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Contents

ABSTRACT

A dichotomous key to the twenty-five families of cephalopods of the order Teuthoidea is presented. A supplementary chart of basic, external teuthoid characters is included. Representatives of each family are illustrated. The current state of systematics within each family is briefly discussed.

Introduction

No comprehensive key to the families of the Teuthoidea has been published since Hoyle's key to the dibranchiate Cephalopoda (1904). Hoyle's excellent work also includes a key to the genera. Three major keys on the suborder Oegopsida also were published around the turn of the century. The first of these keys was presented by Goodrich (1892) and dealt only with the genera of oegopsids. This was followed in 1900 by Pfeffer's synopsis of the oegopsid cephalopods which included a comprehensive key to the twelve known families. The remaining key to appear on oegopsids was published in Pfeffer's extensive monograph (1912); this was a modification of his earlier key, but utilized external characters only. Although not a key, Thiele's handbook (1935) includes brief diagnoses of the genera of Recent cephalopods known at that time. This work should be used with caution, however, because some of the diagnoses are incomplete and misleading.

Advancements in the systematics of recent cephalopods have decisively altered earlier concepts and the former keys no longer reflect current knowledge. The need for a modern key is particularly pressing in the order Teuthoidea in which the number of families has nearly doubled since the last major revision (i.e., Pfeffer, 1912). Furthermore, the rapid expansion in the fields of fisheries science and biological oceanography has created a greater need by nonteuthologists for information about cephalopods. The cephalopods with which the programs in these fields are involved belong primarly to the order Teuthoidea.

The present work is designed for rapid identification of the families of the order Teuthoidea by utilization of a dichotomous key, a supplementary chart of basic characters, illustrations, and discussions of individual families. We believe this is the most effective method of presentation permitting the familial identification of both whole and damaged specimens. This paper is designed for use by the nonspecialist as well as the specialist.

The dichotomous key utilizes only external characters which have been kept to a minimal number. It is designed primarily for the identification of adult specimens; therefore, one should use caution when dealing with larval forms. The order in which the families are presented is not necessarily indicative of phylogenetic relationship; some closely related groups naturally will fall together, while others may be widely separated. The diagrams in Figure 1 illustrate most of the morphological terms presented in the key. The ventral arms are often modified in males (hectocotylization), and the tips of the other arms occasionally may be modified; these modifications should not be confused with the typical characters of the arms used in the key. Some groups are characterized by the absence of tentacles, but lack of tentacles may also result from injury. Injured specimens, however, invariably show stubs of the missing tentacles.

The chart presents a brief summary of the basic characters for each family. It should be particularly useful if damaged specimens lack certain characters that are utilized in the key. Representative species of each family are illustrated, and atypical forms are illustrated where necessary. A discussion is presented which more fully characterizes each family, briefly surveys the genera, and reflects the current status of their systematics. References to recent works dealing with the systematics of families and genera are given where possible.

ACKNOWLEDGMENTS.—Many of the illustrations are reproduced from recent works of the authors and were originally drawn by Miss Constance Stolen, as was the diagram of the basic teuthoid features; we gratefully acknowledge her contribution. The remaining illustra-

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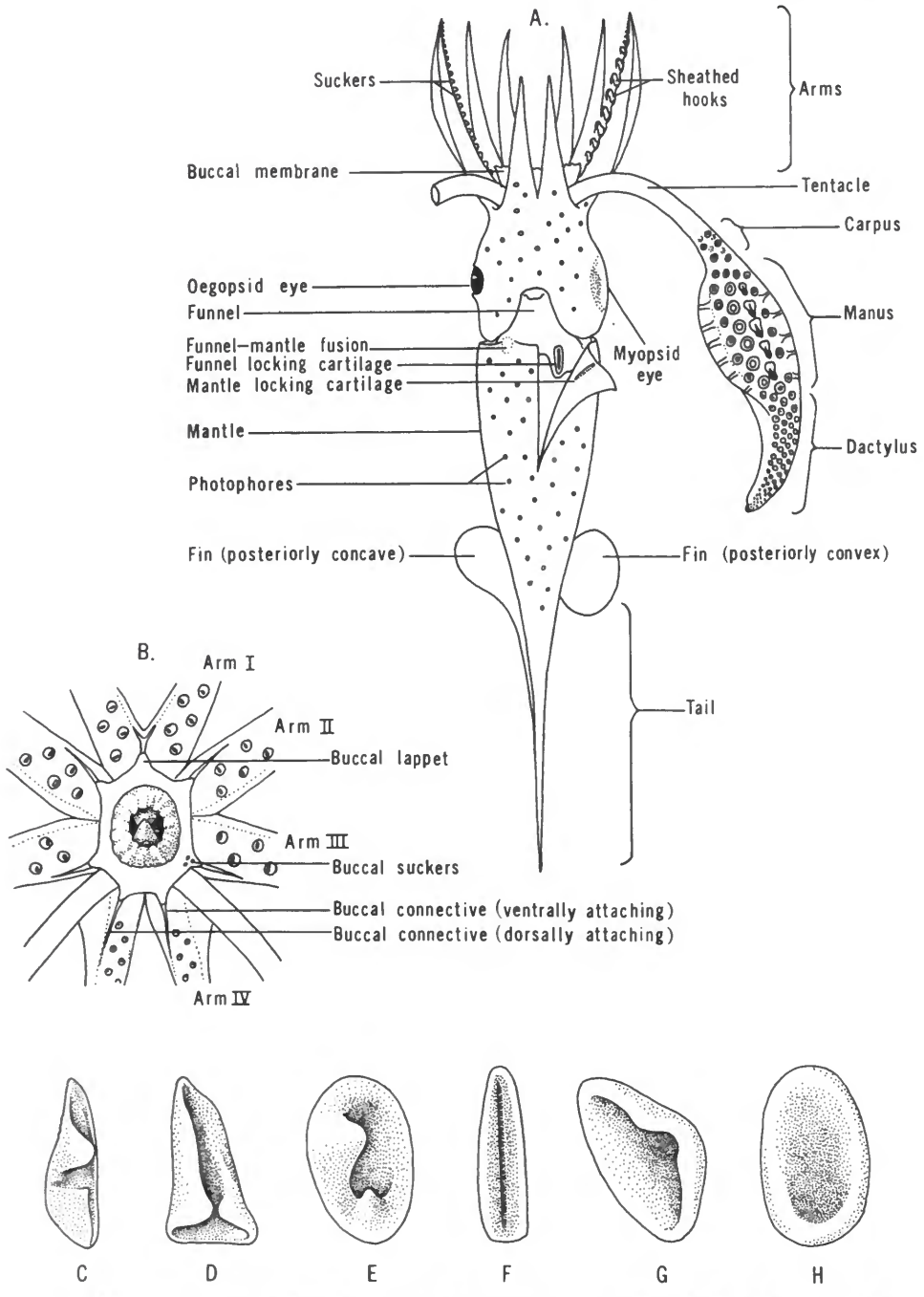

FIGURE 1.—A, A composite diagram illustrating basic teuthoid features. B, Diagram of oral surface of brachial crown and buccal membrane. Basic types of funnel locking-cartilage: C, ⊣-shaped; D, ⊥-shaped; E, oval with inward projecting knobs; F, simple, straight; G, subtriangular; H, oval.

tions come from published teuthological works of other authors. The work was partially supported by grants GB 57294 and GA 1493 from the National Science Foundation. We wish to thank the following persons from the Institute of Marine Sciences for testing and commenting on the key: E. S. McSweeny, G. Y. Hendrix, E. T. LaRoe, and students of the invertebrate taxonomy class.

Key to the Families of the Order Teuthoidea

1. Eye covered by a transparent membrane (cornea) (Figure 1A) (Myopsida) 2
   Eye without cornea and in open contact with seawater (Figure 1A) (Oegopsida) 3
2. Four rows of suckers on manus of tentacular clubs. Medial posterior border of fins concave (i.e., curves posteriorly toward midline) (Figure 1A) . . . . . Loliginidae (Plate 1A, B)
   Two rows of suckers on manus of tentacular clubs. Medial posterior border of fins convex (i.e., curves anteriorly toward midline) (Figure 1A) . . . . . Pickfordiateuthidae (Plate 1C, D)
3. Funnel free from mantle; a funnel-mantle locking apparatus present . . . . . 4[a]
   Funnel fused to mantle on each side; no funnel-mantle locking apparatus present (Figure 1A) . 24
4. Funnel-mantle locking apparatus a simple, straight groove and ridge (Figure 1F) . . . . 5[b]
   Funnel-mantle locking apparatus not a simple, straight groove and ridge (Figures 1C, D, E, G, H) 18
5. Arms with hooks or with suckers in four rows on the proximal half of the ventral arms . . 6
   Arms without hooks and with suckers in two rows on the proximal half of the ventral arms. 8
6. Armature of arms in two rows 7
   Armature of arms in four rows . . . . . Gonatidae (Plate 2A–D)
7. Tentacles present; fully developed clubs present . . . . . Enoploteuthidae (Plate 3A–C)
   Tentacles and clubs absent in adults although present in larvae or occasionally juveniles (*Taningia*) but always with rudimentary clubs . . . . . Octopoteuthidae (Plate 3D)
8. Buccal membrane connectives attach to the ventral sides of arms IV (Figure 1B) 9
   Buccal membrane connectives attach to the dorsal sides of arms IV . . . . . 13[c]
9. Hooks present on tentacular clubs (tentacles and clubs unknown in *Chaunoteuthis*). . . . . Onychoteuthidae (Plate 4A–C)
   Hooks lacking on tentacular clubs 10
10. Cartilaginous scales present on mantle (may be minute) (Figure 2). Tentacular clubs with four longitudinal rows of suckers . . . . . Lepidoteuthidae (Plate 4D)
    Cartilaginous scales lacking. Tentacular clubs with more than four longitudinal rows of suckers on some areas 11
11. Fins nearly as long as the mantle, supported by strong, transverse, muscular ribs. Minute suckers present on oral surface of buccal lappets (Figure 1B) . Ctenopterygidae (Plate 5C)
    Fins less than half the body length and without supporting ribs. No suckers on buccal lappets. 12
12. Tentacular clubs with six uniform rows of suckers. Long spike-like tail present (greater than the fin length) . . . . . Batoteuthidae (Plate 6A, B)
    Tentacular clubs with four rows of suckers on distal portion, numerous rows on proximal portion. No tail present . . . . . Brachioteuthidae (Plate 7A, B)
13. Ventral surface of eye with a row of photophores. Buccal membrane with eight separate lappets. . . . . Lycoteuthidae (Plate 7C, D)
    No photophores on eyes. Buccal membrane with seven lappets or less 14
14. Surface of mantle, head, and arms covered with numerous photophores (usually large and distinct) . . . . . Histioteuthidae (Plate 8A, B)
    Surface of mantle and head without photophores (arms may have a few photophores). . 15
15. Minute suckers present on oral surface of buccal lappets. . . . Bathyteuthidae (Plate 9A–C)
    No suckers on oral surface of buccal lappets 16

[a] See footnote 1 in Table 1.
[b] See footnote 2 in Table 1.
[c] See footnote 3 in Table 1.

Key to the Families of the Order Teuthoidea—Continued

16. Many small to minute suckers (or suckers and knobs) at the proximal end of the manus . . 17
    No cluster of small suckers at proximal end of the manus . . . Psychroteuthidae (Plate 8C, D)
17. Medial posterior borders of fins slightly convex. Carpal knobs in a single dorsal row or absent. Small size . . . . . Neoteuthidae (Plate 10A–D)
    Medial posterior borders of fins concave. Carpal knobs in a cluster alternating with carpal suckers. Attains gigantic size . . . . . Architeuthidae (Plate 11C, D)
18. Funnel locking-cartilage with a longitudinal and a transverse groove, ⊥-shaped or ⊣-shaped (Figure 1D or C) 19
    Funnel locking-cartilage oval, triangular or oval with inward projecting knobs (Figures 1H, G, E) 20
19. Funnel locking-cartilage with a longitudinal groove crossed by a transverse groove at its posterior end, ⊥-shaped (Figure 1D). Fins less than 60% of mantle length . . . . . Ommastrephidae (Plate 11A, B)
    Funnel locking-cartilage with a longitudinal groove from which a shorter groove branches medially, ⊣-shaped (Figure 1C). Fins more than 80% of mantle length . . . . . Thysanoteuthidae (Plate 12A)
20. Funnel locking-cartilage oval with one or two knobs directed toward the center of the concavity (Figure 1E) . . . . . 21[d]
    Funnel locking-cartilage oval or subtriangular, without knobs (Figures 1G, H). 22
21. Club with only four rows of suckers . . . . . Chiroteuthidae (Plate 13A–E)
    Club with many (more than 15) rows of minute suckers . . Mastigoteuthidae (Plate 12B, C)
22. Suckers on arms in four to six rows. Tail extremely long (greater than the mantle length). . . . . Joubiniteuthidae (Plate 6C, D)
    Suckers on arms in two rows. Tail short (less than half the mantle length) or absent. . . 23
23. Suckers on the tentacular clubs in four longitudinal rows. Mantle free dorsally. . . . . Cycloteuthidae (Plate 14A–E)
    Suckers on the tentacular clubs in eight or more longitudinal rows. Mantle fused dorsally to head . . . . . Promachoteuthidae (Plate 5A, B)
24. Mantle free dorsally—articulates with head by ridge and groove. . . . . Grimalditeuthidae (Plate 15A)
    Mantle fused dorsally with head . . . . . Cranchiidae (Plates 15B–D and 16A–D)

[d] See footnote 4 in Table 1.

Suborder MYOPSIDA

This suborder contains two families of near-shore, usually shallow water, squids, many of which form the basis of commercial fisheries (see Fields, 1965). Members of the Myopsida can be recognized by the presence of corneal membranes covering the eyes.

LOLIGINIDAE sensu restricto Steenstrup, 1861

PLATE 1A, B

Presently eight genera are recognized in the family: *Loligo, Doryteuthis, Lolliguncula, Sepioteuthis, Loliolopsis, Loliolus, Alloteuthis,* and *Uroteuthis. Loligo* is the most common and speciose genus. Members of the family are primarily distributed throughout the warm waters of the world, although some species of *Loligo* occur in colder regions.

The characteristic features of this family include a straight, simple locking apparatus, seven buccal lappets each with a few small suckers, buccal connectives that attach to the ventral borders of arms IV, four rows of suckers on the manus, two rows of suckers on the arms, and fins with concave posterior borders. Photophores are present in some species.

PICKFORDIATEUTHIDAE Voss, 1953

PLATE 1C, D

This recently described family (Voss, 1953) contains a single species, *Pickfordiateuthis pulchella,* which is known only from the tropical western Atlantic. It is a small species that has a mantle length of about 13–17 mm at maturity. The family characteristics include the presence of only two rows of suckers on the manus of the tentacular clubs; biserial suckers on the arms; small, round fins with convex posterior borders; buccal membranes with reduced lappets and no suckers; buccal connectives that attach to the ventral sides of arms IV; and a straight, simple funnel locking apparatus. Photophores are absent.

TABLE 1.—*Comparison of basic characters for all families of the Teuthoidea*

Families	*Funnel locking apparatus*					*Buccal connectives to arms IV*		*Arms I–III (excluding tips)* [5]				*Clubs*			
	Simple, straight groove and ridge [2]	⊥, ⊣	*Oval with inward projecting knobs*	*Round or triangular*	*Fused*	*Attached dorsally*	*Attached ventrally*	*Armature in two rows*	*Armature in four rows*	*Armature in more than four rows*	*Hooks present*	*Armature in up to four rows*	*Armature in more than four rows*	*Hooks present*	*No tentacles*
Loliginidae	X						X	X				X			
Pickfordiateuthidae	X						X	X				X			
Gonatidae	X						X		X		X [6]		X	X [16]	X [16]
Enoploteuthidae	X					X		X			X	X		X [17]	
Octopoteuthidae	X						X	X			X				X
Onychoteuthidae	X						X	X				X		X	
Lepidoteuthidae	X						X	X				X [10]			X [10]
Ctenopterygidae	X						X		X [7]	X [7]			X		
Batoteuthidae	X						X	X					X		
Brachioteuthidae	X						X	X					X		
Lycoteuthidae	X					X		X				X			
Histioteuthidae	X					X [3]		X				X [11]	X [11]		
Bathyteuthidae	X					X			X [8]				X		
Psychroteuthidae	X					X		X				X [12]	X [12]		
Neoteuthidae	X					X		X				X [13]	X [13]		
Architeuthidae	X					X		X				X [14]	X [14]		
Ommastrephidae		X [1]				X		X				X [15]	X [15]		
Thysanoteuthidae		X					X	X				X			
Chiroteuthidae			X				X	X				X			
Mastigoteuthidae			X [4]				X	X					X		
Joubiniteuthidae				X			X			X			X		
Cycloteuthidae				X			X	X				X			
Promachoteuthidae				X			X	X					X		
Grimalditeuthidae					X		X	X							X
Cranchiidae					X		X	X			X [9]	X		X [18]	

[1] See, however, *Symplectoteuthis*, under the discussion of the Ommastrephidae.

[2] The classification "simple and straight" includes some locking apparatuses that show considerable variation. For example, in the Octopoteuthidae and the Histioteuthidae the central groove is fairly broad and may curve slightly and in *Gonatopsis borealis* (Gonatidae) the central groove flares broadly at its posterior end. The homogeneity of this classification becomes apparent when this type of locking-cartilage is contrasted with the highly specialized types illustrated in Figure 1.

[3] This character is difficult to detect in some histioteuthids because of the development of secondary connectives.

[4] In some mastigoteuthids the knobs are difficult to distinguish. See also *Mastigoteuthis magna* under discussion of the Mastigoteuthidae.

[5] The arm characters used here refer only to the dorsal three pairs of arms; ventral arms frequently are modified. The characters of the extreme tips of the arms are also excluded from this chart because the tips occasionally are modified by an increase in the number of sucker rows.

[6] Males of *Berryteuthis anonychus* lack hooks. Females of this species have hooks near the bases of arms I–III.

[7] *Ctenopteryx* has sucker rows that increase distally to four or sometimes six rows.

[8] The rows of suckers on the arms of *Bathyteuthis* are irregularly arranged, beginning proximally with one or two rows but increasing to three or four rows.

[9] Only one species, *Mesonychoteuthis hamiltoni*, has hooks on the arms.

[10] Two genera, *Pholidoteuthis* and *Tetronychoteuthis*, have four rows of suckers on the clubs; *Lepidoteuthis* lacks tentacles.

[11] Most, but not all, species of *Histioteuthis* have more than four rows of suckers on the club.

[12] The species of *Psychroteuthis* have from four to seven irregular rows of suckers on the club.

[13] Young members of the Neoteuthidae have four rows of suckers on the clubs, however, with growth numerous rows of suckers appear at the proximal end of the manus and on the tentacular stalk.

[14] Architeuthids have four rows of suckers on the manus and dactylus but more than four rows in the carpal locking region.

[15] *Illex* has eight rows of suckers on the dactylus. Other members of the family have four rows of suckers on the manus and dactylus.

[16] *Berryteuthis* has clubs with only suckers and no hooks; *Gonatus* has some hooks; *Gonatopsis* lacks tentacles.

[17] One genus, *Pterygioteuthis*, has only suckers on the clubs.

[18] Several genera, e.g., *Galiteuthis* and *Mesonychoteuthis*, have some hooks on the clubs.

Suborder OEGOPSIDA

Species of this suborder generally inhabit the open sea from the surface to great depths. The group is very diverse in species and exhibits a wide variety of forms.

The Oegopsida is distinguished from the Myopsida primarily by the absence of a corneal membrane over the eye. The oegopsid eye is directly bathed in sea water. The muscular integument of the head encircles the eye, forming an oval eyelid capable of a sphincter-like contraction. A contracted eyelid in a preserved specimen may give the false impression that the eye is covered by a cornea. If one is careful, however, there should be no difficulty in distinguishing the two suborders of squids.

GONATIDAE Hoyle, 1886

PLATE 2A–D

This family is characterized by tetraserial armature on the arms. Arm tips, however, in one species, *Gonatopsis octopedatus,* are modified and have up to twelve rows of minute suckers. The two medial rows of arms I–III consist of hooks in all species, except *Berryteuthis anonychus,* which has only suckers, except at the bases of some arms in females. All members of the family have a simple, straight funnel locking-cartilage which may flare slightly at the posterior end; buccal connectives that attach to the ventral borders of arms IV; numerous irregular rows of suckers on the clubs with additional hooks in some forms (i.e., *Gonatus* species). Only one species in the family has photophores (*Gonatus,* new species); these are oval patches located on the ventral surfaces of the eyes.

Three described genera, *Gonatus, Berryteuthis,* and *Gonatopsis,* are known. *Gonatus* is characterized by at least a single large hook in the center of the tentacular club and only five longitudinal rows of radular teeth. *Berryteuthis* is characterized by the absence of hooks on the tentacular club and by seven longitudinal rows of radular teeth. This genus has previously been considered a synonym of *Gonatus* or at best a subgenus. However, with the recent discovery of a number of new species of *Gonatus,* the generic differences are now more clearly defined and the evidence indicates that *Berryteuthis* should be considered a valid genus (Young, in manuscript). *Gonatopsis* is characterized by the complete loss of tentacles, except in the early larval forms (Young, in press).

Species in this family are cold water forms and are among the most abundant squids in higher latitudes.

ENOPLOTEUTHIDAE Pfeffer, 1900

PLATE 3A–C

All members of this large family possess a straight locking apparatus; biserial armature (except occasionally at the arm tips) with at least some hooks on the arms; tetraserial armature on the clubs (marginal suckers of the manus may be lost with growth in some species); photophores; eight buccal lappets and buccal connectives that attach dorsally to the ventral arms (*Enoploteuthis dubia* Adam, 1960, is unique in having connectives that attach dorsally to all arms). All species, except those of the genus *Pterygioteuthis,* possess hooks on the tentacular clubs.

The Enoploteuthidae is divided into three long-established subfamilies: Enoploteuthinae, Pyroteuthinae, and Ancistrochirinae. The Enoploteuthinae is characterized by the absence of nidamental glands, presence of numerous, small photophores over the suface of the mantle, head and arms, but not on the tentacles or viscera, and fins with concave posterior borders. This is the most speciose subfamily and contains the following genera: *Enoploteuthis, Abralia, Abraliopsis,* and *Watasenia.* The Pyroteuthinae has nidamental glands, no photophores on the surface of the mantle, head or arms, but large photophores embedded in the tentacles and others present on the viscera, and fins with convex posterior borders. Two genera, *Pyroteuthis* and *Pterygioteuthis,* are included in this subfamily. The Ancistrochirinae has nidamental glands, a few large scattered photophores on the surface of the mantle, head, and tentacles, but not on the arms or viscera, and huge fins with convex posterior borders. Two genera, *Thelidioteuthis* and *Ancistrochirus,* are known, but there is a possibility that the first is a synonym of the latter. Occasionally *Abralia, Abraliopsis,* and *Watasenia* have been split from the Enoploteuthinae as a separate subfamily, the Abraliinae. This division, however, cannot be maintained on the basis of present knowledge.

Enoploteuthids are primarily inhabitants of the tropical and subtropical oceans of the world. Some species of *Pterygioteuthis, Abraliopsis,* and *Watasenia,* however, inhabit temperate waters as well. (Recent works include Roper, 1966, and Voss, in manuscript.)

OCTOPOTEUTHIDAE Berry, 1912

PLATE 3D

The family is characterized by biserial hooks on the arms (usually replaced by small biserial suckers near the arm tips); a lack of tentacles; buccal connectives that attach to the ventral borders of arms IV; a simple, straight, slightly broad funnel locking-cartilage; very large fins; light organs at the tips of at least some of the arms.

The family presently consists of two genera, *Octopoteuthis* and *Taningia*. Tenacles are present in larval forms of all species but are lost very early in *Octopoteuthis,* while they remain for some time in *Taningia* as small rudimentary filaments which bear a few distal suckers. *Octopoteuthis* bears small spindle-shaped photophores at the tips of all eight arms, but *Taningia* bears very large photophores only at the tips of the second arms. The genus *Octopodoteuthopsis* Pfeffer, 1912, was synonymized with *Octopoteuthis* by Robson (1948). Recent workers have retained the genus *Octopodoteuthopsis;* however, this genus does not differ significantly from *Octopoteuthis* and the genus cannot be maintained (Young, in press).

Considerable confusion concerning the correct name of this family and its type genus has existed from the time of Rüppell's original description of *Octopoteuthis sicula* to the present day. Therefore, it is necessary to review the nomenclatural history of the family in detail.

Rüppell's description of *Octopoteuthis sicula* was published in March 1844. The new generic name was mentioned three times, always spelled *Octopoteuthis.* Rüppell stated that the new genus was called *Octopoteuthis* because it united the characters of *Octopus, Loligo,* and *Enoploteuthis.* Regardless of the soundness of such a relationship, Rüppell's intentions are clear—he used the stem of *Octopus* in forming the name.

Krohn (1845) described the species in more detail and discussed the generic relationships. The generic name was used only twice, in the title and in the final sentence. Both times it was spelled *Octopodoteuthis.* Krohn gave no reason for the emended spelling; he simply stated that, following Rüppell's suggestion, he called the genus *Octopodoteuthis.* This is an "unjustified emendation" according to the International Code of Zoological Nomenclature (Article 33). The original spelling was correct, and Krohn's name is a junior objective synonym.

Krohn added to the confusion futher in 1847 when he changed the name of "*Octopodoteuthis*" to *Verania* because he discovered that the young of *O. sicula* have tiny tentacles—thus have 10 appendages—so the original name no longer applied to the condition of the species. A change of this sort, of course, is untenable (Article 18); *Verania* is merely a junior synonym of *Octopoteuthis.*

Chun (1910) accepted the name *Octopodoteuthis* and created it for a new family. Chun, however, based the name of the family, the Veranyidae, on the genus *Veranya* which he admitted was a junior synonym. Therefore, although Chun was the first to have a concept of the family, his name is inadmissible because it was originally based on a generic name that was not currently valid. Berry (1912) correctly pointed out that Chun's Veranyidae is untenable because *Veranya* is an "exact synonym of *Octopoteuthis.*" He concluded that Octopoteuthidae (or Octopodoteuthidae if Krohn's emendation could be accepted) must replace Veranyidae.

Pfeffer's monograph came out in 1912 also; he called the group Octopodoteuthinae, based on the incorrectly emended generic name. This would require subsequent emendation to Octopoteuthinae and elevation to Octopoteuthidae. We have been unable to determine the exact date of publication of Pfeffer's monograph and, therefore, must consider it as published on the last day of the year. The authorship of the family name must then be attributed to Berry.

Adam (1952) correctly used *Octopoteuthis* and gave a good synonymy.

ONYCHOTEUTHIDAE Gray, 1849

PLATE 4A–C

The family is characterized by tetraserial armature generally present on the tentacular clubs (the tentacles of *Chaunoteuthis* are unknown), of which the two median rows consist of hooks and the marginal rows of suckers (in some forms the marginal rows are absent; straight simple locking apparatus; two rows of suckers on the arms; buccal connectives that attach to the ventral sides of arms IV. Most members of the family are strong, active swimmers.

Five genera are currently recogized: *Onychoteuthis, Onykia, Moroteuthis, Ancistroteuthis,* and *Chaunoteuthis.* The generic boundaries, however, are not well defined and the family is in need of revision.

Onychoteuthis is the most widely distributed genus and the only genus of the onychoteuthids known to possess photophores. *Onykia* contains the smallest forms

in the family and has a number of poorly defined species in tropical seas. *Moroteuthis* is the giant of the family; the largest recorded specimen had a total length greater than four meters (Verrill, 1876). *Chaunoteuthis* differs from the other genera by having a gelatinous consistency.

LEPIDOTEUTHIDAE Pfeffer, 1912

PLATE 4D

Formerly only a single species, *Lepidoteuthis grimaldii,* was included in this family. We, however, include two additional genera, *Pholidoteuthis* and *Tetronychoteuthis,* although a detailed analysis of the three genera is necessary to confirm their relationships. The lack of sufficient material has resulted in the uncertain position of these genera. *Pholidoteuthis* was previously placed in its own family, the Pholidoteuthidae; *Tetronychoteuthis* had been included in the Onychoteuthidae, although its placement there is clearly unwarranted.

The family Lepidoteuthidae is characterized by the presence of distinct "scales" on the mantle (Figure 2), buccal connectives that attach to the ventral borders of arms IV, straight, simple funnel locking-cartilage, biserial suckers on the arms, and tetraserial suckers on the tentacular clubs, except in *Lepidoteuthis,* which lacks tentacles in the adults. Photophores are absent.

Species of *Lepidoteuthis* and *Pholidoteuthis* are known to attain large size: 97 cm mantle length in *Lepidoteuthis* (Clarke and Maul, 1962), and 78 cm mantle length in *Pholidoteuthis* (Voss, unpublished).

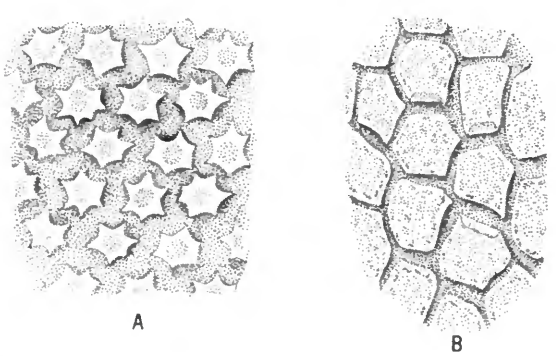

FIGURE 2.—Cartilaginous scales on the surface of the mantle in the Lepidoteuthidae: A, *Tetronychoteuthis;* B, *Pholidoteuthis.*

The most characteristic feature of this family is the existence of distinct cartilaginous "scales" that occur only on the surfaces of the mantle. The posterior end of the mantle, however, is devoid of "scales." The scaleless area on the dorsal side extends nearly to the anterior margin of the fins, but on the ventral side it occurs only on the posterior two-thirds of the area covered by the fins.

CTENOPTERYGIDAE Grimpe, 1922

PLATE 5C

The only genus in this family, *Ctenopteryx,* is readily distinguished by its long, ribbed fins; suckers on the lappets of the buccal membrane; eight to fourteen longitudinal rows of small suckers on the tentacular clubs; four to six rows of suckers on the distal half of arms I–III; buccal connectives that attach to the ventral borders of arms IV; straight, simple, locking-cartilage; photophores in some species. A number of species exist; however, due to the confused state of the systematics within the genus, all forms have long been lumped under the name *C. sicula.*

BATOTEUTHIDAE Young and Roper, 1968

PLATE 6A, B

This family has recently been discovered in Antarctic waters. The arms bear two rows of suckers, and the tentacles bear very elongate clubs with six longitudinal rows of suckers. The buccal connectives attach to the ventral borders of arms IV; the funnel locking-cartilage has a simple, straight groove; the posterior end of the body is drawn out into a long, sharp tail. The single species, *Batoteuthis scolops,* is known only from Antarctic waters.

The title page of the journal (Antarctic Research Series) in which the description of the family first appeared inadvertently listed the publication date as 1967. The actual date of publication was May 1968.

BRACHIOTEUTHIDAE Pfeffer, 1908

PLATE 7A, B

This family is monotypic and characterized primarily by the presence of numerous rows of small suckers on the proximal portion of the tentacular clubs, straight, simple funnel locking-cartilage, ventral attachment of the buccal connectives to arms IV, two rows of suckers on the arms, and long slender bodies

with relatively short terminal fins. Some species of *Brachioteuthis* have peculiar larvae with characteristic, long, slender necks. The family is badly in need of a revision.

LYCOTEUTHIDAE Pfeffer, 1908

PLATE 7C, D

The family is distinguished by biserial suckers on the arms, tetraserial suckers on the tentacular clubs, straight, simple funnel locking-cartilage, buccal membrane with eight lappets and supports, buccal connectives that attach to the dorsal borders of arms IV, and photophores at least on the viscera and the ventral surfaces of eyes.

Two subfamilies are known. The Lampadioteuthinae represented by a single species, *Lampadioteuthis megaleia*, is distinguished by the peculiarities of its pen and by the presence of only four light organs on the eye. The Lycoteuthinae has a characteristic pen and five photophores on the ventral surface of the eye. This subfamily has four genera: *Lycoteuthis, Selenoteuthis, Nematolampas,* and *Oregoniateuthis*. The family recently was monographed by Voss (1962).

HISTIOTEUTHIDAE Verrill, 1881

PLATE 8A, B

This monotypic family is easily distinguished by large, anteriorly directed photophores over the surface of the mantle, head and arms; large head with the left eye considerably larger than the right; six or seven buccal lappets; buccal connectives that attach to the dorsal border of arms IV; a straight or slightly curved and slightly broad, simple, funnel locking-cartilage; suckers on the tentacular clubs arranged in four, or more commonly, greater than four irregular rows; suckers on the arms biserial.

The family is being monographed by N. Voss (in press).

BATHYTEUTHIDAE Pfeffer, 1900

PLATE 9A–C

The family is distinguished by the presence of a straight funnel locking-cartilage, buccal connectives that attach to the dorsal borders of arms IV, suckers on the buccal lappets, small clubs with many rows of minute suckers, round or paddle-like subterminal fins (i.e., posterior margins convex), suckers on the arms arranged in irregular rows (two rows proximally increasing to four distally), and a deep maroon color. A single photophore is embedded at the base of each arm I–III. This is easily apparent in young specimens but may be obscure in adults.

The family contains a single genus, *Bathyteuthis,* and three species. The most common species, *B. abyssicola,* is a deep sea form that has been recorded from all major oceans and is most abundant between 1000 m and 2500 m; *B. abyssicola* is one of the most numerous cephalopods in the Antarctic waters. The systematics and distribution of the family have been recently studied (Roper, 1969).

PSYCHROTEUTHIDAE Thiele, 1921

PLATE 8C, D

The monotypic family is based on *Psychroteuthis glacialis* described from incomplete specimens from the stomachs of penguins and seals. Because of the inadequate description, the status of this family has been considered doubtful. Recently additional material has become available that confirms the validity of the Psychroteuthidae (Young and Roper, in manuscript).

The family is characterized by buccal connectives that attach to the dorsal borders of arms IV, straight, simple funnel locking-cartilage, absence of photophores on the mantle and head, a tentacular club with four to seven rows of suckers on the manus and dactylus, and biserial suckers on the arms.

Two species, one undescribed, are presently known from Antarctic waters.

NEOTEUTHIDAE Naef, 1921a

PLATE 10A-D

The family is characterized by biserial suckers on the arms, four rows of suckers on the distal part of the manus and dactylus, and numerous small suckers on the proximal end of the manus, buccal connectives that attach to the dorsal borders of arms IV, straight, simple funnel locking-cartilage, anterior fin lobes lacking and posterior fin lobes free, the absence of photophores.

Two genera, *Alluroteuthis* Odhner, 1923, and *Neoteuthis* Naef, 1921, are known. Odhner (1923) suggested that *Parateuthis tunicata* Thiele, 1921, might be the larva of the monotypic *Alluroteuthis antarcticus.* Although these species appear superficially to be quite different, new material of both species presently under study indicates that they probably are synonymous and

that the older genus, *Parateuthis,* will, therefore, be the valid name. Before this change can be made, however, the problem will require further investigation.

The validity of *Neoteuthis* has previously been considered doubtful because of the very inadequate early description. Recent findings, however, have confirmed the validity of the genus and have demonstrated its close affinity with *Alluroteuthis.* This information has necessitated the submergence of the family Alluroteuthidae into the synonymy of Neoteuthidae (Young, in manuscript).

ARCHITEUTHIDAE Pfeffer, 1900

PLATE 11C, D

This family includes the largest of all cephalopods. Specimens occasionally are found moribund at the surface of the ocean, but most records are from strandings or whale stomachs.

The Architeuthidae is characterized by tetraserial armature on the tentacular clubs with large suckers in the medial rows of the manus and small suckers in the marginal rows; a distinct cluster of numerous small suckers and knobs at the proximal end of the manus; two longitudinal rows of alternating suckers and pads on the tentacular stalks; a straight simple funnel locking-cartilage; buccal connectives that attach to the dorsal border of arms IV; the absence of photophores.

Many species have been named in the sole genus of the family, *Architeuthis,* but they are so inadequately described and poorly understood that the systematics of the group is thoroughly confused. Total lengths of nearly 60 feet and mantle lengths of nearly 17 feet (not a complete specimen) have been recorded (summary in Clarke, 1966).

Juveniles of species from both the Atlantic and Pacific Oceans have recently been discovered (Roper and Young, in manuscript).

OMMASTREPHIDAE Steenstrup, 1857

PLATE 11A, B

The family is characterized by an inverted T-shaped funnel locking-cartilage, biserial suckers on the arms, tetraserial suckers on the tentacular clubs (except *Illex* which has eight rows of suckers on the dactylus), buccal connectives that attach to the dorsal borders of arms IV, photophores in some genera, and a muscular bridge anterior to the funnel locking-cartilage which passes from the funnel to the ventral surface of the head.

The inverted T-shaped funnel locking-cartilage easily distinguishes this family from all others, even in the youngest stages. One genus, *Symplectoteuthis,* has the funnel and mantle cartilages fused at a single point, but they are otherwise typical.

Three subfamilies are presently recognized: Ommastrephinae, Todarodinae, and Illicinae. The Ommastrephinae is distinguished by the presence of a central pocket (foveola) and several side pockets in the funnel groove, and by the presence of photophores which are often deeply buried in the tissue of the mantle, head and arms. Five genera are present: *Ommastrephes, Symplectoteuthis, Dosidicus, Hyaloteuthis,* and *Ornithoteuthis.* Species of these genera are strong, powerful swimmers that are commonly found in surface waters at night. *Dosidicus,* the giant of the family which inhabits the Peru Current, is reported to attain a total length of about four meters (Duncan, 1941).

The Todarodinae has a foveola, but lacks side pockets in the funnel groove, and lacks photophores. Two genera are known: *Todarodes* and *Nototodarus. Todarodes pacificus* from Japan is the basis of one of the largest cephalopod fisheries in the world. *Nototodarus* is known only from the Pacific Ocean.

The Illicinae lacks both central and side pockets in the funnel groove and lacks photophores. The two genera, *Illex* and *Todaropsis,* are known only from the Atlantic Ocean. *Illex illecebrosus* from Newfoundland is the basis of one of the largest squid fisheries in the Atlantic.

All species of the family in which the developmental stages are known pass through the "rhynchoteuthis" larval stage recognized by the fusion of the tentacles to form a trunklike proboscis. The systematics of the family is unstable and is presently being revised by Roper and by Clarke.

THYSANOTEUTHIDAE Keferstein, 1866

PLATE 12A

This family is characterized by a funnel locking-cartilage with a long, narrow longitudinal groove and a short, broad transverse groove (⊣-shaped, Figure 1c); long broad fins in the shape of a rhombus that extend nearly the full length of the mantle; nuchal-mantle lock with two distinct knobs that fit into opposing pits; extremely long, cirrate trabeculae on the arms; buccal connectives that attach to the ventral borders of arms IV; two rows of suckers on the arms and four

rows of suckers on the manus; the absence of photophores.

Two genera, *Thysanoteuthis* and *Cirrobrachium,* are currently included in the family. *Cirrobrachium* is known only from a few larval forms and a single, larger fragmentary specimen; it is distinguished by long, slender, free cirri (trabeculae) on the arms. So little is known about the characters of the two nominal species of *Cirrobrachium* that the genus is in question. The monotypic species, *Thysanoteuthis rhombus,* attains a large size of at least 80 cm mantle length and 19 kg weight (Nishimura, 1966) and is a very powerful swimmer.

CHIROTEUTHIDAE Gray, 1849

PLATE 13A–E

This family is often divided into two subfamilies: the Chiroteuthinae and the Mastigoteuthinae. We consider these groups to be closely related, but we believe that they are distinct enough to each merit familial ranking.

The family Chiroteuthidae, although distinctive, is rather difficult to characterize because of secondary modifications in certain genera (e.g., *Valbyteuthis, Chiropsis*). The funnel locking-cartilage distinguishes the Chiroteuthidae from all families except the Mastigoteuthidae. The locking apparatus is oval and bears one or two distinct knobs that project toward the center of the cavity. When two knobs are present, one occurs on the medial side and the other on the posterior side of the lock. The arms bear biserial suckers, except occasionally at the tips; the tentacles have tetraserial suckers; the buccal connectives attach to the ventral borders of arms IV; photophores are usually present.

Three genera are presently recognized: *Chiroteuthis, Chiropsis,* and *Valbyteuthis.* Several other genera have been described, but their status is uncertain. *Chirosoma regnardi* Joubin, 1912, was named in a brief note on a collection of cephalopods from the eastern North Atlantic. An inadequate preliminary diagnosis was given, based on a single character (rows of suckers), but a description of the species never appeared. Joubin (1924) discussed the species of the family Chiroteuthidae (as Chiroteuthinae) but did not mention his own species *Chirosoma regnardi.* Apparently he no longer recognized the genus or species as distinct taxa. Clearly, this form must be considered a genus and species dubia. Berry (1920) described a new genus, *Chiroteuthoides,* based on a larval specimen from the western Atlantic. The affinity of this taxon with the Chiroteuthidae is doubtful. *Bigelowia* MacDonald and Clench (1934) possesses the typical characteristics of *Chiroteuthis* and clearly is a synonym of this genus, although, until now, it has never formally been synonymized.

Most chiroteuthids belong in the genus *Chiroteuthis* and possess very elongate tentacles, distinctive clubs with suckers arranged in four rows on long, slender stalks, greatly enlarged ventral arms, and abundant photophores. *Chiroteuthis* larvae are noted for their large size and exotic appearance.

Chiropsis has a single species, *C. mega,* known only from the holotype. It is similar in appearance to *Chiroteuthis* except for the short, broad, blunt ventral arms.

Valbyteuthis differs considerably from *Chiroteuthis* and *Chiropsis;* a recent study, however, has revealed a striking similarity between the species of *Valbyteuthis* and certain larval forms ("*doratopsis*" type) of *Chiroteuthis* (Roper and Young, 1967). Members of the genus are easily recognized by the lack of a funnel valve and by the presence of an oval funnel locking-cartilage bearing only a posterior knob.

MASTIGOTEUTHIDAE Verrill, 1881

PLATE 12B, C

The family Mastigoteuthidae is characterized by an oval funnel locking-cartilage with inward projecting knobs, as in chiroteuthids, but generally the posterior knob is weakly developed and occasionally the medial knob is also poorly developed giving the locking-cartilage an almost oval appearance. The long, whiplike tentacles that bear many hundreds of minute, often microscopic, suckers in many rows (more than 15) are also very characteristic of the family. Suckers are arranged biserially on the arms; the buccal connectives attach to the ventral borders of arms IV; the fins generally are large; the ventral arms are commonly greatly enlarged. Often numerous, small photophores are embedded in the integument of the mantle, fins, head, and arms. The funnel locking-cartilage of *Mastigoteuthis magna* is somewhat peculiar in having lobes that project toward the concavity from both the medial and the lateral sides, giving the groove of the lock a flask-shaped appearance. The Mastigoteuthidae is closely related to the Promachoteuthidae, but, among other characters, the Promachoteuthidae is easily distinguished by the dorsal fusion of the mantle to the

head, while the Mastigoteuthidae has a free mantle margin.

Two genera, *Mastigoteuthis* and *Echinoteuthis,* are included in the family. *Echinoteuthis,* represented only *E. danae* Joubin, 1933, has not been reported since its original description. It is distinguished by numerous, small, cartilaginous tubercles over the surface of the mantle, head, funnel, and arms. Fifteen nominal species of *Mastigoteuthis* are known, several of which have been described from single multilated specimens. The species of *Mastigoteuthis* are common inhabitants of the deep sea.

JOUBINITEUTHIDAE Naef, 1922

PLATE 6C, D

This family is very distinctive and is easily recognized by the extremely elongate, slender arms which have six rows of suckers on each arm I–III and four rows of suckers on each arm IV. The tentacular clubs are elongate, compressed, and bear eight to ten longitudinal rows of small suckers; the funnel locking-cartilage is oval; the buccal connectives attach to the ventral borders of arms IV; an elongate, thread-like tail that is longer than the length of the mantle is present; photophores are absent.

A single species, *Joubiniteuthis portieri,* is known. A recent review of the family has shown that *Valdemaria danae,* a species previously included in the Mastigoteuthidae, is synonymous with *Joubiniteuthis portieri* (Young and Roper, 1969b).

CYCLOTEUTHIDAE Naef, 1923

PLATE 14A–E

The Cycloteuthidae is characterized by buccal connectives that attach to the ventral borders of arms IV; arms with biserial suckers; a tentacular club with tetraserial suckers; a compact, expanded club with a well-defined manus and dactylus, but an ill-defined carpus; a subtriangular funnel locking-cartilage; fins (including tail when present) greater than 70% of the mantle length in adults; the presence of photophores.

Naef (1923) established the Cycloteuthinae as a subfamily of the Onychoteuthidae based on a previously described genus, *Cycloteuthis* Joubin, 1919, that contains a single species, *C. sirventi.* Recently Young and Roper (1969a) elevated the Cycloteuthinae to familial status and included in it another genus, *Discoteuthis.*

C. sirventi has a prominent tail and four rows of equal-sized suckers on the manus of the tentacular club. Species of *Discoteuthis* lack a tail and have greatly enlarged medial suckers on the manus of the tentacular club.

PROMACHOTEUTHIDAE Naef, 1912

PLATE 5A, B

The Promachoteuthidae is known from only a few juvenile specimens; however, its very distinctive features make it easy to recognize. The mantle is fused dorsally to the head in the nuchal region; the eyes are greatly reduced; the funnel locking-cartilage is oval; the tentacular club has numerous longitudinal rows (more than eight) of minute suckers; the buccal connectives attach to the ventral borders of arms IV; the arms have biserial suckers; photophores are absent.

The eye openings are greatly reduced in size corresponding to the small eyes and are difficult to detect. In the past, the misinterpretation of this condition resulted in the placement of the Promachoteuthidae in the Myopsida. Recently the family has been removed from the Myopsida and placed in the Oegopsida (Roper and Young, 1968—inadvertently listed as 1967 in journal). *Promachoteuthis,* the only genus in the family, contains two species, *P. megaptera* from the Pacific near Japan and an unnamed species from the waters off southern Chile.

GRIMALDITEUTHIDAE Pfeffer, 1900

PLATE 15A

The Grimalditeuthidae is easily recognized by the fusion of the funnel and mantle locking-cartilages while the dorsal mantle-nuchal locking apparatus is free. Tentacles are lacking; the arms have biserial suckers; buccal connectives attach to the ventral borders of arms IV. An extremely long tail bears an accessory fin; however, this structure is delicate and may be broken off during capture. Photophores may be present at the tips of the arms.

A single genus, *Grimalditeuthis,* is known. Two nominal species have been described but are probably synonymous.

CRANCHIIDAE Prosch, 1849

PLATES 15B–D; and 16A–D

The Cranchiidae contains a great diversity of species which exhibit a wide variety of basic characters. One

prominent character, however, easily distinguishes all members of the group: the mantle is fused to the head in the nuchal region and to the funnel at its two posterolateral corners. Buccal connectives attach to the ventral borders of arms IV; the armature of the clubs generally is in four longitudinal rows; the arms generally have biserial suckers; photophores are present.

The numerous cranchiid genera are divided into two subfamilies, the Cranchiinae and the Taoniinae. The Cranchiinae is characterized by cartilaginous strips bearing tubercles on the ventral surface of the mantle that originate at the funnel-mantle fusions and extend posteriorly, the lateral fusion of the funnel to the ventral surface of the head in the adult stage, and one or more rows of small, round photophores on the eye. This subfamily contains the following genera: *Cranchia, Liocranchia, Leachia,* and *Drechselia. Pyrgopsis* generally has been regarded as a separate genus; however, a complete series of the developmental stages of a new species of *Leachia* has shown that young specimens possess the generic characters of *Pyrgopsis* and that this genus must fall into the synonymy of *Leachia* (Young, in press). The genus *Egea* was previously placed in this subfamily. One of us (G.L.V.) has recently examined the type and found that there are no cartilaginous strips on the mantle contrary to what Joubin described and that the genus clearly belongs in the Taoniinae. *Liguriella* has also been placed in the Cranchiinae but it is known only from larval specimens and its true affinities are uncertain. Clarke (1966) erroneously placed *Crystalloteuthis,* a member of the Taoniinae, in this subfamily.

The Taoniinae is characterized by the absence of cartilaginous strips that extend posteriorly from the funnel-mantle fusions, by the presence of a funnel that is free laterally, and by the presence of one to three generally crescent-shaped photophores on the eyes. This subfamily contains numerous and diverse species that are arranged in many ill-defined genera. In addition, many of the genera are based on larval forms (e.g., *Fusocranchia, Teuthowenia,* and *Taonidium*); therefore, a listing of the nominal genera would serve no useful purpose.

Mesonychoteuthis, represented only by *M. hamiltoni,* has large hooks on both the tentacles and arms; it attains a total length of at least 3½ meters (Clarke, 1966). A related genus, *Galiteuthis,* has large hooks only on the tentacular clubs. *Taonius* has a few greatly enlarged teeth, closely approximating hooks, that arise from the sucker rings on the tentacular clubs. The systematic position of *Ascocranchia* has been uncertain because of the atypical eye photophores in the only species. However, the close similarity of the peculiar attachment of the paddle-like fins and the large funnel with those of *Helicocranchia* indicates that *Ascocranchia* belongs to the Taoniinae.

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Untenable Families

PARATEUTHIDAE JOUBIN, 1919.—Clarke (1966) reestablished the family Parateuthidae, and it is therefore necessary to make some comments concerning it. The family Parateuthidae was originally erected by Joubin (1919) to include the genera *Lycoteuthis* and *Cycloteuthis.* Not only is the familial name invalid since it is not based on a type genus, but also these genera do not form a natural group. The family Parateuthidae has been rejected by teuthologists since it was first established. Thiele (1921) described the genus *Parateuthis* based on a larval oegopsid captured in the Antarctic Ocean; this genus has no connection whatsoever with Joubin's Parateuthidae. Because of its uncertain position, *Parateuthis* has never been placed in any family, although Odhner (1923) thought it might be a larval *Alluroteuthis.* Larvel specimens of *Alluroteuthis* in the collections of the I.M.S. indicate that this, indeed, probably is the case (see page 9).

The family Parateuthidae is invalid and the four genera that Clarke includes in it (*Cycloteuthis, Psychroteuthis, Parateuthis,* and *Alluroteuthis*) do not form a natural group (except the last two as noted above).

ALLUROTEUTHIDAE ODHNER, 1923.—The Alluroteuthidae has been synonymized with the Neoteuthidae. See page 9 for discussion.

PHOLIDOTEUTHIDAE ADAM, 1950.—The Pholidoteuthidae has been synonymized with the Lepidoteuthidae. See page 8 for discussion.

VALBYTEUTHIDAE JOUBIN, 1931.—The Valbyteuthidae has been synonymized with the Chiroteuthidae. See page 11 for discussion.

VERANYIDAE CHUN, 1910.—The Veranyidae was incorrectly established and has been replaced by Octopoteuthidae. See page 7 for discussion.

Selected Faunal Works

Systematic works of broad general application include Chun (1910), Pfeffer (1912), and Naef (1923).

The following brief list is presented as a preliminary guide to the literature dealing with the teuthoid fauna of local areas:

North Sea—Grimpe, 1925; Jaeckel, 1958
Northwestern Atlantic—Verrill, 1882
Mediterranean—Mangold-Wirz, 1963
Gulf of Mexico—Voss, 1956
West Africa—Adam, 1952
South Africa—Voss, 1967
Indian Ocean—Adam, 1939
Australia—Berry, 1918
New Zealand—Dell, 1952
Philippines—Voss, 1963
Japan—Sasaki, 1929
Hawaii—Berry, 1914
California—Young, in press

References

(Including the works in which the familial names were first introduced.)

Adam, W.
1939. The Cephalopoda in the Indian Museum, Calcutta. *Records of the Indian Museum,* 41(1):61–110.
1950. Un Cephalopode Nouveau: *Pholidoteuthis boschmai* gen. et sp. nov. *Koninklijke Nederlandse Akademie van Wetenschappen,* 53(10):1–8.
1952. Cephalopodes. *Résultats Scientifiques Expédition Oceanographique Belge Atlantique Sud,* 3(3):1–142.
1960. Cephalopoda from the Gulf of Aqaba. Number 16 in "Contributions to the Knowledge of the Red Sea." *Bulletin of the Sea Fisheries Research Station,* Haifa, 26:1–27.

Berry, S. S.
1912. Some Necessary Changes in Cephalopod Nomenclature. *Science,* 36(932):643–646.
1914. The Cephalopoda of the Hawaiian Islands. *Bulletin of the Bureau of Fisheries,* Washington, 32:255–362.
1918. Report on the Cephalopoda Obtained by F.I.S. *Endeavour* in the Great Australian Bight and Other Southern Australian Localities. *Biological Results of the Fishing Experiments by Endeavour,* 1909–1914, 4(5):203–298.
1920. Preliminary Diagnoses of New Cephalopods from the Western Atlantic. *Proceedings of the United States National Museum,* 58(2335):293–300.

Chun, C.
1910. Die Cephalopoden, I: Oegopsida. *Wissenshaftliche Ergebnisse der Deutschen Tiefsee-Expedition, Valdivia,* 18(1):1–410; atlas of 61 plates.

Clarke, M. R.
1966. A Review of the Systematics and Ecology of Oceanic Squids. *Advances in Marine Biology,* 4:91–300.
1967. A Deep-Sea Squid, *Taningia danae* Joubin, 1931. *Symposium of the Zoological Society of London,* 19:127–143.

Clarke, M. R., and G. E. Maul
1962. A Description of the "Scaled" Squid *Lepidoteuthis grimaldi* Joubin, 1895. *Proceedings of the Zoological Society of London,* 139(1):97–118.

Dell, R. K.
1952. The Recent Cephalopoda of New Zealand. *Dominion Museum Bulletin,* 16:1–157.

Duncan, D. D.
1941. Fighting Giants of the Humboldt. *National Geographic Magazine,* 79:373–400.

Fields, W. G.
1965. The Structure, Development, Food Relations, Reproduction, and Life History of the Squid *Loligo opalescens* Berry. *California Department of Fish and Game, Fish Bulletin,* 131:1–108.

Goodrich, E. S.
1892. Note on a Large Squid (*Ommastrephes pteropus* Stp.). *Journal of the Marine Biological Association of the United Kingdom,* 2:314–321.

Gray, J. E.
1849. *Catalogue of the Mollusca in the Collection of the British Museum: I, Cephalopoda Antepedia.* 164 pages. London.

Grimpe, G.
1922. Systematische Ubersicht der europäischen Cephalopoden. *Sitzungsberichte der Naturforschenden Gesellshaft zu Leipzig,* 45–48:36–52.
1925. Zur Kenntnis der Cephalopoden-fauna der Nordsee. *Wissenshaftliche Meeresuntersuchungen der Kommission,* Kiel, 16(3):1–124.

Hoyle, W. E.
1886. Report on the Cephalopoda Collected by H.M.S. *Challenger* During the Years 1873–76. *Report of the Voyage of the Challenger, Zoology,* 16(44):1–246, 33 plates.
1904. A Diagnostic Key to the Genera of Recent Dibranchiate Cephalopoda. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society,* 48(21):1–20.

Jaeckel, S. G. A., Jr.
1958. Cephalopoden. *Die Tierwelt der Nord und Ostsee,* 37(9 b$_2$):479–723.

Joubin, L.
1900. Cephalopodes Provement des Campagnes de la *Princesse-Alice* (1891–1897). *Résultats des Campagnes Scientifiques du Prince de Monaco,* 17:1–135, 15 plates.
1912. Sur les Cephalopodes Captures en 1911 par S.A.S. le Prince de Monaco. *Compte Rendu Academie Sciences,* Paris, 154:395–397.
1919. Etudes Preliminaires sur les Cephalopodes Recuilles au Cours des Croisieres de S.A.S. le Prince de Monaco. 7e Note: *Cycloteuthis sirventi* nov. gen. et. sp. *Bulletin Institut Oceanographique,* Monaco, 351:1–7, 2 figures.

1924. Contribution a l'etude des Cephalopodes de l'Atlantique Nord. 4e Series. *Résultats des Campagnes Scientifiques du Prince de Monaco,* 67:1–113, 16 plates.

1931. Notes Preliminaires sur les Cephalopodes des Croisieres du *Dana* (1921–1922). 3e Partie. *Annales de l'Institut Oceanographique,* new series, 10(7): 167–211.

1933. Notes Preliminaires sur les Cephalopodes des Croisieres du *Dana* (1921–1922). 4e Partie. *Annales de l'Institut Oceanographique,* new series, 13(1):1–49.

Keferstein, W.

1866. Cephalopoda. In Bronn, *Die Klassen und Ordnungen Tierreichs,* 3(2):1307–1464.

MacDonald, R., and W. J. Clench

1934. Descriptions of a New Genus and Two New Species of Squids from the North Atlantic. *Occasional Papers of Boston Society of Natural History,* 8:145–152.

Mangold-Wirz, K.

1963. Biologie des Cephalopodes Benthiques et Nectoniques de la Mer Catalane. *Vie et Milieu,* Supplement, 13:1–285.

Naef, A.

1912. Teuthologische Notizen. I. Die Familien der Myopsiden. *Zoologischer Anzeiger,* 39(7):241–244.

1921a. Das System der Dibranchiaten Cephalopoden und die Mediterranean Arten derselben. *Mitteilungen aus der Zoologischen Station zu Neapel,* 22:527–542.

1921b. Die Cephalopoden. *Fauna und Flora Neapel, Monograph 35,* 1(pt. 1, no. 1):1–148.

1922. *Die Fossilen Tintenfische.* 322 pages. Jena: Gustav Fischer.

1923. Die Cephalopoden: Systematik. *Fauna und Flora Neapel, Monograph 35,* 1(pt. 1, no. 2):i-xiv, 149–863, 473 figures.

Nishimura, S.

1966. Notes on the Occurrence and Biology of the Oceanic Squid, *Thysanoteuthis rhombus* Troschel, in Japan. *Publications of the Seto Marine Biological Laboratory,* 14(4):327–349.

Odhner, N. H.

1923. Die Cephalopoden. In *Further Zoological Results of the Swedish Antarctic Expedition, 1901–1903,* 1:1–7.

Pearcy, W. G., and G. L. Voss

1963. A New Species of Gonatid Squid from the Northeastern Pacific. *Proceedings of the Biological Society of Washington,* 76:105–112.

Pfeffer, G.

1900. Synopsis der oegopsiden Cephalopoden. *Mitteilungen Naturhistorischen Museum in Hamburg* (2 Beiheft z. Jahrbach der Hamburgischen Wissenschaftlichen Anstalten), 17(2):147–198.

1908. Die Cephalopoden. *Nordisches Plankton,* 2(pt. 9, no. 4):9–116.

1912. Die Cephalopoden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung,* 2:i–xxi, 1–815; atlas of 48 plates.

Prosch, V.

1849. Nogle nye Cephalopoder. *Kongelige Danske Videnskabernes Selskabs Skrifter,* series 5, 1:53–72.

Robson, G. C.

1948. The Cephalopoda Decapoda of the *Arcturus* Oceanographic Expedition, 1925. *Zoologica,* 33 (3):115–132.

Roper, C. F. E.

1966. A Study of the Genus *Enoploteuthis* (Cephalopoda: Oegopsida) in the Atlantic Ocean with a Redescription of the Type Species, *E. leptura* (Leach, 1817). *Dana Report No. 66,* 46 pages.

1969. Systematics and Zoogeography of the Worldwide Bathypelagic Squid Genus *Bathyteuthis* (Cephalopoda: Oegopsida). *United States National Museum Bulletin,* 291:1–208.

Roper, C. F. E., and R. E. Young

1967. A Review of the Valbyteuthidae and an Evaluation of Its Relationship with the Chiroteuthidae (Cephalopoda: Oegopsida). *Proceedings of the United States National Museum,* 123(3612):1–9.

1968. The Promachoteuthidae (Cephalopoda: Oegopsida), I: A Reevaluation of Its Systematic Position Based on New Material from the Antarctic and Adjacent Waters. *Antarctic Research Series,* 11:203–214.

MS. First Records of Juveniles of the Giant Squid, *Architeuthis,* from the Atlantic and Pacific Oceans.

Sasaki, M.

1929. A Monograph of the Dibranchiate Cephalopods of the Japanese and Adjacent Waters. *Journal of the College of Agriculture, Hokkaido Imperial University,* 20 (supplementary number): 1–357.

Steenstrup, J.

1857. Oplysning om en ny Art of Blaeksprutter, *Dosidicus Eschrichtii. Oversigt Danske Videnskabernes Selskab Forhandlinger,* 1857: 11–14. [English translation: A. Volse, J. Knudsen, and W. J. Rees. 1962. The Cephalopod Papers of Japetus Steenstrup. *Danish Science Press.* Copenhagen.]

1861. Overblik over de i Kjobenhavus Museer opbevarede Blaeksprutter fra det aabne Hav (1860–1861). *Oversigt Danske Videnskabernes Selskab Forhandlinger* 1861:69–86. [English translation: Volse et al., 1962.]

Thiele, J.

1921. Die Cephalopoden der Deutschen Südpolar-Expedition. *Deutsche Südpolar Expedition (1901–1903) 16, Zoologie,* 8: 433–466.

1935. *Handbuch der systematischen Weichtierkunde,* 2(3):779–1022. Jena: Gustav Fischer.

Verrill, A. E.
1876. Note on Gigantic Cephalopods—A Correction. *American Journal of Science,* Series 3, 14:236–237.
1881a. The Cephalopods of the Northeastern Coast of America, Part II: The Smaller Cephalopods, Including the Squids and Octopi, with Other Allied Forms. *Transactions of the Connecticut Academy of Arts and Sciences,* 5:259–446.
1881b. Report on the Cephalopods, and on Some Additional Species Dredged by the U.S. Fish Commission Steamer "Fish Hawk," During the Season of 1880. *Bulletin of the Museum of Comparative Zoology, Harvard,* 8(5):99–116.
1882. Report on the Cephalopods of the Northeastern Coast of America. *Report of the United States Commissioner of Fisheries,* 1879:1–240.

Voss, G. L.
1953. A New Family, Genus and Species of Myopsid Squid from the Florida Keys. *Bulletin of Marine Science of the Gulf and Caribbean,* 2(4):602–609.
1956. A Review of the Cephalopods of the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean,* 6(2):85–178.
1962. A Monograph of the Cephalopoda of the North Atlantic, I: The Family Lycoteuthidae. *Bulletin of Marine Science of the Gulf and Caribbean,* 12 (2):264–305.
1963. Cephalopods of the Philippine Islands. *United States National Museum Bulletin,* 234:1–180.
1967. Some Bathypelagic Cephalopods from South African Waters. *Annals of the South African Museum,* 50(5):61–88.
MS. A Monograph of the Cephalopoda of the North Atlantic: The Subfamily Enoploteuthinae Exclusive of *Enoploteuthis. Bulletin of Marine Science.*

Voss, N. A.
MS. A Monograph of the Cephalopoda of the North Atlantic: The Family Histioteuthidae.

Young, R. E.
MS. Evidence for Spawning by *Gonatus* in the Arctic Ocean.
MS. Pelagic Cephalopods from the Seas off Southern California, I: Systematics and Areal Distribution.

Young, R. E., and C. F. E. Roper
1968. The Batoteuthidae, a New Family of Squid (Cephalopoda: Oegopsida) from Antarctic Waters. *Antarctic Research Series,* 11:185–202.
1969a. A Monograph of the Cephalopoda of the North Atlantic. The Family Cycloteuthidae (Suborder Oegopsida). *Smithsonian Contributions to Zoology,* number 5:1–24.
1969b. A Monograph of the Cephalopoda of the North Atlantic. The Family Joubiniteuthidae (Suborder Oegopsida). *Smithsonian Contributions to Zoology,* number 15:1–10.
MS. Rediscovery of the Family Psychroteuthidae from Antarctic Waters.

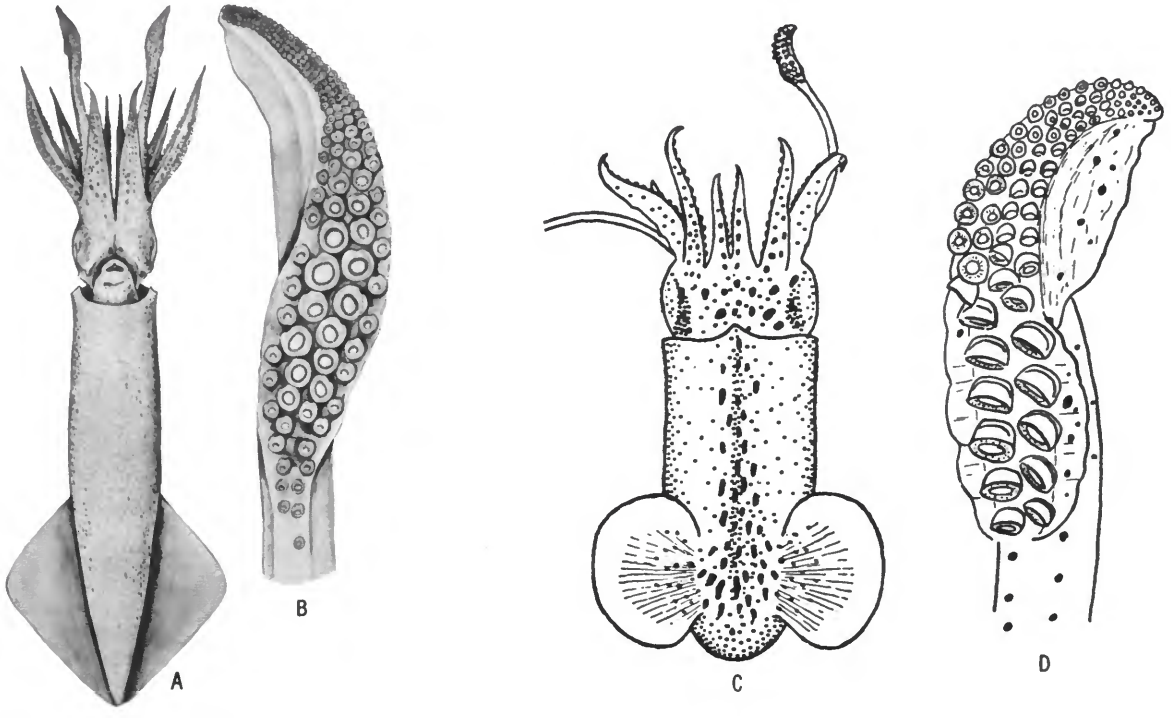

PLATE 1.—Loliginidae: A, *Loligo*, ventral view; B, *Loligo*, tentacular club. Pickfordiateuthidae: C, *Pickfordiateuthis*, dorsal view (from Voss, 1953); D, *Pickfordiateuthis*, tentacular club (from Voss, 1953).

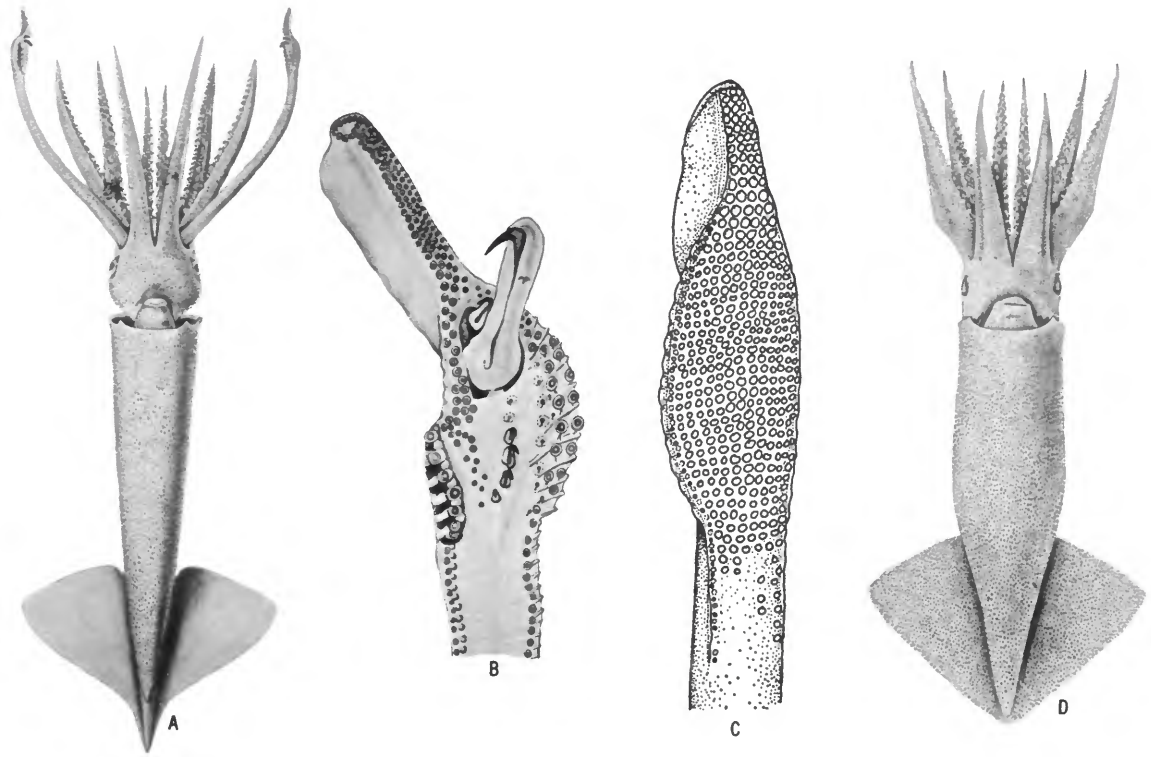

PLATE 2.—Gonatidae: A, *Gonatus*, ventral view (from Young, MS); B, *Gonatus*, tentacular club (from Young, MS); C, *Berryteuthis*, tentacular club (from Pearcy and Voss, 1963); D, *Gonatopsis*, ventral view (from Young, MS).

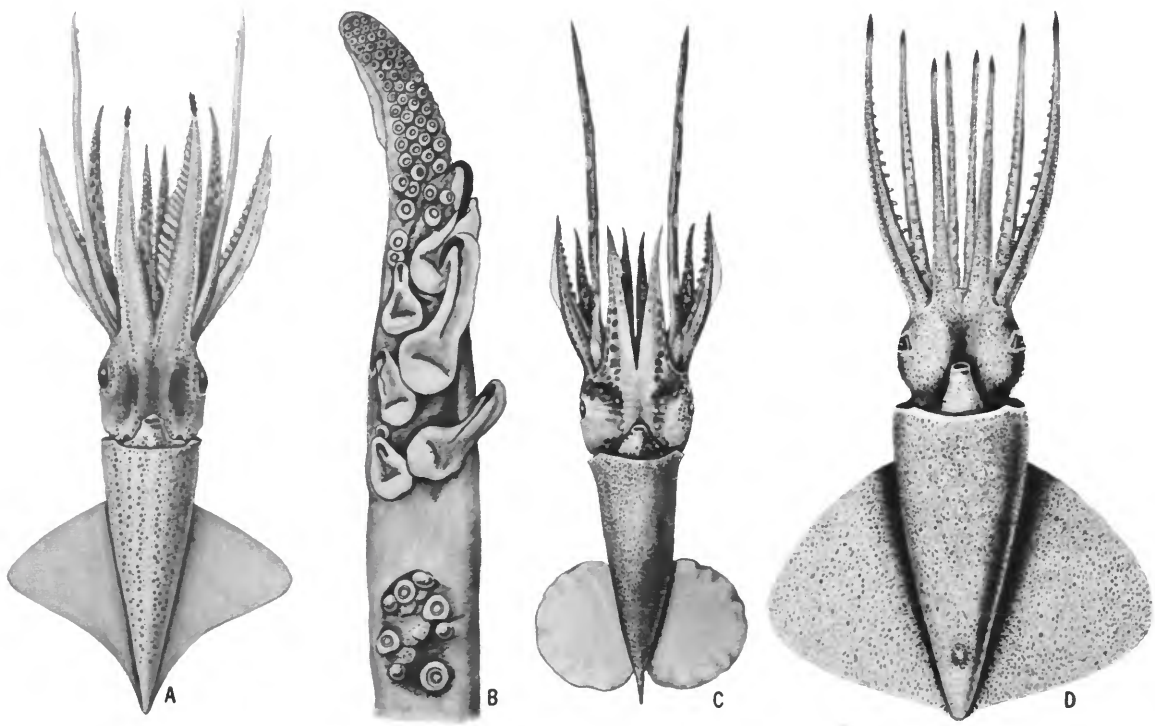

PLATE 3.—Enoploteuthidae: A, *Abraliopsis*, ventral view (from Young, MS); B, *Abraliopsis*, tentacular club (from Young, MS); C, *Pyroteuthis*, ventral view (from Young, MS). Octopoteuthidae: D, *Octopoteuthis*, ventral view.

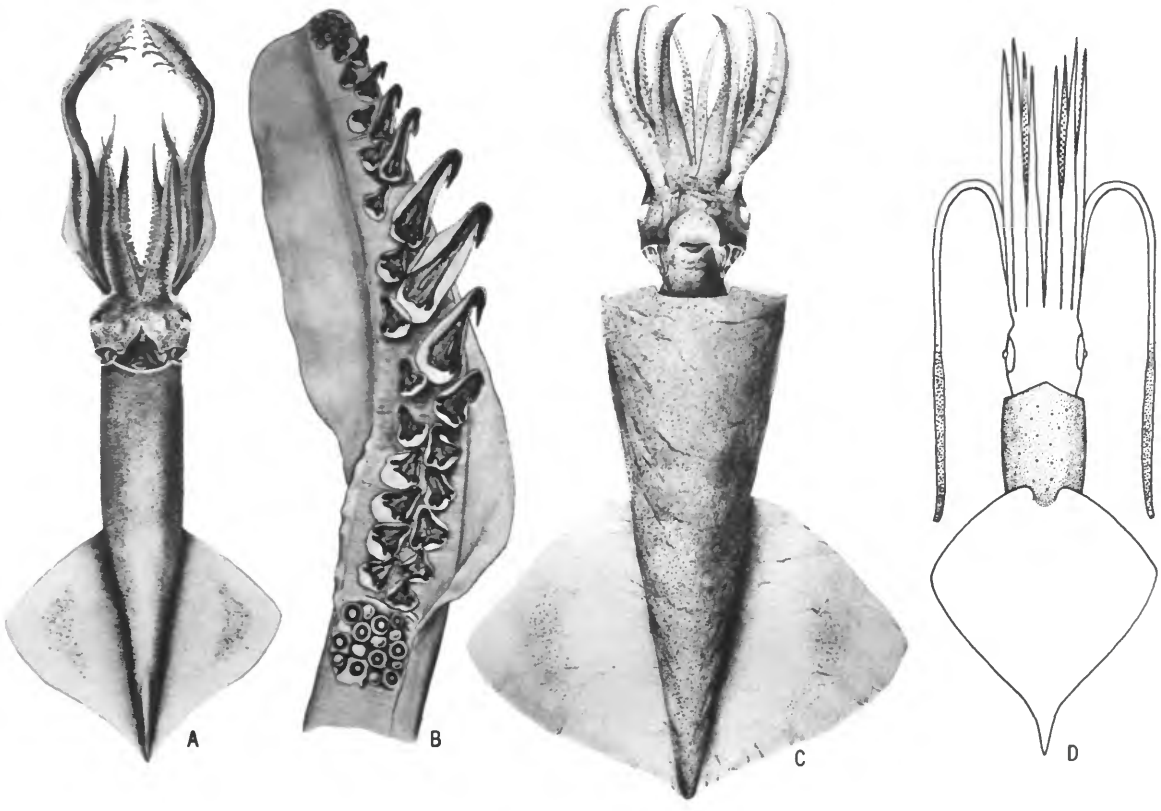

PLATE 4.—Onychoteuthidae: A, *Onychoteuthis,* ventral view (from Pfeffer, 1912); B, *Onychoteuthis,* tentacular club (from Young, MS); C, *Chaunoteuthis,* ventral view (from Pfeffer, 1912). Lepidoteuthidae: D, *Pholidoteuthis,* dorsal view (from Voss, 1956).

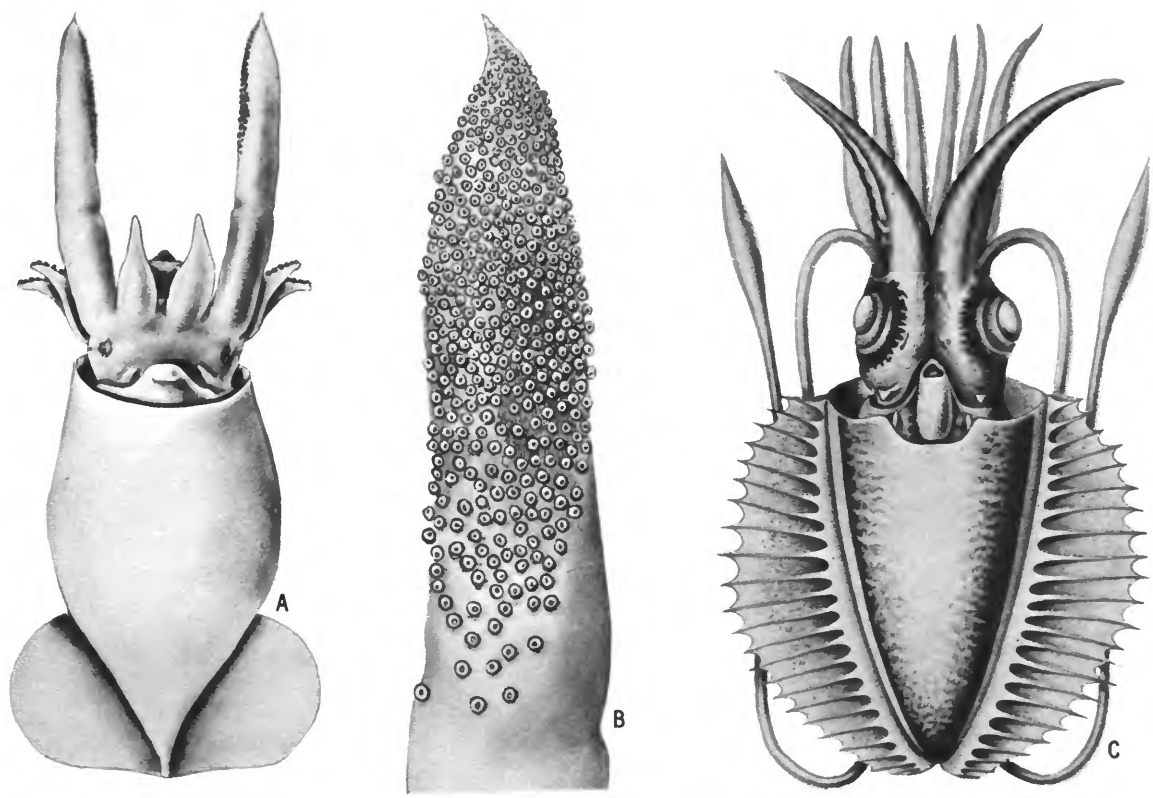

PLATE 5.—Promachoteuthidae: A, *Promachoteuthis,* ventral view (from Roper and Young, 1968); B, *Promachoteuthis,* tentacular club (from Roper and Young, 1968). Ctenopterygidae: C, *Ctenopteryx,* ventral view (from Joubin, 1900).

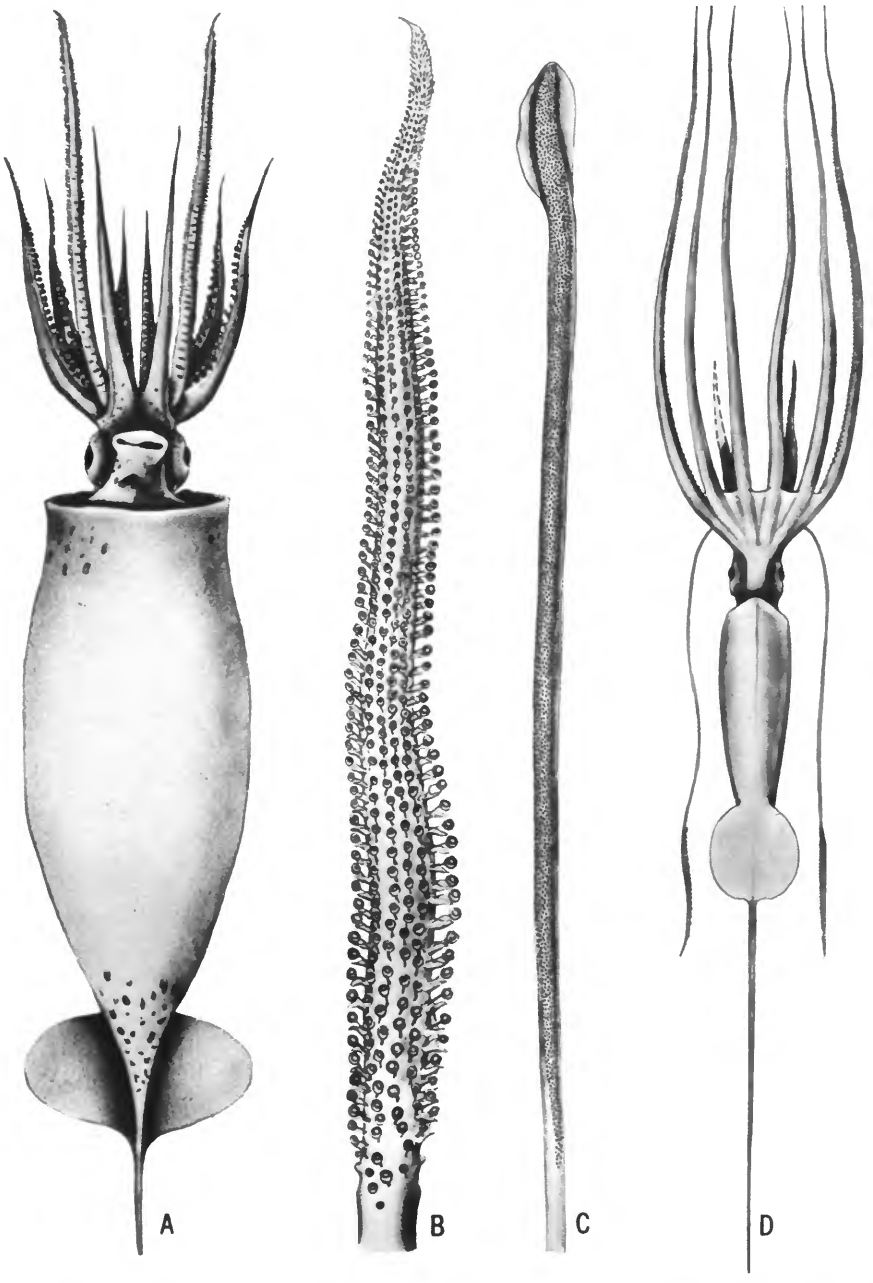

PLATE 6.—Batoteuthidae: A, *Batoteuthis*, ventral view (from Young and Roper, 1968); B, *Batoteuthis*, tentacular club (from Young and Roper, 1968). Joubiniteuthidae: C, *Joubiniteuthis*, tentacular club (from Young and Roper, 1969b); D, *Joubiniteuthis*, dorsal view (from Young and Roper, 1969b).

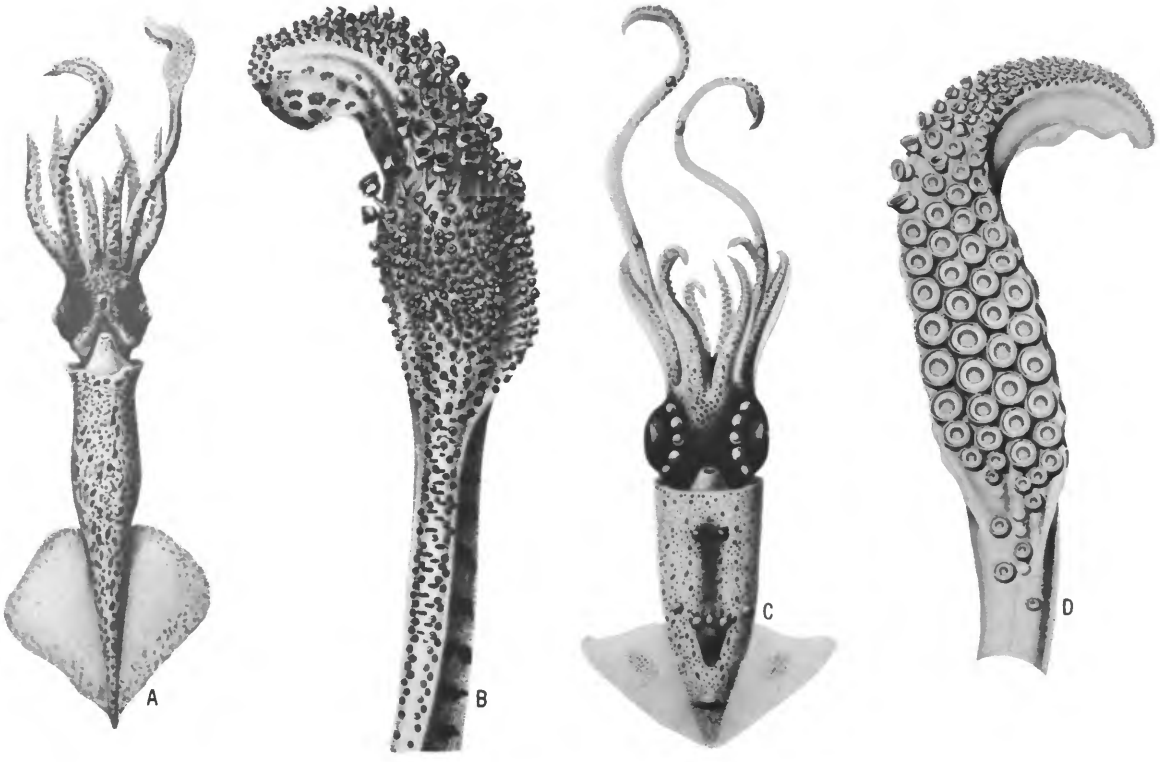

PLATE 7.—Brachioteuthidae: A, *Brachioteuthis,* ventral view; B, *Brachioteuthis,* tentacular club. Lycoteuthidae: C, *Lycoteuthis,* ventral view; D, *Lycoteuthis,* tentacular club. (All from Chun, 1910).

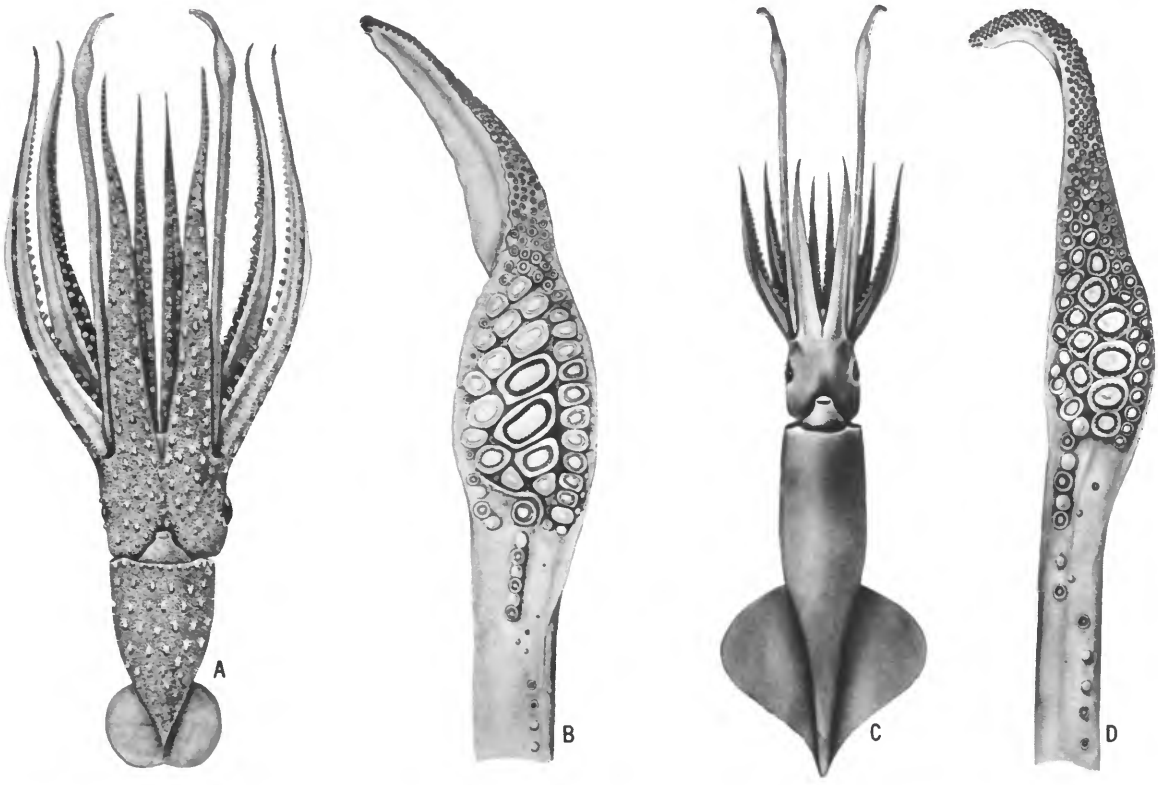

PLATE 8.—Histioteuthidae: A, *Histioteuthis,* ventral view (from Young, MS); B, *Histioteuthis,* tentacular club (from Young, MS). Psychroteuthidae: C, *Psychroteuthis,* ventral view (from Young and Roper, MS); D, *Psychroteuthis,* tentacular club (from Young and Roper, MS).

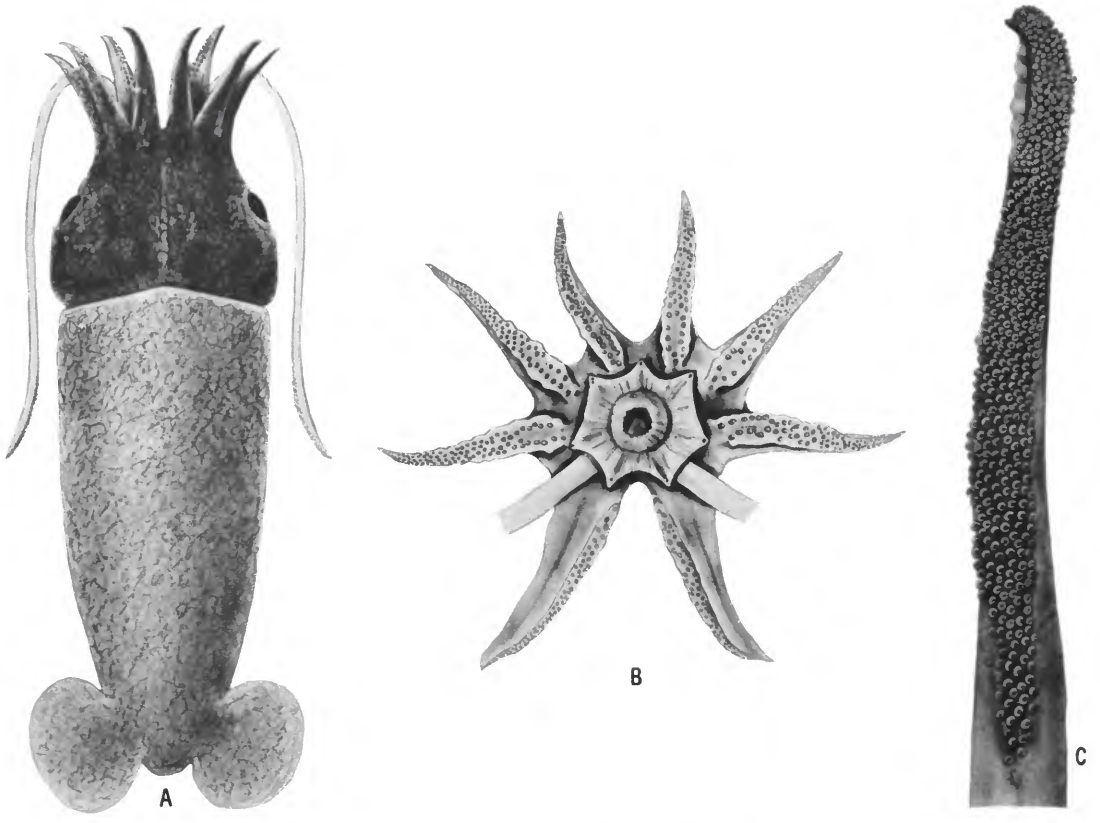

PLATE 9.—Bathyteuthidae: *Bathyteuthis*: A, Dorsal view; B, oral view or arms and buccal membrane; C, tentacular club. (All from Roper, 1969.)

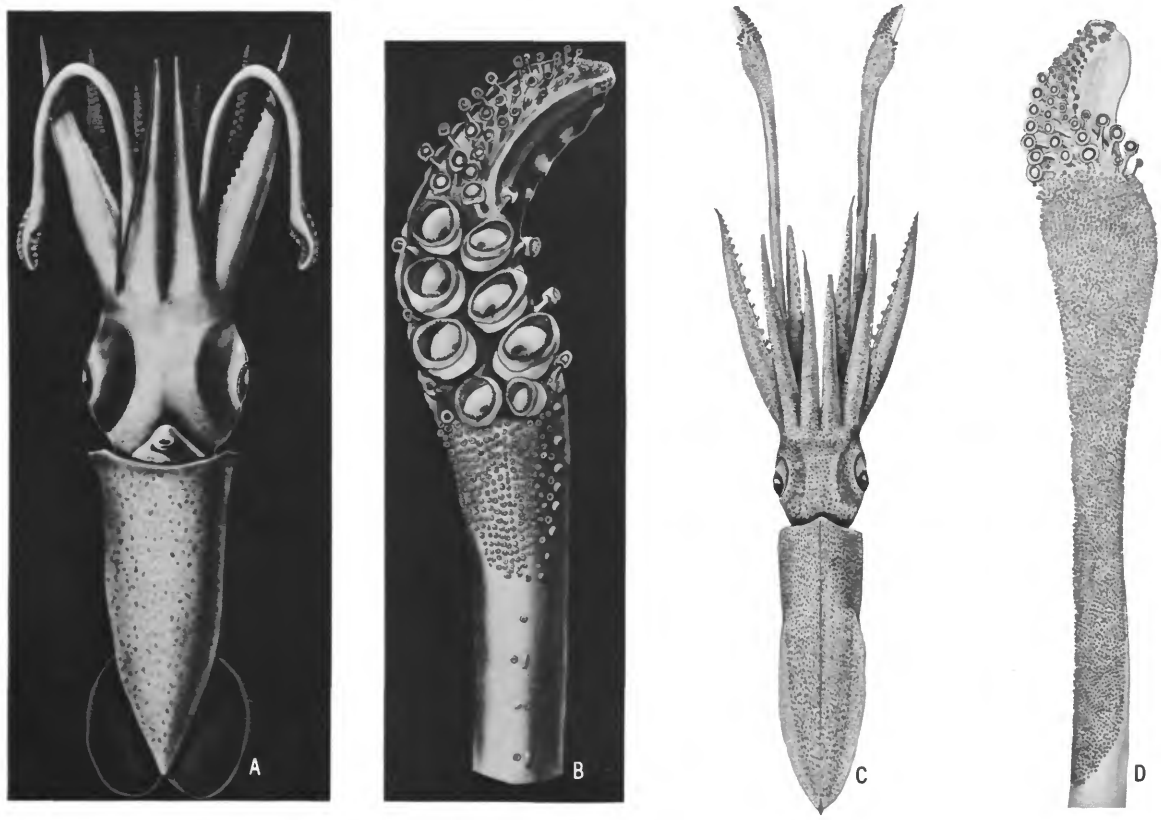

PLATE 10.—Neoteuthidae: A, *Alluroteuthis*, ventral view; B, *Alluroteuthis*, tentacular club; C, *Neoteuthis*, dorsal view (from Young, MS); D, *Neoteuthis*, tentacular club (from Young, MS).

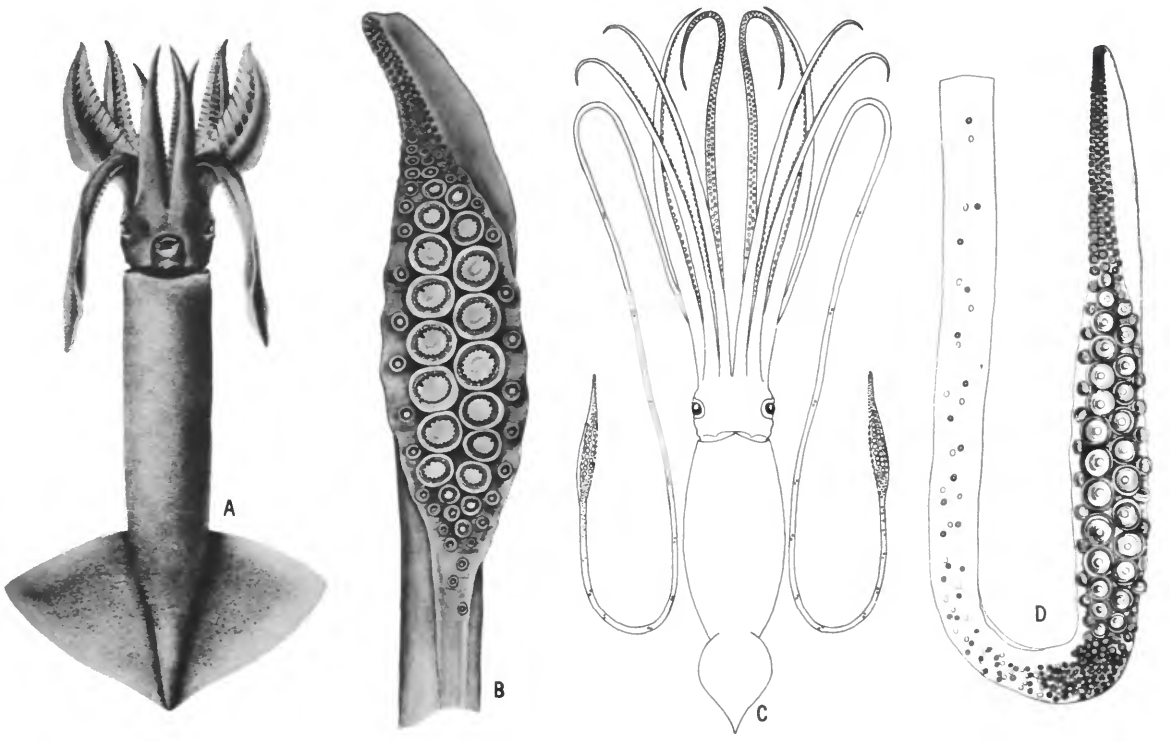

PLATE 11.— Ommastrephidae: A, *Ommastrephes,* ventral view (from Pfeffer, 1912); B, *Symplectoteuthis,* tentacular club (from Young, MS). Architeuthidae: C, *Architeuthis,* dorsal view (redrawn from Verrill, 1882); D, *Architeuthis,* tentacular club (from Verrill, 1882).

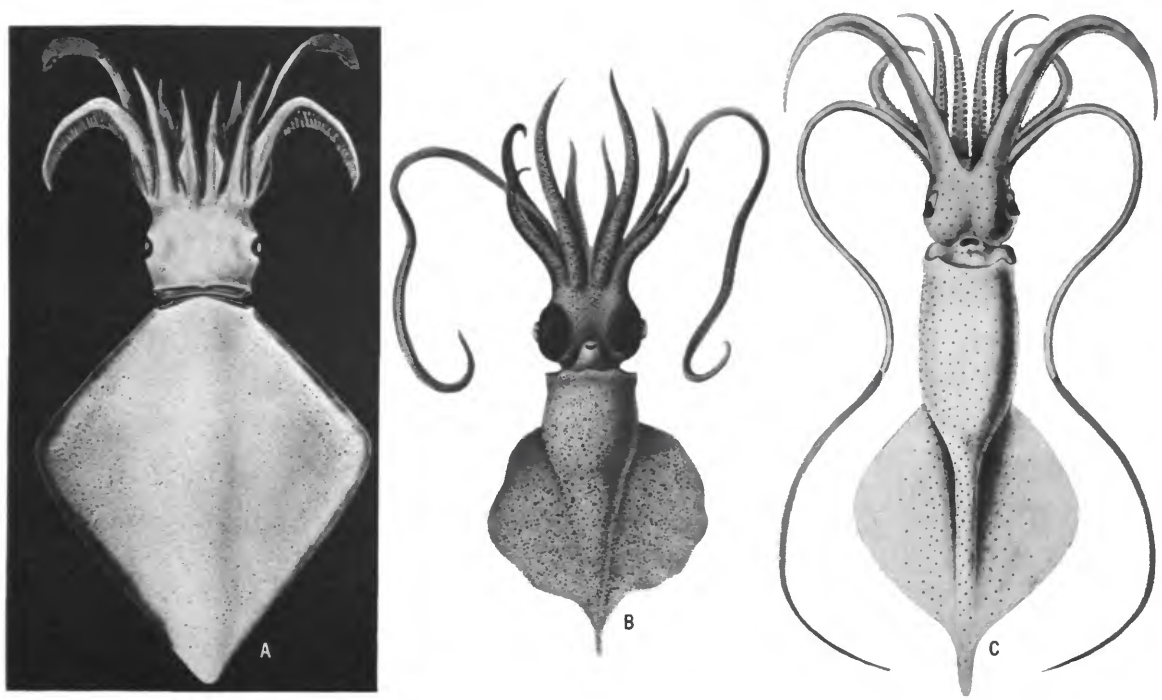

PLATE 12.—Thysanoteuthidae: A, *Thysanoteuthis*, dorsal view. Mastigoteuthidae: B, *Mastigoteuthis*, ventral view (from Chun, 1910); C, *Mastigoteuthis*, ventral view (from Young, MS).

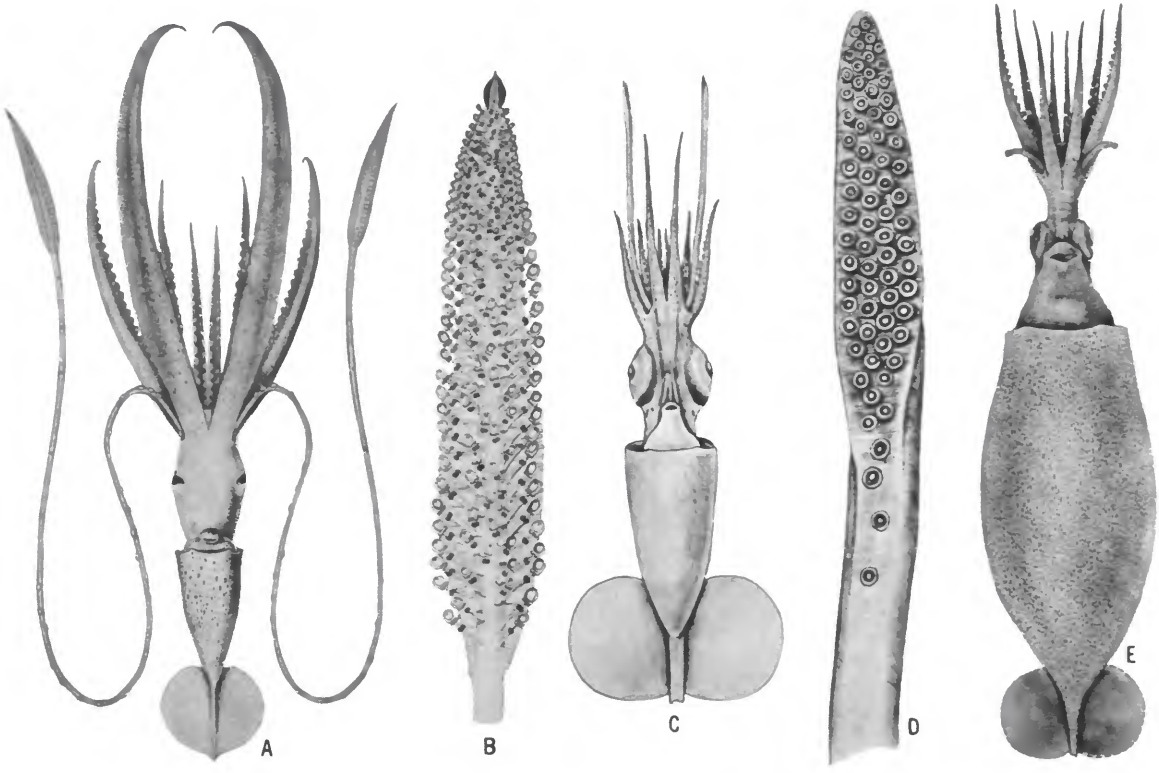

PLATE 13.—Chiroteuthidae: A, *Chiroteuthis*, ventral view (from Young, MS); B, *Chiroteuthis*, tentacular club (from Young, MS); C, *Valbyteuthis*, ventral view (from Roper and Young, 1967); D, *Valbyteuthis*, tentacular club (from Roper and Young, 1967); E, *Valbyteuthis*, ventral view (from Young, MS).

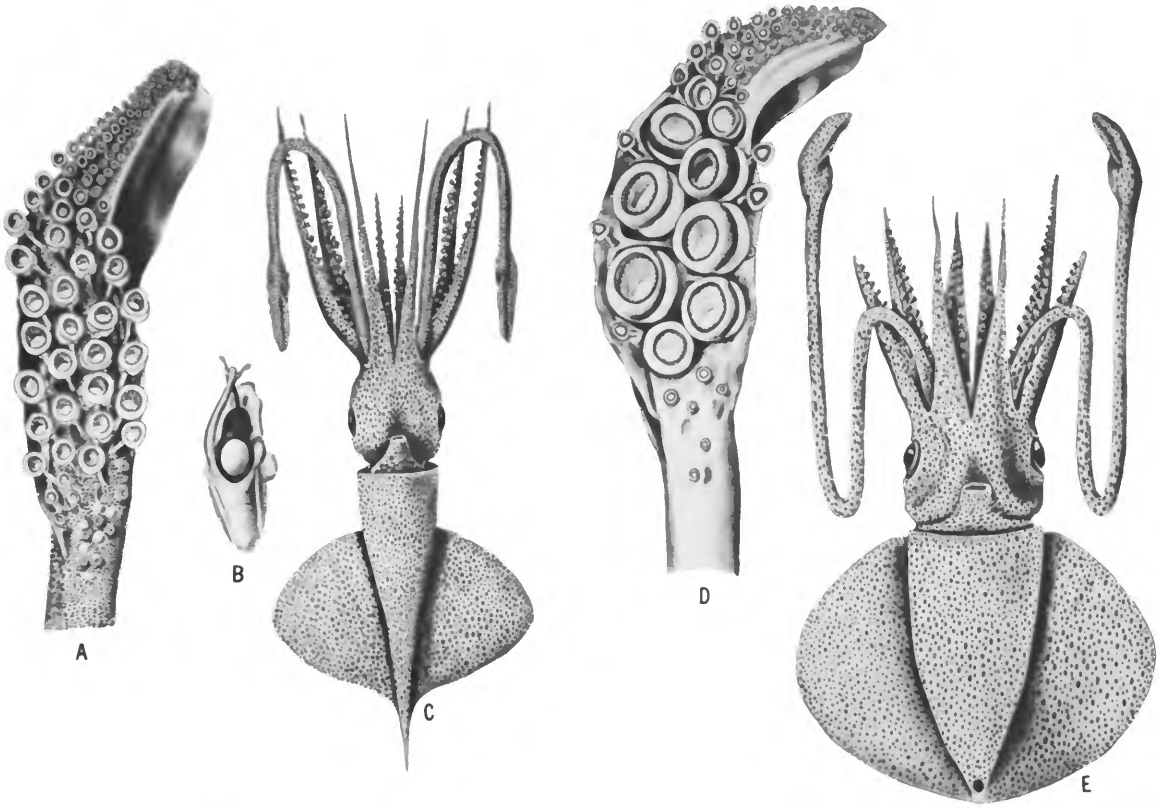

PLATE 14.—Cycloteuthidae: A, *Cycloteuthis,* tentacular club; B, *Cycloteuthis,* visceral photophore; C, *Cycloteuthis,* ventral view; D, *Discoteuthis,* tentacular club; E, *Discoteuthis,* ventral view. (All from Young and Roper, 1969a.)

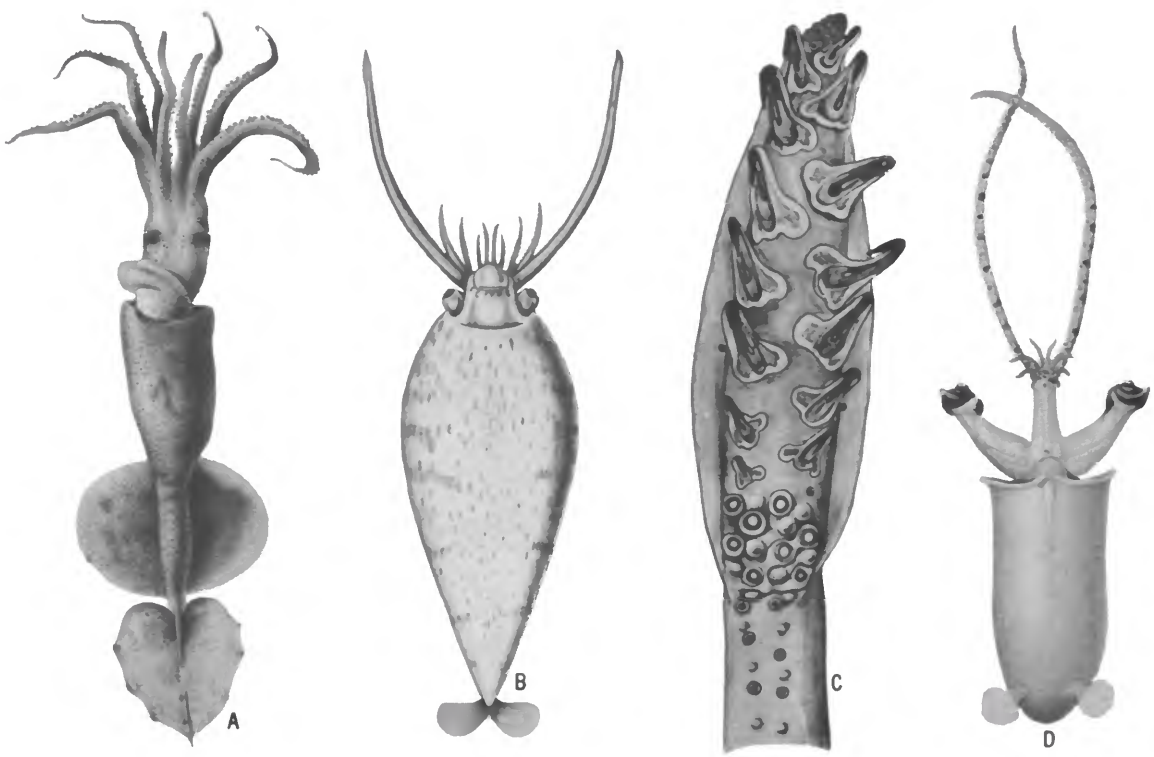

PLATE 15.—Grimalditeuthidae: A, *Grimalditeuthis,* ventral view (from Joubin, 1900). Cranchiidae: B, *Helicocranchia,* ventral view (from Young, MS); C, *Galiteuthis,* tentacular club (from Young, MS); D, *Bathothauma,* dorsal view (from Chun, 1910).

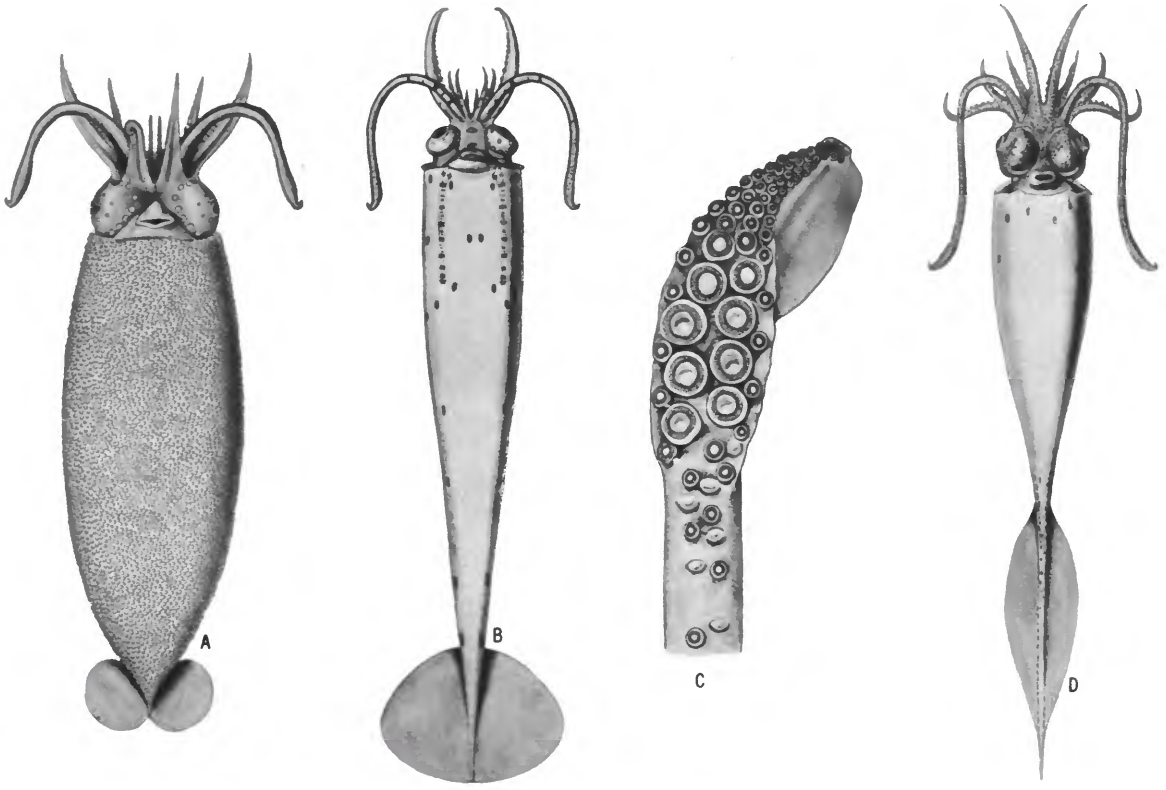

PLATE 16.—Cranchiidae: A, *Cranchia,* ventral view; B, *Leachia,* ventral view; C, *Leachia,* tentacular club; D, *Galiteuthis,* ventral view. (All from Young, MS.)

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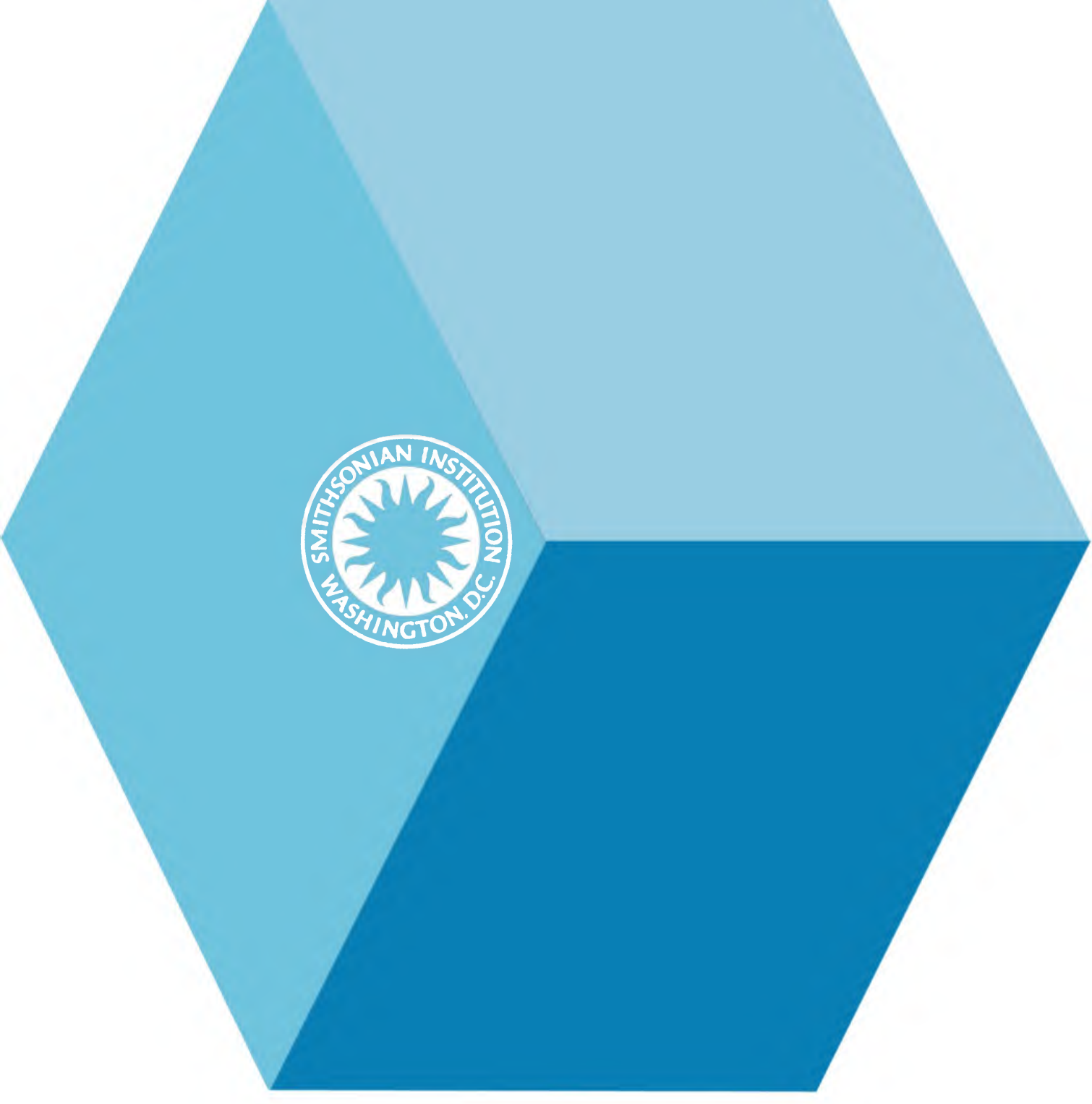
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