

Taxonomy and Zoogeography of the Family Onychoteuthidae (Cephalopoda: Oegopsida)

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ABSTRACT

The Oegopsida family Onychoteuthidae contains five genera, namely, *Onychoteuthis*, *Ancistroteuthis*, *Onykia*, *Moroteuthis*, and *Kondakovia*. The genus *Chaunoteuthis* is considered to represent spent individuals of the other genera of the family. The present study clarified that two well-known nominal species, *Onychoteuthis banksii* (Leach, 1817) and *Ancistroteuthis lichtensteinii* (Férussac and Orbigny, 1839), both represent species complexes in their broad distributional ranges. The genus *Onykia* may represent immature stages of other onychoteuthids. *Moroteuthis robsoni* Adam, 1962, which has hitherto been considered to be a Southern Ocean species, appears to extend its distribution into the warm Atlantic region. Reliable taxonomic records as well as knowledge of distributional differentiation by growth stage are still too scarce to draw a zoogeographical picture of each species in this family.

Introduction

Among the Oegopsida families, Onychoteuthidae is moderately diverse. Some members of this family attain a gigantic size surpassed only by *Mesonychoteuthis* (family Cranchiidae) and by members of the family Architeuthidae. The full life history and the distribution of most species have not been described, but some species, such as certain species of *Onychoteuthis*, are known to spend an epipelagic life from

paralarval to adult stages. *Moroteuthis* species are usually found in the midlayers of cold seas in both the northern and southern hemispheres and contribute a considerable proportion to the sperm whale's diet.

The conventional taxonomic list usually contains six genera, namely, *Onychoteuthis*, *Ancistroteuthis*, *Chaunoteuthis*, *Onykia*, *Moroteuthis*, and *Kondakovia*. Our careful observations on *Chaunoteuthis* during the workshop led us to the conclusion that this genus represents a spent stage or unhealthy condition of multiple species in the family. Some doubt exists as to the validity of the genus *Onykia* as well (Tsuchiya and Okutani, 1992).

The present study was a cooperative undertaking, but Kubodera and Okutani particularly concentrated on the genera *Onychoteuthis*, *Ancistroteuthis*, and *Onykia*, whereas Piatkowski and Clarke concentrated on the genera *Moroteuthis* and *Kondakovia*. The opinions of every author were coordinated by the workshop group leader (TO).

ABBREVIATIONS.—The following abbreviations are used in the text: AL, arm length; DML, dorsal mantle length; FL, fin length; FW, fin width; GL, gladius length; ML, mantle length; MW, mantle width; VLI, ventral length index of gladius rostrum.

Systematics

Family ONYCHOTEUTHIDAE Gray, 1849

DIAGNOSIS.—Mantle cylindrical, muscular, tapering posteriorly to pointed end. Fins posteriorly situated, large, sagittate or transversely oval. Funnel cartilage straight and simple. Neck often with crowded nuchal folds dorsally. Arm suckers biserial, with smooth rings. Tentacle club with 2 rows of strong hooks (with or without marginal suckers) on manus and with well-defined, discoidal fixing apparatus on carpus. Hectocotylization absent. Female with nidamental glands and male with "penis." One genus (*Onychoteuthis*) with subocular and

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intestinal photophores. Buccal connectives 7, attached to ventral side of arms IV. Gladius with strongly ridged rachis, rather broadly lanceolate vanes, and solidified posterior tip or cartilaginous rostrum.

TYPE GENUS.—*Onychoteuthis* Lichtenstein, 1818:1591.

DISCUSSION.—Gray (1849) established this family to comprise the genera *Enoploteuthis*, *Ancistrocheirus*, *Abralia*, *Octopodoteuthis*, *Acanthoteuthis*, *Ancistroteuthis*, *Onychia*, and *Ommastrephes*. Thiele (1935) retained the genera *Tetronychoteuthis*, *Onychia* (= *Steenstrupiola*), *Onychoteuthis* (= *Teleonychoteuthis*), *Chaunoteuthis*, *Ancistroteuthis*, *Moro-teuthis*, and *Mesonychoteuthis*. Roper et al. (1969) and Voss (1977), among others, placed *Tetronychoteuthis* in the family Lepidoteuthidae and placed *Mesonychoteuthis* in the family Cranchiidae. In 1972 Filippova added the genus *Kondakovia*, typified by *K. longimana* Filippova, 1972; however, the generic status of this genus is uncertain (see "Discussion," under *Kondakovia longimana*).

Among the remaining five genera, *Chaunoteuthis* has been considered to represent spent individuals of *Onychoteuthis* (Adam, 1972). We are inclined to think that all specimens of *Chaunoteuthis* hitherto reported (such as Appellöf, 1891; Pfeffer, 1912; Naef, 1923; Nesis, 1970; Okutani and Ida, 1986) represent unhealthy or spent and deteriorating individuals of other onychoteuthid genera. Therefore, we suggest that all species of onychoteuthids may reach a terminal, so-called "*Chaunoteuthis*-stage." Thus, we do not consider this genus to be valid.

The family Onychoteuthidae is generally thought to be close to the family Enoploteuthidae, mainly because of the similarity of tentacular armature.

Onychoteuthis Lichtenstein, 1818

DIAGNOSIS.—Mantle muscular, cylindrical, tapering posteriorly to pointed rostrum. Gladius visible along median line of dorsal mantle. Nuchal folds prominent. Tentacle with 2 rows of strong hooks, without marginal suckers on manus in adult. Two photophores present, 1 on anterior end and 1 on posterior end of intestine. Oval photogenic patch present on ventral periphery of eyeball.

TYPE SPECIES.—*Onychoteuthis bergii* Lichtenstein, 1818:1592, no. 4, pl. 19: fig. a.

DISCUSSION.—This genus was established by Lichtenstein for the hook-bearing *Loligo*. His *O. bergii* was synonymized with *O. banksii* Leach, 1817, by Gray (1849). Since then, this genus has been maintained by subsequent authors.

Onychoteuthis banksii (Leach, 1817)

FIGURE 3

DIAGNOSIS.—Mantle robust, muscular. Fins rhomboidal, length 55%–65% ML, width 65%–78% ML, apical angle 70°–90°. Nuchal folds 9 or 10 pairs. Arm formula

II = III = IV > I, length 35%–45% ML. Tentacle club slightly expanded, length 25%–35% ML, 13–15 small suckers on dactylus, 20–22 hooks on manus in 2 rows, well-defined fixing apparatus with 8–10 suckers and 7–9 pads. Large luminous patch on ventral periphery of each eye. Two large, round, bulbous light organs in ventral mantle cavity, 1 on ink duct behind anal papilla, 1 on ink sac, latter twice as large as former. Medium-sized species maturing at about 150–200 mm ML.

ORIGINAL DESCRIPTION.—Leach, 1817:141.

TYPE LOCALITY.—Gulf of Guinea, west coast of Africa (cf. Leach, 1818:395).

DEPOSITION OF TYPE.—*Holotype*: Natural History Museum, London, England; not available in the workshop.

Paratypes: None.

DISTRIBUTION.—World-wide in tropical and subtropical oceanic waters.

DISCUSSION.—This species is separable from other members of *Onychoteuthis* by having a slender, muscular body, rhomboidal fins with 70°–90° apical angle, 20–22 hooks on the tentacle club, and two large, round visceral photophores. This species has been recorded from the tropical and subtropical waters of all oceans (see Clarke, 1966; Okutani, 1980). In the workshop, several specimens from the Pacific, the Atlantic, and the Mediterranean Sea were examined. Tentacle-club length was observed to vary from less than 20% to over 40% of ML in individuals of nearly the same size. At the extremes, individuals looked quite different; however, numerous intermediate specimens filled the gap and made their demarcation indefinite. We tentatively separated specimens into three groups, i.e., the small-club group having clubs smaller than 25% ML, the intermediate-club group having clubs of 25%–35% ML, and the large-club group having clubs larger than 36% ML.

Geographically, the small- and intermediate-club groups appear broadly in the Pacific, the Atlantic, and the Mediterranean Sea. Young (1972) noted that he recognized two separate groups of *O. banksii* from Florida waters. These might correlate with the present two different club-size groups. On the other hand, the large-club group is known only in the western equatorial Pacific and in the waters off the Hawaiian Islands. Young and Harman (1987) reported that *O. banksii* in Hawaiian waters represented a species complex, judging from the different chromatophore patterns in the early life stages. The present large-club group might be one of the species complexes they mentioned, and it seems to be a western equatorial Pacific endemic. The lack of serial specimens from the larvae to the adult and no information about distribution in the Indian Ocean, however, has prevented us from resolving the species-complex problems of "*O. banksii*."

There has been some confusion on the spelling of the species name, "*banksi*" or "*banksii*." Following the International Code of Zoological Nomenclature (ICZN) and the opinion of F.M.

Bayer, of the Smithsonian Institution and member of the International Commission on Zoological Nomenclature (pers. comm., 1988), the original "ii" ending is considered correct.

***Onychoteuthis borealijaponica* Okada, 1927**

FIGURE 2

DIAGNOSIS.—Mantle muscular but rather thin. Fins rhomboidal, length 55%–60% ML, width 65%–75% ML, apical angle 80°–90°. Nuchal folds 8 or 9 pairs. Arm formula II = III = IV > I, length 35%–45% ML. Tentacle club slightly expanded, length 20%–30% ML, 13–15 small suckers on dactylus, 25–27 hooks on manus in 2 rows, well-defined fixing apparatus with 8–10 suckers and 7–9 pads. Large luminous patch on ventral periphery of each eye. Two oval light organs in ventral mantle cavity, 1 on ink duct behind anal papilla, 1 on ink sac, with intervening silver, iridescent band; former much smaller than latter. Large species maturing at about 250 mm ML in males and about 300–350 mm ML in females.

ORIGINAL DESCRIPTION.—Okada, 1927:4.

TYPE LOCALITY.—Japan.

DEPOSITION OF TYPE.—*Holotype*: Not known.

Paratypes: None.

DISTRIBUTION.—Far northern Pacific, migrating from south to subarctic waters for feeding during summer and returning to subtropical waters for spawning in fall and winter (Naito et al., 1977; Kubodera et al., 1983; Murata et al., 1986).

DISCUSSION.—Okada (1927) described the new species *O. borealijaponica*, from Japanese waters, based on small differences in external appearance and the visceral photophores, and it had long since been considered a synonym of *O. banksii*. In 1972, Young examined onychoteuthids from the seas off southern California and revived the name *O. borealijaponica* with detailed descriptions. He compared *O. borealijaponica* with so-called "*O. banksii*" from off Florida and clarified the differences between them.

This species is very close to *O. banksii*, but it distinctly differs by having smaller tentacle clubs with a larger number of hooks on the manus, two oval visceral photophores, of which the anterior one is much smaller than the posterior one, and a relatively broad mantle with a thin wall. The size at maturity also indicates that this species grows much larger than *O. banksii*. The distribution of *O. borealijaponica* is restricted to the far northern Pacific, and this species favors much cooler waters than does *O. banksii*.

***Onychoteuthis compacta* (Berry, 1913)**

FIGURE 5

DIAGNOSIS.—Mantle nearly cylindrical, ending posteriorly in acute point. Fins enormous, broadly sagittate, length little more than 50% ML, width equal to ML, apical angle 135°.

Arms short, stout, arm formula III > II > IV > I, length 21%–28% ML. Arm suckers in 2 widely spaced rows. Tentacles little longer than arms. Tentacle club not expanded but with well-developed aboral keel and 4 longitudinal rows of armatures, dorsal 2 rows and ventral marginal row being suckers. Only median ventral row with hooks, 10 or 11 in number, proximal 5 hooks small, next 3 hooks much larger, distal 2 or 3 hooks diminishing again in size. Suckers in dorsal 2 rows 16–18, proximal 5 pairs closely set, next 3 pairs widely placed, slightly larger, suckers becoming smaller again distally. Suckers in ventral row exceedingly minute, especially distally, placed very far apart. Suckers on dactylus minute. Well-defined fixing apparatus with 12 suckers and 8 pads. Ocular and visceral photophores present. Animal small (based on juvenile).

ORIGINAL DESCRIPTION.—Berry, 1913:565. (See also Berry, 1914:324–325, fig. 32, pl. LII: figs. 4, 5.)

TYPE LOCALITY.—From RV *Albatross* sta 3989, vicinity of the island of Kauai, Hawaii.

DEPOSITION OF TYPE.—*Holotype*: USNM 214381 (SSB 238); National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; in very poor condition, no detail can be determined.

Paratypes: None.

DISTRIBUTION.—Hawaiian waters.

DISCUSSION.—Berry described *Teleoteuthis (Onychoteuthis) compacta* from Hawaiian waters in 1913, and since then this species has mostly been ignored. In 1978 Young revived the name of *O. compacta* for the species occurring in Hawaiian waters and discussed the relationships between vertical distribution and photosensitive vesicles, but he did not give any systematic characters. Young and Harman (1987) also examined onychoteuthid paralarvae caught in Hawaiian waters and classified them into three sympatric species, *O. compacta*, *O. sp. B*, and *O. sp. C*, primarily on the basis of chromatophore patterns. The latter two species were considered to be paralarvae belonging to an *O. banksii* species complex.

This species is characterized in the original description by having large, broad fins, widely spaced arm-sucker rows, and unique arrangements of suckers and hooks on the tentacle clubs. Paralarvae of *O. compacta* larger than 2.0 mm gladius length can be identified by having a few chromatophores arranged in a complex band that is located farther posteriorly on the ventral mantle belly than it is in other species (Young and Harman, 1987).

Due to the serious damage to the holotype, no important systematic characters could be observed during the workshop. Berry (1913, 1914) described *O. compacta* based on a small specimen, about 21 mm ML. Since then, no available description of this species has been made. Judging from the tentacle-club structures and the body size, the holotype seems to be juvenile and has not developed all of the systematic characters. Detailed descriptions of larger specimens and of mature specimens of this species are badly needed.

***Onychoteuthis meridiopacifica* Rancurel and Okutani, 1990**

FIGURE 4

DIAGNOSIS.—Mantle muscular, elongate-cylindrical. Fins widely rhomboidal, length 40%–50% ML, width 70%–90% ML, apical angle 120°–140°. Nuchal folds 8–12 pairs. Arm formula III > IV > II > I, length 30%–40% ML. Tentacle club slightly expanded, length 20%–25% ML, 10–12 small suckers on dactylus, 16–19 hooks on manus in 2 rows, 3 or 4 small globular suckers on dorsal proximal margin, 1 or 2 small suckers on ventral proximal margin, fixing apparatus with 6–8 suckers and 6 pads. Two very small, oval light organs in ventral mantle cavity, 1 on ink duct behind anal papilla, 1 on ink sac; latter 1.6 times larger than former but never exceeding rectum width. Small species maturing at about 60 mm ML in males.

ORIGINAL DESCRIPTION.—Rancurel and Okutani, 1990:25, figs. 1–6.

TYPE LOCALITY.—21°15'S, 155°11.5'E (southwestern Pacific, between 16°37'S and 23°56'S, 162°00'E and 133°15'W (cf. Rancurel, 1970)).

DEPOSITION OF TYPES.—*Holotype*: NSMT Mo-67008; National Science Museum, Tokyo, Japan.

Paratypes (4): NSMT Mo-67009–12; National Science Museum, Tokyo, Japan.

DISTRIBUTION.—Southwestern Pacific, estimated to be abundant in the central water mass of the Pacific (Okutani and Tsukada, 1988).

DISCUSSION.—Rancurel (1970) found a unique onychoteuthid in the stomach contents of an *Alepisaurus ferox* Lowe caught with long lines in the southwestern Pacific. He recognized apparent differences between his specimens and so-called "*O. banksii*," which had been thought to be the sole *Onychoteuthis* in the South Pacific at that time. Rancurel gave a detailed description of this unique onychoteuthid, but he did not give it a new species name because of the loss or lysis of the fixing apparatus of the arms and tentacles as a result of digestion in the predator. Okutani and Tsukada (1988) also examined the stomach contents of lancetfish and tunas from the tropical Indo-Pacific and found the same *Onychoteuthis* species described by Rancurel. They made a detailed comparison of three species of the genus *Onychoteuthis*, i.e., *O. banksii*, *O. compacta*, and *O. sp.* Rancurel.

During the workshop, a small onychoteuthid squid measuring about 65 mm ML collected off Sydney, Australia, that looked like *Onychoteuthis* sp. Rancurel was identified to *Ancistroteuthis* because of the indistinctness of the light organs in the ventral mantle cavity and some differences among body proportions. Studies after the workshop, however, revealed that this specimen should be included in *O. sp.* Rancurel irrespective of the indistinctness of the light organs. This specimen has tentacular structures and mature male reproductive organs similar to *O. sp.* Rancurel, but it has a more slender mantle (MW/DML, 23% compared with 28%–38%), smaller fins (FW/ML, 67% compared with 73%–90%; FL/ML, 40%

compared with 42%–48%), and shorter arms (AL/ML, 25%–32% compared with 27%–40%) than those of Rancurel's (1970) and Okutani and Tsukada's (1988) specimens. We reexamined Okutani and Tsukada's specimens and recognized that the mantles were strongly constricted in apparent response to the digestive fluid in the predator's stomach, which caused the different body proportions mentioned above. Examination of growth series and specimens in various fixing conditions convinced us that the visceral light organs of *O. sp.* Rancurel degenerate with growth. In 1990 Rancurel and Okutani gave a new species name, *meridiopacifica*, to *O. sp.* Rancurel.

This species is distinguishable from *O. banksii* by having broader fins with an apex angle of 120°–140°, fewer hooks on the manus, and a decidedly small size at maturity. Specimens smaller than about 20 mm ML are almost referable to *O. compacta* except for possessing two rows of immature hooks on the manus. Young and Harman (1987) reported three different paralarvae of *Onychoteuthis* from Hawaiian waters, one of which was identical to *O. compacta*. Although the other two forms have not yet been linked with their adults, one of them might be an early life stage of *O. meridiopacifica*.

***Ancistroteuthis* Gray, 1849**

DIAGNOSIS.—Mantle muscular, slenderly cylindrical, tapered posteriorly, with end acutely pointed and solidified by long spine of gladius. Gladius not visible on dorsal side of mantle. Nuchal folds prominent. Tentacles with double rows of strong hooks but no marginal suckers on manus. No photophore present in pallial cavity. Oval, opaque area with posterior small patch of photogenic tissue on ventral covering of eye.

TYPE SPECIES.—*Onychoteuthis lichtensteinii* Férussac and Orbigny, 1839:334, pl. 8: figs. 8–12.

DISCUSSION.—This genus has been stable since it was established.

***Ancistroteuthis lichtensteinii* (Férussac and Orbigny, 1839)**

FIGURE 1

DIAGNOSIS.—Mantle slender, robust, muscular. Fins lanceolate, attenuated posteriorly into tail, posterior margins concave, length 60% ML, width 57% ML. Nuchal folds 8 or 9 pairs, becoming indistinct dorsally. Arm formula IV > III = II > I, length 40%–53% ML. Tentacle club slightly expanded, length 30% ML, 16 or 17 small suckers on dactylus, 20 or 21 hooks in 2 rows on manus, well-defined, oval fixing apparatus with 9 to 10 suckers and 9 or 10 pads. Medium-sized species maturing at about 200 mm ML in males, maximal ML 300 mm.

ORIGINAL DESCRIPTION.—Férussac and Orbigny, 1839: *Onychoteuthis* pl. 14: figs. 1–3.

TYPE LOCALITY.—Off Nice, Mediterranean Sea.

DEPOSITION OF TYPE.—Not known.

DISTRIBUTION.—Reported from the western Mediterranean Sea and from tropical and subtropical waters of the eastern

Atlantic. This species has also been reported from the Gulf of Mexico (Voss, 1956) and the southwestern Pacific (Rancurel, 1970).

DISCUSSION.—Férussac and Orbigny described *Onychoteuthis lichtensteinii* from Nice, based on the differences in body proportions, fin shape, number of nuchal folds, and tentacular club structures from *O. bergii*, which is considered to be a synonym of *O. banksii*. Gray (1849) recognized that *O. lichtensteinii* lacks visceral light organs and proposed a new genus *Ancistroteuthis* for the species. *Ancistroteuthis lichtensteinii* has often been reported from the western Mediterranean Sea; however, the records outside the Mediterranean are very sparse, being described from the Gulf of Mexico (Voss, 1956), off West Africa (Adam, 1962), and from the southwestern Pacific (Rancurel, 1970). Adam (1962) mentioned some geographical varieties.

During the workshop, four specimens from the eastern Atlantic and two specimens from the southwestern Pacific were available. Detailed comparisons of these specimens showed four different geographical variations, three forms in the Atlantic and one form in the Pacific. One specimen from the northeastern Atlantic at 20°27'N, 21°58'W, was identical to the typical *A. lichtensteinii*, having the characteristics given in the diagnosis. Two specimens from the central Atlantic between 5°S and 22°S apparently differed from the typical form by having larger fins with a less attenuating tail. Moreover, the specimen from the southernmost locality, 34°26'S, 14°43'E, was clearly separable from the typical and central Atlantic forms by having shorter arms, 30%–40% ML, small tentacular clubs of about 20% ML, with smaller and fewer (15 or 16) hooks, and more than 35 small suckers on the dactylus. This specimen was a male and had a mantle length of 138 mm and mature spermatophores. Although three forms are recognized in the Atlantic, no specimen was available that corresponded to the "*A. lichtensteinii*" reported by Voss (1956) from the Gulf of Mexico. Because it had no nuchal folds, Voss's specimen might belong to the genus *Moroteuthis*.

On the other hand, two specimens from off southeastern New Zealand had intermediate characteristics between the central Atlantic and southern Atlantic forms, but the Pacific specimens distinctly differed by having shorter arms of about 30%–45% ML, tentacular clubs of about 30%–35% ML with 18 hooks, and more than 30 small suckers on the dactylus. From the southwestern Pacific, Rancurel (1970) has reported *A. lichtensteinii* in the stomach contents of lancetfish caught at 20°–24°S, 166°–167°E, further north than the locality for the present form. Judging from Rancurel's description and figures, his specimens clearly differed from the above-mentioned forms by having much longer arms of about 89%–95% ML. He mentioned that his specimens also lack nuchal folds and are close to Voss's (1956) specimen of *A. lichtensteinii* from the Gulf of Mexico. Although there is no record of *Moroteuthis* from the tropical southwestern Pacific, Rancurel's specimen also seems to belong to the genus *Moroteuthis*.

There are too few specimens to draw clear-cut conclusions about geographical variations of this poorly known species; however, the Pacific form is considered to have enough specific characters and geographical segregation to separate it from the "*A. lichtensteinii*-complex" in the Atlantic. The central Atlantic and southern Atlantic forms also seem to have adequate specific characters to separate them from the typical *A. lichtensteinii* distributed in the northeastern Atlantic and Mediterranean Sea. As discussed in the geographical variations of *Onychoteuthis banksii*, however, the existence of intermediate forms between the typical form and the central and southern Atlantic forms seems possible. More specimens are necessary to clarify the species complex in the Atlantic.

As to the confusion on the spelling of the species name, "*lichtensteini*" or "*lichtensteinii*," again following the ICZN and the opinion of F.M. Bayer (pers. comm., 1988), as in the preceding case of *Onychoteuthis banksii*, the original "ii" ending is considered correct.

Ancistroteuthis lichtensteinii, Central Atlantic Form

DIAGNOSIS.—Mantle slender, muscular. Fins rhomboidal, length 62% ML, width 70%–78% ML, apical angle 75°–80°, without attenuate tail. Nuchal folds 8 or 9 pairs. Arm formula II = III = IV > I, length 45%–59% ML. Tentacle club slightly expanded, length 29%–31% ML, 15–17 small suckers on dactylus, 19 or 20 hooks on manus in 2 rows, largest hook about 20% of club length, well-defined fixing apparatus with 8 suckers and 8 pads. No light organs in ventral mantle cavity. Examined specimens 134–146 mm ML, mature males.

LOCALITY.—Central Atlantic, R/V *Walther Herwig* sta 467-71, 5°30'S, 16°28'W; R/V *Walther Herwig* sta 443-71, 21°35'S, 16°28'W.

DEPOSITION OF SPECIMENS.—USNM 816698, USNM 817615; National Museum of Natural History, Washington, D.C., United States.

DISTRIBUTION.—Known only from above localities.

DISCUSSION.—See "Discussion" for *A. lichtensteinii*, above.

Ancistroteuthis lichtensteinii, South Atlantic Form

DIAGNOSIS.—Mantle slender, muscular. Fins lanceolate, attenuated posteriorly into short tail, length 59% ML, width 65% ML. Nuchal folds 6 or 7 pairs. Arm formula IV = III = II > I, length 30%–38% ML. Tentacle club small, slightly expanded, length 20%–21% ML, 38 or 39 small suckers on dactylus in 4 rows, 15 or 16 hooks on manus in 2 rows, largest hook about 19% of club length, well-defined fixing apparatus with 10 suckers and 10 pads. No light organs in ventral mantle cavity. Examined specimen 138 mm ML, mature male.

LOCALITY.—Southeastern Atlantic, R/V *Walther Herwig* sta 419-II-71, 34°26'S, 14°43'E.

DEPOSITION OF SPECIMEN.—National Museum of Natural

History, Smithsonian Institution, Washington, D.C., United States.

DISTRIBUTION.—Known only from above locality.

DISCUSSION.—See "Discussion" for *A. lichtensteinii*.

***Ancistroteuthis lichtensteinii*, Pacific Form**

DIAGNOSIS.—Mantle robust, muscular. Fins lanceolate, elongated posteriorly, attenuating into short tail, length 55%–60% ML, width 80% ML. Nuchal folds 5 or 6 pairs. Arm formula III = II = IV > I, length 30%–45% ML. Tentacles robust. Tentacle club slightly expanded, length 30%–35% ML, 32–36 small suckers on dactylus in 4 rows, 18 hooks on manus in 2 rows, largest hook 20%–25% of club length, well-defined fixing apparatus with 8 suckers and 8 pads. No light organs in ventral mantle cavity. Medium-sized species, examined specimens 49–119 mm ML.

LOCALITY.—Southwest Pacific at 46°03'S, 171°37'E, and 44°00'S, 150°09'E.

DEPOSITION OF SPECIMENS.—NMNZ M-94091; Nelson Museum, New Zealand. MVA F-55014; National Museum of Victoria, Melbourne, Australia.

DISTRIBUTION.—Known only from above localities.

DISCUSSION.—See "Discussion" for *A. lichtensteinii*.

Onykia Lesueur, 1821

DIAGNOSIS.—Mantle short, cylindrical, narrowing posteriorly rather abruptly, and ending in pointed tip solidified by endcone of gladius. Fins broader than long, usually roundly ovate in outline. Dorsal nuchal folds absent, photogenic organs lacking. Gladius with strong rachis and lanceolate vanes ending in spoon-shaped hollow with short, conical tip.

TYPE SPECIES.—*Onykia carriboea* Lesueur, 1821:98, pl. 9: figs. 1, 2a–e.

DISCUSSION.—Gray (1849) admitted this genus and followed Menke's (1830) spelling, *Onychia*. Pfeffer (1912) and others preferred to use *Teleoteuthis* Verrill, 1885, the replacement name for *Onychia*, which is the generic name of an insect. Taki (1964) argued for retention of the original spelling *Onykia* and abandonment of the replacement name.

***Onykia carriboea* Lesueur, 1821**

FIGURE 7

DIAGNOSIS.—Mantle muscular, almost ellipsoid in immatures, becoming cylindrical with growth. Fins wider than long, length about 25% ML, width 70%–75% ML, subrhombic, with convex anterior and posterior margins and blunt lateral angles. Tentacle club with medial hooks and marginal suckers, well-defined fixing apparatus with 8 or 9 suckers present. Gladius with short, recurved rostrum. Surface smooth, with crowded purplish chromatophores and silvery sheen. Dorsal mantle and dorsal head particularly deep purplish.

ORIGINAL DESCRIPTION.—Lesueur, 1821:98, pl. 9: figs. 1, 2a–e.

TYPE LOCALITY.—Gulf of Mexico and in Gulf Stream among fuci (= *Sargassum* spp.).

DEPOSITION OF TYPE.—*Holotype*: Academy of Natural Science, Philadelphia, Pennsylvania, United States; probably no longer extant (Voss, 1962).

Paratypes: None.

DISTRIBUTION.—Tropical to warm temperate Atlantic and Indo-Pacific, surface.

DISCUSSION.—This species is characterized by a dark purplish dorsum and a silvery ventrum, and it is frequent in surface collections from the warm-water masses. Subsequent to its description by Lesueur, many names were published by Orbigny (1835, in Férussac and Orbigny, 1835–1848), Gray (1849), Pfeffer (1884, 1900, 1912), Verrill (1885), and others, which were all considered to be synonyms by Clarke (1966).

Another problem is that all the specimens that are identified as *O. carriboea* are immature. This suggests that the name could represent an immature growth stage of named or unnamed larger species that undertake ontogenetic descent or migration to cold-water areas with growth. The problem of an *O. carriboea* complex is fully discussed by Tsuchiya and Okutani (1992).

In connection with this, *O. indica* Okutani, 1981, and specimens from the eastern Atlantic off Congo (R/V *Walther Herwig* sta 482-I-71, 04°34'N, 19°30'W and sta 471-II-71, 02°29'S, 18°58'W; National Museum of Natural History, Smithsonian Institution, Washington, D.C.) also are immature stages. *Onykia indica* seems to be an immature *Moroteuthis*.

Here, too, there has been some confusion on the spelling of the species name, "*carribaea*" or "*carriboea*." As "*carriboea*" appears in the heading of Lesueur's original description, that spelling is correct.

***Onykia rancureli* Okutani, 1981**

FIGURE 6

DIAGNOSIS.—Mantle robust, short, conico-cylindrical, width about 50% ML. Arm I slightly shortest, other arms subequal in length. Sucker counts about 50 per arm. Tentacle robust and rather short, with 26 or 27 biserial hooks and several marginal suckers on manus, 9 or 10 pads on fixing apparatus, and 7–9 small suckers on dactylus. Gladius with strong rachis and small conus and rostrum.

ORIGINAL DESCRIPTION.—Okutani, 1981:155, figs. 1–9.

TYPE LOCALITY.—Central Indian Ocean, 07°51'S, 88°02.5'E, removed from the stomach of a lancetfish measuring 1410 mm fork length.

DEPOSITION OF TYPES.—*Holotype*: NSMT Mo-59498; National Science Museum, Tokyo, Japan.

Paratypes (3): NSMT Mo-59490–92; deposition same as holotype.

DISTRIBUTION.—Central Indian Ocean to entire tropical Pacific. This species is very frequent in the diets of lancetfish and tunas.

DISCUSSION.—This species is characterized by having a unique gladius morphology that could require a new generic name.

***Moroteuthis* Verrill, 1881**

DIAGNOSIS.—Mantle muscular but soft in spent females, anteriorly cylindrical, tapering posteriorly to blunt point. Mantle surface with warts, soft wrinkles, or smooth. Fins rhombic. Dorsal nuchal folds absent. No photophores. Tentacles with 2 rows of hooks, marginal suckers absent in adult but present in early stages. Gladius with cartilaginous endcone.

TYPE SPECIES.—*Ommastrephes robustus* Verrill, 1876:236.

DISCUSSION.—Pfeffer (1908) created the genus *Moroteuthopsis* to separate *Moroteuthis ingens* (Smith, 1881) from *Moroteuthis robusta* (Verrill, 1876). Later, Pfeffer (1912) cast doubt on his earlier decision to create the genus and thought it should perhaps be a subgenus of *Moroteuthis*. In our judgment, after the discovery and our study of the more recent species *Moroteuthis robsoni* Adam, 1962, *M. aequatorialis* Thiele, 1920, *M. lonnbergii* Ishikawa and Wakiya, 1914, and *M. knipovitchi* Filippova, 1972, Pfeffer's subdivision of the genus is not justified.

***Moroteuthis ingens* (Smith, 1881)**

FIGURE 12

DIAGNOSIS.—Adult large (500 mm ML), skin rugose and covered with fleshy warts forming typical paving-stone pattern. Fins large and broad, rhomboidal, not sagittate, fin length 50% ML. Rostrum of gladius triangular in cross section, 10%–12% ML. Carpus with 10–13 suckers, manus with about 14 pairs of hooks, ventral row hooks stronger than dorsal row hooks, largest hooks at 6th–8th pair. Dactylus with 16 or 17 minute suckers. Longest arms (II and III) about 70% ML.

ORIGINAL DESCRIPTION.—Smith, 1881:25, pl. 3: figs. 1–1d.

TYPE LOCALITY.—Port Riofrio, west coast of Patagonia.

DEPOSITION OF TYPE.—*Holotype*: The Natural History Museum, London, England.

Paratypes: None.

DISTRIBUTION.—Sub-Antarctic species, distributed north of the Antarctic convergence and south of the subtropical convergence, off Patagonia and New Zealand. Possibly circumpolar.

DISCUSSION.—Within the genus, this is one of the best described species, and the species characteristics are distinct. *Moroteuthis ingens* is an oceanic epipelagic species with a poorly known biology. According to Nesis (1987), it primarily lives in the lower sublittoral and bathyal zones. It is a prey item in the diets of sperm whales, seals, and sea birds. The beaks of this species were described as *Moroteuthis* A by Clarke (1980). *Moroteuthis ingens* was confused with *Kondakovia longimana* until Filippova (1972) described the latter.

***Moroteuthis knipovitchi* Filippova, 1972**

FIGURE 9

DIAGNOSIS.—Adult moderately large (450 mm ML), skin with smooth-textured surface. Mantle relatively broad and stout, not pointed into tail. Fins large and rhomboidal, about 50%–60% ML. Gladius with terminal cartilaginous conus, conus triangular in cross section. Tentacle club long and slender, with 12 or 13 suckers on carpus, manus with 10–15 pairs of long, narrow hooks, ventral row hooks larger than dorsal row hooks, and with 14–16 minute suckers on dactylus. Longest arms (II) approximately 90% ML.

ORIGINAL DESCRIPTION.—Filippova, 1972:392, figs. 2, 3.

TYPE LOCALITY.—Near South Georgia Island, R/V *Academician Knipovitch* sta 176, 3 Mar 1965, trawling depth 400–550 m.

DEPOSITION OF TYPE.—*Holotype*: Female, 225 mm ML; Zoological Museum, Moscow University, Moscow, Russia.

Paratypes: None.

DISTRIBUTION.—Antarctic, south of the Antarctic convergence in the Scotia Sea, Argentine Basin, and Drake passage, possibly circumpolar (Clarke, 1980; Nesis, 1987).

DISCUSSION.—*Moroteuthis knipovitchi* is characterized by thin, smooth skin, whereas the other species of the genus *Moroteuthis*, except for spent females (see discussion of *M. aequatorialis* in general discussion section, below), have a rugose skin (Filippova, 1972). The species is an oceanic form that is heavily preyed upon by sperm whales.

***Moroteuthis lonnbergii* Ishikawa and Wakiya, 1914**

FIGURE 10

DIAGNOSIS.—Adult moderately large (275 mm ML), skin rugose. Mantle robust and muscular with longitudinal ridges or warts, pointed to a tail. Fins broad, rhomboidal, about 50%–55% ML. Rostrum of gladius narrowly triangular in cross section. Carpus with 7 or 8 suckers, manus with 25 hooks in 2 rows, largest hooks 4th–6th on dorsal row, 6th or 7th on ventral row. Extreme end of dactylus with 10–13 minute suckers. Longest arm (IV) 60% ML.

ORIGINAL DESCRIPTION.—Ishikawa and Wakiya, 1914:445, pls. 45, 46.

TYPE LOCALITY.—Found on the beach of Hayama, Sagami Bay, Japan, probably thrown away by fisherman.

DEPOSITION OF TYPES.—*Syntypes* (5): 147–192 mm ML; deposition not known.

Paratypes: None.

DISTRIBUTION.—Western North Pacific, off eastern Japan, and Indian Ocean (Saya-de-Malha Bank).

DISCUSSION.—This species is very similar to *Moroteuthis robsoni*. It occurs in temperate and tropical oceanic waters from the epipelagic to the bathyal zones and is preyed upon by fur seals and sperm whales.

Concerning the confusion on the spelling of the species name, "*lonnbergi*" or "*lonnbergii*," we have followed the ICZN

and the opinion of F.M. Bayer (pers. comm., 1988) and have retained the original "ii" as the correct ending.

***Moroteuthis robsoni* Adam 1962**

FIGURE 8

DIAGNOSIS.—Adult large (470 mm ML), skin rugose, reddish, and covered with fleshy, irregular warts. Mantle long and slender. Fins very long, not rhomboidal, attenuated to long tail, up to 67% ML. Rostrum of gladius triangular in cross section, ventral length about 23%–36% ML. Tentacle club very narrow, carpus with 10–12 suckers, manus with 13–16 pairs of hooks, dactylus with 12–17 minute suckers. Longest arms (IV) approximately 57%–86% ML.

ORIGINAL DESCRIPTION.—Adam, 1962:24, figs. 2, 3, pl. 1: figs. 1–4.

TYPE LOCALITY.—Angola, 16°35.6'S 11°19.5'E, 26 Feb 1957, chalut, 485–550 m.

DEPOSITION OF TYPE.—*Holotype*: Mission de Biologie Maritime 1957-NO, M 7; deposition not known.

Paratypes: None.

DISTRIBUTION.—North of the southern subtropical convergence, off southwestern Australia, New Zealand, and southern Africa.

DISCUSSION.—This species is very similar to *Moroteuthis robusta*. It is oceanic and lives at the bottom and in the pelagic zone, but its exact depth distribution is unknown. It is heavily preyed upon by sperm whales.

Several specimens from the National Museum of Natural History, Smithsonian Institution (which houses collections of the former United States National Museum (USNM)), that were labeled "*Ancistroteuthis*" were examined and identified as *M. robsoni* (see Table 1). These were as follows: USNM 730692,

271 mm ML (male with large penis but no spermatophores), Gulf of Mexico at 28°36'N, 87°07'W; USNM 575101, 61 mm ML, Gulf of Mexico at 27°18'N, 89°25'W; USNM 730689, 156 mm ML, Gulf of Mexico at 21°33'N, 96°48'W; USNM 730690, 235 mm ML, Gulf of Mexico at 21°41'N, 96°55'W; USNM 730891, ~300 mm ML, Pensacola, Florida; USNM 815468, 370 mm ML, from Bermuda.

The above specimens cannot be distinguished from *Moroteuthis robsoni* from the South Atlantic. Although the rostrum of the gladius is shorter than that in the southern *M. robsoni*, this and other slight differences are probably due to the size of the individual rather than to subspecific differences (Clarke, 1980). The much broader fin of the spent female collected near Bermuda is probably an artifact of preservation. This specimen bridges the gap between *M. robsoni* and *M. aequatorialis* Thiele, 1920.

***Moroteuthis robusta* Verrill, 1876**

FIGURE 11

DIAGNOSIS.—Adult large (1615 mm ML), skin rugose. Mantle robust and relatively broad, surface with longitudinal ridges of soft tissue. Fins large and sagittate, about 50% ML. Rostrum of gladius round or oval in cross section, about 25%–40% ML. Tentacle club slender, with 10–12 suckers on carpus, manus with 16–18 pairs of hooks, 3rd or 4th hooks on ventral row largest. Dactylus with 8–10 suckers. Longest arms (IV) about 90%–100% ML.

ORIGINAL DESCRIPTION.—Verrill, 1876:237.

TYPE LOCALITY.—Coast of Alaska, 3 specimens on beach in April and May 1872.

DEPOSITION OF TYPE.—*Holotype*: USNM 576952, only pieces of pen, buccal mass, fin, and arm extant; National

TABLE 1.—Examined specimens of *Moroteuthis robsoni* from the North Atlantic region that were previously labeled as *Ancistroteuthis*. All specimens are from the collections of the former United States National Museum (USNM), which are now part of the National Museum of Natural History, Smithsonian Institution. (DML = dorsal mantle length; FL = fin length; FLI = fin length index; FW = fin width; FWI = fin width index; - = no measurements available.)

Character	USNM catalog number					
	575101	730689	730690	730692	730691	815468
Sex				male		female
DML (mm)	61	156	235	271	300	370
Tail	no	yes	yes	yes	yes	yes
FL (mm)	29	93	145	150	160	195
FW (mm)	43	85	120	155	155	260
FLI (FL/DML)	0.48	0.60	0.62	0.57	0.53	0.53
FWI (FW/DML)	0.71	0.55	0.51	0.57	0.52	0.70
Number of hooks	28	28	-	28	25/27	-
Number of pairs	14	14	-	14	-	-
Largest hooks	7–8	-	-	-	5–7/4–6	-
Carpal suckers	9	9	-	9	10	8
Dactylus suckers	7–8	15	-	13	11	15
Cone (ventral, mm)	-	35	26	57	-	-
Longest arm (mm)	-	-	126	195	-	-

Museum of Natural History, Smithsonian Institution, Washington, D.C., United States.

Paratypes: None.

DISTRIBUTION.—In offshore waters of the eastern and western far North Pacific, from the Bering Sea and Gulf of Alaska to northeastern Japan and southern California (Okutani, 1980; Nesis, 1987).

DISCUSSION.—Characters distinguishing this species from the other members of the genus *Moroteuthis* are clear. This is a gigantic animal with a maximal mantle length of 2.3 m (Nesis, 1987). When freshly caught, it is very soft to the touch and never as firm as *Ommastrephes* (Sasaki, 1929). It is common in the diets of sperm whales.

Kondakovia Filippova, 1972

DIAGNOSIS.—Because the genus *Kondakovia* is monotypic, diagnoses of the genus and the species are the same (see below).

TYPE SPECIES.—*Kondakovia longimana* Filippova, 1972:395, figs. 4, 5.

Kondakovia longimana Filippova, 1972

FIGURE 13

DIAGNOSIS.—Adult large (740 mm ML), mantle soft and fleshy, broadly cylindrical, slightly tapering posteriorly. No dorsal nuchal folds, no photophores. Fins rhombic, about 42% ML. Gladius thin and fragile, with narrow, longitudinal thickenings, cone 5%–8% ML. Carpus with 9–13 suckers, manus with 27–38 hooks and always 2 rows of marginal suckers, dactylus with 17–40 minute, closely placed suckers. Head and arms more massive than in *Moroteuthis* and larger than mantle portion.

ORIGINAL DESCRIPTION.—Filippova, 1972:395, figs. 4, 5.

TYPE LOCALITY.—North of South Orkney Islands, in areas of high krill (*Euphausia superba*) concentrations, R/V *Academician Knipovitch* sta 970, 20 Mar 1967, surface.

DEPOSITION OF TYPES.—*Holotype:* Female, 260 mm ML; Zoological Museum, Moscow University, Moscow, Russia.

Paratypes: 2 females, 133 mm ML, 210 mm ML; deposition same as holotype.

DISTRIBUTION.—Epi- and mesopelagic in the Southern Ocean, reaching northward to South Georgia and Tasman Sea, possibly circumpolar (Filippova, 1972; Clarke, 1980; Clarke and Macleod, 1982; Nesis, 1987).

DISCUSSION.—*Kondakovia longimana* is distinguished from all *Moroteuthis* species by the possession of marginal suckers on the tentacle club and by different body, gladius, and lower beak proportions. The characters mentioned above, however, overlap somewhat with several *Moroteuthis* species, especially if early life stages are considered. In summary, we believe the generic status created by Filippova (1972) can be justified, although certain body proportions are similar to those of *Moroteuthis* species.

GENERAL DISCUSSION OF ALL *Moroteuthis* AND *Kondakovia* SPECIES

All but the young juveniles of the species *Moroteuthis robusta*, *M. ingens*, *M. robsoni*, *M. knipovitchi*, *M. lonnbergii*, and *Kondakovia longimana* can readily be distinguished using fin and body shape, presence or absence and form of the rugose ornamentation of the skin, the number of carpal suckers or studs, the number of suckers on the dactylus, the number of hooks on the manus, the presence or absence of marginal suckers on the manus, and the ventral length index of the rostrum of the gladius. From the adults, the geographical distributions are shown to be distinct. *Kondakovia longimana* and *M. knipovitchi* are cold-water species and have not been found north of the Antarctic convergence. A few beaks closely similar to those of *K. longimana* were found in stomachs of sperm whales caught off Iceland, which raises the possibility that the species or the genus may be bipolar in distribution (Martin and Clarke, 1986). *Moroteuthis ingens* is probably confined to waters between the Antarctic and southern subtropical convergence. *Moroteuthis robsoni* extends from the southern subtropical convergence to as far north as the Gulf of Mexico and Bermuda. Whether any of the above species are circumpolar has not been established, but the antarctic species are known to extend from Patagonia and Graham Land, Antarctica, eastward to New Zealand.

Moroteuthis robusta and *M. lonnbergii* are North Pacific species, the southern limits of the former extending to south of California, United States, and the latter occurring off Japan. *Moroteuthis pacifica* Okutani, 1983, was based on a juvenile. A serial examination of specimens of different sizes indicates *M. pacifica* could be a juvenile of *M. robusta*; therefore, we believe *M. pacifica* should be reduced to a synonym of the latter species. *Moroteuthis lonnbergii* is similar to *M. robsoni*, but the apparent differences found in the size at maturity and the distributional area lead us to think that *M. lonnbergii* is a valid species segregated in the northwestern North Pacific (and a single locality in the Indian Ocean).

The holotype of *Moroteuthis aequatorialis* Thiele, 1920, collected on the equator at 18°07'W, could not be found for the workshop. We did, however, have available a specimen from Bermuda that closely resembled the type description of that species. The Bermuda specimen (USNM 815468) was clearly a spent female of *M. robsoni* resembling some described by Clarke (1980), and we believe this casts serious doubt on the validity of *M. aequatorialis* as no distinctive characters are given in the original description. Because the type of the latter species is lost, we designate the name a nomen nudum.

The various species grow to different sizes and many of their dimensions increase roughly on the same line, so that many proportional differences given as specific differences in the past are only a function of size (Clarke, 1980). Thus, although fully grown individuals are readily identified on the basis of relative dimensions, these dimensions are much less useful in separating young individuals.

Within these genera, apart from the great changes in form

and features that growth brings about, the females change shape drastically just prior to and during spawning. During this time, proteins are used up to such an extent that the tentacles are lost or change proportions, and the arms become relatively shorter. Additionally, the fins become larger and softer, body tissues become soft and even gelatinous, and the mantle wall loses its warts and becomes smooth (Clarke, 1980). The resultant animals are very like *Chaunoteuthis mollis* Appellöf and, indeed, some of the specimens referred to that species in the past are almost certainly spent females of various species of *Onychoteuthis* and *Moroteuthis*. Another cause for difficulties when comparing measurements of specimens of these species, particularly spent females, is the different affects of preservation times, kinds of preservatives, and position of the animals when preserved.

Zoogeography of the Family Onychoteuthidae

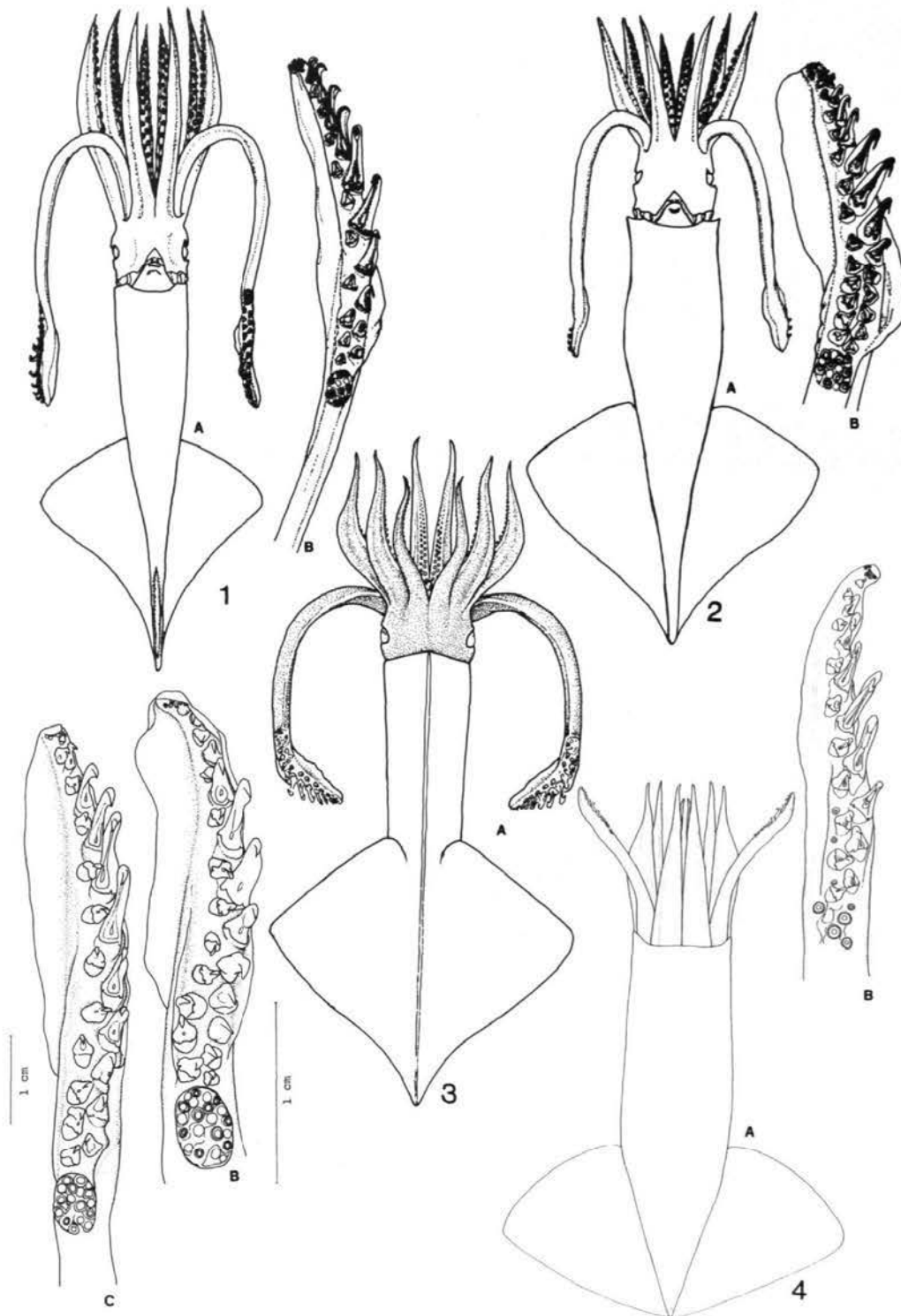
The taxonomic revision of the Onychoteuthidae reveals that there are at least four valid species, including one with three

intraspecific populations, in the genus *Onychoteuthis*, one species with four forms in the genus *Ancistroteuthis*, at least one valid species in the genus *Onykia*, five species in the genus *Moroteuthis*, and a sole species in the genus *Kondakovia*.

We do not have enough reliable distributional data to draw a clear zoogeographical picture for each species, so we instead summarize a general scheme of occurrence by species in Table 2. The genus *Onychoteuthis* seems to be diverging in the Pacific Ocean, as is *Ancistroteuthis* in the Atlantic. Small or medium-sized and epipelagic species belonging to the genera *Onychoteuthis* and *Ancistroteuthis* are distributed in tropical and subtropical waters. Members of the genera *Moroteuthis* and *Kondakovia*, which are usually large in size and may inhabit mesopelagic and/or bathyal benthic realms, are distributed in subarctic, subantarctic, and antarctic waters with the exception of the warm-water species *M. robsoni* and *M. lonnbergii*. Thus the genus *Moroteuthis* seems to be spread from warm-water to cold-water regimes and is divergent especially in the Southern Ocean, as suggested by available information.

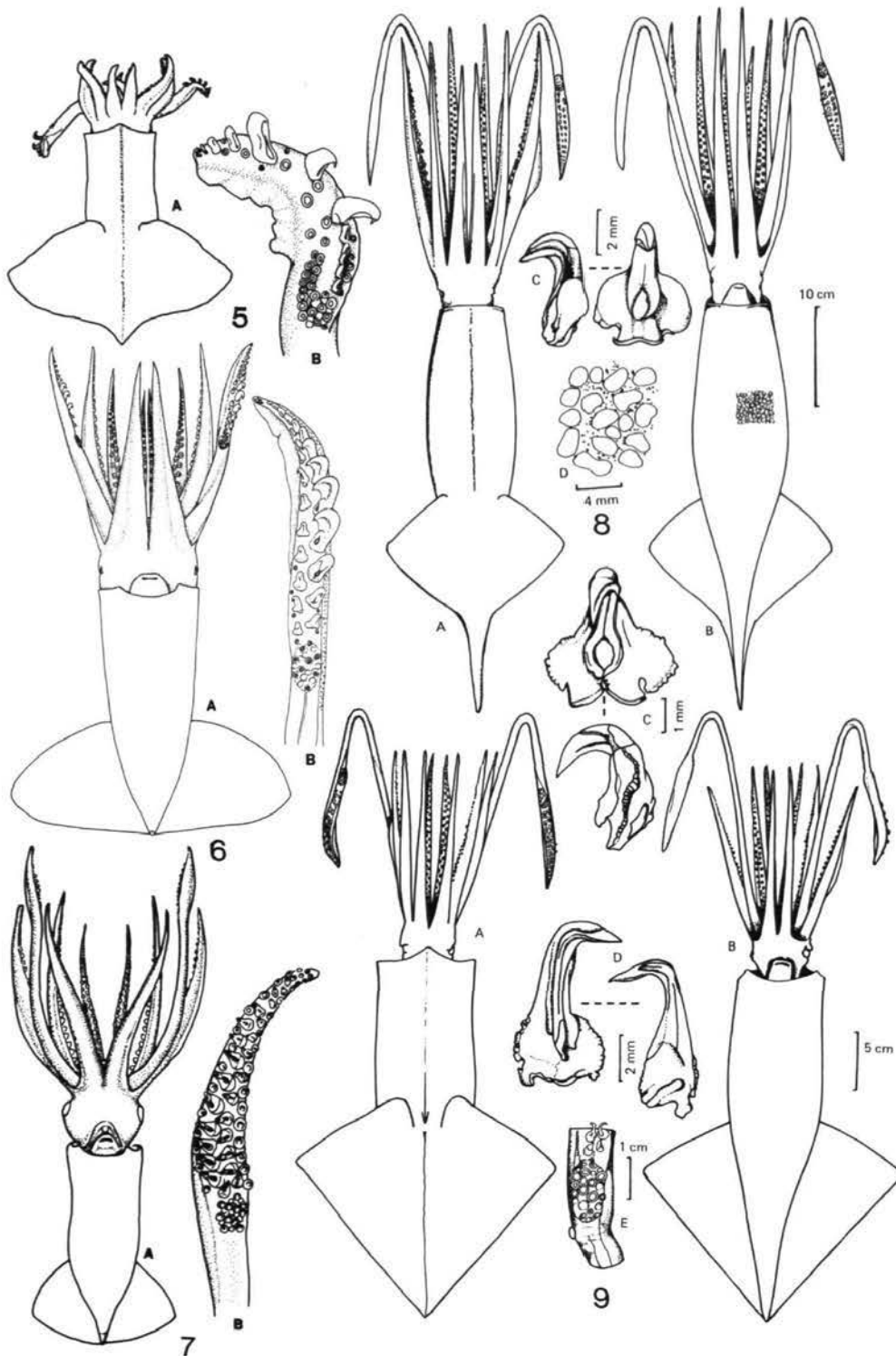
TABLE 2.—The geographical distribution of species in the family Onychoteuthidae. (A = Atlantic sector; C = central; E = east; I = Indian sector; NST = northern subtropical; P = Pacific sector; SA = subarctic; SAA = subantarctic; SST = southern subtropical; T = tropical; U = unpublished occurrence; W = west; X = published occurrence.)

Taxa	Pacific Ocean					Atlantic Ocean					Indian Ocean			Antarctic			Type Locality
	SA	NST	T	SST	SAA	SA	NST	T	SST	SAA	T	SST	SAA	P	A	I	
<i>Onychoteuthis</i>																	
<i>O. banksii</i>																	
small club form		X	X	X			X	X	X			U	U				Gulf of Guinea
medium club form		X	X	X			X	X	X			U	U				
large club form				W													
<i>O. compacta</i>				C													Hawaiian Ids
<i>O. borealijaponica</i>	X	X															Japan
<i>O. meridiopacifica</i>				W													SW Pacific Ocean
<i>Ancistroteuthis</i>																	
<i>A. lichtensteini</i>							E										Mediterranean
central Atlantic form								E									
south Atlantic form									E								
Pacific form				W													
<i>Onykia</i>																	
<i>(O. carriboea)</i>		X	X	X			X	X	X			X	X				Gulf of Mexico
<i>(O. indica)</i>												E					S Indian Ocean
<i>O. rancureli</i>				W								E					SW Pacific Ocean
<i>O. sp.</i>								W									off Congo
<i>Moroteuthis</i>																	
<i>M. ingens</i>					X					X			U	U	U	U	Patagonia
<i>M. robsoni</i>									X	U	X		X				
<i>M. robusta</i>	X	X															Alaska
<i>M. lonnbergii</i>			W														Sagami Bay
<i>M. knipovitchi</i>									W					U	X	U	South Georgia
<i>Kondakovia</i>																	
<i>K. longimana</i>									W					U	X	U	South Orkney



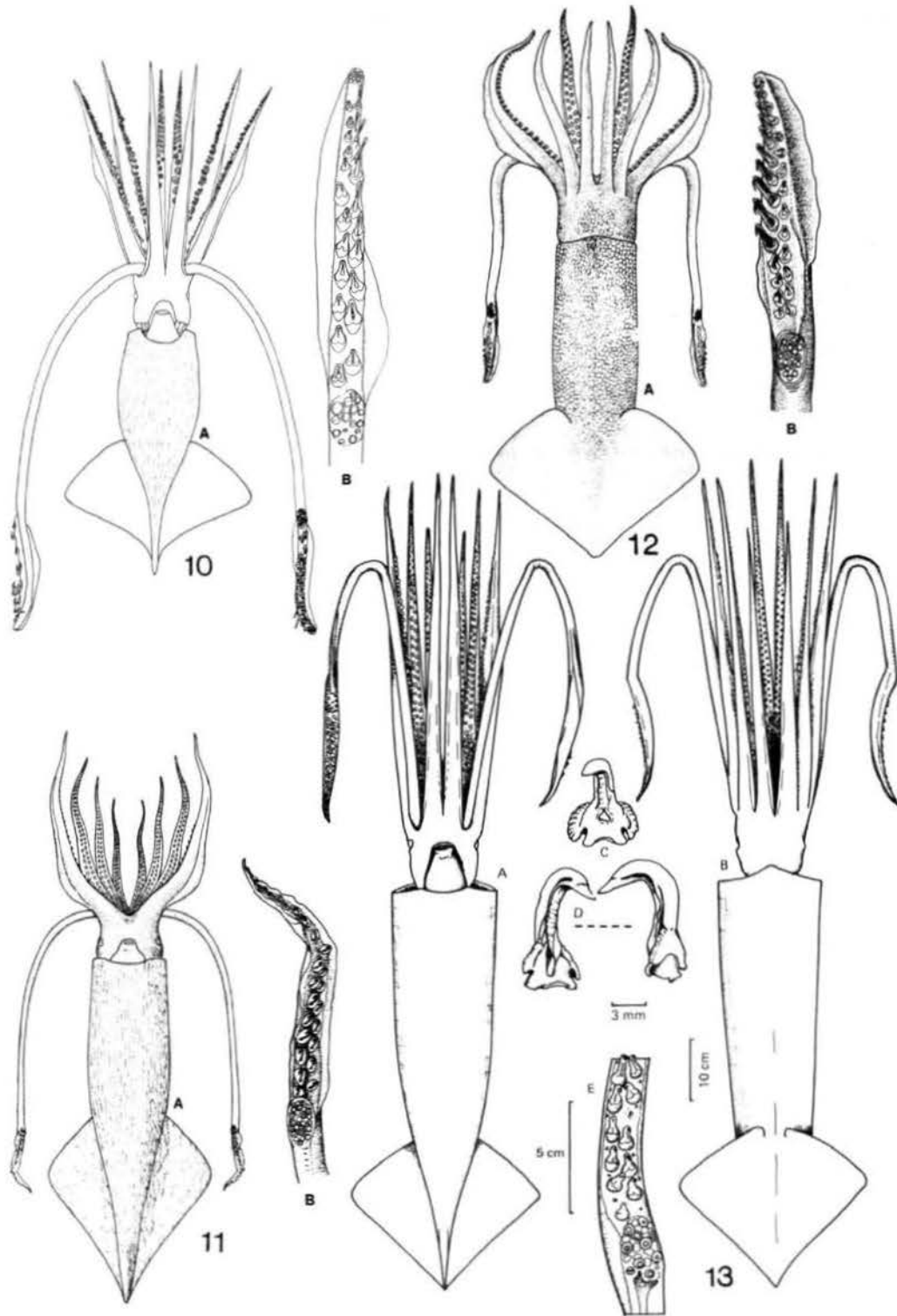
FIGURES 1-4.—1, *Ancistroteuthis lichtensteini*, northeastern Atlantic/Mediterranean Sea form, R/V *Walther Herwig* sta 502-71, 20°27'N, 21°58'W, 116 mm ML: A, ventral view; B, tentacle club. 2, *Onychoteuthis borealijaponica* (modified from Young, 1972, pl. 18: fig. A, pl. 19: fig. A): A, ventral view, 50 mm ML; B, tentacle club, 81 mm ML. 3, *Onychoteuthis banksii*: A, dorsal

view, 133 mm ML (from Pfeffer, 1912, pl. 4: fig. 12); B, tentacle club, large manus type, 04°10'N, 150°29'E, 132 mm ML; C, tentacle club, small manus type, 02°31'N-03°16.6'N, 142°36.44'E-140°54.39'E, 132 mm ML. 4, *Onychoteuthis meridiopacifica*, 21°15'S, 155°11.5'E, 61.7 mm ML: A, ventral view; B, tentacle club.



FIGURES 5-9.—5, *Onychoteuthis compacta* (from Berry, 1914, fig. 32, pl. 52: fig. 4), 21 mm ML: A, dorsal view; B, tentacle club. 6, *Onykia rancureli*, removed from fish stomach in southwestern Pacific, 73.8 mm ML: A, ventral view; B, tentacle club. 7, *Onykia cariboea* (from Pfeffer, 1912, pl. 1: figs. 7, 15), 32 mm ML: A, ventral view; B, tentacle club. 8, *Moroteuthis robsoni* (from

Clarke, 1980, fig. 81): A, dorsal view; B, ventral view; C, largest ventral tentacular hook; D, enlargement of skin sculpture. 9, *Moroteuthis knipovitchi* (from Clarke, 1980, fig. 78): A, dorsal view; B, ventral view; C, largest dorsal tentacular hook; D, largest ventral tentacular hook; E, carpal region of left tentacle club.



FIGURES 10-13.—10, *Moroteuthis lonnbergii*, from Suruga Bay, Honshu, 215 mm ML: A, ventral view; B, tentacle club. 11, *Moroteuthis robusta* (from Roper et al., 1984:134): A, ventral view; B, tentacle club. 12, *Moroteuthis ingens* (from Roper et al., 1984:130): A, dorsal view; B, tentacle club. 13, *Kondakovia longimana* (from Clarke, 1980, fig. 68): A, ventral view; B, dorsal view; C, largest dorsal tentacular hook; D, largest ventral tentacular hook; E, carpal region of left club.

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