

CHIROTEUTHIS VERANYI FROM THE ATLANTIC SECTOR OF THE SOUTHERN OCEAN (CEPHALOPODA: CHIROTEUTHIDAE)

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Chiroteuthis veranyi (Férussac, 1835) (Cephalopoda: Chiroteuthidae) from South Georgia is described from material collected during the British Antarctic Survey's Offshore Biological Programme. The material closely resembles *C. veranyi* from elsewhere and, in common with *C. lacertosa*, *C. imperator* and *C. calyx*, has two round photophores, one on each side of the ink sac. It also resembles *C. lacertosa* and *C. calyx* in the structure of the stalks of the club suckers, which consist of two portions: a broad cylindrical basal portion terminates in a dark purple pleated "skirt" from which arises a slender, sucker-bearing distal portion. The Antarctic material has tentacular club suckers which possess, on the distal half of the ring, a prominent central recurved median tooth flanked by two triangular teeth on each side. The proximal half of the ring is smooth. The proximity of the location where the specimens were collected to the Antarctic Circumpolar Current suggests that the species may be widely distributed in the Southern Ocean.

During the British Antarctic Survey's Offshore Biological Programme (latterly Pelagic Ecosystem Studies Programme), two specimens of a cephalopod belonging to the squid family Chiroteuthidae were caught in the Scotia Sea by rectangular midwater trawl (Baker *et al.* 1973). The material closely resembles *Chiroteuthis veranyi* (Férussac, 1835) from elsewhere, but initially it was suspected to be a new species on the basis of location and the dentition of the tentacular club suckers. Subsequently it was decided, after examining additional material from the Kerguelen Islands, that the Southern Ocean material does not merit the erection of a new species. However, in view of the remoteness of the collection site of the materi-

al from the location of the type material in the Mediterranean, it is described here. The family Chiroteuthidae and the genus *Chiroteuthis* are defined by Roper *et al.* (1969) and Nesis (1987).

MATERIAL AND METHODS

Both specimens were maturing females. They were fixed in 5% formol saline. Suckers were removed from the arms and tentacular club for examination with a Leica S360 scanning electron microscope (SEM). They were transferred through an ascending series of acetone concentrations in water (25, 50, 75 and 100%), put through two changes of 100% dry acetone for 30 minutes, critical-point-dried in liquid CO₂, mounted on SEM stubs with colloidal silver and sputter-coated with gold. Drawings of the suckers were made from SEM photographic images.

This paper follows guidelines given by Roper and Voss (1983) and Clarke (1986) for taxonomic descriptions of cephalopods and their beaks.

SYSTEMATIC DESCRIPTION***Chiroteuthis veranyi* (Férussac, 1835)**

Material: Two specimens. Specimen 1: 52°56.6'S, 36°11.1'W (c. 130 km north of South Georgia), 26 November 1981, RMT1 opened at 250 m, closed at

Table 1: Measurements and indices of two maturing female *Chiroteuthis veranyi* from the Atlantic sector of the Southern Ocean (see text for details of each specimen)

Parameter	Specimen 1		Specimen 2	
	Measurement (mm)	Index (%)	Measurement (mm)	Index (%)
Mantle length	107	–	96	–
Mantle width	34	32	33	34
Fin length	56	52	47	49
Fin width	54	50	50	52
Arm length I	82	77	114	119
Arm length II	124	116	125	130
Arm length III	146	136	135	141
Arm length IV	201	188	245	255
Club length	50	48	52	54
Tentacle length	700	654	670	698
Eye diameter	13	12	14	15

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Fig. 1: Dorsal view of *Chiroteuthis veranyi* from the Atlantic sector of the Southern Ocean before fixation

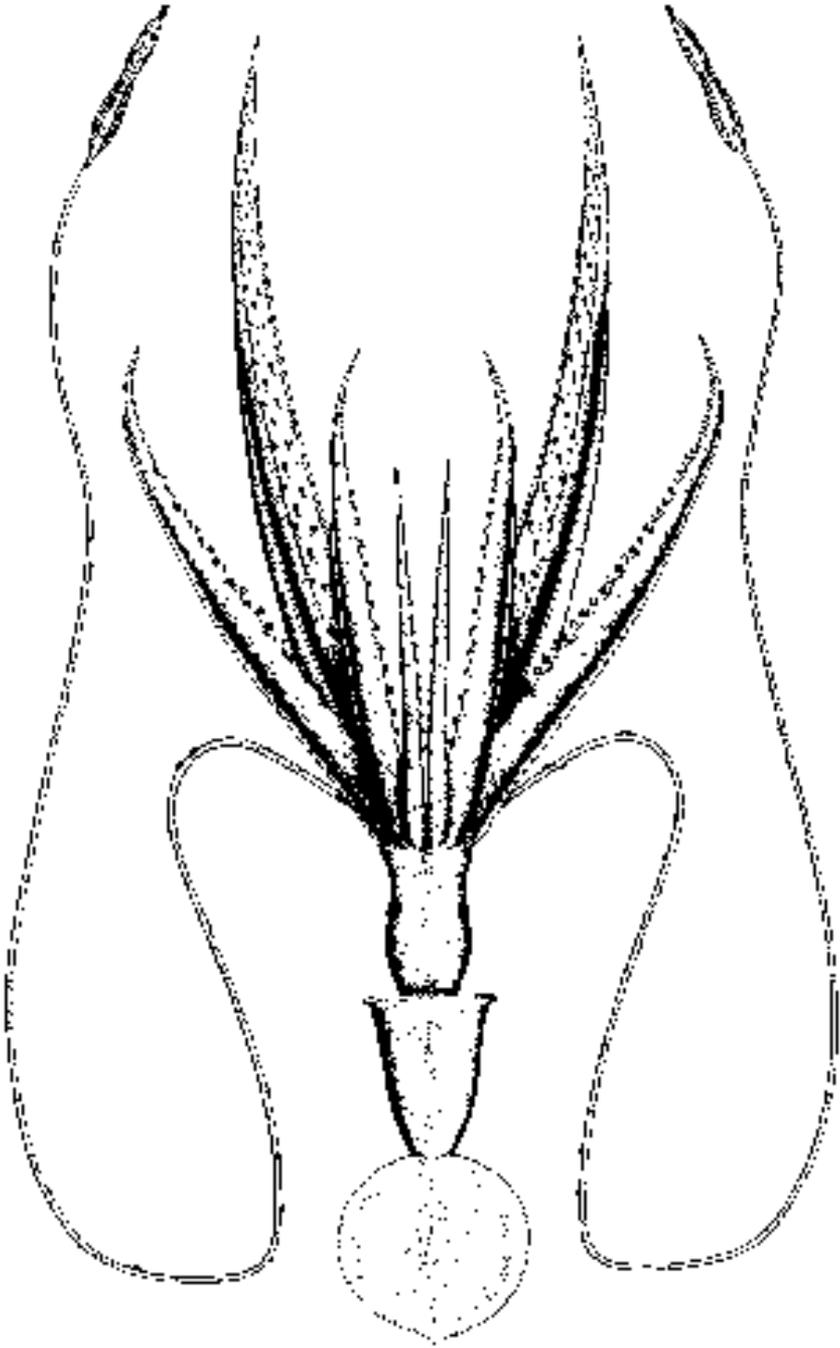


Fig. 2: Dorsal view of *Chiroteuthis veranyi*

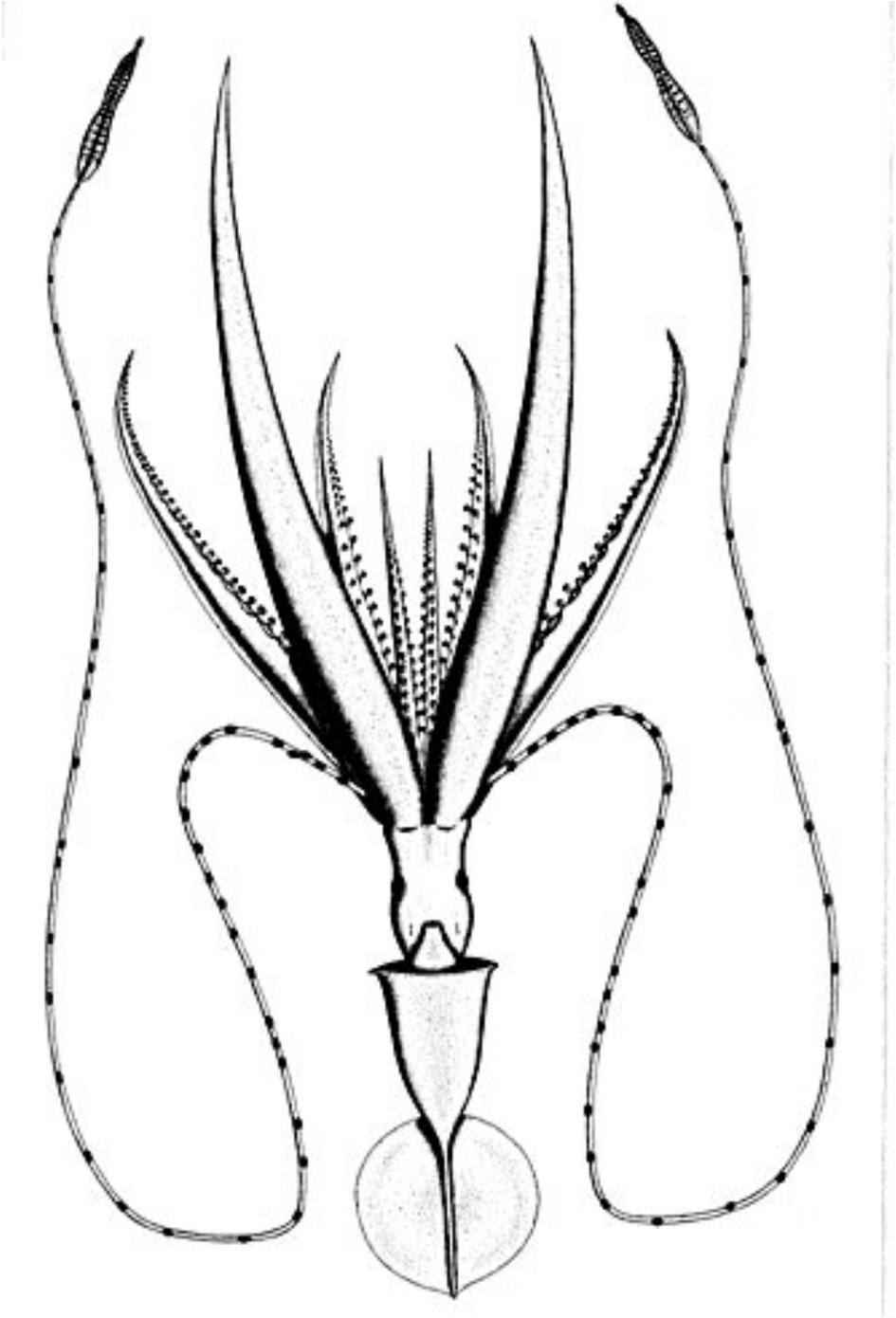


Fig. 3: Ventral view of *Chiroteuthis veranyi*

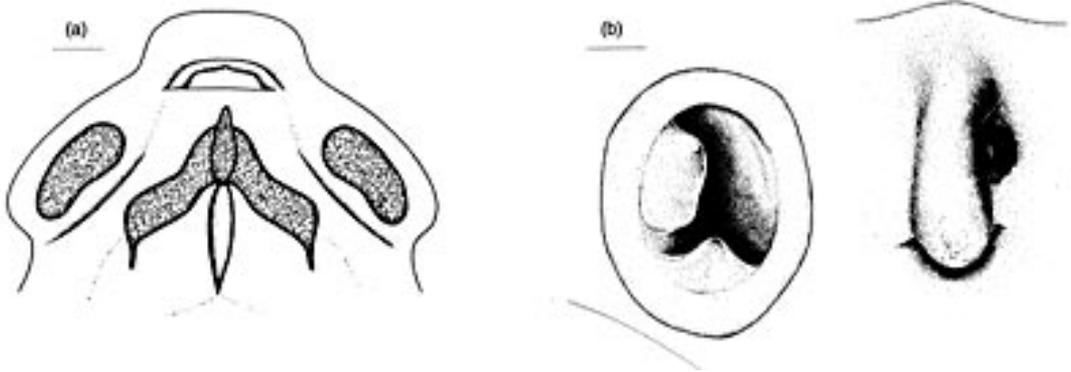


Fig. 4: (a) Funnel organ and valve. (b) Funnel and mantle members of funnel-locking cartilage

2 000 m. Specimen 2 (Fig. 1): 53°22.0'S, 38°33.1'W (c. 65 km north of South Georgia), 30 January 1991, RMT25 opened at 800 m, closed at 1 000 m. Measurements and indices of the two specimens are given in Table I. All drawings were made from Specimen 1.

Description

Mantle (Figs 2, 3): Short, conical, with weak musculature; terminates in a point posteriorly just beyond posterior end of fins; anterior mid-dorsal mantle margin a low point; ventral margin without protruberances.

Fins (Figs 2, 3): Almost circular with free anterior lobes; fins occupy half the mantle length.

Funnel (Fig. 4a): Moderate in size, free from head laterally; *funnel valve* small, well posterior to funnel opening. Dorsal *funnel organ* inverted v-shape with short, wide tapering limbs and a prominent central anterior papilla; ventral pads oval.

Funnel locking-cartilage (Fig. 4b): Oval with two distinct knobs, a larger tragus and a smaller antitragus, projecting towards centre of cavity.

Head (Figs 2, 3): Elongate, cylindrical, slightly swollen in the region of the eyes. Two olfactory papillae, with stalks about 10 mm long with small terminal swellings, arise from ventro-lateral surface of head on each side of funnel opening. *Eyes* large, with a slight anterior and a small posterior sinus. Eyes of both specimens damaged. Buccal connectives attach to dorsal borders of Arms I and II, ventral borders of Arms III and IV.

Arms (Fig. 5): Formula IV>III>II>I in size and length. Arms I–III with thick, low keels, and with low protective membranes supported by trabeculae which are approximately equilateral triangle shape. Arm IV greatly enlarged, about twice mantle length, with a broad tentacular sheath running along its length. No protective membrane or trabeculae on Arm IV. *Suckers* on Arm IV widely separated in two alternating series, converged distally, giving the appearance of single row to arm tip. Largest suckers located basally on Arm IV, one-third arm length from arm base on Arms I–III. Suckers on all arms reduced in size distally towards arm tip, becoming crowded at distal end. Distal two-thirds of largest *sucker rings* (Fig. 6) with 12–16 distinct triangular teeth, proximal one-third of sucker rings scalloped.

Tentacles (Figs 2, 3): Long, slender, about 6–7 times mantle length, white with purplish specks over surface. Numerous loosely adhered “knobs” of unknown function, but thought to be photophores, on aboral surface of tentacular stalk. “Knobs” oval with flattened surface and with purplish pigmentation. An estimate of the number of “knobs” present was impossible because so many had been lost during capture and preservation. “Knobs” decreased in diameter distally towards the club, appeared as dark spots at regular intervals on aboral surface of club.

Club (Fig. 7): Flattened, widest at proximal portion, each side bordered by well developed protective membrane supported by a series of transverse, thick muscular trabeculae. Ends of trabeculae project at edge of membrane. Trabeculae fused with tentacle on oral side. Trabeculae on distal half of club separated by spaces similar in width to their breadth. Trabeculae

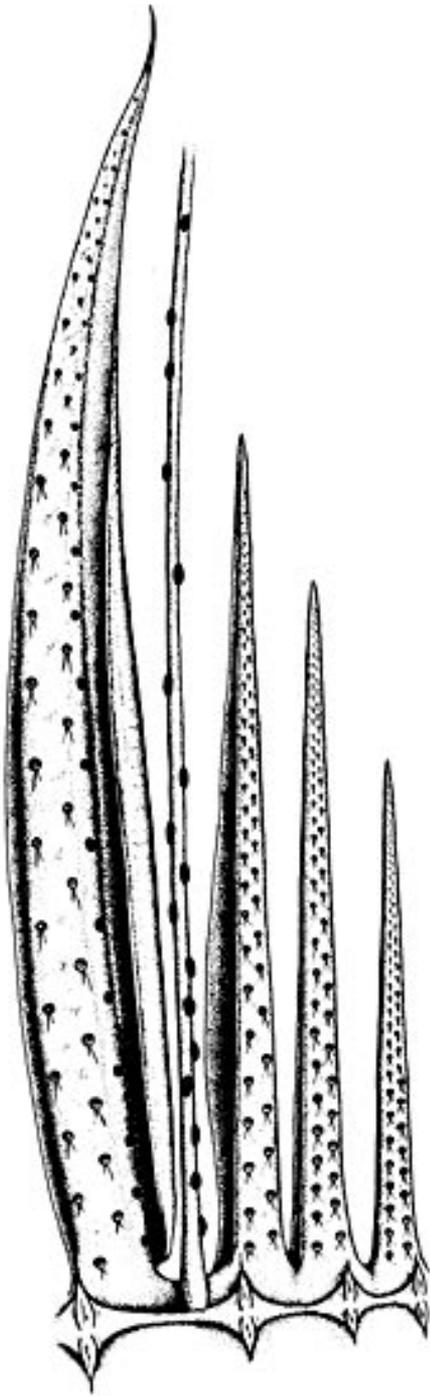


Fig. 5: Brachial crown (right side) of *Chiroteuthis veranyi*

on proximal half of club forked, crowded with narrow spaces in between, those on proximal one-third fused. A thick, ovate dark purple indented photophore, about 2.5 mm long, at tip of club. The spoon-like indentation visible from the aboral side of club.

Club suckers (Fig. 8): A total of 133–136 suckers in about 35 tetraserial rows. Suckers set on long lateral and short medial stalks. Stalks composed of longer basal part and shorter (about half length of basal part) distal sucker-bearing part, separated by a short purple pleated “skirt”. A transparent keel, running along length of each stalk, fuses with protective membrane between trabeculae. Lateral suckers slightly wider than medial suckers. Distal half of *sucker ring* (Fig. 9) with a prominent central recurved median tooth flanked by two triangular teeth on each side, proximal half of sucker ring smooth. Rings on medial suckers about two-thirds the diameter of those on lateral suckers.

Radula (Fig. 10): Seven transverse rows of teeth. Rachidian with a long central tooth flanked by two short, blunt lateral cusps. First lateral tooth bicusped with a long, pointed median cusp and a small blunt lateral cusp. Second lateral tooth pointed, with a broad base and a subtle medial blunt shoulder. Third lateral tooth long, slightly curved, pointed. Marginal plates absent.

Chromatophores (Fig. 1): Numerous pink-purple *chromatophores* cover body, fewer on tentacles, absent on club keels.

Photophores: Two large, round prominent *photophores* lie one on each side of the ink sac. Large regular-spaced photophores lie along oral sides of Arms IV at base of tentacular sheath. Single photophore at tip of each tentacular club and presumed photophores on the tentacular stalks. Eye photophores – strips of golden brown luminous tissue around the eye.

Beak (Fig. 11): Upper mandible with long curved rostrum. Lower mandible with obtuse jaw angle, high wingfold thickened to form a ridge, long wing, short crest; hood long relative to crest and broadly notched in the midline; thickened fold running to lower part of posterior edge of lateral wall.

DISCUSSION

Young (1972) recognized nine species in the genus *Chiroteuthis*: *C. veranyi* (Férussac, 1835), *C. lacer-*

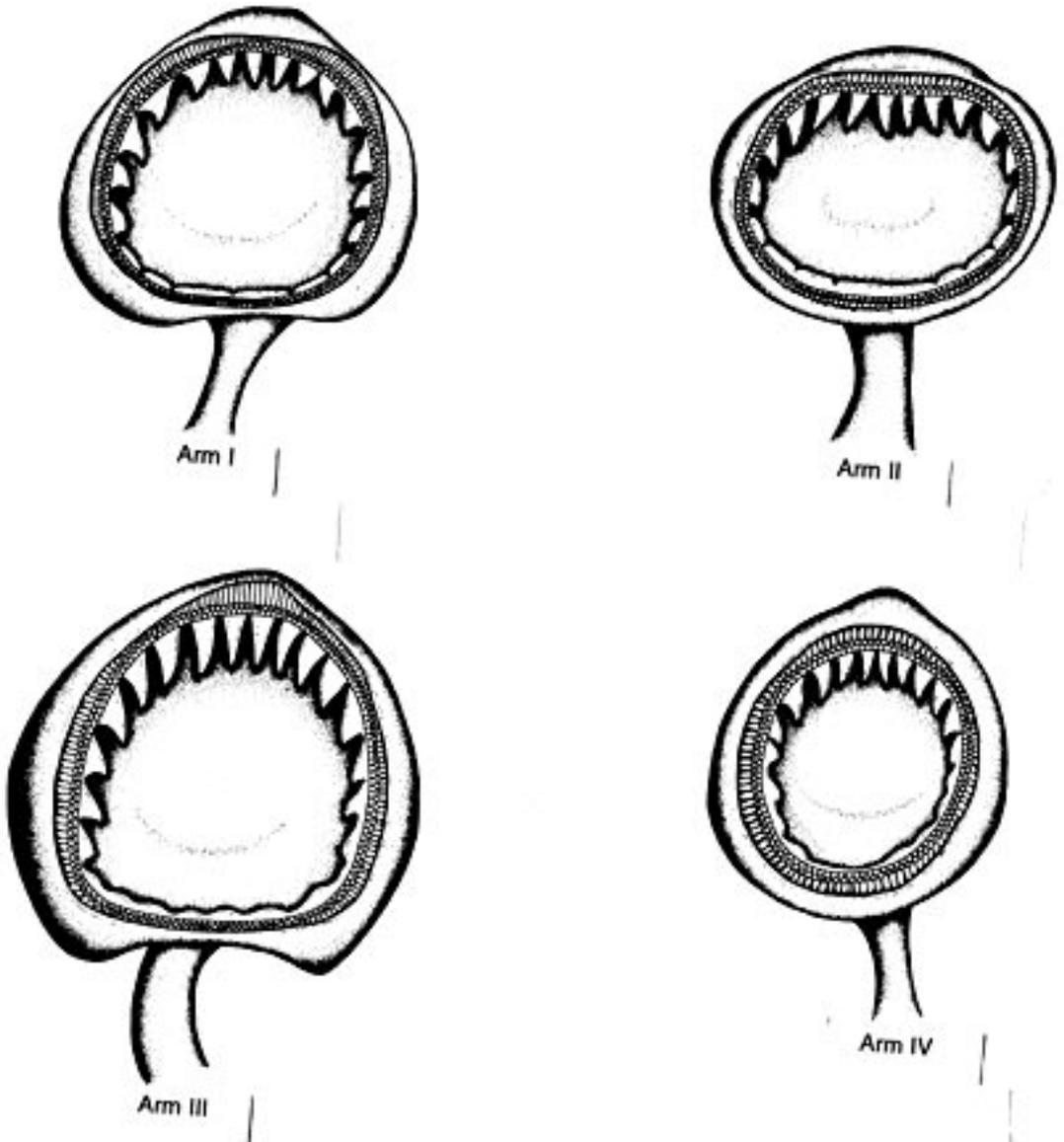


Fig. 6: Largest suckers from Arms I – IV

tosa (Verrill, 1881), *C. picteti* Joubin, 1894, *C. macrosoma* (Goodrich, 1896), *C. imperator* Chun, 1910, *C. atlantica* (MacDonald & Clench, 1934), *C. joubini* Voss, 1967, *C. capensis* Voss, 1967 and *C. calyx* Young, 1972. Nesis (1987) considered *C. lacertosa* to be a subspecies of *C. veranyi*, *C. atlantica* to be a junior synonym of *C. capensis*, and *C. macrosoma* and *C. imperator* to be junior synonyms of *C. picteti*.

Chiroteuthis acanthoderma Lu, 1977 was transferred to a new genus *Asperoteuthis* by Nesis (1980), and recent data indicate that the species possesses secondary fins similar to those in the genus *Grimalditeuthis* (Tsuchiya and Okutani 1993). Recently a new species, *Chiroteuthis spoeli*, and a new subspecies, *Chiroteuthis picteti somaliensis*, from the western Indian Ocean, have been described (Salcedo-Vargas 1996).

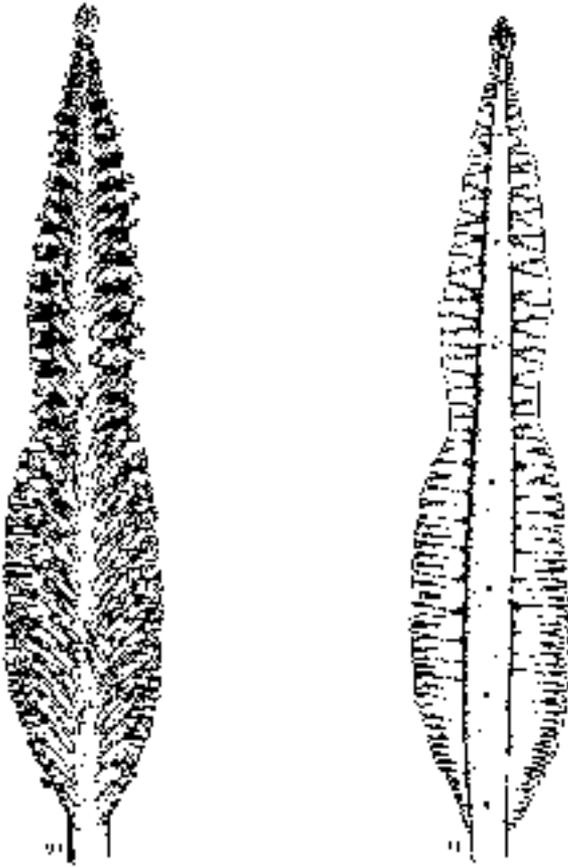


Fig 7: Tentacular club (right side) – (a) oral view, (b) aboral view

The Grimalditeuthidae have been synonymized with the Chiroteuthidae (Young 1991).

The specimens of *C. veranyi* from the Southern Ocean are similar in appearance to material from the north and equatorial Atlantic and Mediterranean (Adam 1952). The tentacular club suckers possess a very prominent central recurved median tooth flanked by two smaller triangular teeth on each side on the distal half of the ring, and a smooth proximal half. However, it is here concluded that the sucker ring dentition is not sufficiently different from other material to merit the erection of a new species. The following are brief comparisons of some important taxonomic characters among the species of *Chiroteuthis* (Young 1972).

C. veranyi has two photophores on the ink sac, one on each side, similar to *C. lacertosa*, *C. calyx* and *C.*

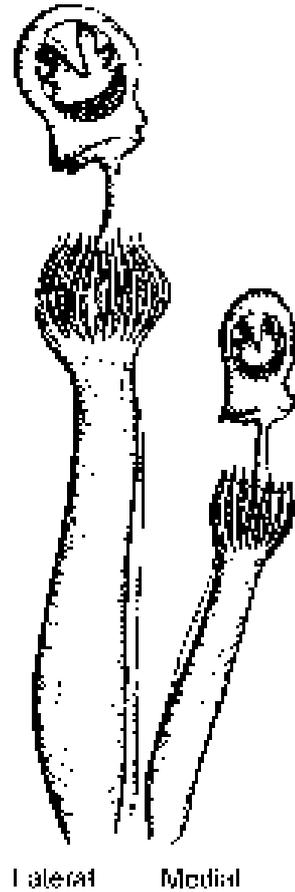


Fig. 8: Medial and lateral tentacular club suckers and stalks from central area of proximal section of manus

imperator. *C. picteti* and *C. joubini* both have one median visceral photophore on the ink sac. The photophore(s) on the ink sac of *C. macrosoma* and *C. atlantica* are unknown. *C. capensis* lacks visceral photophores.

The horny rings of the arm suckers of *C. veranyi* possess 18 small teeth on the distal two-thirds, of which those on the distal one-third are sharply pointed; the proximal margin is smooth. The sucker ring dentition of *C. lacertosa* is similar to that in *C. veranyi*. *C. macrosoma* bears many rounded or squared teeth on the distal margin of the arm sucker rings (10 teeth in Fig. 55 of Goodrich 1896). *C. imperator* possesses 9–16 deeply cleft squarish teeth on the distal half of the sucker ring (Voss 1963). *C. joubini* has long fine teeth on the distal margin of the sucker ring; the

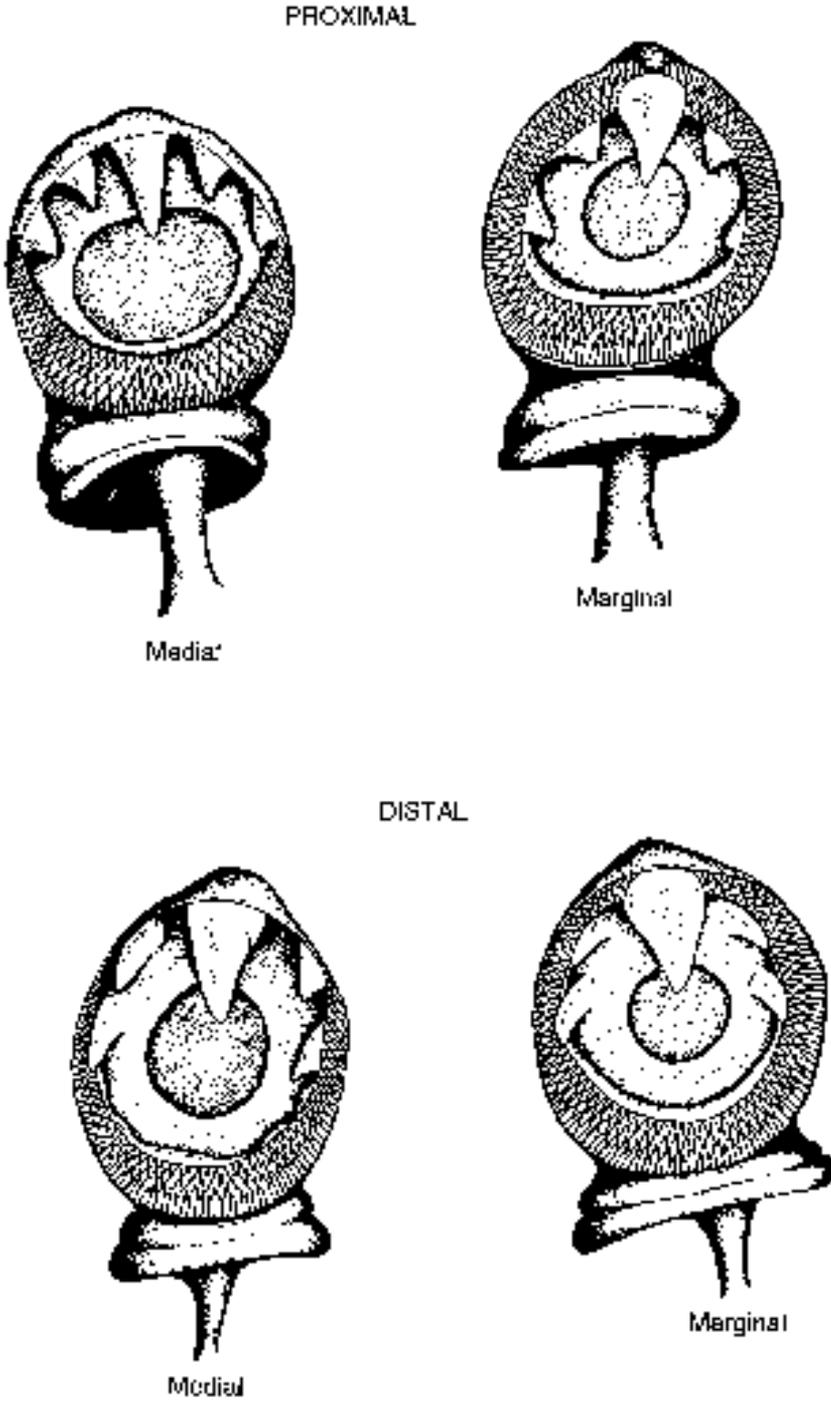


Fig. 9: Medial and lateral tentacular club suckers from the central area of proximal and distal sections of the manus



Fig. 10: Radula tooth row of *Chroteuthis veranyi*

proximal margin is smooth. *C. atlantica* possesses arm sucker rings which resemble those of *C. veranyi*: 12 pointed teeth distally followed by three truncated teeth on each side proximally; the proximal margin is smooth. The arm sucker rings of *C. capensis* possess "about 8–10 long, slender sharp teeth on the distal edge and about 20 low blunt teeth on the rest of the circumference" (Voss 1967). The description of the sucker ring dentition in *C. picteti* is vague, but from the original illustration (Joubin 1894, Plate II, Fig. 7), it appears to have six rounded teeth on the proximal quarter of the sucker ring; the remaining margin is smooth. In *C. calyx* the rings of the enlarged suckers of Arms I – III are smooth, but they may show irregular indentations. The rings of the suckers proximal to the enlarged suckers bear 18 – 20 broad, truncate teeth on the distal two-thirds, the proximal one-third being smooth. The suckers distal to the enlarged suckers have longer, more slender, truncate teeth on the distal margin; proximal margin smooth but irregular. The arm sucker rings of the specimens of *C. veranyi* from the Southern Ocean have 12–16 triangular teeth on the distal two-thirds and are smooth on the proximal one-third, with slight regular indentations.

The horny rings on the suckers on the tentacular club of *C. veranyi* from elsewhere possess seven well-spaced, sharply pointed long teeth on the distal two-thirds, the central tooth being the longest; the proximal margin is smooth. The club sucker ring of *C. lacertosa* described by Verrill in 1881 is similar to that in *C. veranyi*. The club sucker ring dentition is unknown for *C. macrosoma* and *C. atlantica*. In *C. imperator*, the club sucker rings bear 10 sharply pointed teeth with a large median tooth on the distal three-quarters; the proximal margin is smooth. In *C. joubini* the club sucker rings have three long, pointed teeth distally, occasionally with two truncated lateral teeth; the proximal margin is smooth. The club sucker rings of *C. capensis* bear one large hook-like tooth on the distal margin, with 7–8 teeth on each side; the proximal margin is irregular but not toothed. In *C. picteti* the club sucker rings possess one large, triangular, median tooth on the distal margin; the remaining margin is irregular (Joubin 1894, Plate II, Fig. 8). The club sucker

ring of *C. calyx* bears a large recurved median tooth with 10–12 smaller lateral teeth on the distal margin; the proximal margin is smooth. The distal half of the club sucker ring in *C. veranyi* from the South Atlantic possesses a prominent central recurved median tooth, flanked by two triangular teeth on each side; the proximal half of the ring is smooth.

The stalks of the club suckers in *C. veranyi*, *C. lacertosa* and *C. calyx* are composed of two portions: a broad cylindrical basal portion terminates in a dark purple, pleated "skirt" from which arises a slender, sucker-bearing distal portion. *C. capensis* has club suckers bearing an outer raised keel which terminates distally in a lappet-like crest. The club sucker stalks in *C. imperator* are similar to those in *C. capensis*, but the outer keel is lacking on the stalks of the medial suckers. The club sucker stalks in *C. joubini* and possibly in *C. picteti* are similar, with broad basal and slender distal portions.

Beaks from gut contents of predators at South Georgia, that closely resemble those of *C. veranyi*, indicate that it is a regular but minor component of the diet of southern elephant seals (Rodhouse *et al.* 1992a) and wandering, grey-headed and black-browed albatrosses (Rodhouse *et al.* 1987, 1990, Rodhouse and Prince 1993). Predation by albatrosses suggests that *C. veranyi* must at times come within a few metres of the sea surface. Beaks and other material have also been found in the stomachs of sperm whales taken off South Georgia and South Africa (Clarke 1980).

The specimens reported here were caught in the northern ice-free zone of the Scotia Sea. Their proximity to the Antarctic Circumpolar Current suggests that the species may be widely distributed in the Southern Ocean. Two juvenile specimens (mantle length 42 and 48 mm) lacking their tentacles but similar to *C. veranyi* were recorded in Subantarctic/ Subtropical waters off the Patagonian Shelf (Rodhouse *et al.* 1992b). Recently, one of us (CCL) examined a small collection of *Chroteuthis* from Kerguelen. All were typical *C. veranyi*, except one which had club sucker rings of the form described in the specimens from the South Atlantic. All the Kerguelen specimens were from the same area and the one similar to those from the South Atlantic was caught with the typical form. Finally, *C. veranyi* has been recorded twice from the Peru Current, south-eastern Pacific (Nesis 1972, Alexeyev 1994).

It seems paradoxical that the distribution of a pelagic species such as *C. veranyi* can extend across the Antarctic Polar Front, which apparently presents such an impenetrable barrier to benthic invertebrates (Clarke 1996). On the other hand, analysis of molecular genetic markers may in future reveal diversity that cannot be seen at the morphological level. There are

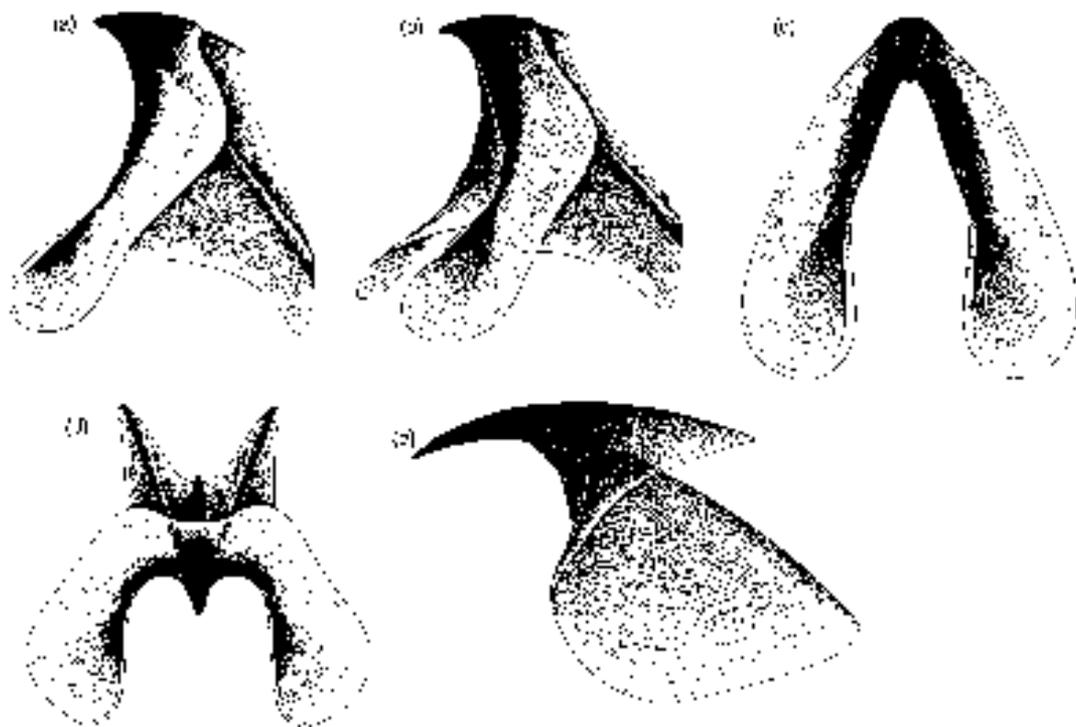


Fig. 11: (a) – (d) Lower beak, and (e) upper beak of *Chiroteuthis veranyi*

instances of apparent cryptic speciation in oceanic squid (Smith *et al.* 1981, Brierley *et al.* 1993) and, in deep-sea fish (Gonostomatidae), molecular genetic markers have revealed cryptic allopatric lineages even in oceanic regions where there are no discernible barriers to gene flow (Miya and Nishida 1997).

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LITERATURE CITED

- ADAM, W. 1952 — Céphalopodes. *Résult. scient. Expéd. océanogr. Belg. Eaux Côtières Afr. Atl. Sud (1948–1949)* 3(3): 142 pp. + 3 Plates.
- ALEXEYEV, D. O. 1994 — New data on the distribution and biology of squids from the southern Pacific. *Ruthenica* 4(2): 151–166.
- BAKER, A. DE C., CLARKE, M. R. and M. J. HARRIS 1973 — The N.I.O. combination net (RMT 1+8) and further developments of rectangular midwater trawls. *J. mar. biol. Ass. U.K.* 53(1): 167–184.
- BRIERLEY, A. S., RODHOUSE, P. G., THORPE, J. P. and M. R. CLARKE 1993 — Genetic evidence of population heterogeneity and cryptic speciation in the ommastrephid squid *Martialia hyadesi* from the Patagonian Shelf and Antarctic Polar Front. *Mar. Biol.* 116(4): 593–602.
- CLARKE, A. 1996 — The distribution of Antarctic marine benthic communities. *Antarct. Res. Ser., Am. geophys. Un.* 70: 19–230.
- CLARKE, M. R. 1980 — Cephalopods in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *“Discovery” Rep.* 37: 1–324.

- CLARKE, M. R. (Ed.) 1986 — *A Handbook for the Identification of Cephalopod Beaks*. Oxford; Clarendon: xiii + 273 pp.
- GOODRICH, E. S. 1896 — Report on a collection of Cephalopoda from the Calcutta Museum. *Trans. Linn. Soc. Lond., Ser. 2* 7: 1–24 + 5 Plates.
- JOUBIN, L. 1894 — Céphalopodes d'Amboine. *Revue suisse Zool.* 2: 23–64 + 4 Plates.
- LU, C. C. 1977 — A new species of squid, *Chiroteuthis acanthoderma*, from the Southwest Pacific (Cephalopoda, Chiroteuthidae). *Steenstrupia* 4: 179–188.
- MIYA, M. and M. NISHIDA 1997 — Speciation in the open ocean. *Nature, Lond.* 389: 803–804.
- NESIS, K. N. 1972 — Oceanic cephalopods of the Peru Current: horizontal and vertical distribution. *Oceanology* 12(3): 426–437.
- NESIS, K. N. 1980 — Taxonomic position of *Chiroteuthis famelica* Berry. *Bull. Mosk. Obshch. Ispyt. Prirody, Sect. Biol.* 85(4): 59–66 (in Russian with English summary).
- NESIS, K. N. 1987 — *Cephalopods of the World*. Neptune City, New Jersey; TFH Publications: 351 pp.
- RODHOUSE, P. G., ARNBOM, T. R., FEDAK, M. A., YEATMAN, J. and A. W. A. MURRAY 1992a — Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can. J. Zool.* 70(5): 1007–1015.
- RODHOUSE, P. G., CLARKE, M. R. and A. W. A. MURRAY 1987 — Cephalopod prey of the wandering albatross *Diomedea exulans*. *Mar. Biol.* 96(1): 1–10.
- RODHOUSE, P. G. and P. A. PRINCE 1993 — Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. *Polar Biol.* 13(6): 373–376.
- RODHOUSE, P. G., PRINCE, P. A., CLARKE, M. R. and A. W. A. MURRAY 1990 — Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Mar. Biol.* 104(3): 353–362.
- RODHOUSE, P. G., SYMON, C. and E. M. C. HATFIELD 1992b — Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 89(2&3): 183–195.
- ROPER, C. F. E. and G. L. VOSS 1983 — Guidelines for taxonomic descriptions of cephalopod species. *Mem. natn. Mus. Vict.* 44: 49–63.
- ROPER, C. F. E., YOUNG, R. E. and G. L. VOSS 1969 — An illustrated key to the families of the order Teuthoidea (Cephalopoda). *Smithson. Contr. Zool.* 13: 32 pp.
- SALCEDO-VARGAS, M. A. 1996 — Cephalopods from the Netherlands Indian Ocean Programme (NIOP) – 1. *Chiroteuthis spoeli* n.spec. and *Chiroteuthis picteti somaliensis* n. subspec. *Beaufortia* 46(2): 11–26.
- SMITH, P. J., ROBERTS, P. E. and R. J. HURST 1981 — Evidence for two species of arrow squid in the New Zealand fishery. *N.Z. J. mar. Freshwat. Res.* 15: 247–253.
- TSUCHIYA, K. and T. OKUTANI 1993 — Rare and interesting squids in Japan – 10. Recent occurrences of big squids from Okinawa. *Venus* 52(4): 299–311.
- VOSS, G. L. 1963 — Cephalopods of the Philippine Islands. *Bull. U.S. natn. Mus.* 234: v + 180 pp.
- VOSS, G. L. 1967 — Some bathypelagic cephalopods from South African waters. *Ann. S. Afr. Mus.* 50(5): 61–88.
- YOUNG, R. E. 1972 — The systematics and aerial distribution of pelagic cephalopods from the seas off southern California. *Smithson. Contr. Zool.* 97: 159 pp.
- YOUNG, R. E. 1991 — Chiroteuthid and related paralarvae from Hawaiian waters. *Bull. mar. Sci.* 49(1–2): 162–185.