Issued May 21, 1968

Reprinted from: ANTARCTIC RESEARCH SERIES, VOL. 11
Biology of the Antarctic Seas III · Edited by Waldo L. Schmitt and George A. Llano
AMERICAN GEOPHYSICAL UNION · Washington, D. C., 1968

THE FAMILY PROMACHOTEUTHIDAE (CEPHALOPODA: OEGOPSIDA). I. A RE-EVALUATION OF ITS SYSTEMATIC POSITION BASED ON NEW MATERIAL FROM ANTARCTIC AND ADJACENT WATERS

CLYDE F. E. ROPER[1] AND RICHARD E. YOUNG
Institute of Marine Science, University of Miami, Florida[2]

Abstract. Two well preserved specimens of the peculiar and poorly-understood family Promachoteuthidae captured by the USNS *Eltanin* have made possible a re-evaluation of its systematic position with the resulting removal of the family from the suborder Myopsida and its placement into the suborder Oegopsida. Considerations are given to the specific status, familial relationships, and habitat of the Promachoteuthidae.

INTRODUCTION

The antarctic Cephalopoda which are collected by the United States Antarctic Research Program's oceanographic research vessel *Eltanin* are being studied at the Institute of Marine Science, University of Miami. The National Science Foundation-sponsored grant, under the direction of Dr. G. L. Voss, calls for the study of the systematics, distribution, and biology of the poorly known antarctic cephalopod fauna. Among the hundreds of specimens of pelagic cephalopods which have been sorted and identified are 2 extremely unusual squids of the genus *Promachoteuthis*. These belong to the aberrant family Promachoteuthidae which was known previously from only a single, mutilated specimen taken by the *Challenger* in the North Pacific Ocean; this form has been the source of considerable systematic confusion since its description by *Hoyle* [1885a].

This, the first of 2 papers on *Promachoteuthis*, presents a literature survey, a description of the external morphology, and a discussion of its systematic position. The second paper will present the results of an anatomical investigation into the peculiar features of this deep-sea cephalopod.

HISTORICAL RÉSUMÉ

Promachoteuthis megaptera was originally described by W. E. Hoyle in the short section on the Cephalopoda in the narrative volume of the voyage of the *Challenger* [1885a]. The description, based on a single specimen, is short and deals mainly with the form of the head, body, fins, and arms. Hoyle mentioned that the eyes were small and not prominent, and he indicated that the globular suckers with lateral apertures recalled those of *Sepiola* and *Rossia*. Since this work was intended as a general introduction, he made no further attempt to classify the new form other than as a "decapod." The specimen was taken from the North Pacific, "perhaps from 1875 fathoms, but more probably from the surface," but he gives no reasons for accepting this latter view.

Hoyle's subsequent short papers on the *Challenger* decapod cephalopods [1885b, 1885c] added details to the description and the species was placed in the "Myopsida." It was in his major work, the *Challenger* Report on the Cephalopoda [1886a], that he dealt with *Promachoteuthis megaptera* in considerable detail, giving a provisional definition of the genus and as detailed a specific description as possible from the single, mutilated specimen. In attempting to place it in his classification scheme he stated that it appeared "to be connected in some way or other with all the principal groups of the Myopsida." At that time the Division Myopsida was understood to encompass the present-day order Sepioidea as well as the current concept of the suborder Myopsida (Loliginidae and Pickfordiateuthidae). Within the "Myopsida" Hoyle placed *Promachoteuthis* in the family Sepiolini of Steenstrup. This decision was based on the similarities of the body, fins, and suckers to those in *Sepiola* and *Rossia*.

[1] Permanent address: Division of Mollusks, U.S. National Museum, Smithsonian Institution, Washington, D.C. 20560.

[2] Contribution No. 853 from the Institute of Marine Science, University of Miami.

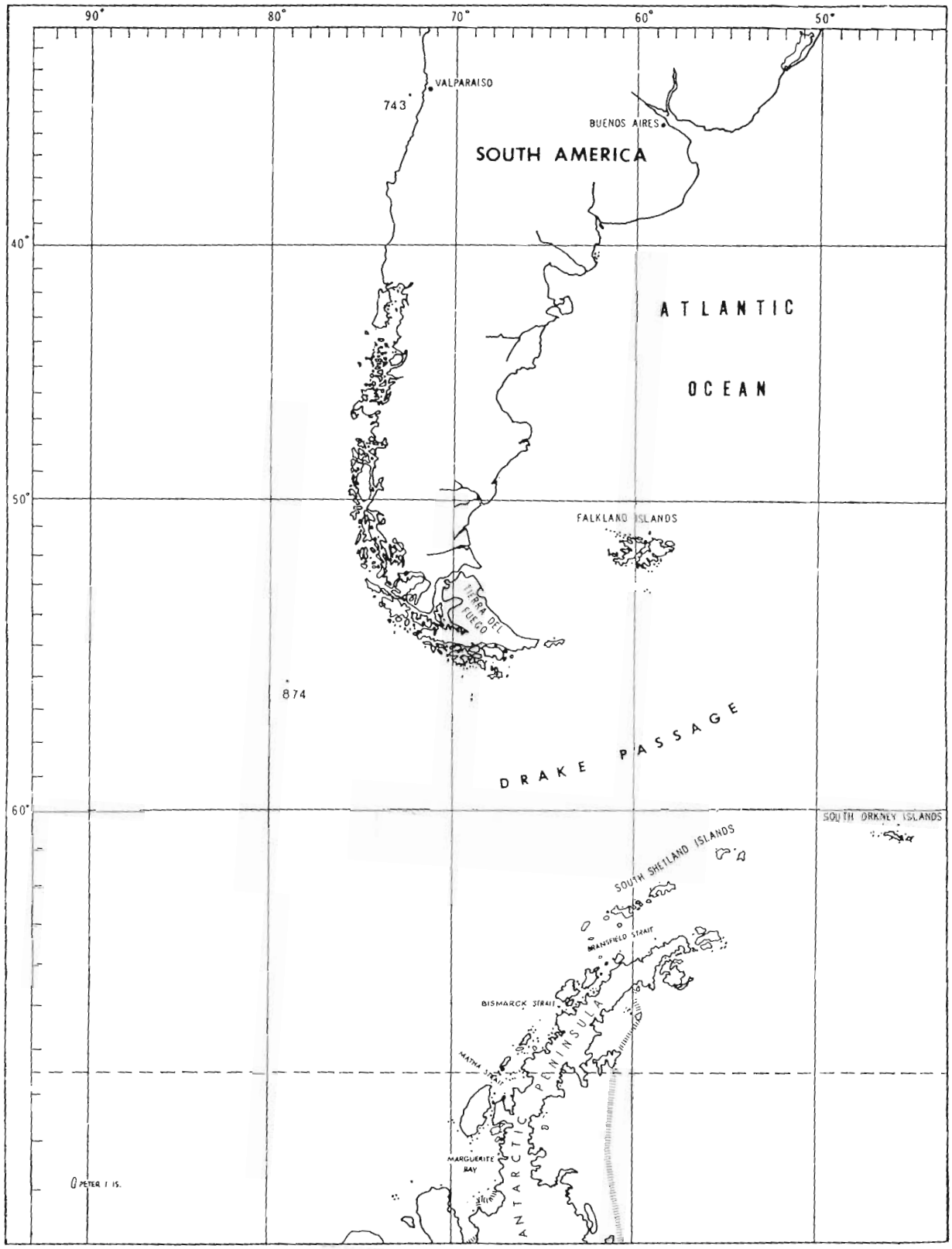


Fig. 1. Location of *Eltanin* Stations where *Promachoteuthis* sp. was captured.

In addition, Hoyle compared *Promachoteuthis* with other "myopsids," noting that it resembled *Loligo* by having the eye covered with integument and by possessing a preocular pore, and that it resembled *Sepia* by having a similar mantle-locking apparatus. However, he felt that those characters which related it with *Sepiola* and *Rossia* were more significant.

In his discussion of *Promachoteuthis megaptera*, Hoyle made several interwoven contradictory statements. In the generic definition he states that *Promachoteuthis* has the dorsal mantle free from the head as in *Rossia*. In the discussion, where Hoyle mentions the similarities with *Sepiola* and *Rossia*, he states, "It resembles the latter genus in that the mantle fold seems to have been continuous across the dorsum" (the head had been severed from the body in capture). This statement contains 2 contradictions: first, it is probable that Hoyle meant to say "the former" (*Sepiola*) since it is this genus, not *Rossia*, which has the dorsal fusion, and second, this contradicts his own previous statement in his generic definition which indicated that the mantle was free from the head. Unfortunately, these opposing statements led to further confusion among subsequent authors.

Joubin, in his revision of the Sepiolidae [1902], included *Promachoteuthis* in the subfamily Sepiolini of Appellöf which Joubin defined (following Appellöf) as having the "dorsal border of the mantle fused with the head; no nuchal adhesive cartilage." This would include *Sepiola* and exclude *Rossia*. Joubin's description is for the most part a direct translation of Hoyle's 1886 work, but he apparently recognized Hoyle's mistaken reference to *Rossia* instead of to *Sepiola*. Joubin, in attempting to correct Hoyle's above quoted statement, however, erroneously decided that Hoyle meant that *Promachoteuthis* "resembled *Rossia* by the fact that the body was dorsally *separated from* the neck" (our italics). Joubin's interpretation immediately eliminates the only character by which *Promachoteuthis* logically could be placed in the Sepiolini Appellöf. However, Joubin apparently was not bothered by this inconsistency and retained *Promachoteuthis* in Sepiolini for reasons he did not enumerate. Beyond this he could add nothing to the knowledge of *Promachoteuthis* since he had not seen the specimen. *Berry* [1912], in his catalogue of Japanese cephalopods, gave the synonymy and type locality (southeast of Japan) and listed *Promachoteuthis megaptera* under the family Sepiolidae, subfamily Rossiinae, obviously basing his decision on Hoyle's description and believing that Joubin's peculiar placement of the form was in error. Berry's paper, which was published in October, 1912, must already have been in press because he does not mention *Naef's* [1912] work, "Die Familien der Myopsiden," which was published in March.

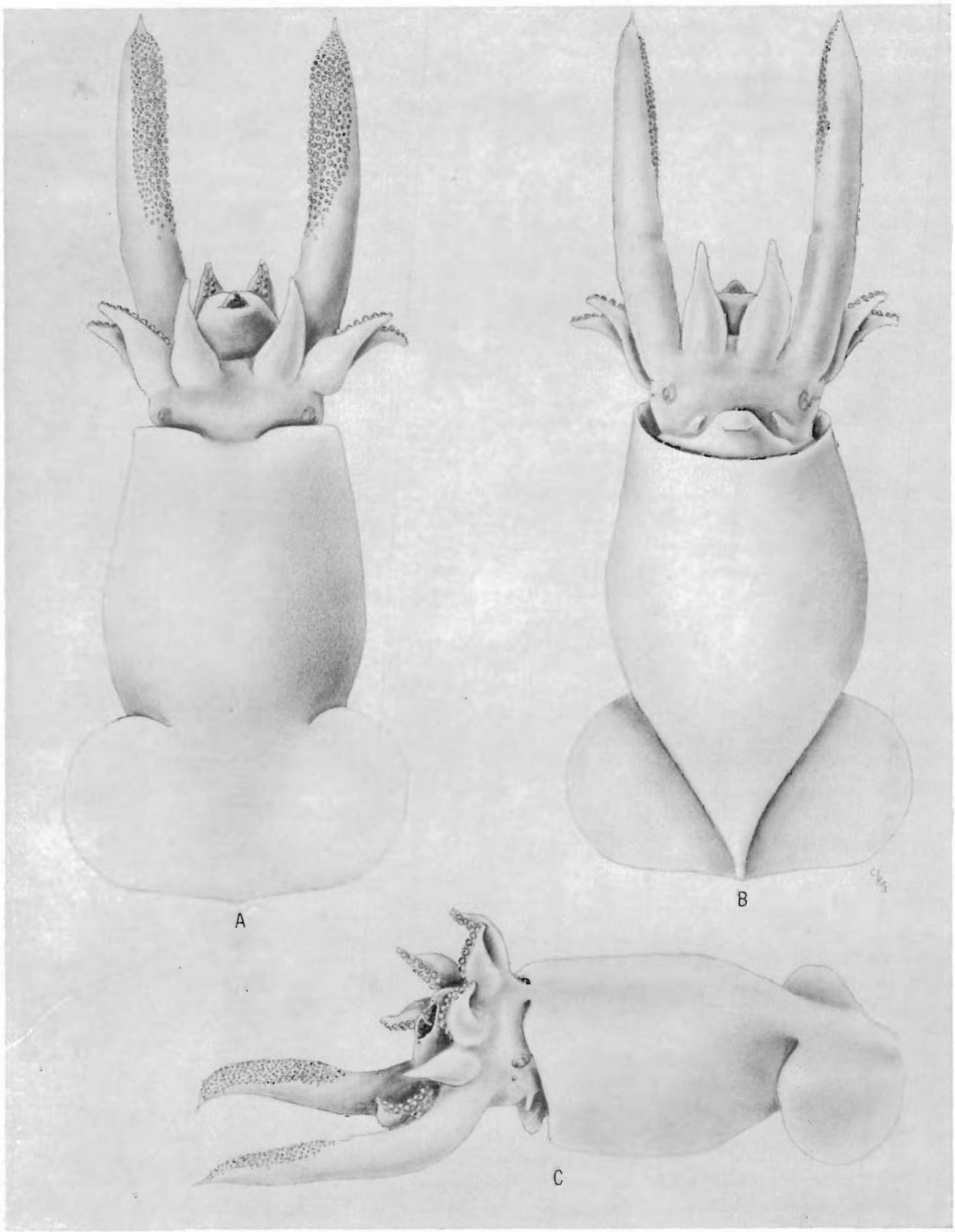
In this work Naef erected the monotypic family Promachoteuthidae and placed it next to the Loliginidae on the basis of the presence of the eye-pore and non-retractile tentacles ("arms"). Naef must have believed these characters to be of greater importance than those which previously had been used to align *Promachoteuthis* with the Sepiolidae. He stated that he could not place *Promachoteuthis* in the Loliginidae because of the great differences in habitats, but that, on the other hand, there was insufficient information to characterize the new family.

Sasaki [1914] listed *P. magaptera* in his notes on Japanese Myopsida and placed it in the Rossiinae, thus sharing Berry's view. Probably he, too, was unaware of Naef's elevation of *Promachoteuthis* to its own family. In 1921 Naef listed the family and genus under his order Teuthoidea [*Naef*, 1916] and his new suborder Metateuthoidea Myopsida which included only 2 other families, the Loliginidae and Lepidoteuthidae. This grouping shows little similarity with the earlier concept of the Myopsida.

In the systematic section of his great monograph *Naef* [1923], relying on his specialized knowledge of the Sepiolidae and agreeing with his earlier views, emphasized that *Promachoteuthis* could not be a member of this family and retained it in his emended Metateuthoidea Myopsida. *Grimpe*, following Naef's classification of the suborder or tribe Myopsida, merely listed Promachoteuthidae and *Promachoteuthis* [1922, 1925].

In his monograph of Japanese cephalopods, *Sasaki* [1929] added some minor details to the knowledge of *P. magaptera* based on his examination of the type, but in the main his description paraphrased Hoyle's. Sasaki, accepting Naef's family, placed the Promachoteuthidae in the old division Myopsida in which he also included the Loliginidae, Idiosepiidae, Sepiolidae, and Sepiidae. In this work the family was first adequately characterized.

Finally, *Thiele* [1935] listed *P. megaptera* and gave the characters of the family and genus. He placed the family in his "suborder" Loliginacea along with the Loliginidae and Lepidoteuthidae thus making his Loliginacea equivalent to Naef's Metateuthoidea Myopsida. Subsequently, the Lepidoteuthidae has been shown to be in the suborder Oegopsida and an addi-


A
B
C

tional family, the Pickfordiateuthidae Voss, 1953, now makes up the third family of the Myopsida. (The term Metateuthoidea has been dropped by most recent authors [*Voss*, 1956].)

In order to make this résumé complete it should be mentioned that *Promachoteuthis megaptera* appeared in *Hoyle's* various catalogues and generic lists [1886b, 1904, 1910], but no additional information was given, and that *Naef* [1916] merely stated that *Promachoteuthis* belonged in the Myopsida.

The foregoing discussion, in addition to tracing the interesting taxonomic history of a cephalopod group known from only a single, mangled specimen, secondarily has graphically pointed out that the classification of the higher taxa of the Cephalopoda has been the subject of considerable discussion and change within relatively recent times.

Family PROMACHOTEUTHIDAE Naef, 1912

Promachoteuthidae Naef, 1912, p. 244; 1921, p. 535.—Grimpe, 1922, p. 45; 1925, p. 95.—Sasaki, 1929, p. 105, 131.—Thiele, 1935, p. 960.

Genus ***Promachoteuthis*** Hoyle, 1885

Promachoteuthis Hoyle, 1885, p. 273; 1886, p. 120.—Joubin, 1902, p. 109.—Hoyle, 1904, p. 8.—Naef, 1912, p. 244; 1916, p. 17; 1921, p. 535; 1923, p. 166.—Grimpe, 1922, p. 45; 1925, p. 95.

Promachoteuthis megaptera Hoyle, 1885

(Type-species by monotypy)

Promachoteuthis megaptera Hoyle, 1885, p. 273; 1885a, p. 182; 1885b, p. 284; 1886, p. 120; 1886a, p. 25.—Joubin, 1902, p. 109.—Hoyle, 1910, p. 412.—Berry, 1912, p. 381, 417.—Sasaki, 1914, p. 588, 599; 1929, p. 131.—Thiele, 1935, p. 960.

Holotype. British Museum (Natural History).

Type Locality. Challenger Sta. 237; 34°37′N., 140° 32′E.; North Pacific Ocean southeast of O-shima, Japan, 17 June 1875.

Promachoteuthis sp.

Material

1 juvenile, 17-mm mantle length; *Eltanin* Sta. 743, 33°18′S., 72°27′W., 26 Sept. 1963; 0–1830 m, 3-m IKMWT.

TABLE 1. Measurements in mm of the *Eltanin* Specimens of *Promachoteuthis* and of the Holotype of *P. megaptera* Hoyle, 1885

	ELT. 743		ELT. 874		*P. megaptera*	
Mantle Length	17.0		10.5		15	
Mantle Width	8.0		6.0		9	
Head Length	4+		3.3		...	
Head Width	7.0		4.0		6	
Fin Length	7.0		4.0		11	
Fin Width	12.0		7.5		23	
Arm Length	R.	L.	R.	L.	R.	L.
I	3.4	4.0	3.0	3.0	13	14
II	4.0	4.0	3.0	3−	14.5	15
III	4.0	4−	3.0	3−	14	14
IV	4.5	4.5	4−	4−	7	12
Tentacle Length	13.0		10.0		22	25+
Club Length	9.0		6.0		...	...
Eye Diameter	0.8		0.8		1.6	

1 juvenile, 10.5-mm mantle length; *Eltanin* Sta. 874, 56°06′S., 79°04′W., 27 Nov. 1963; 1391 m, 3-m IKMWT.

Description

The mantle is broad, bulges in the middle, and tapers to a point posteriorly. It is thick but gelatinous in consistency with 2 weakly developed muscular layers. The mantle opening is broad and considerably wider than the width of the head. The mantle is connected to the head by a broad fusion in the dorsal nuchal region (Plate I, Fig. A–C; Plate III, Fig. A).

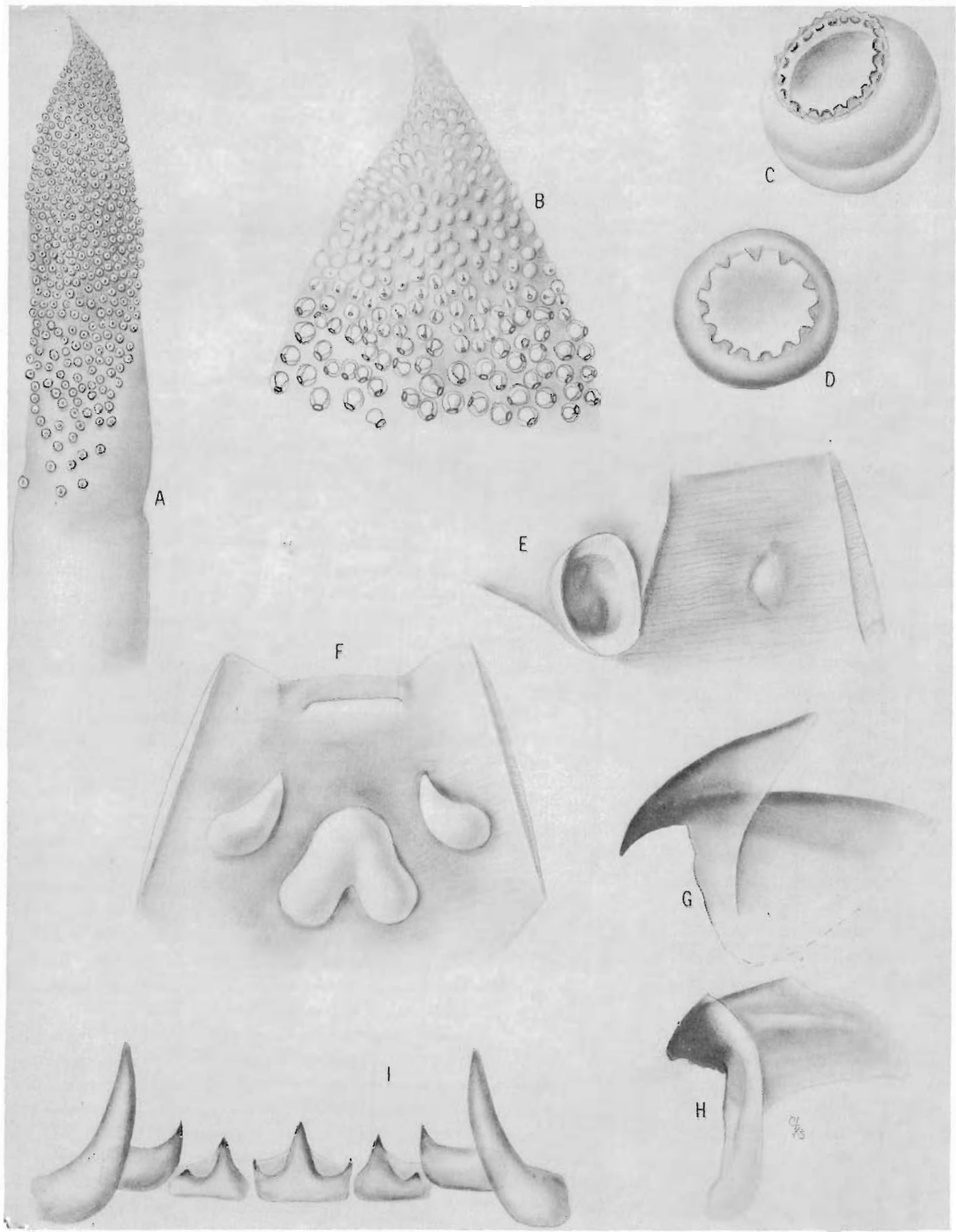
Although the mantle is fused primarily on its inner surface in the area of the nuchal-locking cartilage, the outer integument is continuous with that of the head and somewhat obscures the dorsal anterior border of the mantle. Topographically this fusion is similar to the dorsal fusion of cranchiids.

In the larger specimen the dorsal midline is indistinct. However, in the smaller specimen the dorsal midline is fairly well defined, especially in the middle portion, although anteriorly, where it "fuses" with the head-collar region, the midline is not distinguishable. The gladius cannot be detected in either specimen, and apparently it is greatly reduced or lacking.

The fins are broad and rounded; their length and width are respectively about ⅖ and ⅔ of the mantle length. The fins are poorly muscled but their bases are considerably thickened by gelatinous tissue. Their lateral margins are semicircular in outline; the posterior margins converge forming a nearly flat angle at their junction. In the smaller specimen the posterior tip is slightly more prominent. The anterior lobes are free and the insertions are broadly separated.

Plate II. *Promachoteuthis* sp. Mantle length, 17 mm.

Fig. A. Dorsal view.
Fig. B. Ventral view.
Fig. C. Lateral view.


A
B
C
D
E
F
G
H
I

The funnel is large and thick-walled but is gelatinous in consistency. The exhalent opening extends slightly anterior to the level of the eyes. The funnel components of the locking apparatus are deep bowl-shaped structures without a trace of a tragus or other complexity, and they are relatively large with broad edges (Plate II, Fig. E). The corresponding components on the mantle are distinct rounded knobs in the larger specimen but are barely distinguishable in the younger form. The funnel valve is very weakly developed and forms a thin, narrow ridge-like flap.

The funnel organ of the larger specimen consists of an inverted V-shaped dorsal pad and 2 slightly pear-shaped ventral pads, all of which are extremely swollen (Plate II, Fig. F). The funnel organ of the smaller animal is quite peculiar. The dorsal member is a large, swollen oblong structure, with the long axis extending across the width of the funnel tube. The ventral members are simply small, oval pads (Plate III, Fig. C).

The head is short and swollen with gelatinous tissue which buries the minute eyes. The eyes remain in communication with sea water by a short duct to the surface of the head (Plate I, Fig. A–C). This duct corresponds to the eye opening or eye pore of other cephalopods. The eyes are greatly reduced in size; however, lenses are present, and therefore the eyes are probably still functional. The diameter of the eyes is about 0.8 mm in both specimens, although the large specimen has a 70% greater mantle length.

The olfactory papillae are relatively long, fingerlike projections with no terminal swelling. They arise from the surface of the head ventral and slightly posterior to the eyes. There is no indication of either nuchal folds or a nuchal crest.

The brachial crown and buccal region are quite striking. The arms are extremely short, fat, nearly conical and lack keels, trabeculae, and protective membranes. The arms are subequal, the first and third pair possibly slightly shorter. There is no interbrachial web. The arm suckers are globular and are arranged in 2 rows along the proximal portion of the arm but become irregularly distributed distally.

The chitinous sucker rings possess approximately 20 small, rounded to truncate, regularly spaced teeth. The teeth occupy the entire circumference of the sucker ring (Plate II, Fig. C).

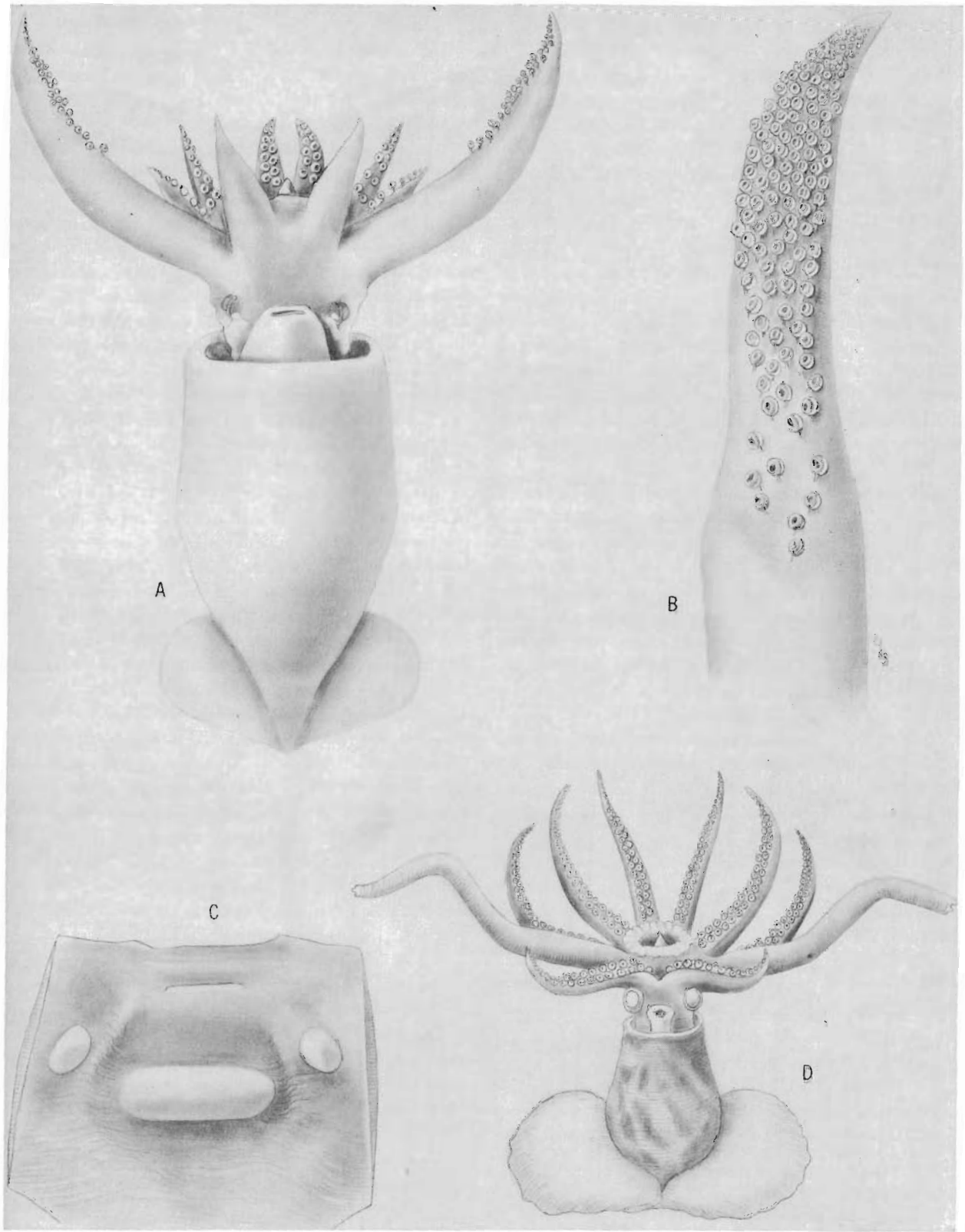
The tentacles are particularly unusual (Plate II, Fig. A; Plate III, Fig. B). The bases originate on the head in the same manner as the arms, and there is no trace of a tentacular sheath or pocket. In fact, at their bases the tentacles look like another pair of arms, with the notable exception that they are extremely thick and robust. In the smaller specimen the tentacles are nearly as long as the mantle, while those of the larger specimen are about 75% of the mantle length. The clubs occupy 60% to 70% of the tentacle length. There are no keels, protective membranes, or carpal clusters. The boundary between the tentacle stalk and club is indicated by a distinct reduction in the diameter of the tentacle. In addition, the stalk is lightly pigmented a pale reddish-brown, while the club is colorless. The proximal suckers of the club originate in 2–3 scattered rows; then as they extend distally they increase rapidly in numbers of rows so that ultimately there are numerous minute suckers closely packed in 20 or more rows in the large specimen and in 6–8 rows in the smaller specimen. The club sucker rings possess approximately 12 small teeth around the circumference; those on the distal margin are slightly pointed, while the remainder are truncate (Plate II, Fig. D). At the distal end of the club the suckers diminish rapidly in size but remain numerous while the club narrows abruptly to a slightly attenuate tip. With the decrease in the sucker size there is a corresponding but accelerated decrease in the diameter of the chitinous rings which soon disappear, leaving undifferentiated suckers. These in turn diminish to minute, fleshy knobs at the termination of the tentacle (Plate II, Fig. B). It is probable that this area represents a zone of sucker proliferation.

The buccal mass is gigantic relative to the size of the animal. Its diameter is greater than the length of the longest arm.

The beaks are extremely large, strongly developed, and protrude from the huge buccal mass. The inner lip is moderately developed and weakly rugose. The outer lip is just a fold of skin encircling the inner lip. The buccal membrane is nearly nonexistent. In the smaller specimen it consists of 7 poorly developed papillalike lappets with indistinct connectives. The connectives attach dorsally to arms I and II and ventrally to arms III and IV. In the large specimen the features

Plate II. *Promachoteuthis* sp. Mantle length, 17 mm.

Fig. A. Tentacle.
Fig. B. Tip of tentacular club.
Fig. C. Sucker from third arm.
Fig. D. Sucker from tentacular club.
Fig. E. Locking apparatus, funnel and mantle components.
Fig. F. Funnel organ and funnel valve.
Fig. G. Dorsal mandible.
Fig. H. Ventral mandible.
Fig. I. Radular teeth.


A
B
C
D

of the buccal membrane are not distinguishable due to the state of contraction.

The beaks are illustrated in Plate II, Figs. G, H. The lower jaw has a slight ridge on the gular lamella, and the rostral lamella is long and narrow. The upper mandible exhibits no unusual peculiarities.

The well developed radula has sharply pointed teeth. The rachidian tooth has a large median cusp and 2 small, sharp, lateral cusps; each first lateral tooth has a large medial cusp and a small conical lateral cusp. The second laterals are broad and low with a sharp cusp arising at the medial end. The third laterals are very elongate and scythe-shaped (Plate II, Fig. I).

The smaller specimen, preserved in 70% ETOH, is nearly colorless and opaque. Although the integument is intact over the entire animal, there is little pigmentation save for around the brachial crown. The oral surface of the brachial crown, the bases of the arms and tentacles, the buccal membrane, and especially the outer lip are lightly pigmented in a pinkish-purple hue. The aboral surfaces are very lightly pigmented. The inner lip is colorless. The beaks are dark brown to black. The eye is reddish-black and the lenses are yellowish-brown. The larger specimen is preserved in 10% buffered formalin and the pigmentation is less apparent.

DISCUSSION

Comparison with Promachoteuthis megaptera

The specimens which have been described here differ greatly from the holotype of *Promachoteuthis megaptera* in a number of important features. These differences are readily apparent when the illustrations of the *Eltanin* specimens (Plate I, Fig. A–C; Plate III, Fig. A) and Hoyle's illustration of *P. megaptera* (re-drawn in Plate III, Fig. D) are compared. It is fortunate that Hoyle's specimen and the larger of the present specimens have nearly the same mantle lengths, making a direct comparison valid (see Table 1).

The arms of *P. megaptera* are very long and slender (about as long as the mantle) and the arm formula is 2·1=3·4, while the arms of the *Eltanin* specimens are very short and stubby (only 20–30% of the mantle length) and are subequal in length, with Arms I & III possibly being slightly the shorter.

The fins in *P. megaptera* are very long and broad (73% and 153% respectively of the mantle length), whereas those of the *Eltanin* specimens are relatively much smaller (their lengths are 33% to 44% of the mantle length and their widths are 70% of the mantle length).

Hoyle states that the sucker rings of *P. megaptera* are smooth, but the rings of the *Eltanin* specimens are finely toothed; however, it is possible that Hoyle was unable to examine his suckers closely enough to detect the minute dentition.

The tentacles of the type specimen of *P. megaptera*, even though the tips are missing, are considerably longer than in the *Eltanin* specimens.

There appears to be a marked difference in the coloration of the 2 species; Hoyle's specimen is considerably more pigmented.

The head of *P. megaptera*, as described, is much smaller than in our material; this, however, may be an artifact of preservation. There is a distinct difference in the diameters of the eyes (*P. megaptera* = 1.6 mm; *Eltanin* specimens = 0.8 mm).

These differences clearly indicate that the *Eltanin* specimens must represent a new species. However, we prefer not to contribute to nomenclatural confusion by the introduction of a specific name based on such small juvenile specimens. Therefore, we will defer naming this species until more material becomes available.

Systematic Position

As shown in the historical review, *Promachoteuthis*, after having been shuffled about between the higher taxa by early authors, presently occupies a familial position within the order Teuthoidea, suborder Myopsida. As a result of our examination of the *Eltanin* specimens we believe this placement to be incorrect, and we find it necessary to reexamine the systematic position of *Promachoteuthis*.

First, the proper ordinal position should be determined. At the ordinal level the characters which are significant in the present discussion are enumerated in Table 2.

Promachoteuthis has no tentacular pockets or sheaths and the tentacles are not retractile. Thus in this character it is aligned with the Teuthoidea. The posterior lobes of the fins are continuous, a feature which is unknown in the Sepioidea. The radula of *Promachoteuthis* is teuthoid in nature. It possesses a rachidian with a long median tooth and 2 small side cusps, and

Plate III

Fig. A–C, *Promachoteuthis* sp., mantle length, 10.5 mm.
Fig. A. Ventral view.
Fig. B. Tentacle.
Fig. C. Funnel organ and funnel valve.
Fig. D. *Promachoteuthis megaptera* Hoyle, 1885; mantle length, 15 mm; ventral view (redrawn from *Hoyle*, 1886).

TABLE 2. Comparison of Sepioid and Teuthoid Ordinal Characters

	Order Sepioidea	Order Teuthoidea
Tentacles	Retractile into pockets	Contractile; not retractile into pockets
Fins	Posterior lobes always free	Posterior lobes usually fused; only occasionally free, e.g., *Pickfordiateuthis, Pyroteuthis, Bathyteuthis*, etc.
Radula	Each tooth, including rachidian, with only 1 projection	Rachidian with a large median projection and 2 small lateral cusps; 1st lateral teeth each with 1 small additional cusp (grades toward sepioid type in some forms, e.g., *Onychoteuthis*)
Gills	No branchial canal between afferent and efferent branchial blood vessels	Branchial canal present between afferent and efferent branchial blood vessels
Liver	Generally divided or bilobed	A single structure

first lateral teeth with additional small single cusps. Although the radula of some teuthoids tends to grade toward the simple sepioid type, the reverse trend does not exist. The gills of *Promachoteuthis* have obvious branchial canals, a clearly distinctive teuthoid character. The liver in *Promachoteuthis* is a single structure and not divided or bilobed as is usual in the sepioids. The combination of these positive characters requires that *Promachoteuthis* be considered an unquestioned member of the order Teuthoidea.

Next, it is necessary to determine with which of the 2 suborders (Myopsida or Oegopsida) *Promachoteuthis* should be aligned.

Naef placed *Promachoteuthis* in the Myopsida because of his belief (based on Hoyle's description) that the animal showed the primary character of the suborder: the possession of a true cornea with a small eye pore. In the present specimens the tissue of the head is gelatinous and transparent with the eyes deeply embedded but each maintaining connection with the exterior through a small pore. If the head were distorted and compressed during capture and preservation, as undoubtedly happened in Hoyle's specimen, the soft, gelatinous tissue over the eye would be reduced to a thin transparent layer which could give the appearance of the "transparent membrane" described by Hoyle and interpreted as a cornea by Naef. In addition, the pore could easily be forced forward to the position occupied by the true preocular pore of myopsids. From this it is easy to understand how earlier authors have accepted the existence of the cornea and preocular pore. This itself, however, does not explain the presence of the pore-like structure in *Promachoteuthis*. When the diameter of the pore is compared with the diameter of the eye it becomes clear that the pore, in fact, is relatively large (about $\frac{1}{5}$ of the eye diameter in the *Eltanin* specimens and $\frac{1}{2}$ the eye diameter in the holotype of *P. megaptera*). In myopsids the preocular pore to eye diameter ratio is approximately 1 to 40, while in the Oegopsida the eye opening to eye diameter ratio is generally between 1 to 2 and 1 to 3. Therefore, *Promachoteuthis* closely approaches the Oegopsida in this important character. It is our opinion that the small eye opening of *Promachoteuthis* merely reflects the reduced condition of the eye, and that this opening actually represents the diagnostic oegopsid trait.

There are 2 other major systematic characters which appear to preclude the placement of *Promachoteuthis* in the Myopsida. The mantle-locking apparatus of the genus is oval, while that of myopsids is always straight. By the possession of many (about 20) rows of small suckers on the tentacular club, *Promachoteuthis* differs radically from any of the myopsids in which the club contains a maximum of 4 sucker rows. *Promachoteuthis*, on the other hand, agrees in both of these characters with certain oegopsids. It should be mentioned also that there are no myopsids known from the deep sea. This group exhibits a considerable uniformity of habitat in the shallow seas of the continental shelf. In our opinion the evidence enumerated here leaves little doubt that *Promachoteuthis* is indeed a member of the suborder Oegopsida.

While *Promachoteuthis* is a truly distinctive form fully deserving its familial ranking, it does have some important traits which indicate possible relationship with the family Mastigoteuthidae Verrill, 1881. The mantle-locking apparatuses of both families are of the same oval shape; however, the tragus and anti-tragus, commonly present in *Mastigoteuthis*, are lacking in *Promachoteuthis*. In addition, both families have unexpanded tentacular clubs bearing numerous rows of minute suckers. The clubs of the 2 families have the same peculiar method of growth by the proliferation of

suckers at the extreme distal end. Although there are many families for which the mode of club growth is not fully known, this peculiar feature of rapid terminal development contrasts with the mode of club growth in several other oegopsid families which have numerous tentacular suckers, e.g., Chiroteuthidae and Batoteuthidae [Young and Roper, 1967]. These latter 2 families proliferate suckers proximal to the area of the manus. Although the familial affinities are vague, these traits are among the more important characters utilized in classification at the family level in the Oegopsida.

Development and Habitat

Although the amount of material available is scanty, it is possible nevertheless to discern 2 clear developmental trends. The smaller specimen has only 6–8 sucker rows on the tentacular club, while the large form in adding slightly more than ⅓ to its mantle length, shows a remarkable increase in the number of suckers, approximately tripling the number of rows. The eyes, however, are the same diameter in both the large and the small specimens. This seems to imply an ontogenetic reduction in the size of the eyes relative to the size of the animal.

The lack of isometric increase in eye size indicates the possibility of a deep-sea habitat for this species. The specimens were captured in open 3-m Isaacs-Kidd midwater trawls which fished at approximately 1400 m and 200 to 1850 m. Therefore, it is possible that the specimens were captured in the bathypelagic zone. This assumption is supported by additional anatomical features. The animal is very gelatinous with a weakly developed muscular system and lacks pigmentation except for traces on the brachial crown and buccal mass. Possession of gelatinous tissue, weak musculature, and reduction in eye size is a characteristic modification of bathypelagic fishes. In addition, many deep sea fishes which are associated with the bottom exhibit a marked loss of pigmentation [*Marshall*, 1954]. Some bathypelagic or deep bottom-associated cephalopods, e.g., *Cirrothauma* and *Stauroteuthis*, also demonstrate the same tendency toward these characteristics [*Chun*, 1914, and personal observation].

The anatomical features and the catch data indicate that this species of *Promachoteuthis* is probably a true inhabitant of the bathypelagic zone.

SUMMARY

1. The literature on *Promachoteuthis* is surveyed in detail, tracing the development of ideas concerning the systematic position of this aberrant genus.
2. Two juvenile specimens captured by the USNS *Eltanin* are described and illustrated. These specimens are compared with *Promachoteuthis megaptera* Hoyle, 1885, and are found to represent a new species. The naming of this species is deferred until adult specimens become available.
3. The study of these specimens has made possible the reevaluation of the systematic position of the family Promachoteuthidae. The family is placed in the order Teuthoidea, suborder Oegopsida, with possible affinities with the family Mastigoteuthidae.
4. The *Eltanin* material available indicates a rapid ontogenetic increase in the number of sucker rows on the tentacular clubs. The eyes seem to undergo an ontogenetic reduction in size relative to the size of the animal.
5. Anatomical features and apparent depths of capture suggest a bathypelagic habitat for this species.

Acknowledgments. The co-authors wish to thank the National Science Foundation, Office of Antarctic Programs, for its encouraging support of the continuing studies of Antarctic Cephalopoda (NSF Grant Numbers GA-103 and GA-253). We also wish to thank Dr. G. L. Voss for his suggestions and encouragement throughout our work. Both of us have examined the type of *Promachoteuthis megaptera* Hoyle at the British Museum (Natural History), and we are grateful to Dr. N. Tebble and Mr. H. O. Ricketts for their kindness during our visit. Dr. Joseph Rosewater of the U. S. National Museum and Dr. S. Stillman Berry of Redlands, California, have read the manuscript, and we are grateful for their valuable comments. The Department of Biology, University of Southern California, is largely responsible for the macrobiological sampling program aboard the USNS *Eltanin;* personnel from the Institute of Marine Science and Smithsonian Oceanographic Sorting Center also participate in the collection of biological specimens. The excellent condition of the material is due to the careful handling and preservation of the specimens by staff members of these institutions. We are most grateful to Miss Constance Stolen for her skillful creation of the illustrations.

REFERENCES

Berry, S. S., A catalogue of Japanese Cephalopoda, *Proc. Acad. Nat. Sci. Philadelphia, 1912:* 380–444, 1912.

Chun, C., Cephalopoda, *Rept. Sci. Res. Michael Sars North Atlantic Deep Sea Exped., 1910, 3*(1) : 1–28, 1914.

Grimpe, G., Systematische Ubersicht der europaischen Cephalopoden, *Sber. Naturf. Ges. Leipzig, 45–48:* 36–52, 1922.

Grimpe, G., Zur Kenntnis der Cephalopodenfauna der Nordsee, *Wiss. Meeresunters. Komm. Kiel, 16*(3) : 1–124, 1925.

Hoyle, W. E., Narrative of the Voyage of the *Challenger* Expedition, The Cephalopoda, *Rept. Voy. Challenger, 1*(1): 269–274, 1885a.

Hoyle, W. E., Diagnosis of new species of Cephalopoda collected during the cruise of H.M.S. *Challenger.* II. The Decapoda, *Ann. Mag. Nat. Hist., Ser. 5, 16:* 181–203, 1885b.

Hoyle, W. E., Preliminary report on the Cephalopoda collected during the cruise of H.M.S. *Challenger*. II. The Decapoda, *Proc. Roy. Soc. Edinburgh, 13*(120) : 281–310, 1885c.

Hoyle, W. E., Report on the Cephalopoda collected by H.M.S. *Challenger* during the years 1873–76, *Rept. Voy. Challenger, Zool., 16*(44) : 1–246, 1886a.

Hoyle, W. E., A catalogue of recent Cephalopoda, *Proc. Roy. Phys. Soc. Edinburgh, 9*: 205–267, 1886b.

Hoyle, W. E., A diagnostic key to the genera of recent dibranchiate Cephalopoda, *Mem. Proc. Manchester Lit. Phil. Soc., 48*(21) : 1–20, 1904.

Hoyle, W. E., A list of the generic names of dibranchiate Cephalopoda with their type species, *Abh. Senckenb. Naturforsch. Ges., 32*: 407–413, 1910.

Joubin, L., Revision des Sepiolidae, *Mem. Soc. Zool. France, 15*(1) : 80–145, 1902.

Marshal, N. B., *Aspects of Deepsea Biology*, 380 pp., Hutchinson's, London, 1954.

Naef, A., Teuthologische Notizen. I. Die Familien der Myopsiden, *Zool. Anz., 39*(7) : 241–244, 1912.

Naef, A., Systematische Uebersicht der mediterranen Cephalopoden, *Pubbl. Sta. Zool. Napoli, 1:* 11–19, 1916.

Naef, A., Das System der dibranchiaten Cephalopoden und die mediterranen Arten derselben, *Mitt. Zool. Sta. Neapel, 22*: 527–542, 1921.

Naef, A., Die Cephalopoden, Systematik, *Fauna u. Flora Neapel, Monogr. 35, 1*, part 1, (2) : 149–863, 1923.

Sasaki, M., Notes on the Japanese Myopsida, *Annot. Zool. Jap., 8*: 587–629, 1914.

Sasaki, M., A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters, *J. Coll. Agric. Hokkaido Imp. Univ., 20*, Suppl.: 1–357, 30 pls., 1929.

Thiele, J., *Handbuch der systematischen Weichtierkunde, 2*(3) : 779–1154, 110 figs., 1935.

Voss, G. L., A new family, genus, and species of myopsid squid from the Florida Keys, *Bull. Mar. Sci. Gulf Carib., 2*(4) : 602–609, 1953.

Young, R. E., and C. F. E. Roper, The Batoteuthidae, a new family of squid (Cephalopoda; Oegopsida) from Antarctic Waters, *Antarctic Res. Ser. 11:* 85–202, 1967.