

A TALE OF TWO SPECIES: TAIL MORPHOLOGY IN PARALARVAL *CHIROTEUTHIS* (CEPHALOPODA: CHIROTEUTHIDAE)

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Abstract.—"Doratopsis" paralarvae of *Chiroteuthis* were observed in-situ and collected intact using a remotely operated vehicle (ROV) in the eastern North Pacific and a manned submersible in the western North Atlantic. These specimens, the first with complete tails, show remarkable interspecific differences in tail morphology but little intraspecific variability. Eleven Pacific specimens had very long rigid tails characterized by pairs of large, fluid-inflated, lateral pouches separated by 4-6 flat, rounded, lateral lobes of tissue (referred to here as flaps, not finlets). The single Atlantic specimen had a long, rigid tail with long, pointed flaps staggered along its sides, each separated by 4-6 short, pointed flaps; when alive, it had what appeared to be very small pouches at the tips of the long flaps. We attribute the Pacific specimens to *Chiroteuthis calyx* Young. Of the species known from the western North Atlantic and Gulf of Mexico, the Atlantic specimen probably is not *C. veranyi* Ferrusac, *C. lacertosa* Verrill, nor *C. joubini* Voss. It most likely is *C. capensis* Voss or an undescribed species.

Squids of the genus *Chiroteuthis* are among the strangest of cephalopods. Adult *Chiroteuthis* look like caricatures of squids. All members of the genus develop through an unusual elongate paralarval stage, designated as the genus *Doratopsis* by Rochebrune (1884) based on *Loligopsis vermicularis* Rüppell, 1845. Ficalbi (1899) demonstrated that "Doratopsis vermicularis" was actually a young stage of *Chiroteuthis veranyi* (Ferrusac, 1835). Although Pfeffer (1900) and Hoyle (1909) disputed this conclusion, Naef (1923) further defended Ficalbi's position and it has been generally accepted since. Recently, Young (1991) redefined the family Chiroteuthidae, giving the primary familial character as development through a doratopsis-type paralarval stage; he provided a detailed unifying diagnosis for the doratopsis stage.

Doratopsis paralarvae have long been known to have a fragile tail that extends

posterior to the fins. However, in all specimens reported in the literature to date, the tails have been either broken or missing. Of the published descriptions of doratopsis paralarvae, only one of Ficalbi's (1899, figs. 1-2) and two of Pfeffer's specimens (1912, plate 46, figs. 1-3) had what until now appeared to be substantial portions of the tail intact. Many other descriptions of doratopsis specimens have been published (e.g., Hoyle 1886, Chun 1910, Issel 1927, Berry 1963); the specimens always lack all but a minute stub of the tail. Young (1991) was forced to omit characters of the paralarval tail in his study because the tails are "invariably broken off."

In the course of studies using submersibles, we have videotaped and collected doratopses with their tails intact. We describe here the details of tail morphology and in-situ behavior of the squids. We include descriptions of the doratopses' general mor-

phology for future taxonomic comparisons. We also discuss the identities of the doratopses and speculate on functions of the tail.

Materials and Methods

Pacific specimens.—These unusual squids were first observed and videotaped in-situ during an ongoing series of remotely operated vehicle (ROV) dives in Monterey Canyon by the Monterey Bay Aquarium Research Institute (MBARI). The ROV operators were then challenged to collect one or more specimens whenever possible in future dives. This effort achieved success when three specimens were collected on separate dives. The "detritus sampler" collecting gear consisted of a large-bore, acrylic tube mounted vertically with remotely actuated, rotating covers to seal both ends. The ROV was maneuvered above the squid and then brought slowly downward until the squid was inside the sampler, which was then closed. These specimens were observed alive by one of us (BHR) aboard ship and one was videotaped through a microscope while alive. All three were then sent to the National Museum of Natural History for detailed morphological observations. Additional specimens have been videotaped and collected and attempts have been made to keep them alive for display at the Monterey Bay Aquarium.

Atlantic specimen.—A single specimen was collected along with several other cephalopods by Marsh Youngbluth of the Harbor Branch Oceanographic Institute using the *Johnson Sea-Link* (JSL) manned submersible for a series of nocturnal dives in Bahamian waters. The doratopsis was collected in a detritus sampler similar to that described above. Its tail broke off when it was transferred from the sampler. The live squid and its tail were photographed in an aquarium aboard ship. The specimen and photographic slides were sent to one of us (CFER) at the National Museum of Natural History (NMNH), but material for com-

parisons was lacking until now. The slides were the source of the details of tail morphology and chromatophore patterns for the live specimen.

All specimens were examined and measured using a dissecting microscope with ocular micrometer. Mantle length (ML) was measured along the dorsal midline from the anterior edge of the mantle to the posterior insertion of the fins (i.e., including the fins beyond the posterior tip of the mantle sensu strictu, which in a doratopsis terminates near the anterior edge of the fins) but excluding the tail.

Observations

Pacific specimens.—Material examined: 1 specimen collected but not videotaped, 44 mm ML, depth 278 m, 6 Aug 1990, 1330–1400 h Pacific Standard Time (PST), 36°42'N, 122°02'W, USNM 817760; 1 specimen videotaped and collected, 49 mm ML, depth 431 m, 7 Nov 1990, 1406 h PST, 36°42'N, 122°02'W, USNM 817761; 1 specimen videotaped and collected, 60 mm ML, depth 302 m, 24–25 Jul 1991, "night-time," 36°42'N, 122°02'W, USNM 884234.

Other observations: 3 squids videotaped but not collected, (#1) depth 366 m, 5 Oct 1989, "daytime," 36°42'N, 122°02'W; (#2) depth 335 m, 27 Nov 1989, "daytime," 36°42'N, 122°02'W; (#3) depth 384 m, 20 Dec 1989, "daytime," 36°43'N, 121°59'W. 5 other specimens 50–55 mm ML were videotaped and collected. The specimens were examined at MBARI and the videotapes reviewed in detail but because of labelling problems resulting from attempts to maintain the squids alive, the specimens could not be associated with specific videotape sequences and dive data. Data for videotape sequences (all daytime) are as follows: (#4) depth 399 m, 17 June 1991, 36°42'N, 122°02'W; (#5) depth 416 m, 12 Jul 1991, 36°45'N, 122°02'W; (#6) depth 457 m, 6 June 1991, same area but position not recorded; (#7) depth 471 m, 9 Sep 1991, same

area but position not recorded; (#8) depth 278 m, 6 Sep 1990, 36°42'N 122°02'W.

Description of animal (Fig. 1A): Tentacles thin but muscular, very long, much longer than ventral arms, with suckers along distal half; tips slightly expanded as clubs with single dorsal keel on all specimens, narrow trabecular membranes present along both sides of sucker-bearing distal half; suckers tetraserial on clubs and stalks. On 44-mm ML specimen single thickened aboral pad at base of each tentacle and series of pad rudiments on aboral side along proximal half of tentacle stalks; on 49-mm and 60-mm ML specimens series of aboral pads well developed along proximal half of stalks. Arms $IV \gg III > II > I$; teeth not apparent on sucker rings of 44-mm ML specimen; on 49-mm and 60-mm ML specimens arm sucker rings with many long sharply pointed teeth across distal half, increasing gradually in length from sides to center. Tentacle sheaths well developed on ventral arms, of vesiculate tissue. Arm-crown pillar gelatinous and vesiculate, short, approximately equal to head length; esophagus centrally located. Head short. Olfactory papillae well developed, finger-like, ventrally located, anterior to statocysts. Eyes of 44-mm ML specimen egg-shaped in lateral view; small end of each oriented anteroventrally, covered with reflective tissue and large ventral chromatophore; eyes on larger specimens round, each covered laterally with reflective tissue, with single, large ventral photophore. Neck very long (ca. $\frac{1}{2}$ ML) and broad (equal to maximum mantle width), longer than head and arm-crown pillar together; gelatinous, strongly and coarsely vesiculate, forming chambers. Digestive gland and gills located near base of funnel at anterior end of mantle cavity; digestive gland bean-shaped, bright red with lateral veneer of reflective tissue in live animal. Ink sac embedded on ventral surface of digestive gland; reflective, with 2 small photophore rudiments on ventral surface; paired photophores on ink sac well developed in 60-mm

ML specimen. Mantle terminates posteriorly near anterior insertion of fins; tissue finely vesiculate posteriorly; very delicate integumentary tissue continues posteriorly from mantle tip, covering gladius ventral to fins. Fins broad, width nearly equals length, round except at anterior and posterior insertions where concavities are partly filled with delicate tissue. Chromatophores orange-brown in live specimen, form pronounced stripe along dorsal midline of mantle and neck, along ventral midline of mantle, scattered around ventral edges and entire dorsal surface of fins, on aboral surface of all arms; 2 rows of very small chromatophores aborally along each tentacle; chromatophore patches on tentacle clubs aborally, ventral and dorsal surfaces of head, laterally at posterior end of mantle and near gills/digestive gland; band of small chromatophores around edge of anterior mantle opening; other chromatophores scattered dorsolaterally on mantle, ventrolaterally on funnel and collar. Chromatophores more numerous on 49-mm ML specimen than on 44-mm ML but patterns very similar; chromatophores on 60-mm ML specimen similar to those of 49-mm ML specimen.

Tail morphology (Fig. 2A): Tail very long, longer than total length of specimen from posterior border of fins to arm tips, constricted near posterior border of fins, gradually broadens to midpoint then tapers to acute posterior tip. In live specimens, 5–6 pairs of knob- or ball-like pouches filled with clear fluid spaced along the lateral edges of the tail. Squeezing one pouch appears to cause fluid to flow into adjacent pouches. Pouches slowly deflate when tail breaks so that in preserved specimens they appear to be tightly rolled flaps of skin. Between pouches, lateral edges of tail form series of obtuse flaps that also roll up in preserved specimens; in live animals these flaps appear as serrations between the ball-like pouches. Tissue of tail vesiculate, especially near central gladius. Gladius box-shaped in cross section, with narrow open gap in ven-

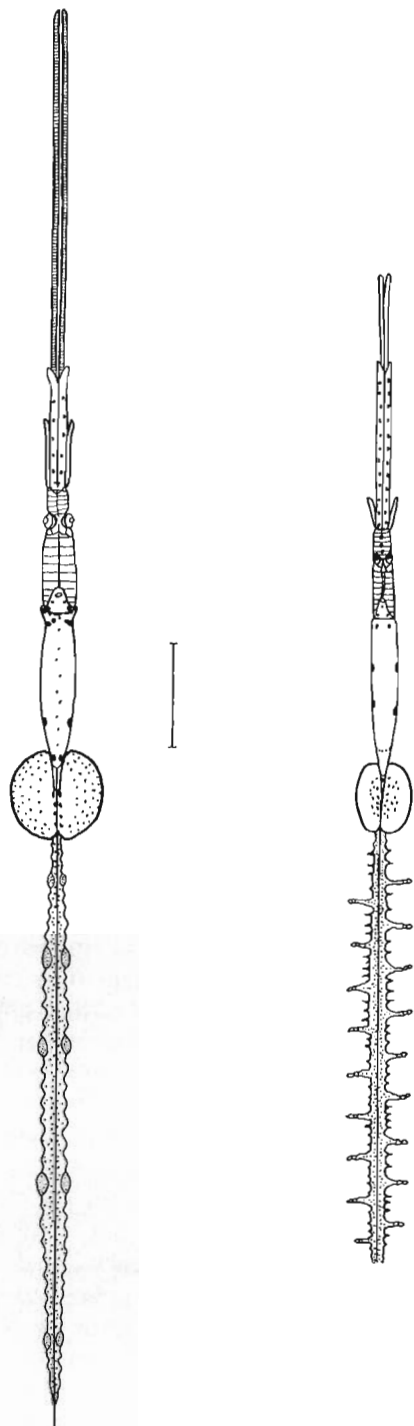


Fig. 1. *Chiroteuthis* spp. Ventral views of doratopsis paralarvae of similar mantle lengths drawn to the same scale. (A, left) Pacific specimen, 44 mm ML, USNM 817760; (B, right) Atlantic specimen, 43 mm ML, USNM 817762. Scale bar = 20 mm.

tral wall and hollow dorsal-midline ridge. Chromatophores concentrated in soft tissue along both sides of gladius, on flaps, and especially on pouches.

Behavior: A typical posture was observed whenever the ROV first approached a doratopsis (Fig. 3). The squids usually orient obliquely, nearly vertically, with the tail pointed downward, the mantle, neck, head, arm-crown pillar, arms, and tentacles approximately in line with the tail. The tentacles extend upward well beyond the tentacle sheaths on the long fourth pair of arms. The arms and tentacles sometimes are spread. The fins undulate slowly. One doratopsis was horizontal in the water when first approached. Another was oriented vertically, head up, but with the arms and tentacles bent 90° at the head so that they hung straight down along the neck and mantle. One individual was observed to bend its gladius more than 45° at the posterior end of the mantle (anterior to the fins) without apparent damage and without breaking the tail.

The doratopsis' escape reaction consists of pointing the tail straight down, then jetting rapidly downward. During the escape, black ink is released in long thin pseudomorphs that undulate slightly in the exhalent current. The pseudomorphs approximate the dimensions and shape of the doratopsis including tail. When attempts were made to collect specimens during videotaping, if they were lightly touched by the side of the sampler, the tail would break completely off close to the narrow constriction near the fins, resulting in the tailless condition always found in net-collected specimens. The breaks always occurred near the fins but not always in exactly the same location, indicating that the break is not associated with a specific weak point in the gladius.

The chromatophores were used by the live animal to form several patterns that, although less complex than those observed in neritic cephalopods, demonstrated the potential for a variety of behavioral patterns

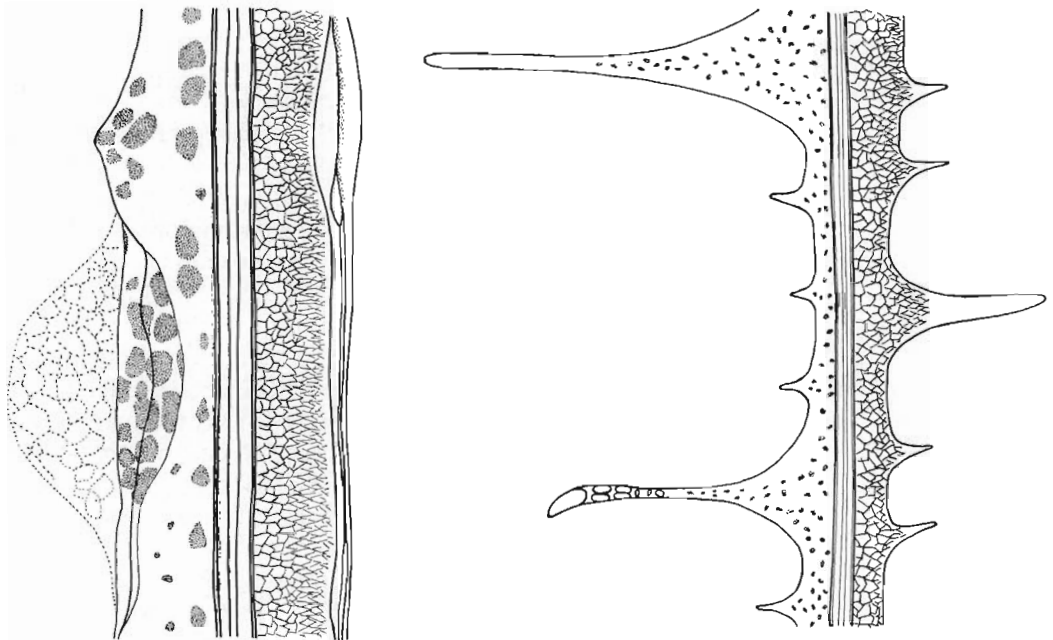


Fig. 2. Composite view of details of tail morphology. Left side of each figure shows chromatophore pattern, right side shows reticulation of tissue. (A, left) Pacific specimen, USNM 817761. In preserved specimens the edges of the tail are tightly rolled. Large stippled area on the left shows approximate shape and chromatophore pattern of deflated pouch when unrolled. (B, right) Atlantic specimen, USNM 817762. Positions of white (distal) and yellow (medial) bead-like structures seen in photographs of the live specimen are indicated on one large flap (lower left of B).

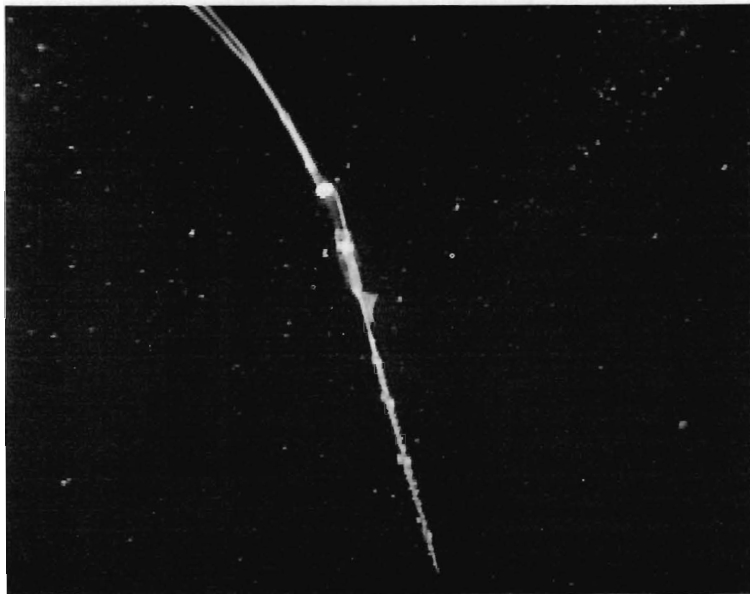


Fig. 3. Still frame from a videotape recorded in-situ, showing a Pacific doratopsis. The squid is oriented obliquely with the tail directed down and the arms and tentacles up.

in these midwater squids. Chromatophore displays observed on live animals aboard ship included: (1) a dark longitudinal stripe along the dorsal midline of the tail, mantle, neck, head, and arms; (2) progression of chromatophore expansion along the dorsal midline from arms toward tail; and (3) independent darkening of separate regions, such as the pouches, fins, tentacle tips, and the mantle in the vicinity of the digestive gland.

All doratopses were observed in-situ within the depth range of 278–471 m.

Atlantic specimen.—Material examined: 1 specimen collected, not videotaped but photographed alive in aquarium, 43 mm ML, depth 142 m, Oct 1979, “nighttime,” “Bahamas,” USNM 817762.

Description of animal (Fig. 1B): Tentacles thin but muscular, very long, longer than ventral arms, with suckers along distal half, tips slightly expanded as clubs with single dorsal keel, narrow trabecular membranes present along both sides of sucker-bearing distal half; no pads on aboral side along proximal half of tentacles; suckers tetraserial on tentacle stalks and clubs. Arms $IV \gg III > II > I$; teeth could not be seen on sucker rings; tentacle sheaths on ventral arms well developed, of vesiculate tissue. Arm-crown pillar gelatinous and long, much longer than head length, strongly and coarsely vesiculate, forming chambers, esophagus located dorsally. Head short. Olfactory papillae well developed, finger-like, located ventrally, anterior to statocysts. Eyes egg-shaped in lateral view, with small end oriented anteroventrally. Neck long (ca. $\frac{1}{3}$ ML), narrower than mantle, gelatinous, strongly and coarsely vesiculate, forming chambers. Digestive gland and gills located near base of funnel at anterior end of mantle cavity; bean-shaped. Ink sac embedded on ventral surface of digestive gland; no trace of chromatophores on digestive gland or ink sac. Mantle terminates posteriorly near anterior insertion of fins, very delicate integumentary tissue continues posteriorly from mantle end

covering gladius ventral to fins. Tissue of posterior mantle finely vesiculated. Fins narrow, width less than length, oval except at anterior and posterior ends where muscular concavities are partly filled with delicate tissue. Chromatophores bleached in preserved specimen; large chromatophores yellow and smaller chromatophores red in photographs of live specimen; form pronounced stripe along dorsal midline of mantle, neck and arm-crown pillar; absent from ventral midline of mantle but present on ventral midline of arm-crown pillar; scattered around centers of ventral surface and entire dorsal surface of fins; on aboral surface of all arms; no chromatophores visible on tentacles but tentacles enclosed within tentacle sheaths of arms IV in photographs; patches of chromatophores on ventral and dorsal surfaces of head; chromatophores laterally on funnel and collar, at posterior end of mantle and on arm-crown pillar; band of small chromatophores around edge of anterior mantle opening; other chromatophores scattered dorsolaterally on mantle and neck.

Tail morphology (Fig. 2B): Tail long, longer than length of specimen from posterior edges of fins to tips of lateral arms, constricted near posterior border of fins, then broad throughout length. Posterior tip missing. Long, narrow, pointed flaps staggered along sides of tail, each separated by 4–6 shorter pointed flaps. In photographs of the live specimen, yellow and white bead-like structures, possibly fluid-filled pouches, were located at the tips of the long flaps; these structures cannot be seen in preserved specimen. Tissue of tail vesiculate, especially near central gladius. Gladius cross-section box-shaped with concave lateral walls, narrow open gap in ventral wall, and with dorsal-midline ridge. Chromatophores concentrated on soft integument along both sides of gladius and on central axes of flaps.

Behavior: This squid assumed the same posture in the shipboard aquarium as was observed in-situ for the Pacific specimens.

When the squid moved in the aquarium, it kept its digestive gland oriented vertically regardless of the orientation of the body axis. The fragility of the tail, which broke at its constriction near the fins during transfer from the sampler, also was similar to the Pacific specimens.

Discussion

Without a complete growth series, inferences about the species identity of these paralarvae of *Chiroteuthis* must be based on assumptions about the systematics and known species distributions within the genus. This is relatively simple for the Pacific specimens but much more complicated for the specimen from the Atlantic.

Chiroteuthis calyx Young, 1972 is the only species known from Californian waters. It is commonly caught in midwater trawls off northern California (Vecchione, unpublished data). Earlier reports of *C. veranyi* from California and Oregon actually represent *C. calyx* (see Young 1972), which is very similar to the Mediterranean/Atlantic *C. veranyi*. A doratopsis described by Berry (1963) was identified as *C. calyx* by Young (1972), as were two doratopses included in the original description of the species. Our Pacific specimens conform to these earlier descriptions of paralarvae. We are therefore confident that our specimens are *C. calyx*. Here we add details about the tail morphology to the description of that species. Intraspecific variation was quite small among our few specimens.

As we mentioned in the introduction, Ficalbi (1899), supported by Naef (1923), demonstrated that "Doratopsis vermicularis" is actually the paralarva of *C. veranyi*. One of Ficalbi's specimens had a fragment of the tail remaining, as did two of Pfeffer's (1912, plate 46) doratopses. Pfeffer's specimens, for which collection location was not presented, clearly represent two separate species of *Chiroteuthis*. Given differences in artistic style (Ficalbi's figures are compar-

atively crude), we believe that the specimen in Pfeffer's figures 1 and 2 belongs to the same species as Ficalbi's specimen, *C. veranyi*. All of these figures show indications of paired lateral pouches on the tail, similar to those described above for *C. calyx*. They also show a proximal constriction of the tail near the fins, as well as tissue expanded laterally from the gladius.

Young (1972) pointed out in the original description that *C. calyx* is very similar to *C. veranyi*. Likewise, strong similarities exist between the paralarvae of *C. calyx* and those of *C. veranyi* as described by Ficalbi (1899) and Pfeffer (1912). These similarities include chromatophore patterns, presence and location of lateral pouches on the tail, and the proximal constriction of the tail. The most noticeable difference between paralarvae of these species is the apparent lack of flaps (tissue lobes) between the pouches on the tail of paralarval *C. veranyi*.

Tail morphology of Pfeffer's other specimen (plate 46, figure 3) is very different from any other described specimens. It appears to have a broad oval pair of flaps about 1 ML from the fins, with no other lateral tissue apparent on the extended gladius of the tail. We cannot associate this specimen with any described species at this time.

The species of *Chiroteuthis* commonly reported from the western North Atlantic are *C. veranyi* and *C. lacertosa* Verrill, 1881 (*Leptoteuthis diaphana* Verrill, 1884 is a juvenile *C. lacertosa*). In addition, *C. joubini* Voss, 1967 and *C. capensis* Voss, 1967, originally described from the equatorial Atlantic and the eastern South Atlantic, respectively, recently have been found in the Gulf of Mexico (Passarella & Hopkins 1991). *Chiroteuthis lacertosa* is so similar to *C. veranyi*, differing only slightly in the shape of the fins and perhaps in details of the club, that their status as separate species is doubtful. The extreme differences between our Atlantic specimen and the *C. veranyi* doratopses of Ficalbi (1899) and Pfeffer (1912, plate 46, figures 1 and 2) convince us that

our specimen is neither *C. veranyi* nor *C. lacertosa*.

Although less compelling, indirect evidence indicates that our specimen probably is not *C. joubini*. We have an early juvenile *Chiroteuthis*, similar to *C. joubini*, 50 mm ML, from the Gulf of Mexico that possesses rows of separate, bead-like ocular photophores, paired photophores on the digestive gland, and central expansions of the trabecular membranes on the clubs. These characters conform to specimens described by Nesis & Nikitina (1984) in a redescription of *C. joubini* which, based on present knowledge, probably represent an undescribed species. The Atlantic specimen reported here, 43 mm ML, shows no indication of any of these diagnostic characters. Whereas our 44-mm ML *C. calyx* has paired photophore rudiments on the digestive gland, none were seen on the 43-mm ML Atlantic specimen. Its ocular photophore rudiments appear to be similar to those of *C. calyx*, which develops a large strip of photogenic tissue on the ventral surface of the eye. The remaining *Chiroteuthis* species now known from the western North Atlantic, *C. capensis*, is characterized by strip-like ocular photophores, lack of photophores on the digestive gland, and lack of the expansion of the trabecular membrane. We therefore feel that our Atlantic specimen is more likely to be *C. capensis* than *C. joubini*, s.l. The possibility remains, though, that it is the paralarva of an undescribed species.

Other genera of Chiroteuthidae possess tails in the subadult/adult stages that are reminiscent of those of paralarval *Chiroteuthis*. These adult tails probably represent paedomorphy, the retention of ancestral larval characteristics in advanced developmental stages. The long tail of an undescribed genus that occurs in Hawaiian waters (R. E. Young, University of Hawaii, pers. comm.) is remarkably like that of paralarval *Chiroteuthis veranyi*, but it apparently lacks the fluid-filled pouches. On *Grimalditeuthis*, the gladius extends well posterior to

the fins and supports a broad, heart-shaped structure that traditionally has been referred to as a "secondary fin." This probably is the source of speculation that the tails of doratopses support one or more secondary fins (e.g., Nesis 1987:241), a terminology that implies an active locomotor function for these structures. Our observations, both of in-situ behavior and of microscopic structure, revealed no muscular movement in any structure of the tail. We have therefore established the nomenclature used above, pouches and flaps, to describe these structures and we advocate their standard use in future studies. While "secondary fin" probably does not accurately describe the tail structure on *Grimalditeuthis* because it is not muscular, it also differs greatly from the pouches and flaps we describe above for doratopses and our terminology would not be appropriate for that structure. It may function as a floatation device and, if so, should be referred to as a float.

Currently, we can only speculate on the functions of the tail structures on paralarval *Chiroteuthis*. The fluid-filled pouches may provide positive buoyancy to counterbalance the weight of the extended gladius. However, the entire tail is filled with vesiculate tissue which is almost certainly buoyant, so the buoyancy contribution of the pouches remains uncertain. A variety of buoyancy mechanisms are known in cephalopods, including fluid-filled vesicles in the arms and bodies of adult chiroteuthids (Denton & Gilpin-Brown 1973). This interpretation is quite different from speculation by Ankel (1974) that the tail functions primarily as a weight to counterbalance the weight of the arms, allowing the center of gravity to match the center of buoyancy provided by the neck (Denton & Gilpin-Brown 1973). Ankel (1974) argued that the typical position of a doratopsis in the water is horizontal in spite of his photograph of a specimen in an aquarium oriented obliquely vertical with the head up.

Patches of chromatophores on mesope-

agic cephalopods often serve to cover structures that are opaque or luminescent. The fluid in the pouches is not opaque, so the concentrations of chromatophores over them may indicate a capability of luminescence, although we have no direct evidence of this yet.

The tail doubles the length of the animal with minimal investment of protein resources, but at the cost of maneuverability. Long thin animals, vertically oriented, are common in the mesopelagic realm (personal observations). The tail also gives the squid a very peculiar appearance which may serve to conceal its identity. In midwater, concealment usually is achieved by attempts to be invisible (e.g., transparency, reflectivity, or bioluminescent counterillumination) or by mimicry. In doratopsis the tail may contribute to mimicry. While reviewing the in-situ videotapes of *C. calyx*, we were impressed with the similarity of its appearance to that of nearby mesopelagic siphonophores (*Nanomia bijuga*) which possess powerful nematocysts; the doratopsis tail pouches looked much like the nectophores and bracts on a siphonophore. The tail may also be important in the escape reaction, as it is almost always pointed downward and because the theoretical maximum velocity of a body through a fluid is proportional to its length. Regardless of its function while attached, the tail is unquestionably designed to detach easily from the animal. Possibly this serves a similar function to the autotomizing tail of a lizard. A predator may be distracted by the detached tail, possibly leaking luminescent fluid, while the squid escapes.

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