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OCTOPUS SCHULTZEI (HOYLE, 1910): A REDESCRIPTION WITH DESIGNATION OF *APHRODOCTOPUS* NEW GENUS (CEPHALOPODA; OCTOPODINAE)

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ABSTRACT

The holotype of *Octopus schultzei* (Hoyle, 1910) was examined, to verify its taxonomic status. The holotype, a male and the only specimen known, possesses unusual characters not referred to in the original description nor in subsequent reports. Most striking are the arm tips, all of which, except the hectocotylus (right third arm), have a mass of long, closely packed finger-like processes instead of suckers. The hectocotylized portion of right arm III is very small, uniform and spongy in structure; the end organ lacks a longitudinal depression and cross-striations; a calamus is absent. These and other characters confirm the specific validity of *O. schultzei* and readily distinguish it from all other known species of *Octopus*. The systematic significance of these and other unusual characters supports the establishment of a new genus, *Aphrodoctopus*.

One of the objectives of the Cephalopod International Advisory Council (CIAC) Workshop sponsored by the Smithsonian Institution in Washington in July 1988 was to clarify the species-level systematics of the subfamily Octopodinae, which encompasses most of the shallow water benthic octopuses of the world. The status of all named species was to be determined through examination of holotypes, additional material and literature. *Octopus schultzei* (Hoyle, 1910) was known to exist on the basis of a single specimen, the holotype, that was not sufficiently well described. A decision was necessary concerning its status which has remained problematical since its original description. The holotype was not available at the CIAC Workshop, where K. M. M. was responsible for studying the species of octopodines of the Eastern Atlantic Ocean and the Mediterranean Sea (Mangold, in press).[1] Subsequently, the holotype was borrowed from the Zoological Museum of the Humboldt University of Berlin and was examined by both of us at the Museum National d'Histoire Naturelle in Paris in June 1989. It was apparent immediately that *O. schultzei* possesses several characters that are so unique as to insure not only the validity of its original specific status, but raised the question of its generic relationship as well. This paper presents a detailed redescription of *O. schultzei* and a discussion of its systematic status and significance.

W. E. Hoyle (1910) reported on the small collection of cephalopods captured during the scientific expedition to western and central Africa in 1903–1905, sponsored by the Royal Prussian Academy of Science of Berlin. Among the few cephalopods available was a single specimen of octopus taken in the Bay of Luederitz, Angra Pequena, German Southwest Africa (now Namibia). Because the specimen was a male with a peculiar hectocotylus and enlarged suckers on arm pairs I, II and III, Hoyle felt the species was distinct and named it *Polypus schultzei*. To the best of our knowledge, no additional specimens have ever been reported in collections. Hoyle (1910) and Robson (1929a), who placed *schultzei* in the genus *Octopus*, are the only zoologists who have examined the unique specimen. In spite of the absence of additional material, we believe a redescription of *O. schultzei*, with its several unusual characters partially overlooked by Hoyle and Robson,

[1] Mangold, K. M. In Press. The Octopodinae of the Mediterranean Sea and the eastern Atlantic Ocean. Smith. Contr. to Zoology.

will contribute to a better understanding of the species and perhaps to a clarification of octopus systematics.

Material and Methods

The holotype of *O. schultzei* was borrowed from the Museum fuer Naturkunde der Humboldt-Universitaet of Berlin through the courtesy of Dr. R. Kilias. Specimens of other species with cirrus- or papilla-like modifications on the arm tips (or closely related species that required examination) were acquired on loan from collections of the National Museum of Natural History, Smithsonian Institution, e.g., *O. penicillifer* Berry, 1954; *O. chierchiae* Jatta, 1889; *O. zonatus* Voss, 1968; *O.* n. sp. Toll and Voss, in prep.[2]; *Eledone massyae* Voss, 1964. Additional specimens were borrowed from the invertebrate museum of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, through the courtesy of N. A. Voss. We examined specimens of *Octopus* species from the collections of the Museum of South Africa through the courtesy of M. Roeleveld, but no specimens of *O. schultzei* were among them.

Measurements, indices and counts are given as defined in Roper and Voss (1983) or, as necessary, in this paper.

Family OCTOPODIDAE
Subfamily Octopodinae

Aphrodoctopus new genus

Type of the Genus.—*Octopus schultzei* (Hoyle, 1910). *Diagnosis.*—An octopodid with suckers on all non-hectocotylized arm tips of males modified into four transverse rows of flexible, tapered, finger-like processes. Hectocotylus simple: end organ of hectocotylus uniform, spongy, with irregular pit near the distal tip, without longitudinal groove, cross-striations, ridges and grooves; calamus absent. Funnel organ a modified inverted W-shape with very short, rounded lateral lobes. Suckers on all arms in two rows. Several pairs of enlarged suckers on arm pairs I, II and III of males. Exposed terminal organ ("penis") very long, without a diverticulum. Intestinal bulb present.

Aphrodoctopus schultzei (Hoyle, 1910)
Figures 1–3

Polypus schultzei Hoyle, 1910: 261, text fig. 1, pl. Va, figs. 1–3.
Octopus (Octopus) schultzei, Robson, 1929a: 48, 148, figs. 52, 53.
Octopus schultzei, Robson, 1929b: 617–618.

Material Examined.—Holotype: male, mantle length 49 mm (50 mm by Hoyle). Type locality: Bay of Luederitz, Angra Pequena, German South West Africa (Namibia); among rocks in shallow water; Museum fuer Naturkunde der Humboldt-Universitaet zu Berlin.

Description.—The animal is small to medium sized with strongly muscular mantle and arms. Table 1 gives measurements, counts and indices. The mantle is globular, about one fifth the total length of the animal and nearly as wide as long (MWI 86); the mantle aperture is broad (type C of Robson, 1929a). The muscular funnel extends anteriorly to the level of the eyes and the base is broad; the free anterior part of the funnel is about two thirds of the total funnel length. The funnel organ is broadly inverted, modified W-shaped, with the median limb angle of about 90° (Fig. 2c; Robson, 1929a, fig. 52); the lateral limbs are represented only by short rounded lobes, about one quarter the length of the medial limbs. The entire funnel organ is broad and flat without sculpture (the irregular wrinkles on the surface of the organ in the holotype are an artifact of preservation).

The head is short and narrower than the mantle (HWI 47), but exact dimensions

[2] Toll, R. B. and G. L. Voss. In prep. *Octopus* new species and a redescription of *Octopus chierchiae* from Panamanian Pacific waters.

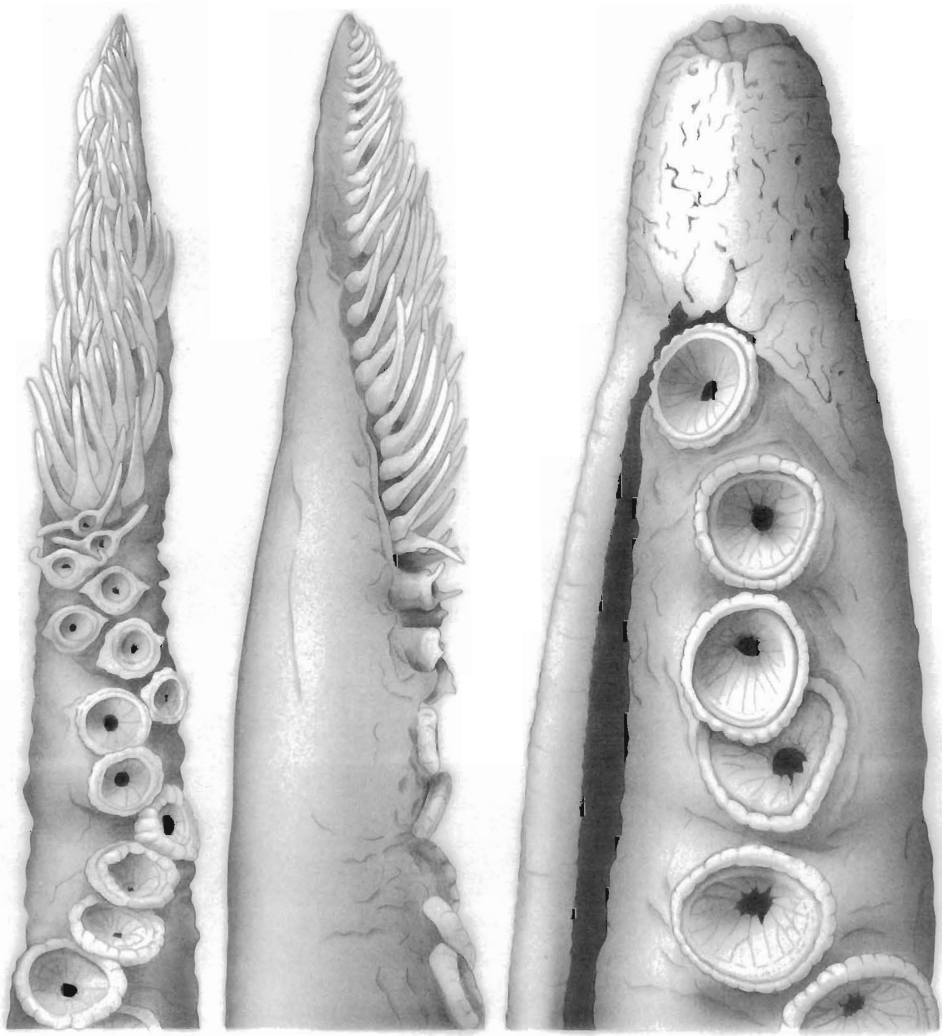

Figure 1. *Aphrodoctopus schultzei,* holotype, 49 mm mantle length. a–b: Modification of sucker rims into digitate processes on tip of right arm IV. a. Oral view. b. Lateral view. c. Hectocotylized right arm III; ligula length, 4 mm.

and shape of the head are difficult to assess because the head was caught or bound by a line (or net), constricting and distorting its natural shape. The eyes can barely be distinguished, except for the presence of flattened occular papillae or flaps.

The arms are robust, muscular, particularly arm pairs I, II and III, and are long, the longest at least four times the length of the mantle. Although the very end of the tips of arms I are missing and the left arm II is partly regenerated, the remaining arms are intact and the arm formula is 2.1.3.4 or 2.3.1.4. The arms are broad with an AWI of 20.4. The suckers occur in two alternating rows along all arms and are set on thick stalks, not deeply set into the arms (Fig. 4). Three to four pairs of suckers are enlarged, especially so on arms I and II, slightly less so on arms III; sucker size and configuration (2 rows) are normal on arms IV. The enlargement begins with the 6th or 7th sucker on arm pairs I, II and III, whereas the largest

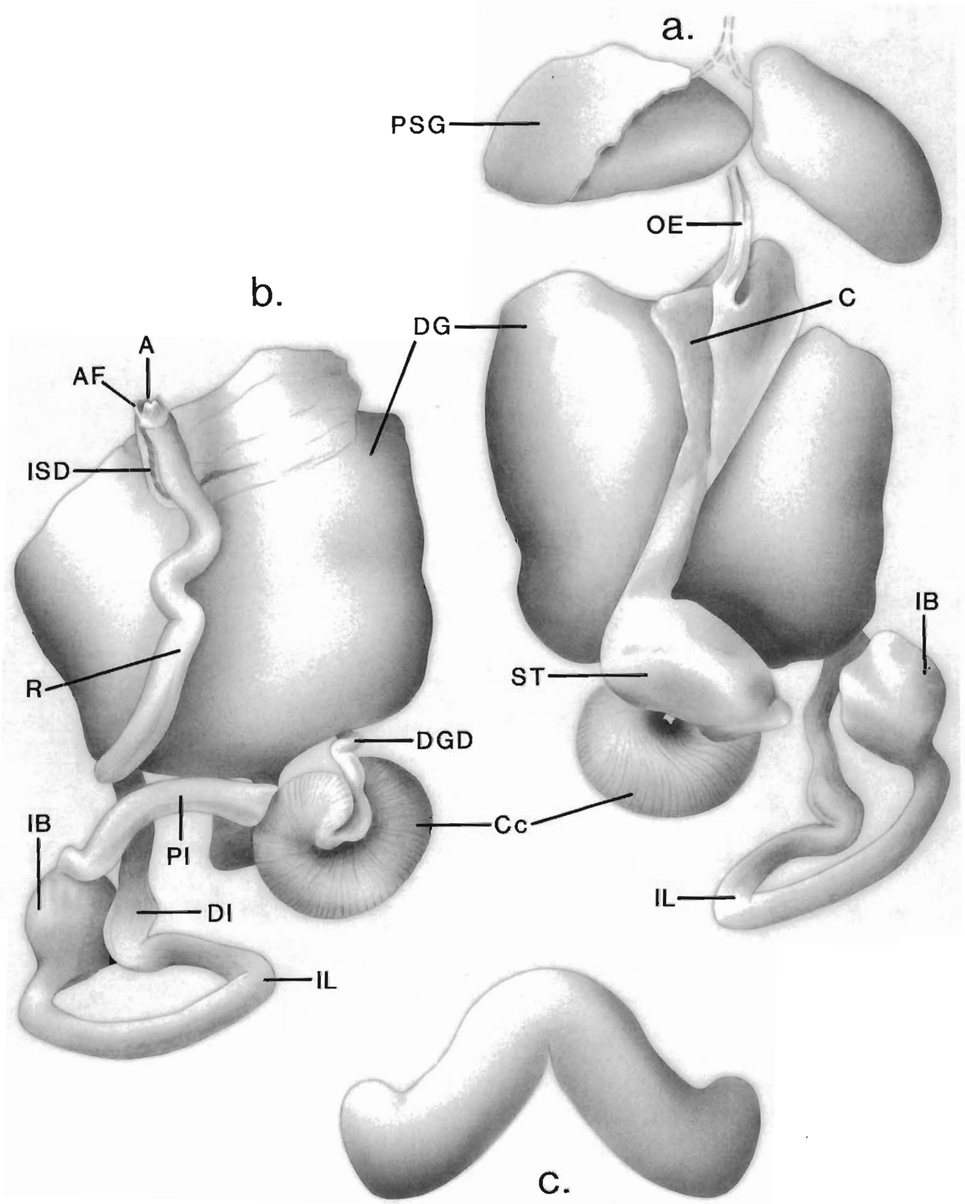

Figure 2. *Aphrodoctopus schultzei,* holotype, 49 mm mantle length. a–b: Digestive system; components expanded for clarity. a. Dorsal view. b. Ventral view. c. Funnel organ. A—anus, AF—anal flap, C—crop, Cc—caecum, DG—digestive gland, DGD—digestive gland duct, DI—distal intestine, IB—intestinal bulb, IL—intestinal loop, ISD—ink sac duct, OE—oesophagus, PI—proximal intestine, PSG—posterior salivary glands, R—rectum, ST—stomach.

normal sucker on arm IV is the 9th or 10th. Table 2 gives counts, maximum sizes of suckers and sucker indices.

The most striking characteristic of *Aphrodoctopus schultzei* is the presence of a brush-like concentration of digitate or finger-like processes on the tips of all the

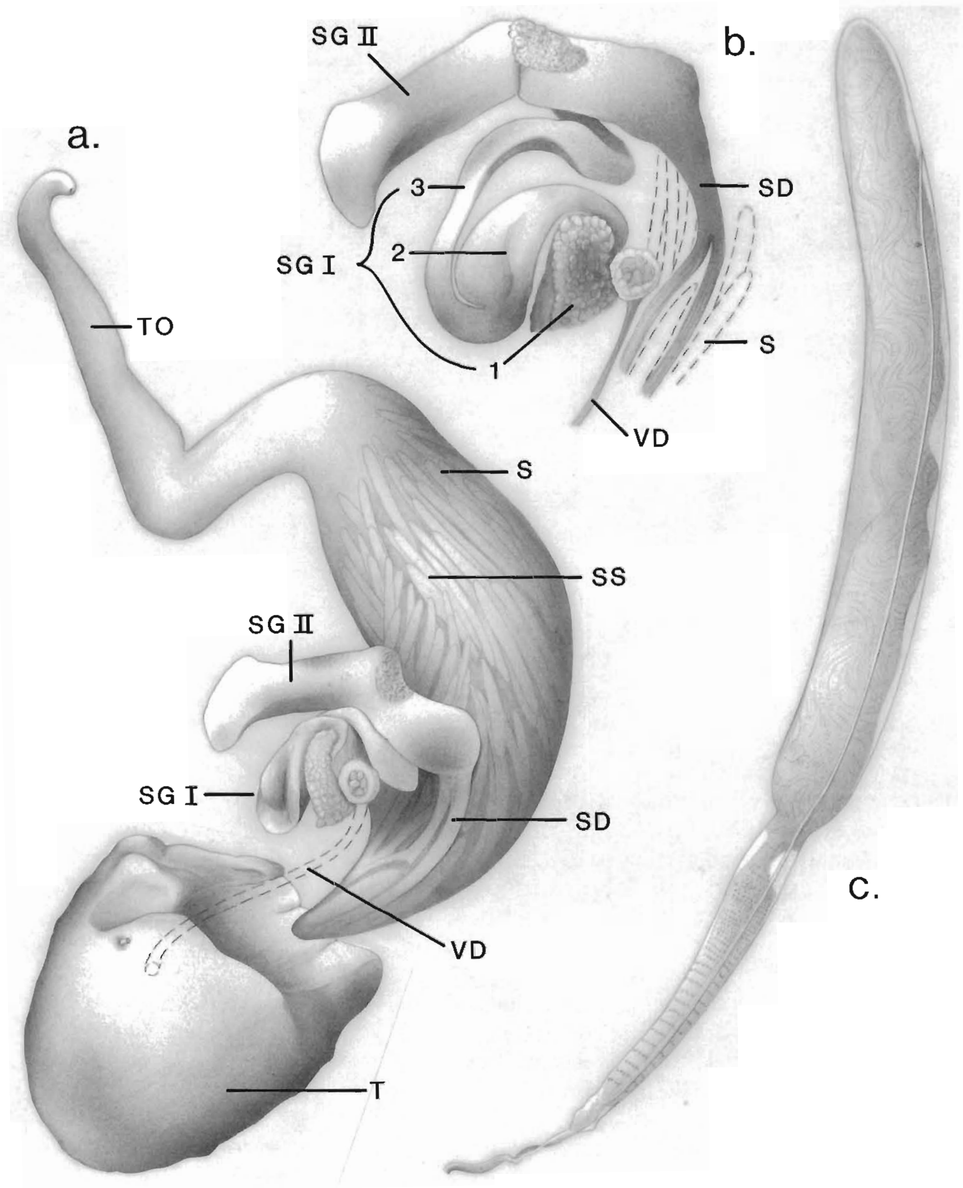

Figure 3. *Aphrodoctopus schultzei,* holotype, 49 mm mantle length. Male reproductive system: a. Entire system with testes displaced posteriorly and spermatophoric gland rotated laterally for clarity. b. Spermatophoric glands I and II; expanded view to show individual components. c. Spermatophore, 10 mm total length. S—spermatophore, SD—spermatophoric duct, SG I—spermatophoric gland I, SG I: 1,2,3—1st, 2nd, 3rd parts of SG I, SG II—spermatophoric gland II, SS—spermatophoric sac ("Needham's sac"), T—testes, TO—terminal organ ("penis"), VD—vas deferens.

arms (Fig. 1a, b), except the hectocotylus. The modified tips occupy about 3 to 6% of the total length of the arms (e.g., 5.6–7.5 mm). The first indication of a modification occurs initially with a small lobe on the lateral edge of the rim of a sucker (marginal ring of Naef, 1923, pl. xii, figs. 1 and 2; fig. 389). A second lobe

Table 1. Measurements (mm), counts and indices of *Aphrodoctopus schultzei*, holotype

	Hoyle		Robson	Present paper		Indices		
Total length	245			238				
Mantle length	50		50	49				
Mantle width	48			42		MWI	86 (96)†	
Head width				23		HWI	47	
Funnel length				18		FLI	37	
Free funnel length				13		FFLI	26	
Arm length	R	L		R	L		R	L
I	140*	180*		100*	140*	I	—	—
II	204	141		170	110*	II	347	—
III	161	193		129	165	III	263	337
IV	149	146		127	126	IV	259	257
Arm formula			2.3.4.1/3.1.4.2	2.3.1.4/2.1.3.4				
Arm width				10		AWI	20.4	
Sucker diameter	11			11		SIe	22.4 (22)†	
Ligula length	4		2.4	4		LLI	3.1	
Web depth				59 (B)		WDI	37	
Web formula			ABCDE/BCADE	BACDE				
Gill length				16		GLI	33	
Gill filaments	9			8 + 1				
Penis length				18		PLI	37	
Spermatophore length				9–10		SpLI	18–20	
Spermatophore width				0.75		SpWI	7.5	

* Arms mutilated or regenerated.
† Robson's Indices.

appears on the next distal sucker; then on each subsequent distal sucker, the lobes become gradually longer until they form two elongate processes on the rim of each sucker. At about the 4th or 5th pair of modified suckers, the cup (adhesive ring and suction chamber, equals infundibulum and acetabulum, respectively) of the sucker disappears and the two processes extend from the remaining base of the sucker, giving a Y-shaped appearance. Distally only processes remain, one pair with a common base in the place of a single sucker, so that four processes occur in a transverse row for the extent of process development to the arm tip. Where fully developed, the processes are cylindrical, elongate and sharply pointed with flat, subtriangular bases. Together they are tightly packed, numerous and give the appearance of toothbrush bristles. The longest processes, about 2 mm in length, occur at the 5th to 8th pair of fully formed processes, then processes gradually become shorter distally. At the arm tip processes become little bumps and the extreme arm tip is granular to smooth. The total number of processes on right arm IV is 86.

The right arm III is hectocotylized by a modification of the tip, unusual in the Octopodinae (Fig. 1c; Hoyle, 1910, pl. Va, figs. 2, 3; Robson, 1929a, fig. 53). The length of the hectocotylized arm is 78% of the length of the left arm III. The spermatophore groove is extremely well developed, thick, broad and deep along the length of the hectocotylized arm; the membrane is 3 to 4 mm wide. A distinct spermatophore guide occurs as a notch and lappet between right arms III and IV. The end organ ("ligula") is very small (LLI 3.1), subcylindrical and blunt; it completely lacks a longitudinal depression, cross-striations, ridges and grooves; calamus is absent. Instead, the entire surface is sponge-like, with a series of irregular, reticulate humps and holes; a singular, irregular, larger deep pit is located near the tip of the end organ.

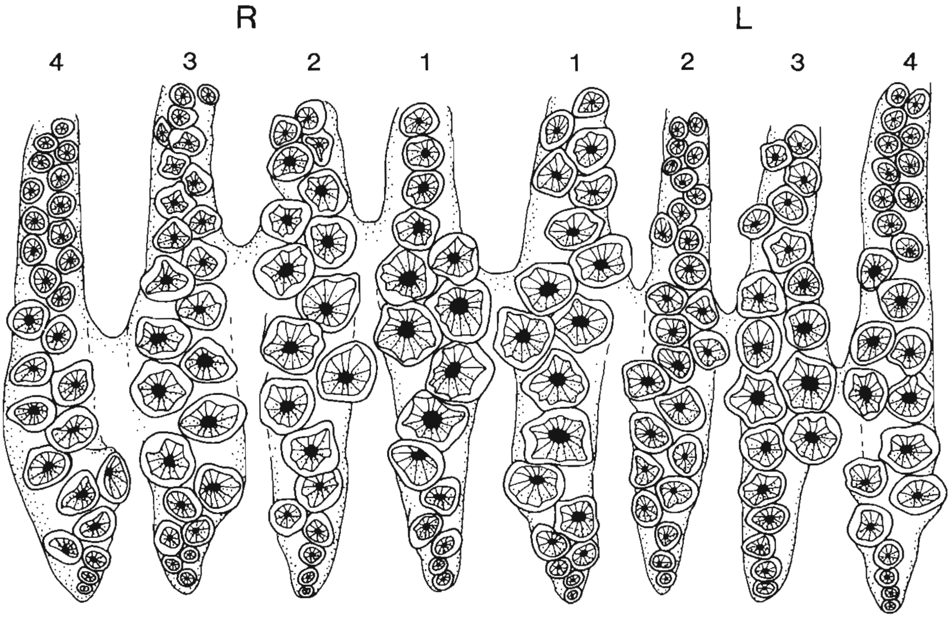

Figure 4. *Aphrodoctopus schultzei,* holotype, 49 mm mantle length. Arms and suckers, oral view. Redrawn from Hoyle, 1910, pl. Va, fig. 1.

The web is moderately well developed and the web depth index (WDI) is 37 (sector B); the web formula is B.A.C.D.E, with E very shallow. No appreciable extension of the web occurs distally along either side of the arms.

The surface of the skin is covered with minute, rounded, conical granules, but no distinct, enlarged cirri or papillae are present, except some small scattered papillae at the base of the dorsal arms. The appearance of an irregular meshwork of wrinkles on the skin is due to contraction and preservation and does not represent a natural condition. The color of the skin in preservation is purple brown, darker on the dorsal than the ventral surface.

Each gill (16 mm long; GLI 33) has eight primary filaments plus the terminal lamella on the outer demibranch.

The radula was figured by Hoyle (1910, fig. 1) and described by Robson (1929a, p. 148) who lists the rhachidian as having a B_3 or B_4 seriation (Fig. 5). The radula and the upper beak were not with the specimen when the holotype was borrowed.

Table 2. Sucker counts, maximum sizes (mm) and indices of *Aphrodoctopus schultzi* (numbers only for left arms)

	Arm				
	Left (No)	Right (No)	Largest diameter	Sucker position	Sucker diameter index
I	*	*	11	6th	22.4
II	67†	89	11	7th	22.4
III	92	64	10	7th	20.4
IV	72	81	7	10th	14.3

* Tip missing.
† Regenerating.

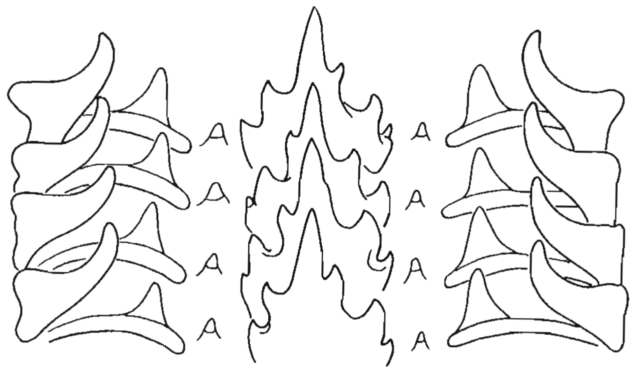

Figure 5. *Aphrodoctopus schultzei,* holotype, 49 mm mantle length. Radula. Redrawn from Hoyle, 1910, fig. 1.

The lower beak has a small, triangular rostrum, a triangular notch and small secondary teeth about half the size of the rostrum.

The buccal mass also is missing, including the anterior salivary glands, so the description of the digestive tract (Fig. 2a, b) begins with the posterior salivary glands. The posterior salivary glands, which cover the anterior half of the dorsal surface of the digestive gland, are very large and lobate (Fig. 2a). The narrow oesophagus enters the dorsal surface of the crop between the posterior salivary glands well posterior to the anterior portion (diverticulum) of the crop. A large portion of the crop lies between the posterior salivary glands and the digestive gland. The crop, or posterior oesophagus, enters the left side of the stomach that lies in a deep depression of the dorso-posterior end of the digestive gland. The stomach is bipartite, with one muscular and one thin-walled section. The vestibulum (Magensinus of Chun, 1910) is short. The spiral caecum lies ventral and posterior to the stomach at the extreme posterior end of the digestive gland in a slight depression, and it is slightly larger than the stomach and has one and one quarter coils. The two ducts of the digestive gland enter the caecum, passing on each side of the proximal part of the intestine. This section of intestine (length 14.3 mm) extends laterally to the right and enters at a right angle a round, muscular, thin-walled intestinal bulb of 6 mm in diameter. The intestine continues posteriorly from the intestinal bulb in a broad curve back toward the midline (16 mm), turns acutely back on itself for 10.8 mm, makes a 90° turn with a slight swelling anteriorly (11.5 mm) where it takes another 90° turn medially. The anterior end of this section passes dorsal to the proximal intestine where this (the proximal intestine) enters the intestinal bulb, and the anterior end parallels the proximal intestine along the posteroventral surface of the digestive gland. The intestine takes a final 90° turn, and the last section, the rectum, passes anteriorly along the ventral surface of the digestive gland (11.2 mm) where it terminates in the anus which has two small lateral flaps. The ink sac is completely embedded in the digestive gland. The ink sac duct enters the anus at its extreme distal end. The digestive gland is subspheroidal with depressions for the stomach, caecum and posterior salivary glands; it is 20 mm long, 24 mm wide and 20 mm thick. The digestive gland appendages are normal.

The male reproductive system is illustrated in Figure 3a, b. The testis is subtriangular in outline with a blunt apex posteriorly; it is semicircular in cross section with a flat dorsal surface and a dome-shaped ventral surface. A deep indentation in the anterior surface contains the posterior part of the spermatophoric sac

(Needham's sac) and the complexes of the spermatophoric glands. The vas deferens arises from the anterodorsal surface of the testis and enters the dorsal part of the spermatophoric gland I as a tightly coiled duct. Gland I is an organ complex that consists of three tightly packed sections: the first part, into which the vas deferens enters, is granular; the second is a hook-shaped sac that empties into a long C-shaped sac, which is the third part of the complex. A spermatophoric duct leads from the anterior surface of the third part into the very large spermatophoric gland II, a large organ complex that nearly surrounds the spermatophoric gland I. The spermatophoric duct empties posteriorly into the spermatophoric sac (Needham's sac). The spermatophoric sac is very large, crescent-shaped (length 25 mm) and is completely packed and swollen with mature spermatophores. The anterior, terminal portion of the spermatophoric sac is L-shaped, non-glandular, muscular, and bends sharply to the left (length 13 mm) then directly anteriorly (length 18 mm) where it terminates. The terminal organ ("penis") entirely lacks a diverticulum. After the last right angle bend the tissue of the "penis" becomes much more muscular than the thin-walled, membraneous spermatophoric sac. The spermatophores are 9–10 mm long (SpLI = 18–20) and 0.75 mm wide (SpWI = 7.5). The sperm mass and cement body cannot be measured because of their contraction within the spermatophore tube, but the ejaculatory apparatus is 2.8 mm long. The surface of the ejaculatory apparatus beneath the translucent outer tunic is sculptured with spiraled rows of minute spines distally; spines become evenly distributed over the proximal half.

Etymology.—The generic name is derived from Greek mythology: Aphrodite, the goddess of love. This name is suggested by the suckers that are modified into processes on the arm tips that could serve a function in courtship behavior. The species was named by Hoyle in honor of Professor Schultz, the leader of the expedition on which the holotype was collected.

Discussion

Two of the primary distinguishing characters of *Aphrodoctopus schultzei* were pointed out by Hoyle (1910) as being unique among all the species of *Octopus*: the structure of the tip (end organ or ligula) of the hectocotylus and the enlarged suckers on all arm pairs I–III. Furthermore, Robson (1929a) noted the unusual ("singular") funnel organ and the very long free extremity of the "penis" devoid of a diverticulum. Thus, it is all the more surprising that these authors seem to have missed what appeared to us first to be the most striking characteristic of this species, the brushlike, digitate processes at the tips of all arms except the hectocotylus. The presence of the conspicuous intestinal bulb in the proximal part of the intestine could not have been seen by Hoyle nor Robson, as the specimen had not been dissected. The presence of these unique or unusual characters in combination is sufficient to confirm the status of the species and even to justify the new generic designation.

In attempting to evaluate these characters to determine potentially closely related species, we believe that the modified arm tip suckers in the genus *Octopus* obviously are significant. We are aware of two other species of *Octopus* that have papillate or finger-like modifications of the suckers on the arm tips: *O. chierchiae* Jatta, 1889 and *O. penicillifer* Berry, 1954. Originally described from coastal Panama, *O. chierchiae* males and females are represented in the S. S. Berry collections from the Gulf of California, now at the NMNH. *Octopus penicillifer,* originally known only from the holotype, a male, also comes from the Gulf of California, where a subsequent female specimen was taken. *Aphrodoctopus schultz-*

ei is known only from the holotype, a male. Our examination of several *O. chierchiae* females and the description of the *O. penicillifer* female (S. S. Berry, ms.) verifies that females do not possess processes. Therefore, we must assume that modified suckers on the arm tips are a male characteristic. In males of *O. chierchiae,* the processes originate on the distal fifth of the arm where the suckers become modified (Fig. 6a, b): the cups (acetabula) become globular/spherical with minute apertures on the relatively long, narrow stalks; the modified suckers/stalks become very closely packed and may be in three to four transverse rows across the arm tips. Some of the sucker stalks lose the remnant apertures (giving a sealed appearance) in the distal half of the modified portion and at this point are properly termed processses. The processes are no higher than normal suckers, they are columnar, blunt-tipped; they are not tapered and pointed as in *A. schultzei.* Jatta illustrated the modifications in 1899, plate 1, figures 12 and 13.

Upon examination of the holotype (USNM 815717), we were able to verify that *Octopus penicillifer* has modified arm tips very similar to those of *O. chierchiae.* The processes arise abruptly near the arm tips without a gradual change-over from normal suckers (Fig. 7). There are no globular suckers. The processes look like columns, truly fingerlike, truncated, blunt, not tapered. They arise from the sucker stalks, are closely packed and appear to be in four transverse rows across the arm.

The processes in *O. chierchiae* and *O. penicillifer* originate from modified sucker stalks, one process per stalk, whereas the processes of *A. schultzei* originate from opposite lateral edges of the sucker rims, giving two processes per sucker. In addition to the comparable arm tip processes, which suggest a close relationship, *O. chierchiae* and *O. penicillifer* have in common other "true" *Octopus* characters such as a well differentiated hectocotylus, a W-shaped funnel organ and the absence of unusually enlarged suckers on arms I–III in males. *Aphrodoctopus schultzei* has a simple, uniform hectocotylus, a modified W-shaped funnel organ with very short lateral limbs and enlarged suckers on arm pairs I-III, and therefore, does not appear to be closely related to these species.

Octopus zonatus Voss, 1968 and *O.* n. sp. Toll and Voss, In Prep.[2] supposedly are closely related to *O. chierchiae* and *O. penicillifer* because of their harlequein coloration pattern, but neither *O. zonatus* nor the new species has any indication of modified arm tip suckers.

Another type of modification of arm tip suckers in *Octopus balboai* Voss, 1971, in which the rims (marginal rings) of the suckers on the distal third of the arms in males including the hectocotylus, are elaborated into a fringe of tiny pointed projections ("papillae"), giving a "star- or flower-like appearance" (p. 17). Voss suggested that this modification could be a sexual character similar to that of the arm tip suckers in *Eledone.* As in *A. schultzei,* the modification in *O. balboai* involves only the sucker rims (marginal rings of Naef), but the suckers maintain their form and are not modified. *Octopus balboai,* furthermore, has a well differentiated hectocotylus and a normal W-shaped funnel organ. *Octopus wolfi* Wuelker, 1913, apparently has a similar pattern of "papillate fringes" around the periphery of the arm tip suckers (Toll and Voss, in press). *Octopus wolfi* also appears to have other characters typical of *Octopus,* but we have seen no specimens of this species. The sucker rim modification in these species is not related to that in *A. schultzei.*

The only species we are aware of that is reported to have modifications on the arm tips in females is *Octopus maorum* (Hutton, 1880). Parker (1885) mentioned and Suter (1913, p. 1064) described "small tubercle-like elevations" in place of suckers "along the extremity" for as much as "one foot" (30 cm) of all arms of a specimen of this large species from New Zealand. The tubercles were "so crowd-

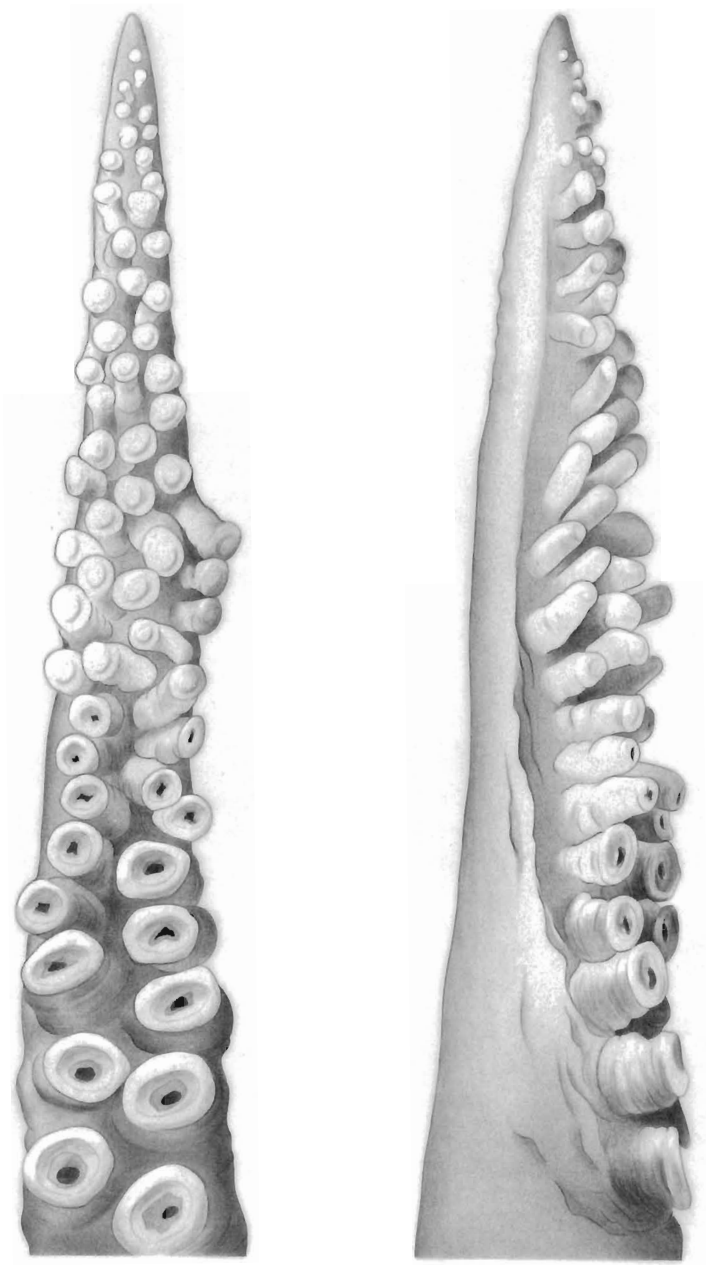

Figure 6. *Octopus chierchiae,* male, 11 mm mantle length, USNM 816247. Modification of suckers and sucker stalks into digitate processes on left arm II: a. Oral view. b. Lateral view.

ed" that they were difficult to count. Benham (1943) examined several specimens of various sizes and found no tubercles; Benham believed that the single specimen reported on by both Parker and Suter was abnormal. Stranks (1988) examined 25 specimens, both females and males, and found no trace of modified suckers, so we must conclude that such a character does not occur in *O. maorum.*

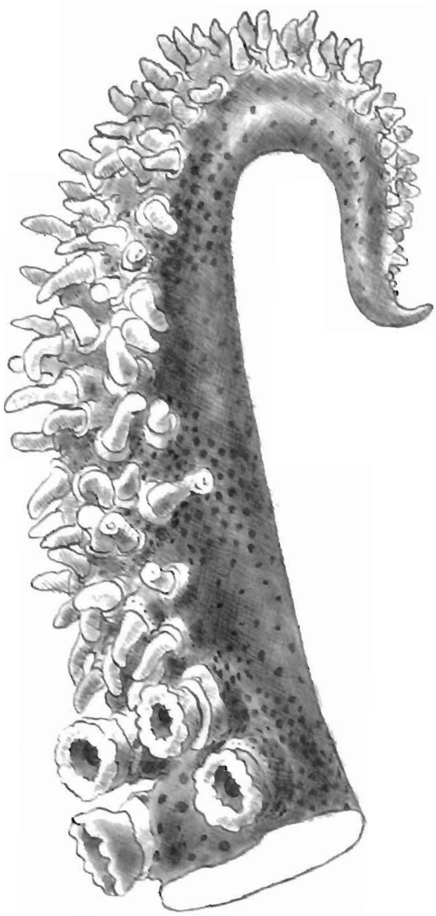

Figure 7. *Octopus penicillifer,* male 15 mm mantle length, USNM 815717. Modification of suckers and sucker stalks into columnar, digitate processes on arm.

Other species in the family Octopodidae exhibit modifications of distal arm suckers into processes or finger- or flap-like structures, namely males of all species of *Eledone*. These modifications occur on the tips of the seven non-hectocotylized arms. In *E. moschata* (Lamarck, 1798) the single row of suckers gradually becomes a double row of flattened laminae or platelets (Naef, 1923, fig. 430); *E. cirrhosa* (Lamarck, 1798) has suckers transversely compressed and drawn out into prolongations (Naef, 1923, fig. 433). In both species the rudimentary suckers are still visible (Haas, 1989, p. 169; Naef, 1923, p. 723). In *E. massyae* Voss, 1964, the suckers decrease in size and become a double row of two minute fleshy papilliform processes that diverge laterally (Roper et al., 1984, p. 219). In *E. thysanophora* Voss, 1962, the normal suckers end without decreasing in size and the last sucker is followed by a brush of tiny processes (papillae) in three to four rows (Voss, 1962, fig. 3a). In *E. caparti* Adam, 1950 suckers are compressed, drawn out laterally, then become double projections (papillae) (not illustrated). In *Eledone palari* (Lu and Stranks, 1991, fig. 1a) arm tip suckers are absent and the entire oral and lateral surface of the arm tips (up to 43% of arm length) is covered with a thickened, spongy pad.

Table 3. Characteristics of octopodid species with dimorphic arm tips in males

Species	Sucker rows	Hectocotylus	Enlarged suckers arms/pair	Penis diverticulum	Funnel organ	Reference
Octopus:						
cheirchiae	2	Octopus-like	none	bulbous	W	Jatta, 1889
penicillifer	2	Octopus-like	none	U-shaped	W	Berry, 1954
balboai	2	Octopus-like	none	long-, tapered	W	Voss, 1971
wolfi	2	Octopus-like	?	small, round (immature ?)	W VV	Toll and Voss, in press
A. schultzei	2	uniform, no calamus, ligula spongy	I–III/6th–10th	none		This paper
Eledone:						
moschata	1	ligula rudimentary, calamus nearly reaches tip	I–IV/4th–12th	none	W	Naef, 1923; Pers. obs.
cirrhosa	1	ligula almost absent, calamus well developed	none	small	W	Neaf, 1923; Pers. obs.
caparti	1	ligula minute, calamus >50% of ligula	I/less so II	?	?	Adam, 1950
thysanophora	1	uniform, no calamus	none, largest at level of web	trace	Λ biparted	Voss, 1962
massyae	1	uniform, no calamus	none	distinct	VV	Voss, 1964
palari	1	ligula medium, calamus large	none	none	VV	Lu and Stranks, this volume

While all known *Eledone* species have dimorphic arm tips in males, dimorphism in the genus *Octopus* appears to be exceptional (we are aware of only four, perhaps five, species out of at least 100 species). The species with modified suckers on arm tips are listed in Table 3. The primary characters that define the genus *Octopus senso lato* are two rows of suckers, a well-differentiated hectocotylus with ligula and calamus and a W-shaped funnel organ (Naef, 1923; Robson, 1929a). *Eledone,* on the other hand, is defined by a single row of suckers, an undifferentiated hectocotylus (but see Adam, 1950 and Lu and Stranks, 1991) and dimorphic arm tips (Voss, 1988). Clearly, *Octopus chierchiae, O. penicillifer* and *O. balboae* conform to the diagnosis of the genus *Octopus. Aphrodoctopus schultzei,* however, an octopus with two rows of suckers, has an undifferentiated hectocotylus similar to that of *Eledone thysanophora* and a modified W-shaped funnel organ. Clearly, *A. schultzei* is not closely related to the three other *Octopus* species with modified arm tip suckers, and its specific validity is confirmed. Its unique modification of arm tip suckers alone would not justify generic distinction. It is the combination of several other important characters that contribute to the concept of separate generic status for *O. schultzei*: 1) the hectocotylus is simple, undifferentiated; 2) the funnel organ is an unusual W-shape with extremely short lateral lobes; 3) several pairs of suckers are enlarged on arm pairs I, II and III; 4) an intestinal bulb is present. This organ is present in other species of Octopoda, especially but not exclusively in the Cirrata, where it is associated with the absence or very weak development of the crop, the posterior salivary glands (or other salivary glands) and/or with a reduction in the size of the digestive gland. *Aphrodoctopus schultzei* has a well developed crop, large posterior salivary glands and a large digestive gland. 5) The very long, free penial terminal organ lacks a diverticulum.

Ultimately, the validity of one row of suckers versus two rows as the principal character that distinguishes the subfamilies Octopodinae and Eledoninae, thus the genera *Octopus* and *Eledone,* might be questioned. But to date this character continues to be used as the primary feature to separate these two subfamilies; for example, see the recent evolutionary tree and classification of the Octopodidae by Voss (1988).

Just a few years ago we would have been reluctant to name a new genus of shallow water benthic octopus that superficially looks so much like an *Octopus.* However, the detailed analyses of the Octopodinae that began at the Cephalopod International Advisory Council Workshop in 1988, Toll's re-evaluation of octopod genera (1991), Mangold and Hochberg's redescription of *Octopus vulgaris* and redefinition of the genus *Octopus* sensu stricto (in prep.[3]), and the monographic work on tropical Indo-Pacific species (M. Norman, pers. comm.), give accumulated evidence that this complex taxon indeed should be subdivided into several genera. Had we not been able to examine the holotype of *Octopus schultzei* in detail, no one could have predicted that it would be one of the subdivided groups. But the combination of so many distinctive characters in this animal, especially in view of the above mentioned modern syntheses, leaves little choice but to designate *O. schultzei* as the type of the new genus *Aphrodoctopus.*

Further comparison of this genus with other genera that arise from *Octopus* sensu lato must await the completion and publication of studies currently in progress by *Octopus* specialists.

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[3] Mangold, K. M. and F. G. Hockberg. In prep. Defining the genus *Octopus*: redescription of *Octopus vulgaris.*

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