

# Systematics and Biogeography of Cephalopods

VOLUME II

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*Nancy A. Voss, Michael Vecchione,  
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# Taxonomy and Zoogeography of the Family Onychoteuthidae (Cephalopoda: Oegopsida)

T. Kubodera, U. Piatkowski, T. Okutani,  
and M.R. Clarke

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## ABSTRACT

The Oegopsida family Onychoteuthidae contains five genera, namely, *Onychoteuthis*, *Ancistroteuthis*, *Onykia*, *Moroteuthis*, and *Kondakovia*. The genus *Chaunoteuthis* is considered to represent spent individuals of the other genera of the family. The present study clarified that two well-known nominal species, *Onychoteuthis banksii* (Leach, 1817) and *Ancistroteuthis lichtensteinii* (Férussac and Orbigny, 1839), both represent species complexes in their broad distributional ranges. The genus *Onykia* may represent immature stages of other onychoteuthids. *Moroteuthis robsoni* Adam, 1962, which has hitherto been considered to be a Southern Ocean species, appears to extend its distribution into the warm Atlantic region. Reliable taxonomic records as well as knowledge of distributional differentiation by growth stage are still too scarce to draw a zoogeographical picture of each species in this family.

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## Introduction

Among the Oegopsida families, Onychoteuthidae is moderately diverse. Some members of this family attain a gigantic size surpassed only by *Mesonychoteuthis* (family Cranchiidae) and by members of the family Architeuthidae. The full life history and the distribution of most species have not been described, but some species, such as certain species of *Onychoteuthis*, are known to spend an epipelagic life from

paralarval to adult stages. *Moroteuthis* species are usually found in the midlayers of cold seas in both the northern and southern hemispheres and contribute a considerable proportion to the sperm whale's diet.

The conventional taxonomic list usually contains six genera, namely, *Onychoteuthis*, *Ancistroteuthis*, *Chaunoteuthis*, *Onykia*, *Moroteuthis*, and *Kondakovia*. Our careful observations on *Chaunoteuthis* during the workshop led us to the conclusion that this genus represents a spent stage or unhealthy condition of multiple species in the family. Some doubt exists as to the validity of the genus *Onykia* as well (Tsuchiya and Okutani, 1992).

The present study was a cooperative undertaking, but Kubodera and Okutani particularly concentrated on the genera *Onychoteuthis*, *Ancistroteuthis*, and *Onykia*, whereas Piatkowski and Clarke concentrated on the genera *Moroteuthis* and *Kondakovia*. The opinions of every author were coordinated by the workshop group leader (TO).

ABBREVIATIONS.—The following abbreviations are used in the text: AL, arm length; DML, dorsal mantle length; FL, fin length; FW, fin width; GL, gladius length; ML, mantle length; MW, mantle width; VLI, ventral length index of gladius rostrum.

## Systematics

### Family ONYCHOTEUTHIDAE Gray, 1849

DIAGNOSIS.—Mantle cylindrical, muscular, tapering posteriorly to pointed end. Fins posteriorly situated, large, sagittate or transversely oval. Funnel cartilage straight and simple. Neck often with crowded nuchal folds dorsally. Arm suckers biserial, with smooth rings. Tentacle club with 2 rows of strong hooks (with or without marginal suckers) on manus and with well-defined, discoidal fixing apparatus on carpus. Hectocotylization absent. Female with nidamental glands and male with "penis." One genus (*Onychoteuthis*) with subocular and

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intestinal photophores. Buccal connectives 7, attached to ventral side of arms IV. Gladius with strongly ridged rachis, rather broadly lanceolate vanes, and solidified posterior tip or cartilaginous rostrum.

TYPE GENUS.—*Onychoteuthis* Lichtenstein, 1818:1591.

DISCUSSION.—Gray (1849) established this family to comprise the genera *Enoploteuthis*, *Ancistrocheirus*, *Abralia*, *Octopodoteuthis*, *Acanthoteuthis*, *Ancistroteuthis*, *Onychia*, and *Ommastrephes*. Thiele (1935) retained the genera *Tetronychoteuthis*, *Onychia* (= *Steenstrupiola*), *Onychoteuthis* (= *Teleonychoteuthis*), *Chaunoteuthis*, *Ancistroteuthis*, *Moro-teuthis*, and *Mesonychoteuthis*. Roper et al. (1969) and Voss (1977), among others, placed *Tetronychoteuthis* in the family Lepidoteuthidae and placed *Mesonychoteuthis* in the family Cranchiidae. In 1972 Filippova added the genus *Kondakovia*, typified by *K. longimana* Filippova, 1972; however, the generic status of this genus is uncertain (see "Discussion," under *Kondakovia longimana*).

Among the remaining five genera, *Chaunoteuthis* has been considered to represent spent individuals of *Onychoteuthis* (Adam, 1972). We are inclined to think that all specimens of *Chaunoteuthis* hitherto reported (such as Appellöf, 1891; Pfeffer, 1912; Naef, 1923; Nesis, 1970; Okutani and Ida, 1986) represent unhealthy or spent and deteriorating individuals of other onychoteuthid genera. Therefore, we suggest that all species of onychoteuthids may reach a terminal, so-called "Chaunoteuthis-stage." Thus, we do not consider this genus to be valid.

The family Onychoteuthidae is generally thought to be close to the family Enoploteuthidae, mainly because of the similarity of tentacular armature.

### *Onychoteuthis* Lichtenstein, 1818

DIAGNOSIS.—Mantle muscular, cylindrical, tapering posteriorly to pointed rostrum. Gladius visible along median line of dorsal mantle. Nuchal folds prominent. Tentacle with 2 rows of strong hooks, without marginal suckers on manus in adult. Two photophores present, 1 on anterior end and 1 on posterior end of intestine. Oval photogenic patch present on ventral periphery of eyeball.

TYPE SPECIES.—*Onychoteuthis bergii* Lichtenstein, 1818:1592, no. 4, pl. 19: fig. a.

DISCUSSION.—This genus was established by Lichtenstein for the hook-bearing *Loligo*. His *O. bergii* was synonymized with *O. banksii* Leach, 1817, by Gray (1849). Since then, this genus has been maintained by subsequent authors.

### *Onychoteuthis banksii* (Leach, 1817)

FIGURE 3

DIAGNOSIS.—Mantle robust, muscular. Fins rhomboidal, length 55%–65% ML, width 65%–78% ML, apical angle 70°–90°. Nuchal folds 9 or 10 pairs. Arm formula

II = III = IV > I, length 35%–45% ML. Tentacle club slightly expanded, length 25%–35% ML, 13–15 small suckers on dactylus, 20–22 hooks on manus in 2 rows, well-defined fixing apparatus with 8–10 suckers and 7–9 pads. Large luminous patch on ventral periphery of each eye. Two large, round, bulbous light organs in ventral mantle cavity, 1 on ink duct behind anal papilla, 1 on ink sac, latter twice as large as former. Medium-sized species maturing at about 150–200 mm ML.

ORIGINAL DESCRIPTION.—Leach, 1817:141.

TYPE LOCALITY.—Gulf of Guinea, west coast of Africa (cf. Leach, 1818:395).

DEPOSITION OF TYPE.—*Holotype*: Natural History Museum, London, England; not available in the workshop.

*Paratypes*: None.

DISTRIBUTION.—World-wide in tropical and subtropical oceanic waters.

DISCUSSION.—This species is separable from other members of *Onychoteuthis* by having a slender, muscular body, rhomboidal fins with 70°–90° apical angle, 20–22 hooks on the tentacle club, and two large, round visceral photophores. This species has been recorded from the tropical and subtropical waters of all oceans (see Clarke, 1966; Okutani, 1980). In the workshop, several specimens from the Pacific, the Atlantic, and the Mediterranean Sea were examined. Tentacle-club length was observed to vary from less than 20% to over 40% of ML in individuals of nearly the same size. At the extremes, individuals looked quite different; however, numerous intermediate specimens filled the gap and made their demarcation indefinite. We tentatively separated specimens into three groups, i.e., the small-club group having clubs smaller than 25% ML, the intermediate-club group having clubs of 25%–35% ML, and the large-club group having clubs larger than 36% ML.

Geographically, the small- and intermediate-club groups appear broadly in the Pacific, the Atlantic, and the Mediterranean Sea. Young (1972) noted that he recognized two separate groups of *O. banksii* from Florida waters. These might correlate with the present two different club-size groups. On the other hand, the large-club group is known only in the western equatorial Pacific and in the waters off the Hawaiian Islands. Young and Harman (1987) reported that *O. banksii* in Hawaiian waters represented a species complex, judging from the different chromatophore patterns in the early life stages. The present large-club group might be one of the species complexes they mentioned, and it seems to be a western equatorial Pacific endemic. The lack of serial specimens from the larvae to the adult and no information about distribution in the Indian Ocean, however, has prevented us from resolving the species-complex problems of "*O. banksii*."

There has been some confusion on the spelling of the species name, "*banksi*" or "*banksii*." Following the International Code of Zoological Nomenclature (ICZN) and the opinion of F.M.



Bayer, of the Smithsonian Institution and member of the International Commission on Zoological Nomenclature (pers. comm., 1988), the original "ii" ending is considered correct.

### *Onychoteuthis borealijaponica* Okada, 1927

FIGURE 2

DIAGNOSIS.—Mantle muscular but rather thin. Fins rhomboidal, length 55%–60% ML, width 65%–75% ML, apical angle 80°–90°. Nuchal folds 8 or 9 pairs. Arm formula  $II = III = IV > I$ , length 35%–45% ML. Tentacle club slightly expanded, length 20%–30% ML, 13–15 small suckers on dactylus, 25–27 hooks on manus in 2 rows, well-defined fixing apparatus with 8–10 suckers and 7–9 pads. Large luminous patch on ventral periphery of each eye. Two oval light organs in ventral mantle cavity, 1 on ink duct behind anal papilla, 1 on ink sac, with intervening silver, iridescent band; former much smaller than latter. Large species maturing at about 250 mm ML in males and about 300–350 mm ML in females.

ORIGINAL DESCRIPTION.—Okada, 1927:4.

TYPE LOCALITY.—Japan.

DEPOSITION OF TYPE.—*Holotype*: Not known.

*Paratypes*: None.

DISTRIBUTION.—Far northern Pacific, migrating from south to subarctic waters for feeding during summer and returning to subtropical waters for spawning in fall and winter (Naito et al., 1977; Kubodera et al., 1983; Murata et al., 1986).

DISCUSSION.—Okada (1927) described the new species *O. borealijaponica*, from Japanese waters, based on small differences in external appearance and the visceral photophores, and it had long since been considered a synonym of *O. banksii*. In 1972, Young examined onychoteuthids from the seas off southern California and revived the name *O. borealijaponica* with detailed descriptions. He compared *O. borealijaponica* with so-called "*O. banksii*" from off Florida and clarified the differences between them.

This species is very close to *O. banksii*, but it distinctly differs by having smaller tentacle clubs with a larger number of hooks on the manus, two oval visceral photophores, of which the anterior one is much smaller than the posterior one, and a relatively broad mantle with a thin wall. The size at maturity also indicates that this species grows much larger than *O. banksii*. The distribution of *O. borealijaponica* is restricted to the far northern Pacific, and this species favors much cooler waters than does *O. banksii*.

### *Onychoteuthis compacta* (Berry, 1913)

FIGURE 5

DIAGNOSIS.—Mantle nearly cylindrical, ending posteriorly in acute point. Fins enormous, broadly sagittate, length little more than 50% ML, width equal to ML, apical angle 135°.

Arms short, stout, arm formula  $III > II > IV > I$ , length 21%–28% ML. Arm suckers in 2 widely spaced rows. Tentacles little longer than arms. Tentacle club not expanded but with well-developed aboral keel and 4 longitudinal rows of armatures, dorsal 2 rows and ventral marginal row being suckers. Only median ventral row with hooks, 10 or 11 in number, proximal 5 hooks small, next 3 hooks much larger, distal 2 or 3 hooks diminishing again in size. Suckers in dorsal 2 rows 16–18, proximal 5 pairs closely set, next 3 pairs widely placed, slightly larger, suckers becoming smaller again distally. Suckers in ventral row exceedingly minute, especially distally, placed very far apart. Suckers on dactylus minute. Well-defined fixing apparatus with 12 suckers and 8 pads. Ocular and visceral photophores present. Animal small (based on juvenile).

ORIGINAL DESCRIPTION.—Berry, 1913:565. (See also Berry, 1914:324–325, fig. 32, pl. LII: figs. 4, 5.)

TYPE LOCALITY.—From RV *Albatross* sta 3989, vicinity of the island of Kauai, Hawaii.

DEPOSITION OF TYPE.—*Holotype*: USNM 214381 (SSB 238); National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; in very poor condition, no detail can be determined.

*Paratypes*: None.

DISTRIBUTION.—Hawaiian waters.

DISCUSSION.—Berry described *Teleoteuthis (Onychoteuthis) compacta* from Hawaiian waters in 1913, and since then this species has mostly been ignored. In 1978 Young revived the name of *O. compacta* for the species occurring in Hawaiian waters and discussed the relationships between vertical distribution and photosensitive vesicles, but he did not give any systematic characters. Young and Harman (1987) also examined onychoteuthid paralarvae caught in Hawaiian waters and classified them into three sympatric species, *O. compacta*, *O. sp. B*, and *O. sp. C*, primarily on the basis of chromatophore patterns. The latter two species were considered to be paralarvae belonging to an *O. banksii* species complex.

This species is characterized in the original description by having large, broad fins, widely spaced arm-sucker rows, and unique arrangements of suckers and hooks on the tentacle clubs. Paralarvae of *O. compacta* larger than 2.0 mm gladius length can be identified by having a few chromatophores arranged in a complex band that is located farther posteriorly on the ventral mantle belly than it is in other species (Young and Harman, 1987).

Due to the serious damage to the holotype, no important systematic characters could be observed during the workshop. Berry (1913, 1914) described *O. compacta* based on a small specimen, about 21 mm ML. Since then, no available description of this species has been made. Judging from the tentacle-club structures and the body size, the holotype seems to be juvenile and has not developed all of the systematic characters. Detailed descriptions of larger specimens and of mature specimens of this species are badly needed.

***Onychoteuthis meridiopacifica* Rancurel and Okutani, 1990**

FIGURE 4

DIAGNOSIS.—Mantle muscular, elongate-cylindrical. Fins widely rhomboidal, length 40%–50% ML, width 70%–90% ML, apical angle 120°–140°. Nuchal folds 8–12 pairs. Arm formula III > IV > II > I, length 30%–40% ML. Tentacle club slightly expanded, length 20%–25% ML, 10–12 small suckers on dactylus, 16–19 hooks on manus in 2 rows, 3 or 4 small globular suckers on dorsal proximal margin, 1 or 2 small suckers on ventral proximal margin, fixing apparatus with 6–8 suckers and 6 pads. Two very small, oval light organs in ventral mantle cavity, 1 on ink duct behind anal papilla, 1 on ink sac; latter 1.6 times larger than former but never exceeding rectum width. Small species maturing at about 60 mm ML in males.

ORIGINAL DESCRIPTION.—Rancurel and Okutani, 1990:25, figs. 1–6.

TYPE LOCALITY.—21°15'S, 155°11.5'E (southwestern Pacific, between 16°37'S and 23°56'S, 162°00'E and 133°15'W (cf. Rancurel, 1970)).

DEPOSITION OF TYPES.—*Holotype*: NSMT Mo-67008; National Science Museum, Tokyo, Japan.

*Paratypes* (4): NSMT Mo-67009–12; National Science Museum, Tokyo, Japan.

DISTRIBUTION.—Southwestern Pacific, estimated to be abundant in the central water mass of the Pacific (Okutani and Tsukada, 1988).

DISCUSSION.—Rancurel (1970) found a unique onychoteuthid in the stomach contents of an *Alepisaurus ferox* Lowe caught with long lines in the southwestern Pacific. He recognized apparent differences between his specimens and so-called "*O. banksii*," which had been thought to be the sole *Onychoteuthis* in the South Pacific at that time. Rancurel gave a detailed description of this unique onychoteuthid, but he did not give it a new species name because of the loss or lysis of the fixing apparatus of the arms and tentacles as a result of digestion in the predator. Okutani and Tsukada (1988) also examined the stomach contents of lancetfish and tunas from the tropical Indo-Pacific and found the same *Onychoteuthis* species described by Rancurel. They made a detailed comparison of three species of the genus *Onychoteuthis*, i.e., *O. banksii*, *O. compacta*, and *O. sp.* Rancurel.

During the workshop, a small onychoteuthid squid measuring about 65 mm ML collected off Sydney, Australia, that looked like *Onychoteuthis* sp. Rancurel was identified to *Ancistroteuthis* because of the indistinctness of the light organs in the ventral mantle cavity and some differences among body proportions. Studies after the workshop, however, revealed that this specimen should be included in *O. sp.* Rancurel irrespective of the indistinctness of the light organs. This specimen has tentacular structures and mature male reproductive organs similar to *O. sp.* Rancurel, but it has a more slender mantle (MW/DML, 23% compared with 28%–38%), smaller fins (FW/ML, 67% compared with 73%–90%; FL/ML, 40%

compared with 42%–48%), and shorter arms (AL/ML, 25%–32% compared with 27%–40%) than those of Rancurel's (1970) and Okutani and Tsukada's (1988) specimens. We reexamined Okutani and Tsukada's specimens and recognized that the mantles were strongly constricted in apparent response to the digestive fluid in the predator's stomach, which caused the different body proportions mentioned above. Examination of growth series and specimens in various fixing conditions convinced us that the visceral light organs of *O. sp.* Rancurel degenerate with growth. In 1990 Rancurel and Okutani gave a new species name, *meridiopacifica*, to *O. sp.* Rancurel.

This species is distinguishable from *O. banksii* by having broader fins with an apex angle of 120°–140°, fewer hooks on the manus, and a decidedly small size at maturity. Specimens smaller than about 20 mm ML are almost referable to *O. compacta* except for possessing two rows of immature hooks on the manus. Young and Harman (1987) reported three different paralarvae of *Onychoteuthis* from Hawaiian waters, one of which was identical to *O. compacta*. Although the other two forms have not yet been linked with their adults, one of them might be an early life stage of *O. meridiopacifica*.

***Ancistroteuthis* Gray, 1849**

DIAGNOSIS.—Mantle muscular, slenderly cylindrical, tapered posteriorly, with end acutely pointed and solidified by long spine of gladius. Gladius not visible on dorsal side of mantle. Nuchal folds prominent. Tentacles with double rows of strong hooks but no marginal suckers on manus. No photophore present in pallial cavity. Oval, opaque area with posterior small patch of photogenic tissue on ventral covering of eye.

TYPE SPECIES.—*Onychoteuthis lichtensteinii* Férussac and Orbigny, 1839:334, pl. 8: figs. 8–12.

DISCUSSION.—This genus has been stable since it was established.

***Ancistroteuthis lichtensteinii* (Férussac and Orbigny, 1839)**

FIGURE 1

DIAGNOSIS.—Mantle slender, robust, muscular. Fins lanceolate, attenuated posteriorly into tail, posterior margins concave, length 60% ML, width 57% ML. Nuchal folds 8 or 9 pairs, becoming indistinct dorsally. Arm formula IV > III = II > I, length 40%–53% ML. Tentacle club slightly expanded, length 30% ML, 16 or 17 small suckers on dactylus, 20 or 21 hooks in 2 rows on manus, well-defined, oval fixing apparatus with 9 to 10 suckers and 9 or 10 pads. Medium-sized species maturing at about 200 mm ML in males, maximal ML 300 mm.

ORIGINAL DESCRIPTION.—Férussac and Orbigny, 1839: *Onychoteuthis* pl. 14: figs. 1–3.

TYPE LOCALITY.—Off Nice, Mediterranean Sea.

DEPOSITION OF TYPE.—Not known.

DISTRIBUTION.—Reported from the western Mediterranean Sea and from tropical and subtropical waters of the eastern

Atlantic. This species has also been reported from the Gulf of Mexico (Voss, 1956) and the southwestern Pacific (Rancurel, 1970).

DISCUSSION.—Férussac and Orbigny described *Onychoteuthis lichtensteinii* from Nice, based on the differences in body proportions, fin shape, number of nuchal folds, and tentacular club structures from *O. bergii*, which is considered to be a synonym of *O. banksii*. Gray (1849) recognized that *O. lichtensteinii* lacks visceral light organs and proposed a new genus *Ancistroteuthis* for the species. *Ancistroteuthis lichtensteinii* has often been reported from the western Mediterranean Sea; however, the records outside the Mediterranean are very sparse, being described from the Gulf of Mexico (Voss, 1956), off West Africa (Adam, 1962), and from the southwestern Pacific (Rancurel, 1970). Adam (1962) mentioned some geographical varieties.

During the workshop, four specimens from the eastern Atlantic and two specimens from the southwestern Pacific were available. Detailed comparisons of these specimens showed four different geographical variations, three forms in the Atlantic and one form in the Pacific. One specimen from the northeastern Atlantic at 20°27'N, 21°58'W, was identical to the typical *A. lichtensteinii*, having the characteristics given in the diagnosis. Two specimens from the central Atlantic between 5°S and 22°S apparently differed from the typical form by having larger fins with a less attenuating tail. Moreover, the specimen from the southernmost locality, 34°26'S, 14°43'E, was clearly separable from the typical and central Atlantic forms by having shorter arms, 30%–40% ML, small tentacular clubs of about 20% ML, with smaller and fewer (15 or 16) hooks, and more than 35 small suckers on the dactylus. This specimen was a male and had a mantle length of 138 mm and mature spermatophores. Although three forms are recognized in the Atlantic, no specimen was available that corresponded to the "*A. lichtensteinii*" reported by Voss (1956) from the Gulf of Mexico. Because it had no nuchal folds, Voss's specimen might belong to the genus *Moroteuthis*.

On the other hand, two specimens from off southeastern New Zealand had intermediate characteristics between the central Atlantic and southern Atlantic forms, but the Pacific specimens distinctly differed by having shorter arms of about 30%–45% ML, tentacular clubs of about 30%–35% ML with 18 hooks, and more than 30 small suckers on the dactylus. From the southwestern Pacific, Rancurel (1970) has reported *A. lichtensteinii* in the stomach contents of lancetfish caught at 20°–24°S, 166°–167°E, further north than the locality for the present form. Judging from Rancurel's description and figures, his specimens clearly differed from the above-mentioned forms by having much longer arms of about 89%–95% ML. He mentioned that his specimens also lack nuchal folds and are close to Voss's (1956) specimen of *A. lichtensteinii* from the Gulf of Mexico. Although there is no record of *Moroteuthis* from the tropical southwestern Pacific, Rancurel's specimen also seems to belong to the genus *Moroteuthis*.

There are too few specimens to draw clear-cut conclusions about geographical variations of this poorly known species; however, the Pacific form is considered to have enough specific characters and geographical segregation to separate it from the "*A. lichtensteinii*-complex" in the Atlantic. The central Atlantic and southern Atlantic forms also seem to have adequate specific characters to separate them from the typical *A. lichtensteinii* distributed in the northeastern Atlantic and Mediterranean Sea. As discussed in the geographical variations of *Onychoteuthis banksii*, however, the existence of intermediate forms between the typical form and the central and southern Atlantic forms seems possible. More specimens are necessary to clarify the species complex in the Atlantic.

As to the confusion on the spelling of the species name, "*lichtensteinii*" or "*lichtensteinii*," again following the ICZN and the opinion of F.M. Bayer (pers. comm., 1988), as in the preceding case of *Onychoteuthis banksii*, the original "ii" ending is considered correct.

#### *Ancistroteuthis lichtensteinii*, Central Atlantic Form

DIAGNOSIS.—Mantle slender, muscular. Fins rhomboidal, length 62% ML, width 70%–78% ML, apical angle 75°–80°, without attenuate tail. Nuchal folds 8 or 9 pairs. Arm formula II = III = IV > I, length 45%–59% ML. Tentacle club slightly expanded, length 29%–31% ML, 15–17 small suckers on dactylus, 19 or 20 hooks on manus in 2 rows, largest hook about 20% of club length, well-defined fixing apparatus with 8 suckers and 8 pads. No light organs in ventral mantle cavity. Examined specimens 134–146 mm ML, mature males.

LOCALITY.—Central Atlantic, R/V *Walther Herwig* sta 467-71, 5°30'S, 16°28'W; R/V *Walther Herwig* sta 443-71, 21°35'S, 16°28'W.

DEPOSITION OF SPECIMENS.—USNM 816698, USNM 817615; National Museum of Natural History, Washington, D.C., United States.

DISTRIBUTION.—Known only from above localities.

DISCUSSION.—See "Discussion" for *A. lichtensteinii*, above.

#### *Ancistroteuthis lichtensteinii*, South Atlantic Form

DIAGNOSIS.—Mantle slender, muscular. Fins lanceolate, attenuated posteriorly into short tail, length 59% ML, width 65% ML. Nuchal folds 6 or 7 pairs. Arm formula IV = III = II > I, length 30%–38% ML. Tentacle club small, slightly expanded, length 20%–21% ML, 38 or 39 small suckers on dactylus in 4 rows, 15 or 16 hooks on manus in 2 rows, largest hook about 19% of club length, well-defined fixing apparatus with 10 suckers and 10 pads. No light organs in ventral mantle cavity. Examined specimen 138 mm ML, mature male.

LOCALITY.—Southeastern Atlantic, R/V *Walther Herwig* sta 419-II-71, 34°26'S, 14°43'E.

DEPOSITION OF SPECIMEN.—National Museum of Natural

History, Smithsonian Institution, Washington, D.C., United States.

DISTRIBUTION.—Known only from above locality.

DISCUSSION.—See "Discussion" for *A. lichtensteinii*.

***Ancistroteuthis lichtensteinii*, Pacific Form**

DIAGNOSIS.—Mantle robust, muscular. Fins lanceolate, elongated posteriorly, attenuating into short tail, length 55%–60% ML, width 80% ML. Nuchal folds 5 or 6 pairs. Arm formula III = II = IV > I, length 30%–45% ML. Tentacles robust. Tentacle club slightly expanded, length 30%–35% ML, 32–36 small suckers on dactylus in 4 rows, 18 hooks on manus in 2 rows, largest hook 20%–25% of club length, well-defined fixing apparatus with 8 suckers and 8 pads. No light organs in ventral mantle cavity. Medium-sized species, examined specimens 49–119 mm ML.

LOCALITY.—Southwest Pacific at 46°03'S, 171°37'E, and 44°00'S, 150°09'E.

DEPOSITION OF SPECIMENS.—NMNZ M-94091; Nelson Museum, New Zealand. MVA F-55014; National Museum of Victoria, Melbourne, Australia.

DISTRIBUTION.—Known only from above localities.

DISCUSSION.—See "Discussion" for *A. lichtensteinii*.

***Onykia* Lesueur, 1821**

DIAGNOSIS.—Mantle short, cylindrical, narrowing posteriorly rather abruptly, and ending in pointed tip solidified by endcone of gladius. Fins broader than long, usually roundly ovate in outline. Dorsal nuchal folds absent, photogenic organs lacking. Gladius with strong rachis and lanceolate vanes ending in spoon-shaped hollow with short, conical tip.

TYPE SPECIES.—*Onykia carriboea* Lesueur, 1821:98, pl. 9: figs. 1, 2a–e.

DISCUSSION.—Gray (1849) admitted this genus and followed Menke's (1830) spelling, *Onychia*. Pfeffer (1912) and others preferred to use *Teleoteuthis* Verrill, 1885, the replacement name for *Onychia*, which is the generic name of an insect. Taki (1964) argued for retention of the original spelling *Onykia* and abandonment of the replacement name.

***Onykia carriboea* Lesueur, 1821**

FIGURE 7

DIAGNOSIS.—Mantle muscular, almost ellipsoid in immatures, becoming cylindrical with growth. Fins wider than long, length about 25% ML, width 70%–75% ML, subrhombic, with convex anterior and posterior margins and blunt lateral angles. Tentacle club with medial hooks and marginal suckers, well-defined fixing apparatus with 8 or 9 suckers present. Gladius with short, recurved rostrum. Surface smooth, with crowded purplish chromatophores and silvery sheen. Dorsal mantle and dorsal head particularly deep purplish.

ORIGINAL DESCRIPTION.—Lesueur, 1821:98, pl. 9: figs. 1, 2a–e.

TYPE LOCALITY.—Gulf of Mexico and in Gulf Stream among fuci (= *Sargassum* spp.).

DEPOSITION OF TYPE.—*Holotype*: Academy of Natural Science, Philadelphia, Pennsylvania, United States; probably no longer extant (Voss, 1962).

*Paratypes*: None.

DISTRIBUTION.—Tropical to warm temperate Atlantic and Indo-Pacific, surface.

DISCUSSION.—This species is characterized by a dark purplish dorsum and a silvery ventrum, and it is frequent in surface collections from the warm-water masses. Subsequent to its description by Lesueur, many names were published by Orbigny (1835, in Férussac and Orbigny, 1835–1848), Gray (1849), Pfeffer (1884, 1900, 1912), Verrill (1885), and others, which were all considered to be synonyms by Clarke (1966).

Another problem is that all the specimens that are identified as *O. carriboea* are immature. This suggests that the name could represent an immature growth stage of named or unnamed larger species that undertake ontogenetic descent or migration to cold-water areas with growth. The problem of an *O. carriboea* complex is fully discussed by Tsuchiya and Okutani (1992).

In connection with this, *O. indica* Okutani, 1981, and specimens from the eastern Atlantic off Congo (R/V *Walther Herwig* sta 482-I-71, 04°34'N, 19°30'W and sta 471-II-71, 02°29'S, 18°58'W; National Museum of Natural History, Smithsonian Institution, Washington, D.C.) also are immature stages. *Onykia indica* seems to be an immature *Moroteuthis*.

Here, too, there has been some confusion on the spelling of the species name, "*carribaea*" or "*carriboea*." As "*carriboea*" appears in the heading of Lesueur's original description, that spelling is correct.

***Onykia rancureli* Okutani, 1981**

FIGURE 6

DIAGNOSIS.—Mantle robust, short, conico-cylindrical, width about 50% ML. Arm I slightly shortest, other arms subequal in length. Sucker counts about 50 per arm. Tentacle robust and rather short, with 26 or 27 biserial hooks and several marginal suckers on manus, 9 or 10 pads on fixing apparatus, and 7–9 small suckers on dactylus. Gladius with strong rachis and small conus and rostrum.

ORIGINAL DESCRIPTION.—Okutani, 1981:155, figs. 1–9.

TYPE LOCALITY.—Central Indian Ocean, 07°51'S, 88°02.5'E, removed from the stomach of a lancetfish measuring 1410 mm fork length.

DEPOSITION OF TYPES.—*Holotype*: NSMT Mo-59498; National Science Museum, Tokyo, Japan.

*Paratypes* (3): NSMT Mo-59490–92; deposition same as holotype.

DISTRIBUTION.—Central Indian Ocean to entire tropical Pacific. This species is very frequent in the diets of lancetfish and tunas.

DISCUSSION.—This species is characterized by having a unique gladius morphology that could require a new generic name.

#### *Moroteuthis* Verrill, 1881

DIAGNOSIS.—Mantle muscular but soft in spent females, anteriorly cylindrical, tapering posteriorly to blunt point. Mantle surface with warts, soft wrinkles, or smooth. Fins rhombic. Dorsal nuchal folds absent. No photophores. Tentacles with 2 rows of hooks, marginal suckers absent in adult but present in early stages. Gladius with cartilaginous endcone.

TYPE SPECIES.—*Ommastrephes robustus* Verrill, 1876:236.

DISCUSSION.—Pfeffer (1908) created the genus *Moroteuthopsis* to separate *Moroteuthis ingens* (Smith, 1881) from *Moroteuthis robusta* (Verrill, 1876). Later, Pfeffer (1912) cast doubt on his earlier decision to create the genus and thought it should perhaps be a subgenus of *Moroteuthis*. In our judgment, after the discovery and our study of the more recent species *Moroteuthis robsoni* Adam, 1962, *M. aequatorialis* Thiele, 1920, *M. lonnbergii* Ishikawa and Wakiya, 1914, and *M. knipovitchi* Filippova, 1972, Pfeffer's subdivision of the genus is not justified.

#### *Moroteuthis ingens* (Smith, 1881)

FIGURE 12

DIAGNOSIS.—Adult large (500 mm ML), skin rugose and covered with fleshy warts forming typical paving-stone pattern. Fins large and broad, rhomboidal, not sagittate, fin length 50% ML. Rostrum of gladius triangular in cross section, 10%–12% ML. Carpus with 10–13 suckers, manus with about 14 pairs of hooks, ventral row hooks stronger than dorsal row hooks, largest hooks at 6th–8th pair. Dactylus with 16 or 17 minute suckers. Longest arms (II and III) about 70% ML.

ORIGINAL DESCRIPTION.—Smith, 1881:25, pl. 3: figs. 1–1d.

TYPE LOCALITY.—Port Riofrio, west coast of Patagonia.

DEPOSITION OF TYPE.—*Holotype*: The Natural History Museum, London, England.

*Paratypes*: None.

DISTRIBUTION.—Sub-Antarctic species, distributed north of the Antarctic convergence and south of the subtropical convergence, off Patagonia and New Zealand. Possibly circumpolar.

DISCUSSION.—Within the genus, this is one of the best described species, and the species characteristics are distinct. *Moroteuthis ingens* is an oceanic epipelagic species with a poorly known biology. According to Nesis (1987), it primarily lives in the lower sublittoral and bathyal zones. It is a prey item in the diets of sperm whales, seals, and sea birds. The beaks of this species were described as *Moroteuthis* A by Clarke (1980). *Moroteuthis ingens* was confused with *Kondakovia longimana* until Filippova (1972) described the latter.

#### *Moroteuthis knipovitchi* Filippova, 1972

FIGURE 9

DIAGNOSIS.—Adult moderately large (450 mm ML), skin with smooth-textured surface. Mantle relatively broad and stout, not pointed into tail. Fins large and rhomboidal, about 50%–60% ML. Gladius with terminal cartilaginous conus, conus triangular in cross section. Tentacle club long and slender, with 12 or 13 suckers on carpus, manus with 10–15 pairs of long, narrow hooks, ventral row hooks larger than dorsal row hooks, and with 14–16 minute suckers on dactylus. Longest arms (II) approximately 90% ML.

ORIGINAL DESCRIPTION.—Filippova, 1972:392, figs. 2, 3.

TYPE LOCALITY.—Near South Georgia Island, R/V *Academician Knipovitch* sta 176, 3 Mar 1965, trawling depth 400–550 m.

DEPOSITION OF TYPE.—*Holotype*: Female, 225 mm ML; Zoological Museum, Moscow University, Moscow, Russia.

*Paratypes*: None.

DISTRIBUTION.—Antarctic, south of the Antarctic convergence in the Scotia Sea, Argentine Basin, and Drake passage, possibly circumpolar (Clarke, 1980; Nesis, 1987).

DISCUSSION.—*Moroteuthis knipovitchi* is characterized by thin, smooth skin, whereas the other species of the genus *Moroteuthis*, except for spent females (see discussion of *M. aequatorialis* in general discussion section, below), have a rugose skin (Filippova, 1972). The species is an oceanic form that is heavily preyed upon by sperm whales.

#### *Moroteuthis lonnbergii* Ishikawa and Wakiya, 1914

FIGURE 10

DIAGNOSIS.—Adult moderately large (275 mm ML), skin rugose. Mantle robust and muscular with longitudinal ridges or warts, pointed to a tail. Fins broad, rhomboidal, about 50%–55% ML. Rostrum of gladius narrowly triangular in cross section. Carpus with 7 or 8 suckers, manus with 25 hooks in 2 rows, largest hooks 4th–6th on dorsal row, 6th or 7th on ventral row. Extreme end of dactylus with 10–13 minute suckers. Longest arm (IV) 60% ML.

ORIGINAL DESCRIPTION.—Ishikawa and Wakiya, 1914:445, pls. 45, 46.

TYPE LOCALITY.—Found on the beach of Hayama, Sagami Bay, Japan, probably thrown away by fisherman.

DEPOSITION OF TYPES.—*Syntypes* (5): 147–192 mm ML; deposition not known.

*Paratypes*: None.

DISTRIBUTION.—Western North Pacific, off eastern Japan, and Indian Ocean (Saya-de-Malha Bank).

DISCUSSION.—This species is very similar to *Moroteuthis robsoni*. It occurs in temperate and tropical oceanic waters from the epipelagic to the bathyal zones and is preyed upon by fur seals and sperm whales.

Concerning the confusion on the spelling of the species name, “*lonnbergi*” or “*lonnbergii*,” we have followed the ICZN

and the opinion of F.M. Bayer (pers. comm., 1988) and have retained the original "ii" as the correct ending.

***Moroteuthis robsoni* Adam 1962**

FIGURE 8

DIAGNOSIS.—Adult large (470 mm ML), skin rugose, reddish, and covered with fleshy, irregular warts. Mantle long and slender. Fins very long, not rhomboidal, attenuated to long tail, up to 67% ML. Rostrum of gladius triangular in cross section, ventral length about 23%–36% ML. Tentacle club very narrow, carpus with 10–12 suckers, manus with 13–16 pairs of hooks, dactylus with 12–17 minute suckers. Longest arms (IV) approximately 57%–86% ML.

ORIGINAL DESCRIPTION.—Adam, 1962:24, figs. 2, 3, pl. 1: figs. 1–4.

TYPE LOCALITY.—Angola, 16°35.6'S 11°19.5'E, 26 Feb 1957, chalut, 485–550 m.

DEPOSITION OF TYPE.—*Holotype*: Mission de Biologie Maritime 1957-NO, M 7; deposition not known.

*Paratypes*: None.

DISTRIBUTION.—North of the southern subtropical convergence, off southwestern Australia, New Zealand, and southern Africa.

DISCUSSION.—This species is very similar to *Moroteuthis robusta*. It is oceanic and lives at the bottom and in the pelagic zone, but its exact depth distribution is unknown. It is heavily preyed upon by sperm whales.

Several specimens from the National Museum of Natural History, Smithsonian Institution (which houses collections of the former United States National Museum (USNM)), that were labeled "*Ancistroteuthis*" were examined and identified as *M. robsoni* (see Table 1). These were as follows: USNM 730692,

271 mm ML (male with large penis but no spermatophores), Gulf of Mexico at 28°36'N, 87°07'W; USNM 575101, 61 mm ML, Gulf of Mexico at 27°18'N, 89°25'W; USNM 730689, 156 mm ML, Gulf of Mexico at 21°33'N, 96°48'W; USNM 730690, 235 mm ML, Gulf of Mexico at 21°41'N, 96°55'W; USNM 730891, ~300 mm ML, Pensacola, Florida; USNM 815468, 370 mm ML, from Bermuda.

The above specimens cannot be distinguished from *Moroteuthis robsoni* from the South Atlantic. Although the rostrum of the gladius is shorter than that in the southern *M. robsoni*, this and other slight differences are probably due to the size of the individual rather than to subspecific differences (Clarke, 1980). The much broader fin of the spent female collected near Bermuda is probably an artifact of preservation. This specimen bridges the gap between *M. robsoni* and *M. aequatorialis* Thiele, 1920.

***Moroteuthis robusta* Verrill, 1876**

FIGURE 11

DIAGNOSIS.—Adult large (1615 mm ML), skin rugose. Mantle robust and relatively broad, surface with longitudinal ridges of soft tissue. Fins large and sagittate, about 50% ML. Rostrum of gladius round or oval in cross section, about 25%–40% ML. Tentacle club slender, with 10–12 suckers on carpus, manus with 16–18 pairs of hooks, 3rd or 4th hooks on ventral row largest. Dactylus with 8–10 suckers. Longest arms (IV) about 90%–100% ML.

ORIGINAL DESCRIPTION.—Verrill, 1876:237.

TYPE LOCALITY.—Coast of Alaska, 3 specimens on beach in April and May 1872.

DEPOSITION OF TYPE.—*Holotype*: USNM 576952, only pieces of pen, buccal mass, fin, and arm extant; National

TABLE 1.—Examined specimens of *Moroteuthis robsoni* from the North Atlantic region that were previously labeled as *Ancistroteuthis*. All specimens are from the collections of the former United States National Museum (USNM), which are now part of the National Museum of Natural History, Smithsonian Institution. (DML = dorsal mantle length; FL = fin length; FLI = fin length index; FW = fin width; FWI = fin width index; — = no measurements available.)

Character	USNM catalog number					
	575101	730689	730690	730692	730691	815468
Sex				male		female
DML (mm)	61	156	235	271	300	370
Tail	no	yes	yes	yes	yes	yes
FL (mm)	29	93	145	150	160	195
FW (mm)	43	85	120	155	155	260
FLI (FL/DML)	0.48	0.60	0.62	0.57	0.53	0.53
FWI (FW/DML)	0.71	0.55	0.51	0.57	0.52	0.70
Number of hooks	28	28	—	28	25/27	—
Number of pairs	14	14	—	14	—	—
Largest hooks	7–8	—	—	—	5–7/4–6	—
Carpal suckers	9	9	—	9	10	8
Dactylus suckers	7–8	15	—	13	11	15
Cone (ventral, mm)	—	35	26	57	—	—
Longest arm (mm)	—	—	126	195	—	—

Museum of Natural History, Smithsonian Institution, Washington, D.C., United States.

*Paratypes*: None.

**DISTRIBUTION.**—In offshore waters of the eastern and western far North Pacific, from the Bering Sea and Gulf of Alaska to northeastern Japan and southern California (Okutani, 1980; Nesis, 1987).

**DISCUSSION.**—Characters distinguishing this species from the other members of the genus *Moroteuthis* are clear. This is a gigantic animal with a maximal mantle length of 2.3 m (Nesis, 1987). When freshly caught, it is very soft to the touch and never as firm as *Ommastrephes* (Sasaki, 1929). It is common in the diets of sperm whales.

### *Kondakovia* Filippova, 1972

**DIAGNOSIS.**—Because the genus *Kondakovia* is monotypic, diagnoses of the genus and the species are the same (see below).

**TYPE SPECIES.**—*Kondakovia longimana* Filippova, 1972:395, figs. 4, 5.

### *Kondakovia longimana* Filippova, 1972

FIGURE 13

**DIAGNOSIS.**—Adult large (740 mm ML), mantle soft and fleshy, broadly cylindrical, slightly tapering posteriorly. No dorsal nuchal folds, no photophores. Fins rhombic, about 42% ML. Gladius thin and fragile, with narrow, longitudinal thickenings, cone 5%–8% ML. Carpus with 9–13 suckers, manus with 27–38 hooks and always 2 rows of marginal suckers, dactylus with 17–40 minute, closely placed suckers. Head and arms more massive than in *Moroteuthis* and larger than mantle portion.

**ORIGINAL DESCRIPTION.**—Filippova, 1972:395, figs. 4, 5.

**TYPE LOCALITY.**—North of South Orkney Islands, in areas of high krill (*Euphausia superba*) concentrations, R/V *Academician Knipovitch* sta 970, 20 Mar 1967, surface.

**DEPOSITION OF TYPES.**—*Holotype*: Female, 260 mm ML; Zoological Museum, Moscow University, Moscow, Russia.

*Paratypes*: 2 females, 133 mm ML, 210 mm ML; deposition same as holotype.

**DISTRIBUTION.**—Epi- and mesopelagic in the Southern Ocean, reaching northward to South Georgia and Tasman Sea, possibly circumpolar (Filippova, 1972; Clarke, 1980; Clarke and Macleod, 1982; Nesis, 1987).

**DISCUSSION.**—*Kondakovia longimana* is distinguished from all *Moroteuthis* species by the possession of marginal suckers on the tentacle club and by different body, gladius, and lower beak proportions. The characters mentioned above, however, overlap somewhat with several *Moroteuthis* species, especially if early life stages are considered. In summary, we believe the generic status created by Filippova (1972) can be justified, although certain body proportions are similar to those of *Moroteuthis* species.

### GENERAL DISCUSSION OF ALL *Moroteuthis* AND *Kondakovia* SPECIES

All but the young juveniles of the species *Moroteuthis robusta*, *M. ingens*, *M. robsoni*, *M. knipovitchi*, *M. lonnbergii*, and *Kondakovia longimana* can readily be distinguished using fin and body shape, presence or absence and form of the rugose ornamentation of the skin, the number of carpal suckers or studs, the number of suckers on the dactylus, the number of hooks on the manus, the presence or absence of marginal suckers on the manus, and the ventral length index of the rostrum of the gladius. From the adults, the geographical distributions are shown to be distinct. *Kondakovia longimana* and *M. knipovitchi* are cold-water species and have not been found north of the Antarctic convergence. A few beaks closely similar to those of *K. longimana* were found in stomachs of sperm whales caught off Iceland, which raises the possibility that the species or the genus may be bipolar in distribution (Martin and Clarke, 1986). *Moroteuthis ingens* is probably confined to waters between the Antarctic and southern subtropical convergence. *Moroteuthis robusta* extends from the southern subtropical convergence to as far north as the Gulf of Mexico and Bermuda. Whether any of the above species are circumpolar has not been established, but the antarctic species are known to extend from Patagonia and Graham Land, Antarctica, eastward to New Zealand.

*Moroteuthis robusta* and *M. lonnbergii* are North Pacific species, the southern limits of the former extending to south of California, United States, and the latter occurring off Japan. *Moroteuthis pacifica* Okutani, 1983, was based on a juvenile. A serial examination of specimens of different sizes indicates *M. pacifica* could be a juvenile of *M. robusta*; therefore, we believe *M. pacifica* should be reduced to a synonym of the latter species. *Moroteuthis lonnbergii* is similar to *M. robsoni*, but the apparent differences found in the size at maturity and the distributional area lead us to think that *M. lonnbergii* is a valid species segregated in the northwestern North Pacific (and a single locality in the Indian Ocean).

The holotype of *Moroteuthis aequatorialis* Thiele, 1920, collected on the equator at 18°07'W, could not be found for the workshop. We did, however, have available a specimen from Bermuda that closely resembled the type description of that species. The Bermuda specimen (USNM 815468) was clearly a spent female of *M. robsoni* resembling some described by Clarke (1980), and we believe this casts serious doubt on the validity of *M. aequatorialis* as no distinctive characters are given in the original description. Because the type of the latter species is lost, we designate the name a nomen nudum.

The various species grow to different sizes and many of their dimensions increase roughly on the same line, so that many proportional differences given as specific differences in the past are only a function of size (Clarke, 1980). Thus, although fully grown individuals are readily identified on the basis of relative dimensions, these dimensions are much less useful in separating young individuals.

Within these genera, apart from the great changes in form

and features that growth brings about, the females change shape drastically just prior to and during spawning. During this time, proteins are used up to such an extent that the tentacles are lost or change proportions, and the arms become relatively shorter. Additionally, the fins become larger and softer, body tissues become soft and even gelatinous, and the mantle wall loses its warts and becomes smooth (Clarke, 1980). The resultant animals are very like *Chaunoteuthis mollis* Appellöf and, indeed, some of the specimens referred to that species in the past are almost certainly spent females of various species of *Onychoteuthis* and *Moroteuthis*. Another cause for difficulties when comparing measurements of specimens of these species, particularly spent females, is the different affects of preservation times, kinds of preservatives, and position of the animals when preserved.

### Zoogeography of the Family Onychoteuthidae

The taxonomic revision of the Onychoteuthidae reveals that there are at least four valid species, including one with three

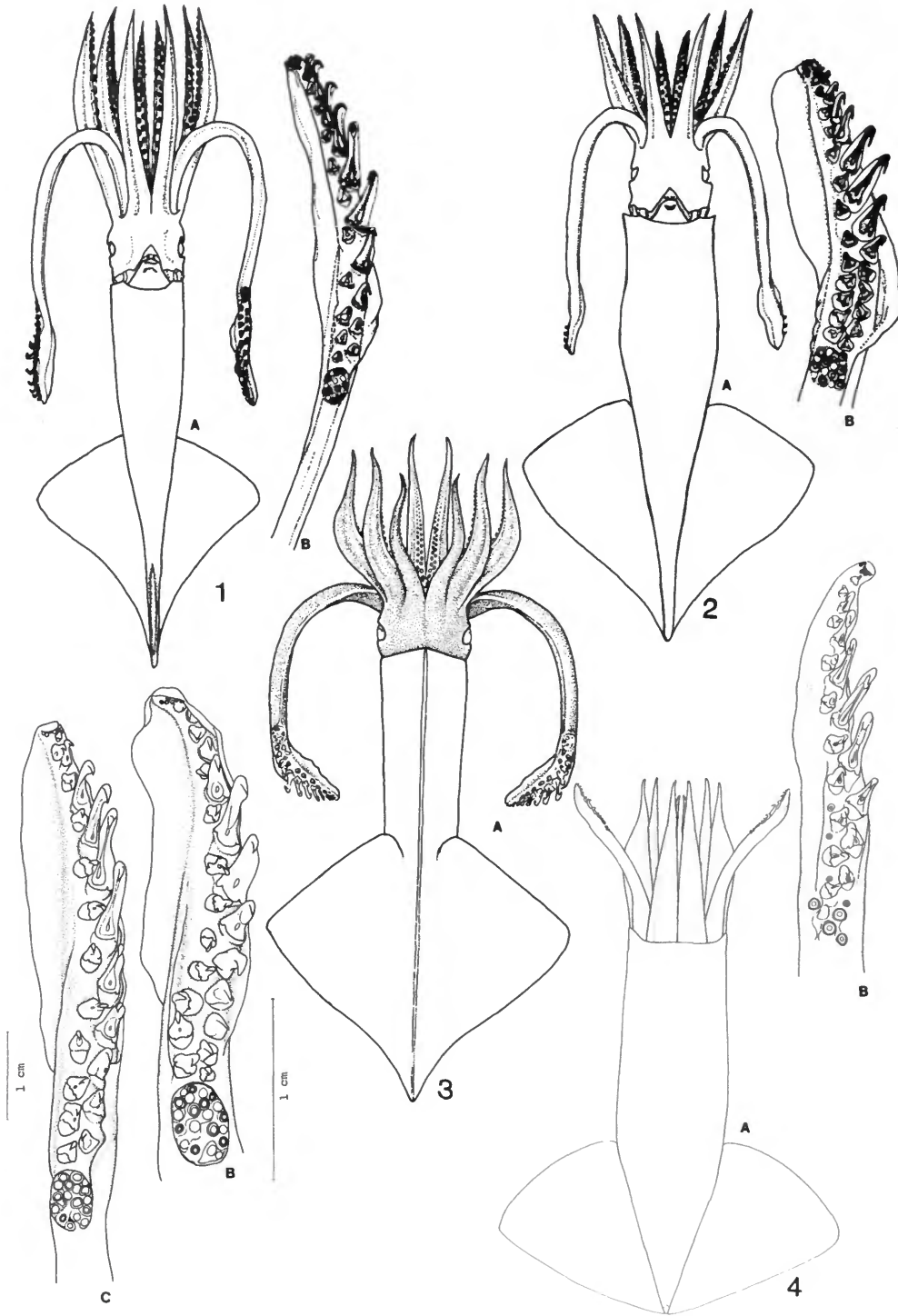
intraspecific populations, in the genus *Onychoteuthis*, one species with four forms in the genus *Ancistroteuthis*, at least one valid species in the genus *Onykia*, five species in the genus *Moroteuthis*, and a sole species in the genus *Kondakovia*.

We do not have enough reliable distributional data to draw a clear zoogeographical picture for each species, so we instead summarize a general scheme of occurrence by species in Table 2. The genus *Onychoteuthis* seems to be diverging in the Pacific Ocean, as is *Ancistroteuthis* in the Atlantic. Small or medium-sized and epipelagic species belonging to the genera *Onychoteuthis* and *Ancistroteuthis* are distributed in tropical and subtropical waters. Members of the genera *Moroteuthis* and *Kondakovia*, which are usually large in size and may inhabit mesopelagic and/or bathyal benthic realms, are distributed in subarctic, subantarctic, and antarctic waters with the exception of the warm-water species *M. robsoni* and *M. lonnbergii*. Thus the genus *Moroteuthis* seems to be spread from warm-water to cold-water regimes and is divergent especially in the Southern Ocean, as suggested by available information.

TABLE 2.—The geographical distribution of species in the family Onychoteuthidae. (A = Atlantic sector; C = central; E = east; I = Indian sector; NST = northern subtropical; P = Pacific sector; SA = subarctic; SAA = subantarctic; SST = southern subtropical; T = tropical; U = unpublished occurrence; W = west; X = published occurrence.)

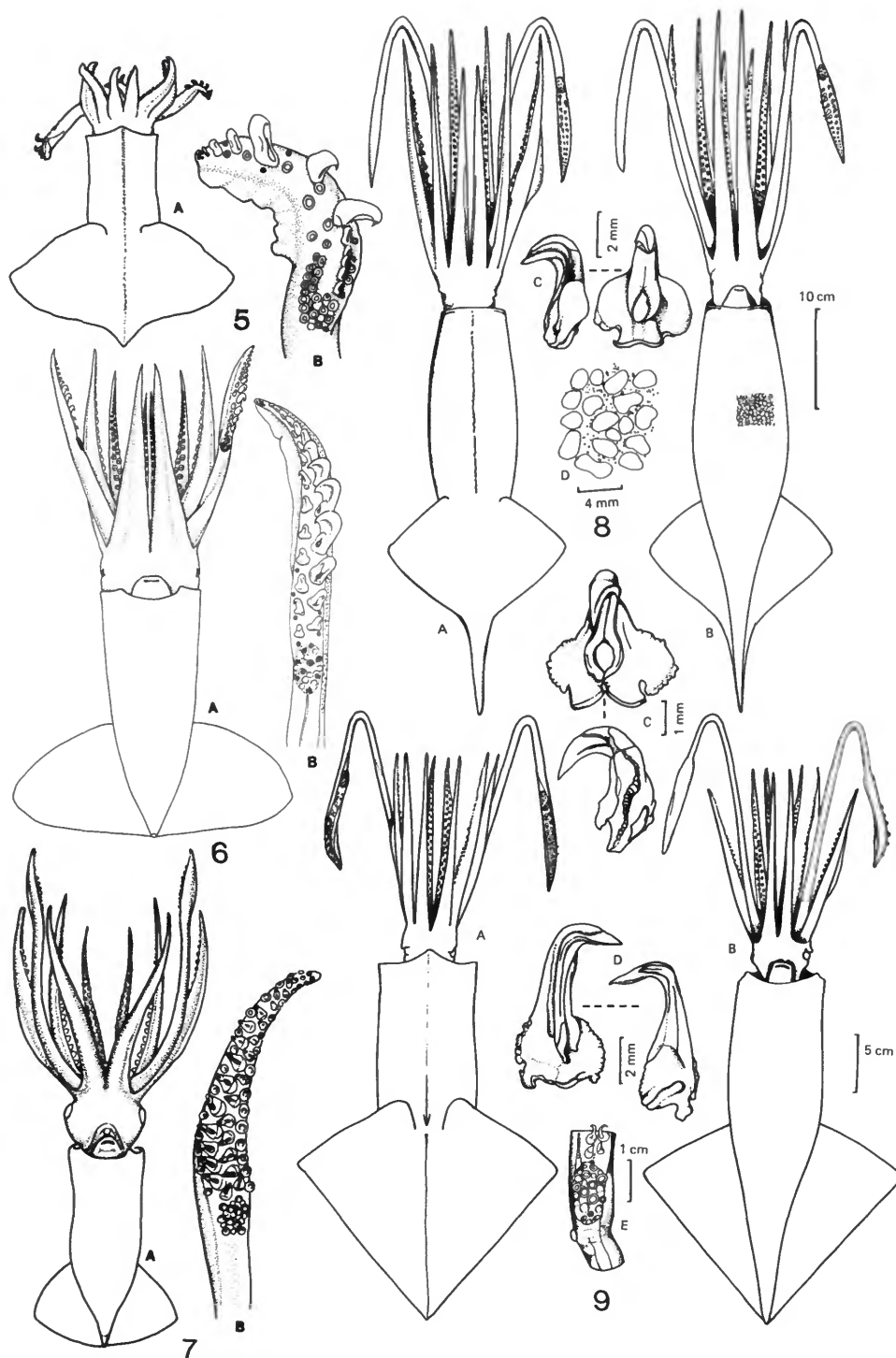
Taxa	Pacific Ocean					Atlantic Ocean					Indian Ocean			Antarctic			Type Locality
	SA	NST	T	SST	SAA	SA	NST	T	SST	SAA	T	SST	SAA	P	A	I	
<i>Onychoteuthis</i>																	
<i>O. banksii</i>																	
small club form			X	X	X			X	X	X			U	U			Gulf of Guinea
medium club form			X	X	X			X	X	X			U	U			
large club form					W												
<i>O. compacta</i>					C												Hawaiian Ids
<i>O. borealijaponica</i>	X	X															Japan
<i>O. meridiopacifica</i>					W												SW Pacific Ocean
<i>Ancistroteuthis</i>																	
<i>A. lichtensteinii</i>							E										Mediterranean
central Atlantic form									E								
south Atlantic form										E							
Pacific form					W												
<i>Onykia</i>																	
( <i>O. carriboea</i> )			X	X	X			X	X	X			X	X			Gulf of Mexico
( <i>O. indica</i> )													E				S Indian Ocean
<i>O. rancureli</i>					W								E				SW Pacific Ocean
<i>O. sp.</i>									W								off Congo
<i>Moroteuthis</i>																	
<i>M. ingens</i>					X					X			U	U	U		Patagonia
<i>M. robsoni</i>								X	U	X			X				
<i>M. robusta</i>	X	X															Alaska
<i>M. lonnbergii</i>					W												Sagami Bay
<i>M. knipovitchi</i>										W				U	X	U	South Georgia
<i>Kondakovia</i>																	
<i>K. longimana</i>										W				U	X	U	South Orkney





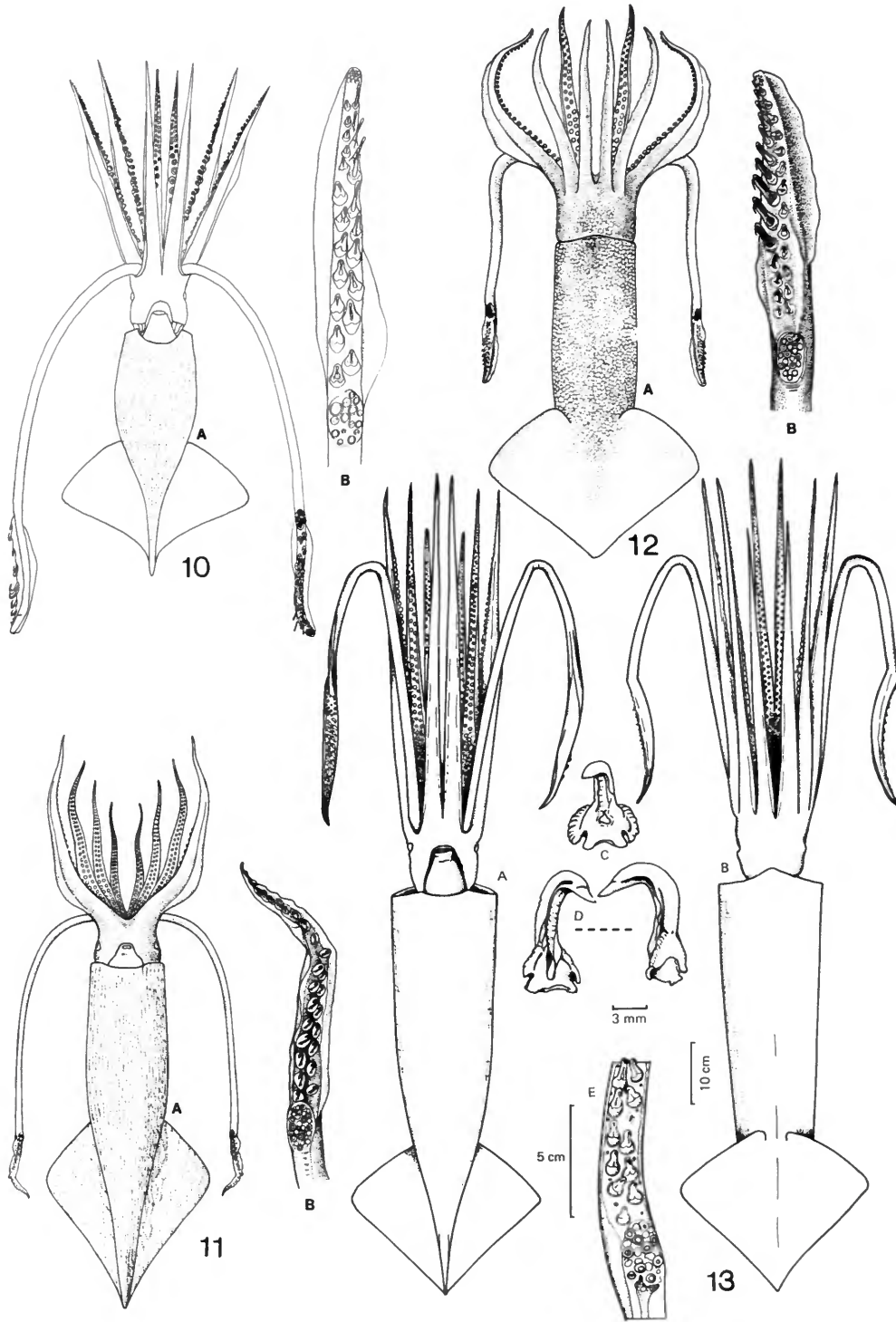
FIGURES 1-4.—1, *Ancistroteuthis lichtensteinii*, northeastern Atlantic/Mediterranean Sea form, R/V *Walther Herwig* sta 502-71, 20°27'N, 21°58'W, 116 mm ML: A, ventral view; B, tentacle club. 2, *Onychoteuthis borealijaponica* (modified from Young, 1972, pl. 18: fig. A, pl. 19: fig. A): A, ventral view, 50 mm ML; B, tentacle club, 81 mm ML. 3, *Onychoteuthis banksii*: A, dorsal

view, 133 mm ML (from Pfeffer, 1912, pl. 4: fig. 12); B, tentacle club, large manus type, 04°10'N, 150°29'E, 132 mm ML; C, tentacle club, small manus type, 02°31'N-03°16.6'N, 142°36.44'E-140°54.39'E, 132 mm ML. 4, *Onychoteuthis meridiopacifica*, 21°15'S, 155°11.5'E, 61.7 mm ML: A, ventral view; B, tentacle club.



FIGURES 5-9.—5, *Onychoteuthis compacta* (from Berry, 1914, fig. 32, pl. 52: fig. 4), 21 mm ML: A, dorsal view; B, tentacle club. 6, *Onykia rancureli*, removed from fish stomach in southwestern Pacific, 73.8 mm ML: A, ventral view; B, tentacle club. 7, *Onykia carriboea* (from Pfeffer, 1912, pl. 1: figs. 7, 15), 32 mm ML: A, ventral view; B, tentacle club. 8, *Moroteuthis robsoni* (from

Clarke, 1980, fig. 81): A, dorsal view; B, ventral view; C, largest ventral tentacular hook; D, enlargement of skin sculpture. 9, *Moroteuthis knipovitchi* (from Clarke, 1980, fig. 78): A, dorsal view; B, ventral view; C, largest dorsal tentacular hook; D, largest ventral tentacular hook; E, carpal region of left tentacle club.



FIGURES 10-13.—10, *Moroteuthis lonnbergii*, from Suruga Bay, Honshu, 215 mm ML: A, ventral view; B, tentacle club. 11, *Moroteuthis robusta* (from Roper et al., 1984:134): A, ventral view; B, tentacle club. 12, *Moroteuthis ingens* (from Roper et al., 1984:130): A, dorsal view; B, tentacle club. 13, *Kondakovia longimana* (from Clarke, 1980, fig. 68): A, ventral view; B, dorsal view; C, largest dorsal tentacular hook; D, largest ventral tentacular hook; E, carpal region of left club.

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# The Cephalopod Family Histioteuthidae (Oegopsida): Systematics, Biology, and Biogeography

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## ABSTRACT

This study is based on the large, mostly unreported collections of histioteuthids that have accumulated since the family was first revised by Voss in 1969. Of primary importance are the collections made in 1971, 1973, 1975/1976, and 1979 by the R/V *Walther Herwig* and the R/V *Anton Dohrn* in the Atlantic and the worldwide collections found in nine Russian or former Russian institutions.

An investigation of the food and feeding of large juvenile to adult *Histioteuthis celetaria pacifica* (G. Voss, 1962) in the western Indian Ocean shows crustaceans and fishes to be the dominant items of prey and of about equal importance in the overall diet. The findings suggest that feeding occurs at approximately equal intensity in the sampled population near the bottom between 364 and 1000 m during both daytime and twilight.

Maturity in the histioteuthids is accompanied by marked changes, not only in the genital organs, but also in the arms, especially arms I, which undergo marked secondary, symmetrical modification; in the photophore patterns, particularly on the arms and mantle where unusual, enlarged, darkly pigmented, simple photophores of different sizes and shapes appear in some species; and in the shape of the gladius and mantle in one species. Characters important in distinguishing among taxa include the photophore patterns on the mantle, around the right eyelid and on the arms, the sculpture of the dorsal pad of the funnel organ, the sucker enlargement pattern on the club, the development and structure of the inner web, the number of elements and the attachments of the buccal membrane, the single or double nature of the male genitalia, the internal structure of the spermatophore, the morphologies of the gladius and the lower beak, and the surface morphology of the skin.

We recognize 13 species of the family Histioteuthidae in a single genus. Subspecies are recognized in two of the species, *Histioteuthis celetaria* (G. Voss, 1960) and *H. corona* (Voss and Voss, 1962), and the available material suggests that more than one taxon is represented in at least two other species, *H. reversa* (Verrill, 1880) and *H. bonnellii* (Férussac, 1834). A key to the species and subspecies is given. *Histioteuthis elongata* (Voss and Voss, 1962) is the mature stage of *H. reversa*. The cosmopolitan, warm-water species *H. hoylei* (Goodrich, 1896), more commonly known in recent literature as *H. dofleini* (Pfeffer, 1912), comprises two separate, closely related species, *H. hoylei* in the Pacific and Indian oceans and *H. arcturi* (Robson, 1948) in the Atlantic. Investigation failed to clearly distinguish the two nominal subspecies of *H. bonnellii*, *H. b. bonnellii* and *H. b. corpuscula* Clarke, 1980, so *H. bonnellii* is restored, for the time being, to the status of an undivided species with two discrete, ecologically distinct northern and southern populations. A survey of the large new collections of *H. meleagroteuthis* (Chun, 1910) confirms that *H. bruuni* N. Voss, 1969, is a variant form of, and synonymous with, the senior species.

Five species groups are characterized: the *H. reversa* species group, comprising *H. reversa*, *H. atlantica* (Hoyle, 1885), and *H. eltaninae* (N. Voss, 1969); the *H. hoylei* species group, comprising *H. hoylei* and *H. arcturi*; the *H. bonnellii* species group, comprising *H. bonnellii* and *H. macrohista* (N. Voss, 1969); the *H. miranda* species group, comprising *H. miranda* (Berry, 1918) and the recently resurrected *H. oceani* (Robson, 1948); and the *H. meleagroteuthis* species group, comprising *H. meleagroteuthis* and *H. heteropsis* (Berry, 1913). Of the two species not belonging to a currently recognized group, *H. corona* and *H. celetaria*, a future, more detailed study than was possible with the available material of *H. celetaria* will probably result in the elevation of its two subspecies to the specific level, and together they will form the sixth distinct group of closely related species in the family.

The distributional patterns nearly equal the number of taxa. The patterns show (1) a close correspondence with patterns of variations in environmental conditions in the oceans; (2) the important role of productivity on the formation of the patterns and in the determination of the abundance of a taxon within its range; and (3) the contiguous nature of the patterns of members of a species group or of subspecies of a polytypic, widespread species. Only three of the eight warm-water species in the family inhabit all three oceans, and of the three cosmopolites, only one is regarded as an undivided

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species. Of the four species or subdivisions of a species that have Southern Ocean-related patterns, two are typically circumglobal, and two are semicircumglobal. For the latter pair, the broad expanse of low nutrient waters of the central Pacific appears to act as an east-west barrier for dispersal. Although there are no strictly cold-water species or recognized subspecies in the northern hemisphere, two histioteuthids normally extend from warm water into north temperate or subarctic waters in the Atlantic. A tendency for some species or subdivisions of a species to be present in the eastern half of the Atlantic and absent in the western half is shared by both groups. The distributions of the four histioteuthids that are confined to the Pacific appear to be more restricted than are the distributions of purely Atlantic taxa. The differences in the patterns appear to reflect important hydrographical differences between the two oceans.

### Introduction

A number of important questions were left unanswered by Voss's (1969) revision of the Histioteuthidae, a monotypic family of pelagic squids that occurs in abundance in the midwaters of the oceans from the subarctic to the subantarctic. For example, among the 13 species recognized in the revision, four of the undivided species, *Histioteuthis reversa* (Verrill, 1880), *H. dofleini* (= *H. hoylei* (Goodrich, 1896)), *H. bonnellii* (Férussac, 1834), and *H. meleagroteuthis* (Chun, 1910), are currently considered to be widespread in the tropical-subtropical-temperate or tropical-subtropical waters of one ocean or multiple oceans. Do each of these broadly distributed, primarily warm-water species actually comprise multiple taxa? And if composed of more than one taxon, are the subdivisions subspecific or specific in nature? What are the distributions of the subdivisions, and how do they relate to ecological conditions in the oceans? How do the occurrence and abundance of a taxon vary within its geographic range? Also, over the years, doubts have arisen about the validity of two of the species, *Histioteuthis elongata* (Voss and Voss, 1962), known until recently only from mature females, and *H. bruuni* (N. Voss, 1969), known until recently only from the holotype. The integrity of a third species, *H. atlantica* (Hoyle, 1885), an inhabitant of the Southern Ocean, also was in doubt. Additionally, we have little understanding of relationships within the family, even though some groupings of apparently closely related species were proposed in the 1969 work, or of relationships of the family with other oegopsids.

Answers are to be found in a detailed study of collections taken over the family's broad geographic range and in which the late growth stages are well represented. Such collections have accumulated, largely unreported, in a number of institutions over the years subsequent to the earlier study as a result of the increased, worldwide interest in marine resources and the use of bigger and more efficient sampling gear. Of outstanding value are the large, Atlantic collections of histioteuthids made during the 1971, 1973, 1975/1976, and 1979 cruises of the German research vessels *Walther Herwig* and *Anton Dohrn*.

These collections, made using a 1600 mesh Engel midwater trawl in depths from the surface 100 m to about 2600 m, are on permanent or temporary loan to the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Also of outstanding value are the worldwide collections housed in the Institute of Oceanology, Russian Academy of Sciences, Moscow, and in eight other Russian and formerly Russian institutions. The 1988 Cephalopod International Advisory Council (CIAC) Workshop on the Systematics and Biogeography of Cephalopods afforded the authors the opportunity to undertake the present study. Two of us (KN and NV) have, over the years, maintained an expressed interest in the family and have watched these collections grow in our respective countries. The third member of our trio (PR) contributed his knowledge of the predators of histioteuthids and of ecological conditions in the Southern Ocean. By integrating the results of our new investigations, which include new comparative studies of several structures, particularly the spermatophore, with those of Voss, 1969, and subsequent works on histioteuthids and those on other pelagic midwater organisms, we attempt to answer the above questions and, in answering, to give a better understanding of the evolution of the family.

### MATERIALS AND METHODS

**SPECIMENS.**—Our study is primarily based on our examination of 1758 mostly unreported specimens of histioteuthids found in the collections of numerous institutions: All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, Russia (VNIRO); Atlantic Research Institute of Fisheries and Oceanography, Kaliningrad, Russia (AtlantNIRO); Atlantic Reference Centre, St. Andrews, New Brunswick, Canada (ARC); Auckland Institute and Museum, Auckland, New Zealand (AIM, formerly AUZ); Azov-Black Sea Institute of Fisheries and Oceanography, Kerch, Ukraine (YugNIRO, formerly AzCherNIRO); Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada (BIO); The Natural History Museum, London, England (BMNH; formerly British Museum (Natural History)); Centre d'Étude des Ressources Animales Marines, Marseille, France (CERAM); Fisheries and Oceans Biological Station, St. Johns, Newfoundland, Canada (SJBS, formerly FOSJ); Fisheries Research Centre, Wellington, New Zealand (FRCW); Huntsman Marine Laboratory, St. Andrews, New Brunswick, Canada (HML); Institute of the Biology of South Seas, Sevastopol, Ukraine (IBSS); Institute of Oceanographic Sciences, Wormley, England (IOS); Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia (IOAN); Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, United States (UMML); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MHNJP); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museum of Comparative Zoology, Harvard University, Cambr-



idge, Massachusetts, United States (MCZ); Museum of Victoria (Natural History), Melbourne, Australia (NMV); National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States (USNM; housing the collections of the former United States National Museum); National Museum of New Zealand, Wellington, New Zealand (NMNZ); National Museum of Wales, Cardiff, Wales (NMWZ); Pacific Research Institute of Fisheries and Oceanography, Vladivostok, Russia (TINRO); Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, Russia (PINRO); Royal Museum of Scotland, Edinburgh, Scotland (RMSE); Scripps Institution of Oceanography, La Jolla, California, United States (SIO); Sea Fisheries Institute, Gdynia, Poland (SFIG); South African Museum, Cape Town, South Africa (SAM); Tokyo Imperial University, Tokyo, Japan (TIU); Western Australian Museum, Perth, Australia (WAM); Zoologisk Museum, Copenhagen, Denmark (ZMUC); Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP, formerly ZIN); and the Zoological Museum of the Moscow University, Moscow, Russia (ZMMU).

**MEASUREMENTS, COUNTS, AND INDICES.**—Our counts, measurements in millimeters (mm), and indices, and their abbreviations, primarily follow the standards defined by Roper and Voss (1983). In one exceptional case, that of the spermatophore, we have modified the measurements, indices, and abbreviations given by Hess (1987). The spermatophore terms, measurements in millimeters, indices, and abbreviations that we used are shown in Figure 1 and are defined below.

SpL	Spermatophore Length; total length of spermatophore.
SpLI	Spermatophore Length Index; total length of spermatophore as percentage of mantle length.
EjApL	Ejaculatory Apparatus Length; length of ejaculatory apparatus measured from point of insertion of ejaculatory tube at oral end of cement body to oral end of spermatophore.
EjApLI	Ejaculatory Apparatus Length Index; ejaculatory apparatus length as percentage of spermatophore length.
CBL	Cement Body Length; length of cement body.
CBLI	Cement Body Length Index; cement body length as percentage of spermatophore length.
SpML	Sperm Mass Length; length of sperm mass or reservoir.
SpMLI	Sperm Mass Length Index; sperm mass length as percentage of spermatophore length.

Because the length of the gladius of a specimen was measured instead of the length of the mantle in the cases of either special studies or where the mantle exhibited noticeable signs of contraction due to preservation (as much as 12% contraction noted), gladius length (GL) and dorsal mantle length (ML) are used interchangeably in our text and tables when referring to the size of an animal. In living squids of this family, the lengths of the gladius and the dorsal mantle are virtually the same.

**TREATMENT OF SPECIES.**—With the exception of the two unassigned species, *Histioteuthis corona* (Voss and Voss, 1962) and *H. celetaria* (G. Voss, 1960), the species are arranged in species groups, with the senior species, which lends

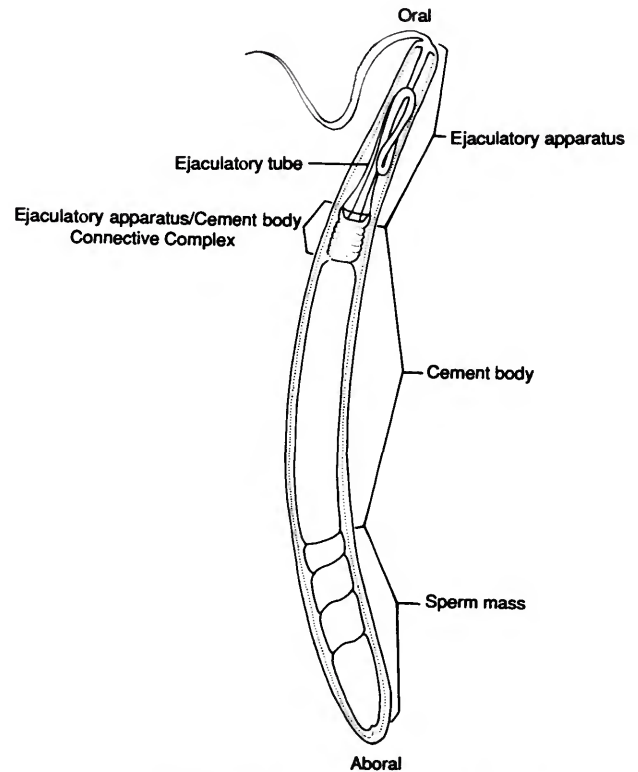


FIGURE 1.—Terms and dimensional limits of spermatophore internal components. See "Materials and Methods" for definitions of spermatophore abbreviations and indices. (Modified from Voss, 1969.)

its name to its respective group, treated first. Our account of each species contains a description, a detailed account of its distribution, and a discussion. In the case of subdivided species, features shared among subspecies are given only in the description of the species. We give a complete synonymy and full illustrations only for the recently resurrected and poorly known species *H. oceani* (Robson, 1948); synonymies and full illustrations for the remaining species, with the partial exceptions of *H. hoylei* and the newly resurrected species *H. arcturi* (Robson, 1948), can be found in Voss, 1969. Aside from those for *H. oceani*, the illustrations in the present paper are mainly restricted to newly found features that distinguish among members of a species group, subspecies, or subpopulations of a polytypic species. Because all species treated in this paper are members of the sole genus in the family, *Histioteuthis*, we frequently dispense with the name of the genus or its initial when referring to the various species in our discussions.

The map we have used, modified from Johnson (1982), shows the approximate boundaries of the upper water-mass regions of the world and the intervening transitional areas as

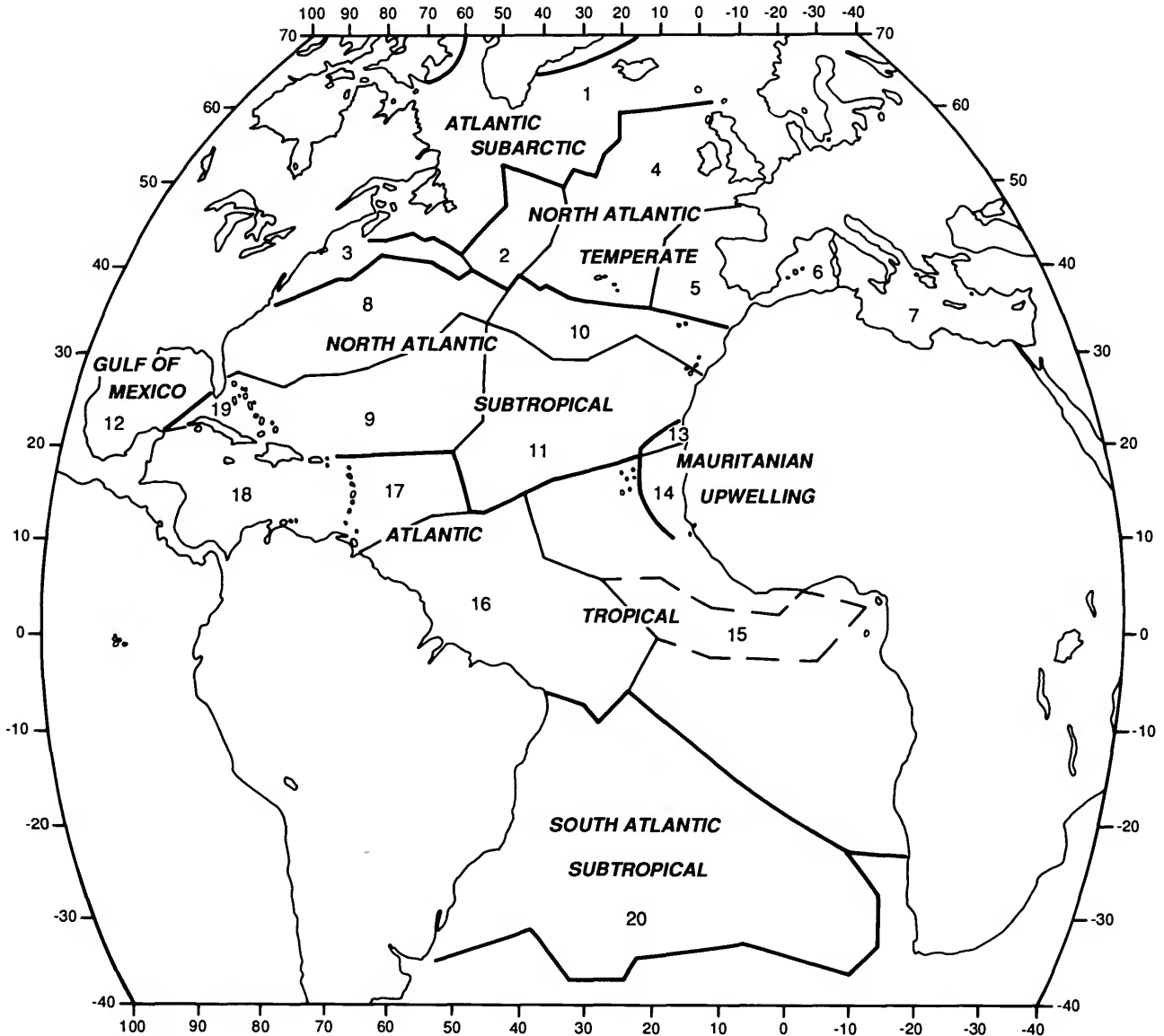


FIGURE 2.—Atlantic Ocean Mesopelagic faunal regions and provinces of Backus et al., 1977. Atlantic Subarctic Region: 1 = Atlantic Subarctic Province. North Atlantic Temperate Region: 2 = Northern Gyre Province, 3 = Slope Water Province, 4 = Azores-Britain Province, 5 = Mediterranean Outflow Province, 6 = Western Mediterranean Sea Province, 7 = Eastern Mediterranean Sea Province. North Atlantic Subtropical Region: 8 = Northern Sargasso Sea Province, 9 = Southern Sargasso Sea Province, 10 = Northern North African Subtropical Sea Province, 11 = Southern North African Subtropical Sea Province. Gulf of Mexico Region: 12 = Gulf of Mexico Province. Mauritanian Upwelling Region: 13 = Northern Mauritanian Upwelling Province, 14 = Southern Mauritanian Upwelling Province. Atlantic Tropical Region: 15 = Guinean Province, 16 = Amazonian Province, 17 = Lesser Antillean Province, 18 = Caribbean Sea Province, 19 = Straits of Florida Province. South Atlantic Subtropical Region: 20 = South Atlantic Subtropical Province. (Redrawn from Backus et al., 1977, with modified numbering of provinces.)

given by Sverdrup et al. (1942). In the Atlantic it shows the mesopelagic faunal regions described by Backus et al. (1977) on the basis of their distributional study of myctophids, the

most speciose family of mesopelagic fishes. Unfortunately, comparable studies, which would have been useful, have not been done for the Indian and Pacific oceans. A redrawing of the

original map of Backus et al. (1977) showing their faunal regions and provinces is shown in Figure 2. These regions and provinces are frequently referred to in our "Distribution" and "Discussion" sections of the species accounts and are referred to in the family "Biogeography" section at the end of the paper. Only specimens that we could identify confidently from either our own examination or the literature were plotted on our maps. Records based solely on beaks found in the stomach contents of predators were not used.

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#### Brief Review of Published Research on Histioteuthids Since the Voss, 1969, Revision

With clarification of the taxonomy of the Histioteuthidae and increased availability of specimens, attention subsequent to the revision focused more on distributions, predators, descriptive and functional morphology, physiology, and other aspects of biology than on systematics.

**SYSTEMATICS AND DISTRIBUTIONS.**—Only two new taxa have been described since 1969, *Histioteuthis corona cerasina* Nesis, 1971, from the southeastern Pacific, and *Histioteuthis bonnellii corpuscula* Clarke, 1980, a small-maturing form described from stomach contents of sperm whales caught off South Africa and in the mid-South Atlantic. Additionally, two inadequately described species, *Histioteuthis inermis* Taki, 1964, from off Japan, and *Histioteuthis oceani* Robson, 1948, from near the Galapagos Islands, were resurrected from the literature by Nesis (1971) and Voss et al. (1992). The reader is referred to Table 1 for a list of the nominal taxa of histioteuthids together with their current identifications.

References to the many papers that contain valuable new data on the systematics and geographical and vertical distributions of histioteuthids can be found in the "Distribution" and "Discussion" sections of the "Species Accounts," and in the "Biogeography" section at the end of this paper.

**PREDATORS.**—Recent investigations of the importance of histioteuthids in the diets of diverse marine animals, as well as the abundance of the different predator species in the various parts of the oceans, are listed in the Appendix and are discussed in the "Oceanic Food Web and Feeding" section of this paper.

**ASPECTS OF MORPHOLOGY.**—The two most striking features in histioteuthids, the numerous photophores, which cover most of the outer body surfaces, and the dimorphic eyes, continue to invite investigations. Based on details of eye anatomy, photophore arrangement, observed positions of the eyes, and the vertical distribution of *dofleini* (= *hoylei*) off Hawaii, Young (1975) hypothesized that the large left eye functions in midwater depths primarily to detect downwelling light, whereas the small right eye functions at the same depths primarily to detect bioluminescent light. In contrast, Bitjukova and Zuev (1976) reported that, based on anatomical and physiological characteristics of the eyes of *bonnellii*, the large eye was similar to that of other cephalopods and fishes and functioned primarily in upper, illuminated waters, whereas the small eye was more specialized and was adapted for use in deep, dark waters.

Photophore morphology and ultrastructure were studied by Young (1977) in *dofleini* (= *hoylei*), and by Dilly and Herring (1981) in *macrohista*, and were discussed in Herring's review papers (1977, 1988) on luminescence and luminescent organs, mainly of cephalopods. The work by Dilly and Herring, which

TABLE 1.—List of nominal taxa of histioteuthids and their current identifications.

Nominal Taxon	As currently recognized
<i>Cranchia bonnellii</i> Férussac, 1834	<i>Histioteuthis bonnellii</i>
<i>Histioteuthis ruppellii</i> Verany, 1846	<i>Histioteuthis bonnellii</i>
<i>Histioteuthis collinsii</i> Verrill, 1879	<i>Histioteuthis bonnellii</i>
<i>Calliteuthis reversa</i> Verrill, 1880	<i>Histioteuthis reversa</i>
<i>Loligopsis ocellata</i> Owen, 1881	nomen dubium*
<i>Histiopsis atlantica</i> Hoyle, 1885	<i>Histioteuthis atlantica</i>
<i>Histiopsis hoylei</i> Goodrich, 1896	<i>Histioteuthis hoylei</i>
<i>Meleagroteuthis hoylei</i> Pfeffer, 1900	nomen nudum
<i>Calliteuthis meleagroteuthis</i> Chun, 1910	<i>Histioteuthis meleagroteuthis</i>
<i>Calliteuthis (Meleagroteuthis) asteroessa</i> Chun, 1910	nomen dubium*
<i>Stigmatoteuthis japonica</i> Pfeffer, 1912	nomen dubium*
<i>Stigmatoteuthis verrilli</i> Pfeffer, 1912	<i>Histioteuthis reversa</i>
<i>Stigmatoteuthis chuni</i> Pfeffer, 1912	<i>Histioteuthis hoylei</i>
<i>Stigmatoteuthis dofleini</i> Pfeffer, 1912	<i>Histioteuthis hoylei</i>
<i>Stigmatoteuthis goodrichi</i> Pfeffer, 1912	nomen dubium*
<i>Calliteuthis (Meleagroteuthis) heteropsis</i> Berry, 1913	<i>Histioteuthis heteropsis</i>
<i>Meleagroteuthis separata</i> Sasaki, 1915	<i>Histioteuthis meleagroteuthis</i>
<i>Calliteuthis miranda</i> Berry, 1918	<i>Histioteuthis miranda</i>
<i>Stigmatoteuthis arcturi</i> Robson, 1948	<i>Histioteuthis arcturi</i> †
<i>Histioteuthis oceani</i> Robson, 1948	<i>Histioteuthis oceani</i>
<i>Histioteuthis cookiana</i> Dell, 1951 (short-webbed series)	<i>Histioteuthis atlantica</i>
(long-webbed series)	<i>Histioteuthis macrohista</i>
<i>Calliteuthis celetaria</i> G. Voss, 1960	<i>Histioteuthis celetaria celetaria</i>
<i>Calliteuthis celetaria pacifica</i> G. Voss, 1962	<i>Histioteuthis celetaria pacifica</i>
<i>Calliteuthis elongata</i> Voss and Voss, 1962	<i>Histioteuthis reversa</i> †
<i>Calliteuthis corona</i> Voss and Voss, 1962	<i>Histioteuthis corona corona</i>
<i>Calliteuthis inermis</i> Taki, 1964	<i>Histioteuthis corona inermis</i>
<i>Histioteuthis eltaninae</i> N. Voss, 1969	<i>Histioteuthis eltaninae</i>
<i>Histioteuthis corona berryi</i> N. Voss, 1969	<i>Histioteuthis corona berryi</i>
<i>Histioteuthis bruuni</i> N. Voss, 1969	<i>Histioteuthis meleagroteuthis</i> †
<i>Histioteuthis macrohista</i> N. Voss, 1969	<i>Histioteuthis macrohista</i>
<i>Histioteuthis corona cerasina</i> Nesis, 1971	<i>Histioteuthis corona cerasina</i>
<i>Histioteuthis bonnellii corpuscula</i> Clarke, 1980	<i>Histioteuthis bonnellii</i> †

\*N. Voss (1969).

†Change of status herein.

found the arm-tip photophores of *macrohista* to be similar to the epidermal photophores in general structure except for the lack of the filter element (formerly referred to as "lens"), supports the hypothesis that "the arm-tip photophores have evolved from terminal skin photophores via intermediate stages such as those presently illustrated by *atlantica*" (Dilly and Herring, 1981:263).

Young's above study of the bioluminescent and counter-shading capabilities of *dofleini* (= *hoylei*) and four other species of midwater squid provided the first description and illustration of the extraocular photoreceptive organs in a histioteuthid. It also provided a discussion of the probable functions of those organs, detecting downwelling light for regulation of vertical migration and counter illumination and monitoring bioluminescent light from their own and outside sources. In 1978 Young gave a more detailed drawing of the photoreceptive organs in *dofleini* (= *hoylei*) and noted the similarities of the organs of two other Hawaiian histioteuthids, *H. celetaria pacifica* and *Histioteuthis* sp. (= *oceani*).

More recently, several other organs of histioteuthids have been the subjects of comparative studies. The large number of body parts and complete specimens of histioteuthids found in the stomach contents of sperm whales of the southern hemisphere permitted Clarke (1980) to do a comparative study of the beaks of the species from that area. Based on several morphological features of the lower beak, Clarke divided the beaks into two groups, which he designated "A" and "B." The number of species represented in the groups was enlarged to include all recognized species of histioteuthids in the results of a 1981 workshop on the taxonomy and identification of cephalopod beaks edited by Clarke (1986b). Toll's (1982) comparative morphology investigations of the gladius in teuthoids, which included 14 of the 17 histioteuthid taxa recognized in the present paper, found the cupped coil at the posterior end of the gladius, initially reported by Voss and Voss (1962), to be a glacial condition shared by all family members and unique among teuthoids. His morphometric data suggested species groups that were not always supported by data from

other known characters. *Histioteuthis bonnellii* represented the family in Maddock and Young's (1984) morphometric study of cephalopod statocysts, and *H. miranda* was used in their (1987) work on the quantitative differences in the brains of cephalopods. In addition to asymmetries in the size of the eyes and optic lobes in histioteuthids, Wentworth and Muntz (1989), working with *atlantica*, *bonnellii*, *dofleini* (= *arcturi*), and *meleagroteuthis*, detected histological differences between the right and left sides both in the optic lobes and in the lenses and retinas of the eyes. Their comparative study of the statocysts of *atlantica* and *bonnellii* showed no change in the volume of the organ between the two sides of the body, but it revealed possible significant differences in statocyst shape between the two species. *Histioteuthis bonnellii* also was a subject of study in Clarke and Maddock's (1988) analyses of statolith shapes in extant cephalopods and their possible use in determining inter- and intrafamilial relationships. The spermatophores of histioteuthids except for *dofleini* (= *arcturi*) were shown to be morphologically distinct among teuthoids by Hess's (1987) comparative morphology investigation of cephalopod spermatophores. Unfortunately, spermatophore data from the 13 histioteuthid species studied failed to suggest discrete species groups in the family that were well supported by other character analyses. The results did support, however, the traditional familial grouping of the histioteuthids with the bathyteuthids.

Two recent observations of *?bonnellii* made from the *Sever-2* submersible on the Hutton Plateau in the North Atlantic, at 540 m in midwater and at 1058 m, 20 m off the bottom, revealed one of the uses of the deep interbranchial web in that species (Moiseyev, 1987; three juveniles of 20–40 mm ML). The animals were seen moving toward the submersible's light with a pulsating movement of the umbrella-like structure formed by the web and arms. The pulsations occurred at a rate of 1–2 per second and appeared to be the primary means of movement.

ASPECTS OF PHYSIOLOGY.—Research on two aspects of the physiology of histioteuthids were subjects of papers by Belman (1978), Clarke et al. (1979), and Lipinski and Turoboyski (1983). Belman's investigations showed the ability of *heteropsis* off southern California to live in the oxygen-minimum layer during the day and to migrate to a nighttime habitat in the oxygen-rich surface waters. These findings suggested to the author that metabolism in *heteropsis* is insensitive to pressure and involves at least partial anaerobiosis at daytime depths. The above works of Clarke et al. and Lipinski and Turoboyski investigated the use of ammonium for buoyancy in squids. Histioteuthids, represented by *meleagroteuthis*, *reversa*, and *Histioteuthis* spp. in the first study and by *macrohista*, *meleagroteuthis*, and *Histioteuthis* sp. in the second, were found to accumulate sufficient ammonium concentrated in specific tissues of the arms and, to a lesser extent, the mantle to provide near-neutral buoyancy for the animals. The often large quantity of oil, orange or red in color, found in the digestive glands of a number of histioteuthids, especially *reversa*, *atlantica*, and *eltaninae* (in the present study, appreciable

amounts of oil were also found in one or more specimens of *hoylei*, *bonnellii*, *macrohista*, *celetaria celetaria*, *celetaria pacifica*, and *heteropsis*), probably acts as an additional buoyancy mechanism. The biochemical composition of this oil has not been studied, but it appears to be similar to the oil contained in midwater crustaceans. Various crustaceans that inhabit the midwater realm are known to form a major portion of the diets of histioteuthids (see following section).

### The Role of Histioteuthids in the Oceanic Food Web and Feeding

PREDATORS.—Histioteuthids are taken by predators at the surface, in midwater, and near the bottom over the family's range of epipelagic to midbathypelagic oceanic zones from the subarctic to the subantarctic. Our list of known predators given in the Appendix, which includes a variety of cetaceans, pinnipeds, seabirds, fishes, and squids, is incomplete (as is our accompanying list of references), especially in the case of fishes, but it is detailed enough to show the substantial role played by histioteuthids in the oceanic food chain.

Of the whales, the sperm whale is by far the most important consumer of cephalopods (Kawakami, 1980; Clarke, 1986a), and histioteuthids have been found in their stomachs from each of the world's oceans. In a review of cephalopod predation, Clarke (1983) reported that numerically histioteuthids are the most important family in sperm whale stomach contents sampled in the northeastern and southeastern Atlantic, southeastern Indian Ocean, and southeastern Pacific. In the Tasman Sea, they are approximately equal in importance to the Octopoteuthidae, whereas in the Southern Ocean (Scotia Sea) and in the northern Pacific, where they are known to be present in considerable numbers, histioteuthids are numerically less important in sperm whale stomach contents than are other families. Because the histioteuthids are smaller on average than some of the members of other families consumed, notably the Cranchiidae, Octopoteuthidae, and Onychoteuthidae, their contribution in terms of biomass is somewhat less than might be expected from their numerical importance. Nevertheless, in the northeastern Atlantic they are the most important family in terms of biomass as well as in numbers.

Among the pinnipeds, the major consumers of cephalopods are the Otariidae (Clarke, 1985a), but only one species, the subantarctic fur seal, *Arctocephalus tropicalis* (Gray), is known to take histioteuthids (Bester and Laycock, 1985). In the diet of this species, histioteuthids are the second most important family of cephalopods after ommastrephids. Two members of the Phocidae known to take histioteuthids are the northern elephant seal, *Mirounga angustirostris* (Gill), in which the family ranks second in importance to the Octopoteuthidae (Antonelis et al., 1987), and the southern elephant seal, *M. leonina* (Linnaeus), in which histioteuthids were found to be the least important family in the diet (Rodhouse et al., 1992).

The major squid predators among the seabirds are the

penguins and procellariiformes. Although histioteuthids are probably eaten by a number of species of penguins, they have only been documented in the diets of the emperor (Offredo et al., 1985) and king penguins (Adams and Klages, 1987; Adams and Brown, 1989). It is well known, however, that they are taken in considerable numbers by procellariiformes. Seabirds breeding at South Georgia are reported by Croxall and Prince (1987) to consume some 466,000 tons of cephalopods annually; one of the most important genera of which, *Histioteuthis*, is taken by albatrosses and petrels. The authors further report that cephalopods comprise 40% by weight of the diet of the wandering albatross, and of this, 53% by numbers and 23% by weight (New Zealand) and 15% by numbers and 1% by weight (South Georgia) are histioteuthids. Histioteuthids in the diets of the light-mantled sooty albatross and the sooty albatross at Marion Island comprise 25% by numbers and 5% by weight of all cephalopods taken. The disparity between composition by numbers and by weight is due to the comparatively small size of the histioteuthids in the diets of these birds (for reviews see Croxall et al., 1985; Prince and Morgan, 1987).

Similarly, although cephalopods are a major component of the food of some fishes, and histioteuthids contribute a large percentage of the numbers of cephalopods taken, they often contribute a relatively minor proportion of the total cephalopod biomass consumed (see Clarke and Stevens, 1974).

Some caution should be exercised in interpreting the information obtained from cephalopod beaks in the gut contents of predators because many squids, as pointed out by Clarke (1962b), cannibalize their own species and prey upon other cephalopods. There is, therefore, the possibility that some beaks, particularly the smaller ones, present in the gut contents of a cephalopod predator have been consumed by the prey species. Clarke et al. (1988) examined the prey of sperm whale in the southeastern Pacific and found it to consist almost exclusively of the large ommastrephid *Dosidicus gigas* (Orbigny). In light of this finding, they concluded that many of the beaks of the presumed prey, including the histioteuthids, reported by Clarke et al. (1976; see also Appendix) were gut contents of the target species, *Dosidicus gigas*, and that the latter authors were incorrect in concluding that sperm whales from the same region prey on a wide range of cephalopods.

**PREY AND FEEDING.**—Little attention has been paid to the prey of histioteuthids. Nixon's (1987) review of the diets of cephalopods mentions the only account of stomach contents for the family to have been published since the first account appeared in Voss (1969). In Voss's (1969) account, remains of fishes (scales, bones, and otoliths), crustaceans (pieces of exoskeleton), and squids (beaks), in that order of predominance, were reported from the stomachs of a number of unspecified histioteuthids. In the second account, Clarke (1980) found the stomachs of six southern hemisphere specimens of *bonnellii* to contain small amounts of unidentifiable debris, and among five specimens of *miranda*, he found two

to contain crustacean parts (one part questionably identified to a midwater, acanthephyrid decapod), one to contain squid sucker rings, and two specimens with only unidentifiable debris. The recent literature contains a third account of the diet of histioteuthids, in which Passarella and Hopkins (1991) found copepods to be the primary food item, followed by euphausiids, for juveniles to 40 mm ML of the two eastern Gulf of Mexico histioteuthids, *H. corona corona* and *H. arcturi* (reported as *dofleini*). With growth of the squids, fish increasingly appeared in the diet.

During the 1988 cruise of the R/V *Vityaz* to the western Indian Ocean, one of us (KN) together with Ch. M. Nigmatullin examined the stomach contents of 26 large juvenile to adult specimens of *H. celetaria pacifica* taken from off the bottom between 364 m and 1000 m. The findings, which are summarized in Table 2, show crustaceans and fishes to be the dominant items of prey and to be of about equal importance in the overall diet of the animal. The tendency for the identifiable remains in a stomach at a given time to be exclusively of one prey is probably more indicative of the more common presence of that prey at the time of feeding than of the preference of *H. c. pacifica* for one prey over the other. Large juveniles, subadults, and adults appeared not to differ in regard to the degree of fullness of stomach, but the data are inadequate for meaningful comment in regard to possible differences that may occur in the composition of the diets between the various growth stages. The findings do suggest that feeding by the population near the bottom occurs with approximately equal intensity during both daytime and twilight. Only one of the 25 (4%) examined specimens caught within this time period had an empty stomach. Whether feeding continues during the nighttime (which is probable), and therefore extends over the full 24 hours, and whether it increases in intensity in at least that part of the population that moves to shallower depths at night (see "Distribution" section in the species account), is not known. The single examined nighttime capture was a spent male that, not surprisingly, had an empty stomach.

#### **Morphological Features and Behavior Related to Maturity**

Maturity in histioteuthids is accompanied by marked morphological changes, not only in the genital organs (and the texture of the body, which shows deterioration in mature females and large, mature males), but also in other parts of the body. Some of the latter modifications are specific or group related; others are familial but are not necessarily developed to the same degree in all species. The arms of the mature male, especially arms I, are the most affected. In all species, arms I are symmetrically modified on the terminal portions with two rows of suckers of uniform size set on elongate, pallsided pedestals and, usually, are modified on the basal or basal and midportions with enlarged suckers. In all of the enlarged suckers, the soft tissue surrounding the sucker ring is greatly swollen to form a fleshy collar. Similar enlarged suckers may

TABLE 2.—Summary of results of feeding study on 26 specimens (52–147 mm ML) of *Histioteuthis celetaria pacifica* taken from off the bottom in two areas (12°N–13°N, 48°E–54°E, and 22°S–26°S, 35°E–44°E) of the western Indian Ocean during the 1988 cruise of the R/V *Vityaz* ( $m = \Sigma[(\text{no. specimens})(\text{stage of fullness})]/n$ ).

Photoperiod	Number of specimens examined	Number of specimens listed by stage of stomach fullness*							Number of specimens listed by identifiable remains in stomachs†		
		0	1	2	3	4	5	m	crustaceans only	fishes only	crustaceans and fishes
Day	17	1	3	0	8	1	4	3.0	10	4	2
Twilight	8	0	1	0	4	2	1	3.3	2	6	0
Night	1	1									

\* Scale is from empty (0) to completely full (5).

†The shrimps *Pasiphaea* aff. *sivado*, *Pasiphaea* sp., and *Sergestes* (*Sergia*) aff. *challengeri* (3–6 cm) were identified among the crustaceans, and myctophids were identified among the fishes from the area between 12°N–13°N, 48°E–54°E.

also occur family wide on the basal portions of arms II and III or II–IV but are known at present only in *reversa*, *atlantica*, *hoylei*, *arcturi*, *macrohista*, *celetaria*, and *heteropsis*. Additional modifications of arms I in the mature male consist of the overall elongation and increased robustness seen in *hoylei*, *arcturi*, and *meleagroteuthis*. The greatest observed increase in robustness occurs in the midportion of arms I in *arcturi*, where the median keel and protective membranes become fleshy and greatly expanded. These secondary male modifications of the arms are presumably used in caressing and holding the typically larger-maturing female during courtship and copulation (Voss and Voss, 1983; Voss, 1985). The enlarged suckers also could have enhanced sensory capabilities (Voight, 1992). The primary use of the symmetrically modified ends of arms I does not appear to be for the transfer of spermatophores to the female, for this, in the absence of a hectocotylus in the family, appears to be accomplished by the penis (two equally developed penises in *hoylei* and *arcturi*), which progressively elongates until, in the advanced stage of maturity, it is capable of extending well out of the mantle cavity. Additional body parts that undergo significant changes during maturity are the mantle and gladius, which uniquely in *reversa* become moderately (in the male) to greatly (in the female) elongate.

The photophore patterns on certain parts of the body, particularly the arms, of several species undergo striking changes during the maturation of both sexes. In all cases, the changes, which show little sexual dimorphism, involve the appearances of unusual, enlarged, darkly pigmented, simple (lacking the anterior filter and associated reflector found in the typical compound photophore) photophores. In the mature stages of both sexes of *celetaria*, a long, narrow, simple photophore (known at present from the female of *H. c. celetaria* and the male of *H. c. pacifica*) develops beneath the low median keel on the distal portions of arms I–III, replacing the distinct terminal group of normal compound photophores that characterize the earlier growth stages of the species. In maturing males and females of *hoylei* and *arcturi*, a small, elongate, simple photophore appears on the ends of arms IV and possibly of other arms, but the latter could not be

determined from our available specimens. In maturing specimens of both sexes of *bonnellii* (except in the case of some early maturing individuals), an enlarged, terminal, simple photophore appears on arms IV. This photophore is somewhat smaller but otherwise is similar to the enlarged, terminal photophore found on arms I–III in younger members of the species. The most unusual maturity-related changes in photophore pattern occur in two closely related species, *reversa* and *atlantica*. In near-mature and mature females and in mature males of the former species, large round to elliptical, dark, simple photophores are found scattered on the distal halves (in females) or the entire surfaces (in males) of all of the arms, on the ventral surface (in females) or ventral and dorsal surfaces (in males) of the mantle, and on the dorsal surface of the head (in males). Until now, the above-described photophore pattern and elongate female mantle were distinguishing characters for *H. elongata*, which is recognized herein as representing the mature stage of the female of *H. reversa*. The final known occurrence in the family of a photophore pattern peculiar to the mature animal is in *atlantica*. In the mature male of this species (mature female not known), a dense concentration of small to medium-sized, simple photophores occurs on the dorsal and ventral surfaces of the posterior one-half to two-thirds of the mantle, filling nearly all available space between the existing compound photophores. All of the maturity-related photophores appear to be structurally similar to the enlarged, arm-tip light organs of *bonnellii* and *macrohista*, which were subjects of studies by Grimpe and Hoffmann (1921) and Dilly and Herring (1981). The large mass of photogenic material present implied to the latter authors that these enlarged simple photophores could “produce a high intensity light compared to that of the smaller skin photophores” (p. 264).

Not all males judged to be mature (on the basis of the presence of large numbers of apparently fully formed spermatophores in the penis and Needham’s sac) display all of the male-maturity features described above. Small, so-judged mature males of several species often lack one or more of the modifications. Frequently missing are the enlarged basal and

midarm suckers, and the terminal modifications on arms I are sometimes missing. Some elements in the unique mature photophore pattern also may be missing or developed to a lesser extent. The absence, too, of a fully elongated penis in these males, which can be only one-half to one-third the size of the smallest known mature or near-mature female of their species, suggests that the ability to produce mature spermatophores precedes the ability to successfully transfer the spermatophores to the female.

Mated individuals have been found for only two of the nine species of histioteuthids in which the near-mature or mature female is known, so we have little knowledge of where the spermatophores are placed. Okutani et al. (1976) reported that all of the many mated females of *hoylei* (reported as *dofleini*) that they found in the stomach contents of sperm whales caught off Japan had clusters of discharged spermatophores on either the anterior ends or other portions of the nidamental glands, the bases of the gills, or the inner wall of the mantle. In a near-mature female of *H. celetaria pacifica* measuring 147 mm ML (IOAN, uncataloged) that is reported in the present study from the western Indian Ocean, two elongate bundles of approximately 30 and 50 discharged spermatophores are attached, one on each side, to the inner wall of the mantle at the level of the gills. Including additional ones on the gills, the number of attached discharged spermatophores in this specimen exceeds 110. In contrast, a fully mature female of *H. celetaria celetaria* measuring 258 mm ML (USNM 816916), also from the present study, has an approximately 26 mm-long streak (clearly not a groove or cut in the surface as seen in the mature female of some onychoteuthids (Nesis, 1970; Okutani and Ida, 1986)) on the external dorsolateral surface of each side of the mantle in the vicinity of the underlying oviducal glands. Numerous sperm reservoirs are deeply embedded in the mantle wall beneath the streaks.

With approaching maturity, all species descend to increasingly greater, daytime depths below about 500 m, extending into unknown depths below 1000 m, or, in the known cases of *atlantica*, *arcturi*, and *bonnellii* (in the eastern tropical Atlantic), below 2000 m. At these depths, they may be found in midwater or near the bottom. Small mature males usually continue to move into the upper 500 m at night, sometimes accompanied by maturing females. Mating in all species probably occurs in deep water. Capture data for the few known spent or near-spent females suggest that both deep-midwater spawning (*H. celetaria celetaria* and *meleagroteuthis*) and near-surface spawning (*reversa*) occur in the family.

### Systematics

#### Family HISTIOTEUTHIDAE Verrill, 1881 (in 1880–1881)

Histioteuthidae Verrill, 1881:431.

DIAGNOSIS.—Oegopsids with asymmetrically developed eyes, left eye larger than right; buccal membrane with connectives attached dorsally to arms IV; arms with biserial

suckers; tentacular club with suckers arranged in approximately 5–8 rows; outer surface of mantle, head, and arms with numerous, compound photophores; funnel-mantle locking cartilage with approximately straight mantle and funnel elements; gladius with ventrally enrolled, cupped coil at posterior end.

DESCRIPTION.—Medium to large oegopsids; mantle conical, short to elongate, with walls usually firm and thick (except in mature females and large mature males of some or all species); fins usually medium to large, transversely oval in combined outline, can extend slightly posterior to free end of mantle, united posteriorly with median notch; head large, usually wider than mantle, with asymmetrically developed eyes, left eye larger (usually markedly) than right; arms medium to long, stout basally, tapering to slender tips, roughly coequal in length (except in mature stage of some species); arm formula typically  $II \cong III > I \cong IV$  or  $II \cong III > I > IV$ ; swimming keel present on distal  $3/4$ – $2/3$  of arms III, moderately expanded on midarm, low on terminal  $1/3$ – $1/4$  of arm; low median keel present on distal  $3/4$ – $1/3$  of arms I and II; arm suckers small to medium, in 2 rows, approximately coequal in size on arms I–III or largest on third  $1/4$  of arms; suckers smaller by usually  $1/3$ – $1/2$  on arms IV; sucker rings smooth to incised on distal and lateral margins; hectocotylus absent; both arms I of mature males with secondary sexual modifications (terminal portions of arms with abruptly reduced suckers of uniform size on elongate, palisaded pedestals; often basal or all normal suckers enlarged and with swollen, fleshy collars; occasionally, entire arm can elongate and portions can show marked increased robustness); inner web connecting basal portions of arms vestigial to in excess of 60% of arm length; buccal membrane 6- or 7-parted, connectives attached dorsally to arms IV (secondary connectives developed in *bonnellii* and *macrohista*); tentacles long, muscular, with expanded club; club with relatively broad manus and approximately coequal-length dactylus; swimming keel and protective membranes present; deep, longitudinal cleft sometimes present on aboral surface of manus; carpal adhesive apparatus composed of alternating single or pairs of suckers and pads arranged in single row extending from dorsal margin of manus to ventral margin of tentacular stalk for distance of 1–3 club lengths; club suckers arranged in approximately 5–8 diagonal rows, slightly to markedly enlarged in median rows of manus, closely arranged and uniformly small on dactylus; rings of manus suckers usually incised around entire margins; anteriorly directed, compound photophores numerous, mostly arranged irregularly in diagonal rows on skin of mantle, head, and aboral surfaces of arms, more concentrated on ventral surfaces.

Funnel-mantle locking apparatus composed of slightly curved mantle ridge and roughly oval, deeply grooved funnel element; funnel with well-developed valve; dorsal pad of funnel organ inverted V-shaped, with small apical papilla, with or without 2 median ridges or flaps on lateral arms; ventral pads oval or kidney-shaped; mantle musculature incomplete across dorsal midline of mantle; male genitalia normally single



(except double in *hoylei* and *arcturi*); spermatophore usually short and relatively stout (except long and narrow in *arcturi*), typically with short sperm mass, long cement body, connective complex at oral end of cement body, single or multiple loops of inner tube of ejaculatory apparatus; mature egg (from oviduct) oval to nearly round, about 1.6–2.3 mm in diameter; gills moderately long, about 30%–50% of mantle length, with about 19–49 lamellae on outer demibranch; digestive duct appendages on entire length of digestive ducts; extraocular photoreceptive organs multivesicular, in triple pairs, composed of flat, approximately coequal-sized dorsal and ventral elements with connecting median, posteriorly curved, narrow strand of vesicles. Gladius with ventrally enrolled, cupped coil at posterior end; free rachis short to moderately long, narrow to broad; vanes narrow to very broad; lower beak typically with thickened median ridge bisecting lateral wall, pronounced wing fold; upper beak with moderately long, curved rostrum, usually with obtuse or false jaw angle; radula homodont to heterodont; outer marginals typically long, curved; marginal plates present (often poorly developed) or absent.

Skin texture, except for numerous epidermal photophores, smooth (with exception of *hoylei* and *arcturi* in which low fleshy papillae give rough appearance to body surfaces); row of small tubercles sometimes present beneath epithelium along midline of anterior portion of dorsum of mantle and basal portions of arms I–III; skin color purplish to brownish red on mantle, head, and aboral surfaces of arms (juvenile, with chromatophores contracted, sometimes appears silvery due

to underlying iridophores); inner web darkly pigmented.

TYPE GENUS.—*Histioteuthis* Orbigny, 1841:xxxvii.

FAMILY SIZE AND RANGE.—Considering current available knowledge, we recognize the histioteuthids to comprise 13 species in a single genus. Subspecies are recognized in two of the species, and sufficient material is available to suggest that more than one taxon is represented in at least two of the remaining 11 species.

The family is distributed circumglobally from the subarctic to the subantarctic, with occurrence in the subarctic Pacific apparently confined to the east and west boundary current systems. All species inhabit the water column from epipelagic waters to mesopelagic depths, and in some cases midbathypelagic depths to in excess of 2000 m. Histioteuthids often occur in great abundance. For some species, occurrence within the range is related to proximity to land or submarine mounts and ridges. Other species are widely dispersed in the open ocean.

**Genus *Histioteuthis* Orbigny, 1842, in Férussac and Orbigny, 1834–1848**

*Histioteuthis* Orbigny, 1842:xxxvii, in Férussac and Orbigny, 1834–1848.

DIAGNOSIS.—Family is monotypic; generic diagnosis is that of family.

TYPE SPECIES.—*Histioteuthis bonelliana* (Férussac, 1834) (= *Cranchia bonnellii* Férussac, 1834:355), by monotypy.

**Key to the Species and Subspecies of Histioteuthidae**

(adults, subadults, and juveniles of > 20 mm ML)

1. Median row of tubercles on dorsal surface of mantle and basal portions of arms I–III present . . . . . 2  
    Median row of tubercles on mantle and arms absent . . . . . 4
2. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head, in 8 to 9 longitudinal rows on basal portions of arms IV, in circle of 19–22 around right eye . . . . . *H. meleagroteuthis*  
    (Atlantic, Pacific, and Indian oceans, tropical–subtropical)  
    Photophores of uniformly medium size, arranged in moderately dense pattern on ventral surfaces of mantle and head, in 4–6 longitudinal rows on basal portions of arms IV, in circle of 16 to 17 (rarely 15 or 18) around right eye . . . . . 3
3. Median row of tubercles 19%–39% of arm length in adults and subadults, 24%–47% in juveniles of 17–38 mm ML; numerous photophores in diagonal rows on basal 1/2 of arms IV, 5 photophores in first 2 to 3 rows, 4 in subsequent rows . . . . . *H. miranda*  
    (S Benguela Current, W Indian Ocean, subtropical waters of Australia–New Zealand)  
    Median row of tubercles 46%–83% of arm length in adults and subadults; 65%–92% in juveniles of 12–22 mm ML; numerous photophores in diagonal rows on basal 1/2 of arms IV, 6 photophores in first 2 to 3 rows, 5 in subsequent rows . . . . . *H. oceani*  
    (equatorial Pacific and certain adjoining areas of N and S Pacific, ? tropical Indian Ocean)

4. Single, large terminal photophore on arms I-III or I-IV present; inner web connecting basal portions of arms deep, 50% or more of arm length in adults, subadults, and large juveniles . . . . . 5  
 Single, large terminal photophore on arms absent; inner web vestigial to moderate in depth, 30% or less of arm length in adults, subadults, and juveniles . . . . . 6
5. Buccal membrane with 6 lappets and 1 connective to arms IV; segment of inner web between right and left junctures of web segments from arms III and IV absent . . . . . *H. bonnellii*<sup>\*</sup>  
 (subarctic, north temperate, and E tropical Atlantic; Mediterranean Sea; Benguela Current; nearly circumglobal in southern half of south subtropical regions)  
 Buccal membrane with 7 lappets and 2 connectives to arms IV; segment of inner web between right and left junctures of web segments from arms III and IV present . . . . . *H. macrohista*  
 (nearly circumglobal in Southern Subtropical Convergence, Benguela Current)
6. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head, in 8-10 longitudinal rows on arms IV, in cirlet of about 19-21 (range, 17-23) around right eye . . . . . *H. heteropsis*  
 (California Current, Peru-Chile Current)  
 Photophores large or intermixed large and small, arranged in widely spaced to moderately dense pattern on ventral surfaces of mantle and head, in 3 to 4 longitudinal rows on arms IV, in cirlet of 16-18 (? rarely 15) around right eye . . . . . 7
7. Photophores large, arranged in widely to moderately widely spaced pattern on anterior  $\frac{1}{3}$ - $\frac{1}{2}$  of ventral surface of mantle; cirlet around right eye composed of 16 to 17 (rarely 18, or ?15) large photophores . . . . . 8  
 Photophores intermixed large and small, arranged in moderately dense pattern on ventral surface of mantle; cirlet around right eye composed of 17 large and 1 small photophores . . . . . 15
8. Photophores in widely spaced pattern on ventral surface of mantle; dorsal pad of funnel organ with 2 lateral flaps; male genitalia paired; skin conspicuously papillated (except in small juveniles) . . . . . 9  
 Photophores in moderately widely spaced pattern on ventral surface of mantle; dorsal pad of funnel organ unsculptured; male genitalia single; skin not papillated . . . . . 10
9. Spermatophore 5%-6% of mantle length, with single loop in ejaculatory apparatus; large adult males with midportions of arms I with moderately increased robustness, median keel moderately expanded, protective membranes low . . . . . *H. hoylei*<sup>†</sup>  
 (Pacific and Indian oceans, tropical-subtropical)  
 Spermatophore 13%-21% of mantle length, with numerous loops in ejaculatory apparatus; large adult males with midportions of arms I with greatly increased robustness, median keel greatly expanded, protective membranes high. . . . . *H. arcturi*, new combination<sup>†</sup>  
 (Atlantic, tropical-subtropical)
10. Terminal group of normal photophores on arms I-IV present, except in mature specimens (? mature male of *H. celetaria celetaria* and mature female of *H. celetaria pacifica*), where terminal groups on arms I-III replaced by single, long, narrow, darkly pigmented photophore; denticulate collars of club suckers in ventral marginal rows on manus asymmetrically broadened . . . . . 11  
 Terminal group of photophores on arms absent; denticulate collars of club suckers in ventral marginal rows on manus not asymmetrically broadened . . . . . 12

- 11. Suckers in median 2 to 3 rows of club manus slightly and approximately coequally enlarged; gladius with shoulders of vanes somewhat flaring and angular . . . . . *H. celetaria celetaria*  
(Atlantic, tropical-subtropical)  
Suckers of median 3 rows of club manus moderately enlarged to 1½ times ventral marginals (except in small juveniles), decreasing in size from ventral to dorsalmost rows; gladius with shoulders of vanes broadly rounded . . . . . *H. celetaria pacifica*  
(Pacific and Indian oceans, primarily equatorial/tropical)
- 12. Longitudinal rows of photophores on arms IV 4 . . . . . *H. corona berryi*  
(North Pacific, subtropical, California Current)  
Longitudinal rows of photophores on arms IV 3 . . . . . 13
- 13. Sucker rings on arms IV smooth; teeth on rings of large suckers of club manus 20–27 . . . . . *H. corona inermis*  
(northwestern Pacific, subtropical)  
Sucker rings on arms IV with teeth; teeth on rings of large suckers of club manus 33–60 . . . . . 14
- 14. Teeth on rings of large suckers of club manus 33–38 . . . . . *H. corona corona*  
(Atlantic, tropical-north subtropical)  
Teeth on rings of large suckers of club manus 50–60 . . . . . *H. corona cerasina*  
(eastern and central equatorial Pacific, Peru-Chile Current)
- 15. Longitudinal rows of photophores on arms IV 3 (of large organs) . . . . . *H. eltaninae*  
(Subantarctic, circumglobal)  
Longitudinal rows of photophores on arms IV 4 (3 rows of large organs, 1 row of small or mixed-size organs) . . . . . 16
- 16. Terminal group of enlarged photophores on arms I–III present; inner web moderately developed, 17%–30% of longest arm length . . . . . *H. atlantica*  
(southern subtropical convergence and northern half of subantarctic, circumglobal)  
Terminal group of enlarged photophores on arms absent; inner web vestigial to low, < 8% of longest arm length . . . . . *H. reversa*  
(Atlantic north temperate and fringing subarctic waters, north subtropical, tropical; Mediterranean Sea)

\*Probably comprises more than one taxon.

†At present, females and immature males of *H. hoylei* and *H. arcturi* can be confidently separated only by geographic location.

**Species Accounts**

***Histioteuthis reversa* Species Group**

This group comprises three closely related species. *Histioteuthis reversa* is confined to the north temperate, north subtropical, and tropical waters of the Atlantic. The other two circumglobal, Southern Ocean species are *H. atlantica*, found in the vicinity of the southern subtropical convergence (SSTC) and in the subantarctic, largely concentrated in the northern half, and *H. eltaninae*, found in the subantarctic, largely concentrated in the southern half. The group members uniquely share photophore patterns composed of intermixed large and small organs on the mantle and 17 large and one small organ

around the right eyelid, glacial vanes that are narrow to moderately wide and diamond-shaped, and a poorly developed median ridge on the lateral walls of the lower beak.

***Histioteuthis reversa* (Verrill, 1880)**

FIGURES 3, 5

*Calliteuthis elongata* N. Voss and G. Voss, 1962:184, figs. 4a–f, 6a [new synonym, herein].

Previously unreported collections of *reversa* comprising approximately 257 juveniles, subadults, and adults mainly taken on cruises of the R/V *Anton Dohrn* (USNM), R/V *Professor Shtokman* (IOAN), R/V *Vityaz* (IOAN), and R/V

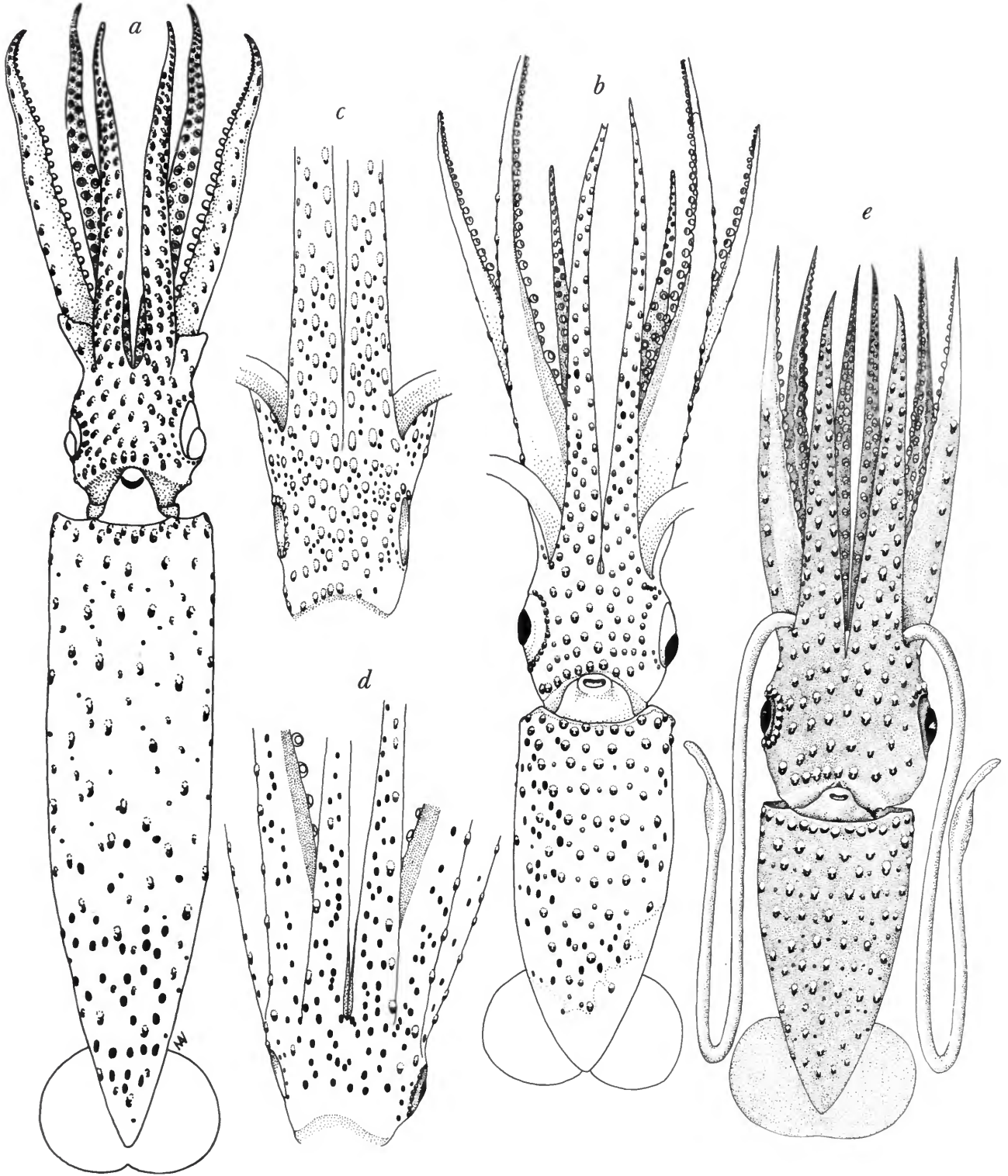


FIGURE 3 (opposite).—*Histioteuthis reversa*. *a-d*, views showing maturity-related elongation of mantle and patterns of darkly pigmented, simple photophores: *a*, ventral view of mature female, MCZ 224813, holotype of *H. elongata*, 183 mm ML, 39°21'N, 70°41'W; *b*, ventral view of mature male, ARC H2209, 85 mm GL, 43°20'N, 59°27'W; *c*, ventral view of head and arms of mature male, USNM 730959, 89 mm ML, 10°52'N, 22°09'W; *d*, dorsal view of head and arms of mature male, HML H7248, 107 mm GL, 42°55'N, 62°13'W; *e*, ventral view of juvenile male, 39 mm ML, UMML 31.1345, 41°27'N, 27°35'W (from Voss, 1969).

*Walther Herwig* (USNM), and recently reported collections of *reversa* and *Histioteuthis elongata* (N. Voss and G. Voss, 1962) from Canadian waters (ARC; Stephen, 1982) permitted us to clearly determine that *elongata* represents the mature stage of the female of *reversa*, as has been long suspected. The new collections also revealed the presence of unusual, maturity-related photophores in the male, as well as new information on distribution and geographic variations that occur in the species.

The following description is based on large juveniles, subadults, and adults, 35–186 mm ML, from over the full range of the species in the Atlantic and from the western Mediterranean. No specimens were available from the eastern Mediterranean.

**DESCRIPTION.**—Small to moderately large histioteuthids, females known to mature at 114–186 mm GL, males at about 49–99 mm GL/ML; mantle moderately elongate to elongate (mature females); fins medium-sized, length about 35%–50% ML, width about 40%–60% ML (fins proportionally smaller in mature females); head large, wider than mantle (except in mature females), usually with 1 to 2 weakly developed nuchal folds; eyes markedly asymmetrical except in mature females; arms of medium length, about 100%–150% ML (about 50%–120% ML in mature females), approximately subequal; sucker rings of arms I–III usually smooth except distal-most sucker rings often distinctly incised; sucker rings of arms IV with numerous low, blunt teeth on distal or entire margins; in mature males, suckers on basal portions of all arms with swollen collars, ends of arms I modified with coequal-size suckers on enlarged pedestals; inner web between arms I, II, and III vestigial to low (about 5%–8% of length of longest arm); buccal membrane 7-membered, with second supports single to dorsal sides of arms II or bifurcate to ventral sides of arms I and dorsal sides of arms II, fourth supports without secondary connectives; tentacles 100%–200% ML; club with deep, longitudinal cleft on aboral surface of manus; suckers on manus in about 6 diagonal rows, markedly enlarged in median ventral row to 3–4 times diameter of ventral marginals; sucker rings with numerous straight-sided, blunt or pointed teeth on entire margins, teeth often heavier and more widely spaced on proximal margins; rings of enlarged,

median suckers sometimes smooth or irregularly incised.

Compound photophores on ventral surface of mantle numerous, intermixed large (arranged in about 7 diagonal rows) and small to near posterior end of mantle; large organs numerous on ventral surface of head; right eye with circlet of 18 organs (17 large and 1 small); basal  $\frac{1}{2}$  of arms IV with 4 longitudinal rows of photophores (3 rows of large organs, 1 dorsal marginal row of small organs) (Figure 3e); near-mature and mature females with large, elliptical, black, simple photophores scattered on posterior  $\frac{1}{3}$  of ventral surface of elongate mantle and distal  $\frac{1}{2}$  of all arms (Figure 3a); mature males with similar but smaller elliptical to round, simple photophores scattered over entire ventral and lateral surfaces and partial dorsal surfaces of mantle, anterior  $\frac{3}{4}$  of dorsal surface of head, entire lengths of arms I–III, and entire or distal  $\frac{1}{2}$  of arms IV (Figure 3b–d); in males, concentration of organs decreases from arms I to IV.

Dorsal pad of funnel organ with low ridge on median  $\frac{2}{3}$  of lateral arms (ridges appear to be independent in small specimens but often appear to merge anteriorly in large individuals); spermatophore short (SpL 2.1–3.6 mm, 2.4%–4.1% ML), sperm mass short to medium (3.7%–25.3% SpL (Atlantic), 30.1%–33.7% SpL (Mediterranean)), cement body medium to long (43.3%–47.4% SpL (Mediterranean), 55.8%–82.5% SpL (Atlantic)), ejaculatory apparatus moderately short (13.2%–19.9% SpL (Atlantic), 20.1%–21.4% SpL (Mediterranean)), with single, long loop of inner tube; ejaculatory-apparatus/cement-body connective complex short; mature egg elliptical, average size 1.8 × 1.5 mm; gills about 36%–42% ML (27%–29% ML in mature females), with about 36–42 lamellae in outer demibranch.

Gladius with strong, moderately wide free rachis; vanes diamond-shaped, moderately wide, ending posteriorly in rounded cupped coil; in mature females gladius with short, narrow free rachis and long, narrow, diamond-shaped vanes, widest at anterior  $\frac{1}{4}$ – $\frac{1}{3}$  length, with gradual posterior taper ending in narrow cupped coil; lower beak with weak median ridge on lateral wall; ridge line, if projected, would intersect posterior margin of lateral wall at point slightly above free corner; hood somewhat flattened in profile; wing fold high, with steep medial side; radula with first and second laterals asymmetrical and of increasing length, marginal plates weakly developed or absent.

Skin color dark, wine red.

ORIGINAL REFERENCE.—Verrill, 1880:393.

TYPE LOCALITY.—Western Atlantic; 39°53'N, 70°59'W, 666 m.

DEPOSITION OF TYPE.—*Holotype*: USNM 574849, female, 51 mm ML, R/V *Fish Hawk* sta 894; fair condition.

DISTRIBUTION.—Confirmed reports show *Histioteuthis reversa* to be confined to the Atlantic Ocean (Figure 5). The species is widely distributed in the North Atlantic Temperate

Region including the eastern and western Mediterranean, and extends northward in the western Atlantic into the subarctic to at least 52°N. The data of Stephen (1982) indicate that *reversa* is the most common histioteuthid taken off the east coast of Canada. To the south, in a study of the cephalopods taken in Gulf Stream cyclonic rings, Lea (1978) showed a strong association between the occurrence of *reversa* and temperate slope water. A similar association was found by Lu and Roper (1979) in their investigation of the vertical distribution and abundance of cephalopods at 39°N, 73°W, off the northeastern coast of the United States. Collections taken by the Sargasso Sea Expedition of the R/V *Anton Dohrn* (USNM), cruise 9 of the R/V *Vityaz* (IOAN), and cruises of various other vessels show *reversa* to be widely distributed in the eastern half of the North Subtropical Region and essentially absent in the western half. The species is abundant in the Mauritanian Upwelling and ranges southward in eastern tropical waters to its southern limit at about 23°S. There, in the high productive area off Namibia, *reversa* has been taken in large numbers by the R/V *Akademik Kurchatov* and R/V *Professor Shtokman* (IOAN). The extension of the range of *reversa* southward in the Benguela Current and into the Agulhas Current by Clarke (1980) on the basis of beaks from stomach contents of sperm whales caught off Donkergat and Durban is questionable. In the northern sector of the Tropical Region, the species extends westward to the northeastern coast of South America (Okutani, 1983) and east of the Lesser Antilles. *Histioteuthis reversa* is absent from the Caribbean Sea and Gulf of Mexico. It also appears to be absent from the South Subtropical Region. The six individuals reported by Nesis (1974) from the southwestern sector of the region between 35°S and 45°S were examined at the workshop and found to be specimens in poor condition of the closely related *atlantica*, which is abundant in the waters of the SSTC. A specimen reported by Toll (1982) from the southeastern Pacific was examined earlier (by NV) and found to be *atlantica*. Retamal and Orellana's (1977) reported capture of *reversa* from the same area off the southwest coast of South America and Lu and Phillip's report (1985) from the Tasman Sea are probably also cases of misidentification.

The abundance of *reversa* near slopes of land masses and submarine topography is probably related to the observed preference of this species for waters of higher productivity.

*Histioteuthis reversa* inhabits the water column from surface waters to in excess of 1000 m. Data from closing nets (Lu and Clarke, 1975a) and open nets (N. Voss, K. Nesis, unpublished data) show small juveniles to about 15 mm ML to be present in the upper 200 m during both day and night. Opening-closing-net captures of all juveniles between depths of 50–630 m during the day and 10–260 m at night (Roper, 1972; Clarke and Lu, 1975; Lu and Clarke, 1975a, 1975b; Lu and Roper, 1979), together with night captures of subadults by open nets fishing as shallow as 80 m, 100 m, and 300 m (N. Voss, K. Nesis, unpublished data) suggest a pattern of diel vertical movement for both growth stages. Daytime, opening-closing-

net captures of mature females at 500 m and 1000 m during the day (Lu and Roper, 1979; reported as *H. elongata*; gladius measurements of two of the three reported specimens corrects the reported sizes of 125 mm ML and 146 mm ML to 180 mm GL and 186 mm GL), daytime, open-net captures of mature females and males in midwaters at 800–1000 m, and nighttime capture in midwaters and near the bottom at approximately 600 m, 640–730 m, 650 m, and 1300 m (N. Voss, K. Nesis, unpublished data) suggest that both sexes mature in deep water. Surface captures of spawning and dead, or near-dead, spent females (Voss and Voss, 1962; Voss, 1969; reported as *H. elongata*) show that the female of *reversa* ascends the water column to spawn, and subsequently die, in shallow water.

DISCUSSION.—The continued absence of mature females identifiable to *Histioteuthis reversa* in the relatively large collections of the species taken in recent years, and the fact that the apparently closely related, sympatric *H. elongata* is known only from near-mature and mature females (with exception of two large males listed, but not described, by Stephen, 1982:122), have created doubts as to the validity of the latter species. We found growth stages unrepresented in earlier studies among the specimens of *reversa* and *elongata* listed by Stephen (1982) from Canadian Atlantic waters and the 48 specimens of the species collected from the eastern tropical Atlantic on the 1971 cruise of the R/V *Walther Herwig*. These growth stages convincingly demonstrate that *elongata* represents the mature stage of *reversa*; consequently, it must be relegated to the synonymy of the older species.

*Histioteuthis reversa* and *elongata* share such attributes as patterns of compound photophores on the ventrum of the mantle, around the right eyelid, and on arms IV, a dorsal pad of the funnel organ with two lateral ridges, a low to vestigial inner web, a gladius with diamond-shaped vanes, and similar geographic ranges. The taxa differ in the presence, in *elongata* (as formerly known from females only) alone, of large, flat, dark, simple photophores intermixed with normal compound photophores on the posterior portion of the mantle ventrum and the distal portions of all the arms, a markedly elongate, narrow gladius, and a markedly elongate, flaccid mantle.

Examinations of one of the largest reported females of *reversa* (Stephen, 1982: ARC H6726, 100 mm ML) and two of the smallest reported females of *elongata* (Stephen, 1982: SJBS H-10, 85 mm ML (94 mm GL); ARC 2204, 119 mm ML/GL) showed them to be identical and to display distinctive characteristics of both taxa. Each specimen is in the maturing stage (indicated by large oviducal and nidamental glands, an enlarged egg mass with nearly round ovarian eggs of ~0.44 mm diameter, and eggs absent in the oviducal ducts), and each possesses the firm-textured, moderately elongate mantle of *reversa* and the large, black photophores on the posterior one-third of the mantle ventrum and the distal ends of the arms that characterize *elongata*. The gladius (extracted from the 94 mm GL and 119 mm GL specimens) resembles that of *reversa* except for having slightly narrower vanes and free rachis than

were illustrated and described for the species by Toll (1982) on the basis of juveniles and subadult and mature males of 30–93 mm GL. The sexually dimorphic elongation of the gladius, which results in the long, narrow gladius and mantle that typifies *elongata*, obviously occurs over a short time period close to maturity of the female.

The poor conditions of the skin and arms of the three mature males available for Voss's 1969 study of the species precluded accurate descriptions of the photophore patterns and secondary sexual modifications of the arms. Our examinations of six new mature males in good condition, four from the northwestern Atlantic (ARC H2209, ARC H7247, reported as *H. elongata* by Stephen, (1982); ARC H7248, reported as *H. reversa* in the same work) and two from the eastern tropical Atlantic (USNM 730959, USNM 817118), show the mature male of *reversa* to have, scattered on the mantle, head, and arms, the same, but smaller, novel, dark simple photophores as found in the mature female (for details of the photophore arrangements, see the species diagnosis and Figure 3a–d). Additionally, some of the new specimens displayed secondary male modifications of the suckers and sucker pedestals on the ends of arms I and modifications of the basal suckers on all the arms. These modifications are found to be typical of other histioteuthids but have not been previously reported for *reversa*. The apparent absence of the modifications in some of the males judged to be mature by the presence of spermatophores may be related to their apparent early stage of maturity.

Evidence suggesting the occurrence of distinct geographical populations of *reversa* has been presented by several authors. In a comparative study of the spermatophores from northwestern Atlantic (2) and Mediterranean (1) specimens, Voss (1969), and later Hess (1987) using the same material, found distinct morphometric differences in the major internal components. Especially striking, and of considered importance, was the proportional difference in the lengths of the sperm mass, short in the western Atlantic specimens and moderately long in the Mediterranean one. In a comparative study of gladii from over the geographic range of the species, Toll (1982) reported a tendency for the gladii from Mediterranean specimens to be proportionally wider than those from the eastern tropical Atlantic. The gladii from northwestern Atlantic material he found to be more variable in width, with the range of width indices overlapping those from the other two areas. The above evidence prompted Voss et al. (1992) to label *reversa* a "group." In an attempt to more clearly define the apparent populational differences, we have measured spermatophores from newly available specimens from the eastern tropical and northwestern Atlantic. Unfortunately, we were unable to locate mature males from the northeastern Atlantic or new ones from the Mediterranean. The ranges of the newly calculated indices for sperm mass length, combined with those from the earlier investigations (some corrected by use of gladius length rather than mantle length), are given in Table 3 together with the results of a companion study of the attachments of the second

TABLE 3.—Comparison among *Histioteuthis reversa* from the Mediterranean, eastern tropical (ET) Atlantic, and northwestern (NW) Atlantic. For explanation of indices, see "Materials and Methods."

Character	Mediterranean	ET Atlantic	NW Atlantic
Spermatophore			
Number of specimens	1	4	5
ML/GL of specimens	93 mm	70–92 mm	61–107 mm
SpLI	3.3–3.8	2.4–3.9	3.3–4.1
SpMLI	30.1–33.7	3.7–10.2	4.9–25.3
2nd buccal membrane support attachments			
Number of specimens	6	10	13
Single to arms II	6	3	8
Bifurcate to arms I and II	0	7	5

buccal membrane supports, another character that we found to vary over the geographic range of the species. Although our expanded spermatophore study shows a broader range of sperm mass length indices for the northwestern Atlantic population than the 4.9–10.8 range from the previous investigations, the range of high values for the Mediterranean form remains distinct. The Mediterranean population of *reversa* appears to be further distinguished by the uniform occurrence of single attachments of the second buccal membrane supports, in contrast to the two types of attachments found in the populations from the other study areas. The two Atlantic populations, on the other hand, cannot be clearly separated from each other on the basis of either the spermatophore or buccal membrane characters. Although the above evidence is strongly suggestive, we consider it to be inadequate at present to grant subspecific status to the Mediterranean form. We hope, however, that it is sufficient to provoke a more detailed comparative study in the future, using additional material, especially from the Mediterranean and the northeastern Atlantic, and employing additional characters.

#### *Histioteuthis atlantica* (Hoyle, 1885)

FIGURES 4, 5

Our examination of previously unreported collections of *atlantica* taken from the Atlantic on the 1971 and 1975/1976 cruises of the R/V *Walther Herwig* (USNM; 269 juveniles, subadults, and adult males), and from Australian (NMV; 30 juveniles and subadults, one adult male) and New Zealand (NMNZ; 41 juveniles, subadults, and adult males) waters, mostly on fisheries survey cruises, permitted us to resolve the recent problem of the questioned integrity of the species (M. Lipinski, pers. comm.; Hess, 1987; Voss et al., 1992) and considerably expand our knowledge of its biology and distribution. The following description is based on large juveniles, subadults, and adult males, 51–258 mm ML that came largely from the Atlantic and the Pacific, the central and

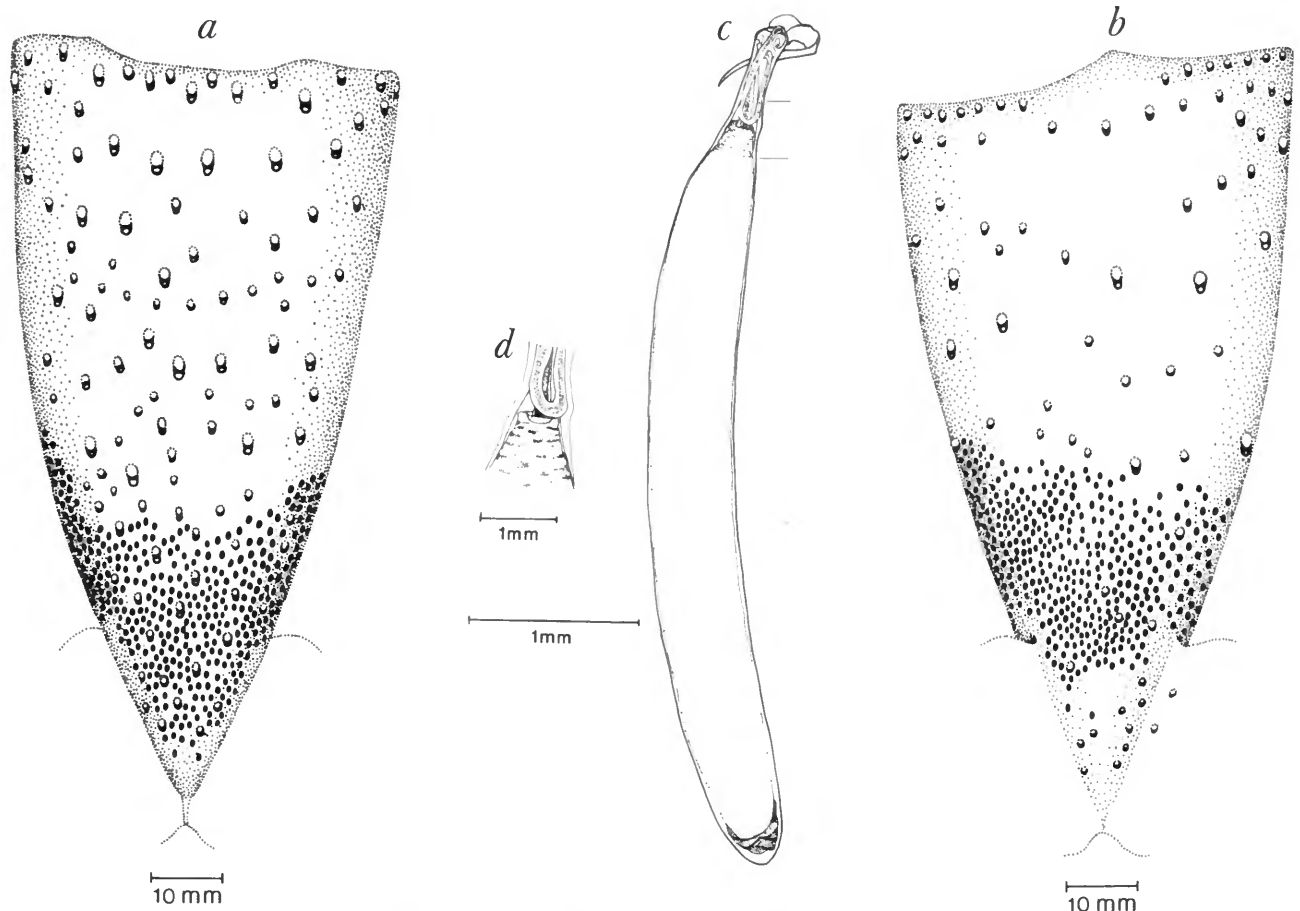


FIGURE 4.—*Histioteuthis atlantica*: *a*, ventral view of mantle of mature male, USNM 816924, 115 mm ML, 40°18'S, 39°12'W, showing maturity-related pattern of darkly pigmented, simple photophores; *b*, dorsal view of same; *c*, spermatophore, SFIG, 87 mm ML, SW Atlantic; *d*, enlargement of area of ejaculatory-apparatus/cement-body connective complex of same.

western sectors of the species' circumglobal range, in the vicinity of the SSTC. The adult female remains unknown.

**DESCRIPTION.**—Small to moderately large histioteuthids; males known to be mature at 51–258 mm ML; female size at maturity not known (females near mature at 114–149 mm ML); mantle moderately elongate; fins of medium size, length about 26%–47% ML, width about 53%–65% ML (at 51–91 mm ML); head with 1 nuchal fold; arms of medium length, about 105%–176% ML (at 51–91 mm ML), length formula usually III > II > IV > I; sucker rings nearly smooth to incised with about 5–10 low teeth on distal and occasionally entire margins; basal suckers on all arms of fully mature males with swollen, fleshy collars; inner web moderately developed, about 17%–30% length of longest arm; buccal membrane 7-membered, with second supports to dorsal sides of arms II; fourth supports without secondary connectives; tentacles long,

about 150%–300% ML; club with deep, longitudinal cleft on aboral surface of manus; suckers on manus in about 6 rows; 3 to 4 suckers in median row disproportionately enlarged to 4 times size of ventral marginal suckers, with rings irregularly incised, often partly smooth in subadults and adults (dentition more regular in juveniles).

Compound photophores intermixed large (arranged in about 6 diagonal rows) and small on ventral surface of mantle to near posterior end; in mature male, posterior  $\frac{1}{2}$ – $\frac{2}{3}$  of dorsal and ventral surfaces of mantle with additional dense concentration of darkly pigmented, small to medium-sized simple photophores (Figure 4*a,b*); in mature female, presence or absence of peculiar pattern of dark, simple photophores not known; circlelet of 18 photophores (17 large and 1 small) around right eye; arms IV with 4 longitudinal rows of photophores (3 rows of large organs, 1 dorsal marginal row of intermixed medium and small



organs); terminal  $\frac{1}{3}$  of arms I, II, and III with row of greatly enlarged, elliptical, heavily pigmented, simple photophores (7 or more in large juvenile and later growth stages) that progressively decrease in size distally; in late growth stages, arms IV with single, less-enlarged terminal photophore.

Dorsal pad of funnel organ with ridge on median line of each lateral arm; spermatophore short (SpL 4.4–10.6 mm, 3.8%–5.2% ML; from 2 specimens: SFIG, 87 mm ML, SW Atlantic; NMNZ P1-7-81, 258 mm ML, SW Pacific), with sperm mass short (5.3%–8.4% SpL), cement body long (74.3%–78.6% SpL), ejaculatory apparatus of medium length (13.8%–17.0% SpL), with 1 (87 mm ML specimen) loop of inner tube (2 to 3 loops that appear in spermatophore of 258 mm ML specimen may or may not be due to partial, interior rupture), ejaculatory-apparatus/cement-body connective complex short (Figure 4c,d); mature egg not known; gills about 30%–33% ML, with about 30–34 lamellae on outer demibranch.

Gladius with strongly developed free rachis, moderately broad, diamond-shaped vanes that end in bluntly rounded, cupped coil; entire gladius moderately thickened, particularly in large specimens; lower beak with poorly developed median ridge on lateral wall; ridge line, if projected, would intersect posterior margin of lateral wall at point slightly above free corner; wing fold high (in large animals) with steep medial side, wing long; radula nearly homodont, with rachidian and first and second laterals of similar size, shape, and base configuration; third laterals longer, slightly curved; marginal plates absent.

ORIGINAL REFERENCE.—Hoyle, 1885:201; illustrated, Hoyle, 1886, pl. 30: figs. 9–15.

TYPE LOCALITY.—South Atlantic; 35°36'S, 21°12'W, 3700 m.

DEPOSITION OF TYPE.—*Holotype*: BMNH 1890.1.24.18, male, 35 mm ML, H.M.S. *Challenger* sta 333, 13 Mar 1876; fair condition.

DISTRIBUTION.—*Histioteuthis atlantica* is found circumglobally between about 30°S–33°S and 50°S (Figure 5). Its normal geographic range includes the SSTC and fringing subtropical waters as well as the subantarctic, where it appears to occur in greatest abundance in the northern half of the region. In the collections from the vicinity of the convergence taken on the 1971 and 1975/1976 cruises of the R/V *Walther Herwig*, *atlantica* was found to be the dominant of the two histioteuthids, *atlantica* and *macrohista*, whose normal range includes the SSTC. During those cruises, a total of 269 specimens of *atlantica* were captured, with mature males, maturing females, and juveniles taken in all sectors of the convergence across the Atlantic. *Histioteuthis atlantica* occurs in the Benguela Current, but distribution appears to be limited to south of 35°S. In the Australian and New Zealand areas, the species occurs north to 33°S in the East Australian Current (C. Lu, unpublished data), is broadly distributed across the Tasman Sea, and extends to about 33°S north and northeast of New Zealand (E. Förch, unpublished data). Westward into central

waters to 125°W, it has been reported from a band between 37°S and 49°S (Voss, 1969; Toll, 1982; Polezhaev, 1986) and from 21°S–47°S in the Peru-Chile Current (Voss, 1969; Toll, 1982, as *H. reversa*; Retamal and Orellana M., 1977, as *H. reversa*; Rocha V. et al., 1991).

*Histioteuthis atlantica* is regularly found over ocean basins as well as over plateau and shelf areas. Our data suggest that *atlantica* may be somewhat geographically isolated from the closely related *eltaninae*, which typically occurs further to the south in the subantarctic, sometimes penetrating south of the Antarctic Polar Front (APF), and is associated with waters of probable higher productivity. There is, however, clearly an overlap in the distributions of the siblings between 45°S and 50°S.

*Histioteuthis atlantica* has been taken in open nets fishing at depths of 40 m to in excess of 2000 m. Juveniles to about 25 mm ML have been taken in open nets fishing both in the upper 100 m and 200 m at night and at about 500–1000 m during both day and night. Mature males and maturing females have been captured by open nets fishing at various depths between 300 m and 2000 m at night and between 900 m and 1000 m during the day. Trawls have caught subadults on the bottom between 700 m and 844 m at night.

DISCUSSION.—Most Southern Ocean species exhibit circumglobal distribution. The question of whether *atlantica* similarly is a single, circumglobally distributed Southern Ocean species or comprises two or more taxa (Hess, 1987; Voss et al., 1992) originated from 1979–1980 correspondence from M. Lipinski to one of us (NV). Lipinski found an unusual concentration of small, simple, dark photophores on the dorsum and ventrum of the mantle of an 87 mm ML mature male (SFIG) from the SW Atlantic that closely resembled *atlantica*. In addition, he described the spermatophore of the specimen as differing in proportional length and in details of interior structure from that described and illustrated in Voss's 1969 family revision for a 51 mm ML specimen of *atlantica* taken off South Africa.

A subsequent examination (by NV) made shortly thereafter of the large, unreported collections of *atlantica* in the USNM (taken on the 1971 R/V *Walther Herwig* cruise) showed the unusual photophore pattern described by Lipinski (Figure 4a,b) to be present on the mantles of all of the 20 mature males that were taken over a wide portion of the species' recognized range across the Atlantic. Among the R/V *Walther Herwig* specimens, which varied in size from 70 to 142 mm ML, the number and density of the photophores increased with the size of the animal. Also at this time, Clarke (1980) illustrated the same feature on a separate mantle of 150 mm GL that he identified as ?*atlantica*, found in the stomach of a sperm whale from off Albany, western Australia. At the workshop, we had the opportunity to examine three additional mature males (121 mm ML, 146 mm ML, and 258 mm ML; NMNZ, NMV) from the Australia–New Zealand area and found all to similarly display the novel photophore arrangement that we now regard

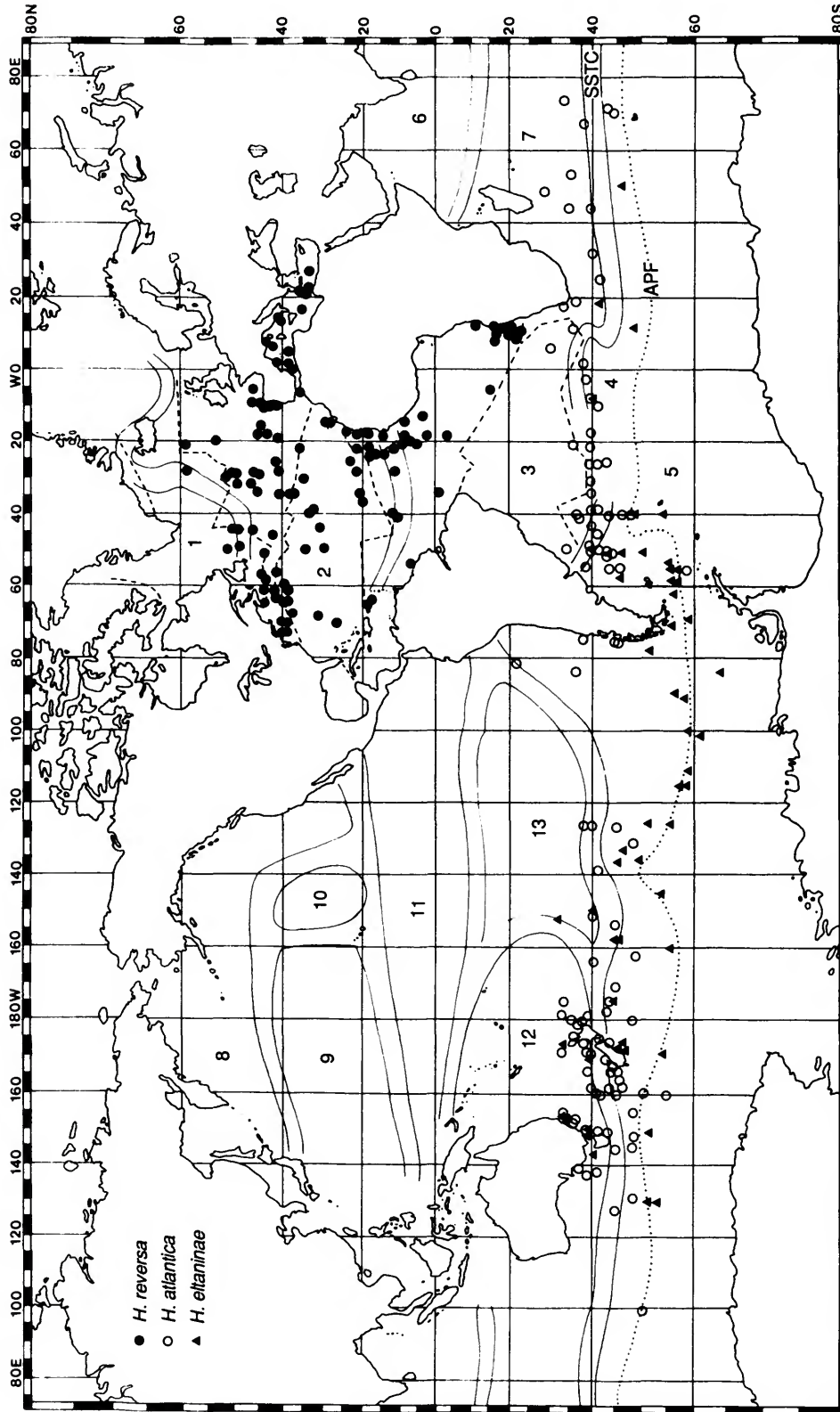


FIGURE 5.—Geographic distributions of members of *Histiotethis reversa* species group. Distribution of *H. reversa* from 260 net hauls (491 specimens), *H. atlantica* from 147 net hauls (419 specimens), and *H. eltaninae* from 68 net hauls (120 specimens). Distributions on this and subsequent maps include locations of all verified species records. Each symbol indicates location of 1 or more specimens; greatly overlapping capture localities not shown. Numbered areas surrounded by solid lines, except in cases of northern and southernmost areas, denote upper water-mass regions (after Sverdrup et al., 1942): 1 = Subarctic Atlantic, 2 = North Atlantic Central, 3 = South Atlantic Central, 4 = Subantarctic, 5 = Circumpolar, 6 = Indian Equatorial, 7 = Indian Central, 8 = Subarctic Pacific, 9 = Western North Pacific Central, 10 = Eastern North Pacific Central, 11 = Pacific Equatorial, 12 = Western South Pacific Central, 13 = Eastern South Pacific Central. SSTC = approximate location of southern subtropical convergence; APF = approximate location of Antarctic Polar Front. Position of SSTC in eastern Pacific E. of ~100°W does not correspond with band of transition water shown on map. Dashed lines in Atlantic indicate boundaries of mesopelagic faunal regions of Backus et al., 1977 (see Figure 2). (Map adapted from Johnson, 1982.)

FIGURE 5.—Geographic distributions of members of *Histiotethis reversa* species group. Distribution of *H. reversa* from 260 net hauls (491 specimens), *H. atlantica* from 147 net hauls (419 specimens), and *H. eltaninae* from 68 net hauls (120 specimens). Distributions on this and subsequent maps include locations of all verified species records. Each symbol indicates location of 1 or more specimens; greatly overlapping capture localities not shown. Numbered areas surrounded by solid lines, except in cases of northern and southernmost areas, denote upper water-mass regions (after Sverdrup et al., 1942): 1 = Subarctic Atlantic, 2 = North Atlantic Central, 3 = South Atlantic Central,

TABLE 4.—Comparison of spermatophores of members of the *Histioteuthis reversa* species group. Number of specimens examined is given in parentheses. For explanation of indices, see "Materials and Methods" (EjAp = ejaculatory apparatus; EjAp/CB = ejaculatory apparatus/cement body).

Character	<i>H. reversa</i> (10)	<i>H. atlantica</i> (2)	<i>H. eltaninae</i> (2)
Specimen size	61–107 mm ML	87 mm ML, 258 mm ML	66 mm ML, 88 mm ML
Geographic area sampled	NW + E tropical Atlantic, Mediterranean Sea	Atlantic + SW Pacific sectors of SSTC	Atlantic sector of subantarctic
SpL (mm)	2.1–3.6	4.4–10.6	4.5–6.4
SpLI	2.4–4.1	3.8–5.2	6.9–7.3
SpMLI	3.7–33.7	5.3–8.4	2.2–4.2
CBLI	43.3–82.5	74.3–78.6	67.3–75.3
EjApLI	13.2–21.4	13.8–17.0	21.3–~26
Loops in EjAp	1 long	1 long ? or 2–3 of varying lengths	1 long
EjAp/CB connective complex	short	short	long
General shape	oral 1/2 and aboral 1/2 of ~ uniform width	oral 1/5 abruptly narrower than remaining stout, aboral portion	oral 1/2 distinctly elongate and narrower than aboral 1/2

as a maturity-related feature of the male of *atlantica*. The appearance of a concentration of similar, but proportionally larger, photophores on the mantle in the mature stages of both sexes in its northern sibling, *reversa*, suggests that the feature could also occur in the mature female of *atlantica*, which is at present unknown.

Concerning the above observed differences in the spermatophores, we concluded that the spermatophore from the South African specimen of 51 mm ML (Voss, 1969) was immature, basing our judgement partly on the specimen's lack of such maturity-related features as the above described photophore arrangement on the mantle and swollen collars on the basal suckers of the arms. The apparent immature features of the spermatophore include an open coil in the oral end of the cement body and the absence of an ejaculatory-apparatus/cement-body connective complex. Further study showed the spermatophore of the largest known male of the species, 258 mm ML taken off New Zealand, and the only other specimen in which we found largely intact spermatophores, compared well, morphologically and morphometrically, with that of Lipinski's 87 mm ML male from the southwestern Atlantic (Figure 4c,d), except for the loops of the inner tube of the ejaculatory apparatus. In the former, the loops varied in length and in number from two to four, in contrast to the single, long loop in the latter and in the spermatophore from the southeastern Atlantic specimen. Whether the multiple loops are the result of partial internal rupture of the ejaculatory apparatus or are a distinguishing feature of the population from the New Zealand area can only be resolved by a future study of new material. Both the New Zealand and southwestern Atlantic spermatophores possess a distinct, short ejaculatory-apparatus/cement-body connective complex, which we consider to be characteristic of *atlantica*. It is similar to that found in *reversa* but differs in proportional length from that of its southern sibling

*eltaninae*. The distinctive general shape of the spermatophore distinguishes it from both species (see Table 4).

Toll (1982) found that the gladius did not vary significantly across the geographic range of *atlantica*. He did, however, detect possible ontogenetic changes, that is, a reduction in the relative width of the gladius and length of the free rachis. In light of Toll's findings and those of our present study, we conclude that *atlantica* represents a single species. The suggestion that the population from the western Pacific can be distinguished from that of the Atlantic on the basis of internal structural differences of the spermatophore demands further investigation.

#### *Histioteuthis eltaninae* N. Voss, 1969

##### FIGURE 5

The study of this species is based on data from Voss's 1969 revision and 76 new, mostly unreported specimens found in the collections of various institutions (AtlantNIRO, IOAN, IOS, NMNZ, NMV, TINRO, UMML, USNM, YugNIRO). Our description is based on large juveniles, subadults, and adult males, 39–105 mm ML, that came largely from the Pacific and western Atlantic sectors of the species' range in the subantarctic. The adult female remains unknown.

DESCRIPTION.—Small to medium-sized histioteuthids; males known to mature at about 66–105 mm ML; female size at maturity not known, largest specimens of 89 mm ML and 98 mm ML immature; mantle moderately elongate; fins of medium size, length about 29%–37% ML, width about 48%–55% ML; head with 1 nuchal fold; arms of medium length, about 100%–127% ML, length formula II = III > I = IV; sucker rings with variable number of low, triangular teeth ranging from about 7–9 confined to distal margins (holotype) to 20 around entire margins; in mature

male, suckers on basal portions of arms I (and possibly of all arms) slightly enlarged, with swollen fleshy collars; inner web low to vestigial; buccal membrane 7-membered, with second supports to dorsal sides of arms II, fourth supports without secondary connectives; tentacles long, often in excess of twice mantle length; club with deep, longitudinal cleft in aboral surface of manus; suckers of manus arranged in about 5 to 6 rows; 4 median suckers greatly enlarged to 3–4 times diameter of ventral marginal suckers; largest suckers with about 36–54 (52, holotype) low, blunt, triangular teeth around entire margins.

Compound photophores intermixed large (arranged in about 6 to 7 diagonal rows) and small on entire ventral surface of mantle; circlet of 18 organs (17 large and 1 small) around right eye; arms IV with 3 rows of large photophores on basal portions.

Dorsal pad of funnel organ with independent, low ridge on median  $\frac{2}{3}$  of each lateral arm; spermatophore short (SpL 4.5–6.4 mm, 6.9%–7.3% ML; from 2 specimens: UMML 31.1340, 66 mm ML, USNM 817751, 88 mm ML); sperm mass short (2.2%–4.2% SpL); cement body long (67.3%–75.3% SpL); ejaculatory apparatus of medium length (21.3%–26.1% SpL), with single loop of inner tube; ejaculatory-apparatus/cement-body connective complex long; mature egg not known; gills about 35%–50% ML, with about 30–33 lamellae in outer demibranch.

Gladius with strongly developed free rachis, moderately wide, diamond-shaped vanes ending posteriorly in moderately broad, rounded, cupped coil; lower beak with poorly developed, or mere trace of, median ridge on lateral wall; ridge line, if projected, would intersect posterior margin of lateral wall at point slightly above free corner; hood slightly rounded in profile, wing fold somewhat rounded; radula with first and second laterals slightly asymmetrical and of slightly increasing length, marginal plates absent.

ORIGINAL REFERENCE.—Voss, 1969:755, figs. 3d–e, 5c, 7d, 12, 13, 14i–m.

TYPE LOCALITY.—Subantarctic; 40°05'S, 149°55'W, about 880 m.

DEPOSITION OF TYPES.—*Holotype*: USNM 576164, female, 53.3 mm ML, R/V *Eltanin* sta 1723, 18 Jul 1966; good condition.

*Paratypes* (8 specimens): UMML 31.1340–41; USNM 576170–75.

DISTRIBUTION.—*Histioteuthis eltaninae* occurs circumglobally in the subantarctic (Figure 5), where it is the most common histioteuthid captured. The northern boundary of its normal distributional range is marked by the SSTC, the transitional waters of which, at least in the Atlantic, are not regularly inhabited by the species. The north–south transects of the convergence and neighboring waters made by the R/V *Akademik Kurchatov* (Nesis, 1974) and during the 1975/1976 cruise of the R/V *Walther Herwig* took no specimens in the convergence. The 1971, east–west transect by the R/V *Walther*

*Herwig* made but a single encounter (a juvenile taken at 40°S, 8°W). Only scattered captures, notably in the vicinity of the Antarctic Peninsula and in the Scotia Sea, have been made south of the Antarctic Polar Front (APF). Exceptional penetrations of *eltaninae* northward of its normal subantarctic range occur in the area of Australia and New Zealand where it occurs with, but is found in lesser number than, its sibling species, *atlantica*. The species ranges to about 33°S in the East Australian Current (C. Lu, unpublished data) and is sparsely scattered to about the same latitude in the northeastern Tasman Sea (E. Förch, unpublished data). Over its range in the subantarctic, it has been taken in greatest number in the southern half of the region. Although *eltaninae* occurs over oceanic basins, its greatest abundance is found in the higher productivity waters associated with submarine ridges and continental shelves.

*Histioteuthis eltaninae* extends vertically from the surface 100 m to unknown depths below 1000 m. Juveniles of 7–20 mm ML have been taken in open nets fishing at night in the upper 200 m and during the day at 200 m. Four nighttime captures with closing nets were made at depths of 30 m, 150 m, and 175 m in the eastern Tasman Sea. Larger animals to 105 mm ML have been taken in open nets fishing maximum depths of 183 m to ~2800 m. Included in the latter size-group are mature males captured in midwater depths of 200 m (night) and ~2000 m, and near the bottom at 620 m.

DISCUSSION.—Morphologically, *eltaninae* appears to be fairly uniform over its circumglobal range in the subantarctic. Toll (1982) compared the gladii of specimens from over broad ranges in the Atlantic and Pacific oceans and reported relatively low morphometric variability. The diamond shape of the gladius of *eltaninae* illustrated and described by Toll closely resembles that of its sibling species, *atlantica* and (the male and immature females of) *reversa*. *Histioteuthis eltaninae* and *reversa* are distinguished from each other by their individual patterns of photophores on arms IV, morphological and morphometric differences in the spermatophores, and by discrete geographic ranges (see Tables 4, 5). In addition, differences could exist in maturity-related features of the photophore patterns on various parts of the body and in body shape in the female and male, but the poor condition of the skin of the two available mature males and the lack of mature females of *eltaninae* makes it impossible for us to say at this time. Marked differences in the development of the inner web and in the pattern of photophores on the arms easily separate *atlantica* from *eltaninae* (see Table 5).

Until the present study, the spermatophore of *eltaninae* was known from only a single specimen, the 66 mm ML paratype (UMML 31.1340). We were fortunate at the workshop to have spermatophores from a second male (USNM 817751, R/V *Walther Herwig* 22/75–76) that was taken from an area in the western South Atlantic near the above paratype. These spermatophores compare well with that of the paratype, which was illustrated and described by Voss (1969) and discussed by

TABLE 5.—Comparison among members of the *Histioteuthis reversa* species group. (For comparison of spermatophores, see Table 3.)

Character	<i>H. reversa</i>	<i>H. atlantica</i>	<i>H. eltaninae</i>
Photophore pattern			
Number of longitudinal rows on arms IV	4 (3 rows large, 1 row small organs)	4 (3 rows large, 1 row intermixed-size organs)	3 (large organs)
Terminal group of enlarged organs on arms I-III	absent	present	absent
Inner web	vestigial to low	moderately developed	vestigial to low
Maturity-related features			
Unusual, dark, simple photophores	present, scattered on portions of mantle, head,* and arms of females and males	present, in dense arrangement on mantle of males; not known in females; single enlarged terminal organ present on arms IV in both sexes	not known
Marked elongation of gladius and mantle in female†	present	appears to be absent	not known
Geographic range	Atlantic north temperate and fringing subarctic waters; north subtropical, tropical	SSTC and fringing subtropical waters; northern half of subarctic; circumglobal	subantarctic, concentrated in southern half; circumglobal

\*On head only in males.

†Mature female known only for *H. reversa*; large subadult known for *H. eltaninae*; near-mature female known for *H. atlantica*.

Hess (1987), with the exception of the ejaculatory-apparatus/cement-body connective complex, which showed increased development in the new, larger specimen. *Histioteuthis eltaninae* can be distinguished from its sibling species, *atlantica* and *reversa*, by the general shape of the spermatophore and the length of the ejaculatory-apparatus/cement-body connective complex (Table 4). Possible differences seen in the proportional lengths of other internal components cannot be evaluated until additional spermatophores of *eltaninae*, taken from over a broader part of the species' distributional range, become available.

#### *Histioteuthis hoylei* Species Group

Our study of new material has shown that the warm-water species *Histioteuthis hoylei* (Goodrich, 1896), formerly considered cosmopolitan and more commonly known in recent literature as *H. dofleini* (Pfeffer, 1912), comprises two separate, closely related species. One species is confined to the Pacific and Indian oceans and is identical to *H. hoylei*, and the other species, for which *Stigmatoteuthis arcturi* Robson, 1948, is available for the specific name, is restricted to the Atlantic. Although the existence of two distinct taxa was long suspected (Voss, 1969; Voss et al., 1992), it required the detailed comparison of mature males from the Atlantic and Pacific to furnish the clenching evidence. Together the two species *hoylei* and *arcturi* form the *hoylei* species group. The group is uniquely characterized by paired male genitalia, a dorsal pad of the funnel organ with two well-developed lateral flaps, and skin that is conspicuously papillated.

#### *Histioteuthis hoylei* (Goodrich, 1896)

FIGURES 6a,b,e, 7

*Histiopsis hoylei* Goodrich, 1896:15, pl. 4: figs. 62-71.

Hoyle's recently found holotype (NMWZ) together with 48 mostly unreported specimens located by one of us (KN) in the collections of the IOAN and ZISP, 22 unreported specimens found in the collections of the NMNZ, NMV, SIO, UMML, and USNM, and captures reported by Voss (1969), Young (1975), Okutani et al. (1976), Jefferts (1983), and Polezhaev (1986) furnished the information on which we have redescribed this species and described its distribution. The species description is based primarily on adults, subadults, and large juveniles, 55-210 mm ML, from the eastern, central, and western North Pacific. Only small juveniles were available from the Indian Ocean; small juveniles and one large juvenile were available from the South Pacific.

DESCRIPTION.—Medium-sized to moderately large histioteuthids; females known to mature at 140 mm ML to ~236 mm ML, males at <100-210 mm ML; skin of mantle, head, arms, and basal 1/2 of fins covered with low, fleshy papillae, imparting overall rough appearance; mantle relatively short, moderately stout; fins of medium size, length about 30%-40% ML, width about 45%-70% ML (55-172 mm ML); head with no nuchal folds apparent; arms long, about 160%-250% ML, except in male in full mating condition, where arms I may extend to >400% ML (see "Discussion," below); arm-length formula usually II  $\cong$  III > I  $\cong$  IV in females and juvenile males, I > III > IV > II or III > IV > I  $\cong$  II in mature and subadult

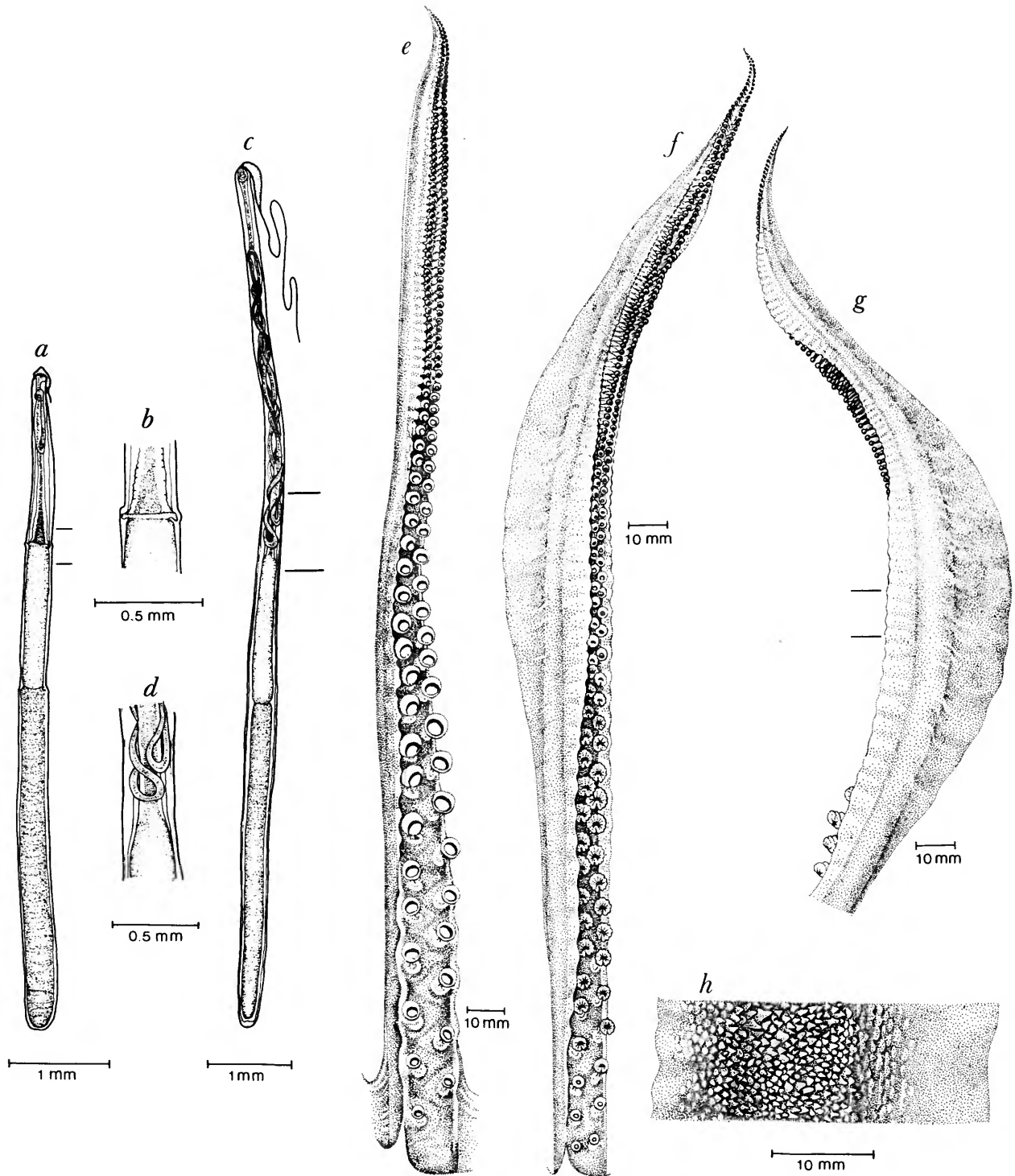


FIGURE 6.—*Histioteuthis hoylei*: *a*, spermatophore, UMML 31.2545, 149 mm GL, 32°N, 124°W; *b*, enlargement of area of insertion of ejaculatory tube on cement body of same; *e*, three-quarters oral view of left of symmetrically modified arms I of same. *Histioteuthis arcturi*: *c*, spermatophore, UMML 31.895, 72 mm ML, 28°58'N, 88°37'W; *d*, enlargement of area

of insertion of ejaculatory tube on cement body of same; *f*, three-quarters oral view of left of symmetrically modified arms I, USNM 816146, 106 mm ML, mature male, 31°51'N, 63°44'W; *g*, ventral view of distal 3/4 of same; *h*, enlargement of indicated portion of same showing papillation of skin. (*c,d*, redrawn from Voss, 1969.)

TABLE 6.—Comparison of measurements, indices, and counts of spermatophores of *Histioteuthis hoylei* from the western and eastern North Pacific. Means are given in parentheses; for explanation of indices see "Materials and Methods." (EjAp = ejaculatory apparatus.)

Character	Chun, 1910*	Sasaki, 1929†	UMML 31.2545	Species
ML(GL) (mm)	140	10 or 140	149	
Locality	35°N, 139°E	39°N, 142°E or 36°N, 142°E	32°N, 124°W	
Spermatophores	?	1	5	
SpL (mm)	7.0–8.5	9	7.8–8.1 (7.9)	7.0–9.0 (8.0)
SpL1	5.0–6.1	4.3 or 6.4	5.3–5.4 (5.3)	5.0–6.1 (5.4)
SpMLI	50.6	45.7	55.6–59.2 (58.0)	45.7–59.2 (55.2)
CBL1	28.3	22.3	18.3–23.2 (20.3)	18.3–28.3 (21.7)
EjApL1	20.5	31.4	25.3–27.2 (26.2)	20.5–31.4 (26.1)
Loops in EjAp	1	1	1	1

\*Indices for sperm mass, cement body, and ejaculatory apparatus based on measurements taken from author's illustration.

†It was not recorded which of Sasaki's two males produced the spermatophore. Indices for sperm mass, cement body, and ejaculatory apparatus based on measurements taken from author's illustration.

males; sucker rings on arms I–IV usually with 6–16 low, flat, truncate or rounded teeth on distal and lateral margins; sometimes rings on arms IV with numerous, truncate teeth around entire margins; in mature male, suckers on midportions of arms III and II and on basal portions of arms I enlarged, with apertures of increased width; greatest sucker enlargement found on arms I; extent of presence of swollen collars on enlarged suckers could not be determined from available material; enlarged suckers occur on all arms in late stage of maturity (see Chun, 1910:130, pl. 1: figs. 1, 2, as *Calliteuthis ocellata* Owen); rings of small suckers on modified ends of arms I with numerous short, stout, pointed teeth on distal and lateral margins or entire margins; in mature male, approximate terminal  $\frac{1}{2}$  of arms I modified with pedestals of biserial, small, coequal-sized suckers elongated to form palisade along each arm margin, with deep, wide, intervening channel; protective membranes low, fused to enlarged sucker pedestals; basal  $\frac{1}{2}$  of modified portions (approximate third  $\frac{1}{4}$  of arms) show moderately increased robustness of arm and moderate development of fleshy median keel (Figure 6e); inner web vestigial; outer web developed to 6%–14% of longest normal arm length; buccal membrane 7-membered, with second supports to dorsal sides of arms II; fourth supports without secondary connectives; tentacles long, about 200%–300% ML; club with deep, longitudinal cleft on aboral surface of manus; suckers on manus in 5–7 rows, markedly dissimilar in size and dentition; 3 to 4 median suckers greatly enlarged to > 4 times size of marginal suckers; suckers with rings incised around entire margins with about 38–85 sharp teeth (55–85 teeth in specimens from N Pacific (19°N–33°N, 123°E–124°W), 38 teeth in only large specimen from S Pacific (40°S, 125°W)); suckers of dorsal and ventral marginal rows minute.

Compound photophores widely spaced on ventrum of mantle, arranged in about 6 diagonal rows, equally large on anterior  $\frac{1}{3}$  with no intermixture of small organs; photophores

progressively decrease in size on posterior  $\frac{2}{3}$  of mantle; circlet of 17 large photophores around right eye; arms IV with 3 longitudinal rows of large organs on basal portions; in adults and subadults, small, elongate, black, simple photophore (2 times length of preceding normal photophore in 172 mm ML, near-mature female; 4 times length in 149 mm ML, mature male) present on ends of arms IV; presence or absence of terminal photophore on arms I–III not known because of poor condition of skin in available specimens.

Dorsal pad of funnel organ with strong, median ridge extending from apical papilla down length of each lateral arm and expanding posteriorly to form 2 broad flaps; male genitalia paired; spermatophore of medium length (SpL 7.0–9.0 mm, 5.0%–6.1% ML; from 3 specimens, 140–210 mm ML, see Table 6, Figure 6a,b); sperm mass moderately long (45.7%–59.2% SpL); cement body of medium length (18.3%–28.3% SpL); ejaculatory apparatus of medium length (20.5%–31.4% SpL), with single loop of inner tube; ejaculatory-apparatus/cement-body connective complex absent; mature egg not known; gills about 40%–50% ML, with about 35–49 lamellae in outer demibranch.

Gladius with broad, moderately short rachis, elongate anterior shoulders of vanes with slightly scalloped outline, broad vanes tapering posteriorly to end in bluntly rounded, cupped coil; lower beak with recessed jaw angle, low shoulder tooth below jaw angle, deep median notch in hood above crest, strong crest fold; well-developed median ridge extends to free corner of lateral wall; radula with stout, unicuspid teeth, rachidian and laterals of approximately coequal length, inner and outer marginals of increasing length, marginal plates vestigial or absent.

ORIGINAL REFERENCE.—Goodrich, 1896:15, pl. 4: figs. 62–71.

TYPE LOCALITY.—Northeastern Indian Ocean, near the Andaman Islands, ~12°N, 92°E, 897 m.

DEPOSITION OF TYPE.—*Holotype*: NMWZ uncat., sex undetermined, juvenile, 22 mm ML, H.M.S. *Investigator* no. 50B-75/7; fair condition.

DISTRIBUTION.—*Histioteuthis hoylei* is restricted to and widely distributed in the Pacific between about 45°N and 45°S and is distributed in the Indian Ocean between about 10°N and the SSTC (Figure 7). In the area south of South Africa and north of the convergence, the ranges of *hoylei* and its Atlantic sibling species may overlap. In the eastern North Pacific, Jefferts (1983) found *hoylei* (reported therein and in the following cited works as *dofleini*) to be common in the California Current system but second to the transitional species *heteropsis* in abundance. In the central North Pacific, Young (1978) found *hoylei* to be the most common of the three histioteuthids, *hoylei*, *oceani* (reported as *Histioteuthis* sp.), and *H. celetaria pacifica*, taken during his vertical distribution study of the cephalopods off Hawaii. High abundance in the western North Pacific is shown by the reports of the species as the major food item of sperm whales caught in eastern Japanese waters (Kawakami, 1976; Okutani et al., 1976). Published (Didenko, 1991) and unpublished data (TINRO cruise reports; K. Nesis, unpublished data) show juvenile to adult *hoylei* to be present in the mesopelagic layer of the northwestern Pacific off the south and middle Kurile Islands in the Okhotsk Sea and in the Bering Sea in certain (probably the warmest) years. Occurrence in the eastern tropical Pacific is known mainly from 25 captures (in 21 net hauls) reported by Okutani (1974), but because of possible errors that we suspect could exist in some of the identifications, we have inserted question marks among the plotted records on our map. To the south, the species appears to be uncommon in the transitional waters of the Peru-Chile Current. Unpublished data (C. Lu, E. Förch) from the southwestern Pacific in the vicinity of Australia and New Zealand show *hoylei* to be normally absent in the transitional waters of the East Australian Current and to be uncommon in the subtropical waters of the Tasman Sea. A recent unpublished study by one of us (KN) also found the species to be uncommon in the western Indian Ocean.

Using opening-closing as well as open sampling gear over bottom depths of 1500–4500 m off Hawaii, Young (1975, 1978) found *hoylei* to inhabit the vertical water column between 100 m and 850 m. During the day, the vertical range was 375–850 m with more than 80% of the 57 captures (56 specimens of ~7–90 mm ML, 1 specimen of 170 mm ML) taken at 500–700 m. At night, the species' range shifted to 100–500 m with more than 85% of the captures taken at 150–300 m. Larger animals tended to be found at slightly greater depths during both time periods. Opening-closing nets have taken a large, near-mature female (170 mm ML; Young, 1975, 1978) during the day off Hawaii at 850 m and a mature male (149 mm ML; UMML) during the night in the California Current at 500 m. An analysis of the data for 252 adult *hoylei* (of which 247 were mated females), taken from the stomachs of 80 sperm whales caught off Japan at 35°N–38°N, 141°E–

143°E, suggests the occurrence of an aggregation of mature females near an isolated oceanic rise in that area (Okutani et al., 1976).

Over its wide range in tropical-subtropical waters of the Pacific and Indian oceans, *hoylei* occurs in open ocean with an apparent maximum concentration in the subtropical North Pacific.

DISCUSSION.—The recent discovery by C. Roper of Goodrich's type in the NMWZ, and its subsequent examination by one of us (NV), led to the recent resurrection of Goodrich's species (Voss et al., 1992), originally described as *Histiopsis hoylei*, from the status of species dubia assigned to it in Voss's 1969 revision of the family. The type specimen is now soft but is in overall fair condition. Although Goodrich's illustration of the right eye (1896, pl. 4: fig. 62) shows a cirlet of 16 photophores, the reexamination clearly revealed the presence of 17 organs. The gladius, which was extracted and illustrated by Goodrich, is no longer with the specimen and is presumed lost. The 1969 work, which recognized *Histioteuthis dofleini* (Pfeffer, 1912) as the valid name for this long-considered, cosmopolitan, warm-water species, stated that more than one taxon was probably involved. The conclusion was based primarily on morphological differences seen between the spermatophores illustrated by Chun (1910; see Voss, 1969:791, for a discussion of this specimen), Marchand (1913; spermatophore from Chun's specimen redescribed and reillustrated), and Sasaki (1929) from Japanese material and those from the single known mature male from the Atlantic (Voss, 1969; Gulf of Mexico). No further action was taken, however, because the range of variations that could occur with maturation of the spermatophore was unknown, as was the spermatophore from over wide geographic ranges in the two oceans. The later designation by Voss et al. (1992) of *hoylei* as a "group" lent further recognition to the existence of multiple taxa.

For the present study, we had available at the workshop eight unreported mature males from the collections of the USNM that were taken by various research vessels (*Walther Herwig* (USNM 816899, USNM 816900, USNM 816902), *Anton Dohrn* (USNM 817758, USNM 817769, USNM 817771), *Discovery* (USNM 816146), *Kaiyo Maru* (USNM 815765)) from the eastern, western, and central Atlantic and from the eastern South Atlantic. Shortly after the workshop, a mature male (UMML 31.2545) taken by the R/V *Melville* from the California Current was sent, quite unexpectedly, by G. Snyder of Scripps Institution of Oceanography. These specimens, together with the mature male (UMML 31.895) from the Gulf of Mexico (spermatophore described and illustrated in Voss, 1969), another male (UMML 31.1706) from the Bahama Islands (spermatophore described and illustrated by Hess, 1987), and unreported subadults and near-mature females from the Atlantic and Pacific, permitted us to compare not only the spermatophores from both sides of each ocean but also to compare additional features of the mature male and other late growth stages from the different oceans (Figure 6, Tables 6–8).



Unfortunately, we were unable to locate any of the earlier described mature males from Japan and, for information on them, have had to continue to rely on the literature. Our comparative study, which was as detailed as the available material permitted, disclosed few clear, consistent morphological or morphometric differences between the Atlantic and Pacific forms except in the late growth stages of the male. We found the spermatophore and the secondary sexually modified arms I of the male from off California to be essentially identical to that of specimens from off Japan, and similarly we found the same features of males from various parts of the Atlantic to closely resemble those of the earlier described males from the Gulf of Mexico and the Bahamas.

The spermatophores from the two oceans markedly differ both in the structure of the ejaculatory apparatus, which contains a single loop of the inner tube in Pacific specimens and numerous loops in Atlantic specimens, and in proportional length. The spermatophore is proportionally short, 5%–6% ML, in animals from the Pacific and is long, 13%–21% ML (the longest known in the family), in those from the Atlantic. In the separate populations, the modifications found on arms I are similar in type but strikingly different in degree of development (Figure 6e–g). In maturing, and especially in mature males, the increased robustness of the basal portions of the modified distal one-half to third quarter of the arms and the increased height and fleshiness of the median keel are markedly greater in Atlantic males. Additionally, in Atlantic specimens, the protective membranes on those portions of the arms are conspicuously expanded to exceed the height of the suckers, in contrast to the low membranes, which only reach midsucker height in Pacific specimens. In all known mature males of both forms, with the exception of one (< 100 mm ML) illustrated by Okutani et al. (1976, pl. IV: fig. 8), there is no elongation of the modified arms. Yet the specimen of Okutani et al., which has all the appearance and described characteristics of *hoylei* (and was taken in the vicinity of an aggregation of mated females of the species), displays elongation of arms I to approximately twice the length of the other arms. Assuming the identifications to be correct, we can only conclude that rapid elongation occurs close to the time of first mating, and that the new California male and those previously described from Japan, all much larger than the specimen of Okutani et al. and containing what we consider to be mature spermatophores, had not yet mated. Chun's (1910:130, pl. 1: figs. 1, 2; as *Calliteuthis ocellata* Owen) described and illustrated condition of the terminal suckers, "arranged more or less distinctly in 4 rows," on the modified arms I in his 140 mm ML male, which is in the apparent late stage of maturity, is probably attributable to contraction and is not the normal condition.

Our comparison between the populations from the two oceans, in which we included adults, subadults, and large juveniles, revealed considerable to complete overlap in most characters unrelated to male sexual maturity. We did, however, find a difference in one character, gladius shape, and we detect

apparent trends in two others, outer-web depth and arm length (see Table 8). In large specimens that we examined from the Pacific, the anterior margins of the vanes of the gladius retain the slightly irregular or scalloped appearance described by Toll (1982) for juveniles from both oceans. This is in contrast to the condition in our large specimens from the Atlantic and that described and illustrated earlier for large Atlantic individuals (Toll, 1982), where the anterior outlines of the vanes assume a convex shape. The detectable difference between the two populations in the position of the median ridge on the lateral wall of the beak can be seen in fig. 5e, f, of Voss's 1969 revision. As to the observed trends, Pacific members tend to have deeper outer webs between arms I–III and shorter arms than their Atlantic counterparts. The significances of additional differences in the morphology of the rings of the ventral submarginal-row suckers on the club manus (Voss, 1969:795) and radula morphology (Voss, 1969, fig. 8a,b) between specimens from the two oceans described or illustrated in the 1969 work invite further investigation.

Considering all of the above, we have no hesitation in recognizing the presence of two separate species in our material from the three oceans, *hoylei*, which inhabits the Pacific and Indian oceans, and a purely Atlantic species, *arcturi* (Robson, 1948). Although we lack the solid evidence from the Indian Ocean that at this stage of our knowledge can only be furnished by mature males, we regard its population as being specifically identical with that of the Pacific, basing our decision on distribution patterns found to be most typical of midwater animals.

All of the illustrations of *Histioteuthis dofleini* found in Voss's 1969 revision, with the exception of figs. 3a,b, 5e, and 8b, are of Pacific specimens and therefore refer to *hoylei*. The exceptional figures show the spermatophore, beaks, and radula from Atlantic specimens and are referable to *arcturi*. The description of *dofleini* given in the revision, on the other hand, was based primarily on Atlantic material and thus largely pertains to *arcturi*.

#### ***Histioteuthis arcturi* (Robson, 1948), new combination**

FIGURES 6c,d,f–h, 7

*Stigmatoteuthis arcturi* Robson, 1948:122, figs. 5, 6.

The high representation of late growth stages in the large, unreported collections of this species (132 specimens) made by the R/V *Anton Dohrn*, R/V *Walther Herwig*, and the Ocean Acre Project (USNM), which were available to us before (NV) and at the workshop, made possible the recognition and the following description of *arcturi*. The above collections and an additionally examined 41 unreported specimens found in the collections of the AtlantNIRO, IOAN, UMML, and VNIRO, and captures reported (as *H. dofleini*) by Voss (1969), Clarke and Lu (1974, 1975), Lipka (1975), Nesis (1975), Roper and Young (1975), Lea (1978), Stephen (1982), and Okutani (1983)

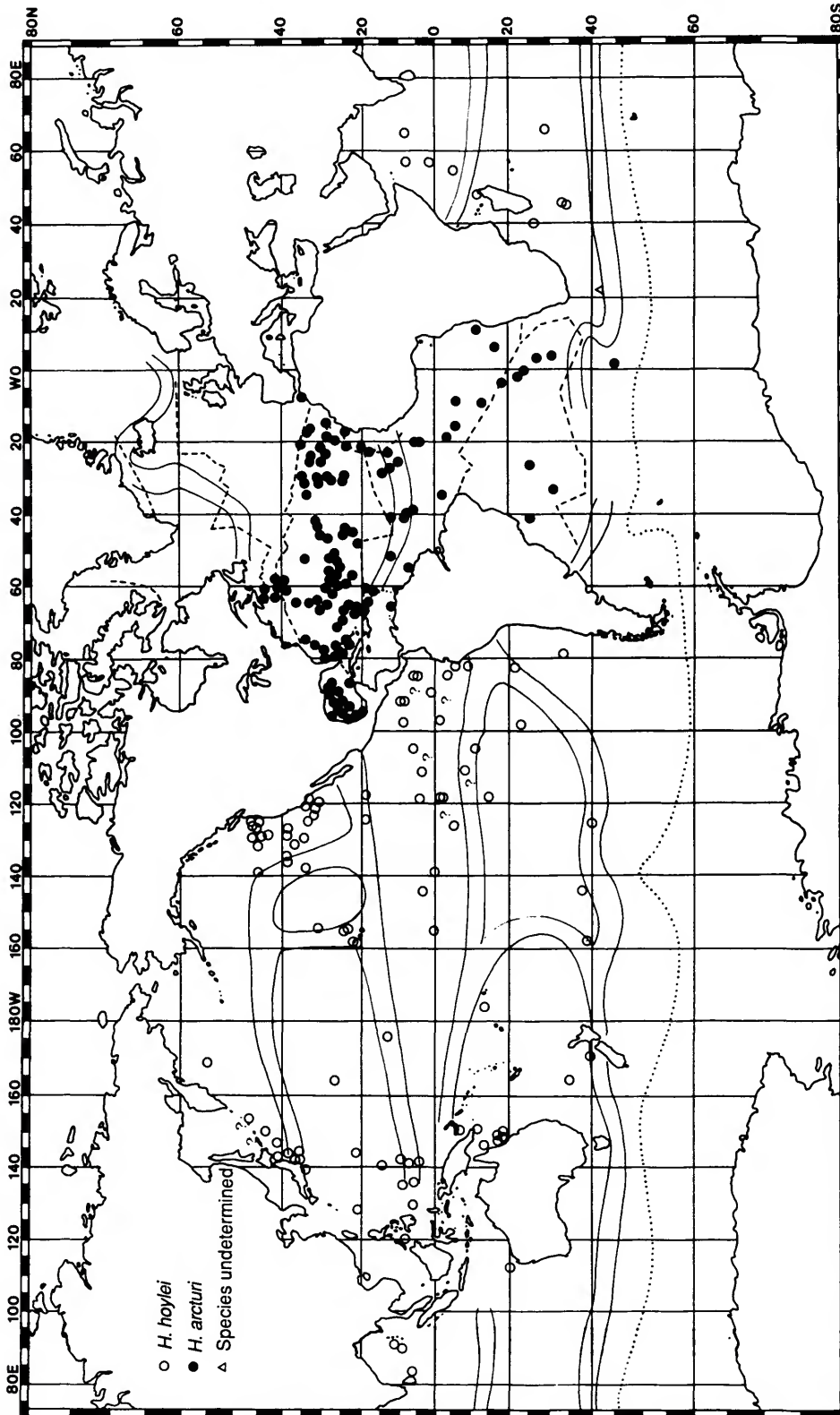


FIGURE 7.—Geographic distributions of members of *Histioteuthis hoylei* species group. Distribution of *H. hoylei* known from 223 net hauls (502 specimens), and *H. arcturi* known from ~276 net hauls (484 specimens). For explanation of question marks, see "Distribution" for *H. hoylei*. For explanation of indicated ocean regions, see Figures 2, 5.

TABLE 7.—Comparison of measurements, indices, and counts of spermatophores of *Histioteuthis arcturi* from over a wide part of the geographic distribution of the species. Means are given in parentheses; for explanation of indices see "Materials and Methods." (EjAp = ejaculatory apparatus.)

Character	UMML 31.895*	UMML 31.1706†	USNM 817758	USNM 815765	USNM 816900	USNM 816899	Species
ML(GL) (mm)	72	111	111	115	106	125	
Locality	29°N, 89°W	25°N, 77°W	25°N, 68°W	37°N, 65°W	27°N, 20°W	5°N, 20°W	
Spermatophores	?	10	3	3	3	3	
SpL (mm)	10.6–11.1	17.4–18.8 (18.0)	21.6–21.9 (21.7)	14.4–17.0 (15.6)	22.2–22.6 (22.5)	18.4–20.8 (19.7)	10.6–22.6 (18.5)
SpLI	14.6–15.4	15.7–16.9 (16.2)	19.5–19.7 (19.6)	12.5–14.7 (13.5)	20.9–21.3 (21.2)	14.7–16.6 (15.8)	12.5–21.3 (17.0)
SpMLI	38.7–42.6	38.2–47.3 (44.0)	40.0–43.0 (41.8)	35.9–46.1 (41.3)	34.6–35.4 (34.9)	42.8–44.3 (43.7)	34.6–46.1 (40.7)
CBLI	15.4–21.4	10.4–12.6 (11.4)	12.2–14.1 (13.0)	15.8–18.9 (17.6)	15.6–18.8 (16.9)	18.7–21.2 (20.0)	10.4–21.4 (16.4)
EjApLI	37.5–43.0	39.4–47.5 (43.1)	42.7–45.9 (43.9)	35.6–47.7 (41.8)	46.0–48.5 (47.1)	33.9–37.0 (35.5)	33.9–48.5 (42.0)
Loops in EjAp	numerous	numerous	numerous	numerous	numerous	numerous	numerous

\*Data from Voss, 1969.

†Data from Hess, 1987.

form the basis for our description of the species' distribution. The following description is based on large juveniles, subadults, and adults, 53–204 mm ML, from over the species' broad range in the Gulf of Mexico and the Atlantic tropical and subtropical regions. The only area not adequately represented in our material is the southwestern Atlantic.

**DESCRIPTION.**—Medium-sized to moderately large histioteuthids; females known to mature at 176–204 mm ML, males at 72–125 mm ML; skin of mantle, head, arms, and basal  $\frac{1}{2}$  of fins covered with low, fleshy papillae, imparting overall rough appearance; mantle relatively short, moderately stout; fins of medium size, length about 30%–40% ML, width about 50%–70% ML (53–125 mm ML); head without nuchal folds; arms long, about 220%–290% ML, with length formula of  $II \cong III \cong IV > I$  in subadults and early mature males,  $I > III > II \cong IV$  in late mature males; sucker rings on arms I–IV usually with 6–14 teeth confined to distal and lateral margins; teeth usually rounded or truncate in females and immature males, sharp pointed in mature males; in mature males, arms I strongly modified (Figure 6f–h), approximate median  $\frac{1}{3}$ – $\frac{1}{2}$  with greatly increased robustness, greatly expanded, fleshy median keels, high protective membranes, and with dorsal surface smooth and ventral surface densely papillated; approximate distal  $\frac{1}{2}$  with pedestals of biserial, small, coequal-sized suckers elongated to form palisades along arm margins, with deep, intervening channel; small suckers with minute, triangular teeth on distal and lateral or entire margins; only suckers on midportions of arms I show noticeable enlargement in specimens up to maximum available size (125 mm ML); basal and midarm suckers on all arms with swollen fleshy collars; inner web vestigial; outer web developed to 3%–8% length of longest arm; buccal membrane 7-membered, with second supports single to dorsal surface of arms II; fourth supports without secondary connectives; tentacles long, about 300%–400% ML; tentacular club with deep, longitudinal cleft on aboral surface of manus; suckers on manus in 5–7 rows, markedly dissimilar in size and dentition; 3 to 4 greatly enlarged median suckers (> 4 times size of marginal suckers)

with about 50–60 sharp, pointed teeth around entire margins; suckers of dorsal and ventral marginal rows minute.

Compound photophores widely spaced on ventrum of mantle, arranged in about 6 diagonal rows, equally large on anterior  $\frac{1}{3}$  with no intermixture of small organs; photophores progressively decrease in size on posterior  $\frac{2}{3}$  of mantle; circlet of 17 (rarely 16) large photophores around right eye; arms IV with 3 longitudinal rows of large organs on basal portions; in adult males and females, small, elongate, black simple photophore present on ends of all arms; terminal photophores 2–3 times length of preceding normal photophore in available specimens with skin intact (males of 94 mm ML and 106 mm ML, female of 115 mm ML).

Dorsal pad of funnel organ with strong, median ridge extending from apical papillae down length of each lateral arm and expanding posteriorly into broad flaps; male genitalia paired; spermatophore long, narrow (SpL 10.6–22.6 mm, 12.5%–21.3% ML; from 6 specimens, Figure 6c,d, Table 7); sperm mass moderately long (34.6%–46.1% SpL); cement body of medium length (10.4%–21.4% SpL); ejaculatory apparatus moderately long (33.9%–48.5% SpL), with numerous loops of inner tube; ejaculatory-apparatus/cement-body connective complex absent; mature egg not available; gills about 30%–50% ML, with about 41–46 lamellae in outer demibranch.

Gladius with broad, moderately short rachis; elongate anterior shoulders of vanes convex in large individuals, slightly scalloped in juveniles and subadults (< ~85 mm ML); vanes broad, tapering posteriorly to end in bluntly rounded, cupped coil; lower beak with recessed jaw angle, low shoulder tooth below jaw angle, deep median notch in hood above crest, strong crest fold; well-developed median ridge extends to point slightly above free corner of lateral wall; radula with stout, unicuspid teeth, rachidian and laterals of approximate coequal length, marginal plates vestigial or absent.

**ORIGINAL REFERENCE.**—Robson, 1948:122, figs. 5, 6.

**TYPE LOCALITY.**—South Sargasso Sea, 26°54'N, 51°15'W, 0–1640 fms (0–3000 m).

TABLE 8.—Comparison between members of the *Histioteuthis hoylei* species group. (Means are given in parentheses; EjAp = ejaculatory apparatus.)

Character	<i>H. hoylei</i>	<i>H. arcturi</i>
Maturity-related features of male		
Spermatophore length	5%–6% (5%) ML	13%–21% (17%) ML
Loops in EjAp	1	numerous
Secondary modifications of arms I	median $1/3$ – $1/2$ of arm with moderately increased robustness, fleshy median keel moderately expanded, protective membranes low	median $1/3$ – $1/2$ of arms with greatly increased robustness, fleshy median keel greatly expanded, protective membranes high
Anterior shoulders of glacial vanes	slightly scalloped in adults	distinctly convex in adults
Median ridge on lateral wall of lower beak	extends to free corner	extends to point slightly above free corner
Outer-web depth*	6%–14% length of longest arm	3%–8% length of longest arm
Arm length*	160%–250% ML	220%–290% ML
Geographic range	Pacific and Indian oceans; tropical–subtropical	Atlantic; tropical–subtropical

\*In adults, subadults, and juveniles >55 mm ML.

DEPOSITION OF TYPE.—*Holotype*: BMNH 1947.7.7.1, female, juvenile, ~32 mm ML, *Arcturus* Oceanographic Expedition (1925) sta 7 (no. 18), PT-1; soft, poor condition but identifiable.

DISTRIBUTION.—The normal range of *Histioteuthis arcturi* is in Atlantic tropical–subtropical waters between about 40°N and 30°S (Figure 7). The southern limit appears to occur somewhat north of the SSTC as shown by the absence of the species in collections made during the various north–south and east–west transects of the convergence and adjacent waters by the R/V *Akademik Kurchatov* (Nesis, 1974) and by the R/V *Walther Herwig* on its 1971 and 1975/1976 cruises (N. Voss, unpublished data). During the Cape Town–Madiera transect of the 1971 R/V *Walther Herwig* cruise, *arcturi* was not found in the Benguela Current but was first encountered in subtropical waters at 28°S and thereafter was taken at 12 out of 19 (63%) Engel-trawl stations made between 25°S and 28°N (31 adults, subadults, and large juveniles captured). In the northwestern Atlantic, the species is transported northward in the Gulf Stream system from its normal warm-water range to about 44°N off Canada (Stephen, 1982). The 1979 Sargasso Sea Expedition of the R/V *Anton Dohrn* found *arcturi* to be the most common and widespread histioteuthid in central north subtropical waters (collection contains 24 adult, subadult, and large juveniles of *arcturi*), with the greatest abundance occurring in the southern Sargasso Sea (14 specimens taken at 11 stations) where, except at two stations in the northern sector where *reversa* and *H. corona* were collected, it was the only histioteuthid taken. In the more productive northern North African Subtropical Sea, *arcturi* ranked third in abundance to *meleagroteuthis* and *reversa*. Our analysis of the cephalopod collections made in the Ocean Acre Area (N. Voss, unpublished data; study area is the water column beneath a 1° rectangle

centered at 32°N, 64°W) in the northern Sargasso Sea, a province not well sampled during the R/V *Anton Dohrn* expedition, showed *arcturi* to occur in high numbers, followed in decreasing order of abundance by *meleagroteuthis* and *H. c. corona*. In his 1978 study of the cephalopods of Gulf Stream cyclonic rings, Lea found the species to be a good indicator of Sargasso Sea water. His later analyses (1984) of the cephalopods taken in a series of transects of the Gulf Stream, between about 26°N and 35°N, showed *arcturi* to occur primarily offshore of the high-speed core of the current, which also demonstrates the Sargasso Sea origin of the species in that area.

To the west and south, the species occurs widely in the Gulf of Mexico, where it has been captured in large numbers, along with *H. c. corona*, in the northern sector in the vicinity of the mouth of the Mississippi River (Voss, 1969; Lipka, 1975). At their study site (27°N, 86°W) in the northeastern gulf, Passarella and Hopkins (1991) found *arcturi* to be the dominant of the two species. The scarcity of *arcturi* in the Caribbean Sea is well demonstrated by the failure of various collecting cruises to take the species in the area (Voss, 1969; Nesis, 1975; N. Voss, unpublished data). The single known capture is a recent one made in the relatively high productivity area off Venezuela (Arocha et al., 1991). *Histioteuthis arcturi* is known to be widely distributed in the western tropical Antillean and Amazonian provinces (Okutani, 1983; Lea, 1984), but the extent of its occurrence in southwestern subtropical waters remains poorly known.

During its life cycle, *arcturi* occupies the vertical column from surface waters to unknown depths below 1000 m. Data from opening-closing nets show that early juveniles of 4–5 mm ML inhabit the surface 200 m at 30°N, 23°W (Clarke and Lu, 1974), and the surface 400 m in the Florida Current and eastern fringing waters (Lea, 1984) during both day and night.

Daytime captures of juveniles of 7–10 mm ML at depths of 400–750 m (Clarke and Lu, 1974; Lea, 1984) are indications of the change to the diurnal vertical distribution pattern found to be typical of larger juveniles. Opening-closing-net data show a concentration of juveniles 10 mm ML to 38 mm ML, the maximum size caught in the studies, between 450 m and 750 m during the day and between surface waters and 400 m during the night (Clarke and Lu, 1974, 1975; Roper and Young, 1975; Lea, 1984). A daytime capture of a 26 mm ML individual in the upper 200 m suggests that an increased vertical spread of the population with a general tendency to seek deeper water probably occurs, rather than a total move of the population to deep water as size increases.

All known subadults, mature males (with one exception), and unmated mature females (mated females not known) were captured in open trawls fishing at night from 600 m to 2700 m, with the majority taken while fishing below 1000 m in both midwater and off the bottom. The exception was a small mature male of 72 mm ML captured while fishing at 403 m off the continental slope in the Gulf of Mexico near the mouth of the Mississippi River.

**DISCUSSION.**—Robson's holotype of *Stigmatoteuthis arcturi* from the Sargasso Sea was examined during the study that led to Voss's 1969 revision of the family, where the species was placed in the synonymy of the then-regarded circumglobal *H. dofleini*. Now that our present work has shown the Atlantic population to be specifically separate from the one in the Pacific and Indian oceans, we have resurrected *arcturi* as an available name for the Atlantic form. The type was reexamined at the workshop and its identity was reconfirmed. Although in soft, poor condition, the approximately 32 mm ML juvenile displays the necessary identifiable features of photophore patterns on the dorsal surface of the mantle, basal portions of arms IV, and around the right eye, the sucker pattern on the club, and the sculpture of the dorsal pad of the funnel organ.

The spermatophore of *arcturi*, previously described and illustrated by Voss (1969) and Hess (1987), is the largest and most atypical in the family. Our new comparative study of the spermatophore (see Table 7) shows that little morphological or morphometric variation occurs in that structure over the broad range of the species. This constancy is probably related to the near-continuous geographic distribution of the species, which includes the more productive as well as the less productive, land-related and open-ocean areas in its range.

#### *Histioteuthis bonnellii* Species Group

Two species constitute this group, uniquely characterized by a single, markedly enlarged, elongate photophore on the ends of arms I–III in the juvenile through adult stages; a group of two or three prominent, round photophores on the left posteroventral margin of the head; a deep inner web between arms I–III that exceeds 50% of the length of the longest arm; multiple attachments of the fourth supports of the buccal

membrane; and broad, roughly triangular glacial vanes. Each group member displays a distinctive distributional pattern (Figure 9). The distribution of the northern member, *bonnellii*, includes portions of the Atlantic, Indian, and Pacific oceans north of the SSTC and the Mediterranean; that of the southern member, *macrohista*, is largely described by the convergence itself.

#### *Histioteuthis bonnellii* (Férussac, 1834)

FIGURES 8a–e; 9

*Histioteuthis bonnellii corpuscula* Clarke, 1980:225, figs. 185–188 (upper right), table 35 [new synonym, herein].

The division of *Histioteuthis bonnellii* into two subspecies by Clarke (1980), when he named *H. b. corpuscula* from the fringing waters to the north of the SSTC in the Atlantic and western Indian oceans, and recent knowledge of reported (Clarke and MacLeod, 1982; Brandt, 1983) and unreported (NMNZ, NMV, UMML) captures of *bonnellii* in the subtropical waters of the Tasman Sea and north of New Zealand called for a detailed study of this mainly Atlantic species over its broad geographic range. Although such a study was not possible because of the lack of sufficient material, before (NV) and at the workshop we were able to critically examine the valuable, unreported collection of 53 mostly large juvenile, subadult, and adult specimens of *bonnellii* (USNM). These specimens were taken from north temperate waters to the SSTC in the Atlantic on the 1971 and 1975/1976 cruises of the R/V *Walther Herwig* and the 1974 and 1979 cruises of the R/V *Anton Dohrn*. In addition, recently reported large juveniles and a mature male from Canadian waters (Stephen, 1982; ARC), unreported Atlantic specimens (IOAN, PINRO, UMML), and certain of the above, unreported, southwestern Pacific specimens were examined. At the workshop, we also had the opportunity to examine a specimen of *bonnellii*, labelled "syntype," from the Paris Museum, and the recently found holotype of Verrill's synonymous *Histioteuthis collinsii* (USNM 730893). A total of 92 specimens were examined.

Our investigations failed to distinguish the two nominal subspecies, *H. b. bonnellii* and *H. b. corpuscula*, using the characters employed by Clarke (1980), and they were too limited by the available material to define new characters that would clearly separate the possible complex of taxa that could be represented in *bonnellii* (see "Discussion," below). Therefore, we have redescribed the species on the basis of mostly late growth stages from over the major portion of its geographic distribution. Unfortunately, the southwestern Pacific was represented only by small juveniles.

**DESCRIPTION.**—Small to large histioteuthids; single reported mature female, 330 mm ML (Kristensen, 1980; subarctic), can mature at about 90 mm ML in tropical Atlantic and southern subtropical waters; males known to mature at 50–~330 mm ML (50–75 mm ML in Atlantic tropical and southern

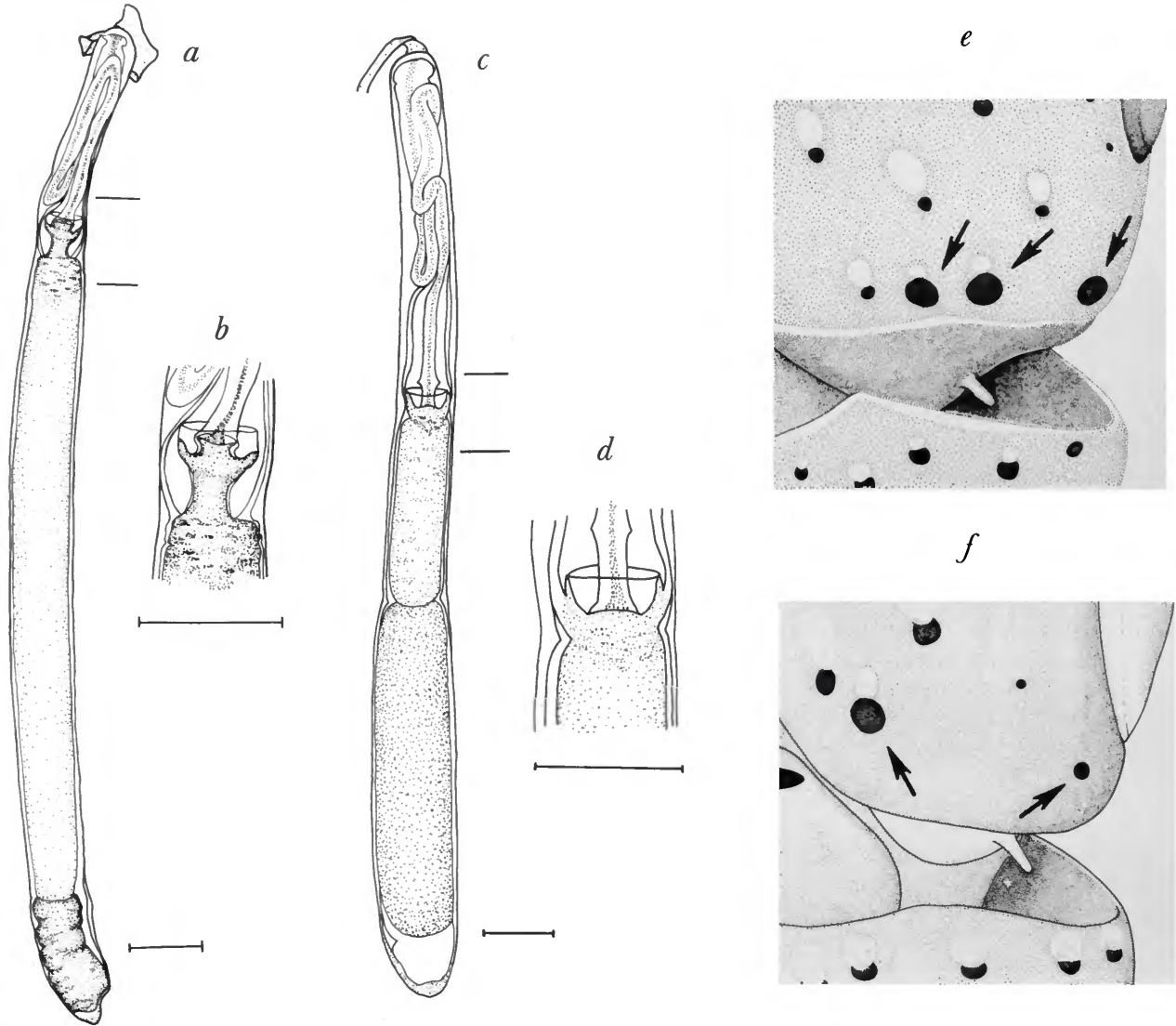


FIGURE 8.—*Histioteuthis bonnellii*: *a*, spermatophore, USNM 817752, 75 mm ML, 38°38'S, 51°55'W; *b*, enlargement of area of ejaculatory-apparatus/cement-body connective complex of same; *c*, spermatophore, USNM 817755, 172 mm ML, 20°27'N, 21°58'W; *d*, enlargement of area of ejaculatory-apparatus/cement-body connective complex of same; *e*, left posteroventral portion of head showing pattern of 3 conspicuous, round photophores, ARC 2205, 42 mm ML, juvenile female, 42°55'N, 60°43'W. *Histioteuthis macrohista*: *f*, left posteroventral portion of head showing pattern of 2 conspicuous, round photophores, UMML 31.1713, 19 mm ML, juvenile, 45°34'S, 147°18'E. Scale bars = 1 mm.

subtropical waters; 172 mm ML in northern Mauritanian Upwelling; 76–~330 mm ML in temperate and subarctic waters); mantle conical, moderately short and stout; fins medium-sized to large, length about 40%–60% ML, width about 50%–90% ML; head with 1 nuchal fold; arms medium long to long, about 130%–300% ML, typical arm length

formula II = III > I = IV; rings of suckers on all arms with 2–7 broad, blunt teeth on distal or distal and lateral margins; in mature male, distal 1/3 of arms I modified with 2 widely spaced rows of uniformly small suckers set on enlarged pedestals; inner web well developed, segments between arms I, II, and III (measured at midpoint) about 50%–60% length of longest

TABLE 9.—Comparison of spermatophores of *Histioteuthis bonnellii* specimens from the southwestern (SW Atl) and eastern tropical Atlantic (ET Atl), South Mauritanian Upwelling (S Maur Upw), North Mauritanian Upwelling (N Maur Upw), and temperate northwestern Atlantic (NW Atl). Means (in parentheses) follow ranges; for explanation of indices, see "Materials and Methods." (EjAp = ejaculatory apparatus.)

Character	SW Atl* (USNM 817752)	ET Atl (USNM 817753)	S Maur Upw (USNM 817754)	N Maur Upw* (USNM 817755)	NW Atl (HML 7913, lot MT 70-2)
ML(GL) (mm)	75	75	73	172	76
Spermatophores measured	3	3	3	3	3
SpL (mm)	4.6–4.6 (4.6)	2.7–2.7 (2.7)	2.7–2.8 (2.7)	2.4–2.6 (2.5)	3.0–3.1 (3.1)
SpLI	6.1–6.1 (6.1)	3.6–3.6 (3.6)	3.6–3.8 (3.7)	1.4–1.5 (1.5)	3.9–4.1 (4.0)
SpMLI	11.0–12.3 (11.8)	9.8–12.6 (11.6)	11.2–11.6 (11.4)	31.3–33.9 (32.8)	30.3–31.5 (31.1)
CBLI	65.2–67.6 (66.2)	57.8–60.9 (59.2)	59.7–61.6 (60.5)	18.6–24.4 (21.6)	26.9–29.6 (28.2)
EjApLI	20.2–20.9 (20.6)	28.7–29.6 (29.2)	26.8–29.1 (28.2)	35.4–39.1 (37.5)	34.2–36.5 (35.2)
Loops in EjAp	1, ≅ apparatus length	2–3, ~ <sup>1</sup> / <sub>2</sub> – <sup>2</sup> / <sub>3</sub> apparatus length	2, ~ <sup>1</sup> / <sub>2</sub> – <sup>2</sup> / <sub>3</sub> apparatus length	2–3, ~ <sup>1</sup> / <sub>2</sub> – <sup>2</sup> / <sub>3</sub> apparatus length	2–3 ~ <sup>2</sup> / <sub>3</sub> apparatus length
Base of cement-body connective complex	constricted	constricted	constricted	not constricted	not constricted

\*Spermatophore illustrated in Figure 8a–d.

arms; junctures of segments from arms III and IV closely spaced, appearing as 1; outer web slightly developed in large specimens; buccal membrane 6-membered, with second supports to dorsal sides of arms II, single fourth support with multiple attachments, 1 each to sides of arms IV and to junctures of web segments from arms III and IV; tentacles long, about 200%–350% ML; tentacular club lacking longitudinal cleft on aboral surface; suckers arranged in 6 rows, with those in median 2 rows enlarged to 2 times diameter of ventral marginal suckers; rings of suckers with numerous sharp teeth around entire margins.

Large compound photophores on ventral surface of mantle regularly set in 7 to 8 diagonal rows; uniformly large on anterior <sup>1</sup>/<sub>2</sub> of mantle, gradually smaller on posterior <sup>1</sup>/<sub>2</sub>; 3 conspicuous, round, dark, usually large photophores on left posterior margin of ventral surface of head (2 median-most organs with small, reduced, anterior filter element set apart from lateral-most organ, which appears to lack anterior filter element; Figure 8e); circlet of 17 (rarely 16 or 18) large photophores around right eye; 3 longitudinal rows of photophores present on basal portions of all arms; single enlarged, elongate, dark, simple photophore present on ends of arms I–IV (photophore about 7%–17% length of arms I–III, 2%–3% length of arms IV; first seen on arms I–III in early juveniles; usually not seen on arms IV until late juvenile or subadult stages and may not appear in some early maturing individuals).

Dorsal pad of funnel organ with fleshy, median ridge on each lateral arm (often indistinct in small juveniles); ridges do not appear to unite anteriorly; spermatophore short (SpL 2.4–4.6 mm; 1.4%–6.1% ML; 15 spermatophores from 5 specimens, 73–172 mm ML); sperm mass short to moderately long (9.8%–33.9% SpL); cement body of medium length to long (18.6%–67.6% SpL); ejaculatory apparatus of medium length

(20.2%–39.1% SpL), with 1 long or 2 to 3 medium long, longitudinal loops of inner tube; ejaculatory-apparatus/cement-body connective complex present (Figure 8a–d, Tables 9, 11); mature egg diameter 2.3 mm (330 mm ML, northwestern Atlantic); gills about 40% ML, with 30–43 lamellae in outer demibranch.

Gladius with short, broad, triangular free rachis; vanes broad, roughly triangular, with long, tapering, nearly straight-sided posterior margins that converge and end in bluntly pointed, cupped coil; lower beak with nearly straight or slightly curved rostral edge; hood (very broad in large specimens) with well-defined notch above crest; wing fold low, broad, often with sharp lateral edge or distinct lateral ridge; lateral wall bisected by well-developed median ridge extending to free corner; radula heterodont; first and second laterals asymmetrical, with rudimentary cusps on outer ends of rather long, narrow bases; weak marginal plates present (Mediterranean juvenile).

ORIGINAL REFERENCE.—Férussac, 1834:355.

TYPE LOCALITY.—Mediterranean, off Nice.

DEPOSITION OF TYPE.—*Holotype*: Whereabouts unknown; sex undetermined, 70 mm ML; neotype not selected.

DISTRIBUTION.—*Histioteuthis bonnellii* is widely, but unevenly, distributed in the Atlantic north of the SSTC and extends eastward across the Indian Ocean and into the western Pacific in subtropical waters fringing the convergence (Figure 9). Occurring throughout subarctic and north temperate waters, including the eastern and western Mediterranean, numerous cruise collections (1980 Amsterdam Mid-North Atlantic Plankton Expedition (USNM); R/V *Anton Dohrn* 1979 Sargasso Sea Expedition; R/V *Atlantis* II-78; and research vessels *Dana*, *Oregon*, *Pillsbury*, and others) have shown the species to be absent from northern subtropical and western tropical waters and from the Gulf of Mexico. The geographic

range of *bonnellii* in the eastern Atlantic south of temperate waters could be disjunct as shown by the extensive cephalopod collections taken on the Cape Town–Madeira transect of the R/V *Walther Herwig* in 1971. On this cruise, 31 large juveniles, subadults, and adults were captured at eight of the 13 (62%) pelagic-trawl stations made in the Mauritanian Upwelling and tropical waters between 21°N and 16°S. No captures were made at the three stations in subtropical waters to the north of the above range or at the six stations to the south until the species was again encountered off Cape Town at 35°S in the southern sector of the Benguela Current. The scarcity or absence of *bonnellii* in the northern sector of the current is further supported by the lack of the species in the collections made by the R/V *Professor Shtokman* (cruise 14, 1985) and R/V *Akademik Kurchatov* (cruise 43, 1986) during their work in Namibian waters between 17°S–26°S and 10°E–14°E. In this area, the closely related SSTC species, *macrohista*, was found to be common, along with *H. reversa*.

Farther south, *bonnellii* inhabits a narrow belt of subtropical waters between about 28°S–40°S that borders the SSTC and extends from off Mar del Plata, Argentina, where the species was encountered by the R/V *Walther Herwig* on both the 1971 and the 1975/1976 cruises, eastward to about 180°. In addition to the above unreported R/V *Walther Herwig* captures, our knowledge of the species' occurrence between these southern latitudes is furnished by the published reports of Voss (1969), Clarke (1980; as *H. b. corpuscula*), Clarke and MacLeod (1982; as *H. b. corpuscula*), and Brandt (1983) and by unpublished records from the Atlantic and western Indian oceans (K. Nesis) and from the Australia–New Zealand area (E. Förch, C. Lu, and N. Voss). During the Socotra Island–Walters Shoal (13°N–34°S) transect of the western Indian Ocean made by the R/V *Vityaz* in 1988/1989, the species was encountered between 25°S and 34°S, with five of the six (83%) stations positive for the species located between 28°S and 34°S in the vicinity of Walters Shoal. There, *bonnellii* was found to be second to *miranda* in abundance among congeners. The cephalopod fauna in southern subtropical waters east of New Zealand is poorly known, but the preference clearly shown by *bonnellii* for high or relatively high productivity waters and the avoidance of oligotrophic areas suggest that the species can not inhabit the less productive central waters of the Pacific. Although the distributions of *bonnellii* and its transitional sibling species, *macrohista*, overlap in the fringing waters immediately to the north of the SSTC, the north-south transects of the convergence in the western Atlantic made during the 1975/1976 cruise of the R/V *Walther Herwig* revealed a total absence of *bonnellii* in convergent waters but an abundance of *macrohista*.

*Histioteuthis bonnellii* inhabits a broad vertical range between the upper 100 m to possibly 2000 m. Lu and Clarke (1975b) report the only closing-net captures, that of a 9 mm ML juvenile at 305–400 m during the day and of a 31 mm ML juvenile at 240–265 m at night in the eastern tropical Atlantic.

Captures by open nets fishing maximum depths of 100–200 m show juveniles of less than 20 mm ML to inhabit these upper waters during both day and night over the entire geographic range of the species. Larger juveniles and subadults have been found at night mostly between about 200 m and 1000 m, but large subadults have been collected at the surface in areas of upwellings in the Mediterranean off Nice and Messina. Mature males were taken by the R/V *Walther Herwig* in the Mauritanian Upwelling and eastern tropical Atlantic while fishing depths of 1300–2200 m. In North Atlantic temperate and subarctic waters, a mature male and a mature female have been reported from the surface 100–325 m (Kristensen, 1980; Stephen, 1982:115 (reported as *H. celetaria celetaria*, see "Discussion").

DISCUSSION.—Clarke (1980) described his southern subspecies of *bonnellii*, *H. b. corpuscula*, from whole specimens found in the stomachs of sperm whales caught off South Africa (holotype from off Durban, 30°S, 31°E; BMNH) and in the mid-Atlantic at 31°S, 33°W, in subtropical waters north of the SSTC. He distinguished *H. b. corpuscula* from the northern *H. b. bonnellii* primarily on the basis of the presence on the head of two or three large, round photophores posteroventral to the left eye, small size at maturity, and a more muscular body in *H. b. corpuscula*. The unusual photophores were known to occur in *macrohista*, in which two widely set organs are present, but were not known for *bonnellii*. Our new material (see text preceding the diagnosis of *bonnellii*) made it possible for us to study, over the entire geographic range of *bonnellii*, the features used by Clarke as well as new ones that may prove useful in distinguishing separate populations in this widespread species. The irregular distribution pattern of *bonnellii*, alone, strongly suggests the existence of more than one taxon.

Considering first the subspecific characteristics employed by Clarke, we found the arrangement of three large, round photophores on the posteroventral margin of the head beneath the left eye described for *H. b. corpuscula* to be present in all specimens of *bonnellii* larger than 18 mm ML that we examined. In fact, the consistent presence of the three-photophore arrangement (two more median, closely spaced organs and one widely spaced lateral organ) becomes a newly recognized feature that further distinguishes *bonnellii* from the closely related *macrohista* (Figure 8e,f). The observed tendency of the lateral-most photophore in *bonnellii* to sometimes be less enlarged than the median pair more likely explains Clarke's statement of two or three photophores in the pattern than does the possibility of a mixture of *bonnellii* and *macrohista* in his original material.

We next looked at size at maturity and found that character to be too variable over the broad geographic range of the species to be useful for clearly distinguishing possible separate taxa. The unreported collections available to us at the workshop contained mature males with mantle lengths of 53 mm (R/V *Walther Herwig* (WH) 412/71) and 75 mm (WH 350/71) from the east and west sides of the Atlantic between 37°S and 40°S



TABLE 10.—Occurrence of an elongate, terminal photophore on arms IV in selected specimens of *Histioteuthis bonnellii*.

Specimen	Sex	Size (mm)	Stage of maturity	Geographic area
Photophore present				
HML Bel 7902-022	male	83	immature	NW Atlantic Temperate
USNM 817755	male	172	mature	N Mauritanian Upwelling
USNM 817776	male	68	immature	N Mauritanian Upwelling
USNM 817775	female	66	immature	S Mauritanian Upwelling
USNM 817775	female	39	immature	S Mauritanian Upwelling
USNM 817774	female	77	maturing	eastern tropical Atlantic
USNM 817773*	male	38	immature	S Benguela Current
Photophore absent				
USNM 817754	male	73	mature	S Mauritanian Upwelling
USNM 817753	male	75	mature	eastern tropical Atlantic
USNM 817753	male	70	mature	eastern tropical Atlantic
USNM 817772	male	72	near-mature	eastern tropical Atlantic
USNM 817752	male	75	near-mature	SW Atlantic Subtropical

\*Photophore in early stage of development.

(the approximate latitudes of Clarke's two mature male paratypes of 70 mm ML) and mature males of 70 mm ML and 75 mm ML (WH 486/71) from 8°N in eastern tropical waters. Collections from the southern and northern Mauritanian Upwelling contained mature males of 73 mm ML (WH 494/71) and 172 mm ML (WH 502/71, the largest known male from the Atlantic), and collections from northwestern temperate waters (42°N, 60°W) contained a mature male of 76 mm ML (ARC HM 7913-70-2). One of us (KN) found a male of the same mantle length, 76 mm, collected in the subarctic at 56°N, 36°W, by the R/V *Artemida* (PINRO), to be near-mature (spermatophoric organ complex contained immature spermatophores). Additionally, we know from Morales (1962) that males grow as large as 330 mm ML in the Mediterranean. Less is known about size at maturity in females. Clarke (1980) reported a 52 mm ML female of *H. b. corpuscula* from off South Africa to be in "spawning condition," but we found none of the numerous females, ranging in size up to 80 mm ML, taken by the R/V *Walther Herwig* from the vicinity of the SSTC and eastern tropical waters to be mature. Several of the larger specimens, however, had enlarged ovaries and nidamental and oviducal glands that indicated a maturing condition. From higher northern latitudes, Stephen (1982) reported a "ripe" female of 225 mm ML caught at 37°N, 56°W, and Kristensen (1980) recorded a 330 mm ML (300 mm after preservation) female from the Davis Strait, West Greenland. The latter is the only female of *bonnellii* documented to be mature by the presence of eggs in the oviducts. Thus it appears that early maturity in males is not confined to any one ecologically distinct area but, rather, occurs throughout the major (if not entire) portion of the range of *bonnellii* in the Atlantic. Lack of data precludes determination of the geographic extent of early maturity in females.

As to body texture, the third character used to distinguish the southern subspecies *H. b. corpuscula*, we compared juveniles, subadults, and adult males of equivalent sizes from temperate waters and from the vicinity of the SSTC and found no consistent differences in body musculature. Clarke stated that his comparisons were made on "large specimens," and it could be that his large temperate material consisted of mature and spent females and spent males that showed deterioration of the body, a condition found to be typical of these stages of maturity in other teuthoids.

During our studies, we observed undescribed variations in two additional features. The first was an elongate, terminal photophore on arms IV. This photophore, morphologically similar to but markedly smaller than those well described for arms I-III, can be seen in the illustrations of *bonnellii* found in Verany (1851) and Pfeffer (1912) of specimens of 69 mm ML and 185 mm ML from the Mediterranean. It was not detected, however, when the species was redescribed (Voss, 1969) on the basis of young juveniles and subadults that happened to have the ends of arms IV in poor condition. The terminal photophore on arms I-III can be seen in juveniles as small as 7 mm ML, but our present investigation, limited by the relatively few available specimens that had the ends of arms IV intact, shows that the terminal photophore on arms IV does not appear until the late juvenile or early subadult stages and can fail to appear even in the mature stage of some early maturing animals (see Table 10). Because the organ occurs in animals taken over the entire latitudinal range of the species, we regard its presence as typical of *bonnellii* and its absence as exceptional to certain early maturing individuals known at present only from the southern half of the species' range.

The availability of mature males from several of the different ecologically distinct areas inhabited by *bonnellii* prompted us

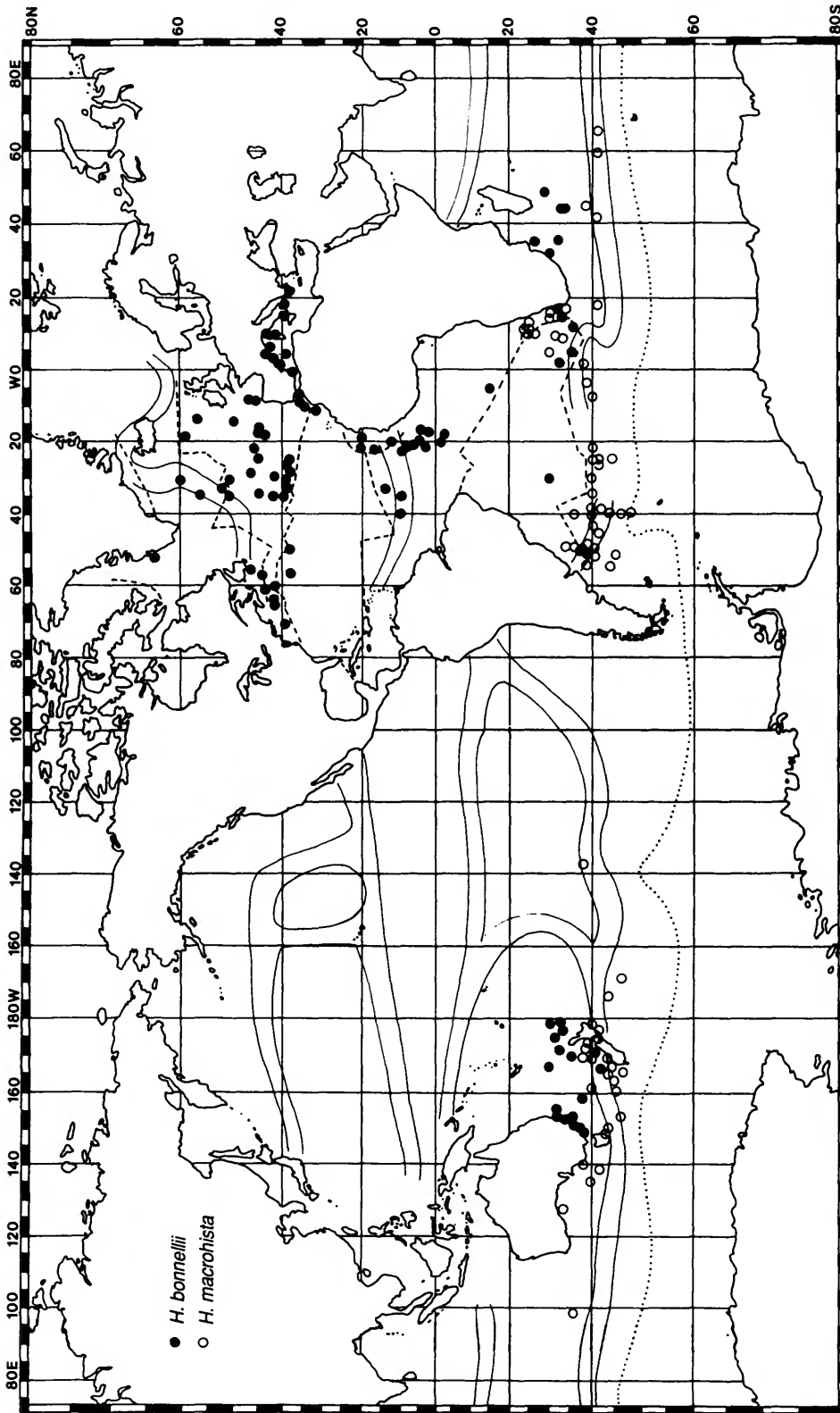


FIGURE 9.—Geographic distributions of members of *Histioteuthis bonnellii* species group. Distribution of *H. bonnellii* known from 141 net hauls (220 specimens), and *H. macrohista* known from 107 net hauls (274 specimens). For explanation of indicated ocean regions, see Figures 2, 5.

TABLE 11.—Distribution of states of spermatophore characters found to vary in *Histioteuthis bonnellii* from the southwestern Atlantic (SW Atl), eastern tropical Atlantic (ET Atl), South Mauritanian Upwelling (S Maur Upw), North Mauritanian Upwelling (N Maur Upw), and temperate northwestern Atlantic (NW Atl). (EjAp/CB = ejaculatory apparatus/cement body.)

Character states	SW Atl	ET Atl	S Maur Upw	N Maur Upw	NW Atl
Loops in ejaculatory apparatus					
Single, long	x				
Multiple, medium long		x	x	x	x
EjAp/CB connective complex base					
Constricted	x	x	x		
Not constricted				x	x
Sperm mass length					
Short	x	x	x		
Long				x	x

to do a comparative study of a second feature that had not formerly been investigated, the spermatophores. Preliminary results revealed intraspecific variations in morphology and morphometrics that could prove valuable in identifying genetically separate populations (Table 9). We were fortunate to find one male with unruptured spermatophores from each of five different geographic areas in the Atlantic, the southwest subtropical, in the vicinity of the SSTC, eastern tropical, southern Mauritanian Upwelling, northern Mauritanian Upwelling, and northwestern temperate areas. All the chosen specimens appeared to be fully mature (penis and Needham's sac packed with spermatophores), and the spermatophores selected for detailed examination were judged to be typical for the individual. A comparison of the spermatophores from the five specimens showed them to be morphologically similar except for two characters, the number of longitudinal loops of the tube of the ejaculatory apparatus and the shape of the base of the ejaculatory-apparatus/cement-body connective complex. In addition, a marked morphometric variation was found in the proportional lengths of the sperm mass and cement body. Although the significance of the observed variations in the present material is unclear at this time, the presence in mature spermatophores of a single loop or multiple loops in the ejaculatory apparatus and of a short or long sperm mass are conditions usually found to be consistent within a taxon in other histioteuthids (Voss, 1969; Hess, 1987; see "Discussion" in *H. hoylei* and *H. arcturi* sections, herein). Obviously, our material and study are inadequate for drawing final conclusions, but if we assume that each specimen is representative of its population of origin, then the distribution of character states shown in Table 11 suggests that three populations of *bonnellii* can possibly be identified on the basis of the spermatophores. If a future study of spermatophores of additional specimens from the various areas supports our findings, then the population from the Atlantic subtropical waters in the vicinity of the SSTC could be identified to *H. b. corpuscula*, the range of which probably will be found to extend eastward into the

western Pacific in the subtropical waters associated with the convergence. At this time, however, based on our above findings, we are unable to sufficiently distinguish this southern population or any other subpopulation, and we regard all material of *bonnellii* as belonging to one, undivided species.

Finally, the new material permitted us to verify the presence in the species of a median ridge on the lateral arms of the dorsal pad of the funnel organ. Sculpture of the dorsal pad was not apparent in the material used in Voss's 1969 study of the species, but weakly developed ridges were described and illustrated by Clarke (1980) for *H. b. corpuscula*. In our new material, we found the median ridges to be present in all specimens that had dorsal pads in good condition. The ridges, which appear not to fuse anteriorly, are well developed in some specimens and are partially obscured by a swollen condition of the pad in others. The possession of two lateral ridges is shared by the closely related *macrohista* and by members of the *reversa* species group.

#### *Histioteuthis macrohista* N. Voss, 1969

FIGURES 8f, 9

Newly available data on largely unreported collections of *macrohista* taken by the R/V *Akademik Kurchatov*, R/V *Professor Shtokman*, and other Russian research vessels (30 specimens; AtlantNIRO, IOAN, YugNIRO), by the R/V *Walther Herwig* (158 specimens; USNM), and by Australian (11 specimens; NMV) and New Zealand (32 specimens; NMNZ) research programs have permitted us to more accurately describe the distribution of this SSTC species. Examination at the workshop of subadults and adults in good condition from these collections allowed us to look more closely at the species over its broad distributional range and, consequently, better characterize it. The following description is based on large juveniles, subadults, and adult males, 25–65 mm ML, from over the full distribution of the species. No mature females were available for our study.

**DESCRIPTION.**—Small histioteuthids; females mature at about 49–65 mm ML, males at about 40–55 mm ML; mantle short, stout, conical; fins large, length about 52%–56% ML, width about 80%–89% ML; head with 1 nuchal fold; arms of medium length, about 120%–200% ML, with approximate length formula  $III = II > IV = I$ ; sucker rings with about 4–10 low, square or rounded teeth on distal and lateral margins; in mature males, suckers on distal  $\frac{1}{3}$  of both arms I abruptly reduced in size, and on elongate, palisaded pedestals; suckers on basal  $\frac{2}{3}$  of all arms with swollen, fleshy collars; inner web between arms I, II, and III well developed, in excess of 50% length of longest arm, with junctures of segments from arms III and IV relatively widely spaced; outer web slightly developed; buccal membrane 7-membered, with second supports to dorsal sides of arms II, 2 fourth supports bifurcate to dorsal sides of arms IV and to junctures of web segments from arms III and IV; tentacles long, about 250%–400% ML; tentacular club without longitudinal cleft on aboral surface; suckers on manus arranged in about 6 rows, moderately enlarged in median rows to  $1\frac{1}{2}$ –2 times size of ventral marginals; rings of enlarged suckers with numerous sharp teeth around entire margins.

Compound photophores uniformly large on anterior  $\frac{1}{2}$  of ventral surface of mantle, arranged in about 6 diagonal rows, progressively decreasing in size on posterior  $\frac{1}{2}$ ; few minute photophores scattered throughout pattern; 2 conspicuous, usually large, round, dark photophores widely set on left posterior margin of ventral surface of head (more median one, with reduced anterior filter element present, usually larger than lateral one, which appears to lack filter element; Figure 8f); circlet of 16 (rarely 15) photophores around right eye; arms IV with 3 longitudinal rows of large photophores on basal portions; ends of arms I, II, and III with single greatly enlarged, elongate, heavily pigmented, simple photophore (photophore about 14%–18% length of arms).

Dorsal pad of funnel organ with heavy, swollen, median ridge that extends entire length of each lateral arm from apical papilla; spermatophore short (SpL 3.3–4.3 mm, 7.1%–8.1% ML; from 2 specimens, 46 mm ML and 53 mm ML); sperm mass short (6.7%–8.3% SpL); cement body long (64.1%–73.7% SpL); ejaculatory apparatus of medium length (25.8%–27.2% SpL), with single longitudinal loop of inner tube; ejaculatory-apparatus/cement-body connective complex present; mature egg not known; gills about 31%–40% ML, with about 19–23 lamellae in outer demibranch.

Gladius with moderately short free rachis; vanes broad, roughly triangular, delicate, ending posteriorly in wide, bluntly rounded, thin cupped coil; lower beak with well-curved rostral edge, rather heavy rostral tip protruding well forward, wing fold distinct but relatively low, lateral wall with moderately heavy median ridge extending to free corner; radula with first and second laterals slightly asymmetrical, weak marginal plates present.

**ORIGINAL REFERENCE.**—Voss, 1969:845, figs. 4a,b, 6f, 8g, 33, 36, 37.

**TYPE LOCALITY.**—Tasman Sea, vicinity of southern subtropical convergence; 45°10'S, 160°10'E; 700–789 m.

**DEPOSITION OF TYPES.**—*Holotype*: USNM 576761, female, 52.0 mm ML, R/V *Eltanin* sta 1834, 11 Dec 1966; good condition.

*Paratypes* (11 specimens): NMNZ 17970, SAM A29637, UMML 31.1342, UMML 31.1734, USNM 576176, USNM 576177, ZMUC (5) uncat.

**DISTRIBUTION.**—*Histioteuthis macrohista* primarily inhabits the transitional and fringing waters of the SSTC (Figure 9), where, over its known range in the Atlantic, Indian, and western Pacific oceans between about 33°S and 47°S, it occurs with *H. atlantica*. The species was found to be common in the collections of the 1971 and 1975/1976 cruises of the R/V *Walther Herwig*, which sampled the entire Atlantic sector of the convergence. In that area, *macrohista* ranked second to *atlantica* in abundance among congeners. Over its Atlantic range in the vicinity of the convergence, mature and near-mature animals were taken close to continental slopes as well as in open ocean. In the eastern Atlantic, the species' range extends northward to 23°S in the Benguela Current, where the R/V *Professor Shtokman* caught the species during cruise 14 (1985) at 11 stations made between 23°S and 26°S, 10°E and 14°E. In this area, the northern limit of *macrohista* and the southern limit of the tropical population of the congener *reversa* were found to overlap between 23°S and 24°S. Neither *macrohista*'s sibling species, *bonnellii*, nor congeners, *atlantica* and *miranda*, were encountered in this northern sector of the current, although the four species are known to co-occur in the current's southern sector. Scattered records are available, but the abundance of *macrohista* in the Indian Ocean portion of the convergence is poorly known. It was not encountered north of the convergence on either the Madagascar Plateau (28°S) or Walters Shoal (34°S), the southernmost areas sampled during the western Indian Ocean cruise of the R/V *Vityaz* in 1988 (K. Nesis, unpublished data). In the area of Australia and New Zealand, published and unpublished (E. Förch, C. Lu, K. Nesis, N. Voss) collecting data show *macrohista* to be common in the vicinity of the convergence and southward to about 47°S. It is uncommon, however, northward in the East Australian Current system and in the subtropical waters of the Tasman Sea, areas normally inhabited by the closely related *bonnellii*.

The R/V *Eltanin* collected the species at only two stations (ELT 1695, ELT 1704) during its numerous transects between New Zealand and the west coast of South America and southward to the Antarctic. Both single captures were made between the east coast of New Zealand and 167°W in the vicinity of the convergence. The scarcity of the species in the central Pacific is further evidenced by Polezhaev's (1986) report of a single specimen of *macrohista* found in a collection of about 500 squids taken between New Zealand and Chile at latitudes of 30°S–45°S. The conspicuous absence of *macrohista* in the eastern Pacific parallels that found for the southern

TABLE 12.—Comparison between members of the *Histioteuthis bonnellii* species group.

Character	<i>H. bonnellii</i> *	<i>H. macrohista</i>
Buccal membrane	6-membered	7-membered
Photophore pattern		
Organs in circlet around right eye	17 (rarely 16 or 18)	6 (rarely 15)
Round organs on left posteroventral margin of head	3	2
Enlarged, terminal brachial organ	present on arms I-IV†	present on arms I-III
Spermatophore		
Sperm mass length	9.8%–33.9% SpL	6.7%–8.3% SpL
Loops in ejaculatory apparatus	1 long or 2–3 medium long	1 long
Gill lamellae in outer demibranch	30–43	19–23
Size at maturity	small–large, 50–330 mm ML	small, ~40–>65 mm ML
Geographic range	Atlantic subarctic, N temperate, E tropical Mediterranean Sea; near circumglobal in southern 1/2 of S subtropical latitudes; Benguela Current; East Australian Current	near circumglobal in SSTC; Benguela Current

\*Probably comprises more than one taxon. See "Discussion" for species.

†On arms IV, photophore approximately 1/3–1/6 size of those on arms I-III; first seen in late juvenile or later growth stages; could be absent in early maturing individuals.

population of *bonnellii* and suggests that the two sibling species are not circumglobal in their distributions.

Although all captures have been made with open nets, data is sufficient to indicate that the vertical range of *H. macrohista* extends from the surface 100 m to depths in excess of 1000 m. Juveniles and subadults have been taken at night in midwaters over the entire known vertical range of the species. At nighttime, subadults also have been captured near the bottom at 700–800 m. Mature males have been captured at night with nets fishing at about 100 m, 300 m, and 600 m.

DISCUSSION.—*Histioteuthis macrohista*, the southernmost member of the pair of species that comprises the *bonnellii* species group, is well distinguished from its sibling species (see Table 12) by a buccal membrane that is seven-membered, rather than six-membered as in *bonnellii*, and by related structural details of the inner web between arms III and IV. In addition, the gladius of *macrohista*, recently described and illustrated by Toll (1982), has vanes with conspicuously wider mid- and posterior portions than those in *bonnellii*. Also, consistent differences between the two species are seen in the presence of two conspicuous, round, dark photophores on the left posteroventral margin of the head in *macrohista* rather than the three present in *bonnellii* (see Figure 8e,f). *Histioteuthis macrohista* also differs by having a slightly reduced number of photophores around the right eye and on the ventral surfaces of the head and mantle and a carpal adhesive apparatus composed of fewer suckers and pads (for a detailed description of the carpal adhesive apparatus of both species, see Voss, 1969).

The spermatophores of *macrohista* are similar to those described here for the specimen of *bonnellii* from southwestern Atlantic subtropical waters, but they differ from those described for *bonnellii* from tropical waters northward in the number of loops in the ejaculatory apparatus. The loops are

single in *macrohista* and in the southwestern Atlantic *bonnellii* and are multiple in *bonnellii* from the more northern areas. Also different is the length of the sperm mass, being short in *macrohista* and long in the two specimens of *bonnellii* from the northern temperate and northern Mauritanian Upwelling areas.

The enlarged, terminal photophores found on arms I–III in *macrohista* were recently shown by Dilly and Herring (1981) to be similar in ultrastructure to those found on arms I–IV in *bonnellii*. Their absence on arms IV in the former species further distinguishes the members of this species pair. The late ontogenetic appearance of the terminal photophores on arms IV in *bonnellii* and their absence in some early maturing individuals of the species suggest that their absence in *macrohista*, a small maturing species, is a derived, pedomorphic condition.

Although a detailed study of the large collections of *macrohista* taken by the R/V *Walther Herwig* on the 1971 and 1975/1976 cruises in the Atlantic and by the New Zealand fisheries survey program around New Zealand remains to be done, a comparison of small lots of specimens from the respective areas revealed no evidence of significant morphological variation. Additionally, new mature males found in both collections showed size of males at maturity to be similar in the two study areas, 44–53 mm ML in the Atlantic and 40–47 mm ML off New Zealand.

#### *Histioteuthis celetaria* (G. Voss, 1960)

This multiple-ocean, warm-water species is currently recognized as comprising two subspecies, *H. c. celetaria*, restricted to the Atlantic, and *H. c. pacifica*, restricted to the Pacific and Indian oceans. Our examination of previously unreported collections (23 specimens of *H. c. celetaria* found in the IBSS,

IOAN, UMML, and USNM; and 87 specimens of *H. c. pacifica* found in the AtlantNIRO, CERAM, IOAN, SIO, TINRO, USNM, WAM, and YugNIRO), which include the mature stages of both subspecies, gave us the opportunity to reassess the described differences between these poorly known taxa and revealed an additional occurrence in the family of maturity-related, simple photophores. The descriptions below are based primarily on large juveniles, subadults, and adults, 35–258 mm ML. Because these growth stages of *H. c. celetaria* are only known from the southeastern Atlantic, knowledge of possible variations that might occur over the range of the subspecies is lacking. Our specimens of *H. c. pacifica* came from over a large part of its known range, with the northern Indian Ocean and eastern Pacific being the areas of poor representation. The characters given in the following species description are common to both subspecies.

**DESCRIPTION.**—Medium-sized to large histioteuthids; mantle stout, conical, becoming elongate with growth (especially in adult female), with moderately thick walls; fins large, length about 40%–60% ML, width about 60%–78% ML (except proportionally smaller in adult female); head large, length 40%–55% ML (except proportionally smaller in adult female), with 2 usually well-developed nuchal folds; arms of medium length, about 80%–130% ML; suckers largest on third  $\frac{1}{4}$  of arms I–III (except in mature male); rings of suckers on arms I–III smooth except on distal ends where rings have few to numerous small, usually blunt teeth on distal and lateral margins; sucker rings on arms IV usually incised on entire or distal and lateral margins; in mature male (not always seen in small mature males), suckers on basal portions of all arms enlarged, with swollen, fleshy collars; ends of arms I modified with coequal-sized suckers on elongate pedestals; inner web between basal portions of arms I–III low to medium, 9%–15% length of longest arm; buccal membrane 7-membered, with second supports to dorsal sides of arms II, fourth supports without secondary connectives; tentacles long, about 150%–220% ML; tentacular club lacking longitudinal cleft on aboral surface; suckers on manus arranged in 6 to 7 rows, slightly or moderately enlarged in median rows; suckers of 2 or 3 ventral marginal rows, and sometimes few proximal suckers of median rows, usually with ventral side of denticulate collar slightly to markedly asymmetrically broadened; rings of manal suckers with numerous (~28–55) sharp-pointed teeth around entire margins; teeth well developed on distal and lateral margins, low and poorly formed, or absent, on proximal margins.

Compound photophores uniformly large and evenly spaced on anterior  $\frac{2}{3}$ – $\frac{3}{4}$  of mantle ventrum, decreasing in size and with interspersed small photophores on posterior end; head with area of reduced number of photophores (or none) often present posteroventral to each eye; cirlet of 17 (rarely 16 or 18) large photophores around right eyelid; arms IV with 3 longitudinal rows of large photophores on basal  $\frac{1}{2}$ ; distinct terminal group of 4–8 normal compound photophores present on ends of arms I–IV in juveniles and subadults and present

only on ends of arms IV in mature stage of both sexes (see below); in mature animals, long, narrow, black, simple photophore present beneath median keel on distal portions of arms I–III (Figure 10*b,c*; not known in mature male of *H. c. celetaria* or mature female of *H. c. pacifica*).

Dorsal pad of funnel organ unsculptured; gills about 33%–43% ML, with 35–43 lamellae in outer demibranch; gladius with free rachis strongly developed, with thickened lateral edges; vanes triangular, with 2 sets of thickened, longitudinal bands; lower beak with rostrum rather narrow; rostral edge long, slightly curved; hood high standing above crest; wing fold low; lateral wall bisected by strong median ridge that extends to free corner.

Skin color dark, wine red.

### *Histioteuthis celetaria celetaria* (G. Voss, 1960)

FIGURES 10*a–d*, 11

**DESCRIPTION.**—Female known to mature at about 258 mm ML (single known mature specimen, USNM 816916, from SE Atlantic); male known to mature at about 87 mm ML (single known mature specimen, USNM 730960, from SE Atlantic); arms about 80%–90% ML; tentacular club with suckers on manus closely arranged, those of median 2 to 3 rows only slightly enlarged (Figure 10*a*); asymmetrically broadened denticulate collar usually present on suckers of 3 ventral marginal rows, asymmetry appears to be most pronounced in juvenile; mature spermatophore not known; mature egg average diameter 1.9 mm; in mature female, long, narrow, black terminal photophore on arms I–III present on distal  $\frac{1}{3}$ – $\frac{1}{2}$  of arms in specimen of 258 mm GL (Figure 10*b,c*), may be proportionally shorter in smaller specimens; in mature male, presence of terminal photophore not known (ends of arms in poor condition in single known specimen); gladius with anterior shoulders of vanes somewhat flaring and angular (Figure 10*d*).

**ORIGINAL REFERENCE.**—Voss, 1960:424, fig. 73.

**TYPE LOCALITY.**—Northwestern Atlantic; 32°10'N, 64°45'W, 730–820 m.

**DEPOSITION OF TYPE.**—*Holotype*: Field Museum of Natural History, Chicago, FMNH 78308, female, 39 mm ML, R/V *Caryn* haul 37, 0405–0838 hours, 5 Aug 1948.

**DISTRIBUTION.**—In Voss's 1969 revision of the family, *Histioteuthis celetaria celetaria* was known from only two small juveniles, including the holotype. Reported captures since then (Nesis, 1974; Toll, 1982; Amelekhina and Zuev, 1988; Amelekhina et al., 1990; Voss et al., 1992) together with unreported ones by the R/V *Akademik Kurchatov*, R/V *Professor Vodyanitsky*, and R/V *Walther Herwig*, show *H. c. celetaria* to be widely distributed in the north subtropical and tropical regions of the Atlantic. It is present but poorly known in the South Atlantic subtropical region, and it appears to be absent from the Caribbean Sea and Gulf of Mexico (Figure 11).

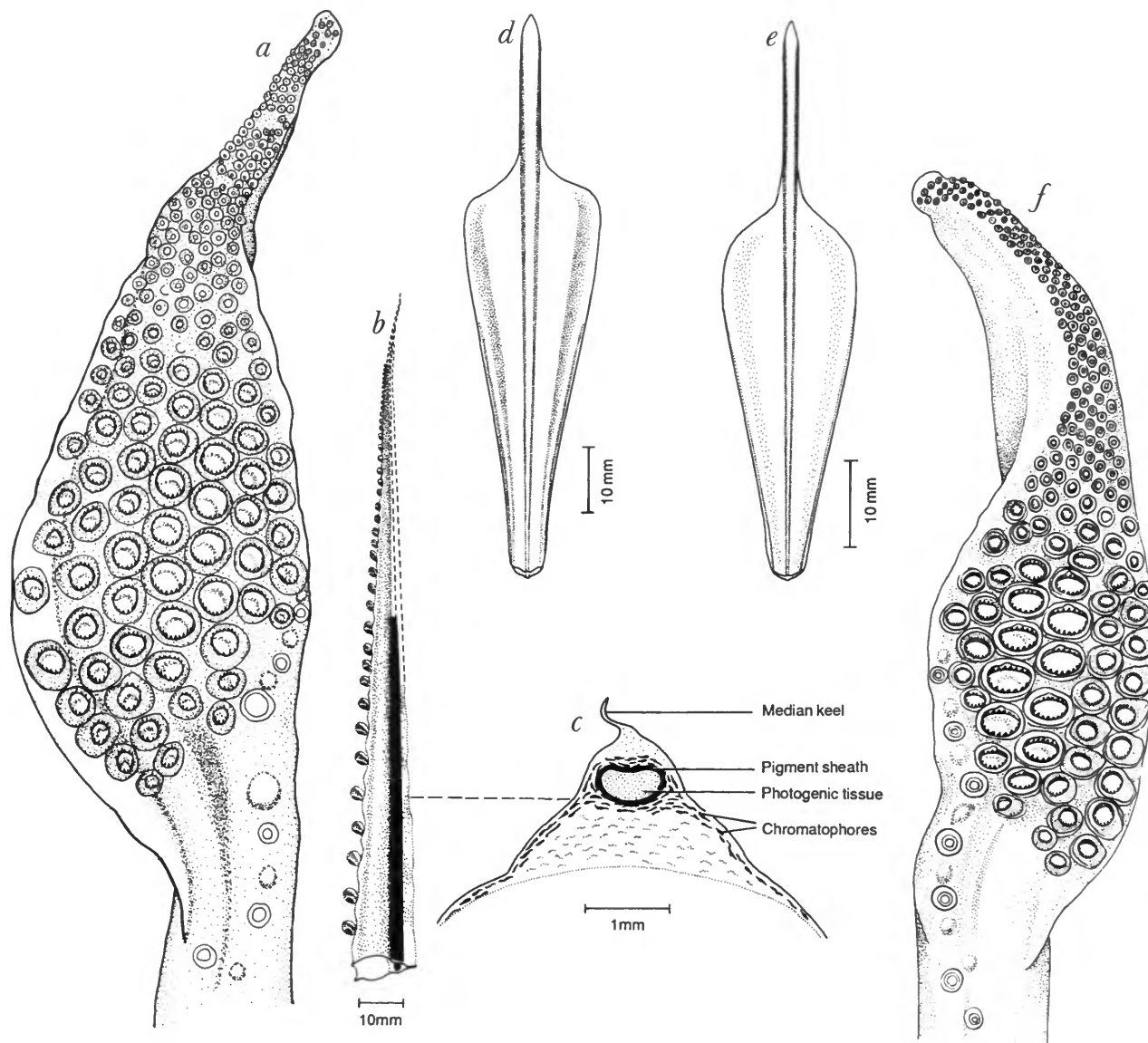


FIGURE 10.—*Histiotueuthis celetaria celetaria*: a, right tentacular club, USNM 730960, 74 mm GL, immature female, 18°36'S, 4°18'W; b, side view of distal  $\frac{2}{3}$  of partially reconstructed left arm I showing maturity-related, long, darkly pigmented, simple photophore beneath median keel, USNM 816916, 258 mm GL, mature female, 13°07'S, 9°02'W; c, diagrammatic cross section of maturity-related photophore and surrounding tissues of same; d, ventral view of gladius, USNM 730960, 87 mm GL, mature male, 18°36'S, 4°18'W. *Histiotueuthis celetaria pacifica*: e, ventral view of gladius, UMML 31.1339, paratype, mature male, ~13°N, 122°E. f, left tentacular club, ZMUC, 74 mm ML, mature male, 25°20'S, 35°17'E. (d,e, redrawn from Toll, 1982; f, redrawn from Voss, 1969.)

All but four of the 25 known specimens were taken in the eastern Atlantic between 33°N and 19°S. The occurrence of *H. c. celetaria* in southern subtropical waters is known only from two small juveniles taken separately in open ocean between 25°S and 26°S, 26°W and 27°W, well north of the SSTC. The

remaining captures of the subspecies have been taken in more productive waters both in open ocean and near land masses and submarine ridges. The capture of five large juveniles and subadults and one adult in a single haul of a 1600-mesh Engel trawl from off the southwestern coast of Africa (19°S, 4°W;

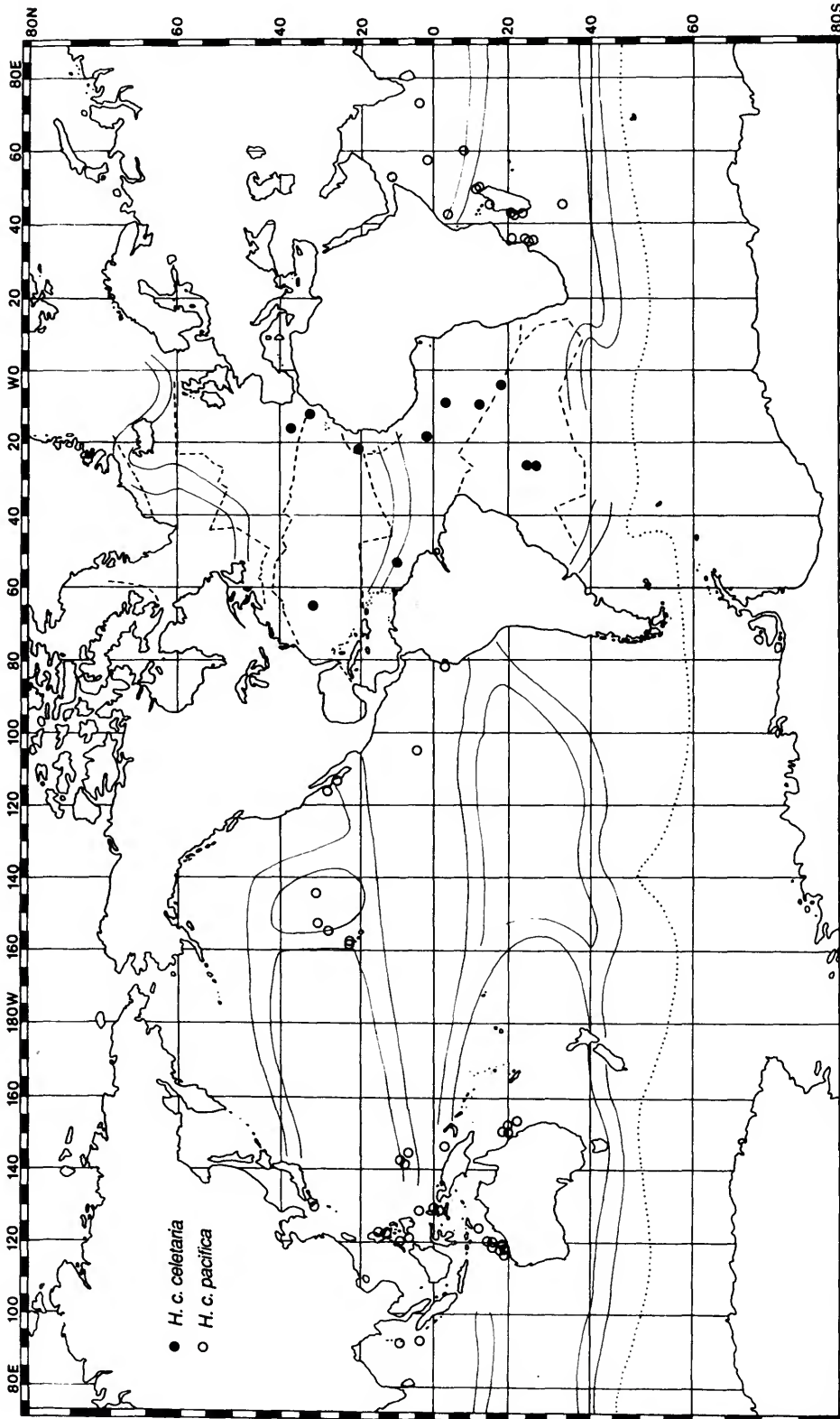


FIGURE 11.—Geographic distribution of *Histioeuthis celestaria*. Distribution of subspecies *H. c. celestaria* known from 11 net hauls (25 specimens), and *H. c. pacifica* known from 76 net hauls (127 specimens). For explanation of indicated ocean regions, see Figures 2, 5.



R/V *Walther Herwig* 447-III/71; misidentified as *H. celetaria pacifica* by Voss et al., 1992) and the capture of 11 small juveniles in one haul by the R/V *Professor Vodyanitsky* at 3°S, 9°W, in the Gulf of Guinea suggest that *H. c. celetaria* probably occurs in abundance in the more productive areas within its distributional range.

Open nets have taken small juveniles to 39 mm ML from the surface 40 m and at fishing depths to about 800 m. Large juveniles, subadults, and adults have all been taken in nets fishing at night between 750 m and 1010 m. The only known mature female, which had mated and was spent (indicated by the flaccid condition of the body and few eggs remaining in the oviducts), was taken while fishing between 990 m and 1010 m at 13°S, 9°W (R/V *Walther Herwig* 455-III/71), over the eastern edge of the Mid-Atlantic Ridge. The sole mature male was captured in open ocean at fishing depths between 750 m and 760 m at 19°S, 4°W. Both captures suggest that mating and spawning in *H. c. celetaria* occur in deep water.

#### *Histioteuthis celetaria pacifica* (G. Voss, 1962)

FIGURES 10e,f, 11

DESCRIPTION.—Female size at maturity not known (largest available specimen, 234 mm ML from 17°S, 119°E (TINRO, uncat.), is immature); male known to mature at 60–>280 mm ML (largest known specimen from 31°N, 129°E, TINRO, uncat.); arms about 100%–125% ML; tentacular club with suckers on manus closely arranged in 6 rows, suckers of median 3 rows moderately enlarged with increased degree of enlargement from dorsal to ventral—most rows, diameter of largest median suckers 1½ times ventral marginals (Figure 10f); asymmetrically broadened denticulate collar usually present on suckers of 2 ventral marginal rows; spermatophore short (SpL 1.3–2.0 mm; 1.7%–3.4% ML; 4 specimens, 65–82 mm ML from Philippines and northwestern Australia); sperm mass of medium length (21%–25% SpL), cement body and ejaculatory apparatus moderately long (35%–40% SpL); ejaculatory apparatus with single longitudinal loop of inner tube; ejaculatory-apparatus/cement-body connective complex well developed; mature egg not known; in mature female, presence of long, narrow, black, terminal photophore on arms I–III not known; in mature male, long, terminal photophore present but extent of development not known because of poor condition of ends of arms; gladius with anterior shoulders of vanes broadly rounded (Figure 10e); radula with stout rachidian; first, second, and third laterals of increasing length; marginal plates weak.

ORIGINAL REFERENCE.—Voss, 1962:174; original illustration, Voss, 1963, fig. 26.

TYPE LOCALITY.—Indo-West Pacific, off Dammi Island, Sulu Archipelago, Philippines; 5°50'N, 120°31'E, 432 m.

DEPOSITION OF TYPES.—*Holotype*: USNM 575453, female, 74 mm ML, R/V *Albatross* sta D5564, 21 Sep 1909.

*Paratypes* (5 specimens): UMML 31.1339, USNM 575454, USNM 575455, USNM 575457 (2 specimens).

DISTRIBUTION.—Recently reported specimens (Nesis, 1977; Young, 1978; Toll, 1982; Lu and Phillips, 1985) and a considerable number of unreported ones found in the collections of various institutes (for list, see text preceding description of *H. celetaria*, above) show the distribution of *H. c. pacifica* to be largely associated with tropical or equatorial waters of the Indian and Pacific oceans (Figure 11). In the Indian Ocean, the subspecies is widely distributed in equatorial waters between 8°N and 10°S and extends into western peripheral waters of the southern gyre to 35°S. Of the seven species of histioteuthids (listed in decreasing order of numbers taken: *H. celetaria pacifica*, *miranda*, *bonnellii* and *meleagroteuthis* (equal number), *atlantica*, and *hoylei* and *corona* ?subsp. (equal number)) captured between 12°S and 34°S, 35°E and 54°E in the southwestern Indian Ocean during the 1988/1989 cruise of the R/V *Vityaz*, *H. c. pacifica* was found to be the most common one between latitudes 8°S and 26°S. Southward to 34°S, it was replaced by *miranda* as the dominant form (K. Nesis, unpublished data).

*Histioteuthis celetaria pacifica* occurs throughout most of the Indo-West Pacific and was taken in large numbers along the northwest shelf and slope of Australia during a recent resource survey of that area (Wadley, 1990; S. Slack-Smith, unpublished data, specimens examined (NV)). The subspecies ranges across the Pacific in equatorial waters to the Americas, where it has been collected from 4°S northward into the southern transitional waters of the California Current to 28°N. It also occurs in peripheral central waters around and north of the Hawaiian Islands to 30°N. It is not known from the Peru–Chile Current or from southern subtropical waters. Although some specimens have been taken from open ocean, most have come from on or near continental and island slopes and submarine rises.

Data from open-net captures and the few available opening-closing-net captures (Young, 1978) show early juveniles to 15 mm ML to be present in the upper 200 m. A daytime opening-closing-net capture of a 10 mm ML specimen at 550 m off Hawaii shows the vertical range of this size group to extend into deeper waters. Older juveniles occur over a broad vertical range extending from deep water (possibly to 1000 m) to about 200 m at night and 400 m during the day. Subadults and adult males have been found day and night in the midwater and near shelf and slope bottoms between about 250–1000 m, with the majority taken deeper than 350 m. An analysis by one of us (KN) of the catch data for 47 specimens (mostly adult males, subadults, and large juveniles) recently taken in eight demersal-trawl hauls by the R/V *Vityaz* from Socotra Island to Mozambique in the western Indian Ocean shows that 34 specimens were caught while fishing depths of 364–500 m, 11 from depths of 501–750 m, and two from 751–1000 m. The largest (147 mm ML) of the 14 mature males taken and the largest female, a near-mature specimen of 146 mm ML, came

from the deepest haul at 980–1000 m. An earlier, unpublished French study of the cephalopods from the same approximate area off Madagascar, between 12°S and 24°S, 43°E and 49°E, similarly showed the subspecies to be abundant and to be the most common histioteuthid taken. The collection of 29 mostly adult males (to 110 mm ML), subadults, and large juveniles were caught with midwater nets during the day at fishing depths largely between 450 m and 720 m (P. Rancurel, unpublished data; part of histioteuthid collection examined (by NV)). The 38 specimens of *H. c. pacifica*, representing the same growth stages as above (with adult males to 110 mm ML), contained in the earlier mentioned collections from off northwestern Australia were taken in trawls from off soft bottom between 400 m and 600 m during both day and night.

DISCUSSION.—*Histioteuthis celetaria* is one of the largest maturing histioteuthids, exceeded in maximum size only by *bonnellii* and possibly *miranda*. Of the combination of characters given in the species diagnosis that distinguishes *celetaria* from all other members of the family, the asymmetrical development of the denticulate collar of certain suckers on the tentacular club manus and a distinct terminal group of normal-sized, compound photophores on the arms are unique. In the mature animal, the appearance of a single long, narrow, simple photophore beneath the median keel on the distal portions of arms I–III, replacing the novel terminal group of photophores on those arms, is another feature found only in *celetaria*. The exact lengths of these maturity-related photophores are not known because of the poor condition of the skin on the arms of the available mature specimens (a single male and female of *H. c. celetaria* and 17 males and no females of *H. c. pacifica*). Those of a specimen whose arms are in the best condition, a 258 mm ML female of *H. c. celetaria*, extend from near the arm tip for  $\frac{1}{3}$ – $\frac{1}{2}$  the lengths of arms I–III (Figure 10b,c). Judging from the remaining fragments in smaller mature animals (all males of *H. c. pacifica*), it appears that the novel photophore first forms on the end of the arm and then progressively extends down the arm with growth. Whether there are subspecific and sexual differences in the proportional length of the organs is not known. Aspects of another feature, the gladius, are also peculiar to the species. It has been described by Toll (1982) to be of the sturdiest construction in the family.

Our examination of new material has confirmed the distinctiveness of the subspecies, *H. c. celetaria* and *H. c. pacifica*, but not on the basis of the previously used characters, which we have found to be unreliable because of variations that occur in both taxa. Originally, the former subspecies was distinguished by the possession of a window-like area, devoid of photophores, posterior to each eye on the ventral surface of the head; four rather than eight or nine small photophores on the lateral margins of the left eye; and, possibly, teeth confined to the distal margins of the manal suckers of the tentacular club. Our present study found the two subspecies to be well distinguished by differences in the sucker pattern of the manus

of the club (Figure 10a,f). In *H. c. celetaria*, suckers of the three ventral-most rows usually display the peculiar, asymmetrically developed denticulate collar, and the suckers of the median two or three rows are slightly and approximately coequally enlarged. In contrast, the suckers of the two ventral-most rows in *H. c. pacifica* usually have asymmetrically broadened collars, and the suckers of the three median rows are moderately enlarged and are graded in size from the largest in the ventral-most, or two ventral-most, row(s) to the least enlarged in the dorsal-most row. This sucker-enlargement pattern is not developed in the small juvenile of *H. c. pacifica*; at this stage, the sucker pattern more closely resembles that of the Atlantic subspecies. An additional subspecific difference found by Toll (1982) in the shape of the anterior shoulders of the gladiol vanes, somewhat flaring and angular in the former subspecies and broadly rounded in the latter (Figure 10d,e), was confirmed by our dissections of new material. The above differences between the siblings are summarized in Table 13. In addition, we detected in *H. c. celetaria* a possible tendency to have proportionally shorter arms than does *H. c. pacifica*.

Unfortunately, we were unable to clarify the differences found by Hess (1987) in the spermatophores of the two taxa. We did, however, determine the presence of the conditions of a single large loop of the inner tube of the ejaculatory apparatus and a sperm mass of about 21%–25% SpL in the spermatophores of specimens from the northwestern shelf of Australia (WAM). These conditions were reported for *H. c. pacifica* from a paratype from the Philippines (UMML 31.1339; Voss, 1969; Hess, 1987), which suggests that they are typical of the subspecies. But the high degree of variation found by Hess in the morphology of the spermatophores of the only known mature male of *H. c. celetaria* (USNM 730960), subsequently verified by our examination of additional spermatophores from the same specimen, leads us to conclude that the specimen is in an early stage of maturity and that the spermatophores are not fully formed, thus precluding a comparison of this organ between subspecies.

Of the above differences between *H. c. celetaria* and *H. c. pacifica*, that in the sucker pattern on the manus of the club appears to be the most significant. Additional large specimens of *H. c. celetaria* from over a broad part of the geographic range of the subspecies and new mature males and females of both subspecies are needed to determine the constancy of our findings and to possibly detect new distinguishing characters. Future study will probably show that these taxa represent two distinct species, but we feel at this stage of our knowledge that they should remain at the subspecific level.

Finally, the single specimen of *H. c. celetaria* listed by Stephen (1982:115) from Canadian Atlantic waters and identified by him as a maturing female of 77 mm ML was examined in order to verify the identification and stage of maturity. The specimen (HML 7913, lot MT 70-2), in poor condition, was found to be a small mature male of *H. bonnellii*. Its size (now measures 69 mm ML, but GL is 76 mm), the

TABLE 13.—Comparison between the two subspecies of *Histioteuthis celetaria*. Both subspecies are poorly known.

Character	<i>H. c. celetaria</i>	<i>H. c. pacifica</i>
Club suckers		
Enlargement pattern	Suckers in median 2 to 3 rows of manus slightly and approximately coequally enlarged	Suckers in median 3 rows of manus moderately enlarged, decreasing in size from ventral- to dorsal-most rows*
Asymmetrical denticulate collar	Usually present on suckers in 3 ventral-most rows	Usually present on suckers in 2 ventral-most rows
Shape of glacial vanes	Shoulders somewhat flaring and angular	Shoulders broadly rounded
Geographic range	Atlantic; tropical-subtropical	Pacific and Indian oceans; largely equatorial or tropical

\*Pattern not developed in small juveniles.

station data on the jar label, and Stephen's handwritten identification label correspond to the information given in his text and minimize the possibility that a mixup of specimens had occurred. We have, therefore, disregarded this record in our above treatment of *H. c. celetaria*.

### *Histioteuthis corona* (N. Voss and G. Voss, 1962)

FIGURE 12

Four subspecies, *H. c. corona*, *H. c. berryi*, *H. c. cerasina*, and *H. c. inermis*, are currently recognized in this cosmopolitan, warm-water species, which possesses a unique, permanently swollen (often appearing deflated after preservation) condition of the dorsal pad of the funnel organ and a distinctive combination of character states. The characters given in the following description are common to all the subspecies and are described from large juveniles, subadults, and adults. Our study material of the relatively well-known, Atlantic *H. c. corona* was composed of 78 mostly unreported specimens (IOAN, UMML, USNM) from over the entire distribution of the subspecies.

The three poorly known, Pacific subspecies were each represented by only a few specimens (five unreported specimens of *H. c. berryi* from the SIO, TINRO, UMML, and the USNM; 29 reported and unreported specimens of *H. c. cerasina* from the IOAN, MHNJP, and the USNM; and two unreported specimens of *H. c. inermis* from the USNM) that came from limited portions of their probable distributions. Unfortunately, subadults and adults are known only for *H. c. corona*.

DESCRIPTION.—Mantle moderately elongate in adults (conical, stout in juveniles), walls thick and firm; fins medium-sized to large, length 30%–60% ML, width 50%–90% ML; head with 2 (occasionally 1) often weakly developed nuchal folds; arms of medium length to moderately long, about 100%–200% ML, arms I–III approximately coequal, arms IV usually slightly shorter; rings of suckers on arms I–III usually smooth except on distal ends of arms where rings usually with numerous, low teeth around entire margins; rings on arms IV

with numerous low, square teeth on entire or distal margins, or teeth absent; inner web connecting basal portions of arms I–III moderately developed, about 11%–25% length of longest arm (? except low to vestigial in *H. c. inermis*); buccal membrane 7-membered, second supports to dorsal sides of arms II (rarely bifurcate to arms I and II), fourth supports without secondary connectives; tentacles long, about 200%–330% ML; tentacular club without longitudinal cleft on aboral surface; suckers on manus arranged in 5 to 6 rows, moderately enlarged in median rows to about 1½–2 times ventral marginals; rings of enlarged suckers with about 20–60 sharp-pointed, conical teeth on entire margins.

Compound photophores uniformly large on anterior ½ of mantle ventrum, arranged in about 8 diagonal rows, progressively decreasing in size on posterior ½; cirlet of 17 (occasionally 16; rarely 18, or ?15) large photophores around right eye; arms IV with 3 (except 4 in *H. c. berryi*) longitudinal rows of large photophores on basal portions; enlarged, maturity-related, simple photophores appear to be lacking (absent in *H. c. corona*, occurrence in other subspecies not known).

Dorsal pad of funnel organ unsculptured, appearing swollen or deflated; mature egg not known; gills about 30%–50% ML, with about 38–44 lamellae on outer demibranch; radula heterodont, with first, second, and third laterals of increasing length, marginal plates appear to be absent.

Gladius with sturdy, relatively short, moderately narrow free rachis (tends to be longer and broader in juveniles); vanes long, moderately narrow (tend to be wider in juveniles), with hourglass-shaped midportion and 2 sets of thickened bands, ending posteriorly in narrow (tends to be broader in juveniles), rounded cupped coil; lateral wall of lower beak with strong median ridge extending to free corner.

Skin color dark cherry or wine red.

### *Histioteuthis corona corona* (N. Voss and G. Voss, 1962)

Previously unreported collections of *H. c. corona* made mostly by the R/V *Anton Dohrn*, R/V *Walther Herwig*, and the

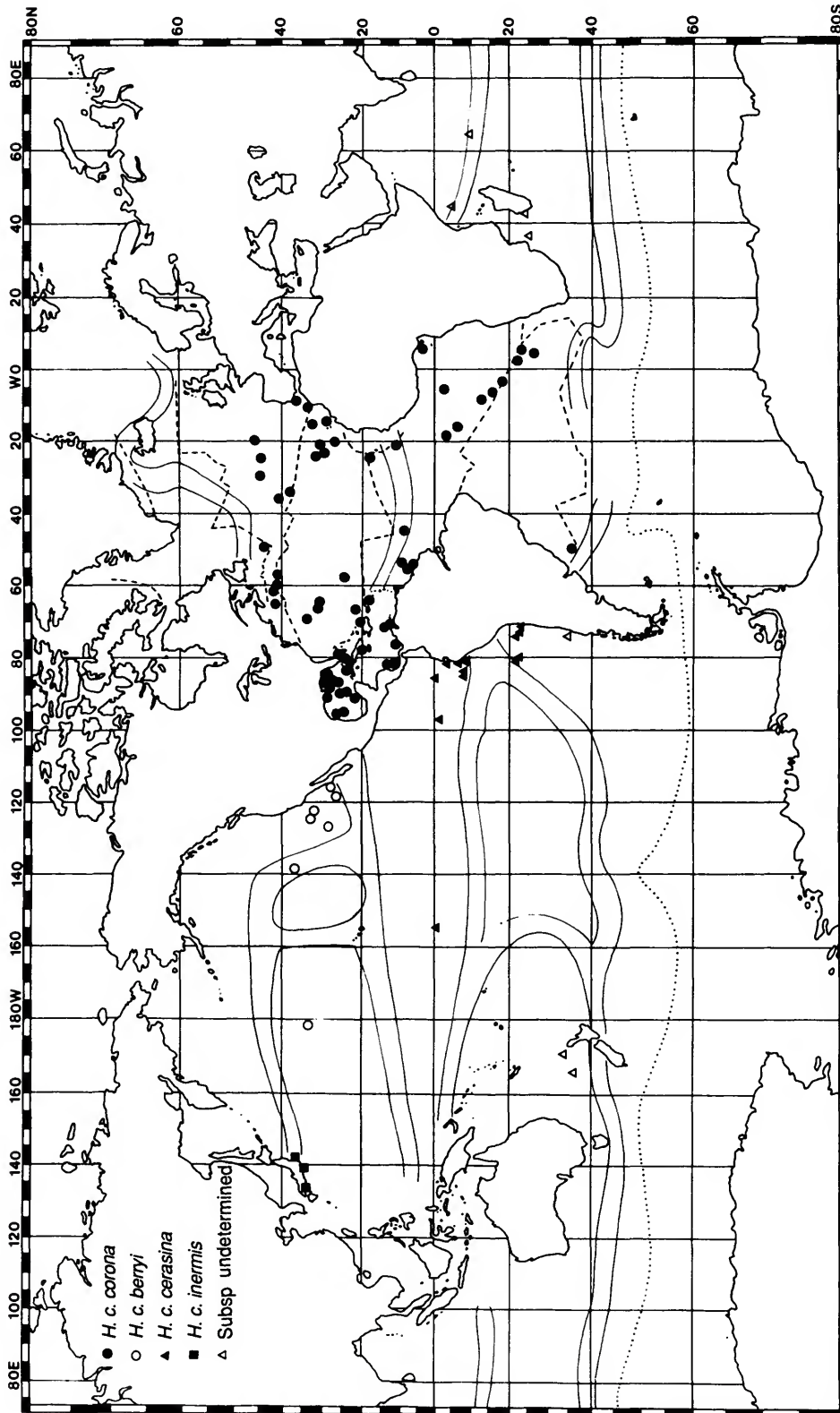


FIGURE 12.—Geographic distribution of *Histiotuleihs coronae*. Distribution of subspecies *H. c. coronae* known from ~94 net hauls (155 specimens), *H. c. berryi* known from 8 net hauls (8 specimens), *H. c. cerasina* known from 19 net hauls (29 specimens), and *H. c. inermis* known from 6 net hauls (10 specimens). For explanation of indicated ocean regions, see Figures 2, 5.

Ocean Acre Program (all deposited in the USNM) and captures reported since Voss's 1969 family revision, particularly those by Clarke and Lu (1974, 1975) and Stephen (1982), have greatly contributed to our understanding of the uneven distribution of this Atlantic subspecies.

**DESCRIPTION.**—Medium-sized to moderately large histioteuthids; males known to mature at about 110–188 mm ML; female size at maturity not known (largest female known, 168 mm ML, immature); fins medium-sized, length about 34%–42% ML, width about 57%–64% ML; in mature male, pedastals of small suckers on ends of arms I swollen and elongate; sucker rings on arms IV with numerous low, square teeth on entire or distal margins; rings on enlarged median suckers on manus of tentacular club with 33–38 triangular or narrow, pointed teeth.

Circlet of 17 (occasionally 16) photophores around right eye; photophores arranged in 3 longitudinal rows on basal portions of arms IV; spermatophore short (SpL 4.2–5.7 mm; 2.5%–3.3% ML; 172 mm ML specimen, UMML 31.1727, off Curaçao in Caribbean Sea), relatively wide; sperm mass short (4.3%–12.3% SpL), convoluted; cement body long (56.7%–71.8% SpL), with ejaculatory-apparatus/cement-body connective complex absent; ejaculatory apparatus of medium length (25.4%–36.8% SpL), with 1 to 2 longitudinal loops of inner tube (see "Discussion" for species, following account of *H. corona inermis*, for description of ontogenetic changes in internal components); lower beak with wing fold low, lateral wall with drawn-out free corner.

**ORIGINAL REFERENCE.**—Voss and Voss, 1962:191, figs. 5a–f, 6b–d.

**TYPE LOCALITY.**—Gulf of Mexico, 29°10'N; 88°00'W, 521 m.

**DEPOSITION OF TYPES.**—*Holotype*: USNM 576160, female, 46 mm ML, R/V *Oregon I* sta 384, 21 Jun 1951.

*Paratypes* (5 specimens): UMML 31.119, UMML 31.414, UMML 31.417, UMML 31.420; Peabody Museum, Yale University, New Haven, YPM 12439.

**DISTRIBUTION.**—*Histioteuthis corona corona* is confined to the Atlantic (Figure 12), where it is the sole recognized subspecies. Known primarily from tropical and north subtropical Gulf of Mexico waters, it occurs in highest abundance in the Tropical Region and Gulf of Mexico. It is the common histioteuthid in most of the gulf and throughout western tropical waters. In the gulf, *H. c. corona* occurs with *arcturi*, whereas in the Caribbean Sea, except off Venezuela, where one specimen of *arcturi* was taken, it is the only histioteuthid encountered. On the Cape Town–Madeira transect of the 1971 cruise of the R/V *Walther Herwig* in eastern tropical waters, during which approximately 50 juveniles, subadults, and adults of *H. c. corona* were taken, the subspecies was first encountered at 27°S and thereafter at 7 (50%) of the 14 stations made to 11°N. It was absent in the collections from the vicinity of the Mauritanian Upwelling but reappeared at the two northernmost stations of the transect between 27°N and 33°N in

subtropical waters. In the western Gulf of Guinea, *H. c. corona* was reported by Arkhipkin and Shchetinnikov (1989) to be the common histioteuthid in their study area, between 3°S and 4°S, 6°W and 7°W. The scattered records in the northern subtropical region indicate that the subspecies is relatively uncommon and is confined to the more productive peripheral waters. *Histioteuthis c. corona* was not found in the central waters by the R/V *Anton Dohrn* during the 1979 Sargasso Sea Expedition. The two captures that were made on that cruise were at separate stations in the southwestern sector of the region between 25°N and 30°N, 58°W and 60°W. Of the three species of histioteuthids taken nearby in the Ocean Acre area, in the vicinity of Bermuda, *H. c. corona* ranked third in abundance to the dominate species, *arcturi* and *meleagroteuthis*. The scattered occurrences in north temperate waters seem to be related to the Gulf Stream system, which transports the subspecies northward from its normal range in warmer waters to about 43°N off Canada (Stephen, 1982) and to 46°N north of the Azores (IOAN). The occurrence of *H. c. corona* in the Gulf Stream in the area to the east and south of the Grand Banks is documented by Khromov (1987). The subspecies appears to be rare or essentially absent in most of the South Subtropical Region. In that region, the lack of encounters in the central waters and the single known capture in the western sector, an 8 mm ML paralarva (UMML) taken at 36°S, 48°W (Rodhouse et al., 1992), suggest that *H. c. corona* could be confined to the more productive peripheral waters as in the northern subtropical region.

The subspecific identifications of two juveniles reported (Voss, 1969) from the southwestern Indian Ocean are highly suspect and are shown on our map as "subspecies undetermined." The specimens identified to *H. c. corona* from the Coral Sea and off the northwestern coast of Australia by Lu and Phillips (1985) appear on reexamination to be damaged juveniles of *H. celetaria pacifica* (C. Lu, pers. comm.).

*Histioteuthis c. corona* inhabits depths from the upper 100 m to probably in excess of 1500 m. Clarke and Lu (1974, 1975) report opening-closing net captures in the eastern Atlantic of juveniles of 7–21 mm ML from 410–700 m during the day and 200–500 m at night. Subadults and adults have been caught in open nets fishing at midwater depths of 375–~2000 m and near the bottom at 735–750 m.

#### *Histioteuthis corona berryi* N. Voss, 1969

Since its original description from the California Current, only one capture of *H. c. berryi* has been reported (Jefferts, 1983). All eight known individuals, including the five new specimens located during the present study, are juveniles. The following description is based on the five largest specimens, 35 to 47 mm ML, which include the two types, all taken in the vicinity of the California Current.

**DESCRIPTION.**—Fins medium-sized, length about 40%–44% ML, width about 56%–65% ML; sucker rings on arms IV with

numerous low, square teeth on entire or distal margins; rings on enlarged median suckers on manus of tentacular club with about 28–34 triangular teeth.

Circlet of 17 photophores around right eye; photophores arranged in 4 longitudinal rows on basal portions of arms IV.

ORIGINAL REFERENCE.—Voss, 1969:781, figs. 19, 20.

TYPE LOCALITY.—Northeastern Pacific; 29°17'N, 125°41'W, 750 m.

DEPOSITION OF TYPES.—*Holotype*: USNM 576079, female, 7.4 mm ML, Wigwam expedition sta 2, 12 May 1955, 1605–2045 hrs.

*Paratype*: Uncataloged, Zooplankton Invertebrate Collections, SIO.

DISTRIBUTION.—The geographic distribution of this distinctive Pacific subspecies is poorly known (Figure 12). Six of the eight known specimens were taken singly between 26°N and 33°N, 115°W and 126°W, in the relatively well-sampled California Current and fringing waters, where *H. c. berryi* appears to be uncommon. The normal range of the species may be in the subtropical waters to the west of the current, where the cephalopod fauna is poorly known. This is suggested by the captures of the remaining two specimens made separately at 37°N, 138°W (Jefferts, 1983), and 32°N, 178°E (K. Nesis, unpublished data).

*Histioteuthis c. berryi* has been taken in open nets over the vertical range of 300 m to about 800 m.

#### *Histioteuthis corona cerasina* Nesis, 1971

Although *H. c. cerasina* has not been reported since the original study of nine juveniles, we located an additional 20 juveniles in the collections of the IOAN, MHNJP, and USNM from the Peru-Chile Current and the eastern and central equatorial Pacific. The following description is primarily based on the seven largest specimens, 34–57 mm ML, including the three type specimens.

DESCRIPTION.—Fins medium-sized, length ~30%–40% ML, width ~50%–68% ML; sucker rings on arms IV irregularly incised into low, blunt teeth; rings on enlarged median suckers on manus of tentacular club with about 50–60 uniformly small, narrow, sharp, conical teeth.

Circlet of 17 (rarely 18) photophores around right eye; photophores arranged in 3 longitudinal rows on basal portions of arms IV.

ORIGINAL REFERENCE.—Nesis, 1971:1463, figs. 1, 2.

TYPE LOCALITY.—Southeastern Pacific; 00°01'S, 84°59'W, 1500 m.

DEPOSITION OF TYPES.—*Holotype*: ZISP, uncataloged, female, 48 mm ML, R/V *Akademik Kurchatov* sta 219, 29 Aug 1968.

*Paratypes*: IOAN, 2 uncataloged specimens.

DISTRIBUTION.—*Histioteuthis c. cerasina* was described from the eastern Pacific, where it was collected in equatorial waters and the Peru-Chile Current between 00° and 24°S, 70°W

and 85°W. Unreported captures from the same area and westward show the species' range to extend to at least 155°W in equatorial waters (Figure 12). To the south at 35°S in the Peru-Chile Current, to the west in subtropical waters around northern New Zealand, and in the western tropical and subtropical Indian Ocean, a number of small juveniles of *H. corona* (subspecific identities are undetermined) have been taken (Voss, 1969; Retamal and Orellana, 1977; E. Förch, K. Nesis, and N. Voss, unpublished data). A detailed study of these and larger specimens from the areas will show whether *H. c. cerasina* has a trans-Pacific or trans-Pacific-Indian Ocean range in equatorial and south subtropical waters, or whether one or more additional subspecies of *corona* remain to be described. The possibility that some of the specimens may be intermediates between subspecies also exists. Over its known geographic range, *H. c. cerasina* has been taken in open ocean and in the vicinity of submarine ridges and continental slopes.

Open nets have captured early juveniles in the upper 300 m (including an 18 mm ML specimen caught at the surface at night) and have captured late juveniles at about 200–1000 m (nighttime) and at about 500–1500 m (daytime).

#### *Histioteuthis corona inermis* (Taki, 1964)

The following description of this least known subspecies of *corona* is based on data from nine juveniles, 34–53 mm ML, including Taki's original three specimens; four recently caught juveniles, 34–53 mm ML, from the localities of the types, Tosa Bay and Suruga Bay, Japan, reported by Okutani et al. (1987); and two unreported juveniles, 39 mm ML and 49 mm ML, from Suruga Bay that we discovered during the workshop in the collections of the USNM (USNM 816306).

DESCRIPTION.—Fins large, length about 45%–60% ML, width about 70%–90% ML; inner web connecting basal portions of arms I–III low to vestigial; rings of suckers on entire lengths of arms I–IV smooth; rings of enlarged suckers on the tentacular club manus with about 20–27 narrow, conical teeth.

Circlet of 16 or 17 (rarely ?15) photophores around right eye; photophores arranged in 3 longitudinal rows on basal portions of arms IV.

ORIGINAL REFERENCE.—Taki, 1964:287, figs. 21–33, pl. 1: figs. 3, 4.

TYPE LOCALITY.—Off Kambara, Suruga Bay, Japan (~35°N, 138°E).

DEPOSITION OF TYPES.—*Holotype*: Zoological Institute, College of Science, Kyoto University, uncataloged, sex undetermined, 42 mm ML, collected by Kiichi Nakazawa, 1932.

*Paratypes*: Two specimens, whereabouts unknown.

DISTRIBUTION.—*Histioteuthis corona inermis* occurs in the northwestern Pacific (Figure 12), where the 10 known specimens were taken in six net collections from off the east coast of Japan between 33°N and 35°N in Tosa, Suruga, and

TABLE 14.—Comparison among the four subspecies of *Histioteuthis corona*.

Character	<i>H. c. corona</i>	<i>H. c. berryi</i>	<i>H. c. cerasina</i>	<i>H. c. inermis</i>
Longitudinal photophore rows (arms IV)	3	4	3	3
Fin length*	39%–47% ML	40%–44% ML	30%–40% ML	45%–60% ML
Fin width*	59%–69% ML	56%–65% ML	50%–68% ML	70%–90% ML
Sucker-ring dentition (arms IV)	present	present	present	absent
Teeth on large manus-sucker rings	33–38	28–34	20–27	50–60
Geographic range	tropical–N Atlantic subtropical	subtropical N Pacific, California Current	E and central equatorial Pacific, Peru–Chile Current	NW subtropical Pacific off tropical Japan

\*In juveniles of 34–57 mm ML (largest size range known for *H. c. berryi*, *H. c. inermis*, and *H. c. cerasina*).

Sagami bays and off the Kii Peninsula (Taki, 1964, 1981; Okutani et al., 1987; USNM 816306). They were collected at depths between about 420–600 m.

DISCUSSION.—*Histioteuthis corona* has been studied in greater detail over its distributional range than many of its congeners. The four recognized subspecies, one in the Atlantic and three in the Pacific, are compared in Table 14. New, unreported specimens of all the subspecies, examined before and at the workshop, have expanded or better described the known geographic ranges and confirmed the originally described differences between taxa. Of the four subspecies, *H. c. berryi* and *H. c. inermis* are the most distinctive. The former is well distinguished by four longitudinal rows of photophores on arms IV rather than three, and the latter is distinguished by markedly larger fins, lack of dentition on the sucker rings of arms IV, and fewer teeth on the rings of the large manus suckers. The exceptionally broad fins of *H. c. inermis* are apparent in the good color-photograph illustrations found in Okutani et al. (1987). A study of the few available specimens of that subspecies suggests that it could further differ by an increased incidence of 16 organs in the circling of photophores around the right eye, rather than the 17 typical of the species, and by an inner web between arms I–III that is low to vestigial, in contrast to being moderate in depth as in the other subspecies. A future comparison of late growth stages is needed to determine the exact taxonomic status of the different subspecies currently considered to constitute *H. corona*.

The gladius from one specimen each of *H. c. inermis* (USNM 816306) and *H. c. cerasina* (R/V *Akademik Kurchatov* 17-1461, IOAN) were extracted at the workshop in order to examine features that were described by Toll (1982) for *H. c. corona* and *H. c. berryi*. We found that all four subspecies possess similar gladiol vanes, which have an hourglass shape to the anterior portions and two sets of thickened longitudinal bands. These features were not shown in Taki's (1964, fig. 25) illustration of the gladius from paratype no. 2 of *H. c. inermis* or described by Nesis (1971) for *H. c. cerasina*.

Interestingly, one character, the attachments of the second buccal membrane supports, which was consistently single to arms II in the four described subspecies, was found to vary in specimens (all young juveniles, unidentifiable to subspecies) from the southern sector of the Peru–Chile Current and from subtropical waters of the South Pacific and the Indian Ocean. From these areas, two (UMML 31.1729, SIO 72-144) of the three individuals that we had the opportunity to examine in detail had second supports that were clearly bifurcate to arms I and II.

The marked differences found in the morphology and morphometrics of the internal components of the spermatophores from two specimens of *H. c. corona* (the only subspecies in which the mature male is known), one of 111 mm ML taken off Surinam in the western tropical Atlantic (Voss, 1969) and the other of 172 mm ML taken off Curaçao in the Caribbean (Hess, 1987; data used in above description) are discussed in Hess (1987). Hess considers the short, convoluted sperm mass and long cement body of the large Curaçao specimen to represent the “mature” condition of the spermatophore of this taxon and considers the elongate, coiled sperm mass and short cement body of the smaller Surinam specimen to be characteristic of the immature spermatophore. At the workshop, we had the opportunity to examine the spermatophores from an intermediate-sized male (145 mm ML, UMML 31.1705) taken in the Straits of Florida. The spermatophores displayed features similar to those of the Surinam specimen. Spermatophores from additional specimens are needed to understand not only the above-described differences in the sperm mass and cement body but also differences seen in the development of the ejaculatory-apparatus/cement-body connective complex. The complex is absent in the spermatophores judged to be mature by Hess, absent or poorly developed in the Straits of Florida specimen, and present but poorly developed in the Surinam specimen. This sequence of changes accompanies those observed in the sperm mass and cement body of the three increasingly larger individuals and supports Hess's conclusions as to the ontogeny of these internal components in

*H. c. corona*. A future comparative study of the spermatophores over the subspecies' broad distributional range and of spermatophores of the remaining subspecies will show if the proposed mature features of the western tropical Atlantic population are common to the species worldwide.

Finally, our examinations of the new, mature specimens of *H. c. corona* that had skin in good, but not perfect, condition confirmed the earlier reported (Voss, 1969) apparent lack of maturity-related, enlarged, simple photophores in this subspecies. We need to know whether these peculiar photophores are also wanting in the other subspecies of *corona*.

### *Histioteuthis miranda* Species Group

This group comprises two closely related taxa, *miranda* and *oceani*. *Histioteuthis miranda*, a typically large-maturing, south subtropical species, appears to be confined to the southern Benguela Current, the western Indian Ocean, and the subtropical waters of the Australia–New Zealand area. *Histioteuthis oceani*, a typically small-maturing, primarily equatorial species, is currently recognized as occurring in the Pacific and Indo–West Pacific regions. The members are united and are together distinguished from other histioteuthids by the shared possession of a uniquely derived photophore pattern consisting of a moderately dense arrangement of organs of nearly uniform, medium size on the ventrum of the mantle and head and on arms IV. A median row of tubercles is present on the dorsum of the mantle and on arms I–III. The latter feature is not a unique derivation as similar tubercles also occur in one member of the *meleagroteuthis* species group.

### *Histioteuthis miranda* (Berry, 1918)

FIGURES 13, 15*f–j*, 16

Data from unpublished collections (11 subadults and adult males taken on the eastern and western slopes of South Africa (SAM), loaned to one of us (NV) by M. Roeleveld; 24 juveniles, subadults, and adults of both sexes taken by various research vessels in the western Indian and southwestern Pacific oceans, found primarily in collections of IOAN and TINRO and examined before and after the workshop by another of us (KN)) together with published information from Voss (1969) and that given by Clarke (1980) on a series of large specimens taken from the stomachs of sperm whales caught off South Africa and southwestern Australia, largely formed the basis for our study of *miranda*. Our knowledge of the species' distribution was much enhanced by unreported collection data on 50 specimens, representing all growth stages, taken in demersal trawls from the slopes of Tasmania and in various other gears from several areas off Australia (NMV). Distribution information also was enhanced by 42 mostly juvenile specimens from New Zealand waters (NMNZ) furnished to us at the workshop by C.C. Lu and E. Förch. The characteristics

given in our description are of subadults and adults, 93–267 mm ML, from over the entire known range of the species.

DESCRIPTION.—Large to medium-sized histioteuthids; females known to mature at 200–267 mm ML; males at 93–262 mm ML; mantle robust, moderately elongate, with thick walls; ridge of low tubercles beneath epithelium extending from near anterior margin of mantle along median line on anterior 1/2 of dorsum, well developed in medium-sized and large juveniles (Figure 13*b,c*) but poorly developed and deeply embedded in body tissue (usually detectable only by dissection or use of probe) in large subadults and in adults (Figure 13*a*); fins of medium size, length about 31%–44% ML, width about 44%–57% ML; head relatively large (Table 15), with nuchal folds usually absent in large specimens but 1 often weakly developed fold usually seen in juveniles; arms of medium length, about 100%–150% ML; typical arm-length formula I = II = III > IV; approximate basal 19%–39% of arms I, II, and III with median row of low tubercles beneath epithelium on aboral surfaces (approximate basal 24%–47% in juveniles of 17–38 mm ML); deeply embedded in body tissue in large specimens), relative length of tubercular row usually greatest on arms I, approximately equal on arms II and III; tubercles number 14–19 on arms I, 11–16 on arms II, 7–13 on arms III (38–249 mm ML); sucker rings usually with about 5–12 low, blunt or square teeth on distal and lateral margins, except on distal ends of arms where rings have more numerous small, blunt or pointed teeth on entire margins; in mature male, both arms I modified with suckers of reduced size on enlarged, palisaded pedestals on distal 1/3 of arm, and basal suckers slightly enlarged with swollen, fleshy collars; inner web unites basal 16%–25% of arms I, II, and III; outer web slightly developed; buccal membrane 7-membered, second supports bifurcate to ventral sides of arms I and dorsal sides of arms II (on 1 side, rarely single to arms II), fourth supports without secondary connectives (Figure 15*i*); tentacles long, about 150%–260% ML; tentacular club without longitudinal cleft on aboral surface; suckers on manus closely arranged in about 6 to 7 rows; median suckers moderately enlarged to about 2 times ventral marginals, with about 45–51 short, irregular, pointed teeth around entire margins of rings.

Compound photophores numerous, moderately widely spaced, arranged in about 9 to 10 diagonal rows on ventrum of mantle, of approximately uniform, medium size; circlet of 16 to 17 (rarely 15) moderately large photophores around right eye; on basal 1/2 of arms IV, first 2 to 3 diagonal rows of photophores contain 5 organs, subsequent rows contain 4 organs (Figure 15*h*); enlarged, maturity-related, simple photophores absent.

Dorsal pad of funnel organ fleshy, without sculpture; spermatophore short (Figure 15*f,g*) (SpL 4.2–5.7 mm, 1.7%–2.3% ML; 10 spermatophores from 249 mm ML specimen from off Cape Town, South Africa, SAM S183); relatively wide (7.4%–8.9% SpL); sperm mass short (10.0%–13.6% SpL); cement body long (61.5%–69.7% SpL); ejaculatory



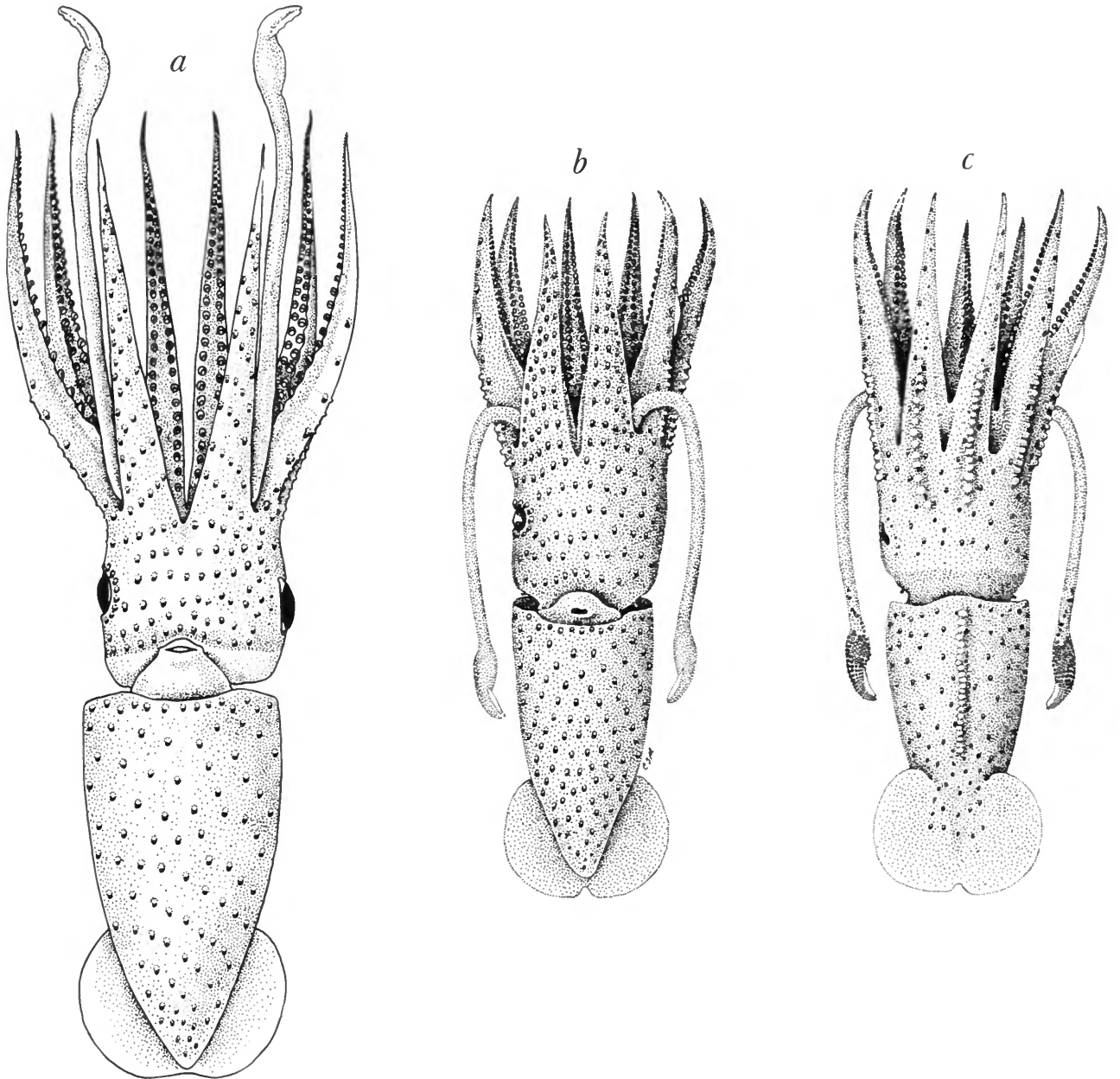


FIGURE 13.—*Histiototeuthis miranda*. *a*, ventral view of neotype, USNM 576165, 182 mm ML, subadult female, 37°54'S, 178°56'E; *b*, ventral view of juvenile, SIO, Lusiad S1b-11, 36 mm GL, 33°47'S, 15°47'E; *c*, dorsal view of same. (*a*, from Voss, 1969.)

apparatus of medium length (24.2%–27.2% SpL), with single long loop of inner tube; ejaculatory-apparatus/cement-body connective complex well developed, with narrow, constricted base; mature egg not available; gills about 35%–49% ML, with 39–41 lamellae in outer demibranch.

Gladius with moderately short free rachis; vanes with hourglass shape to anterior  $\frac{1}{2}$ , 3 sets of thickened longitudinal bands; vanes ending posteriorly in narrow, rounded (in small to medium specimens) to moderately acute, bluntly pointed (in large specimens) cupped coil; lower beak with broad shoulder

TABLE 15.—Comparison between members of the *Histioteuthis miranda* species group. (AL = arm length; EjAp/CB = ejaculatory apparatus/cement body.)

Character	<i>H. miranda</i>	<i>H. oceani</i>
Known geographic range	Southern Benguela Current, subtropical and tropical W Indian Ocean, subtropical waters of Australia–New Zealand	Pacific equatorial and adjoining areas peripheral to central water masses of N and S Pacific
SUBADULTS AND ADULTS		
Buccal membrane	2nd supports bifurcate to arms I + II (on 1 side rarely single to arms II)	2nd supports single to arms II
Head	relatively large, length ~36%–49% ML, width ~46%–53% ML	markedly large, length ~56%–62% ML, width ~56%–80% ML
Tubercles on arms I–III		
Development and position	weakly developed, deeply embedded in body tissue, 19%–39% AL	well developed, on surface, 46%–83% AL
Number	14–19 (arms I), 11–16 (arms II), 7–13 (arms III)	25–36 (arms I), 23–30 (arms II), 17–21 (arms III)
Photophores in diagonal rows on basal 1/2 of arms IV	5 in 1st 2 to 3 rows, 4 in subsequent rows	6 in 1st 2 to 3 rows, 5 in subsequent rows
Gill lamellae in outer demibranch	39–41	26–28
Spermatophore*		
Length	1.7%–2.3% ML	4.0%–4.2% ML
EjAp/CB connective complex	with narrow base	with slender, elongate base
Size at maturity	medium to large, 93–~267 mm ML(GL)	small to ? medium, ~50–?100 mm ML
JUVENILES		
Size	17–38 mm ML	12–22 mm ML
Arm length	87%–103% ML	114%–153% ML
Tubercles on arms I–III	24%–47% AL	65%–92% AL
Photophores in diagonal rows on basal 1/2 of arms IV	as in adult	as in adult

\**H. miranda*, 34°43'S, 17°21'E, SAM S183; *H. oceani*, ~21°20'N, 158°20'W, USNM 729765.

groove; wing fold with flat medial surface, usually with thickened ridge on outer border; hood with broad, shallow notch over crest; lateral wall with sharp median ridge extending to free corner; radula with first, second, and third laterals asymmetrical, of conspicuous increasing length; rachidian with broad, narrow base, outer cusps absent (Figure 15j).

Skin color dark grey blue to purple.

ORIGINAL REFERENCE.—Berry, 1918:221, figs. 5–9, pls. 61, 62.

TYPE LOCALITY.—SE × S of Gabo Island, Victoria, Australia (~38°S, 150°E), 270 fathoms (494 m).

DEPOSITION OF TYPES.—*Holotype*: Australian Museum, Sydney, AMS E5606, female, 140 mm ML, collected by F.I.S. *Endeavour*; not extant.

*Neotype*: USNM 576165, female, 182 mm ML, R/V *Eltanin* sta 1713; designated by N. Voss (1969:797, fig. 4); good condition.

NEOTYPE LOCALITY.—South Pacific, 37°54'S, 178°56'E, 448–732 m.

DISTRIBUTION.—*Histioteuthis miranda* is found in close association with the slopes of continental masses and nearby islands and submarine rises that occur within its known distributional range, which extends from off the southwestern

coast of South Africa eastward in southern subtropical waters to the Australia–New Zealand area (Figure 16). Off Africa, this essentially western Pacific–Indian Ocean species extends in the Agulhas Current system into the southeastern Atlantic, where it occurs in the Benguela Current to about 33°S. Roeleveld et al. (1992) and Roeleveld and Lipinski (in prep.) report the captures of 132 specimens, including subadults and adults, from this area, where *miranda* was found to be abundant by the R/S *Africana* in 1988 at depths of approximately 700–900 m, and from off the east coast of South Africa. Off the east coast of Africa, *miranda* extends into the high-productivity tropical waters of the northwestern Indian Ocean to about 12°N. There, it may occur with its northern sibling species, *oceani*. Although the occurrence of *miranda* in this area is poorly known, it appears to rank in abundance well below its congener *H. celetaria pacifica*. In the subtropical waters to the south, however, the 1988/1989 western Indian Ocean cruise of the R/V *Vityaz* found the species to be common and the dominant histioteuthid encountered between 28°S and 34°S, 43°E and 50°E, on and above the slopes of Walters Shoal (K. Nesis, unpublished data). Between the same approximate latitudes, an earlier South African fisheries survey located an apparently large breeding population off the eastern slopes of Africa (N.

Voss, unpublished data). The species has been taken off Tasmania and off the southwestern and southern coasts of Australia and on the eastern coast as far north as 25°S in the East Australian Current (Wadley, 1990; C. Lu, unpublished data), but it has not been taken on the northwestern shelf, where a resource survey found a large population of *H. celetaria pacifica* (S. Slack-Smith, unpublished data). Around New Zealand, *miranda* has been collected between about 31°S and 45°S, 164°E and 175°W (E. Förch, K. Nesis, unpublished data). Capture data show the species to be abundant and the most common histioteuthid encountered throughout much of its normal range.

Our new material shows that *miranda* displays a restricted south subtropical distributional pattern (see "Biogeography" section, below) in the Pacific and Indian oceans rather than a southern subtropical convergence pattern, which was proposed earlier for the species on the basis of limited distribution data (Voss et al., 1992).

*Histioteuthis miranda* is known to vertically range between subsurface waters to at least 1200 m. At night, open nets fishing at 49 m, 150 m, and between 400 m and 850 m have taken juveniles of 15–25 mm ML, and nets fishing between 200 m and 850 m and on or near the bottom at 700–1200 m have taken larger juveniles. Subadults and mature males and females have been taken both day and night on or near the bottom between about 400 m and 1200 m.

DISCUSSION.—*Histioteuthis miranda* displays little apparent morphological change over its currently recognized geographical range. Differences in the number of rows of photophores on the basal portions of arms IV, three in South African specimens and four in those from western Australia, reported by Clarke (1980) from specimens taken from stomachs of sperm whales are obviously attributable to the poor condition of the material. Our examinations of specimens in good condition showed the pattern of five photophores in the first two to three diagonal rows and four photophores in subsequent rows on the basal one-half of arms IV to be characteristic of the populations from both areas. Unfortunately, we lacked unruptured spermatophores from the Australia–New Zealand area to compare with those described and illustrated by Hess (1987) and those described above by us. The variations seen in the spermatophore of *miranda* (unidentified as to size of animal or capture locality) illustrated by Clarke (1980) are almost certainly the results of partial internal rupture and immaturity of the spermatophore. Our lack of suitable specimens from the eastern end of the species' range precluded another needed comparative study, that of the gladius. The description and illustration of that feature found in Toll (1982) and our characterization given in the diagnosis are based on specimens from the African area.

Our study showed the condition of bifurcate attachments of the second supports of the buccal membrane to arms I and II to be a constant character for *miranda* over its entire known distribution. We found but two instances in which the

attachments were single: one in a specimen (SAM S183) from off South Africa in which the second left support was single to the ventral margin of arms I, an obvious abnormality; and the other in a specimen (USNM 817679) from the northwestern Indian Ocean in which the second left support was single to the dorsal side of arms II. The condition of bifurcate attachments in *miranda* is in sharp contrast to that found in its sibling species, *oceani*, which has, in all specimens examined from over the species known range, second supports single to arms II (Figure 15*d,i*). This and the other differences found between the two members of the *miranda* species group, shown in Table 15, together with questions raised by the specimens labeled "species undetermined" on our map are discussed in the "Discussion" section for *oceani*.

The unavailability of the manuscript from the aforementioned study by Roeleveld and Lipinski, in which the distribution of *miranda* off the southern African west coast is discussed in detail, prevented the incorporation of their findings into the present work. Presumably, the subadult and adult specimens from off the western slope of South Africa on loan from the SAM for the present study are included in Roeleveld and Lipinski's material.

### *Histioteuthis oceani* (Robson, 1948)

FIGURES 14, 15*a–e*, 16

*Histioteuthis oceani* Robson, 1948:123, fig. 7 [examined].

*Histioteuthis miranda*.—Okutani, 1974:66 [locality for specimen from Troll sta 30 in error; examined].—Voss, 1969:797 [part: 17 mm ML, SIO Troll sta 30; holotype of *Histioteuthis oceani*, 7.2 mm ML, R/V *Arcturus* sta 51-T2].

*Histioteuthis* sp.—Young, 1978:593, fig. 14A [vertical distribution and photosensitive vesicles; examined].

*Histioteuthis* sp. (N. Voss).—Clarke, 1986b, fig. 69c [beak, extracted from whole specimen, USNM 729764; examined].

*Histioteuthis* sp. A.—Hess, 1987:362 [spermatophore; examined].

*Histioteuthis oceani*.—Voss et al., 1992 [juvenile figured and distribution].

Our study material for this species was composed of 18 of the 19 known specimens of *oceani*. These included 10 juveniles and subadults and one adult male found in the collections of the USNM (including the specimens from Hawaii referred to as *Histioteuthis* sp. by Young (1978)), four juveniles from the SIO collections (including one misidentified by Voss (1969) and three misidentified by Okutani (1974) to *H. miranda*), and four unreported juveniles and subadults from the collections of the IOAN. Because a synonymy and detailed illustrations of the species were not appropriate for the publication in which *Histioteuthis oceani* was recently reinstated as a valid species (Voss et al., 1992), they are given above. The description is based primarily on large juveniles, subadults, and an adult male, 35–70 mm ML. The specimens came from over the entire currently recognized distribution of the species (Figure 16).

DESCRIPTION.—Small to (?) medium-sized histioteuthids; maximum size possibly to 100 mm ML; female size at maturity not known, largest known female, 70 mm ML, immature

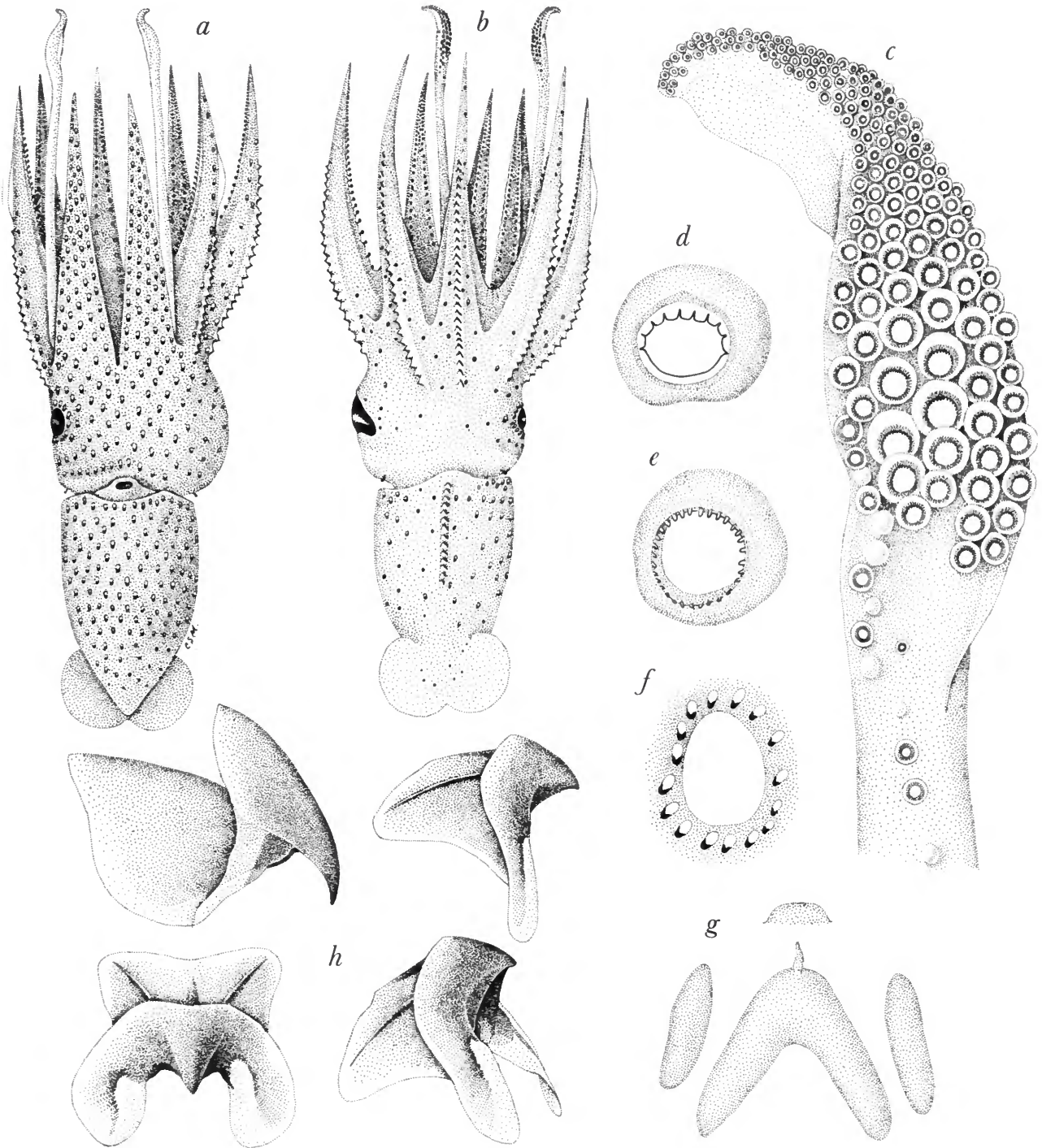


FIGURE 14.—*Histioteuthis oceani*: *a*, ventral view of mature male, USNM 729763, 50 mm GL, ~21°N, 158°W; *b*, dorsal view of same; *c*, left tentacular club of same; *d*, sucker from midarm III of same; *e*, largest sucker on club manus of same; *f*, right eyelid of same; *g*, funnel organ, USNM 729765, 40 mm ML, subadult male, ~21°N, 158°W; *h*, views of upper (upper left) and lower beaks, USNM 729764, 41 mm ML, subadult male, ~21°N, 158°W.

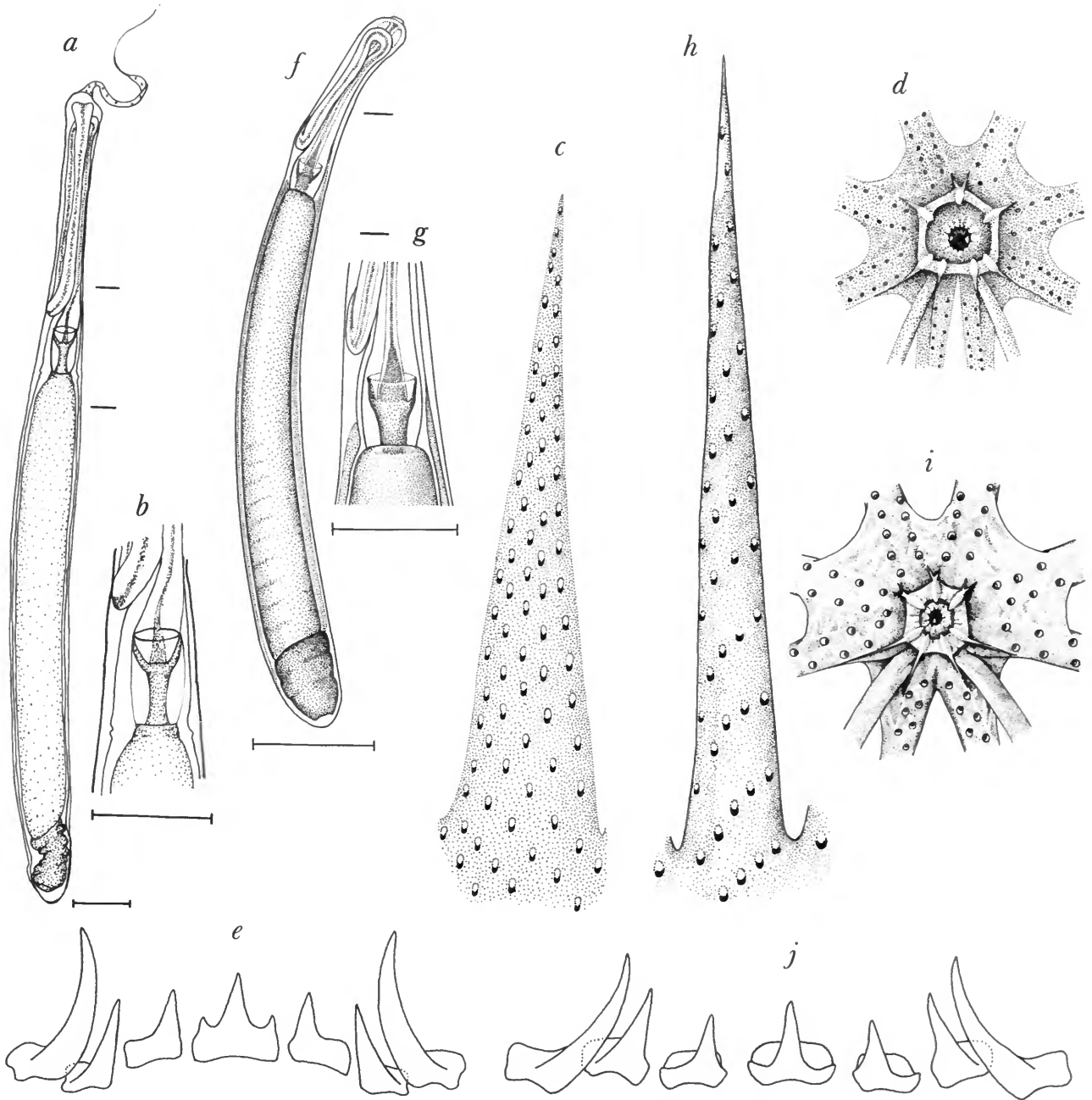


FIGURE 15.—*Histioteuthis oceani*: a, spermatophore, USNM 729763; b, enlargement of area of ejaculatory apparatus/cement-body connective complex of same; c, right arm IV of same; d, buccal view of same; e, radula, USNM 729764. *Histioteuthis miranda*: f, spermatophore, SAM S183, 249 mm ML, mature male, 34°43'S, 17°21'E; g, enlargement of area of ejaculatory apparatus/cement-body connective complex of same; h, right arm IV, USNM 576165; i, buccal view, AUZ 080.04, 17 mm ML, juvenile, 32°27'S, 174°12'E; j, radula, SAM S183, 197 mm ML, maturing female. Scale bars = 1 mm, except b = 0.5 mm. (h, i, from Voss, 1969.)

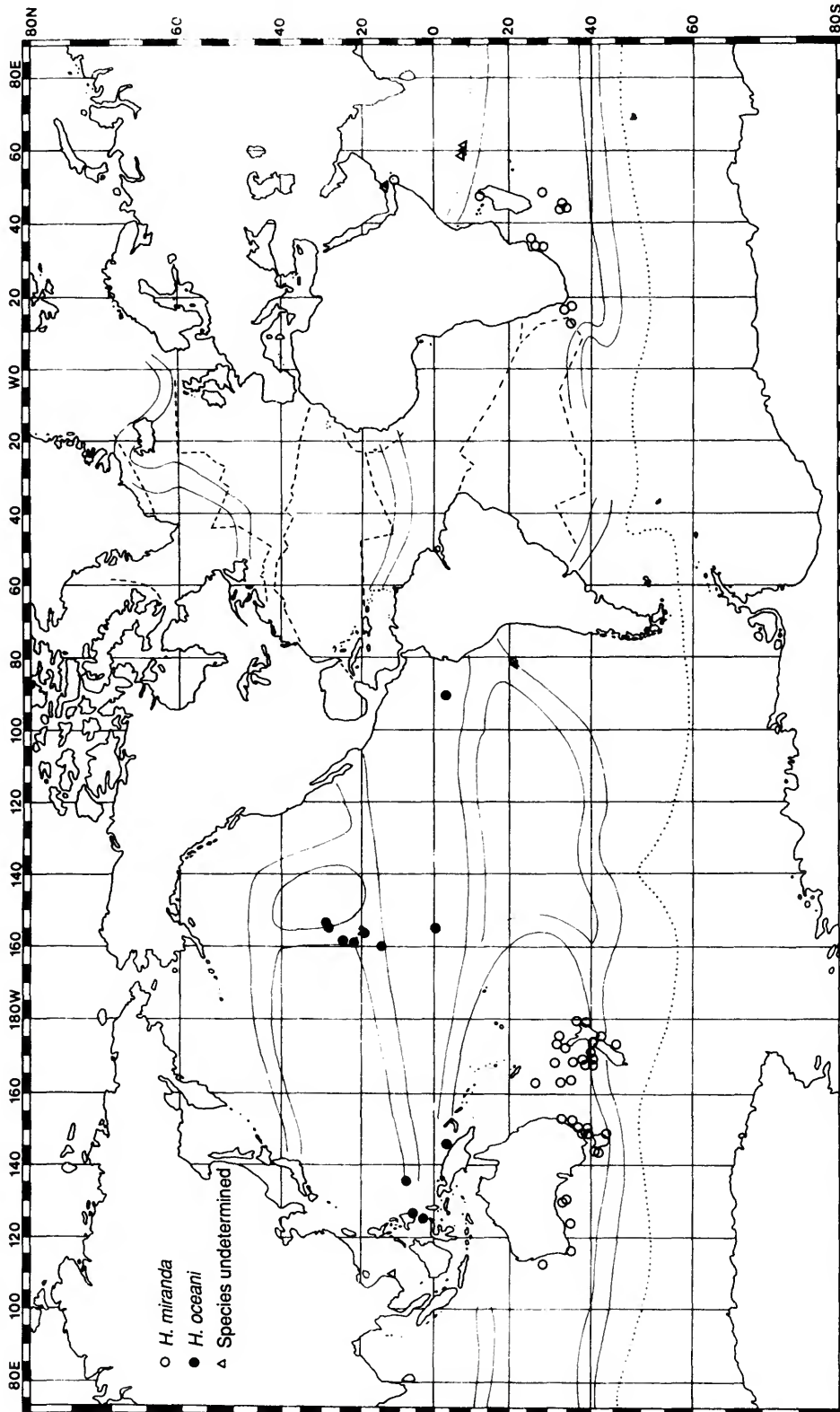


FIGURE 16.—Geographic distributions of members of *Histiotuethis miranda* species group. Distribution of *H. miranda* known from ~109 net hauls (169 specimens), and *H. oceani* known from ~18 net hauls (19 specimens). Because station data for another 121 specimens of *H. miranda* reported by Lipinski and Roeleveld (in prep.) (11 of reported 132 specimens included in present study material) from southern African waters between ~32°S (west coast) to ~33°S (east coast) were not available to us, those records could not be plotted. For explanation of indicated ocean regions, see Figures 2, 5.

(IOAN, central equatorial Pacific); only known mature male, 50 mm ML (USNM 729763, Hawaii); mantle robust, moderately elongate, with thick walls and ridge of low tubercles extending beneath epithelium from near anterior margin along median line on anterior  $\frac{1}{2}$  of dorsum (Figure 14a,b); tubercular ridge well developed in juveniles, subadults, and adults; fins of medium size, length about 37%–43% ML, width about 53%–65% ML; head markedly large, with 1 weakly developed nuchal fold; arms of medium length, about 120%–150% ML; typical arm-length formula I = II = III > IV; approximate basal 46%–83% of arms I, II, and III with median row of low tubercles beneath epithelium on aboral surfaces, well developed in juveniles, subadults, and adults; relative length of tubercular rows decreases from arms I–III; tubercles number 25–36 on arms I, 23–30 on arms II, 17–21 on arms III (12–50 mm ML); sucker rings usually with about 6–10 low, blunt, or square teeth on distal and lateral margins (Figure 14d), except on distal ends of arms where rings bear small teeth on entire margins; in single, available, small mature male, sucker pedestals on distal  $\frac{1}{4}$  of arms I elongate and palisaded; swollen collars and enlargement of basal suckers absent but can occur in larger specimens; inner web unites approximate basal 20%–30% of arms I–III; outer web slightly developed; buccal membrane 7-membered, second supports single to dorsal sides of arms II, fourth supports without secondary connectives (Figure 15d); tentacles long, about 150%–250% ML; tentacular club without longitudinal cleft on aboral surface; suckers on manus closely arranged in about 6 to 7 rows (Figure 14c); median suckers moderately enlarged to  $1\frac{1}{2}$ –2 times ventral marginals, with numerous, acute teeth around entire margins (Figure 14e).

Compound photophores numerous, regularly (roughly in juveniles) arranged in about 9 to 10 diagonal rows on ventrum of mantle, of approximately uniform, medium size; circlet of 16 (rarely 18) moderately large photophores around right eye (Figure 14f); on basal  $\frac{1}{2}$  of arms IV, first 2 to 3 diagonal rows of photophores contain 6 organs, subsequent rows with 5 organs (Figure 15c); enlarged, maturity-related, simple photophores absent in single known mature specimen.

Dorsal pad of funnel organ fleshy, unsculptured (Figure 14g); spermatophore (Figure 15a,b) short (SpL 2.0–2.1 mm; 4.0%–4.2% ML; 5 spermatophores from 50 mm ML specimen from Hawaii, USNM 729763), relatively wide (6.7%–8.7% SpL); sperm mass short (5.9%–7.9% SpL); cement body long (57.8%–60.6% SpL); ejaculatory apparatus of medium length (30.5%–35.6% SpL), with single long loop of inner tube; ejaculatory-apparatus/cement-body connective complex well developed, with slender, elongate base; mature egg not known; gills about 27%–42% ML, with 26–28 lamellae in outer demibranch; gladius with moderately short, broad free rachis; delicate vanes with hourglass shape in anterior  $\frac{1}{2}$  and 3 sets of slightly thickened bands, ending posteriorly in narrow, rounded, cupped coil; lower beak (Figure 14h) with broad, shallow indentation in margin of hood over crest; lateral walls

widely spread with well-developed median ridge extending to free corner; wing fold with flat medial surface; radula (Figure 15e) with first, second, and third laterals asymmetrical, of markedly increasing length; rachidian with broad, stout base and well-defined, small outer cusps.

Skin color light to deep purple.

ORIGINAL REFERENCE.—Robson, 1948:123, fig. 7.

TYPE LOCALITY.—Eastern tropical Pacific, SE of the Galapagos, 2°33'S, 89°44'W, 0–165 fms (0–302 m).

DEPOSITION OF TYPE.—*Holotype*: BMNH 1947.7.8.95, juvenile, 7.2 mm ML, R/V *Arcturus* sta 51 T-2 (no. 29), 23 Apr 1925, 0900 hours; poor but identifiable condition.

DISTRIBUTION.—The distributional range of this species is poorly known. We have plotted on our map (Figure 16) only the localities for the 19 specimens that we have been able to confidently identify. They show a broad, Pacific equatorial distribution for *oceani* from the Galapagos Islands to the Indo-West Pacific that extends northward (to about 30°N, north of Hawaii) and southward in adjoining areas peripheral to the oligotrophic central waters. The species occurs both in the vicinity of islands and submarine rises and in open ocean.

The records of two unreported juveniles that belong to the *miranda* species group taken off the Nazca Ridge in the southeastern Pacific (TINRO), seven taken in the northwestern Indian Ocean by several Russian vessels (IBSS, YugNIRO, ZMMU), and captures reported as *miranda* from off Viet Nam by Khromov (1996) have been labeled “species undetermined” on our map. These specimens are discussed below.

Young’s report (1978; identified as *Histioteuthis* sp.) of opening-closing-net captures of juveniles, subadults, and an adult male from Hawaii at 150–300 m at night and at 550–680 m during the day demonstrates the diel vertical movement of the species. In other areas, open nets have taken subadults while fishing at night at 300–650 m and during the day at 550–800 m. Juveniles were captured at 60–200 m at night and at 300–800 m during the day.

DISCUSSION.—The exceptionally long arms and tubercular rows on arms I–III of a 17 mm ML juvenile from the Philippines compared with those of a 17 mm ML juvenile from off New Zealand were noted in the study of *H. miranda* in Voss’s 1969 family revision. The full significance of the findings was not recognized, however, until the differences were seen to be consistent between new specimens of *miranda* (known in 1969 from only 4 specimens including the above juveniles; now known from 168 specimens) from the south subtropical Pacific and Indian oceans and specimens of an obviously closely related form that inhabited lower Pacific latitudes (Okutani, 1974, reported as *H. miranda*; Young, 1978, reported as *Histioteuthis* sp.; unreported SIO specimens). The subsequent reexamination by one of us (NV) of Robson’s long-armed, 7.2 mm ML holotype of *Histioteuthis oceani* from the Galapagos Islands, which had been questionably placed in the synonymy of *miranda* by Voss (1969), revealed the unreported presence of a median row of tubercles that

extended beyond the basal halves of arms I-III and the five rows of photophores visible on the major portions of the basal halves of arms IV. These new, important characteristics were only revealed after the dark, stiff, distorted specimen (same condition as at the time of the 1969 study) was softened by soaking in Aerosol™ solution. Unfortunately, the arms still remained too rigid to permit examination of the attachments of the second supports of the buccal membrane, conditions of which in the northern and southern forms were observed to vary. As a result of the above studies, Voss et al. (1992) confidently identified the northern population to Robson's species, *oceani*, and included it in their treatment of the valid species of *Histioteuthis*.

*Histioteuthis oceani* is known from relatively few specimens (19) from over a broad geographic area that extends from north of Hawaii to the eastern tropical Pacific and across equatorial waters to the Indo-West Pacific. It consistently varies from the closely related *miranda* in a number of characters (Table 15). The tolerance of *Histioteuthis oceani* for less productive waters further distinguishes it from its sibling species.

Over the distributions of both species, variations were found in relative length of arms in the juvenile, relative length of tubercular rows on arms I-III both in juveniles and in later growth stages, and head size in large animals, but the tendency of *oceani* to have longer arms and tubercular rows and a larger head appears to be distinct. The slightly denser pattern of photophores on the basal one-half of arms IV and the condition of single attachments of the second supports of the buccal membrane were not seen to vary and appear to be good distinguishing characters for *oceani*. Whether the differences seen between siblings in the morphology of the ejaculatory apparatus/cement-body connective complex of the spermatophore (Figures 15b,g) are real or not must await acquisition of additional mature males of *oceani*; at present only a single small one is known. The spermatophore of this specimen was previously described, but not illustrated, by Hess (1987; reported as *Histioteuthis* sp. A). Hess reported difficulty in discerning the configuration of the inner tube of the ejaculatory apparatus, but our examination of seven additional spermatophores from the same specimen clearly shows that the tube makes a single long loop.

As to the reported (Khromov, 1996) and unreported captures that are marked on our map as "species undetermined" because of their unavailability for the necessary detailed examination, those from off Viet Nam and from Nazca Ridge in the southeastern Pacific probably belong to *oceani*. In a recent investigation of the fauna of the latter area, Parin et al. (1988) found the fish fauna to be dominated by broad tropical and Indo-West Pacific species. The unidentified specimens from the northwestern Indian Ocean, on the other hand, may belong to either *miranda* or *oceani*, because the siblings probably co-occur in at least part of that highly productive area. *Histioteuthis miranda* is known to extend northward from its normal southern range, apparently following a path of high

productivity, and the distributional range of *oceani* could normally include the northern half of the Indian Ocean as that area is typically inhabited by all other equatorial/tropical-occurring histioteuthids found in the Pacific.

### *Histioteuthis meleagroteuthis* Species Group

This group is composed of *meleagroteuthis*, one of the three currently recognized, warm-water cosmopolites in the family, and *heteropsis*, an eastern Pacific transitional species. The species group is well distinguished by the possession of a uniformly dense pattern of small compound photophores on the ventral surfaces of the mantle, head, and arms IV, and around the right eyelid.

### *Histioteuthis meleagroteuthis* (Chun, 1910)

FIGURE 17

*Histioteuthis bruuni* N. Voss, 1969:811, figs. 3i,j, 27, 28.—Nesis and Nikitina, 1986:53. [New synonym.]

A total of 109 mostly unreported specimens of this species, including all growth stages (collected mostly in the Atlantic by the R/V *Anton Dohrn*, R/V *Vityaz*, R/V *Walther Herwig*, and other vessels; specimens found in the AtlantNIRO, IOAN, PINRO, SIO, TINRO, USNM, and ZMMU), were examined by us before and at the workshop. Although insufficient in geographic coverage for the detailed comparative study needed for *meleagroteuthis*, the material, augmented by data compiled by E. Förch and C. Lu on specimens contained in the collections of NMNZ and NMV and by reported captures by Lu and Clarke (1975a, 1975b) and Okutani (1983), yielded valuable new morphological and distributional information. At the workshop, we also examined the holotypes of *Meleagroteuthis separata* Sasaki, 1915 (TIU, uncat.), and *Histioteuthis bruuni* N. Voss, 1969 (ZMUC, uncat.), two species considered to be synonymous with *meleagroteuthis* (Voss, 1963; Voss, 1969; Voss et al., 1992).

Our description below is primarily based on large juveniles, subadults, and adults, 38–114 mm ML. The entire range of the species in the Atlantic was well represented in our material, in contrast to the Indian and Pacific oceans from which relatively few specimens were available.

DESCRIPTION.—Small to medium-sized histioteuthids; female known to mature at 114 mm ML, males at 65–102 mm ML; mantle robust, with thick walls (flaccid in spent female), moderately elongate, with row of small tubercles fused basally to form serrate ridge beneath epithelium along dorsal midline of anterior  $1/2$ – $2/3$ ; fins medium-sized, length about 39%–50% ML, width about 58%–68% ML; head with 1 nuchal fold; arms of medium length, about 100%–150% ML, approximately coequal (except in mature male, where arms I distinctly longest), with median row of small tubercles extending from near base to approximately midlength of arms I, II, and III on



TABLE 16.—Measurements and indices of spermatophores of *Histioteuthis meleagroteuthis*. (Means following ranges for "Species" are given in parentheses; for explanation of indices, see "Materials and Methods.")

Character	USNM 728873	USNM 817756	USNM 817756	Species
ML (mm)	102	71	65	
Locality	32°N, 64°W	13°S, 9°W	13°S, 9°W	
Number of spermatophores	3	3	3	
SpL (mm)	1.6–1.7	1.2–1.4	1.3–1.4	1.2–1.7 (1.4)
SpL1	1.6–1.7	1.7–1.9	2.1–2.1	1.6–2.1 (1.8)
SpML1	36.5–38.8	27.9–29.5	33.8–38.8	27.9–38.8 (33.9)
CBLI	15.3–17.7	32.8–36.8	16.4–25.4	15.3–36.8 (24.5)
EjApL1	30.6–36.3	27.9–29.5	29.4–32.8	27.9–36.3 (31.2)

aboral surfaces; arm suckers small, largest basally, gradually decreasing in size distally; rings of arm suckers with about 6–20 low, rounded or square teeth on distal and lateral margins; rings of basal suckers often with fewer, broader teeth; in mature male, arms I elongate, with some increased robustness to distal  $\frac{1}{3}$ , which bears small suckers of equal size on elongated, palisaded pedestals; suckers on basal portions of all arms of mature male slightly enlarged (to greatest extent on arms I), with swollen collars; inner web between arms I, II, and III developed to about 10%–18% length of longest arm; outer web not developed; buccal membrane 7-membered, with second supports to dorsal sides of arms II, or bifurcate to ventral sides of arms I and dorsal sides of arms II (occasionally second supports single on 1 side and bifurcate on other); fourth supports without secondary connectives; tentacles long, about 170%–275% ML; tentacular club without longitudinal cleft on aboral surface; suckers on manus closely arranged in 6 to 7 rows, moderately enlarged in median rows to about 2 times ventral marginals; rings of median suckers on manus with about 25–30 short, pointed teeth on entire margins, with tendency for teeth to be longest on distal margins.

Compound photophores uniformly small (~1.3 mm long in 48.2 mm ML neotype) and arranged in dense pattern on ventral surface of anterior  $\frac{3}{4}$  of mantle, progressively decreasing in size but retaining same approximate spacing on posterior  $\frac{1}{4}$ ; photophores on ventral surface of head of same approximate size and arrangement as on anterior ventrum of mantle except on left side where photophores more widely spaced; circlet of 19–22 photophores around right eye; arms IV with 8 to 9 longitudinal rows of photophores on basal portions; enlarged, maturity-related simple photophores not known to occur on mantle, head, or arms.

Dorsal pad of funnel organ fleshy, unsculptured; spermatophore short (SpL 1.2–1.7 mm; 1.6%–2.1% ML; from 3 specimens, SE and NW Atlantic, 65–102 mm ML); sperm mass moderately long (27.9%–38.8% SpL); cement-body length variable (15.3%–36.8% SpL); ejaculatory apparatus moderately long (27.9%–36.3% SpL), with single long loop of inner tube; ejaculatory-apparatus/cement-body connective complex well developed (Table 16); mature egg not known;

gills about 36%–41% ML, with about 23–35 lamellae in outer demibranch.

Gladius with anteriorly tapered rachis; vanes delicate, triangular in combined outline, with broad, angular anterior shoulders; posterior margins of vanes concave, ending in rounded cupped coil; lower beak with broad hood, slight or no hood notch, slightly curved rostral edge, finely pointed rostrum, high wing fold with steep medial surface; median ridge on lateral wall strong, extending to free corner; radula with first, second, and third laterals of increasing length and asymmetry; marginal plates small.

Skin color dark, wine red.

ORIGINAL REFERENCE.—Chun, 1910:170. (For illustrations and detailed description of holotype see *Meleagroteuthis hoylei* Pfeffer, 1912:291, pl. 22: figs. 1–8; not *Histiopsis hoylei* Goodrich, 1896.)

TYPE LOCALITY.—Tropical eastern Pacific, Fonseca Bay, ~13°N, 88°W.

DEPOSITION OF TYPES.—*Holotype*: Naturhistorischen Museum zu Hamburg, Hamburg, Germany, sex undetermined, 32 mm ML. No longer extant.

*Neotype*: AIM 057.13, male, 48.2 mm ML, Tui Oceanographic Cruise, 35°45'S, 176°20'E, 549–686 m, 21 Jul 1962; designated by Voss, 1969:804.

DISTRIBUTION.—*Histioteuthis meleagroteuthis* is found circumglobally in tropical and subtropical waters between about 35°–45°N and 40°S (Figure 17). The southern boundary of its distribution is well marked by the SSTC. Judging from the absence or near absence of the species in collections taken in the Atlantic SSTC by the R/V *Walther Herwig* and various Russian vessels and its absence in the Pacific near Australia (C. Lu, unpublished data) and New Zealand (E. Förch, unpublished data), it is apparent that the transitional waters of the convergence are not normally inhabited by *meleagroteuthis*. During the 1971 west–east transect and the 1975–1976, north–south transect of the Atlantic sector of the SSTC made by the R/V *Walther Herwig*, the species was encountered at only three stations (six specimens; WH 350/71, WH 106/76, WH 109/76; 35°S–39°S, 40°W–52°W), all from fringing subtropical waters. These captures, plus a spent female of 114

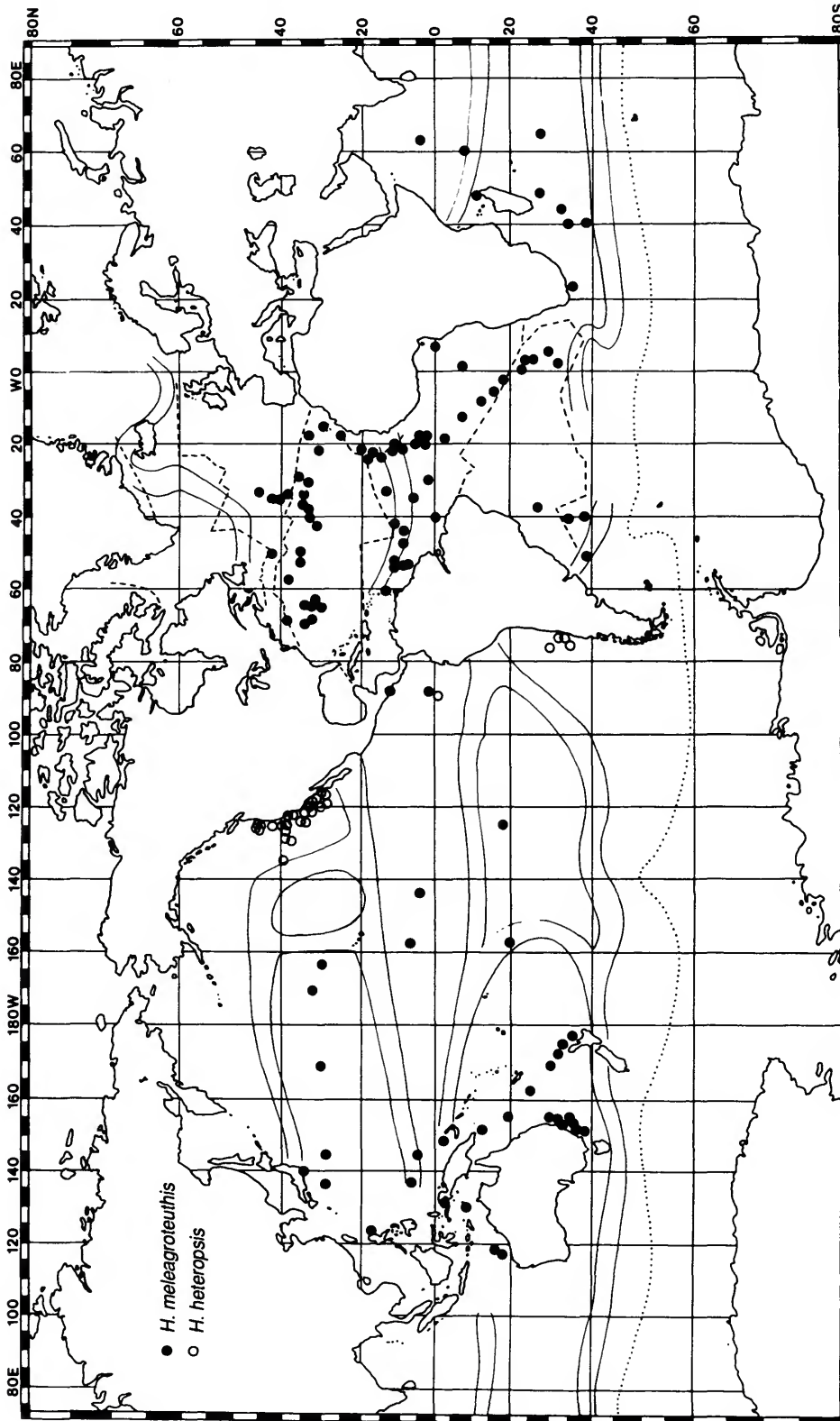


FIGURE 17.—Geographic distributions of members of *Histioteuthis meleagroteuthis* species group. Distribution of *H. meleagroteuthis* known from 136 net hauls (206 specimens), and *H. heteropsis* known from 144 net hauls (296 specimens). For explanation of indicated ocean regions, see Figures 2, 5.

mm ML taken by the R/V *Atlantis II* at 27°S, 37°W (USNM 730185), all from open ocean, constitute the total records of the species from western south subtropical waters. In the southeastern Atlantic, the southernmost record of *meleagroteuthis* is a specimen caught in subtropical waters at 33°16'S, 02°17'E, mistakenly identified by Nesis and Nikitina (1986) as *Histioteuthis bruuni* (see the following section for a discussion of this specimen and the status of the species *bruuni*). During the Cape Town-Madeira transect of the 1971 cruise, the R/V *Walther Herwig* took 45 large juveniles, subadults, and adult males. It first encountered the species at 30°S, 05°E, in subtropical waters, and it subsequently encountered the species at 14 (74%) of the 19 stations occupied using the Engel MWT-1600 in tropical and Mauritanian waters off Africa, with the last encounter made at 20°N, 22°W. Although the R/V *Walther Herwig* failed to collect the species in subtropical waters to the north of that latitude, juveniles were taken by the R/V *Dana* off the northwestern African coast to 29°N (Voss, 1969), by the R/V *Sergei Vavilov* (IOAN) at 31°N, 22°W, by the Amsterdam Mid-North Atlantic Plankton Expedition (USNM) in 1980, and by the R/V *Artemida* (PINRO) to 42°N and 45°N, between 34°W and 35°W, in the area of the south branch of the North Atlantic Current. During the 1979 Sargasso Sea Expedition, the R/V *Anton Dohrn* collected 16 specimens, all taken in subtropical waters, 14 from the proximity of the Mid-Atlantic Ridge and two from near the Bermuda Rise. The collection of 43 juveniles, subadults, and adult males of the species from the Ocean Acre study near Bermuda showed *meleagroteuthis* to be second in abundance to *arcturi* in the area, followed by *H. corona corona*. The species appears to be absent in the less productive subtropical waters to the south of Bermuda and is not known from the Gulf of Mexico and Caribbean Sea, but it is widespread in the western tropical Antillean and Amazonian provinces (Okutani, 1983; Lea, 1984).

The few captures reported from the Indian Ocean are widely scattered between 10°N and the SSTC and are mostly associated with land and submarine rises of the western sector. East of Australia, a number of specimens have been taken between 150°E and 155°E, 07°S and 38°S, with the southernmost captures coming from the East Australian Current (Brandt, 1983; C. Lu, unpublished data). Recent fisheries surveys of subtropical waters to the west and north of New Zealand have taken *meleagroteuthis* between 30°S and 35°S, 166°E and 174°E (E. Förch, unpublished data). The species occurs throughout the Indo-West Pacific and to the north is known to extend to about 35°N in waters off southern Japan. The records of *meleagroteuthis* from the subarctic western Pacific based on Akimuskina's reports (1954a, 1954b, and others; as *Meleagroteuthis separata*) of stomach contents of sperm whales are considered questionable and are not plotted on our map. Distribution in the eastern Pacific is known from only three captures, the holotype and two juveniles briefly described by Okutani (1974) from the eastern tropical Pacific.

The species is absent in the transitional waters of the California and Peru-Chile currents, where it is replaced by the closely related *heteropsis*. Throughout its circumglobal, warm-water range, *meleagroteuthis* appears to be most abundant in the more productive areas, especially those associated with slopes of land and submarine rises.

The species appears to inhabit a vertical range from the surface to well in excess of 1000 m. Opening-closing nets have made daytime captures in the North Atlantic (Clarke and Lu, 1975; Roper and Young, 1975) of juveniles of less than 6 mm ML at 210–300 m as well as a larger juvenile of 16 mm ML and a subadult of 54 mm ML at 610–700 m. Nighttime, opening-closing-net captures of juveniles, 25–35 mm ML, were made at 100–360 m.

Large juveniles and subadults have been taken in open nets in midwater between about 200 m and 1950 m and near the bottom at about 500–1250 m. In the southwestern Pacific (K. Nesis, unpublished data), nighttime captures of large maturing females of 112 mm ML and 110 mm ML at 600 m and (in poor condition) at the surface, and an additional large female of 102 mm ML recovered from the stomach of a shark taken at the surface, show that large females of *meleagroteuthis* could continue to display a diel pattern of vertical movement between deep and shallow depths. The capture of the above-mentioned spent female while fishing at 1875 m in midwater during the day suggests that spawning may occur in deep water.

DISCUSSION.—Our reexaminations of the holotype of *Histioteuthis bruuni* N. Voss, 1969 (ZMUC, uncat.), and the second and only other reported specimen (uncataloged, IOAN; Nesis and Nikitina, 1986), which came from near the type locality in the southeastern Atlantic, confirmed the earlier decisions of Voss et al. (1992) to regard *bruuni* as a variant form and synonym of *meleagroteuthis*. Both specimens, available at the workshop, compared well in all features with *meleagroteuthis* except for the buccal membrane, which is six-membered and asymmetrical in *bruuni* and seven-membered and symmetrical in *meleagroteuthis*. Considering the variability in the buccal-membrane attachments of the latter species discussed in Voss's 1969 paper, the additional cases of such found at the workshop, and the fact that the two specimens of *bruuni* varied differently in their attachments from that found in *meleagroteuthis*, we have no hesitation in concurring that the condition of an unsymmetrical, six-membered buccal membrane is an aberrancy and therefore not a basis for specific distinction.

We also had the opportunity to examine the holotype of *Meleagroteuthis separata* Sasaki, 1915 (TIU, uncat.; specimen soft but otherwise in good condition), which was not available for the 1969 family revision and is distinguished from *meleagroteuthis* only by the shape and sucker arrangement of the tentacular clubs. We are in agreement that the condition of the clubs is a result of injury and subsequent partial regeneration, and we support the earlier relegation (Voss, 1963; Voss, 1969) of *separata* to the synonymy of *meleagroteuthis*.

Mature males, one collected near Bermuda during the Ocean Acre study and two taken in the eastern tropical Atlantic by the R/V *Walther Herwig* (Table 16), permitted us to better describe the spermatophore of the species. No significant morphological or morphometric differences were found in the spermatophores from the two geographic areas, and they compared well with the spermatophore illustrated and described by Voss (1969) for the synonymous *bruuni*. The small size and the general morphology of the ejaculatory apparatus and cement body of the spermatophore of *meleagroteuthis* and the presence of a well-developed ejaculatory-apparatus/cement-body connective complex can be said to be typical for histioteuthids (Hess, 1987). The long sperm mass (> 20% SpL) is a feature shared within the family only by *H. celetaria pacifica*, members of the *hoylei* species group, and certain populations of *reversa* and *bonnellii*. The remaining congeners possess a short sperm mass.

To date, the limited studies on the species show *meleagroteuthis* to have undergone little detectable morphological or morphometric changes over its broad distributional range. The Voss, 1969, study of 14 available specimens found no consistent differences between material from the Atlantic, Indian, and Pacific oceans, and Toll's (1982) study of the gladius, a feature not compared in the earlier work, noted no differences between Atlantic and Pacific specimens. Similarly, our examination of new material revealed no apparent differences in photophore pattern, length of tubercular rows, web depth, arm- and club-sucker dentitions, or number of gill lamellae that we could attribute to geographic variation. For a future, more comprehensive study of *meleagroteuthis*, we recommend the examination of much-needed, additional subadult and adult specimens from the Indian and Pacific oceans, a comparison of spermatophores from the different areas, and a closer look at the sucker enlargement pattern on the club, a feature in which we detected some variation that could prove to be significant.

### *Histioteuthis heteropsis* (Berry, 1913)

FIGURE 17

The second member of the *meleagroteuthis* species group, *H. heteropsis*, replaces its wide-occurring sibling species, *meleagroteuthis*, in the transitional waters of the California Current and Peru-Chile Current. Over the years since the studies of *heteropsis* by Voss (1969) and Young (1972), 89 unreported specimens have accumulated in the collections of the IOAN, SIO, UMML, and USNM. We examined this material before and at the workshop and considered the reports of captures by Nesis (1973a) and Jefferts (1983) in our new study. Our description is based largely on large juveniles, subadults, and adult males, 36–132 mm ML, but because most of the known material from the Peru-Chile Current falls below this size range, we also have included smaller juveniles from that area for information on photophore patterns and on

other characters that essentially are unaffected by growth.

**DESCRIPTION.**—Small to medium-sized histioteuthids; males known to mature at 54–89 mm ML; female size at maturity not known, largest known specimen 132 mm ML (SIO uncat. lot 6303-Cobb 58-7), immature; mantle moderately elongate; fins of medium size, length about 27%–40% ML, width about 48%–56% ML; head with no nuchal fold apparent; arms of medium length, about 100%–135% ML, approximately subequal; rings of suckers on all arms typically with 5–15 low, often poorly defined, round or square teeth on distal and lateral margins, except on distal ends of arms where rings more incised and on entire margins; in mature males, suckers on basal portions of all arms slightly enlarged, approximate distal  $\frac{1}{3}$ – $\frac{1}{2}$  of arms I modified with suckers of equal size on enlarged pedestals; inner web connecting arms I, II, and III approximately 11%–23% of length of longest arm; outer web developed to somewhat lesser degree, resulting in deep pocket between arms and web segments; buccal membrane 7-membered, second supports to dorsal sides of arms II, or bifurcate to ventral sides of arms I and dorsal sides of arms II; fourth supports without secondary connectives; tentacles long, about 140%–200% ML; tentacular club lacking longitudinal cleft on aboral surface; suckers on manus closely arranged in about 6–8 rows, moderately enlarged in median rows to about 2 times ventral marginals; rings of enlarged suckers with about 30–34 sharp or blunt teeth around entire margins.

Compound photophores uniformly small (~1.5 mm long in 63 mm ML specimen) and densely arranged on anterior  $\frac{3}{4}$  of ventral surface of mantle, of diminishing size and density on posterior  $\frac{1}{4}$ ; photophores on ventral surface of head of same approximate size and density as on anterior ventrum of mantle except more widely spaced on left side; circlet of about 19–21 (range, 17–23) photophores around right eye (Table 17); arms IV with 8–10 longitudinal rows of photophores on basal portions; enlarged, maturity-related, simple photophores not known to occur on mantle, head, or arms.

Dorsal pad of funnel organ fleshy, unsculptured; spermatophore short (SpL 1.8–2.8 mm; 2.4%–3.4% ML; from 4 specimens, 54.6–88.5 mm ML, California Current); sperm mass moderately short (10.9%–16.6% SpL); cement body long (55.5%–63.6% SpL); ejaculatory apparatus of medium length (~26.2%–29.5% SpL), with single longitudinal loop of inner tube; ejaculatory-apparatus/cement-body connective complex well developed; mature egg not known; gills about 54%–59% ML, with 37–40 lamellae in outer demibranch.

TABLE 17.—Comparison of the number of photophores in the circlet around the right eye between the two populations of *Histioteuthis heteropsis*.

Population	Number of photophores						
	17	18	19	20	21	22	23
California Current (n = 67)	2	7	36	20	1		1
Peru-Chile Current (n = 20)		1	2	10	7		

Gladius with straight, moderately slender rachis; vanes with rounded, convex (Peru-Chile Current specimens), or slightly angular (California Current specimens) shoulders, with hourglass-shaped midportion; vanes ending posteriorly in rounded cupped coil; lower beak with jaw angle not recessed, visible in profile; hood notch shallow, crest fold weak, median ridge on lateral wall strong, extending to free corner; radula with first and second laterals slightly asymmetrical, third laterals long, saber-shaped; marginal plates weakly developed, tear-shaped.

Skin color purplish red.

ORIGINAL REFERENCE.—Berry, 1913:75; original illustrations, Berry, 1912, figs. 13–16, pl. 50; figs. 1–3, pl. 51, pl. 52; figs. 5–7.

TYPE LOCALITY.—Eastern North Pacific, off Santa Barbara Island, California, 590–818 m.

DEPOSITION OF TYPES.—*Holotype*: USNM 214620, female, 59 mm ML, R/V *Albatross* sta 4416, 12 Apr 1904, by subsequent designation. No longer extant.

*Paratype*: Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, CASIZ 029130, female, 48 mm ML, R/V *Albatross* sta 4538, Monterey Bay, California, 31 May 1904, 1453–1592 m, by subsequent designation.

DISTRIBUTION.—*Histioteuthis heteropsis* is an eastern Pacific transitional species (Figure 17). Collecting data indicates a north-south disjunction in its distributional pattern. In the north, *heteropsis* is restricted to the California Current system where it is common over its known range, between about 24°N and 45°N (Young, 1972; Jefferts, 1983; Voss et al., 1992; unreported SIO collection). In the current, *heteropsis* occurs with its less common congeners, *hoylei*, *H. celetaria pacifica*, and *H. corona berryi*. The species is essentially absent from equatorial waters, which are normally inhabited by the closely related *meleagroteuthis* and where but a single capture of *heteropsis* has been reported (Nesis, 1973a; from 00°38'S, 89°29'W). In the southern sector of its geographic range, *heteropsis* appears to be restricted to the Peru-Chile Current where it is common between about 30°S and 36°S, 72°W and 75°W, judging from unreported collections made during R/V *Eltanin* cruise 25 (USNM) and the South Tow Expedition (SIO) and from several reported captures (Voss, 1969; Nesis, 1973a, 1973b; Retamal and Orellana, 1977) from that area. The exact extent of the distribution of *heteropsis* in the current is not known.

In the California Current, capture data from open nets show that *heteropsis* lives between about 300 m and 900 m during the day, with greatest concentration between about 500 m and 700 m, and at night lives between the surface and about 400 m, with greatest concentration between about 300 m and 400 m (Roper and Young, 1975). One mature male for which we have the time of capture was taken in midwater at 800–850 m during the day. Roper and Young found only juveniles of less than 20 mm ML in the nighttime hauls from the upper 200 m. In the Peru-Chile Current, juveniles of less than 20 mm ML also were

the only size group present in the single known tow from the surface 200 m layer that was successful in capturing the species.

DISCUSSION.—The status of Berry's (1913) original specimens, considered in Voss's 1969 revision of the family to be syntypes of *heteropsis*, has been clarified by Sweeney et al. (1988). On the basis of new evidence from Berry's original jar labels and card catalog, the authors have designated as holotype and paratype (see above) two of the three specimens that were listed in Berry's 1912 description of the material and were used in his 1913 paper, without designation of holotype, for the naming of his new species. The jar label and catalog card for the third specimen (R/V *Albatross* sta 4544; USNM 214624) lacked notations of type status, so that specimen is now regarded as "other material."

The new specimens permitted us to investigate the possible differences discussed by Toll (1982) in gladius morphology and certain body morphometrics that could exist between the northern and southern populations of the species. Toll found the gladius of specimens from the Peru-Chile Current to have vanes with rounded, convex shoulders, an hourglass-shaped midportion, and a relatively broad, rounded posterior end, in contrast to the earlier illustrated gladius of a specimen from the California Current (Voss, 1969) that showed vanes with angular shoulders, a narrow, rounded posterior end, and no hourglass shape at the midportion. Our dissections of additional material from both areas, and a reexamination of the gladius illustrated by Voss, confirmed the findings of Toll for the southern specimens and showed the illustration of the northern specimen to be at fault. The 1969 drawing was an inaccurate reconstruction of a fragmented gladius. Gladii from two new specimens from the northern area (USNM 729898, 50 mm ML; USNM 729901, 38 mm ML) show the hourglass-shaped midportion and relatively broad posterior end typical of the vanes of specimens from the southern area. They show the vane shoulders, however, to be somewhat more angular than those pictured by Toll but not as angular as shown in the 1969 work. Thus, differences in the shape of the gladius of specimens from the two areas appear to be minimal.

The new material available from the Peru-Chile Current, consisting mostly of small juveniles of 15–33 mm ML, was examined but was found to be of little value for determining possible populational differences in arm lengths, posterior fin extension, and inner-web depths suggested by Toll (1982). Concerning other features, we found no significant differences in the dentition of the suckers on the arms or club manus, or in the density of the photophores on the mantle or bases of arms IV. We did find that the specimens from the California Current tended to have slightly fewer photophores in the circling around the right eye than their counterparts from the Peru-Chile Current (Table 17). Unfortunately, the lack of mature males from the southern area precluded a comparison of the spermatophores of the two populations. To summarize our study, we found little evidence of morphological divergence in

TABLE 18.—Comparison between members of the *Histioteuthis meleagroteuthis* species group.

Character	<i>H. meleagroteuthis</i>	<i>H. heteropsis</i>
Median row of tubercles on arms I-III and dorsum of mantle	present	absent
Spermatophore		
Sperm mass length	28%–39% SpL	11%–17% SpL
Cement-body length	15%–37% SpL	56%–64% SpL
Shape of gladiol vanes	strongly flaring anterior margins; combined outline triangular	anterior 1/2 with scalloped margins; combined outline hour-glass-shaped
Geographic range	Atlantic, Pacific, Indian oceans; tropical-subtropical	California Current, Peru-Chile Current; transitional

the two apparently disjunct populations of this antitropical, eastern Pacific, transitional species.

In addition to the shared possession of the uniquely derived dense pattern of uniformly small compound photophores, the two members of the *meleagroteuthis* species group, *meleagroteuthis* and *heteropsis*, are united by shared aspects of funnel organ morphology, arm sucker dentition, buccal membrane attachments, and club sucker pattern. The members are separated by differences in the relative sizes of the internal components of the spermatophore, shape of the gladius, geographic range, and the presence of a median row of tubercles on arms I-III and the dorsum of the mantle in *meleagroteuthis* and their absence in *heteropsis* (Table 18).

#### Relationships among Histioteuthids

The conclusion of Voss's 1969 revision, that the Histioteuthidae is a natural group composed of a number of subgroups of closely related species, is well supported by the present study. Our findings corroborate the earlier proposed groups of *bonnellii-macrohista* and *meleagroteuthis-heteropsis*, show that *atlantica* belongs as a third member to the originally proposed group *reversa-eltaninae*, and describe two new groups, *hoylei-arcturi* and *miranda-oceani*. In addition to characterizing the five species groups, we have given them more formal recognition by labeling them with the oldest name belonging to each: *reversa* species group, *hoylei* species group, *bonnellii* species group, *miranda* species group, and *meleagroteuthis* species group. Of the two species not belonging to a currently recognized group, we believe that a future, more detailed study of *celetaria* will result in elevation of its two subspecies to the specific level and that together they will constitute a sixth distinct group of closely related species in the family. The present scarcity of specimens, the lack of late growth stages in available material, and ignorance of distributions of the three Pacific subspecies of *corona* preclude meaningful speculation now as to the possibility of future recognition of species status for any of the members of that species complex.

The above arrangement of species appears to best fit the morphological evidence presented in the preceding text. A study of histioteuthid phylogeny is planned to supplement the data used herein with information from new characters and to provide evidence for character polarities.

#### Biogeography

The Histioteuthidae can be broadly categorized as meso-upper bathypelagic in subarctic to subantarctic waters in the world's oceans. There is no evidence of horizontal migration in the family, and paralarvae, juveniles, and adults appear to be present in all areas within the normal geographic range of a species.

In this section, we synthesize the detailed distributional data contained in the text and maps of the preceding species accounts, which include (1) horizontal and vertical ranges; (2) observed effects of environmental features, both physical, such as fronts, currents, and warm- or cold-water rings, and biological, such as primary productivity of the water, on the occurrence and abundance within range; (3) data on the vertical distribution of the various growth stages; and (4) suggested spawning sites, whether near the bottom or in midwater in association with slopes of continents, islands, and submarine rises, or in deep or shallower midwater in the open ocean. Differences in a number of these factors affect, to varying degrees, the distributional patterns of the taxa.

Our maps show the approximate boundaries of the major upper water masses of the world's oceans and, in the Atlantic, of the mesopelagic faunal regions described by Backus et al. (1977; see Figure 2 for a redrawing of their original map and the names of their regions and provinces). We plotted separately the distributions of the two cosmopolitan, polytypic species (Figures 11 and 12) and plotted together the distributions of all members of a species group (Figures 5, 7, 9, 16, 17) in order to better demonstrate the importance (or lack of importance) of various environmental features as biogeographic boundaries and the role of ecological features in the formation of the groups.

## DISTRIBUTIONAL PATTERNS

Our classification of the distributional patterns of the histioteuthids is summarized in Table 19 and is discussed below. We have arranged the patterns first by ocean, or oceans if a species or subspecies occurs in multiple oceans (see summary of occurrences in Table 20), and then by association with either oceanic areas or slope areas of continents and islands. The latter association, called "pseudoceanic," has been described for a number of midwater fishes (Krefft, 1974; Nafpaktitis et al., 1977; and others) and at least one species of midwater squid, the cranchiid *Teuthowenia maculata* Leach (Voss, 1985). Among the histioteuthids, two species, *Histioteuthis heteropsis* and *H. miranda*, and possibly one subspecies, *H. corona inermis*, spend their entire life cycle in the proximity of land. The distributional patterns themselves bear the names of the major regions of the oceans primarily inhabited, in whole or in part, by the species or subspecies. The patterns are highly individual, with the number of patterns nearly equalling the number of taxa.

*Atlantic Ocean*

OCEANIC.—1. *Subarctic-North Temperate-Eastern Tropical Pattern*: An apparently disjunct pattern composed of widespread distributions in the Subarctic and North Temperate regions, including the western and part of the eastern Mediterranean Sea, and a distribution to the south that is confined to the Mauritanian Upwelling and the eastern half of the Tropical Region is typical of the northern population of *bonnellii* (= nominal subspecies, *H. bonnellii bonnellii*; Figure 9). Whether the scattered captures in the subarctic are indications of a broad subarctic distribution, as they are interpreted here, or represent expatriates from north temperate waters is not clear. The species is relatively common throughout the western Mediterranean but appears to be restricted in the more subtropical-like, eastern Mediterranean to the northern sector. The southern limit of the species' broad distribution in the North Temperate Region is well marked by the northern edges of the Sargasso Sea and North African Subtropical Sea as drawn by Backus et al. (1977). The absence of *bonnellii* in the North Subtropical Region and its reappearance in the Mauritanian Upwelling and the Tropical Region east of 40°W, which comprises the Guinean Province of Backus et al. (1977), is indicative of the preference of this population for areas of high productivity. The southern limit in the Guinean Province is uncertain. The species was regularly encountered by the R/V *Walther Herwig* in 1971 at stations between the Mauritanian Upwelling and 5°S, in the area of high productivity that extends westward from the Gulf of Guinea, but south of that latitude, in tropical waters, *bonnellii* has only been taken twice, a single juvenile by the R/V *Dana* and another by the R/V *Walther Herwig*, both off St. Helena. These latter captures could be expatriates of either the northern

TABLE 19.—Distribution patterns of histioteuthids in the world's oceans. A question mark precedes the taxa with poorly known distributions; their patterns are regarded as tentative. The northern and southern populations of *Histioteuthis bonnellii* correspond to the two nominal subspecies, which could not be morphologically distinguished in the present study (see "Discussion" for *H. bonnellii*).

Atlantic Ocean	
Oceanic	
Subarctic-north temperate-eastern tropical.	
<i>H. bonnellii</i> northern population*	
North temperate-eastern north subtropical-tropical.	
<i>H. reversa</i> *	
Tropical-north subtropical.	
<i>H. corona corona</i>	
Tropical-subtropical.	
<i>H. arcturi</i>	
<i>H. celetaria celetaria</i>	
Pacific Ocean	
Oceanic	
North subtropical.	
? <i>H. corona berryi</i>	
Eastern tropical.	
? <i>H. cornona cerasina</i>	
Pseudoceanic	
Eastern transitional.	
<i>H. heteropsis</i>	
Western transitional.	
? <i>H. corona inermis</i>	
Pacific-Indian oceans	
Oceanic	
Tropical/equatorial-subtropical.	
<i>H. hoylei</i>	
Tropical/equatorial.	
<i>H. celetaria pacifica</i>	
? <i>H. oceani</i>	
Pseudoceanic	
Semi-south subtropical.	
<i>H. miranda</i>	
Atlantic-Pacific-Indian oceans	
Oceanic	
Tropical-subtropical.	
<i>H. meleagroteuthis</i>	
Semi-south subtropical.	
<i>H. bonnellii</i> southern population	
Southern Ocean	
Oceanic	
Subtropical convergence.	
<i>H. macrohista</i>	
Subtropical convergence/semi-subantarctic.	
<i>H. atlantica</i>	
Subantarctic.	
<i>H. eltaninae</i>	

\*Could comprise more than one taxon. See "Discussion" for the individual species.

or southern population (see below) of the species or could indicate the southern portion of the normal range of the northern population. The latter is unlikely, however, considering the absence of the species in the well-sampled, high

TABLE 20.—The occurrences of histioteuthid species in the world's oceans. Abbreviations of zoogeographic regions and provinces: Atl Subarc = Atlantic Subarctic; N Atl Temp = North Atlantic Temperate (excluding Mediterranean Sea); Med S = Mediterranean Sea (East and West provinces combined); N Atl Subt = North Atlantic Subtropical; G Mex = Gulf of Mexico; Maur Upw = Mauritanian Upwelling; Atl T = Atlantic Tropical (excluding Caribbean Sea); Car S = Caribbean Sea; S Atl Subt = South Atlantic Subtropical; Ben Cur = Benguela Current; Ind O T = Indian Ocean Tropical; Ind O Subt = Indian Ocean Subtropical; N Pac Subt = North Pacific Subtropical; Cal Cur = California Current; Pac T = Pacific Tropical; Per-Chi Cur = Peru-Chile Current; S Pac Subt = South Pacific Subtropical; SSTC = Southern Subtropical Convergence; Subant = Subantarctic.

Taxon	Atl Subarc	N Atl Temp	Med S	N Atl Subt	G Mex	Maur Upw	Atl T	Car S	S Atl Subt	Ben Cur	Ind O T	Ind O Subt	N Pac Subt	Cal Cur	Pac T	Per-Chi Cur	S Pac Subt	SSTC	Subant
<i>H. reversa</i> species group																			
<i>H. reversa</i> *	x	x	x	x		x	x												
<i>H. atlantica</i>										x		x				x	x	x	x
<i>H. eltaninae</i>																	x		x
<i>H. hoylei</i> species group																			
<i>H. hoylei</i>											x	x	x	x	x	x	x		
<i>H. arcturi</i>				x	x	x	x		x										
<i>H. bonnellii</i> species group																			
<i>H. bonnellii</i> *	x	x	x			x	x		x	x		x					x		
<i>H. macrohista</i>										x								x	x
<i>H. celetaria</i>																			
<i>H. c. celetaria</i>				x		x	x		x										
<i>H. c. pacifica</i>											x	x	x	x	x				
<i>H. corona</i>																			
<i>H. c. corona</i>		x		x	x		x	x											
<i>H. c. berryi</i>													x	x					
<i>H. c. cerasina</i>															x	x			
<i>H. c. inermis</i>													x						
<i>H. c. subsp. undetermined</i>											x	x				x	x		
<i>H. miranda</i> species group																			
<i>H. miranda</i>										x	x	x					x	x	
<i>H. oceani</i>											?		x		x	?			
<i>H. meleagroteuthis</i> species group																			
<i>H. meleagroteuthis</i>				x		x	x		x		x	x	x		x				
<i>H. heteropsis</i>														x		x			
Total number of taxa present																			
In region/province	2	3	2	5	2	5	6	1	4	4	5/76	7	6	4	5	6	7	3	3
In ocean	9										7(?)			12(?13)				4	
Atlantic	9										7(?)			12(?13)				4	
Indian	9										7(?)			12(?13)				4	
Pacific	9										7(?)			12(?13)				4	
Southern	9										7(?)			12(?13)				4	

\*Probably comprises more than one taxon.

productivity waters off Namibia at the southernmost end of the Tropical Region. Evidence suggesting that the northern population of *bonnellii* could be composed of subpopulations is presented in the "Discussion" for the species and in Table 11.

2. *North Temperate-Eastern North Subtropical-Tropical Pattern*: Among the histioteuthids, this distributional pattern shown by *reversa* (Figure 5) most closely resembles that described above for the northern population of *bonnellii*. The main differences appear to relate to the increased tolerance of *reversa* for lower-nutrient waters. *Histioteuthis reversa* and *bonnellii* (northern population) are the only members of the

family that are broadly distributed in the North Temperate Region and are the only ones to occur in the Mediterranean Sea. *Histioteuthis reversa* inhabits both the western and eastern Mediterranean including the less productive southern and eastern sectors of the latter province, which are not normally inhabited by *bonnellii*. Evidence that this Mediterranean population of *reversa* could be morphologically distinct from that in the Atlantic is presented in the "Discussion" for the species and in Table 3. Of the two species, *reversa* and *bonnellii*, the former is the more common throughout temperate waters. The scattered records of *reversa* in the subarctic



probably represent expatriates from the species' normal range to the south. In the North Subtropical Region, the species is less abundant than in temperate waters and is largely confined to east of the Mid-Atlantic Ridge, an area named the North African Subtropical Sea by Backus et al. (1977). Exceptions are scattered occurrences in the Sargasso Sea to the west, which appear to be attributable to transport by eddies of the Gulf Stream (Lea, 1978) from the species' normal range in the temperate slope water to the north and tropical, Lesser Antillean water to the south. *Histioteuthis reversa* is abundant in the Mauritanian Upwelling and in high productivity areas of the eastern Tropical Region between the upwelling and 5°S–10°S (Amelekhina and Zuev, 1988; Amelekhina et al., 1990) and is abundant off Namibia where the species finds its southern limit at about 23°S. The arc of the Antilles marks the western boundary of the species in the less productive, western sector of the Tropical Region. It has never been taken in the two westernmost tropical provinces, the Caribbean Sea and the Straits of Florida. Over its distributional range, *reversa* is found in greatest abundance near slopes of land or submarine rises. The broad geographic spread of the species in oceanic waters corresponds to its apparent spawning site in the upper layers of the water column.

3. *Tropical-North Subtropical Pattern*: Over its normal distributional range, *H. corona corona* (Figure 12) is most abundant in the Tropical and Gulf of Mexico regions. In eastern tropical waters, it appears to be common throughout most of the Guinean Province but was noticeably absent in the cephalopod collections taken by the R/V *Akademik Kurchatov* and the R/V *Professor Shtokman* during extensive sampling of the high productivity area off Namibia at the southern end of the province. It was caught regularly, however, by the R/V *Walther Herwig* in the less productive waters found offshore of that area. Similarly, the subspecies is scarce or absent in the very productive Mauritanian Upwelling but is present in nearby, less productive offshore tropical and subtropical waters. To the west, *H. c. corona* occurs in the tropical Antillean and Amazonian provinces, but its distribution and abundance are poorly known. With the exception of a single capture of *arcturi* off the coast of Venezuela, *H. c. corona* is the only histioteuthid encountered in the Caribbean, where it appears to be common in the relatively high productivity areas off the coasts of South and Central America. It has been taken in the tropical Straits of Florida and throughout the Gulf of Mexico, where it occurs with *arcturi* and is the dominant of the two species in most of the area studied. In the gulf, the subspecies is found in greatest abundance in the northern sector in the vicinity of the mouth of the Mississippi River. In the North Subtropical Region, *H. c. corona* inhabits the more productive areas peripheral to the central gyre, where it has been found to be third or fourth in abundance to congeners *arcturi*, *meleagroteuthis*, and, in the eastern sector, *reversa*. The Gulf Stream system expatriates the subspecies northward into north temperate waters off Canada to about 43°N.

The recent capture of a single small juvenile at 36°S, 48°W, in the poorly sampled southwestern Atlantic (Rodhouse et al., 1992) suggests that *H. c. corona* could be found to have the broad, warm-water pattern described below rather than the more restricted tropical-north subtropical pattern described herein for the species.

4. *Tropical-Subtropical Pattern*: Two strictly Atlantic histioteuthids display a tropical-subtropical pattern of distribution, namely *arcturi* (Figure 7), the newly recognized (herein) Atlantic sibling of the Pacific-Indian Ocean species *hoylei*, and *H. celetaria celetaria* (Figure 11), the Atlantic subspecies of one of the three species in the family currently regarded as having cosmopolitan, warm-water distributions. The relatively good distributional data for *arcturi* show the species to be widely distributed between about 35°N–40°N and 30°S. In the northeast, the species is transported northward from the Sargasso Sea into the temperate slope water off Nova Scotia to about 44°N, probably by warm eddies of the Gulf Stream (Fedulov and Arkhipkin, 1986). A southern limit in the South Subtropical Region somewhat north of the SSTC is indicated by the absence of the species in the cephalopod collections made on the east-west and north-south transects of the convergence and adjacent waters during the 1971 cruise of the R/V *Akademik Kurchatov* and the 1971 and 1975/1976 cruises of the R/V *Walther Herwig*. In southeastern tropical waters, *arcturi* appears to be absent in the high productivity area off Namibia, where the north temperate-eastern north subtropical-tropical *reversa* is common, and, instead, finds its southern limit north of that latitude at about 17°S. In the North Subtropical Region, *arcturi* is the most widespread and common histioteuthid in the central waters and occurs in highest abundance in the sector of lowest productivity, the South Sargasso Sea, where it is the sole member of the family present except in the northeastern corner of the province. In the more productive northern subtropical provinces, *arcturi* is the dominant histioteuthid in the North Sargasso Sea but ranks third in abundance to *meleagroteuthis* and *reversa* in the Northern North African Subtropical Sea. The species is less abundant in the warmer waters of the Tropical Region. There, it has been taken in greatest number in the more productive eastern half of the region but appears to largely avoid the areas of maximum productivity. Taken in the Caribbean only in the relatively more productive waters off Venezuela, *arcturi* is common, along with the tropical-north subtropical *H. corona corona*, throughout most of the Gulf of Mexico. In this region the surface water is as warm in the summer as it is in the Caribbean, but it differs in the considerable cooling that occurs in the winter. Data on distribution and relative abundance in the South Subtropical Region are too meager for meaningful comment. Although the spawning site of *arcturi* is not known, the distributional pattern and the abundance of the species in open-ocean areas suggest that it is in midwater not necessarily associated with land or bottom topography.

The 25 known specimens of *H. celetaria celetaria* were

taken at localities in open ocean as well as near slopes of land and submarine rises and were widely distributed in tropical and both northern and southern subtropical waters. The apparent absence of the species from the Gulf of Mexico distinguishes its tropical-subtropical pattern of distribution from that of *arcturi*. All but two nets successful in capturing the subspecies took single specimens. The two exceptional hauls were one by the R/V *Professor Vodyanitsky* that took 11 small juveniles (<10 mm ML) from the surface 35 m in the Gulf of Guinea, and one by the R/V *Walther Herwig* that took five subadults and large juveniles and one mature male while fishing at 750–760 m in tropical waters to the south at 19°S, 4°W. The fact that the two multiple captures and all but six of the single ones came from the Mauritanian Upwelling and eastern half of the Tropical Region suggest that *H. c. celetaria* could occur in greatest abundance in this sector of its geographic range, where productivity is highest. However, of the 24 stations made by the R/V *Walther Herwig* in these waters during the 1971 Cape Town–Madiera transect (using a 1600-mesh Engel trawl), only two were positive for the subspecies, the above-mentioned station and one at 13°S, 9°W, where a spent female was caught between 990 m and 1010 m. Although *H. c. celetaria* could actually occur in lower numbers than sympatric congeners, the scarcity of specimens in the collections from the various areas is nevertheless surprising and is probably less representative of the subspecies' relative abundance than are the catches of the other family members. The scarcity in the collections of the R/V *Walther Herwig* could be explained in part by the lack of ability of the large Engel trawl to catch small specimens, but an explanation of the scarcity of catches over the broad distribution of *H. c. celetaria* must be sought elsewhere and could be partly found in the vertical ranges observed for the different growth stages. Our admittedly limited data describe a life history atypical of histioteuthids, in which the late juvenile, subadult, and adult stages may be confined to deep water, the least sampled segment of the water column. In all other members of the family, late juveniles, subadults, and often adult males continue to move into shallower depths to feed at night, and there the majority of captures have been made.

#### Pacific Ocean

OCEANIC.—1. *North Subtropical Pattern*: Our new data indicate a north subtropical distribution for *H. corona berryi* rather than a transitional, endemic distribution, which was assigned to this distinctive subspecies of the warm-water cosmopolite by Jefferts (1988). The capture localities, between 26°N and 37°N, 115°W and 178°E, for the eight known specimens, all juveniles, show *H. c. berryi* (Figure 12) to be broadly distributed in the subtropical region of the North Pacific, a region poorly sampled for cephalopods. Off the coast of North America, *H. c. berryi* is advected into the California

Current, where extensive sampling has shown it to be present, but uncommon, between 26°N and 33°N, 115°W and 126°W, in the central mixed zone of the current.

2. *Eastern Tropical Pattern*: Our distributional data for *H. corona cerasina* (Figure 12) are scarce. The 29 known specimens, all juveniles, came from the Peru-Chile Current and eastern equatorial waters between 0° and 24°S, 70°W and 85°W, and westward in equatorial waters to 155°W. Because the 19 net hauls successful in catching the subspecies were made within the elongate, wedge-shaped area of the eastern tropical Pacific (ETP), we tentatively assign *H. c. cerasina* to that distribution pattern. Although Okutani's (1974) report on the squids taken during the EASTROPAC studies did not record the subspecies from this area, it is possible that it will be found among the 25 specimens identified to *dofleini* (= *hoylei*) and described by him as mostly juveniles and in poor condition. (These records are plotted with accompanying question marks on our map for *hoylei* (Figure 7).) The ETP is a hydrographically distinct region characterized by the largest oxygen-minimum layer in the world's oceans and by areas of upwelling, divergence, and high biological productivity (McGowan, 1974). The region also is characterized by a distinctive assemblage of midwater species of fishes and various groups of invertebrates, a number of which are endemics (Johnson, 1982). Two species of squid have been reported as endemic to the ETP, the ommastrephid *Dosidicus gigas* by Wormuth (1976) and the cranchiid *Leachia danae* by Voss et al. (1992).

PSEUDOCEANIC.—1. *Eastern Transitional Pattern*: *Histioteuthis heteropsis* (Figure 17) displays a disjunct distribution in the transitional waters of the two eastern boundary currents of the Pacific, both of which are characterized by complex hydrography, and in areas of upwelling and high productivity. All but one of the 296 known specimens, taken in 144 net hauls, came from between 24°N and 45°N, 117°W and 136°W, in the California Current and outer fringes and from between 30°S and 36°S, 72°W and 75°W, in the Peru-Chile Current. The one exceptional capture was made in the intervening equatorial waters, which appear to be normally inhabited by the sibling species *meleagroteuthis*. Because the cephalopod fauna of the area has been relatively well studied, the above range of *heteropsis* in the California Current probably approaches its true range, although the known range in the poorly studied Peru-Chile Current is probably considerably less than that actually inhabited. Among its congeners, *heteropsis*, the dominant histioteuthid throughout the California Current, occurs with the tropical/equatorial-subtropical *hoylei* in the northern zone, with *hoylei* and the north subtropical *H. corona berryi* in the central zone, and with the tropical/equatorial *H. celetaria pacifica* in the southern zone of the current. In the southern portion of the Peru-Chile Current where *heteropsis* has been taken, it is the dominant member of the family present and occurs with *hoylei*, a form of *corona* yet to be identified to subspecies, and the SSTC species *atlantica*. Morphological differences between the two apparently disjunct

populations appear to be minimal (see "Discussion" for the species and Table 17).

2. *Western Transitional Pattern*: The 10 juveniles of the poorly known *H. corona inermis* (Figure 12) all came from the continental slope off the east coast of Japan between 33°N and 35°N, 134°E and 140°E. The subspecies is tentatively regarded herein as displaying a western transitional pattern of distribution, however future studies of the cephalopod fauna of the western Pacific and the Indian Ocean may well show *H. c. inermis* to be more widely distributed.

#### *Pacific-Indian Oceans*

OCEANIC.—1. *Tropical/Equatorial-Subtropical Pattern*: *Histioteuthis hoylei* (Figure 7) has been encountered in almost every open-ocean area that has been sampled for cephalopods in the tropical/equatorial and subtropical regions of the Pacific and Indian oceans. In the majority of these areas, over the species' range between about 45°N and 45°S in the Pacific and 10°N and 35°S in the Indian Ocean, it is the most common histioteuthid taken; however, it is less common and is sometimes scarce in areas associated with continental slopes. Over its broad, open-ocean range in the Pacific, the species appears to be most abundant in north subtropical waters and least abundant in south subtropical waters. Although a number of the records from the ETP are unconfirmed, and some are in doubt, *hoylei* appears to be relatively common and the dominant histioteuthid present in this area of high productivity. Similarly, in the western tropical Pacific, it is the most commonly encountered member of the family in both the Philippine and Coral seas. Several recent studies, the results of which have yet to be published (E. Förch, C. Lu, K. Nesis), show *hoylei* to be uncommon in the subtropical sector of the Tasman Sea and the subtropical and tropical western Indian Ocean. The degree of presence of *hoylei* in the transitional waters of the boundary currents of the Pacific appears largely to reflect the abundance of the species in neighboring oceanic waters. Among the different boundary currents, the greatest known abundance occurs in the California Current. There, it is relatively common and ranks second in abundance (among congeners) to the transitional *heteropsis*. *Histioteuthis hoylei* is uncommon in the Peru-Chile Current and is scarce in the East Australian Current. Its relative abundance in the Kuroshio Current is poorly known, but Okutani et al. (1976) reported the species as common and the dominant squid identified in the whole-specimen remains from stomach contents of sperm whales caught between 35°N and 38°N, 141°E and 143°E, off eastern Japan. Changes in the intensity of the Kuroshio Current could lead to variations in the inflow of warmer intermediate waters into the Okhotsk Sea and account for the unusual reported captures (Didenko, 1991) of *hoylei* in that area in November 1990–January 1991 (species present in 200–500 m layer, absent in 0–200 m layer). Habitation of the central waters of the subtropical gyres, areas of the lowest productivity

in the oceans, and the overall pattern of occurrence of *hoylei* in the Pacific parallels that of its sibling species *arcturi* in the Atlantic, and similarly suggests a midwater site for spawning.

2. *Tropical/Equatorial Pattern*: Our distributional data for *H. celetaria pacifica* (Figure 11), the better known of the two histioteuthids regarded as having a tropical/equatorial pattern of distribution, comes largely from the Indian Ocean and western Pacific, areas where the subspecies appears to occur in greatest abundance. Over its known range in the western Indian Ocean, between about 8°N and 35°S, *H. c. pacifica* inhabits the entire equatorial zone and extends into subtropical waters peripheral to the southern gyre. Between these latitudes, where the R/V *Vityaz* (1988/1989) collected seven species of histioteuthids, *H. c. pacifica* was found to occur in greatest abundance and to be the dominant histioteuthid among congeners between 8°N and 26°S (K. Nesis, unpublished data). In the same approximate area, an unpublished French study also found the subspecies to be abundant and the most common histioteuthid caught off the west coast of Madagascar between 12°S and 24°S (P. Rancurel, pers. comm.). In the eastern Indian Ocean, *H. c. pacifica* has been encountered in large numbers on the tropical northwest shelf and slope of Australia (Wadley, 1990; S. Slack-Smith, unpublished data). The majority of the captures from the Pacific have been made in the vicinity of continental and island masses and submarine rises. Scattered specimens have been taken in the central Pacific off Hawaii and north in transitional and subtropical waters to 30°N and, in the eastern Pacific, in the southern half of the California Current and in the ETP. The patchy occurrence of *H. c. pacifica* within its distributional range relates to its apparent preference for relatively higher productivity waters and a possible spawning site associated with slopes of land or submarine rises.

Distributional data for the recently recognized *oceanii* (Figure 16) is supplied by 19 verified captures, which include juveniles, subadults, and one adult. Captures were made near islands and submarine rises and in open ocean and were widely scattered in tropical/equatorial waters from the Galapagos Islands to the Indo-West Pacific and in central transitional waters to Hawaii and northward to 30°N. With some hesitation, we regard the tropical/equatorial distribution of *oceanii* to be a Pacific-Indian Ocean pattern rather than a Pacific pattern because of the fact that all warm-water histioteuthids that occur in one of the two oceans also occur in the other. It is very likely that *oceanii* will be found in the tropical Indian Ocean in areas of relatively high productivity and could occur with or be replaced by its southern sibling species, *miranda*, in areas where the productivity is highest.

PSEUDOCEANIC.—1. *Semi-South Subtropical Pattern*: *Histioteuthis miranda* (Figure 16) is largely restricted to southern subtropical waters closely associated with land masses and submarine rises in the Indian and western Pacific oceans. Off South Africa, the species extends in the Agulhas Current system into the southeastern Atlantic, where a large

breeding population is known to occur as far north in the southern Benguela Current as 33°S. In the western Indian Ocean, *miranda*, a normally large-maturing species, is abundant and was found by the R/V *Vityaz* in 1988/1989 to be the dominant histioteuthid between latitudes 28°S and 34°S in the vicinity of Walters Shoal. In these subtropical waters, the species occurs with its less common and more broadly distributed congeners, namely (arranged in decreasing order of abundance) *bonnellii* (southern population), *meleagroteuthis*, *atlantica*, and *corona* ?subsp. The capture of a small mature male of *miranda* to the north at 12°N, 51°E, represents an exceptional extension of the species' range into tropical waters. In the northwestern Indian Ocean, the tropical/equatorial *H. celetaria pacifica* is the dominant family member. In this area of high productivity, *miranda* could occur with or replace its tropical/equatorial sibling species, *oceani*. In the western Pacific, *miranda* appears to be abundant on the southern and southeastern shelf of Australia and off Tasmania and is known to extend northward off the west coast of Australia to 28°S and off the east coast to 25°S in the transitional waters of the East Australian Current. Distributional data for histioteuthids off the west coast are scarce, but a survey of the cephalopod fauna of the tropical northwestern shelf showed the species to be absent. Around New Zealand, *miranda* has been caught off the east and west coasts but is rarely caught south of the SSTC. Off the northwestern coast, it is rarely encountered north of about 32°S. A hydrographic feature, the Tasman Front, could correspond to the northern limit of *miranda* and the other histioteuthids with distributions that are primarily associated with the southern half of the subtropical region or more southern areas. The Tasman Front is a meandering thermal front associated with a jet zone that extends across the northern Tasman Sea between 30°S and 35°S and connects the East Australian Current to the boundary current off the east coast of New Zealand (Stanton, 1981; Heath, 1985). A preference for waters of high productivity and a spawning site closely associated with continental masses have apparently prevented *miranda* from crossing the expanse of low-productivity, central waters east of New Zealand to colonize the coasts of South America.

#### *Atlantic-Pacific-Indian Oceans*

OCEANIC.—1. *Tropical-Subtropical Pattern*: Over its wide distributional range, between the SSTC and 35°N–45°N in the Atlantic, Pacific, and Indian oceans, *meleagroteuthis* (Figure 17) occurs in greatest number in the more productive areas of the tropical-subtropical realm and is scarce or absent in the low and least productive areas. In the Atlantic, greatest abundance appears to occur in the Mauritanian Upwelling and the eastern Tropical Region, where the R/V *Walther Herwig*, during its Cape Town–Madeira transect in 1971, made first and last encounters of the species at 30°S in southern subtropical waters and 20°N in the Mauritanian Upwelling. Between these latitudes, the R/V *Walther Herwig* caught *meleagroteuthis* at

more stations than it did any other histioteuthid, although in total number of specimens caught, the species ranked second among congeners in abundance to *reversa*. Westward in tropical waters, *meleagroteuthis* inhabits the Amazonian and Lesser Antilles provinces but has not been taken in the relatively well-sampled Caribbean Sea and Straits of Florida. Considering the occurrence of the species in the upwelling area off Surinam and French Guiana (Okutani, 1983), it would not be surprising if a future study also found it in the nearby upwelling area off Venezuela in the southeastern Caribbean. The species is absent from the Gulf of Mexico and occurs in the North Subtropical Region almost exclusively in the more productive northern half. Its southern limit in the region is found at the northern subtropical convergence, the feature used by Backus et al. (1977) to draw the east-west boundary between the two northern and the two southern provinces. Greatest abundance in the northern North African Subtropical Sea is found in the vicinity of the Mid-Atlantic Ridge, where *meleagroteuthis* and *reversa* closely vie for dominance among congeners caught during the 1979 Sargasso Sea Expedition of the R/V *Anton Dohrn*. In the North Sargasso Sea, greatest abundance occurs in the vicinity of Bermuda, where the species ranks second to *arcturi*. The northern limit of *meleagroteuthis* in midocean could occur slightly north of the northern boundary drawn by Backus et al. for the North Subtropical Region. Between 34°W and 35°W, the Amsterdam-Mid-North Atlantic Plankton Expedition in 1980 and the Russian vessel R/V *Artemida* caught juveniles north to 42°N and 45°N in the vicinity of the southeast-directed branch of the North Atlantic Current. The scarce data from the southern Subtropical Region indicate the species' presence in eastern and southwestern waters as well as a southern limit at the SSTC. Findings of several north-south transects have demonstrated the normal absence of *meleagroteuthis* in the convergence itself. Also, it appears to be scarce or absent in the transitional waters of the Benguela Current. In the Indian Ocean, the species has been taken between 10°N and the SSTC in the more productive western sector, but its occurrence in the less-sampled central and eastern sectors is not known except from records from off the northwestern coast of Australia. In the Pacific, the species has been encountered in greatest abundance in western waters, where it is known to extend from about 35°N off Japan to 38°S in the East Australian Current, but it appears to be scarce or absent in the eastern Tasman Sea. Except in the Tropical Region, where *meleagroteuthis* extends eastward into the ETP to off the coast of Central America, the species has been rarely caught east of 160°W. In the northern and southern midlatitudes of the eastern Pacific, it is replaced by its sibling species *heteropsis*, which has a distribution that is essentially restricted to the California and Peru-Chile currents. In the northern Subtropical Region west of 160°W, *meleagroteuthis* is confined to the more productive area north of about 30°N. The species' distribution across broad expanses of open ocean corresponds with an indicated spawning site in midwater not

necessarily associated with land or submarine rises. Comparative studies focusing on various characters (see "Discussion" for the species) have detected no significant differences in the species over its three-ocean range.

2. *Semi-South Subtropical Pattern*: The southern population of *bonnellii* (Figure 9) corresponds to the subspecies *H. bonnellii corpuscula* named by Clarke (1980), but *H. b. corpuscula* is not recognized herein because of the failure of our comparative study to find significant morphological characters to clearly distinguish this geographically distinct population (see "Discussion" for *bonnellii*). The population appears to be restricted to a narrow band of southern subtropical waters between about 28°S and 40°S, bordering the SSTC, and extending from off the eastern coast of South America to longitude 180° in the Pacific. It has been taken in open ocean over this geographic range, but it has been taken in greatest number in areas associated with land or submarine topography where the productivity is presumably highest. It does not normally occur in the transitional waters of the SSTC, the habitat of the closely related *macrohista*, but appears to regularly occur in the transitional waters of the Benguela and East Australian currents. In the former current, *bonnellii* (southern population) has only been taken in the southern portion, whereas its convergence sibling is distributed over the entire current. The recent western Indian Ocean cruise of the R/V *Vityaz*, which collected cephalopods between 13°N and 34°S, first encountered *bonnellii* (southern population) at 25°S off Mozambique and found it to occur in greatest number between 28°S and 34°S in the area of Walters Shoal, where it ranked second among congeners in abundance to the pseudo-cenotic, semi-south subtropical species *miranda*. Distributional data for cephalopods in the subtropical, eastern Indian Ocean are scarce, so it is not clear if the lack of records from that area indicates a true absence of the species. Off eastern Australia, *bonnellii* (southern population) inhabits the East Australian Current between about 33°S and 38°S and inhabits the Tasman Sea and subtropical waters off the north coast of New Zealand to about 30°S. In these areas, the southern limit is marked by the SSTC and the northern limit appears to correspond to the Tasman Front, as was found above for the semi-south subtropical species, *miranda*. The apparent absence of *bonnellii* (southern population) in the eastern Pacific and in the central waters east of New Zealand closely resembles the absence and scarcity of its southern sibling species, *macrohista*, in the convergence of those areas. The broad expanse of low-nutrient waters that occurs in the central South Pacific is apparently great enough to impose a barrier to the eastward extension of the ranges of these two species.

#### *Southern Ocean*

OCEANIC.—1. *Subtropical Convergence Pattern*: The 274 known specimens of *H. macrohista* (Figure 9) were taken primarily between latitudes 33°S and 47°S in the SSTC and

fringing waters of the Atlantic, Indian, and western Pacific oceans. In the Atlantic, the species was found on the 1971 and 1975/1976 cruises of the R/V *Walther Herwig* to be common and second among congeners in abundance to the convergence/semi-subantarctic species *atlantica* over the entire width and breadth of the convergence. The 1971 west-east transect took *macrohista* (large juveniles, subadults, and adults) in greatest numbers in open ocean between 50°W and 35°W. The 1975/1976 north-south transects along 50°W and 40°W found it concentrated between 36°S and 40°S in the area of the convergence. The encounter of the species on the 40°W transect at two stations, between 47°S and 48°S, well south of the convergence, corresponds to the presence in the area of a pocket of warmer water in the upper 200 m (Hulley, 1981). In the eastern sector of the Atlantic, *macrohista* extends into the Benguela Current where it has been caught in considerable number and regularly occurs in the southern part of the current with its sibling species *bonnellii* (southern population), with *atlantica* and *miranda*, and, in the northern part with *reversa*. The species is known to extend across the Indian Ocean in a narrow belt between 36°S and 42°S and to be concentrated in the Australia–New Zealand area between 39°S and 47°S in the vicinity of the convergence. It is scattered in the Great Australian Bight but is absent or scarce in the East Australian Current system and the subtropical waters of the Tasman Sea, areas normally inhabited by its sibling species, *bonnellii* (southern population). The apparent absence of *macrohista* in the eastern Pacific and its scarcity in the oligotrophic central Pacific indicate a distributional pattern that is semicircumglobal, and not circumglobal, as has been found typical of the cranchiid *Teuthowenia pellucida* (Voss, 1985) and a number of midwater fishes that display the convergence pattern of distribution.

2. *Subtropical Convergence/Semi-Subantarctic Pattern*: *Histioteuthis atlantica* (Figure 5) is distributed circumglobally in the SSTC and in the subantarctic, where it is primarily restricted to north of 45°S–50°S. Additionally, data show the species to be scattered northward of the convergence to about 30°S–33°S in fringing subtropical waters. The large collections of juveniles, subadults, and adults made during the 1971 and 1975/1976 cruises of the R/V *Walther Herwig* show *atlantica* to occur in approximately equally high abundance across the convergence in the Atlantic between 55°W and 1°E and longitudinally between 39°S and 44°S. The only stations where the species was caught further south in the subantarctic during the 1975/1976 cruise were at the two mentioned above, between 46°S and 48°S, where the convergence species *macrohista* was taken in the vicinity of a pocket of warm water. In the eastern Atlantic, *atlantica* inhabits the southern sector of the Benguela Current, where it occurs with those congeners having distributions that are primarily restricted to the convergence and/or the adjoining halves of the subtropical or subantarctic regions. In the vicinity of Australia and New Zealand, the species extends northward to about 33°S in the

East Australian Current system, Tasman Sea, and northeast of New Zealand. The northern boundary in these areas can be described by the Tasman Front. Records from east of the New Zealand area show the species to be present in the area of the convergence, in the northern half of the subantarctic to 125°W, and off the western coast of South America in the Peru-Chile Current northward to 21°S. Distributional data from the South Pacific are too scarce to determine if the lack of reports between 125°W and 85°W shown on our map represents a true absence of the species. Three of the four reports of *atlantica* taken in the vicinity and southward of 34°S in the Peru-Chile Current came from east of 80°W, the faunal boundary found by Craddock and Mead (1970) at 34°S. Those authors showed that east of 80°W, the midwater-fish fauna was dominated by species from the SSTC or more southern waters. Across the broad geographic range of *atlantica*, occurrence appears to be largely confined to waters that, judging by the 100 m nitrate contours (Gordon, 1986, pl. 83), are of relatively low productivity. Concerning the southern limit of those species that display a semisubantarctic pattern of distribution, Hulley (1981:284) suggested that it could possibly correspond to "a zone of subantarctic Divergence, which has been recognized in the southern Indian Ocean in the vicinity of about 53°S in autumn and about 45°S in spring (Ivanov, 1961)."

3. *Subantarctic Pattern: Histiototeuthis eltaninae* (Figure 5) occurs circumglobally between the SSTC and the Antarctic Polar Front, and it has been found in greatest abundance in the probably higher-productive southern half of the region. Data show that the species does not normally inhabit the waters of the SSTC in the Atlantic or of the Benguela Current. In the area of Australia and New Zealand, however, *eltaninae* penetrates northward of the convergence to about 33°S in the East Australian Current system and to the same approximate latitude in the northeastern Tasman Sea. In both areas, it occurs with its more abundant sibling species, *atlantica*. As was found above for *miranda*, *bonnellii* (southern population), and *atlantica*, the northern limit of distribution in the northeastern Tasman Sea appears to occur at the Tasman Front.

### Discussion

The distributional patterns of the histiototeuthids show several striking features: (1) a close correspondence with patterns of variations in environmental conditions in the oceans; (2) the important role of productivity in the formation of the patterns and in the determination of the abundance of a taxon within its range; and (3) the contiguous nature of the patterns of members of a species group or of subspecies of a polytypic, widespread species. The distribution of each species or subdivision of a species that has been adequately studied is congruent with an area of the ocean characterized by a distinct combination of physical and biological features. The geographic area may be

relatively restricted, such as the Pacific eastern boundary currents in the case of *heteropsis*, or the SSTC in the case of *macrohista*, but typically is broad, exceeding the boundaries of a single water-mass region and usually encompassing the whole or parts of two or more adjoining regions.

Of the 13 currently recognized species, eight, *hoylei*, *arcturi*, *celetaria*, *corona*, *miranda*, *oceani*, *meleagroteuthis*, and *heteropsis*, are confined to the warm-water regime. Among these, *arcturi* (Atlantic) and *heteropsis* (Pacific) are confined to a single ocean, *hoylei*, *miranda*, and probably *oceani* inhabit two oceans, the Pacific and Indian oceans, and *celetaria*, *corona*, and *meleagroteuthis* inhabit all three oceans. Of the three warm-water, cosmopolitan species, only *meleagroteuthis* is regarded as being monotypic, with the possibility that a future, more detailed study will show it to comprise more than one taxon. The subspecies of the two polytypic, warm-water cosmopolites, *celetaria* and *corona*, are confined to either the Atlantic or Pacific or to the combined range of the Pacific and Indian oceans. No subspecies occurs in both the Atlantic and Pacific or the Atlantic and Indian oceans. For all of the above wide-ranging, warm-water species, with the present exception of *meleagroteuthis*, the land masses of the Americas and Africa act as geographic barriers to gene flow and dispersal. The semicircumglobal distribution of the southern population of *bonnellii* in the southern half of the southern Subtropical Region of the Atlantic, western Indian, and western Pacific oceans is novel for a warm-water histiototeuthid. Unaffected by the land mass of Africa, the pattern appears to be related to the SSTC and resembles that of a Southern-Ocean form.

Of the three Southern-Ocean patterns in the family, two, that of *atlantica*, which inhabits the SSTC and northern half of the subantarctic, and the closely related *eltaninae*, which occurs in the subantarctic, are typically circumglobal, and one pattern, that of *macrohista*, which is restricted to the SSTC, is semicircumglobal, mirroring the above-described pattern of its sibling species, the southern form of *bonnellii*. The east-west barrier for dispersal for the latter two histiototeuthids appears to be the broad expanse of low-nutrient waters of the central Pacific.

Although there are no strictly cold-water species or subspecies in the northern hemisphere, two histiototeuthids, *reversa* and *bonnellii* (northern population), extend from warm-water into north temperate or north temperate and subarctic waters in the Atlantic. There is evidence, however, suggesting the existence in the northern population of *bonnellii* of two subpopulations, a cold-water one occurring in the Subarctic, northern Temperate, and northern Mauritanian Upwelling regions and a warm-water one in the eastern tropical Atlantic (see "Discussion" of *bonnellii* and Table 10). The distribution pattern of the cold-water subpopulation, which includes a discontinuity between about 32°N and 35°N and the Mauritanian Upwelling Region, parallels that described by

Hulley (1981) for the mesopelagic myctophid *Myctophum punctatum* Rafinesque.

The geographic area in the Atlantic inhabited by a species or subdivision of a species of histioteuthid can be well described in terms of the faunal regions and provinces proposed by Backus et al. (1977). Based on the distributions of mesopelagic myctophid fishes, we have used their zoogeographic scheme in our descriptions of the different distributions and distribution patterns in the family. Although there is good conformity in the areas occupied by histioteuthids and myctophids with respect to the various boundaries used by Backus et al. to define their regions and provinces, there are considerable differences between the distribution patterns of histioteuthids and those patterns described for myctophids (Backus et al., 1977). Of the eight patterns displayed by myctophids in the Atlantic, only one, the Tropical-Subtropical pattern, is similarly found in histioteuthids. Our findings continue to show the highly individualistic nature of the distributional patterns of midwater species.

A conspicuous difference between the distributions of myctophids and histioteuthids is seen among the warm-water forms. Backus et al. (1977) and Hulley (1981) found most of the Atlantic, subtropical myctophids to be bipolar, that is, present in the North and South Subtropical regions but absent in the Tropical Region, whereas none of the histioteuthids are so distributed in the Atlantic or in the Pacific. A notable resemblance between the distributions of the two groups is found in the display of what Backus et al. (1977) called the "eastern effect," that is, the tendency for some species or subdivisions of a species to be present in the cooler, more productive eastern half of the Atlantic and absent in the western half. Among the histioteuthids, this type of distribution is shown by *bonnellii* (northern population) in the Tropical Region and by *reversa* in the northern Subtropical Region. Another resemblance is the occurrence in the Mediterranean Sea of only those species having distributions that normally include the area west of Gibraltar and more northern waters. The histioteuthid examples are *bonnellii* (northern population) and *reversa*. The warm-water histioteuthids *arcturi*, *H. corona corona* and *H. celetaria celetaria* that appear as waifs in the area west of Gibraltar are absent in the Mediterranean.

Among the cold-water species, no histioteuthid displays a bipolar (Krefft, 1974) or bitemperate (Hulley, 1981) pattern of distribution, a category to which both authors assign several species of myctophids. In the histioteuthids, the *reversa* group of closely related species is composed of a northern species, *reversa*, and two clearly distinct, Southern Ocean species, *atlantica* and *eltaninae*, with distributions that overlap in the Subantarctic Region. Hulley's (1981) data for his bitemperate myctophids suggest that the northern and southern populations also may be distinct. The subantarctic distributional pattern that characterizes *eltaninae* is referred to as Holosubantarctic by Hulley and is characteristic of a number of myctophids. He

assigns species that tend to have a more limited distribution in the Subantarctic Region and to be primarily confined to the northern half to his semisubantarctic subpattern. A histioteuthid distributional pattern that includes this portion of the subantarctic together with the SSTC, but excludes the southern portion of the subantarctic, typifies *atlantica*. The temperate, transitional Subtropical Convergence Pattern is common to the histioteuthid *macrohista*, the cranchiid *Teuthowenia pellucida*, and a considerable number of midwater fishes. Although some species of cranchiids, other mesopelagic squids, and various mesopelagic fishes normally occur south of the Antarctic Polar Front and display either an Antarctic Pattern or a Broadly Antarctic Pattern (Krefft, 1974), which includes the Subantarctic Region, no histioteuthid includes the Antarctic Region in its normal distribution range.

Because large expanses of the Pacific and Indian oceans, particularly the central waters (except for around Hawaii) of the Pacific and the northern and eastern (except for the shelf of northwestern Australia) sectors of the Indian Ocean, have been poorly sampled for cephalopods, we know less of the exact distributions of histioteuthids in those oceans than we do of those in the Atlantic. Consequently, we have been tentative in our assignments of distribution patterns to four of the eight taxa that live exclusively in the Pacific or inhabit both the Pacific and Indian oceans. No histioteuthid and few midwater fishes are known to be restricted to the Indian Ocean. The distributions of the four histioteuthids that are confined to the Pacific appear to be more restricted, being confined to a single zoogeographic region (northern Subtropical Region in the case of *H. corona berryi* and the eastern Tropical Region for *H. corona cerasina*) or to a particular transition area (eastern in the case of *heteropsis* and western for *H. corona inermis*), than are those of purely Atlantic taxa. Additionally, although data are scarce, two histioteuthids, *H. celetaria pacifica* and *oceani*, appear to primarily inhabit the large equatorial water masses of the Pacific and Indian oceans and so have been referred to the Tropical Pattern, a distribution pattern not seen among histioteuthids in the Atlantic. The differences between the distribution patterns in the Pacific and Atlantic reflect several of the important hydrographical differences that characterize the Pacific, specifically a distinct equatorial water mass, a well-developed Eastern Tropical Region, and well-developed boundary currents.

To conclude, we propose that the new knowledge of the systematics and distribution patterns of the histioteuthids presented herein, coupled with a planned phylogenetic analysis, will yield an evolutionary picture of this important, pelagic midwater family of squids as well as added insight into the evolution of pelagic midwater organisms in general. We hope that our work will provide a stimulus for additional, comparative morphological and biogeographical studies of histioteuthids and other pelagic cephalopods.

## Appendix

## List of Known Predators of the Histioteuthidae

(Predators identified by the presence of beaks and fleshy remains of histioteuthids in the stomach contents. Histioteuthid names are given as reported by the original authors, except *Histioteuthis* sp./spp. is used herein in place of Histioteuthidae. See Table 1 for names currently recognized.)

Prey	Predator	Geographic Area	Reference
Histioteuthidae Type 1	Pygmy sperm whale	Indian Ocean: southern Africa	Ross, 1984
Histioteuthidae Type 2	Pygmy sperm whale Dwarf sperm whale		
Histioteuthidae Type 3	Pygmy sperm whale		
Histioteuthidae Type 4	Dwarf sperm whale		
Histioteuthidae Type 7	Pygmy sperm whale		
Histioteuthidae unclassified	Dwarf sperm whale		
Histioteuthidae Type 8	Subantarctic fur seal	Southern Ocean: Gough Island	Bester and Laycock, 1985
? <i>Callioteuthis</i> sp.	Sperm whale	N Atlantic: Madeira	Clarke, 1962a
	Waved albatross	E Pacific: Galapagos Islands	Harris, 1973
<i>Histioteuthis</i> sp. A	Sperm whale	N Atlantic: Iceland; Tasman Sea; S Atlantic: Brazil	Clarke and MacLeod, 1976, 1982; Clarke et al., 1980
	Blue shark	N Atlantic: Britain	Clarke and Stevens, 1974
	Northern bottlenosed whale	N Atlantic: Faroe Islands	Clarke and Kristensen, 1980
	Grey-headed albatross	Southern Ocean: South Georgia	Rodhouse et al., 1990
<i>Histioteuthis</i> sp. A1	Sperm whale	Pacific Ocean: Peru, Chile	Clarke et al., 1976
<i>Histioteuthis</i> sp. A5	Sperm whale	Southern Ocean	Clarke, 1980
<i>Histioteuthis atlantica</i>	Wandering albatross	Southern Ocean: New Zealand, South Georgia	Imber and Russ, 1975; Clarke et al., 1981; Rodhouse et al., 1987
	Sooty albatross	Southern Ocean: Marion Island	Berruti and Marcus, 1978
	Sperm whale	Southern Ocean; SW Atlantic	Clarke, 1980; Clarke and McLeod, 1982; Vovk et al., 1978
	Short-tailed shearwater	Southern Ocean; Tasmania	Skira, 1986
	Dwarf sperm whale	S Atlantic: Brazil	Pinedo, 1987
<i>Histioteuthis ?atlantica</i>	Patagonian hake	S Pacific: Chile	Rocha V. et al., 1991
<i>Histioteuthis</i> sp. B	Sperm whale	Southern Ocean: Tasman Sea	Clarke, 1980; Clarke and McLeod, 1982
	Northern bottlenosed whale	N Atlantic: Faroe Islands	Clarke and Kristensen, 1980
	Grey-headed albatross	Southern Ocean: South Georgia	Rodhouse et al., 1990
<i>Histioteuthis</i> spp. B1, B2, B3	Sperm whale	Southern Ocean	Clarke, 1980
<i>Histioteuthis</i> sp. B4	Sperm whale	Southern Ocean; Tasman Sea	Clarke, 1980; Clarke and McLeod, 1982
<i>Histioteuthis bonelliana</i>	Sperm whale	N Atlantic: Madeira	Clarke, 1962a
<i>Histioteuthis bonnellii</i>	Sperm whale	N Atlantic: Iceland, Spain	Clarke and McLeod, 1974, 1976
	Bigeye tuna	E Atlantic: Gulf of Guinea, Benguela Current	Borodulina, 1974; Crawford et al., 1987
	Pygmy sperm whale	N Atlantic: Azores	Martins et al., 1985
	Blue shark	N Atlantic: Britain; Mediterranean	Clarke and Stevens, 1974; Bello, 1990
	Javelin fish	Southern Ocean: Campbell Plateau	Clarke, 1985b
	Albacore	SE Atlantic: Benguela Current	Crawford et al., 1987
	Southern bluefin tuna, Atlantic footballfish	NE Atlantic	Bertelsen and Krefft, 1988
<i>Histioteuthis ?bonnellii</i>	Grey-faced petrel	SW Pacific: New Zealand	Imber, 1973
<i>Histioteuthis b. corpuscula</i>	Sperm whale	SE Atlantic; SW Indian Ocean; Southern Ocean; Tasman Sea	Clarke, 1980; Clarke and McLeod, 1982
<i>Histioteuthis cookiana</i>	Sperm whale	Pacific: New Zealand	Gaskin and Cawthorn, 1967
<i>Histioteuthis corona</i>	Slender bream	SE Pacific	Parin et al., 1990
<i>Histioteuthis corpuscula</i>	Short-tailed shearwater	Southern Ocean: Tasmania	Skira, 1986
<i>Histioteuthis dofleini</i>	Bigeye tuna	Eastern Tropical Atlantic	Borodulina, 1974
	Sperm whale	N Atlantic: Iceland; NE Pacific: California, Canada; Tasman Sea; NW Pacific: Japan; SE Atlantic; SW Atlantic	Clarke and McLeod, 1976, 1980, 1982; Fiscus et al., 1989; Kawakami, 1976; Okutani et al., 1976; Vovk et al., 1978
	Northern elephant seal	NE Pacific	Antonelis et al., 1987
	Swordfish	Western N Atlantic: Florida	Toll and Hess, 1981



## Appendix.—Continued.

Prey	Predator	Geographic Area	Reference
<i>Histioteuthis eltaninae</i>	Wandering albatross	Southern Ocean: New Zealand, South Georgia	Imber and Russ, 1975; Clarke et al., 1981; Rodhouse et al., 1987
	Light-mantled sooty albatross	Southern Ocean: South Georgia	Thomas, 1982
	Grey-headed albatross	Southern Ocean: South Georgia, Edward Isles	Clarke and Prince, 1981; Brook and Klages, 1986
	Sooty albatross	Southern Ocean: Marion Island	Berruti and Marcus, 1978
	Emperor penguin	Southern Ocean: Adelle Land	Offredo et al., 1985
	Sperm whale	SE Atlantic; Southern Ocean	Vovk et al., 1978; Clarke, 1980
	Southern elephant seal	Southern Ocean: South Georgia	Rodhouse et al., 1992
<i>Histioteuthis heteropsis</i>	Northern elephant seal	NE Pacific	Antonelis et al., 1987
	Northern fulmar	NE Pacific: Washington	Hills and Fiscus, 1988
	Sperm whale	NE Pacific: California	Fiscus et al., 1989
	Scalloped and smooth hammer-head sharks	NE Pacific: Gulf of California	Galvan-Magana and Nienhuis, 1989
<i>Histioteuthis macrohista</i>	Wandering albatross	Southern Ocean: New Zealand	Imber and Russ, 1975
	Sooty albatross	Southern Ocean: Marion Island	Berruti and Marcus, 1978
	Sperm whale	SE and SW Atlantic	Vovk et al., 1978
	Short-tailed shearwater	Southern Ocean: Tasmania	Skira, 1986
	Dwarf sperm whale	S Atlantic: Brazil	Pinedo, 1987
	Neon flying squid	SW Atlantic	Lipinski and Linkowski, 1988
	Bigeye tuna	Eastern Tropical Atlantic	Borodulina, 1974
<i>Histioteuthis ?meleagroteuthis</i>	Sperm whale	SE Atlantic; Tasman Sea	Clarke, 1980; Clarke and McLeod, 1982
<i>Histioteuthis miranda</i>	Wandering albatross	Southern Ocean: New Zealand	Imber and Russ, 1975
	Sooty albatross	Southern Ocean: Marion Island	Berruti and Marcus, 1978
	Sperm whale	SE Atlantic; SW Indian Ocean; Southern Ocean; Tasman Sea	Clarke, 1980; Clarke and McLeod, 1982
<i>Histioteuthis reversa</i>	Blue shark	N Atlantic: Britain; Mediterranean	Clarke and Stevens, 1974; Bello, 1990
	Sperm whale	SE Atlantic	Vovk et al., 1978
	Pygmy sperm whale	N Atlantic: Azores	Martins et al., 1985
<i>Histioteuthis</i> sp. (? <i>corpuscula</i> )	Dwarf sperm whale	S Atlantic: Brazil	Pinedo, 1987
<i>Histioteuthis</i> sp. (? <i>meleagroteuthis</i> )	Tiger shark	SW Pacific	Rancurel, 1973
<i>Histioteuthis</i> sp./spp.	Spotted porpoise	N Pacific	Perrin et al., 1973
	Yellowfin tuna, Westland black petrel	SW Pacific: New Zealand	Imber, 1973
	White-chinned petrel, Grey-faced petrel, Rattail	NW Atlantic	Haedrich and Henderson, 1974; Sedberry and Musick, 1978
	Sperm whale	N Atlantic: Iceland; NE Pacific: California; SE Pacific: Peru, Chile; SW Atlantic	Clarke and McLeod, 1976; Clarke et al., 1976; Fiscus et al., 1989; Vovk et al., 1978
	Black petrel	SW Pacific; Southern Ocean: New Zealand	Imber, 1976
	Lancetfishes	NW Atlantic	Matthews et al., 1977
	Northern cutthroat eel	NW Atlantic	Sedberry and Musick, 1978
	Swordfish	NW Atlantic	Toll and Hess, 1981; Stillwell and Kohler, 1985
	Northern shortfin squid	N Atlantic: Newfoundland	O'Dor, 1983
	European squid	Mediterranean	Worms, 1983
	Subantarctic fur seal	Southern Ocean: Gough Island	Bester and Laycock, 1985
	Short-tailed shearwater	Southern Ocean: Tasmania	Skira, 1986
	King penguin	Southern Ocean: Marion Island	Adams and Klages, 1987; Adams and Brown, 1989
	Footballfish	Eastern Tropical Atlantic	Bertelsen and Krefft, 1988
	Blue shark	NE Pacific	Harvey, 1989
<i>Stigmatoteuthis</i> sp.	Sperm whale	N Pacific: Bering Sea, Gulf of Alaska; NE Pacific	Okutani and Nemoto, 1964; Fiscus, 1982
<i>Meleagroteuthis separata</i>	Sperm whale	N Pacific: Kurile Island; Bering Sea	Akimushkin, 1955; Betesheva and Akimushkin, 1955; Tarasevich, 1963, 1968; Fiscus, 1982

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# Workshop Deliberations on the Ommastrephidae: A Brief History of Their Systematics and a Review of the Systematics, Distribution, and Biology of the Genera *Martialia* Rochebrune and Mabile, 1889, *Todaropsis* Girard, 1890, *Dosidicus* Steenstrup, 1857, *Hyaloteuthis* Gray, 1849, and *Eucleoteuthis* Berry, 1916

John H. Wormuth

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## ABSTRACT

The ommastrephid working group reached consensus on two issues: (1) the genus *Ommastrephes* includes only *O. bartramii*, whereas the genus *Sthenoteuthis* includes *S. ovalaniensis*, *S. pteropus*, and a new species presently being described by M. Roeleveld; and (2) the cross-sectional shape of the gladius, a previously neglected character, shows considerable, but not complete, agreement at generic levels.

*Todaropsis* is a monospecific genus and is distinguished from *Illex* in that it has four rows of longitudinal suckers on the dactylus of the tentacular clubs.

Three species of the Ommastrephinae are treated herein, *Dosidicus gigas* (Orbigny, 1835), *Hyaloteuthis pelagica* (Bosc, 1802), and *Eucleoteuthis luminosa* (Sasaki, 1915). They can be separated on internal and external photophore patterns, hectocotylus morphology, size at maturity, and geographical distributions. They represent strong swimming squid of the open ocean and exhibit diel vertical migrations.

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## Workshop Deliberations

This paper is, in part, a result of the Cephalopod International Advisory Council (CIAC)-sponsored workshop held in Washington, D.C., in July 1988. The working group on Ommastrephidae consisted of Malcolm Dunning, Ellen Förch,

Manuel Haimovici, Chingis Nigmatullin, and John Wormuth. The consensus of the group at the time of the workshop is reflected in the following taxonomic structure and in that given in Dunning (1998), Dunning and Förch (1998), Dunning and Wormuth (1998), and Roper et al. (1998).

Although the opinion expressed by Roeleveld (1988:278) concerning the "over-emphasis of the importance of measurements and counts, with the result that significant morphological differences have been overlooked," has some merits, it is impossible to ignore measurements and counts as meaningful systematic characters. The generic interrelationships elucidated by Roeleveld (1988:278) are based on four "of the more important characters," the selection of which is based on (1) tradition, (2) patterns in variation, and (3) development trends. We may have opposite ends of the spectrum in these two approaches, namely, too much data with little or no weighting versus too little data weighted by one experienced researcher.

The majority of active ommastrephid researchers were represented at the workshop. The results represent the group consensus based on two concentrated weeks of comparative laboratory work, constant evaluation and discussion, and consultation with a member of the International Commission on Zoological Nomenclature (F.M. Bayer, Smithsonian Institution). Although biochemical, genetic, or other advanced techniques may clarify or refine our results, and the discovery of new species or new distributional data could fill in present gaps, we feel the workshop papers represent our current understanding of systematics in the Ommastrephidae.

Several things should be highlighted: (1) the genus *Ommastrephes* includes only *O. bartramii*, whereas the genus

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*Sthenoteuthis* includes *S. oualaniensis*, *S. pteropus*, and a new species presently being described by M. Roeleveld; and (2) the cross-sectional shape of the gladius (see Toll, 1990), a previously neglected character, shows considerable, but not complete, agreement at generic levels. The five genera discussed in this paper were selected to assure complete coverage of the Ommastrephidae. The remaining six genera are discussed by Dunning (1998), Dunning and Förch (1998), Dunning and Wormuth (1998), and Roper et al. (1998). *Martialia hyadesi* Rochebrune and Mabile, a species poorly known since its description in 1889, has recently been caught in large numbers over the Patagonian Shelf (southwestern Atlantic) and off New Zealand, and it has recently been thoroughly reviewed by Rodhouse and Yeatman (1990).

ACKNOWLEDGMENTS.—The organizers of the Workshop did a fine job of bringing together a diverse group of specialists and providing an atmosphere conducive to concentrated work. My thanks to Mike Sweeney, Clyde Roper, and Mike Vecchione for their excellent preparations.

#### A Brief History of Ommastrephid Systematics

The first ommastrephid described was *Loligo sagittata* (Lamarck, 1799:14). Bosc (1802:46) described *Sepia pelagica* with only eight lines of text, but he did provide a single character that makes its identification unmistakable. After an examination of generic characters, Lesueur (1821:89) suggested that the two genera were quite different and that *Loligo* constituted a separate family for which he proposed the name Loligoidea. In the same paper he described *Loligo bartramii* and *L. illecebrosa*.

Lesson (1830:240) described *L. oualaniensis*, named for its collection locality, the Caroline (Oualan) Islands. In 1835 some of the recent confusion over generic names began when Orbigny (1835:45) described a new genus, *Ommastrephes*, and two new species, *O. gigas* and *O. cylindraceus*. He also included *Loligo bartramii* in the new genus, but he did not designate a type species. Orbigny also considered the genus to contain *Loligo sagittata*, *L. oualaniensis*, *L. illecebrosa*, and probably *L. pelagica* in addition to those he specifically placed in the genus. Verany (1839:94) described *Loligo coindetii*, and, shortly afterward, Ball (1841:362) described *L. eblanae*. The description of the former species, which is based on a young individual (127 mm total length), is accompanied by a poor figure. The latter species also is based on a young individual (78 mm mantle length (ML)) and the original figures are of poor quality, even with respect to general shape. Herrmannsen (1847:145) fixed *Loligo bartramii* as the type species of the genus *Ommastrephes*, making it the first genus of the Ommastrephidae to be based on a type species. Gray (1847:206) designated *L. sagittata* as the type of the genus *Ommastrephes*, but this was invalid (see Adam, 1939; Okutani, 1962).

Gray (1849) listed the species of *Ommastrephes*. Neither *L.*

*coindetii* or *L. eblanae* was included. He did, however, include all other ommastrephid species previously described and gave an account of a new species, *O. sloanii*, from Maitemata, New Zealand. Gray made an attempt to divide the genus into groups and appears to be the first to mention the fusion of the funnel and mantle cartilage in *O. oualaniensis*. He also named a new genus, *Hyaloteuthis*, for *Sepia pelagica*.

Gould (1852:480) described *O. insignis* based on a specimen from Fiji. He had another specimen from "Antarctic Seas," but it does not appear to be the one used for the original description. Steenstrup (1855:199) described *Ommastrephes pteropus* from a specimen collected in 1661 on the beach near Cattvick, Holland. In 1857 (Steenstrup, 1857a:120) a new genus and species, *Dosidicus eschrichtii*, was described. Based on subsequent literature it would appear that *D. eschrichtii* is a synonym of *O. gigas* and that the latter species is the type species of *Dosidicus*.

The genus *Illex* was erected by Steenstrup (1880:80) to include *Ommastrephes coindetii* and *O. illecebrosus*. In this paper he (1880:83) also erected *Todarodes* to include *O. sagittata* and *O. pacificus*, which he described in the same paper (1880:78). Furtado (1887:5) described a new species, *O. caroli* (= *Ommastrephes bartramii* (Lesueur) fide Dunning, 1998), from Portugal. In the following year, McCoy (1888:255) described a new species, *O. gouldi*, from Australia, which he noted as being similar to both *O. insignis* (= *Nototodarus sloanii* (Gray) fide Nesis, 1987) and *O. sloanii*. Girard (1890:200) named the genus *Todaropsis* with *Loligo eblanae* as the type species.

Rochebrune and Mabile (1889:9) described *Martialia hyadesi*, naming it after the captain of the expedition, M. Martial, of the *La Romanche*, and after the scientist in charge of the study of natural history, M.M. Hyades. The original collection locality was listed as Orange Bay, Cape Horn (55°30'S, 68°2'W). Until recently, the species has remained relatively unknown, but a recent paper by Rodhouse and Yeatman (1990) has provided a thorough redescription. The authors suggest a closer affinity to *Todarodes* than to *Nototodarus*, based on hectocotylus comparisons.

The genus *Symplectoteuthis* was erected by Pfeffer (1900:180) to include *S. oualaniensis*. In 1912 Pfeffer published a very extensive volume on the Cephalopoda with the most comprehensive study on the Ommastrephidae to date. In this monograph he erected a new genus, *Nototodarus*, based on a specimen from Akorua, New Zealand, that he identified as *Ommastrephes insignis* Gould. Subsequent work in the New Zealand area (Dell, 1952) indicated that only one species of *Nototodarus* is found there, the species originally designated *O. sloanii* Gray, and that Pfeffer misidentified his specimen. This makes *N. sloanii* the type species of *Nototodarus*.

In the same year, Berry (1912:338) described *Ommastrephes hawaiiensis* based only on female specimens from the Hawaiian Islands. Specimens collected in the late 1960s support Berry's (1918) contention that *O. hawaiiensis* is a



species of *Nototodarus*. Sasaki (1915:138, 144) described *O. volatilis* and *Symplectoteuthis luminosa* from Japan, and in the following year Berry (1916:60) suggested that *S. luminosa* be placed in a new genus, *Euclideanoteuthis*, because of its unusual photogenic streaks. Okada (1927:13) suggested that *O. volatilis* be placed in a new genus, *Ornithoteuthis*. This separation has been adopted by all subsequent authors except Sasaki (1929).

Adam (1957:3) described a subspecies, *Ornithoteuthis volatilis antillarum*, that was later elevated to species rank by Voss (1957:370). *Illex argentinus* was described by Castellanos (1960:55) from the area off Buenos Aires, Argentina. Two years later, Voss (1962:173) described *Nototodarus sloanii philippinensis* collected near Luzon, Philippines. Roper et al. (1969:299) described *Illex oxygonius* from the western Atlantic. *Nototodarus nipponicus* (Okutani and Uemura, 1973:39) was described from specimens from southern Honshu, Japan. In a more recent paper, Okutani and Kuroiwa (1985) considered *N. nipponicus* to be a junior synonym of *N. sloanii philippinensis*. Dunning (1988a:149) described *Todarodes pacificus pusillus* from northern Australia. Roeleveld (pers. comm.) is describing a new species of *Sthenoteuthis* Verrill to separate the smaller, early maturing form of *S. oualaniensis* that lacks the dorsal light organ from the large-maturing form that possesses the dorsal light organ in the later growth stages.

### Systematics, Distribution, and Biology

#### Family OMMASTREPHIDAE Steenstrup, 1857

DIAGNOSIS.—Locking cartilage an inverted T-shape; biserial suckers on arms, tetraserial suckers on tentacular clubs (except *Illex*, with 8 rows); buccal connectives attached to dorsal borders of arms IV; photophores in some genera.

TYPE GENUS.—*Ommastrephes* Orbigny, 1835.

DISTRIBUTION.—Species are found roughly from 40°N to 40°S in all oceans. Adults vary from approximately 100 mm ML to 1.5 m ML. See Table 1 for family species list.

#### Subfamily TODARODINAE Adam, 1960

DIAGNOSIS.—Funnel groove with anterior foveola, foveola with variable number of longitudinal folds but without side pockets; no carpal-fixing apparatus on tentacular stalk; photophores absent during all phases of life cycle; longitudinal ridge of mantle component of locking cartilage straight; cross section A of gladius (see Toll, 1990) with 2 or 3 lateral lobes.

TYPE GENUS.—*Todarodes* Steenstrup, 1880:83.

DISCUSSION.—In his review of hectocotylization in the family, Adam (1960:2) was the first to recognize the subfamily *Todarodinae*, in which he included *Todarodes* (= *Ommastrestrophes* sensu Pfeffer, 1912:444) and *Nototodarus* Pfeffer, 1912:434. He also used the subfamilial designation *Ommastrestrophinae* to replace Pfeffer's (1912:479) *Sthenoteuthinae*.

Roeleveld (1988:283) considered the *Todarodinae* to be

TABLE 1.—The taxonomic structure of the Family Ommastrephidae.

Taxon	Reference
Family OMMASTREPHIDAE	
Subfamily TODARODINAE	
Genus <i>Todarodes</i>	Dunning and Wormuth, 1998
<i>Todarodes sagittatus</i>	
<i>Todarodes angolensis</i>	
<i>Todarodes filippovae</i>	
<i>Todarodes pacificus</i>	
<i>T. pacificus pacificus</i>	
<i>T. pacificus pusillus</i>	
Genus <i>Nototodarus</i>	Dunning and Förch, 1998
<i>Nototodarus hawaiiensis</i>	
<i>Nototodarus gouldi</i>	
<i>Nototodarus sloanii</i>	
Genus <i>Martialia</i>	Wormuth, herein
<i>Martialia hyadesi</i>	
Subfamily ILLICINAE	
Genus <i>Illex</i>	Roper, Lu, and Vecchione, 1998
<i>Illex illecebrosus</i>	
<i>Illex coindetii</i>	
<i>Illex argentinus</i>	
<i>Illex oxygonius</i>	
Genus <i>Todaropsis</i>	Wormuth, herein
<i>Todaropsis eblanae</i>	
Subfamily OMMASTREPHINAE	
Genus <i>Ommastrephes</i>	Dunning, 1998
<i>Ommastrephes bartramii</i>	
Genus <i>Sthenoteuthis</i>	Dunning, 1998
<i>Sthenoteuthis oualaniensis</i>	
<i>Sthenoteuthis pteropus</i>	
Genus <i>Dosidicus</i>	Wormuth, herein
<i>Dosidicus gigas</i>	
Genus <i>Ornithoteuthis</i>	Dunning, 1998
<i>Ornithoteuthis volatilis</i>	
<i>Ornithoteuthis antillarum</i>	
Genus <i>Euclideanoteuthis</i>	Wormuth, herein
<i>Euclideanoteuthis luminosa</i>	
Genus <i>Hyaloteuthis</i>	Wormuth, herein
<i>Hyaloteuthis pelagica</i>	

“characterized by the apomorphic condition of having the distal trabeculae of the hectocotylus thickened, giving the ventral distal protective membrane the appearance of a picketed flange.” She further considered the genera *Todaropsis* and *Nototodarus* to form a monophyletic group within the subfamily, united by the synapomorphy of the secondary modification of the medial and basal parts of the hectocotylized right arm IV and mirrored on the left arm IV.

#### *Martialia* Rochebrune and Mabile, 1889

DIAGNOSIS.—Protective membranes on arms poorly developed, trabeculae strongly developed and prominent; hectocotylus on distal 1/3 of right arm IV of trabeculae as rounded flaps on ventral side, flaps reduced then distally absent on dorsal side; tentacular club not expanded; largest manus suckers with

15 relatively large, sharp teeth (1 lateral tooth usually larger than others) alternating with 15 smaller, flatter plates or blunt teeth; no carpal-fixing apparatus; cross section A of gladius (see Toll, 1990) with 2 lateral lobes. Monospecific.

TYPE SPECIES.—*Martialia hyadesi* Rochebrune and Mabile, 1889:9, pl. 1.

***Martialia hyadesi* Rochebrune and Mabile, 1889**

DIAGNOSIS.—As for genus.

ORIGINAL REFERENCE.—Rochebrune and Mabile, 1889:9, pl. 1.

TYPE LOCALITY.—Orange Bay (Cook Bay), Cape Horn, South America.

DEPOSITION OF TYPES.—*Syntype*: Museum Nationale d'Histoire Naturelle, Paris, 7-3-512, 7-3-513 (gladius from 7-3-512).

DISTRIBUTION AND LIFE HISTORY.—*Martialia hyadesi* has been collected from Cape Horn (Rochebrune and Mabile, 1889), Macquarie Island, the Patagonian Shelf, and the Antarctic Polar Frontal Zone (Rodhouse and Yeatman, 1990). Rodhouse and Yeatman (1990:141) suggested that "its distribution is related to the cool temperate waters of the Southern Ocean southward to the Antarctic Polar Frontal Zone and possibly extending south of the Front." A recent paper (Uozumi et al., 1991) extends the distribution of this species to New Zealand waters, where immature individuals (101 mm ML and smaller) were collected around and southward of the subtropical convergence zone. The small size of some individuals (<30 mm ML) indicated spawning on or near the Auckland Island Shelf.

The species has been collected in commercial quantities by the Japanese near Shag Rocks (53°33'S, 42°03'W) at bottom depths of 100–200 m and further west on the northern edge of the North Scotia Ridge in water depths of 3000 m (Rodhouse, 1989). This species represents 73%–79% of the biomass in the diet of grey-headed albatross chicks at Bird Island, South Georgia (Rodhouse et al., 1990), and up to 83% of the diet of adult black-browed albatross at South Georgia (Rodhouse, 1990). By analyzing beak measurements, Rodhouse et al. (1990) found evidence of growth of *M. hyadesi* between January and June. This squid also is present in the diet of the wandering albatross but in much lower relative importance (5% of diet) (Rodhouse et al., 1987). This low occurrence may be due to a more southerly distribution of the wandering albatross, which spends much of its time over waters presently thought to be uninhabited by *M. hyadesi*.

**Subfamily ILLICINAE Posselt, 1890**

DIAGNOSIS.—Funnel groove smooth, without foveola or side pockets; dactylus of tentacular club with either 4 or 8 longitudinal rows of suckers; no carpal-fixing apparatus on tentacular stalk; photophores absent during all phases of life

cycle; longitudinal ridge of locking cartilage straight; cross section A of gladius (see Toll, 1990) with either 2 or 3 lateral lobes.

TYPE GENUS.—*Illex* Steenstrup, 1880:82.

DISCUSSION.—The subfamily Illicinae as proposed by Posselt (1890) included only the genus *Illex* Steenstrup. Pfeffer (1912) considered that, on the basis of the characters of the funnel groove, *Todaropsis* Girard, 1890, also should be included in the subfamily. This grouping of genera within the subfamily had been generally accepted until Roeleveld (1988) reviewed important taxonomic characters within the family. She considered the undifferentiated funnel groove to be a secondary loss and homoplastic both in *Todaropsis* and in *Illex*. On the basis of morphological characteristics of the hectocotylus, she placed *Todaropsis* within the Todarodinae. This classification has yet to receive widespread support and was not supported by the CIAC Workshop Group based on consideration of a wider suite of characters. The Illicinae has been considered to be the stem group of the family Ommastrephidae (Pfeffer, 1912:389; Naef, 1923:428), although this proposition has been questioned by Roeleveld (1988).

***Illex* Steenstrup, 1880**

DIAGNOSIS.—Dactylus of tentacular clubs with 8 rows of longitudinal suckers; cross section A of gladius (see Toll, 1990) with 3 lateral lobes.

TYPE SPECIES.—*Loligo coindetii* Verany, 1839:94.

DISCUSSION.—This genus is discussed in detail by Roper et al. (1998).

***Todaropsis* Girard, 1890**

DIAGNOSIS.—Dactylus of tentacular club with 4 rows of longitudinal suckers; medial manus sucker rings with 30 or more evenly spaced, approximately equal, long, pointed teeth; both arms IV hectocotylized in mature males; cross section A of gladius (see Toll, 1990) with 2 lateral lobes. Monospecific.

TYPE SPECIES.—*Loligo eblanae* Ball, 1841:362.

***Todaropsis eblanae* (Ball, 1841)**

DIAGNOSIS.—As for genus.

ORIGINAL REFERENCE.—Ball, 1841:364.

TYPE LOCALITY.—Dublin Bay, Ireland.

DEPOSITION OF TYPES.—Unknown (Science and Art Museum, Dublin at the turn of the century, fide Hoyle (1903)).

*Paratypes*: One designated.

DISTRIBUTION AND BIOLOGY.—*Todaropsis eblanae* is a demersal species of the deeper shelf and continental slope occurring throughout the Mediterranean Sea and in the eastern Atlantic from the Shetland Islands and Skagen, Denmark, in the north, to Capetown, South Africa, in the south (Adam, 1952); in the Indian Ocean on the Agulhas Bank, Mascarenes Ridge,

and western Australian coast; and off the eastern Australian coast to as far as 37°12'S (Korzun et al., 1979; Lu, 1982; Nesis, 1987; Dunning, 1988b).

*Todaropsis eblanae* is usually associated with sandy or muddy bottoms, although small juveniles have been taken in near-surface waters using midwater trawls (Dunning, 1988b). In the Atlantic and in the Mediterranean Sea, this species has been trawled in depths of 20–700 m but appears confined to depths of less than 200 m in the North Sea (Clarke, 1966).

*Todaropsis eblanae* was caught in Australian waters in demersal trawls where depths varied from 200 m to 805 m and bottom temperatures varied from 9.0°C to 17.5°C. The distributions of *Todaropsis eblanae* and *Nototodarus hawaiiensis* overlap significantly off both the east and northwest coasts of Australia. These species were caught in demersal trawls together with *Todarodes pacificus pusillus* (Dunning, 1988a) in depths of 200–250 m off the northeast Australian coast.

Male and female *T. eblanae* were relatively evenly represented (28:34) in material examined from northeastern Australian waters (Dunning, 1988b), in contrast to the female-dominated sex ratios observed in more oceanic ommastrephids (especially *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis*).

Female *T. eblanae* from Australian waters reach maturity at approximately 150 mm ML; males mature from 120 mm ML. Spawning apparently occurs in east coast waters at least from late summer to early winter (Lu, 1982; Dunning, 1988b). Catalanian (Mediterranean) Sea populations of *T. eblanae* were studied by Mangold-Wirz (1963). Males reached maturity at 110–140 mm ML and produced about 200 spermatophores; females matured at 160–190 mm ML and carried 5000 to 10,000 eggs. The spawning season for this population was found to be protracted in this region, lasting at least nine months, from March to November (spring to late autumn).

Prey items are unknown, but predators are known to include *Heptanchus* (Adam, 1952) and *Germo alalunga* (Bouxin and Legendre, 1936).

DISCUSSION.—Roeleveld (1988) reviewed the importance of the characteristics of the funnel groove as a primary taxonomic character within the family Ommastrephidae and reassessed the placement of *Todaropsis* within the Illicinae. She placed this species within the Todarodinae, forming a monophyletic group with *Nototodarus*. This classification has yet to receive widespread support.

#### Subfamily OMMASTREPHINAE Adam, 1960

DIAGNOSIS.—Funnel groove with foveola, foveola with longitudinal folds and with or without side pockets; carpal-fixing apparatus of smooth-ringed suckers and knobs on tentacular stalk; photophores present during all phases of life cycle; longitudinal ridge of mantle component of locking cartilage straight or with anterior bifurcation; cross section

A of gladius (see Toll, 1990) with either 2 or 3 lateral lobes.

TYPE GENUS.—*Ommastrephes* Orbigny, 1835:48.

DISCUSSION.—Steenstrup (1880) divided the “Ommatostrephini” into three groups based on the structure of the funnel groove. One group, with folds both in a single large pocket of the foveola and in smaller lateral pockets, included *Ommatostrephes gigas* Orbigny (1835), *O. pteropus* Steenstrup (1880), *O. bartramii* (Lesueur, 1821), *O. oualaniensis* (Lesson, 1830), *O. pelagicus* Bosc, 1802, and *Dosidicus eschrichti* Steenstrup, 1857. A second group, with only folds in the foveola and with no lateral pockets, included *Todarodes sagittatus* (Lamarck, 1799) and *T. pacificus* (Steenstrup, 1880). The third group, with a smooth funnel groove, included *Illex illecebrosus* (Lesueur, 1821) and *I. coindetii* (Verany, 1839).

Posselt (1890) divided the family into two subfamilies, Illicinae (containing *Illex*) and Ommatostrephinae (the remainder of the above genera). Pfeffer (1912) split the family into three subfamilies: Posselt's Illicinae to include also *Todaropsis*, Ommatostrephinae (with no lateral pockets) to include his *Ommatostrephes* (i.e., *O. sagittatus*, *O. hyadesi*, and *O. sloanii*) and *Nototodarus* (*Ommastrephes insignis* Gould, 1852), and Sthenoteuthinae (with side pockets) to include *Hyaloteuthis pelagica*, *Sthenoteuthis bartramii*, *S. pteropus*, *S. caroli*, *S. incerta* (= *Ommatostrephes gigas* Orbigny), and *Symplectoteuthis oualaniensis* (Lesson).

Thiele (1935) accepted three subfamilies, namely, Illicinae and Ommatostrephinae as given by Pfeffer, with the addition of *Ornithoteuthis volatilis* (Sasaki, 1915) to the latter, and Sthenoteuthinae as given by Pfeffer with the addition of *Symplectoteuthis luminosa* Sasaki, 1915.

Adam (1960) accepted the concept of three subfamilies, as above, but with the name Todarodinae replacing Ommastrephinae to include *Todarodes* (= *Ommatostrephes* of Pfeffer) and *Nototodarus*, and the name Ommastrephinae to replace Sthenoteuthinae.

#### *Dosidicus* Steenstrup, 1857

DIAGNOSIS.—Funnel groove deeply excavated in foveola, rounded anteriorly, with average of 7 longitudinal ridges and 4 to 5 side pockets; dactylus of tentacular club with suckers in 4 longitudinal rows; small subcutaneous photophores on ventral surface of mantle, head, and arms III and IV, 2 intestinal photophores; right or left arm IV hectocotylized; longitudinal ridge of mantle component of locking cartilage with anterior bifurcation; cross section A of gladius (see Toll, 1990) with 3 lateral lobes. Monospecific.

TYPE SPECIES.—*Ommastrephes gigas* Orbigny, 1835:48, pl. 4.

#### *Dosidicus gigas* (Orbigny, 1835)

DIAGNOSIS.—As for genus.

ORIGINAL REFERENCE.—Orbigny, 1835:48, pl. 4.

**TYPE LOCALITY.**—Eastern South Pacific off coast of South America.

**DEPOSITION OF TYPE.**—*Syntype*: Museum Nationale d'Histoire Naturelle, Paris, 7-3-660.

**DISCUSSION.**—Steenstrup (1857a) described a new genus and species, *Dosidicus eschrichti*. He listed three differences between this genus and *Ommatostrephes*: (1) the attenuation of the arms and the small numerous suckers on their distal portions; (2) the four to five fleshy adhesive knobs that compose the carpal-fixing apparatus, "a feature hitherto is known only in the *Onychoteuthis* group" (p. 120); and (3) the shape of the gladius is similar to *Ommatostrephes* but (p. 120) "carries at its posterior end a big funnel-shaped phragmocone whose two-thirds are filled with a solid horny mass giving it greater weight." Based on present knowledge of the family, this latter character has not been attributed to any other species in the family by any other author. Steenstrup did not give a collecting locality in the original paper but later listed the locality as Marseilles (Steenstrup, 1857b). Steenstrup (1857b) used the name *Ommatostrephidae* for the family, having emended the genus to *Ommatostrephes* in 1855. Steenstrup (1862) later decided that the specimen of *Dosidicus eschrichti* probably was collected in the South Seas. In the Paris Museum, Steenstrup saw a specimen of *O. gigas* that was stated to be the type and was supposedly identified by Orbigny himself. Steenstrup claimed that the specimen did not correspond to Orbigny's own description and that he must have sent another specimen to the museum by mistake. He further stated that the gladius of *Dosidicus* is entirely different from that of *O. gigas*. The original description and figures of Orbigny, however, leave little doubt that he described what is now known as *Dosidicus gigas* (Pfeffer, 1900, 1912; Berry, 1911; Clarke, 1966). I conclude that *D. eschrichti* is *D. gigas*.

**DISTRIBUTION AND BIOLOGY.**—*Dosidicus gigas* is the only species ever placed in the genus. It is distributed in the eastern tropical Pacific from about 26°S to as far north, occasionally, as Monterey, California (Figure 1), but usually it does not occur farther north in the Pacific Ocean than mid-Baja, California. This periodic anomalous extension is a result of El Niño-Southern Oscillation events. In the equatorial region, the distribution extends as far west as 140°W, but these individuals probably are expatriates, being advected westward in the equatorial current system. Areas of high density exist from 0° to 18°S and from 16°N to 28°N, including the Gulf of California (Nesis, 1970; Suda, 1973; Sato, 1976; Wormuth, 1976). Immigration into the Gulf of California appears to occur in January and reaches to about 29°N by April (Ehrhardt et al., 1983). In late August and September an emigration takes place back toward the entrance to the Gulf. Populations separate there into a southward migrating group and a northward migrating group. Significant morphometric changes occur in this species from north to south. Specimens from the southern area have proportionately longer arms relative to mantle length (Figure 2) as well as more suckers per arm. In other pelagic species of this

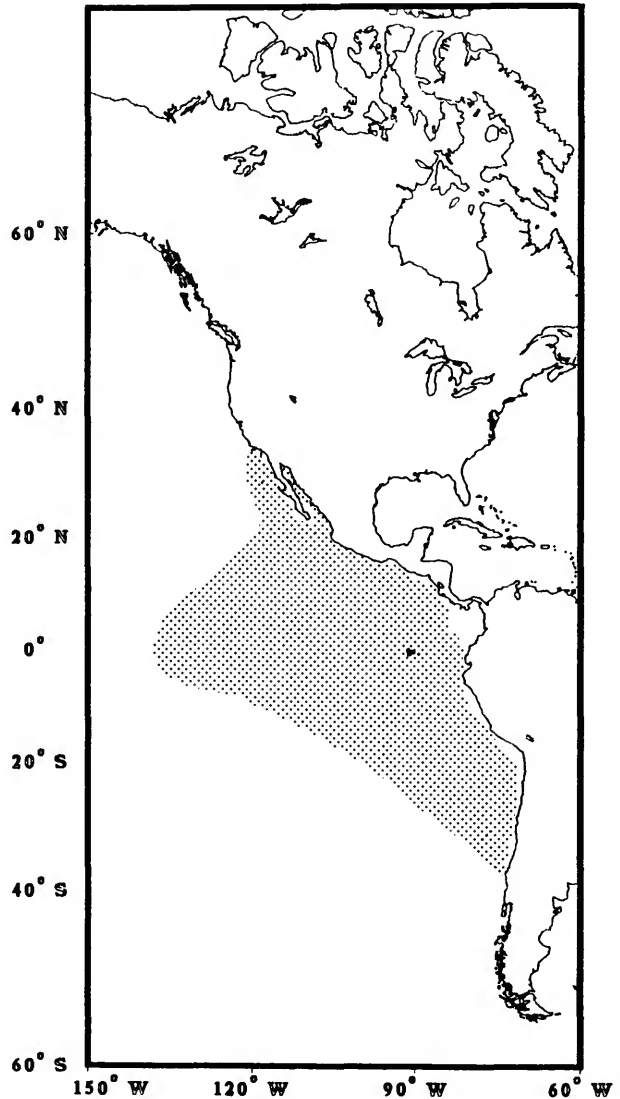


FIGURE 1.—Geographical distribution of *Dosidicus gigas*.

subfamily, no such increase in the number of suckers per arm with increasing mantle length occurs once an individual reaches sexual maturity (Wormuth, unpublished data).

Although Ehrhardt et al. (1983) attribute a diel vertical migration to this species (which populations appear to do in offshore waters), it should be noted that a nearshore fishery occurred off Vina del Mar, Chile (33°02'S, 71°37'W), in which *D. gigas* of up to 120 kg were caught during the day at fairly shallow depths (Voss and Sisson, 1967). The catch in the Gulf of California rose from 14 metric tons in 1974 to 22,000 metric tons in 1980 (Ehrhardt et al., 1983).

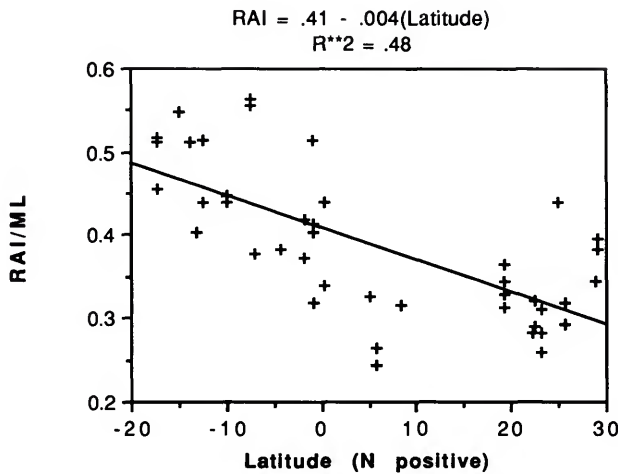


FIGURE 2.—Relationship between proportional length of right arm I/mantle length and latitude for *Dosidicus gigas*.

Recent work by Yamaguchi and Okutani (1990) reported that of juvenile squid collected during jigging of adult *D. gigas* off Peru, >88% were *Sthenoteuthis oualaniensis*. They concluded that the fishing grounds for adults did not coincide with the dispersal area of juvenile *D. gigas*, which “may disperse offshore” (Yamaguchi and Okutani, 1990:7).

*Dosidicus gigas* are cannibalistic and readily attack individuals caught on jigs. Otoliths removed from stomachs of freshly caught specimens show prey to be midwater fishes, such as *Hygophum atratum*, *Myctophum aurolaternatum*, *Lampantactis parvicauda*, *Diogenichthys lateratum*, *Vinciguerria lucetia*, and *Benthosema panamense* (Wormuth, 1971). Predators in this area include the pelagic fishes *Coryphaena hippurus*, *Neothunnus macropterus*, and *Makaira mitsukurri* (Wormuth, 1971). Clarke et al. (1988) found that sperm whales taken within the distributional range of *D. gigas* fed almost exclusively on this species. Growth rates estimated by Ehrhardt et al. (1983) vary from 3.6 to 8.3 cm/month depending on age and hatching time. They report that multiple spawning periods occur in December–January, May–June, and in September.

An excellent overview of this species is given by Nesis (1983).

#### *Hyaloteuthis* Gray, 1849

**DIAGNOSIS.**—Ventral surface of mantle with 19 round photophores, 1 pair on ventral surface of head, 2 pairs on ventral surface of arms IV, 1 intestinal photophore; longitudinal ridge of mantle component of locking cartilages straight; either arm IV hectocotylized in males; cross section A of gladius (see Toll, 1990) with 2 lateral lobes. Monospecific.

**TYPE SPECIES.**—*Sepia pelagica* Bosc, 1802:46.

#### *Hyaloteuthis pelagica* (Bosc, 1802)

**DIAGNOSIS.**—As for genus.

**ORIGINAL REFERENCE.**—Bosc, 1802:46, pl. 1: figs. 1, 2.

**TYPE LOCALITY.**—Unknown.

**DEPOSITION OF TYPES.**—*Holotype*: Unknown.

*Paratypes*: None designated.

**DISTRIBUTION AND BIOLOGY.**—This species is the smallest or one of the smallest of the Ommastrephidae in size at maturity. It appears to be an oceanic, pelagic species but one that is not caught normally at the surface at night. It is distributed in all tropical and subtropical oceans, but, relative to other ommastrephids, its frequency of reported capture has been low, and, therefore, its range is not well defined. Much larger nets in recent sampling have caught this species in large numbers between 20°S and 31°S off Brazil (Warneke-Cremer, 1986), where it was the dominant ommastrephid, with 382 specimens collected. Larvae of this species have been found throughout the year around the Hawaiian Islands (Harman and Young, 1985), with highest abundances in April and lowest in August. Most were caught in the upper 50 m at night and from 100 m to 200 m during the day. The large difference between night and day catch frequencies suggests either diel vertical migration or strong visual net avoidance in the upper 100 m during the day (or both).

#### *Eucleoteuthis* Berry, 1916

**DIAGNOSIS.**—Mantle with 1 pair of yellowish longitudinal stripes of luminous tissue ventrally extending from very near posterior tip to very near anterior margin, 1 stripe on each side of ventral midline, separated by about 45° of mantle circumference; 2 pairs of spots of similar tissue at anterior termination of ventral stripes; 2 large oval patches of luminous tissue at base of arms IV; mantle-funnel locking cartilages fused; longitudinal ridge of mantle component of locking cartilages with anterior bifurcation; cross section A of gladius (see Toll, 1990) with 2 lateral lobes; rings of largest suckers of tentacular club smooth except for 1 large tooth at lateral-most point. Monospecific.

**TYPE SPECIES.**—*Symplectoteuthis luminosa* Sasaki, 1915:144, fig. 4, pl. 4: figs. 7–13.

#### *Eucleoteuthis luminosa* (Sasaki, 1915)

**DIAGNOSIS.**—As for genus.

**ORIGINAL REFERENCE.**—Sasaki, 1915:144, fig. 4, pl. 4: figs. 7–13.

**TYPE LOCALITY.**—Sagami Bay, Japan.

**DEPOSITION OF TYPES.**—*Holotype*: Museum of the Science College, Tokyo Imperial University, Japan.

*Paratypes*: None designated.

**DISTRIBUTION AND BIOLOGY.**—This species is found across the North Pacific from about 20°N to 40°N. In the Southern

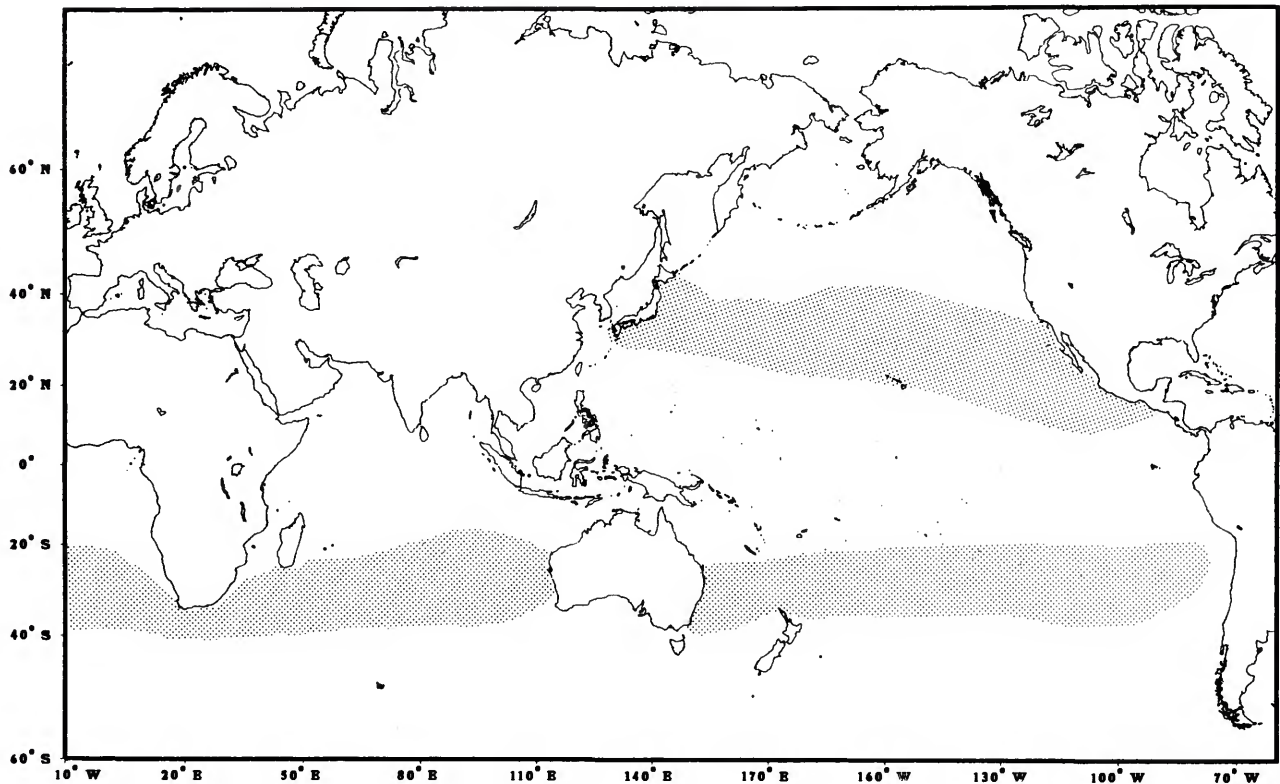


FIGURE 3.—Geographical distribution of *Eucleoteuthis luminosa*.

Hemisphere it is found in all three major oceans at similar south latitudes (Figure 3), but records are not abundant in these areas (Zuev et al., 1975) due to less frequent sampling. It is considered to be a Transition Zone species (McGowan, 1971) by Wormuth (1976).

As is the case for most ommastrephids, little is known of its depth distribution. It occurs with *Ommastrephes bartramii* but

is seen less frequently. This may be because of actual lower abundance or because it rarely approaches the surface. Little is known of its prey species or its reproductive behavior.

Males and females from waters off the east coast of Australia mature at between 120 mm ML and 130 mm ML (Dunning and Brandt, 1985). The broad size range encountered suggests a protracted spawning season.

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# The Ommastrephid Squid Genus *Todarodes*: A Review of Systematics, Distribution, and Biology (Cephalopoda: Teuthoidea)

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## ABSTRACT

The neritic and nerito-oceanic arrow squid genus *Todarodes* (Cephalopoda, Ommastrephidae) includes four nominal species, one consisting of two subspecies. *Todarodes sagittatus* (Lamarck, 1798) occurs in continental slope and oceanic waters of the North Atlantic Ocean and adjacent seas. *Todarodes angolensis* Adam, 1962, shows a parallel distribution in the South Atlantic, its distribution at least partially overlapping that of *T. filippovae* Adam, 1975, in and adjacent to the Southern Ocean. In shelf waters of the western Pacific Ocean around Japan, *T. pacificus* Steenstrup, 1880, forms the basis for the world's largest, single-species squid fishery. Two subspecies have recently been recognized; populations occurring around Japan and as far south as Hong Kong and Taiwan were assigned to *T. p. pacificus*, and those from deeper shelf waters off northern Australia were assigned to *T. p. pusillus* Dunning, 1988. The four species can be separated morphologically on the basis of the relative size, number of rows and dentition of the manus suckers of the club, and the form of modification of the right arm IV in mature males.

*Todarodes sagittatus*, *T. angolensis*, and *T. filippovae* attain mantle lengths of more than 500 mm, with preliminary data showing geographic variation in size at reproductive maturity. By contrast, *T. pacificus pacificus* around Japan rarely exceeds 250 mm mantle length and subpopulations show seasonal variation in size at maturity. Males and females of *T. p. pusillus* reach maturity at less than 100 mm mantle length.

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## Introduction

Arrow squids of the genus *Todarodes* are large, muscular ommastrephids that are abundant in jig and trawl catches in continental slope and oceanic waters of the Atlantic and Southern oceans and adjacent seas. In the Indo-West Pacific, one species is abundant on the continental shelf in both temperate and tropical waters.

The Japanese common squid or surumeika, *T. pacificus* Steenstrup, 1880, is the basis for the world's largest squid fisheries in the northwest Pacific, with jig catches reaching nearly 700,000 tons in 1968. More is known of the life cycle and migrations of this species than is known of any other squid (Okutani, 1983).

The larger *Todarodes* species of the Atlantic and Southern oceans were described earlier than their Pacific congeners and are of local fisheries importance in some regions (e.g., Norway). We have little detailed knowledge, however, of their biology or distributions (Villanueva and Sanchez, 1989), and, indeed, morphological characters separating the species have only recently been clarified (Roeleveld, 1989).

This paper provides a brief overview of the systematics and status of our biological knowledge of *Todarodes*. The need for a rigorous taxonomic revision based on specimens from a broad geographical range and further study of their biology is highlighted.

Measurements and counts used in this paper are as defined by Roper and Voss (1983), and interpretation of tentacular club structure follows Roeleveld (1982).

### Systematics, Distribution, and Biology

#### Family OMMASTREPHIDAE Steenstrup, 1857

#### Subfamily TODARODINAE Adam, 1960

#### Genus *Todarodes* Steenstrup, 1880

DIAGNOSIS.—Ommastrephids with funnel groove, foveola present, side pockets absent; left tentacular club with 2 pairs of carpal suckers, tentacles without fixing apparatus; suckers on dactylus of tentacular club quadrilateral; medial manus sucker rings with 20 or fewer long, pointed teeth, with single larger tooth distally in some species; only right arm IV hectocotylyzed in mature males; ocular, visceral, and mantle photophores absent.

TYPE SPECIES.—*Loligo sagittata* Lamarck, 1798:130.

DISCUSSION.—The genus *Todarodes* includes four nominal species, one of which has two subspecies (*T. pacificus pacificus* Steenstrup, 1880, and *T. pacificus pusillus* Dunning, 1988a). The genus is represented in the North and South Atlantic Ocean, northeastern Indian Ocean, western and southeastern Pacific Ocean, and the Southern Ocean. *Todarodes pacificus* occurs in shelf waters around Japan and Hong Kong and as far south as northern Australia; the southeast Asian and Australian populations that mature at much smaller sizes have been given subspecific status (*T. p. pusillus*, see Dunning, 1988a).

The mantle length (ML) of female *T. pacificus* from around Japan rarely exceeds 350 mm, with males generally less than 250 mm ML (Hamabe et al., 1974; Okutani, 1983). By contrast, males of the larger, nerito-oceanic representatives of the genus, *T. sagittatus* (Lamarck, 1798), *T. angolensis* Adam, 1962, and *T. filippovae* Adam, 1975, can reach more than 400 mm, and females can exceed 500 mm ML (Clarke, 1966; Dunning, 1988b).

Until recently, the lack of sufficient mature specimens of the larger, nerito-oceanic *Todarodes* in collections has meant that morphological characters separating these nominal forms (especially the structure of the hectocotylus in males and the

number, arrangement, and dentition of tentacular carpal and manal suckers) have been poorly defined.

The validity of *T. filippovae* as a distinct species has, until recently, not been recognized by Russian researchers. They considered all *Todarodes* from the Southern Hemisphere to be *T. angolensis*. Hence, little confidence can be placed in the specific identification of larval or adult specimens from the Southern Ocean region and adjacent waters that appeared in the Soviet literature in the 1970s and 1980s.

Recently, morphological characters separating *T. filippovae* from *T. angolensis* and *T. sagittatus* have been clarified further by Roeleveld (1989), based on a review of the literature and her observations of specimens collected off South Africa. These characters are summarized in Table 1, with the inclusion of data from studies by one of us (MCD) in the southwest Pacific Ocean. Specimens of *Todarodes* from the southeast Pacific Ocean also were examined by the authors and colleagues during the Cephalopod International Advisory Council workshop on cephalopod systematics and zoogeography held in Washington, D.C., in July 1988. These specimens, however, could not be assigned with certainty to either *T. filippovae* or *T. angolensis* because they had some features considered distinctive of each of these species. A detailed taxonomic revision of the large species of *Todarodes*, assessing geographic variation in a range of characters over their apparently broad distributions, is clearly warranted.

#### *Todarodes sagittatus* (Lamarck, 1798)

DIAGNOSIS.—Medial manus sucker rings with 17–20 long, pointed teeth; manus with 14–18 quadrilateral sucker rows.

ORIGINAL DESCRIPTION.—Lamarck, 1798:130.

TYPE LOCALITY.—Not indicated (Lamarck, 1798); Atlantic Ocean (Lamarck, 1799).

DEPOSITION OF TYPES.—*Holotype*: ?Museum National d'Histoire Naturelle, Paris (could not be located, June 1988; C.C. Lu, pers. comm.).

*Paratypes*: None nominated.

TABLE 1.—Morphological characters used to separate *Todarodes sagittatus*, *T. angolensis*, and *T. filippovae* at given sizes. The data is from Adam (1962), Roeleveld (1989), and Dunning (unpublished) from specimens collected off South Africa and in the southwest Pacific Ocean.

Characters	Species		
	<i>T. sagittatus</i> 262–355 mm ML	<i>T. angolensis</i> 250–590 mm ML	<i>T. filippovae</i> 180–521 mm ML
Number of manus-sucker rows	14–18	14–18	12–14
Number of teeth in largest median manus-sucker ring	17–20	13–16	7–13
Diameter of largest median manus suckers (% ML)	2.7–4.0	2.0–2.6	2.7–4.5
Distribution	North Atlantic Ocean, Mediterranean Sea	?Temperate southern hemisphere	?Southern subtropical convergence zone

**GEOGRAPHICAL DISTRIBUTION.**—Continental slope and oceanic waters of the Mediterranean Sea and northeastern Atlantic, and seamounts associated with the Mid-Atlantic Ridge as far west as 62°16'W (Korzun et al., 1979).

**DISCUSSION.**—Adult *T. sagittatus* in the North Atlantic Ocean and Mediterranean Sea apparently occupy a broad depth range at night, from the surface to at least 1000 m, and are caught during the day in demersal trawls in depths of 70–800 m. Males reach maturity at between 200 mm ML and 260 mm ML in the Mediterranean Sea and at 300–400 mm ML off the northern British Isles, and mature males of up to 640 mm ML have been caught off Iceland (Mangold-Wirz, 1963; Clarke, 1966). Mature female *T. sagittatus* have rarely been described in the literature. Two mature females of 365 mm ML and 370 mm ML were described from the Mediterranean Sea (Mangold-Wirz, 1963). In the North Atlantic, Clarke (1966) found only two mature females, of 460 mm ML and 470 mm ML, among over 600 specimens examined.

*Todarodes sagittatus* forms the basis for an intermittent jig fishery off the Norwegian coast where, in 1979, the catch reached approximately 2000 tons (Wiborg, 1980).

*Todarodes sagittatus* can be separated from *T. angolensis* on the basis of the larger diameter of the medial manus suckers of the tentacles (2.7%–4.0% ML compared with 2.0%–2.6% ML) and the number of teeth in these suckers (17–20 compared with 13–16) (Roeleveld, 1989; Dunning, unpublished data).

Nesis (1979a) considered most of the rhynchoteuthion larvae described by Pfeffer (1912), Naef (1923), and Degner (1925) from western European and Mediterranean waters to be *T. sagittatus*. It should be noted, however, that characters separating larvae of *Todarodes* from those of *Todaropsis eblanae* (Ball), which also occurs in these waters, have not been clarified; larvae of *T. eblanae* have not been positively described in the literature.

#### *Todarodes angolensis* Adam, 1962

**DIAGNOSIS.**—Medial manus sucker rings with 13–16 long, pointed teeth, diameters of largest suckers < 2.6% ML; manus with 14–18 quadriserial sucker rows.

**ORIGINAL DESCRIPTION.**—Adam, 1962:32.

**TYPE LOCALITY.**—South Atlantic off Angola, Baía dos Elefantes, ~13°10'S, 12°50'E.

**DEPOSITION OF TYPES.**—*Holotype*: Institut Royal des Sciences Naturelles de Belgique, Brussels, female, 350 mm ML, off Angola in Baía dos Elefantes, ~13°10'S, 12°50'E, 13 Sep 1952.

*Paratype*: Institut Royal des Sciences Naturelles de Belgique, Brussels, 1 female, 330 mm ML, collected with holotype.

**GEOGRAPHICAL DISTRIBUTION.**—Continental slope and oceanic waters of the South Atlantic and Southern oceans.

**DISCUSSION.**—*Todarodes angolensis* was originally described as a subspecies of *T. sagittatus* and was elevated to

species status by Nesis (1973) on the basis of the differences in the structure of the carpal region of the tentacular club; see Roeleveld (1989) for a full discussion.

*Todarodes angolensis* is known from the western Mediterranean Sea, South Atlantic Ocean, and southwest Indian Ocean and is known in the Pacific from off the coast of South America, the southeast coast of New Zealand, and south and southwest of Tasmania (Filippova, 1971; Zuev et al., 1976; Nesis, 1979a, 1979b, 1987; Korzun and Sadkov, 1983; Warneke-Cremer, 1986; Roeleveld, 1989; Villanueva and Sanchez, 1989).

As discussed above, Russian researchers have regarded the characters used by Adam (1975) to separate *T. filippovae* from this species to be within the range of either individual, geographic, or ontogenetic variation of *T. angolensis* (Nesis, 1979b, pers. comm., 1982, 1987) and have referred all *Todarodes* (adults and larvae) caught in southern hemisphere waters to *T. angolensis*. The literature is therefore confused and provides little clarification of the distributions of these species.

Morphometrics, sexual maturity, and distribution of *T. angolensis* caught off Namibia were discussed by Villanueva and Sanchez (1989). They found that females reached sexual maturity at between 300 mm ML and 400 mm ML and that males from 240 mm ML carried spermatophores in Needham's sac. Dunning (1988b) described the reproductive condition of female *T. angolensis* (250–590 mm ML) and a single mature male (450 mm ML) that were caught on jigs and in demersal trawls in slope waters off southern New Zealand during the summer months.

Larvae of *T. angolensis* were first described by Nesis (1979a), but, as discussed above, Russian scientists did not consider the (at least partially) sympatric *T. filippovae* to be a distinct species.

#### *Todarodes filippovae* Adam, 1975

**DIAGNOSIS.**—Medial manus sucker rings with 7–13 long, pointed teeth, diameters of largest suckers 2.7%–4.5% ML; manus with 12–14 quadriserial sucker rows.

**ORIGINAL DESCRIPTION.**—Adam, 1975:3.

**TYPE LOCALITY.**—Southern Indian Ocean, 35°S–38°S, 66°E–77°E.

**DEPOSITION OF TYPES.**—*Holotype*: Institut Royal des Sciences Naturelles de Belgique, Brussels, female, 320 mm ML, 35°S–38°S, 66°E–77°E, Dec 1967.

*Paratypes*: Institut Royal des Sciences Naturelles de Belgique, Brussels, 2 males, 210 mm ML, 213 mm ML, and 3 females, 210–220 mm ML, collected with holotype; 3 females, 210–280 mm ML, 35°40'S, 66°10'E, 22 Dec 1967; 2 males, 185 mm ML, 220 mm ML, and 2 females, 182 mm ML, 190 mm ML, 38°15'S, 77°10'E, 28 Dec 1967; 2 males, 220 mm ML, 225 mm ML, 40°S, 49°E, 6 Apr 1970.

**GEOGRAPHICAL DISTRIBUTION.**—Continental slope and oceanic waters of the Southern Ocean and adjacent waters,

apparently abundant in and adjacent to subtropical convergence zone.

DISCUSSION.—*Todarodes filippovae* was originally described from specimens from the southern Indian Ocean. In subsequent studies in southern subtropical and subantarctic waters, Russian researchers have referred all *Todarodes* from these waters to *T. angolensis* Adam, 1960. Okutani (1980) considered *T. filippovae* to have a circum-subantarctic distribution, potentially overlapping that of *T. angolensis* off southern Africa. Roeleveld (1989) considered *T. angolensis* and *T. filippovae* to be associated with different water masses in the Benguela Current system.

In the Tasman Sea, adult *T. filippovae* have been caught near the surface on jigs, in surface driftnets, and in demersal and midwater trawls between 32°45'S and 47°42'S (the most southerly station sampled) where surface water temperatures ranged from 11.5°C to 24.7°C. Temperatures at 250 m ranged from 9.7°C to 11.9°C (Dunning, 1988b).

In contrast to observations in the adjacent Tasman Sea where the sex ratio was approximately 1:1, females dominated trawl catches of larger squid in slope waters along the eastern Australian coast, in some catches by as much as 7:1. Of a total of 175 specimens examined, 125 were females (Dunning, 1988b). A similar preponderance of females was reported for *T. sagittatus* taken in trawls in the North Atlantic and in the Catalanian Sea (western Mediterranean Sea) (Mangold-Wirz, 1963; Clarke, 1966). Male *T. sagittatus* were outnumbered by females by as much as 23:1 off the Norwegian coast (Wiborg, 1980), and female *T. angolensis* outnumbered males in trawl catches off Namibia by 277:86 (Villanueva and Sanchez, 1989). In jig catches of *T. filippovae* from off the north-east Tasmanian coast in November–December 1978 (JAMARC, 1980), the sex ratio of squid with a modal mantle length of less than 200 mm ML was not significantly different from 1:1.

A preliminary study of the parasite fauna of *T. filippovae* from eastern Australian waters was undertaken by Kennedy (1982). Adults of this species, in contrast to specimens of *Ommastrephes bartramii* (Lesueur) from the same region, were found to carry large numbers of encysted nematodes and cestodes in their mantle walls.

The larvae of *T. filippovae* have not been positively described. A single larva, 8 mm ML, was recorded from southwest of Tasmania (sea surface temperature 10.5°C) by Nesis (1979a, pers. comm., 1981) as *T. angolensis*. Although both species are known from the Tasman Sea, *T. filippovae* predominates around Tasmania and this larva could be referable to the latter species.

#### *Todarodes pacificus* Steenstrup, 1880

This species comprises two subspecies, *T. pacificus pacificus*, which inhabits shelf and upper slope waters around Japan and south to Hong Kong and Taiwan, and *T. pacificus pusillus*, from shelf waters around northern Australia.

DIAGNOSIS.—Fin length < 50% ML; largest tentacular sucker rings with 16–20 regularly spaced, equal, conical teeth slightly projecting above ring in all cases; diameters of largest suckers 1.9%–3.0% ML; manus with 6–12 quadriserial sucker rows.

#### *Todarodes pacificus pacificus* Steenstrup, 1880

DIAGNOSIS.—Fin length 30%–45% ML; largest tentacular sucker rings with 18–20 regularly spaced, equal, conical teeth; manus with 11 or 12 quadriserial sucker rows.

ORIGINAL DESCRIPTION.—Steenstrup, 1880:79.

TYPE LOCALITY.—“e mari japonico” [Japanese Seas].

DEPOSITION OF TYPES.—*Syntypes*: Zoological Museum, University of Copenhagen, 2 females, 176 mm ML, 170 mm ML, remains of 2 other specimens (*gladii*, beaks, head with 2 arms and 1 tentacle, 2 arm tips, 5 club suckers, several radular teeth), collected from Hakodate, Japan, Andrea leg., 1869 (fide Kristensen and Knudsen, 1983).

DISTRIBUTION AND LIFE HISTORY.—More is known about this subspecies than about any other ommastrephid due to its economic importance. *Todarodes pacificus pacificus* forms the basis of the largest, single-species squid fishery in the world, although the catch has recently been declining. Okutani (1983) provided a comprehensive review of its life history and fisheries biology.

Japanese researchers consider the subspecies in the waters around Japan to be composed of three seasonal broods, named after the time at which juveniles of the populations are first observed. The winter population ranges from the East South China Sea in the south to the coast of Sakhalin and southern Kamchatka in the north. Larvae are particularly abundant in the waters along the west and south coasts of Kyushu and the south coast of the Korean Peninsula during January and February. Juveniles are often found concentrated around temperature fronts.

The summer population is the most restricted in range and supports only small-scale, local fisheries. It is found in both the Japan Sea and off the Pacific coast. During August, larvae are found around Sado Island and the Oki Islands where they grow and from which they migrate to the southwestern Japan Sea for overwintering.

The autumn population is found from the East China Sea and the west coast of Kyushu north to the coast of Sakhalin. Larvae occur south of 39°N along the shelf of the northern East China Sea from October to December. Although this population is small on the Pacific coast of Japan, the autumn population in the Sea of Japan supports the major fishery, and individuals reach larger sizes at maturity than those in either the summer or the winter populations. The movements of the juveniles of this population are the least well documented (Okutani, 1983).

In Japanese waters, female *T. p. pacificus* reach maturity between 190 mm ML and 300 mm ML depending on whether they belong to the so-called “winter,” “autumn,” or “summer”

populations. Males reach maturity at more than 200 mm ML (Hamabe et al., 1974).

Jig catches of this subspecies in the Northwest Pacific region increased to a maximum of 668,000 tons in 1968. During the 1970s there was a sudden fall in catches, and, except for 1980 (~325,000 tons), annual catches between 1977 and 1984 ranged from 170,000 to 240,000 tons (Okutani, 1977; Murata, 1990). In 1990, the annual reported landings were 164,000 tons (Government of Japan, 1991). Analysis of catch-per-unit-effort versus total effort for the period from 1954 to 1970 clearly indicates overfishing to have been responsible, at least in part, for the sharp and sustained decline in total catch (Araya, 1974; Okutani, 1977).

Larvae of *T. p. pacificus* have been well described and illustrated by Okutani (1965, 1968), who also reviewed earlier Japanese work. The embryology and early growth of hatchlings from egg masses produced by captive females were documented by Hamabe (1962).

#### *Todarodes pacificus pusillus* Dunning, 1988

DIAGNOSIS.—Fin length 25%–31% ML; medial manus sucker rings with 16–18 long, pointed teeth; manus with 6–8 quadriserial sucker rows.

ORIGINAL DESCRIPTION.—Dunning, 1988a:149.

TYPE LOCALITY.—Timor Sea, northeast Indian Ocean, 13°48'S, 124°19'E, bottom depth 102 m.

DEPOSITION OF TYPES.—*Holotype*: Museum of Victoria, Melbourne, Australia, male, 65 mm ML, 28 Mar 1981.

*Paratypes*: Museum of Victoria, Melbourne, Australia, 1 female, 64 mm ML, Timor Sea, 8°53'S, 135°10'E, 27 Jun 1981; 1 male, 63 mm ML, Timor Sea, 9°52'S, 129°12'E, 9 Jul 1980. Queensland Museum, Brisbane, Australia, 1 female, 69 mm ML, off southern Queensland, 27°S, 153°45'E, 5 Mar 1983; 1 male, 62 mm ML, off southern Queensland, 27°S, 153°45'E, 27 Feb 1983; 1 male, 53 mm ML, Northwest Shelf, 19°04'S, 118°57'E, 29 Aug 1983; 1 male, 68 mm ML, Coral Sea, 17°46.2'S, 146°50.2'E, 30 Nov 1985; 1 female, 74 mm ML,

Coral Sea, 17°16.1'S, 146°41.5'E, 1 Dec 1985. National Science Museum, Tokyo, 1 male, 53 mm ML, 1 female, 61 mm ML, Northwest Shelf, 19°31'S, 116°02'E, 13 Oct 1983.

GEOGRAPHICAL DISTRIBUTION.—Continental shelf and upper continental slope off northern Australia.

DISCUSSION.—Until 1988, *T. pacificus* had generally been considered to be restricted to temperate shelf and upper slope waters in the northwestern North Pacific, principally around Japan (Sasaki, 1929; Voss, 1963; Clarke, 1966; Wormuth, 1976; Okutani, 1980; Roper et al., 1984; Nesis, 1987). *Todarodes pacificus* occasionally has been reported from the China Sea (Shojima, 1970; Tung, 1977), around Hong Kong (Voss and Williamson, 1971), and from the southern Philippines (the paratype of *Nototodarus sloani philippinensis* Voss) (Dunning, 1988a). "Juvenile" *T. pacificus* were reported by Rancurel (1976) from the stomachs of yellowfin tuna caught in the northwest Coral Sea, but these specimens have not subsequently been reexamined.

*Todarodes p. pusillus* was collected off the west coast of northern Australia, between 8°53'S in the Timor Sea and 19°31'S on the Northwest Shelf, and off the east coast, between 17°16'S and 27°S. All specimens were caught in demersal trawls where bottom depths varied from 78 m to 357 m. In contrast to *T. p. pacificus*, which is not generally abundant around Japan where the temperature at 50 m depth exceeds 15°C, and which has been caught where temperatures were as low as 5°C (Kasahara and Nasumi, 1976), *T. p. pusillus* was caught where temperatures at 50 m depth were in excess of 23°C and where surface temperatures reached 29°C in summer. Up to 54 individuals were caught in a single trawl sample suggesting that, like *T. p. pacificus* around Japan, this subspecies schools (Dunning, 1988b).

*Todarodes p. pusillus* reaches maturity at considerably smaller sizes than the nominate subspecies. All females larger than 60 mm ML were mature, with eggs in their oviducts, and all males greater than 50 mm ML carried fully formed spermatophores (Dunning, 1988a).

Larvae of *T. p. pusillus* have not been described.

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# A Review of the Systematics, Distribution, and Biology of Arrow Squids of the Genus *Nototodarus* Pfeffer, 1912 (Cephalopoda: Ommastrephidae)

M.C. Dunning  
and Ellen Celia Förch

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## ABSTRACT

The neritic, Indo-Pacific arrow squid genus *Nototodarus* can be separated morphologically from other genera of the subfamily Todarodinae on the basis of the elaborate hectocotylyzation of both arms IV in males and the presence of longitudinal folds in the funnel groove. Of six nominal species, three are considered valid: *N. sloanii* (Gray, 1849), occurring around southern New Zealand; *N. gouldi* (McCoy, 1888), occurring around northern New Zealand and southern Australia; and *N. hawaiiensis* (Berry, 1912), broadly distributed in slope waters in the Indo-Pacific region. The species differ in the structure of the hectocotylus and in the number, arrangement, and dentition of suckers on the sessile arms.

Recent commercial fisheries interest has resulted in a clarification of the distribution of all life stages of these species and has provided a basic understanding of their population structure and biology. All species appear to have complex population structures, do not undertake directed migrations, and grow rapidly. Adult *N. gouldi* have been found to grow at up to 4.5 cm/month. Size at reproductive maturity was found to be variable in all species.

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## Introduction

Although the genus *Nototodarus* was established by Pfeffer in 1912 as part of his extensive reassessment of the ommastrephids of the Pacific, the systematics, distribution, and biology of these ommastrephid squids remained confused until

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the mid-1980s (Smith et al., 1987; Dunning, 1988b). Recent clarification has largely been the result of extensive exploratory surveys undertaken by Japanese and, to a lesser extent, Taiwanese and Soviet vessels throughout the Indo-Pacific commencing in the early 1970s. More recently, major multinational jig and demersal trawl fisheries targeting *Nototodarus sloanii* (Gray, 1849) and *N. gouldi* (McCoy, 1888) have developed on the continental shelf and upper slope around New Zealand and, intermittently, southern Australia, with annual catches in the southwest Pacific approaching 100,000 metric tons in the mid-1980s (Smith et al., 1987). Concurrent fisheries biological studies have significantly advanced the state of knowledge of the life history biology of these species and have provided considerable data on population structure.

This paper provides a brief overview of recent studies of *Nototodarus* and a bibliography of selected useful references from the collections of the authors.

## Species Accounts

### Family OMMASTREPHIDAE Steenstrup, 1857

### Subfamily TODARODINAE Adam, 1960

### *Nototodarus* Pfeffer, 1912

DIAGNOSIS.—Funnel groove with foveola but without side pockets, dactylus of tentacular club with quadriseriate suckers, photophores absent in all life stages, right and left arms IV hectocotylyzed.

TYPE SPECIES.—*Ommastrephes insignis* Gould, 1852:481, pl. 49: fig. 596.

GENUS SIZE.—Of six nominal species, three are considered valid: *N. sloanii* (Gray, 1849), *N. gouldi* (McCoy, 1888), and *N. hawaiiensis* (Berry, 1912).

DISCUSSION.—Pfeffer (1912) erected the genus *Nototodarus* based on a single male specimen assigned to *Ommastrephes insignis* (Gould, 1852) from Akaroa on the east coast of the South Island of New Zealand. Pfeffer distinguished it from other species by the hectocotylization of both arms IV and also by the structure of the funnel groove, characters that he thought allied it to *Todaropsis eblanae* (Ball, 1841).

Gould's type specimen had not been examined by Pfeffer. It has not been redescribed and its present location is unknown. Smith et al. (1987) considered it a species dubium. It is clear from the description and illustration of the hectocotylized arms (Pfeffer, 1912, pl. 31: figs. 2–4) that Pfeffer's holotype of *Nototodarus* was *N. sloanii*, but although Gould's holotype is clearly a *Nototodarus* ("the lower pair [of arms] for one third their length are destitute of cupules, and fimbriated with a double range of compressed, adnate lobules" (Gould, 1852:481)), its specific identity remains unresolved.

Pfeffer (1912) considered *Nototodarus* to be closely allied to *Todaropsis* by the structure of the hectocotylus. In his consideration of the structure of the subfamilies within the family Ommastrephidae, however, Adam (1960) placed greater emphasis on the structure of the funnel groove. On this basis, *Nototodarus* and the genus *Todarodes* were united to form the subfamily Todarodinae, with *Todaropsis* included in the Illicinae. This subfamilial grouping of genera had generally been accepted until a review of taxonomic characters within the family by Roeleveld (1988). She considered the undifferentiated funnel groove to be a secondary loss and homoplastic both in *Todaropsis* and *Illex*. On the basis of her interpretation of morphological characteristics of the hectocotylus, she recognized the close relationship of *Todaropsis* to *Nototodarus* and placed these genera (as the "*Todaropsis*-group") within the Todarodinae.

Six nominal forms of the genus *Nototodarus* have been described from continental shelf and slope waters of the Indo-Pacific region. Of these, three are considered valid and are discussed in detail below, namely, *N. sloanii*, *N. gouldi*, and *N. hawaiiensis*.

The identity of the type species, *N. insignis* (Gould, 1852), described from "Feejee Islands; Antarctic Seas" remains unclear as discussed briefly above and in more detail by Smith et al. (1987).

*Nototodarus nipponicus* Okutani and Uemura, 1973, was described from jig-caught specimens from southern Honshu, Japan. *Nototodarus nipponicus* was characterized by "rough" skin, a very broad fin relative to mantle length (ML), and a large fin angle. In a recent paper, Okutani and Kuroiwa (1985) considered *N. nipponicus* to be a junior synonym of *N. sloanii philippinensis* Voss, 1962.

*Nototodarus sloanii philippinensis* Voss, 1962, was recorded from slope waters around the Philippines and Hong Kong where it is a minor component of the bycatch of domestic trawl fisheries (Voss, 1963; Voss and Williamson, 1971). Perera (1975) assigned squid specimens taken by jig from off Sri Lanka to this subspecies. The sessile arm and tentacular

club suckers illustrated by Perera (1975:58, fig. 10), however, are characteristic of the subfamily Ommastrephinae rather than the Todarodinae, casting doubt on the validity of this identification.

*Nototodarus sloanii philippinensis* was shown by Dunning (1988b) to be a junior synonym of *N. hawaiiensis*. Voss (1962) distinguished *N. sloanii philippinensis* from *N. hawaiiensis* (which he considered to be a subspecies of *N. sloanii*) on the basis of the dentition of the arm and tentacular suckers. Reexaminations of the holotype of *N. sloanii philippinensis* and the holotype and additional specimens of *N. hawaiiensis* from around Hawaii did not provide morphological evidence to justify their separation into distinct species (Dunning, 1988b).

### *Nototodarus sloanii* (Gray, 1849)

FIGURES 1a, 3

*Ommastrephes sloanii* Gray, 1849:61.

*Ommatostrephes sagittatus* var. *sloanei*.—Hoyle, 1909:272 [part].

?*Nototodarus insignis* Pfeffer, 1912:434, pl. 31.

*Ommatostrephes sloanei sloanei*.—Pfeffer, 1912:458, pl. 34: figs. 1, 2, 7 [part].

*Nototodarus sloanii*.—Powell, 1946:99.

*Nototodarus sloanii sloanii*.—Dell, 1952:105, fig. 7, pls. 21–25 [part].

*Nototodarus sloani sloani*.—Voss, 1962:175.

*Nototodarus sloani*.—Kawakami and Okutani, 1981:17: figs. 1A, B, 2.

DIAGNOSIS.—Arms I with more than 60 pairs of suckers, hectocotylized right arm IV with single row of slender, conical papillae distally, ventral protective membrane with supports expanded only opposite extreme tip of arm (Figure 1a).

ORIGINAL REFERENCE.—Gray, 1849:61.

DEPOSITION OF TYPES.—*Holotype*: Smith et al. (1987) considered the holotype to be an immature female, 279 mm ML (with old, printed label, "*Ommatostrephes sloanii* New Zealand," and newer, handwritten label, "*Nototodarus sloanii* (Gray), loc. New Zealand"), that is in The Natural History Museum, London, England (formerly the British Museum (Natural History)), without registration number, in alcohol, and in poor condition. Gray's type specimen came from Waitemata Harbor, northeast coast of New Zealand (36°40'S), which is outside the present range of *N. sloanii*, but this location was stated unequivocally (Smith et al., 1987).

*Paratypes*: None designated, although a second specimen was described by Gray (1849).

DISCUSSION.—The original description was very brief; a full description was given by Wormuth (1976), and the taxonomy of *Nototodarus* in New Zealand waters was reviewed in detail by Smith et al. (1987). Dell (1952) considered only one species of *Nototodarus* to occur in New Zealand waters, although Smith et al. (1987) confirmed that both *N. sloanii* and *N. gouldi* occur there. They suggested that Dell had specimens of both *N. sloanii* and *N. gouldi* in material he examined. His assessment of the differences in the structure of the hectocotylus between his New Zealand "*N. sloanii*" and Australian *N. gouldi* was that the relationship between the two forms was subspecific, i.e., *N. sloanii sloanii* (Gray) occurred around New Zealand and *N.*

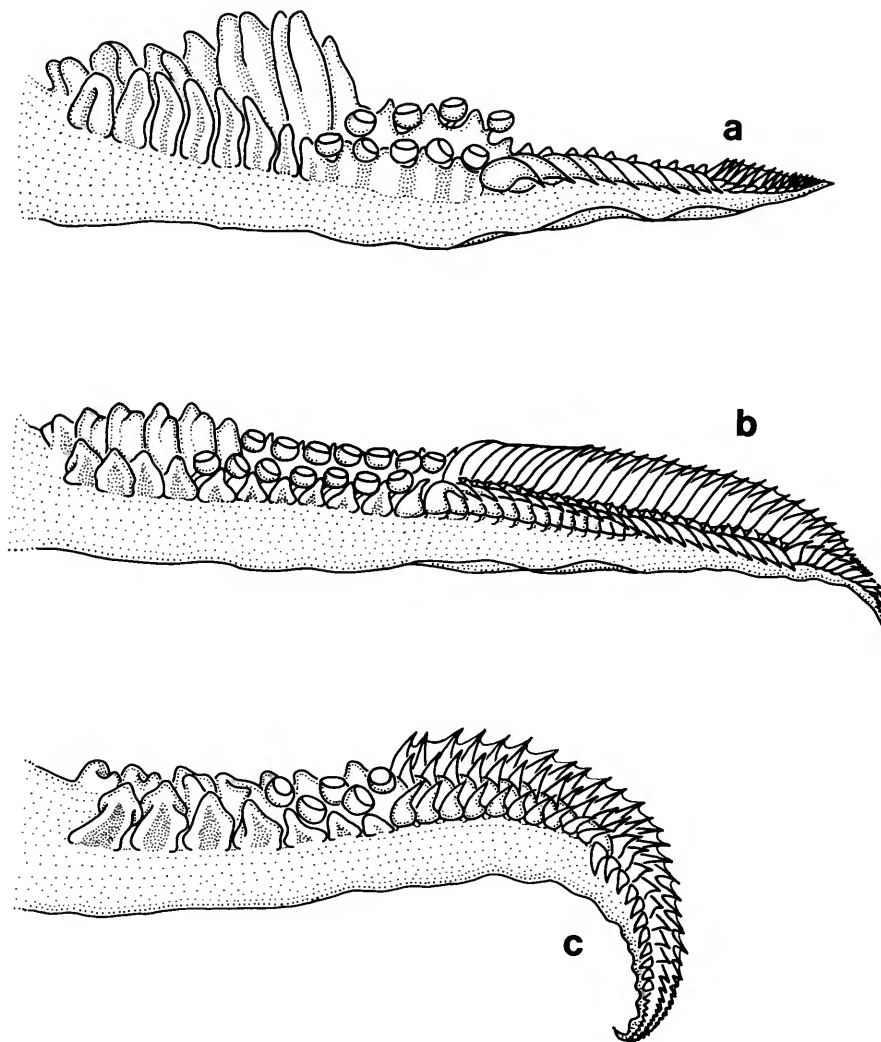


FIGURE 1.—Hectocotylyzed right arms IV of the three species of *Nototodarus*: a, *N. sloanii*; b, *N. gouldi*; c, *N. hawaiiensis*.

*sloanii gouldi* (McCoy) was from southern Australia. The subspecific designations within *N. sloanii* were accepted and extended further by Voss (1962) to include his new subspecies, *N. s. philippinensis*, and subsequently “*Ommastrephes hawaiiensis*” Berry, 1912 (Voss, 1963). Voss considered these subspecies to form a cline within the species *N. sloanii*, but he did not elaborate on the nature of this variation.

*Nototodarus sloanii* forms the basis for major demersal trawl and jig fisheries in New Zealand waters, and its fisheries biology has been the subject of numerous studies (Saito, 1973, 1975, 1976; Saito et al., 1974; Kawakami, 1976; Tung, 1977; Roberts, 1978, 1979, 1983; Mattlin, 1982; Förch, 1983; Hatanaka et al., 1985; Mattlin et al., 1985; Sato, 1985).

DISTRIBUTION.—*Nototodarus sloanii* occurs in New Zealand

and continental shelf waters southward from the northern boundary of the Subtropical Convergence Zone (about 40°S) to the Auckland Islands (51°S) and the Campbell Islands (53°S) where bottom depths vary from 50 m to 500 m. Its distribution extends eastward to southeast of the Chatham Islands (175°40'W) (Figure 2). The jig fishery for this species has concentrated where sea surface temperatures vary from 11.9° C to 16.5° C (Roberts, 1983). *Nototodarus sloanii* is most abundant on the continental shelf in depths of less than 200 m (Mattlin et al., 1985). In the north, its distribution overlaps that of *N. gouldi* (Figure 3) (Sato, 1985; Smith, 1985), and in the south, it has been jigged and trawled together with *Todarodes filippovae* Adam, 1975 (Kawakami, 1976; Dunning and Wormuth, 1998).

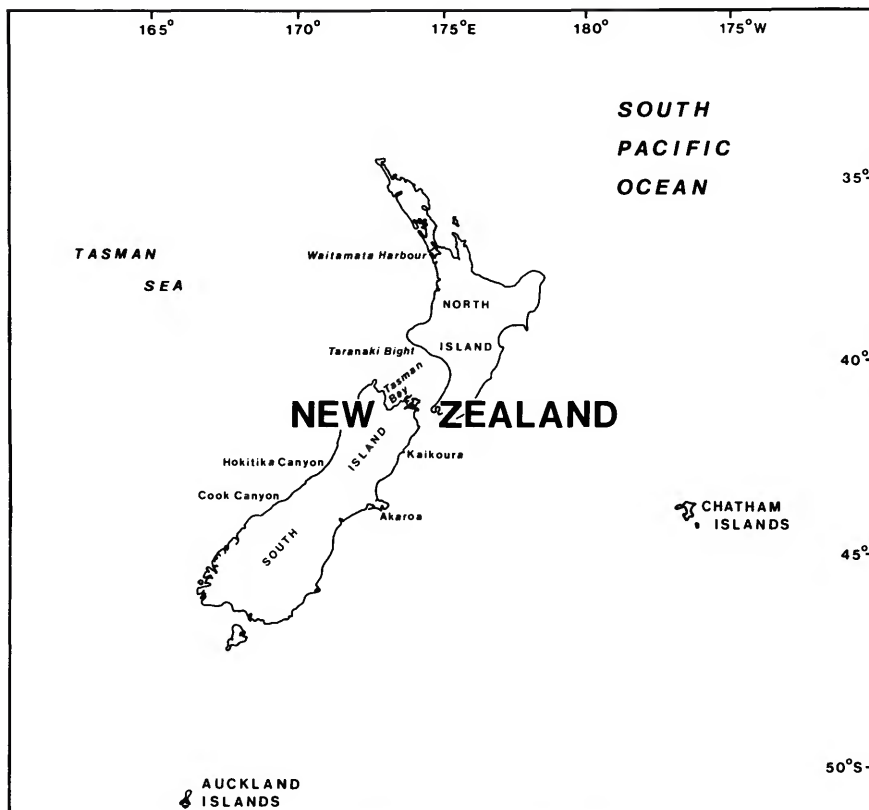


FIGURE 2.—Geographic locations around New Zealand referred to in the text.

Larvae of *N. sloanii* appear to be distributed only on the continental shelf and near submarine canyons. Off the west coast of the South Island where the shelf is very narrow, concentrations have been quite localized near the Cook and Hokitika canyons during winter sampling for ichthyoplankton (Förch, unpublished data).

**MIGRATION.**—Limited tagging studies reported by Sato (1985) failed to identify any directed, large-scale migrations in populations of *N. sloanii* off the east coast of the South Island. The maximum distance traveled was 57 km after 64 days at liberty, and although most recaptured squid from one station on the coastal shelf showed a general northward movement, those from a second station on a bank away from the coast moved in all directions.

**SIZE, MATURITY, AND SEX RATIO.**—Although several modes have often been observed in any one area, length-frequency data (ML) for trawl-caught squid have shown a general increase in modal length with increasing latitude on the Southern Snares shelf and between the northern and southern Auckland Islands shelf (R.H. Mattlin, pers. comm., 1991).

Kawakami (1976) found that male and female *N. sloanii* caught off the east coast of the South Island between October

and December reached maturity from 210 mm ML and 270 mm ML, respectively. Differences in size at maturity between areas and seasons have been noted (Kawakami, 1976; Yamada and Kattoh, 1987).

The sex ratio (males as a proportion of the catch) observed by Sato (1985) for jig catches from the east coast of the South Island varied from 0.37 to 0.65.

**GROWTH.**—Because of the complexity of its population structure, estimates of growth rate from the generally polymodal size-frequency data collected from the jig fishery cannot be made with any confidence (Roberts, 1983). From tagging studies, Sato (1985) measured growth in two male *N. sloanii* of 25 cm ML and 25.7 cm ML at liberty for 31 and 42 days and found they averaged 2.4 and 2.8 cm/month, respectively.

**LARVAE.**—The rhynchoteuthion larvae of *N. sloanii* and *N. gouldi* have been described by Förch (1986). The proboscis tip in these larvae has eight approximately equal-sized suckers and the proboscis begins to split basally at about 5 mm ML, separation into the tentacles being completed at between 8.4 mm ML and 10 mm ML. Morphological differences between *N. sloanii* and *N. gouldi* have not been described, but possible differences in mantle chromatophore patterns are being

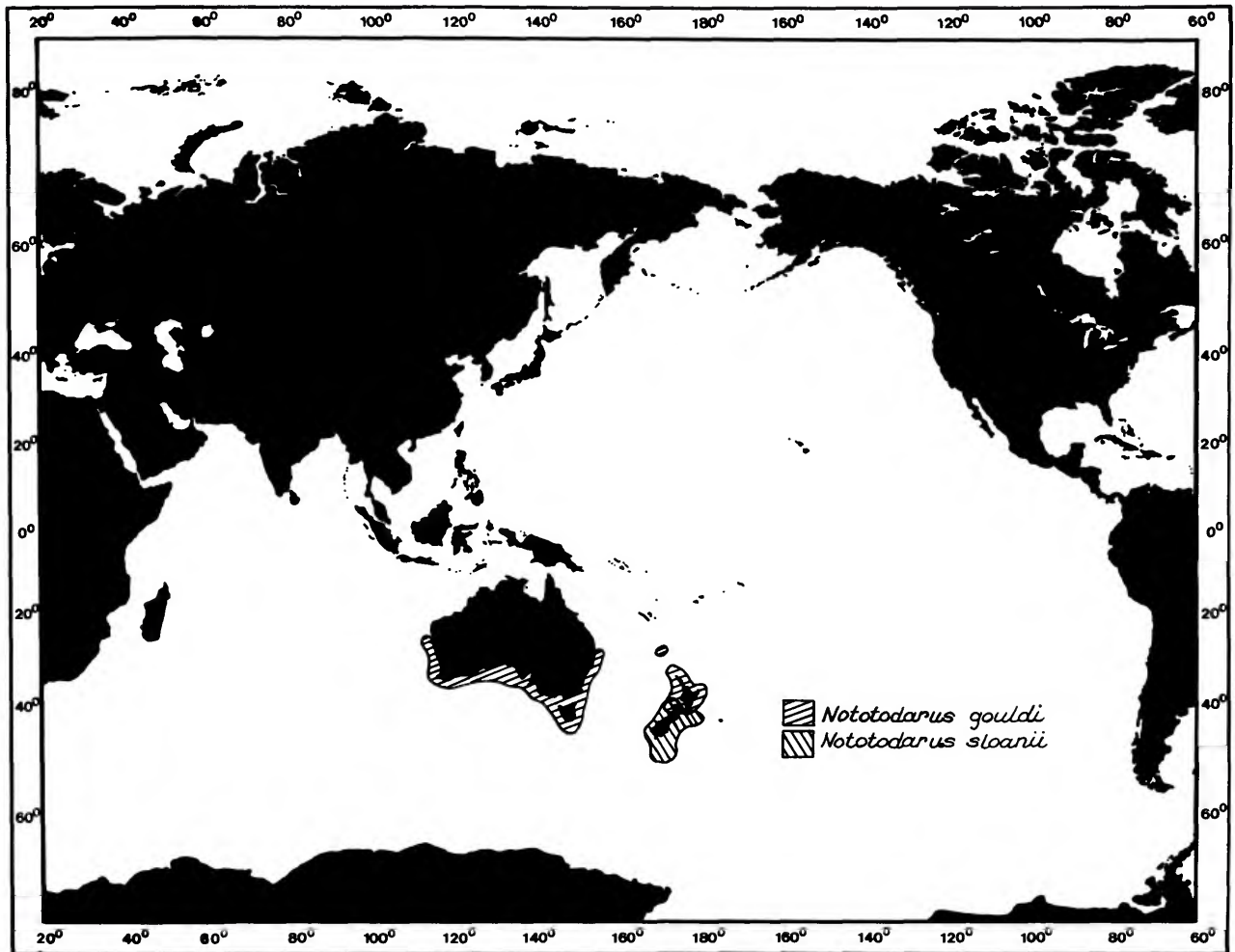


FIGURE 3.—Known distributions of *N. gouldi* (McCoy, 1888) and *Nototodarus sloanii* (Gray, 1849).

investigated by one of us (ECF). Larvae have been captured on the continental shelf off the east coast of the South Island at all times of the year.

#### *Nototodarus gouldi* (McCoy, 1888)

FIGURES 1b, 3

*Ommastrephes gouldi* McCoy, 1888:255, pl. 169.

*Ommastrephes sagittatus sloanei* Pfeffer, 1900:179 [part].

*Ommastrephes sagittatus* var. *sloanei*.—Hoyle, 1909:272 [part].

*Ommastrephes sloanei sloanei*.—Pfeffer, 1912:458, pl. 34: figs. 1, 2, 7 [part].

*Nototodarus gouldi*.—Berry, 1918:228, figs. 10–23, 26, 27, pls. 63–66.

*Nototodarus sloanii sloanii*.—Dell, 1952:105, fig. 7, pls. 21–25 [part].

*Nototodarus sloanii gouldi*.—Voss, 1963:132.

**DIAGNOSIS.**—Right arm I with 28–50 pairs of suckers, hectocotylized right arm IV distally with 1 dorsal row of slender, conical papillae and expanded ventral protective

membrane with supports opposite entire distal row of dorsal papillae (Figure 1b).

**ORIGINAL REFERENCE.**—McCoy 1888:255, pls. 169, 170. Berry (1918) provided a further detailed morphological description of post-juvenile growth stages of this species from southern Australian waters.

**DEPOSITION OF TYPES.**—*Holotype*: Female, 10.4 inches ML (264 mm), Museum of Victoria, Melbourne, Australia, F5104, in alcohol, good condition, collected in Hobson's Bay, Port Phillip, Victoria.

*Paratypes*: None designated.

**DISTRIBUTION.**—*Nototodarus gouldi* is the dominant ommastrephid in continental shelf waters south of 27°S off the Australian coast and off the northern and central coasts of New Zealand. Its abundance has resulted in the development of significant jig fisheries in this region, especially during the

summer months. Around New Zealand, it is partially sympatric with *N. sloanii* between 40°S and 44°S. In slope waters to the north of its range, *N. gouldi* is occasionally caught together with *N. hawaiiensis* (Dunning, 1988c).

*Nototodarus gouldi* has been caught where surface water temperatures vary from 11° C to over 25° C. The largest specimens from Australian waters were a 412 mm ML female and a 320 mm ML male, both were taken in a demersal trawl in the eastern Great Australian Bight in August 1981.

Previous studies of *N. gouldi* in Australasian waters have provided basic information on the population structure during the summer fishing season. Variation in mantle-length distributions during the 1977-1978 summer fishing season from a restricted area in western Bass Strait appeared to conform to a three-"brood" structure similar to that reported for *Todarodes pacificus* (Steenstrup) around Japan (Harrison, 1979). In this same area in the following two summers, however, polymodal mantle-length distributions in the jig catches and the presence throughout the fishing season of recent recruits suggested that the population consisted not of a few discrete broods but rather resulted from temporally and geographically extensive spawning of a number of subpopulations in this region (JAMARC, 1980b, 1987). A complex population structure has also been revealed for *N. gouldi* in the Taranaki Bight region off New Zealand (Sato, 1985).

**MIGRATION.**—Preliminary tagging studies in Bass Strait and adjacent waters and more comprehensive studies off the west coast of New Zealand (Taranaki Bight) (Sato, 1985) provide no confirmation of large-scale migrations for *N. gouldi* of the magnitude reported for *Todarodes pacificus* around Japan (Okutani, 1977). Although some recaptures have been made off the west coast of New Zealand up to 193 km from the tagging site (after 46 days at liberty), recaptured squid had moved in all directions with no relationship between time at liberty and distance traveled. These data were not consistent with a fixed population migration path but supported a complex population structure consisting of many localized schools (Sato, 1985; Yamada and Kattoh, 1987). The few recaptures resulting from tagging in Bass Strait (Machida, 1983) revealed movements of less than 100 km during periods of up to 57 days, suggesting that summer *N. gouldi* populations in southern Australian waters, like the New Zealand populations, are not highly migratory and have relatively restricted distributions. This view of their population structure is further supported by the presence of all life stages of *N. gouldi* from small juveniles to mature and spent adults in Bass Strait during the summer months (Dunning et al., 1981).

Length-frequency data obtained from *N. gouldi* trawled in the eastern Great Australian Bight in late 1981 provided an indication of a general increase in mantle length of squid with increasing bottom depth that may be the result of an offshore movement, either with growth or for spawning, in this species. A similar distribution pattern was observed for *N. sloanii*

off the southeast coast of New Zealand (Mattlin et al., 1985).

**SIZE, MATURITY, AND SEX RATIO.**—Size at maturity of *N. gouldi* shows variation with locality and season although the proportion of males to females in jig catches generally showed little difference from unity throughout the distribution range of this species. Catches from Bass Strait showed proportions of 0.94 in 1979-1980 and 0.96 in 1980-1981 (JAMARC, 1980b, 1987), whereas off southern Western Australia in late 1979 this proportion varied from 0.73 to 1.06 (Western Australian Department of Fisheries and Wildlife, pers. comm., 1980). In trawl samples taken in the eastern Great Australian Bight in November and December 1981, this proportion was 0.67 (235:351). In jig catches reported by Sato (1985) from Taranaki Bight and off the northwest coast of the South Island of New Zealand, the male to female proportion varied from 0.35 to 0.56.

In Bass Strait during the summer months, the majority of males of more than 230 mm ML and females of more than 300 mm ML were fully mature (JAMARC, 1980b, 1987). Among specimens collected during this study in the eastern Great Australian Bight in late winter to early spring, males matured at similar sizes to those in Bass Strait in summer, but the majority of females reached maturity at smaller sizes; most specimens of more than 250 mm ML carried eggs in their oviducts. Off the New South Wales coast near 34°S in spring to early summer, most males of more than 170 mm ML were mature, whereas near 37°S similar reproductive development was not evident until at least 190 mm ML. The smallest mature females at these latitudes were 190 mm ML and 220 mm ML, respectively (Gorman and Graham, 1983).

**GROWTH.**—In the absence of collections obtained throughout the year and given the polymodal mantle-length distributions typical of the major summer fishing ground, the growth rate and the longevity of *N. gouldi* in Australian waters has not previously been estimated with any confidence (Winstanley et al., 1983). Preliminary growth estimates of up to 4.0 cm/month and 3.0-4.5 cm/month were obtained from length-frequency data for this species jigged in Bass Strait and trawled in the Tasman Bay-Kaikoura region of central New Zealand, respectively (Harrison, 1979; Mattlin et al., 1985).

**LARVAE.**—Larvae of this species were described and illustrated by Allan (1945) and Nesis (1979a). They are characterized by the absence of photophores and the possession of eight approximately equal-sized suckers on the tip of the proboscis (the precursor to the tentacles). Morphological differences between the larvae of *N. gouldi* and *N. sloanii* have not been described (Förch, 1986), but *N. gouldi* can be separated from *N. hawaiiensis* on the basis of the two much larger suckers on the extremities of the proboscis tip and the concentrated chromatophore band around the middle of the mantle of the latter species (Harman and Young, 1986).



During summer surveys across the continental shelf and slope off central and northern New South Wales, larvae of *N. gouldi* were most abundant where bottom depth was between 50 m and 200 m rather than in slope waters (Dunning, 1986). When they had reached 9–10 mm ML, most larvae had completed the transition from rhynchoteuthion to the juvenile stage. Larvae close to the probable hatching size (0.8–1.0 mm ML) identified as this species were collected over a broad area of the southern Australian continental shelf from 28°S off southern Queensland to the western Great Australian Bight from late spring to summer. They were present in plankton samples taken off the central New South Wales coast from at least January to July (austral midsummer to midwinter).

### *Nototodarus hawaiiensis* (Berry, 1912)

FIGURES 1c, 4

?*Ommastrephes sloanei*.—Schauinsland, 1899:92.

*Ommastrephes sagittata* near *sloanei*.—Berry, 1909:418.

?*Ommastrephes sloanei sloanei*.—Pfeffer, 1912:458-459 [part].

*Ommastrephes hawaiiensis* Berry, 1912:434.

*Nototodarus sloani philippinensis* Voss, 1962:175.

*Nototodarus sloani hawaiiensis*.—Voss, 1962:175.

*Nototodarus nipponicus* Okutani and Uemura, 1973:39, figs. 1–13, pls. 1–5.

*Nototodarus hawaiiensis*.—Wormuth, 1976:2, 17–21, fig. 3.

DIAGNOSIS.—Arms I with fewer than 30 pairs of suckers, hectocotylized right arm IV with double row of slender, conical papillae and expanded ventral protective membrane distally,

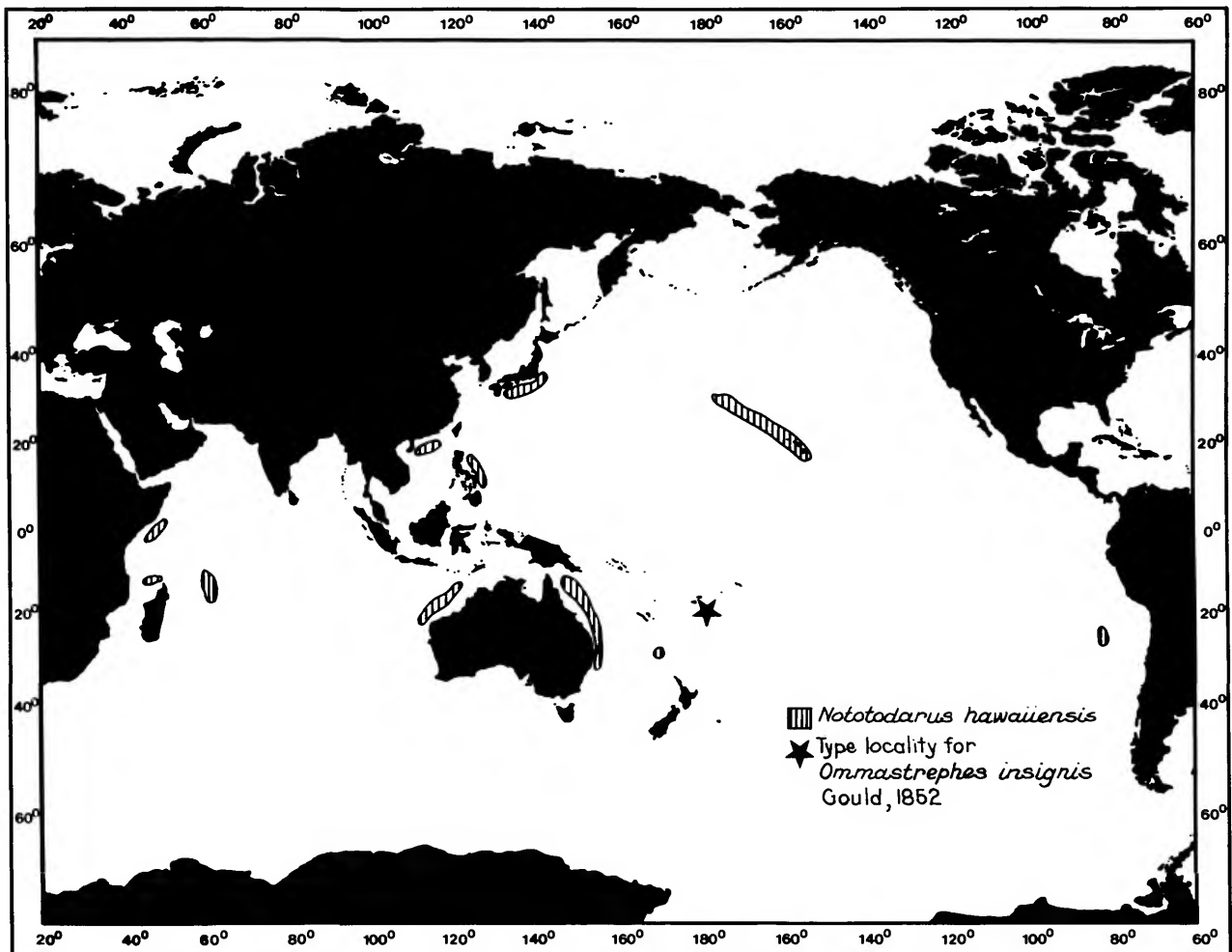


FIGURE 4.—Known distribution of *Nototodarus hawaiiensis* (Berry, 1912), and type locality for *Ommastrephes insignis* Gould, 1852.

TABLE 1.—Comparison of species characters in *Nototodarus*. (See Roper and Voss, 1983, for explanation of indices.)

Character	<i>N. sloani</i> *	<i>N. gouldi</i> *	<i>N. hawaiiensis</i> †
Arms I sucker count	> 60	28–50	19–28
Head-length index	< 20	16–20	19–31
Head-width index	< 24	18–22	21–30
Arms I sucker index	< 1.5	< 1.5	1.5–2.3
Tentacle-sucker index	< 2.5	< 3.0	2.8–3.7
Fin-length index	> 42	> 40	35–43
Arm and tentacular sucker teeth	~equal	~equal	1 tooth much larger
Teeth on largest medial manus sucker	12–15	12–15	14–18
Quadriseserial rows of manus	12–13	12–13	10–11
Skin	smooth	smooth	rough
Hectocotylus			
Proximal-sucker bases enlarged as cushions	~10 pairs	~5–6 pairs	~4–5 pairs
Normal sucker rows (right arm)	~5	~5	1–6
Ventral protective membrane (right arm)	present only on distal 1/3 of arm	wide, with attenuated supports to arm tip	wide, with attenuated supports to arm tip
Ventral-sucker bases (right arm)	rapidly diminish in height distally	rapidly diminish in height distally	modified as thin papillae
Dorsal-sucker bases modifications (right arm)	distally flattened papillae extend to arm tip	broad-based papillae extend to arm tip	broad-based papillae extend to arm tip, equal in length to ventral papillae

\*Synthesis of values from Kawakami and Okutani (1981) and Dunning (1988b).

†Synthesis of values from Wormuth (1976) and Dunning (1988b).

and supports opposite entire distal row of dorsal papillae (Figure 1c).

ORIGINAL REFERENCE.—Berry, 1912:434–437 (very brief description only). Detailed descriptions of adults were given by Berry (1914) and Wormuth (1976).

DEPOSITION OF TYPES.—*Holotype*: Mature female, 138 mm ML, National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States, USNM 214382, in isopropanol, good condition, collected at R/V *Albatross* sta 4117 off Kahuku Point, Oahu, Hawaii, in 253–282 fathoms (463–516 m) on coral sand and foraminifera bottom, 45.6° F (7.6° C), 25 Jul 1902.

*Paratypes*: None designated.

DISTRIBUTION.—*Nototodarus hawaiiensis* has been caught around the Hawaiian and Midway islands (Berry, 1912, 1914; Wormuth, 1976; Young, 1978), the South China Sea near Hainan (Dong, 1963), and the western Indian Ocean (Roeleveld, pers. comm., 1982; Nesis, 1986) (Figure 4). Its distribution throughout the island chains of the central and southeastern Pacific remains unclear although Okutani and Kuroiwa (1985) described specimens trawled at 243 m in depth at a seamount off the coast of Chile (25°39'S, 85°31'W), and further specimens from this region have been examined by Nesis and Nigmatullin (pers. comm., 1988).

Adult *N. hawaiiensis* were caught in demersal trawls south to 19°20'S off the west coast of northern Australia in depths of 162–500 m, where bottom temperatures ranged from 17.2° C to

less than 7.8° C, and off the east coast to 32°34'S in depths of 162–696 m (Dunning, 1988c).

*Nototodarus hawaiiensis* has been taken around Hawaii in shrimp trawls and occasionally on jigs over depths of 230–710 m (Young, 1978; R. Harman, pers. comm.), and specimens of up to 140 mm ML described by Dong (1963) were trawled at a depth of 290 m off Hainan, southern China. The holotype of *N. sloani philippinensis* was trawled at 565 m in soft mud where the bottom temperature was 7.4° C (Voss, 1963). Around Hong Kong, *N. s. philippinensis* has been caught on the bottom at depths of 275–650 m (Voss and Williamson, 1971).

Off the eastern Australian coast between 28°S and 32°S, *N. hawaiiensis* and *N. gouldi* occasionally have been caught together in demersal trawls on the upper continental slope. Off the northern Queensland coast, *N. hawaiiensis* has been caught together with small numbers of *T. pacificus pusillus* (Dunning, 1988a). The latter two species, however, are more abundant in shallower shelf waters (Dunning, 1988c). The distributions of *Todaropsis eblanae* and *N. hawaiiensis* overlap in tropical Australian slope waters, with *N. hawaiiensis* more abundant where these species have been caught together (Dunning, 1988c).

SIZE, MATURITY, AND SEX RATIO.—The largest individuals of *N. hawaiiensis* examined from Australian waters by Dunning (1988c) were a fully mature female, 248 mm ML, taken by demersal trawl in 376 m off the northwest shelf and a mature male of 215 mm ML caught in 555 m off southern

Queensland. Nesis (1986) reported females of up to 290 mm ML from the western Indian Ocean, and Nigmatullin and Nesis (pers. comm., 1988) have examined a female of 318 mm ML from the southeastern Pacific (25°34'S, 85°27'W). The maximum size reported by Voss and Williamson (1971) for "*Nototodarus s. philippinensis*" around the Philippines was 180 mm ML.

Among specimens of *N. hawaiiensis* examined by Dunning (1988c) from northern Australian waters, the smallest mature female was 154 mm ML and the smallest mature male was 152 mm ML. Mature squid were present off both the northwest and northeast Australian coasts at all times when samples were collected, which, together with the broad size range of specimens in all samples, indicates a prolonged spawning period in Australian waters. No significant size disparity was observed between females and males, and an almost equal sex ratio was evident in large samples (northwest shelf: Feb 1983, 60 females:68 males; Jan 1984, 314 females:301 males).

In Hawaiian waters, male *N. hawaiiensis* reach maturity at less than 120 mm ML and females at less than 150 mm ML.

Squid larger than 160 mm ML from Hawaiian waters have not been reported in the literature (Harman and Young, 1986).

**LARVAE.**—The larvae of *N. hawaiiensis* were clearly described and illustrated by Harman and Young (1986). They can be distinguished from other ommastrephid larvae by the absence of photophores and the possession of two enlarged suckers on the tip of the fused tentacle precursor (proboscis). Proboscis division begins at 3–4 mm ML, and the tentacles are completely separated by 8.5 mm ML. Around Hawaii, larvae were present throughout the year but were most abundant in spring. They were caught by Harman and Young (1986) exclusively below the mixed layer (~50 m) to a depth of 150 m.

### Comparison of Species

Morphological characters differentiating the species are given in Table 1, and the characteristic hectocotylized right arms IV of all species are illustrated in Figure 1. The boundaries of the distributions of the three species of *Nototodarus* are shown in Figures 3 and 4.

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# A Revision of the Systematics and Distribution of *Illex* Species (Cephalopoda: Ommastrephidae)

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and Michael Vecchione

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## ABSTRACT

The systematics and distributions of *Illex* species are reviewed. Four species are recognized. All four exhibit a high degree of morphological variability, perhaps related to geography or population structure, that has hindered an understanding of the species relationships and distributions. Neotypes are designated for *I. illecebrosus* and *I. coindetii*. Traditional and newly recognized characters are analyzed so that the three sympatric species in the western Atlantic can be differentiated. The primary characters that distinguish species include dentition of the largest medial suckers on the manus; meristics of the head, mantle, fins, and arms; and the morphology and meristics of several features of the hectocotylus, beak, and spermatophores. Reliance on any single character will not allow species to be identified consistently. A key to the species is presented. *Illex oxygonius* is retained as a separate species because a number of characters distinguish it from *I. illecebrosus* and *I. coindetii*. *Illex coindetii* has the broadest distribution, occurring in the eastern Atlantic southward from the North Sea, throughout the Mediterranean Sea, to Namibia, and in the western Atlantic southward from the mid-Atlantic Bight, throughout the Gulf of Mexico and Caribbean Sea, to French Guiana. *Illex illecebrosus* occurs from northern Florida northward to the Labrador Sea and occasionally to Iceland. The most restricted species, *I. oxygonius*, occurs in the western Atlantic from New Jersey to the eastern Gulf of Mexico. Because this is the zone of overlap between *I. illecebrosus* and *I. coindetii*, the possibility remains that *I. oxygonius* is a hybrid between these species. The southernmost species, *I. argentinus*, occurs from around Rio de Janeiro southward to the tip of Argentina and the Falkland Islands.

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## Introduction

The genus *Illex* was erected by Steenstrup in 1880 to accommodate the species *Loligo illecebrosus* Lesueur, 1821, from the western North Atlantic and *Loligo coindetii* Verany, 1839, from the western Mediterranean. The systematic status of these species remained unresolved, and for many years they were considered subspecies of *I. illecebrosus*, being first designated as such by Pfeffer (1912; see also Adam, 1952; Voss, 1955). Some authors, however, did not accept the subspecies designations and considered these to be separate species (e.g., Voss, 1956; Clarke, 1966). Two other species were described in the 1960s: *Ommastrephes argentinus* Castellanos, 1960, from Argentine waters and *Illex oxygonius* Roper, Lu, and Mangold, 1969, from off the southeastern United States. The description of *I. oxygonius* introduced some elements that seemed to confuse the situation. Based on an extensive analysis of characters, Roper et al. (1969) demonstrated that the four subspecific taxa were indeed four species, but they also recorded *I. coindetii* from the Caribbean Sea, the Gulf of Mexico, and the Straits of Florida. A considerable difficulty in identifying the species confidently, as well as the sympatric occurrence of the pan-Atlantic *I. coindetii* with the new species, *I. oxygonius*, and with *I. illecebrosus* in the northern part of the shared range, led to confusion and misinterpretation.

The very broad distributions of *I. coindetii* and *I. illecebrosus* in the North Atlantic, and especially the disjunct distribution of *I. coindetii* on opposite sides of the Atlantic, has led to problems of identifying species, which in turn has been an impediment to understanding the systematics of the genus. Coupled with this is the remarkable degree of morphological variation that has been observed in all four species throughout their ranges. This has made it extremely difficult to discriminate species in areas of sympatry and often has led to confusion

about identity even in areas of no geographic overlap. Although the full extent of this variation has not been analyzed for all the species, Roper and Mangold (in press) analyzed *I. coindetii* and redefined it on the basis of several characters associated with the hectocotylus. We examine herein all species of *Illex* using the newly found characters as well as traditionally recognized characters in order to define the species more precisely and to delineate their distributions.

This paper deals with the systematics and distribution of the four species of *Illex*, including the designation of neotypes for *I. illecebrosus* and *I. coindetii*. Aspects of the life history, biology and fisheries of these species are discussed in a series of papers published in a book edited by Rodhouse, Dawe, and O'Dor (in press).

#### ACKNOWLEDGMENTS

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#### MATERIALS AND METHODS

A large number of specimens was examined from a broad range of localities, many of which are listed in Lu (1973). Additional material is listed in Roper et al. (1969) and in Roper and Mangold (in press). Most of the material is deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., which houses the collections of the former United States National Museum (USNM). These specimens are designated by a USNM catalog number. Other

materials are deposited in the Invertebrate Museum of RSMAS, University of Miami, and they are designated by UMML (University of Miami Marine Laboratory) catalog numbers. The approximate number of specimens examined for each species is as follows: *I. illecebrosus*, 800; *I. coindetii*, 450; *I. argentinus*, 125; *I. oxygonius*, 60.

Tables 3-7 give comparisons of indices of various morphometric and meristic characters among the four species. The number of specimens measured for these tables and the size range of each sex for each species is presented below:

*Illex illecebrosus*: 122 males, 67-260 mm mantle length (ML); 149 females, 87-317 mm ML.

*Illex coindetii*: 123 males, 43-275 mm ML; 140 females, 44-370 mm ML.

*Illex argentinus*: 69 males, 170-256 mm ML; 46 females, 201-285 mm ML.

*Illex oxygonius*: 10 males, 135-228 mm ML; 11 females, 122-210 mm ML.

The stages of maturity ranged from immature subadults to fully mature adults in spawning condition. Because the entire range of maturity stages is included in the tables, the indices for *I. coindetii* differ slightly from those given in Roper and Mangold (in press) for which only mature specimens were used.

The measurements, indices, and counts are as given in Lu (1973) and Roper and Voss (1983). The terminology for characters of the beaks is given in Clarke (1962, 1986). Because of the newly defined suite of characters associated with the hectocotylized arm, Roper and Mangold (in press) introduced several new measurements, indices, counts, and abbreviations. The diagrammatic illustration of the hectocotylus of *I. coindetii* shows the component parts (Figure 1). Abbreviations and definitions are given below.

AL,I	arms I length
AL,II	arms II length
AL,III	arms III length
AL,IV	arms IV length
AS,I	arms I sucker diameter
AS,II	arms II sucker diameter
AS,III	arms III sucker diameter
AS,IV	arms IV sucker diameter
ASC,I	arms I sucker count
ASC,II	arms II sucker count
ASC,III	arms III sucker count
ASC,IV	arms IV sucker count
CBL	cuttle-bone length
CL	club length
CIS	club suckers
FA	fin angle
FbL	fin-base length
FL	fin length
FW	fin width
GiL	gill-lamellae count
GL	gladius length
HAB	(length of) suckerless area at base of hectocotylized arm measured from V-notch between arms IV to first sucker.



- HALs length of hectocotylied arm measured from most proximal sucker to distal tip (equivalent to HcA in Roper and Voss, 1983).
- HALt total length of hectocotylied arm measured from V-notch between arms IV to distal tip.
- HA1 (length of) proximal sucker-bearing section on hectocotylied arm with normal-sized, graded suckers.
- HA2 (length of) medial section of hectocotylied arm (distal sucker-bearing section) with suckers of reduced diameter, fringed trabeculae, or other modifications.
- HA3 (length of) modified distal tip of hectocotylus characterized by absence of protective membranes and replacement of suckers with lamellae and papillae.
- HL head length
- HW head width
- ML dorsal-mantle length
- MW1 mantle width at mantle opening
- MW2 mantle width at midpoint between mantle opening and fin insertion
- MW3 mantle width at anterior point of fin insertion
- SpL spermatophore length
- SpRL sperm-reservoir length
- SpRW sperm-reservoir width
- VML ventral-mantle length

**Family OMMASTREPHIDAE Steenstrup, 1857**

**Subfamily ILLICINAE Posselt, 1891**

TYPE GENUS.—*Illex* Steenstrup, 1880:82, by original designation.

DIAGNOSIS.—Ommastrephids with smooth funnel groove, without foveola or side pockets; photophores absent; tentacular stalks without carpal-fixing apparatus.

DISCUSSION.—The Illicinae has traditionally been comprised of two genera, *Illex* and *Todaropsis*. Currently, the status of the subfamily is unresolved in view of the phylogenetic analysis by Roeleveld (1988:279), who proposed that *Todaropsis* be separated out of the group and be placed in the Todarodinae with *Todarodes*, *Martialia*, and *Nototodarus*. This leaves only *Illex* in the Illicinae, and the relationship of the Illicinae with the Todarodinae and the Ommastrephinae remains unresolved. Little doubt can be cast on the distinctive nature of Illicinae, excluding *Todaropsis*, however, because it has a number of apomorphic characters, such as club-sucker arrangement and dentition, absence of protective membranes on the hectocotylied tip, and secondary modifications on the medial portion of the hectocotylus (Roeleveld, 1988:287).

**Genus *Illex* Steenstrup, 1880**

TYPE SPECIES.—*Loligo illecebrosa* Lesueur, 1821:95, by original designation.

DIAGNOSIS.—Illicines with 8 longitudinal rows of small to minute suckers on dactylus of tentacular club; tentacular club moderately to broadly expanded; carpal suckers small, biserial; manal suckers tetraserial, suckers in lateral rows small, largest medial suckers with smooth or bluntly crenulated horny rings; either right or left arm IV hectocotylied with equal frequency;

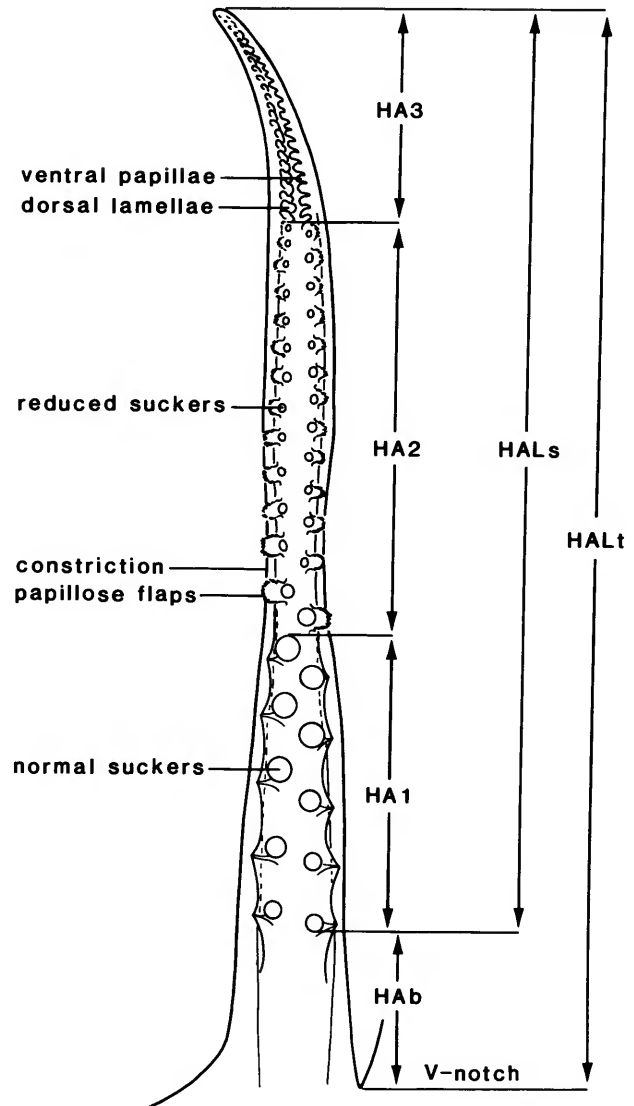


FIGURE 1.—Diagram of *Illex* hectocotylus showing morphological features, portions, and measurements. Definitions given in "Materials and Methods." Drawn from *I. coindetii* (Roper and Mangold, in press).

dorsal and ventral protective membranes of hectocotylus terminate near base of distal modified tip; secondary modification present on medial part of hectocotylied arm.

DISCUSSION.—The genus *Illex* consists of four species, all neritic. The genus is represented in the North and South Atlantic oceans and the Caribbean and Mediterranean seas in waters of the continental shelf and upper slope. It is absent from other oceans. Most members of the family Ommastrephidae are oceanic or nerito-oceanic; however, *Todarodes*, *Todaropsis*,

*Nototodarus*, and *Illex* are primarily neritic, associated with continental shelf and slope waters.

Members of the genus, particularly *Illex illecebrosus* and *I. argentinus*, form the basis of important fisheries in the western North and South Atlantic, respectively, whereas *Illex coindetii* represents a significant by-catch in some Mediterranean fisheries.

***Illex illecebrosus* (Lesueur, 1821)**

FIGURES 2, 3

DIAGNOSIS.—Hectocotylus (see Figure 1) with distal hectocotylized portion of arm IV (HA3) limited to about 22% (13%–30%) of total arm length (HALt); papillae and lamellae weakly developed; basal, suckerless part (HAb) of hectocotylized arm short, about 6% of total arm length; proximal sucker-bearing part (HA1) with 7 to 8 pairs of normal suckers increasing in diameter distally; distal sucker-bearing part (HA2) with slight secondary modification of  $\frac{1}{4}$  reduction in sucker diameter compared to normal proximal suckers; oral surface of arm IV not expanded, sucker rows not abnormally separated; very slight muscular constriction in transition zone between proximal (HA1) and distal (HA2) sucker-bearing parts; trabeculae not modified as fringed lobes; hectocotylized arm shorter than or equal to its opposite arm in length and always equal in thickness. Club expanded; largest distal medial manal sucker rings smooth, without crenulations or notches. Head-width index low, 16.3–17.0. Lower beak with jaw edge straight, short; wing long, wide, no lobe; rostral width narrow; lateral wall short, blunt. Upper beak with hood long, strong; shoulder serrated; rostrum long; wing short; jaw angle with large notch, with tooth; lateral wall short, shallow; crest curved. Fin angle mostly 45° (40°–50°), never > 50°. Spermatophore cone at oral end of cement body, a low, right-isosceles triangle with rounded corners in outline; oral tube long, narrow; aboral neck long, narrow.

ORIGINAL DESCRIPTION.—Lesueur, 1821:95.

TYPE LOCALITY.—Sandy Bay, Massachusetts, United States.

TYPE.—No types were designated. The single specimen illustrated by Lesueur when he caught it at Sandy Bay would have been the holotype (1821:95), but that specimen was not retained according to Lesueur. Based on Lesueur's description and comments, this appears to have been the only specimen available. Extensive searches (individually by CCL, CFER, and G.L. Voss) at the Academy of Natural Sciences, Philadelphia, other museums in the United States, and the Museum National d'Histoire Naturelle, Paris, confirm that no specimen in any way applicable as a holotype or as a neotype is extant.

DESIGNATION OF NEOTYPE.—In the absence of any original type material, and because of exceptional circumstances described below, it is necessary to designate a neotype as follows: mature male, 199 mm ML, National Museum of Natural History, Smithsonian Institution, USNM 727456,

TABLE 1.—Measurements (in mm), indices, and counts of the neotype of *Illex illecebrosus*, USNM 727456.

Character	Measurement (mm)	Index (%)
ML	199	
VML	188	94.5
HL	34.4	17.3
HW	27.5	13.8
MW1	30.8	15.5
MW2	35	17.6
MW3	18.6	9.4
FL	85	42.7
FW	111	55.8
FbL	76	38.2
AL,I	74	37.2
AL,II	95	47.7
AL,III	94	47.2
AL,IV	85	42.7
HALt*	88	44.2
HAb	8	9
HA1	28	32
HA2	35	40
HA3	17	19
CL	49	24.6
AS,I	2.6	1.31
AS,II	4.0	2.01
AS,III	3.9	1.96
AS,IV	2.1	1.06
CIS	2.8	1.41
GL	65	32.7
SpL	21	10.6
SpRL	14.5	69.1
SpRW	0.3	1.43
CBL	2.8	13.3
FA	41°	
ASC,I	102	
ASC,II	100	
ASC,III	98	
ASC,IV	119	
GiLC	69	

\*Right arm IV hectocotylized.

Figure 2; measurements, indices, and counts of the neotype are given in Table 1.

The International Commission on Zoological Nomenclature (ICZN) (Art. 75(b), 1985:157) stipulates that a neotype can be designated "only in exceptional circumstances ... in the interests of stability of nomenclature." In the case of *I. illecebrosus*, the exceptional circumstances occurred with the simultaneous description of *I. oxygonius* and the recognition of this new species and *I. coindetii* as sympatric with *I. illecebrosus* in the western North Atlantic (Roper et al., 1969). The range of inter- and intraspecific variability of characters makes species identification very difficult. A major international fishery exists for *I. illecebrosus* in the north, and it extends southward into the area of sympatry off the mid-Atlantic States. Consequently, all three species are involved in the fishery in the area of sympatry. Any type of rational exploitation and management

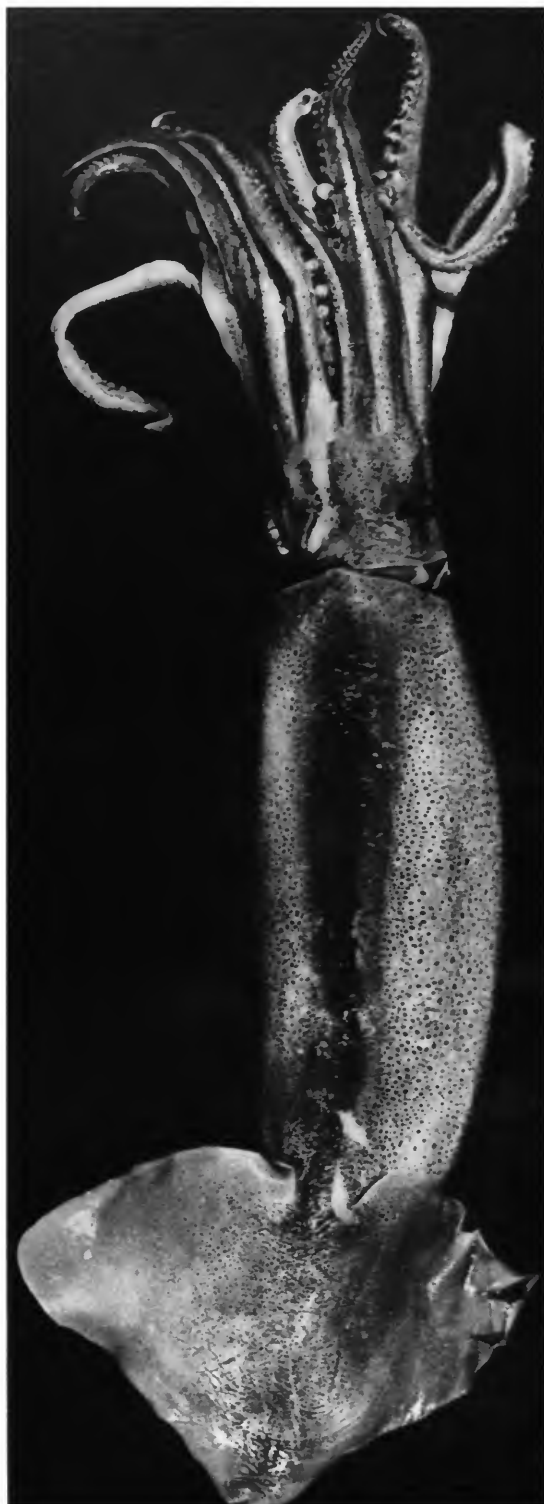


FIGURE 2.—Neotype of *Illex illecebrosus*, mature male, 199 mm ML, USNM 727456.

plan must take into account the three very similar species. The designation of clearly defined neotypes for *Illex illecebrosus* and *I. coindetii* (see below) therefore is necessary for nomenclatural stability.

**NEOTYPE LOCALITY.**—Old Scantum grounds, 12–16 km (8–10 miles) southeast of the Isles of Shoals, New Hampshire, United States, southwest edge of Jeffery's Basin, approximately 43°N, 70°30'W, 17-VIII-1971; otter trawl at 117 m; fishing vessel *Osprey*, Capt. R.A. Stetson, Rye, New Hampshire; collected by C.F.E. Roper. This locality is about 34 km north of Sandy Bay, Massachusetts, Lesueur's type locality.

**GEOGRAPHICAL DISTRIBUTION.**—Western North Atlantic Ocean from 66°N (Iceland, southern Greenland, Baffin Island) southward to around 29°N in the Straits of Florida (Figure 3). *Illex illecebrosus* is a primarily neritic species that normally inhabits continental shelf and upper slope waters.

**DISCUSSION.**—The understanding of the geographical distribution of *I. illecebrosus* has been confused for many years, a result of the unsettled state of the systematics of the genus *Illex*. The northernmost limit recorded in the western Atlantic Ocean for *I. illecebrosus* is "Cumberland Gulf" (Verrill, 1880:289, 1880–1881:280–281). This record was based on one mutilated specimen, probably part of the stomach contents of a predator, collected by L. Kumllein and reported to be deposited in the NMNH, Smithsonian Institution. Our searches of the NMNH collections confirm that this specimen no longer exists. According to Squires (1957:694), the name Cumberland Gulf actually refers to Cumberland Sound, located near the Arctic Circle at 66°N. Until further evidence proves otherwise, this record is accepted as the northernmost limit of the species. Posselt (1898:278) recorded *I. illecebrosus* from Frederikshaab, Greenland, at about 62°30'N, but without an extant specimen, the record apparently cannot be confirmed (Mercer, 1968:268).

The Icelandic records of this species also lack confirmation. Gröndal's (1891) specimen no longer exists in the Museum of Natural History of Reykjavik, and no other specimen is known from Icelandic waters (F. Gudmundsson, pers. comm., 1991; Mercer, 1968:268). Murray and Hjort (1912) reported the species there but did not specify any specimens. If Gröndal's Icelandic specimen belonged to *I. illecebrosus*, we agree with Bruun's opinion (1945:10) that it probably is only an occasional visitor to Icelandic waters. Korzun et al. (1979:472) reported catches of *I. illecebrosus* over the Mid-Atlantic Ridge (~48°N–56°N, 28°W–35°W), but it is unclear to us if this is normal habitat or, we suspect more likely, the result of occasional transport from the west by a meander of the North Atlantic Drift.

Adam (1952:92) reported that his specimens from the Bristol Channel off southwestern England were *I. illecebrosus*. One of us (CCL) examined two specimens (a male of 192 mm ML and a female of 210 mm ML) from Adam's collection, now deposited in the Invertebrate Collections of the RSMAS, University of Miami. These specimens clearly belong to *I. coindetii*, based on the structure of the hectocotylus as well as

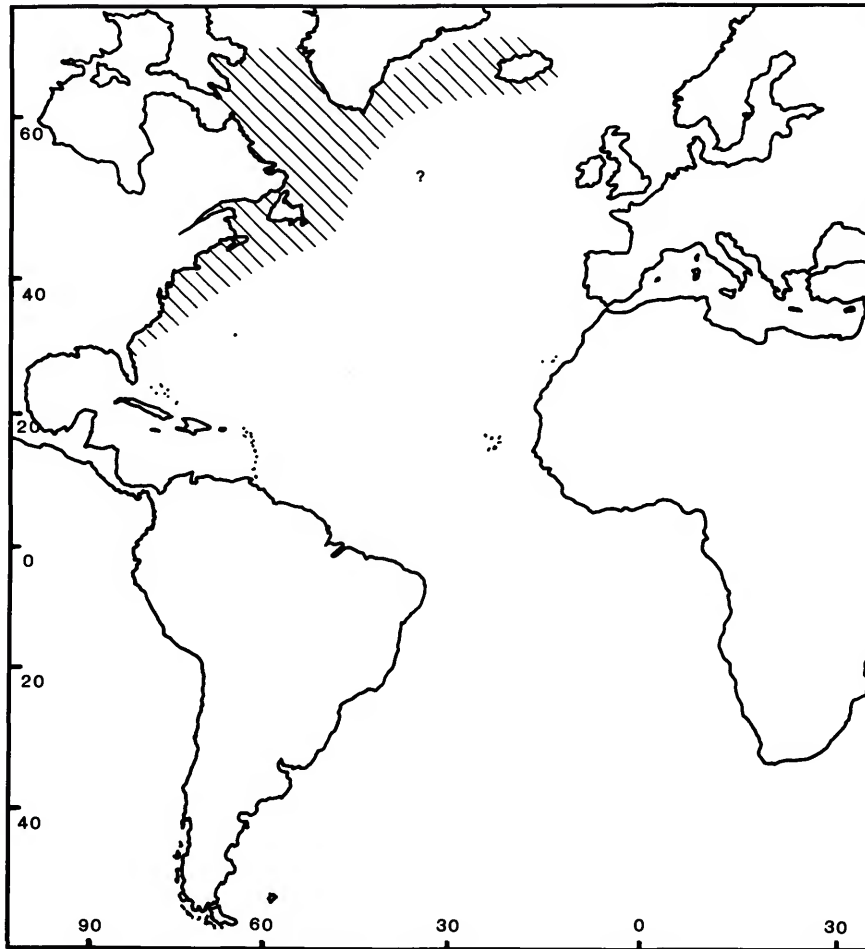


FIGURE 3.—Geographical distribution of *Illex illecebrosus*. (? = northeastern-most distributional limit uncertain.)

body measurements, especially fin angle. It seems probable that Adam's other specimens are *I. coindetii* as well. Therefore, we conclude that *I. illecebrosus* does not occur in the eastern Atlantic Ocean.

The southernmost limit of *I. illecebrosus* along the east coast of North America also is in confusion. Roper et al. (1969:318) pointed out that former records from the Gulf of Mexico and the Caribbean Sea probably are a mixture of *I. coindetii* and *I. oxygonius*, so these records can no longer be used as indications of the true distribution of the species. The southernmost specimens that we have examined and confirmed as *I. illecebrosus* come from off the east coast of Florida at 29°39'30"N, 80°08'30"W (R/V *Oregon* sta 6801). Takeda and Okutani (1983:223) reported the species from off Suriname, but their photograph, together with our new understanding of variability in *I. coindetii*, raises doubts as to the validity of the identification.

*Illex illecebrosus* exhibits strong seasonal migrations in a general pattern of northward/inshore in summer and southward/offshore in winter. Although distinct populations have not been precisely delineated, there appear to be at least two groups, a northern group that spawns in the summer/autumn and a southern group that spawns in the winter/spring (Roper and Vecchione, unpublished). This aspect of the species' distribution needs more research.

The depth distribution of *Illex illecebrosus* extends from the surface to at least 1000 m, but it varies markedly by growth stage, geographically and seasonally. For example, in the inshore summer fishery in the shallow bays of Newfoundland it is jigged in the upper few meters, whereas in the offshore otter trawl fishery to the south (Nova Scotia to Mid-Atlantic Bight) it is taken on the bottom at 250 m. Observations from submersibles record *I. illecebrosus* from both pelagic and benthic habitats at 326–882 m; it commonly rests on the

bottom on the continental slope (Vecchione and Roper, 1992:439, 442). The species undergoes a diel vertical migration during which animals are concentrated on or near the bottom during the day and disperse into the water column at night (Roper and Young, 1975:13). Observations by SCUBA diving in Newfoundland in late afternoon revealed *I. illecebrosus* concentrated at 3–5 m below the surface in water depths of 12–28 m (Williamson, 1965:220). Furthermore, mass strandings of this species occasionally are reported when huge numbers wash ashore, as occurred in eastern Cape Cod Bay in the fall of 1976 (Lux et al., 1978).

***Illex coindetii* (Verany, 1839)**

FIGURES 4, 5

**DIAGNOSIS.**—Hectocotylus (see Figure 1) with distal hectocotylized portion of arm IV (HA3) relatively short, about 25% (17%–30% on fully mature males) of total arm length (HALt); basal, suckerless part (HAb) of hectocotylized arm about 13% (10%–14%) of total length of arm; proximal sucker-bearing part of hectocotylus (HA1) with 5–7 (mostly 5 to 6) pairs of normal suckers increasing in diameter distally; distal sucker-bearing part (HA2) starts with pair of suckers immediately decreased in diameter by  $\frac{1}{2}$  or more in comparison to adjacent proximal pair; rows widely separated, suckers in both rows remain small (but slightly increasing then decreasing in diameter) until termination at distal modified portion; oral surface constricted in transition zone between HA1 and HA2; at proximal origin of HA2, trabeculae distal to largest normal suckers (HA1) transformed into distinctive, round, papillose, fringed flaps; arm musculature conspicuously constricted in transition area where large suckers become reduced; modified distal portion (HA3) starts with 1 to 2 proximal conical knobs on dorsal row followed by fully developed truncate lamellae; ventral row starts with 1 to 2 small conical knobs followed by digitate papillae, no lamellae; hectocotylized arm longer and more robust than opposite arm IV in fully mature males. Club expanded; largest distal manal-sucker rings notched in distal  $\frac{1}{2}$  or all around with low crenulations, not smooth. Head-width index high, 23 (19–26) in mature males, 19 (15–22) in mature females. Lower beak with jaw edge long, strong; wing long, wide, no lobe; rostral width narrow; lateral wall short, blunt. Upper beak with hood long, strong; shoulder smooth; rostrum long; wing short; jaw angle with small notch, no tooth; lateral wall short, shallow; crest curved. Fin angle  $> 50^\circ$ . Spermaphore cone at oral end of cement body, low, rounded triangle, lens-shaped, or diamond-shaped in outline; oral tube broad; aboral neck of cement body very short, broad, indistinct.

**ORIGINAL DESCRIPTION.**—Verany, 1839:94.

**TYPE LOCALITY.**—Off Nice, France, Mediterranean Sea.

**TYPES.**—*Holotype*: Presumably, the holotype was deposited in the Museum of Natural History in Nice at the time of original description, but extensive searches by several investi-



FIGURE 4.—Neotype of *Illex coindetii*, mature male, 132 mm ML, USNM 727457.

gators indicate that the holotype no longer is extant there or at the Museum National d'Histoire Naturelle, Paris. Therefore, the type is assumed to be lost.

**Paratypes:** None designated.

**DESIGNATION OF NEOTYPE.**—In the absence of any type material, and because of exceptional circumstances, it is necessary to designate a neotype as follows: mature male, 132

mm ML, National Museum of Natural History, Smithsonian Institution, USNM 727457, Figure 4; measurements, indices, and counts of the neotype are given in Table 2.

Under the requirements of the ICZN, Art. 75(b), certain circumstances are stipulated under which a neotype can be designated. The same circumstances that apply to *I. illecebrosus* (see above) also apply to *I. coindetii*. In addition, *I. coindetii* occurs in the Mediterranean Sea and eastern Atlantic Ocean where it is a targeted or by-catch species in international commercial fisheries. The extensive morphological variation that exists throughout the range of the species has led to suggestions of a multiple species complex (see discussion in Roper and Mangold, in press). Therefore, a precisely described neotype from the region of the type locality is needed to define the species in order to establish nomenclatural stability throughout the entire range of the species.

**NEOTYPE LOCALITY.**—42°32'N–42°35'N, 03°36'E–03°42'E, off Port Vendres, France; 3-XI-1971, by otter trawl at 200–500 m. Specimen provided by K. Mangold. This locality is approximately 310 km southwest of Nice, the type locality.

**GEOGRAPHICAL DISTRIBUTION.**—*Eastern Atlantic:* European coast of Atlantic Ocean, from Oslo Fjord and North Sea (around 59°N) to Bristol Channel southward; western and eastern Mediterranean Sea; Adriatic and Aegean seas; absent from Black Sea and upper Adriatic; African coast of Atlantic southward to Namibia, around 19°S–20°S. *Western Atlantic:* United States coast from 37°N southward, in Straits of Florida, Gulf of Mexico, Caribbean Sea, to northeastern South America, including Panama, Venezuela, Suriname, and French Guiana to about 3°N (Figure 5). Continental shelf and upper slope.

**DISCUSSION.**—The systematics and distribution of *Illex coindetii* recently have been reviewed (Roper and Mangold, in press). The geographical distribution of *Illex coindetii* is widely spread and disjunct. It has been reported in the eastern Atlantic from as far north as Oslo Fjord, approximately 59°30'N (Lu, 1973). It occurs throughout the North Sea from Helgoland (Grimpe, 1925), along the Atlantic coasts of France, Spain, and Portugal, and down the west coast of Africa southward to Namibia, around 20°S. It also occurs throughout the Mediterranean Sea, the lower Adriatic Sea, and the Aegean Sea. It is absent from the Black Sea and apparently from the upper regions of the Adriatic Sea, possibly because the water depths are too shallow.

Two specimens reported from the Red Sea (Adam, 1942) and deposited in the Museum National d'Histoire Naturelle de Paris appear to be mislabelled. Originally said to be collected from the Red Sea by Clot in 1850 (fide the label accompanying the specimens; also Adam, 1942:14), it is highly unlikely that a strongly stenohaline species like *Illex coindetii* could overcome the rigors of a pre-Lessepsian faunal interchange. Such interchange was accomplished only rarely by euryhaline species prior to the opening of the Suez Canal in 1869 (Por, 1971). As the species subsequently has not been reported from the Red Sea and has never been reported from the Indian

TABLE 2.—Measurements (in mm), indices, and counts of the neotype of *Illex coindetii*, USNM 727457.

Character	Measurement (mm)	Index (%)
ML	132	
VML	122	92.4
HL	29	22.0
HW	28.2	21.4
MW1	30	22.7
MW2	28.4	21.5
MW3	14.7	11.1
FL	52	39.4
FW	75	56.8
FbL	45	34.1
AL,I	66	50.0
AL,II	86	65.2
AL,III	86	65.2
AL,IV	74	56.1
HALI*	84	63.6
HAb	13	15
HA1	27	32
HA2	31	37
HA3	21	25
CL	66	50.0
AS,I	2.9	2.20
AS,II	4.9	3.71
AS,III	4.9	3.71
AS,IV	2.5	1.89
CIS	3.4	2.58
GL	38.9	29.5
SpL	24	18.2
SpRL	12.5	52.1
SpRW	0.3	1.25
CBL	5	20.8
FA	57°	
ASC,I	107	
ASC,II	97	
ASC,III	99	
ASC,IV	119	
GiLC	57	

\*Left arm IV hectocotylized.

Ocean, we must discount Adam's record as mislabelled specimens (Lu, 1973).

The northernmost record of *Illex coindetii* in the western Atlantic Ocean is 37°06'N, 74°35'W, from an otter trawl off the coast of Virginia in the Norfolk Canyon. It is distributed southward along the continental shelf in the edge of the Gulf Stream and the Florida Current, into the Gulf of Mexico and the Caribbean Sea. The southernmost record we have seen in the Caribbean is from 09°02'18"N, 81°23'48"W, in the Golfo de Mosquitos (R/V *Pillsbury* sta 445, UMML 31.1318), but the exact extent of the distribution along the South American coast is undetermined. Arocha et al. (1992) record it along the Venezuelan coast to 62°W. Takeda and Okutani (1983) report it from the waters of Suriname and French Guiana, so it probably reaches around 3°N, 52°W. No records exist from the

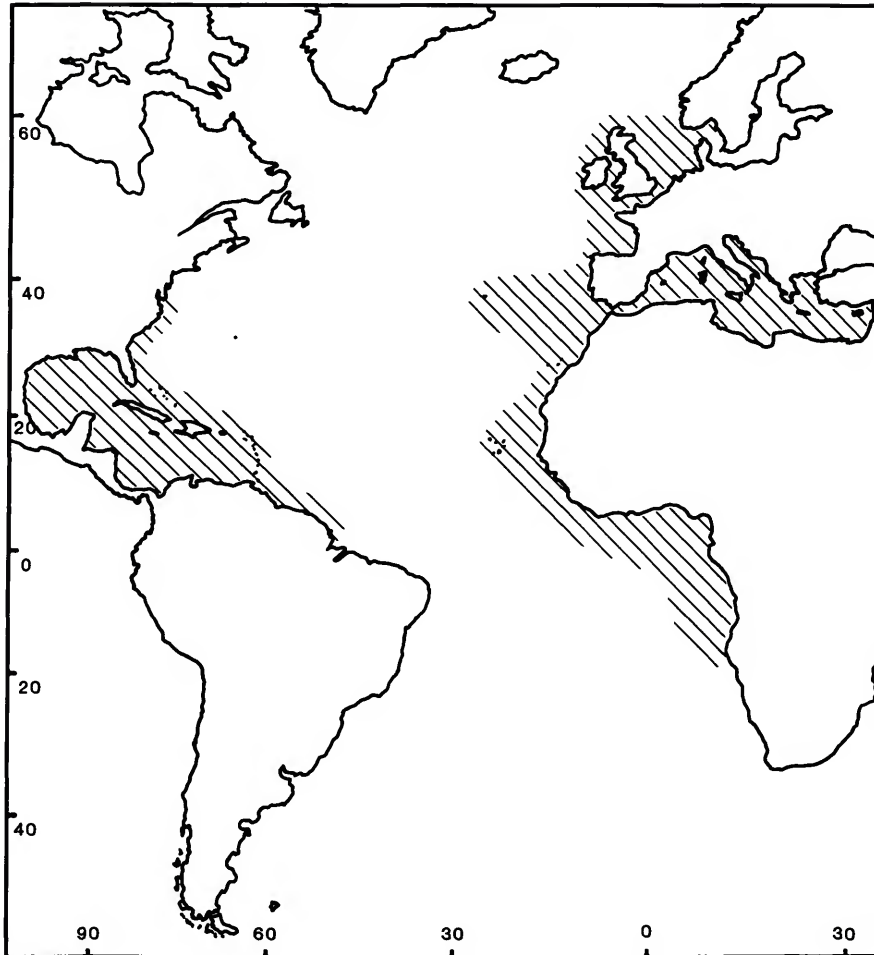


FIGURE 5.—Geographical distribution of *Illex coindetii*.

central Atlantic Ocean between the Antilles Chain and the waters off West Africa.

Thus, our analysis of collections from the Mediterranean Sea and from the Caribbean Sea, Gulf of Mexico, and Straits of Florida confirms that *Illex coindetii* does occur in the western Atlantic as stated by Roper et al. (1969). We have material of two distinct forms of *Illex coindetii* from the Mediterranean. One form is very robust, particularly the head and arms of males, whereas in the other form the head and arms are less strongly developed. The recently completed analysis of *I. coindetii* by Roper and Mangold (in press) demonstrated that the species is highly variable and that a number of morphotypes occur throughout the range of the species.

*Illex coindetii* in the low-latitude, western Atlantic warm waters is similar to the robust form in the Mediterranean Sea. In parts of the western Atlantic, however, specimens get very large, with females up to 319 mm ML and males up to 252 mm

ML, although much smaller, fully mature specimens of both sexes also are found. Some specimens taken off Vigo, Spain, also have been reported to reach an unusually large size: males of 270 mm ML and females of 370 mm ML (A. Guerra and A. Gonzales, pers. comm., 1991).

*Illex coindetii* is a demersal, neritic species that occurs from the surface to about 1000 m deep, with maximal concentrations between 60–600 m depending on geographical location (Roper et al., 1984). Adults, at least, undergo diel vertical migrations, leaving their daytime sites on or near the silty to muddy bottom to disperse into the water column at night. Seasonal migrations are recorded, particularly in the Mediterranean Sea where the species has been studied most extensively (Mangold-Wirz, 1963; Sanchez et al., in press). Large, maturing to mature animals migrate from offshore depths of 200–400 m in the winter into nearshore, shallow water in the summer (Mangold-Wirz, 1963; Sanchez, 1981).

*Illex argentinus* (Castellanos, 1960)

FIGURE 6

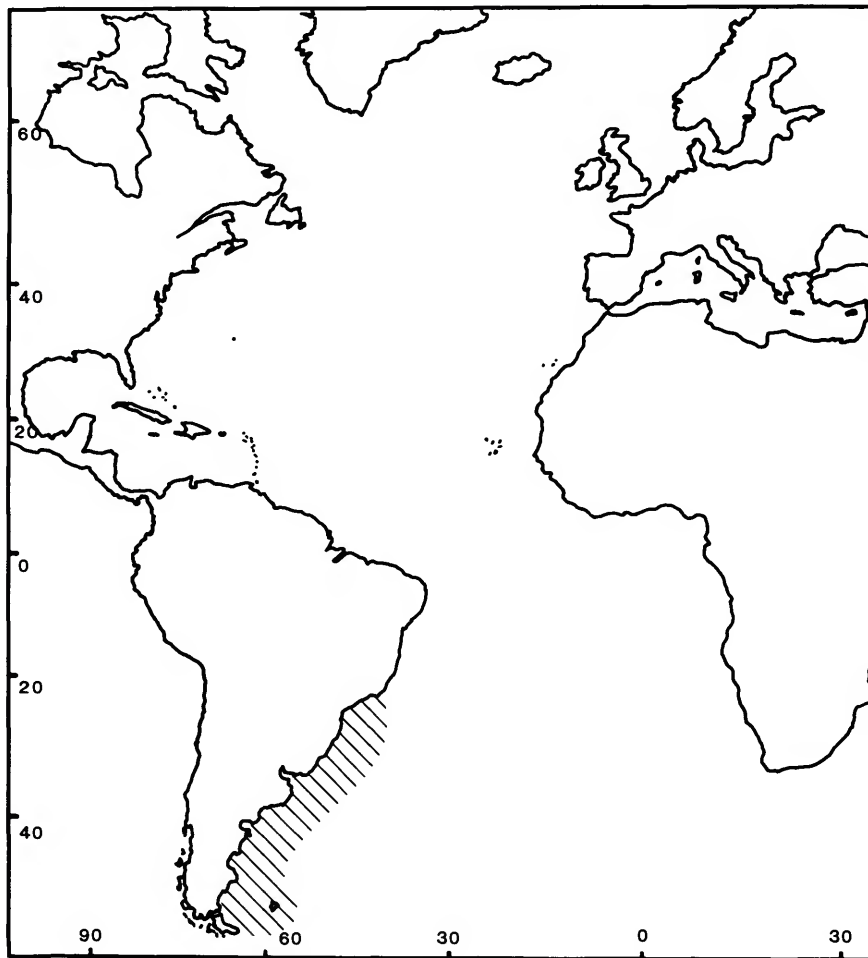
DIAGNOSIS.—Hectocotylus (see Figure 1) with distal hectocotylized portion of arm IV (HA3) and modified HA2 greater than 50% (up to 70%) of total arm length (HALt) (see discussion below); distal tip with 18–22 large, truncate or rounded lamellae on dorsal row and numerous small, indistinct, narrow lamellae on ventral row to tip; medial modified part of hectocotylized arm (HA2) with 10–16 enlarged, rounded, suckerless knobs on dorsal row and 7–10 low, suckerless knobs followed by 7–12 nipple-like papillae on ventral row; proximal sucker-bearing part (HA1) with 8–13 normal suckers; basal, suckerless part (HAb) of hectocotylized arm about 10% of total arm length; hectocotylized arm longer and more robust than opposite arm. Club only slightly expanded;

distal medial manal suckers very enlarged, lateral manal suckers extremely small; largest medial manal-sucker rings smooth or notched with few low, broad crenulate plates. Head-width index low, 16.0–17.8. Lower beak with jaw edge curved, long; wing long, wide, no lobe; rostral width narrow; lateral wall short, blunt. Upper beak with hood long, strong; shoulder serrated; rostrum long; wing short; jaw angle with large notch, with tooth; lateral wall short, shallow; crest curved. Fin angle broad, 45°–55°. Spermatophore cone at oral end of cement body, flat, low, lens-shaped in outline; oral tube broad; aboral neck broad, distinct.

ORIGINAL DESCRIPTION.—Castellanos, 1960:55.

TYPE LOCALITY.—39°S, 55°W, off Argentina, western South Atlantic.

TYPES.—*Holotype*: Museo de La Plata, Argentina, no. 45.001, mature female, 272 mm ML.

FIGURE 6.—Geographical distribution of *Illex argentinus*.



*Paratypes:* Museo de La Plata, Argentina, no. 45.002, mature male, 203 mm ML, and mature female, 287 mm ML.

**GEOGRAPHICAL DISTRIBUTION.**—Western South Atlantic Ocean from 23°S, around Rio de Janeiro and Cabo Frio (Haimovici and Perez, 1992), southward to about 55°S, including the Falkland Islands and Burwood Bank (Figure 6). Continental shelf and upper slope.

**DISCUSSION.**—The hectocotylus of *Illex argentinus* is very distinctive because HA2 loses suckers during development, and it becomes suckerless at full maturity. Consequently it is very difficult to determine the transition point between HA2 and HA3, and the modified part of the hectocotylus traditionally has been reported as 50%–70% (HA2 + HA3). This value is not equivalent to HA3, however, which has been used in the other species. *Illex argentinus*, although relatively restricted in distribution in the western South Atlantic, is extremely abundant and supports a major international fishery. Peak catches occurred in 1987 when 743,189 metric tons were landed (Roper and Rathjen, 1991). The species attains a large size, with fully mature males of 200–240 mm ML and females of 235–285 mm ML. Maximum mantle lengths are reported up to 353 mm ML (Uozumi and Shiba, 1993).

*Illex argentinus* occurs from near the surface to depths of 800 m, with concentrations on the lower shelf at 50–200 m. Preferred water temperatures range between 5°–12° C.

No detailed morphological systematic studies have been conducted on *I. argentinus* specimens from throughout its range. Electrophoretic studies, however, indicate that the species has a marked genetic differentiation among populations. Low levels of genetic variability within separate populations indicate the possibility of several isolated, geographical stocks (Carvalho et al., 1992; Carvalho and Nigmatullin, pers. comm.). The suggestion of these authors that these populations are unrecognized species of *Illex* must be viewed with considerable caution until detailed morphological and, if possible, molecular studies can be undertaken. Because *I. coindetii* shows considerable populational, geographical, and seasonal variation as a single species (Roper and Mangold, in press), we suspect similar mechanisms and phenomena occur in *I. argentinus* populations throughout its range.

Aspects of the distribution and abundance of *I. argentinus* were discussed by Brunetti and Perez Comas (1989). The paralarvae were described by Brunetti (1990), and their distribution was discussed by Brunetti and Ivanovic (1992). Ivanovic and Brunetti (1994) analyzed the diet of *I. argentinus*; it consists primarily of pelagic crustaceans, fishes, and squids. The crustaceans were predominately the amphipod *Themisto gaudichaudii* and euphausiids; the most important fishes were myctophids, particularly in the continental shelf break area. Cannibalism on paralarvae and juveniles was especially evident on the Buenos Aires shelf. Squids preyed mostly on crustaceans in the Patagonian area, whereas fishes were the predominant prey on the Buenos Aires shelf. Vidal (1994) described the morphological changes that occur during growth in paralarvae and juveniles of *I. argentinus*.

### *Illex oxygonius* Roper, Lu, and Mangold, 1969

FIGURE 7

**DIAGNOSIS.**—Hectocotylus (see Figure 1) with distal hectocotylized portion of arm IV (HA3) moderately long, about 29% (24%–32%) of total arm length (HALt); 3 knobs and 2 slightly flattened papillae proximal to well-developed lamellae in dorsal row; basal, suckerless part (HAb) of hectocotylized arm 4% of total arm length; proximal sucker-bearing part (HA1) with 7 pairs of normal suckers; distal sucker-bearing part (HA2) with sucker diameters reduced in size by about 1/4 on both rows; rows normally separated; oral surface of arm constricted slightly in transition zone between HA1 and HA2, but with no distinct reduction of arm musculature between normal and reduced sucker areas; trabeculae not modified as fringed lobes; hectocotylized arm longer and more robust than opposite arm in fully mature animals. Club-sucker rings of largest distal medial manal suckers smooth, without crenulations or notches. Head-width index high, 20.7 (19–23) in mature males, 17.8 (16–20) in mature females. Lower beak with jaw edge curved, long; wing short, narrow, lobate; rostral width wide; lateral wall long, pointed. Upper beak with hood short, very thin, weak; shoulder smooth, straight or slightly curved; rostrum short; wing short; jaw angle with small notch; lateral wall long, deep; crest straight. Fin angle in mature males acute, 25°–35°, occasionally 40°; fin width equal to fin length. Spermatophore cone at oral end of cement body, funnel-shaped, with sides equal, broadly triangular in outline; oral tube relatively broad; aboral neck moderately short, narrow. Mantle long and narrow; tapering gradually to point posteriorly; males with sharp triangular dorsal lobe at mantle opening.

**ORIGINAL DESCRIPTION.**—Roper, Lu, and Mangold, 1969:299.

**TYPE LOCALITY.**—24°13'N, 81°58'W, in Straits of Florida off Key West, Florida, United States.

**TYPES.**—*Holotype:* USNM 577000, mature male, 207 mm ML.

*Paratypes:* USNM 577001–3, USNM 577005, 4 males, 135–205 mm ML; USNM 577004, 577006, 2 females, 181 mm ML, 210 mm ML.

**GEOGRAPHICAL DISTRIBUTION.**—Western North Atlantic, off mid-Atlantic United States from New Jersey southward to Straits of Florida and Gulf of Mexico. Limits of geographical distribution of species not well defined because of lack of comprehensive collections. Neritic, shelf to upper slope waters (Figure 7). Taken at depths of 50–555 m.

**DISCUSSION.**—C. Nigmatullin (pers. comm., 1991) and others have questioned the validity of this species because males of other *Illex* species occasionally are found with acute fin angles. We believe that *I. oxygonius* is a distinct species based on an analysis of multiple distinctive, morphological characters. This is discussed below in “Comparison of Species.”

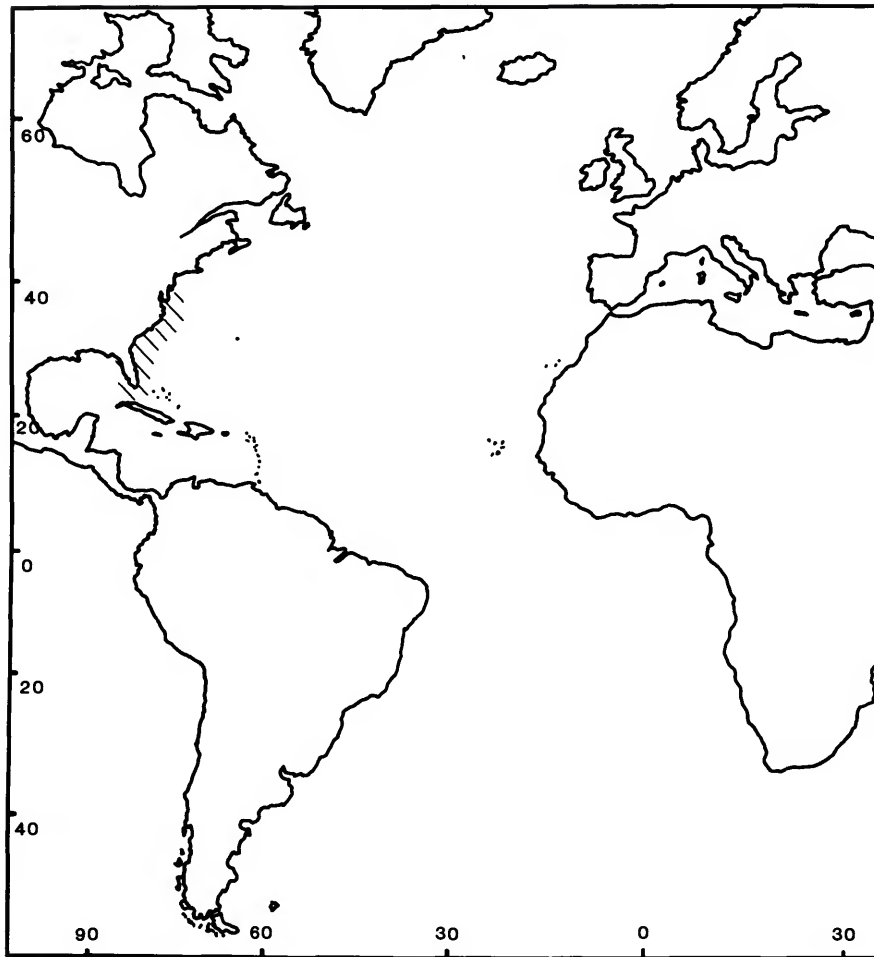


FIGURE 7.—Geographical distribution of *Illex oxygonius*.

*Illex oxygonius* is a neritic species currently known to occur to depths of 555 m in a temperature range of 6°–12° C. It is sympatric with both *I. illecebrosus* in the northern parts of its range and *I. coindetii* in the southern parts. All three species appear to co-occur in the Straits of Florida, but this needs to be confirmed with more precisely located collections.

#### Comparison of Species

The four species of *Illex* differ in several characters. These were discussed in detail to the extent of available knowledge by Roper et al. (1969), but more recent and current studies have provided additional information. The following discussion augments or supplants the 1969 account. The data presented below were derived from approximately 1500 specimens. A complete list of all material used in these analyses is on file at

the National Museum of Natural History, Washington, D.C., and the Museum of Victoria, Melbourne.

**HEAD LENGTH AND HEAD WIDTH.**—*Illex coindetii* has the longest head of the four species (Table 3). In both sexes, the head-length index is (in decreasing order) *I. coindetii*, *I. argentinus*, *I. oxygonius*, and *I. illecebrosus*. Both sexes of *I. coindetii* also have the widest heads of all species, followed by *I. oxygonius*, *I. argentinus*, and *I. illecebrosus* for males, and *I. oxygonius*, *I. illecebrosus*, and *I. argentinus* for females (Table 3).

**MANTLE.**—Mantle width is subject to significant changes during growth, particularly in maturing and mature females due to the enlargement of the developing and mature nidamental glands and ovaries. In general, the mantle is widest at the three selected points measured in preserved specimens of *I. coindetii* and *I. argentinus*, whereas *I. oxygonius* tends to have the

TABLE 3.—Head-length indices (HLI) and head-width indices (HWI) for males and females of the four species of *Illex*. (See "Materials and Methods" for size range (ML) of measured specimens.)

Species	Male		Female	
	Mean	Range	Mean	Range
HLI				
<i>I. illecebrosus</i>	16.4	(10.6–24.7)	15.7	(11.4–22.6)
<i>I. coindetii</i>	21.8	(13.7–29.6)	19.0	(10.0–23.6)
<i>I. argentinus</i>	19.5	(16.0–23.9)	16.8	(14.3–19.7)
<i>I. oxygonius</i>	18.2	(15.0–21.3)	16.3	(12.9–18.6)
HWI				
<i>I. illecebrosus</i>	17.0	(10.0–21.8)	16.3	(12.9–20.4)
<i>I. coindetii</i>	21.1	(13.2–29.1)	18.4	(12.9–25.1)
<i>I. argentinus</i>	17.8	(11.8–21.1)	16.0	(11.7–18.8)
<i>I. oxygonius</i>	20.0	(18.2–22.9)	17.5	(14.7–19.7)

TABLE 4.—Mantle-width indices (MWI) for males and females of the four species of *Illex*. (MW1 is measured at the mantle opening, MW2 is measured at the midpoint between the mantle opening and the fin insertion, and MW3 is measured at the anterior point of the fin insertion; see "Materials and Methods" for size range (ML) of measured specimens.)

Species	Male		Female	
	Mean	Range	Mean	Range
MW11				
<i>I. illecebrosus</i>	18.0	(15.2–23.1)	17.5	(13.9–26.0)
<i>I. coindetii</i>	21.9	(13.7–27.6)	20.3	(16.9–28.0)
<i>I. argentinus</i>	19.8	(14.3–24.2)	18.5	(15.4–21.7)
<i>I. oxygonius</i>	18.7	(16.9–19.9)	17.7	(16.0–20.8)
MW21				
<i>I. illecebrosus</i>	19.7	(15.7–29.1)	19.5	(15.2–28.3)
<i>I. coindetii</i>	21.5	(15.5–30.1)	20.4	(14.7–28.8)
<i>I. argentinus</i>	22.7	(18.7–27.1)	22.3	(18.5–26.5)
<i>I. oxygonius</i>	16.4	(13.1–19.8)	17.8	(15.3–20.5)
MW31				
<i>I. illecebrosus</i>	12.0	(8.2–19.8)	12.0	(9.2–19.3)
<i>I. coindetii</i>	13.6	(8.7–22.8)	13.0	(7.6–19.9)
<i>I. argentinus</i>	13.3	(9.8–17.1)	14.2	(9.6–22.1)
<i>I. oxygonius</i>	10.9	(8.1–16.4)	10.8	(9.0–14.3)

narrowest mantle widths. Table 4 presents mantle-width indices (MWI) measured at three different points along the mantle: (1) MW11, width of mantle at the mantle opening; (2) MW21, width of mantle at the midpoint between the mantle opening and the anterior insertion of the fins; and (3) MW31, width of mantle at a point in line with the insertion of the fins.

The mantle of *I. oxygonius* is long and narrow, and it tapers evenly to a point posteriorly, whereas that of *I. coindetii* is shorter, less narrow, and less drawn out posteriorly. The mantles of both *I. argentinus* and *I. illecebrosus* are more full and robust. Males of *I. oxygonius* have a sharp, triangular dorsal lobe at the mantle opening. Although small lobes may be present in some specimens of the other species, they are not distinct.

Some workers have suggested that the morphological and morphometric characters of the mantle of *I. oxygonius* are artifacts of preservation. A number of freshly collected *I. illecebrosus* were measured, then fixed in the traditional manner (10% buffered formalin solution), and then transferred to 70% ethyl alcohol. More than one year later the specimens were reexamined and remeasured. The morphometric changes were minimal. They certainly did not mimic the habitus of *I. oxygonius*. Therefore, we conclude that it is extremely unlikely that *I. oxygonius* represents an artifact of preservation of *I. illecebrosus* (Vecchione, unpublished).

FINS.—The longest fins (FLI) and the longest base of the fins (FbLI) occur in *I. oxygonius*, followed in decreasing order by *I. illecebrosus*, *I. argentinus*, and *I. coindetii*. *Illex argentinus* has the widest fins (FWI), followed by *I. coindetii* and *I. illecebrosus*; *I. oxygonius* conspicuously has the narrowest fins (Table 5).

The angle of the fins varies greatly among species. In *I. oxygonius* it generally is the most acute, each fin forming an angle of 25°–35°, occasionally 40°, with the longitudinal axis of the mantle. The fin angle in *I. illecebrosus* is 40°–50°, mostly 45°, whereas in *I. coindetii* it exceeds 50°, and in *I. argentinus* it also is broad at 45°–55°. Our experience and that of other workers indicate that fully mature males of *I. coindetii*, *I. illecebrosus*, and *I. argentinus* can have relatively elongate mantles and narrow-appearing fin angles (C. Nigmatullin, M. Lipinski, E. Hatfield, respectively, pers. comm., 1991). Therefore, the fin angle alone is not a reliable character, and, as with other characters in the genus, it must be used in combination with a variety of characters.

ARMS.—Both sexes of *I. argentinus* have relatively longer arms than the other three species. Arm length in males (in

TABLE 5.—Fin-length indices (FLI), fin-width indices (FWI), and fin-base length indices (FbLI) for males and females of the four species of *Illex*. (See "Materials and Methods" for size range (ML) of measured specimens.)

Species	Male		Female	
	Mean	Range	Mean	Range
FLI				
<i>I. illecebrosus</i>	43.8	(31.3–49.3)	44.1	(38.1–53.5)
<i>I. coindetii</i>	39.2	(31.3–46.4)	39.4	(29.4–46.2)
<i>I. argentinus</i>	41.9	(36.3–47.2)	42.3	(37.3–45.2)
<i>I. oxygonius</i>	45.0	(42.0–47.9)	45.0	(42.5–48.1)
FWI				
<i>I. illecebrosus</i>	55.4	(43.0–64.2)	54.6	(40.9–65.8)
<i>I. coindetii</i>	56.4	(45.7–66.5)	53.7	(37.0–65.9)
<i>I. argentinus</i>	58.0	(51.9–66.3)	56.4	(52.2–64.2)
<i>I. oxygonius</i>	51.5	(43.8–62.4)	50.5	(43.1–56.9)
FbLI				
<i>I. illecebrosus</i>	39.5	(28.4–44.3)	39.5	(33.8–50.3)
<i>I. coindetii</i>	33.9	(19.3–40.7)	34.5	(25.0–41.6)
<i>I. argentinus</i>	37.5	(35.2–43.0)	37.8	(34.4–40.3)
<i>I. oxygonius</i>	40.2	(35.8–42.4)	40.0	(37.9–43.2)

TABLE 6.—Arm-length indices (ALI) (hectocotylus not included) for males and females of the four species of *Illex*. (See "Materials and Methods" for size range (ML) of measured specimens.)

Arm	<i>I. illecebrosus</i>		<i>I. coindetii</i>		<i>I. argentinus</i>		<i>I. oxygonius</i>	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Males								
I	39.1	(25.5–56.0)	47.4	(27.1–77.4)	55.6	(45.8–65.0)	43.9	(35.2–53.3)
II	48.2	(32.4–70.0)	62.5	(37.4–96.6)	70.2	(57.9–84.2)	54.8	(45.0–64.2)
III	48.2	(32.4–70.3)	61.0	(37.6–95.9)	71.2	(52.5–86.4)	54.7	(43.8–63.0)
IV	43.0	(27.5–62.9)	54.1	(29.3–87.8)	61.6	(42.6–74.4)	47.9	(39.4–60.6)
Females								
I	36.5	(29.2–49.3)	37.6	(25.0–56.1)	46.2	(39.3–53.7)	34.3	(27.9–39.3)
II	44.5	(35.3–56.8)	48.7	(36.4–67.1)	57.4	(48.5–66.5)	42.9	(34.7–50.9)
III	44.5	(34.7–57.6)	48.3	(36.4–67.7)	58.5	(47.1–70.0)	43.4	(36.5–54.0)
IV	40.4	(29.4–52.6)	42.4	(25.0–63.5)	52.0	(43.4–59.7)	38.1	(31.9–46.0)

decreasing order of arm-length index) of the other species is *I. coindetii*, *I. oxygonius*, and *I. illecebrosus*, but in females it is *I. coindetii*, *I. illecebrosus*, and *I. oxygonius* (Table 6). Males of the genus *Illex* have distinctly longer arms than do females, particularly in *I. argentinus*, *I. coindetii*, and *I. oxygonius*. Sexual dimorphism in arm length is less pronounced in *I. illecebrosus*. Arms II and III are much more robust in males than in females, especially in *I. coindetii*, less so in *I. argentinus* and *I. oxygonius*; no such robust modification occurs in males of *I. illecebrosus*.

Sexual dimorphism also exists in arm-sucker diameter of adults. The largest sucker on each sessile arm is always larger in males than in females of all species, especially so in *I. coindetii*, *I. argentinus*, and *I. oxygonius* (Table 7). The largest suckers on arms II and III of males of these three species are greatly enlarged, whereas no such dramatic enlargement occurs in *I. illecebrosus*.

CLUB SUCKERS.—The dentition on the largest distal, medial sucker rings on the manus of the tentacular club is a useful character in distinguishing *I. coindetii* from *I. illecebrosus* and *I. oxygonius*. We emphasize that these suckers are the most distal of the enlarged, medial manal suckers. On *I. coindetii* the rings are notched distally to make 7 to 8 low, flat, broad teeth with one very broad, low plate proximally (Lu, 1973, fig. 17G). In *I. illecebrosus* and *I. oxygonius* the rings are entire and toothless, rarely with a very shallow notch in the distal margin (Lu, 1973, fig. 6E). *Illex argentinus* has entire, toothless rings, or rings with a few unevenly divided, low, broad plates (Lu, 1973, fig. 24E).

HECTOCOTYLIZED ARM.—The hectocotylus of the four species of *Illex* shows a similar basic structure at the distal tip of either the right or left ventral arm (arm IV), characterized by a series of lamellae, knobs, and papillae and the absence of both protective membranes. In *I. coindetii*, *I. argentinus*, and *I. oxygonius* the hectocotylus is longer than its non-hectocotylized opposite member of the pair, whereas in *I. illecebrosus* it often is slightly shorter. Table 8 gives the

comparative measurements of the hectocotylus based on fully mature specimens that have spermatophores in the Needham's sac. *Illex argentinus* has the longest hectocotylized arm, followed in decreasing lengths by *I. coindetii*, *I. illecebrosus*, and *I. oxygonius* (Table 8). The proportional length of the distal modified portion of the arm varies among the four species. It is greater than 50% in *I. argentinus* (includes HA2, which loses suckers at full maturity and therefore is difficult to distinguish from HA3, the tip), about 29% in *I. oxygonius*, 25% in *I. coindetii*, and 22% in *I. illecebrosus*.

The hectocotylus of *I. coindetii* is unique in that the trabeculae distal to the 5th to 7th pair of suckers (largest normal suckers) are transformed into papillose, fringed, rounded flaps, a feature absent in the other species. These modified trabeculae are larger and more papillose in *I. coindetii* from African waters than in specimens from the Gulf of Mexico, the Caribbean Sea, or the Mediterranean Sea.

The length of the hectocotylized arm and its distal modified portion also vary with geographic location. *Illex illecebrosus* from Newfoundland waters has relatively shorter hectocotylized arms (average HALI 48.5) and modified tips (average HA3LI 20.1) than do specimens from the region off the mid-Atlantic States (55.3, 23.1, respectively). *Illex coindetii* from the Mediterranean Sea has the longest hectocotylized arms (average HALI 71.1), followed by those from the Caribbean Sea (68.5), Gulf of Mexico (59.7), and coastal waters of West Africa (58.6). *Illex coindetii* from the Mediterranean Sea also has the longest modified tips (average HA3LI 27.3) followed by those from the Caribbean Sea and West African waters (both 25.0) and the Gulf of Mexico (23.4). Geographic variation in hectocotylus length is not known in *I. argentinus* and *I. oxygonius*, because of either a lack of comprehensive collections or a relatively narrow distributional range. The size of the lamellae in the dorsal row of the modified tip also varies. *Illex oxygonius* has the largest lamellae, those of *I. coindetii* and *I. argentinus* are slightly smaller, and *I. illecebrosus* has the smallest.

TABLE 7.—Arm-sucker indices (AS) and club-sucker indices (CIS) for males and females of the four species of *Illex*, based on largest sucker diameter on arms I–IV and on club. (See “Materials and Methods” for size range (ML) of measured specimens.)

Index	<i>I. illecebrosus</i>		<i>I. coindetii</i>		<i>I. argentinus</i>		<i>I. oxygonius</i>	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
<b>Males</b>								
AS,I	1.17	(0.80–1.76)	1.61	(0.82–3.12)	1.33	(1.05–1.65)	1.51	(1.31–1.74)
AS,II	1.75	(1.20–2.81)	2.94	(1.18–4.67)	2.71	(1.93–3.27)	2.47	(1.93–3.27)
AS,III	1.73	(1.19–2.74)	2.87	(1.36–5.68)	2.49	(1.92–2.96)	2.44	(2.18–2.49)
AS,IV	1.02	(0.68–1.53)	1.47	(0.69–4.62)	1.43	(1.02–1.74)	1.39	(1.18–1.62)
CIS	1.45	(1.00–2.02)	2.14	(1.27–2.84)	2.19	(1.88–2.84)	1.69	(0.93–1.95)
<b>Females</b>								
AS,I	1.13	(0.86–1.58)	1.35	(0.95–2.00)	1.23	(1.01–1.46)	1.20	(1.07–1.33)
AS,II	1.61	(1.21–2.41)	1.93	(1.42–2.67)	1.88	(1.56–2.28)	1.83	(1.58–2.04)
AS,III	1.61	(1.15–2.41)	1.94	(1.46–2.90)	1.86	(1.43–2.14)	1.80	(1.58–2.21)
AS,IV	1.03	(0.76–1.50)	1.19	(0.79–1.60)	1.10	(0.84–1.28)	1.12	(1.01–1.31)
CIS	1.51	(1.10–2.28)	1.81	(1.36–2.18)	1.95	(1.62–2.18)	1.65	(1.45–2.29)

Knobs and papillae occur in the dorsal row proximal to the fully developed lamellae of the distal modified portion. *Illex oxygonius* has three knobs and two slightly flattened papillae, whereas *I. illecebrosus* and *I. coindetii* have one or two knobs. *Illex argentinus* has the most distinctive hectocotylized arm. The dorsal and ventral sucker rows combined have 8–13 normal proximal suckers (HA1), the dorsal row of the medial modified portion (HA2) continues with 10–16 enlarged, rounded, suckerless knobs, followed by the distal tip with 18–22 large, distinct, truncate or rounded lamellae and terminating with 6–9 (or more) small, narrow, indistinct lamellae at the tip. The ventral row of the medial modified portion (HA2) has 7–10 low, suckerless knobs, then 7–12 nipple-like papillae, and 18–22 (or more) small, indistinct, narrow lamellae extending to the distal tip.

Of the other three species, the medial modified portion (distal sucker-bearing part (HA2)) of the hectocotylus is most distinct in *I. coindetii*. It has a dramatic decrease in sucker size (50% or more) distal to the 5th to 7th pair, constriction of the oral surface and musculature in the transition zone, dorsal and ventral rows of reduced suckers widely separated, and fringed, papillose, round trabeculae. *Illex oxygonius* has a medial modified portion that originates distal to the (5–)7 pairs of normal proximal suckers as a sudden decrease in sucker diameter of about 25%. These sucker rows are not widely separated, but there is a very slight constriction of the oral surface in the transition zone. There are no modified trabeculae. The medial modified portion of *I. illecebrosus* is very slightly developed distal to the 7th to 8th normal proximal sucker, with a sucker diameter reduction of about 25%, a very slight muscular constriction in the transition zone, little separation in sucker rows, and no fringed trabeculae.

The most proximal section of the hectocotylized arm (HAb) is suckerless for varying lengths among the four species. It is

TABLE 8.—Hectocotylized-arm length indices (HALI) and hectocotylized-tip length indices (HA3LI) for mature specimens of the four species of *Illex*. N = number of specimens examined. (The hectocotylized-arm length is measured from the most proximal sucker to the arm tip; the hectocotylized-tip length is measured from the most distal sucker to the arm tip.)

Species	Mean	Range	N	Standard deviation
<b>HALI</b>				
<i>I. illecebrosus</i>	53.0	(39.7–66.0)	7.9	27
<i>I. coindetii</i>	63.7	(42.3–87.1)	9.9	65
<i>I. argentinus</i>	67.6	(49.5–82.0)	7.4	68
<i>I. oxygonius</i>	51.5	(40.6–59.9)	5.7	10
<b>HA3LI</b>				
<i>I. illecebrosus</i>	22.1	(13.0–30.3)	4.6	27
<i>I. coindetii</i>	25.1	(17.1–30.0)	2.7	65
<i>I. argentinus</i> *	50.3	(19.8–70.3)	11.0	68
<i>I. oxygonius</i>	28.8	(23.8–32.0)	2.7	10

\*Includes HA2, which loses suckers at full maturity, making it difficult to determine the junction point of HA2 and HA3.

most conspicuous in *I. coindetii*, with a suckerless part of 13% of the total hectocotylized arm length, followed by *I. argentinus* at 10%, *I. illecebrosus* at 6%, and *I. oxygonius* at 4%. This character alone seems to be an excellent field character for discriminating mature male *I. coindetii* from *I. illecebrosus* and *I. oxygonius* in their region of sympatry in the western Atlantic Ocean.

**SPERMATOPHORES.**—The major difference in the spermatophores of the four species occurs at the oral end of the cement body and the aboral end of the ejaculatory apparatus. In *I. oxygonius* the cone is funnel-shaped, with sides about equal in outline and with rounded corners, the oral tube is relatively broad, and the aboral neck is intermediate in width and length

TABLE 9.—Comparison of the beaks of the four species of *Illex*. Based on Roper et al. (1969) and Lu (1973).

Feature	<i>I. illecebrosus</i>	<i>I. coindetii</i>	<i>I. argentinus</i>	<i>I. oxygonius</i>
Upper beak				
Hood	long, strong	long, strong	long, strong	short, very thin, weak
Shoulder	serrated	smooth	serrated	smooth, straight, or slightly curved
Jaw angle	large notch with tooth	small notch	large notch with tooth	small notch
Rostrum	long	long	long	short
Lateral wall	short, shallow; crest curved	short, shallow; crest curved	short, shallow; crest curved	long, deep; crest straight
Wing	short	short	short	short
Lower Beak				
Jaw edge	straight, short	straight, long	curved, long	curved, long
Wing	long, wide, no lobe; regular outline	long, wide, no lobe; slightly irregular outline	long, wide, no lobe; regular	short, narrow, lobate; irregular outline
Lateral wall	short, blunt	short, blunt	short, blunt	long, pointed
Rostral width	narrow	narrow	narrow	wide

in comparison with *I. illecebrosus* and *I. coindetii*. The *I. illecebrosus* cone is a low, right-isosceles triangle with rounded corners in outline, the oral tube is narrow, and the neck is long and narrow. The cone is either lens-shaped, a rounded triangle, or diamond-shaped in outline in *I. coindetii*, the oral tube is broad, and the neck is very short, broad, and indistinct. In *I. argentinus* the cone is flat and lens-shaped, the oral tube is

broad, and the neck is broad and distinct. Spermatophores of all four species are illustrated in Roper et al. (1969).

BEAKS.—The beaks of the four species of *Illex* differ in a number of features (Table 9); the terminology is defined in Clarke (1962, 1986). The beaks of *I. oxygonius* are illustrated in Roper et al. (1969, pl. 4g,h), and the beaks of the other three species are illustrated in Lu (1973, figs. 6f,g, 16b,c, 24f,g).

### Key to the Species of *Illex*

(for sexually mature or maturing adults only)

- Proportional length (ALI) of all arms long (e.g., 8%–10% larger than in other species); tentacular club not broadly expanded, medial manal suckers exceptionally enlarged, lateral manal suckers extremely small; distal modified portion of hectocotylized arm > 50% of total arm length (= HA2 + HA3); distribution restricted to western South Atlantic Ocean, 23°S–55°S . . . . . *I. argentinus*  
Proportional length (ALI) of all arms moderate to short (e.g., 8%–23% smaller than in *I. argentinus*); tentacular club expanded, medial manal suckers enlarged, lateral manal suckers small (not so markedly disproportionate as above); distal modified portion of hectocotylized arm (HA3) < 33% of total arm length; distribution North Atlantic, Caribbean, Gulf of Mexico, or Mediterranean . . . . . 2
- Distal enlarged manal-sucker rings notched, 7 to 8 low, broad, flat, plate-like teeth; relative lengths of fins and fin bases short; relative length of head (HLI) long; relative length of arms (ALI) long; base of hectocotylized arm (HAb) devoid of suckers for 13% of total arm length; trabeculae on hectocotylus midsection (HA2) modified to papillose, fringed flaps; distribution pan-Atlantic, only *Illex* species in eastern Atlantic and Mediterranean . . . . . *I. coindetii*  
Distal enlarged manal-sucker rings smooth, toothless, rarely with 1 to 2 notches; relative lengths of fins and fin bases long; relative length of head (HLI) short; relative length of arms (ALI) short; base of hectocotylized arm (HAb) devoid of suckers for 4%–6% of total arm length; trabeculae on hectocotylus midsection (HA2) not modified; distribution restricted to western North Atlantic . . . . . 3

3. Relative width of fins broad, 55% of ML; head length and width indices relatively low, 16%–17% of ML; arm lengths relatively short in males, 39%–48% of ML; arm sucker diameter indices relatively small, 1.02–1.75; hectocotylized arm equal to or slightly shorter than opposite arm IV and of equal thickness; lower beak jaw edge straight, short; wing long, wide; lateral wall short, blunt; rostral width narrow . . . . . *I. illecebrosus*  
 Relative width of fins narrow, 51% of ML; head length and width indices relatively high, 16%–20% of ML; arm lengths relatively long in males, 44%–55% of ML; arm sucker diameter indices relatively large, 1.12–2.47, especially in males; hectocotylized arm relatively long, more robust than opposite arm IV; lower beak jaw edge curved, long; wing short, narrow; lateral wall long, pointed; rostral width wide . . . . . *I. oxygonius*

**Discussion**

Because the range of variation of characters within each species of *Illex* heretofore has not been analyzed, it has been difficult to identify the species, especially females, based on field characters. For example, some workers have placed too much emphasis on the single character of the fin angle, a character that now has been shown to exhibit a degree of overlap among the three sympatric species based on larger collections available since the description of *I. oxygonius*. Reliance on this character alone cannot be depended upon to discriminate species. Similarly, reliance solely on the hectocotylized tip can be misleading.

Recent studies have revealed characters that seem to be more conservative and less prone to the extensive geographical variation that has become recognized as a trait of *Illex* species. Roper and Mangold (in press) demonstrated that the proportional length of the suckerless area along the base of the hectocotylus in males is perhaps the best field-identification character for distinguishing *I. coindetii* from the two other sympatric species, *I. illecebrosus* and *I. oxygonius*; the distinctive constriction between HA1 and HA2 is unique to *coindetii*. Other characters of the hectocotylus, formerly unrecognized, also were shown to be important. Although these male characters are not useful for identifying females, they are quite distinctive for males. We believe that they confirm the specific status of all four species of *Illex*. With careful application of additional characters it also should be possible to identify females. As a cautionary note, however, we do not exclude the possibility that hybridization could be taking place in the zone of sympatry in the western Atlantic, in which case *I. oxygonius* could be a hybrid between *I. illecebrosus* in the north and *I. coindetii* in the south. We have seen aberrant specimens from the Gulf of Mexico that also could represent hybridization. We feel that biochemical methods will be required to resolve these problems.

Among other characters that can be applied is the dentition on the largest distal manal rings of the club suckers, which distinguishes *I. coindetii* from the other two sympatric species

in the western Atlantic. The broadly dentate or notched rings on the largest manal sucker of *I. coindetii* contrast with the smooth, toothless corresponding rings of *I. illecebrosus* and *I. oxygonius*.

The beaks, although somewhat cumbersome to extract for analysis, could prove to be the most important source of characters for species discrimination among females. Table 9 presents comparisons of beaks based on Roper et al. (1969) and Lu (1973); illustrations of beaks also are found in these references. *Illex oxygonius* has the most distinctive beaks. The lower-beak wing is short, narrow, lobate, irregular in outline; the lateral wall is long, pointed; the rostral width is wide; the upper-beak hood is short, thin, weak; the rostrum is short; the lateral wall is long, deep, with a straight crest; and the wing is long. All these characters contrast with those in the other three species and should be especially helpful in separating *I. oxygonius* from *I. coindetii* and *I. illecebrosus*.

The long-standing confusion of whether *I. illecebrosus* occurs in the eastern Atlantic also has been addressed by Roper and Mangold (in press), who conclude that only *I. coindetii* occurs in the Mediterranean and eastern Atlantic. The species is distinguished by a highly variable series of geographical (and perhaps physiological) morphotypes that do not merit specific differentiation. The occurrence of *I. coindetii* in the western Atlantic is not such an enigma as some workers have thought. As pointed out by Roper and Mangold (in press), the best way to discriminate *I. oxygonius* is by the suite of characters associated with the hectocotylus, club suckers, and beaks. For example, the suckerless base is especially distinct between *I. coindetii*, at 13% of the total length of the arm, and *I. oxygonius*, at 4%. Furthermore, both sexes of *I. oxygonius* can be distinguished from *I. coindetii* based on the dentition of the largest manal-sucker rings and from *I. illecebrosus* based on the beaks.

We concur with Roeleveld (1988:278) that those who base identification of species primarily on morphometric characters miss the most important distinguishing morphological features. In our view, using morphometric characters can yield rigorous results when clear-cut differences exist, but it is a mistake to

disregard qualitative, structural characters based on careful examination of large numbers of specimens.

*Illex argentinus*, by virtue of its rather isolated distribution in

the far southwestern Atlantic, does not pose a problem with identification; furthermore, it is quite distinct morphologically from its congeners in northern Atlantic waters.

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# A Review of the Systematics, Distribution, and Biology of the Arrow Squid Genera *Ommastrephes* Orbigny, 1835, *Sthenoteuthis* Verrill, 1880, and *Ornithoteuthis* Okada, 1927 (Cephalopoda: Ommastrephidae)

M.C. Dunning

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## ABSTRACT

Within the subfamily Ommastrephinae, the genera *Ommastrephes*, *Sthenoteuthis*, and *Ornithoteuthis* include five nominal species of truly oceanic squids that occur in surface and near-surface waters of tropical and subtropical oceans worldwide.

*Ommastrephes bartramii* (Lesueur, 1821) is the most widespread species in the group, occurring in subtropical waters of all oceans, and is of major fisheries importance, especially in the northwest Pacific Ocean. It reaches sizes in excess of 500 mm mantle length and can be separated morphologically from the partially sympatric *Sthenoteuthis* spp. by the absence of a large dorsal photophore on the mantle in adults and by the absence of visceral photophores in larvae and juveniles. It can be separated morphologically from *Ornithoteuthis* spp. by the absence of photophores ventrally on the viscera and by the more robust mantle and rhomboid fin. *Ommastrephes bartramii* populations in both the Atlantic and Pacific oceans appear to consist of "early"- and "late"-maturing forms.

*Sthenoteuthis* spp. are the dominant surface-schooling ommastrephids in tropical oceans. *Sthenoteuthis oualaniensis* of the Indo-Pacific consists of two forms, one with and the other without a large dorsal photophore on the anterior mantle in adults. The former reaches in excess of 300 mm mantle length, whereas females of the latter form reach maturity at less than 200 mm mantle length. The Atlantic *S. pteropus*, also with a large dorsal light organ on the mantle, has been found to form many local populations associated with different water masses and current systems.

Less commonly encountered at the surface, *Ornithoteuthis volatilis* and *O. antillarum*, both with mantles and fins elongated posteriorly, are restricted to the Indo-Pacific and Atlantic oceans, respectively, and reach maximum sizes of less than 300 mm mantle length. It has been proposed recently that the genus *Ornithoteuthis* be considered as a separate subfamily, but this has yet to receive widespread support.

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## Introduction

The genera *Ommastrephes* Orbigny, 1835, *Sthenoteuthis* Verrill, 1880, and *Ornithoteuthis* Okada, 1927, include the true oceanic squids typically encountered in tropical and subtropical surface and near-surface waters of the high seas. They generally are found near the continental slope only as larvae and reproductively mature adults. One species, *Ommastrephes bartramii* (Lesueur, 1821), is the most widely distributed of all the ommastrephids, occurring in subtropical waters of all oceans and supporting major jig and drift-net fisheries, especially in the North Pacific (Murata et al., 1988).

The differences between the species, and hence generic relationships within this group, have only recently been clarified after a reassessment of the occurrence, location, and development of light organs (photophores) through all life stages, consideration of dentition patterns in the largest club suckers, and consideration of the various forms of hectocotylyzation in the group (Adam, 1960; Zuev et al., 1975; Nigmatullin, 1979, and pers. comm., 1988; Roeleveld, 1988).

In this paper, recent systematic studies are reviewed and a synopsis is presented of current knowledge of the distribution and biology of these abundant oceanic squids.

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### Systematics, Distribution, and Biology

#### Family OMMASTREPHIDAE Steenstrup, 1857

#### Subfamily OMMASTREPHINAE Posselt, 1891

#### *Ommastrephes* Orbigny, 1835

DIAGNOSIS.—Funnel groove with foveola and side pockets; tetraserial suckers on dactylus of tentacular club; medial manus-sucker rings with 1 tooth in each quadrant greatly enlarged; carpal-fixing apparatus consisting of smooth-ringed suckers and knobs on tentacular stalk; small, irregularly shaped, subcutaneous photophores present in adults, embedded in ventral mantle and ventrally in head; no photophores in larvae; either left or right arm IV hectocotylized by complete loss of suckers and sucker bases distally in mature males; mantle-funnel locking apparatus not fused.

TYPE SPECIES.—*Loligo bartramii* Lesueur, 1821:90, pl. 7.

GENUS SIZE.—The genus is monotypic (Zuev et al., 1975).

#### *Ommastrephes bartramii* (Lesueur, 1821)

*Loligo bartramii* Lesueur, 1821:90, pl. 7.

*Ommastrephes bartramii*.—Orbigny, 1835:55.

*Sthenoteuthis bartramii*.—Verrill, 1880:223.

*Ommastrephes caroli* Furtado, 1887:5.

*Ommastrephes caroli stenodactyla* Rancurel, 1976a:81 [the subspecific name, *stenobranchium*, was also used in the text, but this was in error (Rancurel, 1980, and pers. comm., 1988)].

DIAGNOSIS.—As for genus.

ORIGINAL DESCRIPTION.—Lesueur, 1821:90, pl. 7.

TYPES.—*Holotype*: Details of size, sex, and collection locality of specimen not given; originally deposited in the Academy of Natural Sciences, Philadelphia, but specimen no longer extant.

*Paratypes*: None designated.

DISCUSSION.—*Ommastrephes bartramii* is distinguished from other members of the subfamily by the absence of light organs in the larval and early juvenile stages. Light organs in adults are restricted to small, irregularly shaped photophores embedded in the ventral mantle and ventrally in the head. Roeleveld (1988) considered the simplified hectocotylus (absence of sucker stalks and bases distally, no medial or basal modifications, such as thickening of the protective membranes or development of pores between the trabeculae) to be the result of secondary loss.

DISTRIBUTION.—Nesis (1979a) described the distribution of *Ommastrephes bartramii* as "bisubtropical," and this species is the most widespread of all the ommastrephids. Data from the 1966 and 1968 survey transects of the R/V *Walther Herwig* in the Atlantic Ocean also support a bisubtropical distribution of the species in the Atlantic Ocean (Warneke-Cremer, 1986).

*Ommastrephes bartramii* is the dominant surface-dwelling ommastrephid in the North Pacific, occurring in abundance from off the Pacific coast of Japan and occasionally in the

Japan Sea (Okutani et al., 1981) to the west coast of Canada. In the South Pacific Ocean, *O. bartramii* occurs throughout the Tasman Sea and eastward from New Zealand to 80°E off the coast of Chile (Polezhaev, 1986). Its previously reported absence from the southeast Pacific (Nesis, 1973) could reflect variations in the strength of the Peru Current and displacement in waters east of 80°E by the larger, nerito-oceanic ommastrephid endemic to the eastern Pacific, the jumbo squid, *Dosidicus gigas* (Orbigny, 1835).

Filippova (1968, 1971) reported immature *O. bartramii* from the southeast Indian Ocean off Western Australia during the summer months, and Nesis (1979a) considered immature specimens jigged in late summer in the Great Australian Bight as far east as 135°E to be part of an Indian Ocean "superpopulation" (Shevtsova et al., 1979). Nesis (1987) considered North Pacific, North Atlantic, and southern (South Atlantic Ocean + Indian Ocean + South Pacific Ocean) populations to be subspecies.

In the southwest Pacific, adult *O. bartramii* have been caught between 23°42'S and 45°45'S, where surface water temperatures vary from 14.2°C to 25.7°C (Dunning, 1988). In the Atlantic, *O. bartramii* is more abundant in subtropical surface waters of 14°C to 17°C (Zuev et al., 1976). Adult *O. bartramii* are known to occupy a broad depth range, both day and night, from the surface to at least 1500 m (Clarke, 1966). An adult female in the northwest Pacific carrying an ultrasonic tag remained in the upper 100 m (mostly 40–70 m) during the night but stayed below 400 m in depth during the day (Nakamura, 1991). The vertical distribution of larvae and juveniles, however, remains poorly known.

Length-frequency data collected in the Japanese fishing grounds have revealed a complex population structure for *O. bartramii* from the North Pacific. Murata et al. (1988) found from two to four modal size classes in the region. A similar, complex population structure was evident in summer jig catches from the Tasman Sea (Dunning, 1988), with at least four size classes present in some areas.

SIZE, MATURITY, AND REPRODUCTION.—Male *O. bartramii* reach maturity from 320 mm mantle length (ML) in the southwest Pacific. Considerable variation was evident in size at maturity of females in summer catches in this region. The smallest female observed with oviducal eggs measured 420 mm ML, whereas the largest female with no eggs in the oviducts was 550 mm ML. An examination of the degree of development of the web on arms III in *O. bartramii* of both sexes suggests that growth of this structure is correlated with development of reproductive organs (Dunning, 1988).

Rancurel (1976a) examined eight mature males (338–385 mm ML), each with spermatophores (approximately 31 mm long) in the Needham's sac, and reported that the oviducts of a 520 mm ML female washed ashore near New Caledonia in the southwest Pacific filled the mantle cavity. Mature males of 324–406 mm ML and females of 425–491 mm ML caught together off the southeast coast of Japan (30°11'N, 136°43'E) in

late May 1978 were described by Suzuki (1980). Nakamura (1988) reported mature squid (males 29–39 cm ML, females 40–46 cm ML) near the Izu-Ogasawara Islands off southern Japan in April–May 1986 and 1987 (spring).

According to Gaevskaya and Nigmatullin (1976), male *O. bartramii* from the Atlantic reach maturity between 300 mm ML and 350 mm ML, with females represented by two groups according to size of maturity: so called “early-maturing” squid of 400–500 mm ML and “late-maturing” squid of more than 700 mm ML (the latter only reported from the North Atlantic).

LARVAE.—Larvae of *O. bartramii* were first described by Naef (1923) and subsequently were described by Okutani (1965, 1968, 1969) and Nesis (1979b), but the most detailed description was provided by Young and Hirota (1990). These larvae are characterized by the absence of ocular and visceral light organs, lateral suckers on the proboscis tip nearly twice the diameter of the adjacent suckers, and a distinctive chromatophore pattern.

#### *Sthenoteuthis* Verrill, 1880

DIAGNOSIS.—Funnel groove with foveola and side pockets; tetraserial suckers on dactylus of tentacular club; medial manus-sucker rings with 1 tooth in each quadrant greatly enlarged; carpal-fixing apparatus consisting of smooth-ringed suckers and knobs on tentacular stalk; larvae and juveniles with 2 approximately equal-sized light organs present between intestine and ink sac, 1 anterior near anus and 1 posterior; larvae and juveniles also with 1 oval light organ present ventrally on each eye; large dorsal light organ may be present anteriorly on mantle in larger individuals; either left or right arm IV hectocotylized in mature males by loss of sucker stalks and bases distally and development of pores in thickened dorsal and ventral protective membranes basally and medially.

TYPE SPECIES.—*Architeuthis megaptera* Verrill, 1878:207 (= *Ommatostrephes pteropus* Steenstrup, 1855) (see Adam, 1952; Zuev et al., 1975; Roeleveld, 1982).

GENUS SIZE.—Two nominal species are recognized in the genus, *S. oualaniensis* Lesson, 1830, from the Indo-Pacific and *S. pteropus* from the Atlantic Ocean.

#### *Sthenoteuthis oualaniensis* (Lesson, 1830)

*Loligo oualaniensis* Lesson, 1830:240, pl. I: fig. 2.

*Ommastrephes oualaniensis*.—Férussac and Orbigny, 1839:351.

*Symplectoteuthis oualaniensis*.—Pfeffer, 1900:180.

*Sthenoteuthis oualaniensis*.—Zuev, Nesis, and Nigmatullin, 1975:1475.

DIAGNOSIS.—*Sthenoteuthis* with large, oval, dorsal light organ present anteriormost on mantle in adults; mantle and funnel cartilages with muscular fusion on 1 or both sides in postlarval stages; hectocotylized arm with 6–8 pairs of suckers.

ORIGINAL DESCRIPTION.—Lesson, 1830:240, pl. I: fig. 2.

TYPES.—*Holotype*: Museum d'Histoire Naturelle, Paris

(reexamined by Orbigny in 1855, according to Pfeffer (1912); could not be located, Jun 1988, C.C. Lu, pers. comm.), collected near Oualan (= Kusaie or Kosrae), Caroline Islands, northwest Pacific Ocean.

*Paratypes*: None designated.

DISCUSSION.—That “*Symplectoteuthis oualaniensis*” of the Indo-Pacific consisted of two sympatric species, one with and the other without the large, oval light organ on the dorsal mantle, was first suggested by Clarke (1965). Further evidence was provided by Filippova (1968), who found that the second form matured at smaller sizes than its congener. The form without the dorsal light organ is being described as a distinct species by M.A.C. Roeleveld of the South African Museum, Capetown. This species shows a secondary reduction of the pores in and thickening of the protective membranes basally and medially on the hectocotylized arm. Nesis (1977) and subsequently other Soviet workers (e.g., Nigmatullin et al., 1983) refer to this species as the “early-maturing form” of *S. oualaniensis*. A further large form of *S. oualaniensis* reaching mantle lengths of 630 mm has been observed by Soviet researchers in the Arabian and Red seas (K.N. Nesis, pers. comm., 1988).

DISTRIBUTION.—*Sthenoteuthis oualaniensis* occurs throughout tropical surface waters of the Indo-Pacific, with its northern boundary in the Pacific from southern Japan to southern California. It occurs in the Indian Ocean south to southeastern Africa and Cape Leeuwin off Western Australia. In the South Pacific its distribution extends from the Coral Sea eastward to the Line Islands (Zuev et al., 1975; Wormuth, 1976; Nesis, 1977; Dunning, 1988). Adults of *Sthenoteuthis oualaniensis* occur predominantly in tropical oceanic waters, whereas larvae and juveniles also have been caught on the continental slope and shelf.

The distributions of the subtropical *O. bartramii* and *S. oualaniensis* show considerable overlap, especially in the regions of the western boundary currents (the Kuroshio off Taiwan and Japan; the East Australian Current in the Coral and Tasman seas; the Agulhas Current off southern Africa (Filippova, 1971; Okutani and Tung, 1978; Dunning, 1988)).

SIZE, MATURITY, AND REPRODUCTION.—Male *S. oualaniensis* from northern Australian waters reached maturity from 160 mm ML, whereas females from 250 mm ML carried eggs in their oviducts. Spawning appears to be widespread at least in eastern Australian waters and apparently occurs from spring to early winter (Dunning, 1988). The largest specimens reported from northern Australian waters were a 304 mm ML female and a 212 mm ML male.

Reproductive development of *S. oualaniensis* from around Taiwan (19°N–26°N) was described by Tung (1976) for squid caught between March and October (spring to autumn). Males reached maturity at smaller sizes than did females. Spermatophores were evident in squid as small as 110 mm ML. Little development of the ovary was evident in females less than 155

mm ML. At 190 mm ML, the majority of females had ova present in their oviducts.

Nesis (1977) described maturation in *S. oualaniensis* from collections made in the central tropical western Pacific predominantly between 10°S and 15°N. Consistent with Tung's (1976) findings, males of more than 110 mm ML had spermatophores in Needham's sac, whereas ova were first evident in the oviducts of females of 180 mm ML to 190 mm ML. Nesis (1977) concluded that spawning was widespread throughout the region, with larvae caught between February and July.

Specimens of *S. oualaniensis* described by Zuev (1967) from the northwest Indian Ocean mature at sizes larger than have been reported for specimens in the tropical Pacific, and apparently they have a spawning peak in the northern winter, the same time as those in the eastern tropical Pacific (Zuev and Nesis, 1971). A 250 mm total length male was the smallest mature male examined, and the smallest female with ova in its oviducts was 328 mm total length. Considerably larger females of up to 460 mm ML (Okutani and Tung, 1978), 434 mm ML (Raje and Savaria, 1987), and 630 mm ML (K.N. Nesis, pers. comm., 1988) have been reported from the Indian Ocean, although their reproductive condition was not described.

From studies of the distribution of mature adults, Suzuki et al. (1986) concluded that populations of *S. oualaniensis* in the waters adjacent to Hawaii spawn in a restricted area over the continental slope between January and March (winter). Studies by Harman and Young (1986), however, have shown that larvae were present elsewhere in Hawaiian waters throughout the year, with peak abundance in August (summer). An extended spawning season also has been proposed by Nesis (1977) for *S. oualaniensis* from the central western Pacific. Harman et al. (1989) have provided evidence for multiple spawning by individuals in this species, in contrast to the generally accepted dogma of semelparity in teuthoids.

Nesis (1977) recognized that not only did males of *S. sp.* mature at smaller sizes than did those of *S. oualaniensis* (90 mm ML compared with 120–130 mm ML), but females were mature at approximately 130 mm ML. This compared with a size at maturity in excess of 200 mm ML in the "late-maturing" *S. oualaniensis*. Spawning times and locations for *S. sp.* were not defined by Nesis (1977) apart from suggesting that this species did not undertake any spawning migration as had been reported by Tung (1976) for *S. oualaniensis*.

**LARVAE.**—The larvae of *S. oualaniensis* have been illustrated well by Shojima (1970), Nesis (1979b), and Harman and Young (1986). They are characterized by a long proboscis (at least equal to and up to three times the length of the longest arms), eight approximately equal-sized suckers on the proboscis tip, small spherical light organs on the ventral surface of each eye, and two equal-sized photophores posteriorly and anteriorly on the intestine (the rectal photophore first visible in specimens of 3.5–4 mm ML and the intestinal photophore visible at about 6 mm ML).

### *Sthenoteuthis pteropus* (Steenstrup, 1855)

*Ommastrephes pteropus* Steenstrup, 1855:200.

*Ommastrephes pteropus*.—Tryon, 1879:179.

*Architeuthis megaptera* Verrill, 1878:207.

*Sthenoteuthis megaptera*.—Verrill, 1880:223.

*Sthenoteuthis pteropus*.—Pfeffer, 1900:181.

**DIAGNOSIS.**—*Sthenoteuthis* with large, oval dorsal light organ present anteriormost on mantle in adults; mantle and funnel cartilages only rarely fused; 11–13 pairs of suckers on hectocotyliized arm.

**ORIGINAL DESCRIPTION.**—Steenstrup, 1855:200.

**TYPES.**—*Holotype*: Zoological Museum, University of Copenhagen, female, 350 mm ML, St. Croix Island, Caribbean Sea.

*Paratypes*: None nominated.

**DISTRIBUTION.**—*Sthenoteuthis pteropus* is a pelagic species that occurs throughout tropical and warm temperate surface waters of the Atlantic Ocean from 35°N to 30°S where surface water temperatures exceed 16°C (Zuev et al., 1976; Zuev et al., 1985; Warneke-Cremer, 1986). This species is absent in the Mediterranean Sea. Within its range, localized areas of higher abundance have been delineated in association with particular oceanographic characteristics (eddies and frontal zones) (Zuev et al., 1985; Arkhipkin et al., 1988).

Zuev and Tsybal (1982) concluded that adult *S. pteropus* were distributed in the upper isothermal zone and underlying thermocline and did not generally occur below 150–200 m in depth. Although adults were concentrated in surface waters at night, larvae and juveniles were distributed widely in waters above the thermocline. This species undergoes diel vertical migration, with the adults feeding on pelagic fishes in deeper water by day and at the surface at night, and with the juveniles feeding on crustaceans in the scattering layer at the surface by day and deeper at night.

**SIZE, MATURITY, AND REPRODUCTION.**—The reproductive condition of *S. pteropus* from the western Gulf of Mexico was described by Hixon et al. (1981). Males, which constituted 63.9% of the samples, reached maturity at smaller sizes than did females. Spermatophores were evident in squid as small as 142 mm ML, whereas the smallest female with mature ova present in its oviducts was 210 mm ML. It was noted, however, that size at maturity varied considerably among both males and females.

Hixon et al. (1981) concluded that year-round spawning occurred in the Gulf of Mexico. The presence of oocytes of various diameters in the ovary of mature females also provided some evidence of multiple spawning in this species as suggested by Harman et al. (1989) for *S. oualaniensis* around Hawaii.

**GROWTH.**—Sequential size-frequency data for *S. pteropus* from the east-central Atlantic were examined by Zuev et al. (1979). They described growth in these squid by the equation  $L_t = 60 (1 - e^{-0.091(t + 0.13)})$ , where  $L_t$  is mantle length in cm and  $t$  is age in months. On this basis, it was concluded that the life span of this species is from 1 to 1.5 years.

LARVAE.—Nesis (1979b) described and illustrated the larvae of *S. pteropus*. Like larvae of *S. oualaniensis*, they are characterized by a long proboscis (at least equal to and up to 3 times the length of the longest arms), eight approximately equal-sized suckers on the proboscis tip, small, spherical light organs on the ventral surface of each eye, and two equal-sized photophores posteriorly and anteriorly on the intestine (the rectal photophore first visible in specimens of 3–3.5 mm ML and the intestinal photophore visible at about 5–5.5 mm ML).

#### *Ornithoteuthis* Okada, 1927

DIAGNOSIS.—Mantle narrow, drawn out into long, pointed tail; fins long, sagittate; funnel groove smooth, with foveola and side pockets (often obscure); tetraserial suckers on dactylus of tentacular club; tentacular club moderately expanded but without carpal-fixing apparatus; photophores evident on eyes and on intestine in larvae and as photogenic strip along viscera in adults; right arm IV hectocotylized in mature males.

TYPE SPECIES.—*Ommastrephes volatilis* Sasaki, 1915.

GENUS SIZE.—Two species have been recognized, *O. volatilis* (Sasaki, 1915), from the Indo-West Pacific, and *O. antillarum* Adam, 1957, from the Atlantic Ocean.

DISCUSSION.—Roeleveld (1988), in her assessment of the generic relationships within the Ommastrephidae, confirmed the placement of *Ornithoteuthis* within the Ommastrephinae, concluding that, although it was not far removed from the other genera, the combination of plesiomorphic characters present indicated that it was the most primitive genus in the subfamily as suggested by Zuev et al. (1975). Nigmatullin (1979) considered that the genus should be placed within a separate subfamily, Ornithoteuthinae. Although possessing intestinal photophores and pockets on both sides of the foveola in the funnel groove as in the ommastrephin genera *Sthenoteuthis*, *Eucleoteuthis*, and *Hyaloteuthis*, the absence of subcutaneous photophores distinguishes the genus *Ornithoteuthis* from all other ommastrephin genera. The creation of a separate subfamily for this genus, however, has yet to receive widespread support.

LARVAE.—Larvae of *Ornithoteuthis* were described and illustrated by Nesis (1979b). They are characterized by the presence of ocular photophores and two unequal-sized photophores in larvae of more than 3.5 mm ML, a proboscis approximately equal in length to the longest arms, and two lateral suckers on the proboscis tip up to twice the diameter of the remaining six.

#### *Ornithoteuthis volatilis* (Sasaki, 1915)

DIAGNOSIS.—*Ornithoteuthis* without sexual dimorphism in dentition of sessile arm suckers. Midventral surface of right arm IV with honeycomb-like sculpturing and with 2 to 3 longitudinal columns of depressions, 10–15 depressions in each column.

ORIGINAL DESCRIPTION.—Sasaki, 1915:138.

TYPES.—*Holotype*: Museum of the Science College, University of Tokyo, Japan, mature male, 213 mm ML, collected off Atami, Sagami Province, Honshu, Japan, 24 Jun 1906.

*Paratypes*: 1 female, 208 mm ML, collected off Atami, Sagami Province, Japan, 24 Jun 1906; 1 male, 2 females, 152 mm ML, 148 mm ML, and 148 mm ML, respectively, collected off Atami, Sagami Province, Honshu, Japan, 23 Sep 1905, after “they flew from the sea into the sky and, colliding with the sail of his boat, fell down into it” (Sasaki, 1915:138).

DISTRIBUTION.—Prior to a recent study in Australian waters that resulted in the capture of more than 2000 larvae and juveniles and 101 adults (Dunning, 1988), only 62 specimens (17 adults) of *O. volatilis* had been reported in the literature. Along the western margin of the Pacific, *O. volatilis* had been recorded between 36°15'N and 23°S and eastward to the Line Islands (140°W), where its latitudinal range appears very restricted (Rancurel, 1970; Wormuth, 1976; Nesis and Nigmatullin, 1979). *Ornithoteuthis volatilis* has been recorded in the Indian Ocean from the Arabian Sea to south of Madagascar in the west and eastward to the Timor Sea (Fujita and Hattori, 1976; Nesis and Nigmatullin, 1979).

The known distribution of adults off the eastern Australian coast has been extended to 38°13'S (Dunning, 1988), and larvae were abundant in summer plankton tows in the East Australian Current (Dunning, 1986). Off the northwest Australian coast, single adults were caught at each of eight demersal trawl stations in continental slope waters between 13°50'S and 18°37'S.

Although larvae and juveniles are reported to be epipelagic, most adults have been caught in midwater and demersal trawls in continental slope waters or near seamounts and have rarely been caught at the surface. In Australian waters, adult *O. volatilis* were absent from trawl and jig catches on the continental shelf and were caught only in demersal trawls where water depths ranged from 400 m to 732 m (Dunning, 1988). Nesis and Nigmatullin (1979) suggested that, like its Atlantic congener (Roper and Young, 1975), *O. volatilis* could undertake diel vertical migration.

*Ornithoteuthis volatilis* has previously been recorded from the stomachs of longnose lancetfish (*Alepisaurus ferox* Lowe) from the northeastern Indian Ocean (Fujita and Hattori, 1976) and around New Caledonia (Rancurel, 1970) and from the stomachs of yellowfin tuna (*Thunnus albacares* (Bonnatere)) from the Gulf of Papua (misidentified as *Ornithoteuthis antillarum*, the Atlantic congener; Rancurel, 1976b). *Alepisaurus* is considered by Rancurel (1970) and Okutani and Kubota (1972) to feed in the upper 300 m of the water column, although it has been caught at depths as great as 1500 m.

SIZE, MATURITY, AND REPRODUCTION.—No disparity in size at maturity was evident among 93 adult male and female *O. volatilis* from Australian waters. Females reached maturity from 150 mm ML and males from 130 mm ML. Considerable variation in size at maturity was evident for both sexes. Two females, 202 mm ML and 217 mm ML, caught in summer and

a single female of 158 mm ML caught in winter off the northwest coast were mature, with both oviducts and ovary filled with ripe eggs. A 248 mm ML female *O. volatilis* caught off the central New South Wales coast in January 1982 was nearing full maturity, although other specimens of 250 mm ML and 269 mm ML caught in winter in the same region were still maturing. Off the southeast Australian coast in summer, mature males of 160 mm ML and 239 mm ML were caught, although additional specimens of 176 mm ML and 199 mm ML were still maturing (Dunning, 1988).

Both seasonal and geographic variation were evident in size at maturity of *O. volatilis* from Australian waters, although maximum size, at least for males, was similar off both the northwest and southeast coasts.

Only 13 adult specimens of *O. volatilis* have been described from elsewhere in the Indo-Pacific region, and the reproductive condition of these specimens was not reported (Sasaki, 1915, 1929; Okada, 1968; Rancurel, 1970; Wormuth, 1976; Nesis and Nigmatullin, 1979). The advanced state of hectocotylization of arm IV of the 213 mm ML male described and illustrated by Sasaki (1915, 1929) is similar to that of mature specimens examined from Australian waters.

LARVAE.—Off eastern Australia during summer 1983, *O. volatilis* was the dominant ommastrephid species in larval collections in deeper shelf and upper continental slope waters. Small larvae were more abundant in deeper shelf and continental slope waters off the northern New South Wales coast, indicating that spawning is occurring in warm East Australian Current waters of tropical origin. The mantle-length distribution of more than 2000 larvae examined together with the size distribution of adults examined supports a hypothesis of extended, perhaps year-round, spawning occurring in this region (Dunning, 1988).

#### *Ornithoteuthis antillarum* Adam, 1957

DIAGNOSIS.—*Ornithoteuthis* with sexual dimorphism in dentition of sessile arm suckers. Suckers of arms II with distinct

difference in dentition between dorsal (2 small, plate-like teeth on each side with 1 central, sharp, pointed tooth distally) and ventral rows (2 small, medial teeth distally with 2 small, plate-like teeth on each side). Midventral surface of right arm IV with honeycomb-like sculpturing and with 4 to 5 longitudinal columns of depressions, 20–25 depressions in each column.

ORIGINAL DESCRIPTION.—Adam, 1957:3.

TYPES.—*Holotype*: Muséum National d'Histoire Naturelle de Paris, MNHN 7-3-686, mature male, 141 mm ML, collected at Basse-Terre (Guadeloupe Island), Antilles, West Indies, 9 Mar 1951.

*Paratypes*: Institut Royal des Sciences Naturelles de Belgique, Brussels, 1 male, 96 mm ML; Institut Français (now Institut Fondamentale) d'Afrique Noire, Dakar, 1 male, 95 mm ML; Muséum National d'Histoire Naturelle de Paris, MNHN 7-3-687, 1 female, 103 mm ML; all collected at Basse-Terre (Guadeloupe Island), Antilles, West Indies, 9 Mar 1951.

DISTRIBUTION.—*Ornithoteuthis antillarum* has been recorded from tropical/subtropical waters of the western Atlantic from approximately 40°N to 40°S and has been recorded in the eastern Atlantic from 20°N to 25°S (Korzun et al., 1979; Nesis and Nigmatullin, 1979; Warneke-Cremer, 1986; Laptikhovskiy, 1990).

SIZE AND MATURITY.—Maturation in *O. antillarum*, the Atlantic representative of this genus, was described by Nesis and Nigmatullin (1979). In the tropical Atlantic, some squids of both sexes were mature at 80–90 mm ML, although further north and south some squids of more than 100 mm ML were still immature. The maximum size of *O. antillarum* caught at the periphery of the range in the Atlantic (at higher latitudes) also was greater than at the center of the range, i.e., 300 mm ML compared with 125 mm ML (Nesis and Nigmatullin, 1979; Laptikhovskiy, 1990). Warneke-Cremer (1986) described a 213 mm ML male and a 221 mm ML female *O. antillarum* from 23°50'S and 24°28'S, respectively, in the southwestern Atlantic.

LARVAE.—See "Larvae" under genus account.

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# Zoogeography of Arrow Squids (Cephalopoda: Ommastrephidae) in the Coral and Tasman Seas, Southwest Pacific

*M.C. Dunning*

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## ABSTRACT

Fourteen species of the oegopsid squid family Ommastrephidae (including representatives of the genera *Todaropsis*, *Todarodes*, *Martialia*, *Nototodarus*, *Ornithoteuthis*, *Ommastrephes*, *Sthenoteuthis*, *Eucleoteuthis*, and *Hyaloteuthis*) are known from the Coral and Tasman seas in the southwest Pacific.

Adults and larvae are represented in shelf, slope, and oceanic waters from tropical to subantarctic waters. The East Australian Current system, a western boundary current, is considered to be of primary importance in the dispersal of larval ommastrephids in subtropical slope and oceanic waters, whereas the West Wind Drift and its associated currents may affect larval distribution in temperate latitudes. The distribution of adults of the oceanic species is influenced by two oceanographic features, the Subtropical Convergence and the Tasman Front, whereas shelf species appear to be restricted to particular depth and temperature regimes.

Division of the region using a simple scheme of three zoogeographic zones, tropical, subtropical, and subantarctic, is considered to assist in interpretation of the still-limited information on the distribution patterns of ommastrephid squids.

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## Introduction

Since the 1970s, the distribution of arrow squid species of the family Ommastrephidae in the southwest Pacific has become more clearly defined. This increase in knowledge has been the result of exploratory commercial fishing and research surveys undertaken primarily by Japanese, Australian, New Zealand, and Russian vessels (JAMARC, 1978, 1987; Nesis,

1979b, 1979c; Machida, 1984; Dunning and Brandt, 1985; Mattlin et al., 1985; Uozumi et al., 1987; Hatanaka et al., 1989). In parallel with increased fisheries interest, knowledge of the oceanography of the region has seen similar advances (e.g., Godfrey et al., 1980; Stanton, 1981; Cresswell, 1983; Coleman, 1984; Andrews and Clegg, 1989).

The zoogeography of the ommastrephids of the Pacific Ocean was briefly reviewed by Wormuth (1976), although his data for the southwest Pacific were very sparse. Nesis (1979b) provided the most recent overview of the zoogeography of neritic and oceanic cephalopods in the Australasian region, including five of the 14 ommastrephid species now known.

In the present paper, a synopsis is provided of more recent distributional information for both larvae and adults. These data are synthesized with recent knowledge of oceanographic patterns, and conformity of ommastrephid distributions with previously proposed zoogeographic schemes for the region also is briefly discussed.

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## MATERIALS AND METHODS

Recent information on ommastrephid squid distribution synthesized in this paper resulted primarily from (1) exploratory demersal- and pelagic-trawl fish and cephalopod surveys by the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO), since 1981 (Dunning, 1986, 1988c); (2) exploratory demersal- and pelagic-trawl fish and squid surveys by the New Zealand Fisheries Research Division, Ministry of Agriculture and Fisheries, since 1981 (e.g., Förc, 1983, 1986; Mattlin et al., 1985); (3) exploratory squid fishing surveys in the Tasman Sea and around New Zealand by the Taiwan Fisheries Research Institute, Keelung, Taiwan, the Japan Marine Resource Research Center (JAMARC), Tokyo, Japan, and the Far Seas Fisheries Research Laboratory,

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Shimizu, Japan, since 1981 (e.g., Collins and Dunning, 1981; Machida, 1984; JAMARC, 1987; Uozumi et al., 1987); and (4) exploratory trawl, jig, and ichthyoplankton surveys off the New South Wales coast by the Fisheries Research Vessel *Kapala* (e.g., Gorman and Graham, 1983).

#### ACKNOWLEDGMENTS

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Many of the squid studies of the Tasman and Coral seas that provided data referred to in this paper were undertaken as part of the CSIRO Division of Fisheries Research's Living Resources Program between 1981 and 1984, and I am thankful to the many people who supported the project and assisted with the field work. I also thank Saburo Machida of JAMARC (now of KSJ Corporation, Minato-ku, Tokyo, Japan) for providing information from *Ommastrephes bartramii* surveys in the Tasman Sea.

#### Description of the Study Area

Simplified bathymetry of the Coral and Tasman seas is illustrated in Figure 1. To the southwest, the dominant feature is the Tasman Abyssal Plain with maximal depths in excess of 5000 m. The restricted channels between Australia and New Caledonia in the north (the Cato and Norfolk troughs) are separated by the southward projecting Lord Howe Rise, with New Caledonia lying on the north of the Norfolk Ridge. A chain of seamounts, some rising to within 90 m of the surface, occurs along 155°E to 156°E. The northernmost of these, the Lord Howe Rise and the Norfolk Ridge, have an effect on water current dynamics in this region (Hamon, 1979; Stanton, 1981; Coleman, 1984).

Although there is broad agreement among oceanographers regarding the composition of water masses in the Coral Sea north of 30°S, considerable disagreement exists with respect to the details of surface circulation patterns. Surface currents in the Coral Sea (Figure 2) are typically weak and variable with a general westward flow to the north of New Caledonia (the South Equatorial Current (SEC)) dividing at the eastern slope of the Great Barrier Reef near 20°S to flow northwestward in a cyclonic circuit between Australia and Papua New Guinea and

southward as the source water for the East Australian Current (EAC) system (Wyrski, 1962; Andrews and Clegg, 1989).

The presence of a "South Tropical Convergence" in the South Pacific at about the latitude of the Tropic of Capricorn has been hypothesized by Burkov (1966), but this feature has not been identified in subsequent oceanographic studies of the Coral Sea (e.g., Andrews and Clegg, 1989).

The dominant oceanographic feature of the western Tasman Sea is the East Australian Current system, characterized by complex, variable, and strong surface currents with an influence extending to abyssal depths (Mulhearn, 1983). Between 27°S and 32°S, the EAC is generally in evidence as a strong (up to 2 m/sec), narrow, southward flowing current at the edge of the continental shelf. A continuous current is not always present along the shelf slope and can be composed of the western edges of a series of asymmetric anticyclonic eddies extending up to 300 km offshore. Near 32°S–33°S the current leaves the coast along a sharp temperature and salinity front and turns southeastward (Godfrey et al., 1980).

Large anticyclonic "eddies" (up to 300 km in diameter) are frequently encountered in the western Tasman Sea south of 34°S (Figure 2). These are characterized by an isothermal and isohaline warm core extending to as deep as 400 m. Eddies are formed when U-shaped meanders of the EAC are pinched off, enclosing tropical water. Those that escape the EAC usually move south at up to 20/km day, with some persisting as identifiable water masses as far as 39°S and for as long as 14 months (Cresswell, 1983).

A component of the EAC continues eastward as the Tasman Front, a generally coherent, meandering, zonal jet linking at least part of the EAC with western boundary currents east of New Zealand (Figure 2). The meandering results from the variability of the EAC and the topographic effects of the Lord Howe Rise and Norfolk Ridge. The Tasman Front is evident on the Lord Howe Rise as far south as 34°S in summer and 30°S in winter. A smaller latitudinal range is evident where the Front crosses the Norfolk Ridge in the region of Wanganella Bank, and this feature terminates at about North Cape on the North Island of New Zealand (Stanton, 1981; Tate et al., 1989).

Between 40°S and 45°S off eastern Tasmania, tropical and subtropical waters associated with the EAC system meet Subantarctic water in the region of the West Wind Drift, forming the Subtropical Convergence (= Temperate Convergence of Briggs, 1974). This feature, often weak in the western Tasman Sea, usually parallels the 15° C surface isotherm in summer and the 10° C isotherm in winter.

Off the southwest coast of New Zealand, the West Wind Drift (in this region called the Tasman Current) branches, with one component continuing northeast as the Westland Current. The other component extends to the south and east, forming the northward flowing Southland Current on the east coast of the South Island (Heath, 1973).

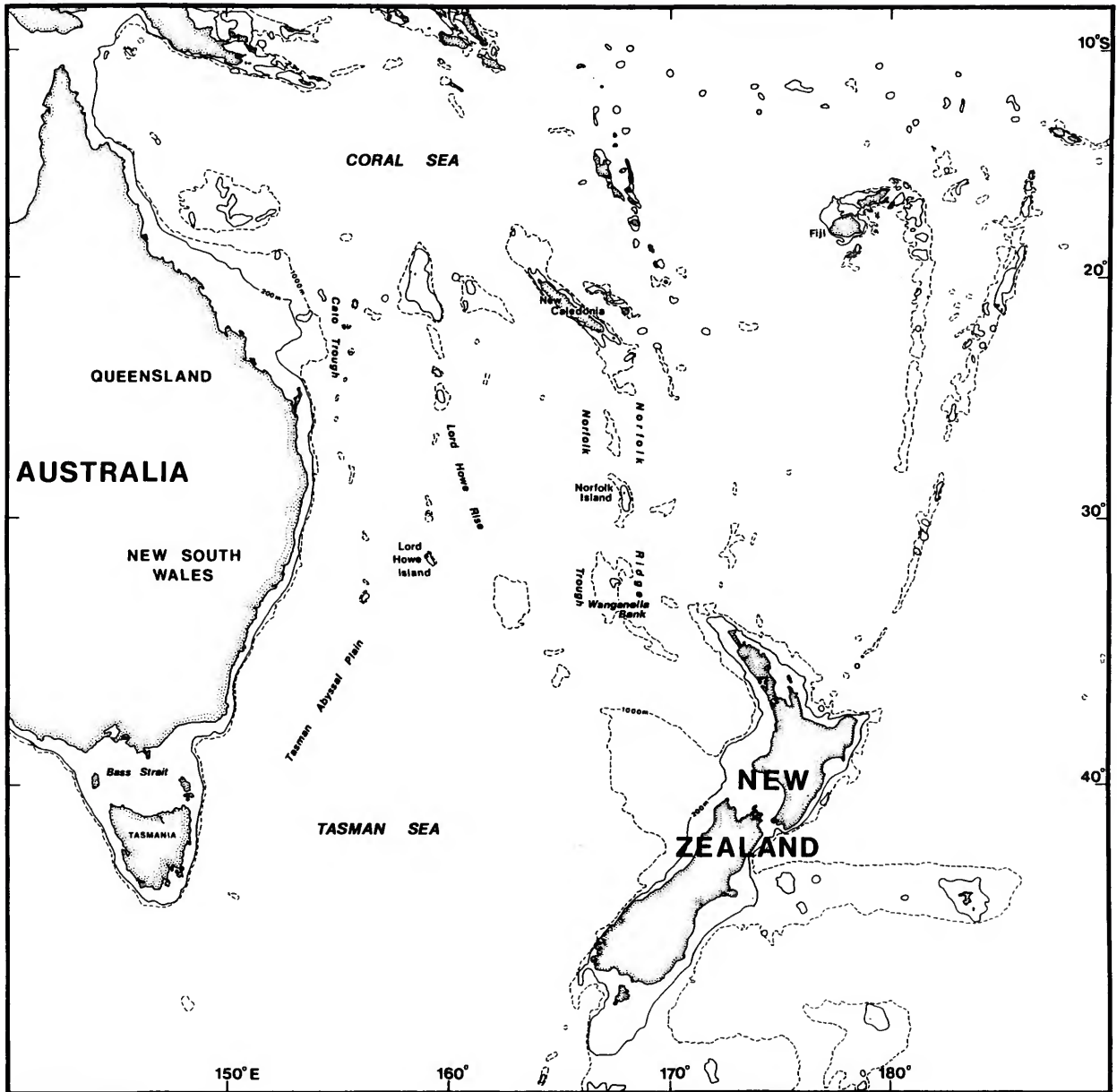


FIGURE 1.—Simplified bathymetry of the Coral and Tasman seas region.

**Distribution of Species**

**Subfamily TODARODINAE**

The Subfamily Todarodinae is represented in the region by

seven species inhabiting shelf, slope, and oceanic waters from tropical to subantarctic waters. Herein, *Todaropsis eblanae* (Ball, 1841) is included in this subfamily as proposed by Roeleveld (1988).

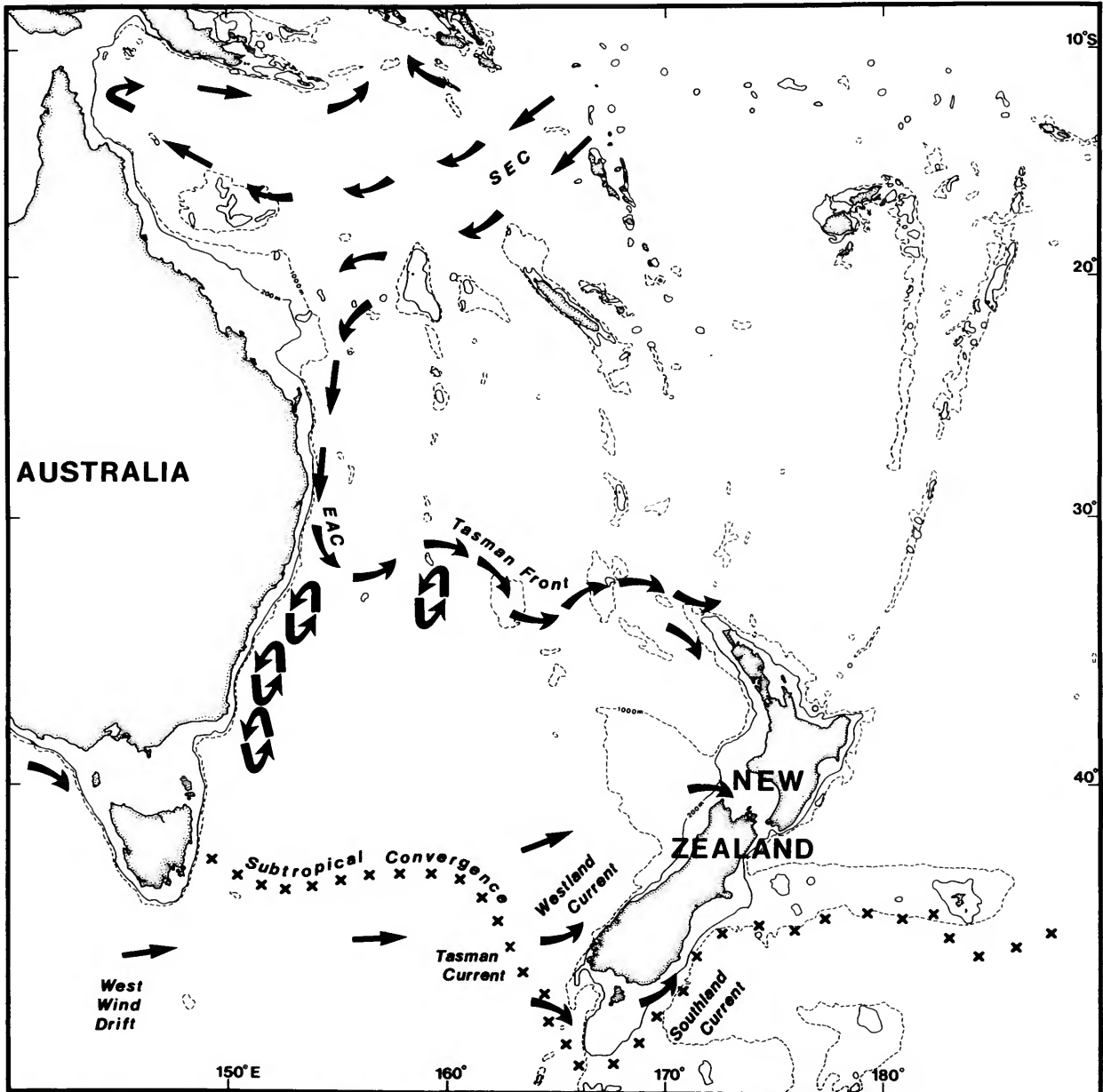


FIGURE 2.—Major currents and oceanographic features of the Coral and Tasman seas region. (EAC = East Australian Current, SEC = South Equatorial Current.)

*Todaropsis eblanae* (Ball, 1841)

FIGURE 3

The golden arrow squid, *T. eblanae*, was first reported from the southwest Pacific by Lu (1982). Additional adult specimens of *T. eblanae* examined by Dunning (1988c) were caught in demersal trawls in eastern Australian waters from 17°44'S to

34°53'S where bottom depths varied from 200 m to 678 m and bottom temperatures (where recorded) varied from 11.4° C to 17.5° C. Specimens described by Lu (1982) were trawled in depths to 805 m and as far south as 37°12'S off the eastern Australian coast. Figure 3 shows locations where *T. eblanae* has been reported from the southwest Pacific.

The available material does not allow a detailed assessment



of this species' distribution with bottom depth, but extensive trawl studies on the continental shelf off the eastern Australian coast suggest that it is restricted to continental slope waters in this region. Adults were not represented in pelagic trawl catches, indicating that *T. eblanae* is predominantly a demersal rather than a midwater species in this region (Dunning, 1988c).

The larvae of *T. eblanae* have not been described in the literature, and no larvae that could be assigned to this species have been reported from the southwest Pacific. Three juveniles of 21 mm mantle length (ML), 22 mm ML, and 33 mm ML were trawled in midwater off central New South Wales (34°S–35°S) in January 1979 and March 1981 (bottom depths of 70–170 m, temperatures at capture depth 16.2°–19.7° C) (Dunning, 1988c).

#### ***Martialia hyadesi* (Rochebrune and Mabile, 1889)**

Since the mid-1980s, *Martialia hyadesi* has become a significant component in the southwest Atlantic Ocean jig fishery off Argentina and the Falkland Islands (Rodhouse and Yeatman, 1990). South Pacific reports of *M. hyadesi* have been from the Eltanin Fracture Zone east of 160°W (Nesis, 1987), from adults stranded on the beach at Macquarie Island (54°30'S, 158°57'E) after a storm (O'Sullivan et al., 1983), and from off the Campbell Islands (~52°30'S, 170°E) (M.J. Imber, pers. comm. cited in Rodhouse and Yeatman, 1990).

Uozumi et al. (1990) provided the first record of this species from southern New Zealand waters. Juveniles (9–101 mm ML), but no adults, were caught using a fine mesh midwater trawl in and south of the Subtropical Convergence Zone (south of 45°S) during midwinter 1985 at the edge of the continental shelf and in deeper water.

#### ***Todarodes filippovae* Adam, 1975**

FIGURES 3, 5

The Southern Ocean arrow squid, *T. filippovae*, was originally described from specimens from the southern Indian Ocean. In subsequent studies in southern subtropical and subantarctic waters, Russian workers have failed to recognize the validity of this species and have referred all *Todarodes* from these waters to *T. angolensis* Adam, 1962 (Zuev et al., 1976; Nesis, 1979a, 1979b, 1979c, 1987; Roeleveld, 1989). Thus, the literature remains confused as to the distribution of these species. Okutani (1980) considers *T. filippovae* to have a circumsubantarctic distribution, and its distribution overlaps that of *T. angolensis* off southwestern Africa (Roeleveld, 1989).

*Todarodes filippovae* has previously been reported from eastern Tasmanian waters by JAMARC (1978), and it is likely that the adult *Todarodes* reported by Nesis (1979c) from south of Tasmania and eastward from New Zealand also are referable to this species (Roeleveld, 1989; K.N. Nesis, pers. comm., 1991). *Todarodes angolensis* is rare in collections from the western Tasman Sea.

Nesis (1979b) considered "*T. angolensis*" to be restricted to waters south of 45°S in the southern Tasman Sea. The results of recent studies have extended the distribution of *T. filippovae* further to the north in summer, and surface driftnet surveys also have shown that although adults are caught near the bottom in slope waters, they apparently migrate throughout the water column and are caught at the surface at night.

Three juveniles of 40 mm ML, 66 mm ML, and 80 mm ML were caught at the surface at night using scoop nets in the extreme west of the Tasman Sea off eastern Tasmania (38°28'S, 154°26'E, and 41°44'S, 153°24'E; surface temperatures 19.5° C and 15.5° C) in late December 1981. None of the plankton collections from the Tasman Sea or eastern Australian coast reported by Dunning (1988c) contain larvae positively identified as this species.

Morphological characters separating the larvae of *Todarodes* spp. from those of *Nototodarus gouldi* (McCoy, 1888), which have been commonly reported from these waters, remain unclear. A single larva, 8 mm ML, was recorded from south of Tasmania (sea surface temperature 10.5° C) by Nesis (1979a, pers. comm., 1981) as *T. angolensis* and may be referable to the more abundant *T. filippovae*.

Off the eastern Australian coast, adult *T. filippovae* have been caught in midwater and demersal trawls and on jigs between 33°08'S and 47°42'S (the most southerly station sampled) where sea surface temperatures ranged from less than 11.5° C to 24.7° C. In the summers of 1981–1982 and 1982–1983 in the central Tasman Sea, adults were caught in surface waters (0–50 m) between 32°45'S and 45°45'S (the most southerly station sampled), with corresponding sea surface temperatures of 20.1° C and 14.2° C. Temperatures at 50 m at these stations ranged from 11.8° C to 18.0° C (Dunning, 1988c).

On the slope and deeper shelf off the west coast of New Zealand, adult and juvenile *T. filippovae* have been caught in demersal and midwater trawls, jigs, and in surface driftnets between 36°S and 50°26'S (on the northern Auckland Shelf) (Kawakami, 1976; Uozumi et al., 1987). Sea surface temperatures where this species has been caught vary from 8.5° C to 19.7° C.

Figure 3 shows the distribution of adults and juveniles in the region.

Variation in abundance with respect to latitude in mean numbers of *T. filippovae* from jig catches in the Tasman Sea (December 1981–February 1982) is shown in Figure 5. Numbers increased toward the southernmost stations sampled (south of 44°S, surface temperatures less than 14° C). No specimens were caught in surface waters with temperatures greater than 20° C (Dunning, 1988c).

*Todarodes filippovae* could be primarily associated with the Subtropical Convergence Zone in the Southwest Pacific, with a similar geographical distribution to the mesopelagic cranchiid *Teuthowenia pellucida* (Voss, 1985), but definition of the southern boundary of its distribution awaits further study.

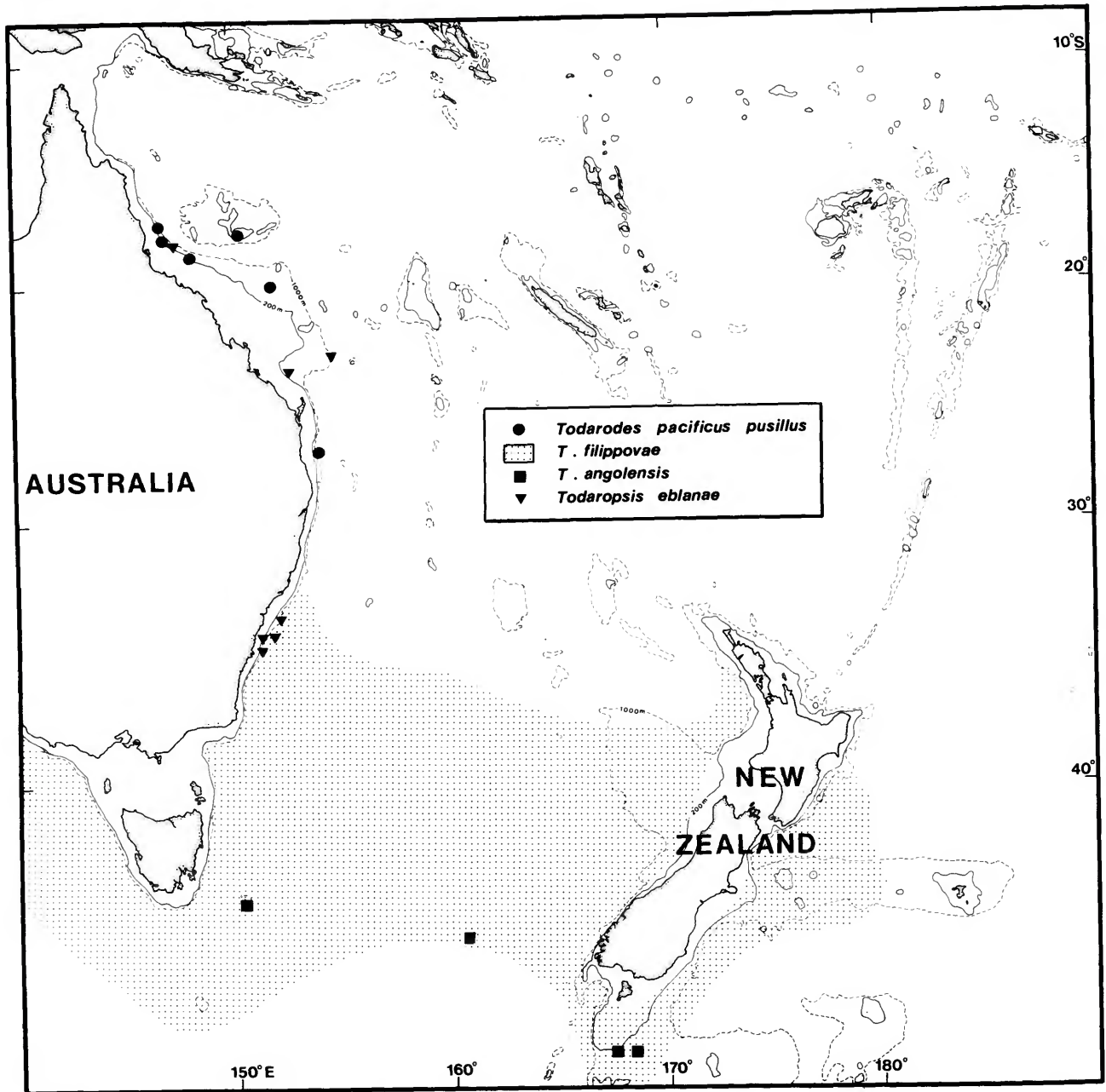


FIGURE 3.—Distribution of representatives of the subfamily Todarodinae in the Coral and Tasman seas region.

*Todarodes angolensis* Adam, 1962

FIGURE 3

*Todarodes angolensis* has previously been reported from the South Atlantic, the southwest Indian Ocean, the South Pacific

off the coast of South America, the southeast coast of New Zealand, and to the south and southwest of Tasmania (Filippova, 1971; Zuev et al., 1976; Nesis, 1979c; Roeleveld, 1989). As discussed previously, however, Russian biologists have confused the literature by referring all

*Todarodes* caught in southern hemisphere waters to *T. angolensis*. They considered the characters used to separate *T. filippovae* from this species to fall within the range of individual, geographic, or ontogenetic variation of the former species (Nesis, 1979c, pers. comm., 1982), a hypothesis not supported by recent studies (Dunning, 1988c; Roeleveld, 1989). *Todarodes angolensis* may be separated from *T. filippovae* on the basis of the number of sucker rows in the manus of the club (14–18 in *T. angolensis*, 12–14 in *T. filippovae*), the number of teeth in the medial manus-sucker rings (13–16 in *T. angolensis*, 7–13 in *T. filippovae*), and the relative diameter of the medial manus suckers (2.3–2.6 mm in *T. angolensis*, 2.7–4.5 mm in *T. filippovae*) (Roeleveld, 1989).

*Todarodes angolensis* was first identified from the southeast Tasman Sea during a jig survey in the austral summer of 1981–1982. The majority of the catch proved to be *T. filippovae* Adam, 1975, although careful examination of four immature females revealed that these specimens were *T. angolensis*. Further investigation revealed the presence of four additional trawled specimens, including two fully mature females and a mature male, in the collections of the National Museum and the New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division, in Wellington, New Zealand (Dunning, 1988c). Another immature female was recently taken by demersal trawl off southern Tasmania (Figure 3).

Specimens of *T. angolensis* have been caught in the southern Tasman Sea between 43°50'S and 52°17'S where sea surface temperatures were less than 13° C and bottom temperatures were as low as 4.8° C. Squids from 250 mm ML to 372 mm ML were jigged together with *T. filippovae* in near-surface oceanic waters in December 1982 (temperatures 11.7°–13.7° C), and specimens from 440 mm ML to 590 mm ML were trawled in slope waters off southern New Zealand and Tasmania in depths of 400 m to 1100 m during the summer months between 1980 and 1989.

Better definition of the distribution of *T. angolensis* in this region, particularly of its southern boundary and its degree of overlap with *T. filippovae*, awaits further study.

#### *Todarodes pacificus pusillus* Dunning, 1988

FIGURE 3

The Japanese common squid, *T. pacificus* Steenstrup, 1880, was described from specimens collected east of Hokkaido, and subsequent workers have considered it restricted to temperate shelf and upper slope waters in the northern North Pacific, principally around Japan (Wormuth, 1976; Okutani, 1983). *Todarodes pacificus* has occasionally been reported from the South China Sea, around Hong Kong, and from the southern Philippines, and a subspecies was recently described from northern Australian waters (Dunning, 1988a).

*Todarodes p. pusillus* has been reported from demersal trawl

catches between 17°16'S and 27°S off the eastern Australian coast, where bottom depths vary from 78 m to 357 m. *Todarodes p. pacificus* is not generally abundant around Japan where temperatures at 50 m depth exceed 15° C; however, it has been caught where temperatures were as low as 5° C. In contrast, *T. p. pusillus* was caught in northern Australian shelf waters where temperatures at 50 m depth were in excess of 23° C and sea surface temperatures reached 29° C in summer (Dunning, 1988a).

#### *Nototodarus sloanii* (Gray, 1849)

FIGURE 4

*Nototodarus sloanii* (Gray, 1849) occurs in New Zealand continental shelf waters southward from the northern boundary of the Subtropical Convergence Zone (~40°S) to the Auckland Islands (51°S) and the Campbell Islands (53°S) where bottom depths vary from 50 m to 500 m. The jig fishery for this species has concentrated where sea surface temperatures vary from 11.9° C to 16.5° C. *Nototodarus sloanii* is most abundant on the continental shelf in depths of less than 200 m (Mattlin et al., 1985). In the north, its distribution overlaps that of *N. gouldi* (Smith et al., 1987), and in the south, it has been jigged and trawled together with *Todarodes filippovae* Adam, 1975, and *Martialia hyadesi* (Kawakami, 1976; Uozumi et al., 1990).

Larvae of *N. sloanii* appear to be distributed only on the continental shelf and near submarine canyons. Off the west coast of the South Island of New Zealand where the shelf is very narrow, concentrations have been quite localized near the submarine canyons during winter sampling for ichthyoplankton (Dunning and Förch, 1998).

#### *Nototodarus gouldi* (McCoy, 1888)

FIGURE 4

The dominant ommastrephid in continental shelf waters off southeastern Australia and around the North Island of New Zealand is *N. gouldi*, and its abundance has resulted in the development of significant jig fisheries in these regions, especially during the summer months (Winstanley et al., 1983).

*Nototodarus gouldi* larvae were first described from eastern Australian shelf and upper slope waters by Allan (1945) from plankton samples taken between eastern Bass Strait (39°20'S) and southern Queensland (26°54'S). They also were caught off central and northern New South Wales in continental shelf and slope waters between 29°S and 36°45'S, between January and May 1983, where sea surface temperatures (where recorded) varied from 17° C to 23.7° C (Dunning, 1988c).

In eastern Australian waters, adult *N. gouldi* have been caught between 27°13'S and 43°40'S where sea surface temperatures varied from 11° C to over 25° C. Although it has been taken in demersal trawls on the upper continental slope to depths of 800 m, it has been most abundant in commercial jig

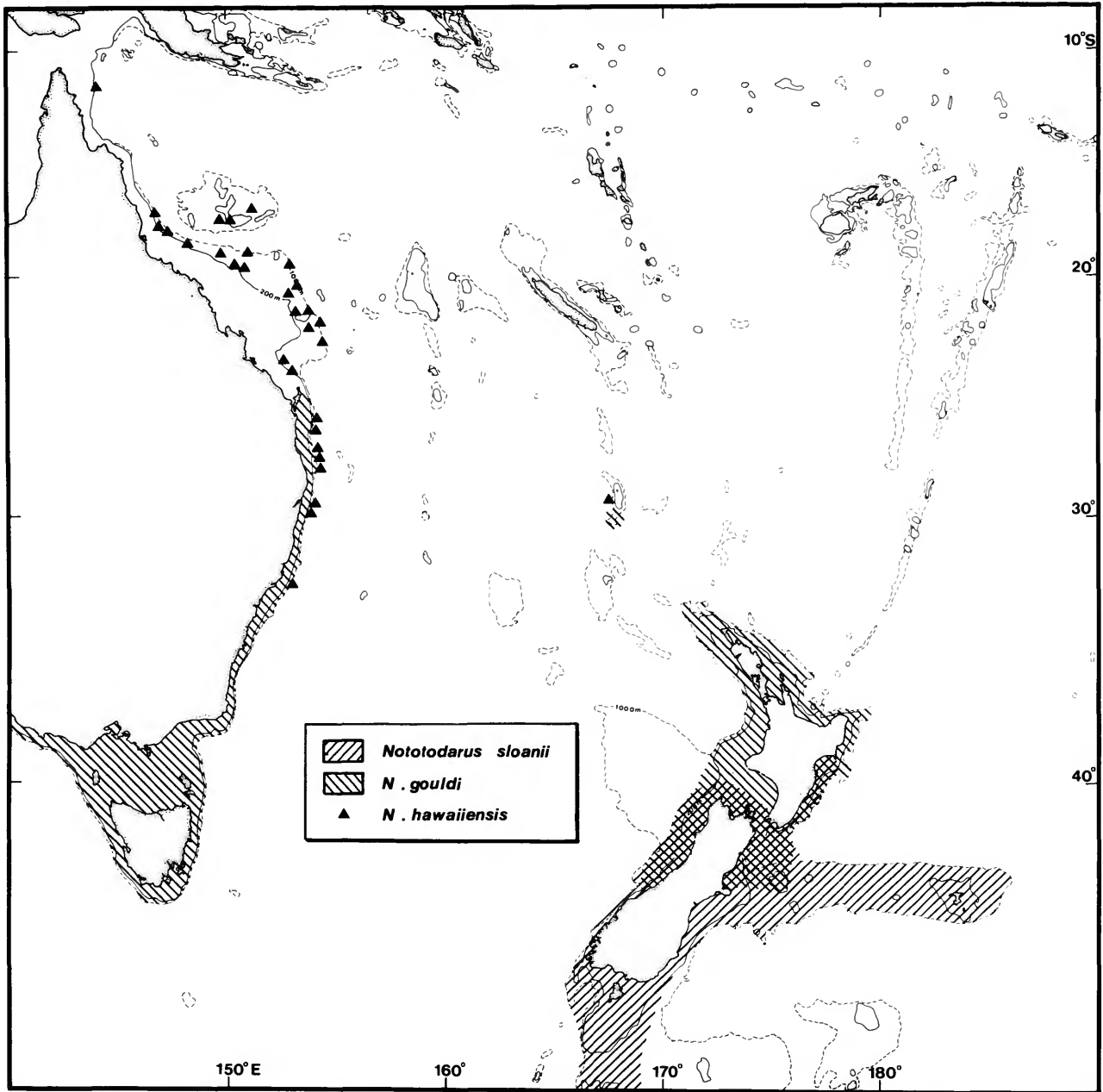


FIGURE 4.—Distribution of representatives of the subfamily Todarodinae in the Coral and Tasman seas region.

catches where bottom depths range from 50 m to 200 m (Winstanley et al., 1983).

*Nototodarus gouldi* occurs in New Zealand waters southward to 44°S off the west coast (Smith et al., 1987). It has been

trawled together with *N. hawaiiensis* (Berry, 1912) north of New Zealand on the South Norfolk Ridge at 29°40'S, 168°E (bottom depth 362–438 m), and off the eastern Australian coast at 27°15'S, 153°54'E (bottom depth 535 m).

*Nototodarus hawaiiensis* (Berry, 1912)

FIGURE 4

*Nototodarus hawaiiensis* has been reported from around the Hawaiian and Midway islands (Wormuth, 1976; Young, 1978), southeastern Honshu, Japan (as *N. nipponicus* Okutani and Uemura, 1973), the South China Sea near Hainan (Dong, 1963), the Philippines (as *N. sloani philippinensis* Voss, 1962), and the western Indian Ocean (Roeleveld, pers. comm., 1982; Nesis, 1987). Its distribution throughout the island chains of the central and southeastern Pacific remains unclear, although Okutani and Kuroiwa (1985) described specimens taken by demersal trawl in 243 m at a seamount off the coast of Chile (25°39'S, 85°31'W), and further specimens from this region have been described by Nesis (1990).

Three *N. hawaiiensis* larvae were caught during ichthyoplankton surveys near Lizard Island on the northern Great Barrier Reef (14°30'S) in November 1984 and February 1985. All were taken in oblique tows in the upper 100 m of the water column where bottom depth exceeded 400 m. A single juvenile (37 mm ML) was scoop-netted at the surface at 23°58'S off the southern Great Barrier Reef in late April 1981 where water temperature was 26.2° C.

Off the eastern Australian coast between 11°35'S and 32°34'S, adults have been caught using demersal trawls between 162 m and 696 m on the deeper continental shelf and continental slope (Dunning, 1988b). *Nototodarus hawaiiensis* has recently been trawled on the South Norfolk Ridge (see discussion of *N. gouldi*, above). *Nototodarus hawaiiensis* was not caught during extensive demersal and pelagic trawling surveys off the east coast south of the point where the East Australian Current turns eastward away from the continental slope (~32°S) (Dunning, 1988c).

The depth range occupied by adult *N. hawaiiensis* across the continental slope was examined using relative abundance data collected during demersal trawl surveys off the northeast Australian coast in depths of 46 m to 1200 m in November–December 1985 (austral midsummer). Highest mean catch rates of *N. hawaiiensis* were obtained between 350 m and 500 m (Dunning, 1988c). The presence of *N. hawaiiensis* in southern Queensland waters was confirmed by its occurrence in demersal trawl catches. Its absence in jig catches at any of the eight stations fished during the R/V *Hoyo-maru* survey in April 1981, however, suggests that this species is primarily demersal rather than pelagic (Dunning, 1988c).

**Subfamily OMMASTREPHINAE**

The subfamily Ommastrephinae is represented in the region by six described and one undescribed species inhabiting tropical and subtropical slope and oceanic waters. Nigmatullin (1979) considers the genus *Ornithoteuthis* Okada, 1927, to be more appropriately assigned to a separate subfamily Ornithoteuthinae, but this has yet to receive wide acceptance.

*Ommastrephes bartramii* (Lesueur, 1821)

FIGURES 5, 6

The red ocean squid or neon flying squid, *Ommastrephes bartramii*, occurs circumglobally in subtropical and temperate waters (Zuev et al., 1976; Okutani, 1980). Nesis (1979c) described its distribution as “bisubtropical.” In the South Pacific Ocean, *O. bartramii* occurs eastward from New Zealand to 80°E off the coast of Chile (Polezhaev, 1986).

Larval *O. bartramii* have been reported from summer collections made off the eastern Australian coast between 28°S and 35°46'S, where sea surface temperatures ranged from 26.9° C to 20.6° C (Nesis, 1979a, pers. comm., 1981; Dunning, 1988c). Small juveniles (<75 mm ML) were collected over a broader latitudinal range, between 23°57'S and 38°25'S, but in similar water temperatures.

Except for single juveniles caught at the surface at 32°59'S, 158°02'E, southwest of Lord Howe Island, and at 34°23'S, 165°38'E, southwest of Wanganella Bank, no larval or juvenile *O. bartramii* were present in 65 plankton and scoop-net samples from the central Tasman Sea over a broad area east of 155°E and south of 32°S during the summers of 1981 and 1982 (Dunning, 1988c).

Off the eastern Australian coast west of 155°E, adult *O. bartramii* were caught in midwater trawls, on jigs, and in surface driftnets between 23°42'S and 43°46'S, where sea surface temperatures varied from 25.7° C to 14.9° C, respectively. Corresponding temperatures at capture depths varied from 25.7° C to 9.0° C. In the central Tasman and southern Coral seas between 155°E and 170°E, this species was caught in summer between 30°S and 45°45'S (the most southerly station sampled), with corresponding sea surface temperatures of 24.7° C and 14.2° C (temperatures at maximum capture depth 23.8°–11.8° C) (Dunning, 1988c).

Nesis's (1979c) conclusion that cold water off the west coast of Tasmania represents a barrier to the westward distribution of Tasman Sea *O. bartramii* into the Great Australian Bight is supported by subsequent demersal trawl and jig studies in this region. No adult *O. bartramii* were identified during extensive trawl and jig surveys made in continental shelf waters (<200 m) off the eastern Australian coast (JAMARC, 1987; Dunning, 1988c).

During a January 1982 extensive midwater and demersal trawl survey where bottom depths varied from 132 m to more than 2000 m, *O. bartramii* was taken only where bottom depth exceeded 600 m. An additional 13 specimens trawled off the New South Wales coast were examined, and all were taken where water depth exceeded 700 m (Dunning, 1988c).

Variation in abundance relative to latitude in mean numbers of *O. bartramii* caught on jigs in the central Tasman Sea and southern Coral Sea between early December 1981 and late February 1982 is shown in Figure 5. *Ommastrephes bartramii*

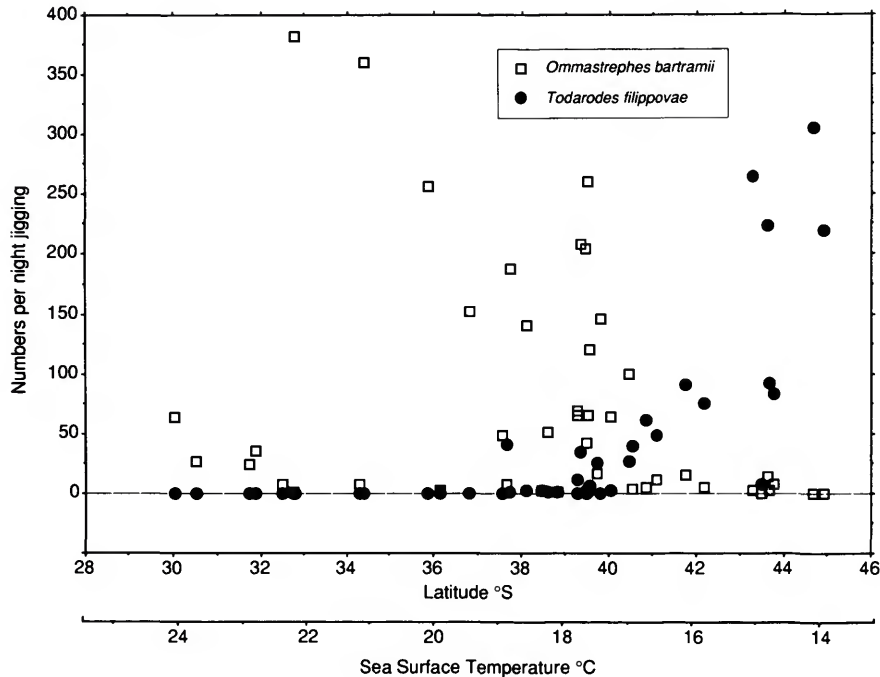


FIGURE 5.—Variation in abundance with latitude and sea surface temperature of *Todarodes filippovae* and *Ommastrephes bartramii* in the Tasman Sea as assessed from jig catches, austral summer, 1981/1982.

was abundant between 32°S and 40°S where sea surface temperatures ranged from 17° C to 24° C. The highest catch in terms of number of squid was obtained at 32°S in waters of 23° C. Further south, catches consisted of fewer squid but with a larger average size (Dunning, 1988c).

#### *Sthenoteuthis oualaniensis* (Lesson, 1830)

FIGURE 6

The yellow-backed squid or purpleback flying squid, *Sthenoteuthis oualaniensis*, is the dominant ommastrephid in tropical oceanic surface waters of the Indo-Pacific region and occurs from the west coast of central America to the east coast of Africa (Clarke, 1966; Zuev et al., 1976; Okutani, 1980). Nesis (1977) described the population structure of this species from the central west Pacific.

In nearshore waters off the eastern Australian coast, larval *S. oualaniensis* were examined from both surface and midwater plankton collections made between 14°33'S (near Lizard Island) and 34°S off the central New South Wales coast, where sea surface temperatures ranged from 20.4° C to greater than 28° C during the summer months. Juveniles were caught in scoop nets at 11 stations sampled between 22°50'S and

38°25'S, east of Bass Strait, in April 1981 (surface temperatures 26.7°–20.8° C).

Larvae of *S. oualaniensis* were the dominant ommastrephids present in ichthyoplankton collections made in Great Barrier Reef Lagoon and oceanic waters off Lizard Island in the summers of 1983/1984 and 1984/1985, and juveniles of this species dominated scoop-net catches made between 23°S and 27°S in April 1981. In the East Australian Current between 28°S and 34°S, however, larvae of this species were rare from January to May 1983, occurring at only 21 of 181 stations sampled. They were absent from samples collected in this same area in July–August 1985 and from 65 plankton stations sampled in the central Tasman Sea during the summers of 1981–1983. Juvenile *S. oualaniensis* represented less than 5% of the ommastrephids caught in a series of 12 midwater trawls taken at 34°30'S in April 1981 (Dunning, 1988c).

Nesis (1979b) considered this species to be restricted to waters north of the Tropic of Capricorn in the Australasian region. During recent studies in nearshore waters off the eastern Australian coast, adult *S. oualaniensis* were caught as far south as 38°40'S in surface waters of 20.7° C. In the southern Coral Sea basin (east of 155°E), adults of this species were caught on jigs only north of 32°S in surface waters of more than 23.5° C, where they replaced *O. bartramii* as the dominant ommastre-

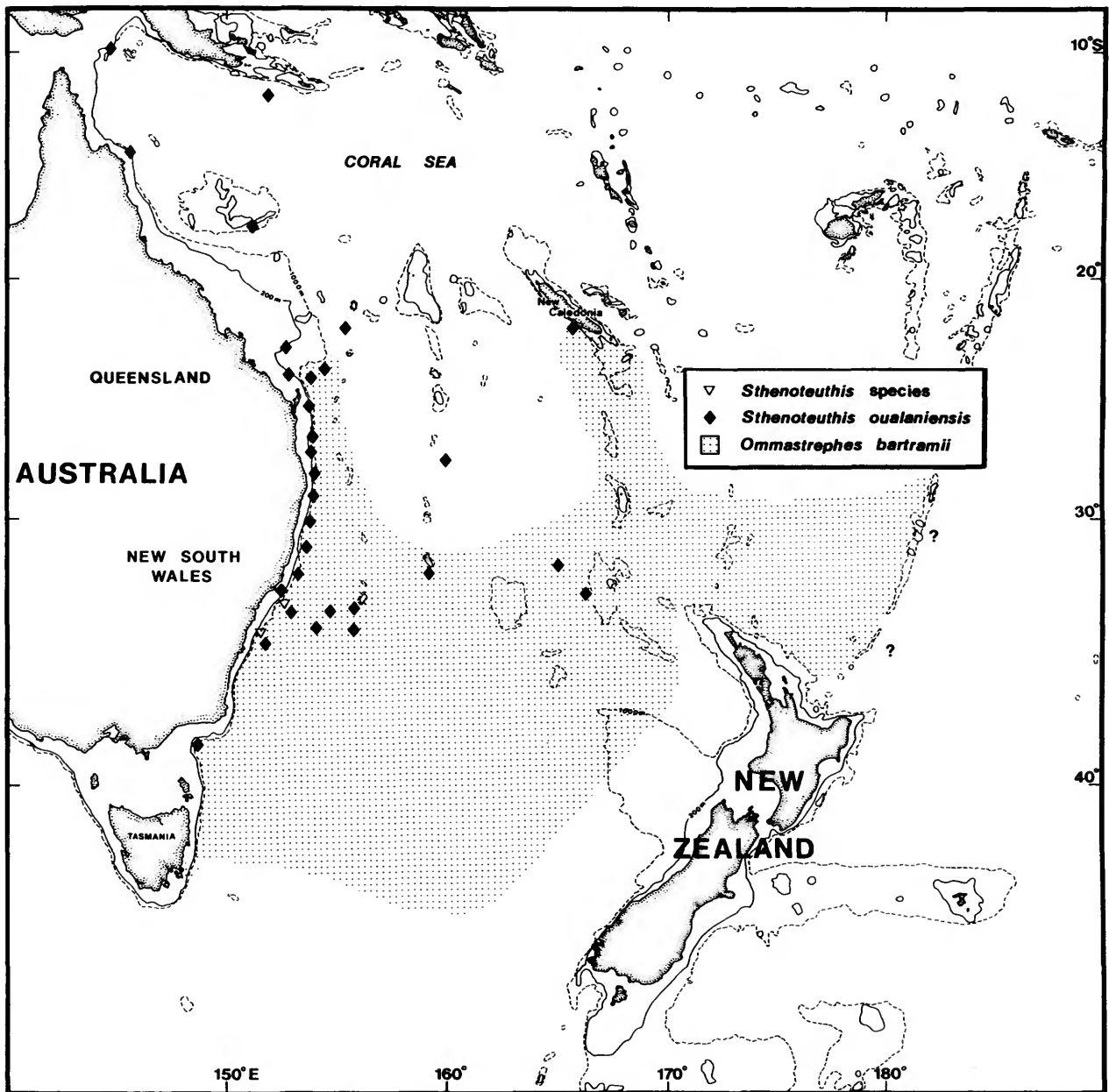


FIGURE 6.—Distribution of representatives of the subfamily Ommastrephinae in the Coral and Tasman seas region (*Sthenoteuthis* sp. being described by M.A.C. Roeleveld, South African Museum) (? = eastward distribution of *O. bartramii* uncertain).

phid (Dunning, 1988c). *Sthenoteuthis oualaniensis* was the dominant species in jig catches from off Fiji (Anonymous, 1980) and off New Caledonia (Rancurel, 1980) and was the dominant species in the diets of *Alepisaurus ferox* Lowe and

yellowfin tuna (*Thunnus albacares* (Bonnaterra)), in the Coral Sea (Rancurel, 1970, 1976).

Although larvae were caught in continental shelf waters of the Great Barrier Reef as shallow as 10 m, adult *S. oualaniensis*

were caught in eastern Australian waters only where bottom depth exceeded 600 m (Dunning, 1988c).

### *Sthenoteuthis* species

FIGURE 6

This species is being described by M.A. Roeleveld, South African Museum (pers. comm., 1982).

Clarke (1965) was the first to recognize the existence of two forms of *S. oualaniensis*, one with and one without a large dorsal photophore patch. The form without the light organ, *S.* species, and the far more frequently encountered *S. oualaniensis* appear to be at least partially sympatric in tropical waters of the Indian and western Pacific Oceans (Clarke, 1966; Nesis, 1977).

Two mature females have been reported from the southwest Pacific. A mature female squid of 134 mm ML was jigged off the eastern Australian coast near the shelf edge at 34°14'S in March 1982, and a second mature female of 150 mm ML was taken together with *S. oualaniensis* at 33°S (sea surface temperature 23.7° C) in late March 1983. At both locations, bottom depth was more than 1000 m and specimens of *S. oualaniensis* were caught at the same location on the same nights (Dunning, 1988c).

### *Eucleoteuthis luminosa* (Sasaki, 1915)

FIGURE 7

The striped squid or luminous flying squid, *E. luminosa*, has a distribution similar to that of *O. bartramii*, occurring in subtropical waters of the North and South Pacific but restricted to south of the equator in the Indian and Atlantic oceans (Zuev et al., 1975; Okutani, 1980). In the South Pacific, this species has previously been reported from around New Caledonia and Norfolk Island (Rancurel, 1970; Zuev et al., 1975) and eastward from the Kermadec Islands to 80°54'E off the coast of Chile (Wormuth, 1976; Polezhaev, 1986). Nesis (1979b) considered *E. luminosa* to be a peripheral species in the Australasian region.

Larval *E. luminosa* have been reported from off the eastern Australian coast between 14°30'S and 35°46'S, where sea surface temperatures (where recorded) ranged from 28° C to 20.6° C. Juveniles (<75 mm ML) were collected between 23°59'S and 37°45'S in water temperatures of 25.6° C to 19.1° C (Dunning, 1988c).

Nesis (1979c) reported larval and juvenile *E. luminosa* between 2 mm ML and 10 mm ML from a depth of 200 m near Norfolk Island; however, no specimens of this species were caught in towed plankton nets or surface scoop nets during summer Tasman Sea and southern Coral Sea surveys undertaken by Dunning (1988c).

Near the eastern Australian coast, adult *E. luminosa* have been caught between 23°59'S and 36°35'S (surface tempera-

tures 25.6°–20.8° C). Single females also were jigged at two stations in the southeastern Coral Sea at 31°44'S, 164°58'E, and 30°03'S, 163°49'E, in late February 1982 and in the southwest Tasman Sea at 35°50'S, 156°38'E, in December 1982 (Dunning, 1988c). During January 1982, three specimens of *E. luminosa* were caught in midwater trawls where bottom depth exceeded 800 m. An additional 18 specimens trawled and jigged off the New South Wales coast were examined, and all were taken where water depth exceeded 600 m (Dunning, 1988c).

### *Hyaloteuthis pelagica* (Bosc, 1802)

FIGURE 7

The luminous *Hyaloteuthis pelagica*, one of the smallest members of the family Ommastrephidae, occurs mainly in the transition zone between tropical and subtropical oceanic waters in the North and South Pacific and Atlantic oceans (Rancurel, 1970; Wormuth, 1976; Nesis and Nigmatullin, 1979; Harman and Young, 1986; Warneke-Cremer, 1986). *Hyaloteuthis pelagica* was first recorded from Australian waters among the stomach contents of yellowfin tuna caught off the northern Great Barrier Reef in October 1971 (Rancurel, 1976).

Seven larvae referable to this species were caught off the eastern Australian coast in surface plankton tows in the EAC between 28°S and 30°S in January and May 1983, respectively, where sea surface temperatures ranged from 23.4° C to 24.4° C. A single larval *H. pelagica* also was caught in an oblique, daytime ichthyoplankton tow to 115 m in oceanic waters off Carter Reef (14°31'S, 145°38'E, bottom depth >1500 m) in January 1985. In late March 1981, two juvenile *H. pelagica* (23 mm ML, 30 mm ML) were caught at night in a single midwater trawl (0–280 m) on the upper continental slope (310 m) at 34°22'S, off the eastern Australian coast (Dunning, 1988c).

A single mature female (46 mm ML) was the only adult reported from Australian waters. It was caught in a midwater trawl in the upper 200 m on the upper continental slope (bottom depth 400 m) off central New South Wales at 34°16'S, 151°21'E, in late March 1981 (Dunning and Brandt, 1985).

### *Ornithoteuthis volatilis* (Sasaki, 1915)

FIGURE 7

Available information suggests that the long-tailed flying squid, *Ornithoteuthis volatilis*, is primarily a tropical/subtropical species. Along the western margin of the Pacific, it has been recorded between 36°15'N and 23°S and eastward to the Line Islands (140°W), where its latitudinal range appears very restricted (Rancurel, 1970; Wormuth, 1976; Nesis and Nigmatullin, 1979). *Ornithoteuthis volatilis* has been recorded in the Indian Ocean from the Arabian Sea to south of Madagascar in the west and eastward to the Timor Sea (Fujita and Hattori, 1976; Nesis and Nigmatullin, 1979).



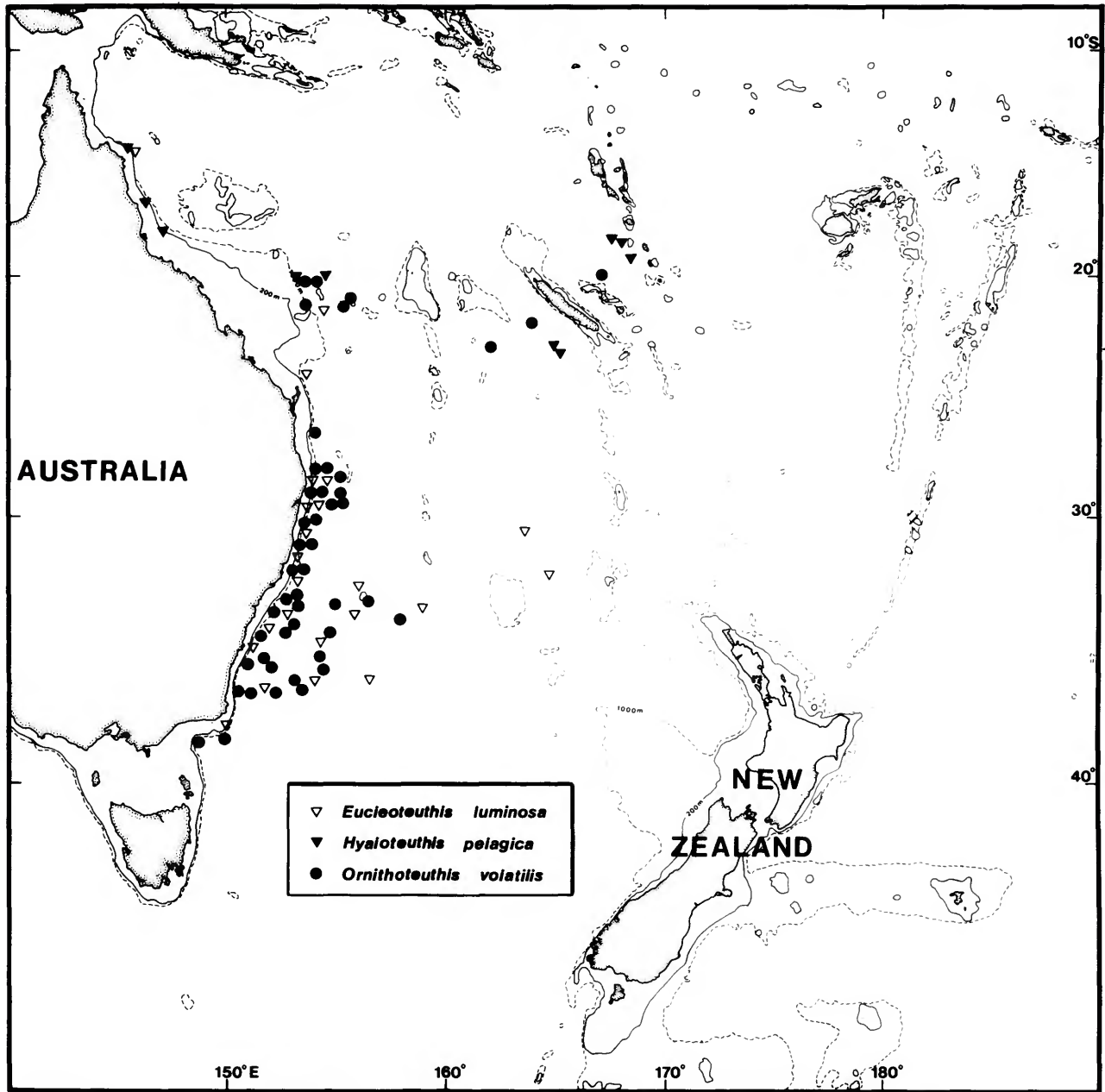


FIGURE 7.—Distribution of representatives of the subfamily Ommastrephinae in the Coral and Tasman seas region. (Includes information from Rancurel, 1976, and Okutani and Tsukada, 1988.)

Larval *Ornithoteuthis volatilis* were caught off the east Australian coast between 27°59'S and 34°33'S, and juveniles were caught between 28°18'S and 38°25'S, where surface temperatures ranged from 26.9° C to 19.6° C. Larvae and juveniles were collected in slope and adjacent waters off the

central New South Wales coast during most of the year (January–May, July–October), with small larvae rare south of the point where the southward flowing EAC turns eastward away from the continental slope. No specimens were present in towed plankton- and scoop-net catches from the central

Tasman Sea basin east of 155°E and south of 32°S made during austral summer 1981/1982.

Adults of *O. volatilis* have been caught using open midwater trawls and jigs at the surface off the eastern Australian coast between 26°30'S and 38°13'S, where surface waters ranged from 25.6°C to 17.3°C. They were absent from trawl and jig catches on the continental shelf, being represented only where water depth exceeded 400 m. They were occasionally caught at the surface on jigs and were caught in demersal trawls fished as deep as 732 m on the continental slope. No specimens were caught during extensive jig surveys of the central Tasman Sea and southern Coral Sea in the summers of 1981–1982 and 1982–1983, although subadult *O. volatilis* were encountered on the eastern boundary of an EAC warm core eddy off the southern New South Wales coast in December 1978, an estimated 250 km seaward of the edge of the continental shelf. Specimens also were caught in trawls near the Taupo Seamount (33°07'S, 156°07'E) in January 1982 (Dunning, 1988c).

### Discussion

**LARVAE.**—The oceanography of the eastern Australian coast south of 27°S is dominated by a major western boundary current, the East Australian Current (Hamon, 1970; Boland and Church, 1981), and this complex feature is likely to have a primary role in the distribution of ommastrephid larvae and subsequently adults in the region. Rather than representing a single continuous flow, satellite-tracked buoy data (Godfrey et al., 1980) suggest that the EAC off northern New South Wales may at times be the resultant western boundary of one or a series of north-south elongated anticyclonic gyres with eastern boundaries east of 156°E.

The EAC carries tropical Coral Sea water southward along the offshore edge of the continental shelf from north of 27°S to a point between 31°S and 32°S, where it turns eastward to form the meandering Tasman Front, dividing the Tasman Sea from the Coral Sea (Godfrey et al., 1980; Stanton, 1981). Also at about this latitude, anticyclonic warm core "eddies" up to 300 km in diameter are regularly "pinched off" from the EAC and drift off to the south, some retaining their hydrological identity for as long as 18 months (Creswell, 1983).

Larvae of at least six ommastrephid species were caught off the northern New South Wales coast in early 1983 (Dunning, 1986), supporting a hypothesis of spawning of many oceanic ommastrephids in slope waters in the northern Tasman Sea during the summer months.

Larvae hatched in the upper 200 m in continental slope or adjacent oceanic waters north of 31°S to 32°S and perhaps as far north as 20°S to 24°S are most likely to be entrained into the EAC system. They are then either carried into the Tasman Sea with water forming a warm core eddy adjacent to the coast west of 156°E or transported further east along the Tasman Front with the potential of subsequent northward or southward

transport around lower intensity gyres. If larvae were able to migrate vertically into deeper northward flowing countercurrents in slope waters or move into the less intense currents of shallower shelf waters, they could extend the time they remain in the more productive waters adjacent to the coast. For species such as *Nototodarus gouldi* and perhaps *Ornithoteuthis volatilis*, shelf waters and slope waters, respectively, also represent their adult habitat.

Off the New South Wales coast, *Ornithoteuthis volatilis* was the dominant species in larval collections in January, March, and May 1983 but was second in abundance to *Nototodarus gouldi*-type larvae in July–August 1985. Larvae of these two forms showed a similar distribution across the shelf and slope, being more abundant where bottom depths were from 50 m to 100 m than they were in deeper slope and oceanic water. Although juvenile *O. volatilis* also dominated midwater trawl samples taken near the continental slope at 34°22'S in April 1981 and at offshore stations near the boundaries of EAC warm core eddies sampled during August 1982 and October 1981, *N. gouldi* juveniles were not represented in samples taken seaward of the continental slope. Both species occur as adults in nearshore waters, *N. gouldi* on the continental shelf and *O. volatilis* in slope waters.

*Ommastrephes bartramii*, the most abundant ommastrephid in the January 1983 survey and second in relative larval abundance in March to *Ornithoteuthis volatilis*, was fourth in abundance in May 1983. Only juveniles of this species were caught off the New South Wales coast in July 1985. Larvae of this species, the adults of which are generally considered restricted to oceanic waters, were relatively evenly distributed offshore from midshelf waters along the northern New South Wales coast in early 1983. A similar pattern was evident for *Sthenoteuthis oualaniensis* larvae caught during the summer months off Lizard Island.

The larvae of *Eucleoteuthis luminosa*, adults of which are oceanic, were more abundant only in deeper slope and oceanic waters in both sampling areas. *Eucleoteuthis luminosa* was the second most abundant ommastrephid in January 1983 but was not represented in March 1983 or July 1985 and outnumbered only *Hyaloteuthis pelagica* in collections made in May 1983.

The northern New South Wales coast appears to be at the southern boundary of the distribution of *S. oualaniensis* larvae, at least from the midsummer to midwinter months. This species was more abundant in samples collected in May 1983 than in either January or March but never represented more than 5% of all ommastrephids. It was not represented in oblique tows made in July 1985. In contrast, *S. oualaniensis* was the overwhelmingly dominant species in the summer months near Lizard Island (Dunning, 1988c).

**ADULTS.**—In the southern Coral and central Tasman seas, boundaries between the distributions of adult ommastrephids appear to be relatively distinct, whereas in continental slope and adjacent waters off the eastern Australian coast, distributions show significant overlaps. As with the distribution of

TABLE 1.—Adult distribution patterns of the fourteen species of the Family Ommastrephidae represented in the Tasman and Coral seas.

Species	Maximum size (ML)	Depth range			Zoogeographic rone		
		Shelf	Slope	Oceanic	Tropical	Subtropical	Subantarctic
TODARODINAE							
<i>Todarodes angolensis</i>	590 mm		x	x		x	
<i>T. filippovae</i>	520 mm		x	x			x
<i>T. pacificus pusillus</i>	100 mm	x	x			x	
<i>Nototodarus sloanii</i>	420 mm	x				x	x
<i>N. gouldi</i>	410 mm	x				x	
<i>N. hawaiiensis</i>	250 mm		x		x		
<i>Todaropsis eblanae</i>	180 mm		x		x	x	
<i>Martialia hyadesi</i>	290 mm	x	?				x
OMMASTREPHINAE							
<i>Ommastrephes bartramii</i>	550 mm			x		x	
<i>Sthenoteuthis oualaniensis</i>	300 mm			x	x		
<i>S. sp. (of Roeleveld)</i>	150 mm			x	x		
<i>Eucleoteuthis luminosa</i>	180 mm			x		x	
<i>Hyaloteuthis pelagica</i>	50 mm			x	x		
<i>Ornithoteuthis volatilis</i>	270 mm		x	x	x	x	

larvae, the warm surface currents of the EAC system appear to have a significant influence on the nearshore distribution of adults of some species in eastern Australian waters. In addition, on the upper continental slope and in deeper water between 28°S and 34°S, poorly defined northward flowing counter currents have been reported at depths of between 200 m and 800 m (Hamon, 1979; Boland, 1979). Such deep counter currents could explain the observed northward extension of the range of *Todarodes filippovae* in slope waters off the New South Wales coast relative to its northern boundary in the central Tasman Sea (~32°S compared to ~38°S).

In the central Tasman Sea and off southern New Zealand, the Tasman Front and Subtropical Convergence appear to represent the major oceanographic factors influencing species distributions. To the north of the Tasman Front, the dominant large ommastrephid is *Sthenoteuthis oualaniensis*, whereas to the south, *Ommastrephes bartramii* dominates. The abundance of this latter species decreases in the northern Subtropical Convergence Zone where *Todarodes filippovae* dominated summer jig and surface driftnet catches.

The fourteen species reported from the Coral and Tasman seas can be divided into four groups on the basis of their adult distribution patterns (Table 1).

Two species, *Nototodarus gouldi* and *Todarodes pacificus pusillus*, occur predominantly on the continental shelf as adults. In southern Australian waters, *N. gouldi* is most abundant in depths of 40 m to 90 m, where surface temperatures range from 15° C to 19° C (Winstanley et al., 1983), and *T. p. pusillus* is most abundant in northern waters with preliminary indications of higher abundance at the shelf edge at depths of ~200 m. Both have been taken off the east coast at ~27°S but in different depth strata (*N. gouldi* in deeper water). From their occurrence in demersal trawl catches, both appear to be associated with the

bottom during the day, with *N. gouldi* migrating into the water column at night where it is taken on jigs.

Adults of *Ornithoteuthis volatilis*, *Todaropsis eblanae*, and *Nototodarus hawaiiensis* have been trawled primarily in continental slope waters. The distributions of the latter two species off the eastern Australian coast overlap significantly, with both taxa more abundant in northern waters (north of 25°S), where bottom depths range from 200 m to 500 m. These species have been caught together with *T. p. pusillus* in depths of 200 m to 250 m off the Great Barrier Reef. *Nototodarus hawaiiensis* appears to be both more widespread and more abundant than *T. eblanae* in northern Australian waters (Dunning, 1988c). *Nototodarus hawaiiensis* has not been caught south of the point where the EAC turns eastward from the slope (31°S–32°S), whereas *T. eblanae* has been caught on several occasions in this region as far south as 37°S, where the continental slope is narrower and the bottom is hard. In the north, the broad continental slope bottom is composed mainly of sandy muds (Maxwell, 1968).

In contrast, adults of *O. volatilis* were regularly caught in midwater trawls off the central New South Wales coast where bottom depths were in excess of 1000 m, indicating a more pelagic life style and possibly higher abundance in deeper slope waters. This species was not trawled off the north Queensland coast during surveys in 1985/1986, although it was taken in small numbers together with *N. hawaiiensis* in demersal trawls at depths greater than 450 m off the northwest Australian coast (Dunning, 1988c).

Both large-maturing *Todarodes* species, *T. filippovae* and *T. angolensis*, occur in slope and oceanic waters. The capture of juvenile and adult *T. filippovae* in demersal and pelagic trawls, on jigs, and in surface driftnets suggests that they occur throughout the water column both day and night. In the central

Tasman Sea, the relative abundance of *T. filippovae* increased to a maximum at the southern boundary of the sampling area, on the southern boundary of the Subtropical Convergence Zone (42°S–44°S, sea surface temperatures < 14° C).

Specimens of *T. angolensis* have been reported from jig catches from the southwest Tasman Sea only (south of 45°S), whereas larger trawled specimens were caught in continental slope waters to the south of New Zealand and off southern Tasmania.

The apparent distribution of *T. filippovae* to the north of *T. angolensis* in the Tasman Sea provides an interesting contrast to Roeleveld's (1989) results, which were based on a trawl survey off South Africa. She concluded that the distribution of *T. filippovae* was centered to the south of *T. angolensis* in the South Atlantic, with specimens of *T. filippovae* trawled in depths of 692 m to 990 m where water temperatures were less than 3.8° C, compared to *T. angolensis* trawled in depths of 247 m to 710 m and temperatures of 5.1° C to 8.2° C. Adults of *T. filippovae* have been reported in abundance in the Tasman Sea in subantarctic waters from the surface to 1200 m, but in the southwest Pacific *T. angolensis* has rarely been reported.

Adults of the larger ommastrephids, *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis*, and of the smaller species, *Eucleoteuthis luminosa*, *S. sp.* and *Hyaloteuthis pelagica*, occur predominantly in oceanic waters. Specimens caught in continental slope waters are generally either juveniles or reproductively mature individuals.

In the southern Coral and central Tasman seas, the distributions of the subtropical *O. bartramii* and the tropical *S. oualaniensis* appear to be separated by the Tasman Front at about 30°S to 32°S and show little overlap. Off the New South Wales coast, the influence of the EAC system promotes the southerly extension of the distribution of *S. oualaniensis* as far as 38°S, and extensive overlap with the distribution of both *O.*

*bartramii* and, to a lesser extent, the more demersal *T. filippovae*, occurs. The distribution of *S. oualaniensis* in the southwest Indian Ocean is similarly affected by the analogous Agulhas Current (Filippova, 1971).

The poor representation of *E. luminosa* and *H. pelagica* in collections from the region provides little clarification of their distributions. The former species appears to occur with *O. bartramii*, at least in the northern Tasman Sea close to the eastern Australian coast, with the majority of specimens of *E. luminosa* taken in subtropical waters. The only adult *H. pelagica* examined was caught in tropical waters of Coral Sea origin in the EAC.

### Zoogeographic Zones and Ommastrephid Squids

Previous studies of the zoogeography of Australasian marine organisms have typically considered coastal fauna, such as demersal fishes (Whitley, 1932) and intertidal invertebrates (Bennett and Pope, 1953; Knox, 1963). The few oceanic groups studied on a regional basis have included largely holoplanktonic species (e.g., pteropods and heteropods; see Newman, 1990). The paucity of our knowledge of the distributions of pelagic biota, especially nektonic forms, in the southwest Pacific relative to that for both the North Pacific and Atlantic oceans has been recognized by recent zoogeographers (e.g., Knox, 1970; Backus, 1986).

In the nearshore, littoral zone, local climatic conditions have a more significant and rapid impact than in offshore, oceanic waters. This is reflected in sometimes sharp boundaries to species distributions and in the larger number of recognizable zoogeographic "provinces" for various littoral species groups in the region (summarized in Briggs, 1974). In oceanic waters, water mass boundaries are poorly defined and pelagic

TABLE 2.—Zoogeographic zones and provinces described by various authors for the Tasman and Coral seas region (after Nesis, 1979b). (SST = summer surface temperature.)

Zones		Provinces	
Nesis (1979b)	Knox (1970)	Knox (1963)	Briggs (1974)
Equatorial (10°S–20°S)	Tropical (SST 20°–28° C)	Great Barrier Reef Solanderian Philippian Norfolkian Flindersian Peronian Aupourian Maugean Cookian Forsterian	Indo-Polynesian   Lord Howe/Norfolk  Southeast Australian Auckland Tasmanian Cookian
South Subtropical (20°S–40°S)	Subtropical (SST 15°–20° C)		
Mixed (peripheral; 40°S–45°S)			
Notalian (S of 45°S)	Subantarctic (SST 5.5°–14.5° C)	Antipodean Kerguelenian	Antipodean Macquarie

organisms are rarely restricted to or characteristic of a single water mass (Backus, 1986). This fact is even more relevant to a consideration of a highly mobile, pelagic group, such as the ommastrephid squids.

I consider the observed distributions of the ommastrephids in the Coral and Tasman seas to be best described by a division of the water masses of the region into the three zoogeographic zones defined by Knox (1970) (Table 2): (1) a tropical zone with surface waters of 20° C to 28° C in summer and bounded to the south by the Tasman Front; (2) a subtropical zone with summer surface waters of 15° C to 20° C bounded to the south

by the subtropical convergence; and (3) a subantarctic zone with summer surface waters of less than 15° C. A further antarctic zone may occur in the adjacent Southern Ocean to the south of the Subantarctic Front, where summer surface waters are less than 3.5° C, but this requires further investigation.

The boundaries of these regions are somewhat at variance with the zones defined by Nesis (1979b) (Table 2), but it is considered that this reflects recent advances in our understanding of both the oceanography of the region and ommastrephid distributions. This simple scheme takes into account the far from perfect data set on which it is based.

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# The Octopod Working Group Proceedings: An Introduction

*Ronald B. Toll*

The octopod working group was originally organized and convened by Dr. Gilbert L. Voss. Gil had devoted considerable time and study during his long and illustrious career to systematics investigations of the Octopoda, beginning his work with the shallow water forms. His instructions to the working group were simple and direct: examine as many of the extant types as could be assembled for the workshop, rely heavily on the use of the original descriptions, rediagnose taxa as necessary and, one-by-one, attempt to establish the systematic standing of each member taxon. The working group focused its attention on the Octopodinae, defined traditionally, and for our purposes, as the shallow water (to about 200 m), benthic octopods with two rows of suckers and an ink sac.

Gil knew that the job placed before the working group was an enormous one. He knew, too, that it would be impossible to establish the systematic status of the several hundred nominal species of Octopodinae within the constraints of time and availability of type material and literature. The goal he placed before us was to move ahead and make as much progress as possible. Never before had so many type specimens of octopodines been assembled in one place at one time, and never before had so many octopod workers congregated to work as a group. The energy and pace of the working group was inspiring, if not frenetic, and I shall always remember with great fondness the long days we spent working around a single, large, laboratory table, huddled together and sharing the expertise that collectively we brought to the task at hand.

Regrettably, Gil died in the year following the workshop, never having had the opportunity to see the immensely valuable product of the workshop that he organized and oversaw: the series of papers that follow and comprise the octopod section of this publication. There is no doubt that this product, his final contribution, as organizer, mentor, and colleague, to the study of the octopods, will serve from this

point on as a primer for all future workers who choose to tackle the particularly vexing problems associated with the systematic study of this group.

It would have pleased Gil to know that the future of octopod research is bright, much more so than just a few years ago. At the time of the workshop there was great concern among all of the participants that the number of octopod workers was dwindling and general interest in octopods was, in comparison to other times in the past, low. Now, the number of persons working on problems of systematics and natural history of the octopods is on the rise, and interest in these fascinating creatures also is increasing from many viewpoints: ecology, evolution, fisheries, and biomedical research. Also, the period of time since the workshop has seen a small torrent of papers dedicated to octopus research. Perhaps we should not be surprised that some of them suggest that at least a portion of our widely held beliefs may not be correct, namely, the separation of the family Octopodidae into the three subfamilies Octopodinae, Bathypolypodinae, and Eledoninae. Indeed, one goal of the proceedings of the octopod section of the workshop was to make it easier for investigators to describe new taxa by making basic knowledge of the systematics of many of the nominal species available for comparison. The recent surge in the discovery of new taxa is, in part, a result of the prepublication dissemination of the results contained herein.

The octopod section comprises six papers, five of which are geographic treatments of the octopodines from major regions of the world: western Atlantic, eastern Atlantic/Mediterranean Sea, Indian Ocean/Red Sea, Australia, and western Pacific. Regrettably, coverage of the octopods from the eastern Pacific and New Zealand is not included herein. In all, about 200 nominal species-level taxa are treated. The final paper is a treatment of the zoogeography of the Octopodinae. The papers conform generally to a common format; however, there are some differences among them, based on the level of our knowledge of a particular region, and to some degree on the philosophy of the individual worker. Furthermore, generic affiliations are not uniformly applied among the papers. This is

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due in part to ongoing generic revisions being conducted by several workers. Finally, several recent papers on octopod systematics, which include the description of several new taxa, are not included among the contributions because they were received late in the review and editorial process. Nonetheless, the papers that follow represent the most comprehensive single treatment of octopodine systematics since Robson's treatise (1929, 1932). It is proposed that these papers serve as

working hypotheses in the continued systematic study of the group. There is little doubt that over time some determinations found therein will need to be revised in light of new information and additional material for examination. This is intended.

It was my pleasure to be included as a member of this workshop and my honor to serve as group leader following Gil's death. His influence over this body of work is pervasive.

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# The Systematics and Nomenclatural Status of the Octopodinae Described from the Western Atlantic Ocean

Gilbert L. Voss\*  
and Ronald B. Toll

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## ABSTRACT

Thirty-three species and subspecies of octopodines described originally from the western Atlantic Ocean, defined herein as the Atlantic Ocean from the Labrador Sea to Cape Horn and including the oceanic islands of the South Atlantic, are reviewed systematically and nomenclaturally. Fifteen species-level taxa are considered herein as valid and are retained (*Octopus briareus* Robson, 1929; *O. burryi* Voss, 1950; *O. carolinensis* Verrill, 1884; *O. filiosus* Howell, 1868; *O. joubini* Robson, 1929; *O. lobensis* Castellanos and Menni, 1969; *O. maya* Voss and Solís Ramirez, 1966; *O. mercatoris* Adam, 1937; *O. occidentalis* Steenstrup in Hoyle, 1886; *Euaxoctopus pillsburyae* Voss, 1975; *O. sanctaehelenae* Robson, 1929; *Pteroctopus schmidtii* (Joubin, 1933); *O. tehuelchus* Orbigny, 1835; *O. verrucosus* Hoyle, 1885; *O. zonatus* Voss, 1968); however, of these, six species (*O. lobensis*, *O. mercatoris*, *O. occidentalis*, *O. sanctaehelenae*, *O. tehuelchus*, *O. verrucosus*) remain problematical and in need of additional study in order to stabilize their systematic status. *Pteroctopus schmidtii* is provisionally retained as distinct; however, it is possible that it will be shown to be a growth stage of another described taxon (Toll, unpublished data). Eight taxa are junior synonyms: *Octopus bakerii* Orbigny, 1826 (= *O. americanus* Baker in Denys de Montfort, 1802 (nomen dubium)); *Callistoctopus bermudensis* (Hoyle, 1885) (= *C. macropus* (Risso, 1826)); *Enteroctopus brucei* (Hoyle, 1912) (= *E. megalocyathus* Couthouy in Gould, 1852); *C. chromatus* (Heilprin, 1888) (= *C. macropus* (Risso, 1826)); *Macrotritopus equivocus* (Robson, 1929) (= *M. defilippi* (Verany, 1851)); *M. gracilis* (Verrill, 1884) (= *M. defilippi* (Verany, 1851)); *O. hummelincki* Adam, 1936 (= *O. filiosus* Howell, 1868); *Macrotritopus scorpio* (Berry, 1920) (= *M. defilippi* (Verany, 1851)). Seven other taxa are nomina dubia: *Octopus americanus* Baker in Denys de Montfort, 1802; *O. eudora* Gray, 1849; *O. furvus* Gould, 1852; *O.*

*geryonea* Gray, 1849; *O. saphenia* Gray, 1849; *O. verrilli verrilli* Hoyle, 1886; *O. verrilli palliata* Robson, 1929. Two are nomina nuda (*O. vulgaris americanus* Orbigny, 1842; *O. vulgaris antillarum* Robson in Pickford, 1946); one is preoccupied (*O. pictus* Verrill, 1883).

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## Introduction

In comparison to octopodines of other geographic regions of the world, the octopodines of the western Atlantic Ocean, defined herein as the Atlantic Ocean from the Labrador Sea to Cape Horn and including the oceanic islands of the South Atlantic, are well known in terms of systematics and natural history. A total of 33 species and subspecies of octopodines have been described from this region, beginning, appropriately enough, with the description of *Octopus americanus* Baker in Denys de Montfort, 1802 (Table 1). In addition, seven species of octopods, originally described as octopodines, are now attributed to the subfamily Bathypolypodinae (Table 2) and are not considered herein.

The study of the Atlantic, American octopodines has a rich history. Important primary and revisionary contributions were

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\*The preliminary literature survey and examination of some type material during the Cephalopod International Advisory Council 1988 Workshop, "The Systematics and Biogeography of Cephalopods," were performed by the late Gilbert L. Voss. Beginning in the late 1940s, Gil Voss almost single-handedly reviewed and revised the octopodine fauna from the western North and Tropical Atlantic Ocean including the description of several new taxa and first accounts of others previously unknown from that region. Just prior to his untimely death in January 1989, Gil had begun to prepare some of the species accounts for this contribution. Completion of the systematic and nomenclatural evaluation of species treated herein was undertaken by the junior author. The present contribution reflects the combined systematic opinions of both authors, who, fortunately, had discussed many of the prevailing systematic problems and had arrived collectively at many of the decisions advanced herein.

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TABLE 1.—Systematic listing and current status of the nominal species of octopodines described from the Western Atlantic Ocean. Nominal taxa are listed in alphabetical order by specific epithet.

Nominal taxon	Current disposition
<i>Octopus americanus</i> Baker in Denys de Montfort, 1802	nomen dubium
<i>Octopus bakerii</i> Orbigny, 1826	= <i>Octopus americanus</i> Baker in Denys de Montfort, 1802 (nomen dubium)
<i>Callistoctopus bermudensis</i> (Hoyle, 1885)	= <i>Callistoctopus macropus</i> (Risso, 1826)
<i>Octopus briareus</i> Robson, 1929	valid
<i>Enteroctopus brucei</i> (Hoyle, 1912)	= <i>Enteroctopus megalocyathus</i> Couthouy in Gould, 1852
<i>Octopus burryi</i> Voss, 1950	valid
<i>Octopus carolinensis</i> Verrill, 1884	valid
<i>Callistoctopus chromatus</i> (Heilprin, 1888)	= <i>Callistoctopus macropus</i> (Risso, 1826)
<i>Macrotritopus equivocus</i> (Robson, 1929)	? = <i>Macrotritopus defilippi</i> (Verany, 1851)
<i>Octopus eudora</i> Gray, 1849	nomen dubium
<i>Octopus filusus</i> Howell, 1868	valid senior synonym (= <i>O. hummelincki</i> , Adam, 1936)
<i>Octopus furvus</i> Gould, 1852	nomen dubium
<i>Octopus geryonea</i> Gray, 1849	nomen dubium
<i>Macrotritopus gracilis</i> (Verrill, 1884)	? = <i>Macrotritopus defilippi</i> (Verany, 1851)
<i>Octopus hummelincki</i> Adam, 1936	= <i>Octopus filusus</i> Howell, 1868
<i>Octopus joubini</i> Robson, 1929	valid
<i>Octopus lobensis</i> Castellanos and Menni, 1969	valid (but possibly = <i>Octopus tehuelchus</i> Orbigny, 1835)
<i>Octopus maya</i> Voss and Solis Ramirez, 1966	valid
<i>Octopus mercatoris</i> Adam, 1937	undetermined (possibly = <i>Octopus joubini</i> Robson, 1929)
<i>Octopus occidentalis</i> Steenstrup in Hoyle, 1886	valid
<i>Octopus pictus</i> Verrill, 1883	preoccupied (replacement name = <i>Octopus verrilli verrilli</i> Hoyle, 1886, considered herein to be a nomen dubium)
<i>Euaxoctopus pillsburyae</i> Voss, 1975	valid
<i>Octopus rugosus sanctaehelenae</i> Robson, 1929	valid (elevated to <i>O. sanctaehelenae</i> )
<i>Octopus saphenia</i> Gray, 1849	nomen dubium
<i>Pteroctopus schmidtii</i> (Joubin, 1933)	valid (provisional)
<i>Macrotritopus scorpio</i> (Berry, 1920)	? = <i>Macrotritopus defilippi</i> (Verany, 1851)
<i>Octopus tehuelchus</i> Orbigny, 1835	valid (in need of redescription)
<i>Octopus verrilli verrilli</i> Hoyle, 1886	nomen dubium
<i>Octopus verrilli palliata</i> Robson, 1929	nomen dubium
<i>Octopus verrucosus</i> Hoyle, 1885	valid
<i>Octopus vulgaris americanus</i> Orbigny, 1842	nomen nudum
<i>Octopus vulgaris antillarum</i> Robson in Pickford, 1946	nomen nudum
<i>Octopus zonatus</i> Voss, 1968	valid

authored by several of the most prominent cephalopod workers based on material collected by some of the most celebrated exploratory expeditions and explorer/scientists of the 19th and 20th centuries. Exemplary of the contributions of the last century are the works of the following scientists: Alcide d'Orbigny (1826, 1835 (in 1835–1847), 1840 (in Férussac and Orbigny, 1834–1848), 1845 (in 1845–1847)), based on collections housed in the Muséum National d'Histoire Naturelle, Paris, and obtained in part by several notable French voyages including those of the *Astrolabe*, *Bonite*, and *Coquille* as well as Orbigny's own eight-year-long voyage to South America; Augustus Gould (1852), based on specimens collected by the United States Exploring Expedition under the direction of Charles Wilkes; William E. Hoyle (1885a, 1885b, 1886), based on collections obtained by HMS *Challenger* under the direction of C. Wyville Thomson; and Addison E. Verrill (1883, 1884), with accounts of specimens collected by the United States Coast and Geodetic Survey steamer *Blake* and

the United States Fish Commission steamer *Albatross*, both under the direction of Alexander Agassiz.

Guy Robson's (1929a) monumental monograph was the first of a long series of modern descriptive and revisionary accounts of the western Atlantic Ocean Octopodinae. These contributions, which include those of Joubin (1933), William Adam (1936, 1937a, 1937b), Grace Pickford (1945, 1946, 1950a, 1950b, 1955), Gilbert Voss (1949, 1950, 1951, 1953, 1956, 1958 (with C. Phillips), 1962, 1964, 1966 (with M. Solis Ramirez), 1968, 1975), and Zulma Castellanos (1967, 1969a, 1969b (the latter two with R. Menni), 1970), define collectively much of the current knowledge of the systematics of the western Atlantic Ocean octopodines and serve as the platform upon which nearly all subsequent work in the field, including the current contribution, is predicated. Despite these combined efforts, complex systematic problems remain, especially with regard to several taxa from the western South Atlantic Ocean, particularly Argentina, and oceanic islands.

TABLE 2.—Western Atlantic Ocean octopod taxa originally described in the subfamily Octopodinae but now attributed to genera in the subfamily Bathypolypodinae.

Nominal taxon	Current disposition	Reference
<i>Enteroctopus eureka</i> Robson, 1929	<i>Benthoctopus eureka</i> (Robson, 1929)	Robson (1930, 1932)
<i>Octopus arcticus</i> Prosch, 1849	<i>Bathypolypus arcticus</i> (Prosch, 1849)	Robson (1932)
<i>Octopus bairdii</i> Verrill, 1873	= <i>Bathypolypus arcticus</i> (Prosch, 1849)	Robson (1932), Kumph (1958)
<i>Octopus januarii</i> Hoyle, 1885	<i>Benthoctopus januarii</i> (Hoyle, 1885)	Toll (1981)
<i>Octopus lenus</i> Verrill, 1880	= <i>Bathypolypus arcticus</i> (Prosch, 1849)	Kumph (1958)
<i>Octopus obesus</i> Verrill, 1880	= <i>Bathypolypus arcticus</i> (Prosch, 1849)	Kumph (1958)
<i>Octopus piscatorum</i> Verrill, 1879	<i>Benthoctopus piscatorum</i> (Verrill, 1879)	Robson (1932)

Systematic treatments of taxa known to occur in the western Atlantic Ocean, but originally described from other regions, can be found elsewhere in this volume (see Mangold, 1998).

ABBREVIATIONS AND DEFINITIONS.—Measurements, indices, and formulas are as defined in Roper and Voss (1983), Toll (1988), and Robson (1929a) with the following exceptions: the term fellow-arm index (FAI) is used in place of opposite-arm index (OAI), but it is defined in the same way; calamus-length index is abbreviated CLI; arm-length index (ALI) is defined as the length of the longest arm as a percentage of the total length (not mantle length as stated by Roper and Voss (1983)). Other abbreviations used in the species accounts are as follows:

ASC	arm-sucker count
AWI	arm-width index
HALI	hectocotylized-arm length index
HASC	hectocotylized-arm sucker count
HWI	head-width index
LLI	ligula-length index
ML	dorsal-mantle length
MWI	mantle-width index
PLI	penis-length index
SIe	enlarged-sucker index
SIn	normal-sucker index
SpLI	spermatophore-length index
SpRI	sperm-reservoir index
TL	total length
WDI	web-depth index

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions are used in the text:

ANSP	Academy of Natural Sciences of Philadelphia
BMNH	The Natural History Museum, London (formerly British Museum (Natural History))
ISBN	Institute Royal des Sciences Naturelles de Belgique
MNHN	Muséum National d'Histoire Naturelle de Paris
MPA	Museo de la Plata, Argentina
NMNH	National Museum of Natural History, Smithsonian Institution
PMY	Peabody Museum, Yale University
RSM	Royal Scottish Museum
UMML	Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami
USNM	collections of the former United States National Museum, now in the NMNH
ZMA	Zoologisch Museum, Amsterdam
ZMK	Zoologisk Museum, Copenhagen

Taxa are arranged alphabetically with regard to the specific epithet. The generic scheme used herein follows that of Toll (1992, MS).

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### Species Accounts

#### *Octopus americanus* Baker in Denys de Montfort, 1802

DIAGNOSIS.—Animals small. Mantle stocky, slightly broader than head. Arms subequal in length. Skin finely papillose.

ORIGINAL DESCRIPTION.—Baker in Denys de Montfort, 1802:38 (but see "Discussion").

TYPE LOCALITY.—Presumed to be the West Indies (fide Haviland pers. comm. to Baker in Baker, 1759:785).

TYPE.—*Holotype*: Not designated (see "Discussion").

DISCUSSION.—The diagnosis is based on the account of Baker (1759). Despite the length of the description, few characters are mentioned that permit recognition of this taxon. Furthermore, the account is based on a single specimen (holotype?) initially provided to Baker for his examination as

well as on additional unspecified material from the collections of BMNH used for comparison. There is no assurance that these specimens (informally constituting a type series?) are conspecific.

In a chronological sense, it is appropriate that the list of nominal octopodine taxa from the Atlantic coast of the Americas begins with *Octopus americanus*. The nomenclatural history of this taxon, discussed previously by Orbigny (1840, in Férussac and Orbigny, 1834–1848), Robson (1929a), and Pickford (1945), is long and complex. The following discussion is based on those accounts and on our examination of most of the pertinent literature involved and cited below. Seba (1758) figured several specimens referred to as “Polype d’Amerique, marin”; however, Pickford (1945:727) noted that “there is no indication, other than the name itself, that any of the several specimens figured actually came from America.” Baker (1759) described superficially and figured multiple views of a distorted, long-preserved octopus alleged to have been collected in the West Indies to which he referred simply as the “Sea Polypus” and, elsewhere in the same account, as “of that species called Bolytaena.” One figure (pl. 29: fig. 3) shows a sacular structure, interpreted by Baker (1759:783) as a seasonal reproductive organ (“milt bag”), extending out of the mantle aperture. The herniated position of this structure, possibly the digestive diverticulum or ink sac, is anomalous, probably induced by the trauma associated with collection and/or preservation. Confusion exists regarding the exact year of publication of Baker’s account. Robson (1929a) gave it as 1758 whereas Pickford (1945) gave 1759. Based on internal evidence, the correct date appears to be 1759.

Denys de Montfort’s (1802) account of “le Poulpe Americain” was based on the accounts of both Seba (1758) and Baker (1759) and includes figures redrawn from each: Seba’s figure 2 as Denys de Montfort’s (1802) pl. 31: fig. 2, labelled “Poulpe Ameriquain de Seba”; Baker’s pl. 39: figs. 3, M, and pl. 29: fig. 2 as Denys de Montfort’s (1802) pl. 30 and pl. 31: fig. 1, respectively, both labelled as “Poulpe Ameriquain de Backer” (incorrect original spelling of Baker, see International Commission on Zoological Nomenclature (ICZN), 1985, Art. 32c,d). Denys de Montfort’s (1802) account has become accepted widely as the first available use of a name with reference to this taxon (e.g., see Blainville, 1826).

Orbigny (1826) erected *Octopus bakerii* (incorrect original spelling of Baker), also based on Baker’s account (see that taxon below) and listed “le Poulpe Americain” of Denys de Montfort (1802) in synonymy. Later, Orbigny (1840, in Férussac and Orbigny, 1834–1848) included “*Octopus Barkerii* Férussac, 1825” (incorrect original spelling of Baker), and *O. americanus* Barker (incorrect original spelling of Baker) in the synonymy of *O. rugosus* Bosc, 1792. Apparently, Orbigny sought to give authorship of the taxon to Férussac; however, Férussac is credited only with the introduction (“prologue”) of Orbigny’s 1826 “Tableau Methodique,” therefore Orbigny (1826) is the correct author of *O. bakerii*.

In view of the absence of a type specimen, inconclusive locality data, and defective original description, we regard *Octopus americanus* as a nomen dubium. If the western Atlantic Ocean “form” of *O. vulgaris* is later shown to be a distinct species, separable from *O. vulgaris* Cuvier, 1797, the name *O. americanus* is available pursuant to the selection of a neotype (see ICZN, 1985, Rec. 75E).

#### *Octopus bakerii* Orbigny, 1826

DIAGNOSIS.—See *Octopus americanus*, above.

ORIGINAL DESCRIPTION.—Orbigny, 1826:144 (as *Octopus bakerii*, incorrect original spelling of Baker).

TYPE LOCALITY.—Presumed to be the West Indies (fide Haviland pers. comm. to Baker in Baker, 1759:785) (see *Octopus americanus*, above).

TYPE.—*Holotype*: Not designated (see “Discussion”).

DISCUSSION.—This taxon was erected solely on the description of the “Sea Polypus” by Baker (1759). As such, *Octopus bakerii* is a junior synonym of *O. americanus* Baker in Denys de Montfort, 1802, itself considered herein to be a nomen dubium (see “Discussion” under that taxon, above).

#### *Callistoctopus bermudensis* (Hoyle, 1885)

DIAGNOSIS.—Mantle ovoid, mantle aperture moderate; head narrower than mantle; eyes small, not prominent. Funnel long. Arms long (ALI 86), distinctly unequal in length, arm order I > II > III > IV. Web shallow. Single supraocular papilla. Color yellow ochre with pale sienna patch on “back,” another on head.

ORIGINAL DESCRIPTION.—Hoyle, 1885a:228, as *Octopus bermudensis*.

TYPE LOCALITY.—Western North Atlantic Ocean, Bermuda.

TYPE.—*Holotype*: BMNH 1889.4.24.38, female, 10 mm ML (erroneously reported as 58 mm in Robson, 1929a; this value is the TL).

DISCUSSION.—The minimal diagnosis is excerpted from the account by Hoyle (1886). Heilprin (1888) considered the possibility that *Callistoctopus bermudensis* was the young of his *C. chromatus*. Robson (1929a) noted that Heilprin’s (1888) assertion could be correct and indicated that if those two taxa were synonymous, his own assertion that *C. chromatus* was allied to or conspecific with *C. macropus* (Risso, 1826) was unwarranted due to the subequal arm lengths in young examples of *C. macropus*. As noted by Pickford (1945), this statement appears to contradict Robson’s (1929a) own understanding of the dissimilar arm lengths in the so-called “alderii” stage of *C. macropus*. Pickford (1945) placed Hoyle’s *Octopus bermudensis* (with Heilprin’s *C. chromatus*) into the synonymy of *C. macropus*. Voss and Phillips (1958) confirmed the occurrence of *C. macropus* from the western Atlantic Ocean, thereby supporting Pickford’s (1945) conclusions. If the western Atlantic “form” of *C. macropus* is a distinct species, *C.*

*bermudensis* would have priority (for an account of *C. macropus*, see Mangold, 1998). Toll (MS) will place *O. macropus* and *O. bermudensis* into *Callistoctopus*.

### *Octopus briareus* Robson, 1929

DIAGNOSIS.—Animals medium-sized to large, to 120 mm ML, wt to 1000 g. Mantle round, widest near middle (MWI 62–92) with slight constriction in neck area; head moderate to wide (HWI 62–83); eyes prominent. Funnel organ W-shaped, with inner and outer limbs subequal in length. Arms long (ALI 80–95), arms II and III larger, thicker, somewhat swollen in midregion (AWI 21–37), arm order II = III > IV > I. Suckers large (SIn 13–22), larger on arms II and III; especially enlarged suckers absent in males and females. Right arm III of males hectocotylized; ligula small but well developed (LLI 3–4), broad, rounded distally, with lateral fringing membranes and with central ridge and about 12–16 transverse laminae; calamus moderate in size (CLI 28–32). Web shallow to moderate in depth (WDI 12–20), web formula A = B = C = D > E. Ink sac present; gill lamellae 6–8. Mature eggs large, capsule 10–14 mm long × 4–5 mm wide, stalk 5–10 mm long, egg masses with 200–500 (rarely to 1000) eggs arranged in clusters of 7–34 (mean = 25). Hatchlings benthonic, mean ML 5.5 mm. Penis small (PLI 31–34), with well-developed diverticulum; entire penial apparatus boomerang-shaped. Spermatophores long (SpLI 126). Radula with A<sub>3</sub> seriation of the rachidian. Color in life iridescent blue-green with chromatophores retracted, frontal white spots absent.

ORIGINAL DESCRIPTION.—Robson, 1929b:612, fig. 1.

TYPE LOCALITY.—Western tropical Atlantic Ocean, Netherlands West Indies, off Curaçao.

TYPES.—*Syntypes*: ZMA, 1 male, 40 mm ML; BMNH 1946.10.8.3, 1 male, 31 mm ML.

DISTRIBUTION.—United States, South Florida, southeastern Gulf of Mexico; Bahamas; Caribbean Sea to northern South America (to ~40°W); in association with coral reefs.

DISCUSSION.—The diagnosis is based on the accounts of Robson (1929b), Adam (1937a), Pickford (1945), and Hanlon (1983). This is a common and well-known species typically found associated with coral reefs. No geographic variation has been discerned. Juveniles and mature specimens are easily recognized by the swollen arms II and III. The eggs are large. In males, the size and structure of the ligula are distinctive. In addition to morphological treatments by Robson (1929b), Pickford (1945), and Adam (1937a), considerable laboratory and field studies have been performed with live specimens, and, as a result, the biology of this species is well known (see Messenger, 1963; Boletzky, 1969, 1973; Borer, 1971; Wolterding, 1971; Opresko, 1974; Hanlon, 1983, 1988; Aronson, 1989; Hanlon and Wolterding, 1989). Humann (1991) included excellent color photographs of adult and juvenile animals taken in the wild.

One male syntype of *Octopus briareus* displays two

anomalies described by Robson (1929b, 1929c (as *O. rugosus*): bilateral hectocotylization and the presence of a supernumerary diverticulum of the penis. The cause or causes of these conditions are unknown.

### *Enteroctopus brucei* (Hoyle, 1912)

DIAGNOSIS.—Animals medium-sized to large (75 ML mm). Mantle ovoid (MWI 80); head slightly narrower than mantle (HWI 67); eyes moderate in size. Funnel short and broad. Arms moderate in length (ALI 76), arm formula I > II = III > IV; males with especially enlarged suckers present on all arm pairs (Sle 20) from 7th–9th pair of suckers. Right arm III of males hectocotylized, shorter than fellow (FAI 77); ligula moderate in length (LLI 8.5), narrow, with deep central groove ornamented with double longitudinal row of small papillae along bottom; groove bordered laterally by thick inrolled cheeks. Radula with tall rachidian of B<sub>3</sub> seriation. Color dull purplish dorsally, pinkish ventrally.

ORIGINAL DESCRIPTION.—Hoyle, 1912:276, figs. 1–3, as *Polypus brucei*.

TYPE LOCALITY.—Western South Atlantic Ocean, Tierra del Fuego, Burdwood Bank, 54°25'S, 57°32'W.

TYPE.—*Holotype*: RSM 1921.143.557, male, Hoyle no. 924 (fide Heppell and Smith, 1983).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. The type was not examined by us. Hoyle (1912) noted that *Enteroctopus brucei* was similar to the sympatric *E. megalocyathus* Couthouy in Gould, 1852, but differed from that taxon in the degree of constriction between the head and brachial crown, presence of a mantle fold, and presence of enlarged suckers on all arm pairs. Robson (1929a) examined the type of *E. brucei* as part of his redescription of *E. megalocyathus* based on new material (three males, one female) from near the type locality. Robson (1929a) noted that the type of *E. brucei* differed from *E. megalocyathus* in body width and radula morphology. Intraspecific radular variation is well documented among octopodids (Robson, 1929a; Adam, 1933, 1941; Pickford, 1945; Arocha, 1989; Toll, unpublished data). Robson (1929a) observed that his specimens of *E. megalocyathus* exhibited enlarged suckers on all arm pairs, thereby potentially removing one of the differences between the two taxa noted by Hoyle (1912). Despite noting that *megalocyathus* “is by no means homogeneous” and that the series of specimens available to him displayed a “marked dimorphism (not sexual) in respect of the head- and body width,” Robson (1929a:178) stated “I have not the least doubt that [*E. brucei*] is identical with *megalocyathus*” and placed *E. brucei* into synonymy.

Ré (1980) redescribed *Enteroctopus megalocyathus* based on new material (seven males, six females) from Golfo Nuevo and Golfo San Jose, Chubut Province, Argentina. Ré discussed Robson's (1929a) account of *E. brucei*, noted that the radula of

the type of *E. brucei*, as figured, was similar to those that she had examined, and suggested that the lack of homogeneity found by Robson could have been due to the inclusion of nonconspecific examples. Ré (1980) maintained the synonymy of *E. brucei* and *E. megalocyathus*.

It is regrettable that the type of *Enteroctopus brucei* has not been examined by recent workers, thereby leaving its status unresolved. Nonetheless, we are of the opinion that *E. brucei* is referable to *E. megalocyathus* and retain it in synonymy.

### *Octopus burryi* Voss, 1950

DIAGNOSIS.—Animals small to medium-sized (to 65 mm ML). Mantle saccular, rounded posteriorly, little wider than long (MWI 51–88); neck slightly constricted; head width moderate (HWI 42–68); eyes small. Funnel organ W-shaped. Arms short to moderate (ALI 53–76), tapering to slender tips, arm formula variable but usually IV > III > II > I. Suckers erect, sucker size sexually dimorphic with males having larger suckers than females (SIn 8–20); especially enlarged suckers absent in males and females. Right arm III of males hectocotylized, shorter than fellow (FAI 72–99); ligula small (LLI 4.1–5.5), triangular, pointed distally, shallowly excavated with about 15 transverse laminae; calamus distinct, moderate to large (CLI 25–45). Web moderate to deep (WDI 24–40), web formula variable, typically D > C > E > B > A or C > D > E = B > A. Gill lamellae 8–11. Mature eggs small, capsule 2.5 mm long; single brood with up to 35,000 eggs; spawn brooded in web of female. Hatchlings small, ~1.5 mm ML, planktonic; ~205 chromatophores covering mantle and head, 8–10 chromatophores in 2 rows along aboral surface of each arm, 2 pairs of chromatophores on funnel, dorsal surface of digestive gland with 13 large visceral chromatophores; arms with 4 uniseriably arranged suckers. Male with short penis (PLI 22–28) with small subspherical diverticulum. Spermatophores moderate in length (SpLI 60.5) with large, coiled sperm mass (SpRI 47). Radula with A<sub>2-3</sub> seriation of the rachidian. Dorsal surface of mantle, head, and arms densely covered with small, round papillae; ventral surface of mantle and oral surface of web and arms smooth; single cirrus over each eye. Color in life light green with white transverse mantle streak and patch and trellis arrangement on mantle; arms with longitudinal, dorsal, brown stripe. Color in preservation (ethanol) deep reddish brown on dorsum, light yellow ventrally on mantle, head, and oral surface of web and arms. Dark brown or black band on dorsal side of each arm and dark bar longitudinally across each eye.

ORIGINAL DESCRIPTION.—Voss, 1950:76, figs. 2, 3.

TYPE LOCALITY.—Western subtropical Atlantic Ocean, Gulf of Mexico, United States, Florida, Florida Keys, Southeast of Sombrero Light, 180 m.

TYPE.—*Holotype*: USNM 574598, female, 30 mm ML.

DISTRIBUTION.—United States, North Carolina; through

Caribbean Sea to northern Brazil; Cape Verde Islands; on sand and mud flats associated with reefs.

DISCUSSION.—The diagnosis is based on the accounts of Voss (1950, 1951, 1956), Pickford (1955), Palacio (1977), Forsythe and Hanlon (1985), and Hochberg et al. (1992). This common and well-known species is easily identified by its surface sculpture, general color, and dark stripe along each arm. In addition to the morphological accounts of *Octopus burryi* by Voss (1950, 1951, 1956), Pickford (1955, as *O. vincenti*), Adam (1960, 1961), Palacio (1977), and Voight (1991), field observations of color patterning are contained in the accounts of Hanlon and Hixon (1980) and Hanlon (1988). Forsythe and Hanlon (1985) report data on growth and development. Detailed descriptions of hatchlings and paralarvae are found in Hochberg et al. (1992). *Octopus vincenti* Pickford, 1955, from the Cape Verde Islands, is a synonym.

### *Octopus carolinensis* Verrill, 1884

DIAGNOSIS.—Animals small to medium-sized (to 46 mm ML). Mantle ovoid (MWI 75–85); head about as wide as mantle; eyes exceptionally large, laterally bulging, occupying entire lateral portions of head. Funnel size moderate, funnel organ W-shaped, with inner and outer limbs subequal in size. Arms short to moderate in length (ALI 65–71), arm order II > III > IV > I. Several especially enlarged, barrel-shaped suckers present on all arm pairs of males. Right arm III of males hectocotylized, shorter than fellow arm; ligula small, acutely pointed. Ink sac present. Mature ovarian eggs small, capsule ~3 mm long × 1 mm wide. Penis with bulbous diverticulum. Surface of mantle, head, and arms densely covered with numerous small papillae; supraocular and special, elongated mantle papillae absent. Color in preservation (ethanol) purplish brown to yellowish tan dorsally, lighter ventrally.

ORIGINAL DESCRIPTION.—Verrill, 1884:235.

TYPE LOCALITY.—Western North Atlantic Ocean, United States, North Carolina, off Cape Hatteras, 260 m.

TYPE.—*Holotype*: USNM 35673, female, 28 mm ML (mantle damaged, reported as 22 mm by Verrill, 1884), in ethanol, general condition fair to good.

DISTRIBUTION.—United States, Cape Hatteras, North Carolina, and south Florida; Caribbean Sea off Nicaragua and Leeward Islands, 183–260 m.

DISCUSSION.—The diagnosis is based on our examinations of the holotype and new material from the NMNH and UMML collections. Verrill's (1884) original description is in good agreement with the holotype except for the mantle length (the mantle is torn at the attachment to the head, and this damage no doubt accounts for the discrepancy). Robson (1929a) retained *Octopus carolinensis* as a distinct species. Pickford (1945) placed *O. carolinensis* in synonymy of *O. vulgaris* Cuvier, 1797, without having examined the holotype. Based on examinations of the holotype and new material from Florida



and the Caribbean Sea, one of us (RBT) has determined that *O. carolinensis* is a distinct taxon, separable from *O. vulgaris* based on a suite of characters including, but not limited to, eye size, dermal ornamentation, depth distribution, maximum size, and sucker morphology, and is currently redescribing this species.

#### *Callistoctopus chromatus* (Heilprin, 1888)

DIAGNOSIS.—Animals small to medium-sized (~240 mm TL). Mantle spherical, acuminate posteriorly. Arms long (ALI ~85), slender, arm formula I > II > III > IV. Mantle granulate, less so anteriorly along neck region. Color milky with ochre and brown splotches and speckles.

ORIGINAL DESCRIPTION.—Heilprin, 1888:324, pl. 16: fig. 1, as *Octopus chromatus*.

TYPE LOCALITY.—Western North Atlantic Ocean, Bermuda, Flatts Village, under stone on beach.

TYPE.—*Holotype*: ANSP A6443, in poor condition (fide Voss, 1962).

DISCUSSION.—The diagnosis is excerpted from the original description. Heilprin (1888) considered the possibility that *Octopus chromatus* was a larger growth stage of *O. bermudensis* Hoyle, 1885, but retained the species as distinct. Peile (1926) considered *O. chromatus* to be a synonym of *O. bermudensis*. Robson (1929a) suspected that *O. chromatus* was a form of *Callistoctopus macropus* (Risso, 1826) but retained it as distinct. Pickford (1945), in part based on calculations of eight indices of external morphological characters taken from Heilprin's (1888) original figure of *O. chromatus*, placed that taxon (along with Hoyle's *O. bermudensis*) into the synonymy of *O. macropus*. Voss (1962) rediscovered the type of *O. chromatus* at the ANSP and retained it as a synonym of *C. macropus* (for a complete account of *C. macropus*, see Mangold, 1998). If the western Atlantic Ocean "form" of *C. macropus* represents a distinct species, *C. bermudensis* (Hoyle, 1885) has priority, and *C. chromatus* is a junior synonym. Toll (MS) will place *O. macropus*, *O. bermudensis*, and *O. chromatus* into *Callistoctopus*.

#### *Macrotritopus equivocus* (Robson, 1929)

DIAGNOSIS.—*Paralarva*: Mantle narrow, elongate (MWI 64), rounded posteriorly; head moderately broad (HWI 59); eyes large, prominent. Arms moderate in length (ALI ~76), slender, arms III elongated. Suckers small. Web shallow. Color in preservation (alcohol) yellowish white with large purplish brown chromatophores, darkest between eyes. Oral surfaces of arms yellowish white with purplish chromatophores in front and behind base of each sucker.

ORIGINAL DESCRIPTION.—Robson, 1929a:169, as *Octopus equivocus* (replacement name for *O. gracilis* Verrill, 1884:236, preoccupied by *O. gracilis* Eydoux and Souleyet, 1852).

TYPE LOCALITY.—Western North Atlantic Ocean, Canada,

Nova Scotia, south of Cape Sable, R/V *Albatross* sta 2084, 40°16'50"N, 67°05'15"W, 0–2358 m.

TYPE.—*Holotype*: USNM 38431, female, paralarva, 11 mm ML.

DISCUSSION.—The diagnosis is excerpted from the original description of *Octopus gracilis* by Verrill (1884). We did not examine the holotype. Robson (1929a) erected *Octopus equivocus* as a replacement name for *O. gracilis* Verrill, 1884 (preoccupied by *O. gracilis* Eydoux and Souleyet, 1852). Robson (1929a) indicated incorrectly that the holotype was maintained at the PMY. Hanlon et al. (1980), Nesis and Nikitina (1981), and Hanlon et al. (1985), collectively, considered all *Macrotritopus* paralarvae from the Atlantic Ocean to be attributable to *M. defilippi* (Verany, 1851), described originally from the Mediterranean Sea and recorded subsequently from the western Atlantic Ocean (Voss, 1964) (for a full account of that taxon see Mangold, 1998). If this is correct, *M. equivocus* is a junior synonym of *M. defilippi*; however, the possibility remains that more than one taxon could have a *Macrotritopus* stage. Toll (MS) will place *O. defilippi* and all suspected synonyms into *Macrotritopus*.

#### *Octopus eudora* Gray, 1849

DIAGNOSIS.—Arms short, arm formula II = III = IV > I. Suckers of moderate size. Web shallow. Skin smooth, "ocular tentacles none" (Gray, 1849:9).

ORIGINAL DESCRIPTION.—Gray, 1849:9.

TYPE LOCALITY.—Western tropical Atlantic Ocean, Jamaica.

TYPES.—*Syntypes*: BMNH 1846.8.31.3, 2 small females, ML undetermined (see "Discussion").

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from Gray's (1849) original description, which is defective, being barely six lines long and lacking mention of most primary systematic characters considered important in the recognition of species-level taxa. We did not examine the types. Robson (1929a:73) referred to "two type specimens" in the collections of the BMNH and attributed them to *Octopus rugosus* Bosc, 1792, later placed into the synonymy of *O. vulgaris* Cuvier, 1797, by Pickford (1945). Pickford's (1946:420) account listed two "very young females," specimens (BMNH 1846.8.31.3.) attributed to "Gray (1850)," with the label information "Jamaica, Mr. Gosse's Coll. C-125-126." There can be little doubt that these specimens are Gray's syntypes that he (Gray, 1849) had indicated originally as having come from Gosse's collection. Although it is entirely possible that *O. eudora* is a junior synonym of *O. vulgaris*, there is insufficient evidence in the accounts cited above to confirm this relationship. Because we are unable to substantiate the systematic position of *O. eudora*, we choose to consider it a nomen dubium. In either event, the name is of little systematic consequence.

***Octopus filusus* Howell, 1868**

DIAGNOSIS.—Animals medium-sized (to 72 mm ML). Mantle saccular, rounded posteriorly (MWI 50–92); neck slightly constricted; head about as wide as mantle (HWI 50–100). Funnel organ W-shaped. Arms short to moderate (ALI 60–80), arm order variable but typically III = II = IV > I. Suckers low, deeply set into arm, moderate to large in size, larger in females (SIn 10–15) than in males (SIn 6–11); males with especially enlarged suckers on arms II and III (Sle 13–18). Right arm III of males hectocotylized, subequal or only slightly shorter in length as compared to fellow arm; ligula small (LLI 3.0–5.0), deeply excavated with thick borders; calamus moderate to large in size (CLI 53–56). Web moderate to deep (WDI 20–56), web formula typically  $C > D > B > E > A$ . Gill lamellae 5–9. Penis short (PLI 16–28), with single, small diverticulum varying in shape from subspherical to digitiform. Spermatophores short to moderate in length (SpLI 27–51), sperm mass moderate in length (SpRI 32–48). Mature ovarian eggs small, 1.6–1.8 mm long, with stalk 1–1.5 times length of egg. Radula with  $A_{3-4}$  seriation of rachidian. Dermal ornamentation of granular elevations covering mantle, head, web, and arms; small to large flat papillae, greatly extensible and multifid in life on mantle and arms; large multifid cirrus over each eye; large terminal cirrus at posterior apex of mantle; skin with patch and groove trellis arrangement. Color in life reddish yellow-brown with yellow mottling; mantle with pair of large white spots; frontal white spots diffuse; single pair of ocelli, consisting of conspicuous iridescent blue ring and dark central spot, present between eye and bases of arms II and III; ocellus occasionally lacking unilaterally or bilaterally. Color in preservation (ethanol) light to dark gray, paler ventrally.

ORIGINAL DESCRIPTION.—Howell, 1868:240.

TYPE LOCALITY.—Western tropical Atlantic Ocean, Virgin Islands, Santa Cruz Island (= St. Croix) (museum label reads “St. Croix, West Indies”).

TYPE.—*Holotype*: ANSP A6450, female, 36 mm ML, in alcohol, fair to good condition.

DISTRIBUTION.—United States, Florida; Bahamas to Recife, Brazil (common in Haiti); associated with coral reefs.

DISCUSSION.—The diagnosis is based on the accounts of Voss (1949, 1962), Burgess (1966), Palacio (1977), and Toll (1990). Voss (1962) rediscovered and examined the type in the ANSP collections. *Octopus filusus* is a common and well-known species. In addition to the morphologic accounts cited above, notes on color patterning and biology can be found in Voss (1953) and Hanlon (1988). A junior synonym, *O. hummelincki* Adam, 1936, described from Bonaire, Lesser Antilles, had been used widely for many years as the name for this species (see Toll, 1990).

***Octopus fuvvus* Gould, 1852**

DIAGNOSIS.—Mantle elongate, pyriform; head long; eyes large, not prominent. Arms long and slender, subequal in

length. Suckers large, crowded, 192 suckers on each arm of arms I; suckers on arms I and II distinctly larger than those on arms III and IV. Web shallow. Mantle smooth to faintly wrinkled. Color “ochreous, but constantly varies, sometimes being nearly black, or mottled with ash-colour, or entirely ash-colored, dark shades being always produced by minute dottings. Underside paler, and shaded with orange-coloured dots” (Gould, 1852:475).

ORIGINAL DESCRIPTION.—Gould, 1852:475, figs. 589, 589a–589d.

TYPE LOCALITY.—Western South Atlantic Ocean, Brazil, “Rio Janeiro [sic],” from fish market.

TYPE.—*Holotype*: Sex undetermined (presumably female), ~150 mm ML, no longer extant (see “Discussion”).

DISCUSSION.—The diagnosis is excerpted from the original description by Gould (1852). The type of *Octopus fuvvus* was collected as part of the United States Exploring Expedition but is absent from the collections of the NMNH and is assumed to have been lost, as apparently was the regrettable fate of all the alcoholic material collected during this historic expedition (see Johnson, 1964; Palacio, 1977; Voss, 1981). Gould (1852) recognized the morphological similarities between his *O. fuvvus* and *Callistoctopus macropus* (Risso, 1826), originally described from the Mediterranean Sea, but noted that the color of *O. fuvvus* was “very different.” Also, *O. fuvvus* is described and figured with the arms “nearly equal in length” as compared to the arm formula of *C. macropus*, which is distinctly  $I > II > III > IV$ . Robson (1929a) noted that *O. fuvvus* superficially reminded him of *C. macropus*, but he could not refer it to that species. Pickford (1945:743) commented that it was “fairly certain” that *O. fuvvus* was a synonym of *C. macropus* but listed it in synonymy preceded by a “?” (for an account of *C. macropus* see Mangold, 1998). Due to the ambiguity of the original description and lack of an extant type specimen, we consider *O. fuvvus* to be a nomen dubium.

***Octopus geryonea* Gray, 1849**

DIAGNOSIS.—Arms moderate in length, thick at base, arm formula  $III > IV > II > I$ . Suckers large, subequal in size, first 3 to 4 adoral suckers uniserial. Web deep. Mantle smooth; head, base of arms, and aboral surface of web finely granular; single supraocular cirrus (“and one behind the eye”? (Gray, 1849:7)).

ORIGINAL DESCRIPTION.—Gray, 1849:7.

TYPE LOCALITY.—Western South Atlantic Ocean, “Coast of Brazils [sic], Bahia” (Gray, 1849:7).

TYPE.—*Holotype*: BMNH 1946.10.8.1 (see “Discussion”), female, large (ML undetermined), “worn” (Robson, 1929a:73).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description, which is defective, being a mere six lines long and lacking mention of numerous primary characters. We did not examine the type. Robson (1929a:73) referred to the type of *O.*

*geryonea* as a "worn specimen from Bahia, probably an old animal" and considered it to be a synonym of *O. rugosus* Bosc, 1792, itself placed in the synonymy of *O. vulgaris* Cuvier, 1797, by Pickford (1945). Pickford (1946) listed a large female specimen (BMNH 1946.10.8.1) attributed to "*Octopus geryonea* Gray (1850) [sic]" as the one Robson had examined and retained *O. geryonea* in synonymy. Although it is entirely possible that *O. geryonea* is a synonym of *O. vulgaris* there is insufficient evidence in these accounts to confirm this relationship. Because we are unable to substantiate the systematic position of *O. geryonea*, we choose to consider it a nomen dubium. In either event, the name is of little systematic consequence.

#### *Macrotritopus gracilis* (Verrill, 1884)

DIAGNOSIS.—See *Macrotritopus equivocus* (Robson, 1929), above.

ORIGINAL DESCRIPTION.—Verrill, 1884:236, as *Octopus gracilis* (preoccupied by *Octopus gracilis* Eydoux and Souleyet, 1852).

TYPE LOCALITY.—Western North Atlantic Ocean, Canada, Nova Scotia, south of Cape Sable, R/V *Albatross* sta 2084, 40°16'50"N, 67°05'15"W, 0–2358 m.

TYPE.—*Holotype*: USNM 38431, female, 11 mm ML.

DISCUSSION.—Robson (1929a) recognized that the name *Octopus gracilis* was preoccupied and erected *O. equivocus* in replacement. Robson (1929a) indicated incorrectly that the holotype was maintained at the PMY. This taxon is most probably a junior synonym of *Macrotritopus defilippi* (Verany, 1851), originally described from the Mediterranean Sea (see Mangold, 1998, for a complete account of *M. defilippi*; see *M. equivocus*, above). Toll (MS) will place *O. defilippi* and its synonyms in *Macrotritopus*.

#### *Octopus hummelincki* Adam, 1936

DIAGNOSIS.—See *Octopus filusos* Howell, 1868, above.

ORIGINAL DESCRIPTION.—Adam, 1936:1.

TYPE LOCALITY.—Western tropical Atlantic Ocean, Netherlands West Indies, Bonaire.

TYPES.—*Syntypes*: ZMA, 1 male, 21 mm ML, 1 female, 18 mm ML, in alcohol, good condition; ISBN, 1 female, 15 mm ML.

DISCUSSION.—This name is a junior synonym of *Octopus filusos* (see Voss, 1962; Toll, 1990; see that taxon above).

#### *Octopus joubini* Robson, 1929

DIAGNOSIS.—Animals small (to 45 mm ML; wt to 30 g). Mantle round or saccular (MWI 90); neck constricted; head moderate in width (HWI 73); eyes prominent, projecting. Funnel organ W-shaped. Arms short (ALI 64). Suckers moderate in size (Sl<sub>n</sub> 9), few in number (ASC 79). Web

shallow to moderate (WDI 28), web formula  $D > B = C = E > A$ , but nearly equal. Gill lamellae 4. Mature ovarian eggs small, 2.3–4.8 mm long; single egg masses of 150–3000 eggs each laid periodically over 4–6 weeks and attached singly to substratum. Hatchlings planktonic, 2.0–2.5 mm ML, with ~420 chromatophores. Surface of head, mantle, and arms smooth; supraocular papillae 3 to 4. Color in life reddish orange. Color in preservation (ethanol) grayish brown.

ORIGINAL DESCRIPTION.—Robson, 1929a:161, figs. 56–58.

TYPE LOCALITY.—Western North Atlantic Ocean, Virgin Islands, St. Thomas, 15 m.

TYPE.—*Holotype*: BMNH 89.4.24.30, female, 15 mm ML.

DISTRIBUTION.—United States, Georgia and Florida; northern Gulf of Mexico to central Caribbean Sea (Virgin Islands); on sand or mud bottom in depths of greater than 10 m.

DISCUSSION.—The diagnosis is based on examination of the female holotype conducted by the authors and K. Mangold and on data contained in the account by Forsythe and Toll (1992). The name *Octopus joubini* has been applied to the western Atlantic Ocean pygmy octopus with large eggs since Pickford (1945) so stated. In the early 1980s, observations of live animals, first performed by J. Forsythe, and preliminary morphological studies of preserved specimens by M. Solis Ramirez, J. Forsythe, S.C. Hess, and the authors confirmed the presence of two distinct, sympatric species, one with large eggs and a second with small eggs, confused under this name. Arocha and Urosa (1982) is the first account of *O. joubini* to refer specifically to the large- and small-egg forms (based on pers. comm., 1980, from G. Voss).

Forsythe and Toll (1992) identified *Octopus joubini* as the small-egg form. A majority of the published accounts of "*O. joubini*" are based on specimens collected from two shallow-water localities: Biscayne Bay and St. Joseph Bay, Florida (e.g., see Boletzky and Boletzky, 1969; Mather, 1972, 1978, 1980, 1982a, 1982b; Thomas and Opresko, 1973; Butterworth, 1982; Hanlon, 1983; Forsythe, 1984). Both populations are attributable to the large-egg form and, therefore, are not conspecific with Robson's holotype. *Octopus mercatoris* Adam, 1937, could be conspecific to either form. If *O. mercatoris* is a synonym of Robson's *O. joubini*, the common large-egg form will need to be described as new (see *O. mercatoris*, below).

#### *Octopus lobensis* Castellanos and Menni, 1969

DIAGNOSIS.—Animals small (26–37 mm ML). Mantle saccular (MWI 81–97), rounded posteriorly; head broad (HWI 59–82); eyes large. Funnel organ VV-shaped. Arms short (ALI 57–64), subequal in length. Right arm III of males hectocotylized (HALI 150–162), subequal in length with fellow (FAI 88.1–105.4); ligula with shallow groove with faint laminae and rugose inrolled sides; calamus small to moderate in length (CLI 29). ASC 76–100. Web formula variable. Gill lamellae 5–11. Mature eggs moderate in length, capsule 9 mm long. Male with

moderate-sized penis with simple, lobate penial diverticulum. Spermatophores long (SpLI ~107), sperm mass with ~37 coils (SpRI ~45). Radula with penticuspid rachidian. Skin rugose, soft to gelatinous.

ORIGINAL DESCRIPTION.—Castellanos and Menni, 1969a:92. figs. 1, 2, 5.

TYPE LOCALITY.—Western South Atlantic Ocean, Argentina, Golfo San Matías, Puerto Lobos.

TYPES.—*Syntypes*: MPA 2073, MPA 2075, MPA 2086–88, MPA 2092, 4 males, 26–37 mm ML, 5 females, 28–37 mm ML.

DISTRIBUTION.—Southern Brazil to south central Argentina.

DISCUSSION.—The diagnosis is based on the original description and additional data contained in Castellanos (1970), which was based on the syntypic series and on new material.

There is considerable confusion regarding the identity of this taxon; *Octopus tehuelchus* Orbigny, 1835 (in 1835–1847), is similar. Palacio (1977) partially redescribed *O. lobensis* based on new material and retained *O. lobensis* as distinct. Based on examination of the syntypic series of *O. lobensis* and 1050 living specimens of *O. tehuelchus*, Pujals (1984) considered the former to be a junior synonym of the latter. It is our opinion that the controversy regarding the identity of these two nominal taxa is far from resolved, and we choose to retain *O. lobensis* as distinct. A definitive study needs to be performed (see also *O. tehuelchus*, below).

#### *Octopus maya* Voss and Solís Ramírez, 1966

DIAGNOSIS.—Animals large (to 119 mm ML; wt to 4 kg). Mantle large, oval, (MWI 42–64), pointed to round posteriorly; neck region constricted; head narrow (HWI 27–48); eyes small, inconspicuous. Funnel organ W-shaped, inner and outer limbs subequal in length. Arms moderate to long (ALI 70–83), stout; arm order variable, but arms I always shortest. Suckers large, sexually dimorphic in size, smaller in females (SIn 8.7–9.5) than in males (SIn 10–13); especially enlarged suckers on arms I and II in males. Right arm III of males hectocotylized (HALI 216–348), shorter than fellow (FAI 72–86); ligula minute (LLI 1.4–1.9), with deep groove with strongly inrolled sides completely obscuring small calamus (CLI 24–27). Web shallow to moderate in depth (WDI 16–30), deeper in males, web formula variable. Gill lamellae 9–10. Mature eggs moderate in size, capsule 11 mm long × 3.9 mm wide at time of spawning, increasing to 17 mm long × 4.5 mm wide just prior to hatching; single egg mass with up to 5000 eggs. Hatchlings benthonic. Penis small, with single, small, subspherical diverticulum. Spermatophores small to moderate in length (SpLI 47); sperm mass short to moderate in length (SpRI 33). Radula with alternating A3–A2 seriation of rachidian. Dermal sculpture in preservation granular with scattered papillae over dorsum of mantle, head, web, and arms; supraocular cirri present. Color in life dark brown flushing to

reddish brown when disturbed; frontal white spots present. Color in preservation (ethanol) brownish purple with greenish cast on arms and web. Paired ocelli between eye and bases of arms II and III consist of iridescent blue or blue-green ring with central large, dark, round spot; iridescent ring absent in adults. Skin with patch and groove trellis arrangement.

ORIGINAL DESCRIPTION.—Voss and Solís Ramírez, 1966:617, figs. 2, 3.

TYPE LOCALITY.—Subtropical western North Atlantic Ocean, Gulf Of Mexico, Mexico, east side of Bay of Campeche, off town of Lerma, 6 m.

TYPE.—*Holotype*: USNM 576060, male, 115 mm ML, in alcohol, good condition.

DISTRIBUTION.—Northeastern Yucatan Peninsula around the Bay of Campeche to near Vera Cruz, Mexico.

DISCUSSION.—The diagnosis is based on the accounts of Voss and Solís Ramírez (1966), Van Heukelem (1983), and Hanlon (1988). *Octopus maya* is common throughout its limited range and supports a local commercial fishery (see Roper et al., 1984). This species is well known; information on its biology and natural history is found in Solís Ramírez (1967), Walker et al. (1970), Van Heukelem (1976, 1977, 1983), and Hanlon (1988).

#### *Octopus mercatoris* Adam, 1937

DIAGNOSIS.—Animals small (to 20 mm ML). Mantle moderate in width (MWI 64–73); neck constricted; head subequal in width to mantle (HWI 71–76); eyes relatively large. Funnel organ W-shaped, inner and outer limbs subequal in size. Arms moderate in length (ALI 78), arm order III > II > IV > I but nearly equal. Suckers elevated, moderate in size, larger in female (SIn 12) than in male (SIn 9.5), ASC 143; in male, 1 or 2 suckers in sucker rows 3 to 4 on arms I–III especially enlarged (SIn 13.5). Right arm III of male hectocotylized (HALI 175), noticeably shorter than fellow (FAI 71); ligula small (LLI 4); calamus small (CLI 20); HASC 80. Web shallow (WDI 16), web sectors nearly subequal in depth. Ink sac present, gill lamellae 6 to 7. Mature ovarian eggs small, capsule ~3 mm long. Penis short, stubby, with simple, subspherical diverticulum (PLI 11). Radula with B<sub>4</sub> seriation of rachidian. Skin of mantle, head, web, and arms smooth; small supraocular papillae present. Color in preservation (ethanol) tan.

ORIGINAL DESCRIPTION.—Adam, 1937b:76, figs. 32–35.

TYPE LOCALITY.—Subtropical western North Atlantic Ocean; Gulf of Mexico, United States, Florida, Dry Tortugas, 120–132 ft (36.6–40.26 m) (male syntype), Tampa Bay, 42–60 ft (12.81–18.3 m) (female syntype).

TYPES.—*Syntypes*: ISBN 10.911, 1 male (with spermatophores), 20 mm ML, 1 female, 20 mm ML.

DISTRIBUTION.—Known with certainty only from the type localities (see “Discussion”).

DISCUSSION.—The diagnosis is based on the original

description by Adam (1937b) and on our examination, with K. Mangold, of the syntypes. *Octopus mercatoris* was placed in the synonymy of *O. joubini* by Pickford (1945). Forsythe and Toll (1992) determined that *O. joubini* is characterized by small eggs that give rise to planktonic young (see *O. joubini* above). *Octopus mercatoris* could either be conspecific to Robson's *O. joubini* or be the valid name of the large-egg form confused with that species. The systematic status of *O. mercatoris* is under investigation by R. Toll.

#### *Octopus occidentalis* Steenstrup in Hoyle, 1886

DIAGNOSIS.—Animals medium-sized (55 mm ML (60 mm ML fide Palacio, 1977)). Mantle wide (MWI 91); head moderate in width (HWI 75.0); eyes prominent. Funnel organ W-shaped, inner and outer limbs subequal in length, outer limbs about twice as wide as inner ones. Arms moderate in length (ALI 76.5), arm formula II > III > IV > I but nearly subequal in length. Suckers large (SIn 13.3). Web shallow (WDI 18.5), web formula C > B > D > E > A. Radula with A<sub>3</sub> seriation of rachidian. Dermal ornamentation of clusters of minute papillae over head, eyes, web, and, to lesser degree, dorsal surface of arms; 2 small supraocular cirri. Color in preservation dark brown to black on dorsal surface of mantle, head, web, and aboral surface of arms, ventrum amber brown, oral surface of web pale yellow with pinkish papillae.

ORIGINAL DESCRIPTION.—Steenstrup in Hoyle, 1886:77.

TYPE LOCALITY.—Central South Atlantic Ocean, Ascension Island.

TYPE.—*Holotype*: BMNH 1889.4.24.14, female, 55 mm ML.

DISTRIBUTION.—Central South Atlantic Ocean, Ascension Island; Western South Atlantic Ocean, Trindade Island, Brazil.

DISCUSSION.—The diagnosis is excerpted from the original description and from Palacio's (1977) account based on his examination of the holotype and a second specimen from Trindade Island (Brazil) (see Massy, 1916). Hoyle (1886) considered *Octopus occidentalis* to be referable to *O. vulgaris americanus* Orbigny, 1842 (considered herein to be a nomen nudum), but chose to use Steenstrup's manuscript name because of the confused nomenclatural history surrounding the use of the name *americanus*. Robson (1929a:73) considered *O. occidentalis* to be a synonym of *O. rugosus* Bosc, 1792 (which was placed into the synonymy of *O. vulgaris* Cuvier, 1797, by Pickford (1945)). Palacio (1977) noted that Robson (1929a) implied that he had examined the radula of the holotype of *O. occidentalis* and compared it to that of Massy's (1916) female specimen; however, this comparison would have been impossible because at the time that Palacio acquired the holotype, the radula had not previously been extracted.

Males of *Octopus occidentalis* are unknown. Palacio (1977) retained *O. occidentalis* as distinct based on characters of the beaks, radula, and general body morphology. We support his decision at present, but confirmation requires additional study.

#### *Octopus pictus* Verrill, 1883

DIAGNOSIS.—See *Octopus verrilli verrilli* Hoyle, 1886, below.

ORIGINAL DESCRIPTION.—Verrill, 1883:112, pl. 3: fig. 3.

TYPE LOCALITIES.—Tropical western North Atlantic Ocean, Flannegan Passage off St. John, R/V *Blake* sta 142, 49 m; off Barbados, R/V *Blake* sta 278, 126 m.

TYPES.—*Syntypes*: Not traced, 2 paralarvae, ~6 mm ML, 6 mm ML.

DISCUSSION.—The name *Octopus pictus* was preoccupied by *Octopus pictus* Blainville, 1828. Hoyle (1886) erected *Octopus verrilli* (= *Octopus verrilli verrilli*) in replacement (see that taxon, below).

#### *Euaxoctopus pillsburyae* Voss, 1975

DIAGNOSIS.—Animals small (to 24 mm ML; to 219 mm TL). Mantle slender, subpyriform (MWI 58–71); neck distinct; head narrow (HWI 39–50); eyes small, protruding. Funnel organ presumably W-shaped (poorly preserved in all type material), limbs pointed. Arms exceptionally long (ALI 88–91), readily autonomized, arm order I > IV > III > II. Suckers small to moderate in size, widely spaced (SIn 6–9); especially enlarged suckers absent in males and females. Right arm III of males hectocotylized, considerably shorter than fellow (FAI < 16); ligula moderate in length (LLI 9–10), lanceolate, with numerous plicae; calamus moderate (CLI 45.5), triangular, acutely pointed, edges strongly inrolled. Web exceptionally shallow (WDI 5.4–5.6). Gill lamellae 7. Mature eggs not known. Penis small (PLI 15–16), with small, blunt diverticulum. Spermatophores small (SpLI 31), spermatophore horn with flat coils. Radula with A<sub>3-4</sub> seriation of rachidian. Surface of mantle, head, and web smooth. Paired "ocelli" located on dorsum of mantle about midway between head and apex of mantle; "ocelli" consist of dark gray, oval splotch outlined by thin, raised, unpigmented, crescent-shaped ridge. Color in preservation (ethanol) grayish brown with fine reticulations.

ORIGINAL DESCRIPTION.—Voss, 1975:346, figs. 1–4.

TYPE LOCALITY.—Caribbean Sea, Surinam, off Surinam River, R/V *Pillsbury* sta 662, 6°49'N, 54°26.5'W, 44 m.

TYPE.—*Holotype*: USNM 729100, male, 24 mm ML.

DISTRIBUTION.—Surinam and the northern coast of South America.

DISCUSSION.—The diagnosis is excerpted from the original description by Voss (1975). This unusual species is still very poorly known. It has the ability to autonomize its arms when handled or placed into preservative.

#### *Octopus rugosus sanctaehelenae* Robson, 1929

DIAGNOSIS.—See *Octopus sanctaehelenae* Robson, 1929, below.

ORIGINAL DESCRIPTION.—Robson, 1929a:74.

TYPE LOCALITY.—Central South Atlantic Ocean, St. Helena Island.

TYPE.—*Holotype*: BMNH 1868.3.12.1, female, ML undetermined.

DISCUSSION.—See *Octopus sanctaehelenae*, below.

#### *Octopus sanctaehelenae* Robson, 1929

DIAGNOSIS.—Web deep (WDI 33). Gill lamellae 11. Skin covered with low, multifid warts, those on sides of body pentastellate, those on dorsum tend to form longitudinal ridges. Warts on skin of arms and web smaller and more densely packed.

ORIGINAL DESCRIPTION.—Robson, 1929a:74, as *Octopus rugosus sanctaehelenae*.

TYPE LOCALITY.—Central South Atlantic Ocean, St. Helena Island.

TYPE.—*Holotype*: BMNH 1868.3.12.1, female, ML undetermined.

DISCUSSION.—The diagnosis is excerpted from the brief original description by Robson (1929a), who erected "*sanctae helenae*" as a varietal form of *Octopus rugosus* Bosc, 1792, (itself later placed into the synonymy of *Octopus vulgaris* Cuvier, 1797, by Pickford (1945)) based on the unique type, which had been dissected and was distorted badly prior to his examination. Robson (1929a) noted that the bottle containing the specimen bore a hand-written label with the name *sanctae helenae*. We did not examine the type.

Pickford (1955) placed *Octopus sanctaehelenae* into the synonymy of *O. vulgaris* without discussion. We are hesitant to support Pickford's (1955) assertion as to the identity of *O. sanctaehelenae* because of the incomplete description of the type and the unresolved systematic problems relating to the octopodines described from central South Atlantic Ocean islands. The gill lamellae count (11), perhaps the only definitive character in Robson's account, indicates to us that *O. sanctaehelenae* may not be attributable to *O. vulgaris*; also, we are unable to attribute this species to any of the octopodines described from these islands. Therefore, we elect to elevate *O. sanctaehelenae* to full species level and retain it as distinct until a complete systematic review of the octopodines from this region can be performed.

#### *Octopus saphenia* Gray, 1849

DIAGNOSIS.—Arms moderate in length, arm formula II = III = IV > I. Suckers subequal. Web shallow. Body, arms, and aboral surface of web finely granular; "ocular beards none" (Gray, 1849:11).

ORIGINAL DESCRIPTION.—Gray, 1849:11.

TYPE LOCALITY.—Western South Atlantic Ocean, east coast of South America (but see "Discussion").

TYPE.—*Holotype*: BMNH, no longer extant (fide Robson, 1929a:160).

DISTRIBUTION.—See "Discussion."

DISCUSSION.—The diagnosis is excerpted from the original description, which is defective, being a mere three lines long and lacking mention of most systematic characters needed for species-level recognition. Gray (1849) gave the distribution ("Habitat") of the species as the Pacific Ocean but listed the type as coming from the east coast of South America as a gift from the Reverend W. Hennah. Robson (1929a) was unable to locate the type in the BMNH collections. In view of the poor description, contradictory locality data, and absence of an extant type specimen, we consider *Octopus saphenia* to be a nomen dubium.

#### *Pteroctopus schmidti* (Joubin, 1933)

DIAGNOSIS.—Immature male small (57 mm TL; 20 mm ML). Mantle moderate in width (MWI 78), rounded posteriorly; head moderately broad (HWI 68.5), slightly set off from mantle by weak neck constriction; eyes deeply set into head. Funnel organ very distinct, VV-shaped, inner and outer limbs subequal in length; funnel with knob-like protrusion at each distal corner near edge of mantle. Arms moderately short (ALI 61.4), arm order I = II = III > IV. Suckers small (Sl<sub>n</sub> 4.6); especially enlarged suckers absent; arms I, II, and III (with exception of right arm III) with 102–107 suckers per arm, arms IV with 98 suckers per arm. Right arm III hectocotylized, slightly shorter than fellow (FAI 91.2); HASC 69; calamus and ligula immature, small, simple. Web deep (WDI 54.3), web formula A > B = C = D > E; edges of adjacent web sectors fused into single pallisades-like keel extended along aboral surface of each arm. Ink sac present; gill lamellae 9. Immature penis small, simple, with simple, bulbous diverticulum. Radula not examined. Pair of moderately sized suprocular cirri and several smaller papillae above each eye; surface of mantle and head finely papillate. General color in preservation (alcohol) light grey without evidence of color patterning.

ORIGINAL DESCRIPTION.—Joubin, 1933:4, as *Danoctopus schmidti*.

TYPE LOCALITY.—Western North Atlantic Ocean, off Abaco, Bahamas, R/V *Dana* sta 1239-XIV, 25°50'N, 76°55'W, 12.2.1922, 1666 m.

TYPE.—*Holotype*: ZMK, male (immature), 57 mm TL, 20 mm ML, in alcohol, good condition.

DISCUSSION.—The diagnosis is based on the examination of the holotype by one of us (RBT). Few specimens of this taxon have been recorded in the literature; the most notable accounts are by Voss (1956) and Cairns (1976). All specimens known to us are small and immature. Nesis (1987) considered *Danoctopus* to be the senior synonym of *Berrya* Adam, 1939. Toll (MS) considers both of these genera to be junior synonyms of *Pteroctopus* Fischer, 1882 (in 1880–1887). *Pteroctopus schmidti* could be a developmental stage of another described species. It could be referable to *Pteroctopus tetracirrhus* (Chiaie) with the exception of the position of the hectocotylus, which is sinistral in *P. tetracirrhus*. One of us (RBT), however,

has examined specimens from the North Atlantic that appear to be extremely similar if not identical to *P. tetracirrhus* except that the hectocotylus is dextral. The problem of the identity of *P. schmidti* currently is under study by one of us (RBT). For the purpose of the present account, *P. schmidti* is provisionally retained as distinct.

***Macrotritopus scorpio* (Berry, 1920)**

DIAGNOSIS.—*Paralarva*: Mantle broad, ovate to pyriform, rounded to rounded-conic posteriorly; mantle aperture broad. Eyes large, conspicuous. Funnel broad, triangular. Arm formula III > II > IV > I, arms III more than twice as long and wide as arms II. Web extremely shallow. Dorsal surface of mantle with minute granular papillation. General color in preservation (alcohol) greyish buff.

ORIGINAL DESCRIPTION.—Berry, 1920:299, pl. 16: fig. 4, as *Polypus scorpio*.

TYPE LOCALITY.—Subtropical western North Atlantic Ocean, United States, Florida, off Biscayne Bay, 0–75 m.

TYPE.—*Holotype*: USNM 338699, paralarva, ~5 mm ML.

DISCUSSION.—The diagnosis is excerpted from the original description by Berry (1920). *Macrotritopus scorpio* is one of several nominal species (subspecies of some accounts) attributed to *Macrotritopus*. Hanlon et al. (1980), Nesis and Nikitina (1981), and Hanlon et al. (1985) concluded collectively that all *Macrotritopus* paralarvae from the Atlantic Ocean are attributable to *M. defilippi* (Verany, 1851), described from the Mediterranean Sea and recorded from the western Atlantic Ocean by Voss (1964). If this is correct, *M. scorpio* is a junior synonym of *M. defilippi* (for an account of that taxon, see Mangold, 1998). Toll (MS) will place *O. defilippi* and all synonyms into *Macrotritopus*.

***Octopus tehuetchus* Orbigny, 1835 (in 1835–1847)**

DIAGNOSIS.—Mantle spherical, about as wide as long (MWI 105); head moderate in width; eyes small. Funnel long and narrow. Arms moderate to long (ALI 81), arm formula IV > I = III > IV; longest arms with about 100 suckers. Web shallow. Mantle smooth. Color in life blackish brown dorsally along mantle and head and aboral surfaces of arms, oral surfaces of arms light blue.

ORIGINAL DESCRIPTION.—Orbigny, 1835:25 (in 1835–1847), pl. 1: figs. 6, 7.

TYPE LOCALITY.—Western South Atlantic Ocean, Argentina, Bahia de San Blas, among rocks.

TYPE.—*Holotype*: MNHN, female?, 164 mm TL, no longer extant (fide Palacio, 1977).

DISTRIBUTION.—Uncertain; given by Palacio (1977) as southwestern Atlantic from Buenos Aires southward to Golfo Nuevo, Peninsula Valdez.

DISCUSSION.—The diagnosis is excerpted from the brief original description by Orbigny (1835, in 1835–1847). The

inadequate diagnosis has resulted in confusion regarding the identity of this taxon. Efforts to clarify its taxonomic status have been hindered by the absence of an extant type, lack of critical comparison with previous published accounts, and insufficient comparative material. Robson (1929a:147) redescribed the species based on specimens in Paris and Leipzig, but because he was “not at all satisfied that they are correctly named,” his account is suspect. Furthermore, Robson (1929a) cautioned against the use of the other records of this taxon because of the difficulties associated with its identification.

*Octopus tehuetchus* was again redescribed by Castellanos and Menni (1969a) based on new material (five males, five females) from several Argentinean localities (Puerto Lobos, Mar del Plata, Puerto Quequén, and Miramar) to distinguish it from their newly erected *O. lobensis* Castellanos and Menni, 1969. According to Castellanos and Menni (1969a), the size and shape of the mantle, head, eyes, and funnel, the distinctiveness of the neck, funnel organ morphology (UU-shaped in *O. tehuetchus* compared with VV-shaped in *O. lobensis*), hectocotylus and radula morphology, and the dermal ornamentation separate the two species. Several of these characters are now known to be inadequate to discriminate species. Castellanos (1970) added additional comparative data on the morphology of the penis, Needham’s sac, spermatophores, and distribution of chromatophores of *O. tehuetchus* and *O. lobensis* as well as the first description of the eggs and embryos of the former.

Palacio (1977) also redescribed *O. tehuetchus* based on nine specimens, four males and four females from La Plata and a single large male from Buenos Aires. The Buenos Aires specimen may not be conspecific with the La Plata material; it is more than twice the size (ML) of any specimen from La Plata. Palacio (1977) described the funnel organ as W-shaped with thick pads but more of a UU in young specimens. The rachidian tooth morphology figured by Palacio (1977) from an unspecified specimen, attributed to *O. tehuetchus*, differs considerably from that figured for *O. tehuetchus* by Castellanos and Menni (1969a).

Ré and Taylor (1981) noted that these two nominal taxa support a single vernacular name (“pulpito”) in Argentina and that their fishery statistics are typically combined. Pujals (1984) examined the type series of *O. lobensis* with particular attention to hectocotylus morphology and presented data on preservation-induced artifacts based on study of 1050 live-collected specimens of *O. tehuetchus* from the Gulf of San Matías, Argentina. She concluded that *O. lobensis* was within the range of variation exhibited by *O. tehuetchus* and placed *O. lobensis* in synonymy.

Clearly, the systematic status of *Octopus tehuetchus* has yet to be resolved. The diagnosis presented above includes only data from the original description because we are unable to assess the reliability of the other accounts of the taxonomy of the octopods of the Argentinean and adjacent coasts. The current confusion regarding the identity of *O. tehuetchus*

*lobensis* can be distilled down to two questions: (1) can specimens of *Octopus* from the Patagonian region of South America be attributed reliably to Orbigny's *O. tehuelchus*; and (2) is the common octopus from this region a single species or two similar but distinct sympatric species, one of them attributable to *O. lobensis*, the other to *O. tehuelchus*. Critical examination of new material, including observation of living specimens, representing the entire geographic range combined with careful reassessment of and comparison to Orbigny's descriptions (1835 (in 1835–1847), 1840 (in Férussac and Orbigny, 1834–1848)) of *O. tehuelchus*, and examination of the type series of *O. lobensis*, are required to reach an informed decision. Until a definitive study is performed, we choose to retain *O. tehuelchus* as distinct (see also *O. lobensis*, above).

#### *Octopus verrilli verrilli* Hoyle, 1886

DIAGNOSIS.—*Paralarva*: Mantle broad (MWI ~100), bluntly rounded posteriorly; neck constriction absent; head wide (HWI ~102); eyes large. Arms moderate in length (ALI ~73), subequal, arm formula I = II = III = IV. Suckers small (SIn ~6). Web shallow to moderately deep. Dorsal surface of head, mantle, and aboral surface of arms covered with large, reddish brown to brown chromatophores. Single supraocular cirrus.

ORIGINAL DESCRIPTION.—Verrill, 1883:112, pl. 3: fig. 3, as *Octopus pictus*.

TYPE LOCALITIES.—Tropical western Atlantic Ocean, Flannegan Passage, off St. John, R/V *Blake* sta 142, 49 m; off Barbados, R/V *Blake* sta 278, 126 m.

TYPES.—*Syntypes*: Not traced, 2 paralarvae, ~6 mm ML, 6 mm ML (see "Discussion").

DISCUSSION.—The diagnosis is excerpted from the brief original description of *Octopus pictus* by Verrill (1883), which is dominated by paralarval characters. Hoyle (1886) erected *O. verrilli* as a replacement name for *O. pictus* (preoccupied by *O. pictus* Blainville, 1828; see *O. pictus* Verrill, 1883, above). Robson's (1929a) account of this taxon reiterates Verrill's (1883) original description. Robson (1929a) erected a varietal form, *O. verrilli palliata* (see that taxon below), thereby making *O. verrilli verrilli* the nominal subspecies. Pickford (1945) tentatively included *O. verrilli verrilli* in the synonymy of *O. macropus*, but we do not support this placement based on the shape of the mantle and the arm lengths.

The syntypes of *Octopus verrilli verrilli* are not now found among the collections of the NMNH despite the fact that many of Verrill's other types are housed there (see Roper and Sweeney, 1978); they are probably no longer extant. *Octopus verrilli verrilli* is almost certainly the paralarval stage of another described taxon; however, we are unable to relate it with certainty to any taxon in particular. Therefore, we choose to consider it a nomen dubium.

#### *Octopus verrilli palliata* Robson, 1929

DIAGNOSIS.—*Paralarva*: Mantle broad (MWI 90). Arms short, subequal in length. Web moderately deep (WDI 42), web formula A = B = C = D > E. Chromatophores in 2 rows along aboral surface of arms.

ORIGINAL DESCRIPTION.—Robson, 1929a:163, fig. 59.

TYPE LOCALITY.—Western subtropical Atlantic Ocean, Bahamas, Harbour Island.

TYPE.—*Holotype*: BMNH 1908.1.30.5, paralarva, female?, 11 mm ML, 29 mm TL.

DISCUSSION.—The diagnosis is excerpted from Robson's (1929a) brief original description, which is little more than a tabular comparison of 10 characters with the nominal subspecies, *Octopus verrilli verrilli*, itself considered above to be a nomen dubium. Robson (1929a:163) was hesitant to refer *O. v. palliata* to Hoyle's *verrilli* but indicated that there was "enough likeness between the two forms to render it probable that they are best treated as conspecific." As is the case with *O. verrilli verrilli*, *O. verrilli palliata* is most certainly the young of another described taxon, but we are unable to relate it to any individual species. Along with the nominal subspecies, we consider *O. verrilli palliata* a nomen dubium.

#### *Octopus verrucosus* Hoyle, 1885

DIAGNOSIS.—Animals medium-sized (to 80 mm ML). Mantle rounded (MWI 69); head narrower than mantle (HWI 50); eyes small ("but slightly prominent" Hoyle (1885a:222)). Funnel long, conical; funnel organ W-shaped. Arms moderate to long (ALI 80), distinctly unequal, arm formula II > III > I = IV. Suckers moderate in size (SIn 10), crowded; about 4 especially enlarged suckers present on arms II and III of males (Sle 23). Right arm III of males hectocotylyzed; ligula minute (LLI 0.8), acutely pointed, with median groove and 3 transverse ridges. Skin of dorsal surface of mantle and head and aboral surface of web covered with irregular, closely set warts of up to several mm in diameter in the nuchal region, larger warts in 2 lines along dorsum of mantle, smaller warts on ventrum; single supraocular cirrus. Color in preservation dull purplish grey, darker dorsally, ventrum considerably lighter.

ORIGINAL DESCRIPTION.—Hoyle, 1885a:222.

TYPE LOCALITY.—Central South Atlantic Ocean, Tristan d'Acunha, Inaccessible Island.

TYPES.—*Syntypes*: BMNH 1889.4.24.16, 2 males, 80 mm ML and ML undetermined.

DISCUSSION.—The diagnosis is excerpted from the accounts by Hoyle (1886) and Robson (1929a) based on the larger syntype. We did not examine the syntypes. Hoyle's (1885a) original description was followed by a slightly expanded description (Hoyle, 1885b). Hoyle (1886) repeated the second description, with minor additions, and included several illustrations of the larger syntype. Robson's (1929a) account



generally agreed with Hoyle's (1886), except Robson gave the SIE as 26. Pickford (1955) placed *O. verrucosus* into the synonymy of *O. vulgaris* Cuvier, 1797. We agree with Robson (1929a) that *O. verrucosus* is distinct from *O. vulgaris* based on several characters, including hectocotylus morphology and pattern of papillae on the dorsum of the mantle. At present, we retain *O. verrucosus* as distinct; however, additional collections from the islands of the South Atlantic Ocean are required to firmly establish its identity.

#### *Octopus vulgaris americanus* Orbigny, 1842

DIAGNOSIS.—None (see "Discussion").

ORIGINAL DESCRIPTION.—Orbigny, 1842, pl. 1: fig. 1.

TYPE LOCALITY.—Tropical western North Atlantic Ocean, Antilles.

TYPE.—*Holotype*: Not designated.

DISCUSSION.—Orbigny (1842) erected *O. v. americanus* as a varietal form of *O. vulgaris* in a figure caption only. According to the ICZN (1985, Art. 45g), *O. v. americanus* sensu Orbigny (1842) constitutes a subspecies. Guppy (1877) elevated *O. v. americanus* to species level and credited Orbigny, 1842, with authorship but in doing so created a homonym of *O. americanus* Baker in Denys de Montfort, 1802.

Because *Octopus vulgaris americanus* was not differentiated from *O. vulgaris vulgaris*, distinctions cannot readily be made from examination of the plate bearing the name *americanus*, and no type was designated. We consider *O. vulgaris americanus* to be a nomen nudum.

#### *Octopus vulgaris antillarum* Robson in Pickford, 1946

DIAGNOSIS.—None (see "Discussion").

ORIGINAL DESCRIPTION.—Robson in Pickford, 1946:420.

TYPE LOCALITY.—Tropical western North Atlantic Ocean, Virgin Islands, St. Thomas.

TYPES.—*Syntypes*: BMNH 1860.4.25.17, 1 male, 5 females.

DISCUSSION.—This subspecies was a varietal form of *Octopus rugosus* (= *O. vulgaris* Cuvier, 1797) that appeared on a handwritten museum label. Robson never published the name. Pickford (1946) contended that Robson (1929a) referred to these specimens in a discussion on the radular morphology

of *O. rugosus*, but this is equivocal because the catalog numbers of the specimens in the BMNH were not listed by Robson (1929a). Because Pickford's use of this name fails to satisfy the requirements for availability (ICZN 1985, Art. 13), *Octopus vulgaris antillarum* is a nomen nudum.

#### *Octopus zonatus* Voss, 1968

DIAGNOSIS.—Animals small (to 30 mm ML; to 88 mm TL). Mantle ovoid to round, widest posteriorly (MWI 66–95); head narrower than mantle (HWI 50–71); eyes moderate in size, protuberant. Funnel organ W-shaped, inner limbs stout, lateral limbs slender, pointed; inner and outer limbs subequal in length. Arms short (ALI 55–66), arm order variable, subequal. Suckers small to moderate in size (SIn 7–10), closely spaced; especially enlarged suckers absent in males and females. Right arm III of males hectocotylized (HALI 85–98), subequal in length to fellow arm (FAI 98); ligula small, slender (LLI 6.3–9.5), pointed, with broad median ridge with slight rugae; calamus large (CLI 40–45), erect. Web moderate in depth (WDI 31–40). Gill lamellae 6 to 7, with 2 to 3 minute lamellae terminally. Mature ovarian eggs moderate in size, capsule 6.1 mm long × 2.8 mm wide. Penis small (PLI 21.6) with small diverticulum. Spermatophores small to moderate in length (SpLI 59), cement body in capsule ornamented with crochets. Radula with A<sub>3</sub> seriation of rachidian. Dorsal mantle surface smooth, with 1 or 2 simple supraocular cirri. Color in life consisting of dark, gray brown transverse bands on dorsum of mantle, longitudinal stripes along head, over eyes, and onto web, and series of transverse bars down arms against yellow-white background color when alarmed; bars and stripes almost indistinguishable from background when at rest.

ORIGINAL DESCRIPTION.—Voss, 1968:647, figs. 1–4.

TYPE LOCALITY.—Tropical western North Atlantic Ocean, Caribbean Sea, Colombia, off Punta Caribana, 8°51.2'N, 77°01.6'W, 73 m.

TYPE.—*Holotype*: USNM 576513, male, 19 mm ML.

DISTRIBUTION.—Caribbean coast of Venezuela west to the Gulf of Darien.

DISCUSSION.—The diagnosis is excerpted from the original description by Voss (1968). A color photograph is presented by Hanlon (1988). This species is the only banded octopus known from the Western Atlantic Ocean.

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# The Systematic and Nomenclatural Status of the Octopodinae Described from the Indian Ocean (Excluding Australia) and the Red Sea

Ronald B. Toll

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## ABSTRACT

Twenty-five species and subspecies of octopodine cephalopods originally described from the Indian Ocean (excluding Australia) and the Red Sea are reviewed, and many are rediagnosed based on examination of the type material. The systematic status and nomenclatural disposition of each taxon is assessed. Twelve species-level taxa are retained as valid: *Octopus arborescens* (Hoyle, 1904); *O. filamentosus* Blainville, 1826; *O. gardineri* (Hoyle, 1905); *O. horridus* Orbigny, 1826; *Pteroctopus keralensis* (Oommen, 1966); *O. microphthalmus* Goodrich, 1896; *O. nanus* Adam, 1973; *Hapalochlaena nierstraszi* (Adam, 1938); *O. prashadi* Adam, 1939; *O. robsoni* Adam, 1941; *O. varunae* Oommen, 1971; *O. winckworthi* Robson, 1926. Several of these taxa are included in this list only provisionally, however, and additional study is required to confirm their systematic status.

Eight taxa are junior synonyms: *O. aranea* Orbigny, 1834, in Férussac and Orbigny, 1834–1848 (= *O. filamentosus* Blainville, 1826); *O. argus* Krauss, 1848 (= *O. horridus* Orbigny, 1826); *O. cyanea gracilis* Robson, 1929 (= *O. cyanea* Gray, 1849); *O. fimbriatus* Rüppell in Orbigny, 1841, in Férussac and Orbigny, 1834–1848 (= *O. horridus* Orbigny, 1826); *O. glaber* Rüppell in Wülker, 1920 (= *O. cyanea* Gray, 1849); *O. herdmani* (Hoyle, 1904) (= *O. cyanea* Gray, 1849); *O. horsti* Joubin, 1898 (= *O. cyanea* Gray, 1849); *Pteroctopus hoylei annae* (Robson, 1929) (= *Pteroctopus hoylei* (Berry, 1909)). Four taxa are nomina dubia: *O. appendiculatus* Blainville, 1826; *Robsonella fontaniana africana* (Robson, 1929); *O. incertus* Targioni-Tozzetti, 1869; *O. taprobanensis* Robson, 1926. One taxon, *O. savignyi* Deshayes in Adam, 1959, is a nomen nudum.

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## Introduction

Historically, the octopodines of the Indian Ocean and Red Sea have been a source of systematic and nomenclatural

confusion. Numerous taxa were erected based on inadequate or inappropriate material (e.g., small juveniles, immature females, damaged specimens). In addition, due to various factors, including the long and arduous journeys involved in the transport of specimens back to centers of study, the practice of maintaining specimens by individual adventurers and scientists rather than deposition of material into systematics museums, varying levels of curatorial care afforded to specimens, and the ravages of age and wartime, many specimens have been damaged, destroyed, or lost. Furthermore, the original descriptions of some taxa were not based on specimens examined firsthand but rather were from a written description and/or illustration provided by an untrained amateur naturalist and/or adventurer who may have seen the animal only briefly or were from prepublication copies of fragmentary text or illustrations distributed among colleagues.

The systematic and nomenclatural confusion regarding Indian Ocean octopodines began in 1826. In that year, Audouin (1826:10) and Orbigny (1826:144) both described the same new taxon, *Octopus horridus*, based on a figure by Savigny (1817). In the same year, Blainville (1826) described *O. filamentosus* from Mauritius. Also in that year, Férussac and Orbigny distributed to interested colleagues prepublication figures of a conspecific specimen under the name of *O. aranea*. Although the actual date of formal publication of this illustration was not until 1834, Orbigny (in Férussac and Orbigny, 1834–1848) contended that his use of the name *O. aranea* had priority over Blainville's *O. filamentosus* based on the distribution of the figure. The systematic disposition of this taxon was further complicated by an apparent subsequent exchange of one of the syntypes of *O. aranea* for a "better" specimen, determined herein not to be conspecific.

Addition of the majority of new taxa throughout the remainder of the nineteenth century and up to the present time is roughly correlated with at least one of two factors: (1) periods dominated by the enthusiasm of voyages of adventure

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and discovery; and (2) the presence of an active cephalopod worker. Hoyle, working with collections and material collected in the Maldivic Islands by the Gardiner Expedition in 1899 and by W.A. Herdman in Ceylon in 1902, described three species: *Polypus arborescens* Hoyle, 1904; *P. herdmani* Hoyle, 1904; and *P. gardineri* Hoyle, 1905. Krauss (1848) described *Octopus argus* from the Natal coast of South Africa. After a nearly one-half century hiatus in the description of new taxa from this region, Goodrich (1896) described *O. microphthalmus* from the Andaman Islands and, two years later, Joubin (1898) described *O. horsti* from the Red Sea.

In 1926, Robson, working at the British Museum (Natural History), erected *Octopus taprobanensis* and *O. winckworthi* from material collected off southern India and Ceylon. Three years later he (Robson, 1929) created a new genus, *Macrochlaena*, for the sole inclusion of *M. winckworthi* and described three new varietal forms, *O. cyanea gracilis* from Madras, *O. hoylei annae* from the Arabian Sea, and *Joubinia fontaniana africana* from the Natal coast of South Africa.

During a 35 year period beginning in 1938, Adam described four new species, three from the Red Sea, *O. nierstraszi* Adam, 1938, *Octopus robsoni* Adam, 1941, and *Octopus nanus* Adam, 1973, and one from the Andaman Islands, *Octopus prashadi* Adam, 1939. A contemporary of Adam's, G. Pickford, following the publication of a lengthy series of papers on the Octopoda of the Americas, produced a manuscript on the octopods from the Indo-Malayan region. Regrettably, this manuscript, completed about 1955 and containing a wealth of descriptive, morphometric data based on the examination of a large series of specimens from the collections of the British Museum (Natural History) (now The Natural History Museum, London), was never published. Prior to her death in 1986, she generously provided copies of her ambitious manuscript to several practicing octopod systematists, including myself, all of whom came to appreciate it as a valuable revisionary work on one of the most complex octopod faunas in the world. Her work is referred to herein as "Pickford (MS)." The most recent additions to the octopods from the Indian Ocean are *Berrya keralensis* Oommen, 1966, and *Octopus varunae* Oommen, 1971, both from the coast of India.

In addition to the systematic and nomenclatural problems noted above, distributional information for the majority of the octopod fauna of the Indian Ocean and adjacent seas is equally uncertain. Although the body of literature on this fauna is replete with distributional records, many of these are suspect due to faulty identifications in turn due to lack of appropriate comparative material. The distribution records given below as part of the species accounts are, by necessity, highly conservative. In many cases, taxa are indicated to be known to occur with absolute certainty from the type locality alone. Although this approach is limiting, it does have the benefit of not perpetuating misleading or erroneous information, a situation that currently plagues the body of literature pertaining to the Octopodinae of the Indian Ocean.

ABBREVIATIONS AND DEFINITIONS.—Measurements, indices, and formulae are as defined in Robson (1929), Roper and Voss (1983), and Toll (1988) with the following exceptions: the term fellow-arm index (FAI) is used in place of opposite-arm index (OAI), but it is defined in the same way; calamus-length index is abbreviated CLI; arm-length index (ALI) is defined as the length of the longest arm as a percentage of the total length (not mantle length as stated by those authors). Other abbreviations used in the species accounts are as follows:

ASC	arm-sucker count
HALI	hectocotylyzed-arm length index
HASC	hectocotylyzed-arm sucker count
HWI	head-width index
LLI	ligula-length index
ML	dorsal-mantle length
MWI	mantle-width index
PLI	penis-length index
SIe	enlarged-sucker index
SIn	normal-sucker index
SpLI	spermatophore-length index
TL	total length
WDI	web-depth index

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions are used in the text:

BMNH	The Natural History Museum, London (formerly, British Museum (Natural History))
IMC	Indian Museum, Calcutta
MNHN	Muséum National d'Histoire Naturelle, Paris
MOLK	Museum of the Oceanographic Laboratory, University of Kerala, India
MRHB	Musée Royal d'Histoire de Belgique, Bruxelles
NMSA	Natal Museum, South Africa
RML	Royal Museum, Leiden
SMF	Senckenberg Museum, Frankfurt
TAU	Tel Aviv University
UMZC	University Museum of Zoology, Cambridge

Regrettably, type material housed in collections of the Indian Museum, Calcutta, was not made available on loan for study. As a result, several acute systematic problems could not be addressed.

The generic scheme used herein follows that given by Toll (1992, MS). Taxa treated herein are arranged alphabetically with regard to the specific epithet (see Table 1).

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TABLE 1.—Nominal taxa treated herein with current systematic disposition. Nominal taxa are listed alphabetically by specific epithet.

Nominal taxon	Current disposition
<i>Octopus appendiculatus</i> Blainville, 1826	nomen dubium
<i>Octopus aranea</i> Orbigny, 1834, in Férussac and Orbigny, 1834–1848	= <i>Octopus filamentosus</i> Blainville, 1826
<i>Octopus arborescens</i> (Hoyle, 1904)	valid
<i>Octopus argus</i> Krauss, 1848	= <i>Octopus horridus</i> Orbigny, 1826
<i>Octopus cyanea gracilis</i> Robson, 1929	= <i>Octopus cyanea</i> Gray, 1849
<i>Octopus filamentosus</i> Blainville, 1826	valid
<i>Octopus fimbriatus</i> Rüppell in Orbigny, 1841, in Férussac and Orbigny, 1834–1848	= <i>O. horridus</i> Orbigny, 1826
<i>Robsonella fontaniana africana</i> (Robson, 1929)	nomen dubium
<i>Octopus gardineri</i> (Hoyle, 1905)	valid
<i>Octopus glaber</i> Rüppell in Wülker, 1920	= <i>Octopus cyanea</i> Gray, 1849
<i>Octopus herdmani</i> (Hoyle, 1904)	= <i>Octopus cyanea</i> Gray, 1849
<i>Octopus horridus</i> Orbigny, 1826	valid
<i>Octopus horsti</i> Joubin, 1898	= <i>Octopus cyanea</i> Gray, 1849
<i>Pteroctopus hoylei annae</i> (Robson, 1929)	= <i>Pteroctopus hoylei</i> (Berry, 1909)
<i>Octopus incertus</i> Targioni-Tozzetti, 1869	nomen dubium
<i>Pteroctopus keralensis</i> (Oommen, 1966)	valid
<i>Octopus microphthalmus</i> Goodrich, 1896	valid
<i>Octopus nanus</i> Adam, 1973	valid
<i>Hapalochlaena nierstraszi</i> (Adam, 1938)	valid
<i>Octopus prashadi</i> Adam, 1939	? valid (? = <i>Octopus winckworthi</i> Robson, 1926)
<i>Octopus robsoni</i> Adam, 1941	valid
<i>Octopus savignyi</i> Deshayes in Adam, 1959	nomen nudum
<i>Octopus taprobanensis</i> Robson, 1926	nomen dubium
<i>Octopus varunae</i> Oommen, 1971	? valid
<i>Octopus winckworthi</i> Robson, 1926	? valid

octopodine material examined during the 1988 Cephalopod International Advisory Council workshop. Special appreciation is reserved for Michael Sweeney for his accomplishments in the enormous task of supervising the assembled type collections during the period of the workshop, help in obtaining copies of rare, old systematics accounts, and for his general assistance, always with good humor. Sue Armentrout and Nancy Voss assisted in obtaining additional literature. This study was supported by a grant from the National Science Foundation (BSR 8508439) and by general research support from The University of the South and Wesleyan College.

### Species Accounts

#### *Octopus appendiculatus* Blainville, 1826

DIAGNOSIS.—Animals moderate in size. Body rounded, arms long, attenuate. Three cirri over each eye.

ORIGINAL DESCRIPTION.—Blainville, 1826:185.

TYPE LOCALITY.—Indian Seas.

TYPE.—*Holotype*: Not designated (the type figures are those by Koelreuter, 1761, pls. 11, 12).

DISCUSSION.—The diagnosis is excerpted from Blainville's (1826) brief original description in which he stated that the

taxon is known only from the account of Koelreuter (1761). Denys de Montfort (1802) also referred to that account. With little substantiative data on locality and morphology and without an extant type, *Octopus appendiculatus* is considered herein to be a nomen dubium.

#### *Octopus aranea* Orbigny, 1834, in Férussac and Orbigny, 1834–1848

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Orbigny, 1834, in Férussac and Orbigny, 1834–1848, atlas, Poulpes, pl. 5.

TYPE LOCALITY.—Western Indian Ocean, Île de France (= Mauritius).

TYPES.—*Syntypes*: MNHN 5-5-1937, immature female, 18 mm ML, collected by Col. Mathieu (also listed as holotype of *O. filamentosus* Blainville, 1826); MNHN 5-5-1938, female, 26 mm ML, collected by Quoy and Gaimard; female, 19.6 mm ML, collected by Mathieu (Île de France) (note: this specimen, labeled as a syntype and bearing the number MNHN 5-5-1939, is not an original member of the syntypic series) (see Lu et al., 1995; see also "Discussion").

DISCUSSION.—One syntype (MNHN 5-5-1939) of *Octopus aranea* was examined. The specimen was apparently on display

at the MNHN at one time; there is a string tied to and extending from the apex of the mantle. At one time this string was connected to a glass float and served to suspend the specimen while on exhibition. Arm pair I is more robust and considerably longer than all other arm pairs. Lu et al. (1995) indicated that another of the syntypes (MNHN 5-5-1938), collected by Quoy and Gaimard, was the actual specimen figured by Orbigny (1834, pl. 5, in Férussac and Orbigny, 1834–1848). Orbigny (in Férussac and Orbigny, 1834–1848) adequately described and illustrated this specimen; the arms are distinctly unequal in length and the arm formula is  $IV > III > II > I$ . Based on this dichotomy between the two “type” specimens and the knowledge of “wanton renaming and re-labelling of specimens” at the MNHN during the period of the turn of the century (Lu et al., 1995), the specimen currently labeled MNHN 5-5-1939 is not conspecific with *O. aranea* and, in all probability, is not the specimen collected in 1826 by Mathieu. The remaining syntype (MNHN 5-5-1937) is also the holotype of *O. filamentosus* Blainville, 1826 (see that taxon, below).

Orbigny (in Férussac and Orbigny, 1834–1848) gave 1826 as the year of publication for his plate (Poulpe, pl. 5) that contains the illustration of *O. aranea* and listed *O. filamentosus* Blainville, 1826, in synonymy. Tillier and Boucher-Rodoni (1994) determined that the actual date of publication for this plate was 22 September 1834, along with livraisons 1–3 of the text. Orbigny (in Férussac and Orbigny, 1834–1848) indicated that he had distributed individually the plate to several colleagues in 1826. The International Code of Zoological Nomenclature (ICZN) (1985:17, Art. 9) states that “distribution only to colleagues or students of a note, even if printed, in explanation of an accompanying illustration . . . does not . . . constitute publication within the meaning of the Code.” Therefore, the first valid publication referable to this taxon is Blainville’s (1826) use of the name *O. filamentosus*, eight years prior to Orbigny’s (1834, in Férussac and Orbigny, 1834–1848) publication of the named illustration of *O. aranea*. Robson (1929) considered *O. aranea* to be a junior synonym of *O. filamentosus*. That decision is supported herein (see that taxon, below).

#### *Octopus arborescens* (Hoyle, 1904)

DIAGNOSIS.—Animals small (to 12 mm ML). Mantle oblong, ending in acuminate point posteriorly (MWI 60–62); head wider than mantle (HWI 70–87); eyes not prominent. Funnel organ W-shaped. Arms short to moderate in length (ALI 70–73), arms I shortest, arms IV longest. Proximal 3 to 4 suckers uniserial, becoming biserial distally; especially enlarged suckers present in male. Right arm III of males hectocotylized, subequal to fellow arm in length; ligula small (LLI 2.5–6.6). Web moderate to deep (WDI 26–50). Gill lamellae 5 to 6. Spermatophores small (SpLI 37). Radula with  $A_2$  seriation of rachidian. Surface of mantle, head, and arms covered with branched papillae to 2 mm tall; largest papillae at

posterior end of mantle, 1 to 2 papillae over each eye, about 12 papillae on dorsal surface of mantle, fewer on ventral surface, 1 to 2 papillae on aboral surface of each arm. Color dull grey with irregular, oval, ring-like markings on dorsal surface of mantle, head, and bases of arms.

ORIGINAL DESCRIPTION.—Hoyle, 1904:189, pl. 2: figs. 8, 9, 12, pl. 3, as *Polypus arborescens*.

TYPE LOCALITY.—Northern Indian Ocean, western Ceylon (= Sri Lanka), Cheval Pearl Bank, Gulf of Manaar; Periya Paar; between Negombo and Chilaw.

TYPES.—*Syntypes*: BMNH 1947.5.5.51, 1, sex undetermined, ~6 mm ML, specimen previously dried, dark and hardened, in alcohol, in poor condition; BMNH 1947.5.5.1–4 (fide Pickford, MS), 4, sex undetermined, condition unknown (see also “Discussion,” below). (Note: the original description lists 10 syntypes. The disposition of the remaining five syntypes, not listed above, is unknown, and these types were not traced; see also “Discussion.”)

DISTRIBUTION.—Northern Indian Ocean?

DISCUSSION.—The diagnosis is based on the original description, my examination of one of the syntypes (BMNH 1947.5.5.51), and data excerpted from the accounts of Robson (1929), Adam (1938a, 1939, 1954), and Pickford (MS). Hoyle (1904) listed 10 syntypes of *Octopus arborescens*. In addition to the syntype that I examined, Pickford (MS) indicated that four additional syntypes (BMNH 1947.5.5.1–4) were extant. Robson (1929) listed the University Museum, Liverpool, as the sole type repository. Therefore, it is possible that the remainder of the syntypic series, or at least some portion of it, is housed there. *Octopus arborescens* is distinctive, and its identification should not prove problematic.

#### *Octopus argus* Krauss, 1848

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Krauss, 1848:132, pl. 6: fig. 26.

TYPE LOCALITY.—Southwestern Indian Ocean, South Africa, Natal Province.

TYPE.—Not designated.

DISCUSSION.—Based on the excellent illustration by Krauss (1848), along with his original description, *Octopus argus* is a junior synonym of *O. horridus* Orbigny, 1826 (see “Discussion,” that taxon); therefore, it is not separately diagnosed.

#### *Octopus cyanea gracilis* Robson, 1929

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Robson, 1929:98.

TYPE LOCALITY.—Northern Indian Ocean, western Bay of Bengal, India, Madras.

TYPE.—*Holotype*: BMNH 1907.9.28.1, female.

DISCUSSION.—This taxon was erected as a varietal form based solely on the holotype, which was not examined herein.



The ICZN (1985:87, Art. 45g) states that “a new name published expressly for a ‘variety’ ... is ... (ii) subspecific if published before 1961.” That is the case here. Robson (1929) noted that this “well marked” form differed from *Octopus cyanea* Gray, 1849, in having a narrow, elongate mantle (MWI 46), the confluence of the pigmented maculations down the arms, and to a lesser extent, more “prominent” eyes, a “freer” funnel, and possible greater attenuation of the arms, a character Robson himself conceded could be artificial in nature. This combination of characters seems insufficient to establish a subspecies, and it is my opinion that *O. c. gracilis* should be considered a junior synonym of *O. cyanea* (for a complete account of *O. cyanea* see Stranks, 1998).

### *Octopus filamentosus* Blainville, 1826

DIAGNOSIS.—Animals small-bodied (18 mm ML). Mantle elongate (MWI 44.4); neck slightly constricted; head narrow (HWI 41.7); eyes small. Arms long (ALI ~88.1), slender, tapering to attenuate tips, arm formula  $IV > III > II > I$ , greatly disparate in length. Gill lamellae 8(?).

ORIGINAL DESCRIPTION.—Blainville, 1826:188.

TYPE LOCALITY.—Western Indian Ocean, Île de France (= Mauritius).

TYPE.—*Holotype*: MNHN 5-5-1937, immature female, 18 mm ML, in alcohol, funnel and buccal mass removed and not with specimen, presumed lost, arms artifactually elongate, overall condition fair to poor (also a syntype of *Octopus aranea* Orbigny, 1834, in Férussac and Orbigny, 1834–1848).

DISTRIBUTION.—Western Indian Ocean?

DISCUSSION.—The diagnosis is based on my examination of the holotype. Although many characters are unavailable due to the present poor condition of the specimen, the disparity in relative arm lengths makes this species easily recognizable. The holotype of *O. filamentosus* is also a syntype of *O. aranea*. Orbigny (in Férussac and Orbigny, 1834–1848) considered the two taxa to be synonyms, with his *O. aranea* having priority (see that taxon, above). Robson (1929) placed *O. aranea* into the synonymy of *O. filamentosus*, a decision supported herein. Pickford (MS) considered *O. filamentosus* to be a synonym of both *O. horridus* Orbigny, 1826 (see that taxon, below), and *O. niveus* Lesson, 1830 (see Toll and Voss, 1998, for an account of that taxon). At present there is insufficient evidence to support her decision, and I retain *O. filamentosus* as distinct.

### *Octopus fimbriatus* Rüppell in Orbigny, 1841, in Férussac and Orbigny, 1834–1848

DIAGNOSIS.—Animals small to medium-sized (19.5 mm ML). Mantle rounded medially, pointed apically (MWI 88.7); neck region relatively long and strongly constricted; head broad (HWI 69.2); eyes strongly projecting. Funnel tapered, narrow at aperture, funnel organ W-shaped, outer limbs about

20% shorter than medial limbs. Arms long (ALI 81.1), tapering to slender tips. Suckers moderate in size (SIn 11.8), deeply set into arms; in males, 6, 14, and 18 suckers especially enlarged on arms II, III, and IV, respectively, beginning with sucker number 10 or 11; enlarged suckers increase in size from arms II to arms IV (Sle 20.5). Right arm III of male hectocotylized (HALI 302.6), shorter than fellow (FAI 76.6); ligula small (LLI 1.8), narrow, pointed apically, with shallow groove with weak transverse laminae; calamus large (CLI 33.3), pointed, HASC 90. Web shallow (WDI 14.8), web formula  $A = E > C = D > B$ , but all sectors subequal. Gill lamellae 6. Male with simple, moderately sized penis (PLI 24.1) with short rounded diverticulum roughly in line with long axis of penis. Surface of mantle, head, and arms with numerous unbranched, warty papillae, general skin texture warty. Color in preservation (alcohol) tan to brown with dark splotches on head and mantle and a reticulated pattern of brown splotches on a dark background down the dorsal and aboral surfaces of the arms; ventral surfaces of mantle and arms lighter.

ORIGINAL DESCRIPTION.—Rüppell in Orbigny, 1841:64, in Férussac and Orbigny, 1834–1848.

TYPE LOCALITY.—Red Sea.

TYPES.—*Syntypes*: SMF 25993/2, 2 males, both 19 mm ML, in alcohol, good condition (label indicates incorrectly that these are also the types of *Octopus horridus*; see “Discussion,” below, see also that taxon).

DISCUSSION.—The diagnosis is based on the better of the two male syntypes examined herein. Orbigny’s (1841, in Férussac and Orbigny, 1834–1848) defective original description of *Octopus fimbriatus* was excerpted from a manuscript by Rüppell and included additional information from a letter by de Haan. Orbigny (1841, in Férussac and Orbigny, 1834–1848) noted that the specimens could actually belong to either *Octopus horridus* Orbigny, 1826, or *O. tuberculatus* Blainville, 1826. The situation was further complicated because the museum label found along with the syntypes of *O. fimbriatus* indicated that they are also the syntypes of *O. horridus* from the Red Sea. Robson (1929:93) stated that “if [these] specimen[s] [were] the one[s] described by de Haan to Orbigny, the latter has to his credit the singular achievement of describing two different species from one and the same type!” Rüppell’s specimens, however, were deposited in Senckenberg in 1827; Rüppell’s voyage to the Red Sea was from 1822–1827 (R. Janssen, pers. comm. to C.F.E. Roper, 9 June 1988). Savigny’s plates of the mollusks and other organisms, including the figure designated by Orbigny (1826) as the type figure for *O. horridus*, were published in 1817 (Bouchet and Danrigal, 1982). Therefore, the specimen illustrated by Savigny (1817) could not have been collected by Rüppell. Wülker (1920), Robson (1929), and Adam (1959) all placed *O. fimbriatus* into the synonymy of *O. horridus*. Based on my examination of the syntypes of *O. fimbriatus* and on comparison to the type illustration of *O. horridus* by Savigny (1817), I concur with these earlier accounts and retain *O. fimbriatus* as a synonym.

***Robsonella fontaniana africana* (Robson, 1929)**

DIAGNOSIS.—Differing from nominal species as follows: arms more unequal in length, with greatest disparity 26% of longest arm; ALI 83. Web sectors unequal, with disparity index (sensu Robson, 1929) 56%. Funnel about 78% web length.

ORIGINAL DESCRIPTION.—Robson, 1929:189, as *Joubinia fontaniana africana*.

TYPE LOCALITY.—Africa, off Natal.

TYPE.—*Holotype*: NMSA, female, ~41 mm ML (measured by Massy (1925) from “end of body to mantle margin,” condition unknown.

DISCUSSION.—Robson proposed *Joubinia fontaniana africana* as a new varietal (= subspecies) form based on Massy's (1925) description of a specimen from Natal. The four characters he used to distinguish this taxon from the nominal subspecies form the diagnosis given above. The generic name *Joubinia* was preoccupied; *Robsonella* was erected by Adam (1938b) in replacement. The specimen is a female. Because the majority of characters used to define species of *Robsonella* are aspects of the male secondary sex characters (penis diverticulum and hectocotylus morphology), it was inadvisable for Robson (1929) to have erected a new subspecies solely on the basis of Massy's description of a female specimen. At present, without examination of the holotype, it is impossible to establish the identity of this specimen. Furthermore, examination of the female type, if extant, could prove inconclusive. Therefore, I recommend that *Robsonella fontaniana africana* be considered a nomen dubium.

***Octopus gardineri* (Hoyle, 1905)**

DIAGNOSIS.—Animals small (12.5–18 mm ML). Mantle elliptical to pear-shaped (MWI 66.6–68.0); neck constricted; head and mantle subequal in width (HWI 55.5–76.0); eyes bulbous, prominent. Funnel elongate, tapering, funnel organ W-shaped, outer limbs 25%–33% shorter than inner limbs. Arm length moderate (ALI 71.0–76.8), arm formula variable (subequal?), arms slender, tapering to tips. Suckers slightly elevated, moderate to large (SI<sub>n</sub> 16.7–16.8); in males, 5th and 6th or 6th and 7th suckers on arms II and III especially enlarged (SI<sub>e</sub> 20–24). Right arm III of males hectocotylized (HALI 208–250), subequal in length to fellow arm; ligula small (LLI 2.4–3.1), triangular, pointed, relatively broad, with central groove; calamus moderate in size (CLI 18.8), pointed, HASC 54. Web deep (WDI 34.8). Gill lamellae 5. Penis with rounded diverticulum extending at approximately right angle to long axis of penis (PLI 17.3–20.0). Surface of mantle, head, and arms smooth. Color in preservation uniformly tan to greenish grey.

ORIGINAL DESCRIPTION.—Hoyle, 1905:976, figs. 144, 145, as *Polypus gardineri*.

TYPE LOCALITY.—North central Indian Ocean, Maldivé Islands, Rotuma, Minikoi, Male Atoll, Hulule.

TYPES.—*Syntypes*: UMZC, 1 male, 12.5 mm ML, Hoyle label no. 860; UMZC, 1 male, 18 mm ML, Hoyle label no. 372; specimens in alcohol, good condition; disposition of 4 additional syntypes unknown, not traced.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—Hoyle's original syntypic series contained six specimens, two of which, indicated above, I examined. These form the basis for the diagnosis. The whereabouts of the remaining syntypes are unknown; it is likely that they are no longer extant. The extant syntypes are adequate to support this taxon. Pickford (MS) considered *Octopus gardineri* to be a synonym of *O. berenice* Gray, 1849; however, as that taxon is now considered to be a nomen dubium (see Toll and Voss, 1998), that conclusion is no longer tenable.

***Octopus glaber* Rüppell in Wülker, 1920**

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Rüppell in Wülker, 1920:51.

TYPE LOCALITY.—Red Sea.

TYPE.—*Holotype*: SMF, female, ML undetermined, in alcohol (R. Janssen, pers. comm., 1988).

DISCUSSION.—The name *Octopus glaber* appears in the account by Wülker (1920) in reference to a specimen in the collections of the SMF collected by Rüppell and with a museum label bearing that binomen. Wülker (1920) noted only two characters: the ocelli between the bases of arms II and III, and the presence of dark spots along the arms near the bases of the suckers. Wülker attributed the specimen to *Polypus horsti* (Joubin, 1898), now recognized as a junior synonym of *O. cyanea* Gray, 1849. Robson (1929) cited Wülker's (1920) account of *O. glaber* and tentatively attributed the specimen to *O. cyanea*. Based on the two characters given by Wülker (1920) in his description of *O. glaber* and the distinctiveness of *O. cyanea*, I support Wülker's judgement and retain *O. glaber* in synonymy. (For a complete account of *O. cyanea*, see Stranks, 1998.)

***Octopus herdmani* (Hoyle, 1904)**

DIAGNOSIS.—Animals medium-sized to large (to 95 mm ML; to 550 mm TL). Mantle width moderate (MWI 61). Arms moderate in length (ALI 65), stout, arm formula II = IV > III > I. Suckers densely spaced, first 4 dorsal suckers uniserial. Surface of mantle with numerous papillae, some elongate anteroposteriorly; 4 papillae form rhombus centered on midline; 2 or 3 minute warts above and behind each eye. Arms I and III with several elongated papillae. Color in preservation dull brownish grey dorsally. Large ocellus present at base of arms III consisting of pale center surrounded in turn by broad dark ring, narrow pale ring, and narrow dark ring.

ORIGINAL DESCRIPTION.—Hoyle, 1904:187, pl. 1, as *Polypus herdmani*.

TYPE LOCALITIES.—Northern Indian Ocean, Ceylon (= Sri

Lanka): Galle; Palk Bay; north of Periya Paar; Pearl Banks, Gulf of Manaar; south end of Cheval Paar.

TYPES.—*Syntypes*: BMNH 1947.5.5.5, 1, sex undetermined, 10 mm ML, Hoyle no. 216, previously dried, blackened, in alcohol, poor condition; BMNH 1947.5.5.6–8, 3, sex undetermined, 6 mm ML, 6 mm ML, 10 mm ML, Hoyle nos. 224–226, previously dried, darkened, in alcohol, poor condition; disposition of 5 additional syntypes unknown, not traced.

DISCUSSION.—The diagnosis is excerpted from the original description by Hoyle (1904) and is based on the largest syntype. Hoyle (1904) designated nine syntypes in his original description. Of those, four are extant (contrary to Robson's (1929:87) assertion that "the type" (= syntypic series?) was no longer extant). The extant specimens are small and in poor condition due to prior desiccation. One (BMNH 1947.5.5.5) was apparently already dry at the time of Hoyle's examination. No substantive information can now be derived from the extant syntypic series. Based on Hoyle's original description, however, there is little doubt that this taxon is a junior synonym of *Octopus cyanea* as suggested by Robson (1929) and Pickford (MS).

#### *Octopus horridus* Orbigny, 1826

DIAGNOSIS.—Animals small to medium-sized (to ~30 mm ML). Mantle rounded medially, pointed apically (MWI 58–88.7); neck region relatively long and strongly constricted; head moderate in width (HWI 50–80); eyes strongly projecting. Funnel tapered, narrow at aperture, funnel organ W-shaped, outer limbs about 20% shorter than medial limbs. Arms moderate to long (ALI 77–84.5), arm formula variable, typically IV = III = II > I; arms tapering to slender tips. Suckers moderate in size, larger in males (SIn 11.8–16.5) than in females (SIn 9.5–13.5), suckers deeply set into arms; in males, 6, 14, and 18 suckers especially enlarged on arms II, III, and IV, respectively, beginning with sucker number 10 or 11, enlarged suckers increase in size from arms II to arms IV (Sle 20.5). Right arm III of male hectocotylized (HALI 302–345), shorter than fellow (FAI 76.6); ligula small (LLI 1.8–4.0), narrow, pointed apically, with shallow groove with weak transverse laminae; calamus large (CLI 33.3), pointed, HASC 90. Web shallow (WDI 9.5–16.5), web sectors subequal but with tendency for sector A to be shallowest. Gill lamellae 5 to 6. Male with simple, moderately sized penis (PLI 24.1) with short, rounded diverticulum roughly in line with long axis of penis. Radula with A<sub>3</sub> seriation of the rachidian; rachidian simple with single denticle on either side of median cusp. Surfaces of mantle, head, and arms with numerous unbranched, warty papillae, single papillae typically present in center of light-colored patches; general skin texture warty. Color in life reddish magenta-purple reticulated with large, circular to oval white spots; when alarmed, ground color deepens and lighter spots become light reddish purple. Color in preservation (alcohol) tan to brown with dark splotches on head and mantle and reticulated pattern of brown splotches on dark background

down dorsal and aboral surfaces of arms; ventral surfaces of mantle and arms lighter.

ORIGINAL DESCRIPTION.—Orbigny, 1826:144.

TYPE LOCALITY.—Red Sea, Egyptian coast.

TYPES.—Not designated. The type figure is that by Savigny, 1817: *Céphalopodes*, pl. 1: fig. 2 (see also "Discussion").

DISTRIBUTION.—Red Sea, Indian Ocean, western and central Pacific Ocean? (see "Discussion").

DISCUSSION.—The diagnosis is based on the accounts by Krauss (1848) (based on the type series of *Octopus argus* (= *O. horridus*), Robson (1929), Boone (1938), Adam (1959), and my examination of the syntypes of *Octopus fimbriatus* (= *O. horridus*, see that taxon, above).

*Octopus horridus* was described as new twice in the same year, 1826, by Orbigny and by Audouin, both based upon Savigny's (1817) figure. Orbigny's (1826) account was apparently published in either January or February of that year (fide Robson, 1929:93). Sherborn (1897) was unable to fix the exact date of publication of Audouin (1826). It is noteworthy that of the 33 species accounts of octopodines in Orbigny (in Férussac and Orbigny, 1834–1848), only *O. horridus* appears without a stated authorship in the boldhead introduction to that taxon. This would suggest that Orbigny himself was unsure of the priority of authorship of *O. horridus*. Robson (1929) noted that although Orbigny had priority, his description, barely five lines long and without accompanying illustrations, could be applied to several species. Unsure of the priority, Robson (1929:91) gave the name "Orbigny" immediately followed by "(? Audouin)." The ICZN (1985:34–35, Art. 12a,b) states that "the proposal of a new ... species group name in association with an illustration of the taxon being named, or by bibliographic reference to such an illustration" is sufficient to be considered an "indication" as this term is applied to the requirements for the criteria of availability. Also, the ICZN (1985, Art. 21c (ii)) dictates that if the specific date of publication of a work cannot be definitively established, then it must be assumed to have been published on the last day of that year. Therefore, despite the defective description, Orbigny's reference to Savigny's (1817) figure constitutes sufficient indication and the valid author of *O. horridus* is Orbigny (1826).

As noted by Robson (1929) and Adam (1959), among others, *Octopus argus* Krauss, 1848, described from the Natalese coast of South Africa, is a junior synonym of *O. horridus*. Krauss' (1848) illustration clearly shows the characteristic pattern of unbranched warts on the head and mantle and the color pattern of the head, mantle, and arms. Adam (1938a, 1939, 1942, 1945, 1959, 1973) noted the similarities between *O. horridus* and *O. niveus* Lesson, 1830, and suggested that the two were separable only on the basis of color pattern. He (Adam, 1939) stated that he was inclined to believe that the two species were synonymous but deferred a final decision until the types could be examined. Pickford (MS) discussed the *O. horridus/niveus* problem in detail and considered the two to be synonyms, with

*O. horridus* having priority. She also placed *O. filamentosus* into the synonymy of *O. horridus*.

Verified records of *O. horridus* are limited largely to the Red Sea and the northern and western Indian Ocean. Rees and Stuckey (1952) stated that there are no records of this species east of the Andaman Islands; however, Adam's (1934) specimen from Mansfield Island, New Guinea, could be attributable to this species (Adam, 1973). Also, Pickford (MS) included an account of a series of small specimens with the characteristic color pattern of *O. horridus* from Christmas Island in the central Pacific Ocean. Further study is required to confirm the distribution of *O. horridus*.

#### *Octopus horsti* Joubin, 1898

DIAGNOSIS.—Animal large. Ocellus present at base of arms III. Irregular series of dark maculations along side of arms between suckers.

ORIGINAL DESCRIPTION.—Joubin, 1898:23.

TYPE LOCALITY.—Red Sea, Djeddah.

TYPE.—*Holotype*: RML, sex undetermined, ML unknown, condition unknown.

DISCUSSION.—The diagnosis is excerpted from the original description by Joubin (1898). This taxon appears to be a synonym of *Octopus cyanea* as previously suggested by Robson (1929) and Adam (1960) (see Stranks, 1998, for a complete account of *O. cyanea*).

#### *Pteroctopus hoylei annae* (Robson, 1929)

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Robson, 1929:220, fig. 89, as *Octopus hoylei annae*.

TYPE LOCALITY.—Indian Ocean, Arabian Sea, R/V *Investigator* sta 360, 13°36'N, 47°32'E, 20 Dec 1905, 130 fms (235 m).

TYPE.—*Holotype*: IMC M8125/1, male, 49 mm ML, condition unknown.

DISCUSSION.—Robson erected *Octopus hoylei annae* as a new variety (= subspecies) based on five specimens from the Persian Gulf, Arabian Sea, and south of Ceylon, described in the account by Massy (1916). He distinguished this new variety on the basis of slightly less prominent eyes, "rather" wider mantle aperture, and size of the calamus. It is informative that Robson indicated that he had not actually seen any specimens referable to *O. h. hoylei*. The differences noted by Robson are not worthy of subspecific recognition for this taxon. Furthermore, the subspecies cannot be sympatric; therefore, *O. h. annae* should be considered a junior synonym of *Pteroctopus hoylei* (Berry, 1909).

#### *Octopus incertus* Targioni-Tozzetti, 1869

DIAGNOSIS.—Mantle subovate; head short and broad; eyes protruding. Arms short. First 3 adoral suckers uniserial,

remainder biserial; ASC about 100. Web shallow, extended along arms. Mantle covered with granulations. Ocular cirri present anterior and posterior to eyes.

ORIGINAL DESCRIPTION.—Targioni-Tozzetti, 1869a:589.

TYPE LOCALITY.—Indian Ocean.

TYPE.—Not designated.

DISCUSSION.—The brief original description (Targioni-Tozzetti, 1869a) was followed by a fuller description including a figure by Targioni-Tozzetti (1869b). Targioni-Tozzetti (1869b) compared this species to *Octopus granulatus* Lamarck, 1798 (= *O. vulgaris* Lamarck, 1798), *O. rugosus* Bosc, 1792 (= *O. vulgaris* Lamarck, 1798), *O. americanus* Baker in Denys de Montfort, 1802 (nomen dubium, fide Voss and Toll, 1998), and *Octopus bakerii* Orbigny, 1826 (junior synonym of *O. americanus* Baker in Denys de Montfort, 1802, fide Voss and Toll, 1998). Robson (1929) tentatively placed *Octopus incertus* in the synonymy of *O. rugosus*. Due to the incomplete description, lack of more specific locality data, and absence of a type, I consider *O. incertus* to be a nomen dubium.

#### *Pteroctopus keralensis* (Oommen, 1966)

DIAGNOSIS.—Animals small to medium-sized (26–49 mm ML). Mantle broad, rounded (MWI 71–94); neck slightly constricted; head broad (HWI 54–82); eyes large, prominent, with small apertures. Funnel stout, compressed, free portion short, funnel organ VV-shaped, conspicuous, inner and outer limbs subequal in length, acutely pointed at ends. Arms short (ALI 65–72), stout, second pair typically longest. Suckers moderate in size, well separated, slightly elevated, no enlarged suckers in males or females. Right arm III of males hectocotylized, shorter than fellow; ligula small to moderate in size (LLI 11–15), conical with deeply excavated median groove and poorly defined transverse laminae; calamus moderate in size (CLI 18.5), conical, acutely pointed. Web exceptionally deep (WDI 38–52), web formula variable but typically A = B = C = D > E. Ink sac present, reduced; gill lamellae 11. Male with large penial apparatus (PLI 32.5), diverticulum tubular, recurved. Spermatophore large. Radula with B<sub>2</sub> seriation of rachidian. Mantle soft, semigelatinous, covered with fine reticulations with minute papillae and with scattered, small warty papillae. Two large, nipple-like and several smaller, warty supraocular cirri. Color in preservation reddish brown dorsally, paler ventrally; papillae surrounded with circlet of minute, reddish brown chromatophores.

ORIGINAL DESCRIPTION.—Oommen, 1966:51, figs. 1–6, as *Berrya keralensis*.

TYPE LOCALITY.—Northern Indian Ocean, India, off Kerala, 09°50'N, 75°36'E, 200–400 m.

TYPE.—*Holotype*: MOLK, male, 40 mm ML, condition unknown.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. Oommen (1966) compared *Berrya keralensis* with

*B. hoylei*, also reported from the Indian Ocean. Differences in web depth, ligula, radula, and number of gill filaments are insufficient to separate the two taxa at the specific level. I have determined (unpublished data) that the coiled ink duct, reported to occur in *B. hoylei*, is an artifact, and it actually has the same conformation as the straight ink duct found in *P. keralensis* by Oommen, thereby eliminating this character as a means to separate the two taxa. It is probable that *B. keralensis* is a synonym of *B. hoylei*. Toll (MS) will place *Berrya* in the synonymy of *Pteroctopus*.

#### *Octopus microphthalmus* Goodrich, 1896

DIAGNOSIS.—Animals small to medium-sized (34–40 mm ML). Mantle cylindrical (MWI 59–83); neck constrictions absent; head narrow (HWI 43–55); eyes small, deeply set. Arms long (ALI 80–88), arm formula I > II > III > IV. Suckers size moderate (SIn 7–9). Web depth shallow (WDI 10–19), web sector A deepest. Gill lamellae 7–9. Eggs large, capsule 10 mm long. Surfaces of mantle, head, arms, and web smooth to finely granular. Color in preservation yellowish brown, darker dorsally.

ORIGINAL DESCRIPTION.—Goodrich, 1896:20, pl. 5: figs. 83, 84.

TYPE LOCALITY.—Northeastern Indian Ocean, Bay of Bengal, Andaman Islands, Port Blair.

TYPE.—*Holotype*: IMC M361/1, female, ~34 mm, condition unknown.

DISTRIBUTION.—Northeastern Indian Ocean?

DISCUSSION.—The diagnosis is excerpted from Robson's (1929) examination of the holotype and Pickford's (MS) account based on new material. Robson's account is difficult to interpret because, in addition to the holotype, he also included data from a specimen reported upon by Massy (1916) that is probably not conspecific. Until additional study can be performed, I choose to retain *Octopus microphthalmus* as distinct.

#### *Octopus nanus* Adam, 1973

DIAGNOSIS.—Animals small (12–13 mm ML). Mantle rounded (MWI 66.7); neck faintly constricted; head broad (HWI 87.8); eyes large, prominent. Funnel moderately sized, funnel organ W-shaped. Arms short to moderate (ALI 69.6), arm formula variable; arms stout basally and tapering to narrow tips. Sucker size moderate (SIn 12.2), elevated; especially enlarged suckers absent in males. Right arm III of males hectocotylized (HALI 191.9), shorter than fellow (FAI 83.4); ligula small (LLI 9.7), pointed; calamus pointed, HASC 36–45. Web moderate (WDI 23.0), web formula C > B > D > A > E. Ink sac present; gill lamellae 5. Males with small penis (PLI ~15). Spermatophores small (SpLI 43–65). Radula with A<sub>3-4</sub> seriation of rachidian. Surfaces of mantle, head, and aboral aspect of arms and web finely granular; single

supraocular cirrus located over each eye. General color in preservation (alcohol) pale grey brown with some darker patches.

ORIGINAL DESCRIPTION.—Adam, 1973:42, figs. 28–32, pl. 1: figs. 1–3.

TYPE LOCALITY.—Red Sea: Cundabilu, 2–8 m (holotype); Landing Bay, Entedebir (= Andeber Deset, 15°42'N, 39°54'E), 2–8 m (paratype).

TYPES.—*Holotype*: TAU E62/2307, male, 13 mm ML, in alcohol, good condition.

*Paratype*: MRHB, male, 12 mm ML, not traced.

DISTRIBUTION.—Known positively only from the type localities.

DISCUSSION.—The diagnosis given above is based on my examination of the holotype and is supplemented with information extracted from the original description. Values from Adam's (1938a) "doubtful specimen" are not included. This taxon is not well known but appears to be distinct.

#### *Hapalochlaena nierstraszi* (Adam, 1938)

DIAGNOSIS.—Animals small (17 mm ML). Mantle round to pear-shaped, (MWI 88.2); neck constricted; head region damaged in holotype, width undetermined but narrower than mantle. Funnel broad, funnel organ W-shaped. Arms short to moderate in length (ALI 71.7), subequal in length, broad at bases and tapered distally, not attenuate. Suckers moderate in size (SIn 8.8), deeply set into flesh of arms. Web deep (WDI 33.7), web formula D > C > E > B > A. Ink sac reduced; gill with 6 to 7 lamellae. Ovarian eggs small, 2.4 mm long, 1.0 mm wide, with short stalk. Radula with multicuspid (?) rachidian of uncertain seriation. Surfaces of head, mantle, and arms papillated. Color in preservation (alcohol) tan with dark maculations on head and mantle and about 7 bands along each arm, each with indication of iridescent ring.

ORIGINAL DESCRIPTION.—Adam, 1938a:14, figs. 6A, 7A,B, 8, 9, as *Octopus nierstraszi*.

TYPE LOCALITY.—Northeastern Indian Ocean, Bay of Bengal, Aves Island (North Andaman Island).

TYPE.—*Holotype*: MRHB, female, 17 mm ML, in alcohol, good condition.

DISTRIBUTION.—Known positively only from the type locality.

DISCUSSION.—The diagnosis is based on the original description and my examination of the holotype. Adam (1938a) originally placed this taxon into *Octopus* sensu stricto, however, he noted its resemblance to the blue-ringed octopuses included in the genus *Hapalochlaena*. Apparently, Adam did not observe the faint indications of the blue iridescent rings that are present in the holotype and which now form the basis for placement of this species into the genus *Hapalochlaena*. Pickford (MS) considered it "highly probable" that this taxon is a synonym of *H. maculosa*, however any further decision must await revision of the genus.

***Octopus prashadi* Adam, 1939**

DIAGNOSIS.—Animals small (27–30 mm ML). Mantle ellipsoid (MWI 66.7–85.1); neck constriction faint; head moderately wide (HWI 56.7–63.0); eyes small, not prominent. Funnel organ VV-shaped. Arms short (ALI 68.9). Suckers small (SIn 6.7); especially enlarged suckers absent in females. Web deep, not continued up arms, web formula  $C > D > B > A > E$  or  $C = D > B = E > A$ . Ink sac present; gill lamellae 8. Radula with  $A_3$  seriation of rachidian. General color in preservation slate blue dorsally, paler ventrally.

ORIGINAL DESCRIPTION.—Adam, 1939:103, pl. II: figs. 1–3.

TYPE LOCALITY.—Indian Seas.

TYPES.—*Holotype*: IMC M4768/1, female, 30 mm ML, condition unknown.

*Paratype*: IMC M361/1, female, 27 mm ML, condition unknown.

DISTRIBUTION.—Known positively from the type locality only. The paratype is from Port Blair, Andaman Islands.

DISCUSSION.—The diagnosis is excerpted from the original description. *Octopus prashadi* bears a strong resemblance to *O. winckworthi* Robson, 1926, with respect to general shapes of the head and mantle, arm lengths, and radular morphology. Pickford (MS) provisionally placed *O. prashadi* into the synonymy of *O. winckworthi*. Because of the lack of comparative material, a final determination as to the systematic status of *O. prashadi* cannot be established unequivocally at this time.

***Octopus robsoni* Adam, 1941**

DIAGNOSIS.—Animals small to medium-sized (28–60 mm ML). Mantle round to oval (MWI 67.5–90.0); neck slightly constricted; head narrow (HWI 36.5–59.0); eyes small, deeply set. Funnel of average size, funnel organ W-shaped, inner and outer limbs subequal in length. Arms moderate in length (ALI 71–77), arm formula variable, arms I typically shortest; arms slender, tapering to fusiform tips. Suckers slightly elevated, of average size (SIn 5.7–10.6); especially enlarged suckers absent in males and females. Right arm III of males hectocotylized; ligula moderate in size (LLI 15.6–23.7), tapering to point, with central groove and weak transverse laminae; calamus small (CLI 15.7). Web moderate to deep (WDI 20–30.5), web formula variable but with sector A consistently shallowest and all others probably subequal. Gill lamellae 8–10. Radula with  $A_{2-3}$  seriation of rachidian. Surfaces of mantle, head, and arms granulated, mantle with larger papillae and up to 6 supraocular papillae in some specimens. Large ocellus, consisting of dark spot surrounded by dark ring, on each side of head between eyes and margin of web. General color in preservation (alcohol) beige with brown maculations on head and mantle; arms with brown band down ventral edges along suckers.

ORIGINAL DESCRIPTION.—Adam, 1941:1.

TYPE LOCALITY.—Gulf of Suez.

TYPES.—*Syntypes*: MNHN 5-3-1038-44, 5 females, 7 males, in alcohol, good condition.

DISTRIBUTION.—Positively known from the type locality only.

DISCUSSION.—The diagnosis is based on my examination of three of the syntypes and on a full description of the entire syntypic series by Adam (1959). Adam (1959) considered the possibility that *Octopus robsoni* could be synonymous with *O. areolatus* Weindl, 1912 (not *O. areolatus* de Haan in Orbigny, 1840, in Férussac and Orbigny, 1834–1848), but, due to the uncertainties regarding the taxonomy of the complex of ocellated octopuses of the Indo-West Pacific, chose to maintain *O. robsoni* as distinct. In a later work on the Red Sea cephalopods, Adam (1973) continued this discussion on the identity of the ocellated forms without resolution (see also Toll and Voss, 1998). Until additional study can be performed, I choose to retain *O. robsoni* as distinct.

***Octopus savignyi* Deshayes in Adam, 1959**

DIAGNOSIS.—None (see “Discussion”).

ORIGINAL DESCRIPTION.—None.

TYPE LOCALITY.—None.

TYPE.—None.

DISCUSSION.—The name *Octopus savignyi* appears in a brief reference by Adam (1959:175), who encountered it on the label with a specimen collected in the Red Sea in 1835, now in the collections of the MNHN, that he attributed to *O. macropus*. A search of all pertinent literature available to me failed to locate any additional reference to this taxon. *Octopus savignyi* is probably a museum name. Without any clear indication to the contrary, *O. savignyi* is herein considered to be a nomen nudum.

***Octopus taprobanensis* Robson, 1926**

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Robson, 1926:165, fig. 7.

TYPE LOCALITY.—Northern Indian Ocean, Ceylon (= Sri Lanka), Periya Paar, Pearl Banks.

TYPE.—*Holotype*: BMNH 1925.11.23.2, sex undetermined (immature), 20 mm ML, in alcohol, generally in good condition.

DISCUSSION.—I examined the holotype; a full diagnosis is not given because the immature specimen has few distinctive characters. The arm order is  $I > II > III > IV$ . Dermal sculpture is lacking entirely. There are 13 or 14 gill lamellae, not 10 as reported by Robson (1929), who also tentatively determined the type to be a female. The greatest likelihood is that this specimen is referable to either *Callistoctopus macropus* (Risso, 1826), *C. ornatus* (Gould, 1852), or *Cistopus indicus* (Rapp in Orbigny, 1835, in Férussac and Orbigny, 1834–1848). Pickford (MS) considered *O. taprobanensis* to be a nomen dubium. I support that decision.

*Octopus varunae* Oommen, 1971

DIAGNOSIS.—Animals medium-sized (38–62 mm ML). Mantle oval (MWI 55–70); neck slightly constricted; head narrower than mantle (HWI 31–47); eyes prominent. Funnel large, stout, conical, funnel organ W-shaped, outer and inner limbs subequal in length. Arms short (ALI 58.7–64.6), arm formula IV > III > II > I; arms stout, gradually tapering to fine tips, fourth arm typically longest, first arms shortest. Suckers small to moderate in size (SIn 6.6–14.5), slightly elevated and well separated; first 3 adoral suckers uniserial, remainder biserial; suckers on arms IV larger than those on other arms; especially enlarged suckers on arms II and III of males only. Right arm III of males hectocotylized, subequal to fellow arm; ligula small (LLI 14.2–15.3), slender, with shallow median groove and 5 to 6 weakly developed transverse laminae; calamus reported not to exist as definite projection; however, illustrated as small and vermiform (CLI 16.5). Web exceptionally deep (WDI 65), web formula  $C = D = E > B > A$  or  $E > D = C > B > A$ . Gill lamellae 10. Ovarian eggs small, capsule 2 mm long, 0.5 mm wide. Penis simple, elongate (PLI 37); penis diverticulum bulbous. Radula with  $A_3$  seriation of rachidian. Dorsal surface of mantle with small papillae extending to oral surface of web sector A, papillae fused into small (3–4 mm) ridge along midsection of mantle, ventral mantle with fewer minute papillae, nearly smooth; 3 prominent supraocular cirri. Ocellus present on each side of head between eyes and margin of web. General color in preservation brownish red dorsally, paler ventrally, dark bands extended down dorsal side of arms near base of suckers.

ORIGINAL DESCRIPTION.—Oommen, 1971:69, figs. 1–6.

TYPE LOCALITY.—Arabian Sea, 14°18'N, 73°35'E, 125–135 m.

TYPE.—*Holotype*: Museum deposition not indicated, assumed to be in collections of MOLK, female, 59 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. The systematics of the ocellated octopods from the Indo-West Pacific are confused at present (see Toll and Voss, 1998). Oommen (1971) compared *Octopus varunae* with only three other ocellate forms chosen on the basis of their reported occurrence in the Bay of Bengal, namely, *O. herdmani* (Hoyle, 1904) (= *Octopus cyanea* Gray, 1849), *O. cyanea* Gray, 1849, and *O. areolatus* de Haan in Orbigny, 1840, in Férussac and Orbigny, 1834–1848. Because of the uncertain distribution of many of the ocellate forms, Oommen's criterion for choosing

these three taxa is defective. Until the types of *O. varunae* can be examined and compared to all other ocellated octopods known to occur in the Indian Ocean, the only recourse is to maintain *O. varunae* as distinct, albeit somewhat doubtful.

*Octopus winckworthi* Robson, 1926

DIAGNOSIS.—Animals small to medium-sized (32.8 ML). Mantle elongate (MWI 58.8), widest medially; neck slightly constricted, nearly confluent to mantle (HWI 51.5); eyes small, deeply set into head. Funnel short, nipple-like, funnel organ VV-shaped, outer limbs about 33% shorter than inner limbs. Arms short (ALI 64.1), subequal in length; arms tapering to tips but not filiform. Suckers small in size (SIn 4.6), slightly elevated; especially enlarged suckers absent in males and females. Right arm III of male hectocotylized (HALI 136.4), shorter than fellow arm (FAI 76.9); ligula short (LLI 4.3), triangular, with shallow medial groove and thickened borders; calamus small (CLI 14.3), triangular, pointed, HASC 40. Web deep (WDI 32.1), web formula  $C > D > B > A > E$ . Gill lamellae 10. Radula simple, with  $A_2$  seriation of rachidian. Surfaces of mantle, head, and arms finely papillose. Ventral and oral surfaces smooth. Several small, warty papillations above and below each eye. General color in preservation (alcohol) tan with darker brown mottling on dorsal surfaces of mantle, head, and arms.

ORIGINAL DESCRIPTION.—Robson, 1926:161, figs. 1–6.

TYPE LOCALITY.—Northern Indian Ocean, southern India, Tuticorin.

TYPE.—*Holotype*: BMNH 1925.11.23.1, male, 32.8 mm ML, in alcohol, good condition, pliable. Beaks, radula, and one gill not with the type and must be considered no longer extant.

DISTRIBUTION.—Known positively only from the type locality.

DISCUSSION.—Toll (MS) considers *Macrochlaena* (erected by Robson, 1929, for this species) to be a synonym of *Octopus sensu stricto* (as defined currently). Pickford (MS) considered *O. winckworthi* to be a synonym of *Octopus prashadi* Adam, 1939 (see that taxon, above). The two taxa share many features, such as small bodied, elongate mantle, short arms, funnel organ morphology, and deep web. Pickford's (MS) assertion as to the systematic relationship of these two taxa is probably correct; however, until the type material of *O. prashadi* can be examined comparatively, I choose to maintain *O. winckworthi* as distinct.

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# The Systematic and Nomenclatural Status of the Octopodinae Described from the West Pacific Region

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## ABSTRACT

Eighty-two nominal species and subspecies of octopodines originally described from the West Pacific region, herein defined as the Pacific Ocean from the Bering Sea to the Straits of Malacca, and eastward to include all of Oceania but excluding Australia, New Zealand, and Tasmania, are treated systematically. Forty-four taxa are retained as distinct; however, many of these are poorly known and are badly in need of additional study in order to clarify remaining systematic problems: *Octopus alatus* (Sasaki, 1920); *O. areolatus* de Haan in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848; *O. bocki* Adam, 1941; *O. brocki* Ortmann, 1888; *O. conispadiceus* (Sasaki, 1917); *O. dofleini dofleini* Wülker, 1910; *Pteroctopus eurycephala* (Taki, 1964); *O. fangsiao etchuanus* (Sasaki, 1929); *O. fangsiao typicus* (Sasaki, 1929); *O. favonius* Gray, 1849; *O. fujitai* (Sasaki, 1929); *O. globosus* Appellöf, 1886; *O. guangdongensis* Dong, 1976; *O. hardwickei* Gray, 1849; *O. hattai* (Sasaki, 1929); *O. hongkongensis* Hoyle, 1885; *P. hoylei* (Berry, 1909); *Cistopus indicus* (Rapp in Orbigny, 1835, in Férussac and Orbigny, 1834–1848); *O. kagoshimensis* Ortmann, 1888; *O. kermadecensis* (Berry, 1914); *O. longispadiceus* (Sasaki, 1917); *Hapalochlaena lunulata* (Quoy and Gaimard, 1832); *O. luteus* (Sasaki, 1929); *O. minor minor* (Sasaki, 1920); *O. minor pardalis* (Sasaki, 1929); *O. minor typicus* (Sasaki, 1929); *O. mutilans* Taki, 1964; *O. nanhaiensis* Dong, 1976; *O. ochotensis* (Sasaki, 1920); *O. oliveri* (Berry, 1914); *Callistoctopus ornatus* (Gould, 1852); *O. oshimai* (Sasaki, 1929); *O. ovulum* (Sasaki, 1917); *O. parvus* (Sasaki, 1917); *Scaeurgus patagiatus* Berry, 1913; *O. rapanui* Voss, 1979; *O. sasakii* Taki, 1942; *O. spinosus* (Sasaki, 1920); *O. striolatus* Dong, 1976; *O. tonganus* Hoyle, 1885; *O. tsugarensis* (Sasaki, 1920); *O. vitiensis* Hoyle, 1885; *O. wolffi* (Wülker, 1913); *O. yendoii* (Sasaki, 1920).

Sixteen taxa are recognized, some provisionally, as junior synonyms of other described taxa or are almost certainly synonyms of an undetermined species: *Octopus aculeatus* Orbigny, 1834, in

Férussac and Orbigny, 1834–1848 (= *O. filamentosus* Blainville, 1826); *Hapalochlaena albidus* Taki, 1962 (= *Pteroctopus hoylei* (Berry, 1909)); *C. arakawai* Taki, 1964 (? = *C. ornatus* Gould, 1852); *O. araneoides* (Taki, 1964) (? = *Octopus* sp.); *O. asper* (Akimushkin, 1963) (= *O. dofleini apollyon* Berry, 1913); *Cistopus bursarius* Steenstrup in Hoyle, 1886 (= *Cistopus indicus* (Rapp in Orbigny, 1835, in Férussac and Orbigny, 1834–1848)); *O. dollfusi* Robson, 1928 (= *Octopus hardwickei* Gray, 1849); *O. harmandi* Rochebrune, 1882 (= *O. filamentosus* Blainville, 1826); *O. madokai* (Berry, 1921) (= *O. hongkongensis* Hoyle, 1885); *O. marmoratus* Hoyle, 1885 (= *O. cyanea* Gray, 1849); *O. megalops* (Taki, 1964) (= *O. hongkongensis* Hoyle, 1885); *O. niveus* Lesson, 1830 (= *O. filamentosus* Blainville, 1826); *O. ocellatus* Gray, 1849 (= *O. fangsiao* in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848); *O. tenuicirrus* (Sasaki, 1929) (= *O. hongkongensis* Hoyle, 1885); *O. tenuipulvinus* (Sasaki, 1920) (? = ssp. of *O. minor* (Sasaki, 1920)); *Pteroctopus witjazi* Akimushkin, 1963 (? = *P. hoylei* (Berry, 1909)).

Twenty taxa are considered herein to be nomina dubia: *O. aegina* Gray, 1849; *O. amboinensis* Brock, 1887; *Macrotritopus bandensis* (Hoyle, 1885); *O. berenice* Gray, 1849; *O. cephea* Gray, 1849; *M. elegans* (Brock, 1887); *O. fusiformis* Brock, 1887; *O. hawaiiensis* Souleyet in Eydoux and Souleyet, 1852; *O. hoeki* Joubin, 1898; *O. inconspicuus* Brock, 1887; *O. machikii* Brock, 1887; *O. marginatus* Taki, 1964; *O. medoria* Gray, 1849; *O. membranaceus* Quoy and Gaimard, 1832; *O. mollis* Gould, 1852; *O. pulcher* Brock, 1887; *O. pusillus* Gould, 1852; *O. sinensis* Orbigny, 1834, in Férussac and Orbigny, 1834–1848; *O. smedleyi* Robson, 1932; *O. teuthoides* Robson, 1929.

*Octopus pustulosus* (Sasaki, 1920) is preoccupied. *Octopus*

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\*The preliminary literature survey and examination of some type material during the Cephalopod International Advisory Council 1988 Workshop, "The Systematics and Biogeography of Cephalopods," were performed by the late Gilbert L. Voss. Just prior to his untimely death in January 1989, Gil had begun to prepare some of the species accounts for this contribution. Continuation of the systematic and nomenclatural evaluation of species treated herein was undertaken by the second author. The present contribution reflects the combined systematic opinions of both authors, who, fortunately, had discussed many of the prevailing systematic problems and had arrived collectively at many of the decisions advanced herein.

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*niveus* Orbigny, 1826, is a nomen nudum. A lectotype has been chosen for *O. areolatus* de Haan in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848. A neotype has been selected for *O. niveus* Lesson, 1830 (= *O. filamentosus* Blainville, 1826).

### Introduction

Since 1830, 24 systematic accounts have included the descriptions of a total of 82 species and subspecies of octopodine cephalopods from the Western Pacific region, defined herein as the Pacific Ocean from the Bering Sea to the Straits of Malacca, eastward to include all of Oceania but excluding Australia, New Zealand, and Tasmania. In addition, three species of octopods, originally described as octopodines, are now attributed to the subfamily Bathypolypodinae (Table 1) and are not considered herein. The first valid account is that by Lesson (1830), who described a single species from Bora Bora in the Society Islands. Two years later, Quoy and Gaimard (1832) described two species based on material collected during the cruise of the *Astrolabe*. Orbigny (in Férussac and Orbigny, 1834–1848) described four species from this region based on original material as well as on previously published accounts and unpublished sources. The most prolific of the 19th century authors of Western Pacific octopodine taxa was Gray (1849), who described seven species based on material in the collections of the British Museum. Brock (1887) erected six species, all from the area around Amboina. Regrettably, five of Brock's types were lost to the destruction wrought by World War II (P. Kuenzer, pers. comm., 1988, to C.F.E. Roper), and none of his taxa can be clearly identified today. Collectively, Gould (1852), Souleyet in Eydoux and Souleyet (1852), Rochebrune (1882), Hoyle (1885), Appellöf (1886), Ortmann (1888), and Joubin (1898) added a total of 14 species.

Following the turn of the century, several prominent cephalopod workers began studies that included octopodines from the West Pacific region. In a series of accounts, Berry (1909, 1913, 1914a, 1914b) described four species from the Hawaiian and Kermadec islands. Wülker (1910, 1913) described two species of octopodines from the western North Pacific Ocean. In a series of two papers and a major monographic revision of the cephalopods of Japanese seas, Sasaki (1917, 1920, 1929) described 22 octopodine taxa from

Japan, the largest contribution of new taxa by a single worker. Robson (1928a, 1929, 1932a) and Adam (1941), collectively, erected four species. Taki (1942, 1962, 1964) added seven species to the octopodine fauna of Japan. Regrettably, none of Taki's types were deposited in museums; however, there is an indication that his type material is extant, held in a private collection by a family member, and that this material could become available for study in the future (T. Okutani and I. Gleadall, pers. comm., 1990). Akimushkin (1963) described two species from the Sea of Okhotsk. Dong (1976) erected three species of *Octopus* from the poorly studied China seas. The most recent addition to the octopodine fauna of the West Pacific region was by Voss (1979), who described *Octopus rapanui* from Easter Island.

Historically, the western Pacific has been one of the areas of greatest confusion with regard to octopod systematics. Some systematics decisions are made herein; however, many complex problems remain. Particularly confusing are several groups of octopods, each representing what, for want of more complete knowledge, have been commonly referred to as "species complexes." One example is the *Callistoctopus macropus/ornatus* complex, long a catch-all taxon for large-bodied animals with long first arms and a distinctive coloration pattern consisting of white spots on a reddish orange background on the mantle, head, and arms. Recent data suggest that so-called *C. macropus* (Risso, 1826) from the Indo-West Pacific Ocean includes several distinct species and that *C. macropus sensu stricto* is an Atlantic Ocean endemic. The so-called *O. aegina/dollfusi* complex, which also includes *O. kagoshimensis* Ortmann, 1888, and *O. hardwickei* Gray, 1849, also is confused. At present, only a single character, ornamentation of the outer tunic of the spermatophore, permits separation of at least two of the species within this complex. The ocellated octopods, including *O. areolatus* de Haan in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848, *O. brocki* Ortmann, 1888, *O. fangshiao etchuanus* (Sasaki, 1929), *O. fangshiao typicus* (Sasaki, 1929), *O. membranaceus* Quoy and Gaimard, 1832, *O. ocellatus* Gray, 1849, and *O. ovulum* (Sasaki, 1917), represent yet another systematically confused group. Also, *Macrotritopus*-like forms (e.g., *O. bandensis* Hoyle, 1885, *O. amboinensis* Brock, 1887, and *O. elegans* Brock, 1887) cannot now be related conclusively to their adult forms. Finally, the so-called "long ligula" complex (*sensu*

TABLE 1.—Pacific Ocean octopod taxa originally described in the subfamily Octopodinae but now attributed to genera in the subfamily Bathypolypodinae.

Nominal taxon	Current disposition	Reference
<i>Octopus abruptus</i> Sasaki, 1920	<i>Benthoctopus abruptus</i> (Sasaki, 1920)	Robson (1932b)
<i>Polypus salebrosus</i> Sasaki, 1920	<i>Bathypolypus salebrosus</i> (Sasaki, 1920)	Robson (1932b)
<i>Polypus glaber</i> Sasaki, 1920 (preoccupied by <i>P. glaber</i> Wülker, 1920)	<i>Benthoctopus hokkaidensis</i> (Berry, 1921)	Berry (1921); Robson (1932b)

Gleadall, 1993), including *O. longispadiceus* (Sasaki, 1917), *O. conispadiceus* (Sasaki, 1917), *O. tsugarensis* (Sasaki, 1920), *O. dofleini* Wülker, 1910, and *O. asper* (Akimushkin, 1963), also is in need of modern revision.

Twenty taxa treated herein have been relegated to the status of *nomen dubia*. Lest our readers feel that too many decisions were simply avoided by the use of this category, it should be understood that the presence of so many inadequately described taxa has had the serious and deleterious effect of inhibiting the descriptions of new taxa. Many workers, keenly aware of the enormous nomenclatural and systematic confusion, have been justifiably reticent to add even more nominal species to the already burgeoning list. The names of those taxa herein considered to be *nomen dubia* remain available if future revisionary work necessitates overturning specific systematic decisions rendered herein. It is our hope that our systematic evaluations will alleviate some of this nomenclatural overburden and facilitate future rigorous, comparative investigations into the systematics of the octopodines from this region.

As much as possible, the diagnoses of taxa are based on examination of the type material or are taken from published accounts of the types. Due to the many systematic and nomenclatural problems regarding the Octopodinae from the Western Pacific region, distributional information and morphometric data from accounts based on unverified specimens have not been included.

**ABBREVIATIONS AND DEFINITIONS.**—Measurements and indices are as defined in Roper and Voss (1983) and Toll (1988) with the following exceptions: the term fellow-arm index (FAI) is used in place of opposite-arm index (OAI), but it is defined in the same way; calamus-length index is abbreviated CLI; arm-length index (ALI) is defined as the length of the longest arm as a percentage of the total length (not mantle length as stated by those authors). Ventral mantle length (VML) as defined by Brock (1887) is the length of the body to the edge of the mantle. The formulae for radular-rachidian tooth symmetry are as defined in Robson (1929). Other abbreviations used in the species accounts are as follows:

ASC	arm-sucker count
HALI	hectocotylized-arm length index
HASC	hectocotylized-arm sucker count
HW	head width
HWI	head-width index
LLI	ligula-length index
ML	dorsal-mantle length
MW	mantle width
MWI	mantle-width index
PLI	penis-length index
SIe	enlarged-sucker index
SIn	normal-sucker index
SpL	spermatophore length
SpLI	spermatophore-length index
SpW	spermatophore width
SpWI	spermatophore-width index
TL	total length
WDI	web-depth index

**INSTITUTIONAL ABBREVIATIONS.**—The following abbreviations for institutions are used in the text:

ACS	Agricultural College, Hokkaido University, Sapporo
BMNH	The Natural History Museum, London (formerly, British Museum (Natural History))
IOAS	Institute of Oceanology, Academia Sinica, Qingdao
MNHN	Muséum National d'Histoire Naturelle, Paris
NRS	Naturhistoriska Riksmuseet, Stockholm
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
SMF	Senckenberg Museum, Frankfurt
TNSM	Tokyo National Science Museum
UMM	University Museum, Munich
UMS	University Museum, Strasbourg
USNM	National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C. (housing collections of the former United States National Museum)
ZMU	Zoological Museum, Upsala
ZMUG	Zoological Museum, University of Göttingen

The generic scheme followed herein is based on that given by Toll (1992, MS). Taxa treated herein are arranged alphabetically with regard to the specific epithet (see Table 2).

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## Species Accounts

### *Octopus aculeatus* Orbigny, 1834, in Férussac and Orbigny, 1834–1848

**ORIGINAL DESCRIPTION.**—Orbigny, 1834, atlas, Poulpe (= *Octopus*) pl. 7: figs. 1, 2, pl. 8: fig. 1, in Férussac and Orbigny, 1834–1848.

**TYPE LOCALITY.**—Western Pacific Ocean, Philippines, Manila (fide Lu et al., 1995).

**TYPE.**—*Syntype*: MNHN 4-7-927, male, 36 mm ML, Perrotet (coll.), 1821 (fide Lu et al., 1995).

**DISCUSSION.**—*Octopus aculeatus* is a junior synonym of *Octopus niveus* Lesson, 1830 (see that taxon, below) (considered herein = *O. filamentosus* Blainville, 1826) and is based, in

TABLE 2.—Systematic listing and current status of the nominal species and subspecies of octopodines described from the Western Pacific Ocean region (\* indicates provisional decision, further study warranted). The nominal taxa are listed in alphabetical order by specific epithet.

Nominal taxon	Current disposition
<i>Octopus aculeatus</i> Orbigny, 1834, in Férussac and Orbigny, 1834–1848	= <i>O. niveus</i> Lesson, 1830; = <i>O. filamentosus</i> Blainville, 1826
<i>Octopus aegina</i> Gray, 1849	nomen dubium
<i>Octopus alatus</i> (Sasaki, 1920)	valid*
<i>Hapaloctopus albidus</i> Taki, 1962	= <i>Pteroctopus hoylei</i> (Berry, 1909)
<i>Octopus amboinensis</i> Brock, 1887	nomen dubium
<i>Callistoctopus arakawai</i> Taki, 1964	? = <i>C. ornatus</i> (Gould, 1852)
<i>Octopus araneoides</i> (Taki, 1964)	? = <i>Octopus</i> sp.
<i>Octopus areolatus</i> de Haan in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848	valid
<i>Octopus asper</i> (Akimushkin, 1963)	= <i>O. dofleini apollyon</i> Berry, 1912
<i>Macrotritopus bandensis</i> (Hoyle, 1885)	nomen dubium
<i>Octopus berenice</i> Gray, 1849	nomen dubium
<i>Octopus bocki</i> Adam, 1941	valid*
<i>Octopus brocki</i> Ortmann, 1888	valid*
<i>Cistopus bursarius</i> Steenstrup in Hoyle, 1886	= <i>C. indicus</i> (Rapp in Orbigny, 1835, in Férussac and Orbigny, 1834–1848)
<i>Octopus cephea</i> Gray, 1849	nomen dubium
<i>Octopus conispadiceus</i> (Sasaki, 1917)	valid
<i>Octopus dofleini dofleini</i> Wülker, 1910	valid
<i>Octopus dollfusi</i> Robson, 1928	= <i>O. hardwickei</i> Gray, 1849
<i>Macrotritopus elegans</i> (Brock, 1887)	nomen dubium
<i>Pteroctopus eurycephala</i> (Taki, 1964)	valid
<i>Octopus fangsiao etchuanus</i> (Sasaki, 1929)	valid
<i>Octopus fangsiao typicus</i> (Sasaki, 1929)	valid
<i>Octopus favonius</i> Gray, 1849	valid
<i>Octopus fujitai</i> (Sasaki, 1929)	valid
<i>Octopus fusiformis</i> Brock, 1887	nomen dubium
<i>Octopus globosus</i> Appellöf, 1886	valid
<i>Octopus guangdongensis</i> Dong, 1976	valid
<i>Octopus hardwickei</i> Gray, 1849	valid
<i>Octopus harmandi</i> Rochebrune, 1882	= <i>O. filamentosus</i> Blainville, 1826
<i>Octopus hattai</i> (Sasaki, 1929)	valid
<i>Octopus hawaiiensis</i> Souleyet in Eydoux and Souleyet, 1852	nomen dubium
<i>Octopus hoeki</i> Joubin, 1898	nomen dubium
<i>Octopus hongkongensis</i> Hoyle, 1885	valid
<i>Pteroctopus hoylei</i> (Berry, 1909)	valid
<i>Octopus inconspicuus</i> Brock, 1887	nomen dubium
<i>Cistopus indicus</i> (Rapp in Orbigny, 1835, in Férussac and Orbigny, 1834–1848)	valid
<i>Octopus kagoshimensis</i> Ortmann, 1888	valid
<i>Octopus kermadecensis</i> (Berry, 1914)	valid
<i>Octopus longispadiceus</i> (Sasaki, 1917)	valid
<i>Hapalochlaena lunulata</i> (Quoy and Gaimard, 1832)	valid
<i>Octopus luteus</i> (Sasaki, 1929)	valid
<i>Octopus machikii</i> Brock, 1887	nomen dubium
<i>Octopus macropus minor</i> (Sasaki, 1920)	= <i>O. minor minor</i> (Sasaki, 1920)
<i>Octopus madokai</i> (Berry, 1921)	= <i>O. hongkongensis</i> Hoyle, 1885
<i>Octopus marginatus</i> Taki, 1964	nomen dubium
<i>Octopus marmoratus</i> Hoyle, 1885	= <i>O. cyanea</i> Gray, 1849
<i>Octopus medoria</i> Gray, 1849	nomen dubium
<i>Octopus megalops</i> (Taki, 1964)	= <i>O. hongkongensis</i> Hoyle, 1885
<i>Octopus membranaceus</i> Quoy and Gaimard, 1832	nomen dubium
<i>Octopus minor minor</i> (Sasaki, 1920)	valid
<i>Octopus minor pardalis</i> (Sasaki, 1929)	valid
<i>Octopus minor typicus</i> (Sasaki, 1929)	valid
<i>Octopus mollis</i> Gould, 1852	nomen dubium
<i>Octopus mutilans</i> Taki, 1942	valid

TABLE 2.—Continued.

Nominal taxon	Current disposition
<i>Octopus nanhaiensis</i> Dong, 1976	valid
<i>Octopus niveus</i> Orbigny, 1826	nomen nudum
<i>Octopus niveus</i> Lesson, 1830	= <i>O. filamentosus</i> Blainville, 1826
<i>Octopus ocellatus</i> Gray, 1849	? = <i>O. fangsiao</i> Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848
<i>Octopus ochotensis</i> (Sasaki, 1920)	valid*
<i>Octopus oliveri</i> (Berry, 1914)	valid
<i>Callistoctopus ornatus</i> (Gould, 1852)	valid
<i>Octopus oshimai</i> (Sasaki, 1929)	valid
<i>Octopus ovulum</i> (Sasaki, 1917)	valid
<i>Octopus parvus</i> (Sasaki, 1917)	valid
<i>Scaeuergus patagiatus</i> Berry, 1913	valid
<i>Octopus pavus</i> (Sasaki, 1920)	= <i>O. parvus</i> (Sasaki, 1917)
<i>Octopus pulcher</i> Brock, 1887	nomen dubium
<i>Octopus pusillus</i> Gould, 1852	nomen dubium
<i>Octopus pustulosus</i> (Sasaki, 1920)	preoccupied (replaced by <i>O. madokai</i> Berry, 1921; = <i>O. hongkongensis</i> Hoyle, 1885)
<i>Octopus rapanui</i> Voss, 1979	valid
<i>Octopus sasakii</i> Taki, 1942	valid
<i>Octopus sinensis</i> Orbigny, 1834, in Férussac and Orbigny, 1834–1848	nomen dubium
<i>Octopus smedleyi</i> Robson, 1932	nomen dubium
<i>Octopus spinosus</i> (Sasaki, 1920)	valid*
<i>Octopus striolatus</i> Dong, 1976	valid
<i>Octopus tenuicirrus</i> (Sasaki, 1929)	= <i>O. hongkongensis</i> Hoyle, 1885
<i>Octopus tenuipulvinus</i> (Sasaki, 1920)	? = <i>O. minor minor</i> (Sasaki, 1920)
<i>Octopus teuthoides</i> Robson, 1929	nomen dubium
<i>Octopus tonganus</i> Hoyle, 1885	valid
<i>Octopus tsugarensis</i> (Sasaki, 1920)	valid*
<i>Octopus variabilis minor</i> (Sasaki, 1929)	= <i>O. minor minor</i> (Sasaki, 1920)
<i>Octopus variabilis pardalis</i> (Sasaki, 1929)	= <i>O. minor pardalis</i> (Sasaki, 1929)
<i>Octopus variabilis typicus</i> (Sasaki, 1929)	= <i>O. minor typicus</i> (Sasaki, 1929)
<i>Octopus vitiensis</i> Hoyle, 1885	valid
<i>Pteroctopus wijazi</i> Akimushkin, 1963	? = <i>P. hoylei</i> (Berry, 1909)
<i>Octopus wolffi</i> (Wülker, 1913)	valid
<i>Octopus yendoii</i> (Sasaki, 1920)	valid*

part, on the same type (see that taxon in Toll, 1998). Orbigny's (1834, in Férussac and Orbigny, 1834–1848) original description of *O. aculeatus* consisted of figures of two specimens that can be considered syntypes. The specimen figured on pl. 7 was from Manila. The specimen figured on pl. 8, as *O. aculeatus* "var.," was obtained in Bora Bora by Lesson and is the holotype of *O. niveus*. The former syntype is extant; the latter syntype was not found in the collections of the MNHN (see Lu et al., 1995).

#### *Octopus aegina* Gray, 1849

DIAGNOSIS.—Mantle elongate. Arm formula IV > III > II > I. Suckers large, distantly spaced, first 5 to 6 suckers uniserial, suckers biserial distally.

ORIGINAL DESCRIPTION.—Gray, 1849:7.

TYPE LOCALITY.—Unknown.

TYPE.—*Holotype*: BMNH 1928.2.14.1 (old collection), female (fide Robson, 1929).

DISCUSSION.—The original description of *Octopus aegina*, excerpted above, was defective. Hoyle (1886) listed it as insufficiently characterized. Robson (1928b, 1929) provided accounts of this species that included a partial redescription of the type; however, nonconspecific material could have been included. Therefore, data from those accounts are not presented as part of the diagnosis above. *Octopus aegina* belongs to the complex of Indo-Pacific octopuses, including *O. dollfusi*, *O. hardwickei*, and *O. kagoshimensis*, characterized as having an exceptionally shallow web sector A; however, only features of the outer tunic of the spermatophore allow for separation of member taxa of this complex (see Adam, 1962). Due to the gender of the type (female) and the lack of locality data, we recommend that *O. aegina* be considered a nomen dubium (see also "Discussion" under *Octopus kagoshimensis*, below).

***Octopus alatus* (Sasaki, 1920)**

DIAGNOSIS.—Animal medium-sized (to 70 mm ML). Mantle compact, widest posteriorly (MWI 69–103); neck indistinct; head broad (HWI 76–93). Funnel organ small, W-shaped. Arms moderate in length (ALI 76–77), arm order I > II > III > IV, very unequal. Sucker size moderate (SIn 7–9). Right arm III of males hectocotylized (HALI 271.4), shorter than fellow (FAI 73–76); ligula short (LLI 4–5), thick, conical. Web moderate to deep (WDI 23–34), continuing up ventral side of arms nearly to tip as broad membrane; web formula  $A > B = C = D > E$  or  $B > A > C > D > E$ . Gill lamellae 11. Penis fusiform with long, slender appendix. Spermatophores slender (SPL 69 mm), swollen at sperm mass. Radula with  $A_2$  seriation of rachidian. Body surface smooth; peripheral keel around mantle (adventitious?).

ORIGINAL DESCRIPTION.—Sasaki, 1920:180, pl. 24: fig. 4, as *Polypus alatus*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Bungo Channel, 32°36'N, 132°23'E, 437 fms (799 m).

TYPE.—*Holotype*: USNM 332978, male, 70 mm ML, in alcohol.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from Sasaki (1929) based on the type series. Sasaki (1929) compared this species with his *Octopus variabilis* (= *O. minor* (Sasaki, 1920)) but considered it distinct based on sucker placement, funnel organ morphology, web morphology, number of suckers on the hectocotylized arm, ligula length, and penis and spermatophore morphology. This species could be related to the *C. ornatus/macropus* complex on the basis of arm order and relative arm lengths, and it could be a congener. We retain *O. alatus* as distinct; further study is warranted.

***Hapaloctopus albidus* Taki, 1962**

See *Pteroctopus hoylei* (Berry, 1909).

***Octopus amboinensis* Brock, 1887**

DIAGNOSIS.—Animal small (78 mm TL, 13 mm VML). Arms moderate in length (ALI 76.9), arm formula III > II > IV > I. First 5 proximal suckers uniserial, suckers biserial distally.

ORIGINAL DESCRIPTION.—Brock, 1887:598.

TYPE LOCALITY.—Western Tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: ZMUG, female, 13 mm VML (no longer extant, see "Discussion").

DISTRIBUTION.—Known from the type locality only.

DISCUSSION.—The diagnosis is excerpted from the original description by Brock (1887), which included few characters that permit positive identification of this taxon. Robson (1929) noted the resemblance of *Octopus amboinensis* to *O. elegans*

Brock, 1887, and indicated that *O. amboinensis* could be referable to the *Macrotritopus* complex based on arm formula. The disparity in arm lengths, however, is not as great as in the typical *Macrotritopus* (arm pair III is only 20% longer than the next longest arm pair, 60 mm compared with 50 mm). Therefore, we do not believe that this taxon should be referred to *Macrotritopus*. The type was destroyed in World War II (P. Kuenzer, pers. comm., 1988, to C.F.E. Roper), and it is doubtful that we will ever be able to determine with certainty the identity of this taxon. In our opinion, *Octopus amboinensis* is a nomen dubium.

***Callistoctopus arakawai* Taki, 1964**

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Taki, 1964:292, figs. 34–41, pls. 2, 3.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Oita Prefecture, Minami-Amabe County, near Kamae Town.

TYPE.—*Holotype*: Not deposited, male, 105 mm ML, 762 mm TL (presumed to be in private collection, see "Introduction").

DISCUSSION.—Voss (1981) reviewed the status of *Callistoctopus arakawai* and placed it in the synonymy of *Octopus ornatus* Gould, 1852, described from Hawaii (see *Callistoctopus ornatus* (Gould, 1852), below). Recent studies by several workers have indicated that "*O. ornatus*" could actually comprise a complex of species found throughout the tropical-subtropical Indo-West Pacific. Toll (1992) retained the genus *Callistoctopus* as distinct from *Octopus sensu stricto*. Without new evidence to the contrary, we tentatively retain *C. arakawai* in the synonymy of *C. ornatus*; however, a critical revision of this complex is necessary to confirm this relationship.

***Octopus araneoides* (Taki, 1964)**

DIAGNOSIS.—Animal moderate-sized (75–83 mm ML). Mantle ovoid to ellipsoid, widest near middle (MWI 43–67); neck slightly constricted; head narrow (HWI 41–53); eyes large. Funnel long, funnel organ broad, W-shaped, outer limbs shorter than inner limbs. Arms short to moderate in length (ALI 66–70), slender, arm order typically I > II > III > IV. Suckers larger in males than in females (SIn 9.0–9.8 and 5.4–7.7, respectively), suckers on arms I larger than on other arms; especially enlarged suckers absent in males and females. Right arm III of males hectocotylized (HALI 207–235), shorter than fellow (FAI 87–95); ligula length moderate (LLI 8–12), with shallow, median groove; calamus short (CLI ~12–13), HASC 90–98. Web moderate (WDI 20–25), web formula  $A > B > C > D > E$ . Gill lamellae 11. Eggs large, capsule 13 mm long × 5 mm wide. Penis long, with long curved diverticulum. Spermatophores long (SPL 75 mm), slender (SPW 0.8 mm). Radula multicuspid with  $B_3$  seriation of rachidian. Surface of head and mantle smooth to finely



pustulate. Mantle pink, web purple, ventral surface slightly lighter than dorsum.

ORIGINAL DESCRIPTION.—Taki, 1964:307, figs. 49–54, pl. 4: fig. 3, as *Paroctopus araneoides*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Hokkaido, off Kushiro City.

TYPE.—*Holotype*: Not deposited, male, 83 mm ML (presumed to be in private collection, see "Introduction").

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Taki (1964). Taki (1964) compared *Octopus araneoides* to *O. dofleini* Wülker, 1910, *O. gilbertianus* Berry, 1912, *O. conispadiceus* (Sasaki, 1917), *O. yendoi* (Sasaki, 1920), and *O. asper* (Akimushkin, 1963). Gleadall (1993) indicated that *O. araneoides* could be a synonym of *O. longispadiceus* (Sasaki, 1917). A final systematic determination of the validity of *O. araneoides* cannot be made until the type is reexamined; however, it is likely that *O. araneoides* will ultimately be shown to be a junior synonym of another described taxon.

***Octopus areolatus* de Haan in Orbigny, 1839–1841,  
in Férussac and Orbigny, 1834–1848**

DIAGNOSIS.—Animal medium-sized (49 mm ML). Mantle elongate, rounded posteriorly (49 mm ML), narrow (MWI 47); neck region constricted; head narrow (HWI 37); eyes large, protruding. Funnel organ W-shaped, elongate. Arms long (ALI 77), stout at base but tapering to slender tips, arm formula III > IV > II > I. Sucker size moderate (SIn 10), erect, closely spaced; 1 or 2 especially enlarged suckers (SLe 13) present on arms II and III in males. Right arm III of males hectocotylized; ligula small (LLI 7), slender, with narrow, shallow groove; calamus moderate in size (CLI 23); HASC 90. Gill lamellae 7. Stylets (shell vestiges) present. Penis moderate in length (PLI 35), slender, with strongly recurved diverticulum. Surfaces of mantle, head, and arms covered with small, flat papillae either single or in groups of 3 to 4 around small central papilla, becoming more scattered laterally, all with fine, dark line between, forming reticulated network; few larger papillae around eyes, 2 large supraocular papillae. Indistinct dark line on each arm; 3 dark lines apparent on head, 1 median line between eyes interrupted by irregular (dumbbell?) light patch between eyes and 1 line across each eye continuing down mantle. Median area of mantle with 2 dark lines; short, dark line on each side of mantle originating at corner of aperture; perhaps some scattered light patches on dorsum of mantle. Large ocellus on each side of head about 1/3 nearer head than edge of web, consisting of large, dark spot enclosing thin, blue gray, iridescent ring.

ORIGINAL DESCRIPTION.—de Haan in Orbigny, 1839–1841: 65, in Férussac and Orbigny, 1834–1848.

TYPE LOCALITY.—Western North Pacific Ocean, Japan.

TYPE.—*Lectotype*: RNHL, male, 49 mm ML, not traced.

DISTRIBUTION.—Uncertain due to numerous misidentifications in the literature.

DISCUSSION.—The diagnosis is based on our examination of the lectotype. Orbigny (1839–1841, in Férussac and Orbigny, 1834–1848) proposed the name *Octopus areolatus* based on a letter received from de Haan. De Haan's specimens, collected by von Siebold, were deposited in Leiden and subsequently were examined by Appellöf (1886) and Robson (1929). Both accounts noted the existence of two syntypes. Robson (1929) and Sasaki (1929), both with some uncertainty, placed *O. areolatus* in the synonymy of *O. fangsiao* Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848.

The type series of *Octopus areolatus*, lent from Leiden, included three specimens, all collected by von Siebold. One is a large, nonconspecific specimen lacking ocelli. The other two are both ocellated. Of those, one is attributable to *O. ocellatus* Gray, 1849 (? = *O. fangsiao*), as previously noted by Robson (1929) (see that taxon, below). The other syntype is designated herein as the lectotype of *O. areolatus*.

Gleadall (1991) supported the assertions of Sasaki (1929) and Pickford (MS) that the Indo-West Pacific ocellated octopod complex comprised two species. Additional critical review of all member taxa must be performed before the systematic relationships of *Octopus areolatus* can be resolved.

***Octopus asper* (Akimushkin, 1963)**

DIAGNOSIS.—Animal medium-sized to large (312–770 mm TL). Mantle pyriform, relatively narrow (MWI 65–84); head narrow. Funnel short, funnel organ W-shaped, outer limbs shorter than inner ones. Arm length moderate (ALI 72–77), thick basally, arm formula typically II > I > III > IV. Sucker size large (SIn 11.0–15.8); especially enlarged suckers absent in males and females; ASC 220–240. Right arm III of males hectocotylized, shorter than fellow arm (FAI ~67); ligula moderate in length (LLI 12.5 in mature specimen), slender, tapered distally, medial groove distinct; calamus minute. Web moderate (WDI 20–27), web formula usually C > D > B > A > E. Gill lamellae 13. Penis long (to 40 mm), narrow. Radula with A<sub>3</sub> seriation of rachidian. Surfaces of mantle, head, base of arms, and web densely covered with circlets of papillae comprised of 1 large central papilla surrounded by smaller ones, most numerous between eyes and at base of arms; 1 large or 2 to 3 small supraocular papillae, 2 papillary rows extended along lateral region of mantle and head. General color in preservation violet brown dorsally, lighter brown ventrally.

ORIGINAL DESCRIPTION.—Akimushkin, 1963:138, figs. 28, 29, as *Paroctopus asper*.

TYPE LOCALITIES.—Western North Pacific Ocean, Kamchatka Peninsula to northern Sea of Japan.

TYPES.—*Syntypes*: Not deposited, 5 males, 312–770 mm TL, 2 females, 475 mm TL, 662 mm TL, no longer extant (see "Discussion").

DISTRIBUTION.—Known only from the type localities.

DISCUSSION.—The diagnosis is extracted from the original description. The types were never deposited and are assumed lost (K. Nesis, pers. comm.). Akimushkin (1963) compared *Octopus asper* to *O. apollyon* Berry, 1912 (considered by Pickford (1964) to be a subspecies of *O. dofleini* (Wülker, 1910)), separating them on the basis of penis and radula morphology and sucker size. Nesis (1987) placed *O. asper* in the synonymy of *O. dofleini apollyon* Berry, 1912. We uphold that decision.

#### *Macrotritopus bandensis* (Hoyle, 1885)

DIAGNOSIS.—*Paralarva*: Animal small (6 mm ML). Mantle rounded. Arms long (ALI 80), unequal, arms III much longer than all others. Gill with 5 to 6 lamellae. Single, large, supraocular cirrus.

ORIGINAL DESCRIPTION.—Hoyle, 1885:227, as *Octopus bandensis*.

TYPE LOCALITY.—Banda Sea, Banda.

TYPE.—*Holotype*: BMNH 89.4.24.40, juvenile, 6 mm ML.

DISTRIBUTION.—Known with certainty from the type locality only.

DISCUSSION.—The diagnosis is based on the holotype, examined herein. It is unfortunate that this species was erected based on such unsatisfactory material. We consider *O. bandensis* referable to *Macrotritopus* based on the great elongation of the third arm pair. It is unlikely, however, that we will learn with certainty the affinities of this juvenile form. Therefore, we consider *M. bandensis* to be a nomen dubium.

#### *Octopus berenice* Gray, 1849

DIAGNOSIS.—*Immature female*: Mantle ovoid; head narrower than mantle. Funnel organ W-shaped. Arms moderate in length (ALI 78). Suckers large in diameter (SIn 16). Web subequal in depth. Dorsal surface of web and mantle with simple and multifid papillae; 4 supraocular papillae on each side of head.

ORIGINAL DESCRIPTION.—Gray, 1849:11.

TYPE LOCALITY.—Unknown.

TYPE.—*Holotype*: BMNH 1928.1.22.3 (old collection), immature female, 18 mm ML.

DISTRIBUTION.—Reported to occur widely throughout the Indo-West Pacific exclusive of Japan; however, because of the uncertainties relating to the identity of this species, these accounts are problematic.

DISCUSSION.—The type of *Octopus berenice*, collected in 1805, was examined by one of us (RBT); it is in poor condition and little substantiative information can now be gained from its study. Gray's (1849) original description is defective, and Robson's (1929) redescription of the holotype, excerpted above, does not contain sufficient information to allow this

taxon to be recognized with reasonable certainty. Furthermore, because the type is a small female and lacks locality data, we treat *O. berenice* as a nomen dubium.

#### *Octopus bocki* Adam, 1941

DIAGNOSIS.—Animal small (21 mm ML). Mantle elongate-pyriform (MWI 57); neck region narrow, head narrow (HWI 50); eyes large, projecting. Funnel organ W-shaped, outer limbs slightly more than 50% of length of inner limbs. Arm length moderate (ALI 73), arm order IV = III > II > I. Sucker size moderate (SIn 9.5). Web moderate to deep (WDI 29), web formula C > D > E > B > A. Gill lamellae 5. Mature ovarian eggs small, capsule ~1 mm long. Radula with A<sub>3-4</sub> seriation of rachidian. Surface of body smooth. Color in preservation (ethanol) grayish with irregular spots on dorsal mantle, head, and arms formed of reddish brown and black chromatophores.

ORIGINAL DESCRIPTION.—Adam, 1941:1.

TYPE LOCALITY.—Fiji Islands, Viti Levu, Namuka, on coral reef.

TYPE.—*Holotype*: NRS, female, 21 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is based on examination of the holotype by one of us (GLV). The type is a fully mature female with darkened nidamental glands. Adam (1941) stated that *Octopus bocki* resembles *O. elegans* Brock, 1887 (*Macrotritopus elegans*, considered herein to be a nomen dubium, see below), but differs from the latter in short arms, well-developed web, small number of gill lamellae, funnel organ morphology, and other features. *Octopus bocki* can be distinguished from *O. dollfusi* Robson, 1928 (= *O. hardwickei* Gray, 1849), by the small number of gill lamellae. Without male specimens, it is difficult to come to any final decision regarding the systematic status of this species; therefore, we retain it, tentatively, as distinct.

#### *Octopus brocki* Ortmann, 1888

DIAGNOSIS.—Animal medium-sized (53 mm ventral ML). Mantle oval (37 mm MW); head short and narrow (21 mm HW). Arms subequal, slender, about twice as long as body. Proximal 5 to 6 suckers uniserial, suckers become biserial distally; 5th and 6th suckers on arms II and III especially enlarged in females. Ligula small, with central longitudinal groove. Skin smooth, papillae absent. Greenish blue iridescent ring between bases of arms III and IV.

ORIGINAL DESCRIPTION.—Ortmann, 1888:645, pl. 21: fig. 4, pl. 22: fig. 1.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Tokyo Bay and Kagoshima.

TYPES.—*Syntypes*: Not traced; 6 females (Tokyo Bay), 2 males, 1 juvenile (Kagoshima). Robson (1929) reported that the two male syntypes are extant in the collections of the UMS.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description; numerical data are from the largest female syntype. Ortmann (1888) compared *Octopus brocki* to *O. areolatus* de Haan in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848 (see that taxon, above), but considered it distinct based on the size of the “eyespot” (= ocellus), absence of dermal sculpture, characteristics of the suckers, and dermal pigmentation. Robson (1929) placed *Octopus brocki* in the synonymy of *O. areolatus*. Sasaki (1929) placed *O. brocki* in the synonymy of *O. fangsiiao etchuanus* (see that taxon, below). The status of *O. brocki* remains unresolved at present; we tentatively retain it as distinct. Future comparative examination of the type series is warranted.

#### *Cistopus bursarius* Steenstrup in Hoyle, 1886

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Steenstrup in Hoyle, 1886:14.

TYPE LOCALITY.—Celbes (= Sulawesi).

TYPE.—*Holotype*: The figure given by Orbigny (1835, pl. 25, in Férussac and Orbigny, 1834–1848) is the type figure.

DISCUSSION.—The name *Cistopus bursarius* appeared in Hoyle (1886) in a footnote in reference to *C. indicus* Gray, 1849. Hoyle (1886:14) stated that just at the time his monograph on the H.M.S. *Challenger* cephalopods was going to press, Steenstrup, in a letter, informed him that Steenstrup doubted “whether Orbigny’s two figures [of *C. indicus*] represent the same species ... [and he was] ... disposed to regard the type of Rapp’s species as having been a true *Octopus*, and the form with pouches between the arms he has adopted the name *Cistopus bursarius*.” Robson (1929) discussed Steenstrup’s opinion, concluded that this action was unwarranted, and considered *C. bursarius* to be a junior synonym of *C. indicus*, a decision supported herein.

#### *Octopus cephea* Gray, 1849

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Gray, 1849:15.

TYPE LOCALITY.—Unknown.

TYPE.—*Holotype*: BMNH 1928.2.2.1 (old collection), female.

DISTRIBUTION.—Unknown.

DISCUSSION.—Gray’s (1849) original description is defective, being devoid of information on many important characters. Gray (1849) noted that *Octopus cephea* was similar to *O. vulgaris* Lamarck, 1798, with the exception of the size of the suckers on arms II and III. Hoyle (1886) considered this taxon to be insufficiently characterized. We examined the type and concur with Robson (1929), who noted that it was in poor condition. The W-shaped funnel organ is preserved. In view of the condition of the type and the complete absence of locality data, we consider *Octopus cephea* to be a nomen dubium.

#### *Octopus conispadiceus* (Sasaki, 1917)

DIAGNOSIS.—Animal large (to ~1200 mm TL). Mantle saccular (MWI 80–98); neck indistinct; head moderate in width (HWI 50–65). Funnel organ VV-shaped, outer limbs shorter than median ones. Arms subequal, moderate in length (ALI 75–79). Suckers large in males (SIn 15), smaller in females; ASC 140–160 in males, 180–190 in females. Right arm III of males hectocotylyzed; ligula moderate to large (LLI 12–20), conical, narrow with deep groove; calamus distinct; hectocotylyzed arm with 52–58 suckers. Web shallow to moderately deep. Gill lamellae 11 to 12. Mature eggs exceptionally large, capsules to 28 mm long. Penis cylindrical, slightly curved, swollen in middle of diverticulum. Spermatophores moderate in length, (SpLI > 50). Radula with A<sub>3-4</sub> seriation of rachidian. Body firm, muscular, with almost no sculpture, few scattered papillae when preserved, single supraocular papillae. Color in life pale grayish blue covered with numerous minute, brownish chromatophores and less numerous yellow chromatophores. Color in preservation (formalin) mauve, faintly and irregularly marbled dorsally.

ORIGINAL DESCRIPTION.—Sasaki, 1917:367, as *Polypus conispadiceus*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Hokkaido, Sapporo, fish market.

TYPES.—Syntypes: ACS (not traced).

DISTRIBUTION.—Waters surrounding Hokkaido, Japan.

DISCUSSION.—The diagnosis is excerpted from Sasaki (1917, 1929). Sasaki (1929) compared *O. conispadiceus* to *O. dofleini* Wülker, 1910. According to that account, it can be differentiated from *O. dofleini* on the basis of hectocotylus and funnel organ morphology, gill lamellae count, reduced dermal sculpture, and lack of large chromatophores on the ventral surface of the mantle. Gleadall (1993) confirmed that the two taxa are distinct. We support that assertion. *Octopus conispadiceus* is a commercial species in Japan (see Okutani et al., 1987; Gleadall, 1993).

#### *Octopus dofleini dofleini* Wülker, 1910

DIAGNOSIS.—Animal large (>190 mm ML). Mantle ovoid; head narrow in adults, proportionally broader in juveniles. Arms moderately long, arm formula typically I = II > III > IV, but arms subequal. Funnel organ W-shaped, with broad limbs, lateral limbs slightly shorter than medial ones. Suckers relatively large, larger in males than in females; especially enlarged suckers absent in males and females. Right arm III of males hectocotylyzed, shorter than fellow arm (FAI typically <80). Ligula long, slender (LLI ~20); calamus short. Web moderately deep, sector E usually shallowest, about 1/2 depth of deepest lateral sector. Gill lamellae 10–15. Eggs moderate in length, capsule 6–8 mm long, attached to substratum in festoons. Penis with exceptionally long diverticulum. Spermatophores enormous, about three times length of mantle, oral end

of spermatophore horn with about 15 spiral coils. Single large supraocular papillae; skin sparsely ornamented with small papillae, 4 larger papillae form rhombus on dorsal mantle in young specimens. General color reddish brown with black reticulations dorsally, paler ventrally.

ORIGINAL DESCRIPTION.—Wülker, 1910:7, pl. 2: figs. 1, 2, pl. 3: fig. 10.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Hokkaido.

TYPE.—*Holotype*: UMM, male, immature?, not extant (see Pickford, 1964); neotype not selected.

DISTRIBUTION.—Subarctic to temperate western Pacific Ocean from Japan to Korea (fide Pickford, 1964).

DISCUSSION.—The diagnosis is excerpted from Pickford (1964). The systematic status of *Octopus dofleini* was reviewed comprehensively by Pickford (1964), who recognized three geographic subspecies, *O. dofleini dofleini* (Japan), *O. d. apollyon* (Gulf of Alaska), and *O. d. martini* (Canada to California). We retain *O. dofleini dofleini* as distinct.

#### *Octopus dollfusi* Robson, 1928

DIAGNOSIS.—See “Discussion.”

ORIGINAL DESCRIPTION.—Robson, 1928a:43, figs. 22–27.

TYPE LOCALITY.—Western Pacific Ocean, Indochina (precise locality unknown).

TYPE.—*Holotype*: MNHN 4-5-899 (fide Lu et al., 1995), male, 34 mm ML, ~119 mm TL, A. Krempf no. 2.129, specimen dried, shrunken.

DISCUSSION.—Adam (1962) examined the type of *Octopus dollfusi* and determined that the spermatophores were armed (= with crochets). As a result, Pickford (MS) determined that *O. dollfusi* was a junior synonym of *Octopus hardwickei* Gray, 1849. We support her conclusion. For a full discussion, see that taxon, below; see also *O. kagoshimensis* Ortmann, 1888.

#### *Macrotritopus elegans* (Brock, 1887)

DIAGNOSIS.—*Paralarva*: Animal small (120 mm TL; 13 mm ML). Arms long (ALI 83.3), arm order III > II > IV > I, arms III much longer than others.

ORIGINAL DESCRIPTION.—Brock, 1887:597, as *Octopus elegans*.

TYPE LOCALITY.—Western Tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: ZMUG, female, 13 mm VML, not extant (see “Discussion”).

DISTRIBUTION.—Known from the type locality only.

DISCUSSION.—The diagnosis is excerpted from the original description by Brock (1887). Robson (1929) redescribed the type of *Octopus elegans*, noted that the specimen was distorted, and recommended that *O. elegans* be included in the *Macrotritopus* complex based on arm formula. The type was subsequently destroyed in World War II (P. Kuenzer, pers.

comm., 1988, to C.F.E. Roper). It is our opinion that this taxon is referable to *Macrotritopus*; however, it is insufficiently characterized at the species level to allow identification, and we recommend that *Macrotritopus elegans* be considered a nomen dubium.

#### *Pteroctopus eurycephala* (Taki, 1964)

DIAGNOSIS.—Animal small (25–26 mm ML). Mantle saccular, broad (MWI 92–96); neck slightly constricted; head broad (HWI 85–108); eyes large, prominent. Funnel broad, short, funnel organ VV-shaped, medial and lateral limbs narrow, pointed apically, subequal in length. Arms moderate in length (ALI 70.0–75.2). Sucker size moderate (SIn 7–8), suckers deeply set in arms. Web deep (WDI 31.6–37.3), subequal in depth. Gill lamellae 8 to 9. Radula with B<sub>4</sub> seriation of thick, tricuspid rachidian. Single, short, conical, supraocular cirrus on each side of head. General color vermillion purple dorsally, old rose ventrally.

ORIGINAL DESCRIPTION.—Taki, 1964:314, figs. 58, 59, pl. 6: fig. 3, as *Sasakinella eurycephala*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Enshu Sea, from Mikawa-Isshiki fish market.

TYPE.—*Holotype*: Not deposited, female, 25 mm ML (presumed to be in private collection, see “Introduction”).

DISCUSSION.—The diagnosis given above is excerpted from the original description. This species, as noted by Taki (1964), is similar in many characters to *Pteroctopus hoylei*, of which it could be a synonym. Until a complete comparison can be performed, we retain *Pteroctopus eurycephala* as distinct.

Toll (MS) considers *Sasakinella eurycephala* (the type species of *Sasakinella* Taki, 1964) to be a junior synonym of *Pteroctopus*.

#### *Octopus fangsiao etchuanus* (Sasaki, 1929)

DIAGNOSIS.—With the characters of *O. f. typicus*, below, except as follows: mantle wide (MWI approximately 100); ligula moderate in size (LLI 8–10), HASC 89–90; eggs moderate to large, capsule 13 mm long. Mantle granulose; circumocular papillae subequal in size.

ORIGINAL DESCRIPTION.—Sasaki, 1929:53, pl. 3: figs. 19, 20, pl. 10: figs. 4–10.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Toyama Prefecture.

TYPES.—*Syntypes*: ACS, 8 males, 6 females, 43–70 mm ML.

DISTRIBUTION.—Japan, Okayama Prefecture, Nagasaki, Toyama Prefecture.

DISCUSSION.—The diagnosis is excerpted from the original description. Sasaki (1929:53) proposed *Octopus fangsiao etchuanus* as a varietal form “with a great deal of hesitation” and tentatively placed *O. brocki* Ortmann, 1888, in synonymy. The difference in HASC suggests that the two taxa are distinct.

As noted by Voight (1998), the apparent sympatry of the subspecies of *O. fangsiao* suggests that their subspecific division is artificial. One course of action would be to raise the nominal subspecies to full species rank; however, we feel that this action is premature and retain the present taxonomy, despite the obvious problem.

*Octopus fangsiao typicus* (Sasaki, 1929)

DIAGNOSIS.—Animal medium-sized (26–52 mm ML). Mantle ovoid (MWI 58–71); neck distinctly constricted; head narrow (HWI 36–46); eyes moderately projecting. Funnel organ large, W-shaped, medial and lateral limbs subequal in length. Arms short to moderate in length (ALI 59.3–71.4), arm formula I > II = III = IV, gradually and evenly tapering to tips. Suckers elevated, proximal 4 to 5 suckers uniserial, suckers become biserial distally, larger on lateral arm pairs; especially enlarged suckers present at level of web margin (in males and females?). Right arm III of males hectocotylized (HALI 211.5–250.0), subequal or only slightly shorter than fellow (FAI 80.3–100); ligula small (LLI 4.5–6.7); calamus rudimentary, HASC 120–140. Web moderate to deep (WDI 20.0–30.2), web formula typically C = D = E > B > A. Gill lamellae 7–9. Eggs moderate in size, egg capsule ~10 mm long. Penis large, with spherical diverticulum. Spermatophores moderate in length (SPL 33–36 mm), slender, with 57–60 coils of sperm cord, horn with 20–30 spiral coils. Radula with symmetrical seriation of pentacuspis rachidian. Dorsal surfaces of mantle, head, and arms variable, smooth to covered with minute conical to rounded papillae; circumocular papillae 5 to 6, 2 supraocular papillae noticeably larger. Ocellus on either side of head between bases of arms II and III consisting of yellowish to greenish iridescent ring surrounding dark central spot and bordered by blackish ring. Twelve to 15 regularly scattered spots on mantle, 4–6 longitudinal, dark strips along mantle. General color in preservation dark dull buff dorsally, light ochre ventrally.

ORIGINAL DESCRIPTION.—Sasaki, 1929:49.

TYPE LOCALITY.—Western North Pacific Ocean, Japan.

TYPE.—*Holotype*: Not selected.

DISTRIBUTION.—Widely distributed along Pacific Coast of Japan; southern Japan Sea (I. Gleadall, pers. comm., 1990).

DISCUSSION.—The diagnosis is excerpted from the original description of *Octopus fangsiao* by Orbigny, 1839–1841, in Féruccac and Orbigny, 1834–1848, and from the account by Sasaki, 1929, wherein two subspecies (“varietal forms”) were erected: *O. f. etchuanus* and *O. f. typicus*. Gleadall and Naggs (1991) reviewed the status of *O. fangsiao* and traced the basis of Orbigny’s description to two accounts of the natural history of Japan, Terajima (1713) and Katsuma (1762). Because Orbigny included only certain portions of the earlier descriptions, in translation, subsequent accounts, including those of Robson (1929) and Taki (1981), rejected Orbigny’s use of the name *O. fangsiao*. Sasaki (1929:51) raised additional concern

about Orbigny’s account by stating that his translation was “not without mistake.” Gleadall and Naggs (1991) determined that these mistakes were trivial in nature and involved the intricacies of transliteration between oriental languages. Based on this recent review, we retain *Octopus fangsiao typicus*. This species is common in local waters (Gleadall and Naggs, 1991). See also “Discussion” under *Octopus fangsiao etchuanus*, above.

*Octopus favonius* Gray, 1849

DIAGNOSIS.—Animal medium-sized (52 mm ML). Mantle moderately wide (MWI 73); neck and head narrow (HWI 61.5). Funnel organ W-shaped, outer limbs shorter than median ones. Arms short, stout (ALI 21), arm order III > II > IV > I. Web moderate in depth (WDI 21), web formula C > D > B = E > A. Gill lamellae 10. Skin nearly smooth, with minute papillae on head and arm bases; oral surface of web with rosette-like papillae; small conical supraocular papillae. Color in preservation grey brown dorsally, paler ventrally.

ORIGINAL DESCRIPTION.—Gray, 1849:9.

TYPE LOCALITY.—Western North Pacific Ocean, Singapore.

TYPE.—*Holotype*: BMNH 1928.1.22.2, female, 52 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from Pickford (MS), who redescribed the type. She believed that this taxon was related to the so-called *Octopus rugosus/vulgaris* complex. We retain it as distinct.

*Octopus fujitai* (Sasaki, 1929)

DIAGNOSIS.—Animal medium-sized (44 mm ML). Mantle globose, broadest in middle (MWI 84.1); neck not constricted; head moderate in width (HWI 75.7); eyes not prominent. Funnel slender, funnel organ unknown. Arms moderate to long (ALI 79.2), slender, tapered, attenuated at tips. Suckers moderate in size (SIn 9.1), about 170 suckers along each arm; especially enlarged suckers absent in female type. Web moderately deep, subequal in all sectors. Ink sac small; gill lamellae 11 to 12. Radula with unicuspid rachidian. Mantle with weakly developed lateral keel. Color in preservation (formalin) brownish pink, darker dorsally than ventrally.

ORIGINAL DESCRIPTION.—Sasaki, 1929:70, figs. 32, 33, pl. 5: fig. 1., pl. 11: fig. 8, as *Polypus fujitai*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Sagami Sea, Toyama Prefecture, Namerikawa.

TYPE.—*Holotype*: ACS, female, 44 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. The unicuspid condition of the rachidian, if real, is unusual among octopodines. We retain *Octopus fujitai* as distinct.

***Octopus fusiformis* Brock, 1887**

DIAGNOSIS.—Animal small to medium-sized (240 mm TL; 35 mm VML). Mantle elongate. Arms moderate to long (ALI 79.1). Right arm III hectocotylized.

ORIGINAL DESCRIPTION.—Brock, 1887:601, pl. 16: figs. 1, 2.

TYPE LOCALITY.—Western Tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: ZMUG, male, 35 mm VML, not extant (see "Discussion").

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Brock (1887). Despite the relatively long original description, which included two figures of a portion of the arms, there is little substantive information regarding diagnostic characters of this taxon. The long slender mantle is similar to that of *Cistopus indicus* and members of the *Callistoctopus* complex. The type was destroyed in World War II (P. Kuenzer, pers. comm., 1988, to C.F.E. Roper), and it is unlikely that the true identity of this taxon will ever be known. We consider *O. fusiformis* to be a nomen dubium.

***Octopus globosus* Appellöf, 1886**

DIAGNOSIS.—Animal small (31–32 mm ML). Mantle spherical (MWI 100); neck distinctly constricted; head almost as wide as mantle (HWI 93). Arms short, stout basally, tapering distally to slender points, arm order II > IV > I > III or II > I > IV > III; several especially enlarged suckers present in males. Gill lamellae 8. Ovarian eggs moderate in size, capsule 9 mm long. Skin with small papillae dorsally, smooth ventrally, 5–7 papillae over eyes, 2 to 3 papillae large. Color in preservation reddish above, pale below.

ORIGINAL DESCRIPTION.—Appellöf, 1886:7, pl. 1: figs. 4, 5.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Nagasaki.

TYPES.—Syntypes: ZMU 138a, 1 female, 31 mm ML, with immature ovarian eggs; ZMU 138b, 1 female, 32 mm ML, with near-mature ovarian eggs.

DISTRIBUTION.—Uncertain outside of Japan due to misidentification and confusion with *Octopus berenice* Gray, 1949, recognized herein as a nomen dubium (see that taxon).

DISCUSSION.—The diagnosis is based on the original description by Appellöf (1886) and on examination of the syntypes by one of us (GLV). The types apparently were purchased from a fish market, causing some workers to doubt the type locality. The label found with the types confirms the published locality. We retain *Octopus globosus* as distinct.

***Octopus guangdongensis* Dong, 1976**

DIAGNOSIS.—Animal medium-sized (190–450 mm TL). Mantle ovoid. Funnel organ W-shaped. Arms subequal, about

8–9 times length of mantle. Ligula minute (LLI 1). Penis slender, diverticulum narrow. Radula with tricuspid rachidian.

ORIGINAL DESCRIPTION.—Dong, 1976:213, pls. 5, 6.

TYPE LOCALITY.—Western North Pacific Ocean, China, Quangdong Province.

TYPE.—*Holotype*: IOAS.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The original description of this taxon was published in Chinese with an English summary, excerpted above; little is known about this species. Dong (1976) compared *Octopus guangdongensis* with *O. mutilans* Taki, 1942, from which he distinguished the former by the arm formula and the morphology of the ligula, penis, and radula. We retain *Octopus guangdongensis* as distinct.

***Octopus hardwickei* Gray, 1849**

DIAGNOSIS.—Animal small to medium-sized (22–29 mm ML). Mantle elongate (MWI 50.0–59.1); neck slightly constricted; head narrow (HWI 40.9–41.4); eyes moderate in size. Funnel damaged in syntype. Arms artifactually elongated in syntype. Suckers moderate in size (SIn 8.3); especially enlarged suckers absent in males and females. Right arm III of males hectocotylized; ligula length moderate (LLI 8.8), relatively narrow; calamus long (CLI 36.5), narrow, acutely pointed. Web shallow (WDI ~15), web formula B = C = D > E > A, sector A noticeably reduced. Gill lamellae 6–8. Penis long (PLI 27.6). Spermatophores armed with teeth-like projections (with crochets) arranged in circlelets. Radula with A<sub>3</sub> seriation of rachidian. General color in preservation (alcohol) dark brown with narrow, dark bands beginning on mantle and extending down head adjacent to distal edge of eyes and down dorsal surface of arms I. Web with reticulated pattern extending down arms II and III (and IV?).

ORIGINAL DESCRIPTION.—Gray, 1849:8.

TYPE LOCALITY.—Singapore? [sic].

TYPES.—*Syntypes*: BMNH 1947.3.11.2–3, 1 male, 29 mm ML, 1 female, 22 mm ML. Specimens in alcohol, in moderate condition, arms disfigured (buccal mass of male syntype not extant). (Robson (1929:115) incorrectly gave the museum registration number as BMNH 1927.12.10.1–2 for the syntypic lot. Pickford (MS) determined there was no such number. The registration number given above is correct.)

DISTRIBUTION.—Eastern Indian Ocean; southwest Pacific Ocean?

DISCUSSION.—The original description of *Octopus hardwickei* is defective, being a mere five lines long and lacking mention of numerous important characters. The diagnosis given above is based on our examination of the syntypes and is supplemented with the accounts of *O. dollfusi* by Robson (1928a) and Adam (1960) (as *O. aegina* Gray, 1849). Examination of the male syntype of *O. hardwickei* confirmed Pickford's (MS) findings that the damaged spermatophores exhibited armored surface sculpture of the outer tunic. This

character alone permitted Adam (1960) to distinguish between *O. dollfusi* and *O. aegina*. Based on other characters still available from the type series of *O. hardwickei*, particularly the very shallow web sector A, and in light of the armored spermatophores, we agree with Pickford (MS) that *O. hardwickei* is the valid senior synonym of *O. dollfusi* Robson, 1928.

#### *Octopus harmandi* Rochebrune, 1882

DIAGNOSIS.—Animal small to medium-sized (30 mm ML). Mantle moderate in width (MWI 70); head slightly narrower than mantle (HWI 60). Funnel organ W-shaped with narrow limbs. Arms long (ALI 87), arm order IV > II = III > I. Male syntype with especially enlarged suckers (S<sub>Ie</sub> 23). Web shallow (WDI 10), nearly subequal in depth, with formula D > C = B > A = E. Ligula minute (LLI 1.3). Dorsal surfaces of mantle and head covered with ridge-like warts.

ORIGINAL DESCRIPTION.—Rochebrune, 1882:39.

TYPE LOCALITY.—Western Tropical Pacific Ocean, China, Cochin (= South Vietnam), Poulo Condoro.

TYPES.—*Syntypes*: MNHN 4-7-928, 1 male, 32 mm ML, 1 female, 7 mm ML, fide Lu et al. (1995).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from Robson (1929), who examined the syntypes. Hoyle (1886) considered *Octopus harmandi* to be insufficiently characterized. Robson (1929) listed *O. harmandi* in the synonymy of *O. niveus* Lesson, 1830 (= *O. filamentosus* Blainville, 1826; for an account of that taxon see Toll, 1998), noting that the hectocotylized arms were identical. We uphold that decision.

#### *Octopus hattai* (Sasaki, 1929)

DIAGNOSIS.—Animal medium-sized to large (90 mm ML, 120 mm ML). Mantle oval, relatively narrow, widest medially (MWI 50–60); neck weakly constricted; head small, about 50% of width of mantle; eyes average in size. Funnel moderately large, funnel organ W-shaped, narrow, inner limbs longer than outer ones. Arms long, distinctly unequal in length; arm formula I > II > III > IV, arms I more than twice length of arms IV. Suckers distinctly unequal in diameter, varying in accordance with arm length, those on arms I twice diameter of those on arms IV; especially enlarged suckers absent. Right arm III of males hectocotylized, slightly more than 50% of length of fellow arm; ligula small (LLI about 5), HASC 82. Web deep, web formula variable but generally A = B = C > D > E. Gill lamellae 12 to 13. Penis large, penis diverticulum recurved and folded back along penis. Spermatophores to 70 mm long and with about 50 turns of sperm mass. Radula with penta- to hexicuspid rachidian (of B<sub>2</sub> seriation?). Surfaces of mantle, head, and basal portions of dorsal arms only with low, poorly defined papillae surrounded by faint, circular

grooves connected to form network. Two to 3 large supraocular papillae in longitudinal row above each eye.

ORIGINAL DESCRIPTION.—Sasaki, 1929:87, figs. 44, 45, pl. 12: fig. 10, as *Polypus hattai*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Chiba Prefecture, Kominato.

TYPES.—*Syntypes*: ACS, 2 males, 90 mm ML, 120 mm ML, 3 females (value of 20 mm ML given by Sasaki (1929) for 1 female syntype, but measurement must be in error as it conflicts with other data from same specimen).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. No new information regarding this taxon is available. This species shares some characteristics with *Callistoctopus*, such as arm formula, relative arm lengths, relative sucker sizes, gill lamellae count, and funnel organ morphology, and could be referable to that genus. We retain *Octopus hattai* as distinct.

#### *Octopus hawaiiensis* Souleyet in Eydoux and Souleyet, 1852

DIAGNOSIS.—Mantle spherical to slightly ovoid; neck distinctly constricted; eyes large and prominent. Arms moderately long (ALI 76), arm order II > I = III = IV. Web short to moderate in depth (WDI ~20), all sectors nearly subequal in depth. Body surface smooth. General color bluish grey with minute, dark chromatophores dorsally, paler ventrally.

ORIGINAL DESCRIPTION.—Souleyet in Eydoux and Souleyet, 1852:9, pl. 1: figs. 1–5.

TYPE LOCALITY.—Central northern Pacific Ocean, Sandwich Islands (= Hawaiian Islands).

TYPE.—*Holotype*: Sex undetermined, 20 mm ML, presumed to have at one time been in collections of MNHN but not currently found there (Lu et al., 1995).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description, which was repeated verbatim (in French) by Berry (1914a) and was paraphrased by Robson (1929). Berry (1914a) could not associate *Octopus hawaiiensis* with any other described species. Robson (1929) maintained *O. hawaiiensis* as distinct but suggested that because the type was relatively small, the taxon could represent the young of another described species. Because the holotype appears to have been lost and the original description lacks sufficient detail to clearly characterize this taxon, we consider *Octopus hawaiiensis* to be a nomen dubium.

#### *Octopus hoeki* Joubin, 1898

DIAGNOSIS.—Animal small to medium-sized (230 mm TL; 65 mm ML). Mantle oval (MWI 40); head narrow (HWI 24); eyes prominent. Arms short to moderate in length (ALI 71), arm order I > II > IV > III (? III > II > IV > I or III > IV > II > I; see "Discussion"). Suckers small in diameter (S<sub>I</sub>n 9.2),

deeply set in flesh of arms; first 3 adoral suckers on each arm uniserial, suckers biserial distally; especially enlarged suckers absent. Web shallow (WDI 19); web formula  $D = C > B = E > A$ . Surface of mantle and dorsal web covered with papillae.

ORIGINAL DESCRIPTION.—Joubin, 1898:24.

TYPE LOCALITY.—Western tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: RNHL, female, 230 mm TL.

DISTRIBUTION.—Known only from type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Joubin (1898) and Robson's (1929) redescription of the type, noted by him to have been badly damaged and mangled. There is some confusion as to several characters exhibited by the type. The arm order as given by Joubin was  $I > II > IV > III$ ; Robson (1929) gave the reverse order. Joubin (1898) noted that the skin of the type was smooth; Robson (1929) indicated that the extant portions of skin were covered with "warts." Also, it is unclear what Joubin (1898:24) meant by the "très curieux petits organes pigments." Pickford (MS) listed *Octopus hoeki* in the synonymy of *O. aegina* Gray, 1849 (considered herein to be a nomen dubium, see that species, above), based on the web formula. We do not think that that action was warranted. Rather, it is our opinion that *O. hoeki* should be treated as a nomen dubium.

#### *Octopus hongkongensis* Hoyle, 1885

DIAGNOSIS.—Animal large (to 200 mm ML). Mantle broad (MWI 100); head relatively narrow (HWI 72). Funnel organ W-shaped, outer limbs shorter than inner limbs. Arms long (ALI 82), arm formula  $I > II > III > IV$ . Suckers large (SI 12); especially enlarged suckers absent in males and females. Right arm III of male hectocotylized (HALI 322), shorter than fellow (FAI 66); ligula long (LLI 11–14); calamus minute. Gill lamellae 8–11. Eggs moderate in length, capsule ~8 mm long. Penis small to moderate in length (PLI < 25). Spermatophores with maximum length of 200 mm. Radula with  $A_4$  seriation of pentacuspoid rachidian. Skin with sparse granular papillae, especially near head.

ORIGINAL DESCRIPTION.—Hoyle, 1885:224.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, off Sagami Bay, Enoshima Island, 345 fms (624 m).

TYPE.—*Holotype*: BMNH 1889.4.24.45, male, 90 mm ML.

DISCUSSION.—The diagnosis is excerpted from the accounts of the type by Hoyle (1886; Steenstrup cited as author), Robson (1929), and Gleadall (1993). Hoyle (1886) included this species in the synonymy of *O. punctatus* Gabb, 1862, from California; however, that name was preoccupied, and the type of *O. punctatus* subsequently was destroyed in the 1906 San Francisco earthquake. Pickford (1964) examined the holotype of *O. hongkongensis* and determined that it was distinct from *O. dofleini* Wülker, 1910. Gleadall (1993) reviewed the

systematic status of *O. hongkongensis* and compared it to other species characterized as having long ligulas. Gleadall (1993) considered *O. madokai* Berry, 1921, *O. tenuicirrus* (Sasaki, 1929), and *O. megalops* Taki, 1964, to be synonyms of *O. hongkongensis* (see those taxa, below).

Hoyle's (1885) original description was based on his comparison of the unique type with four specimens collected from Hong Kong and deposited in the Copenhagen Museum that were attributed to a new species, *Octopus hongkongensis*, in a manuscript by Steenstrup. Gleadall (1993) has determined that Steenstrup's specimens are not conspecific with Hoyle's holotype but represent an undescribed species reaching a maximal mantle length of about 25 mm. As a result, Gleadall (1993) listed Hoyle, 1885, rather than Steenstrup in Hoyle, 1885, as the valid author. That decision is supported herein. It is regrettable that as a valid taxon the name *O. hongkongensis* is actually a misnomer.

#### *Pteroctopus hoylei* (Berry, 1909)

DIAGNOSIS.—Animal small to medium-sized (108–233 mm TL). Mantle rounded; neck slightly constricted; head large, broad; eyes large. Funnel large, funnel organ VV-shaped, limbs narrow, acutely pointed apically, elevated, very distinct, inner and outer limbs subequal. Arms moderate, subequal in length (ALI 70.1–73.8), stout. Suckers small in diameter (SI 4.5–6.0), closely spaced, first 3 proximal suckers uniserial, suckers become biserial distally; especially enlarged suckers absent. Right arm III of males hectocotylized, shorter than fellow (FAI 73.4–96.2); ligula small (LLI 2.7–5.6), bluntly conical, spoon-shaped; calamus acutely conical, deeply grooved. Web deep, dorsal and ventral web extensions along each arm unite aborally to form pallisade-like membrane extending to tip of arm. Mantle musculature gelatinous, surfaces of mantle, head, and basal portion of arms finely granulose, 2 supraocular papillae on each side of head. Color in preservation uniformly brownish red dorsally, paler to pink ventrally and on oral surface of web; distinct pigmentation pattern absent.

ORIGINAL DESCRIPTION.—Berry, 1909:407, fig. 1, as *Polypus hoylei*.

TYPE LOCALITY.—Central northern Pacific Ocean, Hawaii.

TYPE.—*Holotype*: USNM 214310, male, ~55 mm ML, in alcohol, extremely poor condition.

DISTRIBUTION.—Hawaii, Japan?, Indian Ocean (see *Pteroctopus hoylei annae* (Robson, 1929) in Toll, 1998).

DISCUSSION.—The diagnosis is excerpted from Berry (1914a). This distinctive species was originally described in the genus *Polypus*. Robson (1929) tentatively placed it in *Octopus* sensu stricto but noted that the generic position was unclear. Adam (1939) included *P. hoylei* as the type species of a new genus *Berrya*. Toll (MS) considers *Berrya* to be a junior synonym of *Pteroctopus* Fischer. We retain *P. hoylei* as distinct.



Taki (1962) described *Hapaloctopus albidus* in an abstract in Japanese. The following year he (Taki, 1963) placed this taxon in the synonymy of *Berrya hoylei* and provided a lengthy description with several figures of that taxon. Due to the distinctiveness of *P. hoylei*, there is no reason to doubt Taki's reconsideration of *H. albidus*.

#### *Octopus inconspicuus* Brock, 1887

DIAGNOSIS.—Animal moderate-sized (280 mm TL; 40 mm VML). Mantle oval. Arms moderately long (ALI 78.6). Right arm III hectocotylized; ligula small (LLI 2.0). Three supraocular cirri on each side of head, 2 posterior, 1 anterior to each eye. Mantle with 6 papillae on mantle organized in 2 rows, of 2 and 4 papillae, across anterior  $\frac{1}{3}$  of mantle. Additional papillae in longitudinal row along aboral surfaces of arms.

ORIGINAL DESCRIPTION.—Brock, 1887:603, pl. 16: fig. 4.

TYPE LOCALITY.—Western tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: ZMUG, male, 40 mm VML, not extant (see "Discussion").

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Brock (1887). Although lengthy, the description is defective; few diagnostic characters were given that permit positive identification of this taxon. Some characters were artifacts (e.g., torn web). The type was destroyed in World War II (P. Kuenzer, pers. comm., 1988, to C.F.E. Roper). *Octopus inconspicuus* bears some resemblance to *O. horridus* Orbigny, 1826 (for an account of that taxon see Toll, 1998); however, it is highly unlikely that we shall ever know the true identity of Brock's species. Therefore, we consider *O. inconspicuus* to be a nomen dubium.

#### *Cistopus indicus* (Rapp in Orbigny, 1835, in Férussac and Orbigny, 1834–1848)

DIAGNOSIS.—Animal large (to 600 mm TL; to 180 mm ML; wt to 2 kg). Mantle elongate; head narrow; neck constricted. Funnel long, funnel organ W-shaped. Arms long (ALI 80–87), slender, attenuate at tips, arm formula I > II > III > IV or I = II > III > IV. Suckers moderate in diameter (SIn 10); especially enlarged suckers present on arms I and II of males (Sle 17). Right arm III of males hectocotylized, shorter than fellow; ligula small (LLI 1.4–3.0), without concavity; calamus simple, undifferentiated. Web moderate in depth (WDI 13–18), web formula variable, typically A > B > C > D > E or B = C > A > E > D. Web with 8 aquiferous pores leading to individual pouches, 1 per web sector. Ink sac deeply set within digestive diverticulum; gill lamellae 9–11. Mature ovarian eggs small, capsule 4–5 mm in length. Color in preservation dark brown to grey on dorsal surface; ventral surface of mantle with green iridescent sheen. Skin smooth to rugose with fine, low, widely spaced tubercles.

ORIGINAL DESCRIPTION.—Rapp in Orbigny, 1835, pl. 25, in Férussac and Orbigny, 1834–1848, as *Octopus indicus* (see also below).

TYPE LOCALITY.—Western tropical Pacific Ocean, Celebes (= Sulawesi).

TYPE.—*Syntype*: MNHN 5-4-1050, female, 78 mm ML, Rapp (coll.) (fide Lu et al., 1995).

DISTRIBUTION.—Widely distributed in the Indo-Malayan region; Philippines; China; India; Pakistan; spotty records from off east coast of Africa.

DISCUSSION.—The diagnosis is excerpted from the accounts of Robson (1929), Voss and Williamson (1971), Pickford (1974), Roper et al. (1984), and Nesis (1987). *Cistopus indicus* is most easily recognized by the presence of the aquiferous pores and pouches located in each web sector; however, in some material these can be difficult to locate and can go unnoticed.

Some of the poorly described taxa from the Indo-West Pacific that are based on immature types having an elongate mantle and an arm order of I > II > III > IV (or similar) are almost certainly referable to this taxon (see Massy, 1916; Robson, 1929; Adam, 1945, 1959; Pickford, 1974). *Cistopus indicus* supports a large fishery throughout much of its range.

One of us (GLV) has seen material suggesting that there could be a second, cryptic species of *Cistopus* in the Indian Ocean, distinguishable based on hectocotylus morphology.

#### *Octopus kagoshimensis* Ortmann, 1888

DIAGNOSIS.—Animal medium-sized (40 mm ML). Mantle narrow, elongate-oval (MWI 31–42); neck narrow; head narrow (HWI 31–42). Funnel organ W-shaped. Arms moderate in length (ALI 71–79), arm order variable, but arms I always shortest. Suckers large (SIn 10–14); especially enlarged suckers absent in males. Ligula small (LLI 4–8), slender, central groove highly reduced. Web moderate to deep (WDI 22–30), sector D deepest, A shallowest. Gill lamellae 7–10. Mature eggs small, capsule 2.0 mm long  $\times$  0.5 mm wide. Penis long, slender, U-shaped with diverticulum, with connecting crossbar. Spermatophores long, larger than mantle (SpLI 120–250), sperm reservoir unarmed (crochets absent). Radula with A<sub>2-4</sub> seriation (typically A<sub>2</sub>) of rachidian. Body covered with small warts or papillae with single multifid supraocular papillae. Color pale purple or vinous red with purple reticulations. Dark stripe or splotch between sucker bases on dorsal side of arms.

ORIGINAL DESCRIPTION.—Ortmann, 1888:644.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Kagoshima Prefecture.

TYPES.—*Syntypes*: UMS, 5 males, 4 females, now in macerated condition (fide Adam, 1960).

DISTRIBUTION.—See "Discussion."

DISCUSSION.—The diagnosis is based on the original description by Ortmann (1888) and on the accounts by Robson

(1929), Adam (1960), and Pickford (MS). Sasaki (1929) placed *Octopus kagoshimensis* in the synonymy of *O. granulatus* (Lamarck, 1799), but this no longer is tenable. This taxon is referable to the *Octopus aeginalhardwickei* (= *dollfusi*) complex, historically a source of confusion. Member taxa are characterized by the exceptional, deeply excised web sector A and the general, fine papillation of the surface of the mantle, head, and arms. Robson (1928b) placed *O. kagoshimensis* in the synonymy of *O. aegina*. At present, however, the only character that discriminates between the two species in this complex is the form of the spermatophore, either armored (with crochets) or unarmored (crochets lacking).

The type of *O. aegina* Gray, 1849, is a female from an uncertain locality. Due to the uncertainties of attributing new material to that taxon, we consider *O. aegina* to be a nomen dubium (see that taxon, above). *Octopus hardwickei* Gray, 1849, the senior synonym of *O. dollfusi* Robson, 1928, is characterized as having armored spermatophores. Therefore, this taxon is distinct from *O. kagoshimensis*.

Pickford (MS) noted that, based on her examination of material attributable to this complex, specimens with unarmed spermatophores showed a disjunct distribution: Molucca, Celebes (= Sulawesi), and Japan; Suez, Gulf of Aqaba, and Mozambique. Specimens with armed spermatophores have been recorded from Sumatra, Southern China, Singapore, and the Gulf of Siam. This suggests that the complex could contain three species, of which the two with unarmed spermatophores have yet to be distinguished.

#### *Octopus kermadecensis* (Berry, 1914)

DIAGNOSIS.—Animal small to medium-sized (~43 mm ML). Mantle narrow, elongate (MWI 46); neck strongly constricted; head long and narrow (HWI 40); eyes large, protruding. Funnel long, funnel organ damaged in type. Arms moderate in length (ALI 72.4), slender, attenuate; arm formula I > II > III = IV, arms I much longer than others. Suckers elevated, small, proximal 4 suckers uniserial, becoming biserial distally. Surfaces of mantle, head, and arms nearly smooth, few soft papillae located over each eye, and minute papillae scattered on dorsum of mantle; mantle with conspicuous, peripheral, keel-like fold. General color in preservation dull grey brown, mottled, streaked with slate.

ORIGINAL DESCRIPTION.—Berry, 1914b:138, pls. 7, 8, as *Polypus* (*Pinnoctopus*?) *kermadecensis*.

TYPE LOCALITY.—Kermadec Islands, Sunday Island, on beach.

TYPE.—*Holotype*: USNM 816461, female, 43 mm ML, SSB no. 399.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Berry (1914b). The mantle fold is probably adventitious, but its presence prompted Berry (1914b) to suggest that *Octopus kermadecensis* could be referable to

*Pinnoctopus*. Robson (1929) did this with hesitation. Toll (MS) considers *Pinnoctopus* to be a synonym of *Octopus*. We retain *Octopus kermadecensis* as distinct.

#### *Octopus longispadiceus* (Sasaki, 1917)

DIAGNOSIS.—Animal medium-sized (52–63 mm ML). Mantle ovoid (MWI 70–80); neck constricted; head moderate to wide (HWI 73–94); eyes slightly prominent. Funnel organ large, W-shaped, outer limbs about 50% length of inner ones. Arms slender, attenuated at tips, moderate to long (ALI 78–84), arm order I > II > III > IV; especially enlarged suckers present in males on arms I, II, and III at, or just beyond, web margin (10th to 12th pair) (Sle 24), largest on arms I and II. Right arm II hectocotylized, subequal in length to fellow; ligula moderate in length (LLI 9–10), slender, conical, copulatory groove deep and well marked, HASC 49–60. Web moderate in depth (WDI 20–25). Gill lamellae 10 to 11. Penis with long diverticulum. Surface of body covered with single, rounded papillae; single large supraocular papillae on each side of head.

ORIGINAL DESCRIPTION.—Sasaki, 1917:366, as *Polypus longispadiceus*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Iwate Prefecture.

TYPES.—*Syntypes*: Hokkaido University Fisheries Museum, 4 males, 52–63 mm ML (fide Gleadall, 1993).

DISTRIBUTION.—Japan, Miyagi Prefecture; Hokkaido near Hakodate; questionably near Cape Clonard, Korea, and Hyuga-nada.

DISCUSSION.—The diagnosis above is excerpted from Sasaki (1917, 1929). *Octopus longispadiceus* is a member of the complex of western Pacific octopodines characterized by having conical, relatively long ligulas. Gleadall (1993) examined the type series of *O. longispadiceus*, gave a preliminary analysis of this group from Japan, and found that several other taxa, including *O. araneoides* Taki, 1964, *O. yendoi* (Sasaki, 1929), and *O. tsugarensis* (Sasaki, 1920), were related and could be synonyms of *O. longispadiceus*. Further study is required to clarify these relationships. At present we retain *Octopus longispadiceus* as distinct.

#### *Hapalochlaena lunulata* (Quoy and Gaimard, 1832)

DIAGNOSIS.—Animal small to medium-sized (to 55 mm ML). Mantle ovoid to round, pointed posteriorly (MWI 70–93); neck distinct; head width moderate (HWI 57–73); eyes small. Mantle aperture narrow with long pallial septum. Funnel organ W-shaped. Arms short to moderate in length (ALI 69–74), arm order typically IV > III > II > I, but arms subequal. Suckers moderate in size (SIn 8). Right arm III of males hectocotylized, shorter than fellow (FAI 80–90); ligula length moderate (LLI 7–9), simple; calamus small. Web deep (WDI 33). Gill lamellae 7–9. Eggs small, capsule 2.5–3.5 mm long, attached to substratum in festoons of 20–30. Radula with A<sub>2</sub> seriation of rachidian. Skin smooth; mantle, head, web, and

arms with conspicuous pattern of large (7–8 mm), iridescent blue rings with broad, dark maculae around outer periphery and clear centers.

ORIGINAL DESCRIPTION.—Quoy and Gaimard, 1832:86, pl. 6: figs. 1, 2, as *Octopus lunulatus*.

TYPE LOCALITY.—Western tropical Pacific Ocean, Bismarck Archipelago, New Ireland, Carteret Harbour (= Lamassa Bay, 4°43'S, 152°48'E) (not New Zealand as reported in various accounts).

TYPE.—*Syntype*: MNHN 4-12-973, male, 10 mm ML (fide Lu et al., 1995).

DISTRIBUTION.—Western and eastern Australia through the East Indies (but see also "Discussion").

DISCUSSION.—The diagnosis is excerpted from Robson (1929) and Roper and Hochberg (1988). According to Roper and Hochberg (1988), *Hapalochlaena lunulata* can be distinguished easily from the other species of blue-ringed octopuses, *H. maculosa* Hoyle, 1883, and *H. fasciata* Hoyle, 1886, based on the size, configuration, and pattern of the iridescent rings or lines. However, Roper and Hochberg (1988) and Stranks (1988) suggested that *H. lunulata* could include a complex of closely related species or subspecies. Therefore, distributional records are potentially problematic.

#### *Octopus luteus* (Sasaki, 1929)

DIAGNOSIS.—Animal large (110–125 mm ML). Mantle ovoid (MWI 46–56); head narrow (HWI 32–35). Funnel moderate in size, funnel organ W-shaped, medial limbs larger than lateral limbs. Arms short to moderate in length (ALI 61–75), strongly unequal in length, arm formula I > II > III > IV. Right arm III of males hectocotylized (HALI 195), with 88 suckers, shorter than fellow (FAI 61); ligula small (LLI 4). Web shallow (WDI ~18). Gill lamellae 12. Penis elongate, penis diverticulum recurved. Spermatophores moderate in size (SpLI 68.2), slender (SpWI 1.4), with about 25–30 coils of sperm mass. Surface of mantle covered with variously sized, pimple-like papillae, those above eyes slightly larger; ventral surface smooth. Color in preservation reddish brown with darker blotches dorsally, paler ventrally.

ORIGINAL DESCRIPTION.—Sasaki, 1929:45, fig. 160, pl. 27: figs. 6–9, pl. 29: figs. 4, 5, as *Polypus luteus*.

TYPE LOCALITY.—Western North Pacific Ocean, Formosa Strait, Pescadores Islands (= Taiwan, P'eng-hu Lieh-tao).

TYPES.—*Syntypes*: ACS, 1 male, 110 mm ML, 1 female, 125 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Sasaki (1929), who compared this taxon with *Callistoctopus macropus* (Risso, 1826) and separated it based on head size, arm length, sucker number, and web depth. Pickford (1964) considered *O. luteus* to be a junior synonym of *C. macropus*. We retain *Octopus luteus* as distinct. Further study could determine that it is referable to *Callistoctopus*.

#### *Octopus machikii* Brock, 1887

DIAGNOSIS.—Animal small (90 mm TL; 15 mm VML). Arms moderate in length (ALI 77.8), arm order I > III > II > IV. Background color yellow ochre.

ORIGINAL DESCRIPTION.—Brock, 1887:599.

TYPE LOCALITY.—Western tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: ZMUG, female, 15 mm VML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Brock (1887). The holotype, examined herein, has dried out and is now black, hard, brittle, and badly distorted; no new information can be obtained from it. Robson (1929) believed that *Octopus machikii* was attributable to *Callistoctopus macropus* (Risso, 1826) or close thereto. Pickford (MS) thought it was referable to *Cistopus indicus*. Due to the current poor condition of the type and the limited original description, we consider *O. machikii* a nomen dubium.

#### *Octopus macropus minor* (Sasaki, 1920)

See *Octopus minor minor* (Sasaki, 1920).

#### *Octopus madokai* (Berry, 1921)

DIAGNOSIS.—Animal medium-sized to large (380 mm TL; 80 mm ML). Mantle squat (MWI 80); neck distinctly constricted; head relatively broad (HWI 75). Funnel organ W-shaped, inner limbs longer than outer ones. Arms moderate in length (ALI 72), arm order I > II > III > IV. Sucker size moderate (SIn 9.4); especially enlarged suckers absent. Ink sac pyriform, proximal portion of ink sac and duct deeply imbedded in digestive gland. Gill lamellae 10. Dorsal surface of mantle densely covered with low, rounded papillae; about 20 larger papillae and 2 large supraocular papillae on each side of head.

ORIGINAL DESCRIPTION.—Sasaki, 1920:176, pl. 23: fig. 5, as *Polypus pustulosus*, preoccupied; Berry, 1921:352.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Sagami Sea, 35°04'50"N, 139°38'18"E, 70 fms (120 m).

TYPE.—*Holotype*: USNM 332976, female, 80 mm ML (no longer extant, see Roper and Sweeney, 1978).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from Sasaki (1920, 1929) and Gleadall (1993). The original name for this species, *Polypus pustulosus* Sasaki, 1920, was preoccupied (*O. pustulosus* Blainville, 1826). Sasaki (1929) compared this taxon with *Octopus dofleini* Wülker, 1910, and *O. hokkaidensis* Berry, 1921; however, the latter is now recognized as attributable to the genus *Benthoctopus* (see Table 1). Pickford (1964) suggested that *O. madokai* was probably a synonym of *O. dofleini* but was unable to examine the type. Gleadall (1993) placed *O. madokai* in the synonymy of *O. hongkongensis* Hoyle, 1885, which he determined was distinct from *O. dofleini*. We follow that decision herein.

***Octopus marginatus* Taki, 1964**

DIAGNOSIS.—Animal small (43 mm ML). Mantle ovoid, widest near midpoint of length (MWI 72); neck slightly constricted; head moderate in width (HWI 60); eyes small. Funnel short, funnel organ W-shaped, inner and outer limbs subequal in length. Arms moderate in length (ALI 73.7), arm order III > II = IV > I. Sucker size moderate (SIn 10); especially enlarged suckers absent in unique female type. Web shallow (WDI 28), web formula D > E > C > B > A. Gill lamellae 10. Radula with B<sub>4</sub> seriation of rachidian. Surface of head and mantle granular, surface of basal 1/2 of arms covered with elongated pustules arranged in oblique, radiating rows, ornamentation decreases toward arm tips. Color in life brown with lighter colored bar across eyes; narrow, white line borders edge of arms; suckers pink.

ORIGINAL DESCRIPTION.—Taki, 1964:304, figs. 47, 48, pl. 5.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Kyushu, off Oita Prefecture.

TYPE.—*Holotype*: Not deposited, female, 43 mm ML, presumed extant, held in private collection (see "Introduction").

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from Taki's (1964) original description. Taki (1964) indicated that he believed that this species belonged to the *Octopus aegina/dollfusi* complex (discussed above under *O. kagoshimensis*). Taki's female type, lacking characters of the spermatophore crucial for the proper identification of member taxa of this complex, cannot be associated with any previously described taxon. In all probability it is a junior synonym of one of the other species in this complex. It is unlikely that new material, particularly males, could confidently be referred to *O. marginatus*. Therefore, we treat *O. marginatus* as a nomen dubium.

***Octopus marmoratus* Hoyle, 1885**

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Hoyle, 1885:227.

TYPE LOCALITY.—Hawaiian Islands, Oahu, Honolulu.

TYPES.—*Syntypes*: BMNH 1889.4.24.25–26, 1 male, 1 female.

DISCUSSION.—*Octopus marmoratus* is a junior synonym of *Octopus cyanea* Gray, 1849 (for an account of *O. cyanea*, see Stranks, 1998).

***Octopus medoria* Gray, 1849**

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Gray, 1849:14.

TYPE LOCALITY.—Unknown.

TYPE.—*Holotype*: BMNH 1927.2.13.1, female, 29 mm ML.

DISTRIBUTION.—Unknown.

DISCUSSION.—This taxon was incompletely described by Gray (1849). Hoyle (1886) considered it insufficiently diagnosed. Tryon (1879) considered that *Octopus medoria* was likely to be a synonym of *O. cuvieri* Orbigny, 1834, in Férussac and Orbigny, 1834–1848, itself placed in the synonymy of *Octopus macropus* by Robson (1929). Robson (1929) redescribed the holotype of *O. medoria*, which he noted was in poor condition; however, his photograph of that specimen (Robson, 1929, pl. 4: fig. 2) showed it to be in good condition externally. We believe that *O. medoria* is probably attributable to the *Callistoctopus macropus/ornatus* complex; however, without locality data *O. medoria* is best treated as a nomen dubium.

***Octopus megalops* (Taki, 1964)**

DIAGNOSIS.—Animal medium-sized to large (75–78 mm ML). Mantle bursiform (MWI 64–73); neck region distinct; head moderate in width (HWI 49–60); eyes large, prominent. Funnel organ W-shaped, inner limbs longer than outer ones. Arms moderate in length (ALI 74–80), arm order I > II > III > IV. Suckers small (SIn 5–6); especially enlarged suckers absent. Right arm III of males hectocotylized (HALI 202.7), shorter than fellow (FAI 60); ligula length short (LLI 5.2), slenderly conical with narrow groove; calamus small (CLI 12.5). Web depth moderate (WDI 19–25), web formula D > C > B > E > A or C > B > D > E > A. Gill lamellae 8 to 9. Penis small (PLI 13.3), with hook-shaped diverticulum. Radula with B<sub>5</sub> seriation of rachidian. Surface of body smooth; single large supraocular papillae present on each side of head. Color uniformly hermosa pink to cameo pink dorsally, lighter ventrally.

ORIGINAL DESCRIPTION.—Taki, 1964:310, figs. 55–57, pl. 6: figs. 1, 2, as *Paroctopus megalops*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Kōchi Prefecture, Tosa Bay, from fish market.

TYPE.—*Holotype*: Not deposited, male, 75 mm ML, presumed to be held in private collection.

DISTRIBUTION.—Japan, Shikoku, Tosa Bay and Enshu Sea (Okutani et al., 1987:173).

DISCUSSION.—The diagnosis is excerpted from the original description. Taki (1964) noted that this species was similar to *Octopus tenuicirrus* Sasaki, 1929, but differed from it in lack of dermal ornamentation and presence of a single supraocular papillae. Gleadall (1993) reviewed these taxa and concluded that both were synonyms of *O. hongkongensis* Hoyle, 1885. That decision is followed herein.

***Octopus membranaceus* Quoy and Gaimard, 1832**

DIAGNOSIS.—Animal small to medium-sized (93 mm TL). Arm formula II > III = IV > I. Funnel organ W-shaped, inner limbs slightly longer than outer limbs. Gill lamellae 7 to 8. Immature ovarian eggs minute, capsule 0.1–0.3 mm long. Dermal sculpture lacking. Paired ocelli present on web near base of arms II and III.

ORIGINAL DESCRIPTION.—Quoy and Gaimard, 1832:89, pl. 6: fig. 5.

TYPE LOCALITY.—Western tropical Pacific Ocean, New Guinea, Port Dorey.

TYPE.—*Syntype*: MNHN 4-7-922 (see "Discussion"), immature female, 22 mm ML (reported as 20.5 mm by Lu et al., 1995).

DISTRIBUTION.—Known with certainty only from the type locality.

DISCUSSION.—The diagnosis is based on examination of the syntype by one of us (GLV) and on the accounts of Orbigny (in Férussac and Orbigny, 1834–1848) and Gleadall (1991) of the same specimen. The original description and illustration are defective. The specimen labelled as the syntype is an immature female, generally in poor condition; the posterior end of the mantle is torn and macerated, the arms are mutilated and missing the tips. Therefore, measurements of the arms, web, and other characters could not be obtained. The ocellus is poorly preserved as a dark splotch between each eye, and the arm bases are without indication of an iridescent ring.

*Octopus membranaceus* belongs to the much confused western Pacific Ocean ocellated-octopus complex. Gleadall (1991) reviewed and tentatively supported the proposals by Sasaki (1929) and Pickford (MS) that the Indo-Pacific ocellated-octopus complex contained two species that are separable on the basis of egg size. Although we agree that there is substantial evidence to suggest the ocellated octopods from this region are not all attributable to a single species, we are unconvinced that all the nominal species can be attributed to just two species; more than two distinct species of ocellated octopods could exist within this extensive area. As a result, the identity of *Octopus membranaceus*, supported by a single, immature, female type, now in fair to poor condition, is difficult to establish. Therefore, despite the wide use of this name in the literature, we recommend that *O. membranaceus* be considered a nomen dubium.

#### *Octopus minor minor* (Sasaki, 1920)

DIAGNOSIS.—Animal small (20–29 mm ML). Mantle slender (MWI 44–60); neck long; head narrow (HWI 41–55). Funnel organ slender, VV-shaped, inner limbs longer than outer ones (but see "Discussion"). Arms long (ALI 80–82), distinctly unequal, arm order I > II > III > IV. Suckers moderate to large (SIn 8.0–11.0). Right arm III of males hectocotylized, shorter than fellow (FAI 50–53). Gill lamellae 7 to 8. Penis moderate to large in size, with tubular recurved diverticulum. Spermatophores moderate in length (SPL 23 mm; SPW 1 mm), sperm cord with 19 coils. Surface of body tuberculate, supraocular papillae absent. Color greyish brown, deeper and irregularly marbled dorsally.

ORIGINAL DESCRIPTION.—Sasaki, 1920:181, as *Polypus macropus* var. *minor*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan,

Suruga Bay, near Omai Point, 34°40'45"N, 138°18'30"E, 47 fm (86 m).

TYPE.—*Holotype*: USNM 332963, male, 29 mm ML.

DISTRIBUTION.—Sakhalin Peninsula through Japan and along the coast of China from shallow water to 150 m (Okutani et al., 1987:165).

DISCUSSION.—The diagnosis is excerpted from Sasaki (1920, 1929). Sasaki (1920) considered *minor* to be a varietal form of *Polypus macropus* (Risso, 1826). Sasaki (1929) renamed *P. m.* var. *minor* as *P. variabilis* with three varietal forms: *P. v. minor*, *P. v. typicus*, and *P. v. pardalis*. As noted by Taki (1944, 1981) and Okutani et al. (1987), according to the ICZN (1985, Arts. 10–20), *minor* is available and becomes the valid specific epithet of the new species with three subspecies.

There is some confusion with regard to Sasaki's (1929:95) description of the funnel organ. In the text he stated that "the inner lobe is  $\frac{1}{2}$  to  $\frac{3}{5}$  as long as the outer;" however, the figure (pl. 12: fig. 19) clearly shows the inner limbs to be longer. The best course of action is to assume that the figure is correct. Based on the data currently available, we retain *Octopus minor minor* as distinct. Sasaki (1929) distinguished this form from *O. minor typicus* by the shape of the funnel organ, number of gill lamellae, penis morphology, and spermatophore length. As with the other members of this complex, further comparative study is warranted.

*Octopus tenuipulvinus* (Sasaki, 1920:182) is related to this complex and could be the female of *O. minor minor*. Sasaki (1929) stated that he had separated the type of *O. tenuipulvinus* from *Polypus minor* (subspecies not indicated) with hesitation. He gave five characters that he considered to be principle differences: the funnel organ, dermal ornamentation, web, body shape, and gill lamellae count. Sasaki's illustration (1929, pl. 12: fig. 20) of the funnel organ of *O. tenuipulvinus* shows that the inner limbs are more than twice the length of the outer limbs and are extended almost to the aperture of the funnel. Without additional specimens it is difficult to assess this difference. Sasaki's (1929) descriptions of the dermal ornamentation of the various taxa involved do not permit a rigorous comparison. The web as described for *O. tenuipulvinus* is subequal in all sectors, as is the condition in *O. minor pardalis*. Interpretation of body shape can be subjective; however, the MWI of the type of *O. tenuipulvinus* is greater than that reported for all subspecies of *O. minor*. Voss (1981), however, recognized a wide range of mantle shapes in a series of *Callistoctopus ornatus* (Gould, 1852). Finally, the gill count of *O. tenuipulvinus* is within the range of variation seen in *O. minor minor*. Although additional study is warranted, we maintain that *O. tenuipulvinus* is likely a synonym of one of the forms of *O. minor*. *Octopus* sp. B of Voss and Williamson (1971) also could be conspecific.

As noted by Voight (1998), the apparent sympatry of the subspecies of *Octopus minor* suggests that their subspecific division is artificial. One course of action would be to raise the three nominal subspecies to full species rank. We think, however, that this action is premature and retain the present

taxonomy, despite this obvious problem. The *O. minor* complex shows some similarities to the genus *Callistoctopus*.

***Octopus minor pardalis* (Sasaki, 1929)**

DIAGNOSIS.—Animal medium-sized (350 mm TL). Mantle broadly rounded posteriorly (MWI 74); neck weakly constricted; head with small eyes (HWI 70). Funnel organ large, VV-shaped, inner and outer limbs subequal in length. Arms long (ALI 82.9), arms I longest, suckers more numerous than in *Octopus minor typicus*. Right arm III of males hectocotylized, hectocotylus with 110 suckers. Gill lamellae 14. Penis straight, elongate; penis diverticulum short, bulbous. Color in preservation (alcohol) dark brown with 5 lighter, transverse streaks, paler ventrally; arms with numerous round spots (5–7 mm) in regular biserial pattern, most distinct on arms I (at least 30 pairs).

ORIGINAL DESCRIPTION.—Sasaki, 1929:94, pl. 12: figs. 15, 16, as *Polypus variabilis* var. *pardalis*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Chiba Prefecture.

TYPE.—*Holotype*: TNSM?, male, 50 mm ML, presumed no longer extant (I. Gleadall, pers. comm.).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. Sasaki (1929) considered *Octopus minor pardalis* to be similar to *Polypus macropus* (Risso, 1826) but differentiated it on the basis of funnel organ morphology, pigmentation on the dorsal mantle, and number of suckers on the hectocotylized arm. Additional study is warranted; however, until revisionary work can be performed, we retain *Octopus minor pardalis* as distinct. See also "Discussion" under *Octopus minor minor*, above.

***Octopus minor typicus* (Sasaki, 1929)**

DIAGNOSIS.—Animal medium-sized to large (230–578 mm TL; 70–100 mm ML). Mantle elongate, ovoidal (MWI 40.0–53.1); neck strongly constricted; head narrow (HWI 24.3–34.6). Funnel large, funnel organ small, VV-shaped, inner limbs longer than outer ones. Arms long (ALI 76.1–81.5), arm order I > II > III = IV, strongly unequal in length. Suckers prominent, largest on arms I and decreasing in size in relation to decreasing arm length; suckers on arms I about twice size of those on arms IV; suckers larger in males (SIn 5.8–16.7) than in females (SIn 5.3–8.0) of similar size. Right arm III of males hectocotylized (HALI 129.6–164.3), shorter than fellow (FAI 48.4–57.5); ligula long (LLI 11.3–22.9), spoon-shaped, with 10–14 transverse grooves; calamus large, bluntly pointed; HASC 40–60. Web shallow (WDI 6.5–10); web formula A > (=) B > C > D > E. Gill lamellae 10–12. Ovarian eggs moderate in size, capsule 8 mm long. Penial complex shaped like numeral "6," penis short, penis diverticulum large, ovoid. Spermatophores moderate in length (SPL 42 mm) and width

(SPW 2.2 mm), sperm mass with 40 coils. Radula with pentacuspoid rachidian. Surface of body smooth to papillate depending on preservation, 5–8 conical supraocular papillae, 1 distinctly larger than others. Color in preservation (formalin) reddish drab to bluish brown dorsally, lighter ventrally. In life, numerous yellowish spots up to several mm in diameter present on dorsal surface of mantle.

ORIGINAL DESCRIPTION.—Sasaki, 1929:90, figs. 47, 48, pl. 1: fig. 9, pl. 3: fig. 21, pl. 12: figs. 13, 14, as *Polypus variabilis* var. *typicus*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Shizuoka Prefecture.

TYPE.—*Holotype*: ACS (see "Discussion").

DISTRIBUTION.—Numerous localities around Japan.

DISCUSSION.—The diagnosis is excerpted from the original description. Sasaki (1929) indicated that the type series comprised 42 specimens. He gave a single type locality and indicated the disposition of the "type" but did not give a specific data set as having come from the type. Sasaki (1929) noted that this species is highly variable with respect to several characters, notably the morphology of the hectocotylus, penis, and funnel organ. Our review of his data from the type series suggests that it includes nonconspecific material. As with the preceding two subspecies, additional study is required. Until such time, we retain *Octopus minor typicus* as distinct. See also "Discussion" under *Octopus minor minor*, above.

***Octopus mollis* Gould, 1852**

DIAGNOSIS.—Animal small (~75 mm TL). Mantle elongate; eyes prominent. Arms slender, arm order IV > III > II > I; ASC 30–40. Dermal ornamentation absent.

ORIGINAL DESCRIPTION.—Gould, 1852:479, fig. 592.

TYPE.—*Holotype*: Sex undetermined, ~75 mm TL, not extant (see "Discussion").

TYPE LOCALITY.—Western tropical Pacific Ocean, Samoa Islands, Tutuila Island.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The original description is defective, lacking sufficient characterization to adequately recognize this taxon and distinguish it from related forms. Robson (1929) listed it along with taxa he considered to be insufficiently diagnosed. The type was collected as part of the United States Exploring Expedition but is absent from the collections of the NMNH and is assumed to have been lost, as apparently was the regrettable fate of all of the alcoholic material collected from this historic expedition (see Johnson, 1964; Voss, 1981). We recommend that *Octopus mollis* be considered a nomen dubium.

***Octopus mutilans* Taki, 1942**

DIAGNOSIS.—Animal medium-sized (40–55 mm ML). Mantle narrow, ovoid, broadest near posterior 1/3 of mantle (MWI 37–50); neck distinctly constricted; eyes promi-

ment. Funnel organ W-shaped, inner limbs slightly longer than outer ones. Arms long, slender (ALI averaging ~85), length highly variable, tapered gradually toward tips; arm formula typically IV > III > II > I. Suckers moderate in size, sexually dimorphic (SIn 9.4, males; 5.4–7.5, females); proximal 6 to 7 suckers uniserial, suckers biserial distally; maximum of 186 suckers on longest arm; especially enlarged suckers absent in males and females. Right arm III of males hectocotylized, shorter than fellow (FAI about 50); ligula small (LLI ~3), with longitudinal groove; calamus minute, hectocotylized arm with 52–72 suckers. Web exceptionally shallow (WDI 6–7), web formula E = D = C > B > A. Gill lamellae 7 to 8. Penis long (PLI 31), penis diverticulum small. Spermatophores moderate in length (SPL 22 mm), narrow (SPW 0.6 mm); sperm mass with 40 coils. Radula with A<sub>2</sub> seriation of rachidian, alternating between unicuspidate and tricuspitate. Surface of mantle smooth to papillate, mantle with 20–30 low, conical papillae about 3 mm tall, arms with smaller papillae; single small, conical supraocular papilla. Color in life pale dirty grey, ground color yellowish with dark brown reticulations. Row of grey spots extended along each arm, 20–30 on longest arm. Suckers greyish white centrally, brownish around periphery. Mantle becomes uniformly brownish buff without reticulations when stimulated, arms occasionally display dark bars between spots; longitudinal bars can appear along mantle. Color in preservation (formalin) dirty yellowish brown marbled with sooty, reticulated pattern dorsally; pale, ashy yellow ventrally.

ORIGINAL DESCRIPTION.—Taki, 1942:71, figs. 3, 4, 6–14.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Hiroshima Prefecture, Seto Sea off Onomichi.

TYPES.—*Syntypes*: Not deposited, 11 specimens (including males and females), presumed to be held in private collection.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Taki (1942). Taki compared *Octopus mutilans* to *Octopus defilippi* Verany, 1851, *O. niveus* Lesson, 1830 (herein = *Octopus filamentosus* Blainville, 1826), and *O. filamentosus* Blainville, 1826 (see Toll, 1998). *Octopus mutilans* is similar to *O. filamentosus* and could be a synonym; however, the two type localities are far removed from one another and distributional data for both are limited. Therefore, we choose to retain *O. mutilans* as distinct. Further study could demonstrate that these taxa are all referable to the genus *Macrotritopus*. The name *mutilans* reflects the ease by which arms are autonomized during handling.

#### *Octopus nanhaiensis* Dong, 1976

DIAGNOSIS.—Animal small to medium-sized (110–330 mm TL). Mantle ovoid. Funnel organ W-shaped. Arms long, arm order I > II > III > IV. Right arm III of males hectocotylized; ligula small (LLI 6.6), conical. Penis in shape of numeral “9,”

thick, short. Radula with pentacuspitate rachidian. Mantle smooth.

ORIGINAL DESCRIPTION.—Dong, 1976:211, pl. 1.

TYPE LOCALITY.—China, Guangdong Province.

TYPE.—*Holotype*: IOAS Q11JB-47, male, 1960.I.9.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The original description was published in Chinese with English summary, excerpted above. Little is known about this species. Dong (1976) compared it with *Octopus variabilis* (= *O. minor* (Sasaki, 1920)), *O. luteus* (Sasaki, 1929), and *Callistoctopus macropus* (Risso, 1826) but stated that it could be distinguished by ligula, penis, funnel organ, and radula. We agree that *O. nanhaiensis* shows similarities to the *C. ornatus/macropus* complex and could be referable to that genus; however, additional study is needed in order to confirm its identity and generic affiliation. Until then, we retain *O. nanhaiensis* as distinct.

#### *Octopus niveus* Orbigny, 1826

See *Octopus niveus* Lesson, 1830, below.

#### *Octopus niveus* Lesson, 1830

DIAGNOSIS.—Animal small to medium-sized (to 36 mm ML). Mantle elongate; head distinct, subequal in width to mantle; eyes small. Funnel organ W-shaped, inner limbs about twice length of outer limbs, all limbs narrow. Arms long (ALI 82.3), slender, arm formula IV > III > II > I; especially enlarged suckers present in male. Web shallow. Surface of mantle and head covered with small, pointed papillae; papillae dense above eyes; additional papillae on aboral surfaces of arms and web. Color in preservation (alcohol) brownish purple dorsally, yellowish rose ventrally.

ORIGINAL DESCRIPTION.—Lesson, 1830:239, pl. 1: figs. 1, 1bis.

TYPE LOCALITY.—Central, southern tropical Pacific Ocean, Society Islands, Bora Bora Island.

TYPES.—*Holotype*: No longer extant (fide Lu et al., in press).

*Neotype*: The syntype of *Octopus aculeatus* Orbigny, 1834, in Férussac and Orbigny, 1834–1848 (MNHN 4-7-927, male, 36 mm ML) is herein designated as the neotype of *O. niveus*.

DISTRIBUTION.—Reported to occur widely throughout the Indo-Pacific region but, due to taxonomic uncertainties, known with certainty from only the type locality.

DISCUSSION.—The diagnosis given above is based on the accounts of Lesson (1830) and Orbigny (in Férussac and Orbigny, 1834–1848) (see also “Discussion” under *Octopus aculeatus*, above). The name *Octopus niveus* first appeared in Orbigny (1826) without description, so this use represents a nomen nudum. Later, Orbigny (1834, in Férussac and Orbigny, 1834–1848) described a new species, *O. aculeatus*, and placed

the accounts of *O. niveus* by Orbigny (1826) and Lesson (1830) in the synonymy of *O. aculeatus*. This action, however, was unwarranted, and Lesson's (1830) account is the first valid description of this taxon.

Robson (1929) considered *Octopus niveus* as questionably a synonym of *O. filamentosus* Blainville, 1826. Pickford (MS) considered both *O. niveus* and *O. filamentosus* to be conspecific with *O. horridus* Orbigny, 1826. Toll (1998) retained *O. filamentosus* and *O. horridus* as distinct. We concur, however, with Robson and Pickford regarding the systematic status of *O. niveus* and *O. filamentosus* and consider them to be synonyms, with *O. filamentosus* having priority. Both taxa are characterized as being small-bodied, with long arms distinctly dissimilar in length, with the arm formula  $IV > III > II > I$ .

#### *Octopus ocellatus* Gray, 1849

DIAGNOSIS.—Animal small to medium-sized (35 mm ML). Mantle narrower than long (MWI 80), widest in posterior 1/3; neck slightly constricted; head narrower than mantle (HWI 60). Funnel organ W-shaped, inner and outer limbs subequal in length. Arms long (ALI 84), stout basally, slender distally, arm formula  $III = IV > II > I$ . Suckers moderate in size (SIn 11); 1 or 2 especially enlarged suckers on arms II and III (Sle 17.4) of males. Right arm III of males hectocotylized (FAI 77); ligula short (LLI 6.8), slender, with narrow, shallow groove; calamus large (CLI 32), HASC 91. Web shallow to moderate (WDI 19), web formula  $E > C = D > B > A$ . Gill lamellae 7. Penis small to moderate in length (PLI 20), curved. Surfaces of mantle, head, and arms covered with closely spaced papillae, flattened posteriorly but more projecting anteriorly; papillae also on dorsal side only of arms; 2 supraocular papillae on each side of head. Ventrally, papillae on each side of funnel extend to base of dorsal surface of arms IV; few small papillae on ventrolateral corner of mantle. Color in preservation (ethanol) light brownish with dark longitudinal bands. Four full bands on mantle with weak band at corner of mantle aperture and below eyes; 5 bands across length of head, 1 each across eye; 3 bands on base of arms, 1 central band divided anteriorly; 1 dark band on dorsal side of each arm. Ocellus present about halfway between eye and sector C of web; ocellus consists of dark central spot surrounded by clear narrow ring enclosed in turn by dark outer ring; indistinct orange brown area between and slightly posterior to eyes.

ORIGINAL DESCRIPTION.—Gray, 1849:15.

TYPE LOCALITY.—“China Seas” [sic].

TYPE.—*Holotype*: BMNH 1928.12.6.5, male, 35 mm ML.

DISTRIBUTION.—Due to the confusion concerning the ocellated octopods, the distribution outside of Japan and China is unknown.

DISCUSSION.—The diagnosis is based on examination of the holotype by one of us (GLV). Much confusion still remains concerning the ocellated species of the western Pacific Ocean, including *Octopus ocellatus*. *Octopus ocellatus* is distinct from

*O. areolatus* de Haan in Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848 (see also “Discussion,” that taxon). Sasaki (1929), Pickford (MS), and Gleadall and Naggs (1991) considered *O. ocellatus* to be a synonym of *O. fangsiao* Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848. We provisionally support that decision; however, the Indo-West Pacific ocellated octopod complex is in need of comparative revision, and the identity of some member taxa, including *O. ocellatus*, requires confirmation.

#### *Octopus ochotensis* (Sasaki, 1920)

DIAGNOSIS.—Values in brackets refer to the immature male paratype (see “Discussion”). Animal medium-sized (42 [22] mm ML). Mantle broad, globose (MWI 88 [104.5]); head moderate in width (HWI 71 [100]), weakly set off by neck. Funnel organ W-shaped, outer limbs less than 1/2 length of inner limbs. Arms moderate in length (ALI 74 [68]), subequal. Suckers moderate in size (SIn 7.7); especially enlarged suckers absent in females; left arm I with ~110 suckers. Right arm III hectocotylized, shorter than fellow [FAI 85.5]; [LLI 4]; [HASC 84]. Web moderate to deep (WDI 30.8); web formula  $A = B = C > D > E$ . Gill lamellae 9. Ovarian eggs moderate in size, capsule ~9 mm long. Surface slightly rugose in preservation (alcohol); low peripheral keel on mantle.

ORIGINAL DESCRIPTION.—Sasaki, 1920:174, as *Polypus ochotensis*.

TYPE LOCALITY.—Sea of Okhotsk, near Cape Patience, 48°43'30"N, 145°03'E, 75 fm (137 m).

TYPE.—*Holotype*: USNM 332955, female, 42 mm ML, in alcohol, good condition.

DISTRIBUTION.—Known only from the Sea of Okhotsk.

DISCUSSION.—The diagnosis is based on examination of the female type by one of us (GLV) and on the accounts by Sasaki (1920, 1929). Sasaki (1929) noted that he had referred the paratype (immature male) to this species with some hesitation. Little is known about this species. We provisionally retain *O. ochotensis* as distinct; additional study is warranted.

#### *Octopus oliveri* (Berry, 1914)

DIAGNOSIS.—Animal small to medium-sized (“dorsal length of body” 27–30 mm (Berry, 1914b:136)). Mantle broad (MWI 103–137), pyriform, widest posteriorly; neck weakly constricted; head short, narrower than mantle (HWI 77–89); eyes elevated, with small, puckered openings. Arms short (ALI about 75), stout, tapering abruptly near tips, arm formula  $II = III > I = IV$ ; proximal 4 suckers on each arm uniserial, suckers biserial distally. Web thick, shallow. Dorsal surface of mantle and head with numerous conical papillae; eye surrounded by circumocular ring of 5 to 6 low, individual papillae, supraocular papillae absent; ventral surface smooth. Color dark slate dorsally, lighter ventrally. Inner surface of suckers light brown to cream.



ORIGINAL DESCRIPTION.—Berry, 1914b:136, as *Polypus oliveri*.

TYPE LOCALITY.—Sunday Island, Kermadec Islands (intertidal among rocks).

TYPE.—*Holotype*: USNM 816455, female, 30 mm ML, SSB no. 405.

DISTRIBUTION.—In addition to the type locality, Okutani et al. (1987) attributed a specimen from Ishigaki Island, Okinawa, to this species.

DISCUSSION.—The diagnosis is excerpted from the original description. Berry (1916, pl. 6: fig. 2) included a photograph of the type. Okutani et al. (1987) gave two color photographs of a fresh, dead specimen. Little is known about this species. We retain *Octopus oliveri* as distinct.

### *Callistoctopus ornatus* (Gould, 1852)

DIAGNOSIS.—Animal medium-sized to large (to 104 mm ML). Mantle round, bulbular to elongate-tubular (MWI 27–83); neck distinct to indistinct; head narrow (HWI 31–57); eyes moderate in size, slightly protruding. Funnel organ W-shaped, outer limbs slightly shorter than inner ones. Arms long, stout (ALI 80–87), tapering to slender tips, arm order I > II > III > IV. Sucker size moderate to large (SIn 5–14, females; 7.9–15, males); especially enlarged suckers absent in males. Right arm III of males hectocotylyzed, shorter than fellow (FAI 59–82); ligula small (LLI 2.3–6.9), elongate, with strongly inrolled margins completely covering longitudinal groove; calamus large in large specimens (CLI 13–39). Web shallow (WDI 8–14); web formula variable, sector B typically deepest, sector E shallowest. Gill lamellae 12–14. Penis long, with diverticulum as long or longer. Radula with exceptionally tall rachidian with A<sub>7</sub> seriation. Upper mandible with long, well-marked notch along cutting edge; lower mandible with sharp, medial ridge on lateral lamellae, ridge bifurcates posteriorly. Surfaces of mantle, head, and arms with scattered, prominent, flat papillae; some papillae over eyes larger but do not form distinct supraocular cirri. Color in preservation (ethanol) reddish to reddish brown dorsally. Mantle and head with pale to bright buff stripes and spots, about 2 rows of spots extending along arms I and II, all often with raised ridge.

ORIGINAL DESCRIPTION.—Gould, 1852:476, figs. 590, 590a, as *Octopus ornatus*.

TYPE LOCALITIES.—*Holotype*: Central North Pacific Ocean, Sandwich Islands (= Hawaiian Islands).

*Neotype*: Central North Pacific Ocean, Hawaiian Islands, Oahu, Black Point.

TYPE.—*Neotype*: USNM 730020, male, 88 mm ML, in alcohol, good condition.

DISTRIBUTION.—Hawaii; Marshall Islands; other localities could represent misidentifications.

DISCUSSION.—This species was forgotten in the literature until redescribed by G. Voss (1981). Voss (1981) placed *Callistoctopus arakawai* Taki, 1964 (see that taxon, above), in

the synonymy of *Octopus ornatus*. Toll (MS) retains the genus *Callistoctopus* as distinct. New data (Norman, unpublished data; Toll, unpublished data) suggest that *C. ornatus* belongs to a complex of similar species that occurs throughout the central and Indo-West Pacific.

### *Octopus oshimai* (Sasaki, 1929)

DIAGNOSIS.—Animal medium-sized (43–60 mm ML). Mantle ovoid (MWI 44–60); head narrow (HWI 40–51); eyes small, not prominent. Funnel slender, funnel organ W-shaped, outer limbs considerably shorter than inner limbs. Arms moderate in length (ALI 77.1–81.4), slender, tapering uniformly, arm formula typically I = II > III > IV, but arms subequal. Suckers small, about 200 suckers on arms I and II, 190 and 180 suckers on arms III and IV, respectively; especially enlarged suckers absent in males and females. Right arm III of males hectocotylyzed (HALI 186.7–227.3), shorter than fellow (FAI 57.9–65.5); ligula moderate in size (LLI 4.8–9.8), conical, with long, shallow groove, HASC 70–74. Web shallow to moderate (WDI 17.0–23.6), web formula typically A > B > C = D = E or A = B > C = D = E. Gill lamellae 8–10. Ovarian eggs > 6 mm in length. Penis slightly dorsoventrally flattened, “retort-shaped,” inflated posteriorly. Spermatophore 55 mm in length. Surface of mantle finely papillose, smooth elsewhere. General color in preservation purplish grey, marbled with darker areas dorsally; paler, light buff ventrally.

ORIGINAL DESCRIPTION.—Sasaki, 1929:44, pl. 28: figs. 1–5, pl. 30: fig. 12, as *Polypus oshimai*.

TYPE LOCALITY.—Formosa (= Taiwan), fish market.

TYPES.—*Syntypes*: ACS, 4 males (43–48 mm ML), 2 females (50–60 mm ML).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. Sasaki (1929) compared *Octopus oshimai* with *O. globosus* Appellöf, 1886, but distinguished it based on dermal ornamentation, penis morphology, body shape, and relative arm lengths. We retain *Octopus oshimai* as distinct.

### *Octopus ovulum* (Sasaki, 1917)

DIAGNOSIS.—Animal small to medium-sized (24–45 mm ML). Mantle ovoid, broadest medially (MWI 50–74); neck slightly constricted; head relatively broad (HWI 36–53); eyes moderately prominent. Funnel organ W-shaped, medial and lateral limbs narrow, subequal in length. Arms short to moderate (ALI 60.7–75.6), slender, tapering to attenuate tips, arms subequal in length but most often with arm formula IV > III > II > I. Suckers moderately elevated, proximal 5 to 6 suckers on each arm uniserial, suckers biserial distally. Right arm III of males hectocotylyzed (HALI 150.0–183.8), shorter than fellow (FAI 69.3–80.8); ligula small (LLI 5.8–6.3); calamus minute, conical; HASC 118–140. Web depth moderate (WDI 21.6–26.8), web formula typically C = D > B =

E > A, sector A very shallow. Gill lamellae 7 to 8. Mature ovarian eggs small, capsule to 3 mm long. Penis slender, with swollen, recurved diverticulum, collectively shaped like numeral "6." Spermatophores long (SPL 49–61 mm), slender; sperm mass with 230–270 coils. Radula with penticuspid rachidian of unknown seriation. Dorsal surfaces of mantle, head, and arms densely covered with uniform papillae, in places forming longitudinal ridges. Two large supraocular papillae on each side of head, anterior one smaller. Ocellus present below each eye, 4 mm in diameter, consisting of blue to violet iridescent ring surrounding darkened spot. General color in preservation drab with several broad, dark longitudinal stripes on mantle, pale ventrally.

ORIGINAL DESCRIPTION.—Sasaki, 1917:364, as *Polypus ovulum*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Tokyo (fish market); Nagasaki.

TYPES.—*Syntypes*: ?TNSM, 11 males, 5 females, presumed no longer extant (I. Gleadall, pers. comm.).

DISTRIBUTION.—Japan, Nagasaki and Tokyo.

DISCUSSION.—The diagnosis is excerpted from Sasaki (1929), who compared *Octopus ovulum* to both subspecies of *O. fangshiao* Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848. Robson (1929) treated *O. ovulum* as a varietal form of *O. areolatus* Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848, but did not have the benefit of examining Sasaki's type series. Gleadall (1991) reviewed the standing of this taxon and considered the possibility that *O. ovulum* was a synonym of *O. membranaceus* Quoy and Gaimard, 1832, considered herein to be a nomen dubium. The status of *O. ovulum* cannot be addressed fully at present. We retain *Octopus ovulum* as distinct, pending revision.

#### *Octopus parvus* (Sasaki, 1917)

DIAGNOSIS.—Animal small (150 mm TL). Mantle elongated (MWI 61–81); neck distinctly constricted; head small (HWI 50–80). Funnel organ thin, W-shaped, outer limbs 1/2 length of inner limbs. Arms moderate in length (ALI 70–90), arm order II > III > IV > I, but arms nearly subequal. Sucker size large (SIn 16–19), proximal 3 suckers uniserial, suckers biserial distally; especially enlarged suckers absent in males and females. Right arm III of males hectocotylyzed (HALI 271.4–300.0), subequal to fellow arm (FAI 97.4–115.2); ligula short (LLI ~5), narrow, with smooth central groove; HASC 74–83. Gill lamellae 4–6. Ovarian eggs small, capsule 1.8 mm long. Spermatophores small (SPL 12 mm). Radula with symmetrical seriation of rachidian ( $A_{37}$ ). Surface of body covered with beaded papillae.

ORIGINAL DESCRIPTION.—Sasaki, 1917:365, as *Polypus parvus*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Kyushu, Shimizu Harbor.

TYPES.—*Syntypes*: ACS, 1 male, 1 female.

DISTRIBUTION.—Japan, Kagoshima Prefecture?

DISCUSSION.—The diagnosis is excerpted from Sasaki (1917, 1929). Little is known about this species. We retain *Octopus parvus* as distinct. The name *Octopus pavus* (Sasaki, 1920) represents an incorrect subsequent spelling of *O. parvus*.

#### *Scaevurgus patagiatus* Berry, 1913

DIAGNOSIS.—Animal small to medium-sized (60–152 mm TL). Mantle wider in large specimens, narrower in small specimens (MWI 56.5–118.2), widest anteriorly or medially; neck constriction small but distinct; head variable, tending to be broader in small specimens (HWI 64.5–96.2); eyes large, prominent. Funnel large, funnel organ W-shaped, inner and outer limbs subequal in length. Arms moderate in length (ALI 61.7–70.6), robust, tapering rapidly to tips, subequal, but arms II tending to be slightly longer. Suckers moderate in size (SIn 9.1–10.0), proximal 2 to 4 suckers uniserial, suckers biserial distally; single especially enlarged sucker present on arms III (Sle 11.8) in males. Left arm III of males hectocotylyzed (HALI 253.8–271.4), slightly shorter than fellow (FAI 85.7–97.1); ligula large, spoon-shaped, deeply excavated; calamus large (CLI > 50), conical. Web moderate to deep (WDI 24.4–27.0), sector A deepest, sector E shallowest. Dorsal and ventral surfaces of mantle and dorsal surface of head and arms densely covered with small, distinct, rounded papillae formed into ridges on dorsal surface of mantle. Similar smaller ridges on aboral surfaces of arms I, II, and III; peripheral keel present around mantle. Large warted or branched papillae above and behind each eye, smaller papillae in front and above each eye. Color in life light emerald green around eyes, ventral surface of body opalescent blue and pink; reddish brown chromatophores on dorsal surface of mantle, sepia chromatophores over eyes; animal pale green when chromatophores contracted. Color in preservation (alcohol) pale brownish buff, chromatophores small and numerous.

ORIGINAL DESCRIPTION.—Berry, 1913:564.

TYPE LOCALITY.—Central North tropical Pacific Ocean, Hawaiian Islands, off Maui, 261–325 m.

TYPE.—*Holotype*: USNM 214379, male, 34 mm ML, SSB no. 204, no longer extant (fide Roper and Sweeney, 1978).

DISTRIBUTION.—Hawaiian Islands; Japan.

DISCUSSION.—The diagnosis is excerpted from Berry (1914a). Berry (1914a) differentiated *Scaevurgus patagiatus* from *S. unicolor* Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848, from the Atlantic Ocean, based on funnel-organ morphology, dermal ornamentation, and maximum size. Robson (1929) considered the two taxa to be synonymous. Toll (1988) supported Berry's separation of *S. patagiatus* from *S. unicolor* based on average arm-sucker count and hectocotylyzed arm-sucker count (for an account of that taxon, see Mangold, 1998). We uphold the decision that *S. patagiatus* is a distinct species.

#### *Octopus pavus* (Sasaki, 1920)

See *Octopus parvus* (Sasaki, 1917), above.

***Octopus pulcher* Brock, 1887**

DIAGNOSIS.—*Juvenile*: Animal small (50 mm TL; 10 mm VML). Mantle oval. Arms short to moderate in length (ALI 70); arm formula IV > II = III > I. Paired ocelli present between bases of arms II and III.

ORIGINAL DESCRIPTION.—Brock, 1887:607.

TYPE LOCALITY.—Western tropical Pacific Ocean, Banda Sea, Amboina (= Ambon).

TYPE.—*Holotype*: ZMUG, female, 10 mm VML, not extant (see "Discussion").

DISTRIBUTION.—Known from the type locality only.

DISCUSSION.—The diagnosis is excerpted from the original description by Brock (1887). Robson (1929) considered this taxon to be conspecific with *Octopus areolatus* Orbigny, 1839–1841, in Férussac and Orbigny, 1834–1848. Pickford (MS) tentatively included it in the synonymy of *O. membranaceus* Quoy and Gaimard, 1832, considered herein to be a nomen dubium. The type was destroyed in World War II (P. Kuenzer, pers. comm., 1988, to C.F.E. Roper). It is unlikely that we will ever know the true identity of this species; therefore, we consider *O. pulcher* to be a nomen dubium.

***Octopus pusillus* Gould, 1852**

DIAGNOSIS.—Animal small (~75 mm ML). Mantle subglobose; head subequal in width to mantle; neck slightly constricted; eyes large and prominent. Arms short, arm formula I > II > III > IV. ASC 50–60.

ORIGINAL DESCRIPTION.—Gould, 1852:478, fig. 591a,b.

TYPE LOCALITY.—China Sea, Mangsi Island (? = Mangsi Great Reef, 7°28'N, 117°15'E).

TYPE.—*Holotype*: USNM, sex undetermined, ~12 mm ML, not extant (see "Discussion").

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description by Gould (1852), which is defective and lacks sufficient characterization to recognize this taxon. Gould (1852:478–479) considered the possibility that *Octopus pusillus* could represent the young of another species but chose to describe it "as one of the means for enabling others to settle the question." The type of *O. pusillus* was collected as part of the United States Exploring Expedition but is absent from the collections of the NMNH and is assumed to have been lost, as apparently was the regrettable fate of all of the alcoholic material collected from that historic expedition (see Johnson, 1964; Voss, 1981). We consider *O. pusillus* to be a nomen dubium.

***Octopus pustulosus* (Sasaki, 1920)**

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Sasaki, 1920:176, pl. 23: fig. 5, as *Polypus pustulosus*.

TYPE LOCALITY.—Western North Pacific Ocean, Sagami Sea, 35°04'50"N, 139°38'18"E, 70 fms (128 m).

TYPE.—*Holotype*: USNM 322976, female, 380 mm TL, no longer extant (see Roper and Sweeney, 1978).

DISCUSSION.—The original name of this taxon was preoccupied by *Octopus pustulosus* Blainville, 1826. The replacement name is *O. madokai* Berry, 1921 (= *Octopus hongkongensis* Hoyle, 1885) (see that taxon, above).

***Octopus rapanui* Voss, 1979**

DIAGNOSIS.—Animal medium-sized to large (to 550 mm TL, to 115 mm ML). Mantle saccular (MWI 41–74); neck and head narrow (HWI 29–52). Funnel organ apparently W-shaped, lateral limbs slightly longer than medial limbs. Arms moderate in length (ALI 75–80) (ALI of 96 reported in original description in error), stout basally but tapering to long slender tips. Arm order I > II > III > IV. Sucker size moderate to large (SIn 9–11); especially enlarged suckers absent in males and females. Right arm III of males hectocotyized (HALI 212.4–297.1), shorter than fellow arm (FAI 72–95); spermatophoral groove conspicuous, becomes wider and deeper at base of calamus to form pocket-like depression; ligula minute to small (LLI 1.4–4.0), moderately excavated with thickened edges; calamus moderate to large (CLI 29–33). Web shallow to moderate (WDI 18–22), web formula variable. Lower mandible with straight, out-turned rostrum resembling spine. Gill lamellae 11 to 12. Radula with exceptionally tall rachidian tooth with one or two cusps with B<sub>4-5</sub> seriation. Surface of mantle with scattered, prominent, flat papillae, slightly larger over eyes. General color in preservation purple dorsally; lighter, tan ventrally.

ORIGINAL DESCRIPTION.—Voss, 1979:360, figs. 1, 2.

TYPE LOCALITY.—Eastern south-central Pacific Ocean, Easter Island, Hanga Diko.

TYPE.—*Holotype*: USNM 729860, male, 115 mm ML, in alcohol, good condition.

DISTRIBUTION.—Known only from Easter Island.

DISCUSSION.—The diagnosis is excerpted from the original description by Voss (1979). *Octopus rapanui* can be easily distinguished by the peculiar shape of the rostrum of the lower beak.

***Octopus sasakii* Taki, 1942**

DIAGNOSIS.—Animal small to medium-sized (30–45 mm ML). Mantle narrow, rounded posteriorly (MWI 65–67); neck weakly constricted; head nearly as wide as mantle (HWI 62); eyes not prominent. Funnel moderate in size, funnel organ W-shaped, inner limbs slightly longer than outer ones. Arms long (ALI 72–79), arm order I > II > III > IV. Sucker size moderate (SIn 7.4–7.7), suckers elevated, cylindrical, >170 on arms I and II and >150 on arms III and IV, suckers immediately biserial proximally; especially enlarged suckers absent in males and females. Right arm III of males hectocotyized (HALI 240.0), shorter than fellow (FAI 67.9); ligula conical with deep, wide, longitudinal groove; calamus conical, relatively

large (CLI ~33); HASC 76. Web shallow (WDI 13.6–14.6), web formula  $A > B > C > D > E$ . Gill lamellae 8 to 9. Ovarian eggs few in number (~100), eggs moderate in size, capsule 10 mm long. Radula with  $B_4$  seriation of rachidian. Surfaces of mantle, head, and arms with scattered, pustulate papillae. Color in preservation brown or greyish brown. Color in life warm reddish brown, mottled with numerous minute bluish grey circles dorsally, pale grey ventrally.

ORIGINAL DESCRIPTION.—Taki, 1942:75, figs. 5, 15.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Hiroshima Prefecture, Mukaisima, and Ehime Prefecture, Mitu market.

TYPES.—*Syntypes*: Not deposited, 3 males, 11 females, presumed extant in private collection.

DISTRIBUTION.—Japan, Kanagawa Prefecture, Fukui Prefecture, Nagasaki, Fukuoka, Kagoshima, Mukaisima, Okayama Prefecture, Mito, Ehime Prefecture.

DISCUSSION.—The diagnosis is excerpted from the original description by Taki (1942) and from Sasaki (1929, as *Octopus globosus*). Taki (1942) considered his material to be conspecific with *O. globosus* Sasaki (1929) (not *O. globosus* Appellöf, 1886), which he considered allied with the *Callistoctopus ornatus/macropus* complex. Taki (1942) referred to Sasaki's (1929) description of *O. globosus* and added additional descriptions of the radula, male reproductive system, and color patterning. It is regrettable that Taki did not have Sasaki's material at hand in order to perform direct comparisons. Future study could demonstrate that *O. sasakii* is referable to the *C. ornatus/macropus* complex. At present, we retain *O. sasakii* as distinct.

***Octopus sinensis* Orbigny, 1834,  
in Férussac and Orbigny, 1834–1848**

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Orbigny, 1834, atlas, Poulpe (*Octopus*) pl. 9, in Férussac and Orbigny, 1834–1848.

TYPE LOCALITY.—Western North Pacific Ocean, Japan.

TYPE.—*Holotype*: Not designated.

DISCUSSION.—The original description by Orbigny (1834, in Férussac and Orbigny, 1834–1848; see also Orbigny, 1839–1841, in same) was repeated, nearly verbatim, from two early accounts of the natural history of Japan: Terajima (1713) and Katsuma (1762) (see Gleadall and Naggs, 1991). Orbigny (1839–1841, in Férussac and Orbigny, 1834–1848) compared *Octopus sinensis* to *O. vulgaris* Lamarck, 1798. Gleadall and Naggs (1991) considered *O. sinensis* to be a synonym of *O. vulgaris*. There is some doubt, however, whether *O. vulgaris* occurs in the western Pacific; therefore, we do not support this assertion. The original description noted that specimens of *O. sinensis* can attain sizes of up to 3 m (TL?). Therefore, *O. sinensis* actually could be attributable to the so-called "giant octopuses" of the *Octopus dofleini* complex; however, in the absence of a type and with an inadequate original description,

the identity of this taxon cannot be established with certainty. We recommend that *Octopus sinensis* be considered a nomen dubium.

***Octopus smedleyi* Robson, 1932**

DIAGNOSIS.—Animal small (30 mm ML). Mantle ovoid (MWI 73.3); neck constricted; head relatively narrow (HWI 40.0). Arm length moderate (ALI 74), arm order  $IV > III > I > II$ . Web depth shallow (WDI ~20), web formula  $D = E > C > B > A$ . Funnel long, slender; funnel organ W-shaped, inner and outer limbs compressed and broadly fused. Dorsal surfaces of mantle, head, and web densely covered with small, simple papillae.

ORIGINAL DESCRIPTION.—Robson, 1932a:24.

TYPE LOCALITY.—Unknown; presumably the Malayan region based on the one-time presence of the type in the Raffles Museum, Singapore (not traced, presumed no longer extant, see "Discussion").

TYPE.—*Holotype*: Female, 30 mm ML, not extant (see "Discussion").

DISTRIBUTION.—Unknown.

DISCUSSION.—The diagnosis is excerpted from the original description. The shallowness of web sector A suggests that *Octopus smedleyi* is referable to the *O. aegina/hardwickei* (= *dollfusi*) complex. Pickford (MS) attempted to trace the type but was unsuccessful and concluded that the type was lost as a result of World War II. In light of the defective description, uncertain locality data, and without an extant type, we consider *Octopus smedleyi* to be a nomen dubium.

***Octopus spinosus* (Sasaki, 1920)**

DIAGNOSIS.—Animal small (70 mm TL, 85 mm TL; 17 mm ML, 23 mm ML). Mantle subspherical (MWI 94); head relatively broad (HWI 88). Funnel organ W-shaped, outer limbs shorter than median limbs. Arm length short (ALI ~65), subequal. Sucker size small (SIn 1.5). Gill lamellae 10. Dorsal surfaces of mantle, head, and arms covered with moderately closely set, low papillae with smaller papillae scattered between. Single, large supraocular papilla on each side of head. Few large papillae randomly scattered on mantle and head. Color in preservation (ethanol) brownish yellow.

ORIGINAL DESCRIPTION.—Sasaki, 1920:177, pl. 24: fig. 1, as *Polyopus spinosus*.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Tsugaru Strait, 41°18'N, 140°08'40"E, 207 fm (378 m).

TYPES.—*Holotype*: USNM 332968, immature female, not extant (see Roper and Sweeney, 1978).

*Paratype*: USNM 332967, female, 17 mm ML (present measurement) in alcohol, poor condition.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is based on examination of the immature female paratype by one of us (GLV) and the accounts

by Sasaki (1920, 1929). The specimen is now in poor condition, and satisfactory measurements cannot be obtained. The identity of this species remains unclear. We provisionally retain *Octopus spinosus* as distinct.

#### *Octopus striolatus* Dong, 1976

DIAGNOSIS.—Mantle ovoid. Funnel organ *W*-shaped. Arms short. Ligula conical (LLI 2). Penis slender, diverticulum nearly elliptical. Radula with pentacuspoid rachidian. Mantle covered with fine papillae. Few longitudinal stripes on sides of mantle and lateral arms.

ORIGINAL DESCRIPTION.—Dong, 1976:212, pls. 3, 4.

TYPE LOCALITY.—Western North Pacific Ocean, China, Quangdong Province.

TYPE.—*Holotype*: IOAS K65B-50, 1959.VII.1.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The original description, published in Chinese with an English summary, is excerpted above; little is known about this species. Dong stated that this species is similar to *Octopus marginatus* Taki, 1964 (considered herein to be a nomen dubium), but can be distinguished on the basis of color pattern and radula morphology. We retain *Octopus striolatus* as distinct, but further study is warranted.

#### *Octopus tenuicirrus* (Sasaki, 1929)

DIAGNOSIS.—Animal medium-sized to large (to 160 mm ML). Mantle rounded posteriorly (MWI 60–78.1); neck weakly constricted; head large (HWI 50.0–52.3); eyes moderately prominent. Funnel small, funnel organ large, *W*-shaped, broader than long, medial limbs longer than lateral limbs. Arms moderate in length (ALI 74.2–79.3), arm formula typically I > II > III > IV. Suckers large (SIn 13.1 in largest syntype), sucker size varies with arm length, largest suckers on longest arms; ~220 suckers per arm; especially enlarged suckers absent in male syntypes. Right arm III of males hectocotylized (HALI 207.1–250.0), shorter than fellow (FAI 61.5–80.6), HASC 66. Web depth shallow (WDI 15.7–20.9), web formula C > B = D > A > E in largest syntype. Gill lamellae 10–12. Penis small (PLI 14.4), with curved diverticulum. Spermatophores long (SpLI 78.1), slender (SpWI 1.3), with 85 coils of sperm cord. Radula with A<sub>3</sub> seriation of rachidian. Ventral and lateral aspects of mantle, head, and bases of arms I and II with sparse, poorly defined papillae, remainder of surface smooth. Two supraocular cirri on each side of head, posterior one larger. Color reddish ochre, paler ventrally.

ORIGINAL DESCRIPTION.—Sasaki, 1929:78, figs. 36, 37, pl. 11: figs. 14–16, as *Polypus tenuicirrus*.

TYPE LOCALITIES.—Western North Pacific Ocean, Japan, Boso Peninsula, Chiba Prefecture, Kujukurihama.

TYPES.—*Syntypes*: TNSM?, 5 males, largest 160 mm ML, presumed no longer extant (I. Gleadall, pers. comm.).

DISTRIBUTION.—Known only from type localities.

DISCUSSION.—The diagnosis is excerpted from the original description. The specimen from Tosa Bay in the account of Okutani et al. (1987) is probably not conspecific with *Octopus tenuicirrus*; that specimen appears to conform to the characters of *Pteroctopus* sp. Gleadall (1993) considered *O. tenuicirrus* to be a synonym of *O. hongkongensis* Hoyle, 1885 (see that taxon, above). We uphold that decision.

#### *Octopus tenuipulvinus* (Sasaki, 1920)

DIAGNOSIS.—See "Discussion."

ORIGINAL DESCRIPTION.—Sasaki, 1920:182, pl. 24: fig. 5, as *Polypus tenuipulvinus*.

TYPE LOCALITY.—Western North Pacific Ocean, Sagami Sea, 35°04'50"N, 139°38'18"E, 70 fms (128 m).

TYPE.—*Holotype*: USNM 332977, female, 155 mm TL, 22 mm ML, in alcohol.

DISCUSSION.—See *Octopus minor minor* (Sasaki, 1920).

#### *Octopus teuthoides* Robson, 1929

DIAGNOSIS.—*Paralarva*: Animal small (16 mm ML). Mantle exceptionally elongate, spindle-shaped (MWI 31); head long and narrow (HWI 21). Funnel organ *W*-shaped, inner limbs longer than outer ones. Arms short (ALI 57), arm order I > II > III > IV, distinctly dissimilar in length. Suckers small, prominent. Web depth shallow (WDI 17), sectors subequal. Medial adductor muscle reduced. Surface of mantle and head smooth. Color pale yellow with scattered, pale red chromatophores.

ORIGINAL DESCRIPTION.—Robson, 1929:133, fig. 42, pl. 2: fig. 4.

TYPE LOCALITY.—Western tropical Pacific Ocean, New Hebrides, Walla Island (= Wala Island, 15°58'S, 167°22'E).

TYPE.—*Holotype*: BMNH 1928.3.28.1, female, 16 mm ML.

DISTRIBUTION.—New Hebrides; New Guinea; Philippines.

DISCUSSION.—The diagnosis is excerpted from the original description. This species has all of the earmarks of being the juvenile stage of either one of the taxa included in the *Callistoctopus macropus/ornatus* complex or *Cistopus indicus* (see Pickford, MS). Because of the difficulty of relating this paralarval form to any particular adult, we consider *Octopus teuthoides* to be a nomen dubium.

#### *Octopus tonganus* Hoyle, 1885

DIAGNOSIS.—Animal small (30 mm ML, 33 mm ML). Mantle broad, blunt posteriorly (MWI 80, 93); neck narrow to only slightly constricted; head small (HWI 73, 60). Funnel organ *W*-shaped, thick, outer limbs shorter than median limbs. Arms long (ALI 86, 85), arm order irregular, but arms I shortest and arms II and III longest. Sucker size large (SIn 13, 17), deeply set into surface of arms, proximal 3 suckers uniserial,

suckers biserial distally. In males, suckers 11–13 on arms II and III especially enlarged (S<sub>Ie</sub> 23). Ligula minute (LLI 1.3), slender, side inrolled obscuring deep groove, rugae absent. Web exceptionally shallow (WDI 6–7). Gill lamellae 6 (both syntypes). Ovarian eggs minute, capsule 1.2 mm long, stalks short (~0.5 mm). Penis moderate in size (PLI 30), nearly straight, with short diverticulum. Surfaces of mantle, head, and arms rugose, covered with scattered, small, round papillae. Two supraocular cirri on each side of head, anterior one large, multifid; posterior one small, simple. Color dorsally purplish black, ventrally pale yellow tan with few scattered dark spots.

ORIGINAL DESCRIPTION.—Hoyle, 1885:225.

TYPE LOCALITY.—Western tropical Pacific Ocean, Tonga Islands, Tongatapu, from reefs.

TYPES.—*Syntypes*: BMNH 1889.4.24.22–23, 1 male, 30 mm ML, 1 female, 33 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is based on examination of two syntypes by one of us (GLV) (measurements from male and female, respectively). Hoyle's (1885) brief original description was based on three syntypes, which he noted had been damaged during transit to England. Previous identifications based upon that description are suspect. We retain *Octopus tonganus* as distinct.

#### *Octopus tsugarensis* (Sasaki, 1920)

DIAGNOSIS.—Animal small (36 mm ML). Mantle broad (MWI 105.6); neck constriction indistinct; head slightly narrower than mantle (HWI 83.3). Funnel organ W-shaped, stout with shorter outer limbs, median limbs sharply angled. Arms long (ALI 80), subequal. Two pairs of especially enlarged suckers on arms I, II, and III only (S<sub>Ie</sub> 15.8) in unique type. Right arm III of males hectocotylized (HALI 236.1), shorter than fellow (FAI 86.7), HASC 82. Ligula moderate in size (LLI 9), with well-defined longitudinal groove and laminae. Gill lamellae 9 to 10. Penis with long diverticulum, entire penial apparatus curved. Spermatophores large (SpLI 144.4). Color in preservation (alcohol) reddish brown, 3 darker, indistinct, transverse strips on anterior head region.

ORIGINAL DESCRIPTION.—Sasaki, 1920:175, pl. 23: fig. 4.

TYPE LOCALITY.—Western North Pacific Ocean, Japan, Tsugaru Strait, off Fukuyama, 41°17'20"N, 140°07'E, 195 fm (356 m).

TYPE.—*Holotype*: USNM 332972, male, 36 mm ML, in alcohol.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. *Octopus tsugarensis* is a member of the complex of octopodines with conical, relatively long ligulas. Gleadall (1993) gave a preliminary analysis of this complex from Japan and concluded that *O. tsugarensis* could be referable to *O. longispadiceus* (Sasaki, 1917). We tentatively retain *O. tsugarensis* as distinct; further study is required to resolve the systematic status of the taxon.

#### *Octopus variabilis minor* (Sasaki, 1929)

See *Octopus minor minor* (Sasaki, 1920).

#### *Octopus variabilis pardalis* (Sasaki, 1929)

See *Octopus minor pardalis* (Sasaki, 1929).

#### *Octopus variabilis typicus* (Sasaki, 1929)

See *Octopus minor typicus* (Sasaki, 1929).

#### *Octopus vitiensis* Hoyle, 1885

DIAGNOSIS.—Animal small (15 mm ML). Mantle oblong, narrower posteriorly; no neck region; head wider than mantle width; eyes large, prominent. Funnel organ W-shaped with limbs nearly parallel. Arms moderate in length (ALI 72), arm order III > II > IV > I. Suckers large (S<sub>In</sub> 13), deeply set, sucker surface about level with arm surface. Inner margin of sucker ring bears row of about 15 fleshy beads, outer edge of aperture with about 30 beads. Penis small. Dorsal surface of mantle with few granular papillae; few, scattered, larger papillae on head; area around eyes pustulate, with single, large, multifid, supraocular cirrus above and slightly posterior to eye. Surfaces of arms covered with small, round granules that also surround suckers. Color in preservation (ethanol) dark grey, almost black on dorsum and outer surface of arms. Ventral surface of mantle and oral surface of arms pale.

ORIGINAL DESCRIPTION.—Hoyle, 1885:226.

TYPE LOCALITY.—Western South Pacific Ocean, Fiji, Kandavu, on reefs.

TYPE.—*Holotype*: BMNH 89.4.24.24, male, 15 mm ML, poor condition.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is based on examination of the holotype by one of us (GLV). Hoyle (1885) and Robson (1929) stated that the type was a female, but, in actuality, it is an immature male, now in poor condition. The tip of the hectocotylus is missing. Robson (1929) suggested that *Octopus vitiensis* is a synonym of *O. rugosus* Bosc, 1792 (= *O. vulgaris* Lamarck, 1798). There is some uncertainty, however, as to whether *O. vulgaris* is present in the Pacific Ocean; therefore, we retain *O. vitiensis* as distinct.

#### *Pteroctopus witjazi* Akimushkin, 1963

DIAGNOSIS.—Animal small to medium-sized (130 mm TL). Mantle ovoid (MWI 80); head slightly narrower than mantle. Funnel narrow, long, funnel organ W-shaped, inner limbs longer than outer ones. Arms short (ALI 70), arm formula I > II > III > IV. Sucker size moderate (S<sub>In</sub> 11); especially enlarged suckers absent. Left arm III of males hectocotylized, slightly shorter than fellow; ligula conical, small (LLI 5.2). Web deep (WDI 34), web formula A > B > C > D > E. Gill

lamellae 9 to 10. Two supraocular cirri on each side of head. Color violet brown with small white spots on dorsal surface.

ORIGINAL DESCRIPTION.—Akimushkin, 1963:145, figs. 32, 33.

TYPE LOCALITY.—Western North Pacific Ocean, southeastern Sea of Okhotsk.

TYPE.—*Holotype*: Not deposited, male, 130 mm TL, presumed no longer extant (K.N. Nesis, pers. comm., 1988).

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is excerpted from the original description. The type was never deposited and is assumed to be lost or destroyed (K.N. Nesis, pers. comm., 1988). Akimushkin (1963) compared *Pteroctopus wijazi* to *P. tetracirrus* (delle Chiaje, 1830), from the Atlantic Ocean, and separated it on the basis of five characters. Of these, only two, funnel-organ morphology and sucker diameter, potentially represent valid morphologic distinctions between these two taxa. *Pteroctopus wijazi* could be a synonym of *P. hoylei* (Berry, 1909) (Toll, unpublished data).

#### *Octopus wolffi* (Wülker, 1913)

DIAGNOSIS.—Animal small (30 mm TL). Mantle conical, broadest anteriorly (MWI 80); no neck constriction; head wider (HWI 85) than mantle. Funnel organ W-shaped. Arms short (ALI 66), subequal. Sucker size moderate, a few suckers at tip of each arm fringed with small papillae around outer periphery. Ligula short (LLI 10), with central longitudinal groove; calamus moderate to long in length (CLI 27); HASC 40, terminal 9 pairs of suckers fringed around outer periphery with short papillae. Web shallow (WDI 15). Gill lamellae 5, short, stout. Penis small, simple (PLI 15). Spermatophores small, slender. Dorsal and ventral surfaces of mantle covered with small, round granules. Supraocular papillae absent. Color in preservation (ethanol) violet red.

ORIGINAL DESCRIPTION.—Wülker, 1913:458, pl. 23: fig. 3a,b.

TYPE LOCALITY.—South central Pacific Ocean, Society Islands, Tahiti, Popeete.

TYPE.—*Holotype*: SMF, male, 10 mm ML.

DISTRIBUTION.—Known only from the type locality.

DISCUSSION.—The diagnosis is based on examination of the holotype by one of us (GLV). The specimen is now hardened, preventing both extensive examination of internal anatomy and external measurements from being obtained. Robson (1929)

thought that, because of its small size, this specimen was a juvenile. This examination finds that the holotype is a mature adult specimen and therefore belongs to the small group of miniature octopods of which little is known. We retain *Octopus wolffi* as distinct.

#### *Octopus yendoii* (Sasaki, 1920)

DIAGNOSIS.—Animal small to medium-sized (43 mm ML). Mantle subspherical, slightly wider than long; neck slightly constricted; head narrow; eyes only slightly projecting. Funnel free only at tip, funnel organ broadly W-shaped, outer limbs slightly shorter than median limbs. Arms long (ALI 82), arm order I > III > IV > II. Sucker size moderate (SIn 10); especially enlarged suckers absent in male. Ligula short (LLI 6), narrow, with transverse rugae; calamus small to moderate in size (CLI 12); HASC 106. Web depth moderate (WDI 25). Gill lamellae 10. Females with large eggs, capsule 17 mm long × 7 mm wide. Penis mutilated in type. Surfaces of mantle, head, and basal area of arms covered with widely spaced, small, round papillae, less numerous on base of arms III and IV. Peripheral keel around mantle. Color brownish buff.

ORIGINAL DESCRIPTION.—Sasaki, 1920:179, pl. 24: fig. 2, as *Polypus yendoii*.

TYPE LOCALITY.—Western North Pacific Ocean, Sea of Japan, 36°01'30"N, 129°42'E, 70–89 fms (128–163 m).

TYPE.—*Holotype*: USNM 332987, male, 43 mm ML, in alcohol.

DISTRIBUTION.—Sea of Japan.

DISCUSSION.—The diagnosis is based on examination of the type by one of us (GLV). Sasaki (1929) stated that the outer limbs of the funnel organ are strikingly shorter than the median ones. In the type of *O. yendoii*, the outer limbs of the funnel organ are only slightly shorter than the median ones. Robson (1929:206) compared *O. yendoii* to *O. medoria* Gray, 1849 (considered herein to be a nomen dubium), and *O. ochotensis* (Sasaki, 1920). Robson (1929) stated that there is a low peripheral keel but questioned whether it is present in all specimens. Gleadall (1993) considered *O. yendoii* to be a member of the complex of octopodines with conical, relatively long ligulas. Gleadall (1993) gave a preliminary analysis of this complex from Japan and concluded that *O. yendoii* could be referable to *O. longispadiceus* (Sasaki, 1917). Further study is required to resolve the systematic status of the taxon. Until such time, we retain *O. yendoii* as distinct.

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# The Octopodinae from the Eastern Atlantic Ocean and the Mediterranean Sea

*Katharina Mangold*

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## ABSTRACT

Some 50 species of octopodine cephalopods have been described from the eastern Atlantic Ocean and the Mediterranean Sea. Only eight species-level taxa are retained as valid: *Octopus burryi* Voss, 1950; *Octopus defilippi* Verany, 1851; *Octopus macropus* Risso, 1826; *Octopus magnificus* Villanueva, Sanchez, and Compagno Roeleveld, 1992; *Octopus salutii* Verany, 1839; *Octopus vulgaris* Cuvier, 1797; *Scaevurgus unicolor* Orbigny, 1840; and *Pteroctopus tetracirrhus* (Chiaie, 1830). The junior synonyms of these species are given in their respective synonymy sections. Many Mediterranean species are nomina nuda or do not belong to the subfamily Octopodinae. *Aphrodoctopus schultzei* (Hoyle, 1910) is removed from the subfamily Octopodinae pending further study on the systematic placement of this unusual species.

*Octopus defilippi*, *O. macropus*, *O. vulgaris*, *Scaevurgus unicolor*, and *Pteroctopus tetracirrhus* occur in both the eastern Atlantic Ocean and the Mediterranean Sea. *Octopus burryi* is ampho-Atlantic but does not occur in the Mediterranean Sea. *Octopus salutii* is a Mediterranean endemic. *Octopus magnificus* occurs off Southwest and South Africa.

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## Introduction

The science of cephalopods, or teuthology, originated at the Mediterranean Sea. By the time of Aristotle, several cephalopod species, such as *Octopus vulgaris* and *O. macropus*, had been recognized. In the 16th century, several authors, among them Belon (1553), Salviani (1554), and Gesner (1558), described *Octopus* species. Doubtless, the apotheosis of this activity was the very end of the 18th and the first half of the 19th centuries when many French and Italian authors introduced an incredible number of new octopod species names, nearly all of them from the Mediterranean Sea. In comparison, far fewer

octopod species have been described from the eastern Atlantic Ocean (Fischer, 1887; Joubin, 1900; Gray, 1949).

Most of these early octopod species names have since been placed in synonymy. In his monograph of the Recent Cephalopoda, Robson (1929) gave an exhaustive list of synonyms of *Octopus vulgaris* Cuvier, 1797, but maintained *O. rugosus* (Bosc, 1792) as a separate species. In 1955, Pickford concluded that *O. rugosus* also is a synonym of *O. vulgaris*.

The number of octopodine species found in the Mediterranean Sea and the eastern Atlantic Ocean is very low; only eight species are presently recognized. This paucity can hardly be attributed to lack of information because this region is considered to be one of the best known cephalopod areas in the world. More than twice as many octopodine species are present in the western Atlantic Ocean (Voss and Toll, 1998). The absence of coral reefs in the eastern Atlantic Ocean could explain the lower diversity of species present in this area. Coral reefs in many parts of the world harbor numerous octopodine species.

Six species have been described from the Mediterranean Sea; their type localities are situated in the western basin. The type locality of *Octopus burryi* Voss, 1950, is the western Atlantic Ocean, and the species diagnosis is included in the contribution by Voss and Toll (1998).

Although both Cuvier (1797) and Lamarck (1798) correctly named and briefly described *Octopus vulgaris*, a type was never designated. A neotype has been selected from the western Mediterranean Sea (Banyuls-sur-Mer, France), and the species is being redescribed (Hochberg and Mangold, MS). Recent evidence suggests that *O. vulgaris* is not cosmopolitan but is a member of a worldwide species complex. Species complexes also could be involved in the cases of *O. macropus* Risso, 1826, *O. defilippi* Verany, 1851 (a species with *Macrotritopus* juveniles), and perhaps *Scaevurgus unicolor* (Chiaie, 1839–1841, in Férussac and Orbigny, 1834–1848). *Octopus salutii* Verany, 1839, is a Mediterranean endemic occurring outside of this sea only in its outflow off the coast of Portugal and in the

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Gulf of Biscay. *Scaevargus unicolor* and *Pteroctopus tetracirrhus* (Chiaie, 1830) are amphi-Atlantic and Mediterranean species. *Octopus magnificus* Villanueva, Sanchez, and Compagno Roeleveld, 1992, occurs off the south and southwest coasts of Africa.

It should be emphasized that all measurements have been made on fresh material with the exception of a few specimens examined from Sicily and *O. defilippi* specimens from Naples (Hochberg and Mangold, MS).

ABBREVIATIONS AND DEFINITIONS.—Measurements, indices, and formulas are as defined by Roper and Voss (1983) and Robson (1929) with the following exceptions: arm-length index (ALI) is defined as length of the longest arm as a percentage of the total length (not mantle length as stated by those authors); hectocotylus-length index (HALI) is defined as a percentage of the longest arm; calamus-length index is abbreviated CLI. Other abbreviations used in the species accounts are as follows:

FLI	funnel-length index
HWI	head-width index
LLI	ligula-length index
MAI	mantle-aperture index
ML	dorsal-mantle length
MWI	mantle-width index
OAI	opposite-arm index
PLI	penis-length index
Sle	enlarged-sucker index
SIn	normal-sucker index
SpLI	spermatophore-length index
WDI	web-depth index

The following institutional abbreviations are used in the text: MHNN, Muséum d'Histoire Naturelle de Nice; SAM, South African Museum, Cape Town; ZMHU, Zoologisches Museum der Humboldt Universität, Berlin. Taxa are presented in alphabetical order by specific epithet.

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### Species Accounts

#### *Octopus defilippi* Verany, 1851

*Octopus defilippi* Verany, 1851:30, pl. 11: figs. D, E.

*Octopus defilippi* var. *dama* Robson, 1929:140.

*Octopus (Macrotritopus) kempii* Robson, 1929:170, fig. 60.

DIAGNOSIS.—Animals small to medium-sized (33–55 mm ML). Mantle small in relation to total length, elongate or saccular, pyriform, widest in posterior  $\frac{1}{3}$  (MWI 42.0–64.7),

ending in small point. Head narrower than mantle (HWI 42.5–69.7); eyes prominent, projecting. Mantle aperture wide. Funnel elongate, tubular (FLI 27.8–41.2); funnel organ W-shaped, slender, posterior angles rounded, lateral limbs shorter than median limbs. Arms long, slender, with delicate tips, tending to autotomize (ALI 73.3–89.1; MAI 14.3–23.6). Arms III distinctly longer than others; arm formula III > II > IV > I or III > IV > II > I. Suckers widely set, of medium size (SIn males 6.1–9.6, females 5.6–7.4); enlarged suckers absent in both sexes. Right arm III of male hectocotylized (HALI 35.2–60.0), shorter than opposite arm (OAI 34.5–67.0), bearing 60–100 suckers. Ligula minute (LLI 0.5–3.1), well differentiated, with blunt tip and fine cross striations; calamus small (CLI 15.0–25.3). Web exceptionally shallow (WDI 7.0–11.1) but extending to middle of arms along dorsal edge, especially on lateral arms; web formula C > D > B > E > A; sectors A and E distinctly shallower than B, C, and D. Ink sac present. Gills with 11 lamellae per outer demibranch. Proximal oviduct short, distal oviduct very long. Mature ova 2.1 mm long, 1.0 mm wide. Penis small to medium-sized (PLI 13.4–30.0), slender, with small, rounded diverticulum. Spermatophores small (SpLI 20.3–32.5). Radula with A<sub>3</sub> or A<sub>4</sub> seriation of rachidian, usually without ectocones. Skin soft, smooth, loose. Papillae transient except over eyes. Color in life brown yellow, grey brown, or red brown with dark transverse arm bars and heart-shaped pattern on dorsal mantle, often with greenish iridescence, especially around eyes.

ORIGINAL DESCRIPTION.—Verany, 1851:30, pl. 11: figs. D, E.

TYPE LOCALITY.—Western Mediterranean Sea, Italy, Pegli.

TYPE.—*Holotype*: MHNN, specimen in poor condition, only arms and brachial crown present (Voss, 1964).

DISTRIBUTION.—*Mediterranean Sea*: Throughout. *Eastern Atlantic Ocean*: From Morocco to Angola, Cape Verde Islands. *Western Atlantic Ocean*: From the Bahamas to Brazil, in the Gulf of Mexico and Caribbean Sea.

A shallow-water species of the continental shelf that occurs in depths of 6–200 m on sandy or muddy bottoms.

DISCUSSION.—Few differences appear to exist between Mediterranean/eastern Atlantic and western Atlantic specimens. Robson (1929) described a variety, *O. defilippi dama*, from the Gulf of Naples, characterized by the presence of symmetrical ectocones on the rachidian. Specimens from the Catalonian Sea and from Sicily have A<sub>3</sub> or A<sub>4</sub> seriation of the rachidian as do those from the western Atlantic (Voss, 1964). Issel (1925) indicated that *O. defilippi* has planktonic macrotritopus juveniles (arms III distinctly longer and stouter than other arms). The macrotritopus specimens examined by Boletzky (1977) correspond to the variety *O. defilippi dama*. All Atlantic macrotritopus juveniles so far examined appear to belong to *O. defilippi* (Hanlon et al., 1985); however, a species complex, characterized by macrotritopus juveniles, could be represented. *Octopus defilippi* from the Mediterranean (Naples) is being redescribed by Hochberg and Mangold (MS).

MATERIAL EXAMINED.—Six specimens from the Catalanian Sea (western Mediterranean Sea), two from Sicily, and 12 from Naples.

***Octopus macropus* Risso, 1826**

*Octopus macropus* Risso, 1826:3.

*Octopus macropodus* San Giovanni, 1829:319.

*Octopus longimanus* Orbigny, 1840:18.

*Octopus alderi* Verany, 1851:32, pl. 7bis.

*Octopus bermudensis* Hoyle, 1885:228.

DIAGNOSIS.—Animals medium-sized to large (25–155 mm ML). Mantle shape variable, usually elongate or ovoid, widest in posterior  $1/2$  (MWI 32.5–75.0). Stylets present, very reduced in size. Neck often slightly constricted. Head narrower than mantle (HWI 26.5–70.5); eyes medium-sized, bulging. Mantle aperture wide. Funnel long, narrow (FLI 45–48); funnel organ W-shaped, lateral limbs shorter than median limbs. Arms long (ALI 75.5–87.5, MAI 14.1–36.1). Dorsal arms longest and stoutest; arm formula I > II > III > IV. Suckers medium-sized, arms I with largest suckers (SI<sub>n</sub> 6.9–13.5, no noticeable difference between males and females). Right arm III of male hectocotylized (HALI 40–43), shorter than opposite arm (OAI 41–51). Ligula small to medium-sized (LLI 4.5–8.0), narrow, pointed rather than blunt, with swollen margins, deep groove, and numerous delicate transverse lamellae; calamus short (CLI 13–18). Web shallow (WDI 7.3–16.7); web formula A > B > C > D > E; sector A distinctly deeper than B, sector E distinctly shallower than D. Ink sac present, well developed. Gills with 10 to 11 lamellae per outer demibranch. Mature ova 2.5 mm long, 1 mm wide. Penis small (PLI 12–28), distally rounded, with large forward- or backward-directed diverticulum. Spermatophores medium-sized (SpLI ~50). Radula with A<sub>3</sub> seriation of rachidian. Skin smooth, with or without large papillae over eyes. Color in life brick red or brownish with distinct pattern of white spots on dorsal mantle, head, and arms.

ORIGINAL DESCRIPTION.—Risso, 1826:3.

TYPE LOCALITY.—Not indicated in original description; presumed to be western Mediterranean Sea, France, off Nice.

TYPE.—Not designated, presumed to be not extant.

DISTRIBUTION.—*Mediterranean Sea*: Western and eastern basins, Adriatic Sea. *Eastern Atlantic Ocean*: Dakar to St. Helena. *Western Atlantic Ocean*: United States (Florida) to Brazil, and in the Caribbean. Found in tropical to warm-temperate waters.

A shallow-water species that lives on both coral reefs and rocky and sandy bottoms mainly within the upper 20 m, at least in the Mediterranean Sea.

DISCUSSION.—The species is well characterized by its long arms, the arm formula, and the shallow web. Jatta (1896, pl. 6: fig. 1) gave an excellent representation of a live specimen (color pattern). *Octopus macropus* is a member of the “first arms longest and stoutest” species group, which has been widely reported throughout the world. It appears to be closely related to *O. ornatus*. Slight variations appear to exist between

the specimens from the Mediterranean Sea and the western Atlantic Ocean. Among the latter, minor differences exist, especially in male characteristics (Pickford, 1945; Voss, 1957). A detailed comparison is being prepared (F.G. Hochberg, pers. comm., 1994), and a neotype will be selected.

MATERIAL EXAMINED.—One female from the Catalanian Sea and four females from Sicily. For the description of the males (indices), the specimens described by Pickford (1945) from the western Atlantic Ocean and those described by Voss (1957) from the continental United States were included.

***Octopus magnificus* Villanueva, Sanchez, and Compagno Roeleveld, 1992**

*Octopus magnificus* Villanueva, Sanchez, and Compagno Roeleveld, 1992:39.

*Octopus dofleini* Augustyn and Smale, 1989:97 [not Wülker, 1910].

DIAGNOSIS.—Animals large (largest specimen 362 mm ML). Mantle saccular, slightly ovoid (MWI 55.3–90.1). Neck well defined. Head narrower than mantle (HWI males 22.9–99.5, females 26.5–45.3); eyes moderate in size, not prominent. Mantle aperture wide. Funnel elongate, tubular (FLI 28.4–44.7); funnel organ broadly W-shaped, lateral limbs considerably shorter than median limbs. Arms long, muscular and robust proximally, tips attenuated. Arms I and II subequal, longer than arms III and IV; arm formula typically I = II  $\approx$  III = IV. Suckers larger in males than in females; greatly enlarged suckers in males (SI<sub>e</sub> males 9.7–22.7, females 8.9–13.5). Right arm III of male hectocotylized, shorter than opposite arm (OAI 81–95 in mature males), bearing 92–126 suckers; spermatophore groove well defined. Ligula large (LLI 14–22.2 in mature males), tip slightly pointed; calamus small (CLI 4.6–18.7). Web moderately developed; sectors A and E always shallowest, remaining sectors variable, extending 84% along ventral side of arms I and II and 80% along arms III and IV (except hectocotylus). Ink sac present. Gills with 12–15 lamellae per outer demibranch. Penis extremely long (PLI 18.2–104), diverticulum up to 91.8% of penis length. Spermatophores very long (SpLI 161–283). Radula with A<sub>2</sub> or B<sub>2</sub> seriation of rachidian. Skin loose, elongate folds present in live animals, 1 large papillae over each eye, second small supraorbital papillae occasionally present.

ORIGINAL DESCRIPTION.—Villanueva, Sanchez, and Compagno Roeleveld, 1992:39.

TYPE LOCALITY.—Southeastern Atlantic, off Namibia, 29°41'S, 14°41'E, 415 m.

TYPE.—*Holotype*: SAM S2363, maturing male, 275 mm ML, in 80% ethyl alcohol.

DISTRIBUTION.—*Southern Atlantic Ocean*: Africa (from Luderitz to Port Elizabeth).

Collected in depths of 2–560 m on soft bottom sediments. Mature spawning females unknown.

DISCUSSION.—*Octopus magnificus* is closely related to *O. dofleini* and *Enteroctopus megalocyathus* (Villanueva et al., 1992).

MATERIAL EXAMINED.—None; diagnosis and indices after Villanueva et al. (1992).

***Octopus salutii* Verany, 1839**

*Octopus salutii* Verany, 1839:93, pl. 3.

*Octopus saluzzii* Naef, 1923:699.

*Octopus (Octopus) salutii*.—Robson, 1929:157.

DIAGNOSIS.—Animals of medium size (males 30–125 mm ML, females 30–130 mm ML). Mantle short, broadly oval, widest posteriorly (MWI 53.2–55.1), flaccid. Head slightly narrower than mantle (HWI 44.9–~47.5); eyes large, globular. Mantle aperture wide. Funnel moderately elongate (FLI 26.8–38.1); funnel organ W-shaped with rounded angles, lateral limbs slightly longer than median limbs. Arms long, subequal (ALI 70.0–91.9; MAI 15.2–21.7), tapering to narrow rounded tips; arms I shortest. Suckers medium-sized, not deeply set (SI in males 7.2–9.4, females 6.0–7.0); 2 to 3 enlarged suckers can be present. Right arm III of male hectocotylized (HALI 66.1–76.3), shorter than opposite arm (OAI 78–85), bearing 135–150 suckers. Ligula long and slender (LLI 8.6–16.5), with deep groove and numerous fine transverse lamellae, margin slightly swollen; calamus short (CLI 9–11). Web moderately shallow (WDI 12.5–14.5), distinctly larger and thicker on ventral side of arms, extending to  $\frac{2}{3}$  of arm length; web formula  $C > B > D > E > A$ . Ink sac present. Gills with 10 to 11 lamellae per outer demibranch. Mature ova 5.2–5.4 mm long, 1.8 mm wide, with short stalks. Penis moderately long (PLI 25.1–31.2), with rounded diverticulum. Spermatophores medium-sized (SpLI 67.0–67.5). Radula with  $A_2$  seriation of rachidian. Skin slightly gelatinous and swollen. Dorsal mantle covered with tiny irregular papillae. One large papilla over each eye. Color in life bright yellow orange to yellow brown (golden or lemon yellow with blue spots according to Verany's description).

ORIGINAL DESCRIPTION.—Verany, 1839:93, pl. 3.

TYPE LOCALITY.—Western Mediterranean Sea, France, off Nice.

TYPE.—Not traced, presumed to be in MHNN.

DISTRIBUTION.—*Mediterranean Sea*: Western and eastern basins, southern part of Adriatic Sea; in Mediterranean outflow along south coast of Spain, southwest coast of Portugal, north of Cape Finisterre, Bay of Biscay, northern limit 47°35'N, 6°35'W.

A mesobenthic species that lives on muddy bottoms on the continental slope, mostly at depths of 150–350 m. It can be found as deep as 600 m and, on sandy bottoms, as shallow as 30–50 m.

DISCUSSION.—There are no morphological or biological differences among specimens from different parts of the Mediterranean Sea or between specimens from the Mediterranean Sea and the Atlantic (Mediterranean outflow areas). The spawning period is from late May to September (Catalonian Sea). Eggs are interwoven to form strings and are attached to

the substratum (aquarium observations). Hatchlings are planktonic; the arms have four suckers. *Octopus salutii* from the Mediterranean Sea is currently being redescribed (Hochberg and Mangold, MS), and a neotype will be selected.

MATERIAL EXAMINED.—Over 100 specimens from the Catalonian Sea, several from the coasts of Tunisia and Algeria and from the Alboran Sea, five from Sicily, two from the eastern Mediterranean Sea, and two from Portugal. Bay of Biscay specimens identified by B. Mesnil (in Mangold et al., 1976).

***Pteroctopus tetracirrus* (Chiaie, 1830)**

*Octopus tetracirrus* Chiaie, 1830, pl. 72 [According to Robson (1929), the plate was not published with the text. Adam (1952) could not find it nor could 1. The plate was, however, reissued in 1841 as plate 4.]; 1841a:4, pl. 4; 1841b:65.—Orbigny, 1840:36, pl. 22; 1845:175.—Philippi, 1844:202.—Gray, 1849:11.—Verany, 1851:25, pl. 7, 7bis.—Adams and Adams, 1853:20.

*Scaevargus titanotus* Troscchel, 1857:51, pl. 4: figs. 4, 5.—Tryon, 1879:127.

*Octopus tetracirrus*.—Tryon, 1879:119, pl. 27: fig. 17.

*Scaevargus tetracirrus*.—Tiberi, 1880:42.—Hoyle, 1886:14.—Joubin, 1900:36.

*Scaevargus tetracirrus*.—Carus, 1890:461.—Jatta, 1896:230, pl. 5: fig. 2, pl. 25: figs. 2–13.—Lo Bianco, 1903:170, pl. 8: fig. 20.—Naef, 1916:17; 1921:538.—Grimpe, 1922:40; 1925:93.

*Octopus* (“*Scaevargus*”) *tetracirrus*.—Naef, 1923:710, figs. 421a, 422–424.

DIAGNOSIS.—Animals of medium size (males 35–120 mm ML, females 35–130 mm ML). Mantle broadly oval (MWI 61.4–80.5), broadest in young specimens. Neck faintly constricted. Head narrower than mantle (HWI 44.4–64.1); eyes large, bulging. Mantle aperture narrow (A–B, after Robson, 1929). Funnel small to medium-sized (FLI 27.5–41.5), broad at base; funnel organ VV-shaped, lateral limbs slightly shorter than median limbs. Arms subequal, moderately long, stout, especially in small specimens, distinctly longer in adults and longer in females than in males (ALI males 66.5–82.1, females 70.2–86.5; MAI males 22.3–27.1, females 19.2–21.5). Suckers deeply set in arms, small; enlarged suckers absent in both sexes (SI in males 3.0–6.6, females 2.8–4.3). Left arm III of male hectocotylized (HALI 40–66), shorter and stouter than opposite arm (OAI 57–75), bearing 70–80 suckers. Ligula broadly conical, with blunt tip (LLI 2.3–2.9) and deep groove, transverse ridges faint; calamus well developed (CLI 25–40), pointed. Web moderate in depth (WDI 20.2–25.6); web formula  $A > B > C > D > E$ ; sector E distinctly shallower than sectors A–D. Web membranes not continued over outer edge of each arm but fused on dorsal side; muscular cord extended from their point of union along median line of arms. Ink sac present, well developed, more or less embedded in digestive gland. Gills with 9 to 10 lamellae per outer demibranch. Mature ova 7 mm long, 2.5 mm wide, stalks varying in length from 2.0 to 4.5 mm. Male organs in mature specimens very large. Penis moderately long (PLI 13.8–32.7), with distinct, large diverticulum. Spermatophores long (SpLI 79.8–95.5). Radula with  $A_2$  or  $A_3$  seriation of rachidian. Skin loose, subcutaneous tissue

soft and gelatinous. Two distinct slender papillae over each eye. Dorsal mantle, head, and arm bases covered with small tubercles, arranged in regular pattern. Color in life uniformly bright orange red to orange yellow.

ORIGINAL DESCRIPTION.—Chiaie, 1830, pl. 72.

TYPE LOCALITY.—Western Mediterranean Sea, Naples.

TYPE.—Not designated, not extant.

DISTRIBUTION.—*Mediterranean Sea*: Western and eastern basins, southern part of Adriatic Sea. *Eastern Atlantic Ocean*: From west coast of North Africa to just south of the equator, including the Azores and Cape Verde Islands. *Western Atlantic Ocean*: From United States (North Carolina) to Uruguay; in the Gulf of Mexico and the Caribbean.

This species lives on muddy bottoms on the lower part of the continental shelf and the continental slope in depths of 100–720 m (Mediterranean Sea).

DISCUSSION.—There appear to be some minor differences in body proportions between the Mediterranean Sea and the western Atlantic specimens. The mantle and head are broader and the arms are shorter in the latter. The posture of the live animal is very characteristic (see Naef, 1923:711, fig. 422). The colors of the live animals are beautifully represented in Jatta (1896, pl. 4: fig. 2).

The genus *Pteroctopus* is being revised by R. Toll (pers. comm., 1988). According to him, *Beryya* and *Danoctopus* are both synonyms of *Pteroctopus*. Toll reexamined the type of *D. schmidti*. It is a juvenile male consistent with the characters of *B. hoylei*, including the position of the hectocotylus (right arm III). As defined at present, only the position of the hectocotylus (sinistral or dextral) allows for the clear separation of *P. tetracirrhus* and *B. hoylei* (Toll, pers. comm., 1988). Eggs are fixed singly to the substratum, and the hatchlings are planktonic.

### *Octopus vulgaris* Cuvier, 1797

*Octopus vulgaris* Cuvier, 1797:380, pl. 9: fig. 2.

*Sepia rugosa* Bosc, 1792:24, pl. 5: figs. 1, 2.

*Octopus granulatus* Lamarck, 1798:130.

*Octopus vulgaris* Lamarck, 1798:130.

*Octopus tuberculatus* Risso, 1826:3.

*Octopus cassiopeia* Gray, 1849:9.

*Octopus troscheli* Targioni-Tozzetti, 1869:17.

*Octopus rugosus*.—Robson, 1929:63, figs. 8, 9, pl. 2: fig. 3.

A full synonymy is presented in Hochberg and Mangold (MS).

DIAGNOSIS.—*Mediterranean*: Animals of medium to large size (males 20–250 mm ML, females 20–200 mm ML). Mantle broadly oval to saccular, widest in posterior 1/2 (MWI 62.2–80.0). Neck slightly constricted. Head distinctly narrower than mantle (HWI 32.5–53.5). Mantle aperture wide. Funnel elongate, opening relatively narrow (FLI 30.0–48.2); funnel organ W-shaped, lateral limbs usually, but not always, slightly shorter than median limbs. Arms long, robust, tapering to

narrow rounded tips (ALI 76.3–88.7; MAI 18.0–25.2). Lateral arms distinctly longer than median arms; arm formula III > II > IV > I or III = II > IV > I. Suckers very mobile, medium-sized (SIn males 12.5–13.5, females 9.7–10.3); 2 to 3 enlarged suckers (among 15th to 19th) on lateral arms in both sexes (Sle males 18.2–21.1, females 10.5–11.2). Right arm III of male hectocotylized (HALI 56.0–72.2), shorter than opposite arm (OAI 75.2–82.0), bearing 140–180 suckers. Ligula small to minute (LLI 1.2–2.1), tip narrow, transverse striations faint; calamus distinct, relatively long (CLI 47–52). Web moderately shallow (WDI 16.5–18.5); web formula C > D > B > E > A, often variable but sector A always shallowest. Ink sac present, superficial or partially embedded in digestive gland. Gills with 9–11 lamellae per outer demibranch. Mature ova 2.2 mm long, 1.0 mm wide; stalk about 2.5 times ova length. Penis moderately long (PLI 15–21), with small, rounded diverticulum. Spermatophores of moderate size (SplI 31–81). Radula with A<sub>2</sub> to A<sub>5</sub> seriation of rachidian. Skin firm, covered with papillae or smooth. Color in life variable, brown yellow, red brown, dark brown, or greyish.

ORIGINAL DESCRIPTION.—Cuvier, 1797:380, pl. 9: fig. 2.

TYPE LOCALITY.—Not stated in original description, presumed to be the western Mediterranean Sea.

TYPE.—Not designated, presumed to be not extant (Lu et al., 1995).

DISTRIBUTION.—*Mediterranean Sea*: Western and eastern basins, Adriatic Sea. *Eastern Atlantic Ocean*: South coast of England; west, south, and southeast coast of Africa; Azores, Canary Islands, Cape Verde Islands, and St. Helena Islands. *Western Atlantic Ocean*: Described from numerous localities.

This is a shallow-water species that lives on the continental shelf from the surface to 100 (150) m, rarely deeper, on sandy, rocky, or muddy bottoms.

DISCUSSION.—One of the key problems that needs to be addressed is whether *Octopus vulgaris* is a true cosmopolitan or simply a literature cosmopolitan represented by a complex of species. Based on the literature (Pickford, 1945, 1955), *Octopus vulgaris* from the eastern Atlantic cannot be separated morphometrically from specimens in the western Atlantic (Voight, 1991, pers. comm.). Spermatophores are different (G. Voss, pers. comm.), however, and so are the chromatophore patterns of the hatchlings, the skin pattern of adults, and several host specific parasites (Hochberg, pers. comm.). In *Octopus vulgaris* from the Mediterranean Sea, colors combine with papillae texture to produce highly characteristic body patterns (Packard and Sanders, 1969, 1971). The chromatic units making up the different patterns have been described by Packard and Hochberg (1977) and by Frosch and Messenger (1978). Recent evidence suggests that *Octopus vulgaris* is not cosmopolitan but is one member of a species complex (Hochberg and Mangold, MS).

MATERIAL EXAMINED.—Over 200 specimens from the Catalanian Sea, 60 from Naples, and 10 from Sicily.

***Scaeurghus unicolor* (Chiaie, 1839–1841,  
in Férussac and Orbigny, 1834–1848)**

*Octopus unicolor* Chiaie, 1839–1841:70, in Férussac and Orbigny, 1834–1848.

*Octopus cocco* Verany, 1846:17, pl. 4.

*Octopus* ("Scaeurghus") *unicolor*.—Naef, 1923:713.

DIAGNOSIS.—Animals of small to medium size (males 30–72 mm ML, females 30–90 mm ML). Mantle short, ovoid, compact (MWI 52.9–71.6). Stylets calcified. Neck slightly constricted. Head distinctly narrower than mantle (HWI 36.8–46.3); eyes medium-sized, prominent. Mantle aperture medium to wide. Funnel broad at base, conical (FLI 40); funnel organ W-shaped with rounded angles, lateral limbs shorter than medium limbs; sometimes divided into 2 V-shaped parts (Naef, 1923). Arms moderately long, subequal, laterals slightly longer than medians, tapering to delicate tips (ALI 72.7–82.9; MAI 22.9–29.6). Suckers closely set, larger in males than in females (SIn males 7.8–9.7, females 6.5–7.0); enlarged suckers absent in both sexes. Left arm III of male hectocotylized (HALI 46.7–62.6), shorter than opposite arm (OAI 56–74), bearing about 70 suckers. Ligula moderately long (LLI 6.8–11.0), blunt, with heavily infolded margin, deep groove; calamus long (CLI 58–62). Web shallow (WDI 13.3–15.7), extending on ventral side of arms to about 1/2 arm length; sectors subequal. Ink sac present, embedded in digestive gland. Gills with 12–14 lamellae per outer demibranch. Mature ova 2.5 mm long, about 1 mm wide, stalk twice as long as ova. Penis moderate in length (PLI 19.1–37.3), with long diverticulum. Spermatophores long (SpLI 91–100). Radula with A<sub>3</sub> or A<sub>4</sub> seriation of rachidian. Skin firm, body surface granular, uniformly covered with blunt round papillae, often arranged in nearly linear fashion, fused into ridges in some parts of body, especially on arms and around periphery of mantle where distinct keel formed. Single large papilla over each eye. Color in life red brown to red yellow with marked brown mottlings, greenish hue; ventral surface paler, yellow brown, often iridescent. Animals produce wide variety of color patterns, skin textures, and body postures. Skin varies from smooth, with expanded chromatophores, to granular, with contracted chromatophores.

ORIGINAL DESCRIPTION.—Orbigny, 1840:70.

TYPE LOCALITY.—Not stated in original description; very likely western Mediterranean Sea.

TYPE.—Not designated; several collections searched, but holotype considered to be not extant (Lu et al., 1995).

DISTRIBUTION.—*Mediterranean Sea*: Western and eastern basins, southern part of Adriatic Sea. *Eastern Atlantic Ocean*: Southwest coast of Portugal. *Western Atlantic Ocean*: South from United States (Georgia) to Brazil and in the Caribbean (Cuba and elsewhere).

This species lives on the continental shelf and slope, on sandy, coralline, or muddy bottoms, in depths of 50–500 m but mostly deeper than 100 m.

DISCUSSION.—These Mediterranean Sea specimens appear

to differ from western Atlantic specimens in several body proportions (cf. Voss, 1951). The mantle and head are broader, the arms are shorter, and the web is deeper in the western Atlantic specimens; however, the indices for the Mediterranean Sea specimens have been calculated from measurements taken on fresh animals. The spawning period in the Mediterranean Sea is from May to August (Boletzky, 1977; pers. obs.). Eggs are attached to the substratum in festoons. Hatchlings are planktonic, and each arm has four suckers.

MATERIAL EXAMINED.—Thirty-five specimens from the Mediterranean Sea, 20 of these are from the Catalonian Sea.

**Species Removed from the Subfamily OCTOPODINAE**

***Aphrodoctopus schultzei* (Hoyle, 1910)**

DIAGNOSIS.—Animal of medium size (50 mm ML). Mantle short, ovoid, nearly as wide as long (MWI 86). Head short, narrower than mantle (HWI 47); eyes indistinct. Mantle aperture wide. Funnel moderately long (FLI 37), with broad base. Funnel organ W-shaped, median limb angle about 90°, lateral limbs represented only by short rounded lobes. Arms long, stout, particularly arms I and II (ALI 86; MAI 29); arm formula II > I > III > IV. Tips of all arms except hectocotylus covered with mass of long, closely packed, finger-like processes. Suckers set on thick stalks (SIn 14); 3 to 4 pairs of enlarged suckers present (6th or 7th sucker), especially on arms I and II (Sle 22), suckers slightly less enlarged on arms III, arms IV without enlarged suckers. Right arm III of male hectocotylized (HALI 68), shorter than opposite arm (OAI 84), bearing 64 suckers; spermatophore groove well developed. Ligula bluntly rounded, short (LLI 3.1), no longitudinal depression, no transverse striations, ridges, or grooves; calamus absent; entire surface of ligula sponge-like, with series of irregular, reticulate ridges and holes, and with large hole located at tip. Web deep (WDI 37); web formula B > A > C > D > E, sector E very shallow. Penis with long free extremity (PLI 37), without diverticulum. Spermatophores short, armed. Radula with B<sub>3</sub> or B<sub>4</sub> seriation of rachidian. Skin covered dorsally with minute conical granules, no papillae. Color in preservation purple brown.

ORIGINAL DESCRIPTION.—Hoyle, 1910:261, fig. 1, pl. 4: figs. 1–3.

TYPE LOCALITY.—Eastern south Atlantic Ocean, off South-West Africa, Angra Pequena (= Lüderitz, Namibia).

TYPE.—*Holotype*: ZMHU, mature male, 50 mm ML, specimen in poor condition.

DISTRIBUTION.—Known only from the type locality. Collected among rocks in shallow water.

DISCUSSION.—For the purposes of completeness, Hoyle's (1910) *Polypus schultzei* is diagnosed. It is known only from the holotype, a mature male collected off Namibia. The holotype was redescribed in detail by Roper and Mangold (1992), who placed it in a new genus, *Aphrodoctopus*. During a reexamination of octopods from South Africa by Hochberg



(pers. comm.), however, it was noted that *A. schultzei* is identical to the male described by Voss (1962) under the name *Eledone thysanophora*. In addition, it is likely that Hoyle's (1910) description of *E. nigra*, also collected in shallow water at Lüderitz, is a junior synonym of *A. schultzei* and represents the female of the species. On the basis of the above-mentioned synonymies and the suite of combined characters, the species is

tentatively transferred to the subfamily Eledoninae pending further detailed studies. The holotype of *A. schultzei*, a damaged male specimen, is distinct from all other genera and species in the eastern Atlantic Ocean. The arm tips are covered with numerous finger-like processes instead of suckers. The hectocotylus and funnel organ are equally distinct. The penis lacks a diverticulum, and the spermatophores are armed.

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# The Systematic and Nomenclatural Status of the Octopodinae Described from Australia (Mollusca: Cephalopoda)

Timothy N. Stranks

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## ABSTRACT

There are 25 nominal species of Octopodinae originally described from Australian waters. The historical background and systematic status of each of the inshore, benthic octopodine species are reviewed. The revisions have been based where possible on reexaminations of type material. The species are currently placed in three genera: *Octopus*, *Hapalochlaena*, or *Ameloctopus*. Eight taxa from southern temperate waters of Australia are considered valid: *Octopus berrima* Stranks and Norman, 1993; *O. bunurong* Stranks, 1990; *O. kaurna* Stranks, 1990; *O. maorum* Hutton, 1880; *O. pallidus* Hoyle, 1885; *O. superciliosus* Quoy and Gaimard, 1832; *O. warringa* Stranks, 1990; and *Hapalochlaena maculosa* (Hoyle, 1883). Three species from subtropical Australian waters are retained as valid: *Octopus australis* Hoyle, 1885; *Octopus tetricus* Gould, 1852; and *Hapalochlaena fasciata* (Hoyle, 1886). Four taxa from northern tropical waters of Australia are treated as valid: *Octopus cyanea* Gray, 1849; *O. polyzenia* Gray, 1849; *O. tenebricus* Smith, 1884; and *Ameloctopus litoralis* Norman, 1992. Five species are recognized as junior synonyms or homonyms of other taxa: *O. duplex* Hoyle, 1885; *O. flindersi* Cotton, 1932; *O. pictus* Brock, 1882; *O. robustus* Brock, 1887; and *O. westerniensis* Orbigny, 1834. Four species are reported to be nomina dubia: *O. caerulescens* Blainville, 1826; *O. cornutus* (Owen, 1881); *O. pustulosus* Blainville, 1826; and *O. variolatus* Blainville, 1826. Two taxa are recorded as nomina nuda: *O. boscii* (Lesueur, 1821); and *O. peronii* (Lesueur, 1821). Several of the more poorly known species of Australian Octopodinae require additional research to confirm their status.

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## Introduction

Australia has a diverse but poorly known cephalopod fauna. Historically, the situation resulted from the paucity of local cephalopod specialists and an associated lack of detailed

systematic studies of the fauna (see Roper, 1983). With the engagement of cephalopod taxonomists and an increase in research efforts since the late 1970s, the tremendous diversity of Australian cephalopods is now being recognized (see Lu and Phillips, 1985). A case in point is the rich fauna of inshore octopod species inhabiting the temperate, subtropical, and tropical seas around the Australian continent.

There are currently 25 nominal species (representing three genera) of Octopodinae described from Australia (including Tasmania but not New Zealand) (see Table 1). The list does not include species originally described from elsewhere for which there are Australian records (the one exception is *Octopus maorum* Hutton, 1880, from New Zealand, the senior synonym of *O. flindersi* Cotton, 1932).

The history of Australian octopod systematics commences with the early voyages of exploration. Expeditions notably by the French and British, and to a lesser extent by Americans, were the major source of octopod study material during the 19th century. Such collections from Australia were examined by naturalists who either accompanied the expeditions or who studied the material upon its return to European or North American institutions.

The voyage from France of the *Géographe* and the *Naturaliste* (1800–1804) was the first European expedition to collect octopods from Australian waters, collecting at Shark Bay and Rottneest Island (Western Australia) and possibly also from other Australian localities. The material was described by C.A. Lesueur (1821) and H. de Blainville (1826), both authors giving brief accounts that lacked illustrations. The little available information and missing type specimens have made subsequent identification of each of the five involved species very difficult.

A second French expedition, that of the *Astrolabe* (1826–1829), collected octopods from southeastern Australia. The surgeon/naturalists on board, J.R.C. Quoy and J.P. Gaimard

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TABLE 1.—Taxonomic status of nominal species of Australian Octopodinae.

Nominal taxon	Current disposition
<i>Octopus australis</i> Hoyle, 1885	valid
<i>Octopus berrima</i> Stranks and Norman, 1993	valid
<i>Octopus boscii</i> (Lesueur, 1821)	nomen nudum
<i>Octopus bunurong</i> Stranks, 1990	valid
<i>Octopus caerulescens</i> Blainville, 1826	nomen dubium
<i>Octopus cornutus</i> (Owen, 1881)	nomen dubium
<i>Octopus cyanea</i> Gray, 1849	valid
<i>Octopus duplex</i> Hoyle, 1885	junior synonym of <i>Octopus superciliosus</i> Quoy and Gaimard, 1832
<i>Octopus flindersi</i> Cotton, 1932	junior synonym of <i>Octopus maorum</i> Hutton, 1880
<i>Octopus kurna</i> Stranks, 1990	valid
<i>Octopus maorum</i> Hutton, 1880	valid
<i>Octopus pallidus</i> Hoyle, 1885	valid
<i>Octopus peronii</i> (Lesueur, 1821)	nomen nudum
<i>Octopus pictus</i> Brock, 1882	junior homonym of <i>Octopus pictus</i> Blainville, 1828
<i>Octopus polyzenia</i> Gray, 1849	valid
<i>Octopus pustulosus</i> Blainville, 1826	nomen dubium
<i>Octopus robustus</i> Brock, 1887	junior synonym of <i>Hapalochlaena fasciata</i> (Hoyle, 1886)
<i>Octopus superciliosus</i> Quoy and Gaimard, 1832	valid
<i>Octopus tenebricus</i> Smith, 1884	valid
<i>Octopus tetricus</i> Gould, 1852	valid
<i>Octopus variolatus</i> Blainville, 1826	nomen dubium
<i>Octopus warringa</i> Stranks, 1990	valid
<i>Octopus westerniensis</i> Orbigny, 1834	junior synonym of <i>Octopus superciliosus</i> Quoy and Gaimard, 1832
<i>Hapalochlaena fasciata</i> (Hoyle, 1886)	valid
<i>Hapalochlaena maculosa</i> (Hoyle, 1883)	valid
<i>Ameloctopus litoralis</i> Norman, 1992	valid

(1832) described *Octopus superciliosus* from Victorian waters. Although the original description was brief, some extra detail on the type material was given in subsequent publications (e.g., Orbigny, 1840), and, together with the extant type material, this has enabled species identification.

An octopus collected in eastern Australia during the United States Exploring Expedition (1838–1842) was described as *O. tetricus* by A.A. Gould (1852). The type specimen is lost (fide Johnson, 1964), and the identity of the species is now under review.

Two major British expeditions collected octopuses in Australian waters. E.A. Smith (1884) described *O. tenebricus* from specimens collected in eastern Australia during the voyage of the *Alert* (1881–1882). Other material was obtained from southeastern Australia during the *Challenger* cruises (1873–1876) and was named by W.E. Hoyle (1885, 1886). Extant type material and relatively detailed descriptions and plate figures have assisted in confirming the status of these species.

Apart from the expedition reports, other 19th and early 20th century accounts were based by foreign researchers on existing collections in European museums. The studies were often detailed, but as was sometimes the case, the provenance of material was obscure and collection or locality details were

uncertain. A succession of scientists so described octopus species from Australia, including J.E. Gray (1849), R. Owen (1881), and J. Brock (1882, 1887). Commencing in the early 20th century, several scientists in local Australian museums began examining and reporting on regional collections. Among them, B.C. Cotton (1932) diagnosed a new species, *O. flindersi*, from South Australia.

The current renewal of research interest in the Australian octopus fauna after a period of nearly 50 years has to date resulted in four new species of octopuses described from southeastern Australia (Stranks, 1990b; Stranks and Norman, 1993) and another new species described from tropical Australia (Norman, 1992a).

This paper is not intended to be a comprehensive or exhaustive revision of all species described from Australia. Rather, it forms the first installment or progress report on the longer term systematic review of the octopod fauna of the region. The fauna is being conveniently dealt with on a subregional basis. The octopod fauna of temperate southern Australian and tropical Great Barrier Reef waters are now reasonably well known (see Stranks, 1988a; Norman, 1992b, 1993a, 1993b). Other studies on components of the Australian fauna are in progress (e.g., the *Hapalochlaena* and *O. Octopus cyanea/tetricus* species complexes).

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#### METHODS

Systematic decisions in this study relied where possible on reexamination of type material or, alternatively, on published accounts of type specimens. Provisional conclusions were made on the taxonomic status of some species, particularly those for which no type material was available for study. The validity of these conclusions should be confirmed by first-hand examinations of the respective type specimens or, if no extant types are available, by critical evaluation of all other available information.

Within the genus *Octopus*, taxa are arranged by alphabetical order.

ABBREVIATIONS AND DEFINITIONS.—Counts, measurements, and indices are as defined by Roper and Voss (1983) and Toll (1988), with the following exceptions: calamus-length index is abbreviated CLI; funnel-length index is abbreviated FLI; hectocotylied-arm index is abbreviated HAMI; and sucker-diameter index is abbreviated SI. Rachidian-tooth symmetry formulae follow Robson (1929). Where provided, index means are in italics. Three terms used herein to describe skin sculpturing require definition. Tubercles are classified as soft, raised, nonerectile structures (usually rounded or conical in shape) that are expressed over long periods. Ridges are raised, compound, and elongate structures that are not erectile and remain expressed over long periods. Papillae are raised structures that can be intermittently erected into unbranched or branched features. Other abbreviations used in the species accounts are as follows:

ALI	arm-length index
HWI	head-width index
LLI	ligula-length index
ML	dorsal-mantle length
MWI	mantle-width index
OAI	opposite-arm index
PLI	penis-length index
SpLI	spermatophore-length index
SpRI	sperm-reservoir index
SpWI	spermatophore-width index
TL	total length
WDI	web-depth index

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions are used in the text:

AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	The Natural History Museum, London (formerly, British Museum (Natural History))
CMC	Canterbury Museum, Christchurch
MNHN	Muséum National d'Histoire Naturelle, Paris
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NMNZ	National Museum of Wales, Cardiff
NMV	National Museum of New Zealand, Wellington
NMW	Museum of Victoria, Melbourne
OMD	Otago Museum, Dunedin
QMB	Queensland Museum, Brisbane
QVM	Queen Victoria Museum and Art Gallery, Launceston
SAM	South Australian Museum, Adelaide
TMH	Tasmanian Museum and Art Gallery, Hobart
USNM	Collections of the former United States National Museum (now housed at NMNH)
ZMUG	Zoologisches Institut und Museum der Universität, Göttingen

#### Species Accounts

##### *Octopus australis* Hoyle, 1885

DIAGNOSIS.—Animals medium-sized (to 299 mm TL; to 72 mm ML). Mantle broadly ovoid (MWI 56–81–99); head narrow (HWI 41–52–65), demarked from mantle by moderate constriction; eyes small, projecting above surface of head. Funnel large, slender, bluntly tapered (FLI 40–46–55); funnel organ VV-shaped, limbs thin, outer limbs as long as median limbs. Arms long (ALI 191–427), slender, tapering to narrow tips. Arm lengths subequal, arm order usually III > II > IV > I. Suckers raised above arm surface, moderately large (SI females 6–10–14, males 8–11–15), 16th to 20th suckers usually largest, enlarged on arms II and III of mature males. Right arm III of males hectocotylied, shorter than opposite arm (HAMI 171–233–259; OAI 72–78–89); ligula very large, wide and bulbous (LLI 8–13–17); ligula groove well marked and deep, with 2 rows of minute papillae present along groove; calamus very short, acutely pointed (CLI 15–20–29); hectocotylied arm with 62–77 suckers; opposite arm with 124–217 suckers. Web shallow (WDI 15–23–32), web formula C > D > B > A > E to D > C > B > E > A. Radula with B<sub>6-7</sub> asymmetrical seriation of rachidian. Ink sac present. Gill lamellae 7–9 per outer demibranch. Mature female with large eggs (capsule length 8–12 mm; width 1.5–2.0 mm), method of egg attachment to substrate unknown. Penis long (PLI 17–19–20), with single-coiled diverticulum; spermatophores relatively long (SpLI 63–74–85), slender (SpWI 2–3–4), with large, coiled sperm reservoir (SpRI 35–43–56).

Integumental sculpture consists of pattern of fine, rounded, and closely set epidermal tubercles. Tubercles large and most dense on dorsum, similarly sized but more scattered on ventral surface. Unbranched papillae present in ocular region, with row of 1 large and 3 to 4 small supraocular papillae. Ventrolateral

integumentary ridge present around mantle circumference. Color of live animals unknown. Color of specimens preserved in ethyl alcohol light brown to purple dorsally, cream to light brown ventrally. Ocelli absent.

ORIGINAL DESCRIPTION.—Hoyle, 1885:224.

TYPE LOCALITY.—Australia, New South Wales, Port Jackson (33°50'S, 151°17'E), 6–15 fm (11–28 m).

TYPES.—*Lectotype*: BMNH 1889.4.24.28–29, female, 23 mm ML.

*Paralectotype*: BMNH, same lot as lectotype, male, 12 mm ML (designated by Stranks and Norman, 1993).

Specimens in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Endemic to subtropical waters of eastern Australia, from southern Queensland to southern New South Wales. An inshore species, living on sand and mud bottom, and among sponges, at depths of 3–134 m. General biology unknown.

DISCUSSION.—The diagnosis is based on personal examination of the type specimens of *Octopus australis* in the BMNH collection and also on a systematic revision of *O. australis* by Stranks and Norman (1993). Because neither of the type specimens of *O. australis* was originally selected by Hoyle as holotype, the type material should previously have been considered to be two syntypes (F. Naggs, BMNH, pers. comm., 1988) rather than the holotype and paratype as listed by Tait (1982).

*Octopus australis* belongs to the complex of small to medium-sized octopuses with broadly ovoid mantles and long arms from southern and eastern Australia (along with *O. berrima* Stranks and Norman, 1993, *O. superciliosus* Quoy and Gaimard, 1832, and *O. warringa* Stranks, 1990; see those taxa). *Octopus australis* can be distinguished from the other three species by the characteristic integumental sculpture (particularly the small, rounded tubercles on the dorsum and the obvious and continuous ventrolateral ridge around the mantle), the stout, bulbous ligula with papillate rows along the groove, and the large eggs.

*Octopus australis* can be distinguished from other octopod species by a combination of characters that include a broadly ovoid mantle; a skin pattern of small tubercles on the dorsum and a large papilla over each eye; a ventrolateral integumentary ridge; long, subequal arms (3–5 times ML in mature animals); a medium-sized ligula (8%–17% of right arm III length); large eggs (8–12 mm long); and 7–9 gill lamellae.

#### ***Octopus berrima* Stranks and Norman, 1993**

DIAGNOSIS.—Animals medium-sized (to 475 mm TL; to 106 mm ML). Mantle broadly ovoid (MWI 36–74–93); head narrow (HWI 27–49–68), demarked from mantle by moderate constriction; eyes small, projecting above surface of head. Funnel large, slender, bluntly tapered (FLI 31–45–52); funnel organ VV-shaped, limbs thin, outer limbs  $\frac{3}{4}$  length of median

limbs. Arms long (ALI 135–398), slender, tapering to narrow tips. Arm lengths subequal, arm order usually II > III > IV > I or III > II > IV > I. Suckers raised above arm surface, of moderate size (SI 3–7–13), without sucker enlargement. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 196–247–294; OAI 63–80–97); ligula wide, large (LLI 11–13–16); ligula groove well marked and deep, with 2 rows of minute papillae present along groove; calamus very short, acutely pointed (CLI 15–17–20); hectocotylized arm with 66–78 suckers; opposite arm with 138–218 suckers. Web shallow (WDI 20–24–32), web formula C > D > B > A > E to D > C > B > E > A. Radula with B<sub>3-4</sub> asymmetrical seriation of rachidian. Ink sac present. Gill lamellae 7 to 8 per outer demibranch. Mature female with large eggs (capsule 10–14 mm long, 4–5 mm wide), attached singly to substrate by long, thin stalks. Penis long (PLI 14–25–31), with single-coiled diverticulum; spermatophores relatively long (SpLI 57–87–125), slender (SpWI 1.9–2.6–3.0), with large, coiled sperm reservoir (SpRI 38–43–50).

Integumental sculpture consists of pattern of fine, rounded, and closely set epidermal tubercles. Largest tubercles on dorsum; smaller and less prominent tubercles on ventral surface. Unbranched papillae present in ocular region with row of 1 large and 3 to 4 small supraocular papillae, and on mantle dorsum with 4 primary papillae in diamond arrangement. Ventrolateral integumentary ridge present around mantle circumference. In life, color of resting animals grey white with light brown mottling, white to pale cream ventrally. Lateral, dark brown body bar runs from posterior of each eye, passing through eye, to brachial crown. When stimulated, animals become darker in color, uniformly dark brown to purple brown dorsally, cream to light brown ventrally. Dorsal posterior mantle with 2 white spots; white bar present between eyes; 2 thin white stripes along basal length of dorsal arms. Ocelli absent.

ORIGINAL DESCRIPTION.—Stranks and Norman, 1993:355, figs. 3, 6–11.

TYPE LOCALITY.—Australia, Victoria, Port Phillip, off Mordialloc (38°02'S, 145°05'E), no depth data.

TYPE.—*Holotype*: NMV F67132, male, 59 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Endemic to temperate waters of southeastern Australia, from the Great Australian Bight to southern New South Wales, including Bass Strait and Tasmania. An inshore species, living on sand or mud bottom, or among sponges and ascidians, at depths of 5–267 m. Aspects of feeding, growth, and reproduction studied by Tait (1980) (under the name *O. australis*).

DISCUSSION.—The diagnosis is based on personal examination of the type material of *O. berrima* in the NMV collection and on a systematic account of the species by Stranks and Norman (1993). *Octopus berrima* previously has been incorrectly identified and described under the name *O. australis*

Hoyle, 1885 (see Stranks and Norman, 1993, and *O. australis*, above).

*Octopus berrima* belongs to the complex of small to medium-sized octopuses with broadly ovoid mantles and long arms from southern and eastern Australia (the others being *O. australis*, *O. superciliosus* Quoy and Gaimard, 1832, and *O. warringa* Stranks, 1990; see those taxa). *Octopus berrima* can be distinguished from the other three species by the characteristic integumental sculpture (particularly the small, rounded tubercles on the dorsum and the ventrolateral ridge extending partway around the mantle), the long, wide ligula with papillate rows along the groove, and the large eggs attached singly to the substrate.

*Octopus berrima* can be distinguished from other octopod species by a combination of characters that include a broadly ovoid mantle; a skin pattern of small tubercles on the dorsum and a large papilla over each eye; a ventrolateral integumentary ridge; long, subequal arms (2–4 times ML in mature animals); a medium-sized ligula (11%–16% of right arm III length); large eggs (10–14 mm long), attached singly to substrate; and 7 to 8 gill lamellae.

#### *Octopus boscii* (Lesueur, 1821)

ORIGINAL DESCRIPTION.—Lesueur, 1821:101, as *Sepia boscii*.

TYPE LOCALITY.—Australia (as “New Holland”).

TYPE.—Not traced.

DISCUSSION.—F. Péron (as scientist) and C.A. Lesueur (as illustrator) participated in the voyages of the *Géographe* and *Naturaliste* to Australia. Péron made manuscript notes on several octopuses from Australia, including one that he named *Sepia rugosa* (= *Octopus rugosus* (Bosc, 1792)). After Péron's death in 1810, Lesueur reviewed the manuscript and reidentified that taxon as a new species, *Sepia boscii*. Lesueur also sent a copy of Péron's manuscript to France where it appears that H. de Blainville (1826) used the notes on the same taxon to erect another new name, *Octopus variolatus* (quod vide). The names *O. boscii* (Lesueur) and *O. variolatus* Blainville are thus based on the same type material. The type material is not present in the ANSP or the MNHN collections and should be presumed lost or destroyed (Voss, 1962; Lu et al., 1995).

Lesueur's name *boscii* appears with no description or illustration and should be considered a nomen nudum, following Robson (1929). Under provisions of the International Code of Zoological Nomenclature (ICZN; 1985:260) a species name declared a nomen nudum may again be made available. The next use of the name *O. boscii* was by Orbigny (1840), who placed *O. boscii* in synonymy with *O. variolatus* Blainville, 1826, a nomen dubium. The diagnosis of Orbigny's *O. boscii* was transcribed verbatim from Blainville's type description of *O. variolatus*.

#### *Octopus bunurong* Stranks, 1990

*Octopus bunurong* Stranks, 1990b:462, fig. 3a–f.

*Octopus* sp. C, Stranks, 1988a:65, figs. 31–35.

DIAGNOSIS.—Animals medium-sized (to 475 mm TL; to 95 mm ML). Mantle elongate ovoid (MWI 42–59–83); head slightly narrower than mantle (HWI 28–49–65), demarked from mantle by moderate constriction; eyes large, projecting above surface of head. Funnel large, slender, bluntly tapered (FLI 47–55–75); funnel organ VV-shaped, limbs thick, outer limbs  $\frac{3}{4}$  length of median limbs. Arms very long (ALI 167–708), stout at base, tapering to narrow tips. Arm lengths unequal, arm order I > II > III > IV. Suckers raised above arm surface, of moderate size (SI 3–7–12), without sucker enlargement. Right arm III of males hectocotylized, shorter than opposite number (HAMI 167–209–279; OAI 46–62–82); ligula wide, medium-sized (LLI 9–10–12); ligula groove well marked and deep, with incomplete transverse ridges; calamus very short, acutely pointed (CLI 13–18–22); hectocotylized arm with 70–96 suckers. Web very shallow (WDI 9–12–15), web formula usually A > B > C > D > E. Radula with A<sub>3-4</sub> symmetrical seriation of rachidian. Ink sac present. Gill lamellae 9 to 10 per outer demibranch. Mature female with large eggs (capsule 8–10 mm long, 2–3 mm wide); method of egg attachment to substrate unknown. Penis long (PLI 5–21–39), with single-coiled diverticulum; spermatophores relatively short (SpLI 41–65–103), slender (SpWI 3.1–4.4–5.1), with large, coiled sperm reservoir (SpRI 41–50–56).

Integumental sculpture consists of pattern of fine, rounded, and closely set epidermal tubercles and some irregularly spaced, larger, and more elongate tubercles. Tubercles largest on dorsum; tubercles smaller and less prominent on ventral surface. No large papillae in ocular region. Lateral integumentary ridge or fold around mantle circumference absent. Coloring of live animals unknown. Color of specimens preserved in ethyl alcohol light brown to red brown dorsally, creamy red to light brown ventrally. Some regions on dorsum mottled. Surface of raised tubercles usually darker than background, colored brick red to dark brown, giving a speckled appearance. Ocelli absent.

ORIGINAL DESCRIPTION.—Stranks, 1990b:462, fig. 3a–f. See also Stranks, 1988a:65, figs. 31–35.

TYPE LOCALITY.—Australia, Victoria, Wilsons Promontory, Townsend Point (38°49'S, 140°16'E), no depth data.

TYPE.—*Holotype*: NMV F53223, male, 55 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Endemic to temperate waters of southeastern Australia, from the Great Australian Bight to southern New South Wales, including Bass Strait and northern Tasmania. An inshore species, living on reefs, or rocky areas of sand, or among seagrass, at depths from 1–130 m. Biology unknown.

DISCUSSION.—The diagnosis is based on examination of the

type material of *Octopus bunurong* in the NMV collection and on other material from the NMV, QVM, SAM, and TMH collections. The taxonomic history of this species has been examined by Stranks (1990b), who provided a full synonymy and description.

*Octopus bunurong* belongs to the group of medium-sized octopuses with elongate ovoid mantles and very long arms (the other regional member being *O. kaurna* Stranks, 1990; see that taxon, below). The species appears to be closely related to *O. kaurna* but can be distinguished from the latter by the skin patterning, the larger and more prominent eyes, the shorter and more robust dorsal arm pair, the larger suckers on all arms (particularly the dorsal arms), and the longer ligula.

A summary of characters that can be used to distinguish *O. bunurong* from other octopod species includes an elongate ovoid mantle; a skin pattern of rounded and elongate tubercles on the dorsum and the absence of large papillae over the eyes; large and prominent eyes; very long, unequal arms (4–7 times ML in mature animals); moderately large suckers, without enlargement; a medium-sized ligula (9%–12% of right arm III length); large eggs (8–10 mm long); and 9 to 10 gill lamellae.

#### *Octopus caerulescens* Blainville, 1826

ORIGINAL DESCRIPTION.—Blainville, 1826:189.

TYPE LOCALITY.—Australia, Western Australia, Shark Bay, Dorre Island (as “la petite ile de Dorre”) (25°06'S, 113°07'E), stranded on beach.

TYPE.—Not traced.

DISCUSSION.—Blainville (1826) described *O. caerulescens* from Péron's manuscript notes on a specimen collected during the cruises of the *Géographe* and *Naturaliste* (1800–1804). The type cannot be traced in the MNHN collection and should be presumed lost or destroyed (Lu et al., 1995).

The type description is brief and lacks illustrations. The species was characterized by being blue with very small, closely set purple spots on the mantle and having “pointed” suckers on the long arms. It is unlikely that the identity of this species will ever be positively known, although Orbigny (1840:66) might have been correct in attributing the species to “quelques unes de nos espèces de Philonexes.” From information given, and considering the small size (60 mm TL), the species could be an *Argonauta*. To avoid further conjecture, *Octopus caerulescens* should be considered a nomen dubium, following Robson (1929).

#### *Octopus cornutus* (Owen, 1881)

DIAGNOSIS.—Animal medium-sized (approximately 730 mm TL; 95 mm ML). Mantle elongate ovoid (MWI 69); head slightly narrower than mantle (HWI 60), demarked from mantle by minor constriction; eyes large, projecting above surface of head. Arms very long (ALI 374–615), stout at base, tapering to narrow tips. Arm lengths unequal, arm order

III > II > IV > I. Suckers triserial, deeply set in flesh of arms, of moderate size. Web very shallow (WDI 10), dorsal sectors shallowest.

Integumental sculpture consists of sparsely scattered papillae on mantle, head, and base of arms; 4 to 5 large papillae arranged longitudinally on mantle dorsum. Two large, branched and several smaller, unbranched papillae present in supraocular region. In life, color of resting animals pale pink, with parts of “crown” (?brachial crown) pale violet; when stimulated, animals become bluish red to dark violet.

ORIGINAL DESCRIPTION.—Owen, 1881:131, pl. 23, as *Tritaxeopus cornutus*.

TYPE LOCALITY.—Australia (no other details).

TYPE.—*Holotype*: Not traced, ?female, ~95 mm ML.

DISTRIBUTION AND BIOLOGY.—Known only from the type locality.

DISCUSSION.—The diagnosis is based on the type description by Owen (1881). The species is known only from the untraced holotype from an inexact locality; it appears to belong to the complex of octopods with elongate, ovoid mantles and very long arms, but details are scarce.

Owen (1881) selected the taxon as the type species of a new genus, *Tritaxeopus*, based on the presence of three (not two) sucker rows. *Tritaxeopus* was later relegated to a subgenus of *Octopus* by Robson (1929). No other Australian octopus has been observed with such sucker morphology, and without any substantiating material to verify the species, it remains an enigma. The type specimen is in all probability an aberrant form of *Octopus* sensu stricto, and the species should be considered a nomen dubium.

#### *Octopus cyanea* Gray, 1849

*Octopus cyanea* Gray, 1849:15.

*Octopus marmoratus* Hoyle, 1885:227.

*Octopus horsti* Joubin, 1898:23.

*Polypus herdmani* Hoyle, 1904:187, pl. 1.

*Polypus glaber* “Rüppell, MS” [see Wülker, 1920:51].

*Octopus cyanea* var. *gracilis* Robson, 1929:98.

*Callistoctopus magnocellatus* Taki, 1964:298, figs. 42–46, pl. 4: figs. 1, 2 [after Norman, 1991].

DIAGNOSIS.—Animals large (to 900 mm TL; to 160 mm ML). Mantle broadly ovoid (MWI 54–67–81); head narrow (HWI 42–55–67), demarked from mantle by moderate constriction; eyes large, projecting above surface of head. Funnel large, broad, bluntly tapered (FLI 30–38–48); funnel organ W-shaped, limbs broad, outer limbs <sup>3</sup>/<sub>4</sub> length of median limbs. Arms long (ALI 196–582), stout at base, tapering to narrow tips. Arm lengths subequal, arm order IV = III = II > I. Suckers raised above arm surface, moderately large (SI females 7–9–11, males 7–10–12), 10th to 13th suckers usually largest, enlarged on arms II and III of mature males. Right arm III of males hectocotylyzed, shorter than opposite arm (HAMI 296–351–436; OAI 71–82–88); ligula narrow, very small



(LLI 0.4–1.2–1.7); ligula groove shallow, with about 10 fine, transverse ribs; calamus short, blunt (CLI 35–38–41); hectocotylized arm with 160–229 suckers. Web shallow (WDI 14–19–29), web formula  $C > B = D = E > A$  or  $B = C = D = E > A$ . Radula with  $A_{4-5}$  symmetrical seriation of rachidian. Ink sac present. Gill lamellae 9–11 on outer demibranch. Mature female with small eggs (capsule ~2.7 mm long, 0.5 mm wide); method of attachment to substrate unknown. Penis (PLI 4–14–27) with single-coiled diverticulum; spermatophores short (SpLI 32–40–50), slender (SpWI 1.3–1.5–1.6), with large, coiled sperm reservoir (SpRI 30–33–38).

Integumental sculpture consists of fine reticulations forming patch and groove system on dorsum. Ventral surface smoother. Unbranched papillae present on dorsum. Four large, unbranched papillae in diamond pattern present on dorsal mantle. Pattern of large papillae on brachial crown includes unbranched papilla between and slightly below eyes and pair of papillae midway between eyes and edge of dorsal web. Other smaller, unbranched papillae scattered over dorsum. Single large, unbranched papilla obvious in supraocular region, surrounded by 3 to 4 smaller papillae. Lateral integumentary ridge or fold around mantle circumference absent. In life, color of resting animals cream to white with 2 red, longitudinal bands on dorsum from mantle through eyes to brachial crown; when stimulated, animals turn dark brown, or grey white with marked black ocelli, or produce mottled and sculptured cryptic patterns. Large ocellus on each side of head between eyes and web margin, consisting of black central spot (approximately 0.15 times ML) surrounded by pale ring and narrow, black ring. Ventral faces of arms marked by alternating thin, dark brown and cream-colored bands; 3–7 rows of cream-colored spots run along dorsal surfaces of all arms from web margins distally to arm tips. General color of animals preserved in ethyl alcohol cream to drab, slate grey with ocelli and other markings visible, or dark brown to purple with diagnostic markings obscured.

ORIGINAL DESCRIPTION.—Gray, 1849:15.

TYPE LOCALITY.—Australia (as “coast of New Holland”) (no other details).

TYPE.—*Lectotype*: BMNH 1928.2.4.1, 1 male, 106 mm ML (designated by Norman, 1991). Specimen in good condition, preserved in ethyl alcohol. Another type specimen in the BMNH collection listed in the original description (unknown sex and size, from unknown locality, and unregistered) remains untraced.

DISTRIBUTION AND BIOLOGY.—Northern Australia from North West Cape, Western Australia, to the southern end of the Great Barrier Reef, Queensland, and also with a widespread, Indo-West Pacific distribution. Found living on shallow coral reefs and islands, at depths of 0–18 m (Norman, 1991).

Aspects of the biology of *O. cyanea*, including behavioral data, were described by Norman (1991, 1992b). Further information on behavior based on color and body patterns was included in Roper and Hochberg (1988). A review of the life history of *O. cyanea* was given by Van Heukelem (1983).

DISCUSSION.—The diagnosis is based on personal examination of the lectotype of *O. cyanea* in the BMNH collection and also on the revision of the systematics of *O. cyanea* by Norman (1991). The species is one of several octopuses with ocellate color patterns from the Indo-West Pacific region (see Norman, 1993a).

The name *O. cyanea* has been incorrectly applied to an octopod species occurring in subtropical Australian waters, known as the “common Sydney octopus.” The species bearing that common name is currently considered to be *O. tetricus* (quod vide).

*Octopus cyanea* can be distinguished from other octopod species by a combination of characters that include a broadly ovoid mantle; a skin pattern of integumentary wrinkling, unbranched papillae on the dorsum, and a large papilla over each eye; a large, black ocellus on the web, in front of and just below each eye; long, subequal arms (4–6 times ML in mature animals); enlarged suckers on arms II and III of mature males; a very small ligula (approximately 1% of right arm III length); small eggs (capsules about 2.5 mm long); and 9–11 gill lamellae.

#### *Octopus duplex* Hoyle, 1885

ORIGINAL DESCRIPTION.—Hoyle, 1885:226.

TYPE LOCALITY.—Australia, New South Wales, off Two-fold Bay (36°59'S, 150°20'E), 150 fm (275 m), green mud bottom.

TYPES.—*Lectotype*: BMNH 1889.4.24.31–32, 1 female, 19 mm ML.

*Paralectotype*: BMNH, same lot as lectotype, 1 male, 11 mm ML.

Specimens in good condition, preserved in ethyl alcohol.

DISCUSSION.—Personal examination of the two syntypes of *O. duplex* revealed that the animals belonged to different taxa. Based mainly on the animal's size, skin sculpture, and egg morphology, the mature female type was identified as *O. superciliosus* Quoy and Gaimard, 1832. That specimen is herein designated as lectotype, and as such, *O. duplex* is a junior synonym of *O. superciliosus*. The immature male type was determined as *O. berrima* Stranks and Norman, 1993, primarily on the basis of skin sculpture and ligula morphology.

See *O. superciliosus* Quoy and Gaimard, 1832 (below), and *O. berrima* Stranks and Norman, 1993 (above).

#### *Octopus flindersi* Cotton, 1932

ORIGINAL DESCRIPTION.—Cotton, 1932:543, figs. 4, 6.

TYPE LOCALITY.—Australia, South Australia, Largs Bay (34°49'S, 138°29'E), no depth data.

TYPE.—*Holotype*: SAM D10169, male, 176 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISCUSSION.—See *O. maorum* Hutton, 1880 (below).

***Octopus kaurna* Stranks, 1990**

*Octopus kaurna* Stranks, 1990b:460, fig. 2a-f.

*Octopus* sp. B, Stranks, 1988a:61, figs. 26-30.

DIAGNOSIS.—Animals medium-sized (to 420 mm TL; to 85 mm ML). Mantle elongate ovoid (MWI 40-70-107); head wide, slightly narrower than mantle (HWI 37-58-89), demarked from mantle by minor constriction; eyes small, not projecting above surface of head. Funnel large, slender, bluntly tapered (FLI 44-61-89); funnel organ VV-shaped, limbs thick, outer limbs  $\frac{3}{4}$  length of median limbs. Arms very long (ALI 144-686), slender, tapering to narrow tips. Arm lengths unequal, arm order I > II > III > IV. Suckers deeply set in flesh of arms, small (SI 3-5-9), without sucker enlargement. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 144-249-326; OAI 54-61-70); ligula narrow, small (LLI 5-6-8); ligula groove well marked and moderately deep, with incomplete transverse ridges; calamus short, pointed (CLI 33-42-48); hectocotylized arm with 66-129 suckers. Web very shallow (WDI 11-14-19), web formula usually A > B > C > D > E. Radula with B<sub>4-5</sub> asymmetrical seriation of rachidian. Ink sac present. Gill lamellae 9-11 on outer demibranch. Mature female with large eggs (capsule 9-11 mm long, 2-3 mm wide), method of egg attachment to substrate unknown. Penis long (PLI 18-24-36), with large, single-coiled diverticulum; spermatophores relatively short (SpLI 52-83-103), slender (SpWI 3-4-5), with large, coiled sperm reservoir (SpRI 21-29-39).

Integumental sculpture consists of pattern of fine, rounded, and widely set epidermal tubercles. Tubercles largest on dorsum; tubercles smaller and less prominent on ventral surface. Some tubercles on ventrolateral surface more elongate but no more prominent than those on dorsal and ventral surfaces. Papillae in ocular region absent. Lateral integumentary ridge or fold around mantle circumference absent. In life, color of resting animals light brown to pink brown dorsally, cream to light brown ventrally; when stimulated, animals become darker brown to brick-red brown. Color of animals preserved in ethyl alcohol uniformly light brown to dark purple dorsally, creamy red to light brown ventrally. Ocelli absent.

ORIGINAL DESCRIPTION.—Stranks, 1990b:460, fig. 2a-f. See also Stranks, 1988a:61, figs. 26-30.

TYPE LOCALITY.—Australia, Victoria, Hobsons Bay (37°52'S, 144°56'E), no depth data.

TYPE.—*Holotype*: NMV F24494, male, 34 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Endemic to temperate waters of southeastern Australia, from the Great Australian Bight to eastern Australia, including Bass Strait and northern Tasmania. An inshore species, living on sand bottom, and among seagrass, at depths of 0-49 m. Biology unknown.

DISCUSSION.—The diagnosis is based on examination of the type material of *O. kaurna* in the NMV collection and on other material from the NMV, QVM, SAM, and TMH collections.

The systematic background of this species was examined by Stranks (1990b), who provided a full synonymy and description.

*Octopus kaurna* is a member of the regional group of medium-sized octopuses with elongate, ovoid mantles and very long arms (the other member being *O. bunurong* Stranks, 1990; see that taxon, above). The species is apparently closely related to *O. bunurong* but can be distinguished from that species by the skin patterning, the small, nonprojecting eyes, the slender arms, the small, evenly spaced suckers on all arms, and the shorter ligula.

Characters that can be used to distinguish *O. kaurna* from other octopod species include an elongate, ovoid mantle; a skin pattern of rounded tubercles on the dorsum, without large papillae over the eyes; small, not prominent eyes; very long, unequal arms (3-6 times ML in mature animals); small suckers, without enlargement; a small ligula (4%-8% of right arm III length); large eggs (9-11 mm long); and 9-11 gill lamellae.

***Octopus maorum* Hutton, 1880**

*Octopus maorum* Hutton, 1880:1.

*Octopus communis* Park, 1885:198.

*Octopus flindersi* Cotton, 1932:543, figs. 4, 6.

*Paroctopus zealandicus* Benham, 1944:256, pl. 40.

DIAGNOSIS.—Animals large (to 1155 mm TL; to 255 mm ML). Mantle broadly ovoid (MWI 52-69-96); head narrow (HWI 32-53-74), demarked from mantle by moderate constriction; eyes large, not projecting far above surface of head. Funnel large, stout, bluntly tapered (FLI 33-44-57); funnel organ W-shaped, limbs thick, outer limbs  $\frac{3}{4}$  length of median limbs. Arms long (ALI 165-569), slender, tapering to fine tips. Arm lengths unequal, arm order usually I > II > III > IV. Suckers raised above arm surface, large (SI 4-12-22), 15th to 22nd suckers usually largest, enlarged on all arms of mature males and females. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 200-271-317; OAI 57-71-85); ligula narrow, small (LLI 3.4-4.7-6.5); ligula groove well marked and deep, with 10-15 complete transverse ridges; calamus moderately long, acutely pointed (CLI 20-26-35); hectocotylized arm with 94-135 suckers. Web shallow (WDI 14-19-24), web formula A > B > C > D > E. Radula with B<sub>2-3</sub> asymmetrical seriation of rachidian. Ink sac present. Gill lamellae 13-15 per outer demibranch. Mature female with medium-sized eggs (capsule 6-7 mm long, 1-2 mm wide), attached singly to substrate by long, thin stalks. Penis long (PLI 8-14-21), diverticulum single-coiled, marked with 3 lobes; spermatophores relatively short (SpLI 35-69-101), slender (SpWI 0.9-1.5-2.0), with large, coiled sperm reservoir (SpRI 27-45-71).

Integumental sculpture consists of pattern of coarse epidermal wrinkling. Dorsum appears rough, with surface of head covered by numerous, transverse furrows and mantle surface

covered by longitudinal furrows. Epidermal ridges separated into numerous, roughly rectangular patches, most obvious on dorsal mantle. Ventral surface smoother. Unbranched papillae present on dorsum. Papillae on mantle dorsum form ~5 subparallel rows of simple papillae along mantle length. Each row with 3–6 papillae. Unbranched papillae present in ocular region, with 1 large supraocular papilla and numerous, smaller papillae scattered around each eye. Lateral integumentary ridge or fold around mantle circumference absent. In life, color of resting animals uniformly grey to dark brown dorsally, paler ventrally; when stimulated, animals become darker, turning brick red to very dark brown. Preserved animals in ethyl alcohol cream to dark brown dorsally, slightly paler ventrally. In both live and preserved specimens, small, dark red maculations (1%–3% of ML in diameter) scattered over entire dorsal and ventral surfaces. Ocelli absent.

ORIGINAL DESCRIPTION.—Hutton, 1880:1.

TYPE LOCALITY.—New Zealand, Dunedin (45°50'S, 170°30'E), no depth data.

TYPE.—*Lectotype*: OMD A.'89.03, male, 185 mm ML. Specimen in poor condition, preserved in ethyl alcohol. Another type specimen of *O. maorum*, from the CMC collection (male, 43 mm ML, unregistered), was subsequently reidentified as *Robsonella huttoni* Benham, 1943, by Dell (1952).

DISTRIBUTION AND BIOLOGY.—Temperate waters of south-eastern Australia, from the Great Australian Bight to central New South Wales, including Bass Strait and Tasmania, as well as both temperate and subantarctic waters in New Zealand, including the North and South islands and Chatham, Stewart, Auckland, and Campbell islands. No geographic variation detected to date between the Australian and New Zealand populations of the species. A species inhabiting the continental shelf and upper continental slope, living on reefs or rocky areas, or among sponges, at depths of 0–549 m.

Aspects of the biology of *O. maorum*, including the morphology and brooding of eggs and the hatching and behavior of juveniles, were described by Batham (1957). Several parasites have been recorded as occurring in this host in New Zealand, namely, dicyemid mesozoans (*Dicyemeneae kaikouriensis* Short and Hochberg, 1969; *Dicyema knoxi* and *D. maorum* Short, 1971) and digenetic trematodes (*Plagioporus maorum* Allison, 1966; *Lecithochirum* sp. Overstreet and Hochberg, 1975).

DISCUSSION.—The diagnosis is based on personal examination of the lectotype of *O. maorum* in the OMD collection and on another type specimen of *O. maorum* from the CMC collection that has since been reidentified as *Robsonella huttoni* Benham, 1943 (see Dell, 1952). Also examined was the holotype of *Octopus flindersi* Cotton, 1932, from the SAM collection and additional material from the AMS, CMC, NMNZ, NMV, OMD, QVM, SAM, and TMH collections.

Junior synonyms of *O. maorum* include *O. communis* Park, 1885, *O. flindersi* Cotton, 1932, and *Paroctopus zealandicus*

Benham, 1944 (see Stranks, 1988a). The type specimen of *Octopus communis* is no longer extant (Suter, 1913), nor is the type specimen of *Paroctopus zealandicus* (A. Harris, OMD, pers. comm.); nevertheless, the type description of each species is sufficiently detailed to allow each to be recognized and synonymized with *Octopus maorum*. *Octopus maorum* described from New Zealand waters and *O. flindersi* described from Australian waters were determined to be synonymous, with *O. maorum* taking priority. One nomenclatural problem that arose was the reidentification by Dell (1952:39) of one of the types of *O. maorum* as *Robsonella huttoni* Benham, 1943. *Robsonella huttoni* is a different and distinct species from New Zealand. To preserve nomenclatural stability, the male specimen from the Otago Museum is herein designated as the lectotype of *Octopus maorum*.

*Octopus maorum* can be distinguished from other octopod species by a combination of characters that include a broadly ovoid mantle; a skin pattern of longitudinal ridges or folds on the mantle, five rows of unbranched papillae on the dorsum, and a large papilla over each eye; long, unequal arms (3–6 times ML in mature animals); enlarged suckers on all arms of mature males and females; a small ligula (3%–6% of right arm III length); medium-sized eggs (6–7 mm long), attached singly to substrate; and 13–15 gill lamellae.

#### *Octopus pallidus* Hoyle, 1885

DIAGNOSIS.—Animals medium-sized (to 540 mm TL; to 147 mm ML). Mantle broadly ovoid (MWI 67–78–91); head wide but narrower than mantle (HWI 44–58–89), demarked from mantle by moderate constriction; eyes large, not projecting far above surface of head. Funnel large, stout, bluntly tapered (FLI 31–39–52); funnel organ VV-shaped, limbs thick, outer limbs  $\frac{3}{4}$  length of median limbs. Arms short (ALI 134–263), stout, tapering to fine tips. Arm lengths subequal, arm order usually IV > III > II > I. Suckers raised above arm surface, of moderate size (SI females 6–7–8, males 8–9–11), 10th to 13th suckers usually largest, enlarged on all arms of mature males. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 156–184–219; OAI 79–82–89); ligula wide, medium-sized (LLI 9–11–16); ligula groove well marked and deep, with incomplete transverse ridges; calamus long, acutely pointed (CLI 32–40–55); hectocotylized arm with 72–86 suckers. Web moderately deep (WDI 24–30–41), web formula usually D > C > B > E > A. Radula with B<sub>4–5</sub> asymmetrical seriation of rachidian. Ink sac present. Gill lamellae 7–9 per outer demibranch. Mature female with large eggs (capsule 11–13 mm long, 3–4 mm wide), attached singly to substrate by long, thin stalks. Penis long (PLI 13–19–27), with single-coiled diverticulum; spermatophores of medium length (SpLI 43–85–118), slender (SpWI 2.1–2.7–3.3), with large, coiled sperm reservoir (SpRI 35–43–52).

Integumental sculpture consists of pattern of coarse, uni-

formly "rosette"-shaped and closely set epidermal tubercles covering both dorsal and ventral surfaces. Tubercles largest on dorsum near base of arms, smaller and less prominent on ventral surface. Branched and unbranched papillae also present on dorsum. Papillae on mantle dorsum form ~5 subparallel rows of 4–6 simple, usually unbranched papillae along mantle length. Large arborescent papillae obvious in ocular region, with 4 supraocular and 2 subocular papillae. Three rows of 2 papillae each present on dorsal surface of web and dorsal pair of arms. Lateral integumentary ridge or fold around mantle circumference absent. In life, color of resting animals brown and cream mottled dorsally, paler ventrally; when stimulated, animals become uniformly dark brown to purple. Specimens preserved in ethyl alcohol reddish brown to orange dorsally, slightly paler ventrally. In both live and preserved specimens, faint orange stripe often present along length of dorsal arms. Surface of raised tubercles usually darker than background, giving reticulate pattern. Ocelli absent.

ORIGINAL DESCRIPTION.—Hoyle, 1885:223.

TYPE LOCALITY.—Australia, Victoria, off East Moncoeur Island (39°10.5'S, 146°37'E), 38 fm (70 m), sand and shell bottom.

TYPES.—*Lectotype*: BMNH 1889.4.24.19, 1 male, 56 mm ML. Specimen in good condition, preserved in ethyl alcohol.

*Paralectotypes*: BMNH 1889.4.24.20–21, 1 female, 78 mm ML, 1 juvenile. Specimens in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Southeastern Australia, from the Great Australian Bight to central New South Wales, including Bass Strait and Tasmania. A species inhabiting the continental shelf and upper continental slope, living on sand or mud bottom, or among sponges and ascidians, at depths of 7–593 m.

The little information available on the biology of *O. pallidus* has been summarized in Stranks (1988b).

DISCUSSION.—The diagnosis is based on data provided by Hoyle (1885, 1886), Robson (1929), and M.D. Norman (pers. comm., 1990) for the type specimens in the BMNH collection and on personal examination of other material from the NMV, QVM, SAM, and TMH collections. A lectotype is herein designated. The systematics of *O. pallidus* are relatively well known, and Stranks (1988b) provided a taxonomic history, synonymy, and redescription of the species.

*Octopus pallidus* can be distinguished from other species of octopus by a combination of characters that include a broadly ovoid mantle; a skin pattern of "rosette"-shaped tubercles and both branched and unbranched papillae on the dorsum and large branched papillae over each eye; stout, subequal arms (2–3 times ML in mature animals); enlarged suckers on all arms of mature males; a medium-sized ligula (8%–16% of right arm III length); large eggs (11–13 mm long) attached singly to substrate; and 7–9 gill lamellae.

### *Octopus peronii* (Lesueur, 1821)

ORIGINAL DESCRIPTION.—Lesueur, 1821:101, as *Sepia peronii*.

TYPE LOCALITY.—Australia, Western Australia, Shark Bay, Dorre Island (as "island of Dorre, Shark Bay") (25°06'S, 113°07'E), no depth data.

TYPE.—Not traced.

DISCUSSION.—*Octopus peronii* is the second species that Lesueur described from Péron's manuscript notes on octopuses collected at Shark Bay, Western Australia (the other being *O. boscii*). Péron originally identified this taxon as "*Sepia octopa*" (= *Sepia octopodia* Linnaeus; = ?*Octopus vulgaris* Lamarck), but Lesueur reidentified the taxon as a new species, *Sepia peronii*. Blainville (1826) apparently used Péron's notes on the same material to establish another new species name, *Octopus pustulosus* (quod vide). In that case, the names *O. peronii* (Lesueur) and *O. pustulosus* Blainville would have been based on the same type material. The type material has not been located in either the ANSP or MNHN collections and should be presumed lost or destroyed (Voss, 1962; Lu et al., 1995).

No description or illustration appears with Lesueur's name, and *O. peronii* should be classified a nomen nudum following Robson (1929). According to the ICZN (1985:260), the name may again be made available. The name *O. peronii* was next used by Orbigny (1826), again as a nomen nudum, and further by Orbigny (1840), who placed it in the synonymy of *O. pustulosus* Blainville, 1826, a nomen dubium.

### *Octopus pictus* Brock, 1882

ORIGINAL DESCRIPTION.—Brock, 1882:603, pl. 37: fig. 3.

TYPE LOCALITY.—Unknown (specimen was donated by Dr. Schütte of Sydney, New South Wales, which might indicate an Australian locality).

TYPE.—*Holotype*: ZMUG, male, 28 mm ML. Specimen no longer extant.

DISCUSSION.—Brock (1882) gave the name *O. pictus* to a new octopus species from an unknown locality; however, the species-group name *O. pictus* was preoccupied. Blainville (1828) had described a species as *O. pictus* from the Mediterranean Sea (= *Ocythoe tuberculata* Rafinesque, 1814, fide Robson, 1932). The two available species-group names were originally established for different nominal species, in combination with the same generic name *Octopus*. Therefore *O. pictus* Brock, 1882, is a junior homonym of *O. pictus* Blainville, 1828, and is unavailable (ICZN, 1985, Art. 53c).

See *Hapalochlaena maculosa* (Hoyle, 1883) (below).

### *Octopus polyzenia* Gray, 1849

DIAGNOSIS.—Animals small (to 130 mm TL; to 38 mm ML). Mantle ovoid (MWI females 58–69–78, males 50–69–

85); head wide but narrower than mantle (HWI 41-50-63), demarked from mantle by moderate constriction; eyes large, projecting above surface of head. Funnel large, stout, bluntly tapered (FLI 34-40-51); funnel organ W-shaped, limbs thick, outer limbs slightly shorter than median limbs. Arms long (ALI females 236-309, males 201-252), robust, tapering to fine tips. Arm lengths unequal, arm order usually  $IV = III > II > I$  or  $IV > III > II > I$ . Suckers raised above arm surface, of moderate size (SI females 8-9-13, males 10-12-14), 14th to 16th suckers usually largest, enlarged on all arms of mature males. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 152-177-195; OAI 77); ligula conical, small (LLI 5-6-7); ligula groove shallow, with raised, longitudinal midrib; calamus long, pointed (CLI 41-51-69); hectocotylized arm with 45-52 suckers. Web moderately deep (WDI 26-31-39), web formula  $D > C = E > B > A$  or  $D = E > C > B > A$ . Radula with  $A_4$  symmetrical seriation of rachidian. Ink sac present. Gill lamellae 6 to 7 per outer demibranch. Mature female with large eggs (capsule ~8 mm long, 3 mm wide) joined by fine central stalk, attached to substrate in festoons. Penis moderately long (PLI 14-17), with single-coiled diverticulum; spermatophores relatively short (SpLI 34), moderately wide (SpWI 6), with large, coiled sperm reservoir (SpRI 56).

Integumental sculpture consists of pattern of fine, rounded epidermal tubercles. Tubercles present on dorsal and ventral surfaces of mantle, brachial crown, and arms, extending onto arm faces and oral surface of dorsal and dorsolateral webs; tubercles absent from ventral arm crown. Longitudinal, raised skin ridges present on dorsal mantle, with largest forming diamond arrangement; additional shorter ridges present on dorsal and lateral mantle. Arborescent papillae obvious in ocular region, with 1 large and 2 small supraocular papillae. Lateral integumentary ridge or fold around mantle circumference absent. Color of live animals unknown. Color of animals preserved in ethyl alcohol generally cream to pink brown with dark mottling and light patches on dorsum. Dorsal mantle pattern of light-colored, oval patches containing raised skin ridges, central 4 arranged in diamond shape forming faint crucifix pattern. Dark brown, rectangular block between and slightly behind eyes in some specimens. Frontal white spot, consisting of 2 light spots, on dorsal arm crown below midpoint of eyes; anterior cream-colored spot containing primary papillae; posterior spot pink to peach. Dark brown to black ocellus on either side of arm crown between bases of arms II and III (~0.1 times ML), containing small, iridescent blue ring. Dark ocellus can fade in preserved specimens leaving only iridescent ring visible. Dark transverse bars on all arms, widely spaced with 3 to 4 suckers between each bar.

ORIGINAL DESCRIPTION.—Gray, 1849:13.

TYPE LOCALITY.—Australia, Northern Territory, Port Essington (11°16'S, 132°09'E), no depth data.

TYPE.—*Holotype*: BMNH 1845.5.14.78, male, 12 mm

ML. Specimen "not in very good condition" (Robson, 1929:73).

DISTRIBUTION AND BIOLOGY.—Endemic to tropical waters of northern Australia, from Dampier Archipelago, Western Australia, to central Queensland. A species living in shallow coastal waters, on open substrates of sand or mud, at depths of 1-20 m (Norman, 1993a). Biology unknown.

DISCUSSION.—The diagnosis is based on information provided by M.D. Norman (pers. comm., 1990) on the holotype of *O. polyzenia* and on a redescription of the species by Norman (1993a). *Octopus polyzenia* is one of four species of ocellate octopuses reported from Great Barrier Reef waters (Norman, 1993a).

*Octopus polyzenia* can be distinguished from other octopod species by a combination of characters including an ovoid mantle; a skin pattern of raised ridges forming a crucifix pattern on the dorsal mantle, and a large papilla over each eye; a large, black ocellus containing an iridescent, blue ring on the arm crown between the bases of arms II and III; long, unequal arms; moderately large suckers, enlarged on all arms of mature males; a small ligula (5%-7% of right arm III length); large eggs (~8 mm long); and 6 to 7 gill lamellae.

#### *Octopus pustulosus* Blainville, 1826

ORIGINAL DESCRIPTION.—Blainville, 1826:186.

TYPE LOCALITY.—Not stated but presumed to be same as for *O. peronii* (Lesueur, 1821): Australia, Western Australia, Shark Bay, Dorre Island (as "island of Dorre, Shark Bay") (25°06'S, 113°07'E).

TYPE.—Not traced.

DISCUSSION.—See also discussion of *O. peronii* (Lesueur, 1821), above. Blainville's (1826) diagnosis of *O. pustulosus* was based on manuscript notes by F. Péron on an octopod collected during the voyages of the *Géographe* and *Naturaliste*. The brief description and lack of illustration, and the presumed lack of an extant type, mean that the identity of the species may never be established. Following Robson (1929), *Octopus pustulosus* should be considered a nomen dubium.

Sasaki (1920) used the name *O. pustulosus* for a new species from Japan. Berry (1921) noted that the name was preoccupied by Blainville's (1826) taxon and proposed the replacement name *O. madokai*.

#### *Octopus robustus* Brock, 1887

ORIGINAL DESCRIPTION.—Brock, 1887:317.

TYPE LOCALITY.—Australia, New South Wales, Port Jackson (as "Sydney-Docks") (33°50'S, 151°17'E), no depth data.

TYPE.—*Holotype*: ZMUG, male, 28 mm ML.

DISCUSSION.—Details given by Brock (1887) for the type specimen of *Octopus robustus* were investigated. The holotype has not been available for study, and it remains to be confirmed

whether the specimen is extant. The species is recognizable from the type description. Brock (1887) gave details of skin color patterns, including blue rings on the web ventrum and dorsum, but unfortunately omitted important diagnostic details of the color patterning of the head and mantle dorsum (that might have been obscured by the rugose nature of the skin). Based on data on the mantle, head, and arm dimensions, hectocotylus morphology, integumental sculpture and color patterns, and the type locality, *O. robustus* is herein placed in synonymy with *Hapalochlaena fasciata* (Hoyle, 1886) (see that taxon, below).

### *Octopus superciliosus* Quoy and Gaimard, 1832

*Octopus superciliosus* Quoy and Gaimard, 1832:88, pl. 6: fig. 4.

*Octopus westermiensis* Orbigny, 1834, pl. 10: fig. 3.

*Octopus duplex* Hoyle, 1885:226.

**DIAGNOSIS.**—Animals small (to 94 mm TL; to 26 mm ML). Mantle broadly ovoid (MWI 62–79–99); head wide but narrower than mantle (HWI 47–65–92), demarked from mantle by moderate constriction; eyes large, projecting above surface of head. Funnel large, stout, bluntly tapered (FLI 34–45–59); funnel organ VV-shaped, limbs thick, outer limbs  $\frac{3}{4}$  length of median limbs. Arms long (ALI 140–356), stout at base, tapering to fine tips. Arm lengths subequal, arm order usually III > IV > II > I or IV > III > II > I. Suckers raised above arm surface, of moderate size (SI 6–9–14), without sucker enlargement. Right arm III of males hectocotylized, usually shorter than opposite arm (HAMI 172–202–246; OAI 76–92–109); ligula wide, medium-sized (LLI 8–10–14); ligula groove long, well marked, and shallow, with approximately 20 complete transverse ridges; calamus long, acutely pointed (CLI 35–44–53); hectocotylized arm with 46–66 suckers. Web shallow (WDI 21–27–36), web formula usually D > C > E > B > A. Radula with B<sub>3,4</sub> seriation of rachidian. Ink sac present. Gill lamellae 6–8 per outer demibranch. Mature female with large eggs (capsule 8–11 mm long, 2–4 mm wide), attached singly to substrate by long, thin stalks. Penis long (PLI 14–19–27), with single-coiled diverticulum; spermatophores relatively short (SpLI 56–68–84), slender (SpWI 3–4–5), with large, coiled sperm reservoir (SpRI 42–51–61).

Integumental sculpture consists of pattern of unbranched papillae on mantle dorsum and ventrum. Papillae on mantle dorsum form ~7 subparallel, longitudinal rows of 4 to 5 simple, usually elongate papillae along mantle length. Single, large papilla forms posterior point on mantle. Unbranched papillae present in ocular region, with 1 large supraocular papilla and numerous smaller papillae scattered around each eye. Continuous lateral integumentary ridge or fold around mantle circumference absent, but 2 rows of 4 to 5 elongated papillae on ventrolateral surface resemble such lateral ridges. Mantle

surface otherwise smooth. In life, color of resting animals cream to light brown dorsally, white to cream ventrally; when stimulated, animals turn mottled light and dark brown or uniform dark brown to purple. Color of animals preserved in ethyl alcohol uniformly dark brown to purple dorsally, cream to light brown ventrally. Ocelli absent.

**ORIGINAL DESCRIPTION.**—Quoy and Gaimard, 1832:88, pl. 6: fig. 4.

**TYPE LOCALITY.**—Australia, Victoria, Western Port (as “le port Western dans le detroit de Bass, a la Nouvelle-Hollande”) (38°25'S, 145°15'E), no depth data.

**TYPES.**—*Lectotype*: MNHN 5-4-1047, 1 female, 18 mm ML. Specimen in good condition, preserved in ethyl alcohol.

*Paralectotypes*: MNHN, same lot as lectotype, 2 females, 7 mm ML, 13 mm ML. Specimens in good condition, preserved in ethyl alcohol.

**DISTRIBUTION AND BIOLOGY.**—Southeastern Australia, from the Great Australian Bight to southern New South Wales, including Bass Strait. An inshore species, living on sand or mud bottom, or among sponges and polyzoans, at depths of 1–69 m. Biology unknown.

**DISCUSSION.**—The diagnosis is based on personal examination of the type specimens of *O. superciliosus* in the MNHN collection, on *O. duplex* Hoyle, 1885, in the BMNH collection, and on additional material from the NMV, QVM, SAM, and TMH collections. Junior synonyms of *O. superciliosus* include *O. westermiensis* Orbigny, 1834, and *O. duplex* Hoyle, 1885 (see Stranks, 1988a).

The lectotype of *O. superciliosus*, the larger female specimen (18 mm ML, MNHN 5-4-1047), was designated by Orbigny (1840); the two remaining female specimens in the type series are from the same lot (7 mm ML and 13 mm ML) and therefore constitute paralectotypes.

*Octopus superciliosus* belongs to the regional complex of small to medium-sized octopuses with broadly ovoid mantles and moderately long arms, along with *O. australis* Hoyle, 1885, *O. berrima* Stranks and Norman, 1993, and *O. warringa* Stranks, 1990 (see those taxa). *Octopus superciliosus* can be distinguished from the other three species by the characteristic skin patterning (particularly the unbranched papillae on the head and mantle dorsum and traces of a ventrolateral ridge on the mantle but otherwise smooth skin surface), the wide, flattened ligula with many transverse ridges, and the large eggs attached singly to the substrate.

*Octopus superciliosus* can be distinguished from other octopod species by a combination of characters that include a broadly ovoid mantle; a skin pattern of unbranched papillae on the dorsum and large, unbranched papillae over each eye; traces of a ventrolateral integumentary ridge; long, subequal arms (2–3 times ML in mature animals); a medium-sized ligula (8%–13% of right arm III length); large eggs (8–11 mm long); and 6–8 gill lamellae.

*Octopus tenebricus* Smith, 1884

DIAGNOSIS.—Animals small (75–95 mm TL; 17–19 mm ML). Mantle elongate ovoid (MWI 60–78); head wide, slightly narrower than mantle (HWI 47–56), demarked from mantle by strong constriction; eyes very large, projecting above surface of head. Funnel large, slender, bluntly tapered (FLI 37–42); funnel organ W-shaped, limbs thin, outer limbs  $\frac{3}{4}$  length of median limbs. Arms long (ALI 320–381), slender, tapering to narrow tips. Arm lengths unequal, arm order IV = III = II > I or III = II > IV > I. Suckers raised above arm surface, moderately large (SI 8–9), without sucker enlargement. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 279; OAI 87); ligula narrow, small (LLI 4.4); ligula groove well marked but shallow, with very fine transverse ridges and longitudinal medial ridge; calamus moderately long, acutely pointed (CLI 24); hectocotylized arm with 93 suckers. Web shallow (WDI 14–18), web formula  $C > D > B > A = E$ . Ink sac present. Gill lamellae 7 per outer demibranch. Female specimen submature; eggs small (capsule 1.0–1.2 mm long, 0.3–0.4 mm wide). Penis long (PLI 20), with single-coiled diverticulum; spermatophores relatively short (SpLI 41–47), slender (SpWI 3.0–3.5), with large, coiled sperm reservoir (SpRI 37–43).

Integumental sculpture consists of pattern of fine, longitudinal epidermal ridges on mantle dorsum and fine, rounded, and widely set tubercles on dorsum. Ventral surface smoother. Large branched papillae present on dorsum. Papillae on mantle dorsum form approximately 3 subparallel, longitudinal rows of 3 to 4 complex, branched papillae. Larger, arborescent papilla obvious in supraocular region, surrounded by 3 to 4 smaller papillae. Four rows, of 3 complex, branched papillae each, lie on surface of dorsal web and arms. Lateral integumentary ridge or fold around mantle circumference absent. Color of animals preserved in ethyl alcohol uniform dark brown dorsally, slightly paler ventrally. Ocelli absent.

ORIGINAL DESCRIPTION.—Smith, 1884:35, pl. 4: figs. B–B3.

TYPE LOCALITY.—Australia, Queensland, Bowen (as “Port Denison, Queensland”) (20°02'S, 148°15'E), 3–4 fm (5–7 m), sand and rock bottom.

TYPES.—*Lectotype*: BMNH 1881.11.10.13–14, male, 17 mm ML.

*Paralectotype*: BMNH, same lot as lectotype, female, 19 mm ML.

Specimens in fair condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Recorded only from type locality, in tropical waters of northeastern Australia. Biology unknown.

DISCUSSION.—*Octopus tenebricus* is known only from the two type specimens in the BMNH collection. The diagnosis is based on personal examination of this material. A lectotype is herein designated. Smith (1884), Robson (1929), and Norman

(1992b) have also given detailed descriptions of the type material. With no additional specimens available for study, the species remains poorly known.

*Octopus tenebricus* can be distinguished from other octopod species by an elongate ovoid mantle; a skin pattern of epidermal ridges, rounded tubercles, and large, branched papillae on the dorsum, with enlarged papillae over each eye; long, subequal arms (3–4 times ML in syntypes); a small ligula (4% of right arm III length in lectotype); and 7 gill lamellae.

*Octopus tetricus* Gould, 1852

DIAGNOSIS.—Animal medium-sized (~470 mm TL; 55 mm ML). Mantle elongate ovoid (MWI 56); head wide but narrower than mantle (HWI 35), demarked from mantle by moderate constriction; eyes small. Funnel short, bluntly tapered. Arms long (ALI 550–740), stout at base, tapering to narrow tips. Arm order II = III > IV > I. Suckers large (SI 22). Web moderately deep (WDI 25), web formula probably  $C = D > B > A > E$ .

Integumental sculpture consists of pattern of closely set, coarse tubercles. Largest tubercles on dorsum of head and brachial crown; smaller and less prominent tubercles on ventral surface. Tubercles on mantle flattened and sometimes pitted at center, forming reticulate pattern. Longitudinal series of 3 papillae on dorsum between head and base of dorsal arms. Papillae present in ocular region, with 3 supraocular and 1 subocular papillae.

ORIGINAL DESCRIPTION.—Gould, 1852:474, pl. 47: fig. 588.

TYPE LOCALITY.—Australia, New South Wales, near Sydney (33°53'S, 151°13'E), no depth data.

TYPE.—*Holotype*: Not traced, ?female, ~55 mm ML.

DISTRIBUTION AND BIOLOGY.—Known with certainty from type locality only. Other published records require verification.

DISCUSSION.—The diagnosis is based on the type description by Gould (1852) and on information in Robson (1929) and Pickford (MS). Gould (1852:vi of Introduction) reported that the material from the United States Exploring Expedition was lodged in “Washington,” presumably meaning the USNM. The holotype of *O. tetricus* was not located in the NMNH (Roper and Sweeney, 1978), and probably it is among materials lost from the Expedition collection soon after lodgement during the 1840s (Johnson, 1964; C.F.E. Roper, pers. comm., 1988). The type remains untraced and is believed to be no longer extant.

Only the type description was used to construct the diagnosis because of uncertainty about the correct application of the name *O. tetricus*. The name has previously been used for a species occurring near Sydney, New South Wales, and for another species found off southern Western Australia (see Joll, 1983; Roper et al., 1984). Preliminary results of studies in progress by the author and M.D. Norman show that the name *O. tetricus* could be validly applied to the “common Sydney octopus,” whereas the Western Australia taxon could be a separate,

undescribed species. The identity of these octopuses will be confirmed by current studies. One further complicating factor is that the "common Sydney octopus," a subtropical, nonocellated species, has regularly had the name *O. cyanea* (quod vide) applied to it. This is clearly inappropriate, as a revision of the tropical, ocellated *O. cyanea* (see Norman, 1991) has shown, and *O. tetricus* could prove to be the valid name for the species.

#### *Octopus variolatus* Blainville, 1826

ORIGINAL DESCRIPTION.—Blainville, 1826:186.

TYPE LOCALITY.—Australia, Western Australia, Shark Bay, Dorre Island (as "la petite ile de Dorre, dans la baie des Chiens marins à la Nouvelle-Hollande") (25°06'S, 113°07'E), intertidal rockpools.

TYPE.—Not traced.

DISCUSSION.—See also "Discussion" under *O. boscii* (Lesueur, 1821). Blainville (1826) based his description of *O. variolatus* on F. Péron's manuscript notes on an octopus collected during the cruises of the *Géographe* and *Naturaliste*. Identification of the species is hindered by the brief description, lack of illustration, and lack of type material, which is presumed to be lost or destroyed. Following Robson (1929), the species should be considered a nomen dubium.

#### *Octopus warringa* Stranks, 1990

*Octopus warringa* Stranks, 1990b:457, fig. 1a-f.

*Octopus* sp. A, Stranks, 1988a:54, figs. 21-25.

DIAGNOSIS.—Animals small (to 125 mm TL; to 35 mm ML). Mantle broadly ovoid (MWI 56-81-107); head wide but narrower than mantle (HWI 41-66-82), demarked from mantle by moderate constriction; eyes large, projecting above surface of head. Funnel large, stout, bluntly tapered (FLI 33-42-57); funnel organ W-shaped, limbs thick, outer limbs  $\frac{3}{4}$  length of median limbs. Arms moderately long (ALI 149-365), stout, tapering to narrow tips. Arm lengths subequal, arm order usually III > IV > II > I. Suckers raised above arm surface, of moderate size (SI 6-10-14), 6th to 10th suckers usually largest, enlarged on all arms of mature males and females. Right arm III of males hectocotylized, shorter than opposite arm (HAMI 149-206-273; OAI 67-78-86); ligula bulbous, wide, medium-sized (LLI 6-8-10); ligula groove well marked and deep, without transverse ridges; calamus short, acutely pointed (CLI 24-36-50); hectocotylized arm with 51-65 suckers. Web shallow (WDI 19-25-34), web formula usually C > B = D > A = E. Radula with B<sub>3-4</sub> seriation of rachidian. Ink sac present. Gill lamellae 6-8 per outer demibranch. Mature female with small eggs (capsule 2-3 mm long, 1.0-1.5 mm wide), joined by long, twisted stalks, attached to substrate in festoons. Penis long (PLI 15-29-52), diverticulum coiled, with 3 lobes; spermatophores very long (SpLI 72-146-185), slender (SpWI 2.5-3.1-3.6), with large, coiled sperm reservoir (SpRI 29-32-36).

Integumental sculpture consists of pattern of fine, rounded, and closely set epidermal tubercles covering both dorsal and ventral surfaces. Branched and unbranched papillae present on dorsum. Papillae on mantle dorsum form ~7 subparallel, longitudinal rows of 3 to 4 simple, usually unbranched papillae. Single large papilla forms posterior point on mantle. Large arborescent papilla obvious in supraocular region, surrounded by 3 to 4 smaller, usually unbranched papillae. Lateral integumentary ridge or fold around mantle circumference absent. Color of live animals unknown. Color of animals preserved in ethyl alcohol uniformly light brown to purple dorsally, cream to light brown ventrally. Ocelli absent.

ORIGINAL DESCRIPTION.—Stranks, 1990b:457, fig. 1a-f. See also Stranks, 1988a:54, figs. 21-25.

TYPE LOCALITY.—Australia, Tasmania, Maria Island, west of Darlington (42°35'S, 148°03'E), 30 m.

TYPE.—*Holotype*: NMV F57444, male, 17 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION.—Restricted to temperate waters of south-eastern Australia, from the Great Australian Bight to eastern Victoria, including Bass Strait and Tasmania. Also in New Zealand, including the North and South islands and Stewart Island. No geographic variation detected to date between the Australian and New Zealand populations of the species. An inshore species, living on rocky bottoms, or among sponges and polyzoans, at depths of 0-144 m.

The biology of *O. warringa*, including the morphology and brooding of eggs and hatching and behavior of juveniles, was described by Brough (1965) (under the name *Robsonella australis*). Several parasites have been recorded from this species (also under the name *R. australis*), namely dicyemid mesozoans (*Dicyema robsonellae* Short, 1971; *Dicyemenea rostrata* Short and Hochberg, 1969) and a digenetic trematode (*Plagioporus maorum* Allison, 1966).

DISCUSSION.—The diagnosis is based on examination of the type material of *O. warringa* in the NMV collection and on other material from the AMS, NMV, OMD, SAM, and TMH collections. The systematic background of this species was examined by Stranks (1990b), who provided a full synonymy and description.

Previously, several authors had identified and described *O. warringa* from New Zealand material under the name *Robsonella australis* (Hoyle) (i.e., *Octopus australis* Hoyle, 1885) (see Stranks, 1990b). *Octopus warringa* is a separate species, however, and can be distinguished from *O. australis* by the characteristic skin patterning (particularly the absence of a ventrolateral integumentary ridge), the enlarged suckers on all arms of mature males and females, the bulbous ligula, and the small eggs arranged in festoons.

*Ocotopus warringa* can be distinguished from other octopus species by a combination of characters that include a broadly ovoid mantle; a skin pattern of rounded tubercles and both branched and unbranched papillae on the dorsum, and enlarged papillae over each eye; moderately long, subequal arms (2-4



times ML in mature animals); enlarged suckers on all arms of mature males and females; a medium-sized ligula (6%–10% of right arm III length); small eggs (2–3 mm long) arranged in festoons; and 6–8 gill lamellae.

***Octopus westerniensis* Orbigny, 1834, in  
Férussac and Orbigny, 1834–1848**

ORIGINAL DESCRIPTION.—Orbigny, 1834, atlas, *Octopus*, pl. 10: fig. 3.

DISCUSSION.—Orbigny (1834) used the name *O. westerniensis* in the plate legend that accompanied a text description of *O. superciliosus* Quoy and Gaimard (see that taxon, above). It appears that *O. westerniensis* was Quoy and Gaimard's earlier manuscript name for the species (Lu and Phillips, 1985).

***Hapalochlaena fasciata* (Hoyle, 1886)**

*Octopus pictus fasciata* Hoyle, 1886:94, pl. 8: fig. 3.  
*Octopus robustus* Brock, 1887:317.

DIAGNOSIS.—Animals small (to 150 mm TL; to 45 mm ML). Mantle broadly ovoid; head wide but narrower than mantle, demarked from mantle by moderate constriction; eyes small, not projecting above surface of head. Funnel large, slender, bluntly tapered; funnel organ W-shaped. Arms short (2–3 times ML in mature animals), stout at base, tapering to fine tips. Arm lengths subequal, arm order usually  $IV = III = II > I$ . Suckers deeply set in flesh of arms, of moderate size, without sucker enlargement. Right arm III of males hectocotylyzed, shorter than opposite arm; ligula flat, narrow, medium-sized (LLI 7–12); ligula groove shallow and indistinctly marked, with poorly defined transverse ridges; calamus long, pointed; hectocotylyzed arm with 32–43 suckers. Web shallow. Ink sac present; apparently normal-sized and functional in newly hatched juveniles, subadults, and adults. Gill lamellae 5–7 per outer demibranch. Mature female with large eggs (capsule 6–9 mm long, 2–3 mm wide), joined by long, twisted egg stalks, forming festoons; festoons not attached to substrate (carried loose in ventral web and arms).

Integumental sculpture consists of pattern of fine, scattered tubercles and tuberculated ridges on mantle and head dorsum. Ventral surface smoother. Row of 3 to 4 small papillae in subocular region. Large papilla forms prominent posterior point on mantle. In life, background color of resting animals uniform light grey to beige. Maculae, blue lines, and rings not visible on resting animals. When stimulated, animals become uniform dark charcoal or slate grey; maculae in form of streaks or diagonals on mantle and head dorsum, and ovoid patches on dorsal brachial crown, arm bases, and outer surfaces of all arms become darker. Vivid, iridescent, peacock-blue lines pulsate within each dark macula on dorsal mantle and head; blue rings in form of single discrete rings or clusters of several coalesced rings present within each macula on head, web, and arms.

Background color of animals preserved in ethyl alcohol beige with brown maculae; lines and rings appear purplish to dark blue.

ORIGINAL DESCRIPTION.—Hoyle, 1886:94, pl. 8: fig. 3, as *Octopus pictus fasciata*.

TYPE LOCALITY.—Australia, New South Wales, Port Jackson (33°50'S, 151°17'E), 6–15 fm (11–28 m).

TYPE.—*Holotype*: BMNH 1889.4.24.37, female, 45 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Eastern Australia, from southern New South Wales to southern Queensland. An inshore species, living on reefs or rocky areas and common intertidally in rock pools or subtidally in mollusc shells, bottles, or cans, at depths of 0–30 m. A wider western Pacific distribution needs verification.

Aspects of the biology of *H. fasciata*, including the morphology and brooding of eggs and hatching and behavior of juveniles, were described by Dew (1959) and by Tranter and Augustine (1973) (under the name *H. maculosa*).

DISCUSSION.—The diagnosis is based on data provided by Hoyle (1886), Robson (1929), and M.D. Norman (pers. comm.) for the holotype of *H. fasciata* in the BMNH collection and on details given in Roper and Hochberg (1988). The description also was based on details provided by Brock (1887) for the type specimen of *Octopus robustus*. Additional material was studied from the AMS, NMV, and QMB collections. A brief taxonomic background to the species was included both in Roper and Hochberg (1988) and in Stranks (1990a).

*Hapalochlaena fasciata* is a member of the clade of "blue-ringed and blue-lined octopuses" occurring in Australian and adjacent waters, with small bodies, short arms, and color patterns of iridescent blue rings or bars (see Roper and Hochberg, 1988). The systematics of the "blue-lined octopus," *H. fasciata*, are currently undergoing revision by the author. The relationship of *H. fasciata* with "blue-lined octopuses" described from tropical and subtropical regions outside Australia (e.g., from Japan, in Sasaki (1929) and Wülker (1910)) also is being investigated.

***Hapalochlaena maculosa* (Hoyle, 1883)**

*Octopus maculosus* Hoyle, 1883:319, pl. 6.  
*Octopus pictus* Brock, 1882:603, pl. 37: fig. 3.

DIAGNOSIS.—Animals small (to 215 mm TL; to 57 mm ML). Mantle broadly ovoid (MWI 61–81–103); head wide but narrower than mantle (HWI 46–61–82), demarked from mantle by moderate constriction; eyes small, not projecting above surface of head. Funnel large, slender, bluntly tapered (FLI 32–39–47); funnel organ W-shaped, limbs thin, outer limbs  $\frac{3}{4}$  length of median limbs. Arms short (ALI 151–311), stout at base, tapering to fine tips. Arm lengths subequal, arm order usually  $IV = III = II > I$ . Suckers deeply set in flesh of arms, of moderate size (SI 5–8–13), without sucker enlargement. Right arm III of males hectocotylyzed, shorter

than opposite arm (HAMI 166-186-236; OAI 76-81-84); ligula flat, narrow, medium-sized (LLI 7-11-13); ligula groove indistinctly marked and shallow, with poorly defined transverse ridges; calamus long, acutely pointed (CLI 33-45-62); hectocotylized arm with 45-56 suckers. Web shallow (WDI 17-26-32), web formula usually  $D > C > E > B > A$ . Radula with  $A_{2-3}$  seriation of rachidian. Ink sac present; normal-sized and functional in newly hatched juveniles; reduced and nonfunctional in subadults and adults; duct still present. Gill lamellae 6 to 7 per outer demibranch. Mature female with large eggs (capsule 7-9 mm long, 3-4 mm wide), joined by long, twisted egg stalks, forming festoons; festoons not attached to substrate (carried loose in ventral arms and web). Penis long (PLI 19-22-25), with single-coiled diverticulum; spermatophores relatively short (SpLI 43-85-118), slender (SpWI 1.7-2.5-3.5), with large, coiled sperm reservoir (SpRI 33-39-47).

Integumental sculpture consists of pattern of coarse epidermal wrinkling. Dorsum appears rough, with surface covered by numerous, irregularly arranged wrinkles. Ventral surface smoother. Fine, unevenly sized, closely set tubercles cover head and mantle dorsum; numerous larger tubercles surround each eye. Several smaller tubercles occur in center of each blue ring. Large papilla forms prominent posterior point on mantle. Lateral integumentary ridge or fold around mantle circumference absent. In life, background color of resting animals uniform grey to beige with light brown maculae. Dorsal and lateral surfaces of mantle and head marked with 10 maculae in the form of light brown diagonal lines. Dorsal, lateral, and ventral surfaces of brachial crown and arm bases marked with smaller ovoid maculae of light brown color. Outer surfaces of all arms marked with approximately 10 evenly spaced maculae in form of light brown bands. Blue rings not visible on resting animals. When stimulated, animals become darker in color and maculae turn dark brown. Vivid, iridescent, peacock-blue rings in form of single discrete rings or clusters of several rings coalesced into 1 (but not in elongate bands or stripes) pulsate within each dark brown macula. Approximately 50-60 blue rings (diameter 0.5-2.0 mm on mature animals) present on dorsal and lateral surfaces of mantle. Background color of animals preserved in ethyl alcohol is beige with brown maculae as observed in live animals; rings appear purplish to dark blue.

ORIGINAL DESCRIPTION.—Hoyle, 1883:319, pl. 6, as *Octopus maculosus*.

TYPE LOCALITY.—Australia (no other details).

TYPE.—*Holotype*: NMW Z.78.14.421, male, 30 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Restricted to temperate waters of southern Australia, from southern Western Australia to eastern Victoria, including Bass Strait. An inshore species, living on reefs or rocky areas of sand, and common intertidally in rock pools or subtidally in mollusc shells, bottles, or cans, at depths of 0-55 m.

A summary of information available on the taxonomy and biology of *H. maculosa*, as well as cases involving human envenomation by the species, is given in Stranks (1988a). Details on postembryonic development of *H. maculosa* are examined by Stranks and Lu (1991).

DISCUSSION.—The diagnosis is based on data provided by Brock (1882) and Robson (1929) for the holotype of *Octopus pictus* from the ZMUG collection, on a personal examination of the holotype of *O. maculosus* Hoyle, 1883, in the NMW collection, and on examination of additional material from AMS, NMV, QVM, SAM, and TMH collections. The type specimen of *O. pictus* is not extant, having been destroyed during World War II (P. Kuenzer, ZMUG, pers. comm., 1988), but the species is nevertheless recognizable from the type description and figures.

Brock (1882) described *O. pictus* based on a specimen from an uncertain locality. Unaware of Brock's work, Hoyle (1883) described *O. maculosus* from an Australian locality. In a subsequent paper, Hoyle (1886) noted that his *O. maculosus* was the same as Brock's *O. pictus* and relegated *O. maculosus* to junior synonym status. Robson (1929) revised the nomenclature of the taxon and found that the name *O. pictus* was unavailable (because the name *pictus* was preoccupied); he replaced the name with the next oldest available, *O. maculosus* Hoyle, 1883 (now known to be in accordance with ICZN, 1985, Art. 60). Robson (1929) also placed the species in a new genus, *Hapalochlaena*, and hence the name proposed for the species became *H. maculosa* (Hoyle).

*Hapalochlaena maculosa* is a member of the clade of "blue-ringed octopuses" occurring in Australian and adjacent waters. The author presently is reviewing the systematics of this species with reference to other "blue-ringed octopuses" described from subtropical and tropical regions within and outside Australia, such as *H. nierstrazi* (Adam, 1938) (see Toll, 1998, and further details in Stranks, 1988a).

*Hapalochlaena maculosa* can be easily distinguished from other octopod species by a combination of characters that include a broadly ovoid mantle, pointed posteriorly; skin wrinkled, with a pattern of scattered tubercles; a color pattern of dark brown maculae and numerous small (diameter 0.5-2.0 mm), iridescent blue rings on the mantle, head, web, and arms (50-60 rings on mantle); short, subequal arms (2-3 times ML in mature animals); a medium-sized ligula (7%-13% of right arm III length); large eggs (7-9 mm long) arranged in festoons; and 6 to 7 gill lamellae.

#### *Ameloctopus litoralis* Norman, 1992

DIAGNOSIS.—Animals small (to 260 mm TL; to 30 mm ML). Mantle ovoid to greatly elongate (MWI 39-57-80); head narrow (HWI 19-39-66), demarked from mantle by minor constriction; eyes small, not projecting above surface of head. Funnel long, slender, bluntly tapered (FLI 39-47-66); funnel organ consisting of 2 anterior medial pads and 1 posterior

lateral pad on each side. Arms very long (ALI 511-868), slender, tapering to narrow tips. Arm lengths subequal, arm order I = II = III = IV. Arm musculature modified to allow autotomy near 10th sucker of all arms. Suckers raised above arm surface, small (SI 7-10-16), without sucker enlargement. Right arm III of mature males hectocotylyzed, shorter than opposite arm (HAMI 87-201; OAI 21-33); ligula narrow, medium-sized (LLI 6-13-20); ligula groove well marked and shallow, with 10-12 complete transverse ridges; calamus short, pointed (CLI 22-31-38); hectocotylyzed arm with 21-38 suckers. Web very shallow (WDI 4-7-8), web formula A = B = C = D = E. Radula with B<sub>3-4</sub> seriation of rachidian. Ink sac absent. Gill lamellae 5 to 6 on outer demibranch. Mature female with large eggs (capsule ~10 mm long, 3 mm wide), method of egg attachment to substrate unknown. Penis medium-sized (PLI 13-17), without diverticulum; spermatophores short (SpLI 38-41-44), wide (SpWI 5-6-8), with large, coiled sperm reservoir (SpRI 31-37-42).

Integument lacking obvious sculpture, papillae, or patch-and-groove system. In life, color of resting animals pink to brown, with dark brown branchial hearts showing through thin mantle wall. Outer surfaces of all arms marked with evenly spaced maculae in form of purple brown bands. When stimulated, animals become purple black in color and maculae turn darker. Color of animals preserved in ethyl alcohol is beige

background with dark brown maculae as observed in live animals. Ocelli absent.

ORIGINAL DESCRIPTION.—Norman, 1992a:569, figs. 1-5.

TYPE LOCALITY.—Australia, Queensland, Orpheus Island, Pioneer Bay (18°36'S, 146°29'E), 0.1 m.

TYPE.—*Holotype*: NMV F57917, male, 30 mm ML. Specimen in good condition, preserved in ethyl alcohol.

DISTRIBUTION AND BIOLOGY.—Northern Australia, from the Dampier Archipelago, Western Australia, to the southern Great Barrier Reef, Queensland. A species living on inshore, intertidal mud and rubble reef flats (Norman, 1992a).

Biological aspects of *A. litoralis*, including behavior, arm autotomy, and diet, were described by Norman (1992a, 1992b).

DISCUSSION.—The diagnosis is based on personal examination of the holotype of *A. litoralis* in the NMV collection and on the description by Norman (1992a, 1992b). The species is an unusual octopod with elongate arms that readily autotomize and regenerate, and it has no ink sac.

*Ameloctopus litoralis* can be distinguished from other species of octopus by a combination of characters that include an ovoid to elongate mantle; a lack of obvious skin sculpture; small, not prominent eyes; very long, subequal arms (8-10 times ML in mature animals); arm autotomy; small suckers, without enlargement; a medium-sized ligula (6%-20% of right arm III length); large eggs (about 10 mm long); and 5 to 6 gill lamellae.

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# An Overview of Shallow-Water Octopus Biogeography

Janet R. Voight

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## ABSTRACT

Ninety-three species of shallow-water octopuses are recognized in the geographic regions covered by the authors in these volumes. Of these 93 species, 33 are known only from their type locality. Atlantic Ocean and Australian octopuses are the best known.

Octopuses of the Atlantic Ocean form almost discrete north and south faunas, with the northern faunas the better known. Additional research is required to further our understanding of octopuses of the South Atlantic. The Australian octopus fauna forms distinct tropical and warm-temperate components. The many octopuses of the Indo-West Pacific and West Pacific are poorly known. North Pacific octopuses are more diverse than are those of the North Atlantic.

Globally, species with planktonic young tend to have larger areal ranges than do those with benthic young. Data currently available indicate that the octopuses of temperate Australia are significantly more likely than those of either the East or West Atlantic to produce benthic young. Octopus species diversity and endemism are consistent with established vicariance events that have contributed to allopatric speciation. More ancient events, such as the closure of the Tethys Sea, may relate to formation of what are now closely related, but disjunct species.

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## Introduction

Uneven and inadequate taxonomic treatments of shallow-water octopuses have limited our knowledge of octopus biogeography. Some reports have cited the presence of familiar species in areas far removed (sometimes oceans away) from their type localities; others have described new species based on what appear to be trivial characters. Without a consistent taxonomic basis for the world's octopuses, we have been unable to assess global patterns of shallow-water octopus

diversity. Because of this limited perspective, our understanding of octopus history and evolution has suffered.

This paper summarizes our knowledge of shallow-water octopus biogeography using, in general, only the very conservative estimates of species ranges reported in this volume (Mangold, 1998; Stranks, 1998; Toll, 1998; Toll and Voss, 1998; Voss and Toll, 1998). In addition, I discuss distributions in light of both reproductive mode and historical patterns derived from earth history. I avoid imposing schemes of biogeographic provinces on the data; rather, I attempt to find pattern directly from the data.

My goals are to determine whether the available data show patterns and to clearly identify those geographic regions most in need of further research. Because the shallow-water octopuses form a comparatively small, but nearly ubiquitous, group they could be especially important to our understanding the evolution and diversity of the marine near-shore fauna.

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## METHODS

Because the Octopodinae of Voss (1988) appears to be paraphyletic (Voight, 1993a, 1993b), I treat herein the shallow-water octopuses of the world, including species of the genus *Eledone*. Some species of octopuses with distributions to 800 m (e.g., *Pteroctopus*, *Scaevurgus*) also are included; however, as our knowledge of these species differs among areas far more than it does for shallow-water species,

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discussion of their biogeography is precluded. As much as possible, species distributions were tallied from the contributions in this volume (Mangold, 1998; Stranks, 1998; Toll, 1998; Toll and Voss, 1998; Voss and Toll, 1998). These papers are not individually cited throughout this work, rather the reader is referred to the contribution appropriate to the geographic area under discussion for more detailed information and for discussions of taxonomy. Distributional data for species of *Eledone* were taken from species descriptions and from the literature referred to in the tables. I largely excluded from this treatment species from areas not explicitly included in this volume (the East Pacific Ocean, New Zealand) rather than rely on available literature not subjected to critical review.

I attempt to assess world-wide latitudinal patterns of octopus diversity in addition to describing endemism by area. I also consider the associations of reproductive mode with latitudinal distribution and, anecdotally, with areal range.

I treated the production of either planktonic or benthic young as alternate reproductive modes. The type of young typically correlates with egg size, a presumed species-specific character. Although large eggs typically produce benthic young and small eggs typically produce planktonic young, intermediate-sized eggs produce either planktonic or benthic young (Hochberg et al., 1992). To eliminate ambiguity created by intermediate egg lengths and perhaps by immature ovarian eggs, I considered only species for which the hatchling type is reported either by the authors cited above or by Norman (1993a, 1993b). To test whether reproductive mode is associated with latitude, I averaged the extreme latitudes reported for each of the 28 species with known hatchling types and compared the groups by rank sum test ( $r$ ). To test whether adult size is associated with reproductive mode, I compared the maximum reported mantle length for each species by rank sum test. I also tested for correlations between egg length and both body size and latitude for all species with egg lengths reported, excluding the five species known only from their type localities. To test whether reproductive modes differ in frequency among the areas considered, I compared their frequencies with a G-test (log-likelihood ratio test).

I briefly consider the relationship between vicariance events that have affected marine biogeography and octopus distribution and diversity. Congruence of shallow-water octopus distributions with historical events and predictions would offer both a minimal age for cladogenesis and support for null hypotheses for the radiation of the group.

## Results and Discussion

### OCEAN-BASIN PATTERNS

Shallow-water octopuses occur from 60°N (*Eledone cirrhosa* (Lamarck) in the eastern Atlantic Ocean; *Octopus dofleini* (Wülker), *O. ochotensis* (Sasaki) in the Pacific Ocean) to 50°S (*O. lobensis* Castellanos and Menni in the southwestern

Atlantic Ocean). Shallow-water octopuses appear to be more diverse in the North Pacific Ocean than in the North Atlantic Ocean; few shallow-water octopuses have been recorded north of 35°N in the western Atlantic Ocean. Unfortunately, without comparable treatments of the octopus fauna from cold-temperate areas of New Zealand and the East Pacific Ocean, statements about latitudinal diversity gradients can be made only about the Atlantic and West Pacific faunas.

One might predict that the number of species known from an area would accurately reflect our knowledge of the fauna; however, shallow-water octopuses violate this prediction. Forty-one West Pacific species and three subspecies are considered valid, yet of these, one-half are known only from the type locality. In the Indian Ocean, reported distributions of the 12 valid species merely catalog type localities rather than provide the data necessary to understand the biogeography of the area or of the species. The newly reported diversity of octopuses from the Great Barrier Reef (Norman 1993a, 1993b) suggests other Indo-West Pacific areas could also support many undiscovered species. Unfortunately, our meager knowledge of octopuses from the Indo-West Pacific and African coasts prohibits diversity estimates.

ATLANTIC OCEAN.—The cephalopod fauna of the Atlantic Ocean, especially the North Atlantic Ocean, is among the best known of the world. Even distributions of comparatively deep-water taxa (e.g., *Scaevurgus*, *Pteroctopus*) appear to be well established. Our knowledge of the eastern Atlantic fauna can be attributed to generations of European workers; of the seven valid species of *Octopus* in the eastern Atlantic Ocean, six were described before 1850. Our knowledge of the western Atlantic fauna is due largely to Gil Voss, who described four of the eight West Atlantic species discovered in this century and who recorded four eastern species in the West Atlantic Ocean. That one investigator added so much to our knowledge of this area is a tribute to his work and demonstrates how little we know of areas that have yet to be studied over several years.

The distributions of the 21 species of octopuses and nine species of *Eledone* recognized from shallow waters of the Atlantic Ocean are summarized in Tables 1 and 2. Six species have been considered to have ampho-Atlantic distributions, although whether these disjunct populations have diverged is yet to be tested (Voight, 1994). The species assemblages of both the East and West Atlantic coasts can be divided into distinct northern and southern components.

In the western Atlantic Ocean (Table 1), five species of shallow-water octopuses range from the southern United States to northern Brazil; four others appear to be restricted to more tropical waters. Three species have deeper-water distributions; the ranges of two are uncertain. Southwest Atlantic species appear to be endemic to South America.

Most octopus species of the eastern Atlantic Ocean also form distinct north-south assemblages (Table 2), although *Octopus vulgaris* Cuvier ranges throughout the eastern Atlantic Ocean. Of the nine Northeast Atlantic species, including three



TABLE 1.—Egg length and distribution of shallow-water octopuses of the western Atlantic Ocean (\* = amphi-Atlantic distribution).

Taxon	Egg length (mm)	Distribution
Northwest Atlantic species		
<i>Octopus briareus</i>	12	U.S. (South Florida) to northern Brazil
* <i>Octopus burryi</i>	2.5	U.S. (North Carolina) to northern Brazil
<i>Octopus carolinensis</i>	3	U.S. (North Carolina) to Caribbean Sea (183–260 m)
* <i>Macrotritopus defilippi</i>	2.1	Bahamas to northern Brazil
<i>Octopus filosus</i>	1.7	U.S. (Florida) to northern Brazil
<i>Octopus joubini</i>	3.5	U.S. (Georgia) to Central Caribbean Sea
* <i>Callistoctopus macropus</i>	2.5	U.S. (Florida) to northern Brazil
<i>Octopus maya</i>	11	Mexico, Yucatan to Vera Cruz
<i>Euaxoctopus pillsburyae</i>	?	Surinam and northern South America
* <i>Pteroctopus tetracirrhus</i>	7	U.S. (North Carolina) to Uruguay (100–720 m)
* <i>Scaevargus unicolorrhus</i>	2.5	U.S. (Georgia) to northern Brazil (100–500 m)
* <i>Octopus vulgaris</i>	2.2	distribution uncertain
<i>Octopus</i> sp. X†	7	Gulf of Mexico; distribution uncertain
<i>Octopus zonatus</i>	6.1	Venezuela to Gulf of Darien
Southwest Atlantic species		
<i>Eledone gaucha</i>	8	30°–34°S, 56–140 m (Haimovici, 1988)
<i>Octopus lobensis</i>	9	South Brazil to South Central Argentina(?)
<i>Eledone massyae</i>	?	23°–43°S, Trindade Island, Brazil (Voss, 1964)
<i>Octopus tehuelchus</i>	?	distribution uncertain

† *Octopus* sp. X could be *Octopus mercatoris*; see Forsythe and Toll (1991).

TABLE 2.—Egg length and distribution of eastern Atlantic Ocean shallow-water octopuses (\* = amphi-Atlantic species; MS = Mediterranean Sea; TLO = known from type locality only).

Taxon	Egg length (mm)	Distribution
Northeast Atlantic species		
* <i>Octopus burryi</i>	2.5	Cape Verde Islands (additional unconfirmed reports)
<i>Eledone cirrhosa</i>	7.5	MS, Norway, Iceland to Straits of Gibraltar
* <i>Macrotritopus defilippi</i>	2.1	MS, Morocco, Angola, Cape Verde Islands
* <i>Callistoctopus macropus</i>	2.5	MS, Dakar, St. Helena
<i>Eledone moschata</i>	14	MS
<i>Octopus salutii</i>	5.3	MS, Bay of Biscay (150–350 m)
* <i>Pteroctopus tetracirrhus</i>	7	MS, western North Africa just south of 0°. Azores, Cape Verde Islands (100–720 m)
* <i>Scaevargus unicolorrhus</i>	2.5	MS, southwestern Portugal (100–500 m)
*? <i>Octopus vulgaris</i>	2.2	MS, southern England, Southeast Africa, Canary Islands and Azores
Oceanic island species		
<i>Octopus occidentalis</i>	?	TLO (Ascension Islands)
<i>Octopus sanctaehelenae</i>	?	TLO (St. Helena Island)
<i>Octopus verrucosus</i>	?	TLO (Inaccessible Island, Tristan da Cunha Islands)
Southeast Atlantic species		
<i>Eledone caparti</i>	?	5°–8°37'S, 11°21'–13°12'E (60–170 m) (Adam, 1950)
<i>Eledone carlgreni</i>	?	TLO (Sea Point, Cape Peninsula, South Africa)
<i>Octopus magnificus</i>	?	South Africa; Lüderitz to Port Elizabeth (2–560 m)
<i>Eledone nigra</i>	?	TLO? (Angra Pequena, German Southwest Africa)
<i>Eledone schultzei</i>	?	TLO (Angra Pequena, German Southwest Africa)
<i>Eledone thysanophora</i>	?	TLO (Bantry Bay, South Africa)

deeper-water forms, all but *O. burryi* Voss occur in the Mediterranean Sea. Despite its amphi-Atlantic distribution, *Scaevargus unicolorrhus* Féruccac and Orbigny in the East

Atlantic occurs only in the Mediterranean Sea and its outflow along the Portuguese coast. In contrast, *Octopus salutii* Verany ranges as far north as the Bay of Biscay but occurs only in the

eastern Atlantic Ocean. Two species, *Callistoctopus macropus* (Risso) and *Macrotritopus defilippi* Verany, are restricted to the Mediterranean Sea and the coast of northwest Africa.

Taxonomic problems concerning the Atlantic Ocean fauna remain, especially in the South Atlantic assemblages. The abundance of named Southeast Atlantic species of the genus *Eledone* must be addressed through additional taxonomic research, as must the three species suspected as being endemic to oceanic Atlantic islands (Table 2). Recent studies of South American species of *Eledone* (Haimovici, 1988; Levy et al., 1988; Perez et al., 1990) have greatly increased our knowledge of the genus. The North Atlantic Ocean is not free of taxonomic problems. The name *O. joubini* Robson refers to two distinct species (Forsythe and Toll, 1991), and the distribution and systematic status of western Atlantic *O. vulgaris* are uncertain.

Three of nine species, *Octopus salutii*, *Eledone moschata* (Lamarck), and *E. caparti* Adam, are endemic to the tropical East Atlantic Ocean and Mediterranean Sea. In comparison, 12 of 18 species are endemic to the West Atlantic Ocean (Tables 1, 2). The high level of endemism and diversity of West Atlantic octopuses could be due to the history of the area rather than to habitat differences. The uplift of the Central American isthmus and resultant isolation of unique American tropical octopuses (Voight, 1988) could have increased endemism in the western Atlantic Ocean compared to the eastern Atlantic Ocean.

INDO-WEST PACIFIC, INCLUDING THE GREAT BARRIER REEF.—Our knowledge of the octopuses from the Indo-West Pacific Ocean is inadequate for biogeographic discussions. Species that range from the east coast of Africa to Hawaii (Table 3) document that this expanse of tropical ocean could act as a single geographic unit for octopuses; however, only a few species (e.g., *Octopus cyanea* Gray, *Cistopus indicus* Férussac and Orbigny) are currently thought to have such vast ranges (Table 3). Even for these species, additional study is required to assess whether each alleged species is distinct or whether the name has been applied to similar, but distinct, taxa.

For example, at least three species could exist under the name *O. hardwickei* Gray, a species that had been suspected to occur throughout the Indo-West Pacific. Two of these species that are yet to be morphologically distinguished appear to be disjunct, split by the range of the third species, which can be readily distinguished by spermatophore morphology (Toll and Voss, 1998).

Some species groups have been suggested as being uniquely Indo-West Pacific. Norman (1993b) suggested that the region contains a unique clade of ocellated octopuses (*O. mototi* Norman, *O. exannulatus* Norman, *O. polyzenia* Gray). Longitudinal stripes on the mantle, small body size, comparatively few suckers on short arms, and moderate-sized ligulae are characters he cited as separating this group from the octopuses he suspects evolved ocelli in convergence. Toll and Voss (1998) independently recognized a similar group, unified by a shallow web-sector A. The diverse species of *Hapalochlaena* in the Indo-West Pacific initially suggest a similar distribution, but the generic range includes temperate zones of Australia, indicating that its history extends beyond the Indo-West Pacific.

INDIAN OCEAN.—The information currently available for the octopuses of the Indian Ocean is insufficient to estimate levels of diversity or of endemism. Of the 12 species currently recognized as valid described from this ocean and the Red Sea, only one (*O. horridus* Orbigny) has been documented to occur beyond its type locality (Tables 3, 4). Additional taxonomic study is required to assess whether these species are endemic to the Indian Ocean, to determine whether the area harbors additional, undiscovered species, and whether octopuses currently known only from other areas range into the Indian Ocean.

THE GREAT BARRIER REEF.—This shallow-water area occupies a small proportion of the total Indo-West Pacific, yet it is the type locality for 11 octopus species, including the wide-ranging species *O. cyanea*. Recent species descriptions from the Great Barrier Reef (Norman 1993a, 1993b) suggest

TABLE 3.—Egg length and distribution of widely ranging, shallow-water octopuses of the Indian and Pacific oceans; type locality indicated (AU = Australia; WP = West Pacific; IO = Indian Ocean).

Taxon	Area	Egg length (mm)	Distribution
<i>Octopus cyanea</i>	AU	2.7	Africa, Red Sea, Bay of Bengal, Ceylon, northern Australia to southern Great Barrier Reef, Japan, Hawaii
<i>Octopus dofleini dofleini</i>	WP	7	Subarctic to temperate west Pacific
<i>Octopus hardwickei</i>	WP	?	Eastern Indian Ocean (maybe southwest Pacific)
<i>Octopus horridus</i>	IO	?	Red Sea, Indian Ocean to west Pacific?, South Africa?
<i>Pteroctopus hoylei</i>	WP	?	Hawaii, Japan (although reported in Persian Gulf, Arabian Sea, Ceylon, these records suspect)
<i>Cistopus indicus</i>	WP	4.5	Philippines, China, India, Pakistan, East Africa?
<i>Hapalochlaena lunulata</i>	WP	3	Great Barrier Reef, Australia through East Indies
<i>Callistoctopus ornatus</i>	WP	?	Hawaiian and Marshall islands (although reported in E Africa, Japan, China, these records suspect)
<i>Scaevargus patagiatus</i>	WP	?	Hawaii, Japan

TABLE 4.—Distribution and egg length of Indo-West Pacific shallow-water octopuses. Indian ocean species are ordered east to west. (TLO = known from type locality only.)

Taxon	Egg length (mm)	Distribution
Indian Ocean species		
Red Sea		
<i>Octopus nanus</i>	?	TLO (Cundabilu)
<i>Octopus robsoni</i>	?	TLO (Gulf of Suez)
Arabian Sea		
<i>Octopus varunae</i>	2	TLO (Arabian Sea)
Southern India		
<i>Octopus arborescens</i>	?	TLO (Gulf of Manaar)
<i>Octopus winckworthi</i>	?	TLO (Tuticorin, South India)
<i>Pteroctopus keralensis</i>	?	TLO (9°59'N, 75°36'E)
Maldive Islands		
<i>Octopus gardineri</i>	?	TLO (Male Atoll)
Western Indian Ocean		
<i>Octopus filamentosus</i>	?	TLO (Île de France)
Andaman Islands		
<i>Hapalochlaena nierstrazi</i>	2.4	TLO (Aves Island)
<i>Octopus microphthalamus</i>	10	TLO (Port Blair)
<i>Octopus prashadi</i>	?	TLO ("Indian Seas")
Great Barrier Reef species		
<i>Ameloctopus litoralis</i>	10	Dampier Archipelago to southern Great Barrier Reef
<i>Octopus polyzenia</i>	8	Dampier Archipelago to central Queensland
<i>Octopus tenebricus</i>	?	TLO (Bowen, Queensland)
Tropical West Pacific species		
<i>Octopus favonius</i>	?	Singapore
<i>Octopus guangdongensis</i>	?	TLO (off Quandong Province, China)
<i>Octopus kermadecensis</i>	?	TLO (Kermadec Islands)
<i>Octopus nanhaiensis</i>	?	TLO (Quandong Province, China)
<i>Octopus oliveri</i>	?	Kermadec Islands (maybe to Okinawa)
<i>Octopus striolatus</i>	?	Quandong Province, China
Pacific oceanic island species		
<i>Octopus bocki</i>	1	TLO (Fiji)
<i>Octopus rapamui</i>	?	TLO (Easter Island)
<i>Octopus tonganus</i>	1.2	TLO (Tonga)
<i>Octopus vitiensis</i>	?	TLO (Fiji)
<i>Octopus wolfi</i>	?	TLO (Society Islands, Tahiti)

that these octopuses are highly diverse, but, unfortunately, these reports also document the inadequacy of our knowledge of the octopuses of adjacent areas.

**TROPICAL PACIFIC AND OCEANIC PACIFIC ISLANDS.**—Fifteen of the species discussed by Toll and Voss (1998) from the western Pacific Ocean occur in tropical latitudes. Six of these species, *Octopus hardwickei*, *Pteroctopus hoylei* (Berry), *Cistopus indicus*, *Hapalochlaena lunulata* (Quoy and Gaimard), *Callistoctopus ornatus* (Gould), and *Scaergus patagiatus* Berry, range widely throughout the Indo-West Pacific area (Table 3). Five tropical West Pacific species are known only from their type localities (Table 4); *O. oliveri* (Berry), described from the Kermadec Islands (included herein in a broad definition of the Indo-West Pacific), could range as far north as Okinawa (Okutani et al., 1987).

The few species recorded from Pacific islands (Tables 3, 4) offer an insufficient basis for biogeographical discussion. The

13 taxa of octopodid paralarvae collected in Hawaii (Young et al., 1989) suggest that many unknown species of octopuses occur in the oceanic Pacific. Both additional collections and identification of any available specimens currently in museums are required to further our knowledge of this area.

**TEMPERATE AUSTRALIA.**—With five new species described and two species redescribed in the last five years, the octopuses of subtropical and temperate Australia offer a sound basis for biogeographic studies. This data set reveals that regardless of whether the species occurs on soft sediments or on reef or rubble areas, the endpoints of species ranges tend to coincide (Table 5). This coincidence suggests that physical factors limit species distributions within fairly narrow regions.

The endpoints, the Great Australian Bight and southern New South Wales, roughly correspond to the southern extent of warm temperate (Knox, 1980) or subtropical (Stranks, 1998) water. Two species that range from southern Queensland to

TABLE 5.—Distribution, geographic range, and egg length of shallow-water octopuses from subtropical and temperate Australian waters; unless otherwise noted, species occur in upper 20 m. (GAB = Great Australian Bight; NSW = New South Wales; TLO = known from type locality only.)

Taxon	Egg length (mm)	Distribution
GAB—southern NSW species		
<i>Octopus berrima</i>	12	Bass Strait and Tasmania
<i>Octopus bunurong</i>	9	Bass Strait and northern Tasmania
<i>Octopus kaurna</i>	10	eastern Australia, including Bass Strait and northern Tasmania
<i>Hapalochlaena maculosa</i>	8	south Western Australia to eastern Victoria, including Bass Strait
<i>Eledone palari</i>	15	GAB, east and northwest Australia (110–620 m) (Lu and Stranks, 1991)
<i>Octopus superciliosus</i>	9.5	Bass Strait
<i>Octopus warringa</i>	2.5	eastern Victoria, Bass Strait, Tasmania, New Zealand, Stewart Island
GAB—central NSW, Bass Strait, and Tasmania species		
<i>Octopus maorum</i>	6.5	also to New Zealand; Chatham, Stewart, Auckland, and Campbell islands
<i>Octopus pallidus</i>	12	GAB—central NSW, Bass Strait, Tasmania
Southern Queensland—southern NSW species		
<i>Octopus australis</i>	10	southern Queensland—southern NSW
<i>Hapalochlaena fasciata</i>	7.5	could also occur more widely
<i>Octopus tetricus</i>	?	TLO (near Sydney, NSW)

southern New South Wales, *Octopus australis* Hoyle and *O. tetricus* Gould, are apparently restricted to warmer water (Knox, 1980). The southern Australian octopuses cross traditional zoogeographic provincial boundaries, as do many other marine taxa (Knox, 1963; Briggs, 1974). The distribution and diversity of the octopuses are consistent with those of other marine invertebrates (Dartnall, 1974; Knox, 1980). That closely similar species are, or are nearly, disjunct on the eastern and southern coasts of Australia has been taken as evidence of previous northerly shifts in the boundary between the warm- and cold-water masses (Knox, 1980). These shifts, coupled with the emergence of the Bass Strait during low stands of sea level, which has been suggested to amplify temperature differences (Dartnall, 1974), could have forced warm-water marine life northward, bifurcating their distributions at the southernmost tip of Australia. Subsequent southward shifts of the boundary could have allowed these populations to reinvade after periods of isolation. These periods of isolation could have been associated with speciation (Dartnall, 1974; Knox, 1980), a scenario supported by the available octopod data.

Octopus diversity is lower in northern Tasmania than it is in southern Australia, and it is still lower in southern Tasmania. Decreasing diversity with increasing latitude has been reported for other Tasmanian marine animals and could relate to colder temperatures (Dartnall, 1974).

Species distributions from temperate Australia also demonstrate the effect of reproductive mode on areal range. Both

*Octopus maorum* Hutton and *O. warringa* Stanks range to New Zealand; *O. maorum* also occurs on associated oceanic islands (Table 5). That *O. maorum* extends over a greater depth range than does *O. warringa* (0–549 m compared with 0–144 m) could be associated with its occurrence in cold-temperate waters.

Of the 10 temperate Australian species, only these two are known both to have planktonic young and to range beyond Australia. Species with benthic young range continuously along the Australian coast and could extend to Tasmania, an island connected to the continent by a shallow shelf that was probably exposed in recent history. Although the octopuses of New Zealand are not explicitly treated herein, in addition to these two species, Stranks (1998) reported *Robsonella huttoni* Benham to exist as a distinct New Zealand species.

WEST PACIFIC OCEAN.—Lingering taxonomic confusion and poor locality information prohibit discussion of the biogeographic distribution of the 41 species and three subspecies retained as valid from the West Pacific Ocean. The apparent sympatry of subspecies within both *Octopus minor* (Sasaki) and *O. fangsiao* Férussac and Orbigny suggests that they are artificial divisions; therefore, they will not be treated herein. Of the 41 valid species, 17 are from tropical areas and are discussed as part of the Indo-West Pacific zone. Of the remaining 24 valid species, 12 are known from their type localities only and 18 species are restricted to Japanese waters (Table 6).

TABLE 6.—Egg length and distribution of nontropical West Pacific Ocean shallow-water octopuses (ordered north to south in distribution; \* = restricted to Japanese waters; TLO = known from type locality only). (See Toll and Voss, 1998.)

Taxon	Egg length (mm)	Distribution
<i>Octopus ochotensis</i>	9	Sea of Okhotsk
<i>O. minor minor</i>	?	Sakhalin Peninsula through Japan; Chinese coast to Korea?
* <i>O. minor typicus</i>	8	numerous localities around Japan
* <i>O. conispadiceus</i>	28.0	northeastern Japan
<i>O. longispadiceus</i>	?	Japan: Tsugaru Strait; Honshu, Miyagi Prefecture; east Kyushu; to Cape Clonard, Korea?
* <i>O. fangsiao etchanus</i>	?	Japan: Honshu, Seto Sea, Toyama Bay; Kyushu, Nagasaki
* <i>O. fangsiao typicus</i>	10	Pacific coast of Japan; southern Sea of Japan
* <i>O. fujitai</i>	?	Japan: Honshu, Sagami Sea, Toyama Bay
* <i>O. yendoii</i>	17.0	Sea of Japan
* <i>O. sasakii</i>	10	Japan: south Honshu; west Shikoku; Kyushu; west Kyushu
* <i>O. ovulum</i>	3	Japan: Honshu, Tokyo; Kyushu, Nagasaki
* <i>O. globosus</i>	9	Japan: Kyushu, Nagasaki
* <i>O. kagoshimensis</i>	?	Japan: Kyushu, Kagoshima Prefecture (other records uncertain)
* <i>O. spinosus</i>	?	TLO (Japan, Tsugaru Strait)
* <i>O. tsugarensis</i>	?	TLO (Japan, Tsugaru Strait)
* <i>O. alatus</i>	?	TLO (Japan, Bungo Channel (799 m))
* <i>O. mutilans</i>	?	TLO (Japan, Hiroshima Prefecture, Seto Sea off Onomichi)
* <i>O. brocki</i>	?	TLO (Japan, Kyushu; Honshu, Tokyo, Kagoshima)
* <i>O. hattai</i>	?	TLO (Japan, Chiba Prefecture, Kominato)
* <i>O. hongkongensis</i>	8	TLO (Sagami Sea (624 m))
* <i>O. minor pardalis</i>	?	TLO (Japan, Chiba Prefecture)
* <i>Pteroctopus eurycephala</i>	?	TLO (Japan, Honshu, Enshu fishmarket)
* <i>O. parvus</i>	?	TLO (Japan, southern Kyushu, Shimizu harbor (uncertain))
<i>O. luteus</i>	?	TLO (Formosa Strait, P'eng-hu Lieh-tao (Pescadores Islands))
<i>O. oshimai</i>	>6	TLO (Formosa fishmarket)
* <i>O. areolatus</i>	?	TLO (Japan)

Japan's latitudinal position, from subtropical to cold-temperate waters, predicts that its marine fauna will be highly diverse; whether the diversity of octopuses (Table 6) is consistent with this prediction is open to question. Most of the 18 Japanese species are concentrated in warm-temperate waters that extend south from Tsugaru Strait along the coasts of Honshu and Kyushu. One might predict, however, that these species would occur more evenly across the diverse temperatures that Japanese waters offer. Whether the reported diversity represents the most complete knowledge of a local fauna available, due to a traditional reliance on marine resources for food and to the availability of taxonomic surveys (e.g., Okutani et al., 1987), or is a taxonomic artifact must be addressed by additional research.

Of the six non-Japanese Northwest Pacific species, *Octopus minor* and *O. longispadiceus* (Sasaki) range widely, *O. dofleini* (Table 3) also has a very large range, *O. luteus* (Sasaki) and *O. oshimai* (Sasaki) are known only from their type localities, and

*O. ochotensis* appears to be restricted to high northern latitudes (Table 6).

**NORTH PACIFIC OCEAN.**—The North Pacific has traditionally been characterized by high molluscan diversity (Vermeij, 1989), which has been noted among the octopods (Ekman, 1953). Few species, however, are reported north of the Japanese island of Honshu. Whether the Northwest Pacific octopuses represent relics, as Vermeij (1989) discussed for shelled mollusks, is unknown, as neither fossils nor phylogenetic relationships are available for the octopuses. The presence in this area of a species group (*O. longispadiceus*, *O. conispadiceus* (Sasaki), *O. tsugarensis* (Sasaki), *O. hongkongensis* Hoyle) unified by a long, conical ligula and the presence of comparatively diverse, temperate octopuses lends support to this hypothesis.

Shallow-water octopuses are more diverse in the North Pacific than in the North Atlantic (contrast Table 6 with Table 1), as are shelled mollusks (Vermeij, 1989). The Northeast

Pacific octopus fauna remains poorly known, although *O. dofleini* has been reported from the Gulf of Alaska to the warm temperate coast of California, United States, in deeper water. Whether any octopus species ranges continuously from Japan to North America seems unlikely (Pickford, 1964), as intervening areas of low temperatures could form a thermal barrier in the northernmost Pacific Ocean.

**EAST PACIFIC OCEAN.**—Comparatively few species of shallow-water octopuses, such as *O. dofleini* and *O. rubescens* Berry, are thought to occur along the cold-temperate northeast Pacific coast, although deep-water octopuses appear to be diverse (Voss and Percy, 1990). The narrow, warm-temperate coast of southern California supports the endemics *Octopus bimaculatus* Verrill, *O. bimaculoides* Pickford and McConnaughey, and *O. micropyrsus* Berry (Hochberg and Fields, 1980).

A critical nomenclatural review of the shallow-water octopus species from throughout the East Pacific has yet to be completed. Pacific octopuses from South America are virtually unstudied.

The California warm-temperate octopus species could be closely related to species in the northern Gulf of California (Voight, 1988). Their apparently disjunct distributions may relate to Pleistocene shifts in isotherms that created relictual populations (Voight, 1991). Whether eastern Pacific species range around the southern tip of South America to enter the Atlantic Ocean is unknown.

#### PATTERNS OF AREAL RANGES

To determine whether the biological characters of reproductive mode and adult size affect the above distributional patterns requires adopting a more global perspective. The available data for the 93 shallow-water octopus species considered in this paper report egg length for 48 species but report hatchling type for only 28 species. Sixteen species are reported to have planktonic young; 12 species have benthic young. Among these few species, the average latitude of groups with opposing reproductive modes does not significantly differ ( $p > 0.4$ ). Because only nine of these 28 species have an estimated average latitude of at least  $30^\circ$ , these data could be insufficient to assess whether reproductive mode changes toward the poles. Egg length, regardless of hatchling type, is not correlated with latitude ( $n = 43$ ;  $r = 0.2$ ;  $p > 0.2$ ). Species with planktonic young are significantly larger than are species with benthic young ( $p < 0.005$ ), but adult size is not significantly correlated with egg length ( $r = 0.153$ ;  $p > 0.2$ ).

Reproductive mode does appear, however, to affect the areal range of a species. All species with a wide geographic range, such as on both east and west coasts of the Atlantic Ocean (Tables 1, 2), throughout the Indo-West Pacific (Table 3), or from Australia to New Zealand and adjacent oceanic islands (Table 5), have planktonic young. This reproductive mode does not necessarily ensure that a species has a large areal range (see,

for instance, *O. salutii*, Table 2), but species with benthic young do not appear to range across areas of open ocean. With reproductive mode and geographic range unknown for most species, we cannot fully assess how the two are associated.

More data on species ranges and reproductive modes are required to address the dispersal capacity of planktonic young. This question also could have important implications for fisheries biology. If species with planktonic young were able to recolonize a depleted area, populations could be able to sustain a fishery with a margin of safety. In contrast, populations with benthic young could be recolonized only very rarely, making them vulnerable to overfishing.

The distribution of species with alternative reproductive modes differs significantly among the areas considered ( $G = 5.24$ ;  $p < 0.025$ ). Of the nine East Atlantic species for which egg lengths are known (Table 2), only *E. moschata* has benthic young. In contrast, of the six temperate Australian species with a known reproductive mode, five have benthic young. Three (*Octopus* sp. X, *O. maya* Voss and Solís Ramirez, *O. briareus* Robson) of the 12 species restricted to the western Atlantic Ocean (Table 1) have benthic young. The dominance of species with benthic young in temperate Australia could be due to a sampling effect. Because eggs that produce benthic young are large, they develop over a longer period than do small eggs that produce planktonic young. It could be that clutches of large eggs are more likely to be discovered than are clutches of small eggs. If so, as reproductive modes of more species from temperate Australia are discovered, this difference could disappear. The apparent rarity of species with benthic young in the East Atlantic seems unlikely to change with additional discoveries. The apparent deficit in this area is not unique to octopuses; similar low proportions of species with benthic young have been noted among opisthobranchs (Clark and Goetzfried, 1978). Broader geographic and taxonomic comparisons are necessary to determine if the eastern Atlantic is indeed uniquely depauperate in species with benthic young. This deficit, if supported by future research, would suggest that selection has acted differently in the eastern Atlantic than in other areas.

#### EARTH HISTORY AND OCTOPUS DIVERSITY

All areas of high octopus diversity and endemism have been postulated to have had geologically complex histories, or to have been affected by climatic events associated with increasing the chances of allopatric speciation. Such areas include the western tropical Atlantic, where the interruption of the American Seaway is likely to be associated with the many endemic species (Voight, 1988). Pleistocene climatic events, such as shifts in isotherm positions, also are thought to have shifted the distribution of marine invertebrates. Areas where this has been postulated include the temperate regions of Australia, discussed above, the warm temperate zone of the East Pacific (Voight, 1991), and the North Pacific Ocean

(Vermeij, 1989). The observed congruence between species diversity and the opportunity for allopatric speciation suggests that vicariance events have been important in octopus speciation.

Higher-order divergence could be due to much more ancient events. Large-scale distributional patterns appear to be congruent with geologic events associated with plate tectonics. Ancient circumglobal oceanic circulation occurred prior to the closure of the Tethys Sea by the late Paleogene (30–40 MYBP; Cloud, 1988). Lineages that once had nearly continuous distributions may be currently represented by isolated but closely related species.

Table 7 reports five species groups and the characters that I suggest unite each group as a result of having shared a common ancestor millions of years ago. The existence of five species groups, defined by what appear to be uniquely derived characters, that share circumtropical distributions suggests that their ancestors were differentiated prior to 30–40 MYBP. Despite Norman's (1993b) hypothesis that the ocellated octopuses (Table 7, Group 5) are diphyletic, I argue that they are monophyletic, with longitudinal stripes and small body size defining a geographically cohesive group within the clade. The additional characters Norman (1993b) cited, few suckers on short arms and moderate-length ligulae, could be size related and provide only circular support for his hypothesis. The hypothesis that these species groups are monophyletic must, of course, be subjected to analyses designed to test their monophyly. If it is supported, a new minimum age will have been established for the origin of lineages among shallow-water octopuses.

### Conclusions

Biogeographic analysis requires good alpha-level taxonomy, species with well-known range limits, and, ideally, a confirmed phylogeny. What we know about shallow-water octopuses offers only tantalizing glimpses of these data.

The shallow-water octopus species and subspecies recognized to be valid by authors represented in these volumes number 44 in the West Pacific (Toll and Voss, 1998), 15 in Australia (Stranks, 1998), 12 in the Indian Ocean (Toll, 1998), 14 in the western Atlantic (Voss and Toll, 1998), and eight in the eastern Atlantic (Mangold, 1998). Of these 93 species, 33 are known only from their type locality.

The octopuses of the Atlantic Ocean and Australia are best known. In both regions, endpoints of species ranges tend to coincide, indicating that physical factors limit species distributions. Patterns of species diversity and distribution are congruent with hypothesized vicariance events. To test whether these patterns are consistent globally, our current knowledge of octopuses from the Indian and Pacific oceans must be expanded.

Based on the limited data available, whether a species produces planktonic or benthic young appears to be independ-

TABLE 7.—Circumtropical shallow-water octopus species groups that could reflect ancient vicariance events and the characters that are suggested to unite them. Groups 3 and 4 could pertain to *Callistoctopus* and *Macrotritopus*, pending explicit definition of these names (Toll, 1991).

Group 1. <i>Scaevurgus</i> species.
East and West Atlantic: <i>S. unicolor</i>
East Pacific: none
West Pacific: <i>S. patagiatus</i>
Indian Ocean: <i>S. patagiatus</i>
Group 2. <i>Pteroctopus</i> species.
East and West Atlantic: <i>P. tetracirrhus</i>
East Pacific: none
West Pacific: <i>P. hoylei</i> ; <i>P. eurycephala</i>
Indian Ocean: <i>P. keralensis</i>
Group 3. First arms longest, rachidian multicuspids, red and white coloration (possibly <i>Callistoctopus</i> ) (nominal taxa include <i>Callistoctopus</i> and <i>Octopus</i> species).
East and West Atlantic: <i>C. macropus</i>
East Pacific: none
West Pacific: <i>O. alatus</i> ; <i>O. hattai</i> ; <i>O. luteus</i> ; <i>O. minor</i> ; <i>O. nanhaiensis</i> ; <i>C. ornatus</i> ; <i>O. sasakii</i>
Indian Ocean: <i>C. ornatus</i> (?)
Great Barrier Reef: <i>C. ornatus</i> ; <i>O. aspirosomatis</i> ; <i>O. graptus</i> ; <i>O. dierythraeus</i> ; <i>O. alpheus</i>
Group 4. Body form distinctive, with elongate mantle and long, slender arms (possibly <i>Macrotritopus</i> ) (nominal taxa include <i>Amelooctopus</i> , <i>Euaxoctopus</i> , <i>Macrotritopus</i> , and <i>Octopus</i> species).
East and West Atlantic: <i>M. defilippi</i>
West Atlantic: <i>E. pillsburyae</i>
East Pacific: <i>E. panamensis</i>
West Pacific: <i>O. mutilans</i>
Indian Ocean: <i>O. filamentosus</i> ; <i>O. horridus</i>
Great Barrier Reef: <i>A. litoralis</i> (similar specimens reported from Christmas Island, and New Guinea)
Group 5. Ocellated species unified by patch and groove skin pattern, paired ocelli, subequal arms, enlarged suckers present in mature individuals of at least one sex, frontal white spots (nominal taxa include <i>Octopus</i> species).
East Atlantic: none
West Atlantic: <i>O. maya</i> ; <i>O. filiosus</i>
East Pacific: <i>O. bimaculoides</i> ; <i>O. bimaculatus</i> ; <i>O. roosevelti</i> ?, <i>O. oculifer</i> ?
West Pacific: <i>O. areolatus</i> ; <i>O. brocki</i> ; <i>O. fangshiao</i> ; <i>O. ovulum</i> ; <i>O. cyanea</i>
Indian Ocean: <i>O. robsoni</i> ; <i>O. cyanea</i> ; <i>O. varunae</i>
Great Barrier Reef: <i>O. cyanea</i> ; <i>O. polyzenia</i> ; <i>O. exannulatus</i> ; <i>O. mototi</i>

ent of its average latitude. Species with planktonic young are significantly larger than are species with benthic young, and, overall, they appear to have larger ranges than do species with benthic young. Having planktonic young, however, does not ensure that a species has a large areal range. Reproductive modes and areal ranges of more species must be determined before the association of these characters can be fully tested.

Areas with high octopus species diversity are those with geologic or climatic histories that could have isolated populations as a prelude to allopatric speciation. Patterns of octopus diversity and endemism appear to be largely congruent with those of other shallow-water marine invertebrates.

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# Classification, Type Localities, and Type Repositories of Recent Cephalopoda

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## ABSTRACT

An annotated list is presented of the currently accepted classification of the Recent Cephalopoda. The list is based on the most current systematic monographs or revisions available in the literature. The name of each species, its author, year of publication, page citation, general locality of type, and type repository are given. The type species for each genus is listed first, followed by the other species in the genus, listed alphabetically. Synonymies are not included, but species known to be of questionable validity are noted. Type locality is given as a general location to facilitate comparison among species. The "Literature Cited" includes references to all the original descriptions of the species listed in the classification. An index to species also is provided.

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## Introduction

The purpose of this publication is to present a current annotated classification of the Recent Cephalopoda to the species level. One or two unpublished species classifications have been compiled in the past by students of cephalopod systematics as working/reference documents. The genesis for this species classification was the classification that C.F.E. Roper and R.E. Young began as an update to the late G.L. Voss's unpublished "species list." The confirmation of type deposition was based on personal verification by visits to museums by G. Voss and C. Roper and was expanded through references in the literature and queries to colleagues in museums around the world. Previously, no single reference has been published that contains the classification, authorship of

taxa, citation of publication, type locality, and type repository of cephalopod species. A classification of cephalopods to the generic level was published by Voss (1977), and two subsequent generic classifications based on it were published by Roper et al. (1984) and Clarke and Trueman (1988). The classification presented herein expands on these works with the addition of taxa to the species level and subsequently proposed supraspecific taxa. Since the completion of this manuscript, other publications have listed cephalopods to the species level (Nesis, 1987a; Mangold, 1989; Guerra, 1992).

We realize that numerous systematic problems exist at all taxonomic levels of the Cephalopoda. For example, several higher level taxa have been proposed (i.e., superorder Pseudoc-tobranchia Guerra, 1992, and order Cirroctopodida Young, 1989). These newly established taxa are not included at this time because their functional utility remains undebated.

We have addressed the problem cited by Clarke and Trueman (1988:3) concerning the differences in taxon-word endings between Recent and fossil classifications in the endings of ordinal and subordinal names, which are not governed by the International Code of Zoological Nomenclature (ICZN), but which we think should be standardized. Two endings currently are in use, "oidea" and "ida," and both have been used by neontologists and paleontologists, often in the same classification. We have adopted the ordinal ending of "ida" and subordinal ending of "ina" in order to bring consistency to the higher level classification. These endings have a long history of usage by paleontologists and neontologists, and we recommend that both groups of scientists accept both the ordinal and the familial level designations as the standard classification for Recent Cephalopoda.

This paper is intended not to establish taxonomic priority but to be a useful reference for cephalopod systematists. So, although we have derived our data and conclusions from the original publication in every species, systematists who contemplate publishing taxonomic changes are encouraged to check

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original references for specific information. If a user cannot find listed in this classification a previously used specific taxon, it is because that name has been synonymized in the recent literature.

The totals for taxa listed herein are as follows (with several genera not yet fully defined): more than 700 species, 139 genera, and 47 families.

#### MATERIALS AND METHODS

The annotated list of the currently accepted taxa of the Recent cephalopods is based on the most current taxonomic review available in the systematic literature. We realize that conflicting views exist concerning the status of a number of species, particularly in the octopodids, but as these are not yet all published, we are compelled to use those proposed in this volume. Taxa are listed by a hierarchial indentation scheme as follows:

Subclass

  Superorder

    Order

      Suborder

        Family

          Subfamily

            Genus (Subgenus)

              species, subspecies, author, general locality of type, type repository

The name of the taxon, author of the taxon, and year of publication are given for each higher taxon. These data as well as page citation, type locality, and type repository are given for each species. The type species (in bold face) of each genus is listed first, followed by the other species in the genus, listed alphabetically. Synonymies are not included, and those species known or thought to be synonyms that have not yet been synonymized in print remain in the classification. Potentially valid taxa that previously have been declared invalid or synonymized are not listed herein.

The following signs, symbols, and definitions are used in the classification. An asterisk (\*) after a taxon name denotes a taxon whose validity has been questioned but that requires further study to be published either as a synonym or as a valid species. A question mark (?) placed in front of a species name indicates questionable placement of that taxon in the associated genus. "Type locality" is given as a general location to facilitate comparison of species and should not necessarily be construed as the exact published type locality, e.g., Tyrrhenian Sea (general area) compared with Bay of Naples, Cape Miseno, Misenum (exact type locality). Multiple localities indicate that the author of the species did not specify a single type locality, most often found when syntypes came from different localities. "Type repository" is the museum in which the primary type (holotype, lectotype, neotype, syntypes) is deposited and is designated by the acronym of that institution. A question mark

(?) is used following the type repository when a type is thought to have been deposited at that museum (either because it has been listed as "possibly" there or because types from the same publication and collection are known to be there), but its presence has not been verified recently, nor has it been stated to be lost or destroyed. If the primary type has been reported in more than one museum, each repository is listed and separated by "or." The status of such types has not been determined.

In two instances, type material was not deposited in a museum but is now known to be no longer extant; types of species described by A.A. Gould (fide Johnson, 1964:32) and I.I. Akimushkin (fide Kir Nesis, pers. comm., 1988) are listed herein as "lost." Publications included in the "Literature Cited" are those in which the original description of each species listed in this classification is given.

An index of species in this classification also is included, listed alphabetically, followed by the genus in which each species currently is placed, not necessarily in the original or subsequent generic placement. We would appreciate being informed of any omissions, corrections, and/or additions (new species, species synonymized, species resurrected as valid, etc.) that are encountered by the users, as well as suggestions for improvement of this document, for future editions.

The names and abbreviations of the 65 institutions that house the primary types of cephalopod species in this classification are given below. Acronyms for type repositories follow those used for herpetology and ichthyology collections by Leviton et al. (1985) and Leviton and Gibbs (1988) as suggested by the editors of this publication. Also included are references (in parentheses) to published cephalopod type catalogs for the respective institutions.

AIM	Auckland Institute and Museum, Private Bag, Auckland 1, New Zealand.
AMS	Australian Museum, P.O. Box A285, 6-8 College Street, Sydney South, New South Wales 2000, Australia. (Rudman, 1983; Sweeney, Roper, and Hochberg, 1988.)
ANSP	Academy of Natural Sciences, 19th and The Parkway, Philadelphia, Pennsylvania, 19103, United States. (Voss, 1962d.)
ASIO	Academia Sinica, Institute of Oceanology, 7 Nankai Road, Qingdao, China.
BMNH	The Natural History Museum, Cromwell Road, London SW7 5BD, England (formerly British Museum (Natural History)).
CASIZ	California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, United States. (Smith, 1974; Sweeney, Roper, and Hochberg, 1988.)
CMC	Canterbury Museum, Rolleston Avenue, Christchurch 1, New Zealand.
FMHU	Fisheries Museum, Faculty of Fisheries, Hokkaido University, Hakodate, Japan (includes Laboratory of Marine Zoology (HUMZ) collection). (Taki and Igarashi, 1967.)
FMNH	Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605, United States (formerly Chicago Natural History Museum).
FMT	Taiwan Provincial Museum, 2 Siangyang Road, Taipei, Taiwan.

- FUMT University of Tokyo, Department of Fisheries, University Museum, see MSUT.
- HUJ Hebrew University of Jerusalem, Mount Scopus, Jerusalem, 91905 Israel.
- HUMZ Hokkaido University Laboratory of Marine Zoology, Faculty of Fisheries, see FMHU.
- IFLC Integrated Fisheries Project Marine Research Laboratory, P.O. Box 1801, Cochin 682016, India.
- IMC Zoological Museum Calcutta, Indian Museum, 27 Jawaharal Nehru Road, Calcutta 700013, India.
- INPC Indo-Norwegian Project Marine Research Laboratory, Cochin, India (exact address unknown).
- IRSNB Institut Royal des Sciences Naturelles de Belgique, Rue Vautier 29, B-1040 Brussels, Belgium (formerly Musée Royal d'Histoire Naturelle de Belgique).
- LS Linnean Society of London, Burlington House, Piccadilly, London W1V 0LQ, England. (Dodge, 1953.)
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, United States.
- MFDT Marine Fisheries Division, Department of Fisheries, 89/1 Charoen Krung 58, Bangkok 10120, Thailand.
- MHNB Muséum d'Histoire Naturelle, 2 place Bardineau, 33000 Bordeaux, France.
- MHNN Muséum d'Histoire Naturelle (Musée Barla), 60 bis blvd Risso, 06300 Nice, France.
- MLP Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina.
- MNHN Muséum National d'Histoire Naturelle, Laboratoire Biologie Invertébrés Marins et Malacologie, 55, rue de Buffon, 75005 Paris 05, France. (Lu et al., 1995.)
- MOM Musée Océanographique, Avenue Saint-Martin, Monaco-Ville, MC 98000, Monaco. (Belloc, 1950.)
- MORG Museu Océanográfico, Fundacao Universidade do Rio Grande, Caixa Postal 474, 96200 Rio Grande do Sul, Brazil.
- MSNV Museo Civico di Storia Naturale, Gontego dei Turchi-S. Croce 1730, 30135 Venice, Italy.
- MSUT University Museum, University of Tokyo, Hongo 7-3-1, Bunkyo-ku, Tokyo 113, Japan (includes former Tokyo Imperial University (TIU) collection and University of Tokyo Department of Fisheries (FUMT) collection).
- MZUF Museo Zoologico de la Specola, Università di Firenze, Via Romana 17, 50125 Firenze, Italy. (Borri et al., 1988.)
- MZUS Musée Zoologique, Université Louis Pasteur and de la Ville de Strasbourg, 29 Boulevard de la Victoire, F67000 Strasbourg, France.
- MZUSP Museu de Zoologia da Universidade de São Paulo, Av. Nazareth 481, São Paulo, CP7172 Brazil (formerly Departamento de Zoologia La Secretaria de Agricultura do Estado de São Paulo). (Perez and Haimovici, 1991.)
- NELS Nelson Provincial Museum, P.O. Box 645, Nelson, New Zealand.
- NMI National Museum of Ireland, Kildare Street, Dublin 2, Ireland.
- NMNZ National Museum of New Zealand, P.O. Box 467, Wellington, New Zealand (formerly Dominion Museum).
- NMP Natal Museum, Private Bag 9070, Pietermaritzburg 3200, South Africa.
- NMS National Museum, Stamford Road, 0617 Singapore (formerly Raffles Museum).
- NMSZ National Museum of Scotland, Zoology Department, Chambers Street, Edinburgh EH1 1JF, Scotland (formerly Royal Museum of Scotland; formerly Royal Scottish Museum, Edinburgh). (Heppell and Smith, 1983.)
- NMV Museum of Victoria, 285-321 Russell Street, Melbourne, Victoria 3000, Australia (formerly National Museum of Victoria). (Lu, 1983.)
- NMW Naturhistorisches Museum Wien, Burggring 7, Postfach 417, A-1014 Vienna, Austria.
- NMWZ National Museum of Wales, Cathays Park, Cardiff CF1 3NP, Wales.
- NRM Naturhistoriska Riksmuseet, Box 50007, S-104 05 Stockholm, Sweden. (Sandberg and Warén, 1993.)
- NSMT National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 160, Japan. (Kubodera and Tsuchiya, 1993.)
- OLUK Oceanographic Laboratory, University of Kerala, Ernakulam, India.
- OM Otago Museum, Great King Street, Dunedin, New Zealand.
- RMNH Nationaal Natuurhistorisch Museum, Raamsteeg 2, Postbus 9517, 2300 RA Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke Historie).
- SAM South African Museum, Government Avenue, P.O. Box 61, Cape Town 8000, South Africa.
- SAMA South Australian Museum, North Terrace, Adelaide, South Australia 5022, Australia. (Zeidler and MacPhail, 1978; Zeidler, 1983; Sweeney, Roper, and Hochberg, 1988.)
- SBMNH Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105, United States (Hertz, 1984; Scott, Hochberg, and Roth, 1990.)
- SCSIO South China Sea Institute of Oceanology, Academia Sinica, 164 West Xingang, Guangzhou 510301, China.
- SFI Morski Instytut Rybacki (Sea Fisheries Institute), Aleja Zjednoczenia 1, 81-345 Gdynia, Poland.
- SMF Naturmuseum und Forschungsinstitut Senckenberg, Senckenberg Anlage 25, D-60325 Frankfurt, Germany. (Schäfer, 1938.)
- SZN Stazione Zoologica di Napoli, Villa Comunale, 80121 Naples, Italy.
- TAU Tel-Aviv University, Ramat-Aviv, 69978 Tel-Aviv, Israel.
- TIU Tokyo Imperial University, see MSUT.
- UMC University Museum of Zoology, Downing Street, Cambridge University, Cambridge CB2 3EA, England.
- UMM University Museum, Munich, Germany (collections destroyed during World War II fide Pickford, 1964).
- USNM National Museum of Natural History, 10th and Constitution Avenue N.W., Smithsonian Institution, Washington, D.C. 20560, United States (includes collections of the former United States National Museum) (Roper and Sweeney, 1978; Sweeney, Roper, and Hochberg, 1988.)
- WAM Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia. (Slack-Smith, 1983.)
- YPM Peabody Museum of Natural History, Yale University, 170 Whitney Avenue, New Haven, Connecticut 06520, United States.
- YTKC Private collection of the late Iwao Taki stored at the home of Yoshio Taki, Kyoto City, Japan (fide T. Okutani, pers. comm., 1988).
- ZIKU Zoological Institute, College of Science, Kyoto University, Yoshida-Honmachi, Sakyo-ku, Kyoto 606, Japan.
- ZIN Zoological Institute, Russian Academy of Sciences, Universitetskaya Nab. 1, St. Petersburg 199164, Russia.
- ZMA Zoologisch Museum, Universiteit van Amsterdam, P.O. Box 4766, 1009 AT Amsterdam, The Netherlands.
- ZMB Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Invalidenstrasse 43, D-10115 Berlin, Germany.
- ZMH Zoologisches Museum, Universität Hamburg, Martin Luther King Platz 3, 2000 Hamburg 13, Germany.
- ZMMGU Zoological Museum, Moscow State University, ul. Gensena 6, Moscow, Russia.

ZMUB	Zoological Museum, Universitetet i Bergen, Museplass 3, 5000 Bergen, Norway.
ZMUC	Kobenhavns Universitet, Zoologisk Museum, Universitetsparken 15, DK 2100 Copenhagen, Denmark. (Kristensen and Knudsen, 1983.)
ZMUG	Zoologisches Museum der Universität, Berliner Strasse 28, D-W-3400 Göttingen, Germany.
ZMUO	Zoologiske Museum, Universitetet i Oslo, Sarsgt. 1, 0562 Oslo 5, Norway.
ZMUU	Zoologiska Museet, Uppsala Universitets, Villavagen 9, S-751 22 Uppsala, Sweden. (Wallin, 1991a, 1991b.)
ZSI	Zoological Survey of India, "M" Block, New Alipore, Calcutta 700053, India. (Thomson, in prep.)

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## Classification of the Currently Accepted Taxa of Recent Cephalopoda

Taxon	Type locality	Type repository
Class CEPHALOPODA Cuvier, 1797		
Subclass NAUTILOIDEA Agassiz, 1848		
Order NAUTILIDA Agassiz, 1848		
Family NAUTILIDAE Blainville, 1825		
<i>Nautilus</i> Linnaeus, 1758:709		
<i>pompilius pompilius</i> Linnaeus, 1758:709	"In India"	LS
<i>belauensis</i> Saunders, 1981:1	Palau Ids.	USNM
<i>macromphalus</i> Sowerby, 1848:464	not given	unknown
<i>pompilius suluensis</i> Habe and Okutani, 1988:93	Sulu Sea	NSMT
<i>repertus</i> * Iredale, 1944:295	W Australia	AMS
<i>scrobiculatus</i> Lightfoot, 1786:186	New Guinea	unknown
<i>stenomphalus</i> Sowerby, 1848:465	not given	BMNH
Subclass COLEOIDEA Bather, 1888		
Superorder DECABRACHIA Boettger, 1952		
Order SPIRULIDA Stolley, 1919		
Family SPIRULIDAE Owen, 1836		
<i>Spirula</i> Lamarck, 1799:80		
<i>spirula</i> (Linnaeus, 1758:710)	"In America"	LS
Order SEPIIDA Zittel, 1895		
Family SEPIIDAE <sup>1</sup> Keferstein, 1866		
<i>Sepia</i> ( <i>Sepia</i> ) Linnaeus, 1758:658		
<i>officinalis</i> Linnaeus, 1758:658	"Oceano"	LS?
<i>angulata</i> * Roeleveld, 1972:242	South Africa	SAM
<i>apama</i> Gray, 1849:103	S Australia	BMNH
<i>bandensis</i> Adam, 1939b:1	Banda Sea	IRSNB
<i>bertheloti</i> Orbigny, 1835, pl. 11, in Férussac and Orbigny, 1834-1848	Canary Ids.	MNHN or ?IRSNB
<i>chirotrema</i> Berry, 1918:268	S Australia	AMS (not extant)
<i>dollfusi</i> Adam, 1941d:12	S Red Sea	MNHN
<i>elobyana</i> Adam, 1941b:121	Gulf of Guinea	ZMH
<i>gibba</i> Ehrenberg, 1831:[5]	Red Sea	ZMB
<i>hierredda</i> Rang, 1835, pl. 13, in Férussac and Orbigny, 1834-1848	W Africa	MNHN

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>insignis</i> Smith, 1916:25	South Africa	BMNH
<i>irvingi</i> Meyer, 1909:333	W Australia	WAM
<i>latimanus</i> Quoy and Gaimard, 1832:68	New Guinea	MNHN
<i>mestus</i> Gray, 1849:108	Australia	BMNH
<i>novaehollandiae</i> Hoyle, 1909:266	S Australia	MNHN
<i>papillata</i> Quoy and Gaimard, 1832:61	South Africa	MNHN
<i>papuensis</i> Hoyle, 1885c:197	Papua New Guinea	BMNH
<i>pharaonis</i> Ehrenberg, 1831:[4]	Gulf of Suez	ZMB
<i>plangon</i> Gray, 1849:104	SE Australia	BMNH
<i>plathyconchalis</i> Filippova and Khromov, 1991:66	SW Indian Ocean	ZMMGU
<i>rozella</i> (Iredale, 1926:190)	SE Australia	AMS
<i>simoniana</i> Thiele, 1920:436	South Africa	ZMB
<i>tuberculata</i> Lamarck, 1798:130	South Africa	MNHN
<i>vermiculata</i> Quoy and Gaimard, 1832:64	South Africa	MNHN (not extant)
<i>Sepia (Acanthosepion) Rochebrune, 1884b:100</i>		
<i>aculeata</i> Van Hasselt, 1835, pl. 5bis, in Férussac and Orbigny, 1834–1848	Java, Indonesia	MNHN
<i>brevimana</i> Steenstrup, 1875:475	Indian Ocean	ZMUC
<i>esculenta</i> Hoyle, 1885c:188	Japan	BMNH
<i>lycidas</i> Gray, 1849:103	China	BMNH
<i>prashadi</i> Winckworth, 1936:16	Bay of Bengal	BMNH
<i>recurvirostra</i> Steenstrup, 1875:479	South China Sea	ZMUC
<i>savignyi</i> Blainville, 1827:285	Red Sea	MNHN
<i>smithi</i> Hoyle, 1885c:190	Papua New Guinea	BMNH
<i>stellifera</i> Homenko and Khromov, 1984:1150	Arabian Sea	ZMMGU
<i>thurstoni</i> Adam and Rees, 1966:2	Bay of Bengal	BMNH
<i>zanzibarica</i> Pfeffer, 1884:9	Zanzibar	ZMH or ?IRSNB
<i>Sepia (Anomalosepion) Khromov, 1987b:1172</i>		
<i>australis</i> Quoy and Gaimard, 1832:70	South Africa	MNHN
<i>omani</i> Adam and Rees, 1966:92	Gulf of Oman	BMNH
<i>sulcata</i> Hoyle, 1885c:192	Papua New Guinea	BMNH
<i>Sepia (Doratosepion) Rochebrune, 1884b:95</i>		
<i>andreana</i> Steenstrup, 1875:473	Japan	ZMUC
<i>adami</i> Roeleveld, 1972:224	South Africa	SAM
<i>appellöfi</i> Wülker, 1910:14	Japan	UMM? or BMNH?
<i>arabica</i> Massy, 1916:228	N Indian Ocean	ZSI
<i>aureomaculata</i> Okutani and Horikawa, 1987:62	Japan	NSMT
<i>bathyalis</i> Khromov, Nikitina, and Nesis, 1991:13	Madagascar	ZMMGU
<i>braggi</i> Verco, 1907:213	S Australia	SAMA
<i>burnupi</i> Hoyle, 1904a:27	South Africa	BMNH
<i>carinata</i> Sasaki, 1920:192	Japan	USNM
<i>confusa</i> Smith, 1916:24	South Africa	BMNH
<i>cottoni</i> Adam, 1979:193	W Australia	WAM
<i>elongata</i> Orbigny, 1839–1842, pl. 24, in Férussac and Orbigny, 1834–1848	Red Sea	MNHN
<i>erostrata</i> Sasaki, 1929:183	Japan	MSUT
<i>foliopeza</i> Okutani and Tagawa, 1987:67	E China Sea	NSMT
<i>incerta</i> Smith, 1916:23	South Africa	BMNH
<i>ivanovi</i> Khromov, 1982:137	SW Indian Ocean	ZMMGU
<i>joubini</i> Massy, 1927:161	South Africa	BMNH
<i>kobienensis</i> Hoyle, 1885c:195	Japan	BMNH
<i>longipes</i> Sasaki, 1914:619	Japan	MSUT
<i>lorigera</i> Wülker, 1910:12	Japan	UMM?
<i>mascarensis</i> Filippova and Khromov, 1991:63	SW Indian Ocean	ZMMGU

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>?mira</i> (Cotton, 1932:546)	E Australia	SAMA
<i>mirabilis</i> Khromov, 1988:785	W Arabian Sea	ZMMGU
<i>murrayi</i> Adam and Rees, 1966:63	Gulf of Oman	BMNH
<i>pardalis</i> Sasaki, 1914:614	Japan	MSUT
<i>peterseni</i> Appellöf, 1886:23	Japan	ZMUU
<i>saya</i> Khromov, Nikitina, and Nesis, 1991:13	10°N, 61°E (Indian Ocean)	ZMMGU
<i>sewelli</i> Adam and Rees, 1966:61	Gulf of Aden	BMNH
<i>sokotriensis</i> Khromov, 1988:788	W Arabian Sea	ZMMGU
<i>subtenuipes</i> Okutani and Horikawa, 1987:57	Japan	NSMT
<i>tala</i> Khromov, Nikitina, and Nesis, 1991:17	Madagascar	ZMMGU
<i>tenuipes</i> Sasaki, 1929:193	Japan	MSUT
<i>tokioensis</i> Ortmann, 1888:653	Japan	MZUS
<i>trygonina</i> (Rochebrune, 1884b:97)	Red Sea	MNHN (not extant)
<i>vercoi</i> Adam, 1979:190	W Australia	WAM
<i>vietnamica</i> Khromov, 1987a:35	Vietnam	ZIN
<i>Sepia</i> ( <i>Hemisepius</i> ) Steenstrup, 1875:468		
<i>typica</i> (Steenstrup, 1875:468)	South Africa	ZMUC
<i>dubia</i> Adam and Rees, 1966:119	South Africa	BMNH
<i>faurei</i> Roeleveld, 1972:251	South Africa	SAM
<i>pulchra</i> Roeleveld and Liltved, 1985:2	South Africa	SAM
<i>robsoni</i> (Massy, 1927:159)	South Africa	BMNH
<i>Sepia</i> ( <i>Rhombosepius</i> ) Rochebrune, 1884b:82		
<i>elegans</i> Blainville, 1827:284	Sicily, Italy	MNHN (not extant)
<i>acuminata</i> Smith, 1916:21	South Africa	BMNH
<i>cultrata</i> Hoyle, 1885c:198	SE Australia	BMNH
<i>hedleyi</i> Berry, 1918:258	S Australia	AMS
<i>hieronis</i> (Robson, 1924c:645)	South Africa	BMNH
<i>madokai</i> Adam, 1939c:77	Japan	MSUT?
<i>?opipara</i> (Iredale, 1926:191)	E Australia	AMS
<i>orbignyana</i> Férussac in Orbigny, 1826:156	Bay of Biscay, France	MNHN
<i>reesi</i> Adam, 1979:200	W Australia	WAM
<i>rex</i> (Iredale, 1926:193)	SE Australia	AMS
<i>Sepia</i> (subgenus undetermined)		
<i>?bartletti</i> * (Iredale, 1954:67)	Papua New Guinea	AMS
<i>?baxteri</i> * (Iredale, 1940:442)	Lord Howe Id.	AMS
<i>?dannevigi</i> * Berry, 1918:264	S Australia	AMS
<i>?elliptica</i> Hoyle, 1885c:189	Papua New Guinea	BMNH
<i>?whitleyana</i> Iredale, 1926:195	SE Australia	AMS
<i>Metasepia</i> Hoyle, 1885c:199		
<i>pfefferi</i> Hoyle, 1885c:199	Papua New Guinea	BMNH
<i>tullbergi</i> (Appellöf, 1886:26)	Japan	ZMUU
<i>Sepiella</i> Gray, 1849:106		
<i>ornata</i> (Rang, 1837:76)	Gulf of Guinea	MNHN
<i>cyanea</i> Robson, 1924b:13	South Africa	BMNH
<i>inermis</i> (Van Hasselt, 1835, pl. 6bis, in Férussac and Orbigny, 1834–1848)	Indian Ocean	MNHN
<i>japonica</i> Sasaki, 1929:219	Japan	FMHU (not extant)
<i>ocellata</i> * Pfeffer, 1884:13	Java, Indonesia	ZMH
<i>weberi</i> Adam, 1939c:98	Indonesia	ZMA
Family SEPIADARIIDAE Fischer, 1882, in 1880–1887		
<i>Sepiadarium</i> Steenstrup, 1881:214		
<i>kochi</i> Steenstrup, 1881:218	Hong Kong	ZMUC
<i>auritum</i> Robson, 1914:678	W Australia	BMNH
<i>austrinum</i> Berry, 1921a:354	S Australia	SAMA



## Classification.—Continued.

Taxon	Type locality	Type repository
<i>gracilis</i> Voss, 1962a:170	Philippines	USNM
<i>malayense</i> * Robson, 1932a:28	Singapore	BMNH
<i>nipponianum</i> * Berry, 1932:42	Japan	USNM
<i>Sepioloidea</i> Orbigny, 1845:240, in Férussac and Orbigny, 1834–1848		
<i>lineolata</i> (Quoy and Gaimard, 1832:82)	SE Australia	MNHN
<i>pacifica</i> (Kirk, 1882:283)	New Zealand	NMNZ
Order SEPIOLIDA Fioroni, 1981		
Family SEPIOLIDAE Leach, 1817		
Subfamily SEPIOLINAE Appellöf, 1898		
<i>Sepiola</i> Leach, 1817:137		
<i>rondeleti</i> Leach, 1834:230, in Férussac and Orbigny, 1834–1848	Mediterranean Sea	MNHN (not extant)
<i>affinis</i> Naef, 1912e:81	Tyrrhenian Sea	SZN?
<i>atlantica</i> Orbigny, 1839–1842, pl. 4, in Férussac and Orbigny, 1834–1848	Bay of Biscay, France	MNHN
<i>aurantiaca</i> Jatta, 1896:130	Tyrrhenian Sea	SZN?
<i>birostrata</i> Sasaki, 1918:235	Japan	MSUT (not extant)
<i>intermedia</i> Naef, 1912c:270	Tyrrhenian Sea	SZN?
<i>knudseni</i> Adam, 1983:157	6°N, 3°E (Atlantic Ocean)	ZMUC
<i>ligulata</i> Naef, 1912c:271	Tyrrhenian Sea	SZN?
<i>parva</i> Sasaki, 1913:252	Japan	MSUT (not extant)
<i>robusta</i> Naef, 1912c:271	Tyrrhenian Sea	SZN?
<i>rossiaeformis</i> * Pfeffer, 1884:8	Java	ZMH?
<i>steenstrupiana</i> Levy, 1912:LVI	“Villafranca”	unknown
<i>trirostrata</i> Voss, 1962a:172	Philippines	USNM
<i>Euprymna</i> Steenstrup, 1887a:66		
<i>morsei</i> (Verrill, 1881a:417)	Japan	YPM
<i>albatrossae</i> Voss, 1962a:171	Philippines	USNM
<i>berryi</i> Sasaki, 1929:143	Japan	unknown
<i>hoylei</i> Adam, 1986:133	Sulu Archipelago	WAM
<i>penares</i> * (Gray, 1849:95)	Singapore	BMNH
<i>phenax</i> Voss, 1962a:171	Philippines	USNM
<i>pusilla</i> * (Pfeffer, 1884:7)	Atlantic Ocean	ZMH
<i>schneehageni</i> * (Pfeffer, 1884:7)	Banda Sea	ZMH
<i>scolopes</i> Berry, 1913b:564	Hawaiian Ids.	USNM
<i>stenodactyla</i> (Grant, 1833:85)	Mauritius Id.	BMNH?
<i>tasmanica</i> (Pfeffer, 1884:6)	Bass Strait, Australia	ZMH
<i>Rondeletiella</i> Naef, 1921:541		
<i>minor</i> (Naef, 1912c:267)	Tyrrhenian Sea	SZN?
<i>Sepietta</i> Naef, 1912b:248		
<i>oweniana</i> (Orbigny, 1839–1841, pl. 3, in Férussac and Orbigny, 1834–1848)	Tyrrhenian Sea?	MNHN (not extant)
<i>neglecta</i> Naef, 1916a:9	Tyrrhenian Sea	SZN?
<i>petersi</i> (Steenstrup, 1887a:58)	Japan	ZMUU
<i>Inioteuthis</i> Verrill, 1881a:417		
<i>japonica</i> (Orbigny, 1845:234, in Férussac and Orbigny, 1834–1848)	Japan	MNHN (not extant)
<i>capensis</i> Voss, 1962c:255	South Africa	SAM
<i>maculosa</i> Goodrich, 1896:2	Andaman Ids.	ZSI
Subfamily ROSSIINAE Appellöf, 1898		
<i>Rossia</i> Owen, 1834:xcii		
<i>palpebroso</i> Owen, 1834:xcii	“Arctic regions”	BMNH?
<i>brachyura</i> Verrill, 1883a:110	Caribbean Sea	MCZ?

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>bullisi</i> Voss, 1956:101	Gulf of Mexico	USNM
<i>macrosoma</i> (Chiaie, 1830, pl. 17)	Tyrrhenian Sea	unknown
<i>megaptera</i> Verrill, 1881a:349	NW Atlantic Ocean	YPM
<i>moelleri</i> Steenstrup, 1856:198	Greenland	ZMUC (not extant)
<i>mollicella</i> Sasaki, 1920:189	Japan	USNM
<i>pacifica diegensis</i> * Berry, 1912a:292	California	USNM
<i>pacifica pacifica</i> Berry, 1911c:591	Alaska	USNM (not extant)
<i>tortugaensis</i> Voss, 1956:103	Caribbean Sea	USNM
<i>Austrorossia</i> Berry, 1918:252		
<i>australis</i> Berry, 1918:253	SW Australia	AMS
<i>antillensis</i> (Voss, 1955:86)	Cuba	MCZ
<i>bipapillata</i> (Sasaki, 1920:190)	Japan	USNM
<i>enigmatica</i> * (Robson, 1924c:635)	South Africa	BMNH
<i>mastigophora</i> (Chun, 1915:405)	NW Indian Ocean	ZMB
<i>Semirossia</i> Steenstrup, 1887b:90		
<i>tenera</i> (Verrill, 1880c:392)	NW Atlantic Ocean	YPM
<i>equalis</i> (Voss, 1950:73)	Caribbean Sea	USNM
<i>patagonica</i> (Smith, 1881:22)	Patagonia, Argentina	BMNH
<i>Neorossia</i> Boletzky, 1971:968		
<i>caroli</i> (Joubin, 1902a:138)	Azores Ids.	MOM
<i>leptodons</i> Reid, 1992:797	S Australia	NMV
Subfamily HETEROTEUTHIDINAE Appellöf, 1898		
<i>Heteroteuthis</i> ( <i>Heteroteuthis</i> ) Gray, 1849:90		
<i>dispar</i> (Rüppell, 1844:133)	Sicily, Italy	SMF
<i>weberi</i> Joubin, 1902b:401	Indonesia	MNHN
<i>Heteroteuthis</i> ( <i>Stephanoteuthis</i> ) Berry, 1909:408		
<i>hawaiïensis</i> (Berry, 1909:409)	Hawaiian Ids.	USNM
<i>dagamensis</i> Robson, 1924b:11	South Africa	BMNH
<i>serventyi</i> * Allan, 1945:340	SE Australia	AMS
<i>Nectoteuthis</i> Verrill, 1883a:108		
<i>pourtalesi</i> Verrill, 1883a:108	Barbados Id.	USNM
<i>Iridoteuthis</i> Naef, 1912b:24		
<i>iris</i> (Berry, 1909:410)	Hawaiian Ids.	USNM (not extant)
<i>maoria</i> Dell, 1959:3	New Zealand	NMNZ
<i>Stoloteuthis</i> Verrill, 1881a:417		
<i>leucoptera</i> (Verrill, 1878:378)	Gulf of Maine, U.S.	USNM
<i>Sepiolina</i> Naef, 1912b:248		
<i>nipponensis</i> (Berry, 1911a:39)	Japan	CASIZ
Family IDIOSEPIIDAE Appellöf, 1898		
<i>Idiosepius</i> Steenstrup, 1881a:219		
<i>pygmaeus</i> Steenstrup, 1881a:219	South China Sea and 4°N, 107°E	ZMUC
<i>biserialis</i> Voss, 1962c:258	South Africa	SAM
<i>macrocheir</i> Voss, 1962c:259	South Africa	SAM
<i>notoides</i> Berry, 1921a:361	S Australia	SAMA
<i>paradoxus</i> (Ortmann, 1888:649)	Japan	MZUS
<i>picteti</i> (Joubin, 1894:60)	Indonesia	unknown
<i>thailandicus</i> Chotiyaputta, Okutani, and Chaitiamvong, 1991:167	Gulf of Thailand	MFDT
Order TEUTHIDA Naef, 1916b		
Suborder MYOPSINA Orbigny, 1841:220, in Férussac and Orbigny, 1834–1848		
Family PICKFORDIATEUTHIDAE Voss, 1953		
<i>Pickfordiateuthis</i> Voss, 1953:602		
<i>pulchella</i> Voss, 1953:602	SE Florida, U.S.	USNM

## Classification.—Continued.

Taxon	Type locality	Type repository
Family LOLIGINIDAE Lesueur, 1821		
<i>Loligo (Loligo)</i> Lamarck, 1798:130		
<i>vulgaris vulgaris</i> Lamarck, 1798:130	Mediterranean Sea	MNHN (not extant)
<i>vulgaris reynaudi</i> Orbigny, 1839–1841, pl. 24, in Férussac and Orbigny, 1834–1848	Cape of Good Hope	MNHN (not extant)
<i>Loligo (Alloteuthis)</i> Wülker, 1920:56		
<i>media</i> (Linnaeus, 1758:659)	“Pelago”	LS?
<i>africana</i> Adam, 1950b:1	Gabon	IRSNB
<i>subulata</i> Lamarck, 1798:130	Mediterranean Sea	MNHN (not extant)
<i>Loligo</i> (subgenus undetermined)		
<i>bleekeri</i> Keferstein, 1866:1402	“Japan”	unknown
<i>gahi</i> Orbigny, 1835:60 (in 1834–1847)	Chile	MNHN
<i>ocula</i> Cohen, 1976:330	Caribbean	USNM
<i>opalescens</i> Berry, 1911c:591	Washington, U.S.	CASIZ
<i>pealeii</i> Lesueur, 1821:92	South Carolina?, U.S.	ANSP (not extant)
<i>plei</i> Blainville, 1823:132	Martinique Id.	MNHN
<i>roperi</i> Cohen, 1976:346	Bahama Ids.	USNM
<i>sanpaulensis</i> Brakoniecki in Roper, Sweeney, and Nauen, 1984:102	Argentina	USNM
<i>surinamensis</i> Voss, 1974:43	Surinam	RMNH
<i>Loliolus (Loliolus)</i> Steenstrup, 1856:193		
<i>hardwickei</i> (Gray, 1849:69)	India	BMNH
<i>affinis</i> Steenstrup, 1856:194	Indian Ocean	ZMUC
<i>Loliolus (Nipponololigo)</i> Natsukari, 1983:313		
<i>japonica</i> (Hoyle, 1885c:187)	Japan	BMNH
<i>beka</i> (Sasaki, 1929:121)	Japan	FMHU (not extant)
<i>sumatrensis</i> (Orbigny, 1835, pl. 13, in Férussac and Orbigny, 1834–1848)	Japan	MNHN
<i>uyii</i> (Wakiya and Ishikawa, 1921:286)	Japan	MSUT (not extant)
<i>Lolliguncula (Lolliguncula)</i> Steenstrup, 1881a:242		
<i>brevis</i> (Blainville, 1823:133)	Brazil and U.S. (Carolinas)	MNHN (not extant)
<i>mercatoris</i> Adam, 1941b:125	Gulf of Guinea	IRSNB
<i>panamensis</i> Berry, 1911b:100	Gulf of Panama	CASIZ
<i>Lolliguncula (Loliolopsis)</i> Berry, 1929:266		
<i>diomedea</i> (Hoyle, 1904b:29)	17°N, 100°W (Pacific Ocean)	USNM
<i>Sepioteuthis</i> Blainville, 1824:175		
<i>sepioidea</i> (Blainville, 1823:133)	Martinique Id.	MNHN (not extant)
<i>australis</i> Quoy and Gaimard, 1832:77	Port Western, Australia	MNHN
<i>lessoniana</i> Férussac in Lesson, 1830:244	“Dorery”	MNHN (not extant)
<i>loliginiformis</i> (Rüppell and Leuckart, 1828:21)	Red Sea	SMF
<i>Uroteuthis (Uroteuthis)</i> Rehder, 1945:21		
<i>bartschi</i> Rehder, 1945:22	Philippines	USNM
<i>Uroteuthis (Photololigo)</i> Natsukari, 1984:230		
<i>edulis</i> (Hoyle, 1885c:186)	Japan	BMNH
<i>abulati</i> (Adam, 1955:185)	Red Sea	MNHN
<i>arabica</i> (Ehrenberg, 1831:[3])	Red Sea	ZMB
<i>bengalensis</i> (Jothinayagam, 1987:48)	Bay of Bengal	ZSI
<i>chinensis</i> (Gray, 1849:74)	China	BMNH
<i>duvauceli</i> (Orbigny, 1835, pl. 14, in Férussac and Orbigny, 1834–1848)	India, and other locations	MNHN (not extant)
<i>noctiluca</i> (Lu, Roper, and Tait, 1985:59)	S Australia	NMV
<i>reesi</i> (Voss, 1962a:173)	Philippines	USNM
<i>robsoni</i> (Alexeyev, 1992:13)	Mozambique	ZMMGU
<i>singhalensis</i> (Ortmann, 1891:676)	Sri Lanka	MZUS or ?BMNH

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>vossi</i> (Nesis, 1982:144)	Philippines	USNM
Species with undetermined generic affinities		
<i>argus</i> Brakoniecki and Roper, 1985:47	Ecuador	USNM
<i>forbesii</i> Steenstrup, 1856:189	Denmark (?)	ZMUC
<i>pickfordi</i> Adam, 1954:149	Indonesia	ZMA
Suborder OEGOPSINA Orbigny, 1845 (in 1845–1847)		
Family LYCOTEUTHIDAE Pfeffer, 1908a		
Subfamily LYCOTEUTHINAE Pfeffer, 1908a		
<i>Lycoteuthis</i> Pfeffer, 1900:156		
<i>lorigera</i> (Steenstrup, 1875:473)	“South Sea” (= Pacific Ocean)	ZMUC
<i>springeri</i> (Voss, 1956:120)	Gulf of Mexico	USNM
<i>Selenoteuthis</i> Voss, 1959:370		
<i>scintillans</i> Voss, 1959:370	Florida, U.S.	MCZ
<i>Nematolampas</i> Berry, 1913c:208		
<i>regalis</i> Berry, 1913c:208	Kermadec Ids.	USNM
Subfamily LAMPADIOTEUTHINAE Berry, 1916		
<i>Lampadioteuthis</i> Berry, 1916:52		
<i>megaleia</i> Berry, 1916:52	Kermadec Ids.	unknown
Family ENOPLOTEUTHIDAE Pfeffer, 1900		
<i>Enoplateuthis</i> ( <i>Enoplateuthis</i> ) Orbigny in Rüppell, 1844:129		
<i>leptura leptura</i> (Leach, 1817:141)	Gulf of Guinea	BMNH
<i>leptura magnoceani</i> Nesis, 1982:162	unknown (Pacific Ocean)	MNHN
<i>obliqua</i> Burgess, 1982:704	Hawaiian Ids.	USNM
<i>octolineata</i> Burgess, 1982:708	Line Ids.	USNM
<i>reticulata</i> Rancurel, 1970:45	New Caledonia	unknown
<i>Enoplateuthis</i> ( <i>Paraenoplateuthis</i> ) Tsuchiya and Okutani, 1988:120		
<i>chunii</i> Ishikawa, 1914b:401	Japan	MSUT?
<i>anapsis</i> Roper, 1964:140	Caribbean Sea	USNM
<i>galaxias</i> Berry, 1918:211	SE Australia	AMS
<i>higginsii</i> Burgess, 1982:718	Hawaiian Ids.	USNM
<i>jonesii</i> Burgess, 1982:713	Hawaiian Ids.	USNM
<i>semilineata</i> Alexeyev, 1994:167	40°S, 127°W (Pacific Ocean)	ZMMGU
<i>Abralia</i> ( <i>Abralia</i> ) Gray, 1849:50		
<i>armata</i> (Quoy and Gaimard, 1832:84)	Moluccas Ids.	MNHN
<i>multihamata</i> Sasaki, 1929:245	Taiwan	FMT
<i>renschii</i> Grimpe, 1931:149	Sumatra, Indonesia	ZMB
<i>spaercki</i> Grimpe, 1931:150	Banda Sea	ZMUC
<i>steindachneri</i> Weindl, 1912:271	Red Sea	NMW
<i>Abralia</i> ( <i>Asteroteuthis</i> ) Pfeffer, 1908a:292		
<i>veranyi</i> (Rüppell, 1844:131)	Mediterranean Sea	BMNH
<i>Abralia</i> ( <i>Astrabralia</i> ) Nesis, 1987b:1701		
<i>astrosticta</i> Berry, 1909:412	Hawaiian Ids.	USNM
<i>astrolineata</i> Berry, 1914:145	Kermadec Ids.	USNM
<i>Abralia</i> ( <i>Pygmabralia</i> ) Nesis, 1987b:1701		
<i>redfieldi</i> Voss, 1955:99	Bahama Ids.	MCZ
<i>grimpei</i> Voss, 1959:375	Florida, U.S.	MCZ
<i>similis</i> Okutani and Tsuchiya, 1987:141	Japan	NSMT
<i>Abralia</i> ( <i>Heterabralia</i> ) Tsuchiya and Okutani, 1988:128		
<i>andamanica</i> Goodrich, 1896:9	Andaman Sea	ZSI
<i>heminuchalis</i> Burgess, 1992:120	1°S, 150°W (Pacific Ocean)	USNM
<i>robsoni</i> Grimpe, 1931:156	Japan	ZMUC
<i>siedleckyi</i> Lipinski, 1983:255	South Africa	SFI

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>trigonura</i> Berry, 1913b:565	Hawaiian Ids.	USNM
<i>Abralia</i> ( <i>Enigmoteuthis</i> ) Adam, 1973:33		
<i>dubia</i> (Adam, 1960a:12)	Gulf of Aqaba	IRSNB
<i>fasciolata</i> Tsuchiya, 1991:70	Gulf of Aden	USNM
<i>marisarabica</i> Okutani, 1983b:162	Arabian Sea	NSMT
<i>Abraliopsis</i> ( <i>Abraliopsis</i> ) Joubin, 1896:20		
<i>pfefferi</i> Joubin, 1896:20	W Mediterranean Sea	MOM?
<i>hoylei</i> (Pfeffer, 1884:17)	Mascarene Ids. (Indian Ocean)	ZMH (not extant)
<i>pacificus</i> Tsuchiya and Okutani, 1990:48	Japan	NSMT
<i>tui</i> Riddell, 1985:37	Kermadec Ids.	NMNZ?
<i>Abraliopsis</i> ( <i>Micrabralia</i> ) Pfeffer, 1900:167		
<i>lineata</i> (Goodrich, 1896:10)	Andaman Sea	ZSI (not extant)
<i>gilchristi</i> (Robson, 1924b:3)	South Africa	BMNH
<i>Abraliopsis</i> ( <i>Boreabraliopsis</i> ) Tsuchiya and Okutani, 1988:130		
<i>felis</i> McGowan and Okutani, 1968:72	California, U.S.	USNM
<i>Abraliopsis</i> ( <i>Pfefferiteuthis</i> ) Tsuchiya and Okutani, 1988:132		
<i>affinis</i> (Pfeffer, 1912:160)	E Tropical Pacific	ZMH?
<i>atlantica</i> Nesis, 1982:172	2°N, 1°E (Atlantic Ocean)	ZMB
<i>chuni</i> Nesis, 1982:172	2°N, 45°E (Indian Ocean)	ZMB
<i>falco</i> Young, 1972:13	California, U.S.	SBMNH
<i>Watasenia</i> Ishikawa, 1914a:336		
<i>scintillans</i> (Berry, 1911d:93)	Japan	CASIZ
Family ANCISTROCHEIRIDAE Pfeffer, 1912		
<i>Ancistrocheirus</i> Gray, 1849:49		
<i>lesueurii</i> (Orbigny, 1842, pl. 14, in Férussac and Orbigny, 1834–1848)	Indian Ocean	MNHN
Family PYROTEUTHIDAE Pfeffer, 1912		
<i>Pyroteuthis</i> Hoyle, 1904b:42		
<i>margariifera</i> (Rüppell, 1844:129)	S Italy	SMF
<i>addolux</i> Young, 1972:22	California, U.S.	SBMNH
<i>serrata</i> Riddell, 1985:10	Kermadec Ids.	NMNZ?
<i>Pterygioteuthis</i> Fischer, 1896:210		
<i>giardi</i> Fischer, 1896:211	Morocco	MNHN
<i>gemmata</i> Chun, 1908:87	S Atlantic Ocean	ZMB
<i>microlampas</i> Berry, 1913b:566	Hawaiian Ids.	USNM (not extant)
Family OCTOPOTEUTHIDAE Berry, 1912b		
<i>Octopoteuthis</i> Rüppell, 1844:134		
<i>sicula</i> Rüppell, 1844:134	W Mediterranean Sea	BMNH
<i>danae</i> Joubin, 1931:185	Bermuda Ids.	ZMUC
<i>deleton</i> Young, 1972:40	California, U.S.	SBMNH
<i>indica</i> * Naef, 1923:336	South Africa	ZMB?
<i>megaptera</i> (Verrill, 1885:399)	New Jersey, U.S.	USNM (not extant)
<i>nielseni</i> Robson, 1948:120	Cocos Id., Costa Rica	BMNH
<i>rugosa</i> Clarke, 1980:156	South Africa	BMNH
<i>Taningia</i> Joubin, 1931:181		
<i>danae</i> Joubin, 1931:181	Cape Verde Ids.	ZMUC
<i>persica</i> * (Naef, 1923:337)	Gulf of Aden	ZMB?
Family ONYCHOTEUTHIDAE Gray, 1849		
<i>Onychoteuthis</i> Lichtenstein, 1818:1591		
<i>banksii</i> (Leach, 1817:141)	Gulf of Guinea	BMNH
<i>borealijaponica</i> Okada, 1927a:7	Japan	FMHU (not extant)
<i>compacta</i> (Berry, 1913b:565)	Hawaiian Ids.	USNM
<i>meridiopacifica</i> Rancurel and Okutani, 1990:25	Coral Sea	NSMT

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>Onykia</i> * <sup>2</sup> Lesueur, 1821:98		
<i>carriboea</i> Lesueur, 1821:98	Gulf of Mexico and Gulf Stream	ANSP (not extant)
<i>appellöfi</i> (Pfeffer, 1900:158)	Atlantic Ocean	unknown
? <i>indica</i> Okutani, 1981:159	E Indian Ocean	NSMT
<i>intermedia</i> (Pfeffer, 1912:68)	SW Atlantic Ocean	ZMH?
<i>platyptera</i> Orbigny, 1834:41 (in 1834–1847)	Chile	MNHN (not extant)
? <i>rancureli</i> Okutani, 1981:155	7°S, 88°E (Indian Ocean)	NSMT
? <i>verrilli</i> (Pfeffer, 1900:157)	Tasmania	unknown
<i>Ancistroteuthis</i> Gray, 1849:55		
<i>lichtensteini</i> Férussac, 1835, pl. 8, in Férussac and Orbigny, 1834–1848	W Mediterranean Sea	MHNN
<i>Moroteuthis</i> * Verrill, 1881c:298		
<i>robusta</i> (Verrill, 1876:237)	Aleutian Ids.	USNM
<i>ingens</i> Smith, 1881:25	W coast of Patagonia	BMNH
<i>knipovitchi</i> Filippova, 1972:392	S Georgia Id.	ZMMGU
<i>lönnerbergii</i> Ishikawa and Wakiya, 1914:445	Japan	MSUT?
<i>robsoni</i> Adam, 1962:24	Angola	unknown
<i>Kondakovia</i> Filippova, 1972:395		
<i>longimana</i> Filippova, 1972:395	S Orkney Ids.	ZMMGU
Family WALVISTEUTHIDAE Nesis and Nikitina, 1986a		
<i>Walvisteuthis</i> Nesis and Nikitina, 1986a:47		
<i>virilis</i> Nesis and Nikitina, 1986a:47	33°S, 2°E (Atlantic Ocean)	ZMMGU
Family CYCLOTEUTHIDAE Naef, 1923		
<i>Cycloteuthis</i> Joubin, 1919:1		
<i>sirventi</i> Joubin, 1919:1	30°N, 25°W (Atlantic Ocean)	MOM
<i>akimushkini</i> Filippova, 1968:119	9°S, 91°E (Indian Ocean)	ZMMGU
<i>Discoteuthis</i> Young and Roper, 1969:5		
<i>discus</i> Young and Roper, 1969:5	Gulf of Guinea	USNM
<i>laciniosa</i> Young and Roper, 1969:9	33°N, 64°W (Atlantic Ocean)	USNM
Family GONATIDAE Hoyle, 1886		
<i>Gonatus</i> Gray, 1849:67		
<i>fabricii</i> (Lichtenstein, 1818:1592)	Greenland	ZMUC
<i>antarcticus</i> Lönnerberg, 1898:51	Chile	NRM?
<i>berryi</i> Naef, 1923:245	California, U.S.	USNM (not extant)
<i>californiensis</i> Young, 1972:51	California, U.S.	SBMNH
<i>kamtschaticus</i> (Middendorff, 1849:515)	Kuril Ids.	unknown
<i>madokai</i> Kubodera and Okutani, 1977:124	49°N, 168°E (Pacific Ocean)	FMHU
<i>onyx</i> Young, 1972:43	California, U.S.	SBMNH
<i>oregonensis</i> Jefferts, 1985:167	Oregon, U.S.	CASIZ
<i>pyros</i> Young, 1972:49	California, U.S.	SBMNH
<i>steenstrupi</i> Kristensen, 1981:78	NE Atlantic	ZMUC
<i>ursabrunae</i> Jefferts, 1985:160	Gulf of Alaska	CASIZ
<i>Eogonatus</i> Nesis, 1972:1300		
<i>tinro</i> Nesis, 1972:1300	Bering Sea	ZIN
<i>Gonatopsis</i> Sasaki, 1920:198		
<i>octopedatus</i> Sasaki, 1920:198	Okhotsk Sea	USNM
<i>borealis</i> Sasaki, 1923:203	Japan	FMHU (not extant)
<i>japonicus</i> Okiyama, 1969:20	41°N, 138°E (Sea of Japan)	NSMT
<i>makko</i> Okutani and Nemoto, 1964:113	Aleutian Ids.	NSMT
<i>okutani</i> * Nesis, 1972:1304	44°N, 150°E (Pacific Ocean)	ZIN
<i>Berryteuthis</i> Naef, 1921:535		
<i>magister magister</i> (Berry, 1913a:76)	Washington, U.S.	CASIZ
<i>anonychus</i> Percy and Voss, 1963:105	Oregon, U.S.	USNM
<i>magister nipponensis</i> Okutani and Kubodera, 1987:133	Japan	NSMT

## Classification.—Continued.

Taxon	Type locality	Type repository
Family PSYCHROTEUTHIDAE Thiele, 1920		
<i>Psychroteuthis</i> Thiele, 1920:440		
<i>glacialis</i> Thiele, 1920:440	Antarctic Ocean	ZMB
Family LEPIDOTEUTHIDAE <sup>3</sup> Pfeffer, 1912		
<i>Lepidoteuthis</i> Joubin, 1895b:1172		
<i>grimaldii</i> Joubin, 1895b:1172	Azores Ids.	MOM
<i>Pholidoteuthis</i> Adam, 1950a:1592		
<i>boschmai</i> Adam, 1950a:1592	Flores Sea	RMNH
<i>adami</i> Voss, 1956:132	Gulf of Mexico	USNM
<i>Tetronychoteuthis</i> Pfeffer, 1900:161		
<i>dussumieri</i> Orbigny, 1839–1842, pl. 13, in Férussac and Orbigny, 1834–1848	W Indian Ocean	MNHN (not extant)
<i>massyae</i> Pfeffer, 1912:102	48°N, 15°W (Atlantic Ocean)	ZMH?
Family ARCHITEUTHIDAE <sup>4</sup> Pfeffer, 1900		
<i>Architeuthis</i> Steenstrup, 1857b:183		
<i>dux</i> Steenstrup, 1857b:183	31°N, 76°W (Atlantic Ocean)	ZMUC
<i>martensi</i> (Hilgendorf, 1880:65)	Japan	ZMB
<i>sanctipauli</i> (Velain, 1877:81)	38°S, 75°E (Indian Ocean)	MNHN
Family HISTIOTEUTHIDAE Verrill, 1881a		
<i>Histioteuthis</i> Orbigny, 1841:xxxii, in Férussac and Orbigny, 1834–1848		
<i>bonnellii</i> species-group		
<i>bonnellii</i> (Férussac, 1834:355)	W Mediterranean Sea	MNHN
<i>machrohista</i> Voss, 1969:845	Tasman Sea	USNM
<i>reversa</i> species-group		
<i>atlantica</i> (Hoyle, 1885a:273)	35°S, 21°W (Atlantic Ocean)	BMNH
<i>eltaninae</i> Voss, 1969:755	40°S, 149°W (Pacific Ocean)	USNM
<i>reversa</i> (Verrill, 1880c:393)	39°N, 70°W (Atlantic Ocean)	USNM
<i>hoylei</i> species-group		
<i>arcturi</i> (Robson, 1948:122)	26°S, 51°W (Atlantic Ocean)	BMNH
<i>hoylei</i> (Goodrich, 1896:15)	Andaman Sea	NMZW
<i>celetaria</i> subspecies-group		
<i>celetaria celetaria</i> (Voss, 1960:424)	Bermuda Ids.	FMNH
<i>celetaria pacifica</i> (Voss, 1962a:174)	Philippines	USNM
<i>corona</i> subspecies-group		
<i>corona berryi</i> Voss, 1969:781	29°N, 125°W (Pacific Ocean)	USNM
<i>corona cerasina</i> Nesis, 1971:1463	Ecuador	ZIN
<i>corona corona</i> (Voss and Voss, 1962:191)	Gulf of Mexico	USNM
<i>corona inermis</i> Taki, 1964:287	Japan	ZIKU
<i>miranda</i> species-group		
<i>miranda</i> (Berry, 1918:221)	SE Australia	USNM
<i>oceani</i> (Robson, 1948:123)	Galapagos Ids.	BMNH
<i>meleagroteuthis</i> species-group		
<i>heteropsis</i> (Berry, 1913a:75)	California, U.S.	USNM (not extant)
<i>meleagroteuthis</i> (Chun, 1910:170)	New Zealand	AIM
Family NEOTEUTHIDAE Naef, 1921		
<i>Neoteuthis</i> Naef, 1921:540		
<i>thielei</i> Naef, 1921:540	32°S, 8°W (Atlantic Ocean)	ZMB
<i>Alluroteuthis</i> Odhner, 1923:1		
<i>antarctica</i> Odhner, 1923:2	Weddell Sea	NRM
<i>Nototeuthis</i> Nesis and Nikitina, 1986b:290		
<i>dimegacotyle</i> Nesis and Nikitina, 1986b:290	S Chile	ZMMGU
Family BATHYTEUTHIDAE Pfeffer, 1900		
<i>Bathyteuthis</i> Hoyle, 1885a:272		
<i>abyssicola</i> Hoyle, 1885a:272	Antarctic Ocean	BMNH

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>bacidifera</i> Roper, 1968:162	Peru	USNM
<i>berryi</i> Roper, 1968:169	California, U.S.	SBMNH
Family CHTENOPTERYGIDAE Grimpe, 1922		
<i>Chtenopteryx</i> Appellöf, 1890:4		
<i>sicula</i> (Verany, 1851:75)	Messina, Italy	MHNN?
<i>chuni</i> * Pfeffer, 1912:343	28°S, 6°E (Atlantic Ocean)	ZMB?
<i>sepioloidea</i> Rancurel, 1970:39	Tuamotu Ids.	unknown
Family BRACHIOTEUTHIDAE Pfeffer, 1908b		
<i>Brachioteuthis</i> Verrill, 1881a:405		
<i>beani</i> Verrill, 1881a:406	Massachusetts, U.S.	USNM
<i>behni</i> * (Steenstrup, 1882:294)	Indian Ocean	ZMUC
<i>bowmani</i> * Russell, 1909:449	Scotland	unknown
<i>picta</i> Chun, 1910:207	5°N, 7°W? (Atlantic Ocean)	ZMB?
<i>riisei</i> (Steenstrup, 1882:294)	34°S, 7°W (Atlantic Ocean)	ZMUC
Family BATOTEUTHIDAE Young and Roper, 1968		
<i>Batoteuthis</i> Young and Roper, 1968:185		
<i>skolops</i> Young and Roper, 1968:185	49°S, 169°W (Pacific Ocean)	USNM
Family OMMASTREPHIDAE Steenstrup, 1857c		
Subfamily ILLICINAE Posselt, 1891		
<i>Illex</i> Steenstrup, 1880:82		
<i>illecebrosus</i> (Lesueur, 1821:95)	Massachusetts, U.S.	USNM
<i>argentinus</i> (Castellanos, 1960:55)	SW Atlantic Ocean	MLP
<i>coindetii</i> (Verany, 1839a:94)	France, W Mediterranean Sea	USNM
<i>oxygonius</i> Roper, Lu, and Mangold, 1969:299	Florida, U.S.	USNM
Subfamily TODARODINAE Adam, 1960b		
<i>Todarodes</i> Steenstrup, 1880:83		
<i>sagittatus</i> (Lamarck, 1798:130)	Atlantic Ocean	MNHN (not extant)
<i>angolensis</i> Adam, 1962:32	Angola	IRSNB
<i>filippovae</i> Adam, 1975:3	S Indian Ocean	IRSNB
<i>pacificus pacificus</i> (Steenstrup, 1880:79)	Japan	ZMUC
<i>pacificus pusillus</i> Dunning, 1988:149	Timor Sea	NMV
<i>Todaropsis</i> Girard, 1890:204		
<i>eblanae</i> (Ball, 1841:364)	North Sea	unknown
<i>Nototodarus</i> Pfeffer, 1912:434		
<i>sloanii</i> (Gray, 1849:61)	New Zealand	BMNH
<i>gouldi</i> (McCoy, 1888:255)	S Australia	NMV
<i>hawaiiensis</i> (Berry, 1912b:434)	Hawaiian Ids.	USNM
<i>Martialia</i> Rochebrune and Mabile, 1889:H8		
<i>hyadesi</i> Rochebrune and Mabile, 1889:H9	Cape Horn, Chile	MNHN
Subfamily OMMASTREPHINAE Posselt, 1891		
<i>Ommastrephes</i> Orbigny, 1834:45 (in 1834–1847)		
<i>bartramii</i> (Lesueur, 1821:90)	not given	ANSP (not extant)
<i>Sthenoteuthis</i> Verrill, 1880a:222		
<i>pteropus</i> (Steenstrup, 1855:200)	Caribbean Sea	ZMUC
<i>oualaniensis</i> (Lesson, 1830:240)	Caroline Ids.	MNHN (not extant)
<i>Dosidicus</i> Steenstrup, 1857a:120		
<i>gigas</i> (Orbigny, 1835:50 (in 1834–1847))	Chile	MNHN
<i>Eucleoteuthis</i> Berry, 1916:60		
<i>luminosa</i> (Sasaki, 1915:144)	Japan	MSUT?
<i>Ornithoteuthis</i> Okada, 1927b:15		
<i>volatilis</i> (Sasaki, 1915:138)	Japan	MSUT?
<i>antillarum</i> Adam, 1957:3	Guadeloupe Id.	MNHN
<i>Hyaloteuthis</i> Gray, 1849:63		
<i>pelagica</i> (Bosc, 1802:46)	"en pleine mer"	MNHN (not extant)



## Classification.—Continued.

Taxon	Type locality	Type repository
Family THYSANOTEUTHIDAE Keferstein, 1866		
<i>Thysanoteuthis</i> Troschel, 1857:69		
<i>rhombus</i> Troschel, 1857:70	Mediterranean Sea	unknown
? <i>danae</i> * (Joubin, 1933:7)	12°N, 32°W (Atlantic Ocean)	ZMUC
<i>nuchalis</i> * Pfeffer, 1912:531	Yellow Sea	ZMB
Family CHIROTEUTHIDAE Gray, 1849		
<i>Chiroteuthis</i> Orbigny, 1841:xxxii, in Férussac and Orbigny, 1834–1848		
<i>veranii</i> (Férussac, 1835:[5])	Mediterranean Sea	MHNN (not extant)
<i>atlanticus</i> * (MacDonald and Clench, 1934:145)	37°N, 67°W (Atlantic Ocean)	MCZ
<i>calyx</i> Young, 1972:69	California, U.S.	SBMNH
<i>capensis</i> Voss, 1967:76	South Africa	SAM
<i>diaphana</i> * (Verrill, 1884:141)	New Jersey, U.S.	USNM
<i>imperator</i> Chun, 1908:88	Sumatra, Indonesia	ZMB
<i>joubini</i> Voss, 1967:79	8°N, 44°W (Atlantic Ocean)	ZMUC
<i>lacertosa</i> Verrill, 1881a:408	Nova Scotia, Canada	USNM
<i>macrosoma</i> Goodrich, 1896:12	Bay of Bengal	ZSI
<i>pellucida</i> * Goodrich, 1896:14	Bay of Bengal	ZSI
<i>picteti</i> Joubin, 1894:40	Indonesia	MOM
<i>Asperoteuthis</i> Nesis, 1980:59		
<i>acanthoderma</i> (Lu, 1977:179)	Celebes Sea	ZMUC
<i>Grimalditeuthis</i> Joubin, 1898b:111		
<i>bonplandi</i> (Verany, 1839b:99)	29°N, 39°W (Atlantic Ocean)	MHNN?
<i>Plancoteuthis</i> Pfeffer, 1912:571		
<i>danae</i> (Joubin, 1931:188)	Gulf of Panama	ZMUC
<i>levimana</i> (Lönnerberg, 1896:605)	43°N, 24°W (Atlantic Ocean)	ZMUU
<i>oligobessa</i> Young, 1972:72	California, U.S.	SBMNH
Family MASTIGOTEUTHIDAE Verrill, 1881a		
<i>Mastigoteuthis</i> ( <i>Mastigoteuthis</i> ) Verrill, 1881b:100		
<i>agassizii</i> Verrill, 1881b:100	North Carolina, U.S.	USNM
<i>atlantica</i> Joubin, 1933:20	France (Atlantic Ocean)	ZMUC
<i>cordiformis</i> Chun, 1908:88	Sumatra, Indonesia	ZMB
<i>danae</i> (Joubin, 1933:13)	34°N, 33°W (Atlantic Ocean)	ZMUC
<i>dentata</i> Hoyle, 1904b:34	Gulf of Panama	USNM
<i>famelica</i> (Berry, 1909:414)	Hawaiian Ids.	USNM (not extant)
<i>flammea</i> Chun, 1908:88	Gulf of Guinea	ZMB?
<i>glaukopsis</i> Chun, 1908:88	NW Indian Ocean	ZMB?
<i>inermis</i> Rancurel, 1972:25	Gulf of Guinea	ZMUB (not extant)
<i>latipinna</i> (Sasaki, 1916:108)	Japan	MSUT (not extant)
<i>magna</i> Joubin, 1913:2	31°N, 42°W (Atlantic Ocean)	MOM
<i>psychrophila</i> Nesis, 1977:835	59°S, 158°E (Pacific Ocean)	ZIN
<i>pyrodes</i> Young, 1972:64	California, U.S.	SBMNH
<i>schmidti</i> Degner, 1925:50	Bay of Biscay, France	ZMUC
<i>talismani</i> (Fischer and Joubin, 1907:342)	Azores Ids.	MNHN
<i>Mastigoteuthis</i> ( <i>Mastigopsis</i> ) Grimpe, 1922:50		
<i>hjorti</i> Chun, 1913:6	32°N, 34°W (Atlantic Ocean), and other locations	ZMUB
Family PROMACHOTEUTHIDAE Naef, 1912a		
<i>Promachoteuthis</i> Hoyle, 1885a:273		
<i>megaptera</i> Hoyle, 1885a:273	Japan	BMNH
Family JOUBINITEUTHIDAE Naef, 1922		
<i>Joubiniteuthis</i> Berry, 1920a:152		
<i>portieri</i> (Joubin, 1916:1)	Canary Ids.	MOM? or MHNN?

## Classification.—Continued.

Taxon	Type locality	Type repository
Family incertae sedis		
<i>Parateuthis</i> Thiele, 1920:463		
<i>tunicata</i> * Thiele, 1920:463	64°S, 85°E (Antarctic Ocean)	ZMB
Family CRANCHIIDAE <sup>5</sup> Prosch, 1847		
Subfamily CRANCHIINAE Pfeffer, 1912		
<i>Cranchia</i> Leach, 1817:140		
<i>scabra</i> Leach, 1817:140	Congo, W Africa	BMNH
<i>Liocranchia</i> Pfeffer, 1884:25		
<i>reinhardti</i> (Steenstrup, 1856:200)	15°N, 24°W (Atlantic Ocean)	ZMUC
<i>Leachia</i> Lesueur, 1821:89		
<i>cyclura</i> Lesueur, 1821:90	37°S, 33°E (Indian Ocean)	ANSP (not extant)
Subfamily TAONIINAE Pfeffer, 1912		
<i>Taonius</i> Steenstrup, 1861b:84		
<i>pavo</i> (Lesueur, 1821:96)	Massachusetts, U.S.	MNH
<i>Galiteuthis</i> Joubin, 1898a:279		
<i>armata</i> Joubin, 1898a:279	Mediterranean Sea	MHNN
<i>Mesonychoteuthis</i> Robson, 1925:272		
<i>hamiltoni</i> Robson, 1925:272	S Shetland Ids.	BMNH
<i>Helicocranchia</i> Massy, 1907:382		
<i>pfefferi</i> Massy, 1907:382	51°N, 11°W (Atlantic Ocean)	BMNH
<i>Bathothauma</i> Chun, 1906:86		
<i>lyromma</i> Chun, 1906:86	Cape Verde Ids.	ZMB
<i>Sandalops</i> Chun, 1906:86		
<i>melancholicus</i> Chun, 1906:86	Tristan da Cunha Id.	ZMB
<i>Liguriella</i> Issel, 1908:103		
<i>podophtalma</i> Issel, 1908:103	"Atlantic Ocean"	unknown
<i>Egea</i> Joubin, 1933:43		
<i>inermis</i> Joubin, 1933:48	Bermuda Ids.	ZMUC
<i>Megalocranchia</i> Pfeffer, 1884:24		
<i>maxima</i> Pfeffer, 1884:24	Cape of Good Hope	ZMH (not extant)
<i>Teuthowenia</i> Chun, 1910:376		
<i>megalops</i> (Prosch, 1847:71)	W of Faeroe Ids.	ZMUC
<i>maculata</i> (Leach, 1817:140)	1°S, 8°E (Atlantic Ocean)	BMNH
<i>pellucida</i> (Chun, 1910:357)	South Africa	ZMB
Superorder OCTOBRACHIA Fioroni, 1981		
Order OCTOPODIDA Leach, 1818		
Suborder CIRRINA Grimpe, 1916		
Family CIRROTEUTHIDAE Keferstein, 1866		
<i>Cirroteuthis</i> Eschricht, 1836:633		
<i>mülleri</i> Eschricht, 1836:633	Greenland	ZMUC
<i>hoylei</i> Robson, 1932b:161	Chile	BMNH
<i>magna</i> Hoyle, 1885b:233	S Indian Ocean	BMNH
<i>massyae</i> Grimpe, 1920:233	Ireland	NMI
<i>Cirrothauma</i> Chun, 1911:5		
<i>murrayi</i> Chun, 1911:5	N Atlantic Ocean	ZMUB?
<i>Froekenia</i> Hoyle, 1904b:7		
<i>clara</i> * Hoyle, 1904b:7	Gulf of Panama	USNM (not extant)
Family STAURITEUTHIDAE Grimpe, 1916		
<i>Stauriteuthis</i> Verrill, 1879:468		
<i>syrtenensis</i> Verrill, 1879:468	Nova Scotia, Canada	USNM
<i>Chuniteuthis</i> Grimpe, 1916:355		
<i>ebersbachii</i> Grimpe, 1916:357	N Atlantic Ocean	ZMUB
<i>gilchristi</i> (Robson, 1924a:204)	South Africa	BMNH

## Classification.—Continued.

Taxon	Type locality	Type repository
Family OPISTHOTEUTHIDAE Verrill, 1896		
<i>Opisthoteuthis</i> Verrill, 1883a:113		
<i>agassizii</i> Verrill, 1883a:113	West Indies	MCZ?
<i>californiana</i> Berry, 1949:23	California, U.S.	CASIZ
<i>depressa</i> Ijima and Ikeda, 1895:323	Japan	MSUT (not extant)
<i>extensa</i> Thiele in Chun, 1915:537	Sumatra, Indonesia	ZMB
<i>grimaldii</i> (Joubin, 1903:100)	Azores Ids.	MOM
<i>japonica</i> * Taki, 1962:397	Japan	YTKC
<i>medusoides</i> Thiele in Chun, 1915:538	W Indian Ocean	ZMB
<i>persephone</i> Berry, 1918:290	SE Australia	AMS (not extant)
<i>philipii</i> Oommen, 1976:368	SW India	IFLC
<i>pluto</i> Berry, 1918:284	S Australia	AMS (not extant)
<i>vossi</i> Sanchez and Guerra, 1989:1159	22°S, 6°E (Atlantic Ocean)	USNM
<i>Grimpoteuthis</i> Robson, 1932b:136		
<i>umbellata</i> (Fischer, 1883:404)	W Africa	MNHN
<i>albatrossi</i> (Sasaki, 1920:169)	Japan	USNM
<i>antarctica</i> Kubodera and Okutani, 1986:129	62°S, 62°W (Antarctic Ocean)	NSMT
<i>bathynectes</i> Voss and Pearcy, 1990:57	Oregon, U.S.	USNM
<i>bruuni</i> Voss, 1982:426	Chile (Pacific Ocean)	USNM
<i>glacialis</i> (Robson, 1930b:375)	Antarctic Ocean	BMNH
<i>hippocrepium</i> (Hoyle, 1904b:6)	Colombia (Pacific Ocean)	USNM
<i>mawsoni</i> (Berry, 1917:8)	66°S, 145°E (Antarctic Ocean)	AMS
<i>meangensis</i> (Hoyle, 1885b:234)	S Philippines	BMNH
<i>megaptera</i> (Verrill, 1885:405)	North Carolina, U.S.	USNM
<i>pacifica</i> (Hoyle, 1885b:235)	Papua New Guinea	BMNH
<i>plena</i> (Verrill, 1885:404)	37°N, 71°W (Atlantic Ocean)	USNM
<i>tuftsi</i> Voss and Pearcy, 1990:63	Oregon, U.S.	USNM
<i>wülkeri</i> (Grimpe, 1920:235)	Morocco	ZMUB
Suborder INCIRRINA Grimpe, 1916		
Family BOLITAENIDAE Chun, 1911		
<i>Bolitaena</i> Steenstrup, 1859:183		
<i>microcotyla</i> Steenstrup in Hoyle, 1886:16	Atlantic Ocean	ZMUC
<i>Japetella</i> Hoyle, 1885b:231		
<i>diaphana</i> Hoyle, 1885b:232	Papua New Guinea	BMNH
<i>heathi</i> (Berry, 1911c:589)	California, U.S.	USNM
<i>Eledonella</i> Verrill, 1884:144		
<i>pygmaea</i> (Verrill, 1884:145)	Virginia, U.S.	USNM
<i>sheardi</i> * Allan, 1945:345	E Australia	AMS
Family AMPHITRETIDAE Hoyle, 1886		
<i>Amphitretus</i> Hoyle, 1885b:234		
<i>pelagicus</i> Hoyle, 1885b:234	Kermadec Ids.	BMNH
Family IDIOCTOPODIDAE Taki, 1962		
<i>Idioctopus</i> Taki, 1962:397		
<i>gracilipes</i> * Taki, 1962:397	Japan	YTKC
Family VITRELEDONELLIDAE Robson, 1932b:321		
<i>Vitreledonella</i> Joubin, 1918b:1		
<i>richardi</i> Joubin, 1918b:1	30°N, 15°W (Atlantic Ocean)	MHNN
Family OCTOPODIDAE Orbigny, 1840:3, in Férussac and Orbigny, 1834–1848		
Subfamily OCTOPODINAE Grimpe, 1921		
<i>Octopus</i> Cuvier, 1797:380		
<i>vulgaris</i> Cuvier, 1797:380	W Mediterranean Sea	MNHN
<i>adamsi</i> * Benham, 1944:259	New Zealand	OM

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>alatus</i> * (Sasaki, 1920:180)	Japan	USNM
<i>alecto</i> Berry, 1953:56	Gulf of California, Mexico	USNM
<i>alpheus</i> Norman, 1993a:270	E Australia	NMV
<i>araneoides</i> * (Taki, 1964:307)	Japan	YTKC
<i>arborescens</i> (Hoyle, 1904c:189)	Sri Lanka	BMNH or IMC or ?
<i>areolatus</i> de Haan, 1839–1841:65, in Férussac and Orbigny, 1834–1848	Japan	RMNH
<i>aspilosomatis</i> Norman, 1993a:279	NE Australia	NMV
<i>australis</i> Hoyle, 1885b:224	E Australia	BMNH
<i>balboai</i> Voss, 1971:16	Gulf of Panama	USNM
<i>berrima</i> Stranks and Norman, 1993:335	SE Australia	NMV
<i>bimaculatus</i> Verrill, 1883b:121	California, U.S.	USNM
<i>bimaculoides</i> Pickford and McConnaughey, 1949:14	California, U.S.	YPM
<i>bocki</i> Adam, 1941a:1	Fiji Ids.	NRM
<i>briareus</i> Robson, 1929b:612	Curaçao Id., Netherlands Antilles	ZMA or BMNH
<i>brocki</i> * Ortmann, 1888:645	Japan	MZUS
<i>bunurong</i> Stranks, 1990:462	SE Australia	NMV
<i>burryi</i> Voss, 1950:76	Florida, U.S.	USNM
<i>californicus</i> (Berry, 1911c:590)	California, U.S.	USNM (not extant)
<i>campbelli</i> (Smith, 1902:201)	New Zealand	BMNH
<i>carolinensis</i> Verrill, 1884:235	North Carolina, U.S.	USNM
<i>chierchiaie</i> Jatta, 1889:64	Panama	SZN?
<i>conispadiceus</i> (Sasaki, 1917:367)	Japan	MSUT?
<i>cyanea</i> Gray, 1849:15	Australia	BMNH
<i>defilippi</i> (Verany, 1851:30)	W Mediterranean Sea	MHNN
<i>dierythraeus</i> Norman, 1993a:284	NE Australia	NMV
<i>digueti</i> Perrier and Rochebrune, 1894:770	Gulf of California, Mexico	MNHN
<i>dofleini apollyon</i> * (Berry, 1912a:284)	Alaska, U.S.	USNM (not extant)
<i>dofleini dofleini</i> (Wülker, 1910:7)	Japan	UMM (not extant)
<i>dofleini martini</i> * Pickford, 1964:52	Washington, U.S.	YPM
<i>exannulatus</i> Norman, 1993b:321	E Australia	NMV
<i>fangsiao etchuanus</i> (Sasaki, 1929:53)	Japan	MSUT (not extant)
<i>fangsiao typicus</i> Orbigny, 1839–1841:70, in Férussac and Orbigny, 1834–1848	Japan	unknown
<i>favonius</i> Gray, 1849:9	Singapore	BMNH
<i>filamentosus</i> Blainville, 1826:188	Mauritius Id.	MNHN
<i>filosus</i> Howell, 1867:240	St. Croix Id.	ANSP
<i>fitchi</i> Berry, 1953:54	Gulf of California, Mexico	USNM
<i>fujitai</i> (Sasaki, 1929:70)	Japan	FMHU (not extant)
<i>gardineri</i> (Hoyle, 1905:976)	Maldive Ids.	UMC
<i>globosus</i> Appellöf, 1886:7	Japan	ZMUU
<i>graptus</i> Norman, 1993a:296	NE Australia	NMV
<i>guangdongensis</i> Dong, 1976:213	South China Sea	ASIO
<i>hardwickei</i> Gray, 1849:8	Indian Ocean	BMNH
<i>hattai</i> (Sasaki, 1929:87)	Japan	MSUT
<i>hongkongensis</i> Hoyle, 1885b:224	Japan	BMNH
<i>horridus</i> Orbigny, 1826:144	Red Sea	SMF
<i>hubbsorum</i> Berry, 1953:53	Gulf of California, Mexico	USNM
<i>joubini</i> Robson, 1929c:161	Virgin Ids.	BMNH
<i>kagoshimensis</i> Ortmann, 1888:664	Japan	MZUS
<i>kaurna</i> Stranks, 1990:460	SE Australia	NMV
<i>kermadecensis</i> (Berry, 1914:138)	Kermadec Ids.	USNM
<i>?leioderma</i> (Berry, 1911c:590)	Alaska, U.S.	CASIZ

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>lobensis</i> * Castellanos and Menni, 1969:92	Argentina	MLP
<i>longispadiceus</i> (Sasaki, 1917:366)	Japan	FMHU
<i>luteus</i> (Sasaki, 1929:45)	Pescadores Ids.	FMHU (not extant)
<i>macropus</i> Risso, 1826:3	W Mediterranean Sea?	unknown
<i>magnificus</i> Villanueva, Sanchez, and Compagno, 1992:39	Namibia	SAM
<i>maorum</i> Hutton, 1880:1	New Zealand	OM or CMC
<i>maya</i> Voss and Solis Ramirez, 1966:617	Gulf of Mexico	USNM
<i>mercatoris</i> * Adam, 1937:76	Gulf of Mexico	IRSNB
<i>microphthalmus</i> Goodrich, 1896:20	Andaman Ids.	ZSI
<i>micropyrsus</i> Berry, 1953:52	California, U.S.	USNM
<i>mimus</i> Gould, 1852:473	Peru	unknown
<i>minor minor</i> (Sasaki, 1920:181)	Japan	USNM
<i>minor pardalis</i> * (Sasaki, 1929:94)	Japan	MSUT?
<i>minor typicus</i> * (Sasaki, 1929:90)	Japan	MSUT?
<i>mototi</i> Norman, 1993b:329	E Australia	NMV
<i>mutilans</i> Taki, 1942:71	Japan	YTKC
<i>nanhaiensis</i> Dong, 1976:211	South China Sea	ASIO
<i>nanus</i> Adam, 1973:42	Red Sea	TAU
<i>occidentalis</i> Steenstrup in Hoyle, 1886:77	Ascension Id. (Atlantic Ocean)	BMNH
<i>ochotensis</i> (Sasaki, 1920:174)	Okhotsk Sea	USNM
<i>oculifer</i> Hoyle, 1904b:14	Galapagos Ids.	unknown
<i>oliveri</i> (Berry, 1914:136)	Kermadec Ids.	USNM
<i>ornatus</i> Gould, 1852:476	Hawaiian Ids.	USNM
<i>oshimai</i> (Sasaki, 1929:44)	Taiwan	FMHU (not extant)
<i>ovulum</i> * (Sasaki, 1917:364)	Japan	MSUT?
<i>pallidus</i> Hoyle, 1885b:223	SE Australia	BMNH
<i>parvus</i> (Sasaki, 1917:365)	Japan	FMHU
<i>penicillifer</i> Berry, 1954:66	Gulf of California, Mexico	USNM
<i>penterinus</i> * Rochebrune and Mabille, 1889:H7	Patagonia, Argentina	MNHN
<i>polyzenia</i> Gray, 1849:13	N Australia	BMNH
<i>prashadi</i> Adam, 1939a:103	Andaman Ids.	ZSI
<i>pricei</i> * (Berry, 1913a:73)	California, U.S.	CASIZ
<i>rapanui</i> Voss, 1979:360	Easter Id.	USNM
<i>robsoni</i> Adam, 1941c:1	Red Sea	MNHN
<i>rubescens</i> Berry, 1953:51	Gulf of California, Mexico	USNM
<i>salutii</i> Verany, 1839a:93	W Mediterranean Sea	MHNN
<i>sanctaehelenae</i> Robson, 1929c:74	St. Helena Id. (Atlantic Ocean)	BMNH
<i>sasakii</i> Taki, 1942:75	Japan	YTKC
<i>selene</i> Voss, 1971:11	Gulf of Panama	USNM
<i>spinus</i> * (Sasaki, 1920:177)	Japan	USNM (not extant)
<i>striolatus</i> Dong, 1976:212	South China Sea	ASIO
<i>supercilius</i> Quoy and Gaimard, 1832:88	Bass Strait, Australia	MNHN
<i>taprobanensis</i> * Robson, 1926:165	Sri Lanka	BMNH
<i>tehuelchus</i> Orbigny, 1834:27 (in 1834–1847)	Patagonia, Argentina	MNHN (not extant)
<i>tenebricus</i> Smith, 1884:35	NE Australia	BMNH
<i>tenuipulvinus</i> * (Sasaki, 1920:182)	Japan	USNM
<i>tetricus</i> Gould, 1852:474	SE Australia	lost
<i>tonganus</i> Hoyle, 1885b:225	Tonga Ids.	BMNH
<i>tsugarensis</i> * (Sasaki, 1920:175)	Japan	USNM
<i>validus</i> (Sasaki, 1920:183)	Japan	USNM
<i>varunae</i> Oommen, 1971:69	Arabian Sea	?INPC
<i>veligero</i> Berry, 1953:57	Gulf of California, Mexico	USNM

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>verrucosus</i> Hoyle, 1885b:222	Tristan da Cunha Id. (Atlantic Ocean)	BMNH
<i>vitiensis</i> Hoyle, 1885b:226	Fiji Ids.	BMNH
<i>warringa</i> Stranks, 1990:457	SE Australia	NMV
<i>winckworthi</i> Robson, 1926:161	S India	BMNH
<i>wolfi</i> (Wülker, 1913:458)	Tahiti Id., Society Ids.	SMF
<i>yendoi</i> * (Sasaki, 1920:179)	Korea	USNM
<i>zonatus</i> Voss, 1968:647	Colombia (Atlantic Ocean)	USNM
<i>Ameloctopus</i> Norman, 1992:568		
<i>litoralis</i> Norman, 1992:569	NE Australia	NMV
<i>Aphrodactopus</i> Roper and Mangold, 1992:58		
<i>schulzei</i> (Hoyle, 1910:261)	Namibia	ZMB
<i>Cistopus</i> Gray, 1849:20		
<i>indicus</i> (Rapp, 1835:24, in Férussac and Orbigny, 1834–1848)	Sulawesi, Indonesia	MNHN
<i>Enteroctopus</i> Rochebrune and Mabile, 1889:H5		
<i>membranaceus</i> Rochebrune and Mabile, 1889:H7	Tierra del Fuego, Chile	NMHN (not extant)
<i>juttingi</i> * Robson, 1929b:616	Chile	ZMA
<i>megalocyathus</i> (Gould, 1852:471)	Tierra del Fuego, Chile	lost
<i>Euaxoetopus</i> Voss, 1971:25		
<i>panamensis</i> Voss, 1971:25	Gulf of Panama	USNM
<i>pillsburyae</i> Voss, 1975:346	Surinam	USNM
<i>scalenus</i> * (Hoyle, 1904b:13)	7°N, 80°W (Pacific Ocean)	unknown
<i>Hapalochlaena</i> Robson, 1929c:207		
<i>lunulata</i> (Quoy and Gaimard, 1832:86)	Papua New Guinea	MNHN
<i>fasciata</i> (Hoyle, 1886:94)	SE Australia	BMNH
<i>maculosa</i> (Hoyle, 1883:319)	Australia	NMWZ
<i>nierstraszi</i> * (Adam, 1938b:14)	Andaman Ids.	IRSNB
<i>Pteroctopus</i> Fischer, 1882:334 (in 1880–1887)		
<i>tetracirrhus</i> (Chiaie, 1830, pl. 72)	Mediterranean Sea	unknown
<i>eurycephala</i> (Taki, 1964:313)	Japan	YTKC
<i>hoylei</i> (Berry, 1909:407)	Hawaiian Ids.	USNM
<i>keralensis</i> (Oommen, 1966:56)	SW India	OLUK
<i>witjazi</i> * Akimushkin, 1963:145	Sea of Okhotsk	lost
<i>Robsonella</i> * Adam, 1938a:223		
<i>fontaniana</i> (Orbigny, 1834:28 (in 1834–1847))	Chile	MNHN
<i>huttoni</i> Benham, 1943:53	New Zealand	OM
<i>Scaeuergus</i> Troschel, 1857:51		
<i>unicirrhus</i> (Chiaie, 1839–1841:70, in Férussac and Orbigny, 1834–1848)	Mediterranean Sea	unknown
<i>patagiatus</i> Berry, 1913b:564	Hawaiian Ids.	USNM (not extant)
Subfamily ELEDONINAE Grimpe, 1921		
<i>Eledone</i> Leach, 1817:137		
<i>moschata</i> (Lamarck, 1798:130)	not given	MNHN (not extant)
<i>caparti</i> Adam, 1950b:7	Congo, W Africa	IRSNB
<i>cirrhosa cirrhosa</i> (Lamarck, 1798:130)	not given	MNHN (not extant)
<i>cirrhosa zetlandica</i> Russell, 1922:11	Scotland	unknown
<i>gaucha</i> Haimovici, 1988:82	S Brazil	MORG
<i>massyae</i> Voss, 1964:511	Brazil	MZUSP
<i>microsicya</i> * (Rochebrune, 1884c:158)	Red Sea	MNHN
<i>palari</i> Lu and Stranks, 1992:73	E Australia	NMV
<i>Pareledone</i> Robson, 1932b:270		
<i>charcoti</i> (Joubin, 1905:22)	65°S, 64°W (Antarctic Ocean)	MNHN
<i>adelieana</i> (Berry, 1917:17)	66°S, 145°E (Antarctic Ocean)	AMS

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>antarctica</i> * (Thiele, 1920:434)	66°S, 89°E (Antarctic Ocean)	ZMB
<i>framensis</i> Lu and Stranks, 1994:227	67°S, 68°E (Antarctic Ocean)	NMV
<i>harrissoni</i> (Berry, 1917:24)	65°S, 96°E (Antarctic Ocean)	AMS
<i>polymorpha</i> (Robson, 1930b:390)	South Georgia Id.	BMNH
<i>prydzensis</i> Lu and Stranks, 1994:232	66°S, 72°E (Antarctic Ocean)	NMV
<i>turqueti</i> (Joubin, 1905:29)	65°S, 64°W (Antarctic Ocean)	MNHN
<i>Tetracheledone</i> Voss, 1955:107		
<i>spinicirrus</i> Voss, 1955:107	Cuba	MCZ
<i>Vosseledone</i> Palacio, 1978:282		
<i>charrua</i> Palacio, 1978:282	Uruguay	USNM
<i>Velodona</i> Chun, 1915:479		
<i>togata togata</i> Chun, 1915:479	W Indian Ocean	ZMB
<i>togata capensis</i> Robson, 1924a:206	South Africa	BMNH
Subfamily GRANELEDONINAE Voss, 1988		
<i>Graneledone</i> Joubin, 1918b:39		
<i>verrucosa verrucosa</i> (Verrill, 1881b:105)	New England, U.S.	USNM
<i>antarctica</i> Voss, 1976:448	74°S, 175°W (Antarctic Ocean)	USNM
<i>boreopacifica</i> Nesis, 1982:322	50°N, 151°E (Pacific Ocean)	ZIN
<i>challengeri</i> (Berry, 1916:49)	Kermadec Ids.	BMNH
<i>macrotyla</i> Voss, 1976:454	54°S, 55°W (Atlantic Ocean)	USNM
<i>verrucosa media</i> * (Joubin, 1918a:5)	43°N, 63°W (Atlantic Ocean)	MOM
<i>Bentheledone</i> Robson, 1932b:317		
<i>rotunda</i> (Hoyle, 1885b:230)	Antarctic Ocean	BMNH
<i>albida</i> * (Berry, 1917:15)	64°S, 127°E (Antarctic Ocean)	AMS
<i>Thaumeledone</i> Robson, 1930b:392		
<i>brevis</i> (Hoyle, 1885b:230)	Uruguay	BMNH
<i>gunteri</i> Robson, 1930b:392	South Georgia Id.	BMNH
Subfamily MEGALELEDONINAE Taki, 1961		
<i>Megaleledone</i> Taki, 1961:297		
<i>senoi</i> Taki, 1961:297	Antarctic Ocean	YTKC
Subfamily BATHYPOLYPODINAE Robson, 1928a		
<i>Bathypolypus</i> Grimpe, 1921:300		
<i>arcticus</i> (Prosch, 1847:59)	Greenland	ZMUC
<i>faeroensis</i> (Russell, 1909:446)	Iceland	ZMH
<i>proschi</i> Muus, 1962:13	W Greenland	ZMUC
<i>salebrosus</i> (Sasaki, 1920:182)	Japan	USNM
<i>sponsalis</i> (Fischer and Fischer, 1892:297)	W Africa	MNHN
<i>valdiviae</i> (Thiele in Chun, 1915:485)	Agulhas Bank, South Africa	ZMB
<i>Benthoctopus</i> Grimpe, 1921:300		
<i>piscatorum</i> (Verrill, 1879:470)	Nova Scotia, Canada	USNM
<i>abruptus</i> (Sasaki, 1920:173)	Japan	USNM
<i>berryi</i> Robson, 1924c:658	South Africa	BMNH
<i>canthylus</i> Voss and Percy, 1990:69	Oregon, U.S.	USNM
<i>ergasticus</i> (Fischer and Fischer, 1892:298)	W Africa	MNHN
? <i>eureka</i> (Robson, 1929c:179)	Falkland Ids.	NMSZ
<i>fuscus</i> * Taki, 1964:316	Japan	YTKC
<i>hokkaidensis</i> (Berry, 1921b:352)	Japan	USNM
<i>januarii</i> (Hoyle, 1885b:229)	NE Brazil	BMNH
<i>levis</i> (Hoyle, 1885b:229)	Antarctic Ocean	BMNH
<i>macrophallus</i> Voss and Percy, 1990:82	Oregon, U.S.	USNM
? <i>magellanicus</i> * Robson, 1930a:333	Tierra del Fuego, Chile	MNHN
<i>oregonae</i> Toll, 1981:88	Caribbean Sea	USNM

## Classification.—Continued.

Taxon	Type locality	Type repository
<i>oregonensis</i> Voss and Percy, 1990:73	Oregon, U.S.	USNM
<i>profundorum</i> Robson, 1932b:237	Japan	BMNH
<i>pseudonymus</i> * (Grimpe, 1922:41)	Azores Ids.	MOM
<i>robustus</i> Voss and Percy, 1990:67	Oregon, U.S.	USNM
<i>sibiricus</i> Loyning, 1930:1	76°N, 146°E (Arctic Ocean)	ZMUO?
<i>thielei</i> Robson, 1932b:233	Kerguelen Id.	ZMB
<i>yaquina</i> Voss and Percy, 1990:76	Oregon, U.S.	USNM
Family Tereotoptopodidae		
<i>Teretoptopus</i> Robson, 1929b:608		
<i>indicus</i> Robson, 1929b:608	Arabian Sea	ZSI
<i>alcocki</i> Robson, 1932b:251	N Indian Ocean	ZSI
<i>Grimpella</i> * Robson, 1928a:110		
<i>thaumastocheir</i> * Robson, 1928a:110	S Australia	BMNH
Family Tremoctopodidae Tryon, 1879		
<i>Tremoctopus</i> Chiaie, 1830, pls. 70, 71		
<i>violaceus violaceus</i> Chiaie, 1830, pls. 70, 71	Mediterranean Sea	unknown
<i>violaceus gracilis</i> (Eydoux and Souleyet, 1852:13)	8°N, 106°W (Pacific Ocean)	MNHN
<i>gelatus</i> Thomas, 1977:371	E Florida, U.S.	USNM
Family Ocythoidae Gray, 1849		
<i>Ocythoe</i> Rafinesque, 1814:29		
<i>tuberculata</i> Rafinesque, 1814:29	Mediterranean Sea	lost
Family Argonautidae Tryon, 1879		
<i>Argonauta</i> Linnaeus, 1758:708		
<i>argo</i> Linnaeus, 1758:708	Mediterranean Sea	LS
<i>boettgeri</i> Maltzan, 1881:163	unknown	unknown
<i>cornuta</i> * Conrad, 1854:332	not given	ANSP
<i>hians</i> Lightfoot, 1786:44	not given	unknown
<i>nodosa</i> Lightfoot, 1786:96	Cape of Good Hope, Africa	unknown
<i>nouryi</i> Lorois, 1852:10	Marquesas Ids.	unknown
<i>pacifica</i> Dall, 1871:95	California, U.S.	USNM?
Family Alloposidae Verrill, 1881a		
<i>Haliphron</i> Steenstrup, 1861a:332		
<i>atlanticus</i> Steenstrup, 1861a:332	38°N, 34°W (Atlantic Ocean)	ZMUC
<i>hardyi</i> * (Robson, 1930b:397)	0°56'S, 14°08'W	BMNH
<i>pacifica</i> * (Ijima and Ikeda, 1902:87)	Sagami Sea, Japan	MSUT?
Order Vampyromorphida Pickford, 1939		
Family Vampyroteuthidae Thiele in Chun, 1915		
<i>Vampyroteuthis</i> Chun, 1903:88		
<i>infernalis</i> Chun, 1903:88	Gulf of Guinea	ZMB

<sup>1</sup>The classification of the Sepiidae is based primarily on Khromov (1987b), who defined a number of subgenera in an attempt to clarify the complex species structure in the large, unwieldy genus *Sepia*. We have incorporated, however, some of the changes introduced in this publication by Khromov et al. (1998), principally those that transferred species from a designated subgenus into the category "subgenus undetermined." Khromov et al. (1998) retain a "species complex" concept but do not uniformly use subgeneric designations.

<sup>2</sup>See Tsuchiya and Okutani (1992) for evidence that *Onykia* represents a juvenile stage of *Moroteuthis*. Further nomenclatural scrutiny is in progress.

<sup>3</sup>See Roper and Lu (1989) and Nesis and Nikitina (1990) regarding systematic problems in this family.

<sup>4</sup>See Roper and Boss (1982) regarding systematic problems in this family.

<sup>5</sup>This speciose family currently is being monographed by N.A. Voss, and due to considerable amounts of synonymy, only genera and type species are listed (except *Teuthowenia*).



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(Taxa of uncertain validity, which require further study to be published either as a synonym or as a valid species, are indicated by an asterisk (\*). Species with undetermined generic affinities are indicated by family name in brackets.)

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*verrilli*, ?*Onykia*, 572  
*verrucosa media*\*, *Graneledone*, 581  
*verrucosa verrucosa*, *Graneledone*, 581  
*verrucosus*, *Octopus*, 580  
*vietnamica*, *Sepia* (*Doratosepion*), 566  
*violaceus gracilis*, *Tremoctopus*, 582  
*violaceus violaceus*, *Tremoctopus*, 582  
*virilis*, *Walvisteuthis*, 572  
*vitiensis*, *Octopus*, 580  
*volatilis*, *Ornithoteuthis*, 574

*vossi*, *Opisthoteuthis*, 577  
*vossi*, *Uroteuthis* (*Photololigo*), 570  
*vulgaris reynaudi*, *Loligo* (*Loligo*), 569  
*vulgaris vulgaris*, *Loligo* (*Loligo*), 569  
*vulgaris*, *Octopus*, 577  
  
*warringa*, *Octopus*, 580  
*weberi*, *Heteroteuthis* (*Heteroteuthis*), 568  
*weberi*, *Sepiella*, 566  
*whitleyana*, *Sepia* (s.g. undet.), 566

*winckworthi*, *Octopus*, 580  
*witjazi*\*, *Pteroctopus*, 580  
*wolffi*, *Octopus*, 580  
*wülkeri*, *Grimpoteuthis*, 577  
  
*yaquina*, *Bethoctopus*, 582  
*yendoi*\*, *Octopus*, 580  
  
*zanzibarica*, *Sepia* (*Acanthosepion*), 565  
*zonatus*, *Octopus*, 580



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