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DEEP-WATER OCTOPODS (MOLLUSCA; CEPHALOPODA) OF
THE NORTHEASTERN PACIFIC

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ABSTRACT: Descriptions and illustrations are given of nine species of Octopoda from depths of 1,000 m to 4,000 m off the coast of Oregon. Eight are new: *Grimpoteuthis bathynectes*, *G. tuftsi*, *Benthoctopus robustus*, *B. canthylus*, *B. oregonensis*, *B. yaquinae*, *B. macrophallus*, and *Graneledone pacifica*. Four genera are treated: *Cirroteuthis* and *Grimpoteuthis* of the Cirrata and *Benthoctopus* and *Graneledone* of the Incirrata. *Cirroteuthis muelleri* is first recorded from the Pacific Ocean and is redescribed. The genus *Benthoctopus* in the North Pacific is discussed and a provisional key for the nine recognized species is provided. The variability and form of the radula of *Graneledone* are considered to be due to degeneracy and not primitiveness, and to lack of selective feeding pressure.

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INTRODUCTION

The deep-water octopod fauna of the north-eastern Pacific below 2,000 m is poorly known. Little research on the systematics of deep-sea octopods has been completed since Robson's (1932) monograph, with the exception of Voss's (1976) partial revision of *Graneledone*. Two recent papers, however, provide important reviews of the evolution, phylogeny, and biogeography of deep-sea octopods and relevant background for this paper (see Voss 1988a, b).

The present paper is based on a unique collection of about 90 specimens of deep-water octopods, all from the continental slope and two abyssal plains off the Oregon coast. The specimens were collected by the ships CAYUSE, ACONA and YAQUINA of Oregon State University (OSU) in depths from 1,000 to nearly 4,000 m, with most of the material from depths in excess of 2,500 m. Most of the specimens belong to new species in the genera *Grimpoteuthis* and *Benthoctopus*, with the largest series of specimens in the genus *Graneledone*. All three of these poorly known genera consist of a large number of species, most of which were inade-

¹ Deceased January 23, 1989.

quately described and illustrated; thus, reference to type material was necessary.

All of the type specimens of deep-water octopods from the northern Pacific in the collections of the United States National Museum of Natural History (USNM) were borrowed, but their poor condition prevented direct comparison of many features. There was little non-type material at the USNM, although some fine specimens of *Graneledone verrucosa* were borrowed for comparison with the Pacific specimens.

In 1975 Voss traveled to Europe to examine the extensive collections at the British Museum (Natural History), the Muséum National d'Histoire Naturelle in Paris, and the Institut Océanographique in Monaco. Much of the type material was in poor condition and its examination failed to assist in the comparisons except in a few cases which bore indirectly upon the problems of the Oregon material. Specimens of *Benthoctopus* were borrowed from Takashi Okutani, Tokai Regional Fisheries Research Laboratory (currently Tokyo University of Fisheries). Examination of these specimens confirmed the separate identity of *B. canthylus*, but left the others in doubt.

Characters previously used to identify deep-water octopods were not sufficient for species recognition. Therefore the specimens were carefully dissected, and when possible, detailed observations were made for each species of the beaks, radulae, digestive tracts, genitalia, spermatophores, and stellate ganglia, as well as the more traditional counts and measurements. All these features were illustrated.

We hope that the details given here will permit positive identification of new material from the northeastern Pacific without necessitating the onerous, frustrating, and detailed examination of every specimen, as encountered in this study. The deep-sea benthic octopods are, however, in need of monographic revision.

CLASSIFICATION OF NORTHEASTERN PACIFIC DEEP-WATER OCTOPODS

Suborder Cirrata Grimpe, 1916

Family Cirroteuthidae Keferstein, 1866

Genus *Cirroteuthis* Eschricht, 1836

Cirroteuthis muelleri Eschricht, 1836

Family Opisthoteuthidae Verrill, 1896

Genus *Grimpoteuthis* Robson, 1932

Grimpoteuthis bathynectes new species

Grimpoteuthis tufisi new species

Suborder Incirrata Grimpe, 1916

Family Octopodidae Orbigny, 1845

Subfamily Bathypolypodinae Robson, 1928

Genus *Benthoctopus* Grimpe, 1921

Benthoctopus robustus new species

Benthoctopus canthylus new species

Benthoctopus oregonensis new species

Benthoctopus yaquinae new species

Benthoctopus macrophallus new species

Subfamily Graneledoninae Voss, 1988a

Genus *Graneledone* Joubin, 1918

Graneledone pacifica new species

MATERIALS AND METHODS

Collections were made with 2.7 to 3.0 m wide beam trawls with 13 mm (stretch) mesh and with otter trawls having a 7 m foot rope and 38 mm mesh with a 13 mm mesh liner in the cod end. Both nets were towed at two knots (3.7 km hr⁻¹) (see Carey and Heyamoto 1972 for descriptions of nets and sampling methods). Over 600 tows were taken on the continental slope and abyssal plains in the northeastern Pacific from depths of 400 to 5,180 m, 32 to 2,225 km offshore, between 1961 and 1974 (Fig. 1, see Percy et al. 1982 for details). Of these, 164 tows were from 2,500 to 3,045 m on the Cascadia Abyssal Plain, about 400 tows from 400 to 2,780 m on the continental slope off Oregon, and 35 tows from 2,780 to 5,182 m on the Tufts Abyssal Plain. Octopods from this study were captured at depths from 1,000 m on the continental slope to 3,932 m on Tufts Abyssal Plain from the research vessels ACONA, CAYUSE and YAQUINA. One specimen was caught in a trap at 3,660 m on the Aleutian Abyssal Plain.

Collections, including octopods, were preserved in 10% formalin and seawater at sea. Octopods were moribund or dead after capture, so they were not relaxed or killed prior to preservation.

After the cruises, the muscular, firm-bodied specimens were transferred to 70% ethanol, while the soft-bodied forms were stored in 40% isopropyl alcohol. The delicate cirroteuthids were stored in 10% formalin. Most of the material was transferred to 70% ethanol in Miami. Material stored in formalin, especially cirroteuthids, showed signs of deterioration. Storage in ethanol results in some shrinkage but is preferable to loss of the specimens.

All descriptions of color are based upon spec-

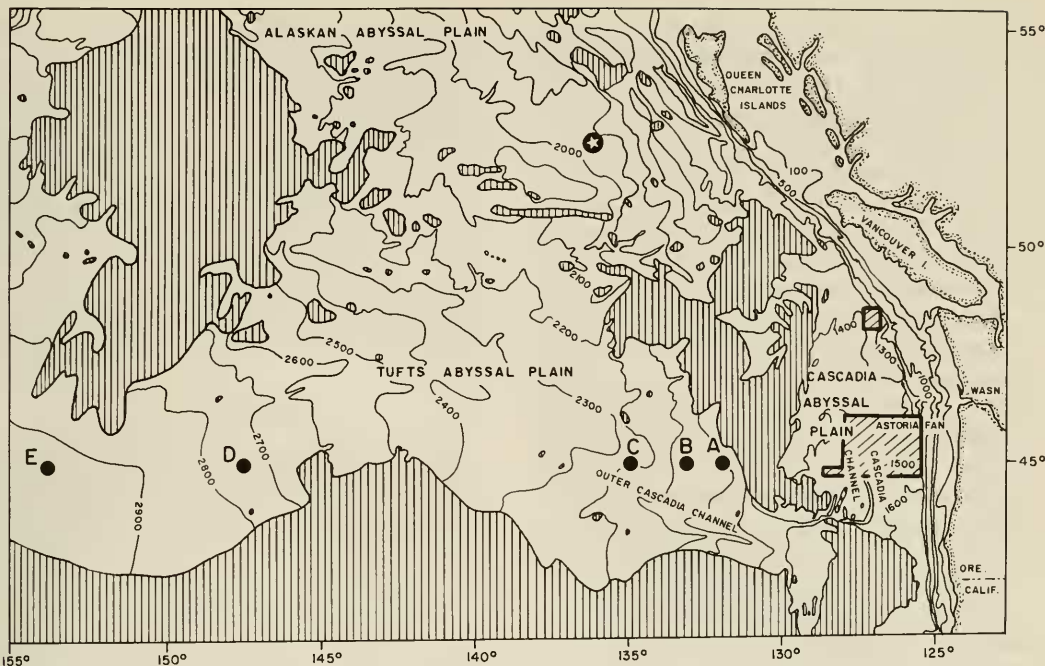


FIGURE 1. Location of trawl collection areas on the continental slope, Cascadia Abyssal Plain, and Tufts Abyssal Plain. Obliquely hatched areas denote general sampling areas on Cascadia Plain, solid dots specific sampling stations on Tufts Plain and the slope. The station on the Alaskan Abyssal Plain shows the location of capture for one *Benthoctopus robustus* in a trap. Vertical hatched areas indicate ridges and hilly topography.

imens preserved in ethanol. No color notes were made of living specimens.

All specimens were carefully examined, and measurements, body proportions, and counts were obtained from the whole animals as described by Voss (1963). The mantle of all specimens was opened to permit examination of the internal anatomy and to count gill lamellae. The digestive tract and genitalia were dissected to permit detailed descriptions and illustrations for each species. Because of the paucity of good specific characters in these octopods, the buccal mass was removed from nearly all specimens and the beaks and radulae extracted, cleaned, and illustrated. The buccal mass was typically immersed in tap water with one or two pellets of potassium hydroxide and gently heated. Beaks and radular ribbons were cleaned in household bleach solution (Chlorox). The beaks were illustrated lying free in a Petri dish, while the radulae were mounted in either Euparal or CMC 10 and drawn with the aid of a camera lucida. The radular ribbon of *Grimpotuthis tuftsi* was destroyed if the buccal mass was treated as described above; even

quick cleaning in bleach caused some radular ribbon deterioration.

Spermatophores were obtained only from *Benthoctopus*. They were so large that mounting was impractical; they were described and illustrated lying free in a Petri dish.

Special attention has been given to the stellate ganglion, particularly in the cirroteuthids, as this structure appears to be of systematic value. The ganglion and its associated nerve fibers were dissected from the mantle wall, mounted on a slide, and drawn with the aid of a camera lucida.

The indices used are those defined by Voss (1963) with the exception of those for fin length (FLI) and width (FWI) of cirroteuthids and the hectocotylized arm index (HcAI), which is expressed as a percentage of the length of its fellow arm on the opposite side. The range and mean of ratios and measurements is given as follows: 60–80–100, in which the italicized number is the mean. All measurements are in mm unless otherwise stated.

The cirroteuthids present certain problems not encountered in other octopods, e.g., the method

of taking measurements of the cirri, the fins, and the mantle length. Some writers have considered that the cirri can contract differentially depending on the type and strength of the preservative. However, cirri lengths do not vary appreciably within a species and average cirri lengths for conspecific animals are the same whether preserved in formalin, isopropyl alcohol, or ethanol. The cirrus length was taken from the longest cirrus on the arms and measured intact from the base to the tip. In some very flaccid specimens the cirrus was removed, stretched out on a glass slide, and measured.

Fin measurements entailed a reconsideration of terms applied both to squid and cirroteuthids. In squid, fin width is the greatest width across the fins measured from outer angle to outer angle, while length is measured from the anterior lobe to the posterior insertion or the tip of the mantle in fins united posteriorly. This measurement is misleading, however, when applied to the paddle-like fins of cirroteuthids, where fin length was measured from the midpoint of a line drawn across the fin base to the outer angle of the fin. There is considerable difference in measurements made along the posterior and anterior margins, particularly if the fins are directed somewhat anteriorly. Fin width is measured across the individual fin at the widest point when the fin is flattened to include the delicate thin anterior border. Fin-width index is expressed as a percentage of fin length. Fin-length index is expressed as a percentage of the interocular width for reasons given below.

Standard length in octopods has conventionally been considered to be the dorsal mantle length (ML) or the length of the body measured from mantle apex to a line drawn across the head from pupil to pupil. In cirroteuthids this measurement is fraught with difficulties. In some species of *Grimpot euthis* the posterior end of the mantle coincides with the posterior surface of the shell vestige. In others, particularly *Cirroteuthis* and *Stauroteuthis* but also in some *Grimpot euthis*, in life or in freshly preserved material, the mantle extends well beyond the shell vestige as a gelatinous, often fluid-filled sac, projecting posteriorly equal to the length of the mantle from the interocular line to the shell vestige. In preservation, this mantle extension is often completely contracted against the shell vestige. As a result, discretion must be used, and as Robson (1932) and others have often given fin length as a ratio of

the interocular width, the fin-length index used here is expressed similarly.

Holotypes of the new species described are deposited in the United States National Museum of Natural History (USNM). Other material examined, including the paratypes, are in the collections of the California Academy of Science (CAS), the Santa Barbara Museum of Natural History (SBMNH), the invertebrate collections of the Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML), and USNM.

THE STUDY AREA

The area of sampling has been described by Pearcy et al. (1982). Briefly, the steep and topographically complex continental slope off Oregon adjoins Cascadia Abyssal Plain, a basin bordered by submarine ridges on the west and south (Fig. 1). Its floor slopes gradually to the south and west. The Astoria and Nitinat fans, two large Pleistocene fans associated with the Columbia and Fraser rivers, are dominant features of the basin, producing a gradual slope from depths of 2,100 m on the fans adjacent to the slope to over 3,000 m in the southern portion of the basin.

Tufts Abyssal Plain is farther offshore and much less influenced by terrigenous sedimentation than is Cascadia Plain. It is bordered by the East Pacific Rise on the east and hilly seamounts on the south; it is connected with the Alaskan and Aleutian Abyssal plains on the north and west. Depth of the Tufts Plain increases gradually to the west. Cascadia Channel, which originates in Cascadia Plain and penetrates the East Pacific Rise, is the only deepwater connection between Tufts and Cascadia plains.

The sediments of these plains are mainly fine muds and clays. In general the rate of sedimentation and organic carbon content of the sediments decrease from east to west across both plains (Griggs et al. 1969). The biomass of benthic megafauna, both invertebrates and fishes, also decreases from east to west (Carey 1965; Pereyra and Alton 1972; Pearcy et al. 1982).

SYSTEMATICS

Order OCTOPODA

Suborder CIRRATA Grimpe, 1916

Deep-sea octopods that live on or just above bottom. Body gelatinous to subgelatinous, with

lateral paddle-shaped fins, uniserial suckers, and cirri alternating with suckers; shell vestige cartilaginous U-, V-, or saddle-shaped, well developed, serving mainly as fin support; radula may be present. Representatives have been reported from throughout the world ocean.

Family CIRROTEUTHIDAE Keferstein, 1866

As currently recognized, this family contains two monotypic genera—*Cirroteuthis* and *Cirrothauma* (see Voss 1988b:296). Body elongate, gelatinous, fragile, colorless to only lightly pigmented except on oral surface of arms and web; cirri long, conspicuous; fins large and wide; simple crop present; radula absent; gills “sepoid”; median pallial adductor vestigial; “secondary” web present; shell vestige saddle-shaped.

Cirroteuthis Eschricht, 1836

With the characters of the family.

TYPE SPECIES: *Cirroteuthis muelleri* Eschricht, 1836, by monotypy.

Cirroteuthis muelleri Eschricht, 1836

(Fig. 2, 3)

Cirroteuthis muelleri Eschricht, 1836:627, pls. 46–48. Mörch 1857:440. Hoyle 1886:60. Lönnberg 1891:6. Appellöf 1893: 1. Posselt 1898:269. Appellöf 1899:7–8, pl. 1, figs. 6–7. Friele and Grieg 1901:123. Pfeffer 1908:23, fig. 13. Robson 1926: Passim; 1932:130, fig. 18. Grieg, 1933:9.
Sciadephorus muelleri Reinhardt and Prosch, 1846:187, pls. 1–5.

MATERIAL EXAMINED (12 specimens all collected by R/V YAQUINA).—2 males, ML 74–79 mm, Cr. Y7102B haul 262, 45°38.3'N, 126°43.8'W in 2,721 m, 17 Feb. 1971, USNM 817580.—1 female, ML 66 mm, Cr. Y7105B haul 276, 45°56.7'N, 127°38.6'W in 2,761 m, 17 May 1971, SBMNH 35142.—1 female, ML 67 mm, Cr. Y7102B haul 263, 45°36.4'N, 126°44.9'W in 2,730 m, 17 Feb. 1971, UMML 31.1935.—1 male ML 72 mm, 1 female ML 21 mm, Cr. Y7105B haul 278, 45°24.0'N, 127°39.0'W in 2,811 m, 18 May 1971, UMML 31.1936.—1 female, ML 64 mm, Cr. Y7102B haul 265, 45°18.6'N, 126°31.5'W in 2,750 m, 18 Feb. 1971, CAS 067786.—1 female, ML 63 mm, Cr. Y7102B haul 270, 44°38.4'N, 126°42.0'W in 2,830 m, 20 Feb. 1971, SBMNH 35143.—2 females, ML 47–63 mm, Cr. Y7102B haul 268, 44°58.8'N, 126°37.4'W in 2,770 m, 19 Feb. 1971, USNM 817581.—1 male, ML 53 mm, Cr. Y7005C haul 230, 44°27.0'N, 132°14.0'W in 3,655 m, 1 June 1970, CAS 067787.—1 female, ML 40 mm, Cr. Y7301F haul 317, 44°44.5'N, 127°29.0'W in 2,810 m, 3 Feb. 1973, CAS 067788.

DESCRIPTION.—Moderately large species with soft, almost gelatinous consistency; body covered by thin, tough, outer layer except on arms

and web where easily torn; all of animal very fragile except for parts of internal anatomy.

Mantle elongate, somewhat tubular but gently rounded posteriorly (Fig. 2a), about half as wide as long (Tables 1–4); head width slightly greater than mantle width with no discernible constriction between head and mantle; mantle aperture narrow, mantle fits snugly around funnel; eyes small, fully formed, with large lenses; eyelid absent but skin transparent over orbit.

Funnel long, conical, narrow, free for about half of its length; funnel organ thin, flat, \wedge -shaped, with sharp median point and truncate lower limbs; small cup-shaped olfactory organ located about midway on either side of funnel on an edge of shallow funnel groove.

Fins approximately median, located slightly nearer apex of mantle than eyes (Fig. 2a); each fin paddle-shaped, about twice as long as wide (Tables 1–4); posterior edge nearly straight, curves anteriorly just past midpoint; anterior margin strongly rounded and proximally turns posteriorly to form narrower base; heavy muscular portion of fins well developed, usually occupies most of fin width near base, extends at least halfway to fin end; outer lobe of fin nearly forms semicircle; fins do not project at 90° angle from body axis but are directed slightly anteriorly.

Arms translucent, not muscular, appear filled with fluids in life but usually collapsed, wrinkled when preserved. Arm lengths difficult to obtain due to contractions of arms and distortion by contraction of web; measurements therefore approximate. Arms (Fig. 3a) subequal with perhaps lateral arms slightly longest; single row of arm suckers as far as distal attachment of primary web, beyond which arms slender, smooth, devoid of suckers, whip-like; inner oral surface of arms broad and bear suckers, aborally arms narrower, triangular in cross-section, outer edge of arm located inside secondary or intermediate web extends as lamella to outer or primary web.

Primary web with thin tough outer layer that keeps web intact in preserved specimens; primary web usually torn from arms during capture, attached only to arm near tip on dorsal side at point where suckers terminate; arms along rest of their length attached to primary web by dorsal and ventral intermediate webs (Fig. 3a); interior spaces appear to be filled with fluids; dorsal intermediate web begins at base of arms, widest at about midpoint, and tapers to terminate near primary web-attachment point; ventral inter-

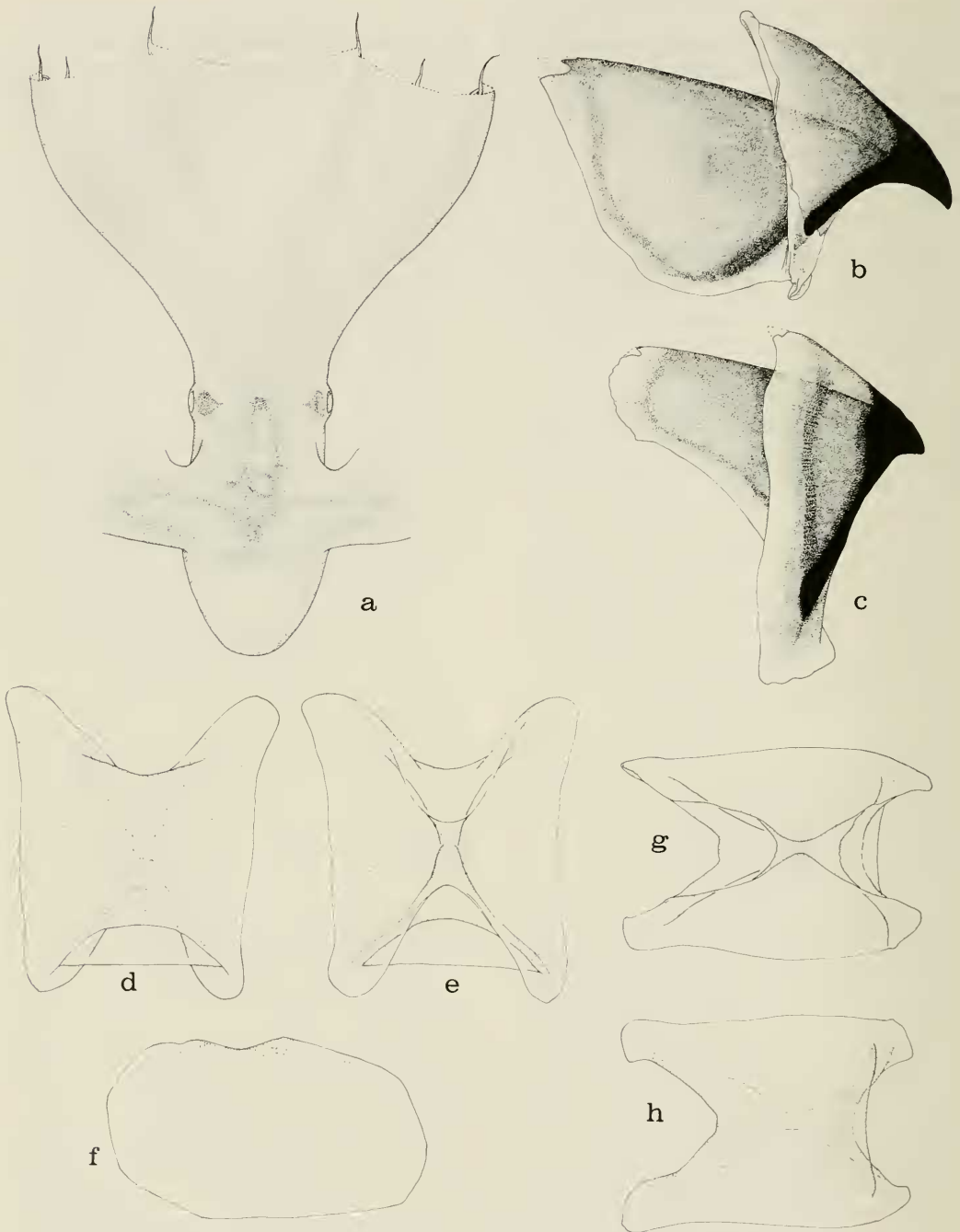


FIGURE 2. *Cirroteuthis muelleri* Eschricht. (a) Dorsal view of male; ML 79 mm. (b-c) Upper and lower beaks. (d-f) Ventral, dorsal, and lateral views of shell vestige of male, 74 mm ML. (g-h) Dorsal and ventral views of shell vestige of male, 53 mm ML.

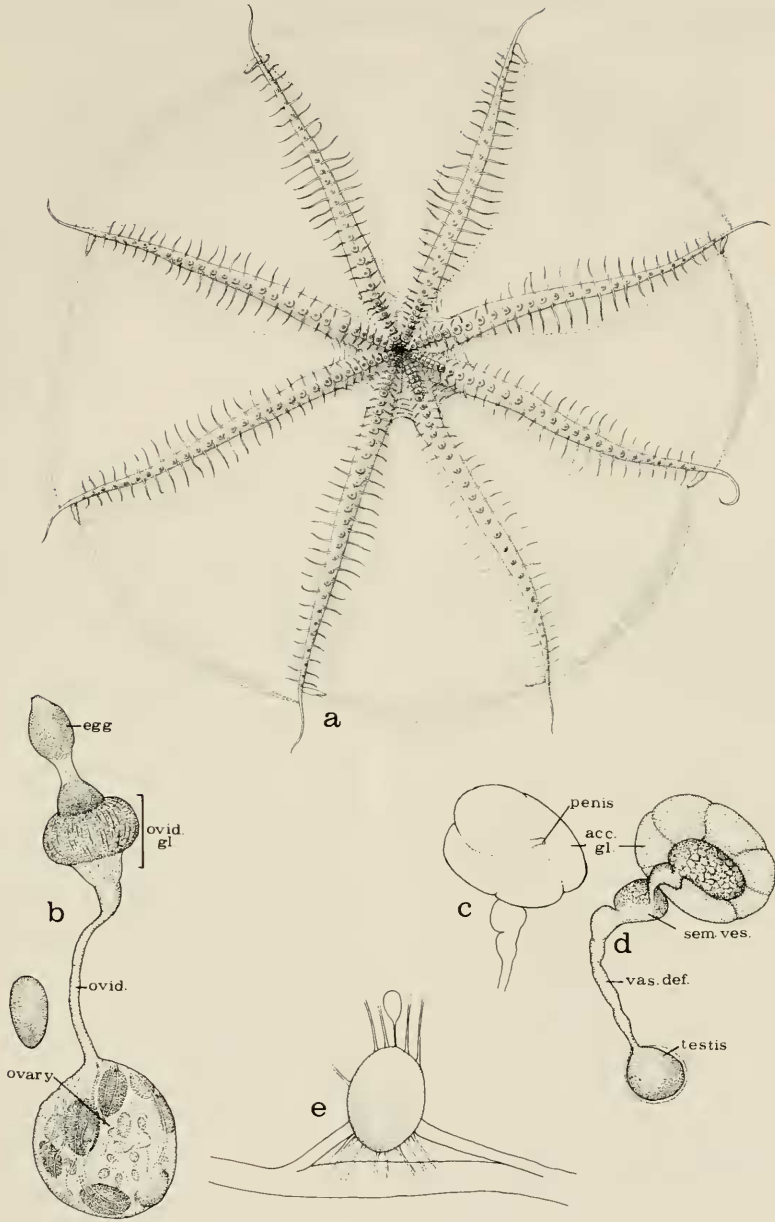


FIGURE 3. *Cirroteuthis muelleri* Eschricht. (a) Oral view of arms and web of male (dorsal side up), 79 mm ML. (b) Genitalia and egg of female, 67 mm ML. (c-d) Genitalia of male, 72 mm ML. (e) Left stellate ganglion.

mediate web originates same as dorsal, is wider, and terminates as moderately wide membrane along inner edge of large, fleshy, thinly tapered process on ventral side of arm a few millimeters proximal to attachment of primary web. This whip-like process (nodule) also the fusion point of primary web, which unites on aboral surface,

intermediate web on its oral surface; no indication of unions of webs when viewing primary web aborally.

Suckers small (Tables 1-4); first suckers surrounding mouth small, 2nd and 3rd succeeding suckers usually largest, then size gradually decreases to about 7th or 8th sucker (Fig. 3a). Seven

TABLE 1. Measurements and counts of four males of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen			
	USNM 817580	USNM 817580	UMML 31.1936	CAS 067787
Mantle length	79.0	74.0	72.0	53.0
Mantle width	47.0	26.0	40.0	27.0
Head width	52.0	34.0	37.0	32.0
Arm length I	170.0	—	145.0	—
Arm length II	178.0	140.0	—	—
Arm length III	170.0	—	—	—
Arm length IV	170.0	—	—	—
Total length	277.0	210.0	222.0	178.0
Fin length	50.0	47.0	47.0	53.0
Fin width	30.0	21.0	30.0	23.0
Sucker diameter	—	1.3	2.1	1.0
Cirrus length	19.2	16.0	18.4	11.0
Gill lamellae	8	9	8	7
Arm formula	21=3=4	—	—	—

or eight basal suckers cup-shaped, usually raised on broad, heavy pads; suckers smaller distal to 8th sucker, often less than half size of basal suckers, delicate, thin-lipped, often with no apparent suction cup, and formed of two, almost parallel, elements. Sucker bases in undamaged specimens widely spaced, formed of large, delicate, mammilar, fluid-filled structures, surmounted by minute, apparently non-functional sucker cups. When fluid-filled bases collapse, suckers lie flat on arm or appear to be mounted on thin delicate pedicels, according to condition of collapsed bases. Distal to small suckers, at about 28th sucker, normal appearance regained. Ventral web nodule joins at about 3rd or 4th enlarged sucker; suckers gradually become smaller, terminate at union of primary web with arm on dorsal surface; largest of terminal suckers about same diameter as basal suckers.

Cirri small, occur in pairs between either suckers 1 and 2, or 2 and 3, one on each side of sucker slightly proximal to base, appear to alternate with suckers, extend distally to terminal sucker; largest in midportion of arm, attain length of over 19 mm, or 9 to 13 times diameter of largest sucker. (Cirri difficult to measure unless removed from arm and placed on glass slide.)

Gills small, little modified, with 7–8–9 lamellae per outer demibranch, including large, partially divided terminal lamella. Thin, transparent, distinct median pallial adductor muscle, 10–16% ML, unites mantle to viscera; inner attachment on membrane overlaying male or female genitalia in median position.

TABLE 2. Indices of bodily proportions and counts of four males of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen				\bar{x}
	USNM 817580	USNM 817580	UMML 31.1936	CAS 067787	
ML	79.0	74.0	72.0	53.0	—
MWI	58.7	35.1	55.5	50.4	49.9
HWI	65.0	45.9	51.3	60.3	55.6
MAI	47.0	52.8	49.6	46.9	49.1
ALI	64.2	66.6	65.3	63.4	64.9
SIn	—	1.7	2.9	1.8	2.1
Cil	24.0	21.6	25.6	20.8	23.0
FLI	96.2	138.2	127.0	165.0	131.6
FWI	60.0	44.7	63.8	43.4	52.9

Posterior third of mantle cavity devoid of structures but filled with tough, viscous, gel-like material that gives body its shape posterior to skeletal structure; may be reservoir for ammonium ions for buoyancy. Area is easily damaged, collapses with too much handling, difficult to measure.

Shell vestige saddle-shaped; originates as flat sheet that curves dorsally on anterior and posterior borders, curls in toward itself, thickens to form supports for large basal fin muscle (Fig. 2d–h).

Beaks thin, weak, and indistinctive (Fig. 2b, c); radula absent, surface normally covered by radula thickened, slightly ridged transversely, bears series of longitudinal folds that resemble lines of various sizes of teeth; cuticular lining not apparent.

Esophagus slender at connection with buccal mass, passes posteriorly between two anterior salivary glands (posterior salivary glands absent); widens into croplike area without diverticulum, but expanded to two to three times diameter of anterior section; posterior to “crop” esophagus narrows, enters distinctly two-parted stomach; spiral caecum nearly as large as both elements of stomach; two large ducts lead into digestive gland through digestive duct appendage; digestive gland round but slightly flattened; intestine large, nearly straight, not divided into parts. Longitudinal folds run full length of intestine, seen clearly through its transparent wall. Ink sac absent; anus without flaps.

Male genitalia unusual (Fig. 3c, d), difficult to compare with those of other octopods: duct from testis large, leads into folded mass with thin-walled out-folding that may correspond to Need-

TABLE 3. Measurements (in mm) of seven females of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen						
	CAS 067788	USNM 817581	USNM 817581	SBMNH 35143	CAS 067786	SBMNH 35142	UMML 31.1935
Mantle length	40	47	63	63	64	66	67
Mantle width	19	22	32	—	46	43	40
Head width	21	23	35	—	42	42	47
Arm length I	—	—	—	—	114	96	—
Arm length II	—	—	—	—	—	96	—
Arm length III	—	—	—	—	—	94	—
Arm length IV	67	95	108	—	—	91	124
Total length	113	157	190	—	180	172	203
Fin length	41	52	61	52	50.5	46.5	49.5
Fin width	18	24	25	38.0	35.0	36.0	30.0
Sucker diameter	0.6	1.0	1.0	2.1	1.6	1.4	2.4
Cirrus length	8.0	9.0	13.0	16.0	19.2	19.2	13.0
Gill lamellae	7	7	8	8	8	8	7
Arm formula	—	—	—	—	—	1=234	—

ham's sac; distal portion of folded mass smooth with small slender duct (penis?) that protrudes from its center; Needham's sac contains about 10 small ovoid structures, apparently spermatophores (similar to structures found in *Grimptoteuthis*); they do not resemble typical octopod spermatophore and probably consist only of sperm reservoir.

Female genitalia (Fig. 3b) unpaired, nearly round ovary contains about 12 large, apparently ripe, ovoid, flesh-colored eggs with light wavy linear markings; 10.4×9.3 mm; numerous small to minute eggs also present; proximal oviduct single, about 4–5 times length of distal oviduct, rather inflated, swollen at distal end at junction with oviducal gland; oviducal gland large, dark colored, forms ring around oviduct; distal oviduct short, strongly flared at distal opening. Mature egg at end of oviduct, with another lodged in oviducal gland (Fig. 3b) exactly as figured by Reinhardt and Prosch (1846, pl. 4).

Optic ganglia distinct, globular, darkly pigmented, almost same diameter as orbit of eye. The stellate ganglion shown in Figure 3e.

Color in ethanol varies from pale white to purple; inner surfaces of arms and web invariably darkest, purple or purplish-brown.

MEASUREMENTS AND COUNTS.—Males: mantle length 53–69.5–79; mantle width 26–35.0–47; head width 32–38.8–52; arm length I 145–170, II 140–178, III 170, IV 170; total length 178–221.8–277; fin length 47–49.3–53; fin width 21–26–30; sucker diameter 1–1.5–2.1; cirrus length 11.0–16.2–19.2; number of gill lamellae 7–8–9.

Females: mantle length 40–58.6–67; mantle width 19–33.3–46; head width 21–35.0–47; arm length I 96–114, II 96, III 94, IV 67–97–124; total length 113–169.2–203; fin length 41–50.4–61; fin width 18–29.4–38; sucker diameter 0.6–1.4–2.4; cirrus length 8.0–13.9–19.2; number of gill lamellae 7–7.6–8.

TYPE.—Zoological Museum, Copenhagen. Robson (1932: 130) erroneously stated that it was in Naturhistorischen Verein of Breslau and Bonn. In a letter to Robson from Sparck dated 8 February 1932, Sparck stated that Robson had made a mistranslation and that the holotype is in the Zoological Museum of Copenhagen (see Kristensen and Knudsen 1983).

TYPE-LOCALITY.—Jakobshavn, West Greenland (Eschricht 1836:627).

DISCUSSION.—A careful examination of the 12 specimens available has revealed no important differences between our material and the descriptions of *Cirroteuthis muelleri* given in the literature (Eschricht 1836; Reinhardt and Prosch 1846; Robson 1932). Some minor differences occur.

Robson (1932:131) drew attention to a peculiar modification of the small suckers on the arms of the British Museum specimen—they were flat. If he referred to the sucker only and not its total base, this condition is also found in our specimens. Eschricht's fig. 1 indicates that the median suckers were smaller in the type, and the coloration seems to indicate that they were on large mammillar bases, just as in our specimens.

The differences in the origin of the cirri (often

TABLE 4. Indices of bodily proportions and counts of seven females of *Cirroteuthis muelleri* Eschricht, 1836.

	Specimen						
	CAS 067788	USNM 817581	SBMNH 35143	USNM 817581	CAS 067786	SBMNH 35142	UMML 31.1935
ML	40	47	63	63	64	66	67
MWI	47.5	46.8	—	50.8	71.9	65.2	59.7
HWI	52.5	48.9	—	55.6	65.6	63.6	70.2
MAI	59.7	49.5	—	58.3	56.1	68.8	54.0
ALI	59.3	60.5	—	56.8	63.3	55.8	61.1
Sl _n	1.5	2.1	3.3	1.6	2.5	2.1	3.6
Ci _i	20.0	19.2	25.4	20.6	30.0	29.1	19.4
FLI	195.2	226.0	—	174.0	120.0	110.7	105.3
FWI	44.0	46.2	73.1	40.9	69.3	77.4	60.6

between the 1st and 2nd suckers in our specimens, only between the 2nd and 3rd in the others) seems to be a matter of individual variation. In our specimens cirri may first appear between suckers 1 and 2 in some arms and between 2 and 3 on other arms. Often only one cirrus is present between 1 and 2, both cirri between 2 and 3.

Robson (1929:26) pointed out the possible systematic value of the size of the mantle aperture, and in *C. muelleri* indicated that while Eschricht's original description showed a wide aperture (Robson's 'C'), the British Museum specimen has a small aperture (at least 'B'). We believe the original illustration is of a very flaccid and perhaps stretched specimen. Our specimens all show at least the B condition and often A.

The shape of the fins also is different. Both Eschricht (1836) and Reinhardt and Prosch (1846) show broad flabellate fins with a very unnatural appearance. We believe that this is artistic treatment; our specimens show a remarkable homogeneity of appearance and closely correspond to the more detailed structure shown in pl. 5, fig. 1 of Reinhardt and Prosch (1846).

A more basic difference is the presence or absence of a median pallial adductor muscle. This is discussed by Robson (1932:119-120), who stated that there was no median adductor in the British Museum specimens. A thin but distinct median adductor is present in our specimens; it is easily overlooked because it is small and transparent. Robson was not noted for the delicacy of his dissections and it is possible that, being familiar with the thick, muscular adductors of the Incirrata, he overlooked the pallial adductor in his specimen. Voss examined two fine USNM specimens of *C. muelleri* obtained by the R/V WALTHER HERWIG in the North Atlantic. Both had the narrow, transparent, easily overlooked median pallial adductor muscle.

DISTRIBUTION.—*Cirroteuthis muelleri* was previously known only from the northern part of the North Atlantic (see Robson 1932:130; Voss 1988b). Its presence in the northeastern Pacific indicates either a very broad distribution or a discontinuous circumboreal pattern (Ekman 1953:161). While the shallow waters of the Arctic Ocean may be a barrier, vertical distribution there is not limited by temperature, as shown by the capture of *Cirrothoaima murrayi* in an ice hole off Point Barrow (Voss 1967:527). Furthermore, cirromorphs resembling *Cirroteuthis* have been photographed in the Arctic Ocean in 2,360 to

3,786 m (Pearcy and Beal 1973), suggesting a continuous distribution through the Arctic Ocean.

Family OPISTHOTEUTHIDAE Verrill, 1896

Body gelatinous to semigelatinous; bell-shaped or disc-like; fins long to small, and lateral to superior (dorsal); simple crop present or absent; radula present or absent; gills "half orange" type; median pallial adductor present; web single; shell vestige U- or V-shaped. This family contains two genera: *Opisthoteuthis* and *Grimptoteuthis* (Voss 1988b).

Grimptoteuthis Robson, 1932

TYPE SPECIES: *Cirroteuthis umbellata* Fischer, 1883:404. By original designation, Robson (1932: 136).

Grimptoteuthis bathynectes new species

(Figs. 4, 5)

MATERIAL EXAMINED (15 specimens all collected by R/V YAQUINA).—Holotype: male, ML 50 mm, Cr. Y7210A haul 308, 44°01.1'N, 133°12.0'W in 3,932 m, USNM 730715. Paratypes: 2 males ML 46.5–48 mm, 1 female ML 31 mm, Cr. Y7210A haul 300, 44°58.1'N, 132°14.7'W in 3,585 m, 10 June 1972, CAS 067789.—1 male, ML 42 mm, Cr. Y7105B haul 281, 44°38.5'N, 127°39.5'W in 2,816 m, 19 May 1971, SBMNH 35144.—1 male ML 30 mm, 1 female ML 85 mm, Cr. Y7210A haul 303, 45°05.1'N, 133°10.9'W in 3,700 m, 10 July 1972, UMML 31.1938.—1 female, ML 57 mm, Cr. Y7005C haul 232, 44°40.2'N, 133°35.7'W in 3,742 m, 3 June 1970, SBMNH 35145.—2 males, ML 17.5–53 mm, Cr. Y7210A haul 299, 44°56.8'N, 132°11.5'W in 3,580 m, 10 June 1972, UMML 31.1937.—1 male, ML 17 mm, Cr. Y7210A haul 307, 45°03.5'N, 134°45.0'W in 3,900 m, 10 Oct. 1972, CAS 067790.—2 males ML 30–36 mm, 1 female ML 29 mm, Cr. Y7210A haul 305, 45°05.2'N, 134°43.4'W in 3,900 m, 9 Oct. 1972, USNM 817582.—1 male, ML 28 mm, Cr. Y7206B haul 288, 44°06.2'N, 125°22.7'W in 2,940 m, 14 June 1972, CAS 067791.

DIAGNOSIS.—A *Grimptoteuthis* with long fins; short cirri; suckers largest proximally, suckers of males larger than those of females; gills compact with 7–9 lamellae; radula absent.

DESCRIPTION.—Mantle saccular (Fig. 4a), little more than half as wide as long, rounded posteriorly; aperture narrow, of type B; head wider than mantle, not set off by neck region; eyes large, somewhat protruding.

Funnel large, projects far beyond mantle margin, distal quarter or less free; funnel organ broad, thick-limbed, \wedge -shaped pad with all angles rounded.

Fins long, moderately wide, situated about halfway between apex of mantle and eyes; posterior margin nearly straight, tips rounded with

slight point, anterior margin convex, turning slightly posteriorly at line of mantle to form minor constriction; fins with narrow muscular base, muscular area extends about three-quarters of length of fins.

Arms gelatinous, moderately long, subequal, stout, deeply set into thick web. Arm formula generally I.II.III.IV.

Web single (secondary web absent), thick, fleshy, soft; web formula variable, usually ABCDE; in most large males sector C on left side noticeably larger than C on right; web depth about half arm length, extensive along arms but unequally distributed; large fleshy nodule or finger-like process located on ventral side of arms (Fig. 4b), about one-half to two-thirds of arm length from base, unites web to ventral side of arms, beyond which web may extend only very short distance; nodules on dorsal side of arms absent, web extends to, or nearly to, tip of each arm. Consequently, sector A lacks processes, so web extends to tip of arm on both sides to make this sector deepest; conversely, web sector E is the shallowest with nodules on each side of arms.

Suckers in single row extend from mouth to tips of arms. Dorsal arms with 47 to 58 suckers set into oral surface, their apertures projecting freely; first four to five suckers small to minute, followed by abruptly larger suckers that gradually increase in size for about one-third arm length, after which they gradually decrease in size to arm tip. Suckers over proximal half of arms largest, abruptly enlarged suckers absent indicating lack of hectocotylization; considerable sexual dimorphism in size and shape of suckers (Tables 5–8); in males, suckers (Fig. 4d) larger (SI_n 4.3–6.7), more globular, with short, narrow apertural rims that rise from free globular bases where web usually joins suckers; suckers in females and small males (Fig. 4c) smaller (SI_n 2.6–3.5), globular base missing or nearly so, and whole sucker smaller, tubular, more erect than those of large males, without webbing between suckers.

Cirri short, about two-thirds to 1.5 sucker diameter in length; located on sides of arms between bases of suckers (Fig. 4c, d), they first appear between suckers 3 and 4 and extend to tips of arms.

Median pallial adductor thin, narrow, length 2.8–9.2% ML. Gills compact, spherical, of "half orange" or *Opisthoteuthis* type (Robson 1932: 124), 7–9 lamellae per gill, closely packed, slightly rugose in appearance.

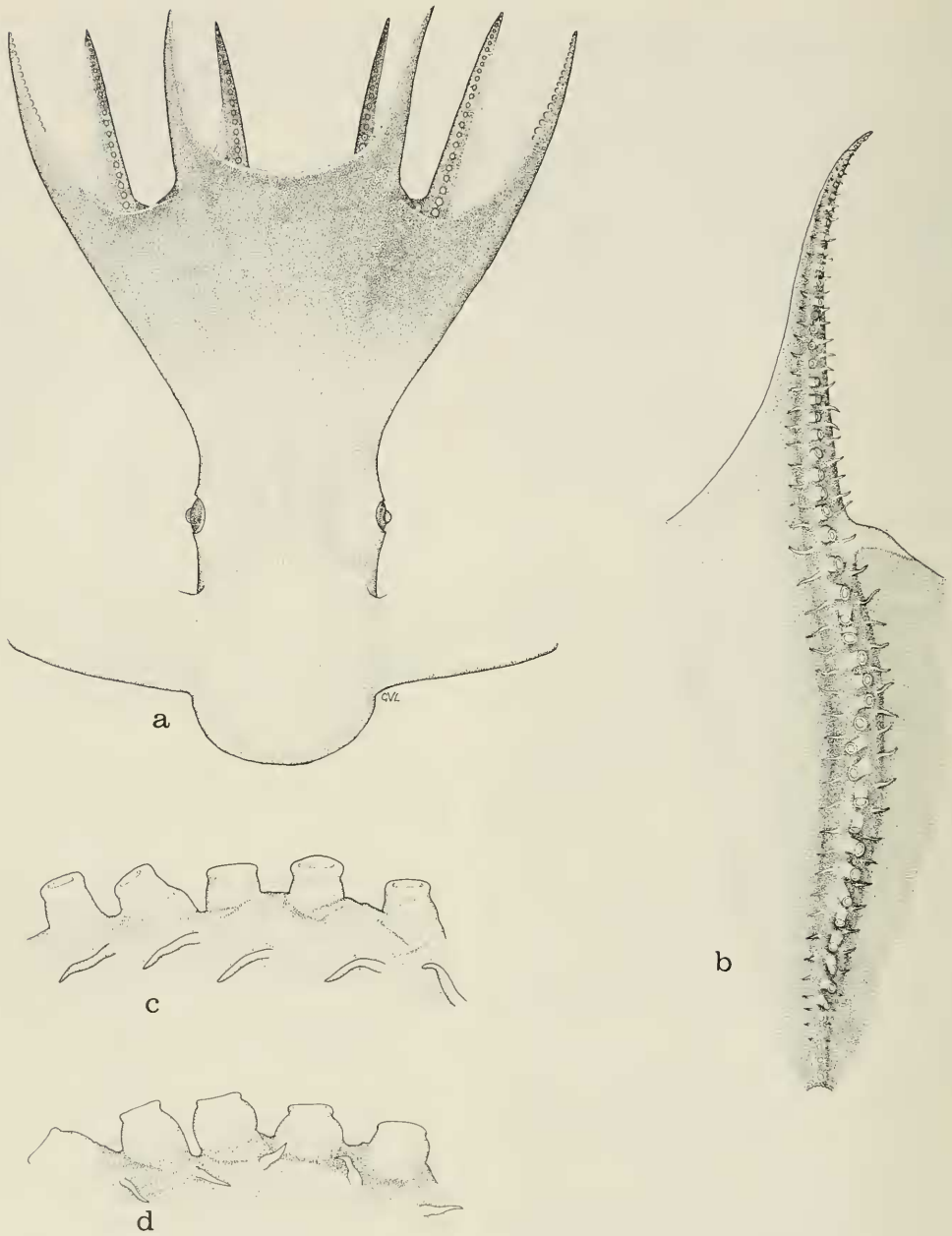


FIGURE 4. *Grimptoteuthis bathynectes* new species. (a) Dorsal view of holotype, USNM 730715, male, 50 mm ML. (b) Oral view of left dorsal arm of male, 50 mm ML. (c) Suckers and cirri of female, 58 mm ML. (d) Suckers and cirri of male, 42 mm ML.

Digestive tract of male shown in Figure 5a; beaks shown in Figure 5d, e. Radula absent; anterior salivary gland apparently absent, two small oval white bodies immediately adjacent and ventral to buccal mass may represent posterior salivary glands; esophagus widens gently posterior

to buccal mass but does not form crop; stomach slightly two-parted; buccal mass, esophagus, and stomach densely covered with deep reddish-purple gelatinous tissue, obscuring details until removed; caecum large with strong, almost complete turn; digestive ducts stout, lead from

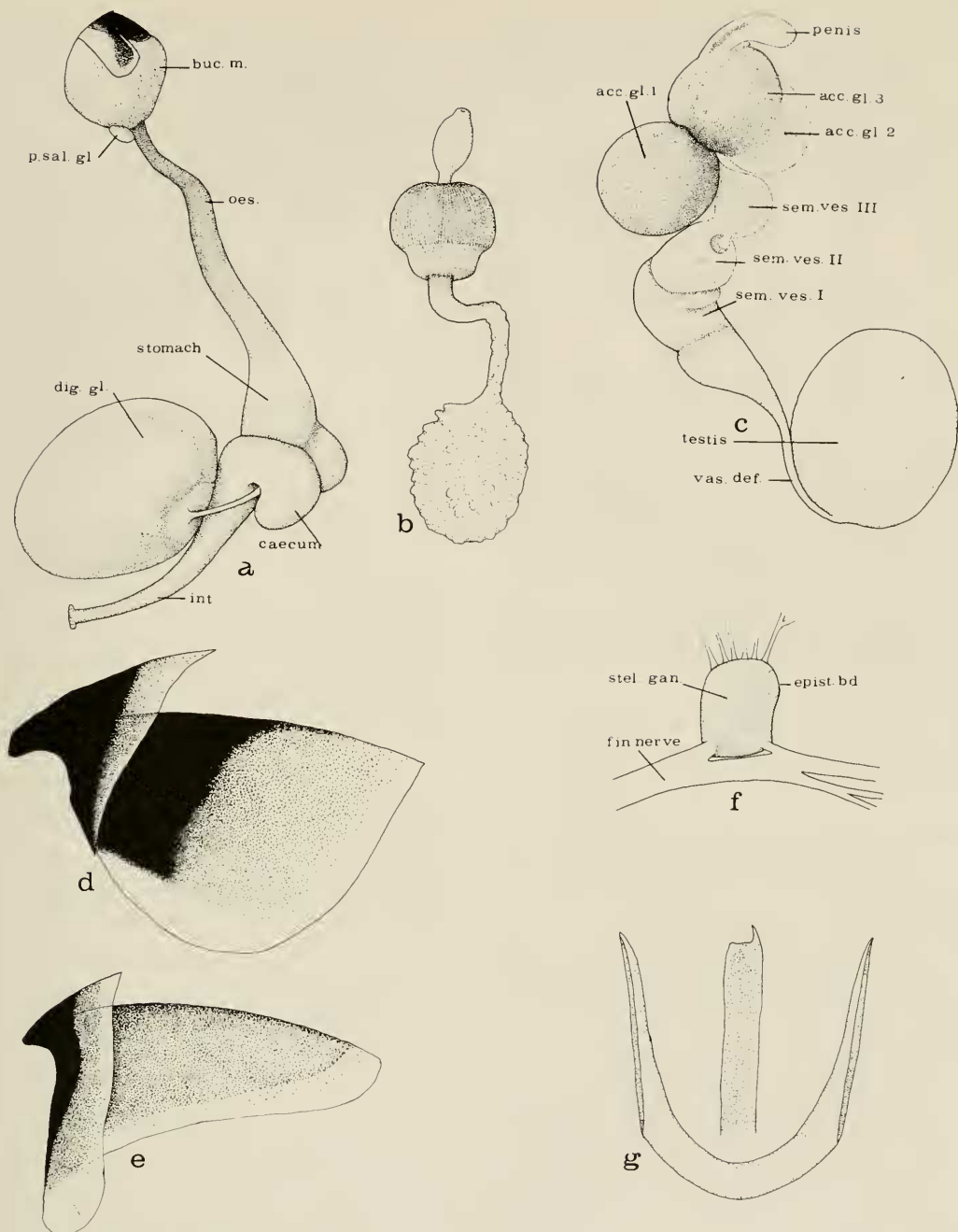


FIGURE 5. *Grimptoteuthis bathynectes* new species. (a) Digestive tract of male, 53 mm ML. (b) Genitalia of female, 85 mm ML. (c) Genitalia of male, 53 mm ML. (d-e) Upper and lower beaks of male, 53 mm ML. (f) Left stellate ganglion of male, 53 mm ML. (g) Dorsal view of shell vestige and lateral view of end, male, 53 mm ML.

caecum-stomach to digestive gland, pass through small but distinct digestive duct appendage area; digestive gland small, globular; intestine small, stout, straight; anal flaps and ink sac absent.

Male genitalia complicated (Fig. 5c). Spermatophores present, similar to those in *Cirro-teuthis*.

Female genitalia (Fig. 5b) simple, unpaired;

TABLE 5. Measurements (in mm) of 11 males of *Grimptoteuthis bathynectes* new species.

	Specimen										
	CAS 067790	UMML 31.1937	CAS 067791	USNM 817582	UMML 31.1938	USNM 817582	SBMNH 35144	CAS 067789	USNM 730715	UMML 31.1937	
Mantle length	17	17.5	28	30	30	36	42	46.5	50	53	
Mantle width	11	14	25	23	16	29	28	34	36	38	
Head width	17	17	28	31	26	35	32	42	41	51	
Arm length I	47	45	73	81	58	116	151	116	132	135	
Arm length II	46	43	67	76	59	103	146	112	124	131	
Arm length III	43	43	63	73	49	100	134	116	115	125	
Arm length IV	39	40	59	70	49	103	129	100	106	119	
Total length	76	70	94	106	85	151	200	156	170	190	
Fin length	—	19	28	24	35	31	40	39	41	43	
Fin width	6	10	12	14	13	16	21	19	21	22	
Sucker diameter	0.6	0.7	1.0	1.2	1.0	2.0	2.8	2.0	3.0	2.7	
Cirrus length	1.0	0.7	1.0	1.0	1.0	2.0	2.5	2.0	2.2	3.0	
Gill lamellae	7	8	8	9	7	7	7	7	9	9	
Suckers on I	47	48	47	52	48	52	49	53	57	50	
Arm formula	1234	1234	1234	1234	2134	1234	1234	1324	1234	1234	

TABLE 6. Indices of bodily proportions and counts of 11 males of *Grimptoteuthis bathynectes* n. sp.

	Specimen										
	CAS 067790	UMML 31.1937	CAS 067791	USNM 817582	UMML 31.1938	USNM 817582	SBMNH 35144	CAS 067789	USNM 730715	UMML 31.1937	
ML	17	17.5	28	30	30	36	42	46.5	50	53	
MW1	64.7	80.0	89.3	76.7	53.3	80.6	66.7	73.1	72.0	71.7	
HW1	100.0	97.1	100.0	103.3	86.7	97.2	76.2	90.3	82.0	96.2	
MA1	34.0	38.0	37.8	36.6	50.0	30.5	27.1	39.7	37.3	38.7	
AI1	65.8	65.7	78.7	77.4	70.6	78.2	77.5	75.0	78.8	72.1	
SI1	3.5	4.0	3.6	4.0	3.3	5.6	6.7	4.3	6.0	5.1	
CI1	5.9	4.0	3.6	3.3	3.3	5.6	6.0	4.3	4.4	5.7	
FL1	—	111.8	100.0	77.4	134.6	88.6	125.0	92.9	102.4	84.3	
FW1	—	52.6	42.9	58.3	37.1	51.6	52.5	48.7	50	51.2	
Arm formula	1234	1234	1234	1234	2134	1234	1234	1324	1234	1234	

TABLE 7. Measurements (in mm) of four females of *Grimpot euthis bathynectes* new species.

	Specimen			
	USNM 817582	CAS 067789	SBMNH 35145	UMML 31.1938
Mantle length	29	31	57	85
Mantle width	16	18	32	67
Head width	24	19	39	59
Arm length I	72	65	124	143
Arm length II	78	72	104	150
Arm length III	73	60	101	143
Arm length IV	67	56	99	141
Total length	95	110	185	240
Fin length	26	28	33	39
Fin width	10	14	21	24
Sucker diameter	1.0	1.0	1.5	3.0
Cirrus length	1.5	1.5	1.5	3.0
Gill lamellae	7	7	8	7
Suckers on I	51	51	58	58
Arm formula	2314	2134	1234	2134

ovary of largest female small with no mature eggs; proximal oviduct long, slender; oviducal gland two-parted, proximal third white, distal two-thirds very dark brown to almost black, both parts strongly and finely plicate; distal oviduct about one-third length of proximal oviduct, slender proximally but broadens distally, appears bulbous.

Shell vestige in male (Fig. 5g) deep, U-shaped, formed of rounded-edged flat strip that tapers to thin flat point distally; fin insertions long and form slight angle near base with rounded apex.

Stellate ganglion of male illustrated in Figure 5f.

Color of mantle and head grayish, tinged with purplish brown; posterior edges of fins lined with dark reddish brown; aboral surface of arms and web dark purple or reddish brown; oral surface of arms and web deep purplish brown or chocolate, often with light brown or flesh-colored suckers.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 50; mantle width 36, head width 41; arm length I 132, II 124, III 115, IV 106; total length 170; fin length 42; fin width 21; sucker diameter 3.0; cirrus length 2.2; number of gill lamellae 9; number of suckers on arm I 57.

Males: mantle length 17–36.2–53; mantle width 11–25.8–38; head width 17–33.0–51; arm length I 45–99.5–141, II 43–95.8–147, III 43–91.5–146, IV 39–86.5–137; total length 70–135.8–200; fin length 19–34.2–43; fin width 6–15.8–22; sucker

TABLE 8. Indices of bodily proportions and counts of four females of *Grimpot euthis bathynectes* new species.

	Specimen			
	USNM 817582	CAS 067789	SBMNH 35145	UMML 31.1938
Mantle length	29	31	57	85
MWI	55	58	56	79
HWI	83	62	69	70
MAI	36	42	46	56
ALI	84	66	67	63
SIn	3.5	3.2	2.6	3.5
CiI	5.2	4.8	2.6	3.3
FLI	108.3	147.4	84.6	66.1
FWI	38.5	50.0	63.6	61.5
Arm formula	2314	2134	1234	2134

diameter 0.6–1.8–3.0; cirrus length 0.7–1.7–3.0; number of lamellae 7–7.7–9; number of suckers on arm I 47–50.5–57.

Females: mantle length 29–50.5–85; mantle width 16–33.3–67; head width 19–35.3–59; arm length I 72–101.0–143, II 78–101.0–150, III 60–94.3–143, IV 56–90.8–141; total length 95–157.5–240; fin length 26–31.5–39; fin width 10–17.3–24; sucker diameter 1–1.6–3; cirrus length 1.5–1.9–3.0; number of gill lamellae 7–7.3–8; number of suckers on arm I 51–54.5–58.

TYPE.—Holotype, male, 50 mm ML, USNM 730715 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, Tufts Abyssal Plain, 45°01.1'N, 135°12.0'W, 3,932 m.

DISCUSSION.—Only two species of *Grimpot euthis*, *G. hippocrepium* (Hoyle, 1904) and *G. albatrossi* (Sasaki, 1920) have been reported from the North Pacific Ocean (Voss 1988b). *Grimpot euthis hippocrepium* was poorly described from a mutilated specimen and is unrecognizable as far as many important characters are concerned. The type (USNM 382467) is in very poor condition and little can be learned from it. *Grimpot euthis albatrossi* is well described (Sasaki 1929: 7) but the type (USNM 332949) dried up, and although it has been realcoholized, it is nearly worthless for comparative studies. As Robson remarked (1932:150), *G. albatrossi* resembles the Atlantic *G. grimaldi* (Joubin, 1903) in having small fins and large suckers near the tips of arms. Neither of these species resembles *G. bathynectes*. It appears closely related to *G. umbellata* (Fischer, 1883), but differs from that species in the shape of the shell vestige, particularly in the muscle insertion, the digestive tract, the male

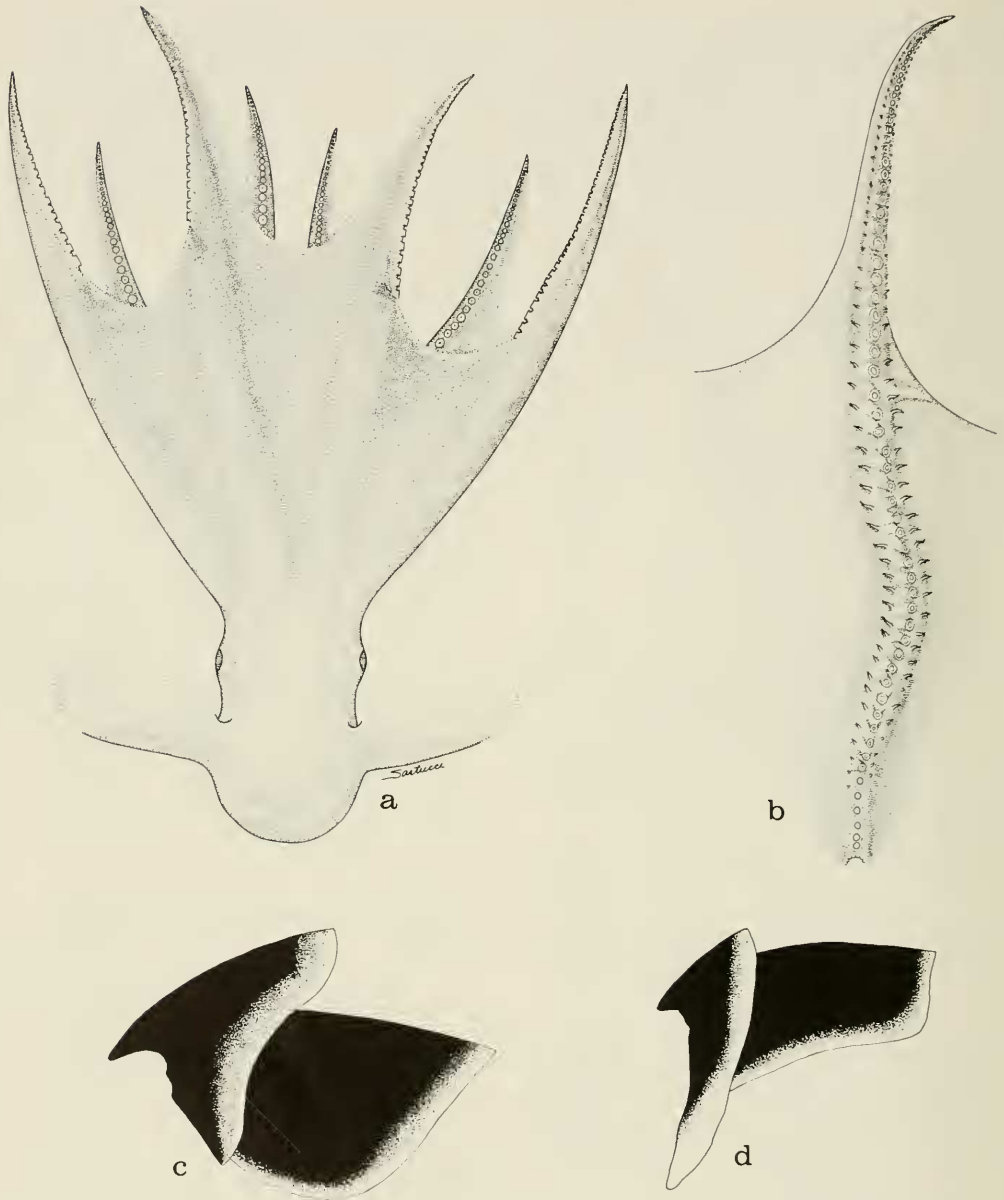


FIGURE 6. *Grimptoteuthis tuftsi* new species. (a) Dorsal view of male, 93 mm ML. (b) Oral view of left dorsal arm of same. (c-d) Upper and lower beaks of male, 72 mm ML.

genitalia, and the shape of the stellate ganglion. Examination of the syntypes in Museum National d'Histoire Naturelle, Paris, did not aid in clarifying the picture; the larger syntype had a different sucker arrangement but the shell vestige was missing; the syntype specimen may be a different species.

While many problems exist in the genus, pres-

ent material is sufficiently distinct to warrant description as a new species. The specific name *bathynectes* is from the Greek and means deep swimmer.

Thirteen specimens of *G. bathynectes* were collected from Tufts Abyssal Plain and two were from Cascadia Plain. Sampling effort was greater on the Cascadia Plain, hence this species inhabits

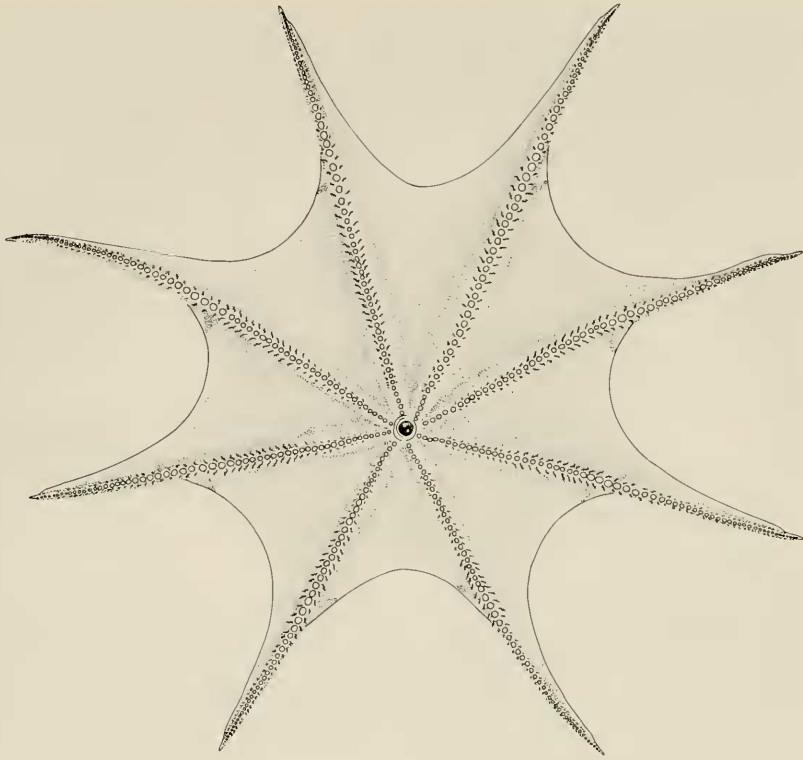


FIGURE 7. *Grimptoteuthis tuftsi* new species. View of web, arms and suckers.

deeper offshore waters and may be found in other abyssal waters of the North Pacific.

Grimptoteuthis tuftsi new species

(Figs. 6–8)

MATERIAL EXAMINED (7 specimens, all collected by R/V YAQUINA):—Holotype: male, ML 101 mm, Cr. Y7210A haul 305, 45°05.2'N, 134°43.4'W in 3,900 m, 9 Oct. 1972, USNM 730714. Paratypes: 1 male, ML 72 mm, Cr. Y7210A haul 300, 44°58.1'N, 132°14.7'W in 3,585 m, 6 Oct. 1972, UMML 31.1939.—1 male, ML 93 mm, Cr. Y7210A haul 302, 44°58.0'N, 133°14.5'W in 3,700 m, 7 Oct. 1972, CAS 067792.—1 male, ML 100 mm, Cr. Y7210A haul 306, 45°02.0'N, 134°42.2'W in 3,900 m, 9 Oct. 1972, SBMNH 35146.—1 female, ML 65 mm, Cr. Y7210A haul 307, 45°03.5'N, 134°45.0'W in 3,900 m, 10 Oct. 1972, UMML 31.1940.—2 females, ML 74–102 mm, Cr. Y7210A haul 305, 45°05.2'N, 134°43.4'W in 3,900 m, 9 Oct. 1972, USNM 817583.

DIAGNOSIS.—A *Grimptoteuthis* with long fins; long cirri; suckers largest distally at web border, suckers of males and females of equal size; gills loosely arranged, with 7–8 lamellae; radula present.

DESCRIPTION.—Mantle (Fig. 6a) saccular, flaccid, width nearly three-quarters length, rounded posteriorly; aperture moderately narrow (27–39%

ML); head wider than mantle, not set off by neck region; eyes large, protrude slightly.

Funnel large, broad, projects well beyond mantle margin, distal third or quarter free; funnel organ thick; \wedge -shaped pad covers most of funnel; olfactory organ distinct round tubercle on each side of funnel at corners of aperture.

Fins long, moderately wide, united to mantle about halfway from apex; posterior margin nearly straight for about three-quarters of its length, then turns forward; anterior margin rounded, tip somewhat pointed, base narrow, stout; muscular portion of fins extend for more than half fin length.

Arms somewhat gelatinous, moderately long, stout, deeply set in web. Arm formula generally I.II.III.IV, but varies.

Web (Fig. 7) simple, thick, fleshy; secondary web absent; web formula variable, generally ABCDE; web depth about half arm length; web unequal on two sides of arms (Fig. 6b): on dorsal side web extends nearly to tip of arm, on ventral side nodule or lappet present at about midpoint of arm, apparently strengthener for web attachment; web ends slightly distal to nodule.

Suckers (Fig. 8a) extend in single row from

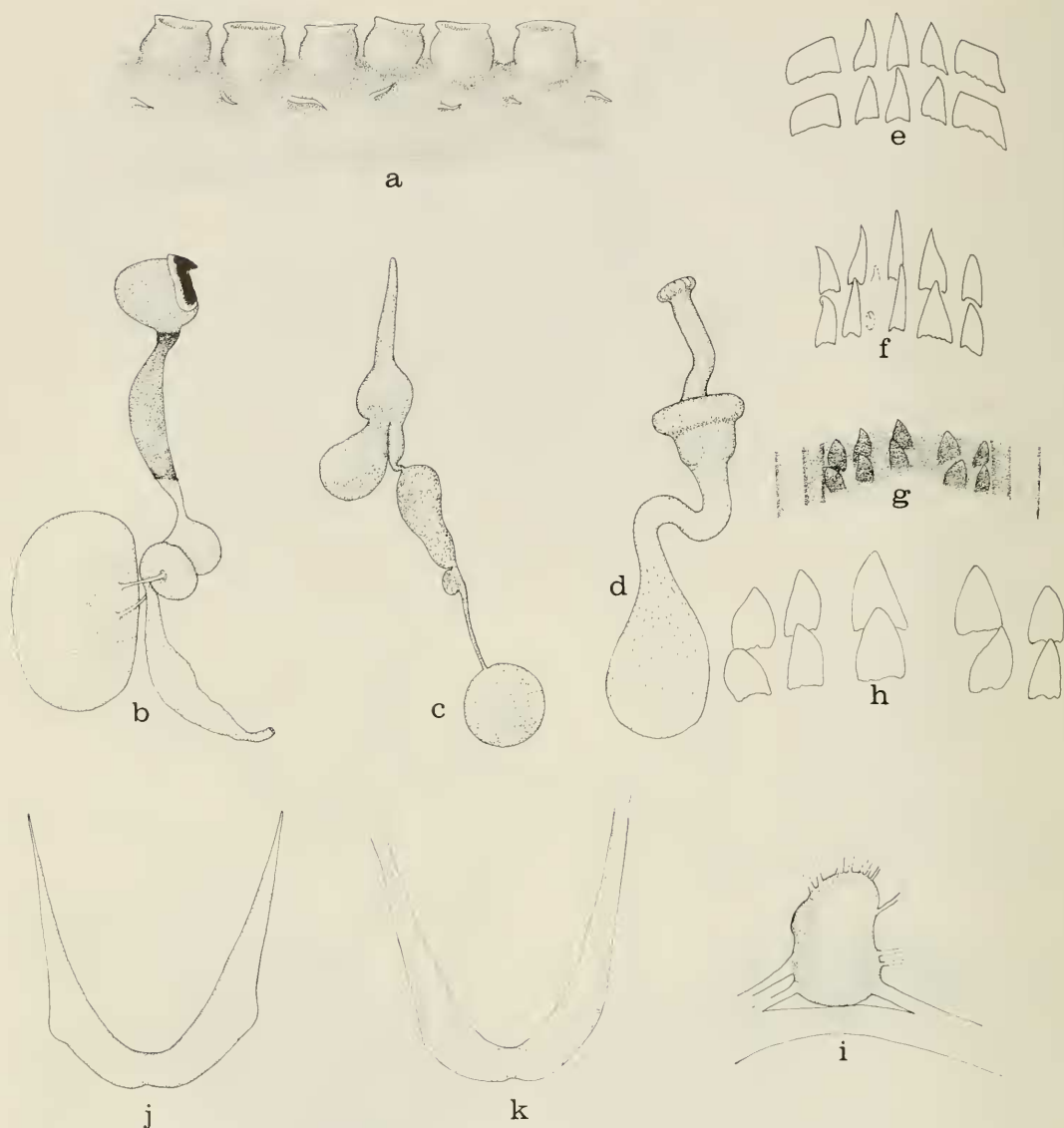


FIGURE 8. *Grimpoteuthis tuftsi* new species. (a) Lateral view of suckers and cirri of male, 93 mm ML. (b) Digestive tract of male, 72 mm ML. (c) Genitalia of male, 72 mm ML. (d) Genitalia of female, 65 mm ML. (e) Radula of male, 72 mm ML. (f) Radula of female, 65 mm ML. (g-h) Radula of male, 93 mm ML; g is uncleaned, h cleaned with ribbon transparent. (i) Stellate ganglion from right side of male, 100 mm ML. (j-k) Ventral and dorsal view of shell vestige of male, 72 mm ML.

mouth to tip of arms; dorsal arms with about 63 to 75 small suckers (SI_n 2.5–5.3) set into oral surface of arms with raised apertures; suckers cylindrical or tubular with small apertures, set about two to three sucker diameters apart in some sections but crowded together in others, united by thin transparent web or membrane along oral surface of arms (Fig. 8a). First 6–7 suckers small, then a gradual increase in size to their maximum

diameter at or just beyond level of ventral node. No sexual dimorphism (Tables 9, 10).

Cirri moderately long, longest 1.5 to 3.5 times longer than diameter of largest suckers; first appear between suckers 5 and 6, or 6 and 7 and extend to arm tip; difficult to distinguish near tip.

Median pallial adductor thin, narrow, length 5.4–11.8% mantle length. Gills nearly spherical

two ducts lead to large round digestive gland; digestive duct appendage prominent; intestine short, inflated; anal flaps and ink sac absent.

Male genitalia complex (Fig. 8c), differ from those of *G. bathynectes*; various glands and their numbering not yet determined; both genitalia similar, spermatophores absent.

Female genitalia (Fig. 8d) simple (immature); large, deflated, thin-walled ovary, eggs absent; proximal oviduct thick, comparatively short; oviducal gland large, two-parted, finely plicate; distal oviduct long, comparatively slender, aperture with flared, incised, or plicate collar.

Shell vestige (Fig. 8j, k) U- or rounded V-shape; stout, strong, somewhat constricted at posterior end; limbs angle slightly at outer posterior inception of fin insertion area, taper to thin, flat, straplike, truncated tips.

Stellate ganglion of male shown in Figure 8i.

Mantle and head pigmented light brownish purple, posterior borders of fins dark purple; web, arms darkish purple aborally, dark purple orally with lighter colored suckers and cirri.

MEASUREMENTS AND COUNTS. — Holotype: mantle length 101; mantle width 63; head width 73; arm length I 312, II 295, III 258, IV 239; total length 460; fin length 85; fin width 31; sucker diameter 2.5; cirrus length 9.0; number of gill lamellae 7; number of suckers on arm 63+.

Males: mantle length 72–91.5–101; mantle width 49–64–75; head width 60–83–101; arm length I 289–308–322, II 275–294.5–320, III 258–267.8–283, IV 217–244.5–261; total length 346–434.5–475; fin length 65–83.8–95; fin width 30–34.8–40; sucker diameter 2.5–3.7–4.5; cirrus length 6–8.0–9; number of gill lamellae 7–7.8–8; number of suckers on arm I 67–70.3–73.

Females: mantle length 65–80.3–102; mantle width 50–55.3–64; head width 60–68.3–78; arm length I 207–238.7–285; II 186–215.3–238; III 170–210–250, IV 208–253; total length 285–355–460; fin length 59–66.7–81; fin width 27–30.3–35; sucker diameter 2.5–2.7–3.0; cirrus length 5–6.7–9; number of gill lamellae 7–7.7–8; number of suckers on arm I 69–72.7–75.

TYPE. — Holotype, male, 101 mm ML, USNM 730714 (fixed in formalin and preserved in 50 percent isopropyl alcohol).

TYPE-LOCALITY. — Off Oregon on the Tufts Abyssal Plain, 45°05.2'N, 134°43.4'W, 3,900 m.

DISCUSSION. — *Grimptoteuthis tuftsi* is somewhat similar to *G. bathynectes* but many characters differentiate them. *Grimptoteuthis tuftsi* has:

lack of sexual dimorphism in sucker shape, longer cirri, different genitalia, more elongate gills with separate lamellae, enlarged suckers near nodules, larger funnel organ, and a radula.

The discovery of a radula in this species, unknown elsewhere in the cirrate octopods, requires a careful reexamination of all species, as its absence has been taken for granted by some earlier students of the group and may have been overlooked. It is obviously degenerate and in its simplicity, variability, and loss of teeth resembles the radula of *Graneledone pacifica* (described in this work) and *G. antarctica* (Voss, 1976). Similarly, the radulae of *Thaumeledone* and *Vosseledone* show degeneration in the near loss of all teeth except the rachidian. We hypothesize that in these genera the radula is degenerate and in the process of being lost because of diet and loss of selective pressure.

All specimens of *G. tuftsi* were caught in bottom trawls on Tufts Abyssal Plain, none in Cascadia Basin nearer the North American continent.

Suborder INCIRRATA Grimpe, 1916

Deep-sea, shallow-water, and pelagic octopods with gelatinous to muscular bodies; fins and cirri absent; shell, when present, reduced to pair of slender cartilaginous or calcareous stylets; radula present in all known species; suckers uniserial or biserial; representatives known from throughout world oceans.

Family OCTOPODIDAE Orbigny, 1845

Benthic octopods with semigelatinous to muscular bodies.

Subfamily BATHYPODIDAE Robson, 1928

Restricted to benthic octopods with biserial suckers; hectocotylus well developed; crop large with diverticulum reduced or absent; ink sac absent; radula *Octopus*-like to degenerate.

Benthoctopus Grimpe, 1921

Deepwater octopods of normal *Octopus*-like appearance with short to long arms; suckers biserial; hectocotylus *Octopus*-like, ligula slightly to moderately excavated with indistinct midrib, smooth or bearing low, often indistinct rugae,

never laminate; crop present, usually with diverticulum; ink sac absent; radula usually with strongly, seldom weakly, multicuspoid rachidian; body entirely smooth, papillae or ocular cirri absent.

TYPE SPECIES: *Octopus piscatorum* Verrill, 1879:470. By original designation, Grimpe 1921:299.

DISCUSSION.—Examination of Verrill's type specimen (USNM 574641) has shown that it probably is not a *Benthoctopus* but more likely belongs to *Bathypolypus* (personal observation by Voss). If this proves correct, the name *Benthoctopus* should be preserved to maintain nomenclatural stability in this group.

***Benthoctopus robustus* new species**

(Figs. 9, 10)

MATERIAL EXAMINED (2 specimens).—Holotype: male, ML 137 mm, R/V ACONA Sta. NAD22, 44°38.5'N, 126°03.8'W in 2,800 m, 1 June 1963, USNM 729994. Paratype: 1 male, ML 114 mm, 140 nautical miles off Tasu Sound, Queen Charlotte Island, B.C., Canada, 52°27'42"N, 135°34'36"W in 3,660 m, 16 Oct. 1978, in sablefish trap, E. Houde, USNM 730895.

DIAGNOSIS.—A *Benthoctopus* with large, strong, transversely ridged lingula; long, sharp calamus; radula with simple rachidian with cusps.

DESCRIPTION.—Body (Fig. 9a) compact, robust, muscular; mantle nearly round, about as wide as long (MWI 80.3), no distinct neck region; head small, narrow (HWI 51.8); eyes and eyelids small; mantle aperture wide.

Funnel large, free for about half of its length, aperture small; funnel organ (Fig. 9f) large, W-shaped, with long, pointed lateral limbs that project slightly anterior to large, round median limb.

Arms (Table 11) moderately long (MAI 64.3; ALI 56.7), stout at base (AWI 12.4), taper to stout, sharp tips, arm formula IV.I.II.III, subequal; web heavy, deep (WDI 34.7), extending along ventral side of arms for about two-thirds their length; web formula DBCAE; suckers biserial, erect on stout bases, well separated, rather small (SIn 5.1) for size of animal; enlarged suckers absent; dorsal arms with about 38–40 suckers.

Third right arm hectocotylized, shorter than its fellow (HcAI 85.1), stout, bordered ventrally by heavy, thickened, in-rolled web that forms incomplete spermatophoral groove, ligula (Fig. 9b) large (LLI 12.4), with deep groove and thickened margins crossed by 14–16 grooves and

membranous ridges or folds; calamus large, long, slender, sharply pointed (CLI 45.4).

Gills large with 11 lamellae per outer demibranch.

Upper beak with very small, sharp, curved rostrum (Fig. 9g); rostrum of lower beak forms right angle at jaw angle (Fig. 9h). Radulae with rachidian somewhat different from other Pacific *Benthoctopus* (Fig. 10d, e), rachidian simple, narrow, with smooth-sided, slender darkened portion bordered by narrow clear portion that bears small, irregular cusps, one on each side; admedians with tall sharp ectocone; inner edges of second laterals strongly, smoothly rounded in holotype, nearly straight in paratype; third laterals slender, sabre-like, curved.

Esophagus slender, leads into distinct crop with anterior diverticulum (Fig. 9d, e); crop of holotype unexpanded, without food; posterior esophagus expanded leading into large muscular stomach; spiral caecum small; digestive gland nearly spherical; intestine three-parted, middle section more inflated and larger than others; anal flaps and ink sac absent.

Male genitalia (Fig. 10a): penis very large (PLI 58.4) with long diverticulum; Needham's sac long, filled with incomplete spermatophores (spermatophore partially reconstructed in Fig. 10b); horn end with three tight turns at oral end (Fig. 10c).

Mantle, head, and arms smooth, cirri and papillae absent. Color in ethanol pale tan with light reddish-brown pigmentation on ventral side of head, around and on funnel, around eyes, and on web, which is darkish purple near margins; no color notes made at time of capture.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 137; mantle width 110; head width 71; length of longest arm (IV) 213; total length 375; length of hectocotylized arm 116.6; ligula length 14.5; calamus length 6.6; number of suckers on arm I 38–40; sucker diameter 7.0; depth of web sector D 73.9; penis length 80; number of gill lamellae in outer demibranch 11.

TYPE.—Holotype, male, 137 mm ML, USNM 729994 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Oregon, off Newport, eastern portion of Cascadia Abyssal Plain, 44°38.5'N, 126°03.8'W, 2,800 m.

DISCUSSION.—This species seems distinct from all other known species on the basis of the simple rachidian and the ligula. Elucidation of its rela-

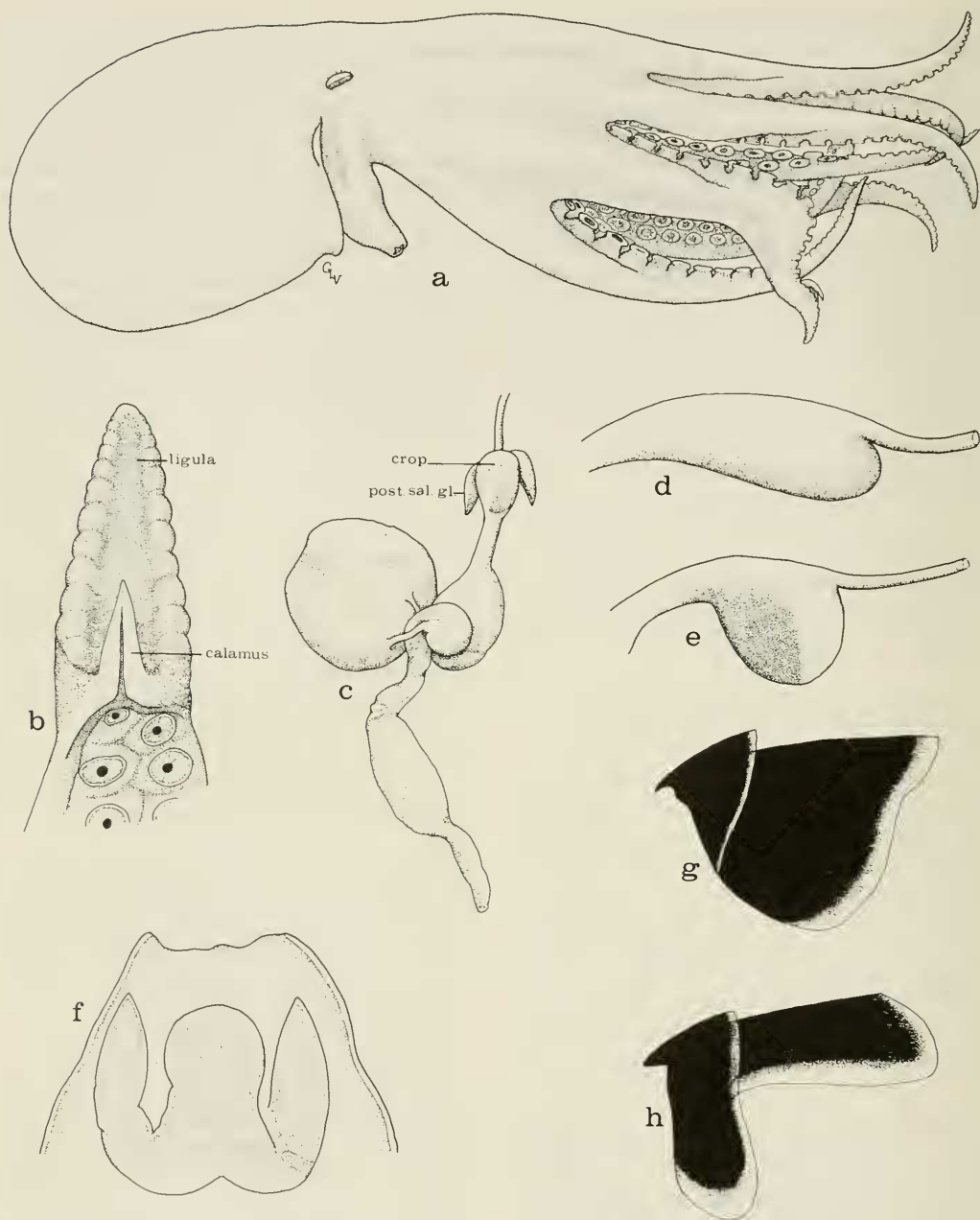


FIGURE 9. *Benthoctopus robustus* new species. (a) Lateral view of holotype, USNM 729994, male, 137 mm ML. (b) Ligula. (c) Digestive tract of paratype, USNM 730895, male, 49 mm ML. (d) Crop of holotype. (e) Crop of paratype. (f) Funnel organ of holotype. (g-h) Upper and lower beaks of holotype.

tionship within the genus must await more material and a full revision of the genus.

The specimen designated as the paratype was found in the collections of the USNM. It was examined to supplement the information on this

new species. Although taken somewhat farther north and in deeper water than the holotype, it corresponds very closely in the meristic counts and morphology of ligula, calamus, and funnel organ. The upper beak, however, has a smooth

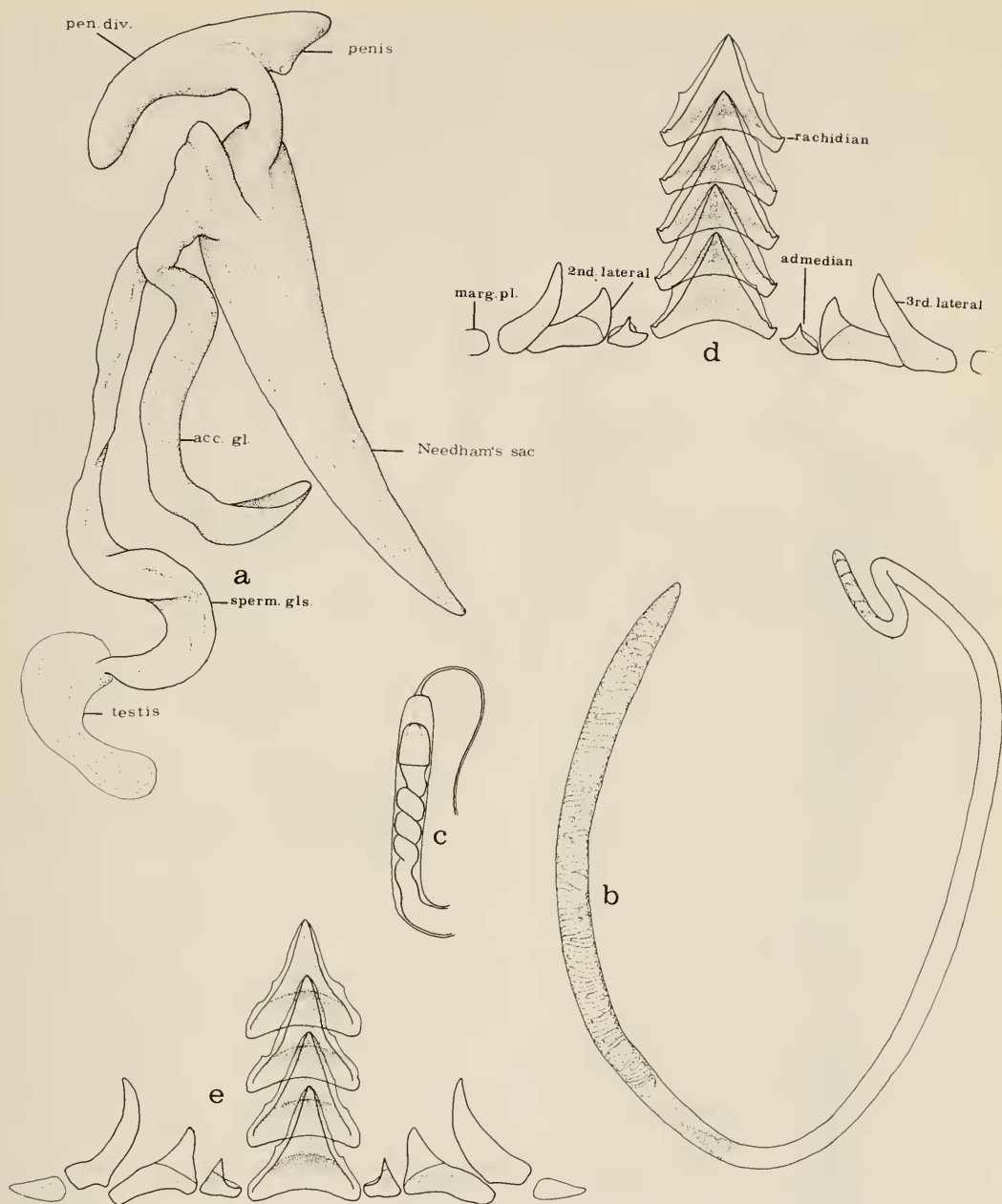


FIGURE 10. *Benthoctopus robustus* new species. (a) Genitalia of holotype. (b-c) Spermatophore of holotype. (d) Radula of holotype. (e) Radula of paratype.

jaw below the rostrum without the rounded tooth. The crest of the lower beak is a little shorter than in the holotype, and the hood wing is a little narrower. These differences probably represent individual variation.

***Benthoctopus canthylus* new species**

(Figs. 11, 12)

MATERIAL EXAMINED.—Holotype: female, ML 54 mm, R/V YAQUINA Cr. Y7102B haul 267, 44°58.1'N, 126°35.8'W in 2,795 m, 19 Feb. 1971, USNM 729993.

TABLE 11. Indices of bodily proportions, counts, and formulae of two male *Benthoctopus robustus*, new species.

	Holotype	Paratype
Mantle length	137	114
MWI	80.3	77
HWI	51.8	48
ALI	56.7	68
MAI	64.3	56
AWI	12.4	15.8
HcAI	85.1	80
LLI	12.4	12.9
CLI	45.4	38.0
WDI	34.7	35.0
SIn	5.1	5.7
PLI	58.4	57.9
Gills	11	11
Web order	DBCAE	CBDAE
Arm formula	4·1=2=3	3214

DIAGNOSIS.—A *Benthoctopus* with thick expansion of midportion of arms I, with greatly enlarged suckers, their diameter 16.3% of mantle length; lower beak with distinct ridge on lateral wall.

DESCRIPTION.—The following description is based upon the holotype and only known specimen. Body (Fig. 11a) (Table 12) firm, overlain by thin semigelatinous layer; mantle broadly elliptical, narrower than long (MWI 77.8); mantle opening wide; head noticeably narrower than mantle (HWI 64.8), no apparent neck region; eyes medium sized with small apertures; funnel moderate sized, free for about half its length, with small aperture; funnel-mantle locking mechanism weakly developed; funnel organ (Fig. 11c) W-shaped with lateral limbs equal in length to median section.

Arms long (MAI 25.1; ALI 74.7), slender (AWI 20.4), taper to fine tips; arms formula I.II.III.IV.; suckers biserial, about 60 pairs on dorsal arms; normal suckers distinct, well separated and small (SIn 6.3).

Dorsal arms (Fig. 11b) normal at base, taper gradually for about 40% of length; arm abruptly swollen for about 25% of length at level of 17th sucker pair; swollen area very muscular, elongate elliptical, with eight pairs of widely spaced, enlarged suckers (Sle 16.3), of which median two to seven pairs greatly enlarged with widely flared apertures; at 26th sucker pair, arm regains normal size and appearance, tapers distally to slender tip; both arms identically modified; other arms normal in all respects.

Web formula BCADE, web moderately deep

(WDI 23.7), extends along ventral side of each arm for little more than half arm length; forms rather strong membrane aborally on modified part of dorsal arms and, through contraction, curls modified area aborally.

Gills with 8 lamellae per outer demibranch, including terminal leaflet.

Digestive tract (Fig. 12a) with buccal mass of normal size; upper beak narrow, with sharp rostrum (Fig. 12b); lower beak with distinct groove on lateral wall (Fig. 12c); radula (Fig. 12d) with multicuspid rachidian with asymmetrically arranged cusps in B_{3-6} formula, cusps on upper part of tooth formed of transparent lamina on each side, lower ones darkened, total arrangement of cusps difficult to determine (usually two cusps on each side of rachidian); admedians with tall sharp ectocone; second laterals with inner heel; third laterals with no distinctive features.

Crop distinct, anteriorly lobed; posterior salivary glands paired on each side (Fig. 12a); stomach and spiral caecum approximately equal in size; digestive gland large, somewhat flattened dorsoventrally, nearly round, slightly bilobed posteriorly; large, inflated intestine strongly reflexed in mid portion; ink sac and anal flaps absent.

Female genitalia (Fig. 12e) with round ovary containing immature eggs, proximal oviducts short; oviducal glands enlarged and only slightly striated; distal oviducts approximately four times length of proximal portion.

Surface in preservation somewhat wrinkled, but no trace of sculpture on any part of body. Color of specimen in ethanol pale liver, slightly darker dorsally and on oral surface of web and arms.

MEASUREMENTS AND COUNTS.—Holotype: 54 mm ML, mantle width 42; head width 35; length of longest arm (I) 215; total length 288; depth of web sector B 51; sucker diameter (normal) 3.4 (enlarged) 8.8; gill lamellae in outer demibranch 8.

TYPE.—Holotype, female, 54 mm ML, USNM 729993 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, eastern portion of Cascadia Abyssal Plain, 44°58.1'N, 126°35.8'W, 2,795 m.

DISCUSSION.—When first examined, this specimen was tentatively identified as *Benthoctopus abruptus* (Sasaki, 1920). Examination of the type specimen (USNM 332935) did not entirely solve

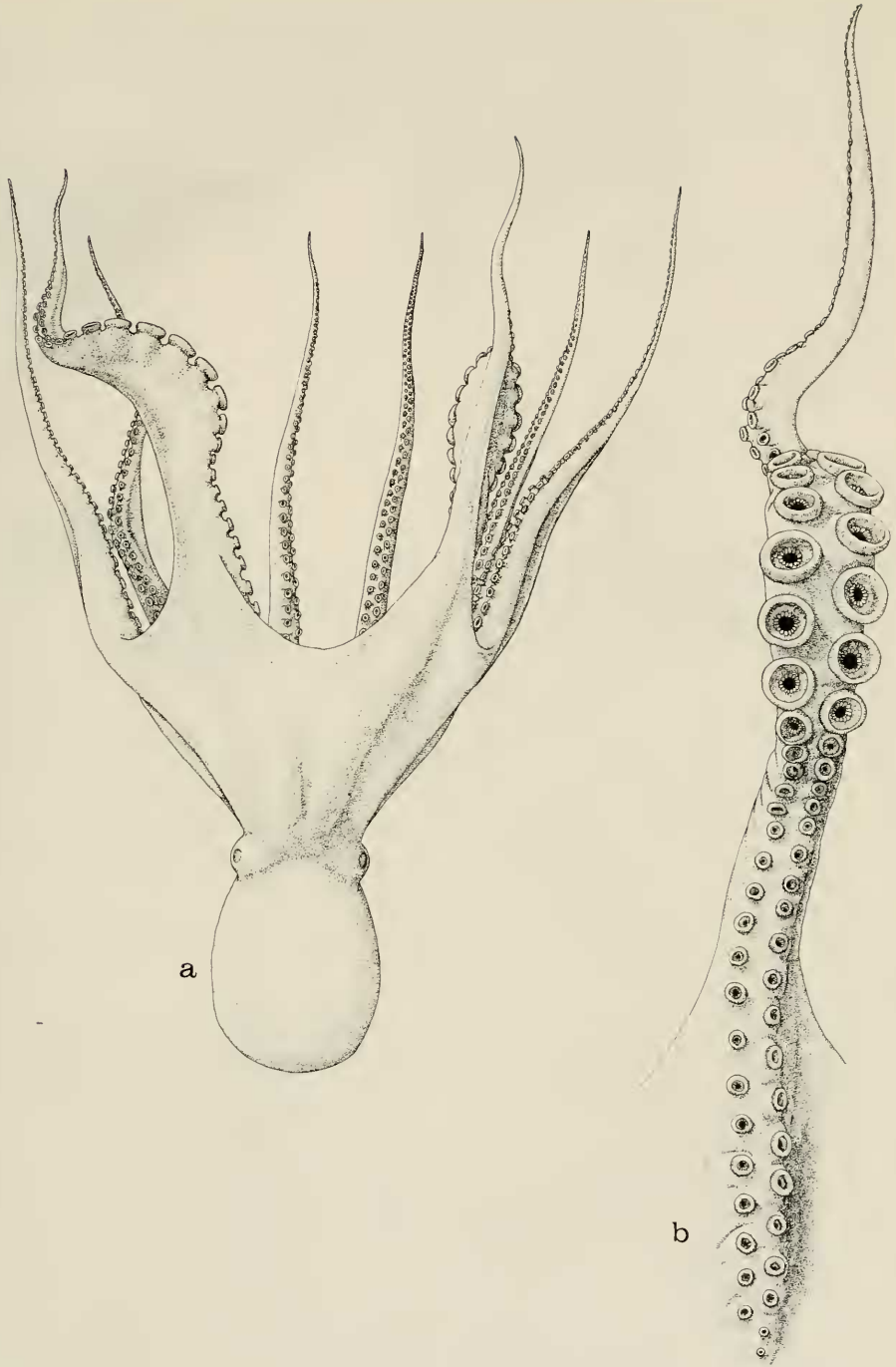


FIGURE 11. *Benthoctopus canthylus* new species. Holotype, USNM 729993, female, 54 mm ML. (a) Dorsal view. (b) Oral view of left dorsal arm.

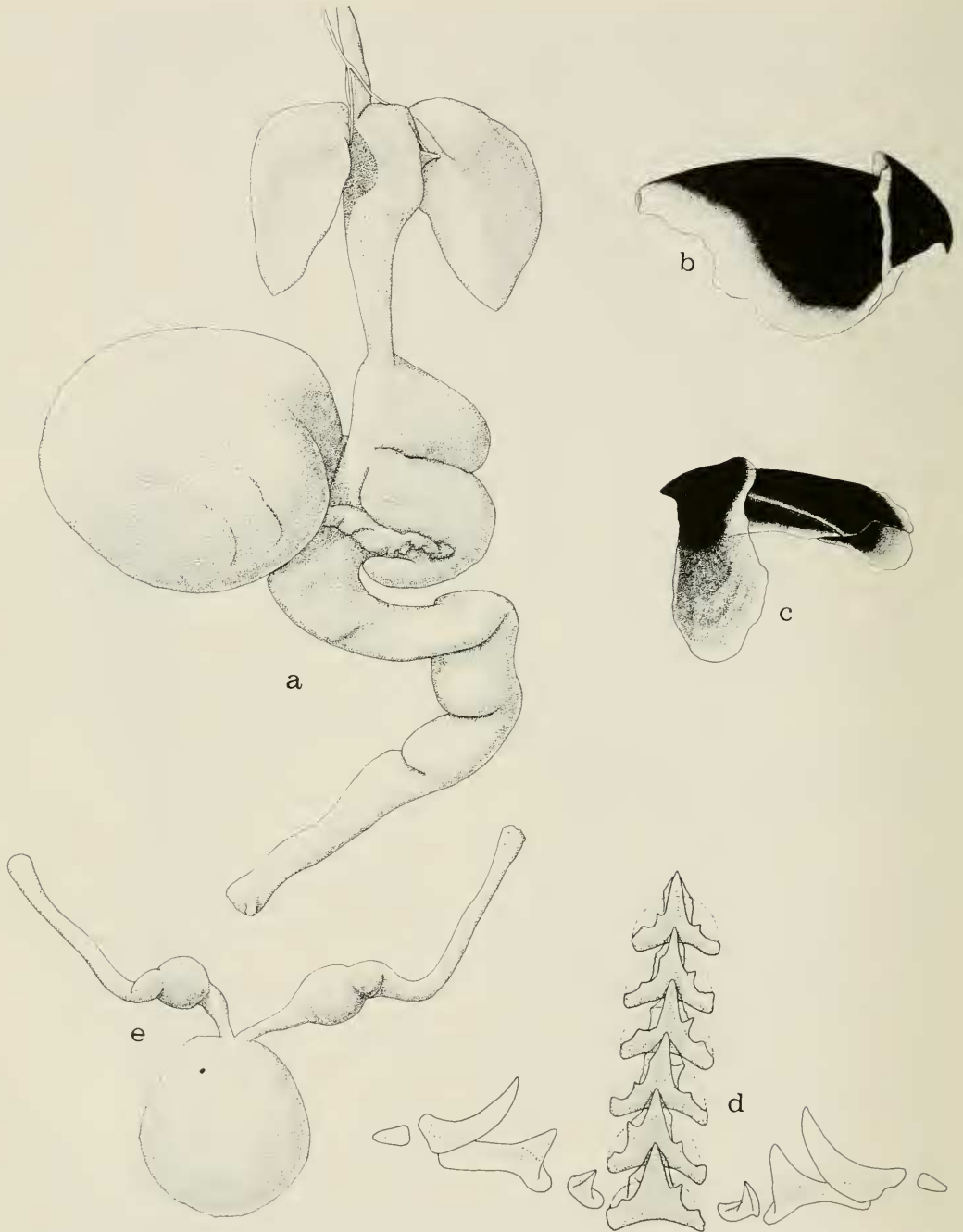


FIGURE 12. *Benthoctopus canthylus* new species. Holotype. (a) Digestive tract. (b-c) Upper and lower beaks. (d) Radula. (e) Genitalia.

the problem because of its poor condition. Dr. Takashi Okutani kindly placed at our disposal a fine series of *B. abruptus* from which it was possible to distinguish the present specimen. In males

of *B. abruptus*, the enlargement of the suckers is by no means as abrupt as in *B. canthylus* and the suckers are expanded differently, with wide, thin, almost leaflike rims. There is also no arm swell-

TABLE 12. Measurements (in mm), counts, and indices of the holotype (female) of *Benthoctopus canthylus* new species.

Mantle length	54		Web depth	
Mantle width	42		Sector A	43
Head width	35		Sector B	51
Arm length			Sector C	48
Arm length I	<u>L</u>	<u>R</u>	Sector D	38
Arm length II	210	215	Sector E	36
Arm length III	205	210		
Arm length IV	184	184		
Arm length IV	175	184	<u>Sucker diameter</u>	
Arm width	11		normal	3.4
Total length	288		enlarged	8.8
Mantle width index	77.8			
Head width index	64.8		Arm width index	20.4
Mantle arm index	25.1		Web depth index	23.7
Arm length index	74.7			
Arm formula	1234		<u>Sucker index</u>	
Web formula	BCADE		normal	6.3
Number of gills	8		enlarged	16.3

ing. The arm suckers in females are unmodified. The funnel organ is W-shaped but the outer limbs are only about half the length of the median portion. *Benthoctopus abruptus* has from 10 to 12 lamellae per outer demibranch, while there are 8 in *B. canthylus*.

Benthoctopus canthylus resembles no other known species of *Benthoctopus*. Unfortunately no males are present in the collection.

The specific name *canthylus* is derived from the Greek *kanthyle*, "swelling," and refers to the peculiar modification of the dorsal arms.

Benthoctopus oregonensis new species

(Figs. 13, 14)

MATERIAL EXAMINED (5 specimens).—Holotype: male, ML 93 mm, R/V YAQUINA Cr. 6606, 44°37.0'N, 125°01.0'W in 1,260 m, 6 Aug. 1966, USNM 729991. Paratypes: 1 female, ML 99 mm, R/V ACONA, 44°24.2'N, 125°10.3'W in 1,000 m, 14 Aug. 1964, CAS 061430.—1 female, ML 115 mm, R/V ACONA, 44°31.3'N, 125°05.4'W in 1,250 m, 15 Jan. 1965. Other material (2 specimens in very poor condition, one partly eaten and both mauled in the net): 1 male, ML 62 mm, R/V ACONA, 44°36'N, 126°06.9'W in 3,000 m, 30 Dec. 1963, UMML 31.1943.—1 male, ML 56 mm, R/V ACONA, 44°36'N, 126°06.9'W in 3,000 m, 30 Dec. 1963.

DIAGNOSIS.—A *Benthoctopus* with stout, transversely ridged ligula; short, blunt calamus; thick, stout funnel organ; 11 gill lamellae in outer demibranch; radula with rachidian with asymmetrical B₃ seriation.

DESCRIPTION.—Body large; mantle globose (Fig. 13a), little narrower than long; head small with prominent, non-projecting eyes; head width considerably narrower than mantle width. Fun-

nel large, stout, free for one-third of its length; funnel organ (Fig. 13b, c) √-shaped, small, compact, rounded, lateral limbs shorter than level of mid-portion of organ (nearly level in some specimens).

Arms (Tables 13 and 14) long (ALI males 81.0–82.3–83.3; females 78.6–82.8–87.1; MAI males 19.3–20.7–22.0; females 22.5–24.3–26.1); arms stout, somewhat rounded in cross-section; soft consistency; arm formula I.II.III.IV. Suckers small (SIn males 5.4–7.4–8.6; females 6.1–6.7–7.6), deeply set into oral surface of arms, protrude somewhat toward ends of arms.

Hectocotylized arm much shorter than its fellow (HcAI 66.7–73.0–81.8); ligula (Fig. 14b, c) short, pointed (LLI 5.0–5.8–6.7), with swollen, inturned margin; oral surface crossed by numerous fine ridges or folds; calamus short (CLI 41.7–42.1–43.0), with short, blunt spout; spermatophoral groove well developed, formed by deep, strong membrane that in preserved specimens curls hectocotylized arm strongly inward.

Upper beak (Fig. 13d) with pronounced terminal hook of rostrum; lower beak (Fig. 13e) with jaw angle of 90°. Radula (Fig. 14a) with prominent rachidian with two sharp cusps on either side, arranged asymmetrically in B₃ seriation; first laterals small, with poorly developed ectocone and endocone; second laterals with sharp prominent endocone and long base; third laterals sharply pointed, sabre-shaped; marginal plates well developed but small, somewhat rectangular.

Esophagus exits buccal mass between large circular anterior salivary glands (Fig. 13f), leads

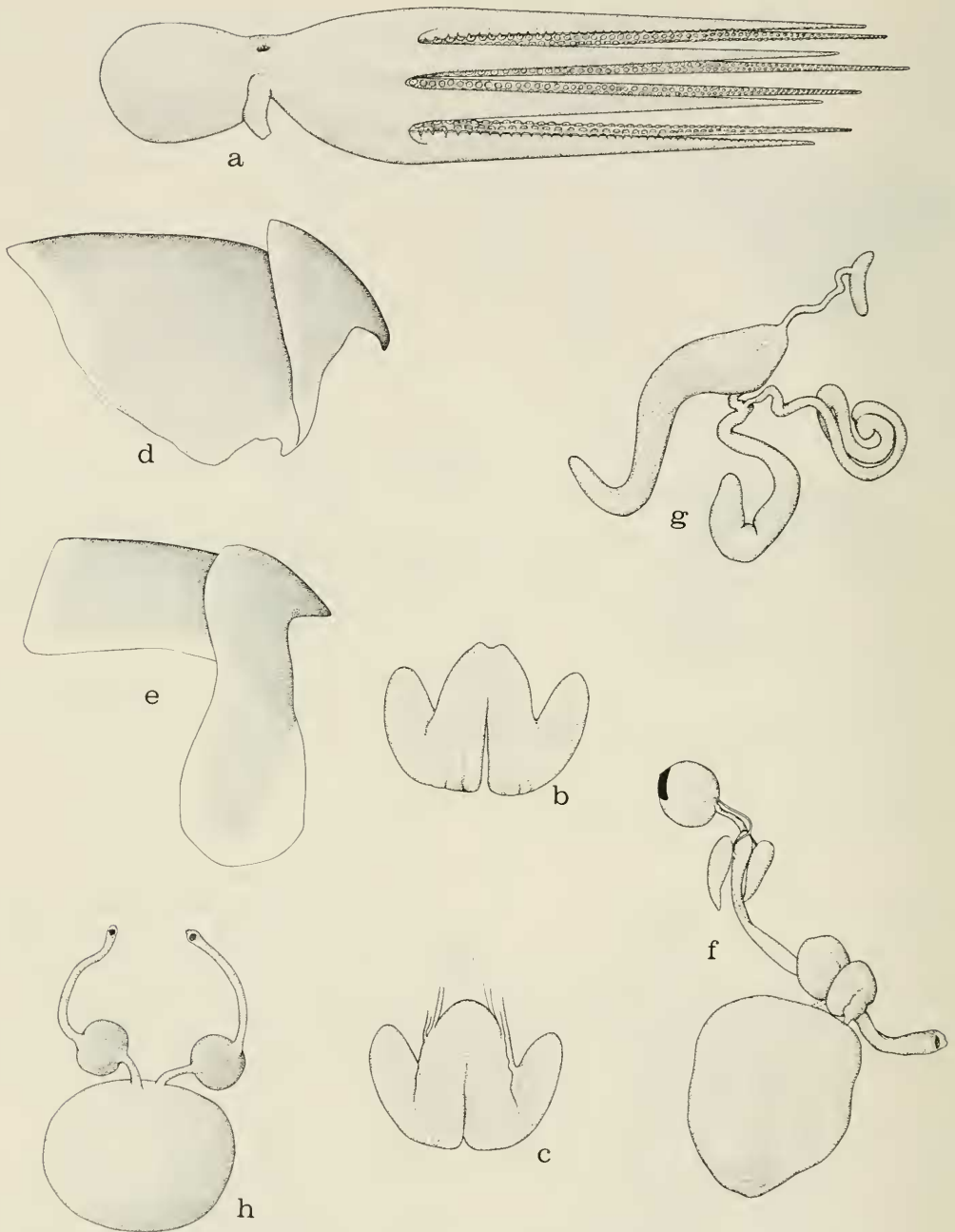


FIGURE 13. *Benthoctopus oregonensis* new species. (a) Lateral view of female, 99 mm ML. (b) Funnel organ of holotype, USNM 729991, male, 93 mm ML. (c) Funnel organ of male, 99 mm ML. (d-e) Upper and lower beaks of holotype. (f) Digestive tract of male, 62 mm ML. (g) Genitalia of holotype, male. (h) Genitalia of female, 99 mm ML.

posteriorly to well-developed crop with anterior diverticulum; posterior salivary glands large, triangular; stomach stout, about one-third larger than spiral caecum; digestive gland very large,

rounded; intestine large, inflated; anal flaps and ink sac absent.

Penis (Fig. 13g) remarkably small in mature animal (PLI 18.3), nearly straight with divertic-

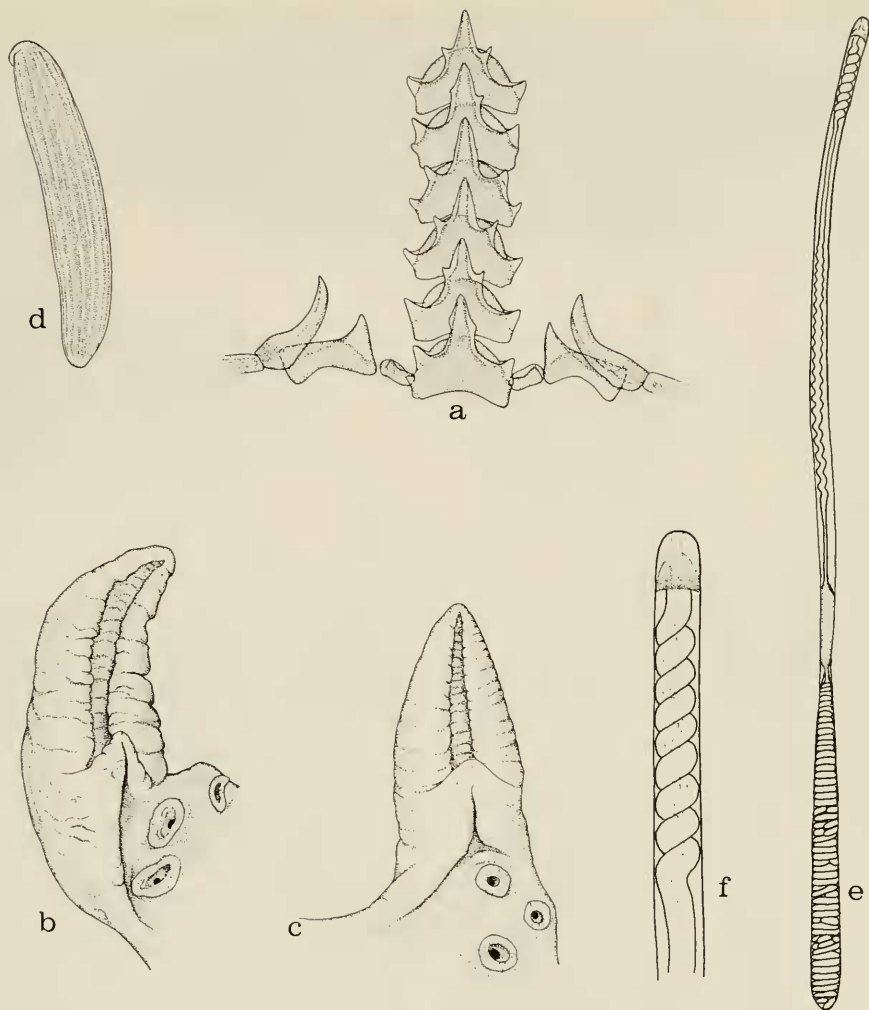


FIGURE 14. *Benthoctopus oregonensis* new species. (a) Radula of holotype. (b) Ligula of same. (c) Ligula of male, 56 mm ML. (d) Egg of female, 99 mm ML. (e–f) Spermatochore of male, 62 mm ML.

ulum about two-thirds of total length. Spermatochores (Fig. 14e, f) long, slender (SpLI 79.6; SpWI 1.6; SpR 32.4); anterior half of horn composed of tightly wound tube of multiple whorls, posterior half of horn straight; about eight tight coils at oral end; sperm mass heavily wound, reservoir slender.

Eggs in females ripe or near-ripe, dark vinous red, lightly striated (Fig. 14d), maximum size 26×6 mm, slender, pointed with clear short stalk; short (Fig. 13h) proximal oviducts lead to comparatively enormous round, dark oviducal glands; distal oviducts slender, three to four times longer than proximal oviducts.

Color in ethanol deep reddish brown to vinous red over most of body, including arms; lighter under head and around funnel; dorsal surface of mantle and head slightly lighter than ventrum, but not distinctly countershaded.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 93, mantle width 70.7; head width 63.3; length of longest arm (I) 421; total length 525; sucker diameter 5.0; depth of deepest web sector (B) 88.4; number of gill lamellae in outer demibranch 11.

TYPE.—Holotype, male, 93 mm ML, USNM 729991 (fixed in formalin and preserved in 50% isopropyl alcohol).

TABLE 13. Indices of bodily proportions and counts of three males of *Benthoctopus oregonensis* new species.

	Specimen			
	—	UMML 31.1943	USNM 729991	
ML	56+	62	93	56.0-70.3-93.0
MWI	98.2	95.2	76.0	76.0-89.8-98.2
HWI	83.9	82.3	68.0	68.0-78.1-83.9
MAI	19.3	20.7	22.0	19.3-20.7-22.0
ALI	82.6	83.3	81.0	81.0-82.3-83.3
AWI	26.8	22.6	20.0	20.0-23.1-26.5
WDI	22.8	25.3	21.0	21.0-23.0-25.3
SIn	8.6	8.2	5.4	5.4-7.4-8.6
HcAI	81.8	66.7	70.6	66.7-73.0-81.8
MHI	31.1	34.4	38.8	31.1-34.8-38.8
LLI	5.6	6.7	5.0	5.0-5.8-6.7
CLI	43.0	41.7	41.7	41.7-42.1-43.0
PLI	—	—	18.3	
SpLI	—	—	79.6	
SpWI	—	—	1.6	
SpRI	—	—	32.4	
AF	1234	1234	1234	
WF	ACDBE	CDABE	BACDE	
Gills	11	11	11	

TYPE-LOCALITY.—On the continental slope off Yaquina Bay, Oregon, 44°37.0'N, 125°01.1'W, 1,260 m.

DISCUSSION.—*Benthoctopus oregonensis* is represented by five specimens, all of which show remarkable homogeneity and very little variation in any of their characters. Their identity, however, offered considerable difficulty because of the confusing descriptions of the possibly closely related taxa *B. profundorum* (Robson, 1932) and *B. hokkaidensis* (Berry, 1921).

Benthoctopus oregonensis can be distinguished from *profundorum* by the former's larger number of gill lamellae (11 vs. 6), and a \surd -shaped fun-

nel organ against a W for *profundorum*. *B. oregonensis* can be distinguished from *hokkaidensis* by its short penis, PLI 18.3 vs. PLI 35; its thick, compact, funnel organ vs. a thin loose one; and by the details of the radula. Neither Sasaki (1929) nor Robson (1932) described the radula of *hokkaidensis*, of which few specimens have been recorded. The radula was extracted from the type of *hokkaidensis* (= *Polypus glaber* Sasaki, 1920: 172) (USNM 332981). The slender rachidian has two cusps on each side of the mesocone in an A₂ seriation. The first lateral has a high narrow ectocone. The second lateral is nearly triangular with a short base, while the third lateral is long and very slender. Marginals are present.

The specific name *oregonensis* is given in recognition of the species' occurrence off the state of Oregon, as well as in honor of the Oregon State University research ships that captured the specimens.

This species occurs on both the continental slope (1,000-1,260 m) off Oregon and the Cascadia Abyssal Plain, 85 nautical miles off the Oregon coast.

Benthoctopus yaquinae new species

(Figs. 15, 16)

MATERIAL EXAMINED (15 specimens).—Holotype: male, ML 90 mm, R/V ACONA Cr. 6501 haul 49, 44°48.8'N, 125°59.5'W in 2,800 m, 12 Jan. 1965, USNM 729992. Paratypes: 1 male, ML 67 mm, R/V YAQUINA, 45°21.6'N, 127°35.7'W in 2,800

TABLE 14. Indices of bodily proportions and counts of two females of *Benthoctopus oregonensis* new species.

	Specimen		
	CAS 061430	—	
ML	99	115	99-107-115
MWI	89.0	80.0	80.0-84.5-89.0
HWI	65.0	57.4	57.4-61.2-65.0
MAI	22.5	26.1	22.5-24.3-26.1
ALI	87.1	78.6	78.6-82.8-87.1
AWI	19.2	18.3	18.3-18.8-19.2
WDI	24.3	22.7	22.7-23.5-24.3
SIn	7.6	6.1	6.1-6.7-7.6
AF	2134	1234	
WF	BACDE	BCADE	
Gills	11	11	

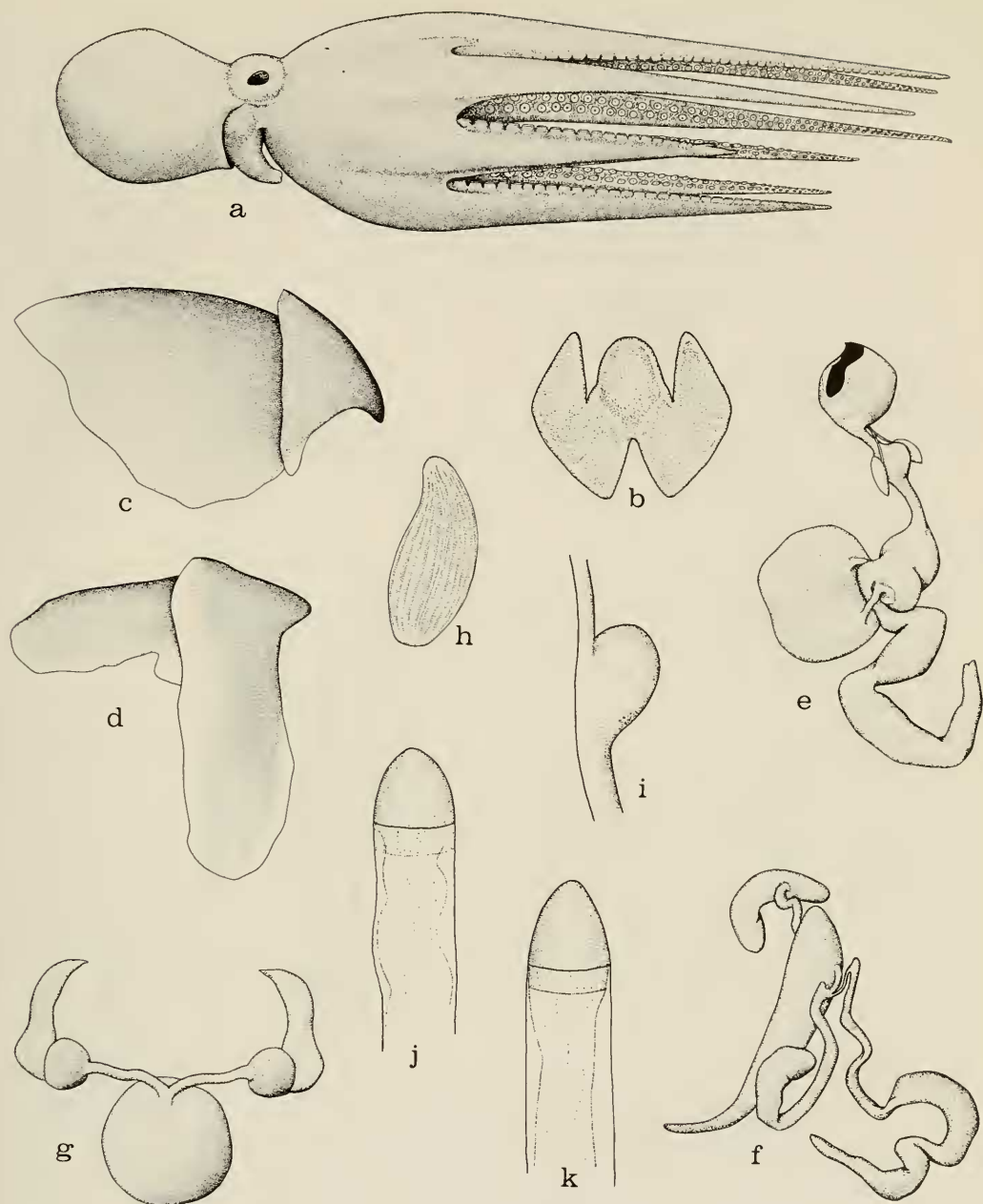


FIGURE 15. *Benthoctopus yaquinae* new species. (a) Lateral view of male, 78 mm ML. (b) Funnel organ of same. (c-d) Upper and lower beaks of male, 78 mm ML. (e) Digestive tract of male, 58 mm ML. (f) Genitalia of same. (g) Genitalia of female, 80 mm ML. (h) Egg of same. (i) Crop of male, 58 mm ML. (j-k) Distal ends of spermatophores.

m, 18 June 1967.—1 male, ML 81 mm, R/V YAQUINA, 45°21.6'N, 127°35.7'W in 2,800 m, 15 May 1971, CAS 061432.—1 male, ML 81 mm, R/V YAQUINA, 44°58.7'N, 124°42.3'W in 2,970 m, 19 Mar. 1970.—1 male, ML 83 mm, R/V YAQUINA Cr. Y72206B haul 294, 43°45.6'N, 125°26.0'W in 3,000 m, 17 June 1972, UMML 31.1945.—1 male, ML 89

mm, R/V YAQUINA Cr. Y7105B haul 278, 45°24.0'N, 127°39.0'W in 2,811 m, 18 May 1971, UMML 31.2544.—1 male ML 82 mm, 1 female ML 23 mm, R/V YAQUINA, 44°06.4'N, 125°24.5'W, in 2,938 m, 15 June 1972.—1 male ML 78 mm, 1 female ML 38 mm, R/V YAQUINA Cr. Y7206B haul 288, 44°06.2'N, 125°22.7'W in 2,940 m, 14 June 1972,

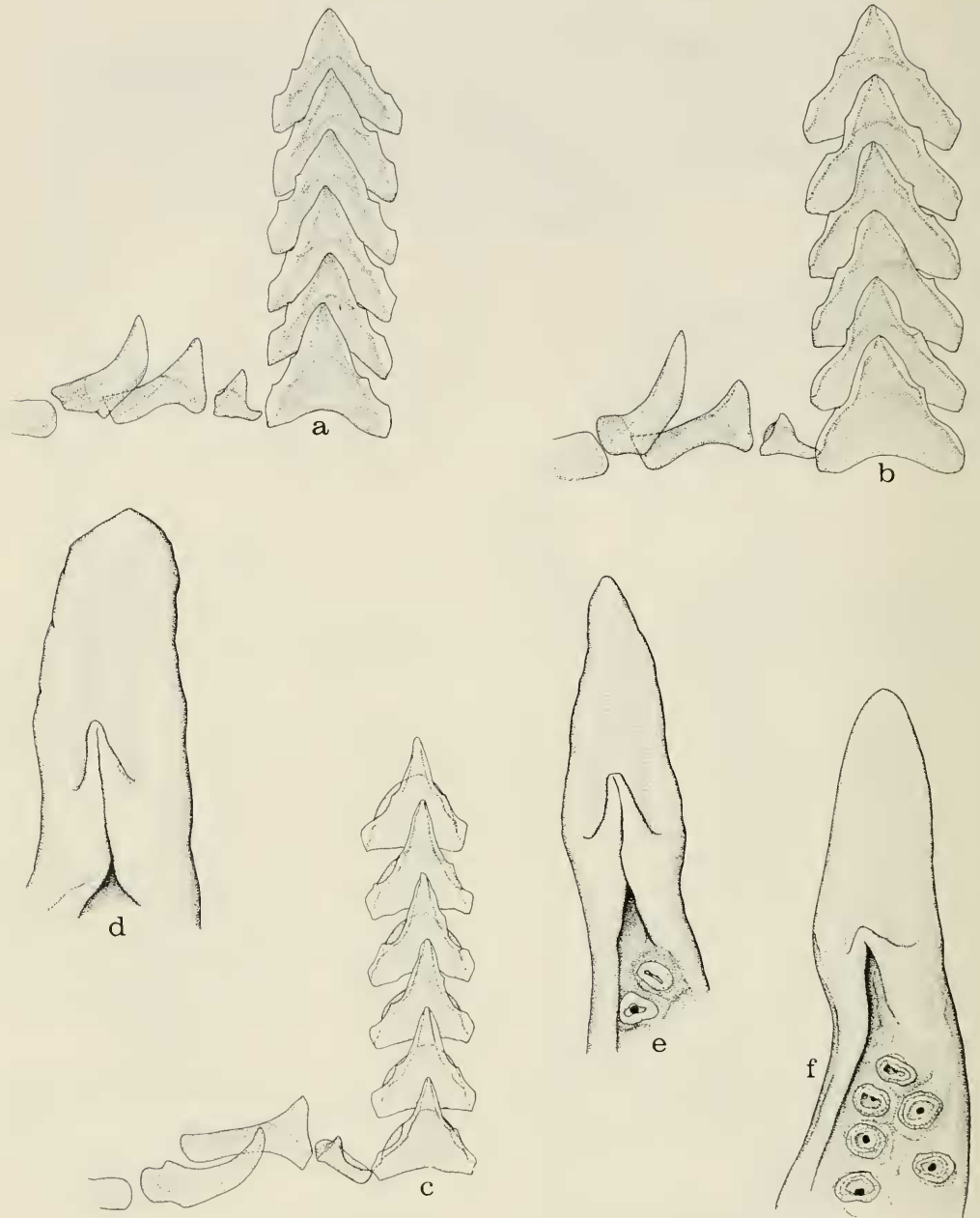


FIGURE 16. *Benthoctopus yaquinae* new species. (a) Radula of male, 78 mm ML. (b) Radula of male, 81 mm ML. (c) Radula of male, 83 mm ML. (d) Ligula of male, 81 mm ML. (e) Ligula of male, 67 mm ML. (f) Ligula of male, 78 mm ML.

UMML 31.2543.—1 female, ML 40 mm, R/V YAQUINA, 44°04.0'N, 125°23.8'W in 2,992 m, 15 June 1972, CAS 061432.—1 female, ML 110 mm, R/V ACONA, 44°39.2'N, 127°27.6'W in 2,800 m, 9 Feb. 1965.—1 female, ML 80 mm, R/V YAQUINA Cr. Y7105B haul 281, 44°38.5'N, 127°39.0'W in 2,816 m, 19 May 1971, UMML 31.1944. Other material: 2 males, ML 30–35 mm, R/V ACONA, 44°24.2'N, 125°10.3'W in 1,000 m, 14 Aug. 1964.

DIAGNOSIS.—A *Benthoctopus* with long, smooth ligula with no transverse ridges and short calamus; rachidian of radula broad with low cusps in irregular asymmetrical seriation; gills with 7–9 lamellae per outer demibranch.

DESCRIPTION (all indices for males are for 11

TABLE 15. Indices of bodily proportions of eight males of *Benthoctopus yaquinae* new species, and other data.

	Specimen							
	30	35	67	78	81	81	82	UMML 31.1945
ML	76.7	68.6	85.1	71.8	85.1	85.2	77.0	83
MWI	83.3	74.3	73.1	53.9	65.4	64.2	60.0	74.7
HWI	32.3	33.7	23.9	32.5	27.0	25.3	31.5	62.7
MAI	77.5	68.9	79.6	75.0	77.7	78.8	75.0	28.6
ALI	20.0	19.4	20.9	23.1	19.8	18.5	24.4	76.7
AWI	30.0	31.7	24.3	25.4	24.0	28.8	26.0	15.7
WDI	6.3	4.9	7.5	6.4	5.2	7.2	6.1	28.3
SIn	73.6	—	72.0	73.9	76.4	73.7	69.0	6.0
HcAI	46.9	41.7	37.2	45.9	38.6	38.6	46.1	76.9
MHI	11.1	9.2	11.1	11.8	10.5	9.1	8.4	41.5
LLI	32.1	44.2	50.0	35.0	31.8	47.4	46.7	9.0
CLI	31.6	33.1	64.2	43.6	49.4	61.7	36.6	36.1
PLI	—	—	—	106.4	—	—	—	51.8
SpLI	—	—	—	3.6	—	—	—	136.1
SpWl	—	—	—	45.8	—	—	—	3.5
SpRI	—	—	—	2134	1234	1234	—	31.0
AF	—	—	—	CDBA=E	ABCADE	CBABDE	1234	1234
WF	—	—	—	8	8	9	B=C=DAE	CDABE
Gills	7	7	9	8	8	9	9	8

TABLE 16. Ranges and means of indices of eight males of *Benthoctopus yaquinae* new species, grouped by sizes (ML) of animals.

	N		
	2	2	4
ML	30.0-32.5-35.0	67.0-72.5-78.0	81.0-81.8-83.0
MWI	68.6-72.7-76.7	71.8-78.5-85.1	74.7-80.5-85.2
HWI	74.3-78.8-83.3	53.9-63.5-73.1	60.0-63.1-65.4
MAI	32.3-33.0-33.7	23.9-28.2-32.5	25.3-28.1-31.5
ALI	68.9-73.2-77.5	75.0-77.3-79.6	75.0-77.1-78.8
AWI	19.4-19.7-20.0	20.9-22.0-23.1	15.7-19.6-24.4
WDI	30.0-30.9-31.7	24.3-24.9-25.4	24.0-26.8-28.8
SIn	4.9-5.6-6.3	6.4-7.0-7.5	5.2-6.1-7.6
HcAI	—	72.0-73.0-73.9	69.0-74.0-76.9
MHI	41.7-44.3-46.9	37.2-41.6-45.9	38.6-41.2-46.1
LLI	9.2-10.2-11.1	11.1-11.5-11.8	8.4-9.3-10.5
CLI	32.1-38.2-44.2	35.0-42.5-50.0	31.8-40.5-47.4
PLI	31.6-32.4-33.1	43.6-53.9-64.2	36.6-49.9-61.7

specimens, including the eight in Table 15, the holotype, and two additional specimens of 83 and 89 mm ML).—Body medium to large (Tables 15 and 16) with soft, somewhat flabby consistency (some specimens firmer); mantle (Fig. 15a) globose, wide (MWI males 68.6-80.3-89.2; females 65.2-76.9-88.5); head small (HWI males 53.9-66.0-83.3; females 51.8-63.7-87.5) with prominent, somewhat protruding eyes and distinct neck section. Funnel large, stout, about distal one-quarter free; funnel organ (Fig. 15b) large, W-shaped, with slender pointed lateral limbs level with, or slightly larger than, anteriorly rounded inner limbs. In some specimens limbs narrow, sharp, with flat organ, but in most organ raised; central and outer limbs padlike with raised rims.

Arm of moderate length (MAI males 25.3-29.6-33.7; females 29.6-34.5-40.0; ALI males 68.9-75.6-79.6; females 68.8-76.1-77.9), soft to muscular, squarish in cross-section (AWI males 13.9-19.1-24.4; females 17.4-19.8-22.5). Arm formula I.II.III.IV, with only two exceptions. Suckers small (SIn males 4.8-5.9-7.5; females 3.6-5.8-7.9), erect, and protrude over most of arm length.

Web formula variable, commonly BCDAE, with B or C usually longest and E always shortest; web shallow (WDI males 24.0-27.1-31.7; females 26.7-28.5-33.4) but extends along ventral side of arms I-III nearly to their tips, inconspicuous on IV.

Hectocotylized arm shorter than its fellow (HcAI 64.1-72.6-76.9; MHcAI 37.2-43.8-55.3); ligula (Fig. 16d-f) large LLI (8.4-10.2-11.8), pointed, flattened, with low median ridge; no

transverse rugae (although some light lines present); calamus small (CLI 31.8-40.5-50.0), well developed, sharply pointed; spermatophoral groove distinct, membrane narrow near midpoint of arm.

Buccal mass exceptionally large; upper beak (Fig. 15c) not distinctive; lower beak (Fig. 15d) with obtuse jaw angle, some with only a shallow smooth curve, low ridge on lower edge of lateral wall.

Radula large, teeth strongly pigmented (Fig. 16a-c). Main modification occurs on rachidian tooth: base broad, stout, darkly pigmented, with somewhat smooth-sided outline; sides of rachidian with supplementary clear rim wholly or partially toothed; dentition variable, usually with two cusps on each side; rachidians with irregular asymmetrical seriation; first laterals with high, very prominent ectocone; second laterals with broad, curved, bladelike endocones on heavy base; third laterals short, sabrelike, rather sharply pointed; marginals vary from elongate-rectangular plates to short buttons.

Buccal mass large (Fig. 15c); anterior salivary glands prominent at base of buccal mass on each side of esophagus; anterior section of esophagus short, stout, followed by small, distinct, anteriorly-lobed crop (Fig. 15i); posterior salivary glands on each side of crop small, elliptical, slightly pointed at each end; stomach large, thick-walled. Stomach and spiral caecum approximately equal in size, closely joined; two ducts from stomach-caecum lead into digestive gland; digestive gland nearly round in outline, but partially divided into two lobes by shallow median

TABLE 17. Indices of bodily proportions of five females of *Benthoctopus yaquinae* new species, and other data.

	Specimen				
	—	UMML 31.2543	CAS 061432	UMML 31.1944	—
ML	23	38	40	80	110
MWI	65.2	79.0	80.0	88.5	71.8
HWI	52.2	65.8	87.5	61.3	51.8
MAI	37.0	34.9	29.6	31.1	40.0
ALI	74.7	77.9	75.0	73.4	68.8
AWI	17.4	18.4	22.5	22.5	18.2
WDI	32.3	29.4	26.7	30.7	33.4
SIn	6.1	5.3	7.9	6.3	3.6
AF	1234	1234	1234	1234	1234
WF	DC=BA-E	ACBDE	C=DB=AE	BCDAE	DCBAE
Gills	9	7	8	8	8

depression; intestine divided into two large, thin-walled sections followed by somewhat narrower distal section; anal flaps and ink sac absent.

Gills large, with 7–9 lamellae per outer demi-branch.

Penis (Fig. 15f) large (PLI 31.6–48.9–67.5), blunt anteriorly with long, broad, blunt diverticulum; penis and diverticulum form slight to strongly bowed curve; Needham's sac large, about twice length of large penial apparatus; accessory gland as long as Needham's sac, well developed with small distinct appendix; seminal glands large, distal half divided into two well-developed, separate sections, proximal half slender, unites to accessory gland slightly posterior to appendix.

Spermatophores long (SpLI 106.4–126.4–136.1), stout (SpWI 2.5–3.3–3.6); sperm reservoir stout, thin-walled, occupies one-third to nearly one-half total length of spermatophore; horn section thick-walled, strong; tube straight with no turns; head (Fig. 15j, k) somewhat pointed with pigmented ring or band around posterior margin.

Proximal oviducts short, narrow, widen perceptibly at junction with small, gray, oviductal glands followed by broad distal oviducts; distal oviducts about three times length of proximal oviducts in largest female, about equal in smaller specimen illustrated (Fig. 15g). Eggs ripe or nearly ripe (Fig. 15h), about 12 × 3.8 mm, bluntly pointed posteriorly, brown with light tan stripes; stalk short, flesh colored.

Surface of body smooth, devoid of sculpture. Color distinctly reverse countershaded; pale slate gray on dorsal arms, head, and mantle; ventral surface and oral surface of arms and web dark bluish red; reverse countershading probably an adaptation to light-colored muds of ocean floor

where animal lives and to near-bottom bioluminescence.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 90; mantle width 66; head width 53; length of longest arm (I) 280; total length 365; length of hectocotylized arm 185; ligula length 21.5; calamus length 8.0; sucker diameter 4.5; depth of deepest web sector (A) 88; gill lamellae per outer demibranch 8.

TYPE.—Holotype, male, 90 mm ML, USNM 729992 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, eastern portion of Cascadia Abyssal Plain, 44°44.8'N, 125°59.5'W, 2,800 meters.

DISCUSSION.—The identity of this species, like *oregonensis*, caused a great deal of perplexity. Few of the descriptions of any species of *Benthoctopus* give sufficient detail to permit identification from the literature and often are based on insufficient or poorly preserved material. The present description is based upon 15 specimens, all from nearly the same locality, so they should represent a single population.

Benthoctopus yaquinae can be separated from *hokkaidensis* by the much greater ligula length (8.4–11.8 for *yaquinae*; 4.5 for *hokkaidensis*), its radula, and its differently shaped penial apparatus. From *profundorum* it can be distinguished by the general shape of the ligula, its greater ligula length (vs. 6.9 for *profundorum*), its funnel organ, and other characters. It is distinct from all other known *Benthoctopus*.

The name *yaquinae* is derived from the R/V YAQUINA, previously operated by the College of Oceanography, Oregon State University, from which most of the specimens were captured.

Of the 15 specimens, all but two were captured

on the Cascadia Abyssal Plain. These two were taken on the continental slope off the central Oregon coast at 1,000 m.

***Benthoctopus macrophallus* new species**

(Fig. 17)

MATERIAL EXAMINED.—Holotype: male, ML 83 mm, R/V YAQUINA Cr. Y7102B haul 267, 44°59'N, 126°31.6'W in 2,795 m, 19 Feb. 1971, USNM 730713.

DIAGNOSIS.—A *Benthoctopus* with long, slender ligula with no transverse ridges and short calamus; long penial apparatus, 67.5% of mantle length; spermatophores very large, 180.7% of mantle length; rachidian of radula tall, slender, somewhat lobulate, without lateral cusps.

DESCRIPTION.—Unique specimen contorted, wrinkled; body and arms muscular; mantle nearly round (MWI 89.2) with slightly narrower neck region; head large (HWI 73.5), eyes large. Funnel large, free for about half its length, stout; funnel organ W-shaped, short, with broad lateral limbs that are longer than round median limb.

Arms long (MAI 26.8; ALI 77.9), stout (AWI 18.1), taper to long slender tips; arm formula I.II.III.IV.; suckers small (SIn 4.8), biserial, erect, raised above arm surface on stout, well-separated pads; about 63–65 sucker pairs on I.

Web shallow (WDI 24.8), order BACDE, extends along sides of arms nearly to tips.

Hectocotylized arm short (HcAI 71.9; FHcAI 39.2), stout; bordered by strong, thick membrane that forms spermatophoral groove; ligula (Fig. 17d) large (LLI 10.9), long, slender, inner surface of ligula shallowly excavated with low central ridge, crossed by numerous very fine lines; calamus short (CLI 34.8) with small sharp spout.

Gills large with 9 lamellae per outer demibranch.

Buccal mass of average size; upper beak (Fig. 17a) stout; rostrum strong with slightly obtuse jaw angle; lower beak (Fig. 17b) with nearly 90° jaw angle with short rostrum.

Radula (Fig. 17c) unique; large, darkly pigmented; rachidian tooth stout; mesocone tall, blunt-tipped with smooth, irregular sides with clear transparent lamina on each side near tip; base comparatively slender with cusp on each outer angle, arrangement symmetrical (A); ad-medians with tall sharp ectocone and short base; second laterals stout with broad blades; third laterals long, curved, slender; marginal plates poorly formed distinct only on inner ends.

Digestive tract not dissected, mantle laid back

to permit examination of esophagus and crop with large anterior diverticulum (Fig. 17e); posterior salivary glands small; anal flaps and ink sac absent.

Penis (Fig. 17i) large with long posterior diverticulum (PLI 67.5); Needham's sac long, slender, contains three spermatophores; accessory gland about as long as Needham's sac. Spermatophores (Fig. 17f) 150 mm long; (SpLI 180.7) with stout horn (SpDI 3.4); sperm reservoir nearly half again as wide; horn little more than half spermatophore length (SpHI 53.3; SpRI 46.7), oral end with brownish cap, with narrow dark-brown band at posterior end (Fig. 17h); horn opaque, no coils visible.

Body sculpture absent. Color in ethanol grayish tan dorsally on mantle, head and base of arms with shades of dark purple on ventral side and on oral and aboral surface of arms and web.

MEASUREMENTS AND COUNTS.—Holotype: mantle length 83; mantle width 74; head width 61; length of longest arm (I) 310; total length 398; length of hectocotylized arm 222.8; ligula length 24.3; calamus length 8.5; number of suckers on arm I 63–65; sucker diameter 4.0; depth of deepest web sector (B) 76.8; number of gill lamellae per outer demibranch 9.

TYPE.—Holotype, male, 83 mm ML, USNM 730713 (fixed in formalin, preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, eastern Cascadia Plain, 44°59'N, 126°31.6'W, 2,795 m.

DISCUSSION.—This species is distinct from all other *Benthoctopus* by the unusual characters of the radula, the beaks, the very large spermatophores, and the unusually long, separate crop diverticulum.

The whole animal is not figured, as it differs little in general appearance from the other species described and illustrated here.

The name *macrophallus* refers to the exceptionally long penial apparatus of this species.

GENERAL DISCUSSION OF NORTH PACIFIC
BENTHOCTOPUS

Approximately 16 species have been described in the genus *Benthoctopus* (Robson 1932; Taki 1964; Voss 1988b), of which few have been well enough described and illustrated to be identifiable. To further confuse the picture, several of the types are in poor condition or essential parts have been removed and are now missing.

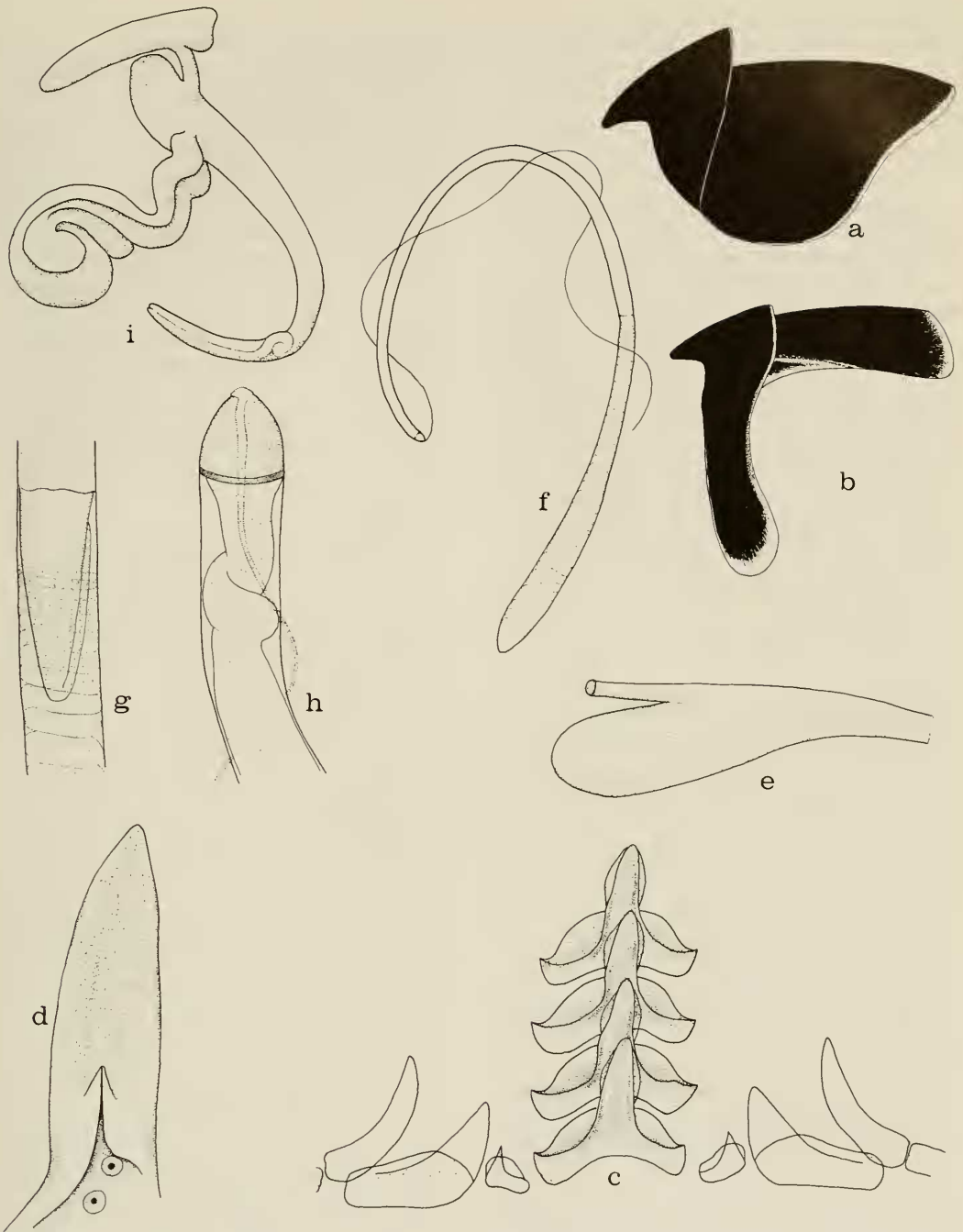


FIGURE 17. *Benthoctopus macrophallus* new species. Holotype, USNM 730713, male, 83 mm ML. (a–b) Upper and lower beaks. (c) Radula. (d) Ligula. (e) Crop. (f) Spermatophore. (g) Cement body. (h) Horn and cap. (i) Genitalia.

Of the 16 species, five are known only from the Atlantic, three from the Southern Ocean, one from the Arctic, and two from the Indian Ocean, for a total of 11. The remaining five species:

abruptus, *fuscus*, *hokkaidensis*, *profundorum*, and *violescens* are from the North Pacific Ocean. To these are now added *robustus*, *canthylus*, *oregonensis*, *yaquinae*, and *macrophallus*, for a total

of 10 North Pacific species. All need to be discussed in evaluating the North Pacific species.

Benthoctopus abruptus was described by Sasaki (1920). It is a well-defined species best characterized by the greatly enlarged, flared suckers on the arms of the males. This character is unique in the genus. *Benthoctopus canthylus*, described here from a single specimen, is the only species with enlarged suckers in females; males are unknown. *Benthoctopus fuscus*, described with a VV-shaped funnel organ (Taki 1964:316), is the only Pacific species with this type of funnel organ.

Benthoctopus hokkaidensis (Berry, 1921) is a replacement name for *Polypus glaber* (Sasaki, 1920). It is known from about four specimens from Japanese waters and was redescribed and illustrated by Sasaki (1929:65). The radula from the type is described here under the discussion of *B. oregonensis*, so the species now is fairly well known. The only discrepancy is the statement by Robson (1932:233) that "the penis has a long diverticle which is bent on itself (?by accident) to confer on the whole structure the shape of S." In the type specimen only the diverticulum is strongly curved inward, not so much as in Sasaki's figure (1929:63; text fig. 25). The funnel organ, also well illustrated, is a wide \checkmark -shape.

No basis exists for separating *B. hokkaidensis* from *violescens* (Taki, 1964). Taki (1964:321) showed that the funnel organ is exactly the same shape as that figured by Sasaki (1929), and both are \checkmark -shaped, not \sphericalangle -shaped as given in his table p. 324-325. The radulae also are the same. Similarly, the penis and its diverticulum have the same curvature, although not as marked in *violescens* as in *hokkaidensis*. In the table, all of the dimensions and indices of *violescens* are within the ranges of *hokkaidensis*. Consequently, *violescens* is placed in the synonymy of *hokkaidensis*.

Throughout this study of *Benthoctopus*, the identity of *B. profundorum* (Robson, 1932) has caused problems. Although Robson (1932:238) stated "this description is largely founded on the type alone," it is a mixture of characters, measurements, and indices of specimens from relatively shallow water and includes specimens from as far away as the Andaman Sea. The type was from off Yokohama in 3,431 m; the other specimens were from depths of 510 to 1,098 m. It is likely that the species as originally described is composed of several species.

The type, BM 1889.4.24.42, was examined by

Voss in London in 1975. Robson stated that the ligula index was 6.9; it is now 6.6. According to Robson, "the copulatory groove is very weak," but it is actually deep and well-defined. The calamus is small and pointed but the CLI is 46.7 as measured from the distal sucker. He stated that the funnel organ was \sphericalangle -shaped, but it is W-shaped with the median section broad and rounded with narrow and pointed lateral limbs. There are six lamellae on the outer demibranch of the gills. The buccal mass has been removed and no trace could be found of either the beaks or the radula. Based upon the type alone, *B. profundorum* must be characterized as having a W-shaped funnel organ, six lamellae on the outer demibranch of the gills, a small ligula (LI 6.6-6.9) with a deep copulatory groove and small pointed calamus, short stout penis with stout diverticulum, ALI 83, SIn 5.9, WDI 34, with beaks and radula unknown.

This leaves *B. robustus*, *oregonensis*, *yaquinae* and *macrophallus* to be considered. *Benthoctopus robustus* has a distinctive radula and genitalia. Both *B. oregonensis* and *yaquinae* have been discussed previously. *Benthoctopus macrophallus*, as the name implies, has a very large penis (PLI 67.5), large ligula, a groove on the lamella of the lower mandible, and a nearly smooth, slender rachidian tooth in the radula.

The characters of the nine recognized species of *Benthoctopus* from the North Pacific Ocean are shown in the following key. The first characters given in the couplets refer to distinguishing characters, those following are diagnostic of the species. We emphasize that this key is provisional. Some characters are not known for all species or sexes of a species. It should be used with illustrations and descriptions of species.

KEY TO THE SPECIES OF *BENTHOCTOPUS* OF THE NORTH PACIFIC OCEAN

1. Funnel organ VV; gills 7-11; radula B₅ with high ectocone on 1st lateral; penis small, straight, PLI 12.2; sucker index normal 6.0. Single male known *fuscus*
1. Funnel organ \sphericalangle , \sphericalangle , or \sphericalangle ; other characters not as above 2
2. Specially enlarged suckers, SLe 15-16.3, present on some or all arms of males or females 3
2. No specially enlarged suckers on either males or females; SIn 4.8-8.6 4

3. All arms normal; in males suckers of mid-portion of arms greatly enlarged, Sle 15, SIn 8; females with normal suckers SIn 8; funnel organ w; gills 10–14; radula B₄₋₅; penis moderate, PLI 7.3 *abruptus*
3. Middle of dorsal arms of females abruptly swollen and bearing greatly enlarged suckers, Sle 16.3; SIn 6.3; funnel organ W; gills 8; radula B₃₋₆; groove on lamella of lower beak. Single female known *canthylus*
4. Groove on lamella of lower beak; funnel organ \sphericalangle ; rachidian with tall, narrow mesocone with undulating margin; 1st laterals with tall, sharp ectocone; gills 9; SIn 4.8; ligula long, slender, LLI 11; calamus short, sharp, CLI 23.3; penis very large, slightly arcuate, PLI 68; spermatophore very long SpLI 180.7. Single male known *macrophallus*
4. No groove on lamella of lower beak; funnel organ W or \sphericalangle ; rachidian teeth broad and/or with lateral cusps with B₄₋₆ seriation 5
5. Funnel organ W shaped 6
5. Funnel organ \sphericalangle shaped 8
6. Arms short, ALI 56, MAI 64; ligula large, deep, rugose, LLI 12.5; calamus long, slender, CLI 45; rachidian broad with nearly smooth margin; gills 11; SIn 5.1; penis large, PLI 58. Single male known *robustus*
6. Arms long, ALI greater than 65; MAI less than 40; ligula small, under LLI 8 or if larger, ligula smooth, shallow (LLI 8.4–10.5); rachidian with lateral cusps on mesocone 7
7. Ligula flattened with low median ridge, medium size, LLI 8.4–10.5; rachidian B₅, broad, triangular, with low cusps on mesocone; gills 7–9; strong reverse countershading *yaquinae*
7. Ligula deeply excavated, small, LLI 6.6–6.9; gills 6; radula unknown; no reverse countershading; type a male, all other specimens doubtful *profundorum*
8. Penis short, nearly straight, with short diverticulum, PLI 18.3; spermatophore small, SpLI 79.6; funnel organ a fat, close \sphericalangle ; ligula short, broad, with deep groove and transverse rugae, LLI 5.0–6.7; gills 11–13 radula B₄₋₅ with strong sharp cusps on mesocone; 1st laterals with low ectocone *oregonensis*
8. Penis long, with long inwardly curved diverticulum, PLI 35; spermatophore long,

SpLI 95.6; funnel organ narrow, widely open \sphericalangle ; ligula short, narrow, with narrow shallow groove, LLI 4.5–5.5; gills about 12; radula B₃₋₆ with strong, sharp cusps on mesocone, 1st laterals with tall, slender ectocone *hokkaidensis*

Subfamily GRANELEDONINAE Voss, 1988a

Deep-sea octopods with uniserial suckers; large eggs; ink sac absent; crop lacks diverticulum, reduced or absent; reduced number of gill lamellae; reduction or degeneration of homodont radula; funnel organ VV, UU or simple paired pads; spermatophores large and few.

DISCUSSION.—Robson (1932:51–56, 257) discussed the “Eledoninae” and his reasons to consider it a polyphyletic group. Voss (1988a) restricted the Eledoninae to the genera *Pareledone*, *Eledone*, *Vosseledone*, *Velodona*, and *Tetracheledone* and erected the new subfamily for the remaining genera with uniserial suckers, *Graneledone*, *Thaumeledone*, and *Bentheledone*.

Genus *Graneledone* Joubin, 1918

With characters of family (see above). Body, head, and arms thickly covered with permanent rugose papillae.

TYPE SPECIES: *Eledone verrucosa* Verrill, 1881: 105. By original designation (Joubin 1918:39).

Graneledone pacifica new species

(Figs. 18–20)

?*Graneledone boreopacifica* Nesis, 1982: 322, fig. k, l.

MATERIAL EXAMINED (28 specimens).—Holotype: male, ML 85 mm, R/V YAQUINA Cr. 6907C haul 95, 44°52.0'N, 125°32.8'W in 2,706 m, 16 July 1969, USNM 730716. Paratypes: 1 male, ML 96 mm, R/V ACONA Cr. A6507 haul 78, 45°59.6'N, 125°44.0'W in 2,500 m, 1 Aug. 1965, UMML 31.2539.—1 male, ML 95 mm, R/V YAQUINA, 45°49'N, 125°34'W in 2,121 m, 7 June 1969, CAS 061434.—1 male, ML 90 mm, R/V Yaquina Cr. Y7003B haul 192, 45°37.9'N, 125°46.5'W in 2,450 m, 19 Mar. 1970, UMML 31.1957.—1 male, ML 86 mm, R/V YAQUINA Cr. Y6907C, 44°52'N, 125°32.8'W in 2,706 m, 16 July 1969, UMML 31.1959.—1 male, ML 85 mm, 1 female, ML 45 mm, R/V YAQUINA Cr. Y7003B haul 195, 45°57.6'N, 125°46.2'W in 2,265 m, 20 July 1970, UMML 31.2542.—1 male, ML 62 mm, R/V YAQUINA Cr. Y6910A haul 116, 45°21'N, 125°37.3'W in 2,500 m, 5 Oct. 1969, UMML 31.2541.—1 male, ML 60 mm, R/V YAQUINA, 45°10.5'N, 125°38.0'W in 2,669 m, 15 July 1964.—1 male, ML 49 mm, R/V YAQUINA Cr. Y6910A, 45°21'N, 125°37.3'W in 2,500 m, 5 Oct. 1969.—2 males, ML 58–59 mm, R/V YAQUINA Cr. Y6910A, 45°09.3'N, 125°35.2'W in 2,652 m, 5 Oct. 1969.—1 male, ML 21 mm, R/V CAYUSE, 44°42.1'N, 125°20.2'W in 2,755 m, 2 Oct. 1970.—1 male, ML

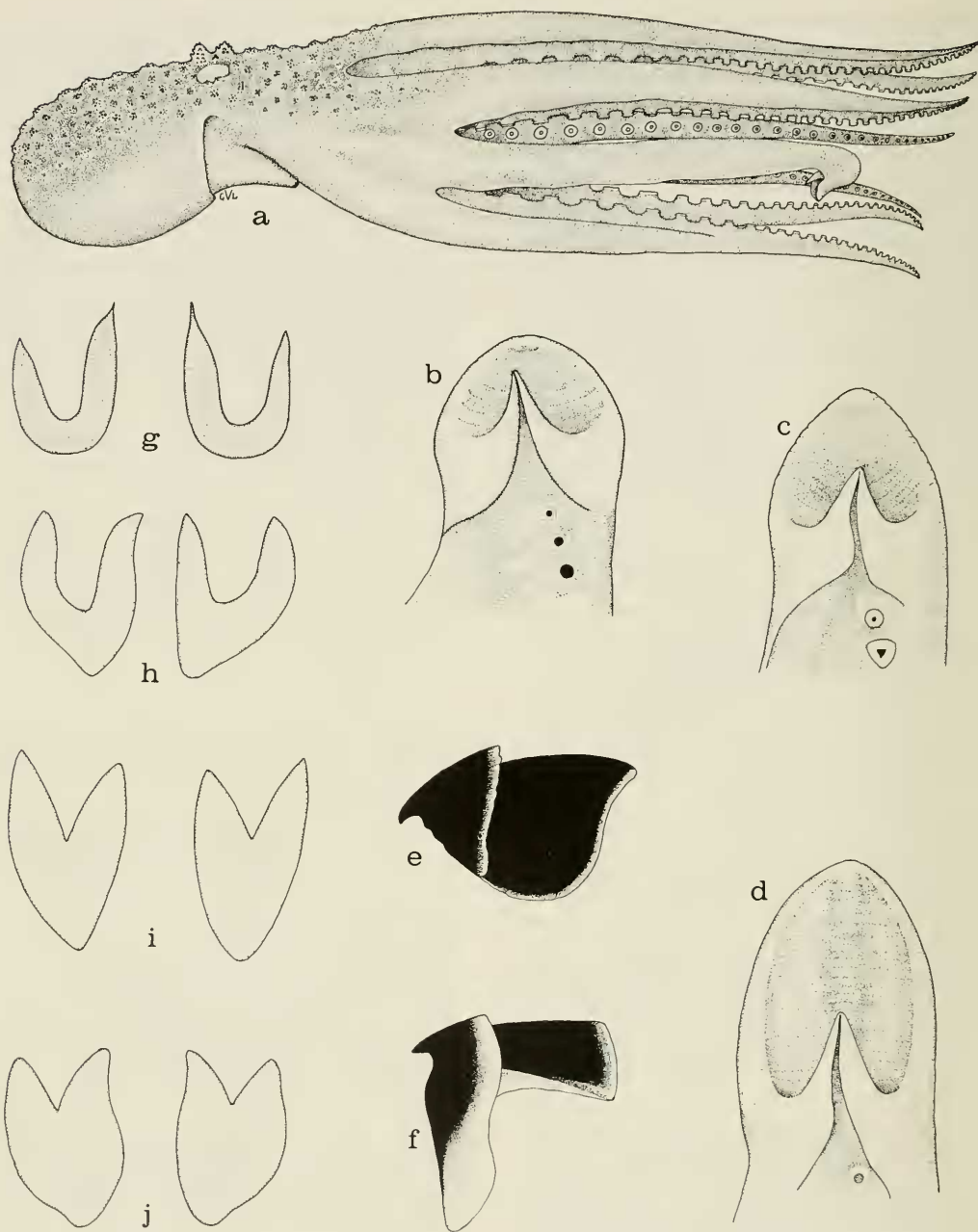


FIGURE 18. *Graneledone pacifica* new species. (a) Lateral view of holotype, USNM 730716, male, 85 mm ML. (b) Ligula of male, 62 mm ML. (c) Ligula of male, 85 mm ML. (d) Ligula of male, 90 mm ML. (e-f) Upper and lower beaks of male, 85 mm ML. (g-j) Funnel organs: g, male, 90 mm ML; h, male, 96 mm ML; i, male, 85 mm ML; j, male, 54 mm ML.

19 mm, R/V YAQUINA Cr. Y6910A, 45°49.2'N, 125°40.1'W in 2,195 m, 4 Oct. 1969.—1 female, ML 105 mm, 1 male, ML 43.5 mm, R/V YAQUINA, 45°59.6'N, 125°44.0'W in 2,500 m, 1 Aug. 1965.—1 female, ML 105 mm, R/V YAQUINA, 45°45.5'N, 125°30.2'W in 2,176 m, 11 Jan. 1967, CAS 061433.—1 female, ML 100 mm, R/V YAQUINA Cr. Y7003B

haul 181, 45°17.4'N, 125°49.0'W in 2,605 m, 18 Mar. 1970, UMML 31.1958.—1 female, ML 97 mm, R/V ACONA, in 1,427 m, 10 Dec. 1961.—2 females, ML 13–88 mm, R/V YAQUINA Cr. Y7003B haul 193, 45°39.0'N, 125°52.9'W in 2,425 m, 19 Mar. 1970, UMML 31.2540.—1 female, ML 75 mm, R/V CAYUSE Cr. 6903 haul 72-01, 45°56.1'N,

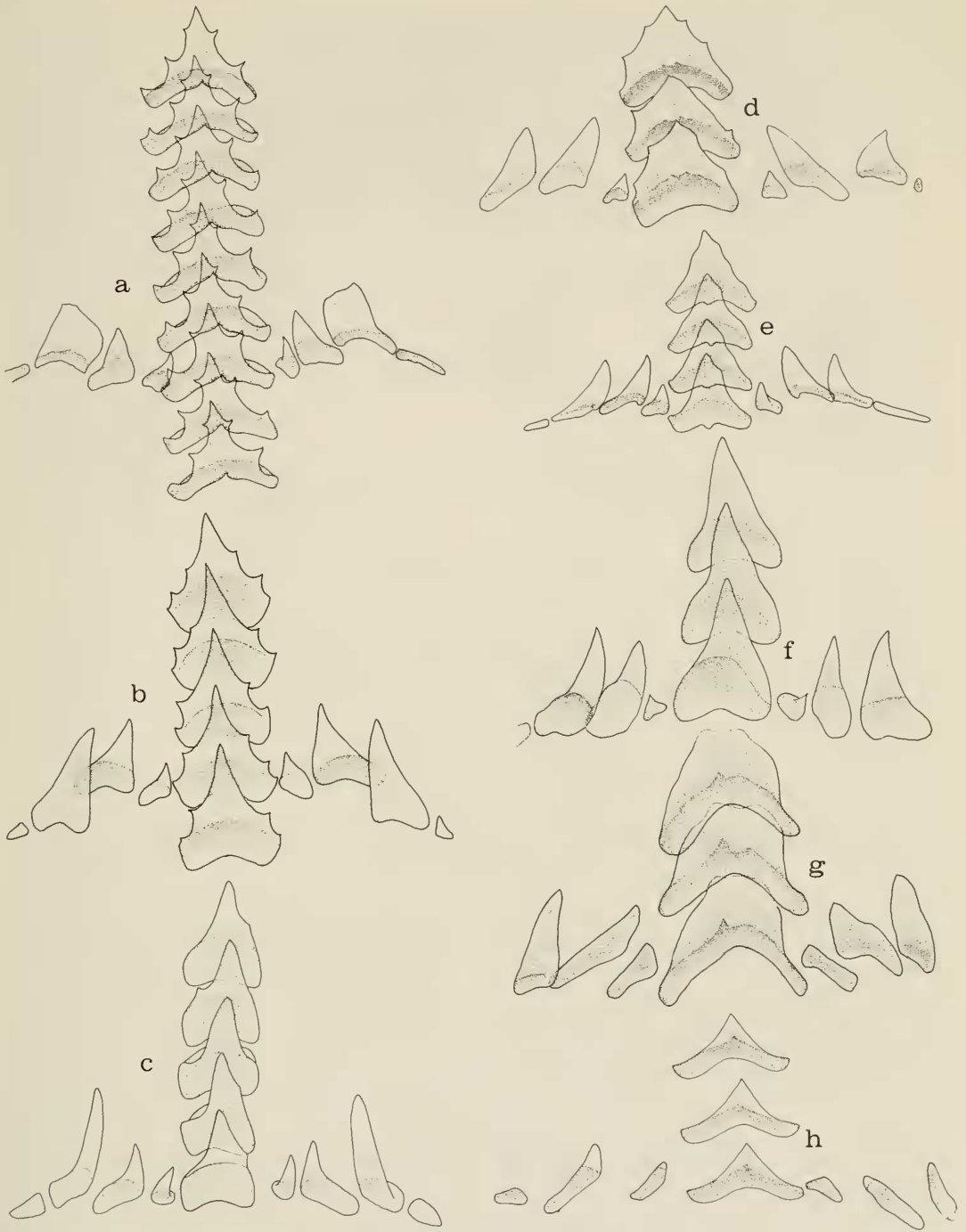


FIGURE 19. *Graneledone pacifica* new species. (a-h) Radulas: a, male, 96 mm ML; b, female, 97 mm ML; c, female, 45 mm ML; d, male, 90 mm ML; e, male, 85 mm ML; f, male, 60 mm ML; g, male, 86 mm ML; h, male, 85 mm ML.

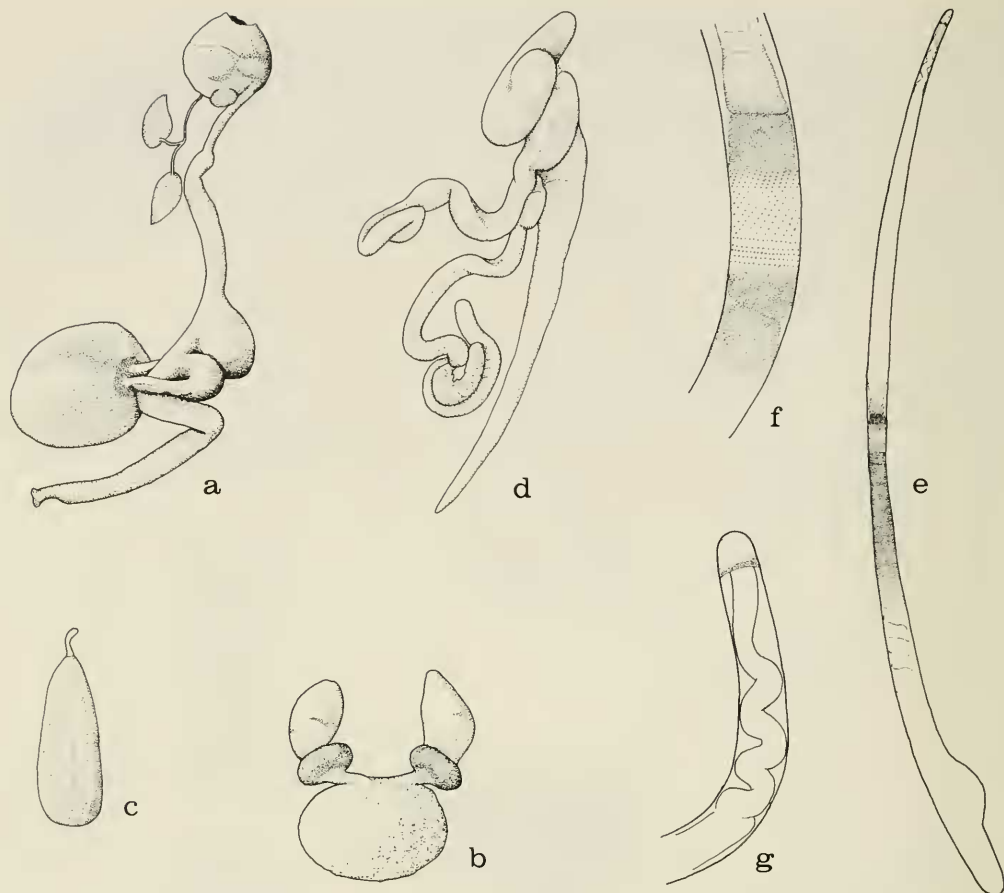


FIGURE 20. *Graneledone pacifica* new species. (a) Digestive tract from female, 75 mm ML. (b) Genitalia of female, 75 mm ML. (c) Egg of same. (d) Genitalia of male, 96 mm ML. (e) Spermatophore of same. (f) Cement body of same. (g) Horn of same.

125°41.8'W in 2,195 m, 30 Mar. 1969, UMML 31.2538.—1 female, ML 60 mm, R/V CAYUSE, 44°49.6'N, 125°33.0'W in 2,756 m, 8 Mar. 1972.—2 females, ML 41–59 mm, R/V YAQUINA, 45°57.6'N, 125°46.2'W in 2,265 m, 20 July 1970.—1 male, ML 65 mm, 1 female, ML 54 mm, R/V YAQUINA, 45°21'N, 125°37.3'W in 2,500 m, 11 Oct. 1974.—1 female, ML 47 mm, R/V ACONA, 44°25.6'N, 125°13.4'W in 1,530 m, 14 Aug. 1964.—1 female, ML 27 mm, R/V YAQUINA Cr. Y6910A haul 113, 46°04.6'N, 125°34.6'W in 2,156 m, 3 Oct. 1969, UMML 31.2537.

DIAGNOSIS.—A *Graneledone* with VV-shaped funnel organ; short, stout spade-shaped ligula with only faint transverse lines; radula very variable, degenerate, often with various teeth missing; mantle, head and arms with rosettes of papillae, often closely packed, with one or two low, rough, supraocular cirri.

DESCRIPTION.—Body medium to large (Tables 18–19), firm and muscular body; skin loose over most of dorsal surface, bears numerous low to

erect wartlike tubercles arranged in small clusters (Fig. 18a). Mantle globose, moderately wide (all indices throughout description from animals in excess of 70 mm ML) (MWI males 87.2–92.9–100.0; females 81.0–92.1–105.3); head narrower (HWI males 63.2–72.7–83.3; females 60.0–72.0–93.3), not distinctly set off from mantle; eyes medium to small with small apertures, project only slightly. Funnel large, stout, less than one-quarter of distal end free; inner edge of funnel forms strong flap which inserts into deep pocket in inner mantle wall, that makes an effective locking apparatus; funnel organ VV-shaped, very variable, each pad grading from slender V-shaped to thick pads split anteriorly (Fig. 18g–j); outer limb usually shorter than inner limb but may be equal in length or inner limb may be shorter than outer one, with all intergradations between two extremes.

Arms moderately long (MAI males 25.0–27.6–31.7; females 25.3–29.1–31.4; ALI males 72.4–78.7–84.4; females 74.4–75.6–77.1), muscular, round in cross-section, rather stout (AWI males 15.8–18.1–20.0; females 18.0–20.2–24.0), taper to long slender points; arm formula I.II.III.IV. Suckers in single row, raised on oral surface of arm, somewhat urn-shaped, well-separated; suckers small (SIn males 5.6–6.0–6.3; females 5.2–5.9–6.7) increase gradually in size from mouth distally, attain greatest size at about margin of web, after which gradually decrease to tips of arms.

Hectocotylized arm shorter than its fellow (HcAI 70.8–82.4–85.8); ligula small (LLI 4.9–5.6–6.5) broad, somewhat heart shaped, may be very small, broad, deep or more slender, pointed (Fig. 18b–d); shape of ligula variable but consistent in length index, usually deeply excavated with numerous low, transverse laminae, some with low longitudinal median ridges on floor of excavation (Fig. 18d); sides raised, thin, muscular, with considerable variation as shown in figures; calamus large (CLI 58.6–62.8–66.7), narrow, sharply pointed, in some smaller specimens calamus length index may exceed 80. Web extends along side of arm, broad, with poorly developed spermatophoral groove but thickened web margin; in preserved specimens contracted web caused end of arm to curl.

Gills large, stout; inner and outer demibranchs about equally developed, 7–8 lamellae per outer demibranch.

Buccal mass large; beaks consistent in all features; upper beak (Fig. 18e) with strong deep jaw angle; lower beak (Fig. 18f) with 90° jaw angle, with distinct groove along lower edge of insertion plate.

Eight radulae extracted and examined (Fig. 19a–h); individual radulae very different. Radulae range from multicuspoid rachidians with a B_s seriation to simple rachidians, to almost completely degenerate ones; some with large, well-developed marginal plates, while others with none; one (Fig. 19h) lacks admedians on one side but has them on other side.

Anterior salivary glands small, free from buccal mass (Fig. 20a); posterior salivary glands small, narrowly elliptical; esophagus slender, expanded into a long, thick-walled pseudocrop with no diverticulum; internal walls strongly plicate; anterior half of stomach muscular, posterior thin-walled; spiral caecum comparatively small; di-

gestive gland large, roundish; paired digestive gland ducts large, thin-walled, may be overlooked in some specimens; intestine stout with sharp bend in anterior quarter; anal flaps and ink sac absent. Crop and stomach contents consisted of crustacean remains, primarily copepods and amphipods.

Genitalia of adult female shown in Figure 20b; ovary moderately large, in near-ripe condition; proximal oviducts short, stout; oviductal glands large, round, somewhat flattened, dark blue-gray; distal oviducts large, short, elliptical, very swollen, terminate in small pores. One of distal oviducts contained mass of whitish material that, under microscope, resolved into minute spherical bodies, probably sperm. Genitalia of other females not developed despite long mantle lengths; oviductal glands small; distal oviducts only moderately larger than proximal ducts; stalk short, white; eggs flesh colored with light transverse striations in largest female; eggs large, measuring 16 × 7 mm, widest part at the posterior end (Fig. 20c).

Penis large, stout, somewhat square-tipped (Fig. 20d); duct enters some distance posterior to pore; diverticulum large, stout, strongly turned back upon itself; Needham's sac long and stout anteriorly, long and slender posteriorly; appendix to accessory gland not visible.

Spermatophores (Fig. 20e–g) large (SpLI 145.0–157.0–169.0), stout (SpWI 4.0–4.5–5.0), with large, flesh-colored sperm reservoir (SpRI 41.0–41.0–41.0); main tube semi-transparent or whitish; cement gland portion purplish red, very dark, almost maroon in some, pale bluish in others; tube narrows posteriorly to connective region, then swells out to large, swollen sperm mass. Spermatophore tube straight to near oral end, makes about three to four coils or turns just prior to end; junction of tube with cement gland surface speckled in regular rows; this area formed by hundreds of small tubular bodies packed in series, radiating outward from center; sperm mass formed of large convolutions. All spermatophores appear similar although indices vary somewhat from specimen to specimen.

Color of specimens preserved in ethanol varies considerably: in some large specimens general coloration pinkish gray, liberally covered with small darker-colored spots with tubercles; in others, ground color reddish brown or purple with tubercles standing out as pale spots; in smaller specimens ground color dark slate gray with red-

dish tinge or dark purple upon which tubercles stand out either lighter or darker, sometimes rather indistinct according to state of contraction. Web and oral surface of arms slightly darker in most specimens. Some specimens show distinct reverse countershading with dorsal surface of mantle, head, and arms lighter than ventral surface; apertures of eyes dark colored in all of lighter-colored specimens.

Surface sculpture distinctive, with little variation other than that from condition of preservation. In well-preserved specimens dorsum of mantle, head, and bases of arms I and II closely covered by small wartlike clusters of tubercles, each cluster raised somewhat from body surface on low fleshy pad; in most specimens pad not discernible, warts set flat on skin; each wart consists of usually six to seven (range 2 to about 11), small blunt tubercles that often, not always, surround somewhat larger central one; warts also surround eyes, but enlarged only dorsally where two, sometimes three, form conspicuous large rough nobs; in life, warts may be erected into tall cirri, but only one specimen exhibits this condition; several specimens, probably preserved in flaccid state, show reverse situation in which warts slightly sunken into general skin surface and even appear as low depressions or pits; examination of these areas under microscope, however, shows similar arrangements of tubercles as found on elevated ones. All stages of conditions between warts and pits present undoubtedly due to flaccidity or contraction at time of fixation, also indicated in that erect warts usually rather close together while flattened ones more widely spaced. Base of lower arms and ventral surface of mantle and head smooth, more darkly colored; two dorsal ocular papillae plainly visible even in smooth or pitted specimens.

MEASUREMENTS AND COUNTS.—Holotype: 85 mm ML; mantle width 85; head width 55; length of longest arm L(I) 346; total length 432; length of hectocotylized arm 290; ligula length 15.6; calamus length 10; sucker diameter 5.0; depth of deepest web sector (D) 91.6; number of gill lamellae in outer demibranch 7.

TYPE.—Holotype, male, 85 mm ML, USNM 730716 (fixed in formalin and preserved in 50% isopropyl alcohol).

TYPE-LOCALITY.—Off Oregon, Cascadia Abyssal Plain near the slope, 44°52.0'N, 125°32.8'W, 2,706 meters.

DISCUSSION.—Six species of *Graneledone* are

TABLE 19. Indices of bodily proportions and other data of 14 females of *Graneledone pacifica* new species.

	Specimen													
	UMML 31.2540	UMML 31.2537	UMML 31.2542	UMML 31.2542	UMML 31.2538	UMML 31.2540	UMML 31.2540	UMML 31.2540	UMML 31.2540	UMML 31.2540				
ML	13	27	41	45	47	54	59	60	75	88	97	100	105	105
MW1	111.5	100.0	85.4	66.7	114.9	90.7	106.8	93.3	105.3	85.2	91.8	96.0	93.3	81.0
HW1	115.4	103.7	78.1	66.7	97.9	83.3	98.8	81.7	93.3	68.2	76.3	60.0	67.6	66.8
MA1	30.9	27.0	50.6	39.1	28.7	32.5	39.3	33.7	25.3	28.9	28.5	31.3	31.4	28.9
AL1	70.0	78.1	66.4	71.9	74.5	75.8	76.5	78.8	77.1	74.4	75.1	75.3	75.4	76.4
AW1	23.1	25.9	20.7	15.6	23.4	20.3	23.7	18.3	24.0	20.5	18.6	18.0	20.0	20.0
WD1	30.9	23.0	—	28.7	30.5	27.7	31.3	25.8	26.9	26.2	27.9	25.3	26.4	22.9
Sl _n	7.7	6.3	4.9	4.4	6.4	5.6	5.1	5.0	6.7	6.3	5.2	6.0	5.7	5.7
AF	1234	1234	2134	1234	1234	1234	2134	1234	1234	1234	1234	1234	1234	1234
WF	CBDAE	BCDAE	—	CBDAE	BDCAE	CBDAE	CBDAE	CBDAE	CBDEA	AB=CDE	DCBAE	DCBAE	CBDAE	CBDAE
Gills	7	8	8	8	7	7	8	7	7	7	8	8	7	7

known—*G. verrucosa* (Verrill, 1881) from the North Atlantic (with a possible subspecies *media* Joubin, 1918), *G. challengerii* (Berry, 1916) from the Kermadec Islands, *G. antarctica* (Voss, 1976) from the Ross Sea, Antarctica, *G. macrotyla* (Voss, 1976) from near the Falkland (Malvinas) Islands, and *G. boreopacifica* (Nesis, 1982) from the northwestern Pacific. *G. setebos* (Robson, 1932) from McMurdo Sound, Antarctica, is considered a nomen dubium (Voss 1976:457). Most of the species are very unsatisfactorily known. Knowledge of variation is known only in *G. antarctica*.

The present material, if we are correct in assigning it to a single species, shows great variation in skin sculpture, radula, funnel organ, and hectocotylus, but surprisingly consistent morphometrics and structure of beaks and spermatophores. *G. antarctica* showed similar wide variation in radula dentition but was remarkably consistent in other features.

In view of our incomplete information concerning *G. verrucosa*, it is difficult to compare it with *G. pacifica*. The type of *verrucosa* was borrowed from the USNM, but its condition did not lend itself for comparison. In the USNM, however, there is now a nice series of *verrucosa* taken by the R/V's KNORR, CHAIN, and WALTHER HERWIG. Detailed examination of these specimens has not been done, but preliminary study shows that, in contrast with *pacifica*, these specimens have a consistently formed radula with little variation. These show rachidians with an A₃₋₄ seriation, strong admedians, second laterals with elongate bases, and third laterals that are rather short and triangular. The warts on the mantle and head are composed of fewer papillae, 3-4, sometimes 5, and show the same general distribution as in *pacifica* but with a number of large warts all around the eye, some quite large, in addition to the 2-3 large supraocular papillae found in both species.

The description of *G. boreopacifica* (Nesis, 1982) is very brief, contained only in a key to the species of the genus accompanied by two figures. Possibly this species is the same as ours, in which case *boreopacifica* takes precedence. The problem cannot be resolved until a detailed description is published.

On the basis of the differences, *G. pacifica* is considered to represent a new species, but it ap-

pears to be closely related to its Atlantic congener.

This species was captured on the continental slope, slope base, and eastern boundary of the Cascadia Abyssal Plain off Oregon. It was not found on the Western Cascadia or Tufts plains and therefore appears to be a bathyal-abyssal species that lives near the continent.

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