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ABSTRACT

A new family of oegopsid cephalopods, Cycloteuthidae, is erected as a result of the elevation of Naef's subfamily Cycloteuthinae. *Cycloteuthis sirventi* Joubin, 1919, is redescribed based on new material from the Atlantic Ocean. A new genus, *Discoteuthis,* and two new species, *D. discus* and *D. laciniosa,* are described from the Atlantic Ocean. Larvae of *C. sirventi* and *D. laciniosa* are described. The distributions of the species of cycloteuthids in the Atlantic and Indian Oceans are presented. The relationships of the family, genera, and species are discussed.

Among the cephalopods captured during the 1964 cruise of the University of Miami, Institute of Marine Sciences' RV *John Elliot Pillsbury* to the Gulf of Guinea, one specimen presented a particular problem in identification even at the familial level. The specimen bore some resemblance to Joubin's poorly known *Cycloteuthis sirventi* on which no additional material has been reported since the original description of the species in 1919. A search through the extensive cephalopod collections at the Institute of Marine Sciences yielded a number of specimens that included not only the new form, but also *Cycloteuthis sirventi.* A study of these specimens, which are primarily from collections of IMS vessels and the RV *Dana* Expeditions, revealed that the species represented by the Gulf of Guinea specimen indeed showed relationship with *Cycloteuthis sirventi* but was generically distinct from it. After further investigation, a second new species was discovered to be referable to the new genus, *Discoteuthis.* The present material of *Cycloteuthis* and *Discoteuthis,* although not great in volume, has provided sound information to confirm that these genera form a taxonomic unit sufficiently distinct from other oegopsid familial groups to necessitate the erection of a separate family, the Cycloteuthidae.

The coauthors wish to thank M. R. Clarke for the loan of a *Discovery* specimen, E. Bertelsen for the *Dana* material, and G. E. Maul for the Madeira specimens. The remaining specimens were taken on the Institute of Marine Sciences' research vessels *Pillsbury* and *Gerda* and during Ocean Acre cruises. We are also grateful to G. L. Voss for his support and for his comments on the manuscript. The illustrations were prepared by Miss Constance Stolen, to whom we are greatly indebted. The work was supported primarily by research grants (GB–3808, GB–2204, GB–5729Y) from the National Science Foundation and the National Geographic Society-University of Miami Deep-Sea Biology Program.

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DEFINITIONS.—The following definitions are designed for the Cycloteuthidae and do not necessarily apply to other groups.

Mantle length (ML): The length of the mantle measured along the dorsal midline from the free anterior margin to the extreme posterior tip of the body. In the Cycloteuthidae, therefore, the mantle length is equal to the pen length.

Tail: The posterior extension of the body beyond the point where the posterior margin of the fins turns abruptly posteriorly near the mantle.

Fin length (FL): The length from the anterior extension of the fin lobes to the extreme posterior tip of the body, measured along the middorsal line of the mantle.

Historical Résumé

Joubin (1919) described a new genus and species, *Cycloteuthis sirventi,* and indicated that it was closely related to *Lycoteuthis diadema;* he placed these two genera in a new family, the Parateuthidae, which he considered to be intermediate between the Enoploteuthidae and the Histioteuthidae. Since a familial name must be based on the name of the type genus, Joubin's name is invalid. Independently, Thiele (1921) erected the genus *Parateuthis* based on a larval oegopsid captured in the Antarctic Ocean (he did not assign it any oegopsid family); this genus, however, has no connection with Joubin's Parateuthidae. Naef (1922, p. 298) recognized that Joubin's family was not a natural grouping and transferred *Lycoteuthis* to the Enoploteuthidae and *Cycloteuthis* to the Onychoteu-

thidae. Shortly afterward, Naef (1923, p. 312) established for *Cyloteuthis* a separate subfamily, the Cycloteuthinae. He also indicated (p. 266) that *Cyloteuthis,* although an onychoteuthid, shares characters with the Enoploteuthidae.

Joubin (1924) repeated his earlier description and retained the position of *Cycloteuthis* in his Parateuthidae, apparently unaware of Naef's changes and Thiele's description of *Parateuthis.*

Although Grimpe (1925) listed *Cycloteuthis* in the Onychoteuthidae, he did not maintain Naef's subfamily and stated that the position of the genus was still uncertain.

Thiele (1935) gave a brief diagnosis of the genus and included it in the Onychoteuthidae, apparently also rejecting Naef's subfamily.

Clarke (1966) resurrected Joubin's invalid family, Parateuthidae, in which he placed four unrelated genera, including *Cycloteuthis;* he gave no explanation for this unwarranted action.

Family CYCLOTEUTHIDAE Naef, 1923

PARATEUTHIDAE Joubin, 1919, p. 2 [in part; refers to *Cycloteuthis* only].

CYCLOTEUTHINAE Naef, 1923, p. 312.

DIAGNOSIS.—Buccal connectives attach to ventral borders of arms IV; arms with biserial suckers; tentacular club with tetraserial suckers; club compact, expanded with well-defined manus and dactylus, ill-defined carpus; funnel locking-cartilage subtriangular; fins large in adults (over 70 percent of mantle length); photophores present.

Genus *Cycloteuthis* Joubin, 1919

Cycloteuthis Joubin, 1919, p. 1.—Naef, 1922, p. 298; 1923, pp. 266, 809.—Thiele, 1935, p. 965.

DIAGNOSIS.—Tail present; gladius only slightly thickened; conus hollow, elongate; suckers in a transverse series on manus nearly equal in size; large photophore on ink sac; a series of small photophores on eye; fins large but not equal to the mantle length in adults.

TYPE-SPECIES.—*Cycloteuthis sirventi* Joubin, 1919. By monotypy.

Cycloteuthis sirventi Joubin, 1919

PLATES 1; 2; 7E, F, H, K; 8C, F; 9O–U

Cycloteuthis sirventi Joubin, 1919, p. 1, figs. 1–2.—Naef, 1923, p. 312.—Joubin, 1924, p. 53, pl. 7: figs. 3–6; pl. 8: figs. 1–11.—Grimpe, 1925, pp. 96, 103.—Thiele, 1935, p. 965.—Clarke, 1966, p. 161.

DESCRIPTION.—The redescription of *Cycloteuthis sirventi* is based primarily on the male specimen with a ML of 42 mm (*Gerda* 212). A clear indication is given when other specimens are discussed. Table 1 lists the measurements of available specimens.

The mantle is conical and tapers posteriorly to a sharp point (Plates 1A, 2C–D). The mantle wall is thin and invaded by gelatinous connective tissue between the inner and outer layers of muscle. Posteriorly the muscular portion of the mantle terminates in advance of the posterior margin of the fins at the beginning of the conus of the pen. In the largest specimen the mantle width is about one-third of the mantle length. The mantle narrows relatively with growth; smallest specimens have mantle widths about 50 percent of the mantle length.

List of Material

Sex	*ML, mm*	*Station number*	*Location*	*Date*	*Estimated depth, m*
1 ♂	42	*Gerda* 212	23°32′N 82°37.5′W	20 I 1964	650
1 ♂	41	Acre 2–2	32°26′N 63°44′W	6 III 1968	140
1 ♂	27	*Dana* 829	25°07′N 19°20′W	13 IV 1920	100
1 ♂	17	*Dana* 4017 VII	29°13′N 14°12′W	27 III 1930	200
1 juv.	15	*Dana* 1172 II	07°22′N 46°51′W	14 XI 1921	200
1 L[1]	10	*Dana* 1157 III	21°57′N 22°58′W	27 X 1921	100
3 L	8. 5	*Dana* 1030	35°31′N 55°58′W	1 XII 1913	10–400
4 L	4–9	*Dana* 830	24°44′N 22°32′W	15 IV 1920	100
1 L	8	*Dana* 1157 XII	21°57′N 22°58′W	27 X 1921	200
1	head only	*Dana* 1157 XII	21°57′N 22°58′W	27 X 1921	200
1	head only	*Dana* 4003 IX	08°26′S 15°11′W	9 III 1930	100

[1] L refers to larval specimens.

TABLE 1.—*Measurements (in mm) of* Cycloteuthis sirventi

Characters	*Gerda 212*	*Dana 829*	*Dana 1172 II*	*Dana 1157 III*	*Dana 1030*	*Dana 1030*	*Dana 1030*	*Dana 1157 XII*	*Dana 1157 XII*	Acre 2–2
Sex	♂	♂	juv.	larva	larva	larva	larva	larva	larva	♂
Mantle length	42	27	15	10	8.5	8.5	8.5	8.0	–	41
Mantle width	14	11	7	4.5	4.0	–	4.0	4.0	–	14
Head length	22	10	6	3.0	2.2	2.5	2.5	4.0	–	18
Head width	13	11	6	4.2	4.0	3.8	4.0	5.0	5.0	15
Fin length	34	19	6.5	3.0	2.0	2.0	1.8	3.5	–	33
Fin width	37	26	8.5	5.2	5.0	5.0	4.2	7.0	–	40
Arms I	26	16	5.5	2.5	1.5	1.8	2.0	2.0	–	23
II	36	22	7.5	5.0	3.2	3.6	3.5	5.5	–	33
III	37	22	7.5	5.0	3.0	3.6	3.0	5.5	–	–
IV	36	21	7.5	4.5	3.0	2.8	2.0	5.0	–	34
Tentacle length	70	40	26	11	7.2	8.0	7.0	13.0	11.0	64
Club length	15	11	4	3.2	2.5	2.2	2.0	3.2	3.2	16

The fins are long, about 80 percent of the mantle length, and broad, about 90 percent of the mantle length. The fins are very muscular and elliptical, except posteriorly where they are drawn out along the lateral sides of the tail. The anterior fin lobes are only slightly produced. The fins are separated by a narrow gap for most of their length and are not fused in the dorsal midline. The bases of the fins insert directly on the shell sac of the gladius.

The funnel is small and reaches just past the posterior edge of the eyelids. The funnel locking-cartilage on either side of the funnel is approximately triangular in shape, with the lateral side nearly parallel to the body axis and the anterior side transverse to the body axis (Plate 7E). The groove of the locking-cartilage is broadly V-shaped paralleling the lateral and anterior sides. A deep, hemispherical depression lies at the anterolateral apex of the lock and is indented into the lateral wall. Medially the groove gradually becomes shallow toward the inner edge of the cartilage. The mantle component is a V-shaped ridge with a large, swollen apical knob. The transverse limb extends ventrally and the oblique limb extends posteriorly. A distinct groove lies anterior to the transverse limb and a more shallow depression parallels the oblique limb.

A long, narrow funnel valve is present. The dorsal portion of the funnel organ is an inverted V-shaped pad (Plate 7H). The limbs are very long and broad; they bear high flaplike median ridges. The apical area bears a separate, flaring median ridge that has an anteriorly directed point located slightly posterior to the apex of the organ. The ventral pads are large and nearly oval, although slightly pointed anteriorly. Two pairs of bridles attach to the dorsal surface of the funnel near its free anterior end.

The head is short and oval with large eyes that occupy almost the entire lateral portions of the head; the circular eyelids have a small anterior sinus. Nuchal folds and the nuchal crest are lacking. A small olfactory papilla lies posterior to each eye and lateral to the funnel. The nuchal locking-cartilage is long and narrow; a deep groove with raised lateral ridges runs along the midline (Plate 7F).

The length of all arms except arms I is approximately 85 percent of the mantle length in the largest specimens. Arms I are about 60 percent of the mantle length. The arm formula is $2=3=4>1$. Gelatinous aboral keels are present on arms I–III and lateral keels are present on arms IV. The arms are slightly damaged and the total extent of the keels cannot be determined. Low, undulating, trabeculate protective membranes are present on arms I–III, but are lacking on the ventral arms. The suckers are arranged biserially in longitudinal rows along the entire lengths of all the arms.

The sucker stalks on arms IV arise from large gelatinous bases that extend transversely across the arms and give the oral faces a ladder-like appearance. The suckers on arms IV are much smaller, more closely packed and more numerous than on the other arms.

The inner rings of the arm suckers bear numerous, low, truncate teeth around the entire margin of the ring. The teeth on the distal part of the rings are larger than those on the proximal part. About 20 teeth occur on the larger suckers, fewer on smaller suckers (Plate 9Q–T). The outer chitinous rings are very narrow; they bear numerous minute granulations. The number of suckers on the arms and clubs of the largest specimen of *C. sirventi* (*Gerda* 212, 42 mm ML) is as follows:

Arm	*Left*	*Right*
I	46+	48
II	–	–
III	66	–
IV	78	70
Club	117	122

The tentacles are long and robust; the tentacular stalks are heavily pigmented and lack suckers. The tentacular club is expanded (Plate 1B); it bears suckers on long, slender stalks in four longitudinal rows; suckers of the manus grade in size into the smaller suckers of the dactylus. Each transverse row on the manus has suckers of nearly equal size. The inner rings of the suckers from the manus bear approximately 20 teeth; a few of the most distal teeth are the longest and most pointed; these grade into teeth on the proximal margin that are short and truncate (Plate 9O). The broad outer rings from the suckers of the manus are made up of narrow, fused radiating strips (Plate 9U).

The suckers of the dactylus grade in size in a transverse series from the largest in the ventral row to the smallest in the dorsal row. The flattened, expanded tip of the dactylus bears an irregular circlet of about 14 suckers with three or four additional scattered suckers. The inner rings of the dactylus suckers have about 22–28 teeth with larger, more pointed teeth distally (Plate 9P).

The carpal locking-apparatus consists of an irregular grouping of 5–6 suckers and pads at the base of the manus with an additional one or two suckers and pads extending up the dorsal margin of the manus.

Well-developed protective membranes, supported by broad, flat trabeculae, occur on the club. The dorsal membrane terminates at the base of the dactylus and the ventral membrane extends to the tip of the dactylus. A broad, aboral keel exists on the distal half of the manus and along the dactylus.

Seven buccal lappets occur on the buccal membrane. The connectives of the buccal membrane attach to the dorsal borders of arms I and II and to the ventral borders of arms III and IV. The oral surface of the membrane is slightly rugose.

The beaks are illustrated on Plate 8F. The rostrum of the upper beak is long and sharply pointed; the palatine lamella is broad. The lower rostrum of the mandible is short and moderately blunt. No lateral ridge occurs across the gular lamella. The beaks, especially the rostrae, are deeply pigmented.

The radula has seven rows of teeth in a transverse series (Plate 7K.) The rhachidian tooth has a long, sharply pointed median cusp and two short, pointed lateral cusps. The first lateral tooth has a moderately long median cusp and two irregularly shaped lateral cusps. The second lateral tooth has a broad base and a single long, pointed cusp. The third lateral tooth has an extremely long, narrow, pointed cusp. Marginal plaques are present.

A large oval photophore is embedded on the ventral surface of the ink sac immediately to the left of the intestine (Plate 1C). Photophores also exist on the eye. Joubin described these photophores around the eye as small, yellow organs but did not give further details.

Although the eyes were damaged, photophores could be distinguished on the specimen from off Bermuda (Acre 2–2). A row of about 20 small round to oval irregularly-spaced photophores with a pale golden sheen rims the edge of the iris (Figure 1). A thick golden band occurs on the ventrolateral surface of the

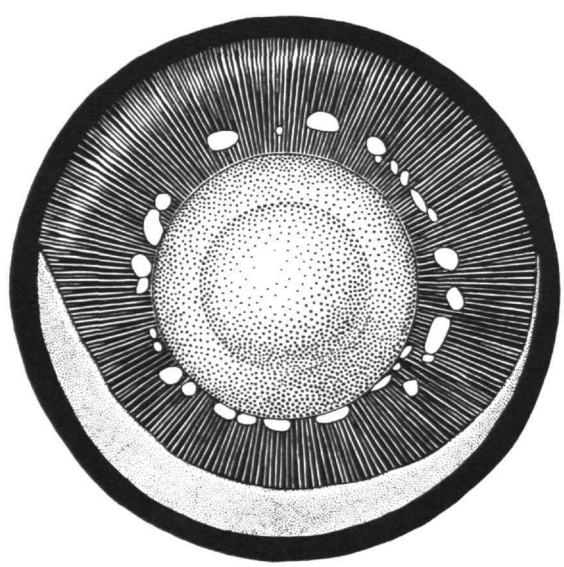

FIGURE 1.—Pattern of photophores on the eye of *Cycloteuthis sirventi* (Acre 2–2; partially reconstructed).

eye and diminishes dorsally. No discrete organs exist along the band, but the entire thickened part, at least, appears to be a luminescent organ. In addition, an inverted U-shaped band of golden tissue lies embedded on the ventral surface of the liver, dorsal to the anal section of the intestine. This organ, too, appears to be a photophore.

The rhachis of the gladius is long and slender; it extends nearly to the posterior tip of the gladius. The vane arises near the anterior end of the gladius, but it remains narrow for nearly half the length of the gladius then broadens suddenly. The edges of the vane fold ventrally in the posterior third of the gladius and fuse to form a long, hollow conus (Plate 8C).

While the largest specimens available are males (41, 42 mm ML), they are not sufficiently mature to have developed spermatophores. In fact, the entire reproductive system at this stage is very weakly developed.

Although Joubin's original and subsequent descriptions of *C. sirventi* were relatively lengthy, they did not include an abundance of pertinent, specific characters. The specific features that he did mention, however, do not differ significantly from those described above.

LARVAE (Plate 2A–B).—The larvae are elongate and bear small terminal fins. The posterior tail that is long in the adult is only a small bump between the posterior margins of the fins in the larvae. The visceral light organ is barely visible and lies ventral to the intestine instead of at the side as in the adult. The photophores on the eyes are not present in larvae. The locking apparatus is similar to that of the adult. The eyes protrude noticeably, but they are not stalked. The arms are short and in the order of $2=3\geqq4>1$. The tentacular clubs are miniature versions of the adult clubs. The larval pen is similar to that of the adult, except that it is not drawn out posteriorly into a long conus. The vane widens at the level of the fins, and posteriorly the margins of the vane turn ventrally to form a very short conus.

LOCATION OF HOLOTYPE.—Oceanographic Museum, Monaco.

TYPE-LOCALITY.—Approximately 800 km west of Madeira at 30°45′N, 25°47′W, 0–500 m.

DISTRIBUTION.—Throughout Atlantic warm waters: Western Atlantic off Brazil, Straits of Florida, off Bermuda; Eastern Atlantic off Northwest Africa, off St. Peter and Paul Rocks (Figure 2). Specimens have been captured at depths between 100 m and 650 m.

Discoteuthis, new genus

DIAGNOSIS.—Tail lacking; gladius greatly thickened; conus absent or only slightly developed; medial suckers on manus greatly enlarged; external photophores present, visceral photophores lacking; fins very large and round, equal to the mantle length in adults.

TYPE-SPECIES.—*Discoteuthis discus*, new species. By original designation.

Discoteuthis discus, new species

PLATES 3; 4; 7A, B, G, I; 8A, D; 9A–G

DESCRIPTION.—The mantle is nearly conical but tapers posteriorly to a slightly rounded point (Plate 3A). The mantle is widest (about 50 percent of the mantle length) at its free anterior end. The anterior margin of the mantle exhibits no pronounced projections or lobes. The mantle wall is relatively thick, but it is not heavily muscled. A central layer of gelatinous connective tissue lies between thin outer and inner sheets of strong, circular muscles. The mantle and head are covered with moderately thick semigelatinous tissue. Table 2 lists measurements of specimens.

List of Material

Sex	*ML, mm*	*Station number*	*Location*	*Date*	*Estimated depth, m*
HOLOTYPE:					
♂	53	*Pillsbury* 36	03°50′N 02°37′W	29 V 1964	750
OTHER SPECIMENS:					
♀	45	*Dana*—no data			
♀	25	*Dana* 1284 I	14°38′N 61°16′W	27 X 1921	300–400
♂	24	*Pillsbury* 473	13°08′N 61°55′W	1 VIII 1966	450
♀?	24	*Dana* 1178 II	10°24′N 54°38′W	19 XI 1921	200
juv.	16	*Dana* 1172 II	07°22′N 46°51′W	14 XI 1921	200

The fins are huge and broadly oval in outline (Plates 3A, 4C). They extend nearly the entire length of the mantle (98 percent of the mantle length in the holotype) and are very broad. Their width is about 40 percent greater than the length of the mantle. For most of their length the fins do not fuse in the dorsal midline but are separated by a narrow gap. The bases of the fins insert directly on the shell sac of the thick, sturdy gladius. The attached median borders of the fins diverge anteriorly forming a distinct V. The anterior fin lobes are short and free. The posterior margin of the fins near the midline is almost straight and has no pronounced posterior projection. The fins are very heavily muscled.

The funnel is short and broad; it extends anteriorly to the level of the posterior border of the eyelids. The musculature of the funnel is similar to that of the mantle. The anterior end of the funnel is free; the remaining portions of the funnel at the collar appear to be bound to the head by a continuous integumentary sheath, but the condition of the specimen makes this uncertain. The funnel locking-cartilage is approximately subtriangular and is encircled by a broad, nearly membranous flange (Plate 7A). Its longest axis lies at a diagonal to the longitudinal axis of the body. The sulcus has a broad, shallow depression anteriorly; it becomes shallower in the midportion and then deepens to a hemispherical depression posterolaterally. The mantle component consists of a diagonally-set, rounded, cartilaginous ridge that has a prominent nose-shaped bulge at the posterolateral end. The bulge articulates with the deep depression on the funnel component. A moderately deep furrow extends along the anterior side of the ridge and curves around the ends; this conforms to the prominent anterior edge of the funnel component.

The dorsal member of the funnel organ is a large, swollen, inverted V-shaped pad (Plate 7G). A large, thumblike papilla protrudes from its apex and a low, indistinct ridge extends partway along each limb. The ventral members are large, elongate, rounded pads. The funnel valve is a small, thin, semicircular flap.

The head is broad and short; it bears huge eyes that occupy nearly the entire lateral region of the head. Each circular eyelid has a small, anterior sinus. The funnel groove is indistinct (or nonexistent). A small olfactory papilla protrudes from the posterolateral surface of the head. No nuchal ridges or folds appear to have been present on the slightly damaged holotype or on the other specimens.

The nuchal locking-cartilage is oval, and it has a distinct ridge on each side of the deep median sulcus. The mantle component has a complementary arrangement with a median ridge and lateral grooves (Plate 7B).

The arms are large (60–85 percent of the mantle length) and robust, but they are not heavily muscled; most of the arm-tips are missing from the holotype. The arms appear to be approximately subequal. The outer integument has been rubbed off the arms and no traces of aboral keels remain. Low, fleshy protective

TABLE 2.—*Measurements (in mm) of* Discoteuthis discus

Characters	*Pillsbury 36*	*Dana*	*Dana 1284 I*	*Pillsbury 473*	*Dana 1178 II*	*Dana 1172 II*
Sex	♂	♀	♀	♂	♀?	juv.
Mantle length	53	45	25	24	24	16
Mantle width	27	25	16	12	14	8
Head length	27	26	–	10	12	5
Head width	27	28	–	13	14	7
Fin length	52	44	23	22	20	10
Fin width	74	65	43	44	30	16
Arms I	34+	–	–	–	–	–
II	44+	–	–	–	18	–
III	33+	–	–	–	–	–
IV	36+	–	–	–	–	–
Tentacle length	132	117	68	–	61	36
Club length	26	25	12	–	11	6

membranes, supported by fleshy trabeculae, occur on all of the arms.

The biserially arranged suckers on the arms are large, globular, and relatively few in number. The suckers are small at the base of each arm but rapidly increase in size and attain their maximum dimensions along the middle one-third of the arm. Suckers on arms IV do not increase greatly in size and are only about half the size of the largest suckers on the other arms. The suckers have narrow stalks which are set on large, robust, conical bases. The inner chitinous rings on the basal suckers are smooth. Distally, however, they have about 7–9 low, broad, rounded teeth on the distal borders (Plate 9C–F). In young specimens the teeth tend to be slightly more pointed.

The numbers of suckers on the arms of the holotype are 43 on right I, 38 on left II, and 46 on right IV. Tips are missing from the remaining arms, so the number of suckers that occur along the proximal portions of the arms for a distance equal to 50 percent of the mantle length are recorded:

Arm	*Left*	*Right*
I	25	25
II	21	22
III	–	21
IV	31	27

There are 81 suckers on the right tentacular club and 80 on the left.

The tentacles are very long—about two and a half times the length of the mantle. The stalks are moderately robust and muscular; they bear no suckers. The clubs are expanded and flattened (Plate 3B). The ill-defined carpal area of the club bears 2 or 3 small, irregularly arranged suckers. A few shallow, round depressions, apparently containing flattened knobs, alternate with the suckers and correspond in position to the location of the suckers on the opposite club. The carpal suckers bear small, irregular teeth around their entire circumference. The carpal area blends distally with 2–4 small to slightly larger suckers with more distinct teeth that are truncate and slightly larger on the distal margin of the sucker ring. It is uncertain whether the smaller of these are true carpal suckers; however, corresponding pads could not be found.

The manus bears four rows of suckers. The 6–9 suckers in the two medial rows on the manus are greatly enlarged; they are closely packed and are set in deep, thin-walled pockets on short, thick stalks. Approximately 32 very low, flattened to slightly rounded teeth line the entire circumference of the inner ring of each of these suckers (Plate 9A); the outer rings are very narrow and smooth. Distally, the large suckers give way to one or two suckers of intermediate size with more elongate, rounded to truncate teeth on the distal margin of the ring. The suckers of the two marginal rows are small and widely spaced; they are attached close to the marginal edges of the club by long, slender stalks. Two proximal suckers of the dorsal marginal row have very short stalks and therefore are closely attached to the club. These two suckers closely resemble the carpal suckers in size and appearance. The stalked marginal suckers bear long, slender, pointed to truncate teeth on the distal margin on the inner ring, but shorter more irregular teeth on the proximal margin; the total number of teeth is about 36.

Four longitudinal rows of small suckers set on long stalks extend the length of the dactylus and terminate just short of the tip. In a transverse series, the suckers grade in size from the largest at the ventral end to the smallest at the dorsal end. The inner rings of the dactylus suckers are each armed with numerous (about 34) sharply pointed teeth; those of the distal half are much longer than those of the proximal half. The dactylus suckers and those of the marginal rows of the manus each have broad outer rings which have several rows of minute bumps; the bumps of the inner row are longer and look like minute teeth. An irregular circle of about 11 or 12 small suckers lies on the flaplike extreme tip of the dactylus.

Protective membranes are present along the dorsal and ventral borders of the manus. The marginal suckers arise from the trabeculae that support these membranes. The dorsal protective membrane disappears along the base of the dactylus while the ventral membrane continues along the dactylus to the tip of the club as a low membrane with flattened trabeculae.

A low keel extends along the distal quarter of the tentacular stalk. A broad swimming keel originates at about the midportion of the aboral surface of the club and extends along the dorsal margin of the dactylus. It terminates abruptly at the base of the flaplike tip of the dactylus.

The buccal mass is large and protruding. The seven strong, muscular supports of the buccal membrane have connectives that attach to the dorsal surfaces of arms I and II and to the ventral surfaces of arms III and IV. The seven buccal lappets are small and triangular. The buccal membrane is fleshy and rugose.

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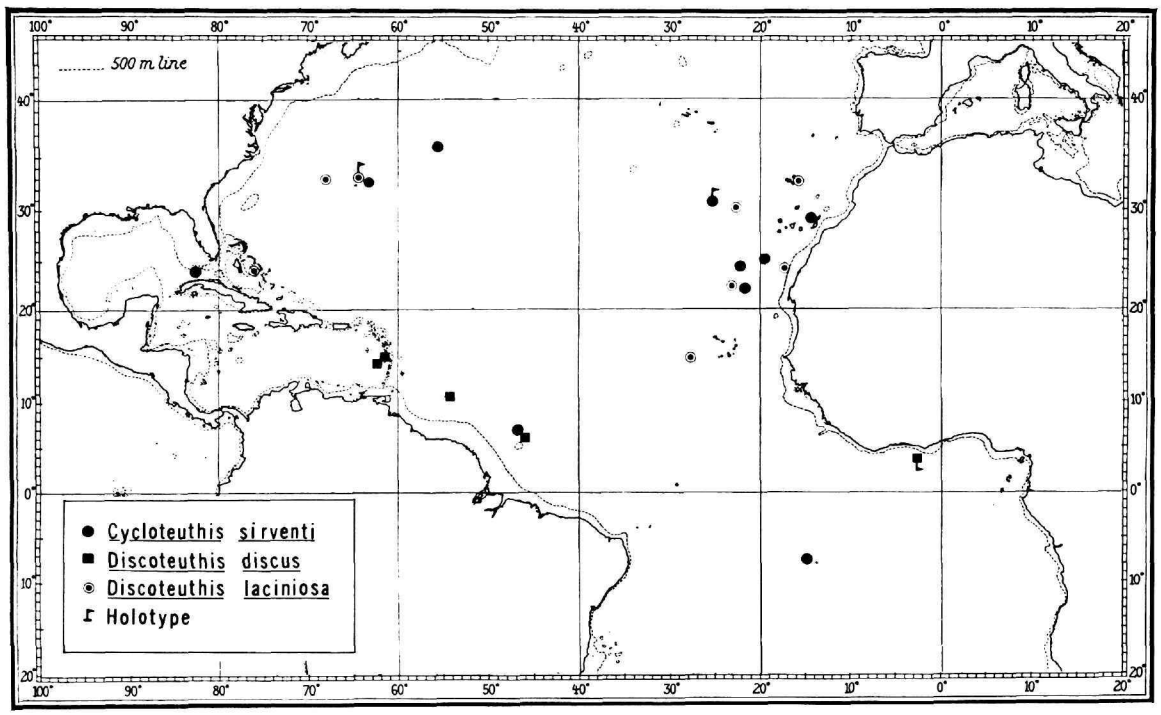

FIGURE 2.—Geographical distribution of *Cycloteuthis sirventi, Discoteuthis discus,* and *Discoteuthis laciniosa.*

The upper and lower mandibles are illustrated on Plate 8D. The upper beak has a long, curved, pointed rostrum and a semicircular palatine lamella. The rostrum of the lower jaw is triangular in silhouette. The gular lamella is large and has a moderate lateral ridge across its surface. The rostrae are darkly pigmented. The dorsal and lateral region of the palatine lamella of the upper jaw is pigmented.

The radula consists of seven rows of teeth in a transverse series (Plate 7I). The rhachidian tooth has a broad, pointed median cusp and two small, triangular lateral cusps. The first lateral tooth has a short, sharp primary cusp and a small, pointed lateral cusp. The second lateral tooth has a broad base that tapers into a single pointed cusp. The third lateral tooth has a single, very long, narrow, curved, sharply pointed cusp. Small marginal plaques are present.

At least four light organs occur around the margin of the eyelid, but this area is damaged so the exact number and arrangement of photophores is uncertain. A dark, round photophore is located on the ventral surface of the posterior tip of the mantle. Reddish-brown chromatophores occur on the mantle, head, fins, and arms where the skin is not damaged.

The gladius has a total length of 47 mm in the holotype, of which the anterior 16–18 percent consists almost exclusively of the rhachis except for a thin, narrow anterior flap 1 mm in length (Plate 8A). The rhachis is widest at the point where the vane originates (3 mm wide); it then gradually tapers posteriorly and disappears 3–4 mm from the terminal end of the gladius; therefore, the posterior portion of the gladius consists entirely of the vane. The vane is long and broad. Soon after its origin near the anterior end of the gladius, the vane widens rapidly, and for the greater part of its length the lateral edges lie nearly parallel. Posteriorly the vane forms a rounded, spoon-shaped end (not a conus) with the terminal edge folded slightly ventrally and anteriorly to form a narrow, delicate lip.

The most striking feature of the pen is its extreme thickness. Almost the entire concavity ventral to the

vane is occupied by a solid amber-colored substance. The pen, which is usually paper-thin in other oegopsids, therefore is approximately 2 mm thick. The vane has the normal thin structure only along its edges; the rhachis is typical (see cross sections). Interestingly, when the pen is submerged in water, the thickened portion becomes nearly invisible and the pen assumes the appearance of a typical gladius (Plate 8A).

SUBADULT STAGES.—The amount of material available for this study is limited, but the specimens represent a wide range of sizes. Some aspects of the changes that occur during growth are apparent on the specimens at hand. The smallest specimen that can be positively identified as *Discoteuthis discus* has a mantle length of 16 mm (*Dana* 1172 II).

The major allometric changes during growth are associated with the length of the fins. At 16 mm ML the fins occupy about 60 percent of the length of the mantle. Around 24–25 mm ML the fins increase proportionally to 80–90 percent of the mantle length. By 45 mm ML and larger the fin length is 98 percent or more of the mantle length (Plate 4A–C). The gladius strongly reflects the allometric increase in the size of the fins by the relative lengthening of the vane during ontogeny (Plate 4D). The basal musculature of the fins attaches to the shell sac which tightly envelops the gladius. Therefore, the allometric growth of the pen and fins is directly related.

LOCATION OF HOLOTYPE.—The holotype of *Discoteuthis discus* has been deposited in the United States National Museum and is designated as catalog number 576214.

TYPE-LOCALITY.—Approximately 100 km SSW of Cape Three Points, Ghana, West Africa, in the Gulf of Guinea at 03°50′N, 02°37′W; *Pillsbury* Sta. 36; 29 May 1964; 750 m.

DISTRIBUTION.—Atlantic warm water: Gulf of Guinea; off northeast coast of South America; and eastern Caribbean Sea (see Figure 2). Captured in open nets at depths between 200 and 750 m.

ETYMOLOGY.—The generic name, *Discoteuthis,* is derived from the combination of the Greek "diskos," a flat, circular plate or disk, and "teuthis," squid; it refers to the huge circular fins. The specific name of the type-species, *discus,* emphasizes this feature of the fins.

Discoteuthis laciniosa, new species

PLATES 5; 6A–E; 7C, D, J; 8B, E; 9H–N

DESCRIPTION.—The mantle is conical and the muscular portion terminates slightly anterior to the posterior margins of the fins. The mantle width is nearly one-half the mantle length (see measurements in Table 3). The mantle musculature is weak and covered externally by a thick layer of gelatinous connective tissue. A few (four or more) small, truncate, integumentary flaps occur along the ventral and lateral borders of the anterior margin of the mantle. In the holotype four flaps occur ventrally between the photophores and some flaps may occur lateral to the photophores, although this is uncertain due to the slightly damaged condition of the mantle margin. The mantle flaps are more pronounced in the smaller specimens (Plate 6A, B).

List of Material

Sex	*ML, mm*	*Station number*	*Location*	*Date*	*Estimated depth, m*
HOLOTYPE:					
?	70	Acre 3–3	33°04′N 64°37′W	4 VII 1968	1000
OTHER SPECIMENS:					
?	56	*Dana* 1157 I	21°57′N 22°58′W	27 X 1921	300–400
?	39	*Discovery* 4840	30°02′N 22°55′W	5 IV 1962	600
♂	35	*Gerda-TOTO*	23°52′N 76°46′W	20 II 1961	750
?	20	*Dana* 1161 IV	14°42′N 28°04′W	5 IX 1921	100
juv.	14	*Dana* 4009 III	24°36.5′N 17°27′W	18 III 1930	100
L	7.5	*Dana* 1341 II	33°15′N 68°20′W	14 V 1922	200
3 L	5–9	*Dana* 4009 II	24°36.5′N 17°27′W	18 III 1930	200

5 additional specimens in poor condition, 55–82 mm ML, taken as stomach contents of the fish, *Aphanopus carbo*, off Madeira.

TABLE 3.—*Measurements (in mm) of* Discoteuthis laciniosa

Characters	Acre *3–3*	*Dana 1157 I*	*Discovery 4840*	*Gerda TOTO*	*Dana 1161 IV*	*Dana 4009 III*	*Dana 4009 II*	*Dana 4009 II*	*Dana 4009 II*	*Dana 1341 II*	*? Dana 3996 VII*
Sex	?	?	?	♂	?	juv.	larva	larva	larva	larva	♀
Mantle length	70	56	39	35	20	14	9	5.5	5.0	7.5	33
Mantle width	30	26	12	12	–	5	3	2.5	2.5	–	11
Head length	31	29	11	11	–	–	3	2.5	2.0	–	14
Head width	40	27	10	–	7	–	4	3.0	2.5	–	12
Fin length	71	59	38	32	19	12	7.5	5.0	2.0	7.5	33
Fin width	95	88	51	52	26	18	12	8.0	6.5	12	44
Arms I	41+	31	–	19	–	–	2.5	2.0	1.5	–	21
II	63	51	–	20	–	–	4.5	2.5	2.5	–	30
III	62	48	28	29	–	–	4	2.5	2.5	–	31
IV	51+	38	28	27	–	–	3.5	2.5	2.2	–	28
Tentacle length	84	80+	68	52	24	–	–	9.0+	–	–	47
Club length	20	19	10	10	5	–	–	–	–	–	9

The round fins are very large and in adults slightly exceed the length of the mantle (Plates 5A; 6A–C). The width of the fins is one and one-third to one and one-half of the mantle length. The fins are extremely muscular, but dorsally, at least in the midportion, they are overlain by a layer of gelatinous connective tissue. The fins, for most of their length, do not fuse in the dorsal midline but are separated by a narrow gap. The bases of the fins insert directly on the shell sac of the thick sturdy gladius. The anterior lobes are free; each medial border forms a deep notch with the surface of the mantle. The notch is more pronounced in the holotype than in the illustrated paratype (Plate 6C). The lateral edges of the fins are semicircular in outline; the posterior margins are nearly straight. No tail exists.

The medium-sized funnel extends nearly to a level with the center of the lenses of the eyes; it lies in a shallow groove on the ventral surface of the head. A small funnel valve is present. The dorsal pad of the funnel organ has an inverted V-shape with long limbs. A low median ridge appears to be present on the anterior half of each limb. A small papilla is present at the anterior apex. The ventral pads are very long and narrow. The funnel locking-cartilage is subtriangular in shape and has a deep, V-shaped groove (Plate 7C). A deep, oval depression lies at the anterolateral angle of the cartilage. The groove becomes more shallow medially and posteriorly, and remains well defined in most specimens, although in the holotype it is somewhat less distinct than in the illustration of a paratype (Plate 7C). A distinct rounded ridge overhangs the groove along the anterior margin of the cartilage. The mantle locking-cartilage consists of a transverse, broadly V-shaped ridge and groove. The ventral end of the groove is deep and pronounced; the groove disappears at the dorsal end. The strong, transverse (ventral) part of the ridge tapers diagonally from the bulb that locks into the deep depression on the funnel cartilage. The posterior sides of both parts of the ridge taper into the inner surface of the mantle.

The head is large, broad and oval; the eyes are enormous and occupy almost the entire lateral portion of the head. A small sinus is present in the anterior margin of each circular eyelid. An olfactory crest is not apparent. A narrow, fingerlike olfactory papilla occurs on the posterior ventrolateral angle of the head. The sensory epithelium is not restricted to the tip of the papilla but covers most of the surface of this structure.

The nuchal cartilage is shield-shaped with a broad anterior end. A broad central ridge that extends the length of the cartilage bears a narrow median groove (Plate 7D).

Although the arms are difficult to measure, they appear to be in the order of $2=3\geqq4>1$. The longest arms are approximately 90 percent of the mantle length and the shortest (the dorsal pair) are about 60 percent of the mantle length. Gelatinous aboral keels are present on arms I–III; those on arms III are the largest and those on arms I, the smallest. Lateral keels are present on arms IV. The medial ventral margin of

each arm IV is sharply angled forming a narrow keel. The arms are very attenuate. Protective membranes occur on all arms; they are supported by the conical bases of the sucker stalks and not by typical independent trabeculae. The arms bear two rows of large suckers with broad apertures. The largest suckers of the ventral arms are considerably smaller than the largest suckers on the other arms. The distal half to two-thirds of each of the large inner sucker rings bears 10-12 low, scalloped teeth; the proximal portion of each ring is smooth. The number of teeth decreases on the rings of smaller suckers (Plate 9J–M). Outer chitinous rings are extremely narrow and poorly developed; they are covered with minute granules. The number of suckers on the clubs and on the proximal portions of the arms for a distance equal to 50 percent of the mantle length of a paratype (*Dana* 1157 I, 56 mm ML) is given below. The total number of suckers on each arm is enclosed in parentheses.

Arm	*Left*	*Right*
I	39 (42–broken)	37 (57)
II	26 (80)	28 (38–broken)
III	25 (90)	27 (84)
IV	36 (60)	38 (66)
Club (total)	67	56 +

The tentacles are robust and relatively short—between one and two times the length of the mantle; the tentacular stalks are naked. The clubs are expanded and bear four transverse rows of suckers on the manus (Plates 5B; 6D). No distinct carpal cluster occurs, but a series of 4 or 5 minute suckers occurs along the dorsal margin of the manus and carpal region. These suckers are about one-tenth the diameter of the largest manal suckers and about one-half the diameter of the suckers in the true marginal series of the manus. The carpal suckers bear small truncate teeth, only slightly differentiated in size, around the entire margins of the inner rings. The proximal three suckers in this series alternate with three smooth, round depressions that are not typical carpal knobs. The distal two suckers in this series do not alternate with depressions and may occur adjacent to small manal suckers of the marginal series. The distalmost "carpal" sucker may be absent.

The manus bears four rows of suckers. Six or seven of the suckers in the two medial rows are enormously enlarged and have very broad apertures. The outer chitinous rings on the large suckers are very narrow and are made up of numerous minute, curved rods; no granulation exists. The dentition on the inner rings is very weak; it consists of numerous (50–60) minute, irregular, low, scalloped teeth around the entire margin (Plate 9H). The suckers of the two medial rows on the manus decrease rapidly in size proximally; these small proximal suckers of the manus have long, curved, pointed teeth distally and shorter, truncate teeth proximally on the inner rings. The suckers on both marginal manal rows have rings that bear numerous, small, pointed teeth around their entire margins. The teeth are larger, more pointed and curved on the distal margin of the inner ring. The outer chitinous rings are well developed with radial striations around the outer margin. The proximal two suckers in the dorsal marginal series of the manus may be absent or may occur adjacent to the distal carpal suckers.

The suckers of the dactylus decrease in size from the ventral to the dorsal row. The suckers of the dorsal row diminish rapidly in size and disappear about halfway out the dactylus. Distal to this point, the suckers of the dorsomedial row decrease abruptly in size but continue to the tip of the dactylus. The suckers of the two ventral rows maintain a relatively large size up to the distal two transverse rows where they decrease rapidly to nearly equal the size of the remaining distal suckers of the dorsomedial row. Eleven to fifteen small suckers are arranged in a circlet or patch around the margin of the slightly expanded, flattened tip of the dactylus.

Protective membranes are present; strong muscular rods connected with membranous integument serve as trabeculae and as support for the small suckers of the marginal rows on the manus. The ventral membrane extends to the end of the dactylus, but the dorsal membrane terminates about halfway out the dactylus. A short, broad swimming keel occurs on the aboral surface of the dactylus .

The buccal membrane bears seven lappets and supports; the connectives of the buccal membrane are attached to the dorsal borders of arms I and II and to the ventral borders of arms III and IV. The buccal membrane is fleshy and rugose.

The beaks are illustrated on Plate 7E. The rostrum of the upper mandible is slightly curved and bluntly pointed; the lateral sides of the palatine lamella are very broad and are rounded in outline. The rostrum of the lower jaw is triangular in outline and has a sharp, projecting tip. The gular lamella is small and

has a slight lateral ridge. The rostrae are darkly pigmented. The pigment on the palatine lamella of the upper beak is concentrated only along the dorsolateral surface.

The radula possesses seven rows of teeth in a transverse series (Plate 7J). The rhachidian tooth has a relatively narrow, pointed median cusp and two, small, pointed lateral cusps. The second lateral tooth has a broad base, a broad, triangular primary cusp, and a small, sharp lateral cusp. The cusp of the second lateral tooth has a broad base that tapers to a sharp point. The cusp of the third lateral tooth is extremely long and narrow; it is slightly curved and sharply pointed. Small marginal plaques are present.

A small photophore is embedded near the edge of the membrane that passes between the third and fourth arms on each side, and two small photophores lie ventrolaterally near the free margin of the mantle (Plate 5A). No photophores are present on the surface of the eye. No other photophores can be detected on the holotype or on other specimens, but all the material is damaged to varying degrees.

The gladius of a paratype (*Dana* 1157 I) is about 55 mm in length (Plate 8B). The free anterior end of the rhachis is U-shaped in cross section, short, and broad (about 7 mm long and 3.5 mm wide) with a small terminal flap. The rhachis tapers posteriorly from the point where the vane arises and terminates short of the end of the gladius. The deep U-shape of the rhachis provides the gladius with a high dorsal ridge. The vane is long and broad. The lateral edges of the vane begin to turn ventrally in the posterior third of the gladius; the edges meet and fuse near the tip of the gladius to form a simple conus. Just posterior to the free portion of the rhachis the gladius becomes very thick dorsoventrally for its entire length; only the sides of the vane remain thin. The thickening consists of a nearly unpigmented, hardened substance (see cross sections on Plate 8B).

LARVAE (Plate 6E).—Four larval specimens which appear to belong to *Discoteuthis laciniosa* are available; they range from 5–9 mm in mantle length. The mantle is short and very broad in the smallest larvae, but it becomes proportionately narrower with growth. The huge, broad, round fins are about 50 percent of the mantle length in the larva of 5 mm ML but rapidly enlarge to 80–90 percent as long as the mantle by 9 mm ML. From 10–15 mm ML the fins have reached their full proportional development and are slightly longer than the ML. The width of the fins is about 133–160 percent of the ML in width. A series of 6–8 papilla-like flaps projects from the ventral two-thirds of the mantle margin.

The eyes protrude from the sides of the head but are not stalked; they are elliptical in an anterodorsal to posteroventral direction. The long axis of the eye from the specimen 9 mm in ML is 1.7 mm and the short axis is 1.1 mm.

The funnel is long and narrow; it extends anteriorly to the base of the oral crown. The funnel locking-cartilages are diagonally set, subtriangular-shaped pits (very similar to those of the adult) that lock with corresponding bumps of the mantle cartilages. The funnel organ is a large V-shaped gland with a small papilla at the apex and a low ridge extending along each limb.

The arms are weak; the arm formula is $2 \geqq 3 > 4 > 1$. No complete tentacles or clubs remain on the specimens.

In the larvae of this genus the large fins are very widely separated from one another by the broad pen. This distinctive feature allows recognition of the larvae at a glance.

LOCATION OF HOLOTYPE.—The holotype of *Discoteuthis laciniosa* has been deposited in the United States National Museum and is designated as catalog number 576215.

TYPE-LOCALITY.—Approximately 40 miles NNE of Bermuda at 33°04′N, 64°37′W; USNS *Gilliss,* Acre 3–3; 4 July 1968; 1000 m, est.

DISTRIBUTION.—North Atlantic warm waters: off West Africa; Madeira; Cape Verde Islands; in the Tongue of the Ocean, Bahamas; and off Bermuda. See Figure 2. Captured in open nets at depths between 100 and 1000 m.

ETYMOLOGY.—The specific name, *laciniosa,* is derived from the Latin word "laciniosus," full of flaps or fringed; it refers to the small flaps that fringe the ventral half to two-thirds of the free margin of the mantle.

Comparison of *Discoteuthis discus* and *D. laciniosa*

The two species differ distinctly in several characters. The most apparent differences concern the distribution of photophores. *Discoteuthis discus* has four light organs embedded in the tissue surrounding each eye and a single, prominent round photophore located ventrally near the posterior apex of the mantle.

Discoteuthis laciniosa has two small, round photophores on the ventral surface of the mantle near the anterior margin and a small, round photophore on each side near the edge of the membrane that connects the bases of arms III and IV (Plates 3A; 5A). The total complement of photophores in each species may not have been detected since our specimens were partially damaged, but, based or present knowledge, no apparent overlap exists in photophore patterns.

The dorsal row of suckers is lacking on the distal half of the dactylus in *D. laciniosa,* but it is complete in *D. discus* (Plates 3B; 5B; 6D). The enlarged suckers on the manus are globular in *D. discus* and flattened in *D. laciniosa.* The percent of the maximum height of the chitinous ring in relation to the diameter is 53–66 percent in *D. discus* and 33–38 percent in *D. laciniosa* (Plate 9G, N).

The funnel locking-cartilage of *D. laciniosa* has a distinct V-shaped groove with a strong apical depression; the posterior limb of the groove is lacking in *D. discus* (Plate 7A, C).

Small flaplike papillae project from the free border of the mantle in *D. laciniosa;* these are most prominent in small specimens. The papillae are absent in *D. discus* (Plates 3A; 4A, B; 5A; 6A, B).

The length of the fins approximates the length of the mantle at 10–15 mm ML in *D. laciniosa,* but this does not occur until a minimum of 25–30 mm ML in *D. discus* (Plates 4B; 6A).

The gladius of *D. laciniosa* has a small, distinct conus, but no conus occurs in *D. discus.* This difference in pens is unusual for such closely related species (Plate 7A, B).

More suckers appear to occur on the arms of *D. laciniosa* than on *D. discus,* but further material is needed to substantiate this condition.

ADDITIONAL MATERIAL.—Our material includes several specimens which do not clearly belong to the species of *Discoteuthis* described here, but they are in such poor condition that we are not able to characterize them sufficiently. Most of these specimens were taken within the distributional ranges of the known species. Additional material is needed in order to delineate more fully the species of the Cycloteuthidae in the central Atlantic region.

One mutilated specimen of *Discoteuthis* about 35 mm in mantle length is available from the Indian Ocean (07°26′N, 64°40′E). Although specific identification is impossible, this specimen extends the known range of the Cycloteuthidae into the Indian Ocean.

A larval specimen, in good condition except for the loss of the tentacles, with a mantle length of 9 mm (*Dana* 1335 XV, 28°02′N, 62°26′W) does not appear to be referable to either *D. discus* or *D. laciniosa,* so it is described here briefly.

The mantle is long and narrow; it tapers to a blunt tip posteriorly (Plate 6F). Several large integumentary flaps project from the mantle margin. The large, round, separate fins are about 72 percent of the ML and about as broad as the mantle is long.

The head is broad, relatively short. The eyes are huge and occupy the entire sides of the head. They are teardrop-shaped with a large rostrum directed posteroventrally. The long axis of the eye is 2.6 mm and the short axis is 1.6 mm. The lenses are very large.

The funnel extends anteriorly to a level with the center of the eyes. The locking apparatus is subtriangular and generally similar to other cycloteuthids.

The arm formula is $2=3>4=1$. Tentacles are missing but the stumps that remain are robust.

Comparison of *Cycloteuthis* and *Discoteuthis*

No difficulty should arise in separating these two distinctive genera. The generic diagnoses list the pertinent differences that are briefly summarized here. *Cycloteuthis:* tail present, gladius thin, conus present, suckers on manus equal-sized, photophores on eyes and viscera, fins moderate—do not attain 100 percent of ML. *Discoteuthis:* tail absent, gladius thick, conus minute or absent, suckers on manus unequal-sized, photophores in integument, fins huge—attain 100 percent of ML.

The fundamental similarities that unite these genera have been listed in the diagnosis of the family. Some features, however, require further comment. Within oegopsid families the gladius is generally a homogeneous structure and is often diagnostic of the family (e.g., Ommastrephidae, Onychoteuthidae), but the differences between the gladii of *Discoteuthis discus* and *Cycloteuthis sirventi* are pronounced. *Cycloteuthis sirventi* has a long, well-developed conus, while *D. discus* completely lacks a conus. *Discoteuthis laciniosa* has a small conus that is somewhat intermediate, but it seems to be a different type than that of *C. sirventi.* Although these differences in the pen are difficult to rationalize in the absence of a comprehensive study on teuthoid gladii, and although they may cast some doubt

on the close relationship of the genera, other characters are sufficiently similar at present to require the inclusion of the two genera in the same family.

Familial Relationships

The attachment of the buccal connectives to either the dorsal or ventral border of arms IV recently has been shown to separate the families of the Oegopsida into two major subdivisions (Young and Roper, 1968) as follows:

Dorsal attachment	*Ventral attachment*
Ommastrephidae	Cycloteuthidae
Bathyteuthidae	Onychoteuthidae
Lycoteuthidae	Gonatidae
Enoploteuthidae	Thysanoteuthidae
Histioteuthidae	Ctenopterygidae
Psychroteuthidae	Octopoteuthidae
Architeuthidae	Brachioteuthidae
Neoteuthidae	Lepidoteuthidae
	Batoteuthidae
	Chiroteuthidae
	Mastigoteuthidae
	Promachoteuthidae
	Joubiniteuthidae
	Grimalditeuthidae
	Cranchiidae

As the list shows, the Cycloteuthidae is aligned by this fundamental character with the majority of the oegopsid families. In the group with ventral attachments to arms IV, the gladius exhibits three basic modifications. The most common type has a narrow, generally elongate conus formed by a ventral folding of the vane with a fusion of the edges in the ventral midline. This type of gladius is characteristic of the Brachioteuthidae, Lepidoteuthidae, Batoteuthidae, Chiroteuthidae, Mastigoteuthidae, Joubiniteuthidae, Grimalditeuthidae, and Cranchiidae (secondary modifications occur in some genera). The Promachoteuthidae, although aligned with this group, apparently lacks a pen. The second type of gladius, found in the Onychoteuthidae and Gonatidae, has a small, short conus without evidence of a ventral fusion. The remaining families, Thysanoteuthidae, Ctenopterygidae, and Octopoteuthidae, lack a conus. The Cycloteuthidae has representatives with two of these types of gladii: (1) *C. sirventi* has a conus with a ventral fusion; (2) *D. discus* lacks a conus. *Discoteuthis laciniosa* has a small conus, but it does not seem to conform to either of the two basic types found in the family. Present knowledge does not enable us to establish definitely which type of gladius is primitive in the family. On the basis of the pen, the Onychoteuthidae and Gonatidae can be excluded from close relationship with the Cycloteuthidae. In determining relationships with the other families, however, the pen is of little value.

The straight, simple funnel locking-cartilage seems to be primitive in the Oegopsida. Independent modifications of this type of locking-cartilage have arisen that are stable traits at least at the familial level. Of the

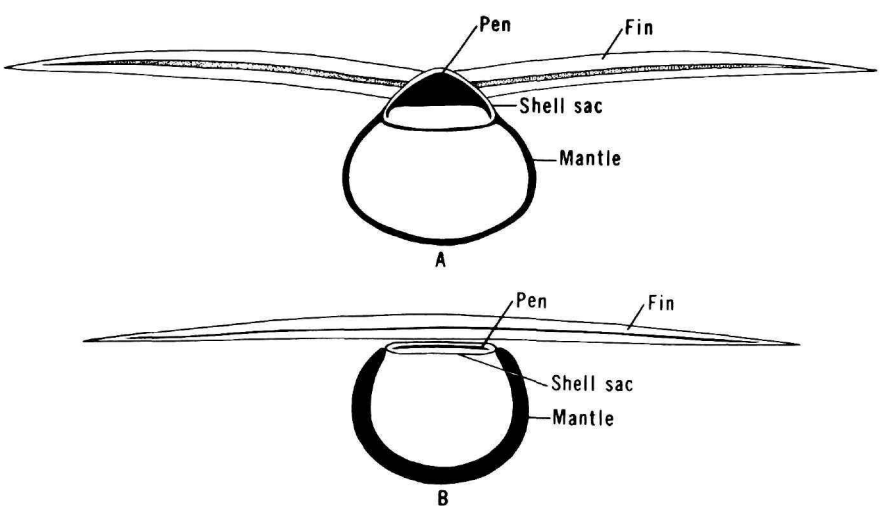

FIGURE 3.—Diagrammatic cross section of body showing relationships between structure of gladii and attachment of fins: A, *Discoteuthis;* B, *Octopoteuthis.*

families with ventral attachments of the buccal connectives to arms IV, an ear-shaped funnel locking-cartilage is present, with a few exceptions, in the Chiroteuthidae and Mastigoteuthidae; and oval lock occurs in the Promachoteuthidae and Joubiniteuthidae; a fused lock occurs in the Grimalditeuthidae and Cranchiidae; a lazy-T lock (i.e., a straight longitudinal groove with a medial groove projecting from its mid-region) exists in the Thysanoteuthidae. The remaining families have a straight, simple cartilage, except the Cycloteuthidae, which has a subtriangular lock with a deep depression at the anterolateral corner. This distinctive locking apparatus separates the Cycloteuthidae from all other families and gives no clear indication of its familial relationships.

Specialized tentacular clubs may indicate relationship between families (e.g., Promachoteuthidae, Joubiniteuthidae, and Mastigoteuthidae), but the generalized structure of the clubs of cycloteuthids offers few clues to indicate relationships.

Superficially, *Discoteuthis* resembles *Octopoteuthis* in the shape and size of the fins. The attachment of the fins, however, is fundamentally different in the two genera. The fins of *Discoteuthis* are separate and insert directly onto the shell sac, whereas the fins of *Octopoteuthis* are fused and continuous across the dorsal midline, thereby passing over the shell sac (Figure 3). This basic difference is also reflected in the structure of the pens. The pen of *Discoteuthis* is a very thick, rigid supporting structure, while that of *Octopoteuthis* is very thin and fragile. The possession of hooks on the arms and the lack of tentacles in *Octopoteuthis,* among other features, further substantiate the remoteness of the relationship between these two groups.

At our present state of knowledge, it is difficult to determine the relationships of the Cycloteuthidae, other than to align it with the families that possess the ventral attachment of the buccal connective to arms IV. Within this group, the family must be assumed to occupy an isolated position.

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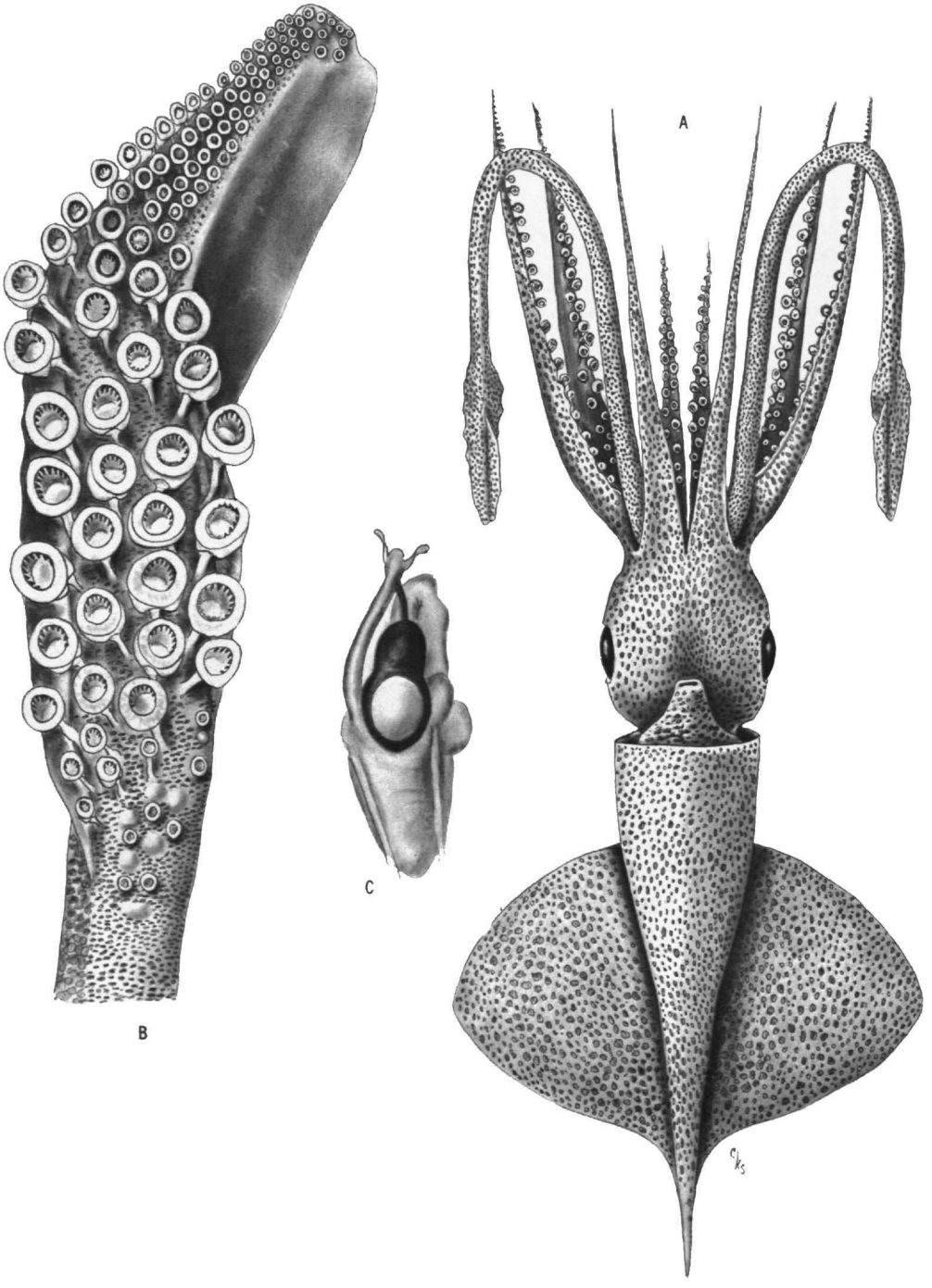

PLATE 1.—*Cycloteuthis sirventi, Gerda* Sta. 212, 42 mm ML: A, ventral view; B, right tentacular club; C, photophore on ink sac.

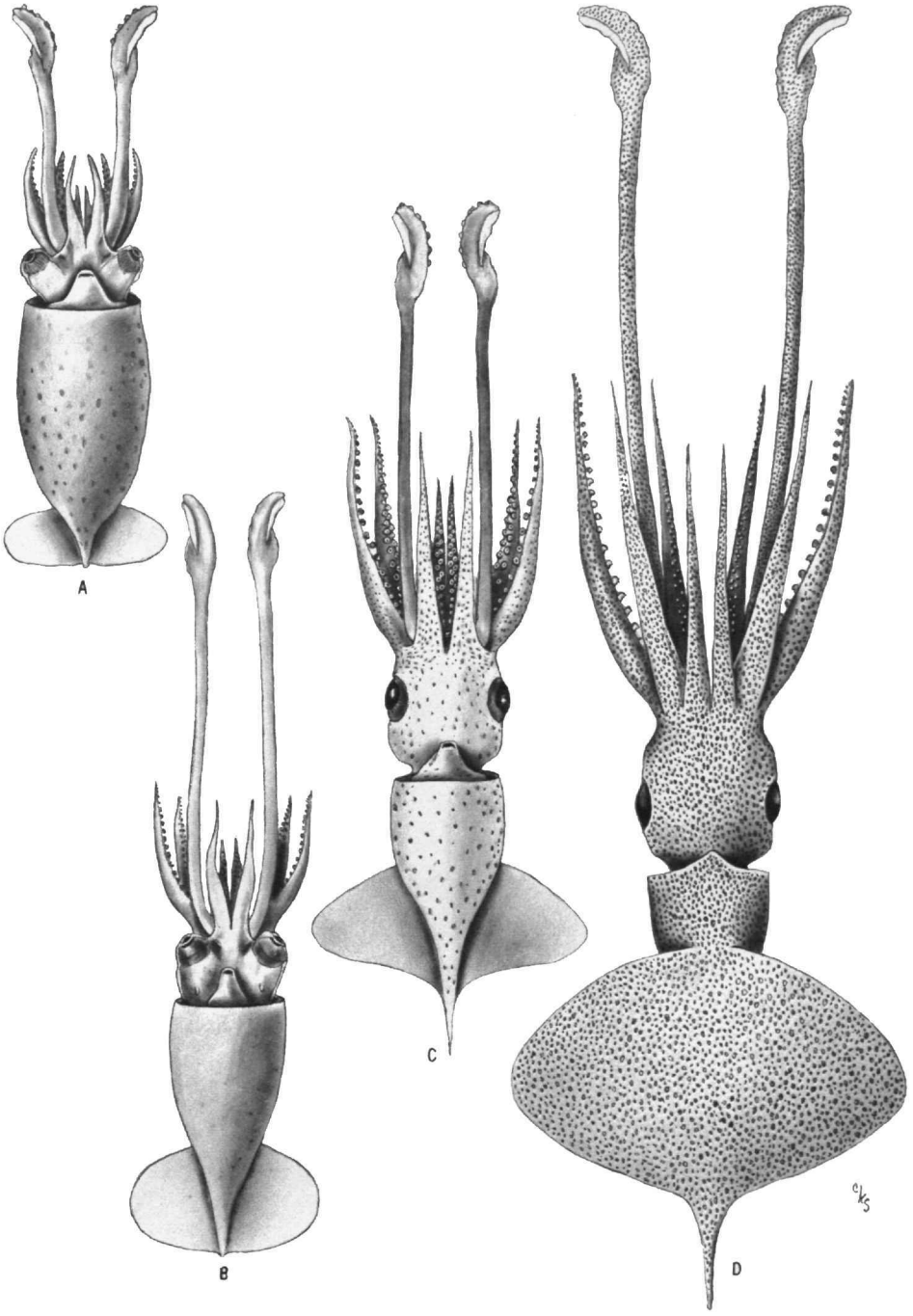

PLATE 2.—*Cycloteuthis sirventi:* A, *Margrethe* Sta. 1030, 8.5 mm ML, ventral view; B, *Dana* Sta. 1172 II, 15 mm ML, ventral view; C, *Dana* Sta. 829, 27 mm ML, ventral view; D, *Gerda* Sta. 212, 42 mm ML, dorsal view.

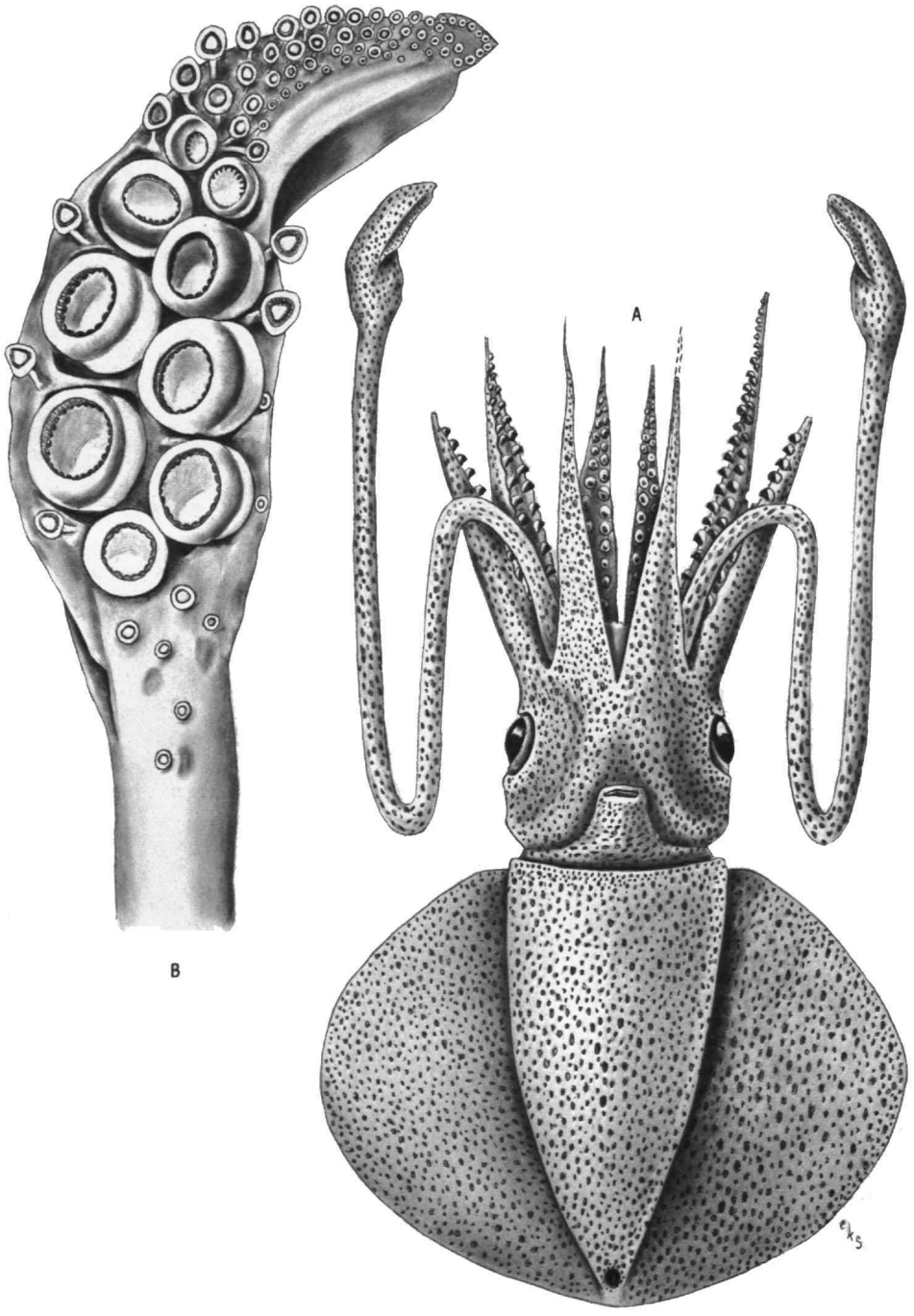

PLATE 3.—*Discoteuthis discus,* holotype, *Pillsbury* Sta. 36, 53 mm ML: A, ventral view; B, right tentacular club.

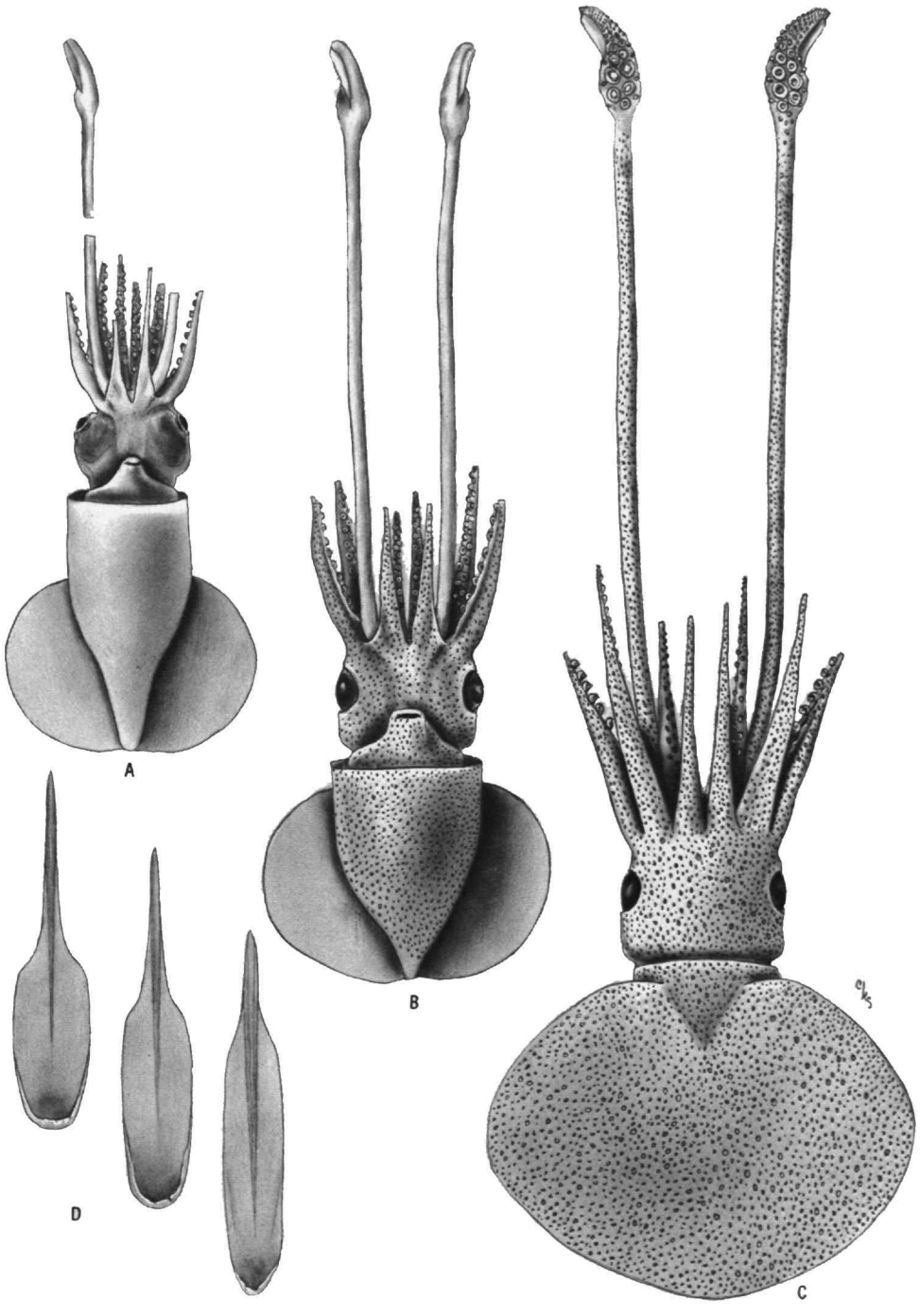

PLATE 4.—*Discoteuthis discus:* A, *Dana* Sta. 1172 II, 16 mm ML, ventral view; B, *Dana* Sta. 1178 II, 24 mm ML, ventral view; C, *Pillsbury* Sta. 36, 53 mm ML, dorsal view of holotype; D, gladii of A–C respectively.

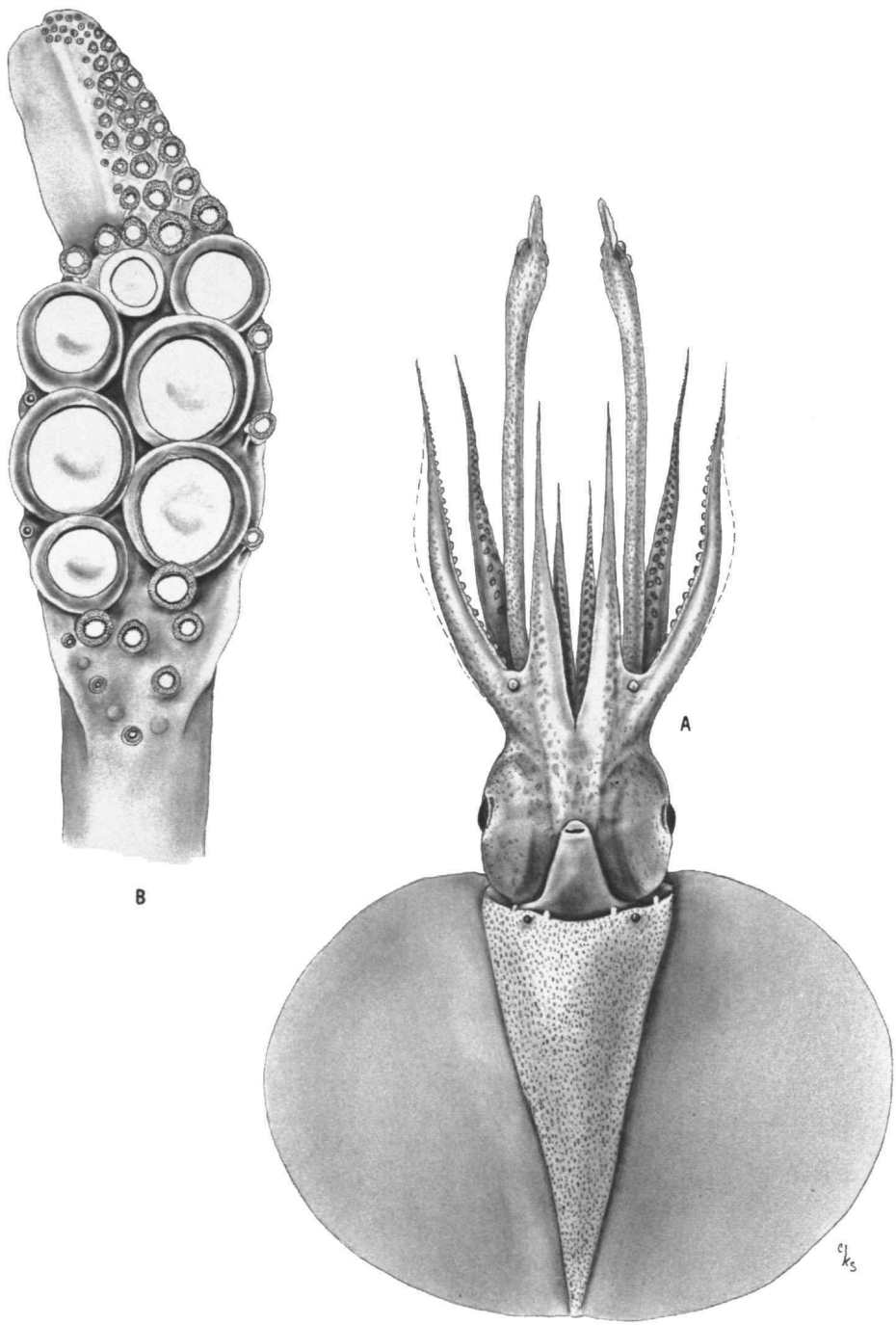

PLATE 5.—*Discoteuthis laciniosa,* paratype, *Dana* Sta. 1157 I, 56 mm ML: A, ventral view; B, left tentacular club.

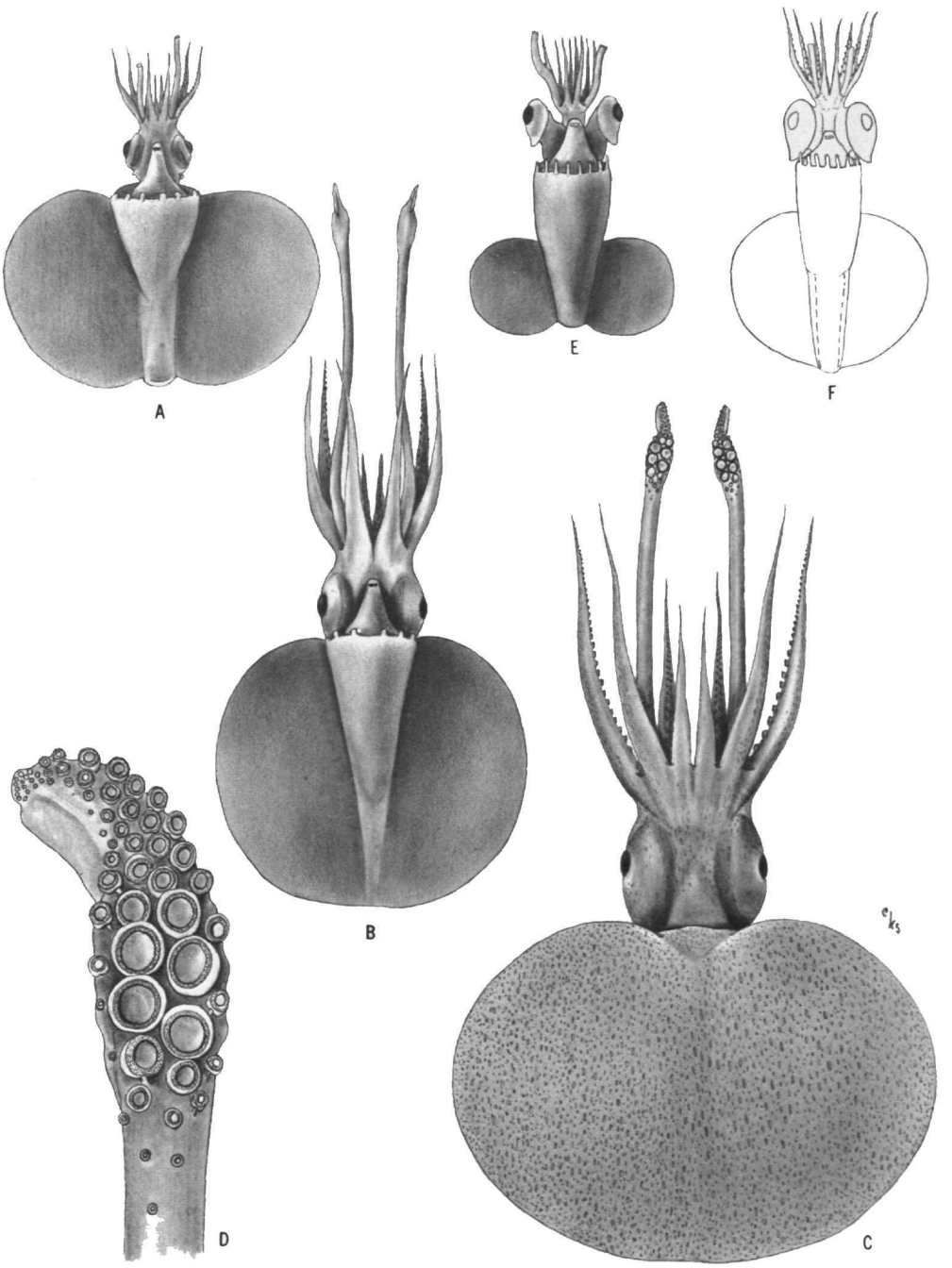

PLATE 6.—*Discoteuthis laciniosa:* A, *Dana* Sta. 4009 III, 14 mm ML, ventral view (eyes reconstructed); B, *Dana* Sta. 1161 IV, 20 mm ML, ventral view; C, *Dana* Sta. 1157 I, 56 mm ML, dorsal view of holotype; D, *Dana* Sta. 1161 IV, 20 mm ML, left tentacular club; E, *Dana* Sta. 4009 II, 5 mm ML, ventral view of larva. *Discoteuthis* species: F, *Dana* Sta. 1335 XV, 9 mm ML, ventral view of larva.

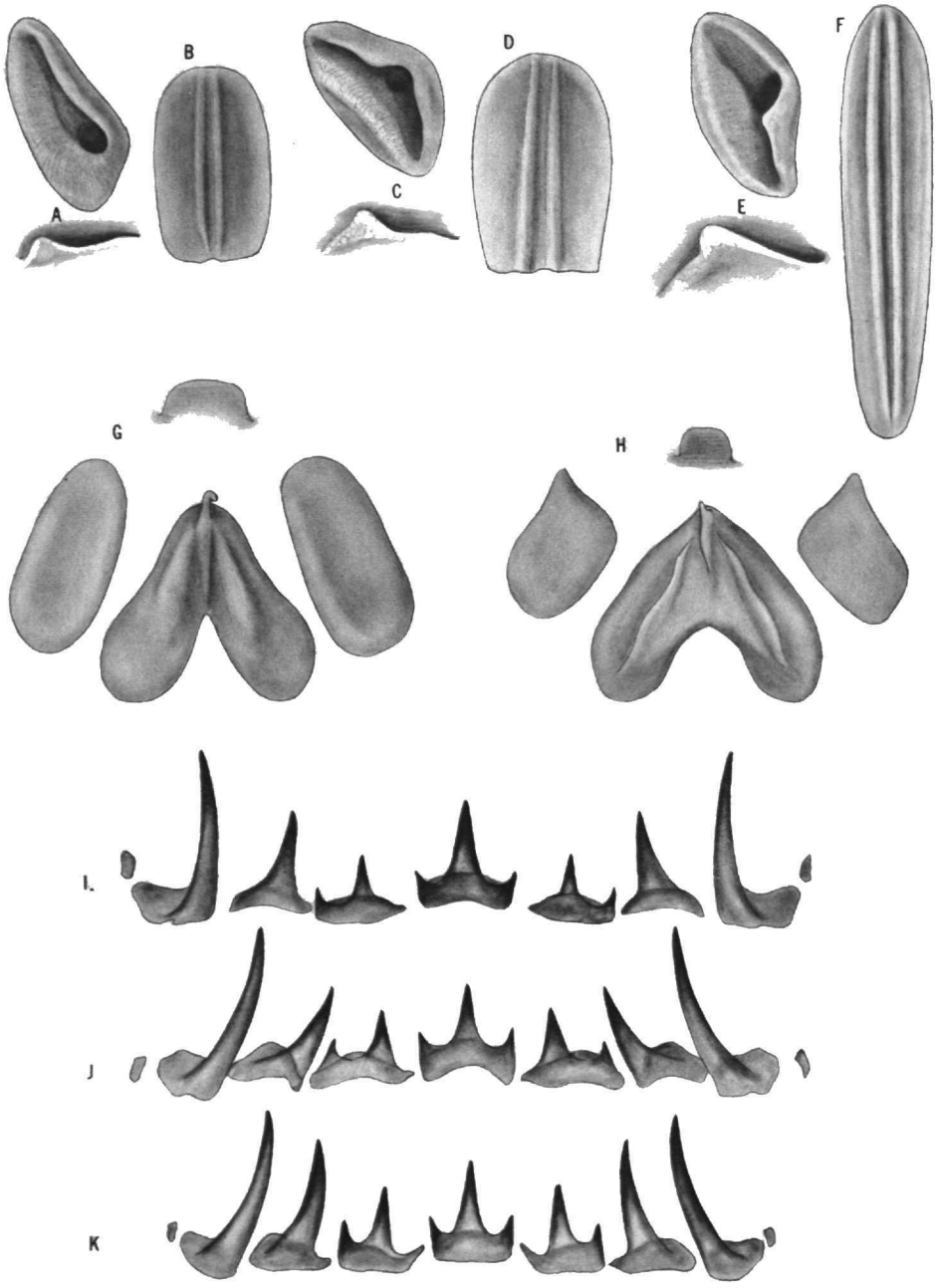

PLATE 7.—*Discoteuthis discus:* A, *Dana* Sta. unknown, 45 mm ML, funnel-mantle locking apparatus; B, holotype, *Pillsbury* Sta. 36, 53 mm ML, nuchal locking apparatus; G, holotype, funnel organ and funnel valve; I, holotype, radula. *Discoteuthis laciniosa:* C, funnel-mantle locking apparatus; D, paratype, *Dana* Sta. 1157 I, 56 mm ML, nuchal locking apparatus; J, paratype, radula. *Cycloteuthis sirventi, Gerda* Sta. 212, 42 mm ML: E, funnel-mantle locking apparatus; F, nuchal locking apparatus; H, funnel organ and funnel valve; K, radula.

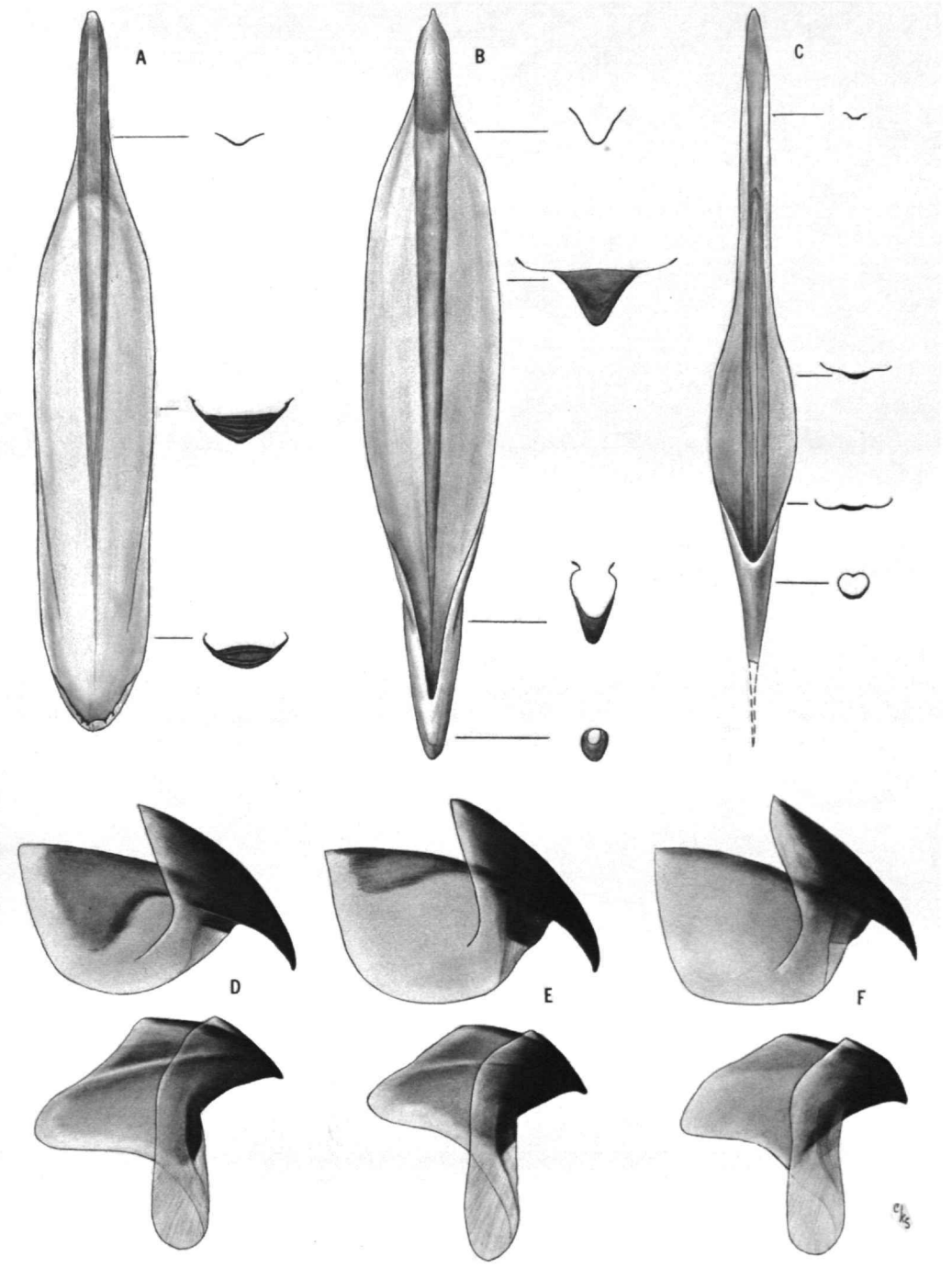

PLATE 8.—Gladii (ventral views and cross sections) and upper and lower beaks: A, D, *Discoteuthis discus,* holotype, *Pillsbury* Sta. 36, 53 mm ML; B, E, *D. laciniosa,* paratype, *Dana* Sta. 1157 I, 56 mm ML; C, F, *Cycloteuthis sirventi, Gerda* Sta. 212, 42 mm ML.

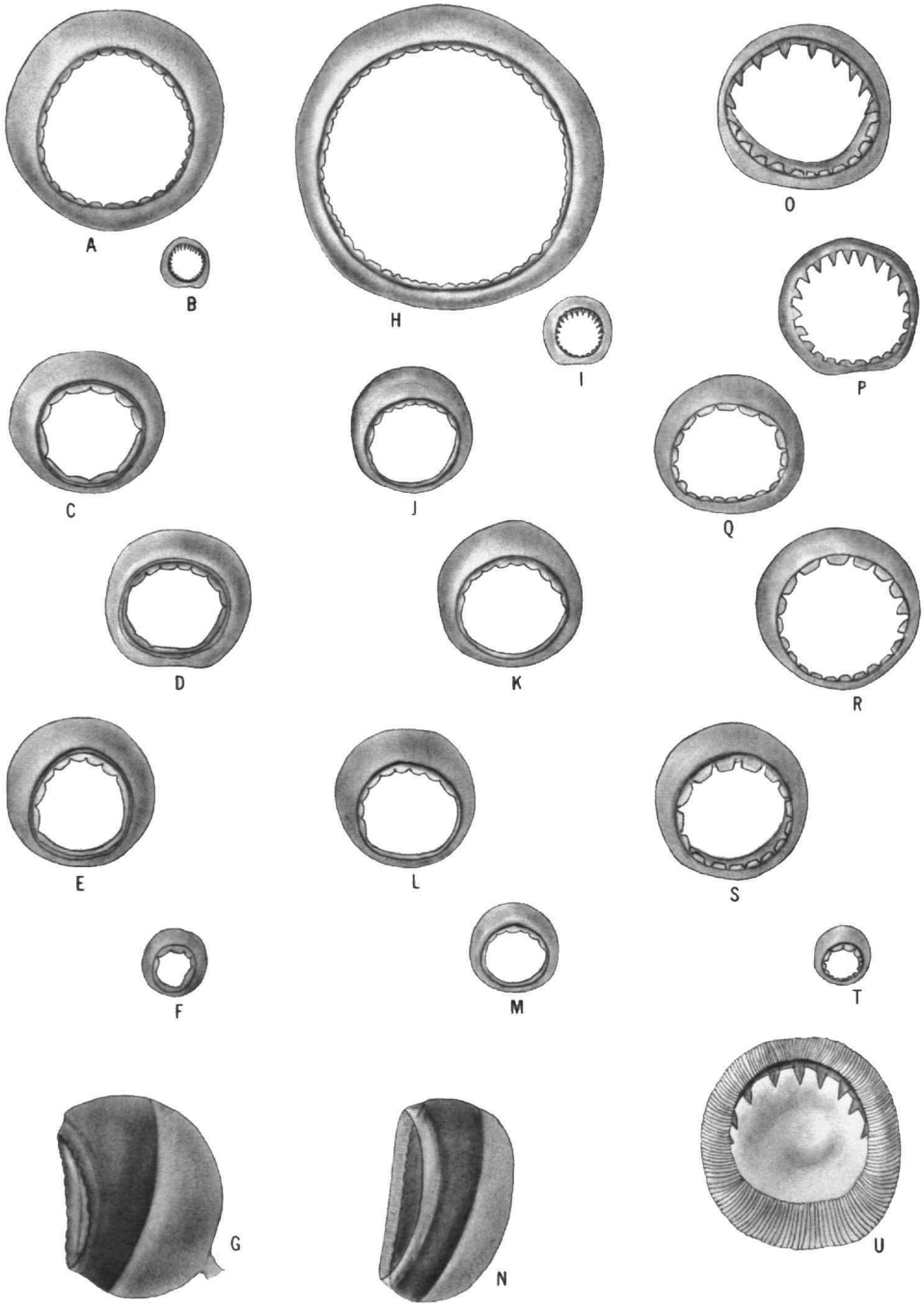

PLATE 9.—*Discoteuthis discus, Dana* Sta. unknown, 45 mm ML, suckers: A, G, from manus of tentacular club; B, from dactylus; C–F, from arms I–IV respectively. *Discoteuthis laciniosa,* paratype, *Dana* 1157 I, 56 mm ML, suckers: H, N, from manus; I, from dactylus; J–M, from arms I–IV respectively. *Cycloteuthis sirventi, Gerda* Sta. 212, 42 mm ML, suckers: O, from manus; P, from dactylus; Q–T, from arms I–IV respectively; U, from manus showing striated outer chitinous ring.

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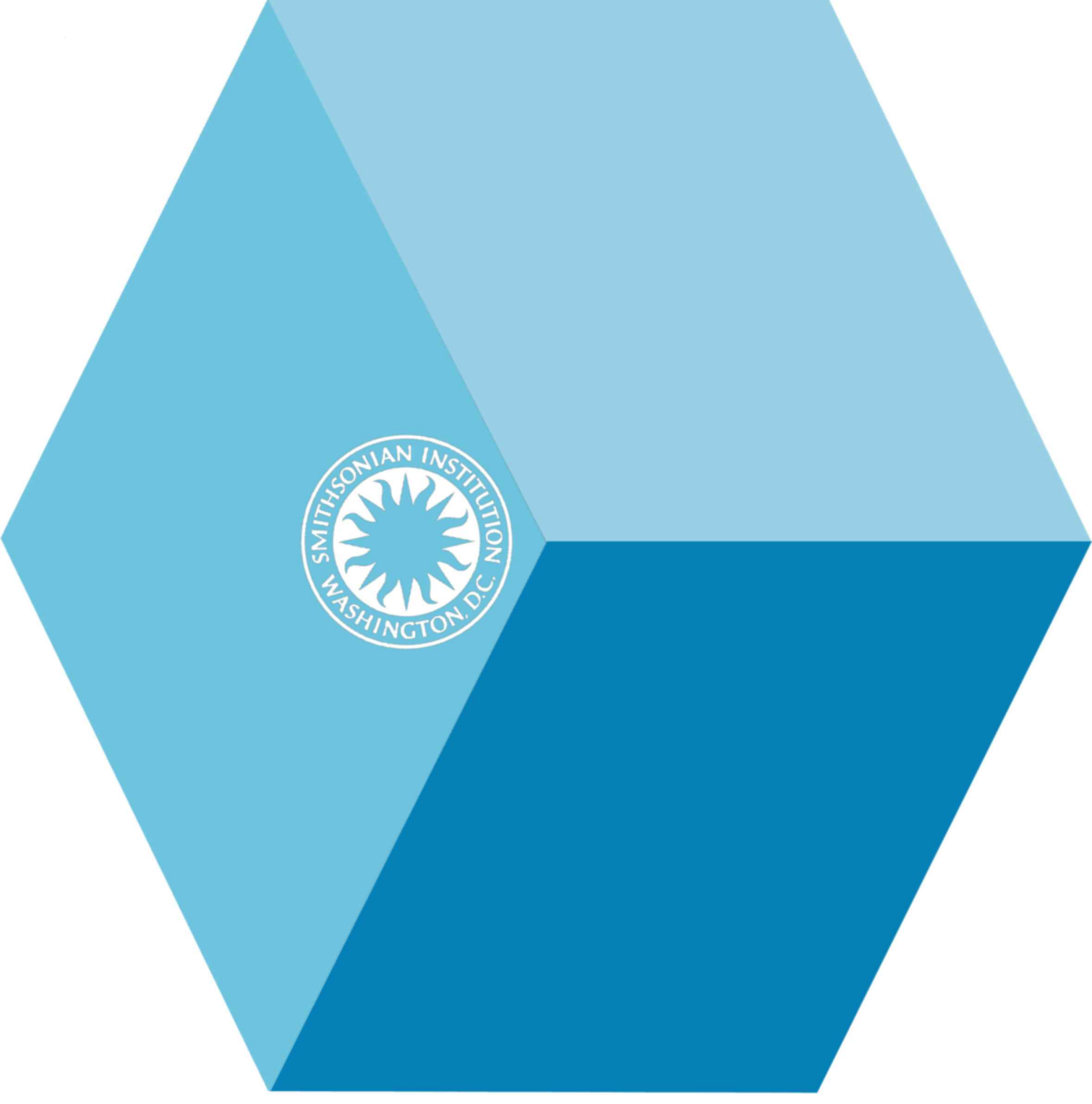
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