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REDESCRIPTION OF THE DEEP-SEA CIRRATE OCTOPOD *CIRROTEUTHIS MAGNA* HOYLE, 1885, AND CONSIDERATIONS ON THE GENUS *CIRROTEUTHIS* (MOLLUSCA: CEPHALOPODA)

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ABSTRACT

The deep-living octopod *Cirroteuthis magna* Hoyle, 1885 is redescribed, based on the only three specimens known of the species: a mature female (holotype) captured in the south Indian Ocean between Prince Edward and Crozet islands at 2557 m and two specimens, one submature female and one mature male, recently captured in the central Atlantic at 1300 and 3351 m depth, respectively. Video images from the capture of the latter specimen were recorded. This species is characterized by its very great size (to 1300 mm TL), making it the largest known cirrate octopod; butterfly-like shell with open wings ; very voluminous eyes with large lenses; arm length 73–79% of the total length; primary web inserted at different levels on the dorsal and ventral ends of the dorso- and ventrolateral arms on both sides, and at the same level on both ends of the dorsal and ventral arms; each arm is independent of the primary web, and is connected with it by a single vertical membrane or intermediate web that is attached along the dorsum of the arm; absence of nodule at the fusion point of both webs. Very large cirri, the first cirri commencing between the 4th and 5th suckers, with three types of suckers on all the arms; cylindro-conical form and those with the acetabulum highly deformable on the first 2/3 of arms and barrel-like on the rest of the arm; absence of particularly enlarged suckers. *C. magna* is compared with *C. muelleri* and other related species. Sperm sacs and spermatozoids from *C. magna* and *C. muelleri* are described and compared. The *Cirroteuthis* genus is reviewed and a diagnosis is proposed. This study confirms that the members of the Cirroteuthidae family show several unusual features of great interest.

Cirrate octopods are a group of cephalopods typically adapted to the deep-sea environment, invertebrates attaining the largest size in the abyssal and hadal ecosystem where they have been captured at depths of up to 7280 m (Voss et al.,1977). This group probably comprises the oldest evolutionary lineage of octopods (Aldred et al., 1983; Voss, 1988a).

Due to the difficulties involved in deep-sea trawling before the advent of modern gear and techniques, few specimens of cirrate octopods were known and most species were represented by unique, poorly preserved specimes. To date, 30 species of cirrate octopods have been described, of which only a few species are represented by more than a dozen specimens (Nesis, 1987; Voss, 1988b; Voss and Pearcy, 1990). As a result, the systematics of cirrate are confused (Voss, 1988a).

Hoyle (1886), Verrill (1896), Chun (1913), Ebersbach (1915), Grimpe (1916, 1920), Robson (1926, 1932) and Sasaki (1929) were the first to discuss the cirrate octopods. Recent studies provide important reviews of cirrate octopods and relevant background for this paper. The work of Aldred et al. (1983) has greatly assisted in clarifying details of the morphology of *Cirrothauma murrayi* Chun, 1913 and has given a solid foundation on which comparision of the genera can be based (Voss, 1988a). The works of Nesis (1987) and Voss (1988a,b) have shed new light on the systematics, phylogeny and biogeography of these cephalopods. The work of Voss and Pearcy (1990) recorded *Cirroteuthis muelleri* Eschricht, 1838 from the Pacific Ocean and redescribed this species. There are also re-

ports of eggs and embryos of cirrate octopods (Boletzky, 1982), reproductive strategy (Villanueva, 1992), and feeding ecology (Villanueva and Guerra, 1991).

The recent use of submersibles has provided the opportunity to observe these organisms in their natural environment. In the past, information has only been available from net-captured specimens which are frequently damaged, due to their extreme fragility and gelatinous consistency. The works of Jahn (1971); Roper and Brundage (1972); Pearcy and Beal (1973); Boletzky (1985); Nesis and Sagalevich (1983) and Vecchione and Roper (1991) have highlighted the fact that photographs taken with cameras mounted on deep-sea search vehicles or submersibles all of great use for the understanding of the biology and ecology of these organisms, besides their morphology and systematics. This methodology has now been perfected with the use of high resolution video cameras that provide whole sequences on the behaviour of deep-sea cephalopods in their natural environment. Boletzky et al., (1992) described the "ballooning response" reaction in a cirrate octopod, based on one such sequence.

During the course of the French FARANAUT cruise (15 March–15 April 1992) conducted over the fracture area 15°–20°N on the Mid Atlantic Ridge, 11 cirrate octopods were filmed and photographed between 2702 and 4527 m, and one of which was captured at a depth of 3351 m., this being the male specimen of *Cirroteuthis magna* described in this paper.

The aim of this paper is to redescribe *Cirroteuthis magna* Hoyle, 1885 on the basis of the three known specimens: holotype, a female captured in 1873 by the CHALLENGER expedition between Prince Edward and the Crozet islands; a second female captured in 1976 by the RV KARA-DAG off Cape Blanc (central-western Africa), and the above male captured in 1992 over the fracture zone 15°–20°N on the Mid Atlantic Ridge (Fig. 1). Also, the genus *Cirroteuthis* Eschricht, 1836, is reviewed, and its diagnosis expanded.

HISTORICAL SUMMARY OF THE GENUS *CIRROTEUTHIS*

The first description of a cirrate octopod coincides with the naming of the genus *Cirroteuthis* in the work published by Eschricht in 1838, where *C. mülleri (muelleri)* is described based on a specimen captured off the coast of Greenland. Reinhard and Prosch (1846) identified two specimens captured "off of Greenland" (probably off the northern part of west Greenland) in the Prince Napoleon Expedition, which were named *Sciadephorus mülleri.* Besides these two specimens, Robson (1932: 130) cites another of this species collected "to the north of the North Sea". There are no subsequent references until 1988 when Nesis (1988) gave a map of the North Polar Ocean and its seas with 19 dots representing actual records of *C. muelleri*, including new specimens taken by Russian research vessels. Voss and Pearcy (1990) redescribe the species based on 12 specimens collected in the northeastern Pacific, likewise highlighting the existence of two further specimen from the North Atlantic (no additional data given), which had not been cited previously. In the National Museum of Natural History of Paris, two more specimens of *C. muelleri* have been found (see material examined), captured in 1963 and 1964 respectively, in the North Atlantic, with more detailed information not given. In total this species is known from 31 specimens from the sites shown in Figure 1.

After Eschricht (1838) a number of species of cirrate octopods were described and attributed to the genus *Cirroteuthis.* In 1932, Robson created the genus *Grimpoteuthis* to which he transferred from *Cirroteuthis* the following species: *C. umbellata* Fischer, 1883,

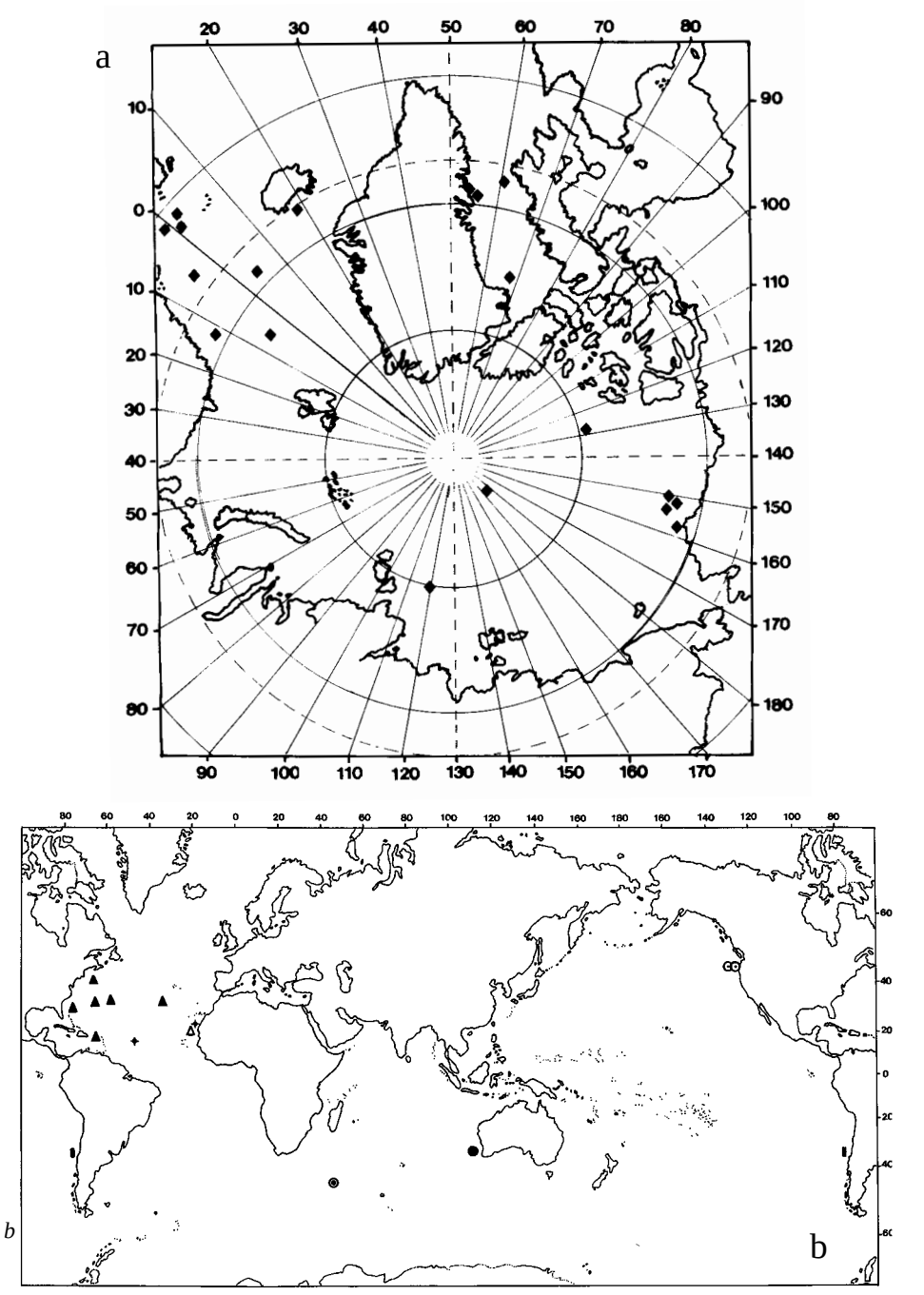

Figure 1. The localities for species of *Cirroteuthis*. 1a Polar projection showing the distribution of *C. muelleri* (from Nesis, 1988 with one added record); 1b. Mercator projection illustrating the distribution of all other studied species. ◉: *Cirroteuthis magna* holotype; + : *Cirroteuthis magna*, Faranaut and Kara-Dag specimens; ♦ : *Cirroteuthis muelleri* (from Nesis, 1988); ʘ: *Cirroteuthis muelleri* described by Voss & Pearcy (1990); Δ: *Cirroteuthis* sp. Golovan & Nesis, 1975; ▲: *Cirroteuthis* n. sp. Roper and Brundage, 1972; ▮: *Cirroteuthis* sp.(holotype for *Cirroteuthis (?) hoylei* Robson 1932); ●: *Cirroteuthis* n. sp. A Nesis, 1982

C. megaptera Verrill, 1885, *C. plena* Verrill, 1885, *C. pacifica* Hoyle, 1885, *C. meangensis* Hoyle, 1885, *C. caudani* Joubin, 1896, *C. grimaldii* Joubin, 1903 and *C. glacialis* Robson, 1932. In the same work, Robson transfered *C. gilchristi* Robson, 1924 to Grimpe's 1916 genus *Chunioteuthis,* and considered as uncertain the generic position of *C. magna* Hoyle, 1885, *Cirroteuthis* (*Cirroteuthopsis*) *massyae* Grimpe, 1920, and Robson's new species *C. hoylei* (see below).

On the basis of the two specimens collected on 29 December 1873 and 17 November 1875 respectively by the CHALLENGER Expedition at two different sampling stations (Fig.1A), Hoyle (1885) described *Cirroteuthis magna,* a description later amplified and illustrated (Hoyle, 1886). Robson (1932) considered that the two specimens belonged to different species, identifying the smallest captured in 1875 off Valparaiso as a new species, *C.* (?) *hoylei,* while identifying the other captured off the Crozet Islands as *C.* (?) *magna.* Robson doubted that the two specimens belonged to the genus *Cirroteuthis,* as the shapes of the gills and the length of the body seemed different to those in *C. muelleri* (Robson, 1932: 133). Nesis (1987: 283) used quotation marks for the two species to indicate their provisional placement in the genus. In his key to the species of *Cirroteuthis,* Voss (1988b) did not include either *C. magna* or *C.* (?) *hoylei* in his list of cirrate octopods.

A reexamination of the holotype and two new specimens reported in this paper confirm the validity of *C. magna* Hoyle, 1885.The species, the largest known cirrate octopod, is herein redescribed.

MATERIAL AND METHODS

Definitions of counts, measurements and indices used here are according to Roper and Voss (1983) and Voss and Pearcy (1990). Our cirrus length, fin length, fin width and fin-length and fin-width indices are as given by the later authors. What Robson (1932) and Voss and Pearcy (1990) measured as fin length was measured as fin width by Hoyle (1886); i.e., the distance between its insertion and the outer end of the fin. Finspan (Table 1) is the distance between the apices of the fins. The Finspan Index (FSI) is defined here as the ratio between the finspan and the total length (TL) multiplied by 100 (Table 2). A second new index is proposed for the cirrate octopods of the Cirroteuthidae family, the Shell Width Index (SWI) or the medial length of the shell (MLS) being a percentage of the maximum width of the shell (MWS). The medial length of the shell is the depth between the anterior and the posterior edges of the transverse bar (or intermediate body) which join the wings of the shell (Fig. 4C). All the abbreviations used are explained in Appendix 1.

The sperm sacs from the FARANAUT specimen were removed from the seminal vesicle, cleaned in a phosphate buffer, counted, measured and then drawn with the aid of a camera lucida on a stereomicroscope with a micrometric viewfinder. Some of the sperm sacs were dehydrated in an ethanol series, and later tranferred to 100% acetone. To observe the interior and the morphology of the spermatozoids, some sperm sacs were torn before drying. These were critical-point dried on a Polaron E-3000, using CO_2. Sperm sacs were mounted on aluminium stubs and coated with 20-nm thick gold in a sputter coating Bio-Rad SC-515 with Peltier stage to maintain the sample at 4°C during the process. Observations were made with a Philips XL-20 Scanning Electron Microscope at accelerating voltages varying between 15 and 30 kv. Measurements of the spermatozoids were made on the screen using the automatic mode on the microscope control program.

Table 1. *Cirroteuthis magna*. (Measurements [in mm] and counts of specimens after fixation)

	Holotype	Faranaut	Kara-Dag
Catalogue number	BMNH 1890.1.24.1	MNHN	ZMMSU Y-372
Sex	Female	Male	Female
Dorsal mantle length	175h	220	140
Total length	1,155h	1,075	870
Ventral mantle length	163h	185	115
Mantle width	125h	170	86
Fin length	200r	156	130
Fin width	76h	74	65
Finspan	513h	483	321
Eye diameter	—	85	60
Interocular width	100r	105	89
Lens diameter	29	28	25
Funnel length	52	50	60
Pallial aperture	22	22	20
Arm length			
I	R 875 L 875h	R 748 L 790	R 690 L —
II	R 870 L 875h	R 710 L 700	R — L —
III	R 870 L 890h	R 685 L 690	R — L —
IV	R 838 L 915h	R 745 L 565	R — L —
Cirrus length*	80h	72	85
Sucker diameter**	8h	9	6
Gill length	37	25	24
Gill width	30	27	20
Gill filam. no (demibranch)	R5–L5 h	R6–L6	R5–L6
Terminal organ (penis) length		6	
Ovarian oocyte length	11		10
Upper beak			
Hood length	28	20	25
Crest length	39.6	32	37
Rostral length	5.1	4.1	3.7
Lower beak			
Hood length	10.6	9.1	—
Crest length	33.8	23	28
Rostral length	4.6	3.4	3.8
Shell width	85 h	66.5	61.5
Shell medial length	22 h	20	18.7

R: right arm; L: left arm; *length of the longest cirrus; **diameter of the largest sucker; h: measured by Hoyle; r: measured by Robson; – : broken.

Systematics

Cirroteuthis magna Hoyle, 1885

Fig. 1–29, Tables 1–4

Cirroteuthis magna Hoyle, 1885: 233; Hoyle, 1886: 56 (pars), text-fig. 2, pl. XII; pl. XIII, figs. 1–2.
Cirroteuthis (?) magna, Robson, 1932: 162.
"Cirroteuthis" magna, Nesis, 1987: 283

Material examined.—Type material. Holotype, mature (?) female, 175 mm ML (BMNH 1890.1.24.1), from Challenger Sta. 146, 45°46′S,45°31′E, between Prince Edward and Crozet Islands, 2557 m,

Table 2. *Cirroteuthis magna.* (Indices of bodily proportions of specimens measured after fixation)

Sex	Holotype Female	Faranaut Male	Kara-Dag Female
ML	175	220	140
MAI	19.1	27.8	20.3
MWI	71.4	77.3	61.4
ALl-I	R 500 L 500	R 340.0 L 359.1	R 492.8
-Il	R 497 L 500	R 322.7 L 318.2	—
-III	R 497 L 508	R 311.4 L 313	—
-IV	R 479 L 523	R 338.6 L 257.8	—
ASIn	4.6	4.1	4.3
CiLI*	80	71	95.6
FLI*	200	148.6	146.1
FSI	44.4	44.9	36.9
FWI**	38	47.4	50
EDI	n/a	39	42.8
FuLl	29.7	24.6	42.8
LDI	16.6	12.7	17.8
PAl	12.6	10.8	14.3
TOLl		2.9	
SWI	26.8	30.1	30.4

*Length of the longest cirrus and of the fin length as percentage of the interocular distance; **width of the fin as percentage of the length of the fin; n/a: not appreciable.

29 December 1873; globigerina ooze. Preserved in 70% ethyl alcohol, in relatively good condition; dissected specimen; beaks now separated, illustrated by Hoyle (1886, pl.XII, figs. 6–7); stomach and gills separated; shell presumably lost, illustrated by Hoyle (1886, pl. XIII, figs. 1,2), although not cited by Robson (1932). There are remains of the oviductal gland; the ovary is voluminous. The present authors completed the measurements noted in Table 1; the shell measurements were calculated from a diagram in Hoyle (1886, pl. XIII, fig.1).

Other material .—Cirroteuthis magna: —1 female, 140 mm ML, (ZMMSU Y-372), RV Kara-Dag, 23°00′N,17°34′W, 18 February 1976, 1300–1350 m, pelagic otter trawl 92.5 m moth-opening in bottom version, collected by M. A.Tsymbal. Very much damaged; preserved in 4% formalin. Specimen measured, dissected and drawn prior to preservation in 70% ethyl alcohol; digestive tract, beak, shell and genitalia separate. —1 mature male, 220 ML, (MNHN, not registered), from the Faranaut cruise, R/V Atalante, captured by the mechanical arm of the submersible Nautile. The capture was filmed, and photographs were also obtained (Plate 1); Sta. FR14, 15°28.75′N,46°33.56′W, 3351 m., 1 April 1992. Collected by T. Triger, the submarine pilot, and preserved in 4% formalin. In good condition, although all webs are damaged; suckers missing from large portions of the arms except on the 4th left. Specimen measured, photographed and drawn, then preserved in 70% ethyl alcohol; digestive tract, beak, shell, genitalia and sperm sacs separate.

Comparative material examined.—Cirrothauma murrayi Chun, 1913: 1 female (IIMV 1990.11.1), 85 mm ML, 500 mm TL, Abyplane cruise, CP.16, 45°50.2′N,15°55.6′W, 4190–4370 m, bottom trawl, 10 June 1981. Preserved in 70% ethyl alcohol, in good state of preservation, dissected, shell separate. The shell is, in general terms, as described by Aldred et al. (1983) although asymmetric, measuring: 33.4 mm wide (MWS), 9.4 mm medial length of the shell (MLS), SWI = 28.1.

Cirroteuthis muelleri Eschricht, 1838: 1 male (USNM 730984), 77 mm ML, RV Oceanus, Sta.5-608, 36°44.36′N 68°36.12′W, 4602–4639 m, R/V Oceanus, 41 ft shrimp trawl, 30 April 1976, determined by G. L.Voss, in acceptable state of preservation, whole specimen. - 2 males, (USNM 817580), 74 and 79 mm ML, Cr. Y. 7102 B, Sta. 262; 45°38.3′N,126°43.8′W, 2721 m, RV Yaquina, bottom trawl, 17 February 1971, determined by G. L.Voss (Voss and Pearcy, 1990, figs. 2,3), in acceptable state of preservation, dissected by G. L.Voss, shells separate, in the first specimen MWS

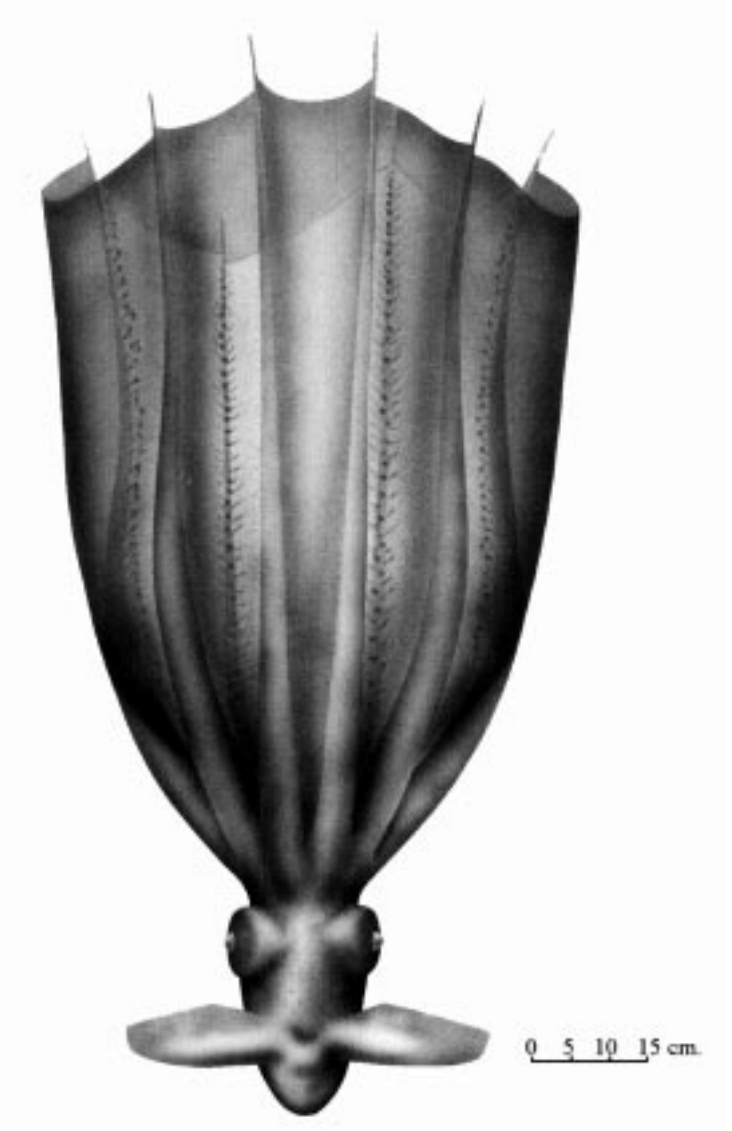

Figure 2. *Cirroteuthis magna*, dorsal view of mature male (220 mm ML, MNHN). Reconstructed based on the specimen captured and video images.

= 20 mm, MLS = 13.2, SWI = 66.0; in the second specimen MWS = 22.6 mm and MLS = 15.7, SWI = 69.5. - 1 male, (BMNH 52.1.1.1), ML unknown, "North Sea" (in fact Norwegian Sea: see Muus, 1962: 10), preserved in alcohol, very much damaged; now dissected, shell, beak (only lower) and viscera separate; described by Robson (1932: 130). Present authors measured the beak (lower rostral length: 2.7 mm, lower hood length: 5.6 mm, lower crest length: 9.7 mm), the cirri (length of the longest: 18 mm) and the suckers (from the 1st to the 7th are conical, diameter of the largest: 1.9 mm; from the 8th to the 21st, are flattened, diameter of the largest: 2.7 mm; diameter of the 22nd: 1.8 mm, from this one onwards, size decreases to the apex; no modified suckers; webs not very well preserved; MWS = 20.4, MLS = 13.9, SWI = 68.1. - 2 specimens (MNHN 3.6.697), described and illustrated by Reinhard and Prosch (1846, p.187, pls. 1-V) as *Sciadephorus mülleri*, captured off Greenland (probably off the northern part of west Greenland), Prince Napoleon Expedition; in

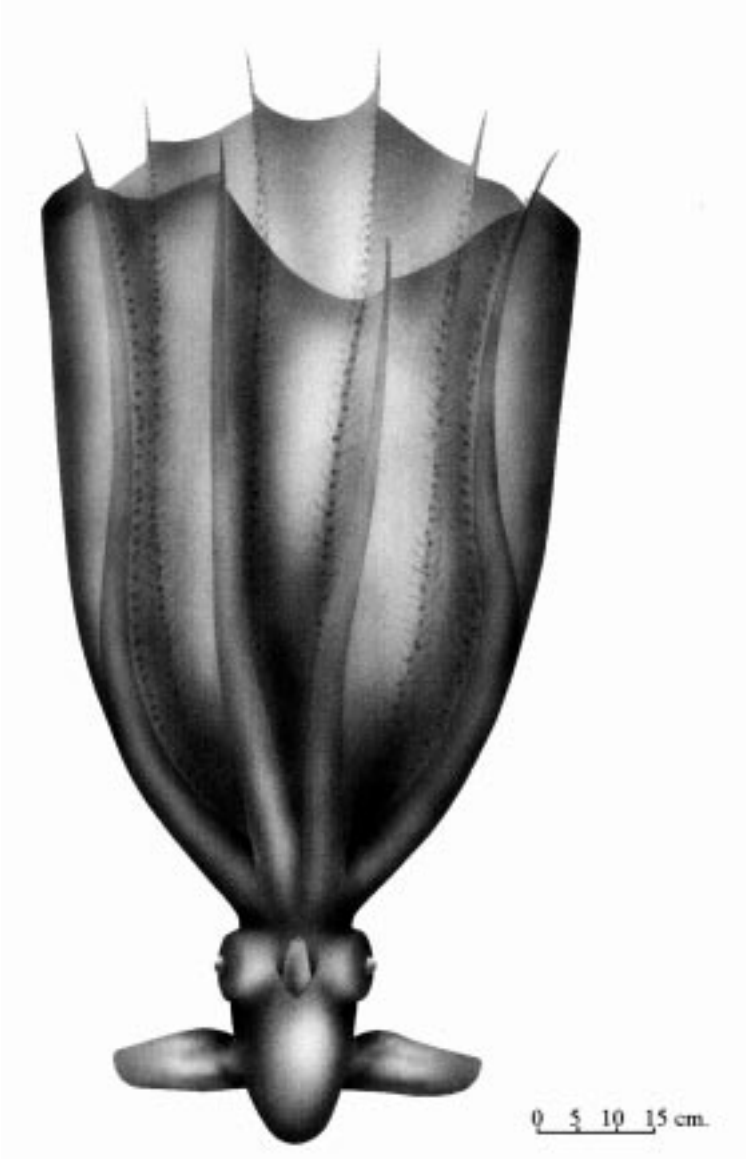

Figure 3. *Cirroteuthis magna*, Ventral view of mature male (220 mm ML, MNHN).

ethyl alcohol, not dissected, in good state of preservation. -1 mature male, 78 mm ML (MNHN, no catalogue number) collected by ISTPM Boulogne, 6 August 1963, origin unknown, in ethyl alcohol, in excellent state of preservation although the web is almost completely missing, labelled as *Cirroteuthis* sp., SWI = 61.2. -1 male immature (MNHN, no catalog number), 58 mm ML, ISTPM Boulogne, RV THALASSA, 27 April 1971, St.X 109, 66°42′N,24°53′W (off Greenland), 400 m, in 4% formalin, in excellent state of preservation, SWI: 66.4.

Cirroteuthis sp: 1 specimen sex unknown, (BMNH1890.1.24.2), 155 mm TL approx., CHALLENGER Sta. 298, off Valparaiso, 34°7′S,73°56′W, 418 m, 17 November 1875, blue mud. Preserved in ethyl alcohol, in very poor state. Hoyle (1885) indicated that this was a "mangled specimen", identifying it as *Cirroteuthis magna.* Considered by Robson (1932: 161) to be the holotype of a new species, *Cirroteuthis (?) hoylei.*

Stauroteuthis syrtensis Verrill, 1879, 1 male, (USNM 730879), 56 mm ML, GS.74.04.89,

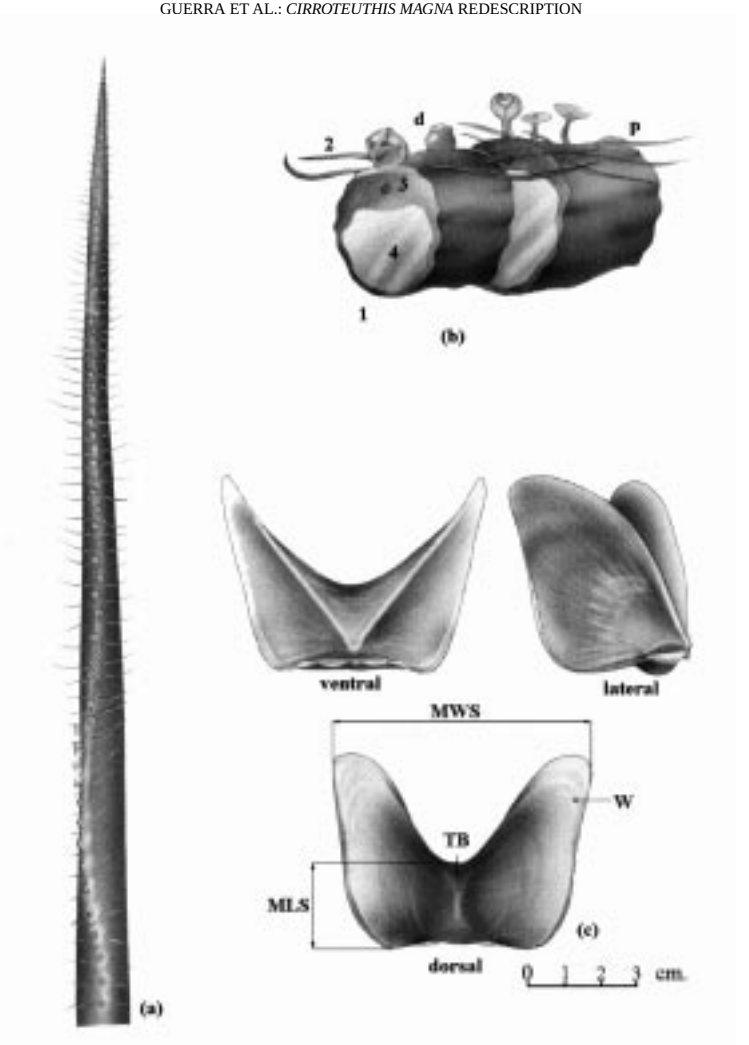

Figure 4. *Cirroteuthis magna,* mature male (220 mm ML, MNHN). (a) Arm oral view; (b) diagram showing transverse sections of one arm in two different zones; p: proximal part of the arm showing stalked suckers and d: distal part of the arm with barrel-shaped sessile suckers; 1: aboral; 2: oral; 3: brachial nerve; 4: fluid filled brachial chamber; (c) shell of the male in dorsal, ventral, and lateral views. MLS: medial length of the shell; MWS: maximum width of the shell; TB: transverse bar; W:

36°32.3′N,74°40.06′W, 860–960 m, RV Gilliss, 45-ft otter trawl, 20 November 1974, determined by G. L.Voss, preserved in 55% isopropyl alcohol, in good condition, complete specimen.

*Grimpoteuthis glacialis (*Robson, 1930): holotype, 1 male, (BMNH1951.4.26.1), 52 mm ML, 231 mm TL, Discovery Exp. Sta. 182, 64°21′S, 62°58′W, Schollaert Channel, Palmer Archipelago, 278–500 m, 14 March 1927, mud, larger otter trawl; labelled as *Cirroteuthis glacialis* Robson, 1930. Preserved in alcohol, in very good condition; dissected, shell, beak and stomach separate.

Grimpoteuthis pacifica (Hoyle, 1885): holotype, 1 specimen of unknown sex and dimensions, (BMNH 1890.1.24.3), Challenger Sta. 181, 13°50′S,151°49′E, Coral Sea off Papua New Guinea, 4538 m, 25 August 1874, red clay. Labelled as *Cirroteuthis pacifica* Hoyle 1885, classified by Robson (1932: 142) as *Grimpoteuthis;* preserved in ethyl alcohol, in very poor condition; dissected, shell, beak and viscera missing; specific characters not distinguishable due to poor condition of specimen.

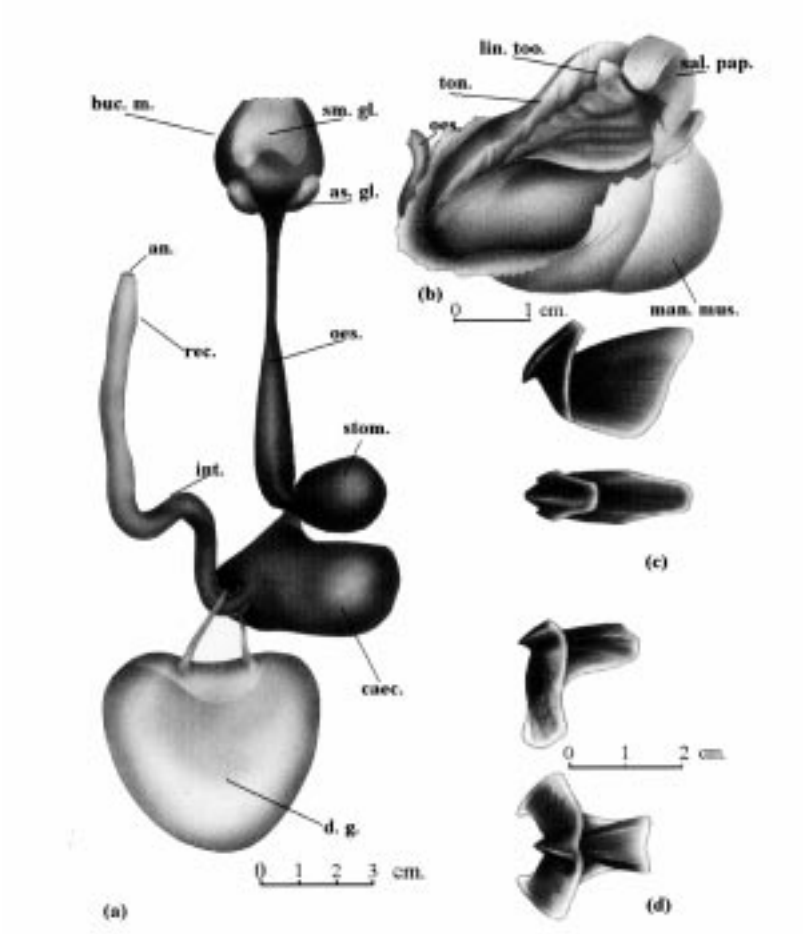

Figure 5. *Cirroteuthis magna*, mature male (220 mm ML, MNHN). (a) Alimentary canal; (b) buccal anatomy, showing lingual tooth; (c) upper beak; d) lower beak.

Grimpoteuthis meangensis (Hoyle, 1885): holotype, 1 mature female, impossible to calculate size (BMNH 1890.1.24.4), CHALLENGER Sta. 214, 4°33′N,127°06′E, off Meanges Islands, 930 m, 10 February 1875, blue mud. Labelled as *Cirroteuthis meangensis* Hoyle 1885, classified by Robson (1932, p. 143) as *Grimpoteuthis;* preserved in ethyl alcohol, in very poor condition; now dissected, shell and beak separate; specific characters still distinguishable despite poor condition of the specimen.

Grimpoteuthis umbellata (Fischer, 1883): syntype, 50 mm ML, sex unknown,(MNHN 3.6.698), 6 April 1883, TALISMAN Exp., dredge 130, 37°55′N,29°22′W, from Faial to Sao Miguel Island, Azores, 2235 m, in ethyl alcohol, arms and suckers in favourable state, web missing, remains of body in poor state, no shell or viscera, labelled as *Cirroteuthis umbellata* P. Fisher "1883", 1884.

-*Grimpoteuthis* sp, 1 female (IIMV 1990.11.2), 50 mm ML, ABYPLANE cruise; 50°31′N,11°31′W., 5280 m, bottom trawl, 12 June1981. Preserved in ethyl alcohol, in good condition, dissected; SWI = 17.8; described and illustrated in Guerra (1992: 223) as *Cirroteuthis* sp.; SWI: 14.6.

Opisthoteuthis grimaldii Joubin, 1903: 2 males, (MNHN 6.8.1961),150 mm TL submature, 165

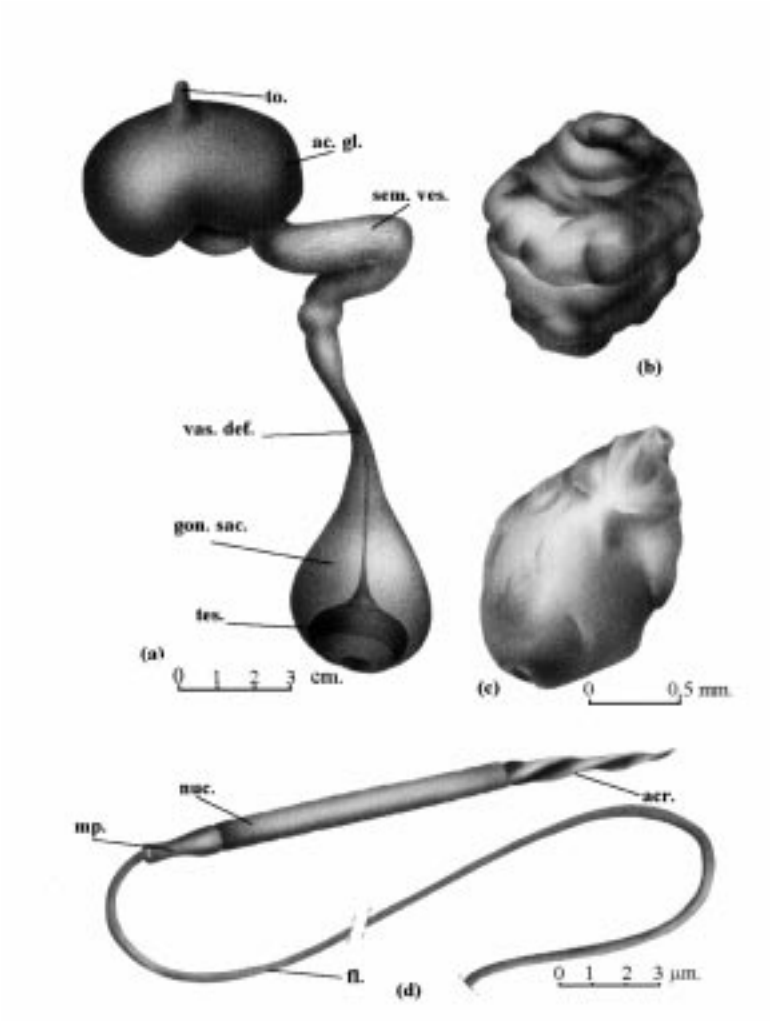

Figure 6. *Cirroteuthis magna*, mature male (220 mm ML, MNHN). (a) Reproductive system ; (b) sperm sac of *C. magna* ; (c) sperm sac of *C. muelleri* (77mm ML, USNM 730984); (d) spermatozoa from sperm sacs of *C. magna* .

mm TL mature, collected by ISTPM Séte, R/V P.T. Tissier Sta. 73, no locality information, February 1959, in formalin, in excellent state of preservation, not dissected, labelled as *Grimpoteuthis grimaldii*.
Opisthoteuthidae, probably *Opisthoteuthis* sp: 1 mature male (IO RAS, no catalogue number), 275 mm TL, R/V Salekhard, cruise 12, trawl 67, sample 18, 3 January 1980, 47°59.38′S, 8°47.2′E, 18:40–19:40, 540–650 m; preserved in alcohol, in poor condition.
Chunioteuthis gilchristi (Robson, 1924): holotype, 1 male (BMNH 1924.9.9.7), Sta. 526, off Cape Town, 2604 m; preserved in ethyl alcohol, in very poor condition; previously dissected, shell, gill, stomach and reproductive tract in separate jars. Labelled as *Cirroteuthis gilchristi* Robson, 1924, in 1932 (p. 158). Robson considered it to be *Chunioteuthis;* it was not possible to observe generic characters due to poor state.
Chunioteuthis sp: 1 specimen of unknown sex and dimensions, (BMNH 1924.9.9.8), severely damaged. Cape Town?, Sta. ?, Gilchrist. Labelled as *Cirroteuthis* sp near *gilchristi* Robson, 1924

Table 3. *Cirroteuthis magna*. (Mature male, 220 mm ML, MNHM). Measurements of the sperm sacs of the seminal vesicle and spermatozoids.

	Max.	Min.	Mean	SD	No
Sperm sac (length in mm)	1.812	0.938	1.469	0.204	196
Sperm sac (width in mm)	1.562	0.938	1.304	0.169	196
No of spermatozoids/100 μm²	108	64	86.08	1.65	—
Spermatozoid (in μm)					
Acrosome length	6.80	4.38	5.76	0.65	67
Acrosome width	0.61	0.40	0.52	0.04	67
Acrosome thickness	0.22	0.13	0.18	0.03	67
Nucleus length	11.00	7.94	9.94	0.64	67
Nucleus width	0.98	0.72	0.83	0.07	67
Mid-portion length	2.37	2.00	2.19	0.09	67
Mid-portion width 1	0.73	0.57	0.65	0.05	67
Mid-portion width 2	0.58	0.34	0.42	0.05	67
Mid-portion width 3	0.62	0.43	0.54	0.06	67
Flagella width	0.37	0.25	0.32	0.03	67

(pt. 2, p. 680). Not referred to by Robson (1932).

Diagnosis.—Deep-sea animals of very great size (up to 1300 mm TL). Butterfly-like shell. Shell Width Index: 26-31. Very voluminous eyes (Eye-ball Diameter Index: 39-43), with large lenses (Lens Diameter Index: 12-18). Arm length 73–79% of the total length. Primary web inserting at a different levels on the oral and aboral ends of the dorso-lateral and ventro-lateral arms on both sides, and at the same levels on both ends of the dorsal and ventral arms. Each arm is not directly connected to the primary web except at its distal margin and at the base of the arms, but each arm is connected with the primary web by the intermediate web that is attached along the aboral side of the arm; absence of a nodule at the fusion point of both webs. Very long non retractile cirri (Cirrus Length Index: 96-71); the first cirri commence between the 4th and 5th suckers. Three types of suckers on all arms: cylindro-conical form and those with the acetabulum highly deformable on the first 2/3 and barrel-shaped on the rest of the arm; no enlarged suckers in male or female. Ovarian oocyte diameter up to 11 mm. Between 5 and 6 gill lamellae per outer demibranch.

External morphology.—For measurements and indices see Tables 1 and 2. The male was measured fresh on board ship by M. Segonzac, and the measurements were: 1300 mm TL, 300 mm ML, 190 mm MW and 950 mm dorsal arm length. A comparison with the measurements subsequently obtained from the fixed specimen and given in table, reveals shinkages of 11–27%. Animals large (up to 1300 mm TL, fresh measure) with soft, gelatinous and fragile consistency. Mantle short (MAI 19 and 20 in females-28 in male); oblong, relatively elongated (i.e., not compressed) and gently rounded posteriorly (Figs. 2,3,8); mantle width approximately 2/3 of mantle length (MWI 61-77). Posterior portion of mantle, posterior to fins, easily lengthened and widened. Pallial aperture narrow, (PAI 10.8-14.3), and slightly larger than base of funnel (Fig. 3).

Head superficially continuous with, and somewhat narrower than mantle; with no discernible constriction between head and mantle (Figs. 2,3,8). Eyes very large and voluminous (EDI: 39-42.8; eyeballs in poor condition and measurement not possible in holo-

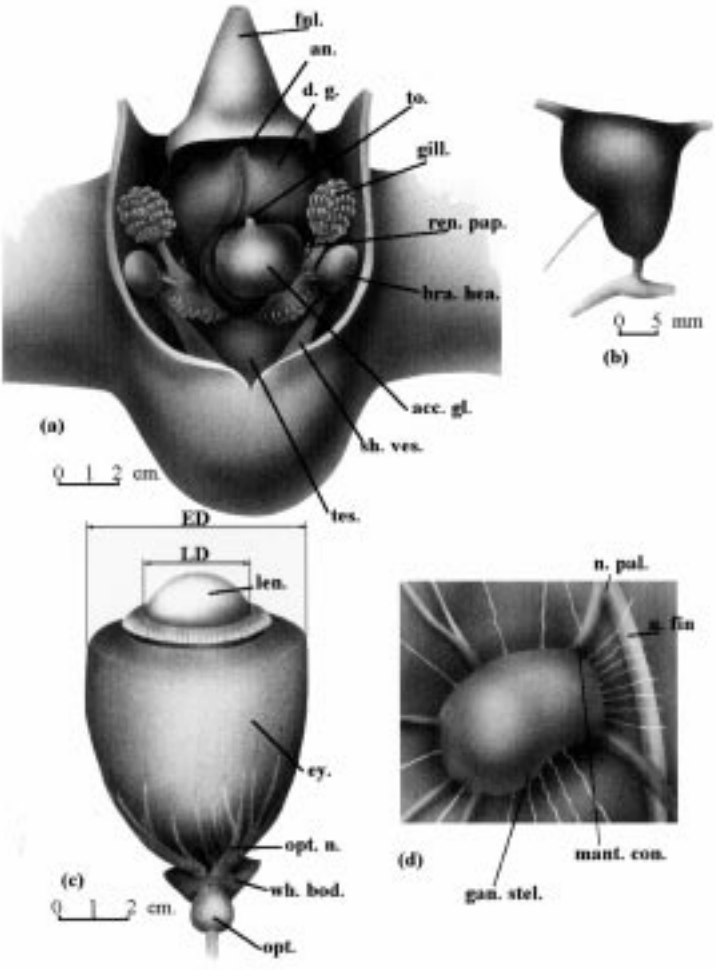

Figure 7. *Cirroteuthis magna*, mature male (220 mm ML, MNHN). (a) Diagram showing the features of the mantle cavity; (b) systemic heart; (c) eye, ED: eye diameter, LD: lens diameter; (d) stellate ganglion from right side.

type), protuberant, fully formed and with large semispherical lenses (Figs. 2,3,7,8,15,16); eyelid absent.

Funnel relatively long (FuLI 24.6 and 42.8 in male and KARA-DAG female, respectively), conical, narrow, slightly swollen at tip, free for about half of its length (Fig. 3). Inside mantle cavity of male base of funnel considerably expanded, funnel opening narrow, pallial aperture surrounds funnel closely but not fused with it. Funnel organ and olfactory pits not seen.

Fins approximately halfway along mantle in live male, but located nearer to apex of mantle than to eyes in preserved specimens (Figs. 2,3,8; Plate 1). Fins large and wide, slightly longer than interocular width. Each fin paddle-shaped, about two or three times as long as broad (FWI: 38-50). Posterior edge of male fins nearly straight, curving ante-

Figure 8. *Cirroteuthis magna*, submature female (140 mm ML, ZMMSU). Dorsal view.

riorly just past 2/3 of length; anterior margin slightly rounded, concave in proximal portion to form narrow base (35 mm). Fins of KARA-DAG female have a more lanceolate form than fins of male (Fig. 8); Hoyle (1886: 56) indicates that fins of holotype are: "obovate in form, about four times as broad as long". Heavy muscular portions of fins well developed, occupying most of fin width near base; outer lobe of fin close to semicircular. Fin thickened along posterior margin.

Arms difficult to measure in KARA-DAG female. In the holotype, arm formula is right I=II=III>IV, left IV.III.I=II according to Hoyle, but in order I>II>III>IV according to Robson (1932: 163). FARANAUT male arm formula I>IV>II>III. Arms 3.5-5 times mantle length. Fourth left arm of the male extremely short (75.8% of opposite arm). Arms translucent. As Hoyle (1886: 56) points out, arms "more resemble thickenings of the web than

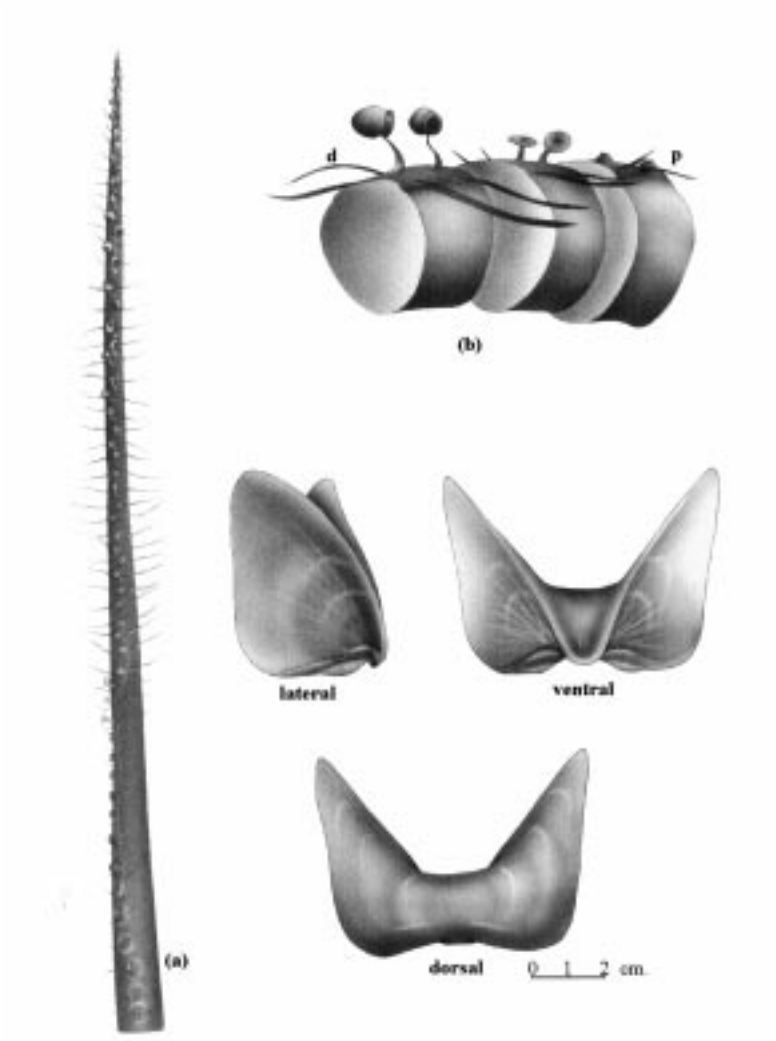

Figure 9. *Cirroteuthis magna* submature female (140 mm ML, ZMMSU). (a) oral view of the arm; (b) arm diagram showing the three types of suckers and the cirri; d: distal; p: proximal. In this diagram the barrel-shaped sessile suckers on the distal part of the arm are shown with membrane straps inserted into suckers laterally (see p. 17 in the text for explanation) (c) shell in dorsal,ventral, and lateral views.

independent arms." Figure 4B shows transverse section of one arm. Oral face of arm is fleshy or muscular part where suckers and cirri are located. Brachial nerve also situated in this face. Underneath lies an ample cavity or compartment, surrounded by very elastic membrane where several fibres observed leading out into many directions. Cavity runs whole length of arm, attaining its broadest width in proximal two thirds, gradually becoming narrower and virtually disappearing at distal end, pinched where both webs inserted. In FARANAUT male, preserving alcohol penetrated this cavity, forming elongated sacs in orange segment-like forms many of which were turgid according to amount of liquid contained. In holotype and KARA-DAG female, membranous walls withdrawn and wrinkled, adhering to oral base of arm, without forming any type of swelling. Oral surface of arms relatively broad and bears single row of suckers. Suckers commence ap-

Table 4. Comparison between males of *Cirroteuthis muelleri* and *C. magna*. Sources for the first species are Eschricht (1838), Robson (1932), Clarke (1986, beak) and Voss and Pearcy (1990).

Species Character	*C. muelleri*	*C. magna*
Shell	saddle-shaped wings slightly flaring	saddle-shaped butterfly wings open
SWI	66–69	30
SDI	1.7–2.9	4.1
CiLI	21–25	71–95
Web	intermediate web single* with nodule in the fusion point	intermediate web single without nodule
EDI	10	39
FuLl	29.8	24.6
Gill lamel. (per demibranch)	7–9	5–6
Stellate ganglion	5 anterior fibres 6 laterals	4 anterior fibres 15 laterals
Lower beak	sharp rostrum; small hook hood long no fold in lateral wall	sharp rostrum; no hook hood short fold in lateral wall

*Intermediate web of *C. muelleri* only double in specimens described by Voss and Pearcy (1990).

proximately 1 cm from mouth; almost covered by lateral margins of web. 29 prominent suckers, small in diameter, on all arms of holotype (largest diameter: 3.4 mm), first 5–7 cylindrical and separated by at least 1 cm, then spread out at intervals of 2–3 cm and "seem to contract by folding the lateral margins over towards each other, so as to present the appearance of a half-closed eyelid" (Hoyle, 1886: 57); from sucker 29 onwards, a sudden appearance of different firm, muscular suckers with a spherical basal portion, embedded in arm, and slightly protruding, shallow cylindrical or conical distal portion. These barrel-shaped suckers gradually increase in size until Sucker Diameter Index reaches 4.6, then decrease towards apex of arms (Hoyle, 1886, pl. XII, Figs. 2,3). FARANAUT male and KARA-DAG female, arrangement, form and size of remaining suckers match those of holotype. In both specimens, especially in male, three types of suckers observed. 1) Those nearest to mouth small, cylindrical and closely spaced, connected with arm by thick, stout stalk, and surrounded by web margins; subsequently increase in size and more widely spaced. 2) The following suckers have long stalk; these stalked suckers have small circular opening surrounded by very narrow rim in the upper part, with narrow infundibulum; acetabulum of these suckers consists of broad chamber surrounded by highly deformable fleshy membrane in such a way that the acetabulum is able to inflate and deflate, forming spherical, flattened or half-closed eyelid (Fig. 4B). Both types of suckers occupy proximal two thirds of arm. 3) On distal third of arm, another type of sucker appears bearing large, fleshy, radiating rim surrounding small, circular orifice, and fairly rigid muscular base, general appearance varying between bowl-like, amphora-like or barrel-like sucker (Fig. 4B). These suckers embedded in arm and are sessile. When the membranes surrounding these suckers unravel, they usually remain connected with arm via straps or threads which insert into suckers laterally and not at base (Fig. 9B).

Pairs of very long, conspicuous and none retractile cirri (Figs. 4A,9A,17) situated between all suckers. First cirri commence between fourth and fifth proximal suckers as very minute prominances which gradually increase in length until halfway along arm where

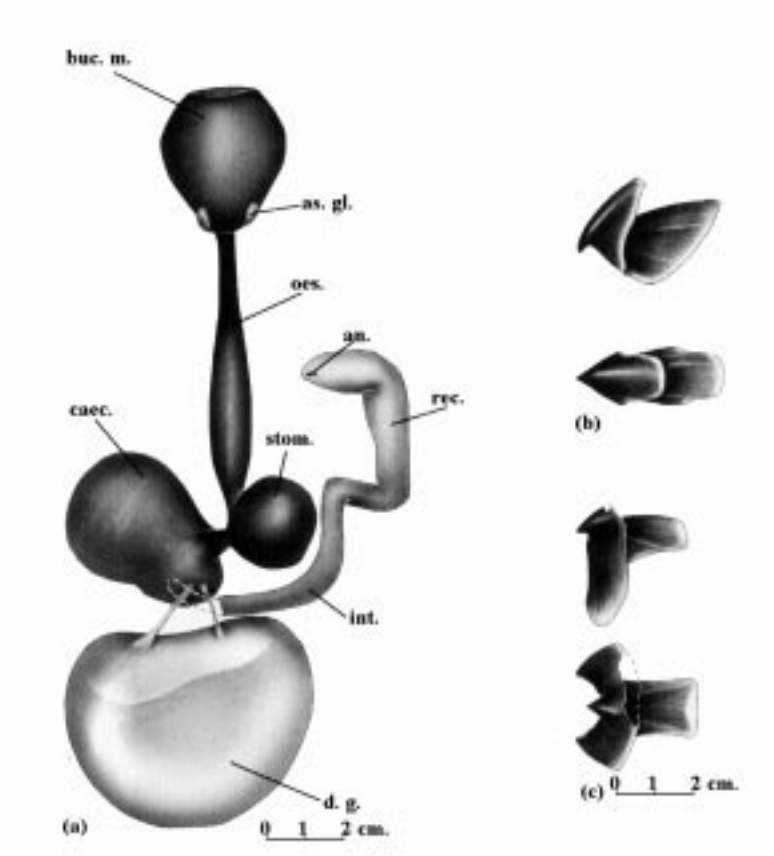

Figure 10. *Cirroteuthis magna*, submature female (140 mm ML, ZMMSU). (a) Alimentary canal ; b) upper beak; (c) lower beak.

they attain their maximum length (CILI 71–95 or 10–14 times diameter of suckers), after which they decrease rapidly, ceasing on opposite side to attachment of web.

Web almost completely missing in FARANAUT male and *Kara-Dag* female specimens. From images of live male (Pl. 1), web appears as very delicate and well-developed (deep) membrane. In male all but tip of arms enclosed in primary web; intermediate web present; primary web apparently inserts at different level on either side of each arm (Figs. 2,3). Webs of holotype quite well preserved and described and illustrated by Hoyle (1886) and Robson (1932). Web arrangement described as follows. Proximal two thirds of each arm independent of primary web, and connected with it by single vertical membrane or "intermediate web" (Hoyle, 1886: 59) which attaches to aboral surface of arm. This intermediate web has form of segment of very wide circle, arms held horizontally being arc. It therefore follows that web, when arms all stretched horizontally, sags downwards in each sector. Each sector of primary web connected with each arm throughout distal third, from point where intermediate web inserts onwards. In sector A (between the dorsal arms), end of primary web almost reaches apices of dorsal arms, inserting at same level on right arm

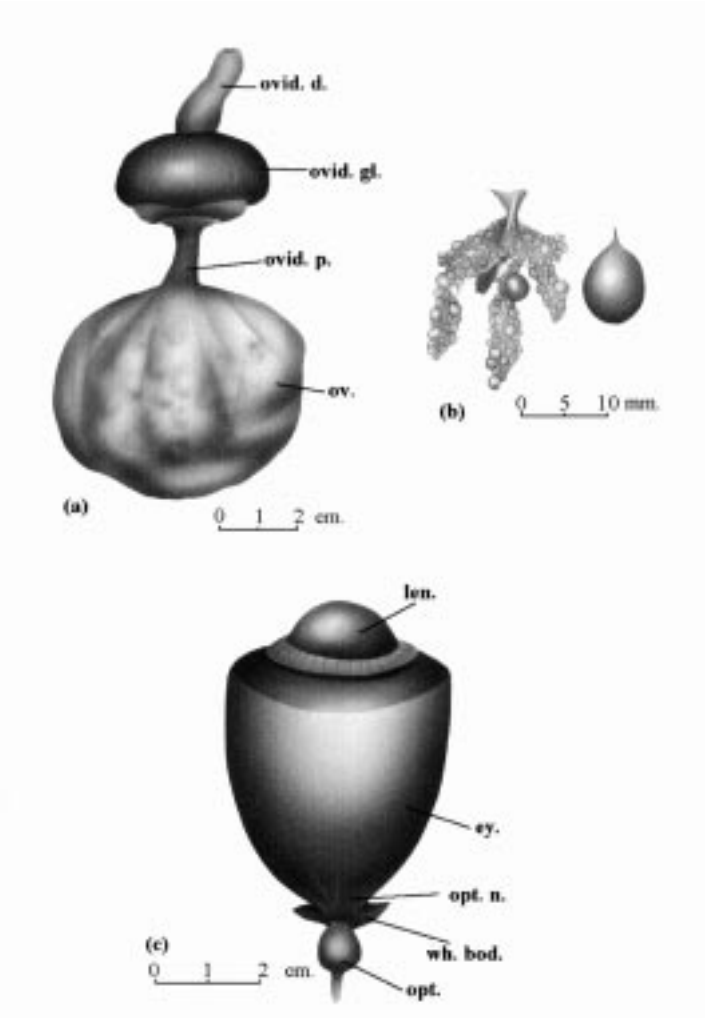

Figure 11. *Cirroteuthis magna*, (140 mm ML, ZMMSU). (a) Reproductive tract; (b) ovarian oocytes; (c) eye.

as on left one. In sector B, anterior end of primary web connected with dorsal arm where intermediate web terminates, while dorso-lateral arm at end of primary web connects near apex. This arrangement repeated in sectors C and D, both on right and left symmetrically, whereas in E (between the ventral arms), end of primary web connected with both arms at fusion points on intermediate web via primary web. At all points where both webs connected, there is thickening, but, "there is no trace of anything horny or cartilaginous" (Hoyle, 1886: 59). Interesting to point out that in this area, sac under each arm pinched (Hoyle, 1886: pl. XII, fig. 2). "The effect of this arrangement is that when the primary web is extended, the arms do not lie in its plane, but each is separated from it by the intermediate web." Hoyle (1886: 59) also points out that primary membrane "would form deep pouches between the several arms owing to the presence of the intermediate web."

Hoyle (1886, fig.2) and Robson (1932: 163) gave web formula as A.B.=C.D.E., but bearing in mind asymmetry of insertions at end of the primary web on dorso-lateral and ventro-lateral arms, this formula has little meaning.

Supraocular papilla not seen in either live or preserved animals. Color of holotype, so far as it is preserved, is dull madder (Hoyle, 1886: 57). Color of body and arms of other two specimens preserved in formalin varies from pale white, in the male, to purple, in the female; inner surfaces of arms and web are darkest, purple or purplish-brown, increasing in density towards mouth in FARANAUT and KARA-DAG specimens. No chromatophores seen in live or preserved specimens. Hoyle pointed out that holotype specimen was "rose" colored when captured. Live FARANAUT male observed to be bluish white in color and violet-pink in body areas. Unpigmented areas of fin almost perfectly translucent. Suckers lacked pigmentation and cirri had chestnut-brown pigmentation (Fig. 14; Pl. 1).

Internal anatomy.—Gill "sepioid" in form, small (Figs. 7A,18), with 5 lamellae per outer demibranch in holotype, with 6 lamellae per outer demibranch in FARANAUT male, and 6 and 5 lamellae in right and left outer demibranchs, respectively, in KARA-DAG female.

Shell or fin support cartilage translucent and thick; its general shape may be described as saddle-shaped, especially when seen dorsally or ventrally in elevation (Figs. 4C,9B; Pl. 3), whereas when seen laterally, with wings extended, has butterfly-like appearance. Consists of relatively narrow central body or transverse bar connecting two lateral expansions; relationship between maximum width of shell and its average length (Shell Width Index: SWI) varied between 26.8 and 30.4. Holotype shell illustrated by Hoyle (pl. XIII, 1–2), but has since been lost. Robson (1932) did not describe it and not found in collection at British Museum. Its general appearance and SWI closely coincide with shell of FARANAUT male and KARA-DAG female, although Hoyle's drawing does not enable precise comparisons. Shells of the FARANAUT male (Fig. 4C; Pl. 3) and KARA-DAG female (Fig. 9C) do, however differ in certain details: a) intermediate body of shell slightly larger and narrower in the KARA-DAG female than in male; b) in female, upper margins of two wings connected at ventral end of shell under transverse bar at more obtuse angle than in male; and (c) connection of both wings curved in female, whereas almost straight in male.

Digestive system of holotype not described either by Hoyle (1885, 1886) or by Robson (1932), although former illustrated beak (Hoyle, 1886: pl. XII; figs. 6,7). Currently, only buccal complex, stomach (now dissected), and beak all that remain of digestive system. Both upper and lower mandibles similar to those of FARANAUT male and the KARA-DAG female. No lingual tooth as found in Faranaut male (see below) observed.

Digestive system of the FARANAUT male (Fig. 5A) in form of single loop, fitting closely around digestive gland, green-olive in color and heart-shaped. Buccal mass contains large, thick, and robust beaks (Fig 5C,D). Lower mandible with obtuse jaw angle, sharp rostrum without hook, and marked infold in lateral wall. Upper mandible jaw angle close to right angle, sharp rostrum without hook, and no infold in lateral wall, and hood distinctly rounded in profile near rostral tip.

Anterior part of buccal cavity of male specimen, behind salivary papilla and radular groove, and between two infolds of tongue, very conspicuous, hard, and cylindro-conical lingual tooth (Fig. 5B). Radula absent, and no signs of minute toothed structures between salivary papilla and tongue. Buccal mass externally shows single sub-mandibular salivary gland and two round anterior or lateral salivary glands arranged on either side of tongue. Posterior salivary gland not observed externally, but in sagittal section of buccal

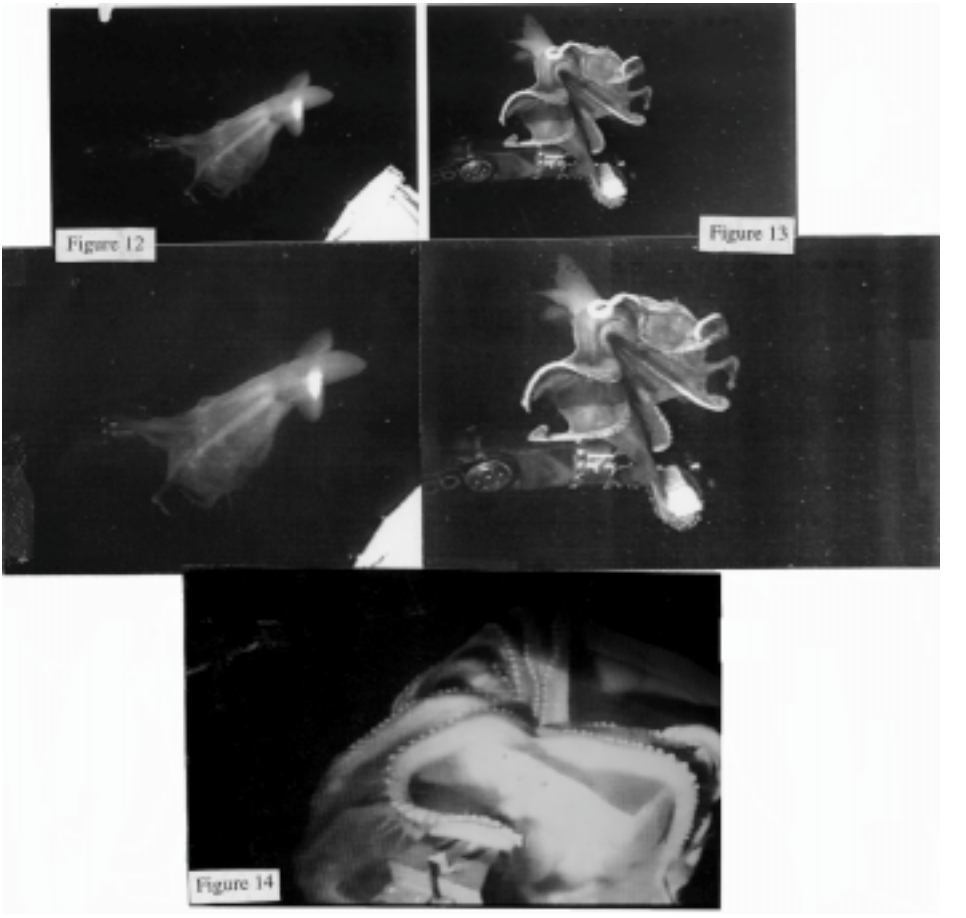

PLATE 1. Figures 12–14. *Cirroteuthis magna* mature male (220 mm ML, MNHN) from the Faranaut cruise approaching the collecting bag of the submersible Nautile. The web is visible(12). The animal captured by the mechanical arm of the submersible (13). The male in the sample collecting bag. Suckers and long cirri are clearly visible (14).

mass near midline, a single gland extending from floor of buccal mass to apex of salivary papilla. Presumably "posterior" salivary gland, lying here in front of brain, as observed in *Cirrothauma* by Aldred et al., (1983). Duct leading to salivary papilla not seen in our specimen.

Oesophagus leaves buccal mass dorso-posteriorly. Initially narrow, widening about half way along its length, 75 mm in total length. Swelling at point of maximum diameter appears homologous with simple crop. Stomach oval and lies on digestive gland dorso-posteriorly, in deep groove, displaced slightly to right, 21 mm wide and 18 mm long. Caecum, into which stomach opens via wide duct, larger than stomach (43×26 mm) and bagpipe-like in shape, not forming spiral. Close to underside of digestive gland, attached by two short, narrow ducts.

Intestine initially narrow than widens distally. In first third, makes 90° curve, then extends 60 mm in straight line (rectum) to anus. No anal flaps or ink sac.

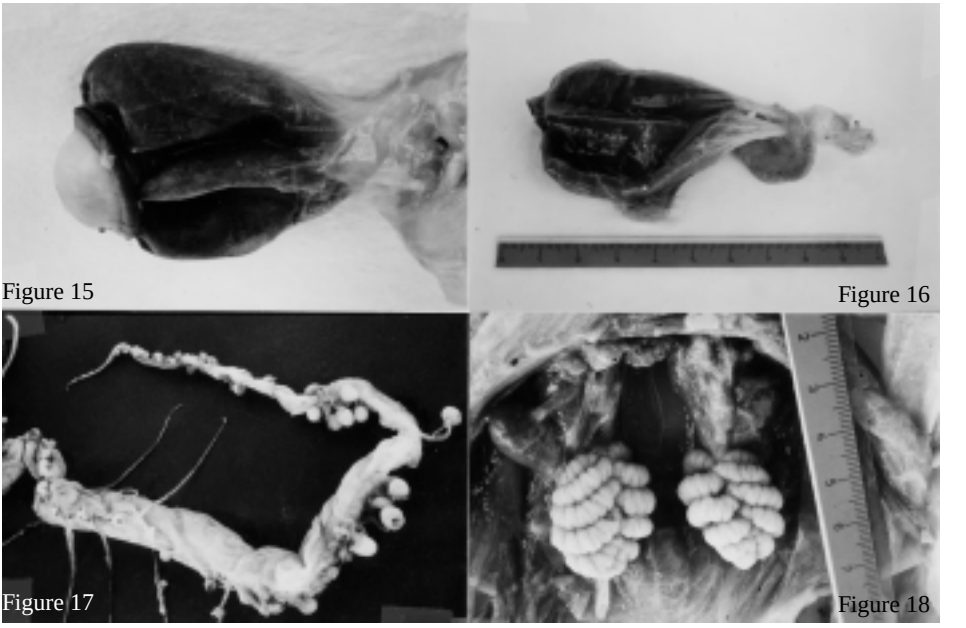

PLATE 2. Figure 15–18. *Cirroteuthis magna*, mature male (220 mm ML, MNHN). Eye (15). Eye without lens. Optic nerves, white body and optic lobe visible (16). Detail of left ventral arm (IV) illustrating long cirri and two types of suckers (17). Detail of inner pallial cavity where both gills can be clearly seen (18).

Oesophagus and dorsal side of stomach deeply pigmented, with dark purple-black color in oesophagus and brown in stomach. Caecum is grey, and color of intestine dark purple in preserved specimens. Only sand deposits found in stomach of male.

Digestive system of KARA DAG female (Fig. 10A), in general terms, has similar structure to that of male, differs in following aspects: (a) buccal mass proportionally larger; (b) no submandibular gland observed externally, probably due to preservation state; (c) lateral salivary glands considerably smaller; (d) beaks (Fig. 10B,C) larger and have different appearance. Hood's posterior end of upper beak larger and wider than in FARANAUT male (Fig. 5C), and lower margin of lateral wall showning more obtuse angle. Main differences in lower beak in rostrum, more pointed in female that in male (Fig. 5D), and in jaw angle, obtuse in male whereas form 90° angle in female (Fig. 10C); (e) no lingual tooth; (f) digestive gland more rounded in shape than cordate, and anterior areas have different shape, which may be due to perservation ; and (g) rectum (Fig. 10A) wider and shorter than that of male. Stomach empty.

The FARANAUT male mature. No spermatophores seen, but in seminal vesicle numerous sperm sacs filled with spermatozoa, as described in *Cirrothauma* by Aldred et al. (1983). The oval testis (16 × 12 mm) enclosed in thin-walled sac situated posteriorly in mantle. On ventral side, ridges radiate from small central circular area (Fig. 6A). First portion of vas deferens (40 mm) extremely narrow, widening abruptly into sort of reflexed tube (Ebersbach's seminal vesicles) measuring 31 mm in length. Proximal section of vas deferens thick-walled and highly folded internally. Duct turns sharply through 90°, then it widens and turns sharply again 180°. In this portion, wall is very thin and numerous

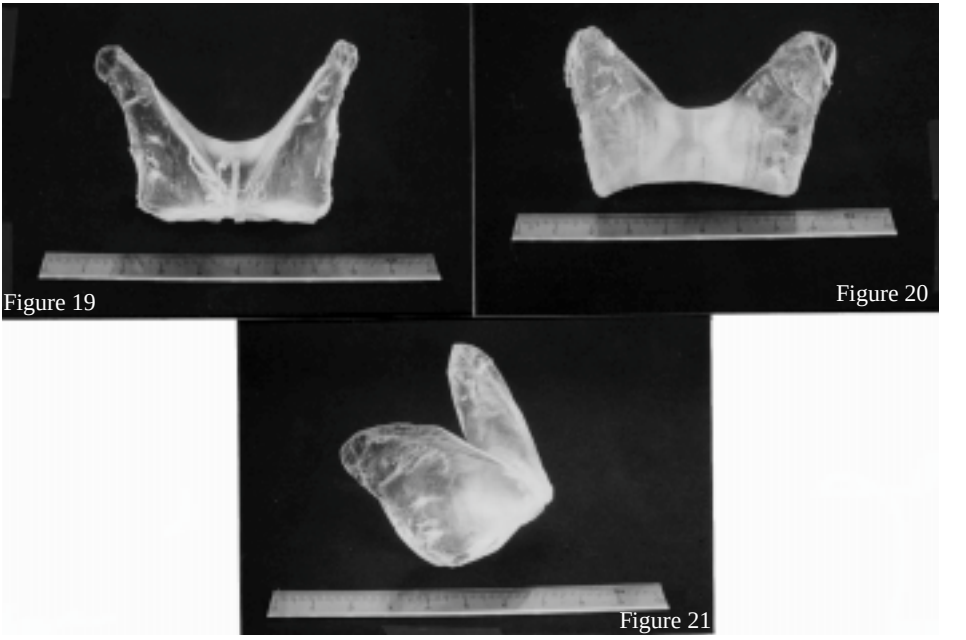

PLATE 3. Figure 19–21. *Cirroteuthis magna*, mature male (220 mm ML, MNHN). Ventral view of shell vestige or fin support cartilage (19). Dorsal view (20). Dorso-lateral view (21).

sperm sacs seen within. Vas deferens passes through voluminous (27×29 mm) mass of accessory glands, expands slightly and curves into small (6×2 mm), cylindrical terminal organ, without "body wall" as exists in *Cirrothauma murrayi* (Aldred et al., 1983). Three accessory glands covered by deeply pigmented walled sac, with dark purple color.

One hundred and ninety six sperm sacs counted inside seminal vesicle. Each sperm sac tapered, and slightly broader than long (Figs. 6B,22), 1.47 ± 0.04 mm $\times$ 1.30 ± 0.003 mm. Outer part of sperm sac presents infolds, more or less spiral-shaped (Fig. 23). No special pores or opercular structures observed in sperm sac. Numerous spermatozoids (Fig. 6D) packed and embedded in granular substance (Figs. 24,25). In interior of sperm sac, spermatozoids arranged perpendicular to infolds, with flagella inwards and acrosomes outwards (Fig. 26). Flagella folded over, and parallel to main axis of sperm sac. Average of 86.1 ± 2.5 spermatozoids counted per each 100 μm^2 sperm sac surface. Impossible to measure total length of spermatozoids since flagella coiled up, but approximately 90% of total length of spermatozoid corresponds to flagellum. Table 3 shows measurements of each portion. In its outer morphology, acrosome flattened, with blunted spearhead shape presenting helical keel of approximately one and half turns. In connecting area between acrosome and nucleus, small constriction appears. Nucleus cylindrical, elongate and flat (Fig. 27). Between nucleus and flagellum lies truncated, cone-shaped mid portion, with slight depression in center (Fig. 28). Flagellum very long, reaching some 250 μm in length and approximately 0.32 μm in diameter (Fig. 29).

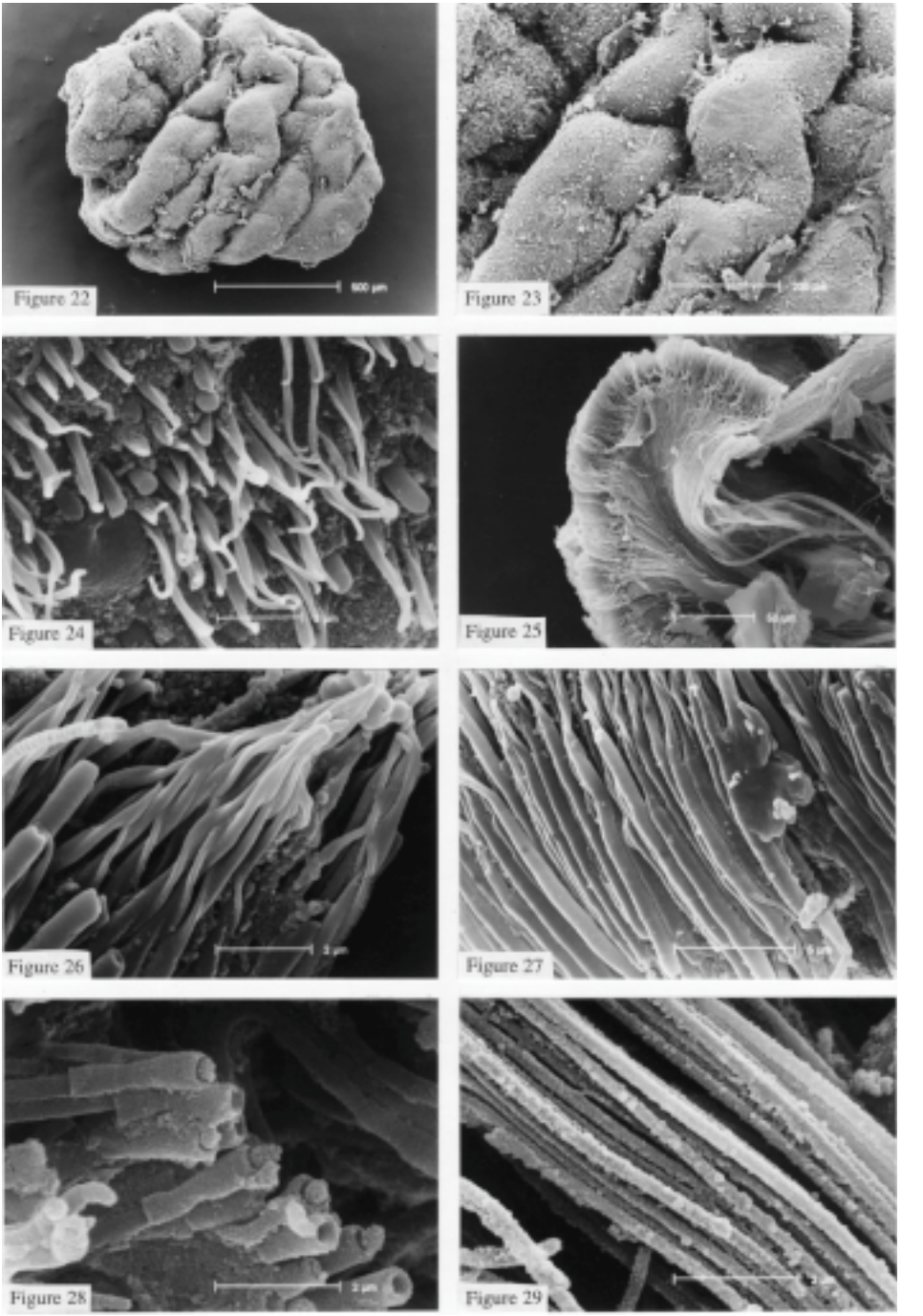

PLATE 4. Figure 22–29.*Cirroteuthis magna*, mature male (220 mm ML, MNHN). Scanning electron photomicrograph of complete sperm sac (22). Detail of folds on surface of sperm sac (23). Detail of inner wall of sperm sac containing free ends of spermatozoid acrosomes (24). Fracture of infold in sperm sac (25). Details of acromes of spermatozoids inside sperm sac (26). Details of nuclei of spermatozoids (27). Details of the mid portions of spermatozoids (28). Detail of a flagella bundle of spermatozoids (29).

Female holotype remains of oviductal gland, reconstructed, spherical with two clearly differentiated regions with different diameters, distal one of 54 mm, and proximal of 27 mm; distal oviduct leads out from former, and proximal oviduct leads out from latter. No oviductal eggs observed. Ovary enormous (approximately 100×80 mm) and full of practically spherical oocytes of various sizes, up to 11.3 mm in diameter.

KARA-DAG female submature. Figure 11A illustrates form of female genital system. Distal and proximal oviducts very short. Oviductal gland large and spherical with very shortened poles and two clearly differentiated regions. Inside ovary 84 loose immature oocytes, with 50 to 70 forming clusters (Fig. 11B). No oocytes in proximal oviduct, oviductal gland or distal oviduct. Oocytes with wide range of sizes observed. Size of larger oocytes 10×8 mm. Outer surface of oocytes smooth.

Figure 7B shows form of systemic heart of FARANAUT male. Systemic heart of females not adequately observed. Branchial hearts of all three specimens oval, and dark green in color in male (Fig. 7A). On each side of branchial hearts of male, well-developed renal papilla, deeply pigmented violet coloring present (Fig. 7A). This papilla not observed in the females. Pallial adductor muscles weakly developed.

Eyes (Figs. 7C,11C,15,16) in three specimens voluminous (EDI 39.0–42.8) and dark violet in color. In holotype, deflated and not measured. Equipped with large semispherical lenses (LDI 12.7–17.8). Configuration of ocular nervous system in FARANAUT male and KARA-DAG female very similar, but not observed in holotype. In posterior part of eye, optic nerves evident and show no chiasma. Back of eye attached to large "white body", form shown in Figures 7C,11C,16. Optic ganglia globular lying close to "white body". Each ganglion attached to brain by broad optic tract.

Stellate ganglia of male shown in Figure 7D. Contour has form of reniform-shaped. Mantle connective leaves fin nerve which runs on past ganglion. Nine stellar nerves, one larger than others. Fifteen lateral and posterior stellar nerves lead out, one bi-branched. Due to state of preservation of stellate ganglia epistellar body not distinguishable.

Holotype.—Female, 175 mm ML, mature (?), preserved in ethyl alcohol, BMNH 1890.1.24.1.

Type locality.—South Indian Ocean, between Prince Edward and Crozet islands, 2557 m.

Etymology.—Although Hoyle (1885) does not indicate so, the specific name of *magna* is derived from the Latin adjective *magnus*: "large," which refers to the large size of the specimen.

DIAGNOSIS OF THE GENUS *CIRROTEUTHIS* ESCHRICHT, 1838

Type Species: *Cirroteuthis mülleri* Eschricht, 1838

Emmended diagnosis.—Eye large, well developed, with lens; fin cartilage (shell) shape variable, compact saddle-shaped with wings slightly flaring to butterfly-shape with spread out wings; SWI >25; primary web well developed, extends almost to the tips of all arms; ends of the primary web inserted, at a different level, into the lateral sides opposite the dorsolateral (II) and ventrolateral arms (III); intermediate web present; cirri evident from suckers 2–5 to the apex of the arms; pair of cirri situated between each sucker, with cirri

lengths greater than the diameter of the largest sucker; highly modified, enlarged suckers absent; fins large, longer than the interocular width; pallial aperture narrow; funnel long (FuLI 25–43); longitudinal gill shape "sepioid".

Remarks.—The above redescription of *magna* reveals that it definitively belongs to the genus *Cirroteuthis*. *C. magna* shares the diagnostic characters given by Robson (1932: 134) and Voss (1988a,b) for the genus *Cirroteuthis*, based solely by those authors on *C. muelleri*, excluding the form of the shell.

The Family Cirroteuthidae

The characters of the family Cirroteuthidae Keferstein, 1886, have recently been discussed by various authors (Nesis, 1987; Voss, 1988a; Hochberg et al., 1992). In accordance with these authors, and taking into account the characteristics of the species redescribed in this paper, the diagnostic characters of the family are as follows.

Diagnosis.—Mantle sac-shaped, not dorso-laterally compressed; underlying tissues fragile, gelatinous; eyes well-developed or degenerate; all but tips of arms enclosed in web; secondary or intermediate web present; cirri long, conspicuous; lateral fins large, wide, longer than head width, not retractable; shell thick, wing- or saddle-shaped, Shell Vestige Index >25; crop diverticulum absent; gills "sepioid"; posterior salivary gland present; radula absent; lingual tooth present; pallial adductor muscle weakly developed.

The family as we know it currently contains two genera: *Cirrothauma* Chun, 1913, with eyes reduced, without lens or iris, embedded within the jelly of the skin, and *Cirroteuthis* Eschricht, 1838, with eyes well developed with lens and iris.

Our study confirms the conditions in *Cirrothauma*, which show that members of this family have several unusual features of great interest (Aldred et al., 1983). The presence of the "posterior" salivary gland in front of the brain suggests this to be the original position, which has been already suggested by the fact that in *Octopus* the posterior salivary nerve runs forward and then backwards (Young, 1971). The absence of chiasma of the optic nerves suggests that this also is an ancestral condition. It has interesting physiological implications (Young, pers. comm.). The absence of spermatophores and the presence of sperm in sacs is an unexplained condition.

Hoyle (1904) created the genus *Froekenia* for a very damaged specimen, which he named *Froekenia clara*. Based on a memorandum by Mr. Agassiz written immediatly after capture, Hoyle (1904: 8) concluded that the absence of the web in this specimen was not due to defective preservation. U-shaped shell, short cirri and the possibility that the web was torn away in capture, brings the validity of the genus *Froekenia* into question. Voss (1988b) considered *F. clara* as a "nomen dubium". Nesis (1986: 126) had reported *Froekenia* n. sp., from the tropical western Indian Ocean, which he included in Cirroteuthidae. His study on five specimens in good condition, showed that *Froekenia* is a valid and well distinguishable webless genus with a buckle-shaped shell. Following Voss's (1988a) diagnosis, *Froekenia* belongs to the latter family.

The validity of *Cirroteuthopsis* is the subject of controversy. Robson (1932: 160) raised the subgenus created by Grimpe (1920) for *C. massyae* to the category of genus, but it seems that all the characters of *Cirroteuthopsis* could easily be preservation artifacts. Voss (1988a) and Hochberg et al. (1992) do not recognbize *Cirroteuthopsis* as a valid genus, but Nesis (1987: 283) considers Grimpe's species *massyae* to be a member of the

genus *Cirroteuthis*. At present, we see no reason to contradict Voss, Hochberg or Nesis, and feel that additional material in good condition is required to resolve the problem.

Intraspecific Variations

The exteranl morphology of the *Cirroteuthis magna* male and the females described here show certain differences (Table 2). Internally, they also differ in: (a) the number of gill lamellae; (b) the form and size of the buccal complex and beaks; (c) the absence of lingual tooth in females; (d) the form of the digestive gland and of the rectum, and (e) in certain details of the shell. It is very difficult to differentiate between what are, in fact, diagnostic characters and what may be due to sexual dimorphism or preservation artifacts.

Despite these differences, the three specimen are quite similar in various characters, of which the following are considered diagnostic for species: (a) the large body size; (b) the presence of large, obovate-shaped fins; (c) voluminous eyes with large lens; (d) long cirri; (d) the arrangement, sizes and types of suckers; (e) the arrangement of the web; (f) the general appearance of the shell and the value of the SWI (26.8–30.1–30.4); (g) the form of the funnel; h) the pallial aperture; and (i) the similar ocular nervous system.

Although characteristics of the three specimens enable partial or preliminary redescription of this species, additional material is required to fully describe the morphology and anatomy of *C. magna.*

Furthermore, placement of these three specimens in the species *C. magna* may be questioned considering the huge distance between the subantarctic Indian Ocean, where the holotype was captured, and the subtropical North Atlantic, where the other two were collected. This argument may be countered by the similarity in morphological characters, the capacity of movement of these organisms, the absence of topographic barriers between the two areas, and the homogeneity (temperature, salinity) of the deep water mass where these cephalopods were collected (Gage and Tyler, 1991).

Comparison with Other Species of *Cirroteuthis*

Cirroteuthis magna has various morphological characters in common with *C. muelleri*. Both species differ, at least in the characters shown in Table 4.

Voss and Pearcy (1990: 51) found that their *C. muelleri* specimens have a double intermediate web, while the *C. muelleri* Eschricht figures and all the specimens of *C. muelleri* examined by the present authors have single intermediate web. A double intermediate web was not clearly observed in the three animals of the Voss and Pearcy collection (see comparative material) examined for this work.

The shell of *C. magna* is more similar to that of *C. murrayi* (Aldred et al. 1983: fig. 9) than to that of *C. muelleri* (Voss and Pearcy, 1990: fig.2). The SWI of *C. magna* varied between 26.8–30.4 (Table 1), values close to those for the male *C. murrayi* examined (IIMV 1990.11.1) and to the male illustrated by Aldred et al. (1983), with SWI of 28.1 and 31.4, respectively. The SWI for *C. muelleri* in the two males we examined (USNM 817580) varied between 66–69, the specimen illustrated by Voss and Pearcy (1990) has a value of 67, calculated from measurements taken from illustration.

The external morphology of the sperm sac in *Cirroteuthis magna* (Figs. 6B,22) appears to be different from that of *C. muelleri* described in this paper for the first time (Fig. 6C). The sperm sac in *C. muelleri* (specimen USNM 730984) presented a completely smooth surface (Fig. 6C) while the sperm sac in *C. magna* had folds (Fig. 6B). The possibility that these folds may be an artifact produced by fixation and treatment may not be totally rejected.

Furthermore, the arrangement of spermatozoids within the sperm sacs, their size and form, are practically identical in *C. magna* and *C. muelleri.* Spermatozoids in both species are considered typical for an octopod, because they lack the skirt membrane which is present in Sepioidea and Teuthoidea, and the insertion of flagella is central (Healy, 1989, 1990). Also, the nucleus is elongated and large in size, resembling *Octopus* in the form of the acrosome with a prominent helical keel (Healy, 1990).

The spermatozoids of *C. magna* and *C. muelleri* are different from those of *Vampyroteuthis infernalis* in the form of the acrosome, as well as in morphology and size of the nucleus and of the mid portion (Healy, 1989). Also they are quite different from the spermatozoids of *Opisthoteuthis agassizii* and *O. vossi* (Villanueva, 1992) in size and morphology of the acrosome, nucleus and mid portion. Nevertheless, they present similarities with those of *O. persephone* (Healey, 1993).

Future research, with spermatic material from specimens of cirrate octopods species, may provide a clearer view of the phylogenetic relations and may help to clarify the confused systematics of the group.

The identification of the specimen from CHALLENGER Sta. 298 (BMNH 1890.1.24.2; see comparative material examined) as *C. magna,* as made by Hoyle (1885), must be considered very doubtful. Robson (1932) recognized this specimen as constituting a new species, *C. (?) hoylei.* He based this decision on the form of the shell, the size and distribution of cirri and the size of suckers. This decision also appears questionable. In our opinion, it is valid to place this specimen in the genus *Cirroteuthis* on the basis of the saddle-shaped shell and the length of the cirri, but we prefer to recognize this very damage specimen as *Cirroteuthis* sp. rather than ascribing it to a new species.

Nesis (1987: 283) considered two other species: *Cirroteuthis* n. sp. A Nesis, 1982 (in Nesis, 1987) from the Naturalist Plateau off Southwestern Australia (Fig.1B), and *Cirroteuthis* n. sp. B Roper and Brundage, 1972 (in Nesis, 1987). The latter species was described on the basis of five photographs, and one captured specimen of 1500 mm TL. Unfortunately, this specimen taken by the trawler ZVEZD KRYMA off Cape Blanc (Mauritania, Africa) was not preserved, although it was photographed (Golovan and Nesis, 1975). The area of distribution of *Cirroteuthis* n. sp. B would cover the North Atlantic from the Canary Islands to Dakar and the Caribbean Sea (Fig. 1B), living in the abyssal depths from 2500 to 5200 m, and in the upwelling off Cape Blanc ascending to depths of 1300–2000 m. In this same area, the KARA-DAG female described above was caught, and some months later, two additional cirrate octopods were caught by trawling, one very large and the other very small, which the collector (M. A.Tsymbal, pers. comm.) considered belonged to the same species as the female referred to here. Unfortunately, neither specimen was preserved or photographed, so it is not possible to confirm their identification.

Nesis (1987: 283) distinguished between an asymmetrical and symmetrical web. In the asymmetrical condition, the web is attached to the lateral arm on the dorsal side at a point distal to that on the ventral side. This is the case in *C. magna*. Nesis considered symmetrical web as: a) attached to both sides of an arm at approximately the same level, as in

Opisthoteuthis, or b) not being attached to arm sides but adjacent web sectors are fused together on aboral surface of the arm, as in *C. muelleri* (Eschricht, 1838; Voss and Pearcy, 1990) and in the *Cirroteuthis* of Roper and Brundage (1972: 13). In *C. magna*, the web is strongly asymmetrical as it inserts at different levels on both lateral faces of each arm; however this would be symmetrical, according to Nesis' definition, as there is an additional or intermediate membrane between the primary web and each arm. This contradiction is echoed in the key given by Nesis (1987: 283) to the *Cirroteuthis* species where he states that *C. magna* lacks a secondary web. In fact, the terms "intermediate web" and "secondary web" are analogous. Thus, the concept of asymmetry and symmetry in the web must only be applied if these sectors are connected to each arm at different or the same levels. Nesis' interpretation (1987) that *C. magna* has an intermediate but not a secondary web, is mistaken.

Furthermore, the species with an asymmetrical web may adopt a "bell-shaped pose", as their arms are stretched by a web attached to very different points, causing the arm tips to bend. Those species with a symmetrical web, adopt the so-called "open umbrella pose". This pose is visible in some of the cirrates shown in Roper and Brundage (1972: figs. 9,10,22,25), perhaps suggesting that these animals may be neither *C. magna* nor *C. muelleri.* Moreover, the condition in the specimen photographed in Golovan and Nesis (1975) is unclear, but in other respects it is very like those photographed by Roper and Brundage (1972), considered by the authors represent more than one species. There is insufficient data to considerer any of the specimens photographed in Roper and Brundage (1972) and in Golovan and Nesis (1975) as *C. magna.*

The poor state of the holotypes examined of certain cirrate species such as *Grimpoteuthis pacifica, G. meangensis* and *Chunioteuthis gilchristi* make it imperative to collect additional well-preserved specimens, permit detailed redescriptions of these delicate cephalopods.

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Literature Cited

Aldred, R. G., M. Nixon and J. Z. Young. 1983. *Cirrothauma murrayi* Chun, a finned octopod. Phil. Trans. R. Soc. Lond. B. 301: 1–54.

Boletzky, S. V. 1982. On eggs and embryos of cirromorph octopods. Malacologia 22: 197–204.

_____. 1985. Le vol du pulpe. L' Univers vivant. no. 3: 42–47.

_____, M. Rio and M. Roux. 1992. Octopod "ballooning" response. Nature 356: 199.

Clarke, M. R., ed. 1986. A Handbook for the identification of cephalopod beaks. Clarendon, Oxford. 273 p.

Chun, C. 1913. Cephalopoda from the "Michael Sars" North Atlantic deep-sea expedition 1910. Rep. Scient. Results Michael Sars N. Atlant. deep sea exped. 3: 1–21.

Ebersbach, A. 1915. Zur Anatomie von *Cirroteuthis umbellata* Fischer und *Stauroteuthis* sp. Z. Wiss . Zool. 113: 362–483.

Eschricht, D. F. 1838. *Cirroteuthis mülleri,* eine neue gattung der cephalopoden bildend. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinesche Akademie der Naturforsher, Breslau und Bonn. 18: 627–634.

Fischer, P. 1883. Note préliminaire sur une nouvelle espéce du genre *Cirroteuthis*. J. Conchyliol. Paris. 31: 402–404.

Gage, J. D. and P. A. Tyler.1991. Deep-sea biology. A natural history of organisms at the deep-sea floor. Cambridge Univ. Press, Cambridge, U.K. 504 p.

Golovan, G. A and K.N. Nesis. 1975. Giant deep-water octopus. Priroda 5: 112–113 (in Russian).

Grimpe, G. 1916. *Chunioteuthis*.- Eine neve Cephalopodengattung. Zool., Anz. 46: 349–359.

_____. 1920. Teuthologische Mittheilungen V. Zwei neue Cirraten-Arten. Zool. Anz. 51(11): 230.

Guerra, A. 1992. Mollusca, Cephalopoda. Pages 1–327 *in* M. A. Ramos, J. Alba, X. Belles, J. Gosalbez, A. Guerra, E. Macpherson, F. Martin, J. Serrano and J. Templado, eds. Fauna Ibérica, vol.1, Museo Nacional de Ciencias Naturales, CSIC. Madrid. 327 p.

Healy, J. M. 1989. Spermatozoa of the deep-sea cephalopod *Vampyroteuthis infernalis* Chun: ultrastructure and possible phylogenetic significance. Phil. Trans. R. Soc. Lond. B 323: 589–600.

_____. 1990. Ultrastructure of spermatozoa and sperminiogenesis in *Spirula spirula* (L.): systematic importance and comparison with other cephalopods. Helgoländer Meeresunters. 44: 109–123.

_____. 1993. Sperm and spermiogenesis in *Opisthoteuthis persephone* (Octopoda: Cirrata): Ultrastructure comparison with other cephalopods and evolutionary significance. J. Moll. Stud. 59: 105–115.

Hochberg, F. G., M. Nixon, M. and R. B. Toll. 1992. Order Octopoda Leach, 1818. Pages 213–280 *in* M. J. Sweeney et al. "Larval" and juvenile cephalopods: a manual for their identification. Smithson. Contrib. Zool. 513.

Hoyle, W. E.1885. Diagnosis of new species of cephalopoda collected during the cruise of H.M.S "Challenger". Part 1. The Octopoda. Ann. Mag. Nat. His. Ser. 5. 15: 222–236.

_____. 1886. Report on cephalopods collected by H. M. S. "Challenger" during the years 1873–1876. Report on the scientific results of the Voyage of H. M. S. "Challenger" 1873–76. Zoology 16: 1–245.

_____. 1904. Reports of the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, on the U.S. fish commission steamer "Albatross" from August, 1899, to March, 1900, Commander Jefferson T. Moser, U.S.N., Commanding. V. Report on the Cephalopoda. Bull. Mus. Comp. Zool., Harvard College. 43: 1–71.

Jahn, W. 1971. Deepest photographic evidence of an abyssal cephalopod. Nature. 232: 487–488.

Joubin, L. 1896. Résultats scientifiques de la campagne du "Caudan" (...). Ann. Univ. Lyon, 4: 247–250.

_____. 1912. Etudes préliminaires sur les céphalopodes recueillis au cours des croisières de S.A.S. le Prince de Monaco. 2e Note: *Cirroteuthis Grimaldii*, nov. sp. Bull. Inst. Océanogr. Monaco. 9: 1–13.

Muus, B. J. 1962. Cephalopoda. The Godthaab-expedition, 1928. Meddr. Om Grønland, 81: 1–23.

Nesis, K. N. 1983. Finned octopuses. Pages 46–49 *in* Y. I. Starobogatov and K. N. Nesis, eds. Taxonomy and ecology of cephalopods. Leningrad. Zool. Inst. Acad. Sci. U.S.S.R. (in Russian). 286 p.

_____. 1986. Cephalopods from the seamounts of the Western Indian Ocean. Okeanologia 26: 123–130 (in Russian, English summary).

_____.1987. Cephalopods of the world. T.F.H. Publications, Inc., Ltd., Neptune City, USA. 351 p. (Russian original version published in 1982)

_____.1988. Cephalopods of the north polar ocean and it seas. Pages 115–136 *in* A. I. Kafanov, ed. Fauna and distribution of mollusks: North Pacific and Polar Basin. Vladivostok, Far Eastern Scientific Center, Acad. Sci. U.S.S.R. (in Russian).

_____ and A. M. Sagalevich. 1983. Deep-sea cirrate octopuses observed from submersibles. Priroda 11: 23–25 (in Russian; abridged English translation in Deep Sea Newsletter 9: 7).

Pearcy, W. G. and A. Beal. 1973. Deep-sea cirromorphs (Cephalopoda) photographed in the Arctic Ocean. Deep Sea Res. 20: 107–108.

Reinhard, J. T.and V. Prosch. 1846. Om *Sciadephorus muelleri*. (*Cirroteuthis* Eschricht). K. Dansk. Vid. Selsk. Afh., Kjøbenhavn 12: 165–224.

Robson, G. C. 1924. On the Cephalopods obtained in South African waters by Dr. J. D. F. Gilchrist in 1920–21. Proc. zool. Soc. Lond. 3: 589–686.

_____. 1926. The Deep-sea Octopoda. Proc. Zool. Soc. Lond., 1925. 4: 1323–1355.

_____. 1930. Cephalopoda, I. Octopoda."Discovery" Rep. 2: 371–402.

_____. 1932. A monograph of the recent Cephalopoda. Part II. The Octopoda, excluding Octopodinae. Lond. Brit. Mus. (Nat. Hist.), p. I-XI, 1-359.

Roper, C. F. E.and W. L. Brundage. 1972. Cirrate octopods with associated deep sea organisms: new biological data based on deep benthic photographs (Cephalopoda). Smithson. Contrib. Zool. 121: 1–46.

_____ and G. L. Voss. 1983. Guidelines for taxonomic descriptions of cephalopod species. Mem. Nat. Mus. Victoria 44: 49–63.

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

Vecchione, M. and C. F. E. Roper. 1991. Cephalopods observed from submersibles in the western North Atlantic. Bull. Mar. Sci. 49: 433–445.

Verrill, A. E. 1885. Third catalogue of Mollusca recently added to the fauna of the New England coast (...). Trans. Conn. Acad. 6: 395–452.

_____. 1896. The Opisthoteuthidae. A remarkable new familly of deep-sea Cephalopoda, with remarks on some points in molluscan morphology. Amer. J. Sci . 4: 74-80.

Villanueva, R. 1992. Continous spawning in the cirrate octopods *Opisthoteuthis agassizii* and *O. vossi* : features of sexual maturation defining a reproductive strategy in cephalopods. Mar. Biol. 114: 265–275.

Villanueva, R. and A. Guerra. 1991. Food and prey detection in two deep-sea cephalopods: *Opisthoteuthis agassizii* and *O. vossi* (Octopoda: Cirrata). Bull. Mar. Sci. 49: 288–299.

Voss, G. L. 1988a. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). Pages 253–275 *in* M. R. Clarke and E. R. Trueman, eds. The Mollusca, Vol, 12, K. M. Wilbur, ed. Paleontology and neontology of cephalopods. Academic Press, San Diego, California.

_____. 1988b. The biogeography of the deep-sea Octopoda. Malacologia 29: 295–307.

_____ and W. G. Pearcy. 1990. Deep-water octopods (Mollusca; Cephalopoda) of the Northeastern Pacific. Proc. Calif. Acad. Sci. 47: 47–90.

_____, C. R. Robins and J. C.Staiger. 1977. Pages 483–503 *in* Study of the macro-fauna of the tropical western Atlantic. FAO Fish. Rep. no. 200.

Young, J. Z. 1971. The anatomy of the nervous system of *Octopus vulgaris*. Clarendon Press, Oxford, U.K. 690 p.

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APPENDIX 1

ABBREVIATIONS USED

ac. gl. = accesory gland; **acr.** = acrosome; **ALI** = arm length index; **a. s. gl.** = anterior salivary gland; **ASIn** = arm sucker index; **an.** = anus; **BMNH** = The Museum Natural History (formely the British M.N.H.); **bra. hea.** = branchial heart; **buc. m.** = buccal mass; **Caec.** = caecum; **CiLI** = Cirrus length index; **d. g.** = digestive gland; **ED** = eye diameter; **EDI** = eye diameter index; **ey.** = eye; **d** = distal; **fl.** = flagellum; **FLI** = fin length index; **fnl.** = funnel; **FuLI** = funnel length index; **FSI** = finspan index; **FWI** = fin width index; **gan. stel** = stellate ganglion; **gon. sac.** = gonadal sac; **IIMV** = Instituto Investigaciones Marinas of Vigo; **int.** = intestine; **IO RAS** = Institute of Oceanology, Russian Academy of Sciences, Moscow; **ISTPM** = Institut Scientifique et Technique des Pêches Maritimes; **LD** = lens diameter; **LDI** = lens diameter index; **len.** = eye lens; **lin. too** = lingual tooth; **MAI** = mantle arm index; **man. mus** = mandibular muscle; **ML** = dorsal mantle length; **MLS** = medial length of the shell; **MNHN** = Muséum National Histoire Naturelle Paris; **m. p.** = mid portion; **MWI** = mantle width index; **MWS** = maximun width of the shell; **n. fin** = fin nerve; **n. pal.** = pallial nerve; **nuc.** = nucleus; **oes.** = oesophagus; **opt.** = optic lobe; **opt. n.** = optic nerve; **ovid. d.** = distal oviduct; **ovid. gl.** = oviducal gland; **ovid. p.** = proximal oviduct; **ov.** = ovary; **p** = proximal; **PAI** = pallial aperture index; **rec.** = rectum; **ren. pap.** = renal papilla; **sal. pap.** = salivary papilla; **SDI** = sucker diameter index; **sem. ves.** = seminal vesicle; **sh. ves.** = shell vestige; **sm. gl.** = submandibular gland; **stom.** = stomach; **SWI** = shell width index; **TB** = transverse bar of the shell; **tes.** = testis; **TL** = total length; **to.** = terminal organ (penis); **ton.** = tongue; **TOLI** = terminal organ (penis) length index; **USNM** = United States National Museum of Natural History; **vas. def.** = vas deferens; **w** = wing of the shell; **wh. bod.** = white body; **ZMMSU** = Zoological Museum of the Moscow State University