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 BATOTEUTHIDAE, A NEW FAMILY OF SQUID (CEPHALOPODA; OEGOPSIDA) FROM ANTARCTIC WATERS

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Abstract. The first new family of oegopsid cephalopods to be described in over 30 years, the Batoteuthidae, is recorded from Antarctic waters. A discussion of a number of the more important oegopsid familial characters is presented, and the Batoteuthidae is compared with other families of the suborder. The value of the buccal membrane connectives as a stable systematic character at the family level is established for the first time. The family is based on the new genus and species, Batoteuthis skolops. Observations are presented concerning the peculiar internal anatomy and the broad geographic distribution of the species.

INTRODUCTION

Since 1962 the USNS Eltanin, chartered by the National Science Foundation, has conducted a continuous series of oceanographic cruises in the southern Atlantic, Pacific, and Indian oceans as one part of the United States Antarctic Research Program. The USARP cephalopod collections are currently being studied at the Institute of Marine Science of the University of Miami under the direction of Dr. G. L. Voss in an effort to delineate the Antarctic cephalopod fauna and to determine its zoogeographic relationships. Of the numerous interesting and unusual cephalopods captured by the Eltanin, 4 specimens have been discovered that represent a new family of pelagic squids. The significance of this discovery is emphasized by the fact that a new family of oegopsid squids has not been described in over 30 years.

Family BATOTEUTHIDAE, new family

The characters of this monotypic family are combined with those of the genus.

Type-genus: Batoteuthis, new genus.

Genus Batoteuthis, new genus

Diagnosis

Funnel-mantle locking apparatus straight, simple. Buccal connectives attach dorsally to arm pairs I and II, ventrally to arm pairs III and IV. Gladius with long, slender rachis; true vane lacking. Conus extremely elongate; mid-ventral fusion apparent. Club 80% or more of tentacle length; 6 distinct longitudinal sucker rows; dactylus and carpus not present. Head extremely small. Fins short. Mantle long, slender, produced into long, pointed tail posteriorly. Viscera compact, located near anterior end of mantle cavity (except gonads).

Type-species: Batoteuthis skolops, new species.

Batoteuthis skolops, new species

External Characteristics

The Holotype. The mantle wall is very thin but muscular, similar to the mantle wall of most cranchiids. The mantle is sac-like and bulges in the middle, but it tapers to a point posteriorly; its muscular portion terminates just anterior to the posterior margin of the fins. The free mantle opening is very broad and is considerably wider than the head. The gladius is visible in the dorsal mid-line and extends posteriorly beyond the fins as the supporting element of the long, thin "tail", much of which is missing (Pl. I, Figs. A, B).

The fins are small and short; their length is about half their width. Taken together, the 2 fins are broadly oval in outline. Anterior lobes are not developed, and the posterior margins extend for a short distance along the narrow tail.

Because of the peculiar long, tapering tail-like posterior extensions of the mantle and fins, it is necessary to measure mantle and fin length exclusive of this "tail"; therefore the mantle and fin length are defined

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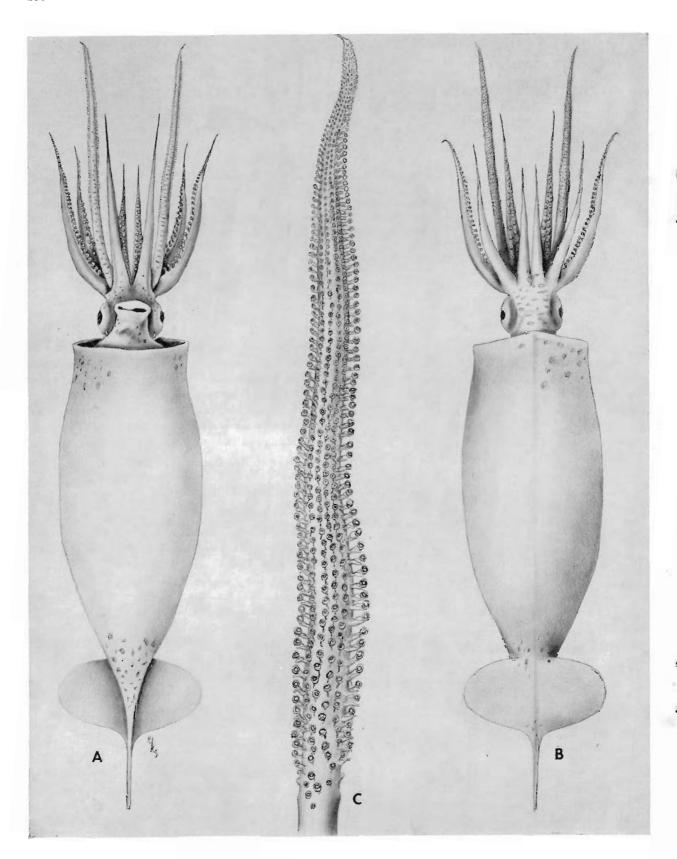


TABLE 1. List of Material of Batoteuthis skolops, New Species

Eltanin Sta. No.ª	Mantle Length, mm	Sex	Location	Apparent Depth of Capture, m	Date of Capture	Gear
1396 ^b	51	Female ?	49°57′S, 169°01′W	2525	26 XI 1964	3m IKMT
1314	30	?	59°11'S, 105°04'W	366	24 X 1964	3m IKMT
846	95	Female	57°52'S, 74°43'W	1866	10-11 XI 1963	3m IKMT
382	90	Female	55°23'S, 55°45'W	1257	23 XII 1962	3m IKMT

[&]quot;These represent the University of Southern California's station numbers assigned for Eltanin cruises.

b Holotype.

here as extending to the level of greatest inflection on the concave posterior border of the fins. It must be emphasized that the method of measurement differs from the usual method in which the tail, if present, is included in the mantle length. Whenever the term mantle length is used here with reference to the Batoteuthidae, it refers to the convenient definition stated above.

The funnel is huge and thin walled like the mantle; its exhalant opening is very broad. The funnel extends nearly to the base of the ventral arms (Pl. I, Fig. A). The dorsal member of the funnel organ is an inverted U-shaped structure that has an inverted V-shaped inner notch. A small papilla extends anteriorly from the apex. The ventral members are basically oval but exhibit some variation in shape (Pl. IV, Fig. G). The funnel valve is the typical semicircular flap.

The funnel component of the locking apparatus is nearly straight, deeply grooved, and slightly broader and deeper in the posterior end. The mantle component extends posteriorly from the free edge of the mantle as a nearly straight, narrow ridge which broadens posteriorly (Pl. IV, Fig. D).

The head is exceedingly small and is slightly shorter than broad. The eyes are proportionately large and occupy about $\frac{3}{4}$ of the lateral surface of the head. The eye opening is oval with a small anterior optic sinus. Small olfactory papillae are present just posterior to the eye on the ventrolateral surface of the head. Both nuchal crest and nuchal folds are absent.

Arms are long and slender; they taper distally to terminate in long, attenuate tips. The arm formula is 4.3.2.1. No evidence of swimming keels exists except on the ventral arms, where keels are weakly developed. Trabeculae and sucker stalks arise from a common

base (Pl. II, Fig. D). The protective membranes are variable but generally very low and weakly developed. However, the membranes appear to be more strongly developed on the right ventral arm of the type specimen, where they reach as high as the trabeculae.

Suckers are arranged in well separated, biserial rows and stand considerably above the oral surface of the arms on long stalks. The slender portion of the sucker stalk arises abruptly from a broad, conical base. At the tips of the arms the size and arrangement of the suckers cannot be determined because of damage to the specimen.

The largest suckers of the second and third arms are approximately ½ greater in diameter than the largest suckers of the first and fourth arms. The globular arm suckers possess broad apertures. The rings of the lateral arm suckers possess approximately 8–10 large, broadly spaced, sharply pointed, conical teeth, while the sucker rings of the dorsal and ventral arms possess 11–12 small, closely packed, sharp teeth (Pl. II, Figs. B, F, G, H, I).

Tentacles are relatively short (about 11/2 times longer than the arms) and robust. The extremely long clubs oecupy approximately 80% of the tentacle length; they are flattened but not appreciably expanded (Pl. I, Fig. C; Pl. II, Fig. E). Numerous pointed trabeculae are distributed along the entire lateral margins of the club. A trace of a protective membrane can be detected between the trabeculae, especially between the first few proximal trabeculae on the ventral margin of the club. The clubs have 6 well defined longitudinal rows of small, closely packed suckers that are situated on long slender stalks. The chitinous rings bear approximately 6 small, conical, widely spaced teeth (Pl. II, Fig. A). The bases of the stalks of the marginal sucker rows join with the bases of the trabeculae (Pl. II, Fig. C).

No dactyl or carpal areas are present on the club. The 2 median sucker rows and the lateral-most rows appear to originate in the same proximal region of the

Plate 1. Batoteuthis skolops, new species, holotype. Elt. 1396, 51-mm mantle length.

Fig. A. Ventral view.

Fig. B. Dorsal view.

Fig. C. Tentacular club, oral surface.

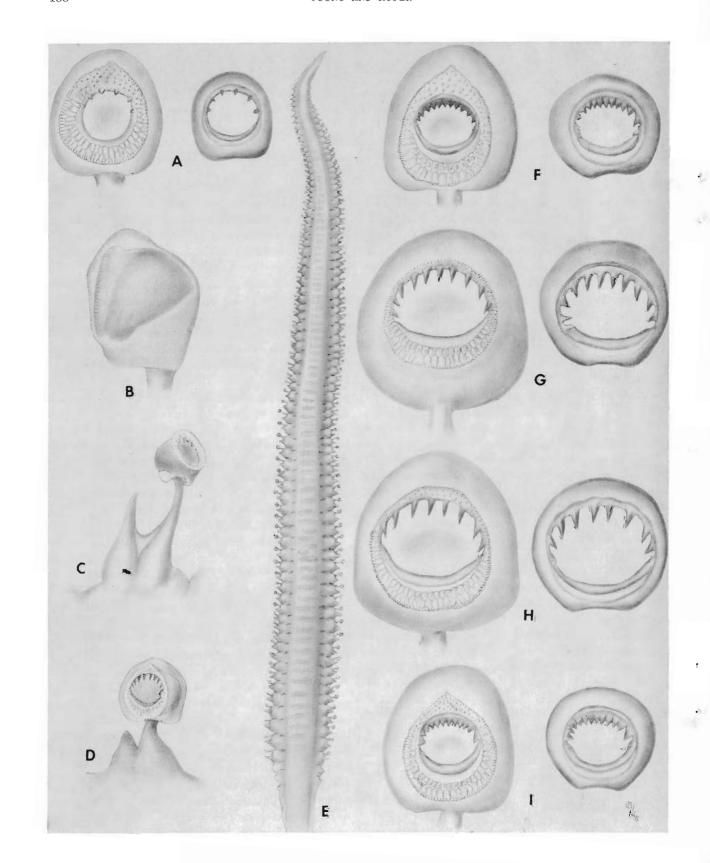


TABLE 2. Measurements and Indices" of Batoteuthis skolops, New Species

	Elt. 1396 Holotype Female?			Elt. 1314 Paratype ?			Elt. 846 Female		Elt. 382 Female		
	Measur ments mm		Indices	me	sure- nts,	Ind	ices	Measure- ments, min	Indices	Measure- ments, mm	Indices
Mantle Length	51			5	30			95		90	
Tail Length	10+	-c		2	25.5+	85	.0	42+		29+	
Mantle Width Opening	14		27.4		7	23	.1	13	13.7	15	16.7
Mantle Width Widest	19		37.2	1	.2	40	.0	20	21	18	20
Head Width	8.5	5	16.6		4.5	15	.0	Missing		Missing	
Fin Length	9		18.0		4	13	.3	20	21	18	20
Fin Width	18		35.2		7	23	.4	40	42.1	33	36.7
	R.	L.	R. L.	R.	L.	R.	L.				
Arms I ^d	14)	3+	27.9 25.5	4.5	3.5+	15.0	11.7	Missing		Missing	
11	18 1	17+	35.2 33.4	4+	4.5 +	13.3	15.0	,,		,,	
III	19.5 2	20	38.2 39.3	2 5.5-	+ 5.5	18.3	18.3	27		"	
IV	21.5 2	22.5	42.1 44.2	2 5.5-	+ 5.5	23.4	23.4	37		"	
Tentacle Length	30 3	30	58.9 58.9	21	22	70.0	73.4	"		"	
Club Length ^c	24 2	24.5	47.0 48.) 19	20	63.4	66.7	77		"	

^{*} Indices are expressed as % of mantle length.

b Mantle measured to a level with the points of greatest inflection on the concave posterior border of the fins (see text).

club, while the remaining 2 rows seem to converge proximally with the lateral-most rows.

The buccal membrane possesses 7 lappets and 8 connectives which are attached dorsally to arm pairs I and II and ventrally to arm pairs III and IV. The oral surface of the buccal membrane is nearly smooth, marked only by minute crenulations (Pl. IV, Fig. A).

The beaks are figured in Pl. IV, Fig. C. Their rostra are strong and darkly pigmented, while their lamellae are extremely fragile and transparent. A definite ridge is present on the insertion plate of the gular lamella of the lower mandible.

The radula is extremely small and the finer details are difficult to detect with certainty (Pl. IV, Fig. B). There are 7 teeth in a transverse row. The first and

second laterals are very small, while the third laterals are extremely elongate.

The gladius (taken from Elt. 846) is long and slender, with the anterior half consisting of only a narrow rhachis. A narrow vane arises at about the midpoint and very shortly folds ventrally with the edges fusing in the midline to form a long, hollow, tapering conus (Pl. III, Fig. B).

A few dark brown chromatophores are present on the posterior ventral surface of the mantle, around the head, along the tentacle, and particularly on the aboral surface of the club, where they are regularly spaced between the trabeculae.

Table 2 presents the measurements and indices of the specimens of *Batoteuthis skolops*.

Large Specimens. The shape of the mantle in the larger specimens (Elt. 846 and 382) differs greatly from that seen in the 2 younger specimens (Pl. III, Fig. A). The mantle is very elongate, slender and conical; the widest point is just posterior to the free mantle opening, which is slightly constricted. The mantle wall remains thin, though proportionately thicker than in the smaller specimens. The gladius is visible in the dorsal midline only in the anterior region and along the tail. The tail is extremely long (nearly half the mantle length) and slender, and, although the ex-

[°]A + mark indicates that a portion of the measured character is missing (c.g., arm tips) and that the complete specimen would have greater dimensions.

^d Arms measured from the dorsal notch between the bases of the arms, e.g., II is measured from the notch between II and I. ^e In Elt. 1314 this refers to the entire sucker-bearing portion of the tentacle (see text).

Plate II. Batoteuthis skolops, new species, holotype. Elt. 1396, 51-mm mantle length.

Fig. A. Tentacular sucker and chitinous ring.

Fig. B. Sucker from Arm II, side view.

Fig. C. Trabecula and sucker from tentacular club.

Fig. D. Trabecula and sucker from arm II.

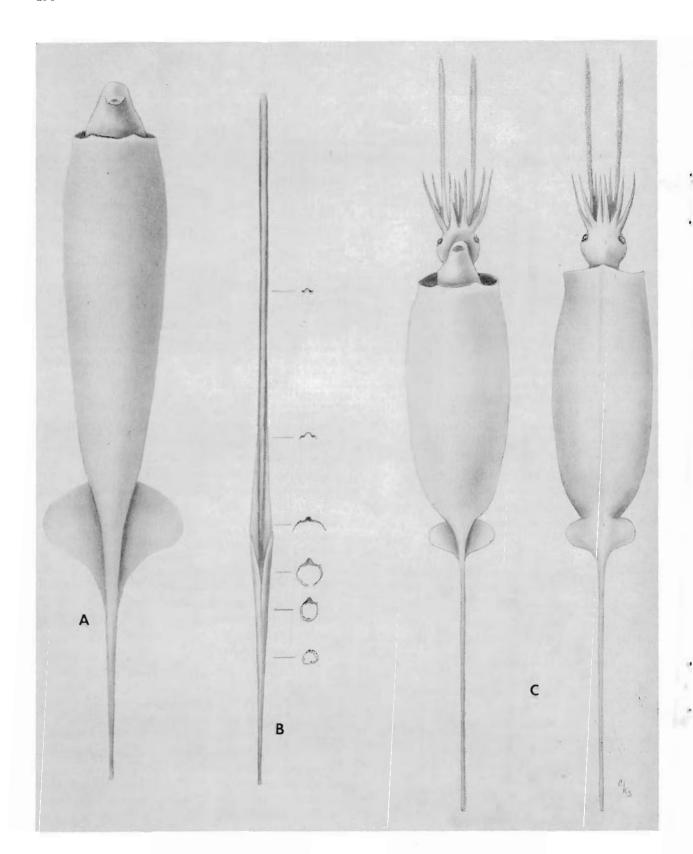
Fig. E. Tentacular club, aboral view.

Fig. F. Arm I sucker and chitinous ring.

Fig. G. Arm II sucker and chitinous ring.

Fig. H. Arm III sucker and chitinous ring.

Fig. I. Arm IV sucker and chitinous ring.



treme tip is missing, it undoubtedly tapers to a sharp point.

The fins are short and occupy about $\frac{1}{5}$ of the mantle length. Their posterior borders are concave and extend posteriorly to form part of the tapering tail.

The funnel is strongly developed. The locking apparatuses are similar to those of the smaller specimens. The dorsal member of the funnel organ is the same shape as in the holotype, but each ventral member has a skewed diamond shape with rounded corners (Pl. IV, Fig. H).

The head is missing from both large specimens.

The outer integument has been rubbed off from nearly the entire mantle. However, some shreds remain on the posterior mantle and under the fins to reveal numerous typical reddish-brown chromatophores.

Larval specimen. The mantle is sac-like, membranous, and transparent (Pl. III, Fig. C). The flaring mantle opening is considerably wider than the head. The gladius is clearly visible along the midline. The muscular portion of the mantle terminates shortly before the posterior border of the fins, but the gladius continues posteriorly, covered by the mantle integument, to form an extremely long, needle-like tail. The tail is nearly equal to the mantle in length. However, the tip of the pen is missing, and it is possible that the tail would be longer in uninjured specimens.

The fins are extremely small and occupy only 13% of the mantle length. They are nearly 13¼ times broader than long. The fin margins are broadly ovoid and exhibit no free lobes.

The thin-walled funnel is large and extends to the level of the anterior border of the eyes. The inverted U-shaped dorsal member of the funnel organ is broad and possesses a long, flattened papilla that extends anteriorly from the apex. The ventral pads are only slightly longer than broad and appear nearly square, although the corners are rounded; there is a slight anterior bulge.

The head is extremely small and rounded. The eyes are proportionately much smaller than in the type, and they appear to be directed slightly forward.

The arms are lacking in details and it is not possible to determine the extent of development of keels and protective membranes. The suckers are situated in 2 biserial rows. The arm tips are missing. The buccal mass, surrounded by an indistinct buccal membrane, protrudes slightly from the base of the oral crown.

The tentacles are proportionately longer than in the adult and are more robust than the arms. The proportion of tentacle length to mantle length is 75% in the larva and 59% in the adult. The sucker-bearing portion of the larval tentacle occupies about 90% of the tentacle length. However, only the distal 55% of this portion bears a club structure similar to that in the larger specimen. Proximal to the distal area there is a gradual decrease in the number of sucker rows. The larval clubs have more distinct protective membranes than do those of adults.

A few scattered chromatophores are distributed over the dorsal surface of the head.

Internal Anatomy

Although the specimens were not completely dissected, it has been possible to determine the general orientation and form of parts of the major organ systems (Pl. V, Figs. A-E; Pl. VI, Figs. A-D).

Kidney (Pl. V, Fig. B). Numerous venous appendages are present along the vena cavae, as these vessels lead from the cephalic vein to the branchial hearts. Appendages also occur along the initial part of each posterior mantle vein. Two additional kidney lobes arise near the junction of the cephalic vein and the vena cavae. These peculiar lobes extend anteriorly and lie parallel to and dorsal to the intestine. Both appear to be blind extensions of the kidney. Nephridial pores are located anterior to the branchial hearts. Typical nephridial papillae are lacking, and the pores open nearly flush with the surface of the body wall ventral to the kidneys.

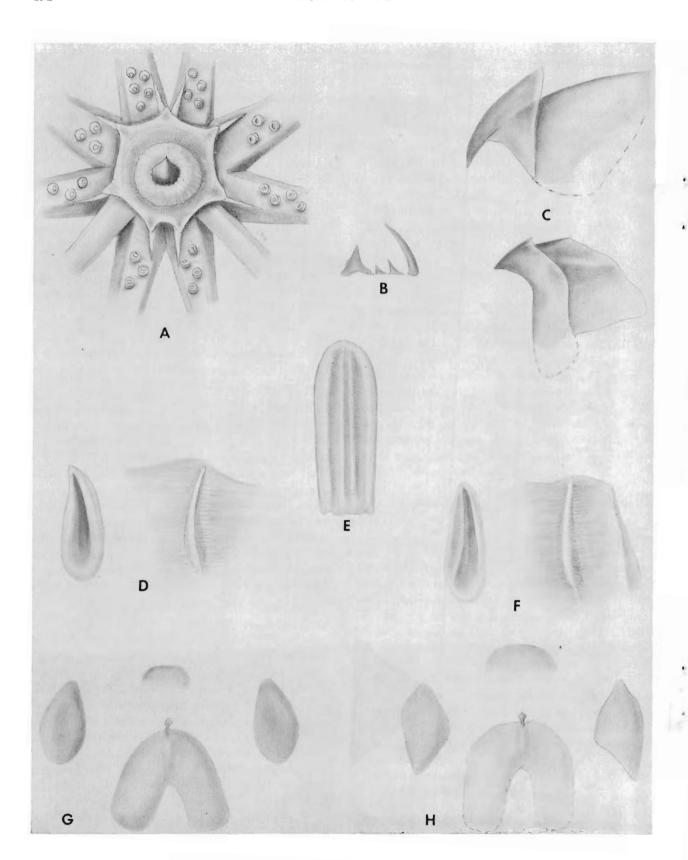
Branchial heart complex (Pl. V, Fig. B). The vena cavae, as they emerge from the kidney, enter the branchial hearts near their extreme anterior ends. Immediately lateral to these points the afferent branchial vessels arise from the branchial hearts and pass into the gills. A distinct swelling that appears to be a sphincter muscle surrounds each of these branchial vessels a short distance from the branchial heart. The branchial hearts are unusually elongate, oval structures with their long axes paralleling the body axis. The branchial hearts are in a peculiar position—they lie near the body midline, almost completely enclosed in the visceral-pericardial coelom, and are far removed from the posterior end of the gills. The accessory branchial

Plate III. Batoteuthis skolops, new species.

Fig. A. Ventral view of Elt. 846, 95-mm mantle length.

Fig. B. Gladius, ventral view and cross sections. Elt. 846.

Fig. C. Larva, Elt. 1314, 30-mm mantle length, ventral and dorsal views.



hearts are attached to the posterior tips of the branchial hearts.

Gills (Pl. V, Figs. A, C). Each gill is slender and possesses approximately 40 pairs of filaments in the larger specimens. The gills are long relative to the size of the viscera; however, they are very small in comparison to the size of the body. The branchial glands are well developed. A cross section through the gill reveals a very short, blunt inner demibranch supported by a slender stylet and a long, outer demibranch which is almost completely fused to the base of the gill. The branchial canal is large.

Female reproductive system (Pl. V, Figs. A, B; Pl. VI, Figs. B, C). The visceral-pericardial coelom forms an extremely long, slender sac that extends approximately from the base of the gills posteriorly into the tail. The immature ovary is a single organ situated far posteriorly in the visceral-pericardial coelon near the anterior edge of the fins. It is boomerang-shaped and is suspended from the dorsal wall of the coelom by a short mesentery.

An oviduct lies along each anterior lateral side of the visceral-pericardial coelom adjacent to the branchial hearts. Each oviduct is subdivided into 3 distinct sections. The posterior portion arises from the coelom by a small crenulate pore just dorsal to the nidamental glands. It extends forward to the middle area as a tightly coiled duct lined by closely packed lamellae that run parallel to the duct. The funnel-shaped middle portion consists of a central duct with an outer surface of thin lamellae. These lamellae are independent of those that run along the inner surface of the first section of the oviduct. The orifice of the middle portion opens into the third, anteriormost section, which is a bilobed, elongate, hood-like structure. The inner surface of each side of the hood bears separate rows of lamellae. The hood has a broad, slit-like orifice which opens into the mantle cavity just anterior to the afferent branchial vessel.

The nidamental glands are small, narrow, cigarshaped structures that lie near the midline ventral to the visceral-pericardial coelom and immediately posterior to the branchial hearts. These glands open into the mantle cavity via broad slit-like pores across their anterior ends.

Visceral blood vessels (Pl. V, Figs. A, B). The cephalic artery arises from the anterior end of the large heart and passes laterally around the side of the liver instead of passing directly dorsal to this organ, as is often the case in other teuthoids. The efferent branchial vessels enter the ventricle well posteriorly.

The posterior mantle artery arises from the posterior end of the ventricle and runs along the ventral surface of body wall just below the visceral-pericardial coelom. Near the level of the anterior border of the fins it sends a branch, the median mantle artery, into the ventral portion of the mantle. This very short branch runs along the anterior edge of a median membrane. This membrane is extremely narrow and barely visible. Further posteriorly the mantle artery forks to form the paired lateral mantle arteries.

The posterior mantle veins leave the kidney, pass dorsal to the nidamental glands, and run along the lateral edge of the visceral-pericardial coelom to the region of the fins, where they enter the mantle wall and the fins.

Digestive tract (Pl. V, Fig. D). The esophagus extends from the head along the dorsal surface of the liver and passes laterally around the liver near its posterior end. The esophagus enters the stomach near the midline ventral to the liver. Both stomach and caecum have been severely damaged during capture and it is not possible to give a meaningful description. The intestine leaves the stomach-caecum complex and passes almost directly forward to the anus, which lies at the base of the funnel. Anal flaps are present.

The ink sac lies embedded in the ventral surface of the liver and gives off a short duct that leads into the rectum.

The liver is very large in relation to the size of the other viscera, and its long axis coincides with the body axis.

The pancreas is composed of 2 compact and separate organs, each of which lies on the posterior ventral surface of the liver. The organs are well defined, sausage-shaped structures, and each bears a small lobe on its medial side from which the hepatic ducts probably arise, although they cannot be observed in the present material.

Plate IV. Batoteuthis skolops, new species.

Fig. A. Buccal crown showing buccal membrane connectives, holotype.

Fig. B. Rachidian and 3 lateral teeth of bradula, holotype.

Fig. C. Upper and lower mandibles.

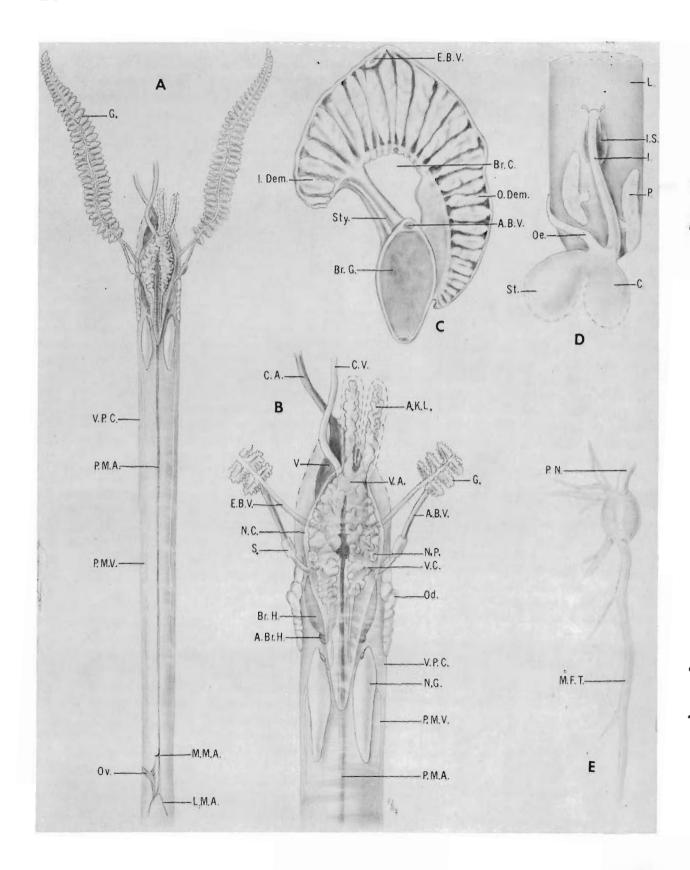
Fig. D. Locking apparatus, funnel and mantle components, holotype.

Fig. E. Nuchal cartilage, holotype.

Fig. F. Locking apparatus, funnel and mantle components, Elt.

Fig. G. Funnel organ and funnel valve, holotype.

Fig. H. Funnel organ and funnel valve, Elt. 846.



Mantle and fin nerves (Pl. V, Fig. E). The pallial nerve enters the stellate ganglion without giving off a distinct fin nerve, although in some specimens a few fibers may pass over the surface of the ganglion to rejoin the large nerve trunk that emerges from the posterior end of the ganglion. In the specimens where they exist, these superficial fibers probably represent at least a portion of the fin nerve fibers; the remaining fin nerve fibers pass through the ganglion. A few large nerves emerge laterally from the ganglion and pass into the anterior portion of the mantle. A large nerve trunk that incorporates both posterior mantle and fin nerve fibers arises from the posterior end of the ganglion. The trunk extends to the fins and during its passage gives off nerves to the middle and posterior portions of the mantle.

Many of the features discussed in the foregoing sections exhibit peculiarities in their structure and position. However, until all the families of the Oegopsida are better understood anatomically, it is impossible to evaluate the systemic significance of these features.

Growth

Position of viscera (Pl. V, Fig. A; Pl. VI, Fig. A, D). One of the most remarkable features of Batoteuthis skolops is the position of the viscera in the far anterior region of the mantle cavity, with the exception of the gonad, which is near the posterior end of the mantle.

The relative location of different internal organs undergoes drastic change during ontogeny. However, the gills seem to maintain a constant position within

Plate V. Batoteuthis skolops, new species.

Abbreviations for anatomical terms:

A.B.V., afferent branchial vessel; A.Br.H., accessory branchial heart; A.K.L., anterior kidney lobes; Br.C., branchial canal; Br.G., branchial gland; Br.H., branchial heart; C., caecum; C.A., cephalic artery; C.V., cephalic vein; E.B.V., efferent branchial vessel; G., gill; I., intestine; I.Dem., inner demibranch; I.S., ink sac; L., liver; L.M.A., lateral mantle artery; M.F.T., mantle-fin nerve trunk; M.M.A., median mantle artery; N.C., nephridial coelom; N.G., nidamental gland; N.P., nephridial pore; O. Dem., outer demibranch; Od., oviduct; Oe., oesophagus; Ov., ovary; P., pancreas; P.M.A., posterior mantle artery; P.M.V., posterior mantle vein; P.N., pallial nerve; S., sphincter; St., stomach; Sty., stylet; V., ventricle; V.A., venous appendages; V.C., vena cava; V.P.C., visceral-pericardial coelom.

the mantle cavity. In the youngest specimen available (Elt. 1314, 30-mm mantle length) the visceral organs are exceedingly small and are concentrated in a small area dorsal to the posterior base of the funnel and well anterior to the bases of the gills (Pl. VI, Fig. D). The liver is small and oval. The stomach and ceacum lie in the midline anterior to the branchial hearts.

In holotype (*Eltanin* 1396, 51-mm mantle length) the liver is greatly enlarged and the rest of the organs have been displaced posteriorly during growth (Pl. VI, Fig. A), bringing the stomach-caecum near the bases of the gills and posterior to the branchial hearts, which have remained in approximately the same position as in the smaller specimen.

The branchial hearts of the larger specimen (Elt. 382, 90-mm mantle length) have migrated well posterior to the bases of the gills (Pl. V, Fig. A). Although the stomach and caecum are missing, it is probable that they too would occur somewhat posterior to their former position.

Tentacular clubs. The club of the holotype occupies 80% of the tentacle length. In the smaller specimen, however, the fully developed portion of the club occupies about 55% of the tentacle length, but the suckerbearing portion continues proximally along the stalk (36% of the tentacle length), where the suckers occur in progressively fewer rows and become more scattered. Apparently this segment of the tentacular stalk serves as the zone of proliferation of club suckers.

Etymology

The generic name is derived from the Greek "batos" meaning thorn-bush. The one term combines two distinctive features of the genus: the long thornlike tail and the large bushy clubs. The Greek word "skolops" concerns anything pointed, again referring to the long pointed tail of the species.

Types

The type specimen is deposited in the United States National Museum. Holotype, USNM 576029.

Type Locality

South Pacific Ocean approximately 1000 km southeast of Wellington, New Zealand, at 49°57′S, 169°01′W in the region of the Antarctic Convergence. *Eltanin* Sta. 1396.

Distribution

This species has been captured in the South Atlantic and South Pacific oceans between approximately 49° and 60°S and between 55° and 170°W.

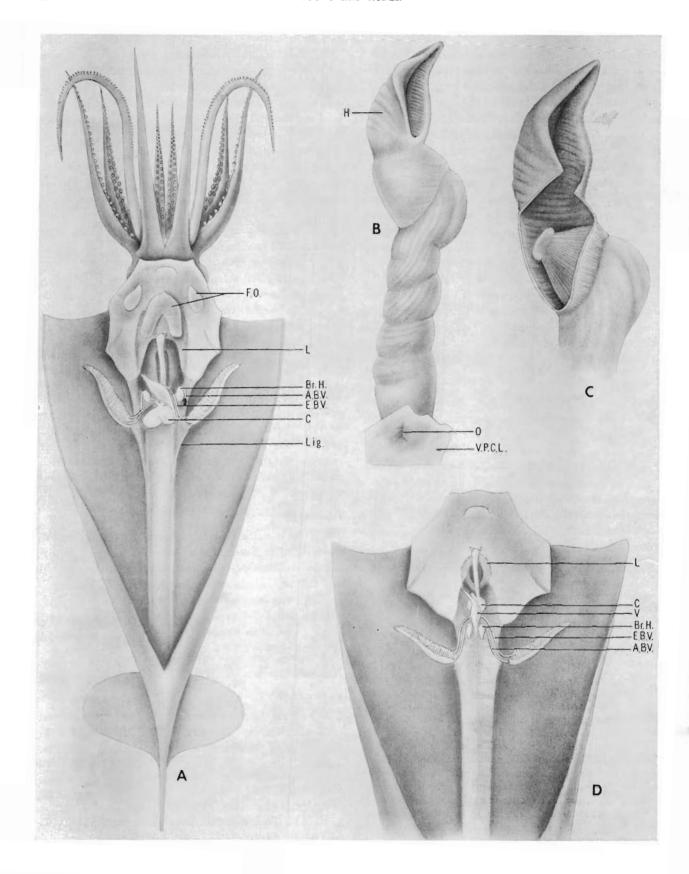
Fig. A. Ventral view of viscera, Elt. 382, 90-mm mantle length.

Fig. B. Detailed view of viscera, Elt. 382.

Fig. C. Cross-section of gill, Elt. 382.

Fig. D. Digestive organs, holotype.

Fig. E. Stellate ganglion, Elt. 382.



The vertical distribution is difficult to ascertain with certainty because of the use of open nets. The specimens were taken in 3-m Isaacs-Kidd Midwater Trawls, which fished at depths of 366, 1257, 1866, and 2525 meters.

DISCUSSION

An adequate comparative evaluation of the familial characters in the Oegopsida has never been undertaken. While we have not gone into an exhaustive study of the characters, we feel that it is necessary to give at least a general summary of the more important features of oegopsid families so that the establishment of a new family will be soundly based.

In the following section the families are placed in convenient character groupings in order to simplify the discussion. We do not necessarily imply close relationships between the families included in the various groupings.

Locking Apparatus

The funnel-mantle locking apparatus has long been recognized as one of the most stable familial characters used in classification in the Oegopsida [Pfeffer, 1900, 1912; Hoyle, 1904; Voss, 1956, 1963]. In several families it is the primary character upon which the family is established (e.g., Ommastrephidae, Thysanoteuthidae). The oegopsid locking apparatus falls into three major categories: funnel and mantle components separate and simple; funnel and mantle components separate and complex; funnel and mantle components completely fused.

In the first type, each cartilaginous funnel component is indented by a straight median sulcus. This furrow corresponds to a straight cartilaginous ridge on the opposing inner surface of the mantle. The majority of the oegopsid families exhibit this simple type of locking apparatus. Enoploteuthidae, Onychoteuthidae, and Architeuthidae are typical examples. A certain

amount of variability exists; for example, in the Histioteuthidae and Octopoteuthidae there is a tendency toward a broadening and shortening of the grooves.

The more complex locking mechanism is found in only a few families. In the Ommastrephidae the apparatus forms a strong, inverted T-shaped lock. The T-lock is homogeneous throughout this large family, varying only slightly in Symplectoteuthis, in which there is a slight fusion of the funnel and mantle components. The Thysanoteuthidae possess an oddly formed apparatus that is roughly T-shaped, but the long, narrow cross-bar lies parallel with the body axis, and the short, deep leg of the T lies transverse to the body axis. The Chiroteuthidae and Mastigoteuthidae possess ovoid locking structures that usually bear 1 or 2 inwardly-directed protuberances which give an earshaped appearance to the funnel component of the apparatus. In Mastigoteuthis magna Joubin, atypical protuberances impinge from opposite sides, producing a straight groove anteriorly and a very deep, bowl-shaped depression posteriorly. We have examined a number of specimens of M. magna and these clearly have a distinct flask-shaped locking apparatus and not a straight groove as suggested by Clarke and Maul [1962]. Also, in contrast to Clarke and Maul, we can find no valid reasons for supposing that the larval chiroteuthid, "Doratopsis" sagitta Chun, 1908, diverges significantly from the pattern of other chiroteuthids. The Joubiniteuthidae apparatus is oval, lacks protuberances, but has an extremely deep, posteriorly-directed concavity [see Young and Roper, 1967a]. In the Promachoteuthidae the funnel-locking cartilage is ovoid and bowl-shaped.

The locking apparatus is most highly modified in the Grimalditeuthidae and Cranchiidae. The funnel and mantle components in these families are completely fused, and in some genera (e.g. *Helicocranchia*) all trace of the cartilage has disappeared. It is interesting to note that in the Cranchiidae the mantle is fused to the head even in the nuchal region.

The complex and the fused types of locking apparatus are highly distinctive and in all cases clearly separate the families that possess them from those with the more simplified type.

The Batoteuthidae have a straight locking apparatus that tends to be slightly divergent from the typical form by having the sulcus gently flaring at its posterior end. The locking apparatus, nevertheless, clearly belongs to the simple type exhibited by the majority of oegopsid families. This highly significant feature, by itself, is sufficient to preclude placement of the genus

Abbreviations for anatomical terms:

A.B.V., afferent branchial vessel; Br.H., branchial heart; C., caecum; E.B.V., efferent branchial vessel; F.O., funnel organ; H., hood of oviduct; L., liver; Lig., ligament; O., orifice of the oviduct; V.A., venous appendages; V.P.C.L., visceral-pericardial coelom lining.

Plate VI. Baioteuthis skolops, new species.

Fig. A. Position of viscera in holotype.

Fig. B. Oviduct, Elt. 382.

Fig. C. Cut-away view of anterior end of oviduct showing middle section, Elt. 382.

Fig. D. Position of viscera in larva, Elt. 1314.

in the families Ommastrephidac, Thysanoteuthidae, Chiroteuthidae, Mastigoteuthidae, Promachoteuthidae, Joubiniteuthidae, Grimalditeuthidae, and Cranchiidae.

Tentacular Club

The tentacular club in oegopsids is another of the more stable characters used in classification at the familial level. An understanding of club structure and variation throughout the suborder is essential to the establishment of a coherent classification. Not only is the club of primary importance in defining families, but it is often diagnostic at the generic and specific levels as well. A number of widely diverse types of clubs exists within the Oegopsida; however, many of them are merely modifications of a common basic type.

The "typical" club occupies a relatively small proportion of the tentacle, is at least somewhat expanded and flattened, and is easily divisible into 3 distinct areas: the carpus, the manus, and the dactylus. The expanded manus possesses marginal trabeculate membranes and 4 rows of suckers that extend distally onto the narrow dactylus, where the suckers become greatly reduced in size. Each club usually exhibits a more or less distinct pattern of small suckers and knobs, which, when held together, form a locking device, the carpal structure. The Lycoteuthidae, Ommastrephidae (except Illex), Thysanoteuthidae, Lepidoteuthidae (except Lepidoteuthis, which lacks tentacles), and Cycloteuthidae are examples of groups which possess the basic club type. However, all of these groups are distinctive in the more detailed structure of the club. The Cranchiidae also possess the basic type of club, but some genera have secondarily developed extreme modifications (e.g., large hooks in Galiteuthis and Taonius, and tentacles lacking in some species of Leachia and Ascocranchia).

The type of club found in the Enoploteuthidae and Onychoteuthidae is very similar to the more typical club but differs by having the suckers of 1 or both median rows on the manus developed into hooks. In some genera (Onychoteuthis, Moroteuthis) there is also a tendency toward the loss of the lateral sucker rows on the manus. A distinct carpal cluster is generally present. Chaunoteuthis, an onychoteuthid, lacks tentacles.

The tentacular clubs of the Histioteuthidae, Psychroteuthidae, and Gonatidae are also similar to the basic type, but they possess additional rows of suckers on the manus. The gonatids often show a further increase in sucker rows on the dactylus. A few club suckers in some species of *Gonatus*, moreover, develop into large

hooks in the central portion of the manus. Tentacles are completely lacking in Gonatopsis.

The Architeuthidae and Alluroteuthidae have nearly typical clubs, but a small cluster of irregularly arranged small suckers is present at the proximal end of each manus.

The Chiroteuthidae possess a nearly typical club in the larval stages. With growth, however, additional suckers on long pedicels are added along the carpal region and on a portion of the tentacular stalk [Roper and Young, 1967a]. The adult club is therefore very long and narrow.

A number of families exist in which the tentacular clubs show no apparent similarity to the typical type discussed above. These families are the Brachioteuthidae, Bathyteuthidae, Ctenopterygidae, Promachoteuthidae, Mastigoteuthidae, Joubiniteuthidae, Octopoteuthidae, and Grimalditeuthidae.

The Brachioteuthidae possess expanded clubs that bear 3 to 4 rows of suckers on the distal portion. The proximal portion (perhaps corresponding to manal and carpal areas) bears many rows of suckers that extend down the tentacular stalk. Within the family there is considerable variation of this general arrangement.

The Bathyteuthidae and Ctenopterygidae exhibit an uncommon type of club that has no differentiation into carpus, manus, or dactylus. It is very short and bears many irregular rows of closely packed, minute suckers.

The Mastigoteuthidae, Promachoteuthidae, and Joubiniteuthidae possess very characteristic clubs. In these families the club is very long and narrow and may occupy as much as 70% of the tentacle length. The suckers are minute and are arranged in numerous rows. Further, there is no differentiation into carpus, manus, and dactylus.

A severe modification of the club occurs in the Octopoteuthidae and Grimalditeuthidae. These families lack proper tentacles entirely. The larvae of all octopodoteuthids have small tentacular filaments, but these are usually lost in adulthood. However, a remnant of the tentacles remains in the adult *Taningia*; the minute "club" bears only a very few suckers. *Grimalditeuthis*, the sole representative of the Grimalditeuthidae, completely lacks tentacles.

From this general survey of club types in the Oegopsida, it can be seen that the club of the Batoteuthidae shows almost no similarity to any of these forms. It possesses a unique feature among the Oegopsida: 6 discrete rows of suckers that extend the full length of the elongate, slightly expanded club. In addition there

is no differentiation into the carpal and dactyl areas. The club occupies over 80% of the tentacle length. This very high proportion of club to tentacle length is approached only in the families Mastigoteuthidae and Promachoteuthidae.

These features of the tentacular club provide the new family with one of its most distinctive characteristics.

Buccal Membrane Connectives

The importance of the connectives between the buccal membrane and the arms was suggested by *Chun* [1910] as a possible familial character. However, this character has never been thoroughly evaluated. For that reason, we have made a general survey of all the oegopsid families and the majority of genera in order to determine the stability of this character within families. The results of this study are presented in Table 3. We have been able to examine specimens of most of the species mentioned. In addition, we have consulted *Chun* [1910], *Pjeffer* [1912], *Sasaki* [1929], *Kjennerud* [1958], and *Adam* [1960].

Table 3 reveals some very surprising facts. Every oegopsid family shows complete uniformity in the position of the buccal connectives. Furthermore, families that have been shown to be closely related by similarities of other characters, also agree in the arrangement of their buccal membrane connectives (e.g., Lycoteuthidae and Enoploteuthidae; Mastigoteuthidae, Promachoteuthidae [Roper and Young, 1967b], and Chiroteuthidae).

It is apparent from this analysis that the position of the buccal membrane connectives provides one of the most stable and conservative familial characters within the Oegopsida.

Arm Suckers and Hooks

Most families of Oegopsida contain species which bear 2 rows of suckers on the oral surface of each arm. Five families, however, differ drastically from this pattern. Two of these families, the Octopoteuthidae and the Enoploteuthidae, have suckers replaced by hooks on the arms. In the majority of species these hooks occupy almost the entire length of the arms, but 2–4 rows of minute suckers remain at the arm tips. In the third family, the Gonatidae, most members have 2 median rows of hooks and 2 lateral rows of suckers on the dorsal and 3 pairs of arms that give way to 4 or more rows of suckers at the arm tips. The ventral arms always bear at least 4 rows of suckers. This arrangement in the Gonatidae varies somewhat in one species, Gonatus anonychus, in which hooks are lack-

ing in the males and are present only at the bases of the arms in the females; the arms bear primarily 4 rows of suckers. In the Bathyteuthidae suckers are arranged in 2 rows at the bases of the arms, but they become irregular in *Bathyteuthis*, with a tendency toward the formation of 4 rows. *Ctenopteryx*, the only genus of the family Ctenopterygidae, has as many as 6 rows of suckers on the distal half of the arms. Finally, the Joubiniteuthidae possess 5–6 sucker rows on the dorsal and 3 pairs of arms and 4 rows on the fourth arms.

Therefore, in a few families the arrangement of hooks and suckers on the arms is highly diagnostic. Within the other families the arrangement of 2 rows of suckers is a constant feature.

The Batoteuthidae bear 2 rows of suckers on each arm and therefore are clearly aligned in this regard with the majority of oegopsid families and are separated distinctly from the Octopoteuthidae, Enoploteuthidae, Gonatidae, Joubiniteuthidae, and to a lesser extent, Bathyteuthidae.

Gladius

One would expect the gladius in oegopsids to be a very stable and useful character in the higher taxa. While this is true within some families, it is by no means a general rule.

There has never been a comprehensive analysis of the gladius within the families of Oegopsida; therefore, it is difficult to determine which features of the pen are the most useful in helping to define families. In fact, for many species the gladius has never been described. We are nevertheless able to find apparent similarities between the pens of the Batoteuthidae and those of the following diverse groups: Chiroteuthidae, Mastigoteuthidae, Grimalditeuthidae, Joubiniteuthidae, some Cranchiidae, Lepidoteuthidae, Cycloteuthis, and Brachioteuthidae. The primary feature shared by these groups is a long (usually) conus formed by the infolding and fusion of the lateral edges of the vane. Also, these groups generally possess a long, slender rachis with a reduced or absent free vane. However, these features show considerable variation.

As indicated above it is difficult to evaluate these similarities on the basis of existing knowledge of pen structure.

General Appearance

The general appearance of squid (i.e. fin size and shape, arm formula, body shape, head shape, etc.) is

TABLE 3. Position of Buccal Membrane Connectives in the Families of the Oegopsida

Family	$DDVV^n$	$DDVD^a$	Family	$DDVV^{a}$	DDVD
Batoteuthidae Batoteuthis skolops Young and Roper (monotypic)	X		Alluroteuthidae Alluroteuthis antarcticus Odhner (monotypic)		х
Lycoteuthidae Lycoteuthis diadema (Chun) Selenoteuthis scintillans Voss		X X	Bathyteuthidae ^t Bathyteuthis abyssicola Hoyle Bathyteuthis sp.		X X
Enoplotenthidae Abralia veranyi (Ruppell) Abraliopsis hoylei (Pfelfer) Enoplotenthis anapsis Roper Enoplotenthis leptura (Leach) Enoplotenthis dubia Adam ^b Thelidiotenthis alessandrinii (Verany) Ancistrochirus lesuenri		X X X X	Ctenopterygidae ^t Ctenopteryx sicula (Verany) Brachioteuthidae Brachioteuthis picta Chun Brachioteuthis riisei (Steenstrup) Ommastrephidae	X X X	
(Ferrusac and Orbigny) Pyroteuthis margaritifera (Ruppell) Pterygioteuthis gemmata Chun Octopoteuthidae ^c Taningia danae Joubin Octopoteuthis sicula Ruppell Octopoteuthopsis megaptera (Verrill)	X X X	X X X	Illex illecebrosus (Lesueur) Todaropsis eblanae (Ball) Todarodes pacificus (Steenstrup) Ommastrephes bartrami (Lesueur) Ommastrephes pteropus Steenstrup Symplectoteuthis luminosa Sasaki Symplectoteuthis oualaniensis Lesson Dosidicus gigas (Orbigny)		X X X X X X X
Onychoteuthidae Moroteuthis ingens (Smith) Chaunoteuthis mollis Appellof Onychoteuthis banksi (Leach) Onykia appellofi (Pfeffer) Onykia verrilli (Pfeffer)	X X X X		Ornithoteuthis antillarum Adam Ornithoteuthis volatilis (Sasaki) Hyaloteuthis pelagicus (Bosc) Thysanoteuthidae Thysanoteuthis rhombus Troschel	X	X X X
Ancistroteuthis lichtensteini (Ferrusac and Orbigny) Gonatidae Gonatus fabricii (Lichtenstein)	X X X		Chiroteuthidae Chiroteuthis veranyi (Ferussac) Chiroteuthis imperator Chun Chiroteuthis sp.	X X X	
Gonatus berryi Naef Gonatus anonychus Pearcy and Voss Gonatopsis sp. Architeuthidae	X X		Valbyteuthis danae Joubing Mastigoteuthidae Mastigoteuthis dentata Hoyle	X X	
Architeuthis sp. Architeuthis japonica Pfeffer Histioteuthidae ^d		X X	Mastigoteuthis flammea Chun Mastigoteuthis cordiformis Chun Mastigoteuthis hjorti Chun	X X X	
Calliteuthis menghinii (Verany) Calliteuthis reversa (Verrill) Calliteuthis dofteini Pfeffer		X X X	Echinoteuthis danae Joubin Mastigoteuthis latipinna (Sasaki) Promachoteuthidae ^h	X X	
Calliteuthis heteropsis (Berry) Calliteuthis corona (Voss and Voss) Calliteuthis meleagroteuthis (Chun)		X X X	Promachoteuthis sp. Grimalditeuthidae Grimalditeuthis bonplandi Verany	X	
Psychroteuthidae* Psychroteuthis glacialis Thiele		X	(monotypic)	X	

[&]quot;The initials refer to the location of the attachment points on the dorsal or ventral surfaces of Arms I-IV consecutively.

^bThe order of attachment in this species is DDDD [see *Adam*, 1960].

^c The connectives are usually obscure except in the finest preserved specimens. Peculiarly, Octopoteuthis sicula and Octopoteuthopsis megaptera possess both dorsal and ventral connectives to each of the arms. However, the ventral attachments on Arms III and 1V appear to be the true connectives.

^d G. L. Voss [1963] believed that all species of this family belong to Calliteuthis with the exception of one, Histioteuthis bonelli Ferussac. However, he stated (p. 127), "... future study may show that all should be united under the genus Histioteuthis..." The Histioteuthidae are currently being revised by N. A. Voss.

A number of specimens of Psychroteuthis are in our collections. These verify the validity of the family, which has been suspect because of the fragmentary condition of Thiele's specimens. We are redescribing the family and delineating the growth stages.

t Ctenopteryx and Bathyteuthis usually have been placed in separate subfamilies of the Bathyteuthidae, but recent work has shown that familial distinction is justified. One of us (CFER) is currently revising these groups.

^{*} See Roper and Young [1967a] for a discussion of the systematic position of the genus Valbyteuthis.

^h The Promachoteuthidae have been shown to be oegopsid and not myopsid squids [Roper and Young, 1967b].

TABLE 3. Position of Buccal Membrane Connectives in the Families of the Oegopsida. (Continued)

Family	DDVV ^a	DDVD
Cranchiidae		
Cranchia scabra Leach	X	
Helicocranchia pfefferi Massy	X	
Liocranchia valdiviae Chun	X	
Megalocranchia pellucida (Chun)	X	
Galiteuthis armata Joubin	X	
Galiteuthis phyllura Berry	X	
Drechselia danae Joubin	X	
Pyrgopsis sp.	X	
Crystalloteuthis glacialis Chun	X	
Bathothauma lyromma Chun	X	
Taonius pavo (Lesueur)	X	
Egea inermis Joubin	X	
Joubiniteuthidae ⁱ Joubiniteuthis portieri Joubin (monotypic)	X	
Lepidoteuthidae ^j		
Pholidoteuthis adami Voss	X	
Lepidoteuthis grimaldii Joubin	X	
Tetronychoteuthis dussumieri (Orbigny)		
Tetronychoteuthis massyae Pfeffer	X	
Cycloteuthidaek		
Cycloteuthis sirventi Joubin	X	
Undescribed genus, species A	X	
Undescribed genus, species B	X	

¹The connectives are difficult to find, but they are nevertheless clearly ventral on Arms III and IV.

The scaled-squid complex represents a natural familial

grouping.

of considerable importance in determining familial status, but it is extremely difficult to evaluate.

Most families exhibit a characteristic general appearance; however, there exists so much variation within families that any attempt to discuss these features in detail would be too cumbersome to include in the present work. Here it is sufficient to emphasize that the Batoteuthidae have a very peculiar appearance. The short, broad outline of their muscular fins is unlike that found in other oegopsid families. The very small size of the head relative to the body size is also distinctive. The closest similarities in head size perhaps are found among some of the Cranchiidae, which, however, possess a quite distinctive head in other respects.

The Batoteuthidae possess an extremely long tail supported throughout its entire length by the gladius. Only a few families of oegopsids have representatives with long tails similar to this type (i.e., gladius present throughout the length of the tail). The tail of the

larval specimen of Batoteuthis is proportionally much longer than in the larger specimen (about $\frac{5}{6}$ of the mantle length compared with about $\frac{1}{2}$ of the mantle length). This peculiar larval condition recalls a similar structure in the larvae of chiroteuthids and mastigoteuthids, and in all stages of the joubiniteuthids. However, in the adults of chiroteuthids and mastigoteuthids the tail becomes proportionately shorter than in the adult of Batoteuthidae. The extreme length of the adult tail in Batoteuthis is exceeded only in the Joubiniteuthidae and the Grimalditeuthidae. The Grimalditeuthidae, however, possess an entirely different type of tail that even supports an additional pair of fins.

Thus, the striking general appearance of the Batoteuthidae is, in itself, a very distinctive feature of this group.

The preceding discussion clearly establishes the Batoteuthidae as a distinct family. However, it is more difficult to establish the phylogenetic position of the family within the Oegopsida. Table 4 summarizes the correlation of certain basic characters of the Batoteuthidae with those of the other oegopsid families.

TABLE 4. Summary of Selected Familial Characters of the Oegopsida^a

	Straight Locking Apparatus	Buccal Mem- brane Connec- tive DDVV	Vane Modified into Conus	Long Tail
Batoteuthidae	X	X	X	X
Lycoteuthidae	X			
Enoploteuthidae	X			
Octopoteuthidae	X	X		
Onychoteuthidae	X	X		
Gonatidae	X	X		
Architeuthidae	X			
Histioteuthidae	X			
Psychroteuthidae	X			
Affuroteuthidae	X			
Bathyteuthidae	X			
Ctenopterygidae	X	X		
Ommastrephidae				
Thysanoteuthidae		X		
Brachioteuthidae	X	X	X	
Lepidoteuthidae	X	X	X	
Cycloteuthidae		X	Хь	
Chiroteuthidae		X	X	X
Mastigoteuthidae		X	X	X
Promachoteuthidae	е	X		
Joubiniteuthidae		X	X	X
Grimalditeuthidae		X	X	X
Cranchiidae		X	Хь	

^a A more comprehensive list of familial characters is given in Roper, et al. [1967].

b Character present in only part of the family.

^{*} Cycloteuthis sirventi Joubin, 1919, was previously considered an onychoteuthid [Thiele, 1935], but our examination of several well preserved specimens reveals that it cannot be a member of this family. The undescribed genus, with 2 species, shares familial characteristics with Cycloteuthis [see Young and Royer, 1967b].

The characters listed in Table 4 reveal some possible familial relationships. The distribution of straight locking apparatus, however, requires some explanation.

The straight locking apparatus is presumably the primitive type within the oegopsida. The more complex types have been derived along several different lines; therefore it is possible in an evolutionary series for a family possessing a straight locking apparatus to be more closely related to a family possessing a complex apparatus than to a family with a straight apparatus. This is apparently the situation with the Batoteuthidae.

Table 4 indicates a possible evolutionary branch within the Oegopsida, with the Brachioteuthidae located near the base and leading eventually to Mastigoteuthidae and Chiroteuthidae. Promachoteuthidae, Joubiniteuthidae, and possibly Grimalditeuthidae also probably occur near the end of this evolutionary pathway. We suggest that the Batoteuthidae lie on this line somewhere between the Brachioteuthidae and the terminal complex.

SUMMARY

- A new family of oegopsid cephalopods from Antarctic waters, the Batoteuthidae, is described and illustrated.
- 2. Familial characters within the Oegopsida are reviewed and compared with the new family.
- 3. Analysis of the position of the buccal membrane connectives throughout the Oegopsida reveals that this is an extremely stable family character.
- 4. The Batoteuthidae family is thought to be on an evolutionary branch that has the Brachioteuthidae near the base and the Mastigoteuthidae near the extreme end.

Acknowledgments. The co-authors express their gratitude to the National Science Foundation for its continued support and encouragement of the studies on Antarctic Cephalopoda (NSF Grant Numbers GA-103 and GA-253); the work could not have been accomplished without this aid. The University of Southern California has been largely responsible for the macro-biological sampling program aboard the Eltanin. In addition, personnel from the Institute of Marine Science and the Smithsonian Oceanographic Sorting Center have participated in the work. We wish to acknowledge the representatives of these institutions for their careful handling and sorting of the cephalopod material.

We wish to thank Dr. G. L. Voss for his assistance with the

manuscript. His continuous interest and support of our studies is much appreciated.

The value of a descriptive paper such as this depends greatly upon adequate illustrations. We wish to acknowledge very gratefully the contribution of Miss Constance Stolen, who has so skillfully and accurately produced the illustrations.

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