PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
119(1):91–136. 2006.

Cephalopods of the Indian Ocean. A review. Part I. Inshore squids (Loliginidae) collected during the International Indian Ocean Expedition

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Abstract.—Cephalopods collected during the International Indian Ocean Expedition (IIOE; 1959–1965) and preserved at the Smithsonian Institution Oceanographic Sorting Center were analysed. This present work reports on the squids of the Loliginidae. A total of 378 specimens of Loliginids was identified: *Loligo chinensis*, *Loligo duvaucelii*, *Loligo edulis*, *Loligo singhalensis*, *Loligo (?) sumatrensis*, *Loliolus hardwickei*, and *Sepioteuthis lessoniana*. A systematic description is provided for each species, as well as its geographic distribution. Extensive updated information on the biology and fishery of each species also is discussed. Basic measurements were taken on each specimen and main morphological indices were computed; these were compared with those reported in the literature for each species. Tables provide measurements, morphological indices and comparisons with other studies. Appendices present information on capture sites, measurements and indices of individuals by sex and stage of maturity. These are located on the internet at www.biolsocwash/Jerebroper and http://www.nmnh.si.edu/iz/cephs/morphology/

The International Indian Ocean Expedition (IIOE; 1959–1965) was a cooperative, multidisciplinary, multiship scientific venture (Wooster 1984), the need of which was first recognized during the International Geophysical Year (IGY) in 1957. The Scientific Committee on Ocean Research (SCOR) decided first to support a two-year international program of physical measurements in the waters of the deep oceans, then to investigate more comprehensively the deep waters of the Indian Ocean during the third and fourth years.

In spite of the many different views on the organization, objectives, and systematic planning of the Expedition, an agreement on the program was eventually reached. It stressed the importance of inter-calibration of data acquisition methods and techniques. It was designed to obtain basic data on the geomorphology of the ocean bottom and to gather all possible biological data and information, from the baseline productivity of the waters to the main fisheries species as well as the status of commercial fish stocks for exploitation.

The Expedition witnessed the evolution of "old time oceanography into new time oceanography" (Aleem & Morcos 1984), since oceanography experienced dramatic changes in techniques, instrumentation and ships during the six-year-span of the Expedition. Forty ships from 13 countries

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participated, equipped with the most advanced electronic devices. The initial cost of the expedition was estimated at 12 million dollars US; the final costs exceeded 60 million dollars U.S. (Aleem & Morcos 1984).

The fundamental observations made in geology led to the elaboration of the theory on seafloor spreading, which then became a central unifying theory in marine geophysics. The study of the seasonally reversing currents associated with the monsoon system stimulated the development of more elaborate research programs on the interaction between the oceans and the atmosphere. An example of such comprehensive programs is the Global Weather Experiment carried out in 1979, which used satellite observations on a world-wide scale and pioneered modern satellite-based oceanographic studies. (Aleem & Morcos 1984). Among the results were important consequences for local nations, such as training programs for students and the origin of oceanographic studies. The Expedition also drew attention to the high productivity of Indian Ocean waters, leading to an increased interest in the development of sea fisheries in many countries; e.g., see Meiyappan & Mohamed (2003).

The phenomenal amount of biological material gathered during the Expedition required appropriate initiatives by participating countries to process and distribute it and to provide for appropriate research. In Washington, D.C., a working unit was established in 1962 as a mechanism to receive, sort and distribute to specialists the mass of specimens expected from United States participation in the IIOE. This was the Smithsonian Oceanographic Sorting Center (SOSC) (Wallen & Fehlmann 1974). About ten years after opening, SOSC had sorted nearly 3.7 million specimens from over 4,500 samples received, about 1.5 million of which had been sent to 140 specialists in the U.S.A. and 17 other countries (Wallen & Fehlmann 1974). The work of sorting and dispensing specimens continues to the present, although in a very much reduced capacity in recent years. The SOSC function now is incorporated into the Smithsonian National Museum of Natural History, Department of Invertebrate Zoology.

In spite of all the work done, 40 years later, material still needs to be examined. It is available for research by interested scientists.

The present work is the result of a joint research project between the Italian Consiglio Nazionale delle Ricerche (CNR) (National Research Council) and the North Atlantic Treaty Organization (NATO). This enabled the first author to spend one year in Washington, working with the Smithsonian Institution and the Rosenstiel School of Marine and Atmospheric Sciences (Miami, Florida) to analyse some of the cephalopod material collected during the IIOE.

Materials and Methods

The bulk of material came from cruises of the research vessels R/V *Anton Bruun* and R/V *Ambariaka*; a few additional samples from other sources also were examined. Once identified to species level, specimens were classified by an alphanumerical code and information on sampling area, depth and gear were recorded. Appendices 1A–G provide information by species on locality of capture, sex and number.

Measurements and indices (see Appendices 2A–G) used throughout this paper are those given by Roper & Voss (1983), using dorsal mantle length (ML) as a standard. If the measure was repeated on symmetrical structures, "r" and "l" indicate the right and left sides. The following additional parameters also were recorded. Nidamental Gland Length (NGL) was measured as an additional parameter to assess female maturity and Nidamental Gland Index (NGLI) was computed as the length of the gland as a percentage of mantle length. All measurements are in mm, if not otherwise indicated.

A three-stage maturity scale developed for the squid, *Illex coindetii* (Jereb & Ragonese 1995, see below), where 1 = immature, 2 = maturing, and 3 = mature, was applied to describe sexual maturity in the specimens. No maturity stage was assigned to specimens too small to be sexed; these are referred to either as "juveniles" or "unsexed" in the text. Number and shape of teeth on sucker rings of arm suckers and largest tentacular club suckers also were recorded.

Selected indices of biological parameters were chosen for each species according to sex, stage of maturity, and specific locality in the Indian Ocean, to enable intraspecific comparisons when sufficient material was available (see Tables 1 to 7, A and B). Also, our results were compared with analogous measurements taken on the same species by other authors (see Tables 1C to 7C for each species). Specimens for which maturity stage or sex was not assessable were not considered in these tables. Table 8 summarizes measurements and indices by sex for all seven species examined in this study.

The published information available on the biology and fishery of each species is reviewed and summarized following the systematic description and geographical distribution sections. Nomenclatural references conform to those provided in Sweeney and Vecchione (1998).

All Appendices and Tables are available on the Internet at the following websites: www.biolsocwash/Jerebroper and http://www.nmnh.si.edu/iz/cephs/morphology/

Results

Class Cephalopoda Cuvier, 1797
Subclass Coleoidea Bather, 1888
Superorder Decabrachia Boettger, 1952
Order Teuthidea Naef, 1916
Suborder Myopsina d'Orbigny, 1841 in Ferussac and d'Orbigny, 1834–1848
Family Loliginidae Lesueur, 1821

Macroscopic scale used to assess stage of maturity in the present material (from Jereb & Ragonese 1995:374) as presented in Table 3 and Appendix 2 (see on-line websites).*

	Females	Males
Stage 1 (Immature)	NG are visible but thin and almost transparent. The ovary is filamentous and transparent.	The gonad is small and inconspicuous. The testis and the SO are hardly visible. The penis is a small appendage protruding close to the left gill. Hectocotylus not formed.
Stage 2 (Maturing)	NG are whitish and well formed but do not cover the underlying visceral mass. The ovary is conspicuously developed and granular but does not occupy all the posterior half of the mantle cavity. The ova are visible.	The testis is a white, flat, lanceolate body. The SS is well-developed and may contain a few spermatophores. The penis is clearly visible. Hectototylus almost completely formed.
Stage 3 (Mature)	NG large and ripe, milk-white, almost completely cover the visceral mass. Ovary very large, occupies fully half of the mantle cavity. Anterior portion of the ovary and the oviducts filled with eggs that are amber-coloured in fresh specimens.	The testis is conspicuous, fusiform and slightly yellowish. The SS is filled with spermatophores. A slight pressure is sufficient to force them to extrude from the penis.

* NG = Nidamental gland; SO = Spermatophoric organ; SS = Spermatophoric sac.

Distinctive features.—Transparent skin (corneal membrane) covers eye lens. Funnel-locking apparatus a simple, straight groove and ridge. Fins attach to lateral regions of mantle. Arm suckers in two longitudinal series. Tentacular clubs with suckers in four series (except two series in manal region of *Pickfordiateuthis* clubs). Hooks never present. Buccal connectives attach to ventral margins of ventral arms, arms IV. Seven buccal lappets possess small to minute suckers (except in *Pickfordiateuthis* and *Sepioteuthis*). Left ventral arm usually hectocotylized in males; structure of the modified portion of the hectocotylus useful as a diagnostic character in most species. Eggs spawned in gelatinous finger-like egg masses attached to substrate. Color usually reddish-brown, darker dorsally, but quite variable depending on species and behavioural situation.

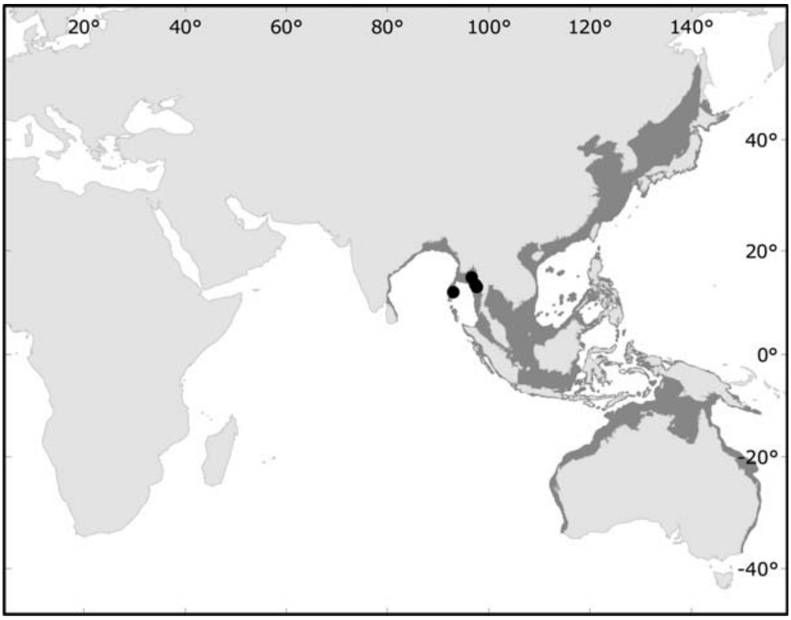
Remarks.—The systematics of the family Loliginidae [seven genera, 41–50 species, Nesis (1987)] recently has been the object of studies to clarify the position of some of its species and genera (Cohen 1976; Natsukari 1976, 1983, 1984a, 1984b; Lu et al. 1985; Natsukari & Okutani 1975; Brakoniecki 1986; Alekseev 1989, 1991; Korzun & Alekseev 1991; Vecchione et al. 1998; Vecchione et al. 2005).

A noteworthy testimony to the importance of the many unsolved systematic problems is that one of the main sections of the 1988 Cephalopod International Advisory Council (CIAC) Workshop (Washington, July, 1988) was devoted entirely to the Family Loliginidae. The decisions made during the Workshop required some modifications to the traditional classification (Vecchione et al. 1998) that tentatively assigned the nine recognized groups of species into five genera and four subgenera. These are *Sepioteuthis, Lolliguncula* (*Lolliguncula*), *Lolliguncula* (*Loliopsis*), *Uroteuthis* (*Uroteuthis*), *Uroteuthis* (*Photololigo), Loliolus* (*Loliolus*), *Loliolus* (*Nipponololigo*), *Loligo* (*Loligo*) and *Loligo* (*Alloteuthis*). However, in the years following the 1988 Workshop, new observations and cladistic analyses on morphological (e.g., Alekseev 1989, Anderson 1996) and molecular (e.g., Brierley et al. 1996, Anderson 2000) characters added new parameters to the still-problematic status within the family. Another workshop on loliginid systematics was convened during the CIAC 2003 meeting in Thailand. One goal of the workshop was to resolve differences in generic-level classification of the family. The loliginid taxonomists reached consensus that a new classification is appropriate, which includes ten genera and nine subgenera as valid (Vecchione et al. 2005). Additional subgenera remain undescribed or undetermined. The revised classification is: *Loligo, Afrololigo, Alloteuthis, Doryteuthis* (*Doryteuthis*), *Doryteuthis* (*Amerigo*), *Heterololigo, Loliolus* (*Loliolus*), *Loliolus* (*Nipponololigo*), *Lolliguncula* (*Lolliguncula*), *Lolliguncula* (*Loliopsis*), *Pickfordiateuthis*, *Sepioteuthis*, *Uroteuthis* (*Uroteuthis*), *Uroteuthis* (*Photololigo*), *Uroteuthis* (*Aestuariolus*).

Since these recent nomenclatural changes are rather complex and not yet universally accepted, we choose to use the former, long-standing classification summarized by Nesis (1987), as these generic and specific names are well established both in the scientific literature and in the fisheries. The newly proposed classifications of Vecchione et al. (2005), however, are reported within brackets as a matter of information.

Genus *Loligo* Lamarck, 1798
Subgenus *Loligo* Lamarck, 1798 (s.s.)
Loligo chinensis Gray, 1849
[*Uroteuthis* (*Photololigo*) *chinensis*, Vecchione et al. 1998, Vecchione et al., 2005]
Fig. 1A–J

Loligo chinensis Gray, 1849: 74 (original description); type locality: China.—



Map 1. Geographical distribution of *Loligo chinensis*, (shaded areas); black dots, present material, site-specific localities.

Tryon, 1879: 145 (re-description of the type).—Natsukari & Okutani, 1975: 85, text-Figs. 1–4 (re-description of the type).—Okutani, 1980: 33, Fig. 38.—Nesis, 1982: 141, Figs. 37i–k; 1987: 151, Figs. 37i–j.— Roper et al. 1984: 86.—Brakoniecki, 1986: 28–29.—Okutani et al. 1987: 97.

Loligo indica, Hoyle, 1886: 156, pl. 26 Fig. 1–10 (non Pfeffer 1884); type locality: Arafura Sea, south of Papua New Guinea.

Loligo etheridgei Berry, 1918: 243, Figs. 28–38, pls. 67–69, 1 table, type locality: Australian Sea.—Adam, 1954: 136, Figs. 7–9, 1 table, Dobo, Aru Is., Arafura Sea.

Loligo formosana Sasaki, 1929: 109, text-Fig. 161, pl. 30, Fig. 13, 1 table, type locality: Tainan market.—Voss & Williamson, 1971: 58, Figs. 19, 20, 22, pl. 14, Hong Kong.

Loligo singhalensis, Okutani, 1980.—Nesis, 1982, 1987.

Doryteuthis singhalensis, Voss, 1963.—Voss & Williamson, 1971.—Roper et al. 1984.—Silas, 1986.

Photololigo chinensis, Natsukari, 1984a: 232.—Dunning, 1998: 774.

Loligo (*Photololigo*) *chinensis*, Okutani, 1990: 61, Fig. 74.

Uroteuthis (*Photololigo*) *chinensis*, Vecchione et al. 1998: 218.—Vecchione et al. 2005.

FAO vernacular names.—En-Mitre squid; Fr-Calmar mitre; Sp-Calamar mitrado.

Type locality.—Canton fish market, China.

Distribution.—*Loligo chinensis* is an Indo-Pacific species (Map 1). Its distribution extends from the western Pacific: Japan, South China Sea by Gray (1849), Wakiya & Ishikawa (1921); Hong Kong by Voss & Williamson (1971), as *L. formosana*; Philippines by Voss (1963), as *L. singhalensis*; Indonesia by Adam (1954) as *L. etheridgei*; northern, western and eastern Australian waters by Berry (1918), as *L. etheridgei*; Yeatman & Benzie (1994); to the eastern Indian Ocean: Andaman Sea, Thailand by Natheewathana (1992); Bay of

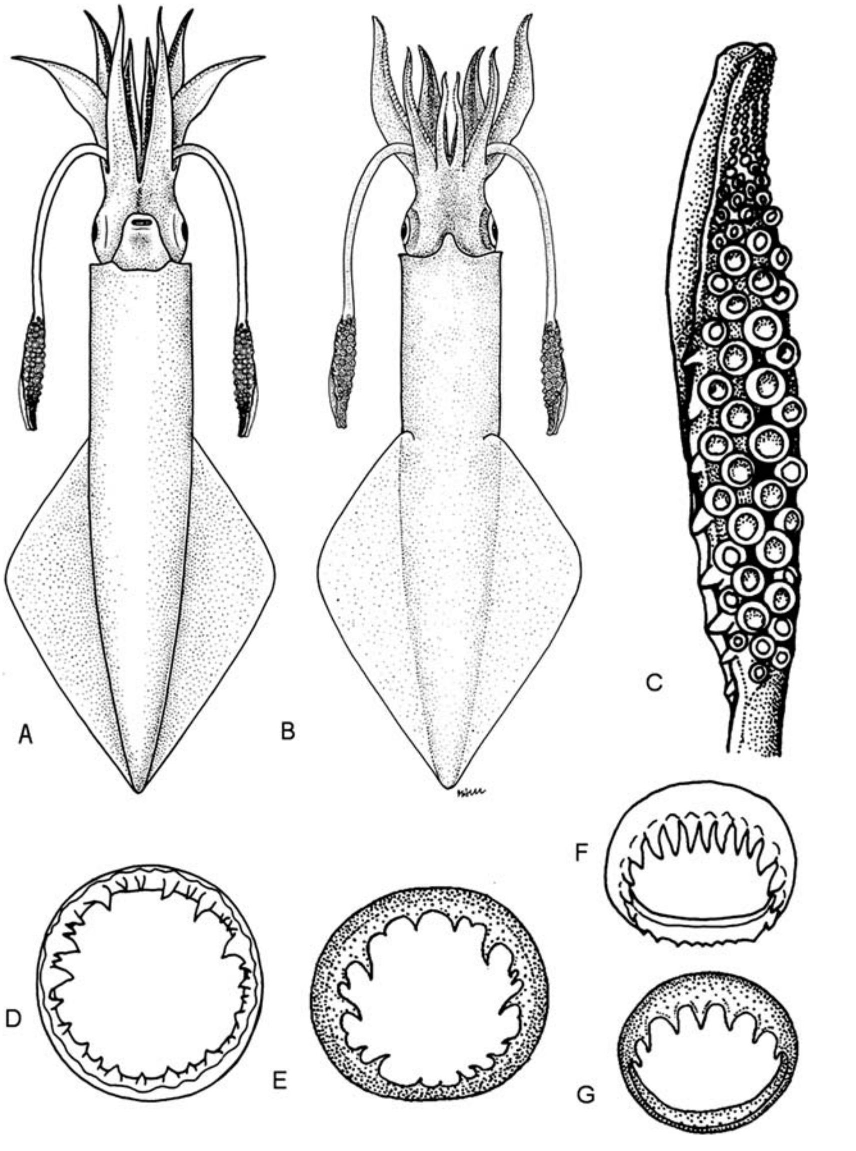


Fig. 1. A–G. *Loligo chinensis* Gray, 1849. A, ventral view (Roper et al. 1984). B, dorsal view (redrawn from Roper et al. 1984; as *Loligo singhalensis*). C, tentacular club (Roper et al. 1984). D, tentacular club sucker ring (Roper et al. 1984). E, tentacular club sucker ring (Roper et al. 1984; as *L. singhalensis)*. F, arm III sucker ring (Roper et al. 1984). G, arm III sucker ring (Roper et al. 1984, as *L. singhalensis*). H–J. *Loligo chinensis* Gray, 1849. H, hectocotylus (Dunning and Lu 1998). I, hectocotylus (Roper et al. 1984, as *L. singhalensis*). J, gladius (Nateewathana 1992).

Bengal in the present work; Chikuni (1983), Silas (1986) as *Doryteuthis singhalensis*.

Material examined.—Forty-five specimens of *Loligo chinensis* (24 males, 21 females) from the eastern side of the Bay of Bengal (IIOE) were examined. See Appendix 1A for detailed locality and capture data. All measurements and relative indices are reported in Appendix 2A. Table 1A gives data on measurements and indices of morphometric characters by sex and stage of maturity. Selected ranges of indices are reported in Table 8.

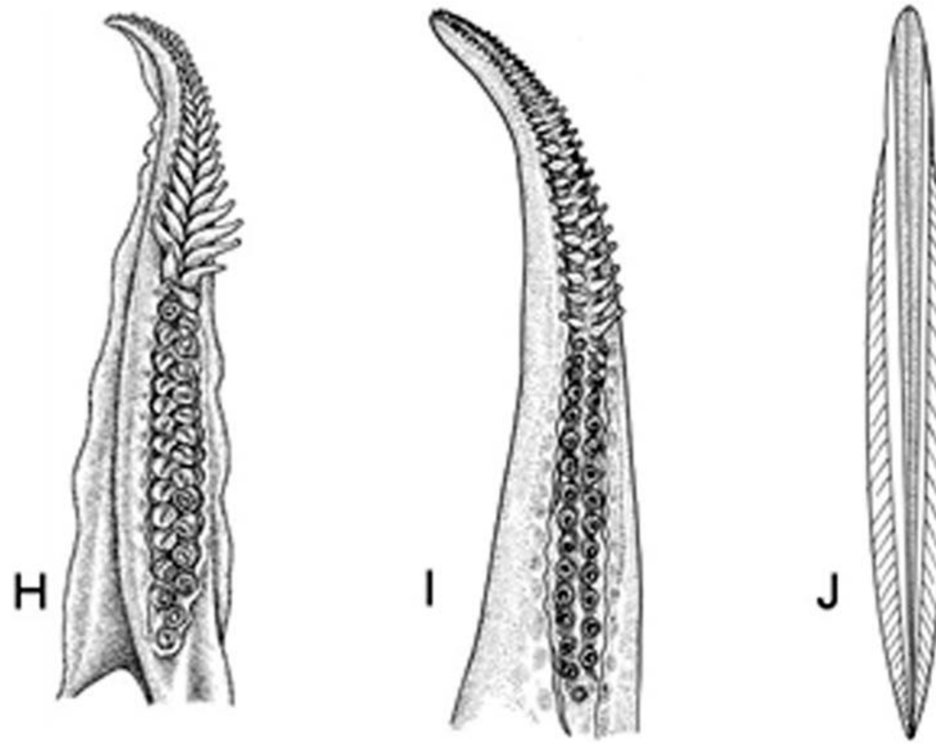


Fig. 1.—Continued.

Diagnosis.—Fin length in adults greater than 60% of mantle length (Fig. 1A, B). Hectocotylized portion of the left arm IV from 33% to 50% of total arm length (Fig. 1H, I). Arm sucker rings with 10–15 stout, pointed, conical teeth distally, the proximal margin smooth; occasionally with rudimentary teeth only (Fig. 1F, G). Largest club sucker rings with 20–30 teeth, very unequal in size: large teeth (about ten) alternate with small, sometimes very small, teeth (Fig. 1D, E). Gladius rather narrow: gladius width 6–8% of gladius length (Fig. 1J). One photophore present on each side of the ink sac.

Description.—The mantle is cylindrical and tapers posteriorly to a bluntly conical tip; mantle width 20–30% of ML, widest in its anterior part. A cutaneous ridge may be present or absent on the ventral surface of mantle in adult males: Voss & Williamson (1971), as *Dorytheuthis singhalensis*, present; Nesis (1987), as *Loligo chinensis*, absent; Okutani (1980), as *L. chinensis*, present; present material, absent.

The fins are rhombic, with anterior and posterior margins almost straight (posterior margin only slightly concave). Fins are longer than wide, become more accentuated with growth; fin length reaches 0.67 of mantle length, fin length index (FLI) up to 65–70%; fin width is about half the length of the mantle, fin width index (FWI) up to 58%, present work.

The head is stout, slightly narrower than the mantle at the mantle opening.

The arms are muscular, moderately long (longest arm attains 35% of mantle length (Okutani et al. 1987); the arm formula is 3.4.2.1 (Natsukari & Okutani 1975).

The arm suckers are biserial and of medium size. Proximal suckers on arms II and III in males slightly enlarged (Brakoniecki 1986). Chitinous sucker rings bear from 10–15 stout, acutely pointed, conical teeth on the distal margin. The proximal margin is smooth, but sometimes bears rudimentary "teeth-like" projections. The left arm IV is hectocotylized in males in its distal half by the modification of suckers and stalks into fleshy, cone-shaped papillae; hectocotylized arm index (HcLI) up to 70%; mature males have a secondary sexual modification of enlarged proximal suckers on arms II and III (Brakoniecki 1986). Suckers on the ventral series are slightly larger than those on the dorsal series.

The tentacles are moderately long and slender. Clubs are slender and rather long; club length index (ClLI) 20–35% (Fig. 1C). Club suckers quadriserial, those of the median rows slightly larger (1.2–1.5 times larger, Natsukari & Okutani 1975, Okutani et al. 1987) than those of the lateral rows. The large suckers of the manus bear 20–30 conical, stout, sharp teeth around the whole margin, greatly variable in size; among these, about 10 large teeth alternate with smaller, and even very small, inconspicuous teeth (0–4) in a line.

Buccal lappets with small suckers.

A pair of photophores is present on the ink sac, one on each side. Based on this character alone, the species should be included in the genus *Photololigo* (Natsukari, 1984a).

The gladius is rather narrow; gladius width 6–8% of gladius length (Okutani et al. 1987).

The relative indices obtained for this species in different studies, as well as data in the present work, are reported in Table 1C for comparison.

Biology.—The biology of *L. chinensis* is still poorly known, and most basic biological information is lacking (see also Natsukari & Tashiro 1991). A neritic species, *L. chinensis* has been reported within a depth range of 15–170 m, and its spawning period is likely to extend throughout the year (Roper et al. 1984, as *D. singhalensis*).

A thorough review of the cephalopod resources of Thailand (Chotiyaputta 1993a) reports a year-round spawning season with two main peaks (March–June and August–November), a fecundity of 3000–11,000 eggs and a length at 50% maturity of 160 mm and 140 mm mantle length (ML) for males and females, respectively. Subsequent age analysis revealed that *L. chinensis* matured earlier during the warmer summer period than in the cooler winter period, suggesting that maturity is governed more by individual size than by age (Jackson 1993). Probably one of the largest loliginid species of the Indo-Pacific region, its mantle length has been reported up to 490 mm for males and 310 mm for females (Voss & Williamson 1971, as *D. singhalensis*), and a length-weight relationship was computed for the population from the Gulf of Thailand (Chotiyaputta 1993b).

Our material consists of *L. chinensis* specimens caught during the month of March at depths between 36 and 81 m; no specimen was sexually mature, although several were in a maturing stage.

Fishery.—A commercially important species throughout its range (Roper et al. 1984), *L. chinensis* is reported to be exploited currently in the Yellow Sea and East and South China Sea, and it probably constitutes, together with *L. edulis,* the majority of the Chinese squid catch (Guo & Chen 2000). It is quite extensively exploited by the Hong Kong fishery (Voss & Williamson 1971, Okutani 1980, Chikuni 1983) and the Taiwanese trawlers.

Of occasional commercial relevance in Japanese waters (Voss 1973), *L. chinensis* is likely to represent a small part of the squid catch around the Philippine Islands, as well, and it constitutes about half of the trawl catch of squid in the South China Sea (Chikuni 1983, Chan & Noor 1986).

Loligo chinensis is one of the most important species for the Gulf of Thailand fishery (Chotiyaputta 1993a, Chantawong & Suksawat 1997). It also is likely to constitute a substantial portion of the catch in the Malaysian waters (Chikuni 1983), where it is reported as the dominant squid species for some local fisheries (Ashirin & Ibrahim 1992). Probably it is also well represented in the Indonesian fisheries (Arafura Sea, Java Sea; Chikuni 1983), and it is one of the most important commercial cephalopod species in northern Australian waters (Dunning 1982), along with *L. singhalensis*.

As far as the Indian Ocean fishery is concerned, this species is well represented in squid catches from the southeastern waters of the Bay of Bengal (Thai coasts, Andaman Sea; Chikuni 1983, Chotiyaputta 1993a, Chantawong 1994). It is reported among the commercially exploited squid species of India (Silas 1986, as *D. singhalensis*) and Sri Lanka (Chikuni 1983). This species also is assumed to be present in the Arabian Sea (Chikuni 1983, Siraimeetan 1990, as *D. singhalensis*), even though it is not clear what proportion it contributes to the fishery landings there because of the confusion in the loliginid nomenclature.

Remarks.—After its original description, this species was re-described several times under different names, as summarized by Natsukari & Okutani (1975), who also give a re-description of the type-specimen. Those authors synonomized *L. indica* Hoyle 1886, *L. etheridgei* Berry, 1918, and *L. formosana* Sasaki, 1929 with *L. chinensis*.

Our specimens agree fairly well with the re-description provided by Natsukari & Okutani (1975), even though many specimens are in poor condition. The long-term confusion inherent in the convoluted regional loliginid nomenclature makes it very difficult to assess the true importance of this species to the fisheries. However, it seems probable that *L. chinensis* is under-reported, at least in the western areas of its range.

Loligo duvaucelii d'Orbigny, 1835, in Ferussac and d'Orbigny 1834–1838
[*Uroteuthis* (*Photololigo*) *duvaucelii*, Vecchione et al. 1998, Vecchione et al. 2005]
Fig. 2A–E

Loligo duvaucelii d'Orbigny, 1835, in Ferussac and d'Orbigny, 1834–1838: 318, pl. 14, pl. 20, Figs. 6–16.—Adam, 1954: 132–136, Figs. 5–6.—Voss & Williamson, 1971: 60–62, pl. 17, Figs. 19, 20, 22.—Okutani, 1980: 35, Fig. 42.

?*Loligo sumatrensis*, Brock, 1887: 595 (in Adam 1954).

Loligo duvauceli d'Orbigny, 1835, 1839, 1848; Voss, 1963: 71–74, Fig. 12.—Adam, 1973: 18–19, Figs. 1–3; Nesis, 1982: 145, Fig. 37s–u.—Roper et al. 1984: 87–88.—Brakoniecki, 1986: 29–30.—Jothinayagam, 1987: 43–46, Fig. 15.—Nesis, 1987: 154, Fig. 37 q–s.—Nateewathana, 1992: 7–10, Fig.2.

Loligo indica Pfeffer, 1884: 64, Figs. 3, 3a.—Goodrich, 1896: 7, Figs. 20–28.—Massy, 1916: 218, pl. 23, Fig. 9, pl. 24, Fig. 11.

Loligo galatheae Hoyle, 1885: 183–184, 1886: 159–160, pl. 27, Figs. 1–12.

?*Loligo oshimai* Sasaki, 1929: 123–125, pl. 30, Fig. 14, text Figs. 162–164.

Photololigo duvaucelii, Natsukari, 1984a: 231.—Dunning, 1998: 775.

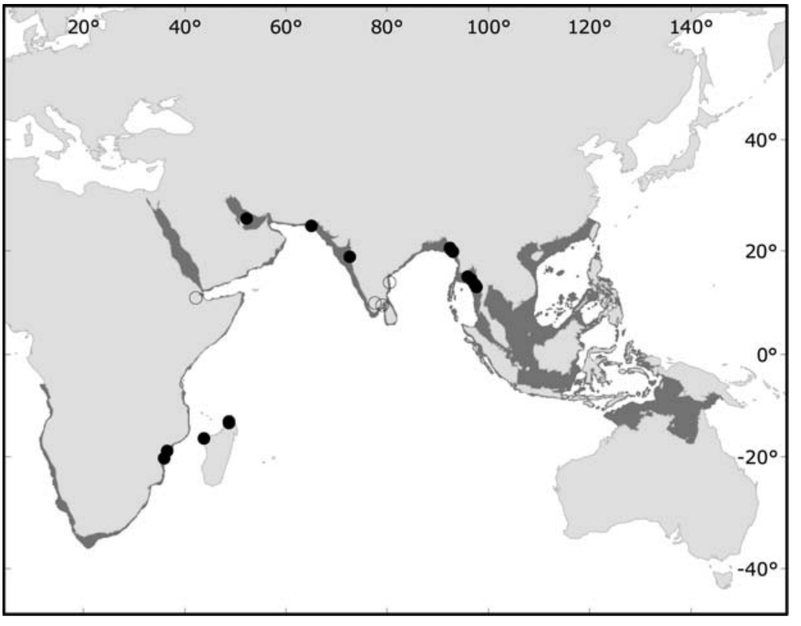
Loligo (*Photololigo*) *duvaucelii*, Okutani, 1990: 61, Fig. 75.

Uroteuthis (*Photololigo*) *duvaucelii*, Vecchione et al. 1998.

FAO vernacular names.—En - Indian squid; Fr - Calmar indien; Sp - Calamar indico.

Type locality.—India and other sites. (Indo-Pacific: Sumatra, coast of Malabar, Bombay, Pondichery, Batavia, Moluccas, fide d'Orbigny 1835 and Adam 1973).

Distribution.—An Indo-West Pacific species (Nesis 1982, 1987; Roper et al. 1984), *Loligo duvaucelii* extends its distribution throughout the Indian Ocean (Map 2), from the South African coasts



Map 2. Geographical distribution of *Loligo duvuacelii*, (shaded areas); black dots, present material, site-specific localities; open circles, present material, general localities.

(Angola, Mozambique by Adam 1962), the Red Sea (Adam 1973) and the Arabian Sea (Sarvesan 1974, Perera 1975, Oommen 1976, Chikuni 1983, Kasim 1985, Silas 1986, Rao 1988, Siraimeetan 1990, Vidyasagar & Desmukh 1992, Mohamed 1993, 1996), eastward to the Bay of Bengal, Sri Lanka (Voss 1973, Sarvesan 1974, Chikuni 1983, Silas 1986, Mohan and Rayudu 1986, Jothinayagam 1987, Jasmine et al. 1989) and the Andaman Sea (Voss 1973, Chikuni 1983, Nateewathana 1992, Chotiyaputta 1993a, 1997). A common Malaysian squid (Sumatra, Malaysia, Thailand by Voss & Williamson 1971, Voss 1973, Latif 1982, Chikuni 1983, Chotiyaputta 1993a), *L. duvaucelii* also is very abundant in Philippine waters (Voss 1963, Voss & Williamson 1971, Chikuni 1983) and moderately abundant in the South China Sea (Shin 1982, Chikuni 1983). It has also been recorded in the West Pacific north to Formosa Island and the Taiwan Strait (Adam 1962, Voss 1963, Roper et al. 1984) and south to the Java and Arafura Seas (Chikuni 1983).

Material examined.—208 specimens of *L. duvaucelii* (65 males, 132 females, 11 juveniles) were examined from Indian Ocean, mostly IIOE: 24 from the Arabian Sea, eight from Djibuti (Somalia), 52 from Madagascar and 124 from the Bay of Bengal. See Appendix 1B for detailed localities and capture data. All measurements and relative indices are reported in Appendix 2B. Table 2A, B give general and regional data on morphometric measurements and indices by sex and stage of maturity. A comparison of measurements and indices reported by various authors is provided in Table 2C. Selected ranges of indices are reported in Table 8.

Diagnosis.—Fin length in adults up to 60% of mantle length (see Table 2C) (Fig. 2A). More than half the length of the left ventral arm hectocotylized in males, up to 75% in present work (see Table 2A, C) (Fig. 2D). Suckers of lateral arms of males (greatly) enlarged. Arm

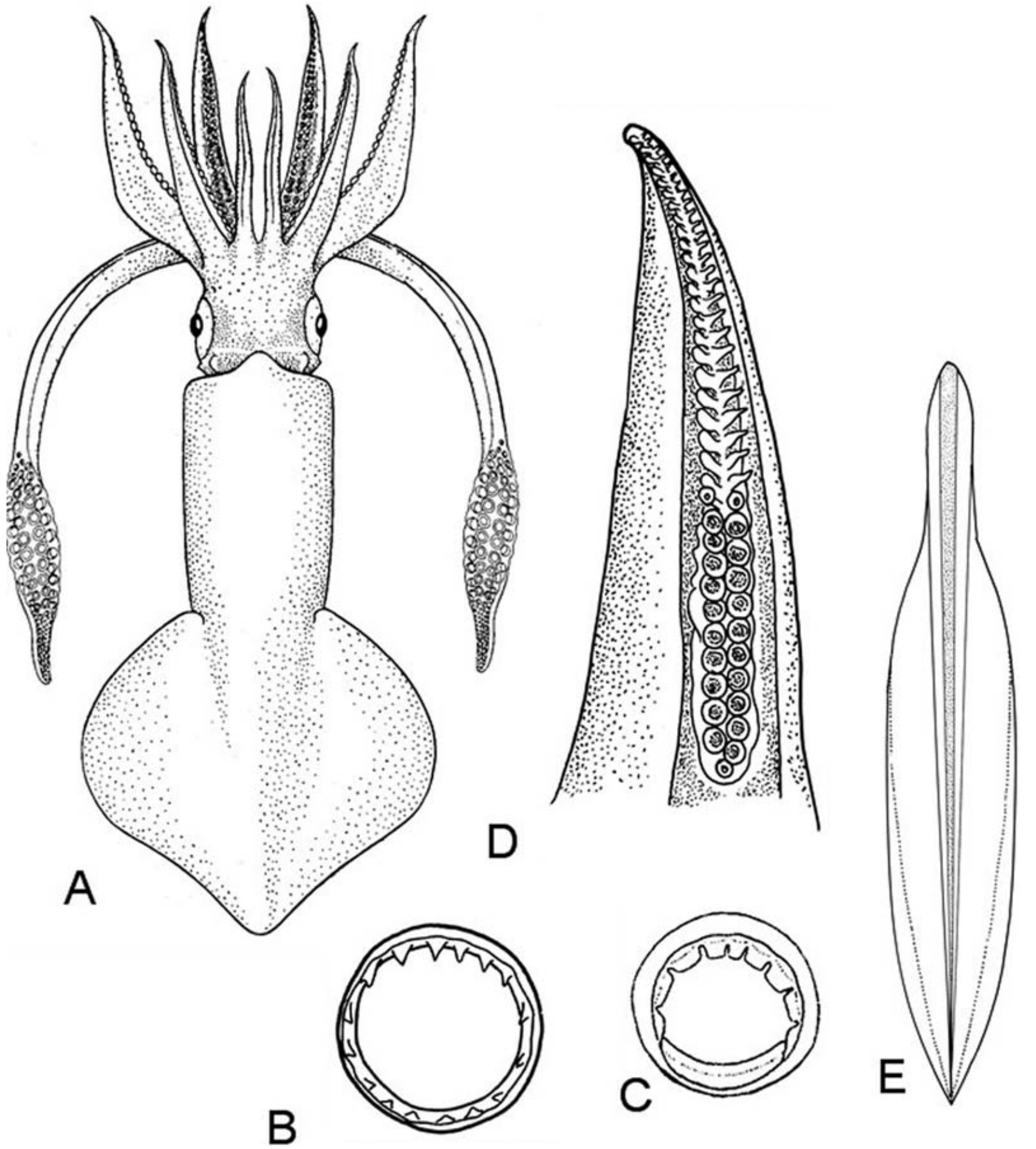


Fig. 2. *Loligo duvaucelii* d'Orbigny, 1835. A, dorsal view (Roper et al. 1984). B, tentacular club sucker ring (Roper et al. 1984). C, arm III sucker ring (Roper et al. 1984). D, hectocotylus (Nesis 1982/1987). E, gladius (Voss & Williamson 1972).

sucker rings with broad, large, square teeth (five to nine) on the distal margin in females and around the entire ring (up to 18) in males (Fig. 2C). Club sucker rings with 14 to 20–22 short, sharp teeth regularly spaced around the entire margin (Fig. 2B). Two oval luminous organs (photophores) present along the ink sac, one on each side.

Description.—When in good condition, our material conforms to the general descriptions given by Adam (1954) and Voss (1963). A more delicate appearance (i.e., more slender mantle, smaller head), however, is evident in the specimens from Djibuti (Somalia) (Table 2B-2).

Mantle moderately long and slender, cylindrical for about half (slightly more than half) its length, then it tapers gently into a blunt tip. Anterior margin with a small rounded lobe in the dorsal midline.

Fins gently rhombic, broad, widest approximately at the middle point of their length; fin length occupies more than half of mantle length (up to 60%). The anterior and posterior margins are nearly straight, the lateral angles very rounded.

Head broad, slightly narrower than the mantle; eyes large.

Arms moderately long; arm formula 3.2.4.1 (Voss 1963). Sexual dimorphism is noticeable in sucker size and dentition, even though not always as strongly evident in the material we examined as stressed by other authors (e.g., Voss 1963).

The suckers of all arms in females are similar in size and dentition: 4–10, usually 6–7, broad, square, bluntly edged teeth occur along the distal margin whereas the proximal margin is smooth. Very often the central tooth (teeth) is (are) more slender and slightly pointed, as evidenced also in the present material. As a secondary sexual modification in males, suckers of arms II and III usually are enlarged, sometimes greatly so, and sucker rings bear several [usually around ten, but up to 18 according to Adam (1954)] broad, square, truncate teeth that occupy almost the entire margin. These teeth are shorter than those of females. Small, inconspicuous denticles may be present along the proximal margin (Adam 1973).

Left ventral arm hectocotylized in males. Usually about half of the arm bears from 12–22 pairs of normal suckers; up to 30 pairs are present on our specimens from the east African coast, in which the modified portion of the hectocotylized arm is unusually short. Two rows of fleshy papillae occur distal to the suckers. They vary in size and form: those of the ventral row are cone-shaped, sometimes very "fat" and long (e.g., present material, Bay of Bengal). Generally they are fused with the protective membrane for at least their basal portion (more generally up to 0.33 of their length). The papillae of the dorsal row usually are thinner and shorter. Minute suckers are present on the tips of these papillae. The modified portion extends for more than half of the arm length, up to 75% in some of our material (Tables 2A, C). A peculiar feature is noted in some of the specimens we examined: at the base of the arm the dorsal protective membrane is slightly expanded to form a kind of crest that enfolds the first basal suckers. This crest is present in a few specimens from the southwestern and southeastern coasts of India, i.e., off Cochin (PJ 308 and 309) and off Mandapam (PJ 313).

Tentacles long; clubs large, up to 45–50% of ML; club suckers quadri-serial, those of the medial rows slightly larger (about 1.5 times) than those on the lateral rows. Sucker rings have 14–22 acute, conical, regularly spaced teeth around the entire margin. Smaller, almost inconspicuous denticles may be present between adjacent conical teeth.

Buccal membrane seven-pointed; each lappet bears up to 5 small suckers.

A pair of ovoid luminous organs (photophores) is located on the ventral side of the ink sac, near the anus. Details of the morphology and physiology of these organs are presented by Prinngennies & Jorgensen (1994) and Prinngennies et al. (2001). On the basis of this character, the species should be included in the subgenus *Photololigo* Natsukari (1984a).

Gladius with a long, straight edged vane in mid-portion and a short rachis (Fig. 2E).

Biology.—In recent years, increased attention has been paid to the biology of *L. duvaucelii*, principally because of the importance of the fishery for this species in the Indian (both west and east coasts) and Thai waters. A list of local names of this species in Indian waters is given in Meiyappan & Mohamed (2003).

While its embryonic development and hatching were observed in the laboratory (Asokan & Kakati 1991), the biology of the species by field data and information was studied from the Indian waters by Oommen (1976), Silas (1986), Rao (1988), Vidyasagar & Deshmukh (1992), Mohamed (1993, 1996), Mohamed & Rao (1997), Rahim & Chandran (1984), Karnik & Chakraborty (2001), Karnik et al. (2003). Field studies also were conducted from the Gulf of Thailand and the Andaman Sea by Chotiyaputta (1982, 1993a, 1993b, 1994, 1997), Supongpan (1984, 1988), Manoch & Shunji (1992) and Supongpan & Sinoda (1998).

According to information from statolith age readings (Chotiyaputta 1997), the life cycle of *L. duvaucelii* would be about one year, which, as expected, is shorter than estimates obtained by length frequency analysis (e.g., Kasim 1985, Mohamed 1996, Mohamed & Rao 1997). The spawning period appears to be quite prolonged, almost all year round, with peaks in different months, principally in spring and autumn. Spawning aggregations occur in the post-monsoon months along the west coasts of India (Mohamed 1993) and seem to be dependent upon the SW and NE monsoons in the western part of the Gulf of Thailand (Supongpan & Sinoda 1998). Size at 50% maturity is 90–130 mm ML for females and 70–150 mm ML for males. Observations on growth after sexual maturity is reached indicate an extended reproductive phase within the life cycle, i.e., a non-strictly semelparous reproduction (Mohamed 1993), as is the case in other squid (Rocha et al. 2001). Other studies have confirmed an allometric growth (Silas 1986, Mohamed 1996, Karnik & Chakraborty 2001), with females growing faster than males; however, males ultimately attain a greater size and age. Maximum reported size of males is 320 mm ML from Thai waters (Chotiyaputta 1993a) and 330 mm ML along the west coast of India (Meiyappan & Mohamed (2003).

Recently, a first attempt to culture *L. duvaucelii* was made from eggs collected in the field (Prinngennies et al. 2000). Hatchlings were fed with rotifers and *Artemia* and survived for several weeks.

Fishery.—*Loligo duvaucelii* is one of the most common species among the Indo-Pacific loliginids, and it was reported to be the most important squid species for the Indian fishery during the years 1972–1984 (Ramachandran 1987). It was considered the most promising species for the Indian dried squid industry (Sarvaiya 1991), and it constituted, along with *L. chinensis*, about 90% of the squid catches of Thailand during the year 1988, probably a typical situation for that area (Chotiyaputta 1993a).

Known to be fairly important for the fisheries of the eastern Arabian Sea (Chikuni 1983), this species constituted 68% (i.e., 4795 metric tons) of the squid caught north of and off the Gujarat coast during December 1983–March 1984 (northwest coastal India, Siraimeetan 1990). The catch continued at a median annual value of over 5000 metric tons into the middle 1990's (Mohamed & Rao 1997). It formed about 8% of the trawl landings at Bombay with a standing stock of 990 metric tons and an annual stock of 2150 metric tons, according to Vidyasagar & Deshmukh (1992). In this area, cuttlefish (Sepiidae) constitute the dominant species among cephalopods for all capture techniques (Siraimeetan 1990), but *L. duvaucelii* represented 68% of the catches of the Mangalore trawlers of central west India (Silas 1986). The species is present in small quantities throughout the year in the trawl fishery off Cochin, southwest India, and it is the dominant squid caught as a by-catch by the shrimp trawlers (Silas 1986).

Loligo duvaucelii also is reported to constitute a significant fraction of the total cephalopod production of Vizhinjam, southwestern India (i.e., about 42%, Silas 1986), where it is caught by shore seine, boat seine, and hook and line.

Loliginid squids constitute 48% of the total Indian cephalopod captures versus 51% for sepiioids (1% for octopods). *Loligo duvaucelii* is by far the predominant squid species in that total, representing 49% of the west coast cephalopod landing (20–330 mm ML) and 24% of east coast landings (30–180 mm ML). Peak Indian cephalopod landings occurred in 1995 at 116,753 metric tons and averaged around 110,000 metric tons from 1996 through 2000 (Meiyappan & Mohamed 2003).

As for the Bay of Bengal, *L. duvaucelii* is important for all the main eastern Indian landing places (i.e., Waltair, Kakinada, Madras, Mandapam, Vishakhapatnam), where it constitutes the most abundantly caught squid species (Mohan & Rayudu 1986, Silas 1986, Kripa et al. 1996). It also is reported as the most common species landed along the Andaman Sea coast of Thailand (Nateewathana 1992, Chantawong 1994).

In the Gulf of Thailand, *L. duvaucelii* is caught by various fishing gears, such as otter trawl, pair trawl, squid night-light attraction, push net, and hook and line; in 1988 the species contributed about 45% of the 67,176 metric tons of landed squid (Chotiyaputta 1993a).

Loligo duvuacelii is one of the main commercial squid species for the Philippine fishery (Voss 1963, 1973; Chikuni 1983), and it is reported among the five major squid species known in the Malaysian area (Latif 1982). It is among the most common squid species caught in the Java Sea (Sudjoko 1987).

Loligo duvaucelii is abundant in the South China Sea (Chikuni 1983, Guo & Chen 2000), and it is reported among the commercial squid species of the Hong Kong fishery (Shin 1982). However, very little information is known about the abundance and landings of this species in the Yellow and East China Seas (Chikuni 1983).

Loligo edulis Hoyle, 1885
[*Uroteuthis* (*Photololigo*) *edulis*, Vecchione et al. 1998, Vecchione et al. 2005].
Fig. 3A–H

Loligo edulis Hoyle, 1885: 186; 1886: 152, pl. XXIII, Figs. 1–9.— Sasaki, 1929: 107–109, Figs. 57–59, pl. XIII, as form *nagasakiensis* and form *grandipes*.—Voss, 1963: 67, Figs. 11a–e.—Voss & Williamson, 1971: 57, Figs. 19,20,22, pls. 14–15.—Adam, 1973: 19, Figs. 4–5.—Okutani, 1980: 33, Figs. 36–37.—Nesis, 1982: 141, Figs. 37a–e, 1987: 151, Figs. 37b–f.—Roper et al., 1984: 88.—Brakoniecki, 1986: 27–28.—Okutani et al., 1987: 99.

Loligo chinensis, Sasaki, 1914: 601.—Wakiya and Ishikawa, 1921: 279 (non Gray 1849).

Loligo kensaki Wakiya and Ishikawa, 1921: 283, pl. 2, Fig. 9.

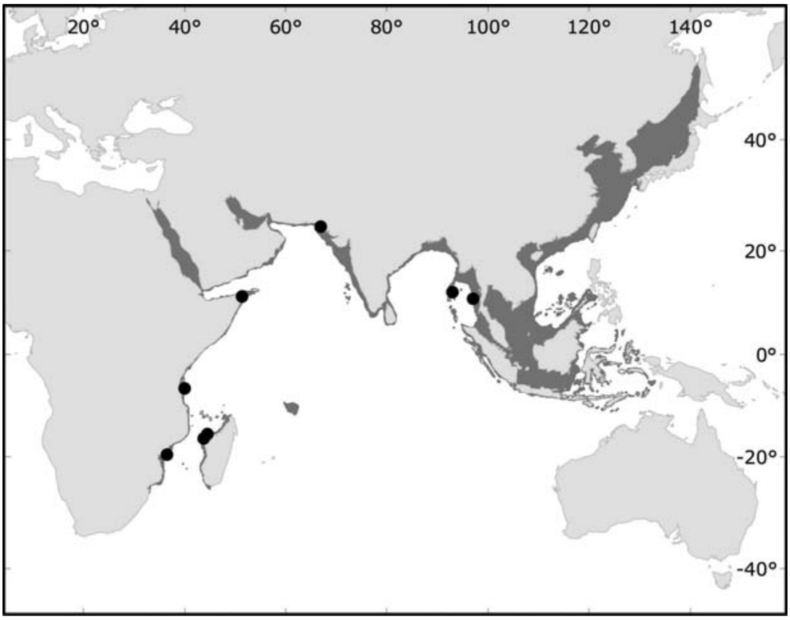
Loligo budo Wakiya and Ishikawa, 1921: 258, pl. 2, Figs. 1,10.—Okada, 1927: 174, Fig. 2.—Roper et al. 1984: 89–90.—Nesis, 1982: 144, Figs. 37z, 37zh, 1987: 151, Figs. 37G–H.—Okutani et al. 1987: 101.

Loligo singhalensis, Adam, 1954 (fide Korzun & Alekseev, 1991), non Ortmann, 1891.

Doryteuthis kensaki Wakiya and Ishikawa, 1921: 283, Fig. 4, pl. 1: Fig. 9.—Okutani, 1973: 94, Fig. 40.

Photololigo edulis, Natsukari, 1984a: 230.—Dunning, 1998: 776.

Loligo (*Photololigo*) *edulis*, Okutani 1990: 57, Fig. 67.



Map 3. Geographical distribution of *Loligo edulis*, (shaded areas); black dots, present material, site-specific localities.

Uroteuthis (*Photololigo*) *chinensis*, Vecchione et al. 1998: 318.

FAO vernacular names.—En - Swordtip squid; Fr - Calmar epee; Sp - Calamar espada.

Type locality.—Yokohama Fish Market, Japan.

Distribution.—An Indo-Pacific species (Nesis 1987), *Loligo edulis* is fairly common and relatively abundant in the western Pacific (Map 3), from northern waters (East China Sea, Japan Sea by Okutani 1973, 1975, 1980; Okutani et al. 1987; Chikuni 1983; Natsukari & Tashiro 1991; Kubota et al. 1993; Zheng 1994) to the tropical seas (Indonesia, Java Sea, Malaysia, Thailand by Latif 1982, Shin 1982, Chikuni 1983, Chan & Noor 1986, Okutani et al. 1987, Sudjoko 1987, Sodikin 1992, Chotiyaputta 1993a), south to northern Australia (Okutani 1980, Okutani et al. 1987, Dunning 1982, Chikuni 1983, Yeatman & Benzie 1994). The distribution of *L. edulis* also extends throughout the Indian Ocean, from its southeastern waters, i.e., the Andaman Sea, Thailand, (Nateewathana 1992, Chotiyaputta 1993a) and the Bay of Bengal (Chikuni 1983, present work), to the Arabian Sea, including the Gulf of Aden, the Gulf of Oman, and the Persian Gulf (Zuev 1971, Voss 1973, Shvetsova 1974, Chikuni 1983, present work), the Red Sea (Adam 1973), and southward to Mozambique (East African coast by the present study; Saja de Malha Bank by Zuev 1971, Voss 1973; Mozambique Channel by Korzun 1992).

Material examined.—Thirty-six specimens of *L. edulis* (11 males, 15 females, 10 juveniles), 13 from the Bay of Bengal, 6 from the Arabian Sea and 17 from the coasts of East Africa (Indian Ocean, IIOE). See Appendix 1C for detailed locality and capture data. All measurements and relative indices are reported in Appendix 2C. Data on measurements and indices of morphometric characters by sex and stage of maturity are given for the total collection of study material (Table 3A) and for regional areas (Tables 3B, 1–3). Selected ranges of indices are reported in Table 8.

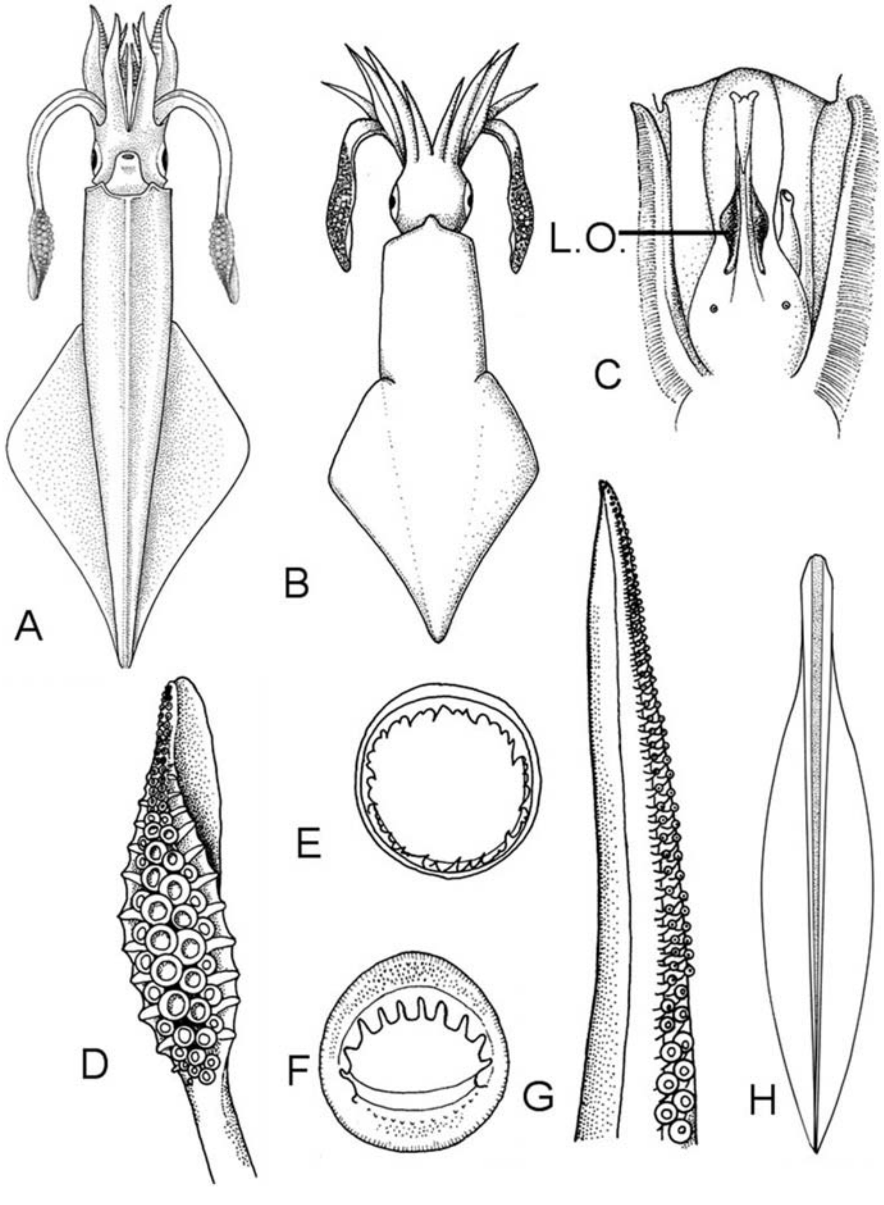


Fig. 3. *Loligo edulis* Hoyle, 1885. A, ventral view (Roper et al. 1984; as *L. edulis* form *edulis*). B, dorsal view (Roper et al. 1984; *as L. edulis* form *budo*). C, photophores (L.O.) on ink sac (Roper et al. 1984). D, tentacular club (Roper et al. 1984). E, tentacular club sucker ring (Roper et al. 1984). F, arm sucker ring (Roper et al. 1984). G, hectocotylus (Roper et al. 1984). H, gladius (Voss & Williamson 1972).

Diagnosis.—Fin length in adults ranges from a little more than 50% up to 70% of mantle length (see Table 3A) (Fig. 3A, B). Hectocotylized portion of the left arm IV very long, up to 65–80% of its length (Fig. 3G). Arm sucker rings with up to a dozen (more often 6–8) long, slender, square-cut (bluntly-pointed) teeth on the distal margin; the proximal margin smooth, or only irregularly denticulate with inconspicuous denticles (Fig. 3F). Largest club sucker rings with up to 30–40 teeth very unequal in size: usually about 15–20 large, stout, sharp, conical, widely-spaced teeth, alternating with smaller ones, sometimes minute (from one to groups of three to four) (Fig. 3E). The gladius of "…usual form, the narrow anterior portion being less than 0.25 of the total length…" (Hoyle 1885: 187), has a broad rachis, with a large, oval vane with rounded margins (Voss 1963) (Fig. 3H). One luminous organ present on each side of the ink sac (Fig. 3C).

Description.—As far as many characters are concerned, the following description deals with very broad distributional limits, due to the polymorphic characteristics of *L. edulis* (see *Remarks* and Table 3A, B).

The mantle is moderately stout to elongate, cylindrical anteriorly, gradually tapered posteriorly to a blunt point. Mantle width 30–40% of mantle length. Mature males may be more slender (Okutani et al. 1987) and often are reported to bear a cutaneous ridge on their ventral mantle surface (Sasaki 1929: "…ordinarily present …"; Adam 1954 (as *L. singhalensis*, alias *L. edulis* following Korzun & Alekseev, 1991, Roper et al. 1984, Okutani et al. 1987, Nesis 1987). This cutaneous ridge, however, is not mentioned by Voss (1963) nor Adam (1973) in their description of specimens from the Philippines and from the Red Sea, respectively. No mature male was available in the present work, and no ridge was detected on the specimens examined.

Fins large, rhombic with the anterior margin slightly convex, the posterior margin gently concave, and the lateral angles rounded. Fins become slightly longer than wide in adult specimens (up to 70% of mantle length), their width reaching 60% of mantle length (usually slightly larger in females).

The head seems quite variable in its relative dimensions, having been described alternatively as "large" (Sasaki 1929, on "full length specimens"; Voss 1963), "small" (Hoyle 1885, Sasaki 1929, on "medium size specimens", Adam 1954) and even "cubic" (Okutani et al. 1987), with prominent eyes. Head width varies between 10–11% and 20–37% of mantle length (Voss 1963, Okutani et al. 1987).

Arms moderately long, 25–45% of mantle length. The arm formula is variable, 3.4.2.1 (Hoyle 1885, Sasaki 1929, Voss 1963, Okutani et al. 1987) or 4.3.2.1 (Okutani et al. 1987). The suckers are biserial, oblique and of medium-size, sometimes slightly larger in males (Voss 1963) and in the lateral arms (Adam 1973). The suckers on arms II and III of mature males are noticeably enlarged as a secondary sexual character (Brakoniecki 1986). Arm sucker rings bear up to a dozen (more often 6–8) long, slender, mostly squared, sometimes conical, but always flat-topped (blunt) teeth on the distal margin. They can be widely spaced or closely packed (also present material). The proximal margin is either smooth or slightly irregularly denticulate, with very low, rounded denticles (Adam 1973).

The left arm IV is hectocotylized in males for more than 0.75 of its length (HcLI up to 70–80 in mature males, Table 3A), by the modification of the suckers and stalks into fleshy, conical papillae, which may or may not bear small suckers on the tips. On the proximal part of the arm from six to then up to 27–30 pairs of normal suckers are present. The existence of different "forms" within the species *L. edulis* is based primarily on these variations.

Tentacles moderately long, slender. Clubs expanded, lanceolate; club length varies between 15% and 40% of mantle length (Fig. 3D). Club suckers quadriserial; medial suckers larger than the lateral ones (about 1.2 times greater diameter, Okutani et al. 1987). The largest club sucker rings bear up to 30–40 teeth around the entire margin, very unequal in size: often 15–20 large, sharp, widely-spaced, conical teeth alternate with much smaller ones, sometimes rather regularly (one to four smaller between two larger, Okutani et al. 1987).

Buccal lappets with several small suckers (from 2–3 up to14–15; Voss 1963, Sasaki 1929, Adam 1954, 1973). A pair of oblong photophores is present on the ink sac, one on each side.

The gladius is long and moderately narrow, 6–7 times longer than wide; the vanes are distinctly curved laterally; the rachis is about 0.2 the length of the gladius.

The relative indices obtained for *L. edulis* by different authors, as well as in the present work, are reported in Table 3C.

Biology.—An extensive review of the status of the biology and resources of *L. edulis* in the Japanese waters was published by Natsukari & Tashiro (1991). According to those authors, this species inhabits continental shelf waters in Japan and winters close inshore in shallow water. The spawning season extends throughout the year, with three detectable peaks in spring, summer and autumn, but the season is shorter in the northernmost part of the area. The life span is reported to be about one year (see also Natsukari et al. 1988). Juveniles feed preferentially on crustaceans, whereas the main food for the adults is fishes.

The size at which individuals become sexually mature shows great variability, depending on the season and locality. Most specimens of both sexes reach full maturity by 150–200 mm ML. The smallest size recorded for full maturity was 52 mm and 59 mm ML for males and females, respectively, while some specimens were not sexually mature at a size larger than 300 mm ML. Spawning grounds were recorded at different depths, from 30–40 m down to 100 m, on sandy bottom in coastal waters where warm oceanic currents inflow.

The analysis of several length-weight relationships obtained for *L. edulis* in different seasons and locations of the northwestern Pacific indicate a highly variable growth depending on season and area (Natsukari & Tashiro 1991). Data from northern Australia support an extended spawning season for the species and show that *L. edulis* in the Gulf of Carpentaria reaches sexual maturity at smaller sizes (70–80 mm ML) than the northern form (Dunning et al. 1994). *Loligo edulis* in the northwestern part of the Indian Ocean also is reported to reach sexual maturity at the small size of 70–80 mm (Shvetsova 1974) and even smaller (50–60 mm, Adam 1973), and its spawning period extends from fall to spring or even to the beginning of summer.

Fishery.—A medium to large-sized species, *L. edulis* has excellent flesh quality, and it is exploited throughout its distributional range (Roper et al. 1984). One of the principal commercial squid species of the Japanese market (Wray 1996), it constitutes one of the most important resources for the coastal fisheries of Kiushu and the southwestern Japan Sea, where the annual catch is estimated around 25,000 metric tons. It is caught throughout the year by jigging, set netting, bottom trawling and other gears (Natsukari 1991, Kubota et al. 1993).

Loligo edulis also is very abundant in the Yellow and East China seas (Chikuni 1983, Zheng et al. 1999), where, together with *L. chinensis*, it is believed to account for the majority of the Chinese squid catch (Chikuni 1983, Zheng 1994, Song et al. 1999, Ling & Zheng 2000).

It is vigorously exploited by the Hong Kong fishery, where it constitutes, together with *L. chinensis*, a large proportion (50–60%) of the annual cephalopod landings (Voss & Williamson 1971, Shin 1982), and it is believed also to be rather abundant in the South China Sea (Chikuni 1983). *Loligo edulis* is fished in the Malaysian waters (Latif 1982, Chan & Noor 1986), and it represents one of the main species of the Philippine and Indonesian fisheries (Voss 1973, Sodikin 1992, Sudjoko 1987). It also constitutes one of the most important commercial cephalopod species in the northern Australian waters (Dunning 1982).

Loligo edulis is highly abundant in the Andaman Sea, where it represents one of the main Thai squid resources (Chotiyaputta 1993a), but it is not mentioned within the cephalopod resources of India (Silas 1968, Rao 1973, Perera 1975, Silas et al. 1982, Silas 1986, Mohan & Rayudu 1986, Jothinayagam 1987, Siraimeetan 1990). However, its presence in the western Indian Ocean (i.e., Arabian Sea, Red Sea, East African waters) was confirmed (Zuev 1971, Adam 1973, Voss 1973, Shvetsova 1974, Chikuni 1983, Korzun 1992), even though its potential to the fishery there is still unknown. We suggest that the apparent absence of its occurrence in Indian waters is a matter of misidentification rather than of disjunct distribution.

Remarks.—*Loligo edulis* is characterized by a marked polymorphism, both by locality and by season (Okutani et al. 1987, Nesis 1987, Natsukari & Tashiro 1991). The existence of such a variety of "forms" whose taxonomic relationships are still not clear, makes the confident identification of the species rather complicated and the assessment of populations (stocks) rather difficult. After the original description by Hoyle (1885), who referred to one male specimen from the Yokohama Fish Market, Japan, the condition of maturity of which was not specified, the species was repeatedly redescribed by subsequent authors, as reported below and summarized in Table 3D.

Among the so-called *L. edulis*-type squid distributed throughout the western Pacific (Natsukari & Okutani 1975, Natsukari & Tashiro 1991), four species originally were recognized by Wakiya and Ishikawa (1921): *L. edulis* Hoyle, 1885, *L. chinensis* (non Gray, 1849), *L. kensaki* Wakiya & Ishikawa, 1921, and *L. budo* Wakiya & Ishikawa, 1921.

Three "forms" subsequently were identified by Sasaki (1929): *L. edulis* (non Hoyle, but corresponding to *L. kensaki* Wakiya & Ishikawa, 1921); *L. edulis* form *nagasakiensis* (corresponding to *L. edulis* Hoyle, 1885), to which Sasaki referred three specimens previously described by him (Sasaki 1914) as *L. chinensis* Gray, 1849; *L. edulis* form *grandipes* (corresponding to *L. budo* Wakiya & Ishikawa, 1921). Sasaki did not consider *L. chinensis* (non Gray 1849) a valid form.

Okutani (1975), in the revision of his catalogue of Japanese squid, synonymized two of the three forms, erecting two subspecies: *L. edulis edulis* Hoyle, 1885 (corresponding to *L. kensaki* Wakiya & Ishikawa, 1921 and *L. edulis* form *nagasakiensis* Sasaki, 1929) and *L. edulis budo* Wakiya & Ishikawa, 1921 (corresponding to *L. edulis* form *grandipes* Sasaki, 1929).

Natsukari (1984a:230), in one of his studies of loliginid squids, proposed the new genus *Photololigo*, distinguished from the other loliginids essentially by the presence of luminous organs (photophores) on the ink sac, and he designated *L. edulis* Hoyle, 1885 as the type species of the new genus. Later Natsukari et al. (1986, 1988) stated the opinion that the two subspecies recognized by Okutani (1975) could be different seasonal "forms" of the same species, probably not genetically isolated, and that the differences between the two forms were evident only in late (subadult) stages. Okutani et al. (1987:101) took into account these considerations but still referred to the two forms as valid, *L. edulis* Hoyle, 1885 and *L. edulis* form *budo* Wakiya & Ishikawa, 1921. Okutani et al. (1987:99) also clearly pointed out that *L. edulis* Hoyle, 1885, is a species characterized by "…polymorphism by locality and by season within the range of the distribution…."

Nesis (1987) reported two species: *L. edulis* Hoyle, 1885 distributed from the Red Sea and Mozambique into the western Pacific, and *L. budo* Wakiya & Ishikawa, 1921 from Southern Japan. However, he actually considered *L. budo* to be a "doubtful species," possibly a "form" of *L. edulis* (Nesis 1987: 151). Also, referring to the northwestern Pacific population, Nesis (1987: 151) discussed two different forms "…of unclear taxonomic relationship…": *L. edulis* form *edulis* Hoyle, 1885 (includes *L. edulis* form *nagasakiensis* Sasaki, 1929), and *L. edulis* form *kensaki* Wakiya and Ishikawa, 1921 (includes *L. edulis* form *edulis* Sasaki, 1929, non *L. edulis* Hoyle, 1885).

While *L. edulis* form *budo* is characterized by very large clubs, long arms and large suckers in comparison with the typical *L. edulis*, the two *L. edulis* "forms" differ essentially in the hectocotylized structure: 7–8 pairs of normal suckers at the base of the arm, no small suckers on the papillae of the modified portion (=*L. edulis* form *edulis*), versus 20–27 pairs of normal suckers and rudimentary suckers on the papillae of the modified portion (=*L. edulis* form *kensaki*).

Natsukari & Tashiro (1991) again stated that they consider *L. edulis* form *kensaki* Wakiya & Ishikawa, 1921 and *L. edulis* form *budo* Wakiya & Ishikawa, 1921 as two seasonal forms of the same species, based on some evidence that the forms probably are not genetically isolated (Natsukari et al. 1986, 1988).

Subsequently, four species of *Photololigo* from the northern waters of Australia were identified using allozymes (Yeatman & Benzie 1994). Two of these species fitted the gross morphology of *Photololigo edulis* from Japan, supporting the opinion that a number of widely distributed species (such as *P. edulis*) may represent a series of morphologically similar allopatric sibling species.

Unfortunately, among those we examined, only the specimens from the Arabian Sea (2 males and 4 females, 48–65 mm ML) were in good condition, but none was fully mature. Their general morphology closely resembles that of *L. duvaucelii*, as already noted by Adam (1973) for his specimens from the Red Sea. From these, *L. edulis* is distinguishable essentially by the arm sucker dentition: it strictly conforms to the *L. edulis*-type, with six to eight long, slender, blunt teeth on the distal margin of the ring and by the longer modified portion of the hectocotylized arm. The hectocotylized arm in our two males is very well developed in spite of the small size of the specimens (48–65 mm ML, Table 3B-1; see also Adam, 1973). It bears six and eight pairs, respectively, of normal suckers at the proximal base of the arms, followed by the sucker stalks modified into cone-shaped papillae with minute suckers on the tip, exactly as described by Voss (1963). The club sucker dentition conforms to the alternating large and small tooth pattern and, according to Adam (1973), "…hardly more than one small tooth…" is distinguishable between two large teeth.

Our material from the East African coasts (6 males, 5 females, 6 juveniles of undetermined sex, ML 30–87 mm) is in poor condition, but it also is morphologically very similar to the appearance of *L. duvaucelii*. The arm sucker dentition, in some cases (i.e., specimens 154 n.1–2 and 159 n.1), is very close to the *chinensis*-type, in the sense that the teeth are rather conical and appear sharply pointed; under higher magnification, the teeth have blunt tips. Other specimens have an obvious *edulis*-type dentition, with long, squared, widely spaced teeth. Also, the hectocotylus is rather variable, with regard to the number of normal suckers at the base of the arm, between 11–12 and 16–18 pairs. The morphology of the cone-shaped papillae, whether longer and more slender or shorter and more stout, always includes small suckers on the tips. The club sucker rings have 10–11 large teeth that alternate with 1 or more (two to three) small, inconspicuous teeth.

The specimens from the Bay of Bengal (3 males, 6 females, 4 juveniles of undetermined sex) also are in poor condition. They appear to be morphologically quite different at first glimpse, almost indistinguishable from our *L. chinensis* specimens from the same area, with slender mantles, smaller heads, and slightly more narrow and more "rhombic" fins (clearly longer than wide). It is impossible to know how much the variations are ascribable to effects of fixation. This situation reminds us of what Natsukari et al. (1975) reported concerning the misidentification of *Loligo edulis* as *Loligo chinensis* by Wakiya & Ishikawa (1921), and it certainly supports the more general statement by Okutani et al. (1987) about the polymorphic characteristics of the species.

Again, ultimately the identification is possible on the basis of the arm sucker dentition, clearly *edulis*-type. While the modified arms in males are hardly detectable, nevertheless the relatively very long modified portion possesses the minute suckers on the tips of the cone-shaped papillae.

The above-mentioned differences in the general appearance among our specimens from the different areas are not numerically quantifiable, nor even numerically evident. Although quantitatively few, our observations tend to confirm the marked polymorphism of the species already emphasized by several authors in relation to different geographical areas and, possibly, different seasons within the same area. Our results also underline the need for more detailed observations, information, and clarification on *L. edulis* throughout the Indian Ocean, especially because of its well-documented importance as a fisheries resource in the western Pacific.

Loligo sumatrensis d'Orbigny, 1835, in Ferussac and d'Orbigny 1834–1838 [*Loliolus* (*Nipponololigo*) *sumatrensis*, Vecchione et al. 1998; Vecchione et al., pers. comm.].
Fig. 4A–I

Loligo sumatrensis d'Orbigny, 1835, in Ferussac and d'Orbigny 1834–1838: 317–318, *Loligo* pl. 13, Fig. 1–3.—Natsukari, 1984b: 259–263, Figs. 1–2, tab.1.—Okutani et al. 1987: 91.—Nateewathana, 1992: 14–17, Fig. 4, tab. 5.

Loligo kobiensis Hoyle, 1885: 184–186.—Roper et al. 1984: 94.—Brakoniecki, 1986: 39–41, Fig. 2B.

Loligo yokoyae Ishikawa, 1926: 30–32, Fig.1.

Loliolus rhomboidalis Burgess, 1967: 319–329, Figs. 1–5, tab. 1.

Nipponololigo kobiensis, Natsukari, 1983: 314–315.

Nipponololigo sumatrensis, Natsukari, 1984b: 262.—Dunning, 1998: 773.

Loligo sumatrensis d'Orbigny, 1839.—Nesis 1987: 154, Fig. 34 g–i; 157, Fig. 37 t–v.

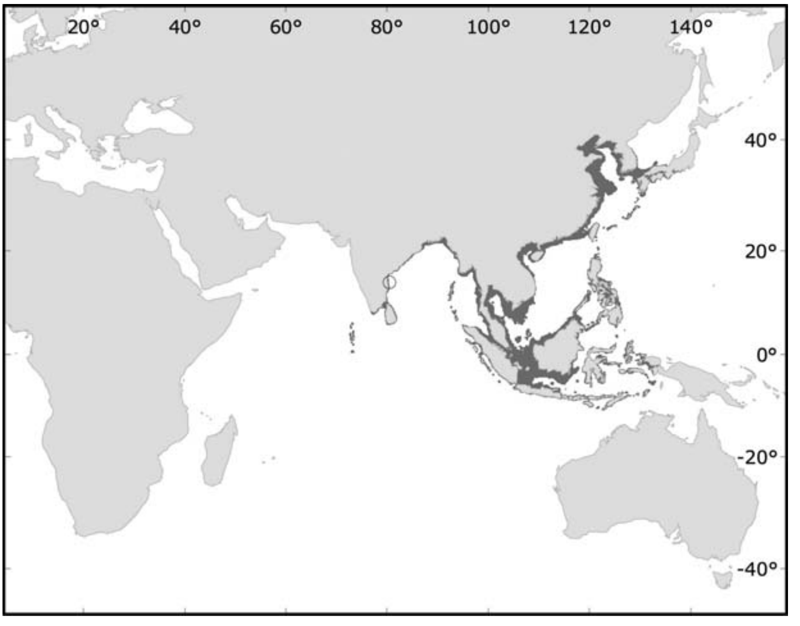
Loliolus (*Nipponololigo*) *sumatrensis*, Okutani, 1990: 59, Fig. 92.—Vecchione et al. 1998.

FAO vernacular names.—En—Kobé squid; Fr—Calmar kobi; Sp—Calamar kobi.

Type locality.—Japan

Distribution.—Western Pacific (Map 4), from southern Japanese waters southwestward to Sumatra, including South Korean waters, China, Thailand, Philippines and Indonesia (Roper et al. 1984, Okutani et al. 1987, Nesis, 1987), westward to the Bay of Bengal from the Andaman Sea to the east coast of India and the Maldive Islands (Burgess 1967, Nesis, 1987, Nateewathana 1992, present work).

Material examined.—Five specimens of *Loligo sumatrensis* (3 males, 2 females) from Madras, central east coast of India.



Map 4. Geographical distribution of *Loligo sumatrensis*, (shaded areas); open circle, present material, general locality.

See Appendix 1D for detailed localities and capture data. All measurements and relative indices are reported in Appendix 2D. Selected ranges of indices are reported in Table 8.

Diagnosis.—Squids of small size up to 120–130 mm ML (Fig. 4A, B). Fin length generally about 60–65% ML; fin width slightly larger at 60–70% ML. In males most of the left ventral arm is hectocotylized, up to 87% (see Table 4A), and the basal part of the right ventral arm bears about 4 pairs of greatly enlarged suckers (Fig. 4G, H). Largest arm sucker rings with 6–9 large, very obtuse, square teeth, almost as wide as high (Fig. 4F). Largest medial manus sucker rings smooth (Fig. 4E). Smaller lateral manus sucker rings with acute teeth (Fig. 4D).

Description.—The material we examined is in relatively good condition, and the general aspect conforms closely to the description given by Burgess (1967; the species, as *L. rhomboidalis*, is fully illustrated in this work based on *Anton Bruun* IIOE material), including the coloration of the preserved specimens, a pale yellowish ground color with purplish red chromatophores. These chromatophores are broadly distributed over the body surface without a distinctive pattern, except for a dark purplish midline dorsally, in correspondence with the underlying gladius.

The mantle is sub-cylindrical and gradually tapers posteriorly into a blunt point (slightly more pointed in females). Mantle width is about 30% of mantle length. Fins are rhombic, rather wide (up to 70% of mantle length), with straight margins. Fin length is about 55–57% of mantle length. The head is small, with large eyes. Only minor differences in general morphological features are noticeable between males and females. The arms are moderately long (slightly shorter in females), with an arm formula of 3.4.2.1. Several (up to 8) very enlarged globular suckers are present on the proximal end of the right ventral arm of males. Suckers of the other arms are similar in shape and size in males and females, except the proximal suckers on arms III of males are secondarily enlarged at sexual maturity (Brakoniecki 1986).

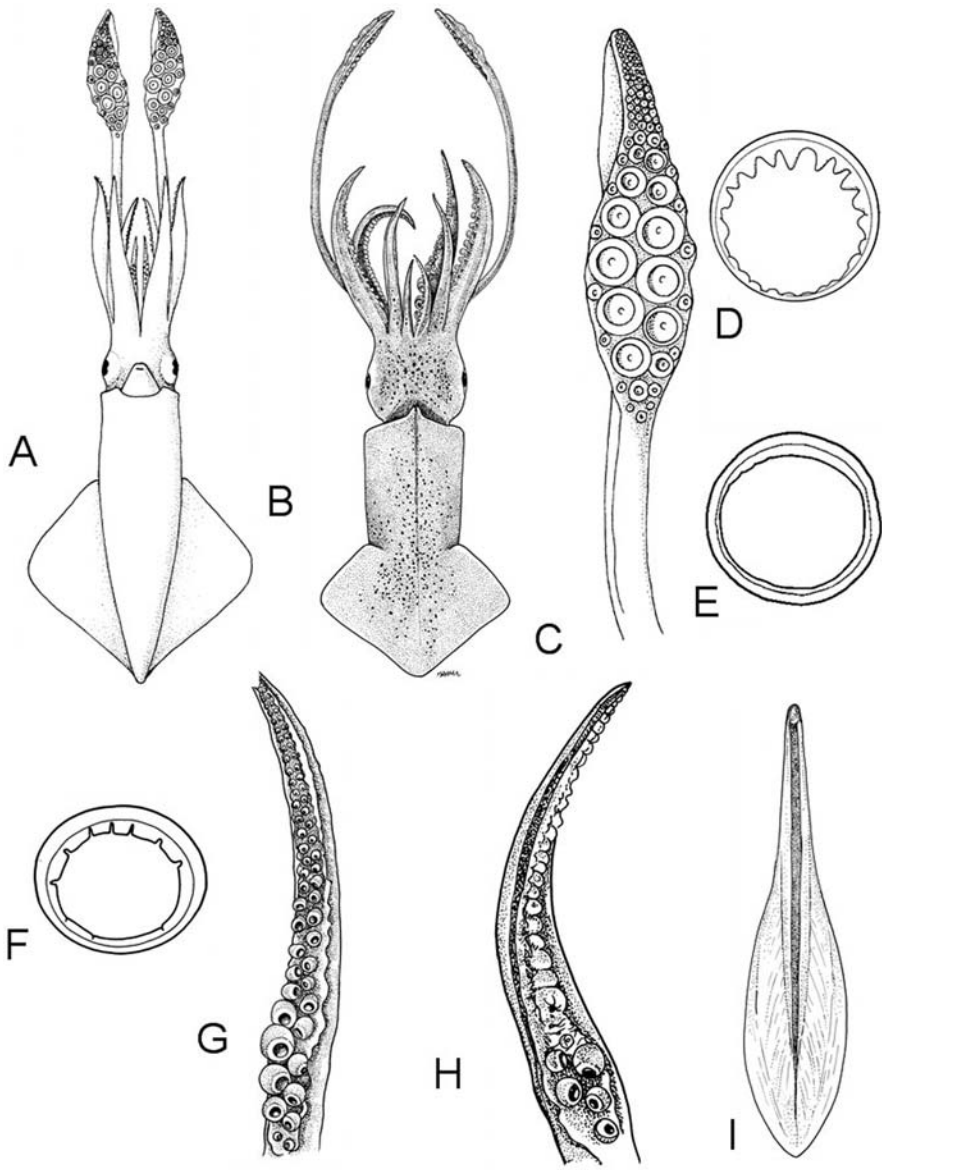


Fig. 4. *Loligo sumatrensis* d'Orbigny, 1835. A, ventral view (Roper et al. 1984; as *Loligo kobiensis*. B, dorsal view (redrawn from Burgess 1967). C, tentacular club (Roper et al. 1984). D, tentacular club, small toothed sucker ring, lateral row (Roper et al. 1984). E, tentacular club, large smooth sucker ring, medial row (Natsukari 1984). F, arm III sucker ring (Roper et al. 1984). G, hectocotylus, right arm IV (Nesis 1982/1987). H, hectocotylus, left arm IV (Nesis 1982/1987). I, gladius (Burgess 1967).

The left ventral arm is hectocotylized in males; 6–7 normal suckers are present on the proximal portion of the arm. The unmodified portion follows, with the suckers modified into two series of fleshy papillae: those of the dorsal series are reduced, stump-like, and gradually decrease in size distally; those of the ventral series are more robust, palisade-like. The distal-most part of the arm remains unmodified in two thirds of the specimens in our study.

Tentacles weak, with clubs rather strongly developed in comparison

(Fig. 4C). Suckers of the median series about 2–4 times larger than those on lateral series and flattened, with smooth, non-dentate rings. Suckers on the marginal series with small, acute teeth.

The gladius is broad, paddle-like, with broad, curved vane and long rachis (Fig. 4I).

A comparison of selected measurements, indices and sucker dentition from various authors is given in Table 4C.

Biology.—*Loligo sumatrensis* is a neritic species that commonly inhabits coastal waters. Its biology has not been specifically investigated in this study, because of its marginal interest to fisheries. A synopsis of the available biological knowledge, however, is given by Chotiyaputta (1993a), for the Gulf of Thailand and the Andaman Sea populations. Accordingly, *L. sumatrensis* is common in captures at sizes that range between 20 and 70 mm ML, and its spawning period extends year round.

Fisheries.—Taken as by-catch in fisheries for other squids in most of its distributional area, e.g., southwestern Japanese waters. It is highly abundant in the Gulf of Thailand and in the Andaman Sea (Chantawong & Suksawat 1997), whereas it appears to be scarce in the Bay of Bengal.

Remarks.—Manoch (1998) hypothesised that *Loligo uyii* from the eastern side of the Gulf of Thailand is synonymous with *Loligo sumatrensis*.

Subgenus *Doryteuthis* Naef, 1912
Loligo (*Doryteuthis*) *singhalensis* Ortmann, 1891
[*Uroteuthis* (*Photololigo*) *singhalensis*, Vecchione et al., 1998].
[*Uroteuthis* (subgenus undetermined) *singhalensis*, Vecchione et al. (2005)].
Fig. 5A–F

Loligo singhalensis Ortmann, 1891: 676, pl. 46, Fig. 3a–d.—Brakoniecki 1986: 25–26, Fig. 1F.

Loligo singhalensis var. *beryllae* Robson, 1928: 15, Figs. 4–10.

Doryteuthis singhalensis, Naef, 1912: 472.

Doryteuthis sibogae Adam,1954: 146, Fig. 16–18, pl. I, Fig.4.—Silas 1986:31, pl. VIII, A–B.

Loligo sibogae, Natsukari, 1976: 15, Fig. 1–14.

Photololigo sibogae, Natsukari, 1984a: 232.—Dunning, 1998: 777.

Loligo (*Photololigo*) *singhalensis*, Okutani 1990: 61, Fig. 76.

Uroteuthis (*Photololigo*) *singhalensis*, Vecchione et al., 1998.

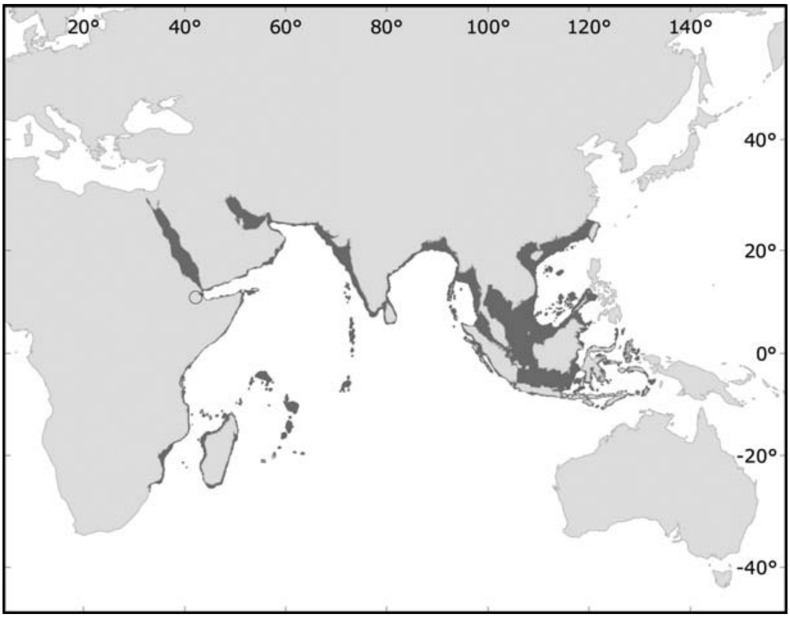
FAO vernacular names.—En—Siboga squid; Fr—Calmar siboga; Sp—Calamar siboga.

Type locality.—Sri Lanka (Indian Ocean).

Distribution.—*Loligo singhalensis* is an Indo-Pacific species. Its distribution (Map 5) extends in the western Pacific from the South China Sea [Singapore, Indonesian waters by Adam (1954)], north to Formosa Island (Natsukari 1976) and westward into the Indian Ocean from the Andaman Sea, Thailand (Nateewathana 1992, Chantawong & Suksawat 1997); the Bay of Bengal (Perera 1975, Silas et al. 1985, Jothinagayam 1987), westward (Dayratne 1993) to the Arabian Sea (Zuev 1971) and the eastern African coasts (Somalia by Rocha et al. 1998, present work; Seychelles by Okutani 1970; Mozambique, at Mascarene underwater ridge by Pinchukov & Makarova, 1984).

Material examined.—Twenty-four specimens of *L. singhalensis* (13 males, 11 females), from Djibuti, Somalia. See Appendix 1E for details of locality and data collection. All measurements and relative indices are reported in Appendix 2E. Selected ranges of indices are reported in Table 8.

Diagnosis.—Fin length in adults up to 50–60% of mantle length (Fig. 5A). Hectocotylized part of left ventral arm up to 45% of total arm length (Fig. 5E). Arm suckers with 6 (5)–11 wide, squared,



Map 5. Geographical distribution of *Loligo singhalensis*, (shaded areas); open circle, present material, general locality.

plate-like teeth distally (Fig. 5D). Club suckers with 15–20–25 conical, sharply-pointed teeth around the entire margin, that occasionally may be interposed by smaller, almost inconspicuous, pointed teeth (Fig. 5C). Gladius narrow, widest in its anterior 0.33, with nearly straight margins on the vane (Fig. 5F). One photophore present on each side of the ink sac.

Description.—The mantle is long, slender, cylindrical, and it tapers posteriorly into a sharply-pointed tip. Mantle about 4–7 times as long as wide, widest at the midpoint of its length; MWI around 19 in mature animals (males) (Table 5A). The fins are narrow, rhombic in outline, with the anterior margin slightly convex and the posterior margin slightly concave. Fins are relatively short in young specimens and become longer with growth (Natsukari 1976, Korzun & Alexeev 1991), their length half or slightly more than half the length of the mantle in adults. The relation between fin length and mantle length has been mathematically described by Korzun & Alekseev (1991).

The head is comparatively small and short; the eyes are of medium-size.

The arms are slender and proportionally short. The arm formula varies: 3.2.4.1, as well as 3.4.2.1 (Ortmann 1891, Robson 1928, Adam 1954, Okutani 1970, Natsukari 1976, Silas et al. 1985, Jothinayagham 1987). The suckers are biserial, medium-sized, largest on arms II and III; sucker index = 0.8–1.4 (Natsukari 1976). The chitinous sucker rings are smooth or wavy proximally, while the distal margin bears 6–11 (most commonly nine) plate-like, truncate, squared teeth.

The left arm IV is hectocotylized in mature males for 40–45% of its length, by the modification of suckers and stalks along both rows into uniform, cone-shaped, pointed, fleshy papillae, devoid of minute suckers on their tips. The papillae on the ventral row are only slightly longer than those of the dorsal row. On the proximal part of the arm are

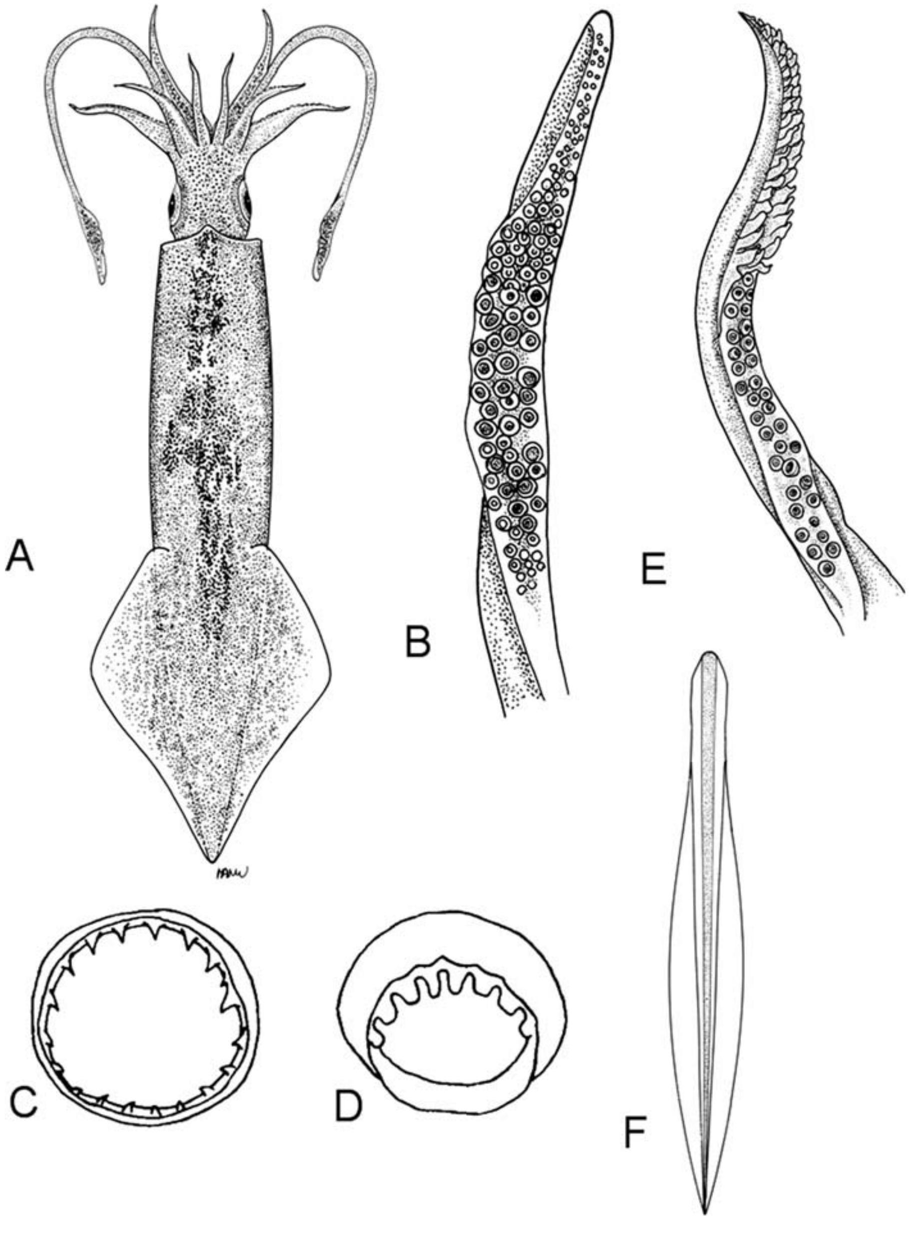


Fig. 5. *Loligo singhalensis* Ortmann, 1891. A, dorsal view (FAO original). B, tentacular club (Nateewathana 1992). C, tentacular club, largest sucker ring (Roper et al. 1984; as *Loligo sibogae*). D, arm III, largest sucker ring (Roper et al. 1984; as *L. sibogae*). E, hectocotylus (Nateewathana 1992). F, gladius (Voss & Williamson 1972).

15–20 pairs of normal suckers. While the hectocotylized portion of the arm becomes relatively longer with maturity (Natsukari 1976), the number of suckers on the proximal part seems to remain constant.

The tentacles are short and slender. Clubs are rather short (ClLI = 12–25, present work) (Fig. 5B). Club suckers quadriserial, those of the median two rows of the manus slightly larger than those of the lateral two rows. The largest suckers bear 15–20 incurved, conical, very sharp (="thorn-like", Ortmann 1891), widely-spaced teeth around the entire chitinous ring. Occasionally a few smaller, almost inconspicuous and sharp, secondary teeth are interposed between the primary teeth: their presence is indicated by the symbols (±) in Appendix 2E.

The buccal membrane is well developed, and each of its seven lappets bears up to 12 small suckers.

Luminous organs are present, one on each side of the ink sac. Based on this character, the species should be included in the proposed genus *Photololigo* (Natsukari 1984a).

The gladius is very narrow and slender, with almost straight lateral margins along the vane; it is widest at its anterior (0.33) part.

Table 5A and C present the relative indices obtained for this species in the present work, as well as those computed by other authors.

Biology.—A semipelagic, neritic species that occurs mainly in coastal (inshore) waters, *L. singhalensis* has been reported to inhabit bottom depths down to 220 m (Pinchukov & Makarova 1984). The biology of this species is still poorly known. Data from the southwest coast of India (Silas 1986) indicate that males in that area attain sexual maturity at a size range of 70–170 mm ML (50% mature at 97 mm ML), and females mature at a size range of 70–130 mm ML (50% mature at 84 mm ML). All males and females are fully mature at a size of 170 and 130 mm, respectively. Mature specimens of both sexes occur from October to April, suggesting a protracted spawning season. Juveniles are caught along the coast from January–February up to June (in some years), supporting this hypothesis. Based on the analysis of the length frequency distributions, a life cycle of over two years has been estimated (Pinchukov & Makarova 1984, Silas 1986). Adults in the Vizhinjam coastal waters are 70–205 mm ML in the fishery (Silas 1986).

Data from the southeastern slope of the Mascarene submarine ridge (Pinchukov & Makarova 1984), western Indian Ocean, indicate that this species is represented by two sympatric groups which differ slightly in size at first maturity. Males of the first group, which is widespread over the distributional area, reach sexual maturity at a size range of 80–210 mm ML and females at a size range of 100–170 mm ML. The second group occurs only in the northern part of the area, where males and females become mature at a size of 100-230 mm ML and 110–170 mm ML, respectively.

Among the specimens examined in the present work, 6 males and 2 females were mature (46% and 18%, respectively, of the total number available), with a ML range of 125–150 mm and 111–119 mm, respectively; they were collected during the month of February.

Fishery.—Reported mainly as a by-catch in the Indonesian and South China Sea fin fisheries (as *L. sibogae*, Roper et al. 1984), *L. singhalensis* is likely to be more important to the fisheries in Indian Ocean waters, even though the extent of its contribution is difficult to assess because of confusion with the nomenclature (see *Remarks*). For example, Chikuni (1983) listed *L. singhalensis* among the major species of loliginid squid that occur in the Indo-Pacific region, with small catches recorded from the China Sea to the eastern Arabian Sea, but it is not clear to what extent he actually referred to different species.

Included among the important species for the commercial squid fishery of Thailand (Chantawong & Suksawat 1997), *L. singhalensis* seems consistently present in the Andaman Sea (Chotiyaputta 1993a), where it is one of the target species of a light-attraction fishery in Phuket and Phang-Nga provinces (Chantawong 1994). It is definitely among the important species for the Indian fishery (Ramachandran 1987). Reported as present on both coasts of the Indian peninsula (Silas et al. 1982, as *Doryteuthis* sp. by Silas et al. 1985, Silas 1986, as *Doryteuthis sibogae*), it seems particularly important for the local fisheries off the southwestern coast (Silas 1986). It also is likely to contribute consistently to the small pelagic local fishery in Sri Lankan waters (Dayaratne 1993, as *L. singhalensis*). The species also probably is important in the northern part of the Bay of Bengal (Mohan & Rayudu 1986, as *Doryteuthis* sp.). However, it is not clear to what extent the references to this species as the second most important squid resource of India in general (Ramachandran 1987), and off the north-western coast in particular (Siraimeetan 1990), might include other species as well. Recent data (Meiyappan & Mohamed, 2003) on Indian landings, however, seem to confirm that *L. singhalensis* (listed as *Doryteuthis sibogae*) is the second most frequently caught squid, representing 11% of east coast catches and about 2% of the catch from the southwestern coast.

Remarks.—The systematic position of this species has been the object of several discussions and various contradictions during the past (Naef 1912: Adam 1939b, 1954; Voss 1963: Silas 1968: Okutani 1970, 1980; Voss & Williamson 1971: Perera, 1975: Natsukari 1976, 1984a; Nesis 1982, 1985; Silas et al. 1982, 1985: Silas 1986; Roper et al. 1984: Alekseev 1989, 1991; Jothinayagam 1987), and of specific attention during the 1988 CIAC Workshop (Vecchione et al. 1998).

Korzun & Alekseev (1991) gave a synthesis of the historical pathway of the systematics of the species and came to the conclusion that *Doryteuthis sibogae* Adam, 1954 is the earliest synonym of *Loligo singhalensis* Ortmann, 1891. Those authors did not object to the inclusion of *L. singhalensis* into the newly-created genus *Photololigo* of Natsukari (1984a), and presented a summary of the situation concerning this species in the literature, by indicating those references they consider valid for the species and those they do not consider valid, as follows:

Photololigo singhalensis
(Ortmann 1891)

Valid references:

Loligo singhalensis Ortmann, 1891.

Loligo singhalensis var. *beryllae* Robson, 1928.

Doryteuthis singhalensis, Naef, 1912.—Okutani, 1970*.—Perera, 1975*.—Pinchukov & Makarova, 1979, 1984.—Zuev, 1971, Zuev & Nesis, 1971.

Doryteuthis sibogae Adam, 1954.—Natsukari, 1976.

Loligo sibogae, Alekseev, 1989.—Nesis, 1982, 1987.—Roper et al. 1984.

Photololigo sibogae, Natsukari, 1984.

Invalid references:

non *Loligo singhalensis* (= *L. chinensis*), Okutani, 1980.—Nesis, 1982, 1987.—Alekseev, 1989.

non *Doryteuthis singhalensis* (= *L. edulis*), Adam, 1939b, 1954.

non *Doryteuthis singhalensis* (= *L. chinensis*), Voss, 1963.—Voss & Williamson, 1971;.—Roper et al.1984.

non *Photololigo singhalensis* (= *L. chinensis*), Natsukari, 1984.

After our examination of the literature we think it reasonable to agree with the view of Korzun & Alekseev (1991). We also now refer to *Loligo singhalensis* the following references as valid:

Doryteuthis singhalensis, Jothinayagam, 1987*.

Doryteuthis sp., Silas et al. 1982.—Mohan & Rayudu, 1986.

Doryteuthis sibogae, Silas et al. 1985, Silas 1986.

We do not refer to *Loligo singhalensis* the following reference:

Doryteuthis singhalensis, Silas et al. 1986 (= *Loligo chinensis* ?).

In some cases (noted by*) the description of some characters is ambiguous, i.e., the fin length is reported to be greater than the range limits given for the species by most authors; for example, Jothinayagham (1987) reported "about 70%", Okutani (1970) measured "62%" and Perera (1975) stated "…more than half…" of mantle length, even though in the latter case it is impossible to calculate a numerical FL/ML ratio. However, the other characters defined and the illustrations of their specimens tend to support the identity of the subject species with *L. singhalensis* Ortmann, 1891 (Jothinayagam 1987: 52, Fig. 18a, Okutani 1970, pl. 8 Fig. 4, Perera 1975: 54, Fig. 6).

We consider the reference to *Doryteuthis* sp. by Mohan & Rayudu (1986) as valid for *L. singhalensis*, since these authors appear to adhere to the nomenclature used by Silas in numerous papers before 1985. Other species-specific references, mainly those reporting fishery statistics, unfortunately remain doubtful, and their validation requires knowledge about species-specific characters.

As for the ultimate assignment of this species to a genus and subgenus, it seems that the solution of this problem will require some additional investigation. The revision accomplished by Vecchione et al. (1998), who consider the correct designation to be *Uroteuthis* (*Photololigo*) *singhalensis*, has been questioned again, and following the CIAC meeting in Phuket (February 2003) the species now is considered to belong to the genus *Uroteuthis*, but to an undetermined subgenus (Vecchione et al. 2005).

Following its original description (Ortmann 1891), this species was illustrated by Naef (1912), Robson (1928) and Adam (1954). More recently, exhaustive and accurate descriptions have been given by Okutani (1970), Natsukari (1976), Silas et al. (1985) and Nateewathana (1992). Since our material agrees especially well with the description given by Natsukari (1976), we suggest the reader refer to this work for further details about the species.

Genus *Loliolus* Steenstrup, 1856
Loliolus hardwickei (Gray 1849)
[*Loliolus* (*Loliolus*) *hardwickei*,
Vecchione et al. 1998].
Fig. 6A–L

Loligo hardwickei Gray, 1849: 69. Nesis, 1982: 132.—Lu et al. 1985: 70–74, Fig. 7a–h, 8, tab. 3.—Nesis, 1987: 146.

Loliolus typus, Steenstrup, 1856: 194, pl. 1, Figs. 5, 5′.—Silas, 1968: 307.

Loliolus investigatoris Goodrich, 1896: 8–9, pl. 2, Figs. 29–37.—Massy, 1916: 222.—Adam, 1939b: 66, Fig. 1.—Adam, 1954: 29, Figs. 2–4.—Silas, 1968: 307.—Oommen, 1975: 189.—Nesis, 1982: 132, Fig. 34 a,b,c,g.—Silas, 1968: 307.—Silas, 1986: 21, 32, 33.—Silas, 1986: 116–118.—Jothinayagham, 1987: 57–59, Fig. 20 a–g.—Nesis, 1987: 146.

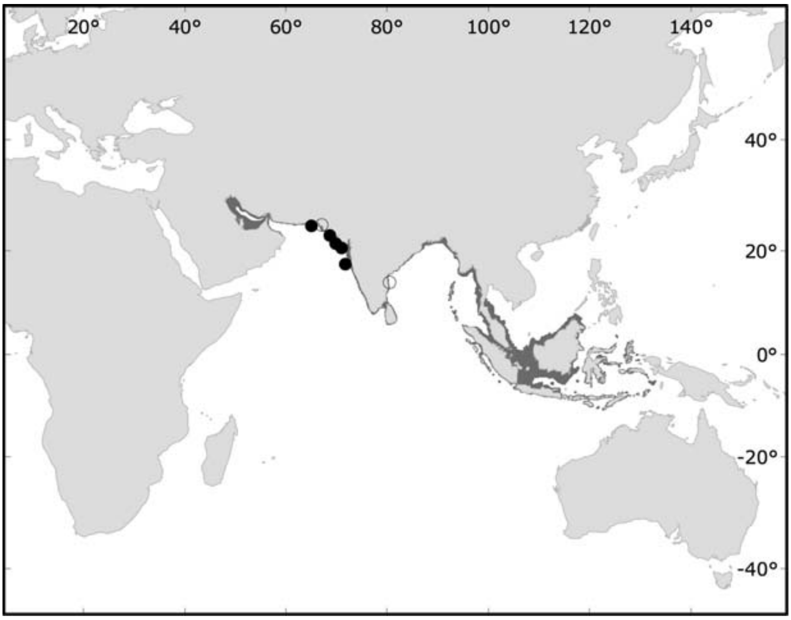
Loliolus hardwickei, Brakoniecki, 1986: 34–35, Fig. 2A.

FAO vernacular names.—none.

Type locality.—India (Bay of Bengal ?).

Distribution.—*Loliolus hardwickei* (Map 6) is a common species throughout the Indian Ocean, from the Persian Gulf, along the western and eastern coasts of India, to the Andaman Sea and into Indonesia waters (Silas 1968, Silas 1986; Jothinayagam 1987, Nesis 1987). A single specimen was reported from the Chinese coast (Lu et al. 1985).

Material examined.—Forty-seven specimens of *L. hardwickei* (20 males, 27 females): 42 from the Arabian Sea and five from the Bay of Bengal, off Madras; all Indian Ocean, mostly from the IIOE. See Appendix 1F for detailed localities



Map 6. Geographical distribution of *Loliolus hardwickei*, (shaded areas); black dots, present material, site-specific localities; open circles, present material, general localities.

and capture data. All measurements and relative indices are reported in Appendix 2F. Table 6A, B present general and regional measurements and indices; Table 6C provides a comparison of selected measurements, indices, and sucker dentition from various authors. Selected ranges of indices are reported in Table 8.

Diagnosis.—Squid of small size, mantle short, stout; fins posterior, broad, heart-shaped, their width up to 100–110% of mantle length (Table 6A; Fig. 6A–D). Left ventral arm hectocotylized (Fig. 6J). The modification extends along the entire length of the arm (i.e., no normal suckers at the proximal base), and a peculiar fleshy crest is present at the proximal end. Arm suckers rings with 2–7 large, blunt, rounded, trapezoidal teeth (Fig. 6H, I). Club sucker rings with 20–40 small, sharp and/or truncate teeth (Fig. 6F, G).

Description.—Most of the examined material is in a rather poor condition of preservation (i.e., quite flabby), and some have already been dissected. However, the general appearance and the main characters are almost exactly as described by Lu et al. (1985), enabling a confident identification of the species.

The mantle is short and stout (MWI up to 58, Table 6A) with a conspicuous, rounded anterior dorsal lobe. Fins large, heart-shaped, with anterior and lateral edges rounded; they occupy up to 76% of mantle length and their width is greater than their length (FW 100–110% of ML). The fins continue past the posterior end of the body, where they are fused.

Head short, a little narrower than the mantle.

Arms rather short, sub-equal, usually shorter in females than males. Arm formula 3.4.2.1 (3.2.4.1 in type).

Arm sucker rings with only 2–7 large, low, stout, broad teeth on the distal margin; their number varies depending on the arm and on the sex of the specimen. The proximal suckers on arms II and III of males are enlarged as secondary sexual modifications (Brakoniecki 1986).

Left ventral arm hectocotylized in males by the modification of both ventral and dorsal series of suckers along its entire length: suckers are missing, except at the very tip where two to three minute suckers may be present. Ventral sucker stalks enlarged and fused entirely with the ventral trabeculate membrane, making it "…greatly enlarged and thickened into a fleshy ridge." (Lu et al. 1985:70). The proximal-most 2–3 trabeculae are further enlarged (up to twice the membrane height) to form a peculiar crest. Dorsal series of sucker stalks reduced to small, free, lobate papillae.

Tentacles short. Clubs small (ClLI 15–40, Table 6A), scarcely expanded; manus club suckers sub-equal; suckers of median series 1.0–1.3 times diameter of suckers of marginal series (Lu et al. 1985) (Fig. 6E). Largest club sucker rings with 20–40 small, acute or bluntly triangular teeth around the entire margin.

Buccal membrane with seven-pointed lappets; each lappet bears 1–6 minute suckers.

Gladius broad (GWI 22-37, Lu et al. 1985); vane thin and fragile (Fig. 6K, L).

Photophores absent.

Additional details of the morphology of *L. hardwickei* are presented in Lu et al. (1985).

Biology.—Very little information is available on the biology of *L. hardwickei*. This species was not included with the squids examined by Silas (1986), nor was it in the resumé of biological information given for squids of the Andaman Sea by Chotiyaputta (1993a). Such limited attention undoubtedly is related to the meagre importance of *L. hardwickei* for the commercial fisheries, in spite of its common occurrence in these areas.

Loliolus hardwickei is known to inhabit estuarine and coastal waters to a maximum recorded depth of 30 m (Lu et al. 1985). Males and females reach sexual maturity at a size of about 30–40 mm ML (Table 6A; Lu et al. 1985). Maximum reported size is 88 mm ML for a male captured at the mouth of the River Hughli, India (Massy 1916).

Fishery.—In spite of its common occurrence in the Indo-Pacific region, few data on catch statistics are available. With so many other species of much larger loliginid squids in high abundance, probably not much demand exists for such a small squid as *L. hardwickei*. Perhaps artisanal fisheries are developed in local situations. *Loliolus hardwickei* (as *L. investigatoris*) is reported among the cephalopod resources of the northern part of the Arabian Sea, i.e., the Guajarat coast (Siraimeetan 1990) and the eastern coast of India (Silas 1986).

Genus *Sepioteuthis* Blainville, 1824
Sepioteuthis lessoniana Ferussac in Lesson, 1830
Fig. 7A–H

Sepioteuthis lessoniana Lesson, 1830: 244, pl. 11.—Sasaki, 1929: 127, pl. 14, Figs. 15–17, pl. 29, Figs. 8–9, text Figs. 74–77.—Adam, 1939a: 21, pl. I, Figs. 1–2.—Voss, 1963: 77–81, Fig. 13.—Voss & Williamson, 1971: 66–67, pl. 20, Figs. 19, 20, 26.—Lu & Tait, 1983: 183–190, Figs. 1–4, 8a.—Roper et al. 1984: 109–111.—Brakoniecki 1986: 15–16, Fig. 1A.—Jothinayagam, 1987: 54–57, Fig. 19.—Nesis, 1987: 146–147, Fig. 35 i–m.—Okutani et al. 1987: 105.—Nateewathana, 1992: 3–7, Fig. 1a–n, tab. 2.— Dunning 1998: 778.—Nateewathana et al. 2000.

Sepioteuthis hemprichii Ehrenberg, 1831: [2].

Sepioteuthis guinensis Quoy & Gaimard, 1832: 72, pl. 3, Figs. 1–7.

Sepioteuthis lunulata Quoy & Gaimard, 1832: 74, pl. 3, Figs. 8–13.

Sepioteuthis mauritiana Quoy & Gaimard, 1832: 76, pl.4, Figs. 2–6.

Sepioteuthis sinensis Orbigny, 1848: 304.

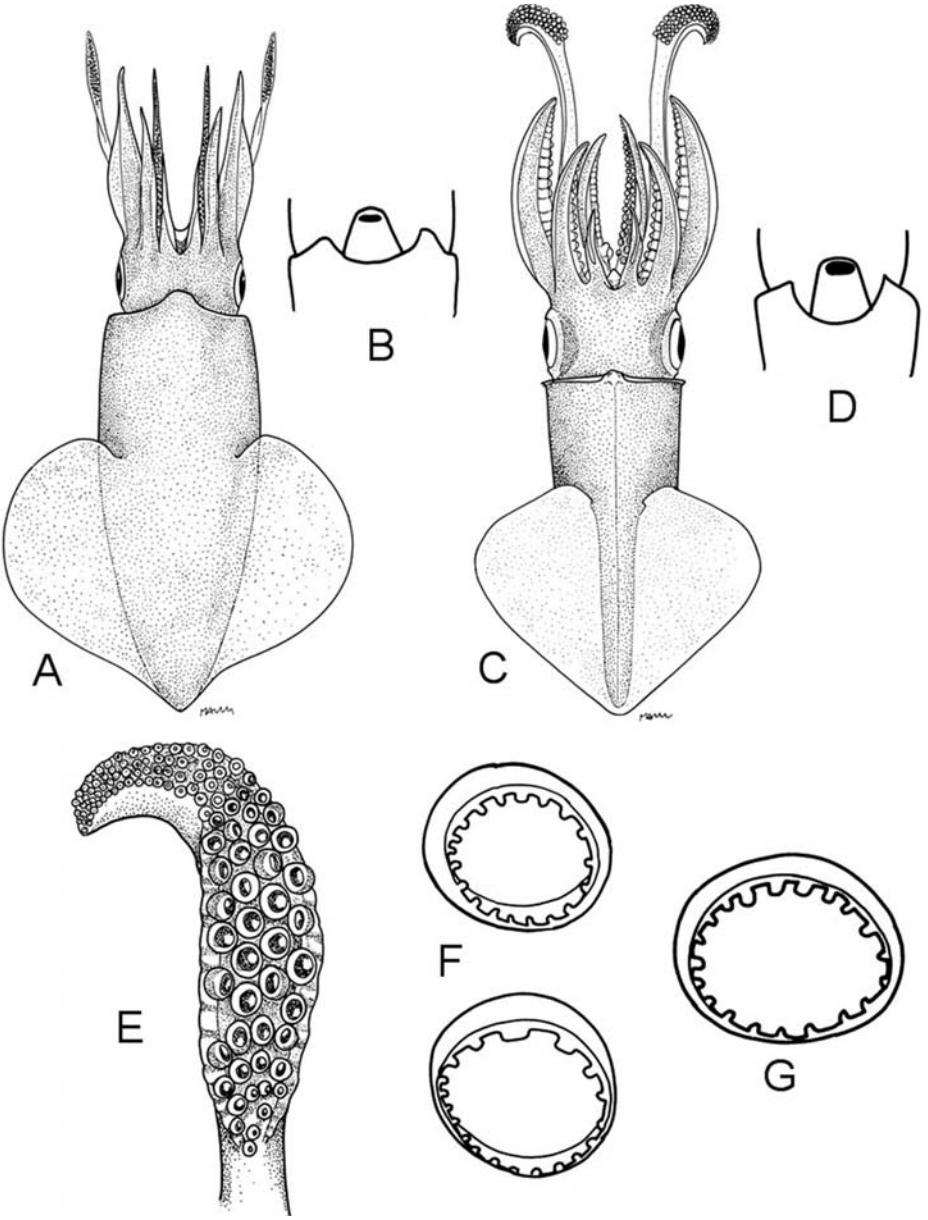


Fig. 6. A–G. *Loliolus hardwickei* (Gray 1849). A, dorsal view, female (Adam 1954). B, funnel notch on ventral mantle, female (Adam 1954). C, dorsal view, male (Adam 1954). D, funnel notch on ventral mantle, male (Lu et al. 1985). E, tentacular club (Lu et al. 1985). F, tentacular club sucker rings, female (Adam 1954). G, tentacular club sucker ring, male (Adam 1954). H–L. *Loliolus hardwickei* (Gray 1849). H, arm III sucker rings, female (Adam 1954). I, arm III sucker rings, male (Adam 1954). J, hectocotylus (Lu et al. 1985). K, gladius, female (Adam 1954). L, gladius, male (Adam 1954).

Sepioteuthis arctipinnis Gould, 1852: 479, Fig. 593.

Sepioteuthis brevis Owen, 1881: 137, pl. 26, Fig.1.

Sepioteuthis neoguinaica Pfeffer, 1884: 4, pl. I, Fig. 2, pl. II, Fig. 2a.

Sepioteuthis indica Goodrich, 1896: 5, pl.1, Figs. 9–19.

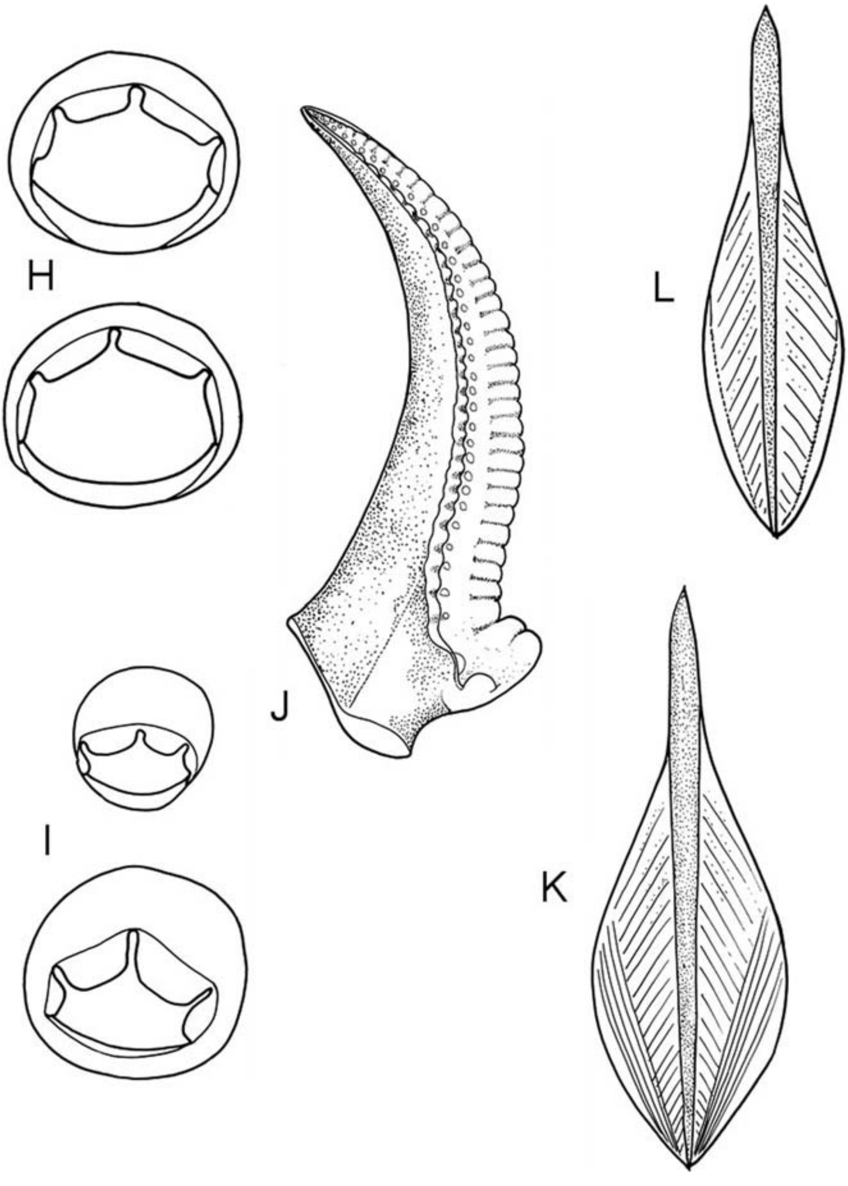


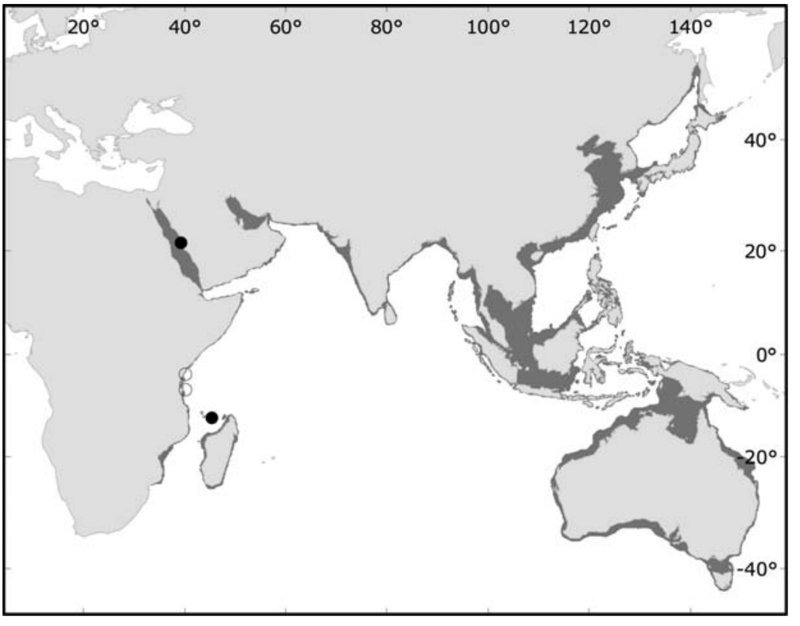
Fig. 6.—Continued.

Sepioteuthis sieboldi Joubin, 1898: 27.
Sepioteuthis malayana Wülker, 1913: 478, Fig. 7a–f.
Sepioteuthis krempfi Robson, 1928: 28, Figs. 3–4.

FAO vernacular names.—En—Bigfin reef squid; Fr—Calmar tollelet; Sp—Calamar manopla.

Type locality.—"Dorery." Type not extant.

Distribution.—One of the most widely distributed loliginid squids (Map 7) of the Indo-West Pacific region, *Sepioteuthis lessoniana* reportedly occurs from Japan to Australia and New Zealand and from Hawaii to the east African coast, north to the Red Sea and south to Madagascar (Adam 1939a, Chikuni 1983, Roper et al. 1984, Nesis 1987, Okutani et al. 1987, Rocha et al. 1998,



Map 7. Geographical distribution of *Sepioteuthis lessoniana*, (shaded areas); black dots, present material, site-specific localities; open circles, present material, general localities.

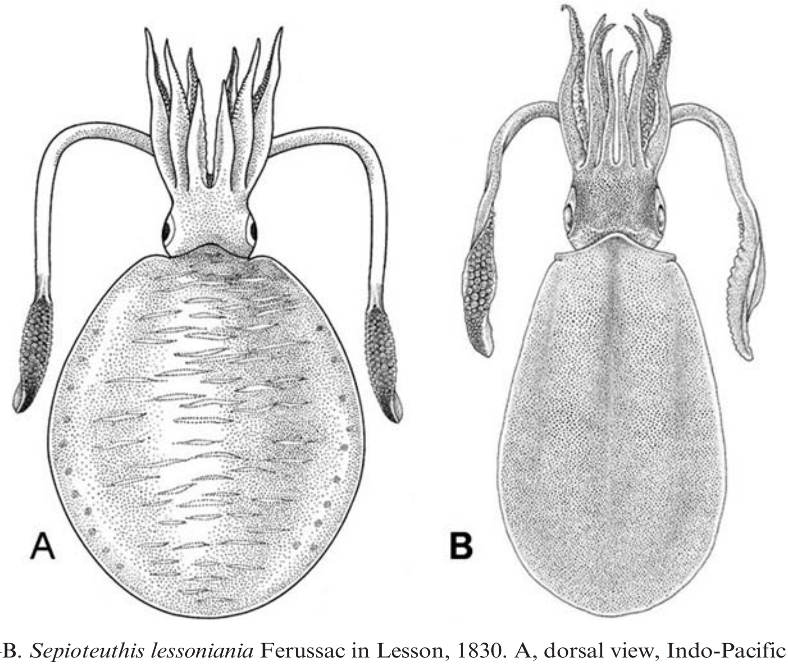


Fig. 7. A–B. *Sepioteuthis lessoniania* Ferussac in Lesson, 1830. A, dorsal view, Indo-Pacific form (Roper et al. 1984). B. dorsal view, northeastern Australian form (Dunning and Lu 1998). C–H. *Sepioteuthis lessoniana* Ferussac in Lesson, 1830. C, tentacular club (Roper et al. 1984). D, tentacular club sucker ring (Roper et al. 1984). E, arm III sucker ring (Roper et al. 1984). F, hectocotylus, Indo-Pacific form (Roper et al. 1984). G, hectocotylus, northeastern Australian form (Dunning and Lu 1998). H, gladius (Voss & Williamson 1972).

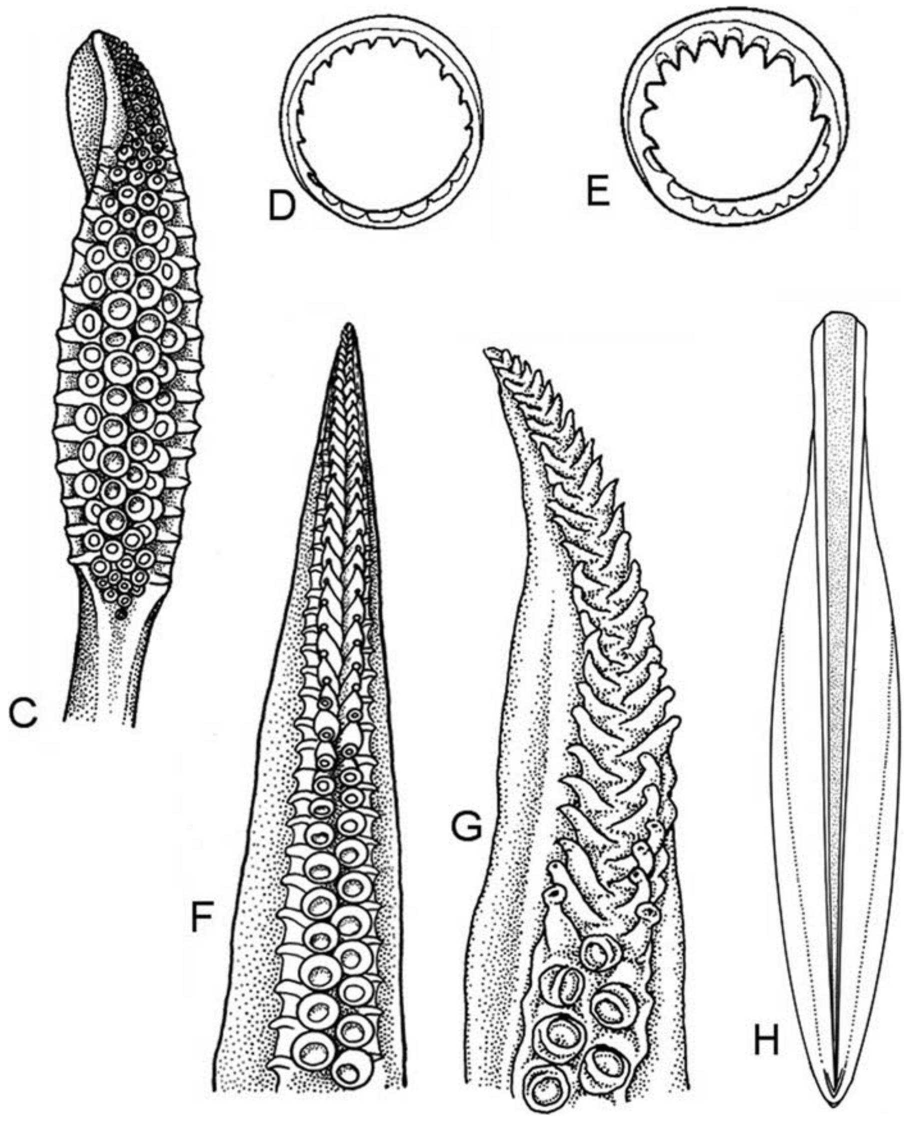


Fig. 7.—Continued.

Nateewathana et al. 2000, present material).

Material examined.—Thirteen specimens of *S. lessoniana* (5 females, 8 juveniles): 12 from East Africa, off Mombasa and the western Madagascar coast, and 1 from the Red Sea. See Appendix 1G for detailed localities and capture data. All measurements and relative indices are reported in Appendix 2G. Table 7A gives data on measurements and indices. A summary of selected measurements, indices and sucker dentition from various authors is provided in Table 7C. Selected ranges of indices are in Table 8.

Diagnosis.—Fins broadly oval in outline, extend to the anterior edge of the mantle, their length over 90% (up to nearly 100%) of mantle length except in paralarvae and small juveniles (Fig. 7A, B). Fins narrow in width uniformly from the point of maximum width, located at about the posterior 0.4 of the body (i.e., distance from widest point to the anterior edge of the mantle on average 60–65% of mantle length). Each lappet of buccal membrane bears from 2–11 small suckers (present material 4–6).

Description.—A large loliginid squid (size exceeds 300 mm ML) with the *Sepia*-like body of the genus, unique among squids (Fig. 7A, B). The mantle is long and robust, with the posterior end not sharply pointed, rather more bluntly rounded. Fins very long, occupying almost the entire length of the mantle, their width up to 75% (on average 60–65%) of mantle length. Head large with prominent eyes. Arms strongly developed; arm formula 3.4.2.1, the first pair smaller, more slender than pairs II–IV. Arm sucker rings with 18–29 triangular, sharply pointed teeth around the whole margin, but most pronounced on distal 0.67 of ring (Fig. 7E). Tentacles long, robust; tentacular clubs long (up to 35% of mantle length), only slightly expanded (Fig. 7C). Club sucker rings with 14-23 small, sharp, regularly spaced teeth around entire ring (Fig. 7D).

Left ventral arm hectocotylized in males by the modification of the distal one third (about 25–35%) of arm length, where the two series of suckers are transformed into long, conical, fleshy papillae with a minute sucker with smooth chitinous ring on each tip. Long, fleshy papillae connected by low folded ridge that extends along arm between the rows of papillae; papillae on dorsal row thicker and longer than those on ventral row (Brakoniecki 1986) (Fig. 7F, G).

Gladius very wide, width about 20% of length. Rachis stout, broad, short anteriorly, gradually narrows posteriorly. The vane is slightly curved ventrally at its posterior end (Fig. 7H).

Biology.—*Sepioteuthis lessoniana* is the subject of fisheries of various degree and importance, and it also is a very promising species for aquaculture and biomedical purposes. Consequently, the biology of this squid has been studied rather intensively, both in the field and in the laboratory (e.g., Rao 1954; Suzuki et al. 1983; Silas 1986; Segawa 1987; Jackson 1989; Ueda & Jo 1989; Hanlon et al. 1991; Segawa et al. 1993a; Lee et al. 1994; Ueta & Segawa 1995; Ueta et al. 1995, 1999; Wada & Kobayashi 1995; Wada et al. 1995; Balgos & Pauly 1998; Boal & Gonzalez 1998; Ueta et al. 1999; Forsythe et al. 2001; Mhitu et al. 2001; Pecl 2001; Jackson & Moltschaniwskyj 2002; Samuel & Patterson 2002).

Sepioteuthis squids, particularly *S. sepioidea* of the western Atlantic, also are known as "reef squids", due to their preference for coral reef environments, i.e., warm, clear, tropical and subtropical waters (Vecchione et al. 1998).

Sepioteuthis lessoniana is a neritic species that occurs from the surface down to about 100 m depth throughout its area of distribution. Rather common in coastal environments on sea grass beds, coral reefs, and sandy bottoms, it usually migrates consistently inshore after the winter is over to start mating and spawning (Rao 1954, Suzuki et al. 1983, Segawa 1987, Segawa et al. 1993b, Ueta & Segawa 1995).

Spawning season depends on the hydrographical conditions and can be quite extended. It occurs from January to June off southern India (Rao 1954) and from mid-June to late August and September in the cooler southern Japanese waters (Segawa 1987, Ueda & Jo 1989). Several peaks of two to three months during the year are reported for the Andaman Sea and the Gulf of Thailand populations (Chotiyaputta 1993a).

Recent observations confirm the existence of flexible reproductive strategies in this species (Pecl 2001) and affirm its potential to spawn multiple batches of eggs at discrete times throughout the adult life span. Therefore, even though field observations of spawned-out females do exist that show a consistent degeneration of the tissues of the whole body (e.g., Rao 1954) and confirm that egg-laying is the final event of the life cycle, the spawning "phase" itself may be quite prolonged, as also indicated by rearing observations (e.g., Wada & Kobayashi 1995).

Another example of the great flexibility of the *S. lessoniana* life cycle is given in the study of Jackson & Moltschaniwskyi (2002), who observed significant spatial and temporal variation in growth rates and maturity of the equatorial, tropical, and subtropical Indo-Pacific populations. In the "hot" shallow equatorial waters of the Gulf of Thailand, *S. lessoniana* grow faster and mature earlier, at a much smaller size, than *S. lessoniana* that inhabit the "cool" subtropical waters of southern Australia. The tropical population off Townsville (northeastern Australia) shows an intermediate situation between the two extremes, as well as an alternation of generations that depends on the season of hatching.

Eggs are embedded in milky white, soft, gelatinous, slender, finger-like capsules, each of which usually contains up to 13 eggs in a row (Segawa et al. 1993b). These capsules are attached in clusters to the substrate. Based on the number of eggs in a single capsule, on the mode of capsule attachment to the substrate, and on the season of spawning, it was suggested that *S. lessoniana* actually is a complex of species in the Japanese waters (Segawa et al. 1993a, Izuka et al. 1994; see *Remarks*).

Length frequency analyses and field observations indicate a life span that ranges between 1 and 3 years for this species (Rao 1954, Silas et al. 1982, Segawa 1987, Ueda & Jo 1989). Rearing experiments, however, evidenced a considerably shorter life cycle, with females reaching sexual maturity and spawning at ages between 110 and 140 days (ML between 105 and 145 mm, Segawa, 1987).

The employment of direct ageing techniques (i.e., statolith reading and analysis) on field-captured animals revealed that *S. lessoniana* of the tropical Australian waters indeed do grow at a very fast rate. Individuals reached maturity and completed the whole life cycle in less than 100 days, at a size of about 180–200 mm ML (Jackson 1990). A very large animal (a mature male of 364 mm ML) was captured and age-analysed by statolith at 164 days (Jackson, pers. comm.), supporting the hypothesis of a very rapid growth during the entire life cycle.

The discrepancies between the results of length frequency analyses and statolith ageing were attributed, at least in part, to underestimation of the age of older squid (Balgos & Pauly 1998) in the latter case; however, it must be remembered that length frequency analysis is not considered to be an entirely adequate method to assess squid growth (e.g., Caddy 1991, Alford & Jackson 1993, Jackson et al. 2000).

A rapid growth rate certainly is one of the characteristics that makes *S. lessoniana* especially suitable to laboratory experiments and to aquaculture projects (Lee et al. 1994, Nabhitabhata 1995). In addition, the life cycle in captivity is completed in 4–6 mo, with adult weights between 0.4 and 2.2 kg. Feeding rate is high; a variety of prey items, e.g., live fishes and crustaceans, is eaten, and late juveniles and adults also can be trained to accept and ingest food pellets (Hanlon et al. 1991). Crowding in captivity can be a problem during the crucial juvenile phase (Danakusumah 1999), but it is tolerated afterwards; the incidence of disease and cannibalism is low. Reproduction is easily achieved in captivity.

All of these biological characteristics make *S. lessoniana* very interesting and quite promising for future aquaculture projects focused not only on the needs of biomedical research but also to those of human food production (Hanlon et al.

1991). Successful cephalopod mass-culture experiments in Thailand on three cephalopod species, including *S. lessoniana*, have led to the production and release of a consistent amount of cephalopod paralarvae (about 2 million each year since 1990) to enhance natural stocks (Nabhitabhata 1995). Recent information reported that *S. lessoniana* has been cultured through several successive generations (Walsh et al. 2002).

Fishery.—*Sepioteuthis lessoniana* is of commercial interest throughout its distributional range, being marketed mostly fresh but also dried (e.g., Roper et al. 1984, Sarvaiya 1991). It is captured throughout the year with a variety of gear, including lure-hooks, set nets, spears, beach seines or purse seines, and jigs in inshore waters (e.g., Dunning et al. 1994), and by trawlers on the continental shelf.

In Japanese waters, most squids are caught by directed trawl fishery and also as a by-catch, but a purse seine fishery directed at *S. lessoniana* occurs from May to September around Hong Kong (Chikuni 1983); squid jigging also is efficiently practiced (Tokai & Ueta 1999).

The bigfin reef squid is one of the loliginid species caught in the waters of the South China Sea (Nateewathana et al. 2000), and it probably represents one of the main components of the captures in Indonesian waters (Chikuni 1983), as evidenced by local studies (e.g., Soselisa et al. 1986, Sudjoko 1987). It also is one of the cephalopod species that supports a minor domestic fishery in northern Australian waters (Dunning et al. 1994).

This species is highly abundant in the Gulf of Thailand and in the Andaman Sea, where it represents one of the most important commercial species for the cephalopod fishery (Chotiyaputta 1993a, Chantawong & Suksawat 1997). It is caught in smaller quantities all along the east coast of India (Silas 1986), and it supports a fishing industry in Madras state (Rao 1954). In recent years, *S. lessoniana* accounted for 7% of Indian east coast cephalopod landings, all from Palk Bay and the Gulf of Mannar (Meiyappan & Mohamed 2003).

Sepioteuthis lessoniana is reported as moderately abundant in Sri Lankan waters but rather scarce on the west coast of India (Silas 1986). Very poor information is available for the remaining part of the Arabian Sea (Chikuni 1983) and eastern African waters, although we expect that significant local fishery production occurs.

Remarks.—The systematic status of the genus has long been stable (Vecchione et al. 1998), and since the generic revision by Adam (1939a, four species are considered valid, including *S. lessoniana*. One of them, *S. loliginiformis*, is considered doubtful by Nesis (1987).

The hypothesis that two different infraspecific populations of *S. lessoniana* inhabit the Okinawa area was postulated by Segawa et al. (1993a) on the basis of the differences observed in the spawning season, spawning substrate, attachment of capsules, number of eggs per capsule and the arrangement of the deposited capsules themselves. The "usual" egg capsules are found attached to an "exposed" substrate, contain a medium number of 4–8 eggs, and are deposited in April–May. The "unusual" egg capsules are attached to the underside of hard substrata, contain only 2 eggs per capsule, and are laid from June to October. Subsequent observations by isozyme and other morphological analysis (Izuka et al. 1994, 1996a, 1996b; Yokogawa & Ueta 2000) indicate the presence of three different taxa within the *S. lessoniana* complex off the Okinawa islands. They appear to be demonstrably reproductively isolated; thus the species requires a systematic revision.

Acknowledgments

The authors acknowledge with gratitude the support of the Italian Consiglio

Nazionale delle Ricerche (CNR) (National Research Council); the North Atlantic Treaty Organization (NATO); the Smithsonian U.S. National Museum of Natural History, Department of Invertebrate Zoology; the Smithsonian Oceanographic Sorting Center, and the Rosensteil School of Marine and Atmospheric Sciences (RSMAS). We also acknowledge colleagues M. Vecchione (National Marine Fishery Service Systematics Laboratory, Smithsonian U.S. National Museum of Natural History) for helpful discussions about loliginid systematics, and Nancy Voss (RSMAS) for valuable comments on the manuscript. The technical support of I. H. Roper is very much appreciated, as always. The comments and suggestions of two reviewers were most helpful and appreciated.

Note added in proof:

While this paper was in press, an important volume was published that addresses many aspects of loliginid systematics, life history, biology, and fisheries.

Chotiyaputta, C., E.M.C. Hatfield and C.-C. Lu, Guest Editors. 2005 Cephalopod Biology, Recruitment and Culture; International Symposium and Workshop, Phuket, Thailand, 2003. Phuket Marine Biological Center Research Bulletin No. 66, 2005. 365 p.

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Associate Editor: Stephen L. Gardiner