

BEAUFORTIA

INSTITUTE FOR SYSTEMATICS AND POPULATION BIOLOGY
(ZOOLOGICAL MUSEUM) UNIVERSITY OF AMSTERDAM

Vol. 47, no. 3

December 19, 1997

CEPHALOPODS FROM THE NETHERLANDS INDIAN OCEAN PROGRAMME (NIOP)- II. MASTIGOTEUTHID LINEAGE AND RELATED FORMS

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Keywords: Cephalopoda, *Planktoteuthis*, *Chiroteuthis*, *Idioteuthis*, *Mastigoteuthis*, Taxonomy, West Indian Ocean, Deep seasquids.

ABSTRACT

Seven species of bathypelagic squids from the West Indian Ocean are described. Two species from the chiroteuthid lineage are recorded: *Planktoteuthis* sp. and *Chiroteuthis mega*. The family Mastigoteuthidae is divided in two genera: *Idioteuthis* and *Mastigoteuthis*. As members of the former are *Idioteuthis danae* (= *Echinoteuthis danae*) and two species new to science, and for the latter *Mastigoteuthis glaukopsis* and *Mastigoteuthis grimaldii*. The mastigoteuthid lineage is defined by: 1) short neck and brachial pillar; 2) whip-like tentacle; 3) ovate pseudoconus in cross section view, and 4) arm formula: $IV > II > III \geq I$. The family Mastigoteuthidae as now defined consist of seventeen species.

INTRODUCTION

The taxonomy of mastigoteuthid-like squids is mainly based on juvenile and a few pre-adult forms. Mastigoteuthid and chiroteuthid squids used to form two subfamilies of the family Chiroteuthidae (Chun, 1910; Pfeffer, 1912; Naef, 1923; Sasaki, 1929). After their elevation to familial level (Roper et al., 1969), some species were placed in one family and later trans-

ferred to the other, such as *Chiroteuthis grimaldii* Joubin, 1895, *Tankaia borealis* Sasaki, 1929, *Chiroteuthoides hastula* Berry, 1909 or *Chiroteuthis famelica* Berry, 1920 (Joubin, 1895; Sasaki, 1929; Clarke, 1966; Berry, 1909, 1920; Nesis, 1987).

On the other hand, the complex of chiroteuthid paralarval forms characterized by the "doratopsis" stage, present in various genera (Chun, 1910; Pfeffer, 1912; Naef, 1923), has been partially solved by Young (1991), who

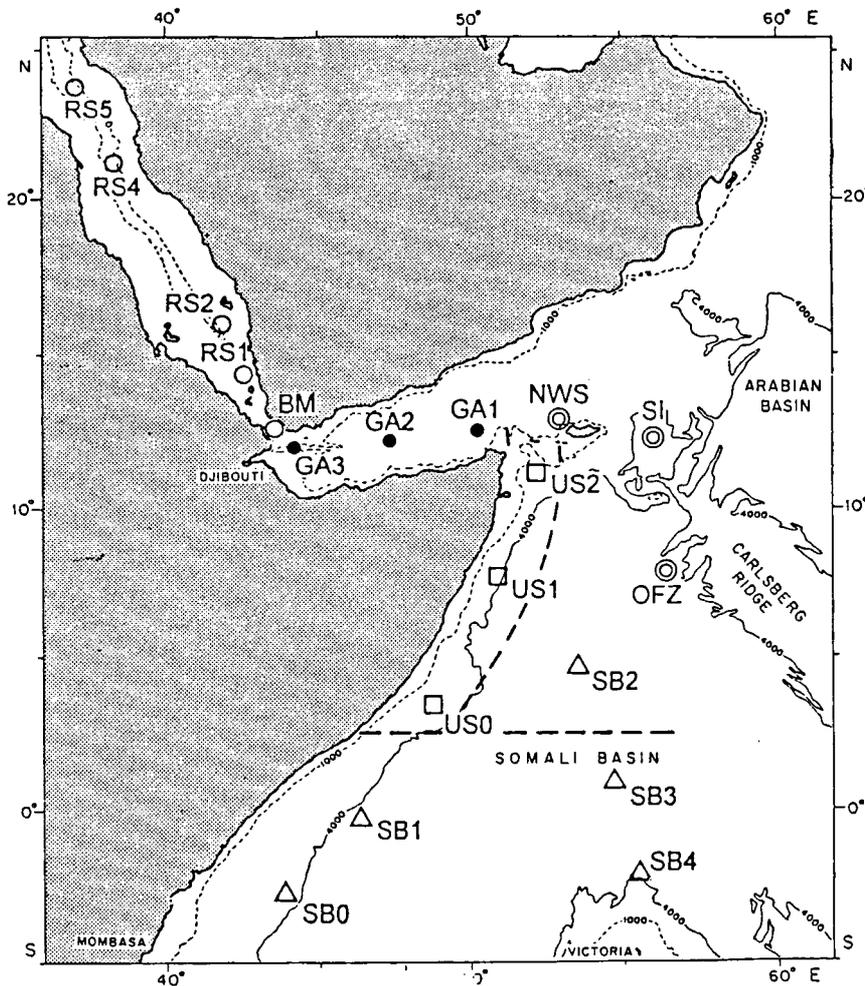


Fig. 1. RMT8 stations of the R/V Tyro during the cruises in 1992-1993. Dashed lines indicate the border of the areas used for pooling data. Abbreviations: RS = Red Sea; BM = Bab-el-Mandab; GA = Gulf of Aden; US = Upwelling Somalia; NSW = NW of Socotra; SI = Socotra Island; OFZ = Owen Fracture Zone; SB = Somalia Basin.

defined the "chiroteuthid lineage" for several genera with common morphology. However, the "mastigoteuthid-lineage", without a common larval form, has remained poorly characterized.

Young (1991) described several mastigoteuthid larval forms, but all of them still remained lumped together under the single genus *Mastigoteuthis* Verrill, 1881. Studies on the Mastigoteuthidae (Salcedo-Vargas, 1993; 1995; Salcedo-Vargas & Okutani, 1994) added new information to these taxa in order to improve their taxonomic position.

The present paper deals with part of the cephalopod fauna from the West Indian Ocean collected during the NIOP expeditions (Salcedo-Vargas, 1994). In this study, the paralarval stages of some species, some of which have been poorly studied systematically, are described. Representatives of the chiroteuthid lineage (CH) from the NIOP collection are divided into two papers.

The first one (Salcedo-Vargas, 1996) describes the new chiroteuthid forms, and is separate from this paper because those specimens are larger forms (50-90 mm ML), whereas in this one we will deal with paralarval and some juvenile specimens of up to 47 mm ML. Two representatives of the chiroteuthid lineage, *Planktoteuthis* sp. and *Chiroteuthis mega* (Joubin, 1933) are studied here. The members of the "mastigoteuthid lineage" (MA) are also defined in the following pages, and consist of the genus *Idioteuthis* including the species *Idioteuthis danae* Joubin, 1933 (= *Echinoteuthis danae*) and two new species to science. The genus *Mastigoteuthis* consist of *Mastigoteuthis grimaldii* Joubin, 1895 and *Mastigoteuthis glaukopis* Chun, 1910.

MATERIALS AND METHODS

The material examined is from the West Indian

Ocean and is incorporated in the collections of the Zoological Museum of Amsterdam (ZMA), Netherlands. The samples were collected by the large net Rectangular Midwater Trawl (RMT) (mesh size 4.5 mm, net opening 8 m²) from 0 to 600m depth. Samples were fixed in 4% formalin on board. They were sorted, measured and identified in the laboratory, and later transferred into 70% ethyl alcohol. The sampling area is indicated in Fig 1.

Abbreviations: CH: Chiroteuthid lineage; MA: Mastigoteuthid lineage; SAM: South African Museum; ZMC: Zoological Museum of Copenhagen; ZMA: Zoological Museum of Amsterdam; NHML: Natural History Museum London; ZMB: Zoological Museum of Berlin.

TAXONOMY

Family Chiroteuthidae

Genus *Planktoteuthis* Pfeffer, 1912

Doratopsis Chun, 1910: 227-234, pl. 39, figs. 12, 15; pl. 45, figs. 1-5, 6, 7; pl. 46, figs. 6, 7; pl. 47, figs. 1, 5, 6.

Planktoteuthis Pfeffer, 1912, (in part): 554, 570-578, pl. 46, figs. 6-7; Young, 1991: 169-174, figs. 3D, E, I, J; 4E, 3A-C, F, H; 4C.

Diagnosis: (Doratopsis stage) Mantle narrow and elongate; funnel cartilage has well-developed antitragus or no tubercles at all; head round, either very evident from long neck and brachial pillar or fused to neck; tentacle muscular and cylindrical; all arms vesiculate, thin and long; fins leaf-shaped or round; suckers in arm IV form a single series; sometimes enlarged suckers on arm II or III; distal part of club has enlarged suckers in one or both ventral longitudinal rows; keel and carpal suckers developed from 12 mm ML; eyes small, round or oval; if oval, eyes have ventral projection, which appears as tubercle in youngest stages.

Type species: *Valbyteuthis danae* Joubin, 1931.

Planktoteuthis spec.

Figs. 2a-d; 6a; table 1

Material examined: 1 paralarva, 22 mm ML, 13/Jan./93, No. 640, Sta. SB3, night-time, depth 0-100 m; 1 paralarva, 18 mm ML, 13/

Jan./93, No. 639, Sta. SB3, night-time, depth 0-100 m.

Description: Mantle moderate to large, conical, slightly wider than head; tail long and usually truncated; antero-dorsal margin of mantle protruding and sharpened; fins antero-posteriorly ovate, 55% ML; AF IV>III>II>I; arm IV 95-100% ML; head rounded, brachial pillar long, 30% ML; neck thin and long, 40% ML; nuchal cartilage, thin, long and round in distal part, 6 times longer than wide; eyes relatively small; funnel medium; funnel cartilage small, tragus and antitragus well-developed; tentacular stalk thin but muscular, 1.5 times ML, with well-defined club of 3.5 mm, keel present; 12 small carpal suckers; manus has 16 rows of 4 suckers arranged transversally; suckers in border of manus larger than interior ones; 4 small suckers in dactylus; armature large, all arms gelatinous, vesiculate and transparent; arm III most robust with slightly larger suckers; arm II slightly shorter than arm III but much thinner; arm I extremely thin; all arms have suckers larger than those in arm IV; all arms have row of single chromatophores along ventral side, most evident in arms III and IV, and in oral side between each row of suckers; some large chromatophores exist at base of armature between most proximal corner of arms and buccal mass; a few more around eyes and head and on shoulders of funnel; evidence of luminous tissue on ventral side of eyeballs but no photophores; olfactory papillae not observed.

Remarks: This species can be recognized by its elongate body, neck, and brachial pillar, and round head. The chromatophore patterns were not completely discernible. They seem to resemble those of *Planktoteuthis danae* (Joubin, 1931, redefined by Young 1991), although they can be distinguished from it by the presence of enlarged suckers on arms and the fin shape. By its arm formula and general appearance, this species could also be related to *Doratopsis exophthalmica* Chun, 1908, but more information should be gathered before defining its specific level.

Genus *Chiroteuthis* d'Orbigny, 1841

Doratopsis Chun, 1912 (in part): 224-226, 228-231, pl. 42, fig. 5; pl. 39, fig. 11, 13, 14; pl. 46,

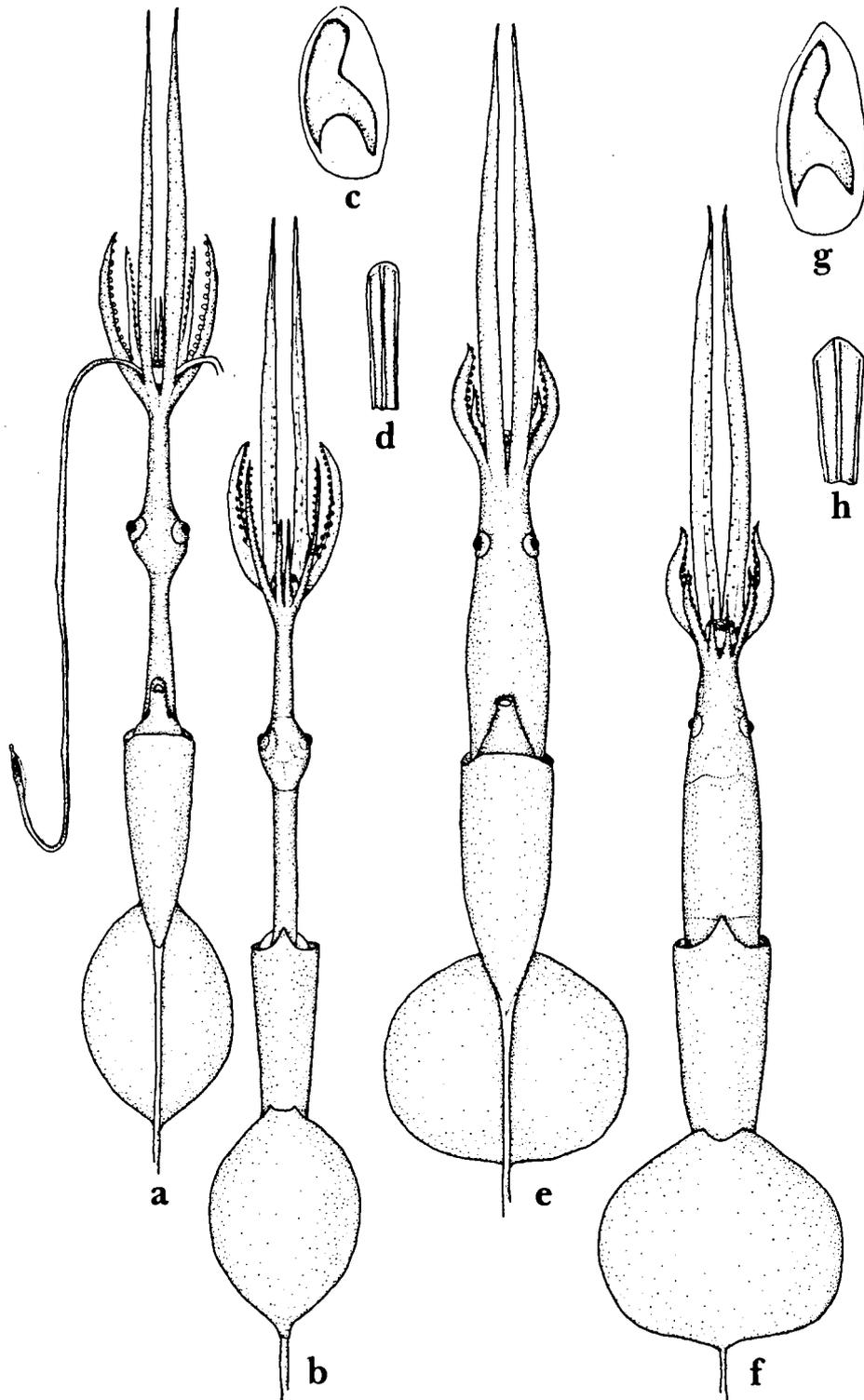


Fig. 2. Chiroteuthid lineage. *Planktoteuthis* sp. A, 22 mm ML, a: ventral view, b: same specimen, dorsal view, c: funnel cartilage, d: nuchal cartilage; *Chiroteuthis mega* (Joubin, 1933), 25 mm ML, e: ventral view, f: same specimen, dorsal view, g: funnel cartilage, h: nuchal cartilage.

Table 1. Measurements and indices. Abbreviations: DML: Dorsal Mantle length; MW: Mantle Width; FL: Fin Length; FW: Fin Width; ALI: Arm Length Index, I to IV; TL: Tentacle Length; CL: Club-area Length; HL: Head Length; HW: Head Width; ED: Eye Diameter; LnD: Lens Diameter. I: In all cases means Index; (*) in all cases means truncated or damaged; The figures in brackets are the real measurements in mm. Abbreviations after Roper and Voss, 1983.

| Sample # | 639 | 640 | 503-1 | 718 | 984 | 882 | 882 | 882 | 842 |
|-------------------|-----------------|-----------------|-------------|------------------|------------------|------------------|------------------|------------------|------------------|
| Species | <i>P. sp. A</i> | <i>P. sp. A</i> | <i>mega</i> | <i>grimaldii</i> | <i>glaukopis</i> | <i>glaukopis</i> | <i>glaukopis</i> | <i>glaukopis</i> | <i>glaukopis</i> |
| Sex | indef. | indef. | indef. | indef. | indef. | indef. | indef. | indef. | indef. |
| DML | 22 | 18 | 25 | 44 | 47 | 30 | 30* | 30* | 25 |
| MWI (MW) | 15.9 (3.5) | 16.6 (3) | 24.0 (6) | 27.2 (12) | 29.7 (14) | 20.0 (6) | 20.0 (6) | 20.0 (6) | 24.0 (6) |
| FLI (FL) | 50.0 (11) | 47.2 (8.5) | 52.0 (13) | 56.8 (23) | 57.4 (27) | 56.6 (17) | --- | --- | 48.0 (12) |
| FWI (FW) | 50.0 (11) | 44.4 (8) | 52.0 (13) | 50.0 (25) | 61.7 (29) | 50.0 (15) | --- | --- | 72.0 (18) |
| ALI | | | | | | | | | |
| I1 (I) | 22.7 (5) | 11.1 (2) | 12.0 (3) | 45.4 (20) | 29.7 (14) | 20.0 (6) | 20.0 (6) | 23.3 (7) | 16.0 (4) |
| II1 (II) | 34.0 (7.5) | 22.2 (4) | 24.0 (6) | 63.6 (28) | 53.1 (25) | 33.3 (10) | 33.3 (10) | 36.6 (11) | 36.0 (9) |
| III1 (III) | 40.9 (9) | 44.4 (8) | 36.0 (9) | 50.0 (22) | 38.2 (18) | 30.0 (9) | 30.0 (9) | 30.0 (9) | 34.0 (8.5) |
| IV1 (IV) | 100 (22) | 83.3 (15) | 108 (27) | 147 (65) | 95.7 (45) | 96.6 (29) | 100 (930) | 100 (30) | 80.0 (20) |
| TLI (TL) | 168 (37) | 138 (25) | --- | 409 (180) | --- | --- | --- | --- | --- |
| CLI (CL) | 15.9 (3.5) | 19.4 (3.5) | --- | 181 (80) | --- | --- | --- | --- | --- |
| HLI (HL) | 72.2 (16) | 66.6 (12) | 52.0 (13) | 29.5 (13) | 31.9 (15) | 28.3 (8.5) | 26.6 (8) | 30.0 (9) | 32.0 (8) |
| HWI (HW) | 11.3 (2.5) | 16.6 (3) | 16.0 (4) | 22.7 (10) | 21.2 (10) | 16.6 (5) | 16.6 (5) | 18.3 (5.5) | 18.0 (4.5) |
| ED / LnD | 0.7/0.2 | 0.5/0.2 | 2/0.5 | 5/1.5 | 10/4 | 4.5/2 | 4.5/2 | 4.5/2 | 3/1.5 |

figs. 1-5; pl. 47, fig. 2; Pfeffer, 1912 (in part): 555-570, pl. 46, figs. 1-5, 8-12.

Chiroteuthis Young, 1991: 163-168, figs. 1E-G, M, N, 2; 1A, B, I, J; 4D.

Diagnosis: (Doratopsis stage) Body slim and elongate; gladius long, extending far beyond posterior fins-mantle insertion point; some species develop secondary fins on long tail; neck long, not differentiated from head; tentacle has sucker buds arranged in 6-8 rows in distal part, and 2 suckers in proximal part in specimens from 2-8 mm ML; from 10-18 mm ML, number of sucker buds decrease and proximal suckers gradually become 4 transverse rows, while in distal part some suckers toothed and larger than others; olfactory papilla evident; from 35 mm ML, club-area has typical arrangement of suckers in 4 rows; AF: IV>>III>II>I from 20 mm ML, in smaller specimens arm III generally smaller than II or equal to I.

Type species: *Chiroteuthis veranyi* (Férussac, 1835)

Chiroteuthis mega (Joubin, 1933)

Figs. 2e-h; table 1

Chiropsis mega Joubin, 1933: 30-41, figs. 30-39.

Chiroteuthis capensis Voss: 1969: 76-79, pl. 4, figs. A-G; pl. 5, figs. A-G.

Material examined: 1 paralarvae, 22 mm ML, 1/Aug./92, No. 503-1, Sta. SB1, night-time, depth 00-212 m.

Type specimen: *Chiropsis mega* Joubin, 1933

Type locality: 25° 50' N; 76° 55'S, near The Bahamas.

Type depository: Zoological Museum of Copenhagen, Denmark.

Description: Mantle elongate and cylindrical; tail long, normally truncated; antero-dorsal margin of mantle strongly protruding; fins round and wide, 40% ML; AF IV>III>II>I; arm IV 100% ML; arm IV vesiculate and transparent, but others stiffer and opaque; brachial pillar vesiculate with central esophagus; head-neck ill-defined; lower part opaque and stiff, narrows just above funnel opening; upper part vesiculate, thick, and

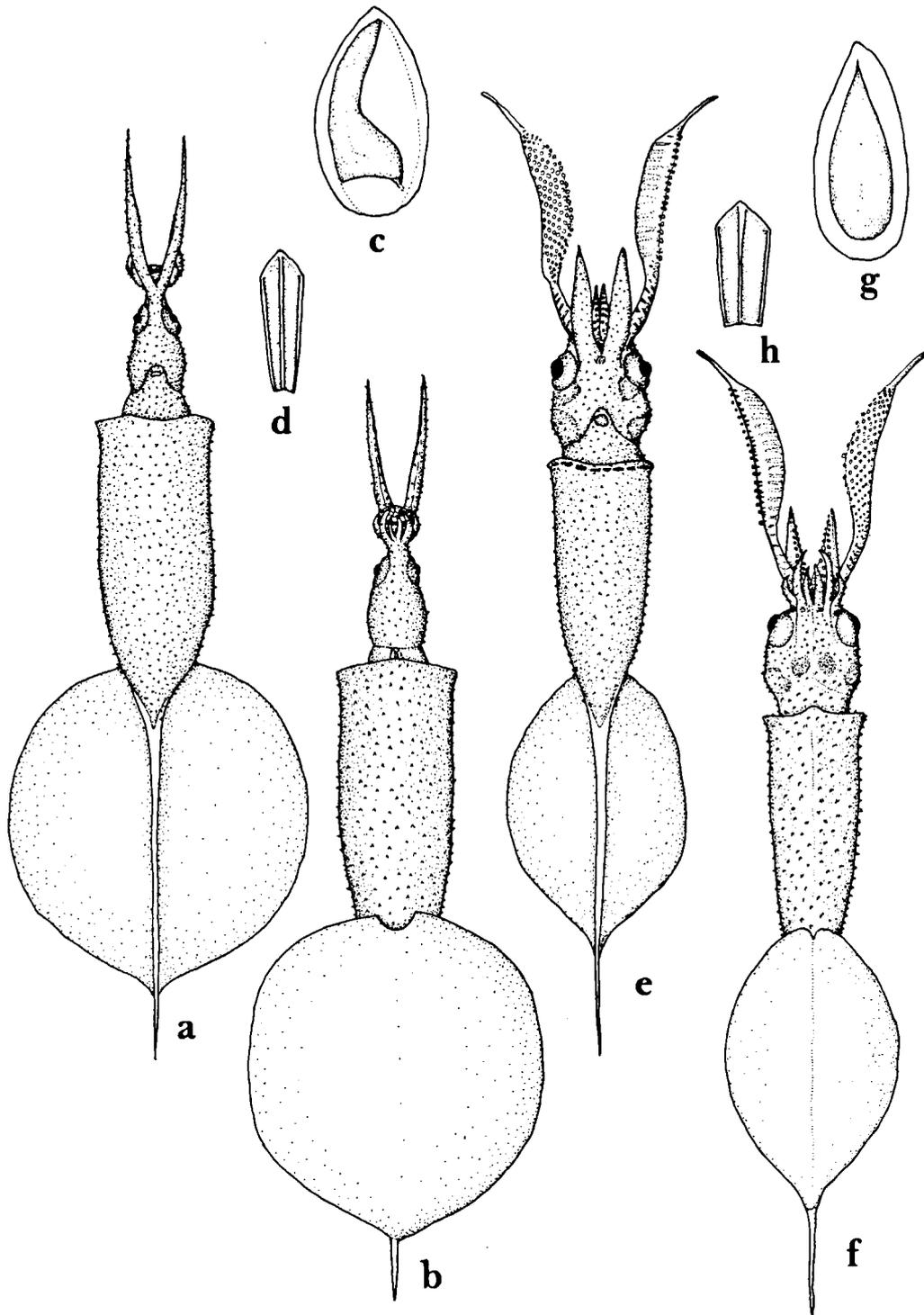


Fig. 3. Mastigoteuthid lineage. *Idiotheuthis danae* (Joubin, 1933), 30 mm ML, , a: ventral view, b: same specimen, dorsal view, c: funnel cartilage, d: nuchal cartilage; *Idiotheuthis tyroi* new spec., 15 mm ML, e: ventral view, f: same specimen, dorsal view, g: funnel cartilage, h: nuchal cartilage.

40% ML; eyes relatively small; funnel medium size, fused laterally and clearly differentiated from neck; nuchal cartilage slightly spatulate, length 3.5 times width; funnel cartilage small, tragus and antitragus well-developed; tentacular stalk truncated, but muscular and cylindrical; no evidence of photophores; chromatophores only observed on ventral side of fins, next to gladius; olfactory papillae not observed.

Remarks: The present specimen is assigned to *C. mega* because of its closely related funnel and nuchal cartilage morphology and large fins. The paralarva is characterized by the shorter brachial pillar and longer neck, and the relatively broad conus of the gladius, which immediately separates it from the other *Doratopsis* described (Pfeffer, 1912; Clarke, 1966; Young, 1991) and examined material (SAM, ZMC and ZMA).

Vecchione, et al. (1992) defined two chiroteuthid paralarval; the one from the Atlantic was related to *C. capensis* Voss. Because of the lack of measurements, indices and detailed illustrations of the specimen, comparison was not possible. However, the descriptions of both species (Vecchione's and the present paper's) coincided in most of their characters and should be related to the same species. On the other hand, Salcedo-Vargas (1996) organized the genus *Chiroteuthis* into two groups based on tentacular and general morphology. This characterization and a further examination of a collection of *C. capensis* Voss (9 specimens from 50-180 mm ML, South African Museum) by the author provided the clues to evaluate *Chiroopsis mega* Joubin, 1933 as the type species, after examination of the type specimen and considering *Chiroteuthis capensis* Voss, 1969 as the junior synonym by applying the rule of priority.

Family Mastigoteuthidae

Genus *Idioteuthis* Sasaki, 1916

Mastigoteuthis Chun, 1913: 6-7, pl. 2, fig. 1.

Idioteuthis Sasaki, 1916: 108, pl. 3.

Mastigoteuthis Sasaki, 1929: 310-314, text fig. 143, pl. 24, figs. 15-20.

Mastigoteuthis Adam, 1954: 159, pl. 2, fig. 1.

Mastigoteuthis Rancurel, 1973: 27-32, figs. 1-8.

Mastigopsis Nesis, 1987: 258, fig. 67 A-C.

Mastigoteuthis Roper & Sweeney, 1992: 175-176, fig. 211a-b.

Idioteuthis Salcedo-Vargas and Okutani, 1994: 124-125, figs.

1, 2, 5, 6.

Diagnosis: Mantle short to moderate, generally gelatinous; elongate and narrow in paralarval forms; fins large and wide, 50-95% of ML; tentacle whip-like with enlarged suckers in proximal part of club-area in some species, eyes small to very large, in *I. latipinna* one eye larger, usually left one; in some species single or pair of photophores on eye ball; photophore in eye sinus absent; arms never reach 100% of ML; AF: IV>II>III≥I; neck short; nuchal cartilage broad and short; tragus and antitragus poor to moderately developed or absent; tentacular suckers enlarged in proximal part and very small distally; round, wart-like cartilaginous tubercles with single spiny-like protuberance covers all body.

Type species: *Idioteuthis latipinna* Sasaki, 1916

Idioteuthis danae (Joubin, 1933)

Fig. 3a-d; table 2

Echinoteuthis danae Joubin, 1933: 13-20, text figs. 10-17;

Nesis, 1987: 258, fig. 67D-G; Roper & Sweeney, 1992: 177, fig. 212.

Material examined: 3 paralarvae, 22 and 15(2) mm ML, 1/Aug./92, No. 503-2, Sta. S1, night-time, depth 100-212 m; 1 paralarva, 30 mm ML, 22/July/92, No. 409-5, Sta. US2, night-time, depth 103-298 m.

Type specimen: *Echinoteuthis danae* Joubin, 1933.

Type locality: Tropical Atlantic.

Description: Mantle elongate, cylindrically shaped; conus long and thin; antero-dorsal margin of mantle straight; fins large and heart-shaped, 50-55% ML; AF IV>>II>III≥I; arm IV 30-36% ML, thin and stiff, suckers present proximally and apparently absent from middle to distal part; arms I to III very small in relation to arm IV, gelatinous and closer in size to each other, suckers similar size to those in arm IV; head small, ovoid in profile, triangular in ventral view, narrower than mantle width, neck short, clearly demarcated; nuchal cartilage short and slightly spatulate, 2 mm; eyes small and ovate; funnel large; funnel cartilage medium, tragus well-developed and antitragus not observed; no evidence of photophores; chromatophores not observed; tentacles lost; mantle, head and arms

Table 2. Measurements and indices. Abbreviations: DML: Dorsal Mantle length; MW: Mantle Width; FL: Fin Length; FW: Fin Width; ALI: Arm Length Index, I to IV; TL: Tentacle Length; CL: Club-area Length; HL: Head Length; HW: Head Width; ED: Eye Diameter; LnD: Lens Diameter. I: In all cases means Index; (*) in all cases means truncated or damaged; SAM: South African Museum; Albatross: original data from *Mastigoteuthis famelica* (Berry, 1909); Dana: original data from *Echinoteuthis danae* (Joubin, 1933). The figures in brackets are the real measurements in mm. Abbreviations after Roper and Voss, 1983.

| Sample # | N°. 485 | N°. 485 | N°. 485 | N°. 485 | SAM-78 | Albatross | Dana | N°. 409-5 |
|-------------------|-----------------|-----------------|-----------------|-----------------|---------------|-----------------|--------------|--------------|
| Species | <i>okutanii</i> | <i>okutanii</i> | <i>okutanii</i> | <i>okutanii</i> | <i>hjorti</i> | <i>famelica</i> | <i>danae</i> | <i>danae</i> |
| Sex | indef. | indef. | indef. | indef. | indef. | indef. | indef. | indef. |
| DML | 18 | 18 | 18 | 15 | 16 | 39 | 40 | 30 |
| MWI (MW) | 22.2 (4) | 22.2 (4) | 22.2 (4) | 26.6 (4) | 25.0 (4) | 10.2 (4) | 12.5 (5) | 18.3 (5.5) |
| FLI (FL) | 55.5 (10) | 52.7 (9.5) | 52.7 (9.5) | 66.6 (10) | 53.1 (8.5) | 53.8 (21) | 62.5 (25) | 50 (15) |
| FWI (FW) | 66.6 (12) | 61.1 (11) | 55.5 (10) | 66.6 (10) | 125 (20) | 37.1 (14.5) | 42.5 (17) | 46.6 (14) |
| ALI | | | | | | | | |
| II (I) | 22.2 (4) | 22.2 (4) | 22.2 (4) | 20.0 (3) | 31.2 (5) | 12.8 (5) | 7.5 (3) | 5.0 (1.5) |
| III (II) | 33.3 (6) | 33.3 (6) | 30.5 (5.5) | 26.4 (4) | 43.7 (7) | 16.6 (6.5) | 12.5 (5) | 6.6 (2.0) |
| III1 (III) | 22.2 (4) | 22.2 (4) | 22.2 (4) | 20.0 (3) | 34.3 (5.5) | 14.1 (5.5) | 10.0 (4) | 5.0 (1.5) |
| IV1 (IV) | 50.0 (9) | 50.0 (9) | (---) | 50.0 (7.5) | 50.0 (8) | 51.2 (20) | 35.0 (14) | 33.3 (10) |
| TLI (TL) | --- | --- | --- | --- | --- | --- | --- | --- |
| CLI (CL) | (---) | --- | --- | --- | --- | --- | --- | --- |
| HLI (HL) | 30.5 (5.5) | 30.5 (5.5) | 30.5 (5.5) | 30.0 (4.5) | 43.7 (7) | 12.8 (5) | 17.5 (7) | 15 (4.5) |
| HWI (HW) | 22.2 (4) | 22.2 (4) | 22.2 (4) | 23.3 (3.5) | 37.5 (6) | 10.2 (4) | 12.5 (5) | 6.6 (2.0) |
| ED / LnD | 2.5/1.5 | 2.0/1.5 | 2.0/1.5 | 1.5/1.0 | 3.5/2.0 | --- | --- | 1.0/0.5 |

Table 2. continued.

| Sample # | N°. 503-2 | N°. 503-2 | N°. 503-2 | N°. 503-2 |
|-------------------|--------------|--------------|--------------|--------------|
| Species | <i>danae</i> | <i>danae</i> | <i>danae</i> | <i>tyroi</i> |
| Sex | indef. | indef. | indef. | indef. |
| DML | 22 | 15 | 15 | 15 |
| MWI (MW) | 22.7 (5.0) | 20 (3.0) | 20 (3.0) | 23.3 (3.5) |
| FLI (FL) | 54.5 (12) | 60 (9.0) | 60 (9.0) | 53.3 (8.0) |
| FWI (FW) | 54.5 (12) | 60 (9.0) | 60 (9.0) | 80 (12) |
| ALI | | | | |
| II (I) | 3.6 (0.8) | 4.0 (0.6) | 4.0 (0.6) | 8.0 (1.2) |
| III (II) | 5.5 (1.2) | 6.6 (1.0) | 6.6 (1.0) | 12.0 (1.8) |
| III1 (III) | 3.6 (0.8) | 2.6 (0.4) | 36.0 (9) | 8.0 (1.2) |
| IV1 (IV) | 36.6 (8.0) | 30 (4.5) | 30 (4.5) | 16.6 (2.5) |
| TLI (TL) | --- | --- (12)* | --- (12)* | 40 (6.0) |
| CLI (CL) | --- | --- | --- | 23.3 (3.5) |
| HLI (HL) | 18.2 (4.0) | 16.6 (2.5) | 16.6 (2.5) | 23.3 (3.5) |
| HWI (HW) | 9.1 (2.0) | 10 (1.5) | 10 (1.5) | 16.6 (2.5) |
| ED / LnD | 1.0/0.5 | 0.7/0.4 | 0.7/0.4 | 1.3/0.8 |

completely covered by small, cartilaginous, transparent, tricuspid spiny-like tubercles.

Distribution: The range of distribution of *Idioteuthis danae* extends from the Tropical Atlantic to Southern Africa and the West Indian Ocean.

Remarks: These specimens can be distinguished from the other mastigoteuthid forms by the relatively small size of the head, the small and thin armature, and the large fins. The basic differences with other idioteuthid and mastigoteuthid species are the lack of photophores on the eye sinus and especially the consistency and size of the armature, particularly arm IV, which is stiffer and thinner than in other species described here.

The general morphology of this species fits the description of *Mastigoteuthis famelica* (Berry, 1909), as well as *Echinoteuthis danae* Joubin, 1933. Analysis of their morphometry (Table 2) and key taxonomic characters make it clear that the NIOP specimens resemble *E. danae* more than *M. famelica*. Joubin (1933) also indicated that his species was more closely related to *M. famelica* than to any other mastigoteuthid.

During the study of the mastigoteuthid forms from the Northwest Pacific (Salcedo-Vargas, 1993), several specimens labeled as *Mastigoteuthis* and resembling *E. danae* were examined. Further examination of the paralarvae of other species of mastigoteuthids of the same mantle length and from the same area, indeed indicate that Joubin's specimens are not *Mastigoteuthis* spp. according to its present characterization.

Young (1972) indicated that the elucidation of *M. famelica* from Hawaii depended on new materials, which he presented in a recent paper (Young, 1991). In his publication, he not only defined this species, but also offered the theory that the genus *Chiroteuthoides* was a synonym of *Mastigoteuthis* because of the underdeveloped arm III and the presence of skin tubercles. Nesis (1987), who also noted the skin tubercles in *M. famelica*, had made it the type specimen of the genus *Asperoteuthis* Nesis, but this was also corrected by Young (1991).

It is possible to conclude that, although the tentacle in the two nominal species of the former genus *Echinoteuthis* has not been properly described, the other taxonomic characters that typify these species are enough to transfer them from the *Mastigoteuthis* into the *Idioteuthis*.

***Idioteuthis tyroi* new spec.**

Figs. 3e-h; 6b-c; table 2

Material examined: Holotype, a paralarva, 15 mm ML, 1/Aug./92, No. 503, Sta. SI, night-time, depth 212 m.

Type locality: Coast of Somalia.

Type depository: Zoological Museum of Amsterdam (ZMA), University of Amsterdam.

Description: Mantle moderate to long, conically shaped anteriorly; tail long and thin, extends 20% of fin length; antero-dorsal margin of mantle slightly protruding; fins ovate antero-posteriorly, 55-60% ML; armature small; arms muscular but soft; AF IV>II>I≥III; arm IV 45% ML, with well-developed membrane on external side; head slightly swollen in "cheeks"; neck short and clearly demarcated; eyes medium; funnel medium to large; funnel cartilage large and simple, without clear evidence of tragus or antitragus; luminous tissue covers eyeballs ventrally; arm suckers slightly enlarged in arms III and IV, reducing in size gradually toward tip; tentacular arm short but strongly developed, stalk short and thicker than arm IV, 50% ML; club-area 70% TIL, flattened orally and covered in small suckers (47 rows, from 4 to 9 suckers transversally arranged on oral side), on aboral side striped with chromatophores which extend to base of stalk; dactylus-like extension, elongated and naked; large chromatophores on both sides of head and at base of armature; small chromatophores around edge of anterior end of mantle; no evidence of photophores or luminous organs; transparent, cartilaginous, spiny-like tricuspid tubercles cover body.

Etymology: The specific name *tyroi* is taken from the research vessel the *Tyro*, on which the expeditions were carried out, as an acknowledgement to the crew and the scientists who participated in the NIOP cruises.

Remarks: This single specimen can be related to *I. danae* mainly by the tentacle morphology, and also due to the presence of skin tubercles. The presence of the elongate tail, leaf-like fins, and the morphology of the funnel-mantle cartilages make it akin to the mastigoteuthid lineage, but not to the *Mastigoteuthis* species. In addition, because of the small size of arm IV and the lack

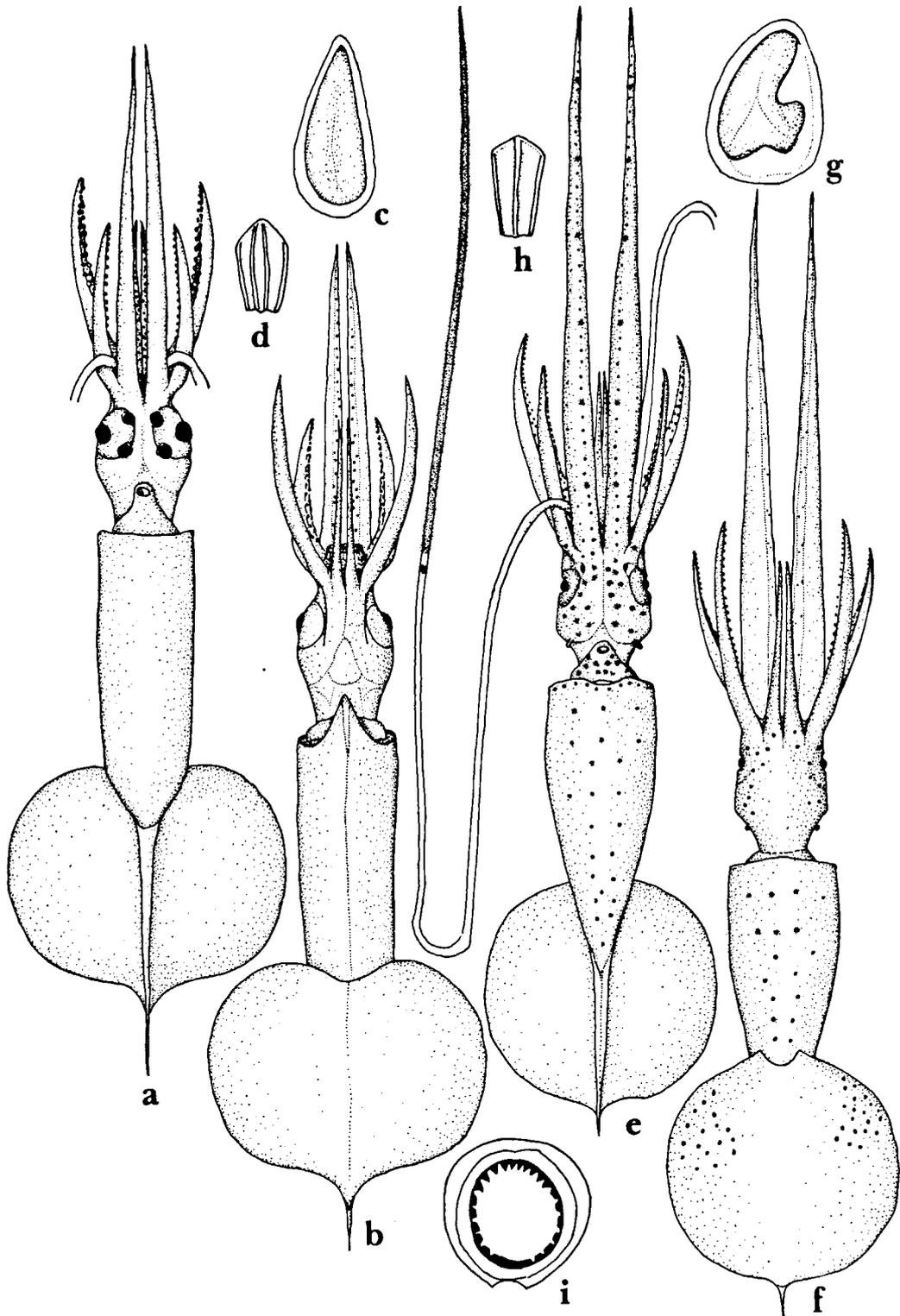


Fig. 4. Mastigoteuthid lineage. *Idoteuthis okutanii* new spec., 18 mm ML, a: ventral view, b: same specimen, dorsal view, c: funnel cartilage, d: nuchal cartilage; *Mastigoteuthis agassizii* Verrill, 1881, 44 mm ML, e: ventral view, f: same specimen, dorsal view, g: funnel cartilage, h: nuchal cartilage, i: proximal sucker arm III.

of photophores in the eyeball, this specimen is placed in the genus *Idioteuthis*. Therefore, taking into consideration the guidelines for taxonomic descriptions of cephalopods (Roper & Voss, 1983), this single specimen has enough unique morphological characters to be designated as a new species.

Idioteuthis okutanii new spec.

Figs. 4a-d; table 2

Material examined: Holotype, paralarvae, 20 mm ML, 29/July/92, No. 485, Sta. US1.5 (3), nighttime, depth 0-100 m. Paratypes: 4 specimens, 20(2), 16(2) mm ML, same date, same locality.

Type locality: Coast off Somalia.

Type depository: Zoological Museum of Amsterdam (ZMA) of the University of Amsterdam.

Description: Mantle long, cylindrically shaped; antero-dorsal margin of mantle wide and strongly protruding; fins strong, transversely oval, 40% ML; tail short; AF IV>II>III≥I; arm IV 60% ML, arm II slightly shorter than arm IV; armature large, very soft, gelatinous and vesiculated; suckers in all arms similar size until distal extremes; head outline rounded, neck clearly demarcated; eyes large; funnel medium; funnel cartilage large; tragus and antitragus not developed; two round, large, white photophores on ventral side of eye ball; no evidence of photophores on body; tentacular stalk truncated; cartilaginous tubercles wart-like and observed only around eyes; small chromatophores cover entire body and arms, mainly on ventral side.

Etymology: The specific name was chosen to honour Dr. Takashi Okutani former professor of the Tokyo University of Fisheries for his great contribution to the knowledge of the Phylum Mollusca, and for providing me with the opportunity to study his collections.

Remarks: The general morphology of the body, armature, AF, and the presence of skin tubercles place these squids in this genus, in spite of the truncated tentacular arms. But they can be primarily differentiated from the other species described here by the two photophores on the eyeball and the morphology of the funnel-mantle cartilages.

This species differs clearly from the type

species because of the fin length and the position of the eyeball photophores. In *I. okutanii* the mantle is longer, the fins just reach 50% ML, and the eyeball photophores are both placed ventrally. This species is related to some of the species of the genus *Mastigoteuthis* (this paper) by its general appearance, but can be differentiated by the lack of tragus and antitragus in the funnel cartilage. Another form that closely resembles *I. okutanii* is *Mastigoteuthis cf. hjorti* (Roper & Sweeney, 1992), but this differs due to having only a single photophore in the eyeball.

A reference specimen, 16 mm ML (Table 2) from the South African Museum identified as *M. hjorti* Chun, clearly differs from the NIOP specimens by its larger eyes, short tail, position of the eyeball photophores, mantle shape, and fin size. Therefore, the features that distinguish the NIOP specimens from their closely-related species are so unique as to deserve definition as a new species.

Genus *Mastigoteuthis* Verrill, 1881

Chiroteuthis Joubin, 1985: 38-46, figs. 1-6.

Mastigoteuthis Verrill, 1881: 100, pl. 1, fig. 1; pl. 2, fig. 2, 3; Chun, 1910: 174-176, 181-183, pl. 33, figs. 3, 4; pl. 35, figs. 3, 4, 7, 9; pl. 36, figs. 1, 2; pl. 37, figs. 2-4; Pfeffer, 1912: 615-620; Dilly, Nixon and Young, 1977: 527-599, pl. 1-16; Nesis, 1987: 249-252, fig. 66; Salcedo-Vargas and Okutani, 1994: 119-120, figs. 2, 3.

Diagnosis: Mantle cylindrical, tapering gradually after reaching anterior part of fin insertion; fins round or heart-shaped, 40-55% ML; tail short; arms long, AF:IV>>II>III≥I; arm IV longest, attains 100%ML from 25 mm ML; single photophore embedded in eye sinus; funnel cartilage ovate with tragus and antitragus; arm suckers small with sharp teeth mainly located in distal margin; tentacle long and narrow, longer than mantle length; whip-shaped, small suckers in 6 to 18 rows transversely arranged covering oral and aboral sides from distal to medial part of club-area; suckers covering 60% of stalk; in adult stages develop cushions in tentacular suckers.

Type species: *Mastigoteuthis agassizii* Verrill, 1881.

Type locality: East Coast of the U.S.A., "Blake Expedition", Summer 1880, Sta. 325, 33°35'N, 76°W, 674 path.; Sta. 328, 34°28'N, 75°22'W, 1632 path.

Type depository: Museum of Comparative Zoology, Harvard College, U.S.A.

Mastigoteuthis grimaldii (Joubin, 1895)

Figs. 4e-i; 6d-e; table 1

Chiroteuthis grimaldii Joubin, 1895: 38-46, figs. 1-6.

Chiroteuthopsis grimaldii Fisher and Joubin, 1906: 345-347, figs. 5-8

Mastigoteuthis grimaldii Rancurel, 1971: 125-145, figs. 1-11.

Material examined: 1 immature female, 44 mm ML, 16/I/93, No. 718, Sta. SB2, daytime, depth 940-1560 m.

Type specimen: *Chiroteuthis grimaldii* Joubin, 1895.

Type locality: Tropical Atlantic.

Description: Mantle short, conically shaped; antero-dorsal margin of mantle slightly protruding; fins nearly circular, FL-FW: 56-50% ML; AF: IV>II>III≥I; arm IV 100-140% ML; head squarish, neck clearly demarcated; nuchal cartilage wide, slightly spatulate, length (5.5mm) is 2.5 times width; eyes relatively small, 5 mm diameter; funnel medium; funnel cartilage large, 3.5 mm, tragus poorly developed in upper part and antitragus poorly developed, forming deep cavity; small single photophore embedded in integument next to eye sinus, 0.25 mm; series of photophores alternating 5 small and one larger along ventral side of arm IV; small white photophores on ventral and dorsal sides of head, funnel and mantle, mainly distributed on central parts and on proximal margin of mantle; tentacular stalk narrower than arm I, whip-shaped, 2.5 times ML, club-area 40% TIL, covered in rows of small suckers (from 4 to 18 rows arranged transversally); arm suckers not enlarged and decreasing in size distally, smallest on arm IV, with 18-26 small teeth: 14-16 sharp in distal margin and 4-10 crenelate in lateral and proximal margins; proximal teeth fuse to form smooth margin in later stages; body covered in small dark brown chromatophores.

Distribution: The *Mastigoteuthis grimaldii*, according to the present data is incorporated as one of the Indo and Northwest Pacific species.

Remarks: The paralarvae and juveniles of this species can be recognized by the squarish shape of the head, the poorly developed antitragus and

the weak tragus, the small size of the eyes and eye sinus photophore, the arrangement of photophores on the ventral side of arm IV, and by the tentacle shape and number of sucker rows.

About 70 specimens from the Northwest Pacific (Salcedo-Vargas, 1993) and 35 specimens from the South African Museum from 18 to 145 mm ML were examined. Sexually mature female specimens have been observed at 90 mm ML, suggesting that this is a medium-sized species. The smallest specimens observed from the Northwest Pacific collection ranged from 18-22 mm ML. Except for an increase in the number of photophores in the arms, head and mantle, no metamorphic changes in later stages were apparent in the forms or in the tentacles. These observations proved that the tentacular stalks of *Mastigoteuthis* Verrill do not go through a metamorphosis, at least after 18 mm ML, as those of the chiroteuthids or other members of the mastigoteuthid lineage probably do.

The NIOP specimen as well as the Northwest Pacific and Southern African ones with their respective ontogenetic variations were identified as members of this species. Small morphological variations have been observed due to growth stage, maturity, and in many cases artifacts of preservation. The usually shrunken or loose mantle may indicate a wide variation in its ML-MW, ML-FL and ML-FW ratios, since the ML is taken as a base for calculating the indices. Another key character easily modified by handling and preservation is the funnel cartilage, which may cause the tragus to appear either absent or well-developed. Variations in some indices among populations around the world can certainly be observed, however the diagnostic features of other *Mastigoteuthis* spp. indicate that *M. flammea* is the junior synonym of *M. grimaldii*, and *M. schmidti* of *M. agassizii*.

Mastigoteuthis glaukopsis Chun, 1910

Figs. 5a-j; table 1

Mastigoteuthis glaukopsis Chun, 1910:184-185, pl. 33, figs. 1, 2; pl. 34, figs. 2, 15, 16; pl. 37, fig. 1.

Material examined: 1 juvenile, 47 mm ML, No. 984, Sta. S1; 3 juveniles, 30(3) mm ML, No. 882,

Sta. US2; 1 juvenile damaged, No. 806, Sta. US1; 1 juvenile 25 mm ML, No. 842, Sta. US2.
Type specimen: *Mastigoteuthis glaukopsis* Chun, 1910
Type locality: Indian Ocean.
Type depository: Berlin Museum of Zoology, Germany.

Description: Mantle elongate, slightly conical in shape; antero-dorsal margin of mantle moderately protruding; fins oval to round, FW-FL: 57-61%ML; AF IV>II>III≥I; arm IV 95% ML; head ovate, slightly narrower than mantle opening, neck clearly demarcated; nuchal cartilage spatulate, length (5.5 mm) 3 times width; eyes large, 10 mm; funnel medium size; funnel cartilage medium, 3 mm; tragus strong in upper part of the cavity and low, poorly developed antitragus, inside cavity; large single photophore embedded in integument next to eye sinus, 1.7 mm; tentacular stalk narrow, whip-shaped (truncated in these specimens); suckers in all arms medium but not enlarged, do not decrease gradually in size distally; suckers in all arms similar size, with 12-16 large teeth, of which 12 sharp in distal margin and 4 crenelate in lateral margin; proximal margin smooth; single row of small chromatophores along gladius on dorsal side up to anterior fin-mantle insertion; small specimens differ from larger ones only by shape of mantle and size of buccal mass.

Specimens from 25-30 mm ML: Mantle elongate, slightly conical; FW: 48-72% ML, arm IV 80-100%ML; middle and distal arm suckers have 22-24 teeth in all margins; in proximal suckers teeth from proximal margin fused, lateral margin teeth (4-8) became crenelate and distal margin teeth (8-12) remain sharp.

Remarks: The larger size of the eyes and eye sinus photophore and the well-developed and strong tragus distinguish this species from other nominal species of the genus *Mastigoteuthis*. Small photophores embedded on the epidermis are observed, but are easily rubbed off by handling and preservation.

At present, the members of this group can be characterized as: *M. glaukopsis* for the Indo-Pacific, typified by its large eyes, moderate eye sinus photophore and strong tragus; *M. atlantica* for the Central and South Atlantic, characterized by its large eyes, very large eye sinus photophore

and strong tragus; and *M. pyrodes* for Eastern and Northwestern Pacific, identified by large eyes, small eye sinus photophore and small antitragus.

M. iselini and *M. pschychrophila* have been poorly studied and need more data to be re-evaluated.

DISCUSSION

Two *Doratopsis* forms are included in this paper. The *Planktoteuthis* sp. is closely related to *P. danae* (Joubin, 1931), however, the lack of growth series and the few available specimens of this species from the sampled area limits its identification. The *Chiroteuthis mega* (Joubin, 1933) is defined here as the senior synonym of *C. capensis* Voss, 1969. The paralarva fits the definition of *C. mega* more than in any other *Doratopsis* diagnosis. The taxonomic arrangement of the *Chiroteuthis* spp. was published in an earlier paper by the author (Salcedo-Vargas, 1996). The type specimen of *C. mega* was only examined after the publication of that paper.

From the definition of the genus *Mastigoteuthis* (Verrill, 1881) to the most recent paper by Young (1991), all the species with whip-like or similarly shaped tentacles were included in this genus. Sasaki (1916) defined the genus *Idioteuthis*, but he synonymized it with *Mastigoteuthis* in 1929 in spite of the evident differences of *Idioteuthis latipinna* with other mastigoteuthids. It is assumed that the morphology of the tentacle is the character that unifies all the nominal species in the genus. However, there are other characters that can lead to a subdivision within the family and reflect a better arrangement. In an attempt to review the family, Young (1991) suggested that the skin tubercles might differentiate two lineages. Salcedo-Vargas & Okutani (1994), in their reorganization of the mastigoteuthids, revived the *Idioteuthis* Sasaki and named four subgenera. They mistakenly placed the *Echinoteuthis* as subgenus in *Mastigoteuthis* and synonymized some valid species.

Information gathered from the present study and the examination of type specimens (*M. atlantica*, *M. pyrodes*, *M. schmidtii* and *I. latipinna*), in addition to the examination of the collections of the SAM, ZMC, ZMA, NHML and ZMB, indicate that the species with skin tubercles may

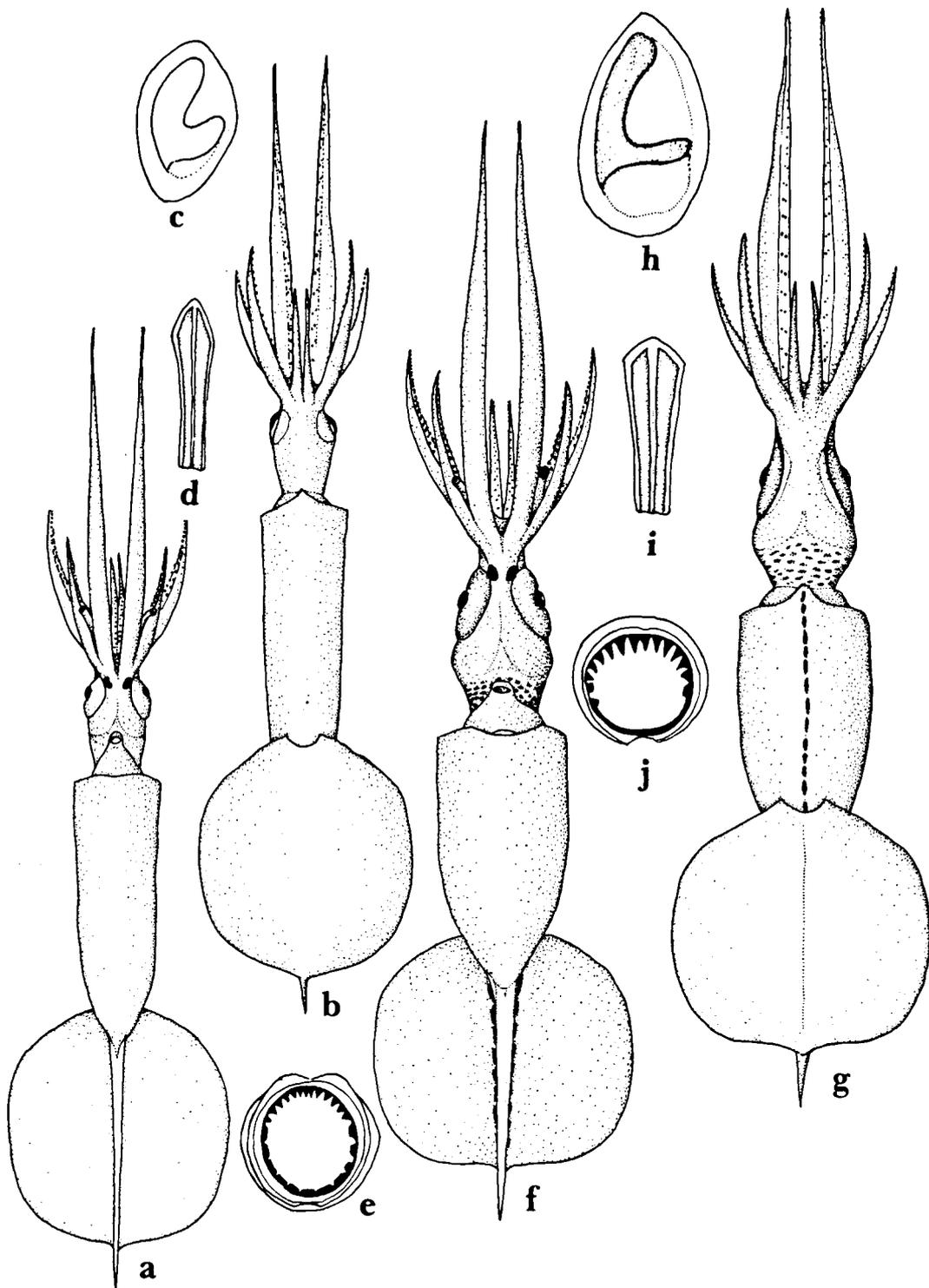


Fig. 5. Mastigoteuthid lineage. *Mastigoteuthid glaukopis* Chun, 1910, a: 30 mm ML ventral view, b: same specimen, dorsal view, c: funnel cartilage, d: nuchal cartilage, e: proximal sucker arm III, f: 47 mm ML, g: ventral view, h: dorsal view, i: funnel cartilage, j: nuchal cartilage, k: proximal sucker arm III.

indeed form a different lineage that can also be characterized by the presence of eyeball photophores and the absence of an eye sinus photophore.

On the other hand, it was thought that small mastigoteuthids have an under-developed arm III (Berry, 1909, 1920), and this was confirmed by Young (1991) after having observed small specimens and having compared them with the paralarvae of chiroteuthids. Arm III of chiroteuthids, which is underdeveloped in early stages, grows larger than arm II in juvenile stages. However, in mastigoteuthids arm III is smaller than arm II and sometimes equal to arm I, and this remains so throughout the life cycle. This is a typical feature of mastigoteuthids, which is probably of more use for phylogenetic studies than for taxonomic purposes.

The present findings agree with the data from Hawaii (Berry, 1909, 1920; Young, 1991) in indicating that all the properly characterized species of the family Mastigoteuthidae have a less-developed arm III, but differ by keeping them as members of the genus *Mastigoteuthis*.

Rather than being characterized by a common paralarval form, the mastigoteuthis lineage as outlined in the present paper is recognized by common set of characters such as: 1) short neck and brachial pillar; 2) whip-like tentacle; 3) ovate pseudoconus in cross section view and 4) AF: $IV > II > III \geq I$, and includes the genera *Mastigoteuthis* and *Idioteuthis*.

SUMMARY OF TAXONOMY

Organizing mastigoteuthid forms into two genera clarifies the presence of two lineages based on the presence and absence of photophores and skin tubercles. However, the subgeneric division (Salcedo-Vargas and Okutani, 1994) does not agree with the present findings, and limits a better array of species. Thus, instead of subgenera, each genus was divided into three groups, basically organized by similarities and differences. Further cladistic analysis will help to offer a proper subgeneric arrangement of the present seventeen members of the Mastigoteuthidae.

The genus *Idioteuthis* Sasaki, is divided into three groups. The first group characterized by the lack of paired eyeball photophores and with single

cusped wart-like skin tubercles, consists of two species, *I. latipinna* Sasaki, 1916, and *I. cordiformis* (Chun, 1908). The second group, with two photophores on the eyeball, and also by single cusped dermal tubercles, includes *Idioteuthis hjorti* (Chun, 1913), and the new species, *I. okutanii*. The third group bears tricuspid or more spiny tubercles and lacks photophores in the eyeball and includes *I. famelica* Berry, 1912 (former *Mastigoteuthis famelica*), *I. danae* (Joubin, 1933) (former *Echinoteuthis danae*), and the other new species, *I. tyroi*.

The genus *Mastigoteuthis* Verrill also forms three groups. The first group is characterized by the large fins, enlarged arm suckers, very small tentacle suckers and bottle-like cavity of the funnel cartilage. The eye sinus and eyeball photophores have not yet been observed. It consists of two closely related species: *Mastigoteuthis magna* Joubin, 1913 and *Mastigoteuthis inermis* Rancurel, 1972. The second group can be recognized by the small eye sinus photophore and poorly developed tubercles in the funnel cartilage, and consists of *Mastigoteuthis agassizii* Verrill, 1881, *Mastigoteuthis grimaldii* Joubin, 1895, *Mastigoteuthis pyrodes* Young, 1972 and the poorly studied *Mastigoteuthis dentata* Hoyle, 1904. The third and last group can be defined by the large eye sinus photophore, the strongly developed tragus, and large eyes. The species included in this third group are *Mastigoteuthis atlantica* (Joubin, 1933) and *Mastigoteuthis glaukopis* Chun, 1910. Other species such as *M. iselini* Clench and Mac Donald, 1934 and *M. psychrophila* Nesis, 1977, are included in this group because of their funnel cartilage morphology, but need to be properly characterized.

Comparison of the taxonomic systems of the Mastigoteuthidae, as set out by Salcedo-Vargas and Okutani (1994), with the present study are shown in Fig. 7.

ACKNOWLEDGMENTS

The anonymous reviewers are acknowledged for their comments and suggestions on ways to improve this manuscript. I also thanks to M. Roeleveld (South African Museum), Mr. Tom Schiøtte (Zoological Museum of Copenhagen) and Dr. Fred Naggs (Natural History Museum,

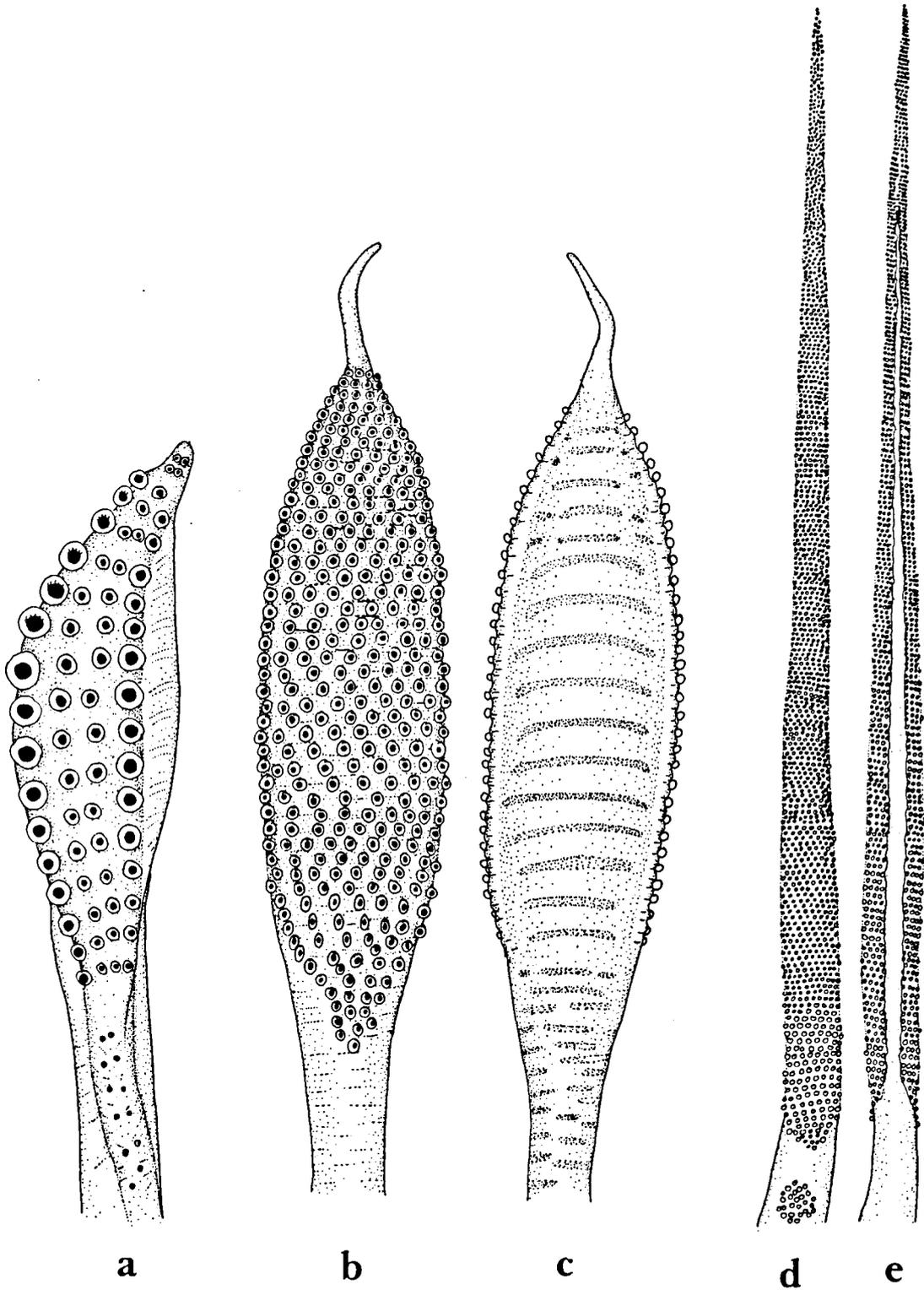


Fig. 6. Tentacles. a: *Planktoteuthis* sp. A, oral view. Club length 3.5 mm; b: *Idioteuthis tyroi* new spec., oral view, c: aboral view. Club length 3.5 mm; d: *Mastigoteuthis agassizii* Verrill, 1881, oral view, e: aboral view. Club length 80 mm.

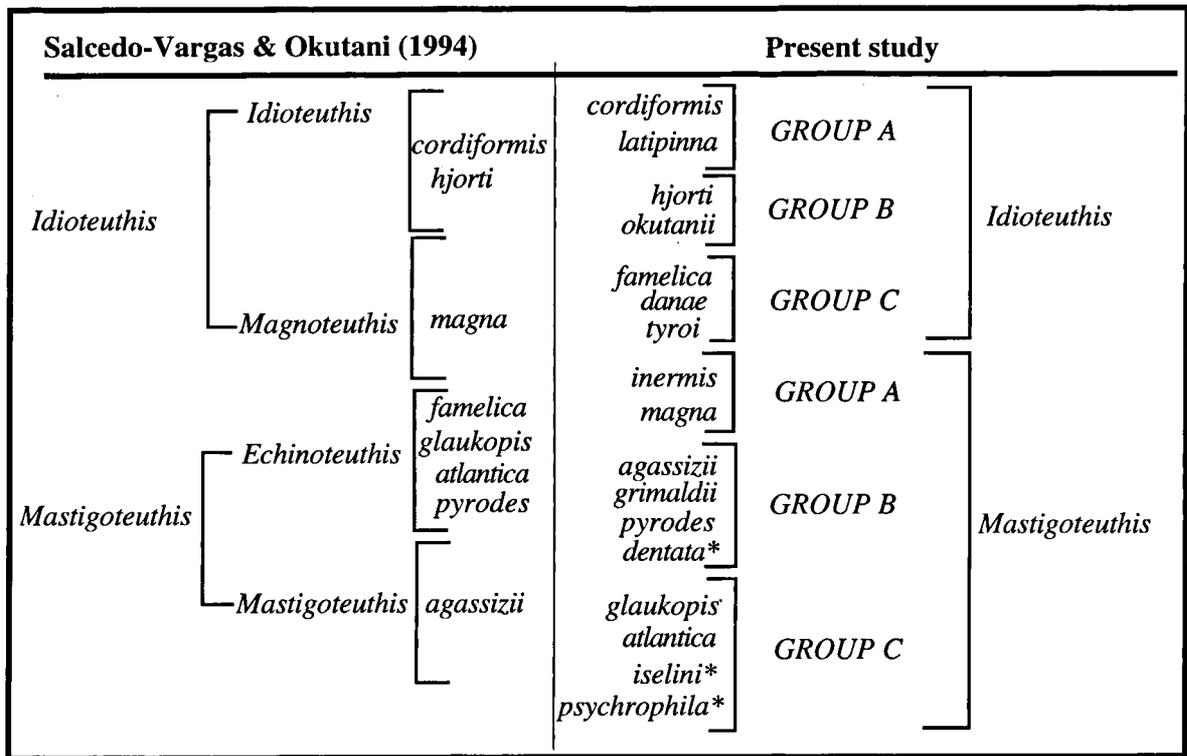


Fig. 7. Comparison of the taxonomic systems of the Mastigoteuthidae, as set out by Salcedo-Vargas and Okutani (1994), with the present study. (*) Species to be re-evaluated.

London) for the loan of the reference material. Dr. Richard E. Young (University of Hawaii) offered fruitful and opportune advices, which were highly appreciated. Special acknowledgment to Ms. N. Baird, M.A. for the corrections of the English language.

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Received: February 7, 1997.