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FAO Species Catalogue for Fishery Purposes No. 4, Vol. 1

CEPHALOPODS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF SPECIES KNOWN TO DATE

Volume 1. Chambered Nautiluses and Sepioids

(Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)

FIAT PANIS

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Volume 1

Chambered Nautiluses and Sepioids

(Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)

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The First Volume of this New Edition of the Cephalopods of the World Catalogue

is warmly dedicated to the memory of

Kir N. Nesis

an accomplished scientist and teuthologist,

a true gentleman

and a cherished friend and colleague.

PREPARATION OF THIS DOCUMENT

This document has been prepared by the Marine Resources Service, Fishery Resources Division, FAO Fisheries Department. It is part of the regular programme activities and a partial fulfilment of the Organization's role with regards to the marine fisheries resources identification and biodata (FAO Programme Element 232A3). It received support through contributions from the Ministry of Agriculture and Forestry Policies of the Government of Italy and from the Ministry of Foreign Affairs of the Kingdom of Norway to the FAO Global Partnerships for Responsible Fisheries (FISCODE).

This publication is the first of three volumes of the second edition of the original FAO Catalogue of Cephalopods of the World (Roper *et al.*, 1984), and it constitutes Volume I of Number 4 in the new series: *FAO Species Catalogue for Fisheries Purposes*, that evolved as an independent series in 2001 from the former *FAO Fisheries Synopsis* No. 125.

Because the new Catalogue has expanded apace with recent research and fisheries information and revisions, it now is necessary to publish it as three free-standing volumes. Each volume has separate pagination, terminology/glossary, systematic sections, list of species and a volume-specific bibliography. This allows readers to use each volume independently without having to consult the other volumes for technical terms, measurements or bibliographic purposes. We hope that this added flexibility will provide convenience and utility for users of the Catalogue.

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ABSTRACT

This is the first volume of the entirely rewritten, revised and updated version of the original FAO Catalogue of Cephalopods of the World (1984). The present Volume is a multiauthored compilation that reviews six families: *Nautilidae*, *Sepiidae*, *Sepiolidae*, *Sepiadariidae*, *Idiosepiidae* and *Spirulidae*, with 23 genera and the 201 species known to the date of the completion of the volume. It provides accounts for all families and genera, as well as illustrated keys to all taxa. Information under each species account includes: valid modern systematic name and original citation of the species (or subspecies); main synonyms; English, French and Spanish FAO names for the species; illustrations of dorsal and ventral aspect of the whole animal (as necessary) and other distinguishing illustrations; field characteristics; diagnostic features; geographic and vertical distribution, including GIS map; size; habitat; biology; interest to fishery; local names when available; a remarks section (as necessary) and literature. The volume is fully indexed and also includes sections on terminology and measurements, an extensive glossary, an introduction with an updated review of the existing biological knowledge on cephalopods (including fisheries information and catch data for recent years) and a dedicated bibliography.

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Authors
FAO Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SC

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Reid, A. 2005. Family Sepiadariidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 1. Rome, FAO. pp. 204–207.

Reid, A. 2005. Family Idiosepiidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 1. Rome, FAO. pp. 208–210.

Reid, A. 2005. Family Spirulidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 1. Rome, FAO. pp. 211–212.

Reid, A. & Jereb, P. 2005. Family Sepiolidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 1. Rome, FAO. pp. 153–203.

Reid, A., Jereb, P. & Roper, C.F.E. 2005. Family Sepiidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae)*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 1. Rome, FAO. pp. 57–152.

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In particular, for this Volume, we want to thank: **Eero Aro** (Finnish Game and Fisheries Research Institute, Helsinki, Finland), **Eduardo Balguerias** (Centro Oceanografico de Canarias-IEO, Santa Cruz de Tenerife, Spain), **Giambattista Bello** (Acquario Provinciale, Bari, Italy), **Alexei Birkun** (Crimean State Medical University, Simferopol, Ukraine), **Teresa Borges** (Centre of Marine Sciences, University of Algarve, Lisbon, Portugal), **Julia Filippova** (Russian Federal Institute of Marine Fisheries and Oceanography, Moscow, Russia), **Ian Gleadall** (Tohoku Bunka Gakuen University, Sendai, Japan), **Angel Guerra** (Instituto de Investigaciones Marinas, Vigo, Spain), **Eugenia Lefkaditou** (Institute of Marine Biological Resources-NCMR, Athens, Greece), **Marek Lipinski** (Marine and Coastal Management-DEAT, Cape Town, South Africa), **Piero Mannini** (Marine Resources Services-FIR, FAO, Rome, Italy), **Joanne Murphy** (University of Aberdeen, Aberdeen, Scotland, UK), **Chingiz Nigmatullin** (Atlantic Research Institute of Fisheries and Oceanography, Kaliningrad, Russia), **João Pereira** (Instituto Nacional de Investigação Agrária e das Pescas, Lisbon, Portugal), **Sergio Ragonese** (Istituto per l'Ambiente Marino Costiero–CNR, Mazara del Vallo, Italy), **Francisco Rocha** (Instituto de Investigaciones Marinas, Vigo, Spain), **Alp Salman** (Ege University, Izmir, Turkey), **Bruce Saunders** (Bryn Mawr College, Bryn Mawr, Pennsylvania, USA), **Ignacio Sobrino** (Centro Oceanografico de Cádiz-IEO, Cadiz, Spain), **Tooraj Valinassab** (Iranian Fisheries Research Organization, Teheran, Iran), **Peter Ward** (University of Washington, Seattle, USA).

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Pere Oliver (Instituto Español de Oceanografía, Palma de Mallorca, formerly of FAO, Rome) initiated this revised edition, followed by **Michel Lamboeuf** (FAO, Rome) and **Jordi Lleonart** (FAO, Rome), who were our contacts at FAO. This publication would not have been forthcoming without their very much appreciated support and encouragement. We especially thank **Michel Lamboeuf** for his help with the use of the FAO FISHSTAT database and for his revision of the graphic sections thereafter.

Of course, a compilation of this nature must rely heavily on already-published works; we acknowledge these publications with gratitude. In particular, we acknowledge here that many illustrations from these works have been used for the purposes of this Catalogue, for which we are most appreciative.

We also acknowledge with deep thanks the members of the FAO technical staff who so efficiently contributed to the preparation of this Volume: **Emanuela D'Antoni** for her excellent job in creating the many illustrations needed for the Catalogue and for greatly enhancing many illustrations from the literature; **Nicoletta De Angelis** and **Michèle Kautenberger** for their skilful collaboration in completing this highly technical and complex document and **Fabio Carocci** for his help in preparing the distribution maps.

Colour photographs are included in this new version of the Catalogue to enrich the quality and utility of the book. Therefore we acknowledge with gratitude those who contributed with great generosity by offering photographic material: **M. Demestre**, **J.W. Forsythe**, **M. Lamboeuf**, **J. Lleonart**, **M. Norman**, **W.F. Rathjen**, **P. Sanchez and W.B. Saunders.**

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TABLE OF CONTENTS

1. INTRODUCTION

by Patrizia Jereb, Clyde F.E. Roper and Michael Vecchione

With the increasing exploitation of finfish resources, and the depletion of a number of major fish stocks that formerly supported industrial-scale fisheries, increasing attention continues to be paid to the so-called 'unconventional marine resources', which include numerous species of cephalopods. Cephalopod catches have increased steadily in the last 30 years, from about 1 million metric tonnes in 1970 to more than 3 million tonnes in 2001. This increase confirms a potential development of the fishery predicted by G.L. Voss in 1973, in his first general review of the world's cephalopod resources prepared for FAO. The rapid expansion of cephalopod fisheries in the decade or so following the publication of Voss's review, meant that a more comprehensive and updated compilation was required, particularly for cephalopod fishery biologists, zoologists and students. The FAO Species Catalogue, 'Cephalopods of the World' by C.F.E. Roper, M.J. Sweeney and C.E. Nauen was published in 1984 to meet this need.

The number of cephalopod species that enter commercial fisheries has continued to grow significantly since 1984, as a result of a still-growing market demand and the expansion of fisheries operations to new fishing areas and to deeper waters. It has been suggested that the cephalopod 'life-strategy' may guarantee survival against environmentally stressful conditions, including those caused by heavy fishing. However, as cephalopod fisheries experienced further extensive development, parallel concern developed regarding potential overexploitation. Thus, a broad consensus developed among fishery biologists to apply the experience gained from errors made in finfish management to avoid possible failures in cephalopod exploitation. To help prevent potential failures, refined species identification capabilities are required, as well as a more detailed and accurate compilation of information on cephalopod species, distribution, biology, fisheries and catch statistics. Consequently, FAO recognized that a new edition of the 'Cephalopods of the World' catalogue was needed. To achieve this expanded goal, several authors with particular areas of specialization were assembled to enhance the accuracy, coverage and utility of this revised catalogue.

In our attempt to make this document as comprehensive and as useful as possible, the taxonomic coverage of this edition of the catalogue is organized into 3 levels of interest:

Level 1 : species of cephalopods currently exploited commercially and species utilized at the subsistence and artisanal levels;

Level 2 : species of occasional and fortuitous interest to fisheries; this includes species considered to have a potential value to fisheries, based on criteria such as edibility, suspected abundance, accessibility, marketability, etc.;

Level 3 : species with no current interest to fisheries, which are listed only with the basic information available.

The inclusion of such a wide range of species is necessary to provide the most comprehensive inventory of species possibly useful to mankind, regardless of their current commercial status. For example, this work should be useful for the ever-expanding search for development and utilization of 'natural products', pharmaceuticals, etc.

The catalogue is based primarily on information available in published literature. However, yet-to-be-published reports and working documents also have been used when appropriate, especially from geographical areas where a large body of published information and data are lacking, and we are particularly grateful to colleagues worldwide who have supplied us with fisheries information, as well as bibliographies of local cephalopod literature.

The fishery statistics presented herein are taken from the FAO official database, FISHSTAT, now available on the Worldwide web (FISHSTAT Plus 2000). This information is supplemented by field observations made by the authors in many parts of the world, both in preparation of the 1984 volume, as well as for the current edition. These field visits provided opportunities to examine fresh material at landing sites, markets and laboratories, as well as to obtain first-hand information about local cephalopod fisheries from regional fisheries workers.

During the 20-plus years separating the two editions, the rapid development of cephalopod fisheries worldwide and the simultaneous increase in the population of fisheries scientists, their research and publications, made available an enormous amount of new data and research results. Sometimes it is difficult to evaluate the reliability of published data, especially with regard to the identification of species in areas where the cephalopod fauna has not been sufficiently studied. It is entirely understandable that field workers isolated from good library and museum/collection facilities have difficulties in correctly identifying the species they encounter in the field. Moreover, the discovery of new species, the more accurate delimitation of known species, or even the introduction of nomenclatural changes, may cause confusion and lead to the use of scientific names that are incorrect by modern standards. Although great care was exercised to evaluate and correct such published information used in the catalogue, some incorrect interpretations may have occurred. Another difficulty, in the taxonomic literature especially, is that information on the economic importance of species is rather scarce or of a very general nature. Also, we may have overlooked important information published only in relevant local fisheries literature that is unavailable on a broader scale. All of these potential difficulties, however, have been significantly mitigated during the preparation of the new edition because of the availability on-line of fisheries databases and bibliographic search capabilities.

With regard to the limitations mentioned above, we heartily request that readers who detect any errors in the information presented, or who have any additional information and data that will enhance the accuracy and utility of this book, please contact and inform one of the authors or the Species Identification and Data Programme (SIDP) of the Marine Resources Service, Fisheries Resources Division, Fisheries Department, FAO Rome.

For further reading and information on cephalopod biology, fishery and resources, additional references and websites are listed at the end of references.

1.1 Plan of the Catalogue

This catalogue is organized by families and their appropriate genera within major cephalopod groups, then alphabetically by species.

Level 1, the most important species for fisheries, consists of detailed information in all 12 categories listed below. **Level 2**, which comprises those species of occasional, fortuitous or potential interest to fisheries, consists of whatever information is available and appropriate in the 12 categories. **Level 3**, those species for which there is no current interest to fisheries, consists of basic information (i.e. scientific name, size, geographical distribution, literature). The format within the species sections includes the first two levels of treatment (Level 1 and Level 2) presented together. Species included in Level 3 are presented at the end of each family.

Consequently, each major group and family is introduced with general descriptive remarks, illustrations of diagnostic features, highlights of the biology and relevance to fisheries. The information that pertains to each species in Levels 1 and 2 is arranged by categories as follows: (1) scientific name; (2) synonymy; (3) misidentifications; (4) FAO names; (5) diagnostic features with illustrations; (6) maximum known size; (7) geographical distribution with map; (8) habitat and biology; (9) interest to fisheries; (10) local names; (11) remarks and (12) literature.

(1) Scientific Name: Reference to author, date and publication is given for the original description of each species.

(2) Frequent Synonyms: Principal synonyms and name combinations are listed.

(3) Misidentifications: Misidentifications as other species are reported here and discussed in detail under section 11, Remarks, along with other nomenclatural points.

(4) FAO Names: English, French and Spanish names for each species, used primarily within FAO, are selected on the basis of the following criteria: (i) each name must apply to one species only, in a worldwide context; (ii) the name must conform to FAO nomenclatural spelling; (iii) the name should apply only to a cephalopod species, and should not lead to confusion with species names in other major animal groups. Wherever possible, these names are selected based on vernacular names (or parts of names) already in existence within the areas where the species is fished. FAO species names, of course, are not intended to replace local species names, but they are considered necessary to overcome the considerable confusion caused by the use of a single common name for many different species, or several names for the same species.

(5) Diagnostic Features: Principal distinctive characters of the species are given as an aid for identification, accompanied by pertinent illustrations. Species identifications should be attempted only after verification of the family through use of the illustrated key to families. Reference to FAO Species Identification Guides is given wherever relevant.

(6) Size: The known mantle length (or total length in some cases) of both males and females is provided where possible. Sizes or measurements might not be completely comparable because they were taken mostly from preserved or fixed specimens, but measurements of commercially important species often come from fresh material. Because of the elasticity of tentacles and arms total length is not a very accurate measurement. Where both total length and mantle length are given, the respective figures do not necessarily pertain to the same specimen but may have been obtained from different sources. The available information on the size attained by some species often is very meagre, so the maximum reported size cited here might be considerably smaller than the actual maximum size. Maximum weight is given when available.

(7) Geographical Distribution: The entire known geographic range of the species, including areas of seasonal occurrence, is given in the text and shown on a map. In cases where only scattered records of occurrence are available, question marks have been used to indicate areas of suspected or unconfirmed distribution.

(8) Habitat and Biology: The known depth range of the species and information on salinity and temperature of its habitat are given where available. For the sake of exactness actual depth data are reported, as given in the literature referenced. Information on biological aspects, such as migrations, spawning seasons and areas, longevity, food, and predators, is also included.

(9) Interest to Fisheries: This paragraph gives an account of the areas where the species is fished and of the nature of the fishery; its importance is either qualitatively estimated (minor, moderate, major or potential) or actual figures of annual landings are provided. Data on utilization (fresh, dried, cooked, frozen, canned, etc.) are also given where available. Here, too, the quality and quantity of the available information varies considerably among the species.

(10) Local Names: These are the names used locally for the various species. The present compilation is necessarily incomplete, since only a fraction of the local names applied to specific entities is actually published. In many cases, local names are available only for species that support traditional fisheries. Apart from possible omissions due to limitations of literature available, some of the names included may be somewhat artificial, i.e. through transliteration of indigenous words into English. The local species name is preceded by the name of the country concerned in capital letters and, where necessary, by geographical specifications in lower case letters.

(11) Remarks: Important information concerning the species, but not specifically linked to any of the previous categories, is given here. For example, in some cases the taxonomic status of certain scientific names requires further discussion. Other nomenclatural problems are discussed in this section, such as the use of subspecies names.

(12) Literature: This includes references to the most important publications relevant to the species, the emphasis being on biology and fisheries. Additional references are included in the bibliography. In the case of a few uncommon species, only systematic papers are available.

1.2 General Remarks on Cephalopods

The group known as cephalopods (class **Cephalopoda**) is the most complex in the phylum Mollusca, and indeed, in all of the invertebrate phyla. It includes exclusively marine animals that live in all oceans of the world with the exception of the Black Sea, from the Arctic Sea to the Antarctic Ocean and from the surface waters down into the deep sea.

Cephalopods first appeared as a separate molluscan taxonomic entity, the nautiloids, in the Upper Cambrian period (over 500 million years ago), but more than half of these ancestors were already extinct by the end of the Silurian, 400 million years ago, when only the nautiluses survived. Meanwhile, other forms arose in the late Palaeozoic (between 400 and 350 million years ago), including those of the Subclass Coleoidea, but most of them became extinct by the end of the Mesozoic, about 150 million years ago. The only members of the subclass Coleoidea that exist today are the forms that developed in the Upper Triassic and Lower Jurassic (between 200 and 150 million years ago).

Although there is a long fossil record of many different groups, all living cephalopods belong to two 'subclasses': the **Coleoidea**, which includes the major groups known as squids, cuttlefishes *sensu lato*, octopods and vampires, and the **Nautiloidea**, containing two genera, ***Nautilus*** and ***Allonautilus***, the only surviving cephalopods with an external shell.

At the present time the status and understanding of the **Systematics and Classification** of the Recent Cephalopoda is under considerable discussion. The families of living cephalopods are, for the most part, well resolved and relatively well accepted. Species-level taxa usually can be placed in well-defined families. The higher classification, however, still is not resolved. The classification above the family level is controversial and a broad consensus still needs to be achieved. This situation is not unexpected for a group of organisms that has undergone explosive research attention in recent decades.

Consequently, rather than accept and promote any particular scheme of classification, before consensus and stability are achieved, we will use an 'operational breakdown' that is satisfactory for the objectives of this Catalogue. For practical purposes we separate the cephalopods into several groups, without assigning or implying taxonomic relationships. Figure 1 diagrams several of the classification schemes currently under discussion.

In this work the following groups are used, as illustrated in Figure 2[1/]:

Nautiluses
Cuttlefishes
Bobtail squids
Bottletail squids
Pygmy squids
Ram's horn squid
Myopsid squids
Oegopsid squids
Vampires
Cirrate octopods
Incirrate octopods

[1/] The endings used in the group names do not imply any level of classification.

Unresolved taxa:

Spirula
Idiosepius
Bathyteuthis
Chtenopteryx
Sepiadariidae

Plural versus singular usage of cephalopod common group names is standardized as follows:

squid, cuttlefish, octopod, octopus, vampire, nautilus refer to one individual or one species;

squids, cuttlefishes, octopods, octopuses, vampires, nautiluses refer to two or more individuals and/or species. These terms are also used to indicate the major groups.

The term **'cuttlefishes'** is also used '*sensu lato*' to indicate the following groups: Cuttlefishes, Bobtail squids, Bottletail squids, Pygmy squids and the Ram's horn squid.

We differentiate between the members of the family Octopodidae, which are called **octopus/octopuses** and the members of the whole group (Incirrate and Cirrate or any combination of non-Octopodidae taxa), which are called **octopod/octopods**.

Cephalopods **occur in all marine habitats** of the world: benthic forms are found on coral reefs, grass flats, sand, mud and rocks; epibenthic, pelagic and epipelagic species occur in bays, seas; and epipelagic, mesopelagic, bathypelagic and benthopelagic species are all present in the open ocean. Salinity is considered to be a limiting factor in cephalopod distribution; they are generally restricted to salinity concentrations between 27 and 37‰. However, ***Lolliguncula brevis***, which lives and reproduces in waters of 17‰, demonstrates a capacity for a higher degree of salinity tolerance (Hendrix *et al.*, 1981). Some species inhabit the Red Sea and the southern coasts of the Iberian Peninsula (Guerra, 1992), where the salinity is higher than 37‰ and other species have been found in waters where salinity ranges between 25 and 18‰ (Sea of Marmara; Unsal *et al.*, 1999). The habitat depth range extends from the intertidal to over 5 000 m. Many species of oceanic cephalopods undergo diel vertical migrations: they occur at depths of about 200 to 700 m during the day, then at the onset of twilight and increasing darkness, they ascend into the uppermost 200 m for the night. A deeper-living layer of diel migrators occurs from about 1 000 m to 600 m during the daytime. The abundance of cephalopods varies, depending on group, habitat and season, from isolated, territorial individuals (primarily benthic octopods and sepioids), through small schools of squids with a few dozen individuals, to huge schools of neritic and oceanic species with millions of specimens.

The **size of adult** cephalopods ranges from less than 1 cm (Jackson, 1989) to the giant squid at approximately 20 m in total length, including the tentacles. The largest specimens may weigh well over 500 kg, but the average size of commercial species is 20 to 40 cm mantle length and about 0.1 to 2.0 kg total weight.

Cephalopods are **soft-bodied, bilaterally symmetrical** animals with a well-developed head and a body that consists of the muscular mantle, the mantle cavity that houses the internal organs, and, when present, the external fins. The head bears an anterior circumoral (surrounding

Roper *et al.* (1984)

Order	Suborder
Teuthoidea	Myopsida
	Oegopsida
Sepioidea	
Vampyromorpha	
Octopoda	Cirrata
	Incirrata

Engeser and Bandel (1988)

Superorder	Order	Suborder
Decapoda	Spirulida	
	"higher decapods" (name not given)	Teuthina
		Sepiina
Vampyromorphoidea	Vampyromorpha	
	Octopoda	Cirrata
		Incirrata

Clarke (1988)

Order	Suborder
Sepioidea	
Sepiolioidea	
Teuthoidea	Myopsida
	Oegopsida
Vampyromorpha	
Octopoda	

Sweeney and Roper (1998)

Superorder	Order	Suborder
Decabrachia	Spirulida	
	Sepiida	
	Sepiolida	
	Teuthida	Myopsina
		Oegopsina
Octobrachia	Vampyromorphida	
	Octopodida	Cirrina
		Incirrina

Young *et al.* (1998)

Division	Superorder	Order	Suborder
Neocoleoidea	Decapodiformes	Oegopsida	
		Myopsida	
		Sepioidea	Sepiida
			Sepiolida
			Spirulida
			Incertae sedis
	Octopodiformes	Vampyromorpha	
		Octopoda	Cirrata
			Incirrata

Boletzky (1999)

Grade	Superorder	Order
	Decabrachia	Spirulida
		Sepiida
		Sepiolida
		Idiosepiida
		Teuthida
Vampyropoda	Pseudooctobrachia	Vampyromorpha
	Octobrachia	Cirroctopoda
		Octopoda

Haas (2002) ranks not given

1	2	3	4	5
Neocoleoidea	Decabrachiomorpha	Oegopsida		
		Uniductia	Spirulida	
			Myopsida	Loliginida
				Sepiida
	Octobrachiomorpha	Vampyromorpha		
		Octopoda	Cirrata	
			Incirrata	

Fig. 1 Some conflicting suprafamilial classifications of living coleoid cephalopods

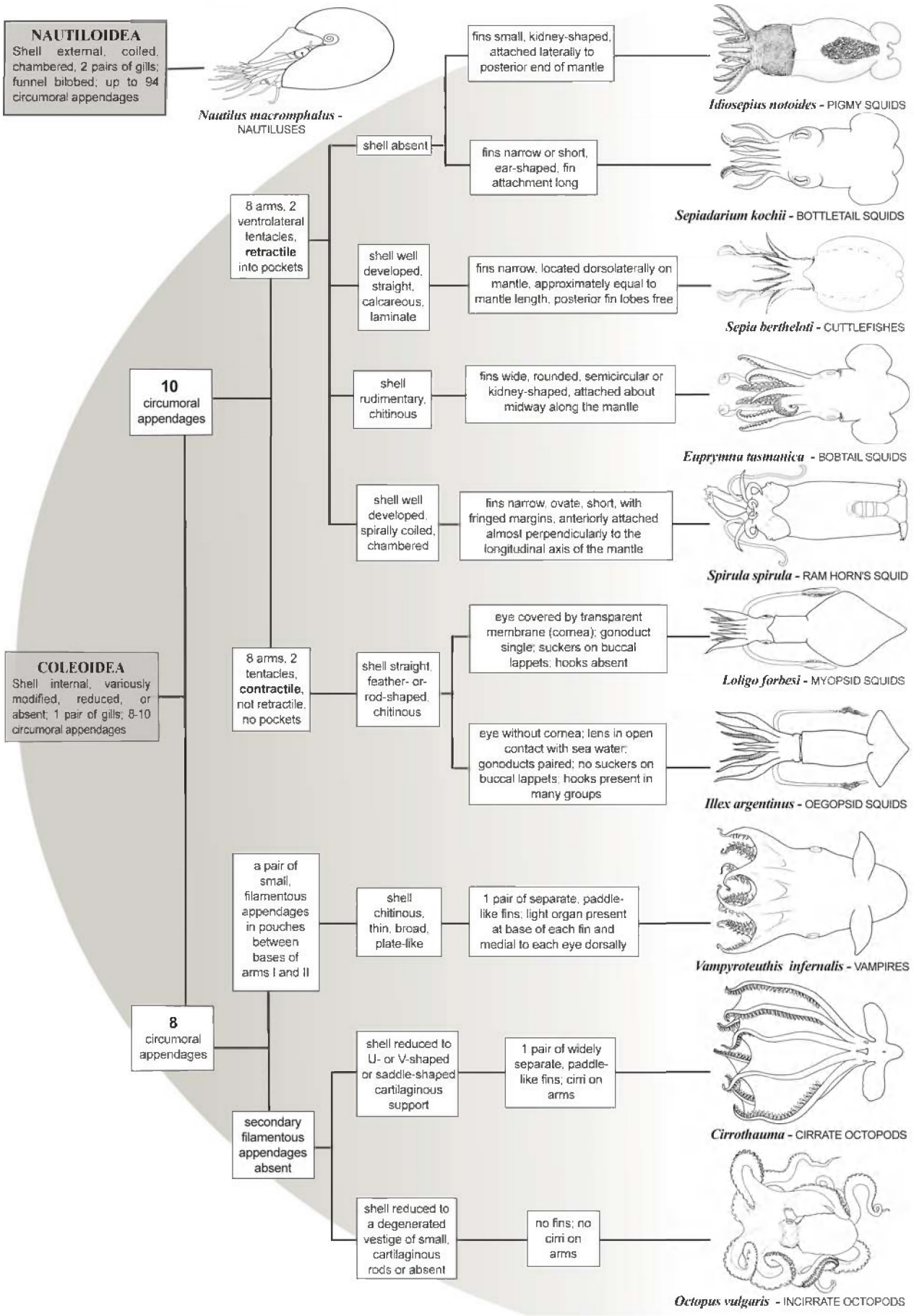


Fig. 2 Living cephalopods

the mouth) crown of mobile appendages (arms, tentacles). This characteristic feature reflects the origin of the name Cephalopoda, which derives from the union of the two Greek words: 'kefale', head, and 'pous', feet. The name was erected by Schneider in 1784, and it became permanently in use within the scientific context with the publication of Cuvier's work (1798). Arms and tentacles bear suckers and/or hooks (except in ***Nautilus***), which are powerful tools to seize prey. The mouth has a pair of chitinous jaws (the beaks) and, as in other molluscs, a chitinous tongue-like radula (band of teeth) occurs in most cephalopod species. The ancestral mollusc shell is variously modified, reduced, or absent in living coleoids. It is a calcium carbonate structure in cuttlefishes (the cuttlebone of sepiids and the ram's horn shell of ***Spirula***), reduced to a rigid structure composed of chitin in squids (the gladius or pen, sometimes quite flexible) and to a cartilaginous structure in finned octopods. In some sepiolids no vestige of shell is found. A true external shell occurs only in the primitive nautiluses (restricted to the Indo-Pacific), although a shell-like egg case is produced and carried by female argonauts (pelagic octopods often misnamed 'paper nautilus').

The loss of the external shell allowed the development of a **powerful muscular mantle** that became the main locomotory organ for fast swimming, via water jetting from the funnel. The funnel (siphon) is a unique, multifunctional, muscular structure that aids in respiration and expulsion of materials in addition to locomotion. Oxygenated water is drawn through the mantle opening around the head (neck) into the mantle cavity, where it bathes the gills for respiration. Mantle muscular contraction expels the deoxygenated water from the mantle cavity through the ventrally located funnel. The discharge jet serves to eliminate nephridial and digestive wastes, as well as to complete the respiratory cycle and for locomotion. Female reproductive products (eggs, egg masses) also are discharged through the funnel. Most coleoids produce ink, a dark, viscous fluid also expelled through the funnel. The ink may take the form of a mucoidal 'pseudomorph' (false body) to decoy potential predators, or of a cloud to obscure the escaping cephalopod.

One pair of gills (ctenidia) is present, except in ***Nautilus*** and ***Allonautilus***, which have two pairs for **respiration**, i.e. to extract the oxygen from the water. However, in contrast with coleoids, ***Nautilus*** makes use of anaerobic respiration during periods of high activity and can survive in water with very low oxygen content. Coleoids also use anerobic muscle layers. Cutaneous respiration also occurs in some cephalopods.

The cephalopod **circulatory system** is distinctive within the Mollusca. It is a closed system (blood contained within vessels), similar in many respects to that of vertebrates and fulfilling the demand for the more efficient circulation required by an active locomotory system. There is a principal, or systemic, heart, two branchial hearts and developed arterial, venous and capillary systems supplying blood to the muscles and organs. From the gills, the oxygenated blood goes through the efferent branchial vessels to the systemic heart, where it is expelled from the ventricle through three aortas: the cephalic or dorsal aorta, which supplies the head and the anterior part of the gut; the posterior, minor or abdominal aorta that supplies the mantle and fins along with the posterior part of the gut and the funnel; and the gonadal aorta that develops gradually with sexual maturation of the animal. The blood is collected through sinuses and capillaries into the veins, through which it goes to the branchial hearts that pump it through the filaments of the gills. The circulating respiratory pigment used for oxygen transport is copper-containing haemocyanin, a system of rather lower efficiency than the iron-containing haemoglobin of vertebrates. In living cephalopods blood sinuses are much reduced and replaced functionally by muscles. The circulatory system therefore has to work against the peripheral muscle-induced pressure, which increases with increasing activity (maximum during jet-swimming). It also has to cope with the resistance of the small diameter of the final capillary blood vessels, and the low oxygen carrying capacity of the blood (less than 4.5% by volume). In spite of these limitations, the system has other functional modifications (see for example Wells and Smith, 1987; Martin and Voight, 1987) that achieve the capacity to deliver oxygen at a rate comparable to that of active fishes, enabling cephalopods to accomplish extraordinary performances.

The **excretory system** also differs markedly from that of other molluscs and, along with the closed circulatory system and the branchial circulation, enables unique relationships between blood and the final secretion, the urine. The excretory system differs between living nautiloids and coleoids and also among coleoids, but the general organization is similar, consisting basically of the renal sac with the renal appendages (organs comparable to vertebrate kidneys), the pericardial glands, the branchial hearts and the gills. Cephalopods are ammoniotelic, and ammonium ions are continuously released by the gill epithelium and by renal appendages into the surrounding water. Ammonium ions are used by buoyant squids to replace denser chloride ions in fluids in the coelom and in the body tissues. Because this solution is less dense (and hence more buoyant) than seawater, it provides lift.

The **nervous system** is highly developed in recent cephalopods, with a large brain and peripheral connections, contrasting with the original molluscan circumesophageal nerve ring. Among its most remarkable features is the giant fibre system of squids and cuttlefishes that connects the central nervous system with the mantle muscles. This system consists of three orders of cells and fibres and ensures the immediate and simultaneous contraction of mantle, fins and retractor muscles of both sides, rather than an anterior to posterior sequential contraction that would be counter-productive for water movement (expulsion). Also remarkable is the eye development of most coleoids, for which vision plays a major role in life. Their eyes are large, have a design generally similar to that of fishes and other vertebrates (e.g. a lens focuses images on the retina), and all the available evidence suggests the ocular/visual performance to be comparable to that of vertebrates. The cephalopods also developed a system to keep the focused image stationary on the retina while the animal turns, by moving the eyes in coordination with the head/body movement. This is extremely important for hunters that rely on sight, and it is accomplished by connections of the eye muscles with the statocysts, a mechanism similar to the vestibulo-optic system of fishes. The statocyst system provides cephalopods with information on their orientation, as well as changes in position and direction of movement. The statocyst system is highly developed in coleoids, where it consists of separate cavities located in the cartilaginous skull, posteroventral to the brain. The statocysts contain

nervous cells and receptors differentiated to detect both linear acceleration, with the aid of calcareous stones called statoliths, and angular acceleration. Many coleoids also have extra-ocular photoreceptors (photosensitive vesicles) about which little is known; in mesopelagic squids they appear to monitor light intensity in order to enable the animals to match the counter-illumination with the ambient light by their own photophores (light-producing organs). Cephalopods are provided with numerous mechano- and chemoreceptors and recent evidence indicates that in some species, like ***Loligo vulgaris***, ***Sepia officinalis*** and ***Octopus*** sp., ciliate cells form lines in several parts of the body, a system analogous to the lateral-line system in fishes.

Most Coleoidea are able to change colour by using a complex system of **chromatophores** under nervous control. The chromatophores are pigment-filled sacs present in the skin, and capable of remarkable expansion and contraction. This system responds to current situations in the environment, e.g. background coloration and threatening predators, and it is critical for survival, especially for shallow-water benthic forms. Coloration capabilities are variable depending on taxonomic group and habitat. Most species also have **iridocytes** (shiny, reflective platelets) in the skin. Most cephalopod behaviour includes rapid changes in overall colour and colour patterns, as well as changes in the texture of the skin, from smooth to heavily papillate, tubercular, or with erected flaps. While shallow-living cephalopods are able to conceal themselves by chromatophore-produced colour patterns, chameleon-like colour changes and textural presentations, many deep-sea forms camouflage themselves by producing bioluminescent light from photophores which eliminate their silhouettes against the downwelling sunlight in the dimly-lit mid-depths.

Locomotion is achieved by any of, or a combination of, the following methods, depending on the taxonomic group: 1) jet propulsion; 2) flapping or undulating the fins on the mantle; 3) crawling along the bottom on the arms; 4) medusoid swimming with arms and interbrachial webs. The fins on the mantle also provide balance and steering during jet propulsion. Many families of midwater squids have evolved to 'low energy life styles' and achieve neutral buoyancy by producing and storing in tissues or in different organs substances/elements with specific properties, such as oils or solutions of ammonium ions. This capability enabled coleoid cephalopods to inhabit open water, even in the great depths in the ocean, the greatest volume of living space on earth.

Cephalopods are voracious, active **predators** that feed upon crustaceans, fishes, other cephalopods and, in the case of some benthic octopods, on bivalved molluscs. The speed of cephalopods, their high mobility and powerful visual systems, along with strongly-muscled arms and tentacles, both equipped with suckers and/or hooks, make them extremely efficient hunters. A common hunting technique in sepioids and loliginids involves extremely rapid shooting forward of the tentacles to capture the prey, while in some oegopsid squids the tentacles may be used like long, sucker-covered fishing lures. Some octopods use their web to envelop crabs and occasionally may wait until prey touches them before attacking. The captured prey of cephalopods is brought to the mouth and killed by bites of the strong, chitinous beaks, equipped with powerful muscles. Sometimes the prey are first paralysed with a fast-acting toxin, immobilization being a strong advantage in case of large and/or very active prey such as large crabs. The Incirrate octopods and ***Sepia*** species usually poison their prey before eating them, while squids do not seem able to produce such strongly toxic secretions. Digestion in cephalopods is rapid and efficient and cephalopod metabolism is essentially proteinic: there is little or no digestion/assimilation of carbohydrates and lipids. Food conversion is highly efficient, especially in octopuses, where up to 50% of the food eaten can be converted into body mass. More active cephalopods like squids, however, need several times the amount of food required by octopuses and can eat from 3 to 15% of their body weight each day.

All cephalopods are **dioecious** (separate sexes) and many, though not all, exhibit external sexual dimorphism, either in morphological or in size differences. Females frequently are larger than males, a phenomenon which reaches its extreme in some pelagic octopods (such as ***Argonauta***) where males are truly dwarf forms. Males of many species possess one, occasionally two, modified arm(s) (the hectocotylus) for transferring spermatophores to females during mating. The males of some species also exhibit modifications to other arms, in addition to the hectocotylus. The hectocotylus may be simple or complex and can consist of modified suckers, papillae, membranes, ridges and grooves, flaps. The one or two limbs function to transfer the spermatophores (tubular sperm packets) from the male's reproductive tract to an implantation site on the female. The spermatophores may be implanted inside the mantle cavity (where they may penetrate the ovary), into the oviducts themselves, around the mantle opening on the neck, on the head, in a pocket under the eye, around the mouth or in other locations. Females of a few species also develop gender-specific structures (e.g. arm-tip photophores) when mature. Mating is often preceded or accompanied by courtship behaviour that involves striking chromatophore patterns and display. Copulatory behaviour varies significantly among species, in colour and textural display, proximity of male and female, duration of display and spermatophore transfer, and the location of implantation of the spermatophores on the female.

The **gonads** form a single mass at the posterior end of the mantle cavity, and female gonoducts may be paired (in oegopsids and incirrate octopods) or single, as in other coleoids and in the nautiluses. Cephalopod reproductive systems are highly complex structures with ducts, glands and storage organs. Female octopods have oviducal glands, while decapods, in addition, have nidamental glands and, in some families, accessory nidamental glands. Spermatophores are produced in the multi-unit spermatophoric gland and stored in the Needham's sac, from which they are released through the terminal part of the duct, the penis. This term is not strictly accurate in many groups, because the spermatophores are passed to, or taken by, the hectocotylized arm(s), which in turn transfer(s) the spermatophore(s) to the female. Some families do not possess a hectocotylus. Instead, the terminal portion of the male reproductive tract forms a functional penis that can be greatly enlarged and elongated, often extending out of the mantle cavity and past the head. It is likely that these structures directly transfer the spermatophores to the female. The number and size of spermatophores vary greatly, depending on the species and group (for reviews on spermatophore structures and function see Mann *et al.*, 1966, 1970; Mann, 1984). Once in contact with seawater, the so called 'spermatophoric reaction' begins. The spermatophores evert, with the resultant extrusion of the

sperm packet caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher. The resulting extruded sperm packet is named spermatangium (or sperm bulb or body). Sperm are able to survive several months once stored in the female, at least in some species, and fertilization of mature ova may take place either in the ovary, the oviducal glands, the mantle cavity or the cone formed by the outstretched arms while the eggs are laid. Males of the pelagic octopod ***Argonauta*** (and its relatives) insert sperm into a detachable hectocotylized arm. Mating occurs by the arm severing and crawling into the female's mantle cavity.

Fertilized **eggs** are embedded in one or more layers of protective coatings produced by the oviducal and nidamental glands and generally are laid as egg masses. Egg masses may be benthic or pelagic, varying among the major taxonomic groups. Some oceanic mesopelagic and deep-sea species, however, lay individual eggs.

Eggs of neritic, inshore squids, except in ***Sepioteuthis***, generally are very small (only a few millimetres in diameter) and frequently are laid in finger-like pods each containing from a few to several hundred eggs. Deposited in multifinger masses (sometimes called 'sea mops'), these eggs are attached to rocks, shells or other hard substrates on the bottom in shallow waters. Many oceanic squids lay their eggs into large sausage-shaped or spherical gelatinous masses containing tens or even hundreds of thousands of eggs that drift submerged in the open sea. Other pelagic species lay individual eggs, not enmeshed in gelatinous masses.

Cuttlefishes *sensu lato* lay few, relatively large (around 10 to 40 mm in diameter), grape-like eggs that are attached to hard substrates. Some species camouflage the eggs from predators by making them dark using a coating of ink deposited by the female at egg laying.

Cirrate octopods lay rather large (from 10 to 25 mm length) single eggs, enclosed in a tough protective coating (see Boletzky, 1982, 1986), and they are laid individually or in small clusters of a very few eggs.

Benthic incirrate octopods lay their eggs singly or in grape-like clusters and strands. Most species attach the eggs to hard surfaces such as rock or shells while some carry the eggs within their arms and webs. The eggs vary in size from a few millimetres to 40 mm long. They are attached to each other and/or to the substratum by cement produced by the oviducal gland. They lack the gelatinous outer matrix found in squid and cuttlefish eggs and the outer shell found in the Cirrate octopod eggs: the protective function has been 'replaced' by the brooding behaviour of the female parent. The female of the pelagic octopod ***Argonauta*** constructs a thin, decorative shell-like egg case, which encases her mantle and into which she periodically lays and attaches festoons of minute eggs.

The mode of reproduction and egg-laying still is unknown for many species, especially those of oceanic and deep-sea environments.

Development of cephalopod embryos is direct, without true metamorphic stages. Hatchlings of species with large eggs look like miniatures of the adult, while hatchlings of species with small eggs undergo gradual changes in proportions during development. The young of some species, however, differ conspicuously from the adults. Thus, the term 'paralarva' has been introduced for these early stages of cephalopods that differ morphologically and ecologically from older stages. Hatchlings from large-egged benthic octopods are either benthic crawl-away young or temporarily planktonic, quickly settling back to the adult benthic habitat. Small-egged benthic octopuses produce planktonic hatchlings with very simple skin patterns of large chromatophores. The paralarvae of many deep-sea species of squids and octopods occur in the upper 100 m of the open ocean; then they exhibit an ontogenetic descent, gradually descending to deeper depths with increasing size until the adult depth is attained. Time of embryonic development varies widely, from a few days to many months, depending on the species and the temperature conditions. Hatching may occur synchronously from a single clutch or be extended over a period of 2 or 3 weeks.

In spite of the large number of studies and research carried out on cephalopods, especially in recent decades, the **life history** of the majority of species is still unknown, and our knowledge of the life cycles of the members of this interesting class remains fragmentary. Information comes from studies in the field as well as from observations in the laboratory. However, little is known of life history for species that are not targets of regular fisheries, and only a handful of cephalopod species have been reared successfully in the laboratory.

Studies and monitoring of **growth** in cephalopods are complicated by the high variability in individual growth rates. This makes it difficult to apply conventional methods, e.g. length frequency analysis, used for more traditional resources such as fishes and crustaceans. Determination of age in Recent coleoids is also difficult, because they have few hard structures that show daily marks (rings) that would enable direct estimates of age. In the last 15 years, progress has been made on the study and analysis of statoliths that has resulted in an increased knowledge of age, in squids at least. This has led to changes in our perspectives about the physiology and ecology of many teuthoids, but more research is required before a full understanding is achieved (see Jereb *et al.*, 1991; Okutani *et al.*, 1993; Jackson, 1994 and Lipinski and Durholtz, 1994 for reviews and discussions). Principle results obtained from the research generally confirm a very high growth rate in cephalopods, comparable to that of the fastest-growing fishes.

Nautilus species have a **life span** of about 20 years, during which they spawn intermittently when first mature, then annually when fully mature, laying a few large eggs at a time. The life expectancy of most coleoids appears to range from a few months to one or two years. Many small oceanic squids, such as pyroteuthids may complete their life cycles in less than six months, while some minute forms of sepioids have a life span of only 2 to 3 months. Recent evidence, however, suggests that larger species of squids and octopods, for example the giant squid (***Architeuthis*** spp.) and the giant octopus (***Enteroctopus dofleini***), as well as those that live in coldest habitats, may live for several years.

A general consensus exists that **spawning** is a terminal event, in spite of the high variability in the duration of individual spawning periods (5 to 50% of ontogenesis; Nigmatullin, 2002) as well as the type of spawning, e.g. from one-time, total spawning, to prolonged, intermittent, multiple batches. A recent review of coleoid reproductive

strategies (Rocha *et al.*, 2001) defined five comprehensive, flexible strategies:

A) **Single event spawning**, formerly termed semelparity, consists of synchronous ovulation, and monocyclic, simultaneous terminal spawning; ***Octopus vulgaris*** is the typical example of this life strategy.

B) **Multiple event spawning**, formerly termed iteroparity, with the following possibilities:

1 - polycyclic spawning: egg-laying occurs in separate batches during the spawning season and growth occurs between production of egg batches and subsequent spawning events (e.g. ***Nautilus*** species);

2 - multiple spawning, with group-synchronous ovulation, monocyclic spawning and growth between egg batches (e.g. ***Sthenoteuthis oualaniensis***);

3 - intermittent terminal spawning with group-synchronous ovulation, monocyclic spawning and no growth between egg batches (e.g. ***Sepia officinalis***, ***Loligo vulgaris***, ***Illex coindetii***);

4 - continuous spawning, with asynchronous ovulation, monocyclic spawning and growth between egg batches (e.g. ***Idiosepius pygmaeus***, ***Opisthoteuthis*** spp., ***Argonauta*** spp.).

All coleoids die after their spawning period.

The **total number** of living species of cephalopods that have been described is fewer than 1 000; over 720 are listed in the present catalogues. However, many species still wait to be described and this is particularly true for the octopuses, where at present at least another 100 undescribed species are estimated to exist.

The status of the **systematics** of cephalopods has changed in the last 30 years, as research and associated scientific discussions have increased substantially. However, phylogenetic relationships among most families within the major groups remain uncertain, and new species are described fairly frequently as new habitats are explored and as families are gradually better-understood.

The major groups of living cephalopods, i.e. squids, cuttlefishes, bobtail and bottletail squids, octopods, vampires and chambered nautiluses, are easily distinguished by external characteristics.

The **squids** have an elongate, cylindrical body with posterolateral fins on the mantle (rarely, the fins extend for the length of the mantle); 10 circumoral appendages anteriorly on the head, not connected at bases with a web (except Histioteuthidae); 8 arms with 2 (occasionally 4 or more) series of stalked suckers with chitinous rings (and/or chitinous hooks in some groups) that extend along the entire arm length; 2 longer tentacles with an organized cluster of 2 or more series of stalked suckers (and/or hooks) at the distal section (tentacular club); the proximal tentacular stalks usually are devoid of suckers or hooks.

The **cuttlefishes** have broad sac-like bodies with lateral fins that are narrow and extend along the length of the mantle; posterior lobes of the fins free (subterminal) and separated by the posterior end of the mantle; 10 circumoral appendages, the longest 2 (tentacles) are retractile into pockets on the ventrolateral sides of the head; the 8 remaining arms frequently with 4 series of stalked suckers with chitinous rings, never hooks (otherwise 2 series); eyes covered with a transparent membrane and eyelids present; dorsal, internal, finely chambered shell, thick, chalky, calcareous (cuttlebone).

The **bobtail** and **bottletail squids** have sac-like bodies with short, round and flap-like fins, attached laterally about midway along the mantle, with pronounced anterior lobes and free posterior lobes; 10 circumoral appendages as above, 8 short arms, 2 retractable tentacles, each with a well defined club; large eyes covered with a transparent membrane; shell thin, chitinous or lost.

The **octopods** have a short, sac-like body, either with no lateral fins or with separate, paddle-like fins in the deep-sea cirrate octopods; 8 circumoral arms only (no tentacles) with bases connected by a membranous web, and unstalked suckers in one or two series, without chitinous rings or hooks, along the length of the arms.

The **vampires** have 8 circumoral arms, plus an additional pair of long, thin, suckerless filaments, retractile into pockets, located between arms I and II; one pair of posterior, elongate-oval fins (2 pairs in juveniles); numerous small photophores over body, posteriorly a pair of large, external photophores; single series of suckers bordered with cirri on each arm.

The chambered **nautiluses** are characterized by an external, smooth, coiled, chambered shell, numerous circumoral appendages without suckers (up to 100 appendages), a 'funnel' of rolled muscular flaps or lobes not fused in the ventral midline and simple eyes without lenses.

More detailed descriptions of these groups are presented in the appropriate systematic section.

Cephalopods are important experimental animals in **biomedical research** with direct applications to humans. Because of their highly developed brains and sensory organs, they are valuable in behavioural and comparative neuroanatomical studies. In addition, the extremely large single nerve axons of some cephalopods, the largest in the animal kingdom, are used extensively in neurophysiological research.

The bite of cephalopods, especially octopuses, can be painful at the least to humans, poisonous or secondarily infected, or, rarely, lethal. Several human deaths have been recorded in the western Pacific Ocean and Australia as a result of poisonous bites from the small blue-ringed octopus, ***Hapalochlaena*** spp.; the lethal toxin is a neural blocker considered a form of tetrodotoxin. Another documented threat by squids to humans is from the large ommastrephid squid, ***Dosidicus gigas***, which forms large aggressive schools that are known to have attacked fishermen that have fallen in the water, causing several confirmed deaths. Scuba divers also have been attacked. Therefore, cephalopods must be handled carefully.

1.3 Interest to Fishery and Role in the Ecosystem

Cephalopods are very important for human consumption. They have been fished on an artisanal basis for several thousand years and were already well known and highly valued as food by ancient Greeks, Romans and Chinese. In more recent times, increasingly heavy demand for cephalopods by the Japanese led to the development of a commercial fishery that started in the 1960s and rapidly expanded to become global in scope. Fishing pressure on cephalopods has increased as stocks of finfishes have been depleted worldwide, and cephalopod resources now are exploited throughout the world oceans.

A catch of around 3.3 million tonnes was reported for 2001 by FAO statistics (FAO, 2000); this figure represents about 3.6% of the world total marine catch for the same year. Estimated value for this catch was around US$5 billion, a value that positions cephalopods in fifth place in the monetary value scale, following miscellaneous coastal fishes, shrimps, tunas, cods and hakes.

Table 1 reports the world catch of cephalopods since 1950, by major fisheries 'categories'. The discrepancies in the last digit of the totals in the tables are caused by rounding off the individual figures. Squids, both inshore and oceanic, are by far the main component in the world cephalopod fishery production, accounting for about 70% of the total catch, followed by cuttlefishes (species of ***Sepia***, ***Sepiella*** and allied genera), then by octopuses (mainly ***Octopus*** spp. and ***Eledone*** spp.). The impressive increase in production during the last 20 years is due mainly to the increase of squid catches, from a little more than 1 million tonnes in 1980 to over 2.2 million tonnes for 2001; this value represents an increase of 250%. Such a significant increase in production was mostly related to the 'discovery' and increasing exploitation of squid resources in the southwest Atlantic (Fig. 3b), principally for ***Illex argentinus***, (Fig. 4b), as well as an increase in the production of other major squid target species, mainly ***Todarodes pacificus*** in the northwest Pacific and ***Dosidicus gigas*** in the eastern Pacific (Figs 3d–e and 4b). ***Illex argentinus*** catches exceeded 1 million tonnes in 1999 (Table 2), a record peak which placed this species at the eleventh position in value of the total world marine-species production of that year. Fluctuations in squid catches are responsible for the major fluctuations in total cephalopod landings, changes usually related to a combination of environmental, marketing and/or political reasons. For example, the low cephalopod catch in 1998 in the eastern Pacific, reflected the poor catch of ***Dosidicus gigas*** as a result of the El Niño weather system in the southern and central areas that year. By contrast, the low catch in the southwest Atlantic and in the northwest Pacific in the same year was mainly a result of low fishing activities by the main squid-producing countries (i.e. Korea, Japan and Taiwan Province of China). This was caused by a lower market demand due to very high catches of the previous year, together with higher fishing fees set by Argentina on foreign trawlers fishing in its waters that year.

Cuttlefishes *sensu lato* production also increased strikingly over the last two decades, doubling between 1980 and 2001 (Table 1; Fig. 4d). The main producer is China (over 50% of the total), followed by Thailand (western Pacific and central Indo-Pacific areas) and by Morocco (eastern central Atlantic), where production increased steadily in recent years.

Octopus catches have increased as well, but not as conspicuously (Table 1; Fig. 4e). The main producer is Morocco, which accounted for slightly more than 35% of the total reported octopus production in 2001, followed by Japan (about 14% of total world production). Mexico ranks first in the '***Octopus vulgaris***' landings, with over 20 000 tonnes reported for 2001, followed by Spain (nearly 15 000 tonnes); Mexican production accounts for more than one-third (38.7%) of total '***Octopus vulgaris***' species-complex reported production.

Cephalopod fisheries and landings are unevenly distributed in the world's oceans, as shown in Table 3 (Antarctic zone captures are not reported in the figure because they are minimal; these catches are discussed in the individual species sections). More than half of the total cephalopod catch (about 58% in 2001) is taken in the northwest Pacific and the southwest Atlantic combined. Other important areas are the western central Pacific, eastern Atlantic and eastern Pacific, but smaller-scale fishing activities in other areas also developed consistently in the last decades (see, for example, the Indian Ocean fisheries). Cephalopod fisheries are especially intense in Japan, southeastern Asia and China and in the Mediterranean Sea, where, however, cephalopod catches show a decreasing trend for all three main groups in the last decade (Fig. 3g).

Japan remains the leading cephalopod-producing country; over 560 000 tonnes were caught by Japanese fleets in 2001, which represents about 17% of the total world cephalopod catch (Table 4). However, China, Korea and Argentina follow closely. In fact, Korea was the main producer in 1999, principally as a consequence of the peak in ***Illex argentinus*** production.

International commerce of cephalopod products also increased strikingly during the last 20 years. Imported and exported cephalopod products were estimated at around 325 000 and 240 000 tonnes, respectively, in 1980, compared with more than 1.3 million tonnes estimated for 2001 (Table 5).

Estimated cephalopod import value reached US$ 2 700 billion in 2001. This represents about 4.6% of the value of the total world fisheries commodities imports for the same year, while the value of cephalopod exports was a little higher than US$ 2 500 billion, i.e. about 4.5% of the total world fisheries commodities export value.

Argentina was the lead exporter in the 2001 statistics in terms of quantity, followed by Spain, then by Morocco and the United States (Table 5). However, the highest monetary values of exports are those attained by Morocco (frozen ***Octopus*** spp. and squids, both ***Loligo*** spp. and ***Todarodes sagittatus***), followed by Thailand (frozen cuttlefishes and squids, as well as cephalopod 'preparations') and Viet Nam (dried squids, followed by various frozen cephalopods, including ***Octopus*** spp.).

European countries are the main market at present for imported cephalopod products, with Spain, Italy, Greece, Portugal and France accounting for 49.6% of the world total (Table 5). Spain has been the leading European importer (by tonnage) in the world since 1997. The highest import values, however, remain those spent by Japan, mainly for frozen ***Octopus*** spp., followed by various other cephalopod commodities.

Table 1
Total world cephalopod catch in thousand metric tonnes since 1950, by major fisheries categories

	Squids Total[1/]		*Loligo* spp.	Ommastrephidae	Non-identified Squids	Octopuses		Cuttlefishes		Non-identified Cephalopods		World Cephalopod Total
	mt	%	mt	mt	mt	mt	%	mt	%	mt	%	mt
1950	494.5	85	12.4	431.4	50.7	35.8	6.20	47.2	8.10	3.0	0.50	580.5
1951	548.5	85	9.9	483.1	55.5	39.9	6.20	55.6	8.60	3.0	0.50	647.0
1952	686.4	85	15.7	605.3	65.4	49.7	6.20	67.9	8.40	3.0	0.40	807.0
1953	505.9	81	14.8	429.4	61.7	53.6	8.60	62.6	10.00	3.0	0.50	625.1
1954	470.4	78	13.4	400.2	56.8	56.6	9.40	69.6	11.60	3.0	0.50	599.7
1955	477.2	78	16.9	393.8	66.5	60.0	9.80	72.7	11.80	4.0	0.70	613.9
1956	402.4	75	16.7	313.7	72.0	60.9	11.30	70.4	13.10	4.0	0.70	537.7
1957	479.6	76	17.8	393.5	68.3	67.4	10.70	77.3	12.30	4.6	0.70	628.9
1958	468.2	75	18.4	391.4	58.4	68.4	10.90	86.7	13.80	4.8	0.80	628.0
1959	611.9	78	17.8	512.1	82.0	70.7	9.00	95.0	12.10	4.3	0.50	781.9
1960	612.2	78	23.1	510.7	78.4	76.0	9.70	94.6	12.00	4.5	0.60	787.3
1961	575.1	76	24.1	481.2	69.8	79.9	10.60	94.3	12.50	4.1	0.50	753.4
1962	708.1	78	24.6	592.4	91.1	93.0	10.30	100.6	11.10	4.1	0.50	905.8
1963	830.2	81	24.8	705.4	100.0	95.1	9.30	96.2	9.40	4.8	0.50	1 026.3
1964	448.8	66	27.2	348.4	73.2	97.9	14.50	125.5	18.50	5.0	0.70	677.2
1965	616.3	70	33.9	498.9	83.5	116.4	13.20	144.4	16.40	4.8	0.50	881.9
1966	602.8	71	33.5	481.5	87.7	111.1	13.00	133.6	15.70	5.7	0.70	853.1
1967	684.6	70	31.8	539.6	113.2	146.1	14.90	146.8	14.90	5.0	0.50	982.5
1968	902.1	72	37.1	764.2	100.7	188.9	15.10	154.4	12.40	4.8	0.40	1 250.2
1969	697.5	69	34.9	548.6	114.1	163.8	16.10	151.2	14.90	4.6	0.50	1 017.1
1970	680.3	69	76.4	501.7	102.1	153.1	15.50	151.4	15.30	6.3	0.60	991.1
1971	640.1	66	79.3	427.0	133.8	150.6	15.40	178.8	18.30	7.6	0.80	977.1
1972	805.4	66	112.3	550.9	142.2	212.1	17.50	181.3	15.00	13.5	1.10	1 212.4
1973	717.5	68	111.3	434.4	171.9	178.9	16.80	150.0	14.10	15.6	1.50	1 062.0
1974	718.0	66	117.9	388.1	211.9	228.0	20.80	139.5	12.70	10.3	0.90	1 095.8
1975	797.8	67	120.6	458.5	218.7	249.1	20.80	137.3	11.50	13.7	1.10	1 197.9
1976	782.5	64	104.6	429.9	248.0	232.0	19.10	186.5	15.40	12.9	1.10	1 213.9
1977	800.6	64	117.6	357.5	325.5	206.2	16.50	223.0	17.90	17.5	1.40	1 247.3
1978	873.4	64	114.5	418.3	340.6	203.7	15.00	263.3	19.30	21.4	1.60	1 361.7
1979	1 059.8	70	114.5	571.6	373.7	157.9	10.40	285.8	18.80	19.6	1.30	1 523.1
1980	1 091.0	71	118.5	536.3	436.1	181.7	11.70	252.9	16.40	20.9	1.40	1 546.5
1981	944.7	68	124.2	448.0	372.5	222.2	16.10	198.6	14.40	17.5	1.30	1 383.1
1982	1 114.2	69	136.5	457.1	520.6	202.3	12.50	281.0	17.40	18.6	1.10	1 616.1
1983	1 085.5	65	175.0	392.8	517.6	250.3	14.90	316.5	18.90	22.4	1.30	1 674.6
1984	1 125.8	68	150.5	511.9	463.3	213.3	12.80	294.8	17.70	32.3	1.90	1 666.2
1985	1 260.2	70	178.9	530.9	550.4	211.1	11.80	280.8	15.70	36.2	2.00	1 788.3
1986	1 205.7	69	250.5	467.2	488.0	250.5	14.20	275.3	15.70	26.5	1.50	1 758.1
1987	1 756.5	76	328.4	871.1	557.0	245.5	10.70	247.5	10.80	47.6	2.10	2 297.1
1988	1 644.0	74	293.3	846.9	503.8	253.7	11.30	268.6	12.00	69.1	3.10	2 235.4
1989	1 973.8	75	357.7	968.9	647.2	275.1	10.40	279.3	10.60	115.9	4.40	2 644.0
1990	1 720.0	73	296.6	822.2	601.2	294.4	12.40	299.1	12.60	57.5	2.40	2 371.1
1991	1 856.1	72	293.7	1 072.4	489.9	319.3	12.50	301.0	11.80	84.7	3.30	2 561.1
1992	2 095.3	76	310.2	1 362.4	422.7	297.4	10.70	267.4	9.70	106.9	3.90	2 767.0
1993	1 973.6	73	317.1	1 390.4	266.1	296.6	11.00	310.5	11.60	107.1	4.00	2 687.8
1994	1 959.5	70	318.4	1 322.3	318.8	275.4	9.80	383.6	13.70	184.9	6.60	2 803.4
1995	2 001.8	68	328.0	1 313.0	360.8	304.3	10.40	421.7	14.40	210.6	7.20	2 938.4
1996	2 276.2	72	305.2	1 607.4	363.7	305.6	9.70	381.4	12.10	186.5	5.90	3 149.7
1997	2 487.9	72	269.2	1 909.8	308.9	273.4	7.90	469.4	13.60	225.9	6.50	3 456.6
1998	1 883.5	66	295.4	1 243.6	344.5	319.6	11.20	441.5	15.50	213.0	7.50	2 857.6
1999	2 582.1	72	268.3	1 860.2	453.6	352.5	9.80	453.1	12.60	210.0	5.80	3 597.7
2000	2 560.7	70	304.9	1 773.8	482.0	312.2	8.50	497.4	13.60	284.8	7.80	3 655.2
2001	2 242.6	67	288.9	1 574.5	379.2	317.2	9.50	533.3	15.90	253.7	7.60	3 346.8

(Source: FAO, 2000)

[1/] Squids are broken down into Loliginids, Ommastrephids and unidentified squids to show each group's relative importance.

Table 2
Total world cephalopod catch in thousand metric tonnes since 1980, by major species (Source: FAO, 2000)

Cephalopod species	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Illex argentinus	16.0	33.3	79.7	56.2	106.1	204.9	271.3	546.3	564.3	558.5	410.1	559.5	609.8	638.5	505.7	520.9	656.5	980.3	693.5	1145.0	930.8	743.0
Todarodes pacificus	405.4	290.4	274.2	245.9	286.5	214.3	141.5	262.0	227.8	319.8	321.5	403.0	545.2	548.4	504.4	513.4	715.9	603.4	378.6	497.9	570.4	528.5
Dosidicus gigas	19.1	9.8	1.2	0.1	0.4	15.9	1.2	0.3	1.7	10.4	14.9	45.8	109.4	124.4	195.2	136.3	142.2	162.5	27.5	134.8	182.4	223.8
Nototodarus sloani	0.8	48.8	48.9	55.7	90.1	67.1	28.1	32.7	38.5	53.0	29.8	35.1	64.4	45.1	79.4	94.1	53.7	64.6	55.6	31.4	25.6	45.1
Ommastrephes bartrami	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	49.9	55.0	36.1	47.4	23.9
Illex illecebrosus	88.7	50.2	31.3	12.0	10.6	6.9	6.7	18.1	5.9	17.7	25.6	19.7	23.9	25.6	30.7	18.6	29.0	34.8	26.6	9.9	11.2	5.7
Todarodes sagittatus	6.4	15.5	21.8	22.5	18.1	21.8	9.8	11.4	8.4	8.3	8.3	7.5	7.8	6.5	5.8	5.2	5.9	5.6	6.6	4.9	4.9	4.3
Illex coindetii	0.0	0.0	0.1	0.4	0.1	0.1	0.2	0.3	0.2	1.2	0.5	0.6	0.8	0.8	0.7	0.6	0.4	0.4	0.2	0.3	0.4	0.3
Martialia hyadesi	0.0	0.0	0.0	0.0	0.0	0.0	8.4	0.0	0.0	0.2	11.6	1.4	1.0	1.3	0.4	24.0	3.8	8.4	0.1	0.0	0.7	0.0
Ommastrephids	**536.3**	**448.0**	**457.1**	**392.8**	**511.9**	**530.9**	**467.2**	**871.1**	**846.9**	**968.9**	**822.2**	**1 072.4**	**1 362.4**	**1 390.4**	**1 322.3**	**1 313.0**	**1 607.4**	**1 909.8**	**1 243.6**	**1 860.2**	**1 773.8**	**1 574.5**
Loligo spp.	93.1	99.6	114.0	131.6	113.9	148.4	189.5	245.4	224.8	234.7	218.3	221.4	215.9	244.3	234.6	216.8	216.7	227.6	218.1	199.8	215.0	213.6
Loligo gahi	0.0	0.0	0.0	16.0	13.0	9.2	39.7	68.6	44.0	89.2	57.1	45.8	71.8	44.3	55.5	85.2	68.5	21.7	51.7	42.5	67.0	57.7
Loligo pealei	23.6	22.5	20.8	25.7	22.4	17.0	17.1	11.7	19.1	23.0	16.3	19.6	19.7	22.2	22.5	18.9	12.5	16.2	18.9	18.7	16.9	14.2
Loligo reynaudi	1.9	2.1	1.7	1.7	1.2	4.3	4.2	2.7	5.4	10.7	5.0	7.0	2.8	6.3	5.8	7.0	7.5	3.7	6.7	7.2	6.0	3.4
***Loligo* species**	**118.5**	**124.2**	**136.5**	**175.0**	**150.5**	**178.9**	**250.5**	**328.4**	**293.3**	**357.7**	**296.6**	**293.7**	**310.2**	**317.1**	**318.4**	**328.0**	**305.2**	**269.2**	**295.4**	**268.3**	**304.9**	**288.9**
Non-identified squids	**436.1**	**372.5**	**520.6**	**517.6**	**463.3**	**550.4**	**488.0**	**557.0**	**503.8**	**647.2**	**601.2**	**489.9**	**422.7**	**266.1**	**318.8**	**360.8**	**363.7**	**308.9**	**344.5**	**453.6**	**482.0**	**379.2**
SQUIDS	**1 091.0**	**944.7**	**1 114.2**	**1 085.5**	**1 125.8**	**1 260.2**	**1 205.7**	**1 756.5**	**1 644.0**	**1 973.8**	**1 720.0**	**1 856.1**	**2 095.3**	**1 973.6**	**1 959.5**	**2 001.8**	**2 276.2**	**2 487.9**	**1 883.5**	**2 582.1**	**2 560.7**	**2 242.6**
Octopodidae	113.2	131.5	137.8	146.1	145.4	144.5	183.3	180.1	192.4	210.8	229.2	235.7	218.0	223.6	205.2	235.0	230.8	210.8	245.4	295.0	259.7	261.8
Octopus vulgaris	66.4	88.7	61.9	99.8	65.1	62.9	64.4	62.5	57.8	61.8	62.2	80.2	75.8	69.4	66.3	66.8	72.9	60.3	72.5	56.1	50.5	53.1
Eledone spp.	2.1	2.0	2.6	4.3	2.7	3.7	2.7	2.9	3.6	2.5	3.0	3.4	3.6	3.5	3.9	2.5	1.9	2.3	1.8	1.4	2.0	2.4
OCTOPUSES	**181.7**	**222.2**	**202.3**	**250.3**	**213.3**	**211.1**	**250.5**	**245.5**	**253.7**	**275.1**	**294.4**	**319.3**	**297.4**	**296.6**	**275.4**	**304.3**	**305.6**	**273.4**	**319.6**	**352.5**	**312.2**	**317.2**
Sepiidae, Sepiolidae	248.1	194.7	**275.8**	311.3	288.2	273.2	266.7	236.4	253.3	262.1	283.1	289.2	254.1	297.9	371.0	411.4	370.0	455.7	429.1	438.3	484.7	519.3
Sepia officinalis	4.8	4.0	5.2	5.2	6.6	7.6	8.6	11.1	15.3	17.2	16.0	11.8	13.2	12.6	12.5	10.4	11.4	13.8	12.4	14.9	12.7	14.0
CUTTLEFISHES	**252.9**	**198.6**	**281.0**	**316.5**	**294.8**	**280.8**	**275.3**	**247.5**	**268.6**	**279.3**	**299.1**	**301.0**	**267.4**	**310.5**	**383.6**	**421.7**	**381.4**	**469.4**	**441.5**	**453.1**	**497.4**	**533.3**
Non-identified cephalopods	**20.9**	**17.5**	**18.6**	**22.4**	**32.3**	**36.2**	**26.5**	**47.6**	**69.1**	**115.9**	**57.5**	**84.7**	**106.9**	**107.1**	**184.9**	**210.6**	**186.5**	**225.9**	**213.0**	**210.0**	**284.8**	**253.7**
WORLD TOTAL	**1 546.5**	**1 383.1**	**1 616.1**	**1 674.6**	**1 666.2**	**1 788.3**	**1 758.1**	**2 297.1**	**2 235.4**	**2 644.0**	**2 371.1**	**2 561.1**	**2 767.0**	**2 687.8**	**2 803.4**	**2 938.4**	**3 149.8**	**3 456.7**	**2 857.6**	**3 597.7**	**3 655.2**	**3 346.8**

Table 3
World cephalopod capture production in thousand metric tonnes, by FAO areas during the years 1980–2001

Area	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	%
NW Pacific	882.3	691.9	761.6	738.8	717.3	709.3	596.0	706.6	691.4	877.9	861.7	815.6	913.8	873.7	937.9	1 006.5	1 165.5	1 154.1	1 033.6	1 117.8	1 222.0	1 137.5	34.0
SW Atlantic	31.0	54.1	208.4	205.2	252.1	352.9	410.5	763.9	681.4	764.3	550.9	696.9	734.3	719.5	586.2	645.2	747.9	1016.6	750.0	1 192.7	1 001.0	802.9	24.0
WC Pacific	119.6	130.0	153.6	183.1	170.2	182.6	195.5	204.9	215.7	239.1	259.8	270.0	279.8	314.2	359.3	355.8	343.9	360.0	366.1	364.6	435.3	390.5	11.7
EC Atlantic	138.0	190.5	175.9	211.6	156.6	154.0	194.3	167.7	165.0	184.5	202.4	238.8	188.4	195.0	179.1	191.2	190.6	150.4	183.7	250.3	216.4	212.9	6.4
SE Pacific	0.3	1.2	3.0	2.8	3.4	19.5	5.9	4.8	7.2	9.8	20.6	72.5	117.5	135.5	199.6	109.2	36.0	32.1	11.4	82.8	127.6	175.0	5.2
EC Pacific	30.7	32.3	19.8	16.0	17.7	24.7	35.5	67.9	76.6	80.8	80.2	64.6	40.8	38.2	58.8	111.3	201.5	213.1	30.4	150.6	202.5	167.1	5.0
W Indian Ocean	23.7	11.9	11.8	10.1	20.0	27.3	24.0	32.0	42.0	45.1	37.5	70.5	77.2	81.7	102.0	110.6	94.9	148.6	112.4	121.3	119.0	140.1	4.2
E Indian Ocean	27.4	22.6	23.4	25.4	34.3	32.9	39.1	53.6	60.5	92.5	51.8	62.3	84.1	73.3	71.3	88.4	104.6	109.4	115.7	111.8	124.1	116.0	3.5
SW Pacific	80.2	63.3	71.1	81.0	116.8	88.8	72.1	73.6	75.0	107.1	67.9	63.7	113.0	69.7	116.7	139.6	73.3	84.8	71.0	43.6	35.5	57.3	1.7
Mediterranean & Black Sea	51.7	47.1	49.4	55.3	56.7	65.7	68.4	67.7	83.3	76.9	72.5	67.8	71.7	65.4	68.7	62.5	59.3	60.1	54.3	50.7	53.8	53.8	1.6
NE Atlantic	29.2	37.4	41.9	48.5	37.2	38.2	25.4	43.4	42.4	49.7	55.5	41.2	49.9	49.0	44.0	54.0	53.4	51.0	49.9	53.1	58.8	44.5	1.3
WC Atlantic	8.4	8.9	9.3	12.3	10.2	10.4	13.3	11.5	12.0	18.2	19.3	20.3	21.5	18.8	20.0	20.7	31.1	20.8	24.1	20.1	24.4	23.2	0.7
NW Atlantic	111.3	72.0	52.1	39.9	33.1	23.9	23.7	23.5	22.0	37.6	39.0	36.3	40.7	46.4	52.0	35.6	38.9	48.7	44.7	26.8	26.4	18.4	0.6
SE Atlantic	8.5	11.1	10.1	10.0	8.3	12.1	12.6	20.2	11.4	14.7	7.8	9.9	8.2	7.1	6.5	7.4	8.2	4.1	7.8	8.3	7.5	4.7	0.1
NE Pacific	4.3	8.9	24.7	34.7	32.4	46.0	41.7	55.8	49.7	45.7	43.9	30.9	26.0	0.3	1.4	0.3	0.7	2.8	2.3	3.1	0.7	3.0	0.1
TOTAL	**1 546.5**	**1 383.1**	**1 616.1**	**1 674.6**	**1 666.2**	**1 788.3**	**1 758.1**	**2 297.1**	**2 235.4**	**2 644.0**	**2 371.1**	**2 561.1**	**2 767.0**	**2 687.8**	**2 803.4**	**2 938.4**	**3 149.7**	**3 456.6**	**2 857.6**	**3 597.7**	**3 655.2**	**3 346.8**	

(Source: FAO, 2000)

Table 4
World cephalopod capture (in metric tonnes) ranked by the 10 main producing countries from 1990 to 2001

Country	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Japan	622 235	595 516	772 777	639 683	647 090	599 685	728 759	700 036	446 927	558 527	668 147	566 371
China	69 918	70 167	70 836	122 159	193 561	225 421	175 835	246 690	379 056	417 031	482 802	504 287
Korea, Republic of	333 709	411 673	475 625	432 160	381 040	421 492	449 352	481 960	310 631	591 087	426 679	412 513
Argentina	27 778	46 375	77 746	194 653	197 971	200 400	292 851	414 041	291 993	342 934	279 914	229 874
Thailand	135 072	154 402	150 315	153 237	144 436	156 397	173 183	173 648	188 156	174 382	171 990	170 945
Taiwan Province of China	223 868	280 878	207 948	219 926	191 257	187 820	171 847	250 811	237 060	297 528	258 907	165 521
Morocco	74 143	92 162	82 368	91 685	83 047	90 134	91 324	63 963	68 553	112 829	147 727	140 829
Viet Nam	23 000	28 000	32 000	33 000	87 000	103 000	92 000	92 500	103 000	110 000	180 000	130 000
India	30 907	55 273	72 682	70 423	95 109	103 739	85 120	117 624	95 834	93 709	96 408	114 681
USA	43 497	63 307	50 975	73 646	97 879	104 119	108 878	101 506	45 240	117 124	143 808	105 125
World Total	**2 371 064**	**2 561 100**	**2 766 970**	**2 687 779**	**2 803 421**	**2 938 392**	**3 149 764**	**3 456 670**	**2 857 620**	**3 597 670**	**3 655 150**	**3 346 828**

(Source: FAO, 2000)

Table 5
World cephalopod export and import quantities and values in 2001 for the 10 leading countries

2001 Exports				2001 Imports			
Quantity (Thousand tonnes)		Value (Millions US$)		Quantity (Thousand tonnes)		Value (Millions US$)	
Argentina	158.5	Morocco	399.7	Spain	286.2	Japan	812.8
Spain	126.1	Thailand	319.0	Japan	198.7	Spain	567.3
Morocco	111.9	Viet Nam	269.7	China	195.9	Italy	421.9
USA	108.1	Spain	254.7	Italy	186.2	USA	143.6
China	101.4	China	213.1	Korea, Republic of	66.2	China	131.0
Thailand	92.4	Argentina	149.4	USA	62.1	Korea, Republic of	124.2
Korea, Republic of	76.6	India	106.1	Thailand	49.8	Thailand	65.9
Taiwan Province of China	62.5	USA	85.9	Greece	33.5	Portugal	61.0
India	60.1	Korea, Republic of	71.7	Portugal	31.2	Greece	56.2
Viet Nam	59.8	Mauritania	65.5	France	25.8	France	55.4
World Total	**1 310.8**	**World Total**	**2 506.0**	**World Total**	**1 329.4**	**World Total**	**2 750.9**

(Source: FAO, 2000)

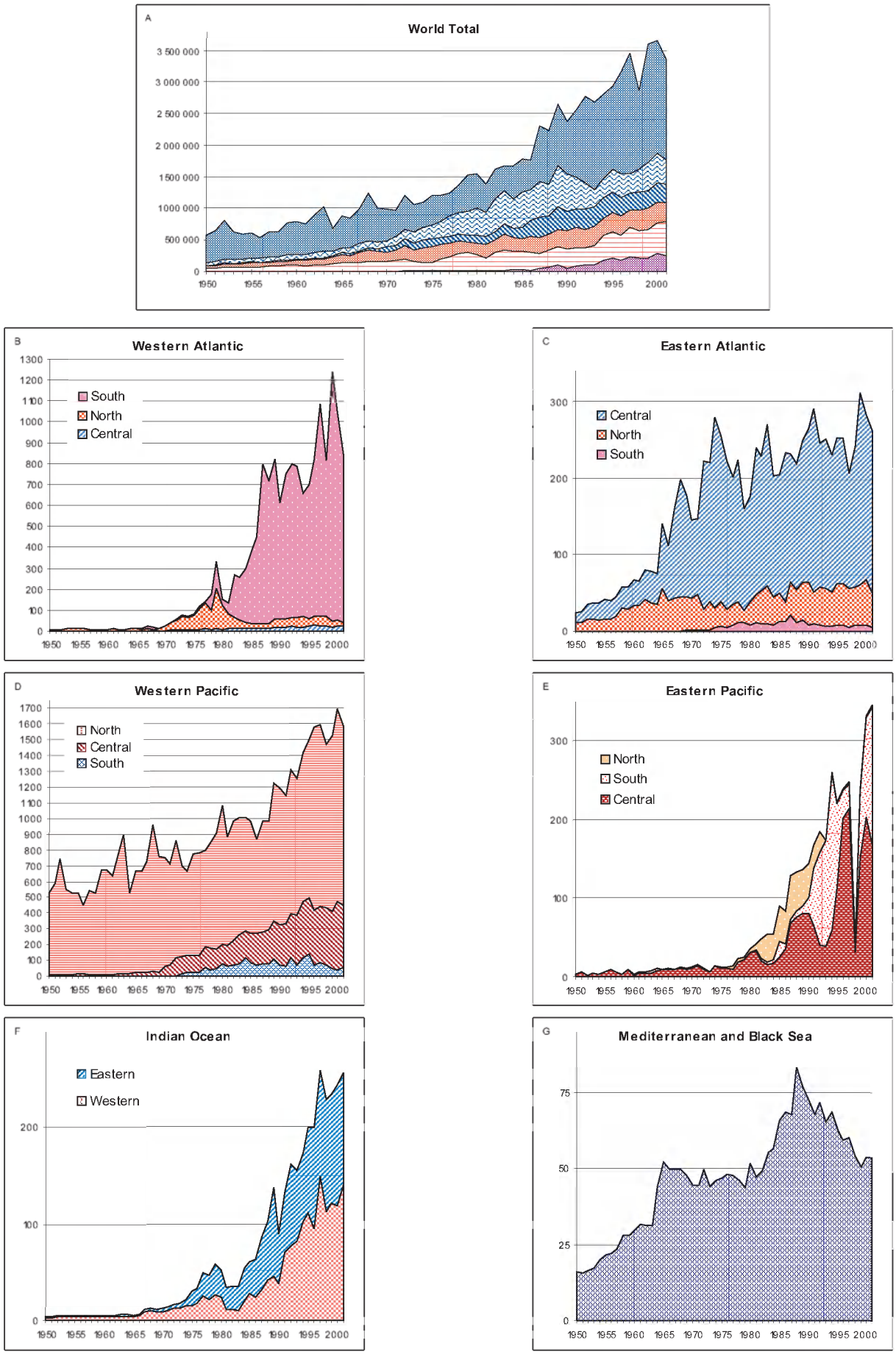


Fig. 3 Cephalopod capture (tonnes) by main FAO fisheries areas
(Source: FAO, 2000)

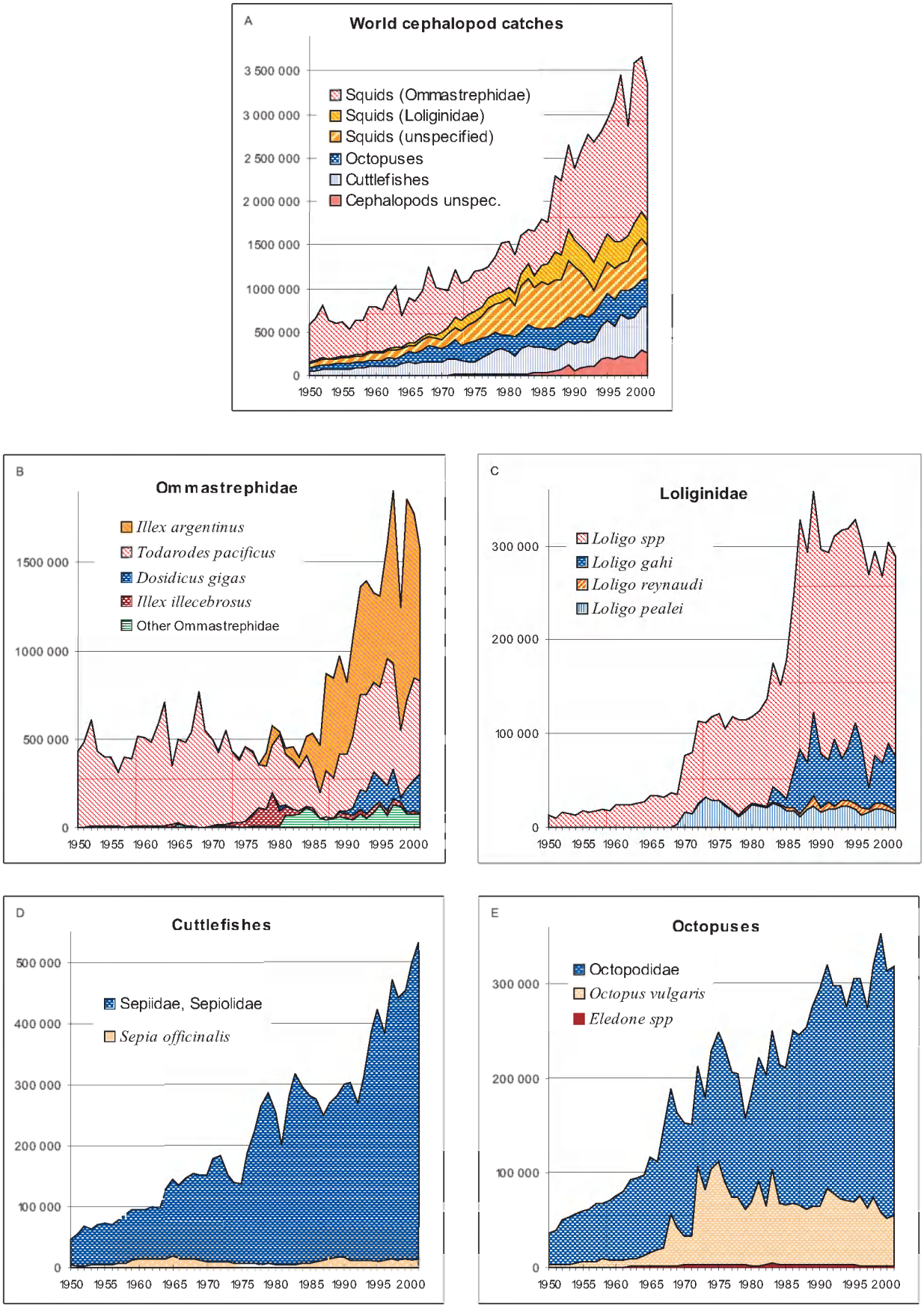


Fig. 4 Total world cephalopod capture (tonnes) by main species groups or species
(Source: FAO, 2000)

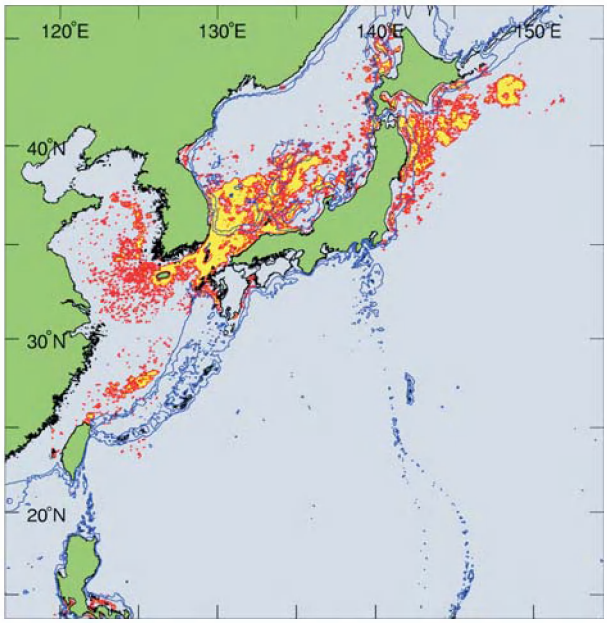
Numerous fishing techniques and methods to capture cephalopods have been developed over time. These were extensively reviewed, for example, by Rathjen (1984, 1991) and Roper and Rathjen (1991). They include hand collection, small traps, spears, lures, jigs, lampara nets, chemical flushing, midwater trawls and otter trawls.

Jigging is the most widely used method, which accounts for almost half of the world cephalopod catch: all squids, primarily ommastrephids, but also a few loliginids. This technique is employed primarily at night, when many species of squids are attracted to the fishing vessel by lights. Figure 5 shows the distribution of the world's light fishery for some of the most important squid species. Jigs, which feature numerous, variously-arranged, barbless hooks (Plate IX, 60), are lowered and retrieved by jigging machines that simulate the constant swimming behaviour of natural prey, inducing the squids to attack them. While simple hand-jigging machines are still used in small-scale, artisanal fisheries, large modern vessels for industrial fishing activities are equipped with scores of automated, computer-controlled jigging machines, each capable of catching several tonnes per night (Plate VIII, 50; Plate IX, 56). Occasionally, cuttlefishes also are captured by hand jig.

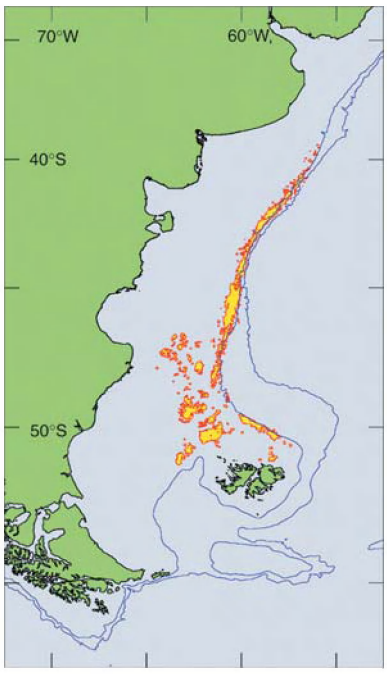
Trawling is the secondmost productive fishery method to catch cephalopods (Plate VIII, 51). Formerly, many species of squids, octopods and cuttlefishes *sensu lato* were caught as bycatch in trawl fisheries for finfishes and shrimps, but some specialized small-scale fisheries trawling for cephalopods also existed (e.g. for cuttlefishes in the Mediterranean Sea). The amount of cephalopods taken as bycatch in bottom trawls for finfish fisheries drove increasing attention to the resource by the 1980s; this led to the development of the (principally) midwater trawl fisheries specifically targeting squids, particularly the South Atlantic/ Subantarctic fishery for ***Illex argentinus***. Trawling is a very efficient technique to catch benthic and epibenthic species, but soft-bodied animals like cephalopods are often damaged by the other species in the catch, particularly in benthic and epibenthic otter trawls. Even in fisheries in which squid-specific trawling occurs, the huge catches of squids per tow often result in crushed and damaged product. Consequently, trawled squid product generally is less valuable than jig-caught squids. However, modern oceanic trawlers can process on board many metric tonnes of cephalopods per day, which helps insure a high-quality product. Bottom trawling can be very dangerous for benthic habitats because of the physical damage it causes to the seabed and associated fauna and because of its lack of selectivity. Consequently, less intense exploitation by this traditional fishing technique and an approach toward diversification of methods and redistribution of the fisheries through different areas were encouraged and still are highly recommended, especially in situations where small-scale fisheries still exist and new, more efficient methods can be implemented.

The remaining cephalopod catches come from **several different methods** (Plate VIII, 47, 49, 52-54; Plate IX, 55, 59). Cuttlefishes are captured by dredges, seines, jigs and pots specifically developed for these species and very popular in some regions, e.g. the Mediterranean Sea. Nearshore, neritic squids are caught by purse seines, octopuses are taken by pots, dragnets, hooks and spears, while ***Nautilus*** spp. are caught in deep-set wicker or wire traps.

The **utilization of cephalopods** for human consumption is extensive and diverse. Products range from fresh food, eaten raw as 'sashimi' in Japan and, in recent years, worldwide, and fresh-cooked, as well as various types of processed product (dried, canned, frozen, reduced to meal, etc.). The high protein and low fat content of cephalopods make them an important and healthy element in the human



a) Kuroshio Current Province
(*Todarodes pacificus* and *Ommastrephes bartrami*)



b) Southwest Atlantic Province
(*Illex argentinus*)

Fig. 5 Distribution of the world's light fisheries for ommastrephids (illustrations based on night-time satellite imagery) (from Rodhouse *et al.*, 2001)

diet. With the increasing demand for food for human consumption, cephalopod resources probably will receive even more attention in the future.

Considering the present level of exploitation of the commercially-fished cephalopod populations, a further increase in such fishery production is likely to occur first by expansion of the fisheries into the less-fished regions of the oceans, e.g. the Southern Ocean, probably the 'last frontier' in the field of marine fisheries. There, a standing stock of squid biomass as high as 100 million tonnes was estimated by scientists, based on an estimate of 30 million tonnes consumed by vertebrate predators (see Rodhouse *et al.*, 1994 for details), even though squid captures are rarely successful. Therefore, a priority for the future research in the field of Antarctic cephalopod biology will be to assess the squid biomass there, quantitatively and qualitatively, with the objective of determining a sustainable fishery production. However, polar cephalopods probably are longer living and slower growing than species currently harvested. Therefore, caution must be exercised in assumptions and decisions for management of polar cephalopod fisheries.

In the future, it is likely that attention will be focused on finding other species and families to replace fish stocks that become severely reduced by overfishing. Even though clear evidence reveals the existence of large cephalopod resources available for exploitation in the open oceans, based on the estimated consumption by predators (see Clarke, 1996; Piatkowski *et al.*, 2001 for reviews), many oceanic squids are distasteful for human consumption as their tissues have a high ammonium content. Research is being carried out on how to remove this factor on a commercial scale, but results will take time and catches will need to be processed before utilization. A number of ommastrephid squids that lack ammonium are considered to be underexploited. These include: ***Sthenoteuthis pteropus***, ***Ommastrephes bartrami***, ***Martialia hyadesi***, ***Todarodes sagittatus***, ***Sthenoteuthis oualaniensis***, ***Nototodarus philippinensis*** and ***Dosidicus gigas***, and the circumpolar, subantarctic ***Todarodes filippovae***. Exploitation of these species would provide large tonnages of high quality cephalopods and would require only minor development in catching techniques. However it will be necessary to determine where these species congregate for feeding and spawning activities. An analysis of biomass, production and potential catch for the 21 species of Ommastrephidae is presented in Nigmatullin (2004).

Although a number of other oceanic squid families have large populations and high quality flesh, they are not currently exploited on a commercial scale except for a few seasonal fisheries. These include members of the families Thysanoteuthidae, Gonatidae and Pholidoteuthidae, for example. Increased exploitation of these groups, however, would also require some research and development of catching techniques. Commercial exploitation of the cosmopolitan family Histioteuthidae also could be considered, since at least one large commercial-level catch has been made in the North Atlantic (see Okutani, personal communication, *in* Clarke, 1996). However, the increased exploitation of these oceanic squid species might have unpredictable, far-reaching negative effects on the mesopelagic ecosystem. Therefore, great caution must be exercised in developing this kind of fishery.

Almost all of our knowledge of the general biology of cephalopods, in fact, is limited to the shelf-living species as well as to those ommastrephids that move onto the shelf at certain seasons. These represent only about 15% of all cephalopod species (Clarke, 1996). Even so, many gaps still exist in our knowledge about their life cycles, especially as far as the relationships among species are concerned (e.g. prey-predator balances). Some populations of harvested species have shown sudden, occasionally catastrophic, declines before adequate biological data could be gathered and analysed. Squid stocks, for example, experienced true collapses at least in two well-known and documented cases. These were the northwest Pacific ***Todarodes pacificus*** fishery failure in the 1970s and the northwest Atlantic ***Illex illecebrosus*** fishery collapse in the 1980s. While the ***T. pacificus*** fishery has recovered, the ***I. illecebrosus*** fishery has remained insignificant. These collapses are thought to have occurred mainly as a consequence of temporarily unfavourable environmental conditions or actual long-term environmental changes, probably aggravated by heavy fishing pressure (Dawe and Warren, 1993).

A significant challenge thus exists to deepen our knowledge and learn the details of distribution, life history and biology of exploited species in order to allow rational utilization of the stocks. The necessity for research as a key factor towards attaining this goal has been stressed by many authors (e.g. Lipinski *et al.*, 1998) and it is especially important in the fields of life-cycle clarification, stock structure and genetics, role in the food web and interactions with the environment. The last topic seems of particular interest within the more general context of climate/environmental global changes, since the unusual biological characteristics and short life cycles of cephalopods are strongly linked to immediate, temporal environmental circumstances. Therefore, cephalopods are potentially very good 'indicator species' to predict or reflect changes in environmental conditions, both locally and on a broader scale (O'Dor and Dawe, 1998; Arkhipkin *et al.*, 2001; Bendik, 2001; Dawe *et al.*, 2000, 2001; Jereb *et al.*, 2001; Laptikhowsky and Remelso, 2001; Roberts, 2001).

Perhaps even more significant is the challenge that exists for future exploitation of new species or populations. The **role** of cephalopods **in the ecosystem**, in fact, is more complex than it was thought to be only a few decades ago. Cephalopods can be considered subdominant predators that tend to increase in biomass when other species, particularly their predators and competitors for food, become depleted, as a result of a combination of heavy or excessive fishing, other human impacts, oceanographic fluctuations and competition for food (see Caddy, 1983, and Caddy and Rodhouse, 1998 for a detailed analysis of the transition from finfish-targeted fisheries to cephalopod-targeted fisheries). A thoroughly studied case is that of the snapper fishery on the Endeavour Bank (Balguerias *et al.*, 2000), which was replaced by a cephalopod fishery between 1960 and 1970. In turn, cephalopods are major food items in the diets of innumerable species of fishes, toothed whales (e.g. sperm whales, beaked whales, dolphins, porpoises), pinnipeds (seals, sea lions) and seabirds (penguins, petrels, albatrosses).

Muscular cephalopods derive their energy from crustaceans, fishes and other cephalopods. At the same time, they are a very efficient food store for the large, oceanic predators, by rapidly converting oceanic resources into high energy food. On the other hand, neutrally buoyant ammoniacal squids, which probably greatly outnumber the

muscular squids in biomass, also provide food to many of the same predators, but not over the continental shelf and with consistently lower energy per unit body mass. We know virtually nothing about the details of feeding, growth, life cycles, periodicities, distribution and spawning in ammoniacal species.

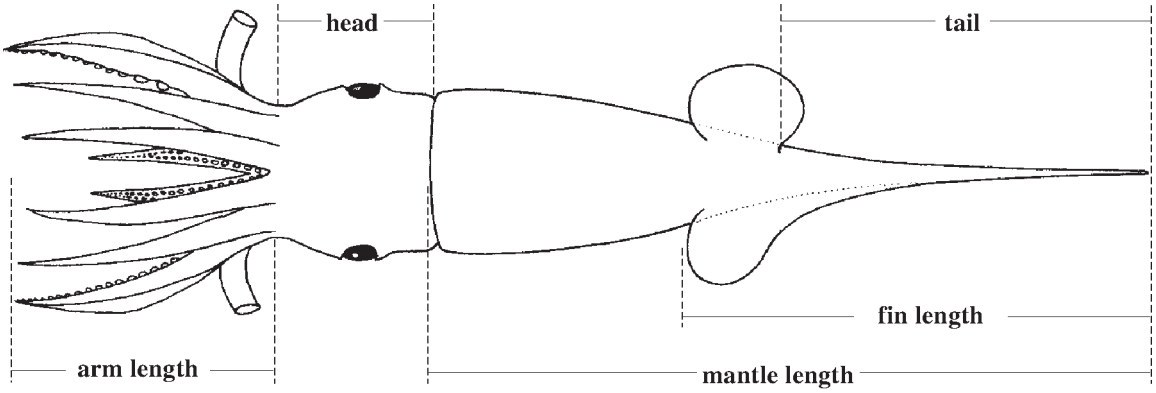
In spite of our relatively poor knowledge, it is now clear that cephalopods are a dominant component within marine ecosystems and that their abundance ultimately may influence the abundance of their predators and prey populations. Recent studies of the effects of consumption of important pelagic squids and fishes by predatory fishes on the northeastern shelf of the United States (Overholtz *et al.*, 2000), concluded that changes in predator abundance may have important implications for the long-term fishery yields of pelagic species.

What seems consistent with our present knowledge is that removal of cephalopods through fisheries would have a consistent impact on the environment: populations of small midwater fishes would increase, while top predators like cetaceans, seabirds, seals and even some fish populations would decrease.

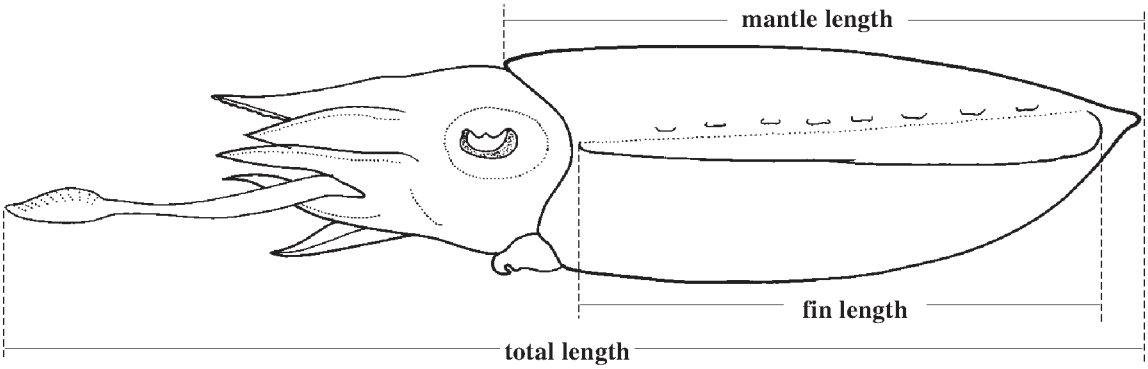
Taking into consideration these factors, increasing effort should be focused on improving our scientific knowledge of this group. Cephalopod catches need increased monitoring, especially in those areas of major environmental fluctuations and where fisheries management is complicated by multiple countries fishing the same resource. Cooperation, collaboration and commitment are required to better understand these important and fascinating animals.

NEXT PAGE

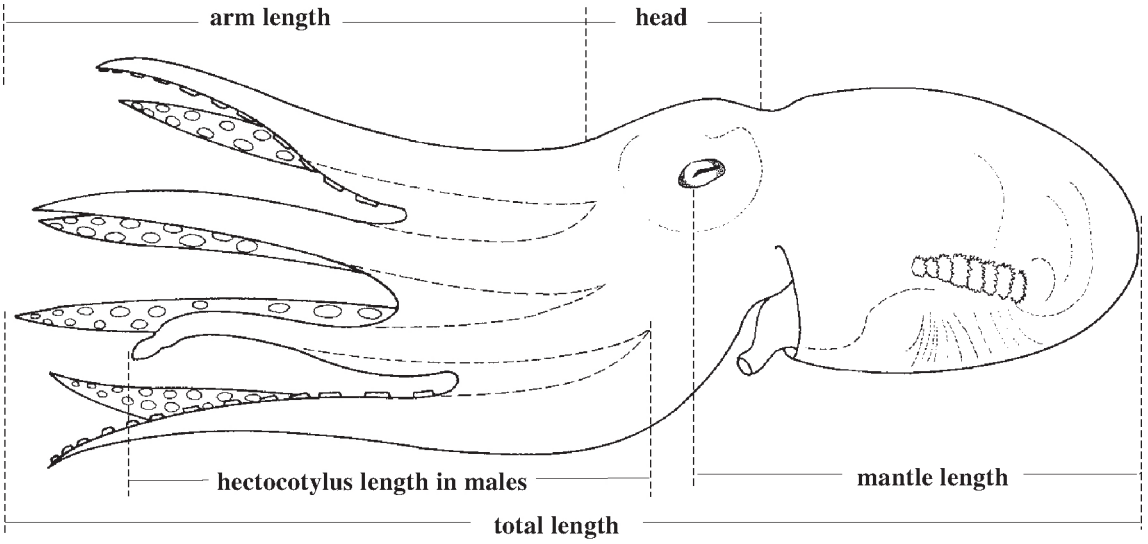
1. 4 Illustrated Glossary of Technical Terms and Measurements



a) Schematic illustration of a squid



b) Schematic illustration of a cuttlefish



c) Schematic illustration of an octopus

Fig. 6

Abdominal septum – Median septum that traverses the mantle cavity parallel to the body axis. It extends from the visceral mass to the ventral mantle wall. The ventral mantle artery runs along the dorsal edge of this septum.

Aboral – Away from or opposite to the mouth.

Abyssal – The great depths of the ocean: from 2 000 to 6 000 m.

Accessory nidamental glands – Glands of unknown function; consist of tubules containing symbiotic bacteria. Found in all **decapodiformes** except oegopsid squids.

Adult – A female that has mature eggs (these frequently are stored in the oviducts), or a male that has produced spermatophores (these are stored in Needham's sac).

Afferent blood vessel – Artery vessel carrying blood toward an organ.

Afferent nerve – Nerve carrying impulses toward the brain or specific ganglia.

Anal flaps – A pair of fleshy papillae involved in directing releases of ink, one flap situated at each side of the anus (Fig. 7).

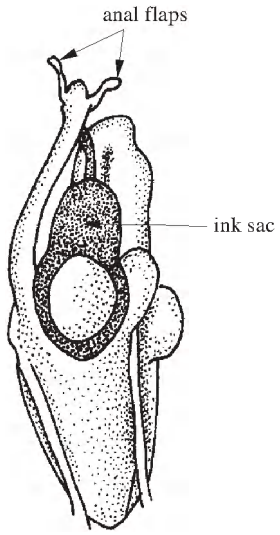


Fig. 7 Terminal portion of the digestive tract

Anal pads – Ovoid pads of unknown function, apparently glandular, one located on each side of the anus in some squids (e.g. bobtail squids).

Anterior – Toward the head-end or toward the arm-tips of cephalopods.

Anterior salivary glands – Glands on or in the buccal mass that aid in preliminary digestion.

Antitragus – Knob that projects inward from the posterior surface of the central depression in the funnel-locking cartilage of some squids (Fig. 8).

Anus – Terminal opening of the digestive tract in the anterior mantle cavity, sometimes extending to inside the funnel, through which digestive waste products, as well as ink, are expelled.

Apomorphic – Derived from a more ancestral condition. Loosely considered the 'advanced' condition.

Arm – One of the circumoral appendages of cephalopods. Arms are designated by the numbers I to IV, starting with I as the dorsal (or upper) pair. In **decapodiformes** each appendage of the fourth original pair is modified to form a tentacle. The second pair of arms is modified in vampires into a long filamentous structure. It has been lost in cirrate and incirrate octopods.

Arm formula – Comparative length of the 4 pairs of arms expressed numerically in decreasing order: the largest arm is indicated first and the shortest last, e.g. IV>III>II>I. If IV>III=II>I, then arm IV is the longest, followed by arm III which is the same size as arm II and both are longer than arm I. In octopods, the non-hectocotylized arm III is used in this formula.

Armature – The grappling structures of the arms and tentacular clubs, including suckers and/or hooks.

Bactritida – A fossil taxon that existed about 428 to 216 million years ago and is thought to be the ancestral stock of the Ammonoidea and Coleoidea.

Bathypelagic – The deep midwater region of the ocean.

Beak – One of the 2 chitinous jaws of cephalopods, bound in powerful muscles. The dorsal beak is referred to as the 'upper' beak and it inserts within the 'lower' (ventral) beak to tear tissue with a scissors-like cutting action.

Belemnoidea – A fossil group of cephalopods that is thought to be the sister group of the Coleoidea. Belemnoids are distinguished by the presence of hook-like structures on the arms rather than suckers.

Benthopelagic – A free-swimming animal that lives just above the ocean floor but rarely rests on the ocean floor.

Bilateral symmetry – The symmetry exhibited by an organism or an organ if only one plane can divide the animal structure into 2 halves that are mirror images of each other.

Bioluminescence – The production of light by living organisms, sometimes called 'living light'. The light is produced through a chemical reaction that generally takes place in complex organs called photophores or light organs.

Brachial – Pertaining to the arms.

Brachial crown – The combination of arms and tentacles that surround the mouth.

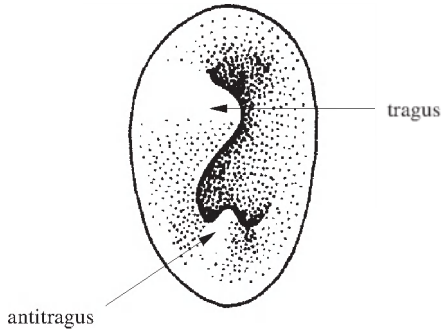


Fig. 8 Funnel-locking cartilage

Brachial lobe (of the brain) – The anteriormost part of the brain located ventral to the oesophagus. The large axial nerve cords that run down the centres of the arms connect to this lobe. The proper name is 'anterior suboesophageal mass'.

Brachial photophore – Photophore located on the arms.

Brachial pillar – A narrow, elongate anterior region on the paralarval or juvenile head of some families, between the eyes and the base of the brachial crown; especially well developed in young cranchiid squids.

Brain – Medial portion of the central nervous system that includes the suboesophageal and supraoesophageal masses but generally does not include the large optic lobes.

Branchial – Pertaining to the gills.

Branchial canal – A large opening at the base of each gill lamella and between the primary afferent and efferent blood vessels of the gill. A branchial canal is absent in nautiluses, cuttlefishes, bobtail squids, bottletail squids, pygmy squids, ram's horn squids, and cirrate octopods.

Branchial gland – Elongate or spheroidal gland adjacent and parallel to the gill attachment to the mantle wall.

Brooding – Incubation of eggs by the female. A characteristic feature of incirrate octopods, but also found in some squids (e.g. **Gonatidae**).

Buccal – Pertaining to the mouth.

Buccal connective – Thin muscular band that attaches the buccal support of the buccal membrane to the base of the adjacent arm. The position of attachment of the connective on the fourth arms was recognized in the early twentieth century as an important character for phylogenetic relationships among **decapodiformes** (Fig. 9).

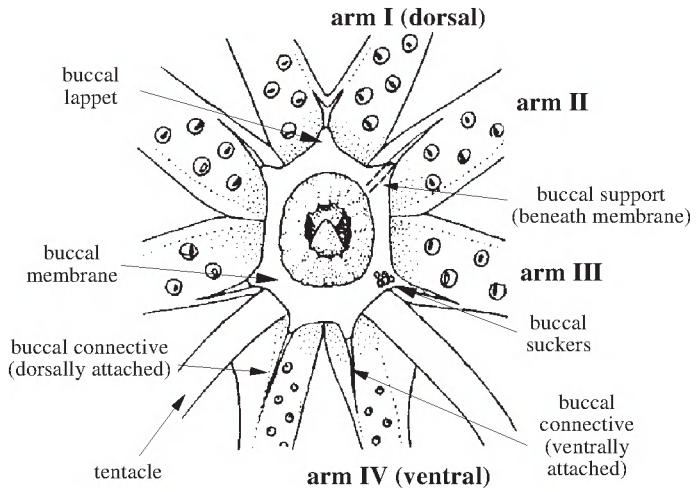


Fig. 9 Buccal anatomy of decapods

Buccal crown – Umbrella-like structure that surrounds the mouth and in turn is enveloped by the brachial crown. It consists of buccal supports and the buccal membrane. The buccal crown is present in most **decapodiformes** but absent from all **octopodiformes**.

Buccal lappet – A small, subtriangular flap at the tip of each buccal support of the buccal membrane; thought to be homologous with the inner ring of tentacles that surrounds the mouth of nautiluses. May bear suckers (Fig. 9).

Buccal mass – Muscular bulb at the anteriormost part of the digestive system that consists of the mouth, beaks, radula, muscles and pairs of salivary glands.

Buccal membrane – The muscular membrane that encircles the mouth like an umbrella (Fig. 9). It connects to the buccal supports to form the buccal crown. The pigmentation of the buccal membrane often differs from that of the adjacent oral surfaces of the arms.

Buccal membrane connectives – See buccal connective (Fig. 9).

Buccal suckers – Small suckers on the buccal lappets/membrane of some species (Fig. 9).

Buccal support – Muscular rod fused to buccal membrane as supporting rib (Fig. 9); 6 to 8 in number.

Buoyancy (neutral, positive, negative) – The tendency to float in seawater. A neutrally buoyant object does not rise or sink but maintains its position in the water; a positively buoyant object will rise and a negatively buoyant object will sink.

Bursa copulatrix – The wrinkled area present in most bobtail squids near the female genital opening for the attachment of the spermatophores; it is more differentiated in members of the subfamily **Sepiolinae** and forms a characteristic structure called 'bursa', which is used during copulation (Fig. 10). It differs conspicuously among species and can be used as a key character to identify ***Sepiola*** and ***Sepietta*** species females.

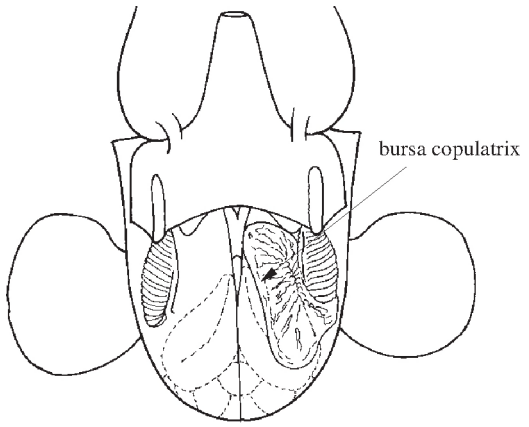


Fig. 10 Mantle cavity of female *Sepiola rondeletii* showing the bursa copulatrix

Caecal sac – The sac-like, thin-walled posterior portion of the caecum in the digestive tract that lacks the internal, ciliated leaflets characteristic of the anterior portion of the caecum.

Caecum – Region of the digestive tract of all cephalopods between the stomach and intestine. It is the primary site of food absorption.

Calcified – Chalky, calcareous material of calcium salts (calcium carbonate), formed by deposition.

Calamus – The conical papilla or projection at the base of the ligula on the hectocotylus of octopods, at the distal terminus of the sperm groove, distal to the last sucker (Fig. 11) (see **Ligula**).

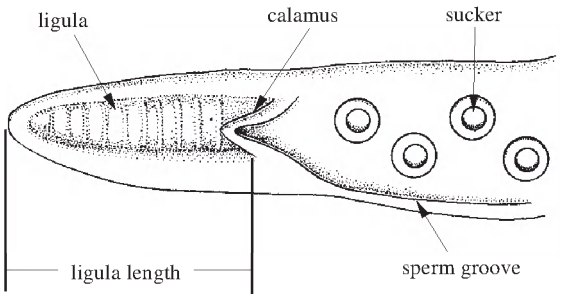


Fig. 11 Distal tip of hectocotylus of cirrate and incirrate octopods

Cambrian period – Oldest period of the modern geological timescale.

Carpal cluster (= **Carpal pad**) – An usually distinct group of suckers and knobs on the carpus of the tentacular club (Fig. 12).

Carpal knobs – Small, rounded, hemispherical, muscular protuberances on the carpus to which carpal suckers from the opposite club adhere during the locking of the clubs (Fig. 12).

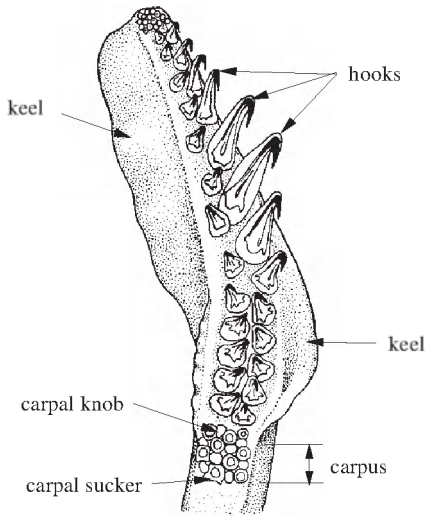


Fig. 12 Tentacular club of squid

Carpal suckers – Small suckers on the carpus of the club that adhere to the carpal knobs on the opposite carpus during the locking of the clubs (Fig. 12).

Carpus – The proximal zone of small suckers and knobs on the base of the tentacular club in some families (Fig. 12).

Cartilaginous structures or 'scales' – Cartilage-like structures in the skin of certain squids; may be overlapping and scale-like, or multifaceted platelets, knobs or papillae (Fig. 13).

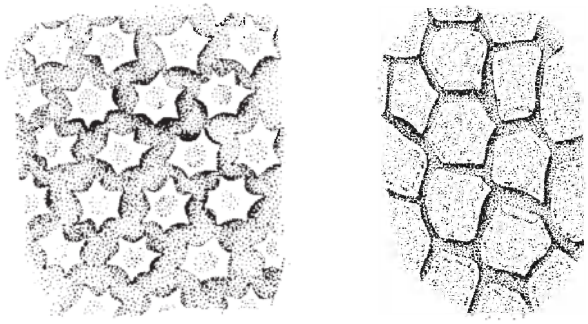


Fig. 13 Two types of cartilagineous structures or 'scales'

Cement body – Structure in the spermatophore that allows adhesion of the discharged spermatophore to a female (Fig. 38).

Cephalic cartilage – Cartilage-like tissue that envelops the posterior part of the brain of cephalopods and encompasses the statocysts. Anteriorly the cartilage thins and entwines with muscular tissue, which makes a well-defined limit difficult to distinguish. The cartilage has a large central foramen through which the oesophagus passes and minor foramina for nerves and blood vessels.

Cephalic vein – Large vein that drains blood from the head region; it lies along the ventral surface of the visceral sac, beside or dorsal to the intestine. The cephalic vein terminates by dividing into the two venae cavae, each of which passes through the 'kidney' (nephridium), the branchial heart and into the gill.

Cephalopoda – The class within the Mollusca characterized by bilateral symmetry, internal 'shell' or absence of shell (except nautiluses), anterior head appendages and funnel, posterior mantle, mantle cavity with organs, and shell and fins when present.

Character state – A particular condition of a taxonomic character. For example, the character 'sucker' may include the two states: sucker with a horny ring or sucker without a horny ring.

Chemotactile – Refers to chemical and touch sensitivity.

Chitin(ous) – A horny polysaccharide substance (fingernail-like) that forms the sucker rings, hooks and beaks.

Chorion – A tough secreted membrane that encapsules the egg.

Chromatophores – Pigment-filled muscular sacs in the skin under individual nervous control that collectively provide the background colour, colour patterns and colour dynamics (play) of cephalopods.

Circumoral appendages – The eight arms of **decapodiformes** and **octopodiformes**, plus the two tentacles of **decapodiformes** and the very numerous arms of nautiluses. All arise from the head and encircle the mouth (Fig. 9).

Cirri (singular **cirrus**): **1) Arm**: elongate, fleshy, finger-like papillae along the lateral edges of the oral surface of the arms, especially in cirrate octopods (Fig. 14).

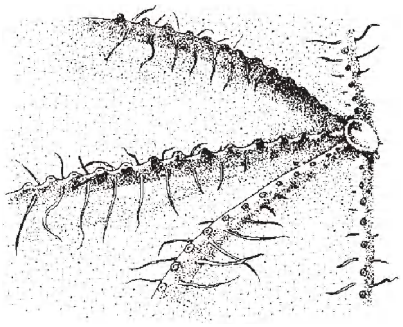


Fig. 14 Cirri on arms of cirrate octopods

2) Body: fleshy protuberances of the skin that can be erected as papillae, usually over the eyes (Fig. 15).

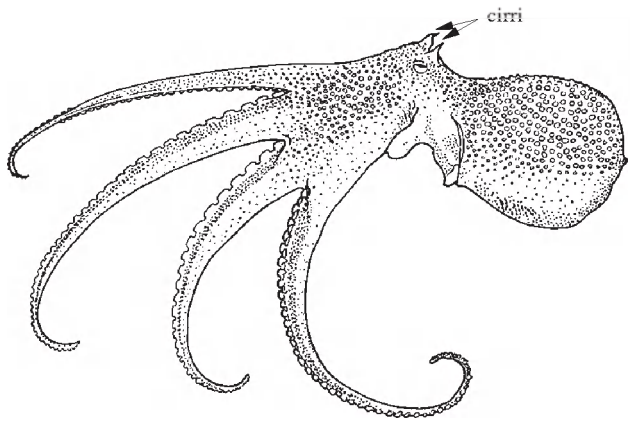


Fig. 15 Cirri dorsal to eyes of incirrate octopods

Club-fixing apparatus – Arrangement of suckers and matching knobs on the carpal region of the tentacular club that permits the two clubs to be locked together (Fig. 12).

Coelom – An internal body cavity of mesodermal origin that is lined by an epithelium. Cephalopods have two coeloms, the viscero-pericardial coelom and the nephridial coelom.

Collar – Muscular, flange-like structure that extends from the nuchal cartilage to the funnel; it forms a one-way valve that allows water to enter the mantle cavity but closes as the mantle contracts, thereby forcing exhalant water out through the funnel.

Cone, conus – The spoon-like, cup-like, spiked or simple conical posterior terminus of the gladius or cuttlebone; homologous to the phragmacone of fossil squids (Fig. 16).

Conus fields – The sides of the conus that continue anteriorly along the vanes of the gladius.

Cornea – Smooth, thin, turgid, transparent skin without muscles that covers the eyes to protect the eye lenses of incirrate octopods and some **decapods** (myopsids and sepioids) (Fig. 17).

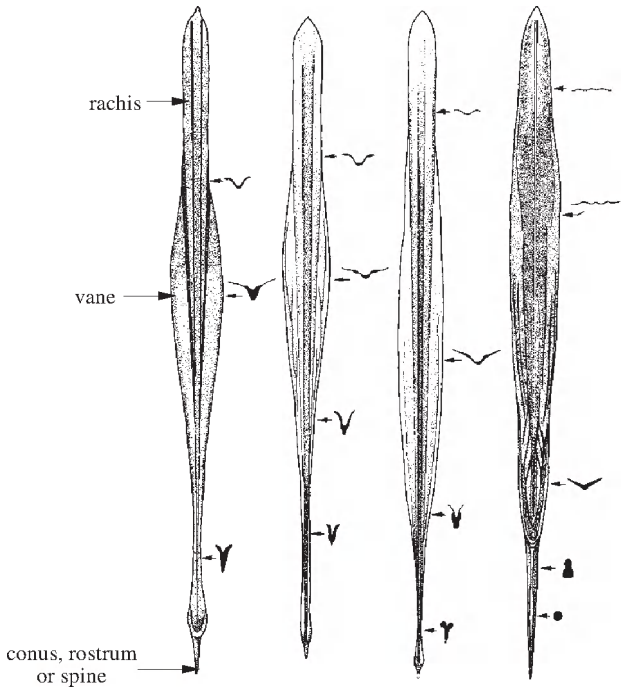


Fig. 16 Gladii of some squids

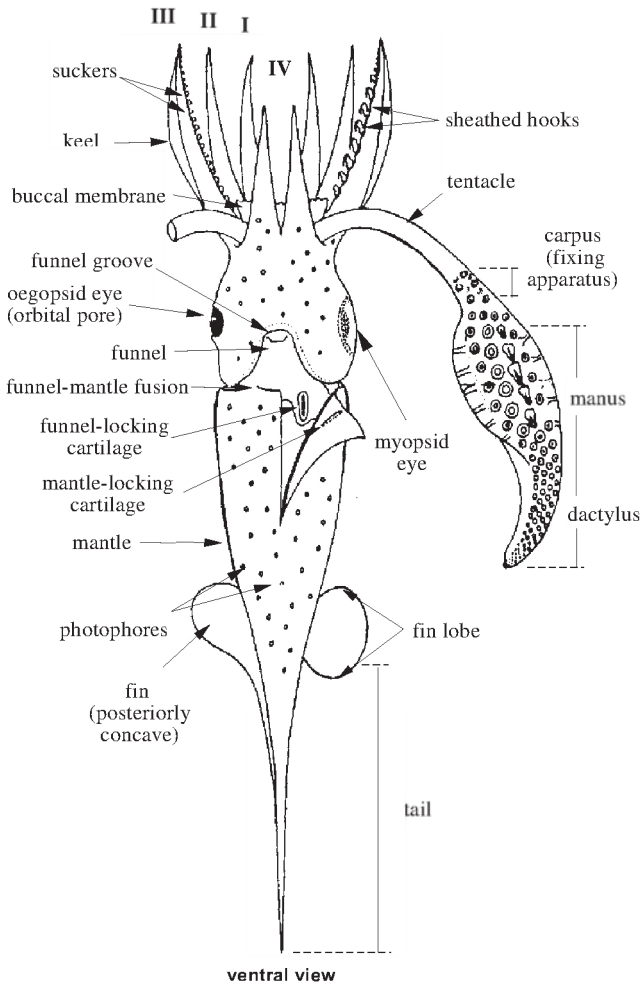


Fig. 17 A composite diagram illustrating basic squid features

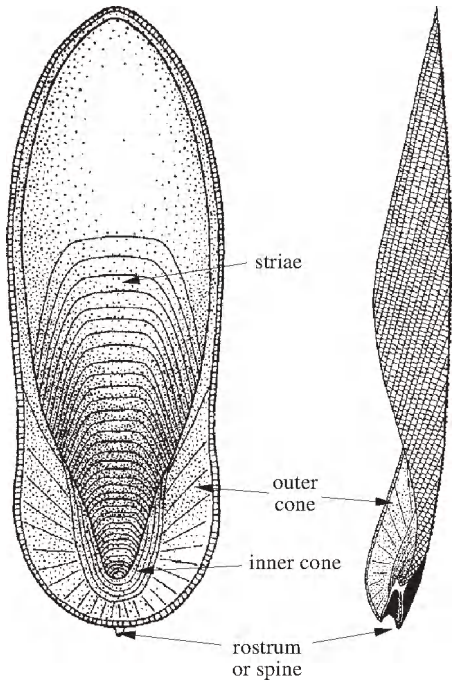
Counter illumination – The production of bioluminescent light by an animal to conceal its silhouette against a lighted background. The process can allow an animal to become virtually invisible under dim directional light.

Cretaceous – The last period of the Mesozoic Era.

Crop – Expansion (i.e. a broadening or a side pocket) of the oesophagus for storing ingested food, prior to entering stomach. Present in **nautiluses** and most **octopods**.

Cusp – A point or projection on a tooth of the radula or on a cartilagenous tubercule in the skin.

Cuttlebone (= **sepion**) – The calcareous (chalky) oblong, supporting protective and buoyancy shield in the dorsal part of the mantle of cuttlefishes (Fig. 18).



a) ventral view **b) lateral view**

Fig. 18 Cuttlebone

Dactylus – The distal, terminal section of the tentacular club, often characterized by suckers of reduced size (Fig. 17).

Decapodiformes – Higher-level taxon that includes all 10-limbed cephalopods: cuttlefishes, bobtail squids, bottletail squids, pygmy squids, ram's horn squids, myopsid squids and oegopsid squids (Fig. 2 Living Cephalopods). Because of the long history of referring to these cephalopods by the common name '**decapods**', the latter is maintained as the common name for the **Decapodiformes**.

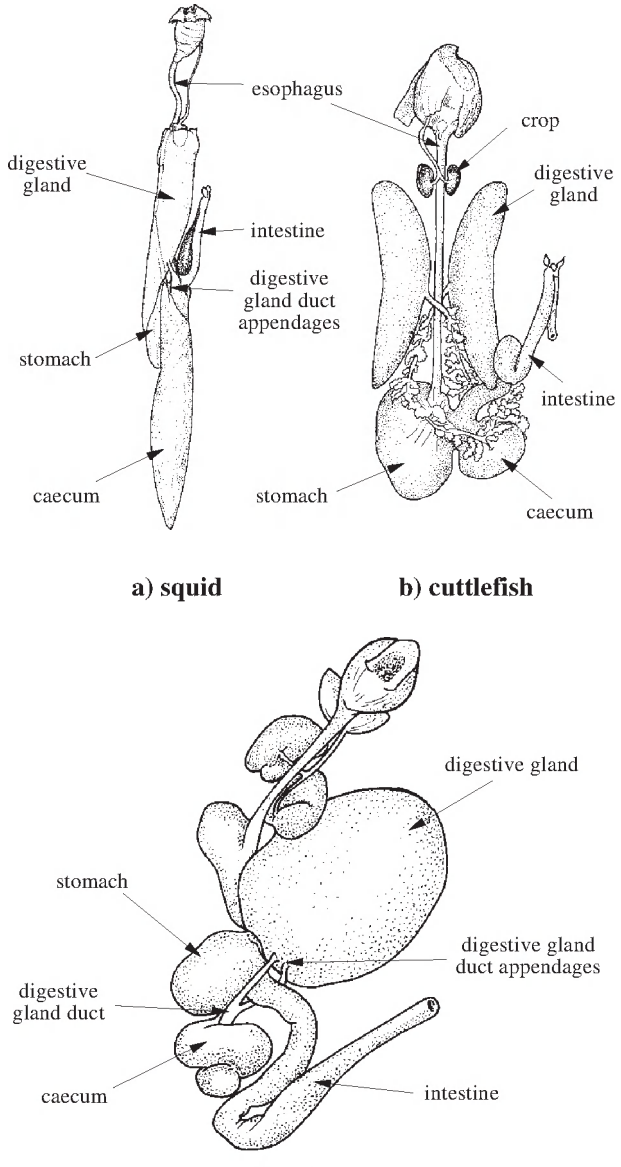
Decapods – Common name for the **Decapodiformes**.

Demersal – Organisms that live close to the ocean floor.

Diel vertical migration – Vertical animal migration during twilight periods. Many mesopelagic animals migrate to shallow depths at sunset, where they spend the night feeding. Then they descend at sunrise from near-surface waters to spend the day hiding at greater, darker depths. Some animals migrate vertically over 1 000 m, others migrate less than 100 m.

Digestive gland – Primary organ in cephalopods that secretes digestive enzymes. It is also important in absorption and excretion (Fig. 19).

Digestive gland duct appendages – Outpockets of the ducts leading from the digestive gland that are covered with glandular epithelium (Fig. 19).



a) squid **b) cuttlefish**

c) octopus

Fig. 19 Digestive system
(after Bidder, 1966)

Distal – Away from the central region of the body or point of origin; toward the peripheral parts (opposite of proximal).

Doratopsis – The peculiar paralarval stage that is characteristic of all members of the oegopsid squid family **Chiroteuthidae**.

Dorsal – The uppermost or back surface of a cephalopod, opposite the ventral surface where the funnel is located (Fig. 20).

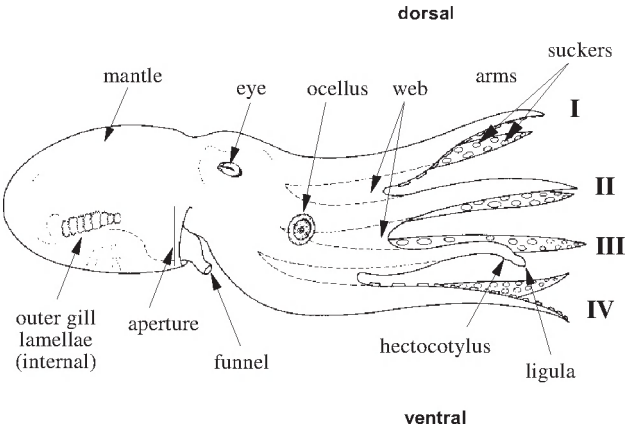


Fig. 20 Schematic lateral view of octopus features

Efferent vein – Vein that carries blood away from the heart or an organ.

Efferent nerve – Nerve carrying impulses away from the brain or specific ganglia.

Egg mass – A large number of eggs encapsulated in a gelatinous matrix or a large number of such structures that are attached together. The pelagic egg mass of an oceanic squid can be a large, fragile, gelatinous ball that carries many thousands of eggs. In contrast, the egg mass of a neritic squid (loliginid) can be composed of hundreds of very tough, encapsulated eggs in strings, attached together at their bases and to the substrate.

Ejaculatory apparatus – Portion of the spermatophore involved in the vigorous extrusion of the sperm mass (Fig. 38).

Epipelagic zone – The uppermost pelagic zone of the ocean.

Epithelial pigmentation – The pigmentation contained in epithelial cells that are unable to change their shape in the absence of muscles and nerves. Colour in most cephalopods, however, is created by pigment granules that are contained in specialized organs, the chromatophores, that can change shape rapidly by muscular action under nervous control (see **Chromatophores**).

Exploitation rate (E) – When fishing mortality (F) and natural mortality (M) operate concurrently, the exploitation rate represents the fraction of dead animals due to the fishery (i.e. caught by the fishery), which is, F/Z where Z denotes the total (i.e. M+F) mortality rate.

Eye (**position** and **size**) – Eyes are the primary sensory organs of cephalopods; they usually are large and located one on each side of the head. However, some species have small eyes, eyes on stalks or telescopic eyes.

Eyelid sinus (= **optic sinus** = **orbital sinus**) – Indentation, often complex, of the anterior margin of the eyelid (Fig. 28).

Family – The taxon above the genus level, comprised of the most closely related genera.

Fin(s) – The pair of muscular flaps that arise along the dorsolateral surface of the mantle of **decapodiformes**, **vampires** and **cirrate octopods**; used for locomotion, steering and stabilization (Fig. 17).

Fin angle – The angle between the longitudinal axis of the mantle and the posterior border of one fin (Fig. 21).

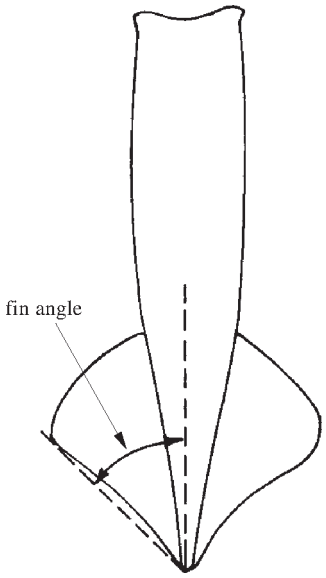


Fig. 21 Fin angle on squid

Fin attachment – A fin attaches to the shell, the mantle, the opposite fin or some combination of these.

Fin cartilage – Cartilage associated with the fins of all fin-bearing cephalopods.

Fin length – Length from anterior lobe, or anteriormost attachment of lobe, to posteriormost attachment of fin to mantle or tail. Extremely long, spike-like tails usually do not include fin tissue.

Fin lobe – The portion of a fin that extends anteriorly from the fin's anterior point of attachment, or posteriorly from the fin's posterior point of attachment of the fin, to the mantle (Fig. 17). This often is called the 'free' lobe.

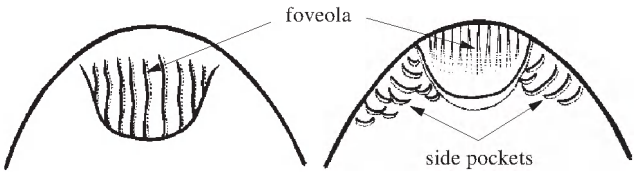
Fin position – Fins are located anterior to the termination of the muscular mantle (subterminal position) or mostly posterior to it (terminal position) or in an area of overlap between the two.

Fin shape – Fins are classified, somewhat arbitrarily, by their shape as sagittate, rhomboid, circular/elliptical, lanceolate, ear-shaped, ribbed, lobate or skirt-like.

Fixing apparatus – The mechanism of suckers and knobs on the carpal region of the tentacular club that permits the two clubs to be locked together during capture of prey (Figs 12 and 17) (see **Carpus**).

Foot – See **Molluscan foot**.

Foveola – Transverse, membranous fold of skin that forms a pocket in the anterior end of the funnel groove of some oegopsid squids (Fig. 22) (see **Side pockets**).



a) Todarodinae b) Ommastrephinae

Fig. 22 Funnel groove

Funnel – The ventral, subconical tube through which water is expelled from the mantle cavity during locomotion and respiration (reproductive and waste products and the ink also pass through the funnel) (Figs 17 and 20). Archaic term: **siphon**.

Funnel-adductor muscles – Muscles that support the lateral attachment of the funnel to the head.

Funnel groove – The depression in the posteroventral surface of the head in which lies the anterior portion of the funnel (Fig. 17).

Funnel-locking cartilage – The cartilaginous groove, pit, pocket or depression on each ventrolateral side of the posterior part of the funnel that joins with the mantle component to lock the funnel and mantle together during locomotion and respiration, so that water is expelled only through the funnel and not around the mantle opening (Figs 17 and 23) (see **Mantle-locking cartilage**).

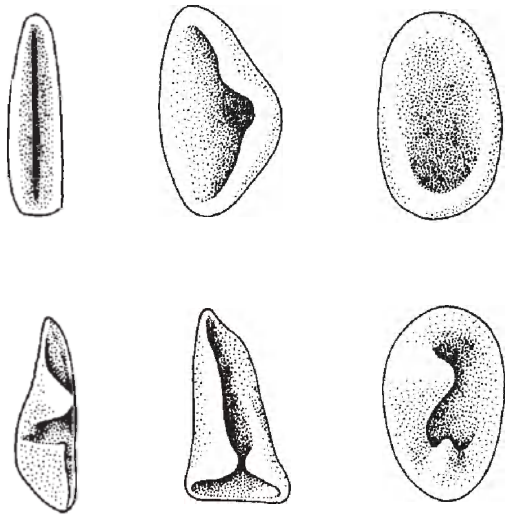


Fig. 23 Funnel-locking cartilage; examples of shapes and structures

Funnel organ – The glandular structure fused to the internal surface of the funnel, generally a single W-shaped form in **octopodiformes** and a dorsal inverted V-shaped component with opposed ventral oblong components in **decapodiformes** (Fig. 24).

Funnel-retractor muscles – Large muscles that attach to the corners of the funnel and run posteriorly to attach to the sides of the shell sac (generally near the base of the gills) or, in some species, insert on the interior mantle wall.

Funnel valve – The semi lunar muscular flap in the dorsal inner surface near the distal opening of the funnel in some species (Fig. 24).

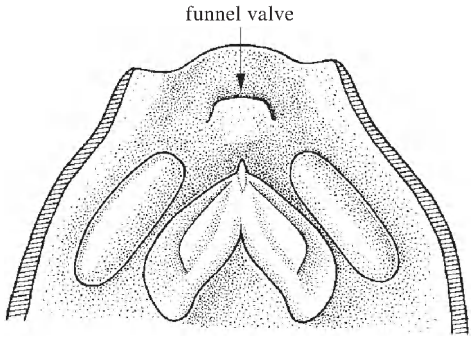


Fig. 24 Funnel organ and funnel valve components on inner surface of funnel of squids

Genus – The taxon below the family level and above the species level.

Gill – Primary organ for the exchange of respiratory gases with seawater (Fig. 30).

Gill lamellae – The leaf-like convoluted individual components of the gill through which gas exchange occurs (Figs 25 and 30).

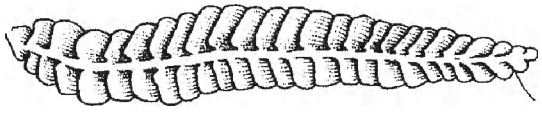


Fig. 25 Gill lamella, a single element from a complex structure

Gladius (= **pen**) – The feather or rod-shaped chitinous supporting structure in the dorsal midline of **squids**; the homologue of the shell of ancestral forms (Fig. 16).

Gladius length (**GL**) – Sometimes used as a measurement of the body (= mantle) length when direct measurement of the mantle is unreliable (usually due to deformation).

Gonoduct(s) – Tubular structure(s) of the reproductive system which serves to transport reroductive products from the gonad(s) to the exterior (see **Oviducts**).

Hatchling – Young cephalopod newly hatched from the egg.

Head length (**HL**) – A standard measurement within species growth stages and for species comparisons; measured from posterior limit to V-notch at base of Arms I (Fig. 6).

Head-mantle fusion – Zone of fusion of head and mantle; it varies among groups/families; of systematic and biological significance.

Hectocotylus – One (or more) modified arm in male cephalopods used to transfer spermatophores to the female; modifications may involve suckers, sucker stalks, protective membranes, trabeculae (Figs 11 and 26) (see **Calamus**, **Ligula**).

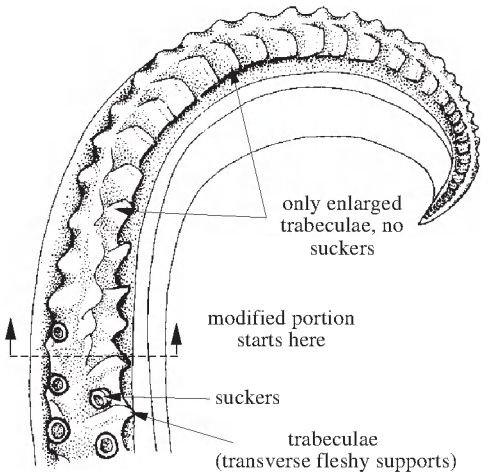


Fig. 26 Hectocotylized arm (*Illex oxygonius*)

Hood – Leathery cap or trapdoor of nautiluses that can be retracted to protect the animal within the shell.

Holotype – The single specimen designated by the original author to represent the new species name. It is an international standard of reference that provides objectivity and stability for the species name.

Hooks – Chitinous, claw-like structures ontogenetically derived from the suckers on the arms and/or clubs of some oegopsid squids (Fig. 12).

Horizontal arm septa – Septa extending the length of the arms (i.e. parallel to the arm axis), that roughly divide the arms into oral and aboral regions. This feature is a characteristic of the arms of cirrate octopods and the incirrate octopods of the family **Bolitaenidae**. The functional significance is unknown.

Horny rings of suckers – Suckers of **decapods** have two types of hard, horny rings. One, the inner ring, lies around the inner walls of the *acetabulum* (cup) and often bears teeth. The other, the outer ring, is composed of numerous minute platelets and lies on the surface of the *infundibulum* (outer rim) (Fig. 40).

Inferior frontal lobe system – A system of lobes in octopod brains: the paired posterior buccal, lateral inferior frontal and subfrontal lobes, and the single median inferior frontal lobe. They form a functional unit concerned with the chemotactile information from the arms and its use.

Ink sac – The structure that manufactures and stores the ink of cephalopods; it lies parallel with the intestine and empties via a duct into the rectum (Figs 7 and 30).

Intestine – Distal region of the alimentary canal between the stomach/caecum complex and the anus (Fig. 19).

Juvenile – Life history stage between the hatchling and the nearly-mature subadult stages.

Keel – **(1)** A flattened, muscular extension along the aboral surface of some arms to render them more hydrodynamic (Fig. 17); **(2)** 1 or 2 expanded muscular membranes along the tentacular club of some groups (Fig. 12); **(3)** the lateral ridge of skin around the lateral margin in incirrate octopods (Fig. 27).

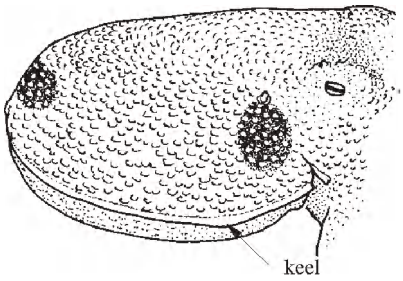


Fig. 27 Incirrate octopod

Lateral – Pertaining to the side(s) of an organism or structure, away from the centre or midline.

Lateral funnel-adductor muscles – See **Funnel-adductor muscles**.

Lateral membranes of arms IV – See **Tentacular sheath**.

Lateral-line analogue – Sensory structure analogous to the lateral line of fishes. The lateral-line analogue, which senses vibrations transmitted by seawater, is located along a series of lines on the dorsal surface of the head, with some sensory cells extending onto the bases of the arms.

Lateral ridge – A narrow, horizontal, muscular structure along the lateral side of the mantle of incirrate octopods. Also referred to as a keel (Fig. 27).

Length at 50% maturity – Mantle length at which 50% of specimens examined in a representative sample is sexually mature, according to the maturity scale and the statistical model used.

Lens (in photophores) – Structure in a photophore that can focus or disperse bioluminescent light.

Light guides – Structures in photophores that specifically direct light via internal reflection.

Light organ (= **photophore**) – A simple or complex structure that produces bioluminescence (cool light) by intrinsic (self generated) or extrinsic (bacterial) means (Figs 17 and 28).

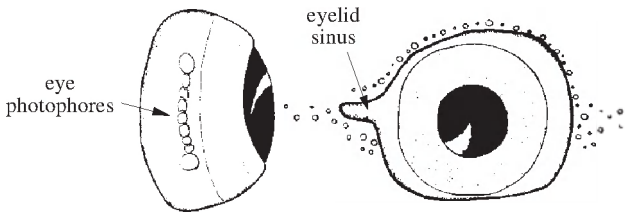


Fig. 28 Light organs (photophores) on ventral surface of squid eyeball; eyelid or orbital sinus

Ligula – The spatulate to spoon-shaped, terminal structure of the hectocotylus of many incirrate octopods, that contains the **calamus** basally (proximally) and usually a series of transverse ridges and grooves on the oral surface (Fig. 11) (see **Calamus**, **Hectocotylus**). Spermatophores

transferred along the sperm groove of the hectocotylized arm are presumably gripped by the ligula. Details of the function of the ligula are unknown.

Lips – Two concentric, muscular, glandular rings of skin that surround the mouth and beaks.

Living chamber – Largest and most recently formed chamber of **nautilus** shell in which the animal resides (also refers to numerous shells of fossil cephalopods).

Macrotritopus – A complex of paralarval forms in the incirrate octopod family **Octopodidae**, characterized by the third pair of arms being extremely elongate.

Mantle – The fleshy (muscular) tubular or sac-like body of cephalopods; provides propulsion through jet-like expulsion of water; contains the viscera (Figs 17 and 20).

Mantle cavity – Space enclosed by the mantle. In cephalopods the mantle cavity contains the visceral sac, gills, anus, openings of the gonoducts, nephridial pores and various muscles and septa (Fig. 30).

Mantle length (ML) – The standard measure of length in coleoid cephalopods. In **decapods** ML is measured along the dorsal midline from the mantle margin to the posterior tip of the body (Fig. 6). In **octopods** ML is measured from a line joining the mid-point of the eyes (rather than the anterior mantle margin, since the latter is obscured by the head/mantle fusion) to the posteriormost area of the mantle (Fig. 6).

Mantle-locking cartilage – The cartilaginous ridge, knob or swelling on each side of the ventrolateral, internal surface of mantle that locks into the funnel component of the locking apparatus during locomotion (Figs 17 and 23) (see **Funnel-locking cartilage**).

Manus – Central or 'hand' portion of club between the dactylus distally and the carpus proximally (Fig. 17).

Mature – In cephalopods this term refers to sexual maturity which is determined for females by the presence of ova (mature eggs) free in the coelom or oviducts (Fig. 30), and for males by the presence of spermatophores in Needham's sac (Fig. 29) (see **Adult**).

Medial(n) – Pertaining to a structure located toward, on, or along the dorsal or ventral midline.

Mesopelagic zone – The middle-depth zone of the pelagic realm of the ocean.

Mollusca – One of the major invertebrate phyla. Some of the common molluscs are snails and clams. The **Cephalopoda** is a class within the Mollusca.

Molluscan foot – A major structure in molluscan morphology. In gastropods the foot is the muscular sole that the animal crawls with. In cephalopods the funnel, and possibly the arms and tentacles are derived from the molluscan foot. The evolutionary origin of the latter is still uncertain. They may represent outgrowths of the head (favoured by anatomical evidence of the nerve connections) or modifications of the molluscan foot that have migrated around the mouth (favoured by embryological evidence, the migration of arm primordia).

Monophyletic group – A natural group (taxon) that shares a common ancestor.

Myopsida – A high-level taxon (order) within the **Decapodiformes**. In recent classification, the **Myopsida** (including the family Loliginidae) have been considered the sister group of the **Oegopsida** and the two groups together compose the **Teuthoidea** (squids). In contrast, at the beginning of the twentieth century, the **Myopsida** included the Loliginidae and the **Sepioidea** (cuttlefish and relatives) and the presence of a cornea covering the eye lens defined the group. At present the phylogenetic relationships within the **Decapods** are unresolved.

Neck – The region that separates the posterior end of the cephalic cartilage and head musculature. Only those cephalopods with elongate heads (e.g. the oegopsid squid family **Chiroteuthidae**) have distinct necks.

Needham's sac (= **spermatophore/spermatophoric sac**) – The elongate, membranous organ of males where completed, functional spermatophores are stored. It opens into the mantle cavity or directly into the water through the penis (Fig. 29).

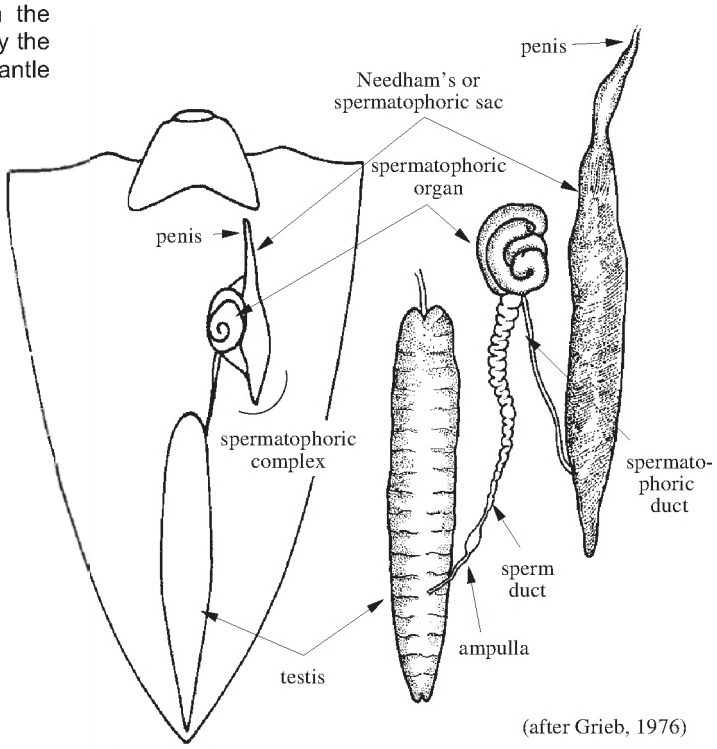


Fig. 29 Male squid reproductive apparatus

Nephridial coelom – The cavity of the renal (kidney) sac. It connects with the exterior via the renal pore and with the viscero-pericardial coelom via a pair of slender ducts from the latter.

Nephridial papillae – Small raised openings to the renal cavities.

Neritic – The region of the ocean that overlies the continental shelf.

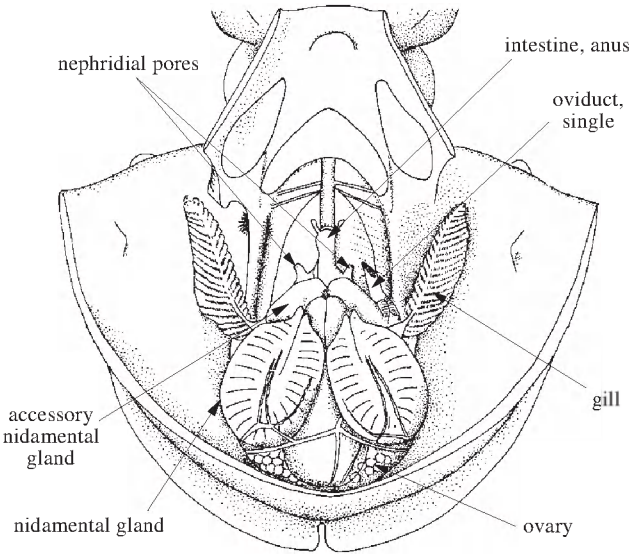
Nidamental glands – Large glandular structures in females of most **decapods** and **nautiluses** that lie in and open directly into the mantle cavity. The glands are composed of numerous lamellae that are involved in secretion of egg cases or the jelly of egg masses (Fig. 30).

Nominal species – A species that has been formally described and is based on a morphological type. It is an available name but not necessarily a valid species.

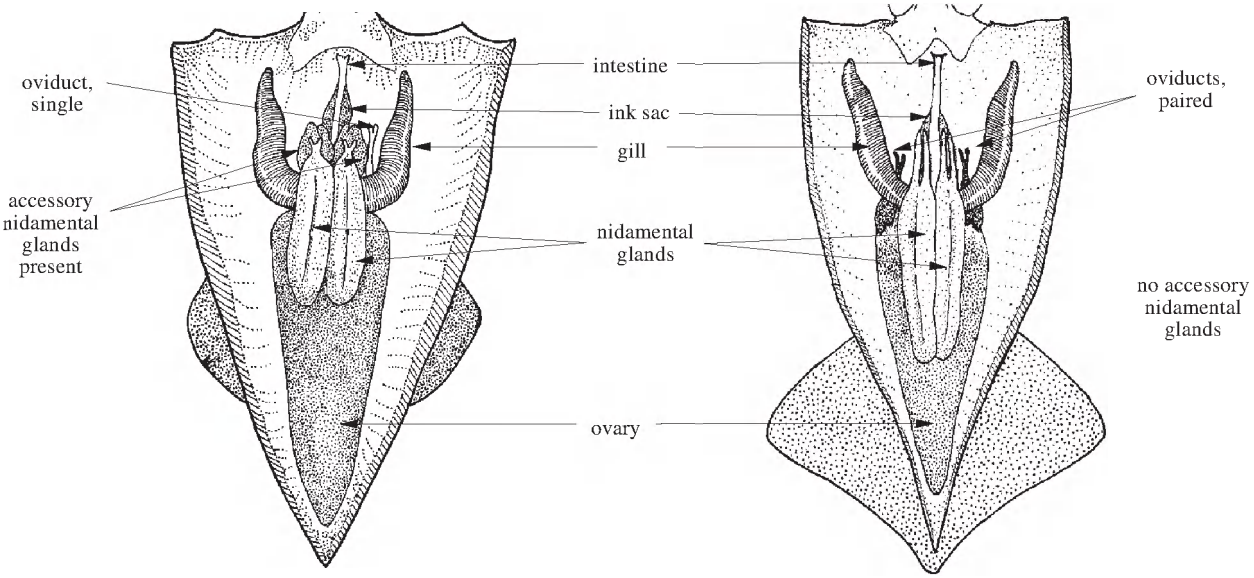
Nuchal cartilage – See **Nuchal-locking apparatus**.

Nuchal crest – Prominent transverse ridge in most **decapods** that extends across the dorsal head and down the lateral head surfaces at its posterior end (Fig. 31).

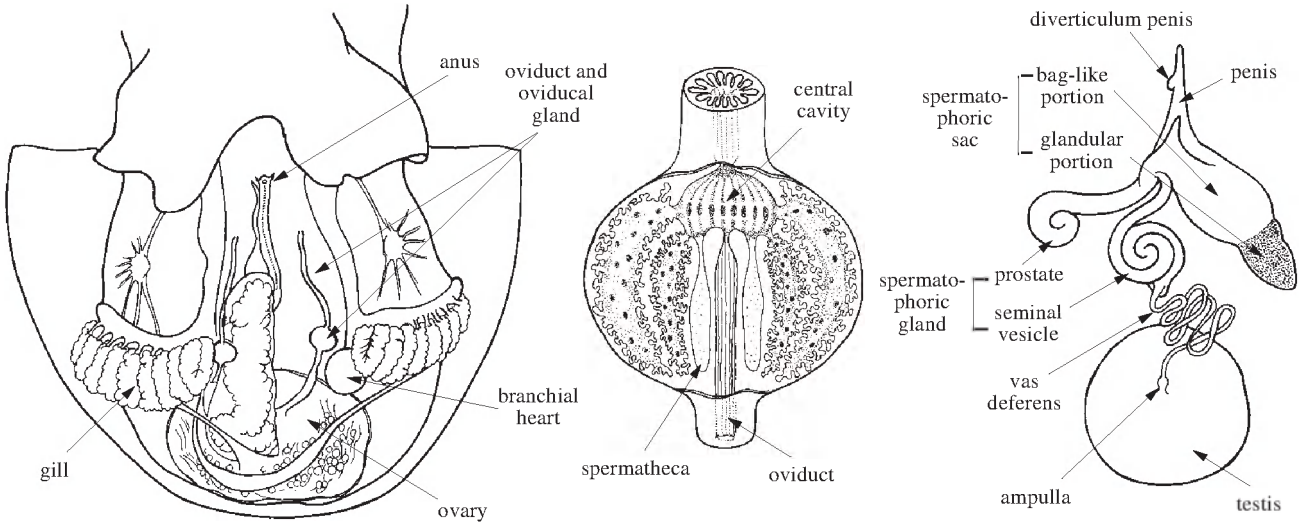
Nuchal folds – Fixed folds or pleats of the head integument that adjoin the nuchal crest posteriorly and are perpendicular to it. The function of the folds is uncertain (Fig. 31).



a) Sepiidae



b) Loliginidae **c) Ommastrephidae**

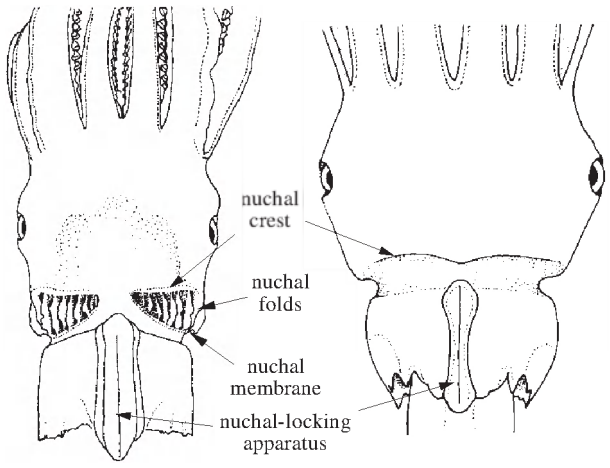


d) female Octopus **e) oviducal gland** (after Froesch and Marthy, 1975) **f) male reproductive tract** (after Mann, 1984)

Fig. 30 Internal organs
[a, b and c - Decapodiformes; d, e and f - Octopodiformes]

Nuchal-locking apparatus – An oblong, cartilaginous-locking structure in **decapods** located mid-dorsally just posterior to the head. It is composed of the nuchal cartilage, which also forms an attachment site for collar and head retractor muscles, and an interlocking, complementary cartilage on the mantle that underlies the gladius. The apparatus keeps the head and mantle aligned dorsally during mantle contractions (Fig. 31).

Nuchal membrane (= **occipital membrane**) – A thin membrane that connects the main nuchal folds at their posterior ends (Fig. 31).



a) *Onychoteuthis* b) *Onykia*

Fig. 31 Nuchal folds and nuchal crest

Nuchal organ – Small sensory organ with photoreceptor-like sensory cells that is located in the nuchal region of apparently all **coleoid** cephalopods.

Nuchal region – The dorsolateral area around posterior part of the head and the area immediately posterior to it, normally covered by the anterior mantle wall.

Occipital crest – See **Nuchal crest**.

Occipital folds – See **Nuchal folds**.

Occipital membrane – See **Nuchal membrane**.

Ocellus – A pigmented spot or patch that usually consists of a central locus of concentrated chromatophores with one or more outer concentric rings of chromatophores. Ocelli occur on some octopuses, and their normally vivid iridescence and pigmentation cause them to stand out against the background coloration of the skin. Also called '**false eyespot**' (Fig. 20).

Octopodiformes – Higher-level taxon that includes all 8-limbed cephalopods: vampires, cirrate octopods, incirrate octopods. (Fig. 2 Living Cephalopods). Because of the long history of referring to these cephalopods by the common name '**octopods**', the latter is used as the common name for the **Octopodiformes**.

Octopods – Common name for **Octopodiformes**.

Ocular photophore – Photophore(s) that lie(s) on the eyeball (Fig. 28).

Oegopsida – A high-level taxon within the **Decapodiformes**. In recent classification, the **Oegopsida** (oceanic squids) has been considered the sister group of the **Myopsida** and the two groups together compose the **Teuthoidea** (squids). At present the composition and affinities of the **Oegopsida** are unresolved.

Oesophagus – The portion of the digestive tract between the buccal mass and the stomach (Fig. 19). Often a portion of the oesophagus is expanded to form a crop for food storage (see **Crop**).

Olfactory papilla – A pit, or bump-like to finger-like protuberance on the posterolateral surface of each side of the head; of olfactory function.

Olfactory organ – A chemosensory organ present in all coleoid cephalopods thought to be the homologue of the **rhinophore** of *Nautilus*.

Ontogenetic descent – The progressive descent into a deeper-water habitat as a mesopelagic cephalopod grows older and larger. This distribution pattern is particularly common in many pelagic chiroteuthid and cranchiid squids.

Opening/closing trawl – A trawl whose mouth is open during fishing at a selected depth but is closed during descent and retrieval.

Optic lobes of brain – Large lobes of the brain associated with the eyes. In octopods and some squids the optic lobes may be separated from the rest of the brain by an optic stalk of varying length.

Optic sinus – See **Eyelid sinus**.

Oral – Toward or pertaining to the mouth.

Orbital pore – Minute pore in the anterior part of the transparent tissue (cornea) that covers the eyes of decapods except for the oegopsid squids; remnant of the primary eyelids (Fig. 17).

Orbital sinus – See **Eyelid sinus**.

Order – The taxonomic category above the family level.

Outer cone – Rim that surrounds the phragmocone in cuttlebones.

Oviduct(s) – Female gonoduct(s). The oviduct conducts eggs from the visceropericardial coelom, that encompasses the ovary, to the mantle cavity and often is used to store eggs. In some argonautid octopods eggs are fertilized and undergo either partial (*Argonauta*) or complete (*Ocythoe*) embryonic development within the oviduct (Fig. 30).

Oviducal gland – Glandular structure that surrounds the anterior end of the primary oviduct and secrets some of the external coatings around spawned eggs.

Paralarva – The term that indicates the first free-living life history stage (typically planktonic) for those cephalopods that differ in morphology and ecology from older juveniles.

Pedicel (= **sucker stalk**) – A short, muscular stalk that supports a sucker in sepioids and teuthoids (Fig. 32).

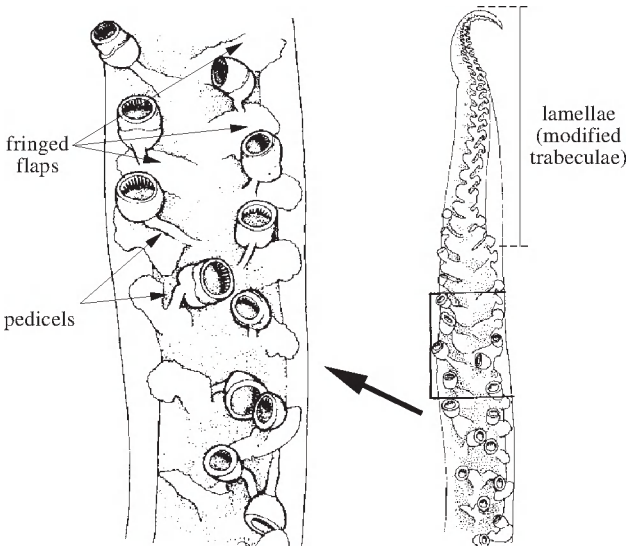


Fig. 32 Hectocotylized arm of males

Pelagic – **(1)** Free swimming in open ocean; **(2)** the region of the ocean away from the ocean floor.

Pen – See **Gladius**.

Penis – The long, muscular terminal section of the male gonoduct that serves to transfer spermatophores to the female (Fig. 29). Apparently, in species with a hectocotylus, the penis transfers spermatophores to the hectocotylus which in turn transfers them to the female. In species without a hectocotylus, the penis often is greatly elongate, capable of extending beyond the mantle opening and apparently can transfer spermatophores directly to the female.

Photocytes – Cells that produce bioluminescence in photophores.

Photophore – An organ that produces and distributes bioluminescence or 'living light', either intrinsically through biochemical reaction or extrinsically through luminescent bacteria (Figs 17 and 28) (see **Light organ**).

Phylum – The major, formative, principal taxonomic level; above 'Class'.

Phragmocone – System of plates that comprise the cuttlebone.

Pocket, tentacular – An open depression in the anteroventral surface of the head between the bases of arms III and IV of **decapods**, except myopsid and oegopsid squids, into which the ejectable feeding tentacles are retracted when not in use (Fig. 33).

Polarity (Evolutionary) – The direction of evolution. That is, one state is 'primitive' (plesiomorphic) and another is 'derived' (apomorphic).

Polarize (Evolutionary) – To determine the direction of evolution. That is, to determine which state is 'primitive' (plesiomorphic) and which is 'derived' (apomorphic).

Posterior – Toward the closed, tail-end of the mantle, away from the head and arms.

Primary conus – A solid conus on the gladius that is not formed by the in-folding of the lateral vanes.

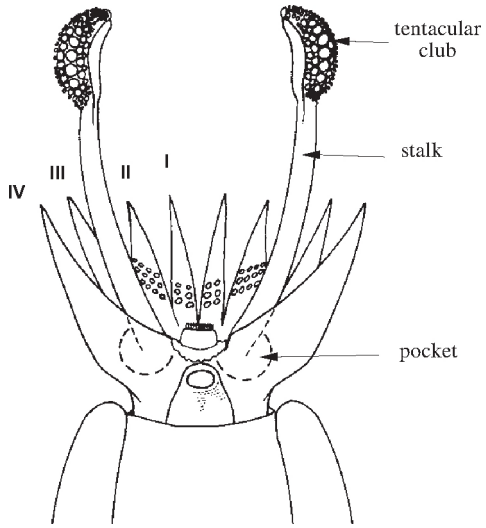


Fig. 33 Diagramatic sketch of arms and tentacles of decapods other than myopsid and oegopsid squids

Protective membrane – Thin web-like integument along the lateral angles of the oral surface of the arms and clubs lateral to the suckers, supported by muscular rods called trabeculae (Fig. 34) (see **Trabeculae**).

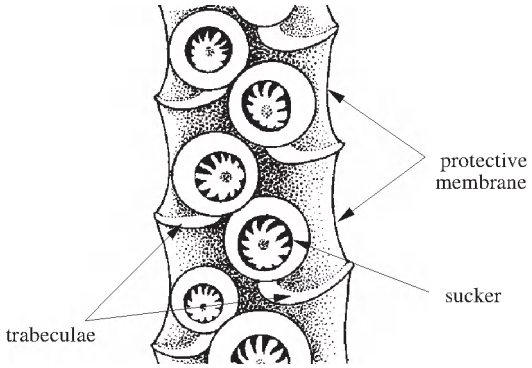


Fig. 34 Trabeculae, protective membranes and suckers on arm of squid

Proximal – Situated nearest or next to the centre of the body or nearest the point of origin or attachment of a muscle, appendage, etc. (opposite of distal).

Pseudomorph – An ejected mass of ink and mucous that approximates the size and shape of the cephalopod that released it; i.e. a false body that fixes the attention of a predator while the cephalopod escapes.

Rachis – The thickened central axis that usually extends the entire length of the gladius. Free rachis is the portion that does not support vanes (Fig. 16) (see **Gladius, Vane**).

Radula – The chitinous, ribbon-like band in the mouth of cephalopods that contains up to seven transverse rows of teeth that aid in transport of food into the oesophagus (Fig. 35). Has a significant higher taxonomic value.

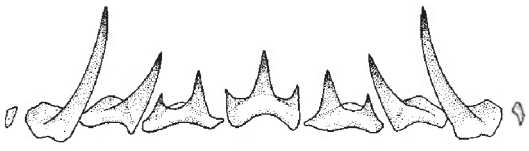


Fig. 35 Radula

Recent – Geological term referring to an organism or species that is living or has lived within the past 10 000 years, or to an object formed or events that have occurred within the past 10 000 years.

Renal appendages – Structures that form the nephridium (= kidney). The renal appendages are out-pockets of the veins within the renal sac (primarily the venae cavae) that are covered with renal epithelium. The renal sac empties into the mantle cavity via the nephridial (or renal) pore.

Renal pore – The opening(s) of the renal cavities into the mantle cavity, through which urine is discharged.

Rhinophore – A short sensory tentacle in **nautiluses**. Four in total, one on both sides of each eye.

Rhynchoteuthion – Paralarval stage of the Ommastrephidae characterized by the fusion of the tentacles into a trunk-like proboscis.

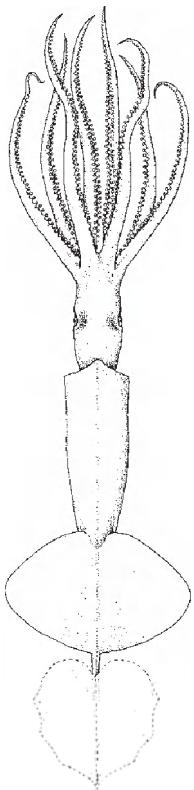
Rostrum (= **spine**) – A spike-like posterior projection of the gladius or cuttlebone, exterior to the conus (Figs 16 and 18).

Secondary conus – A conical region at the posterior end of the gladius that is formed by an in-rolling and fusion of the vanes. The ventral line of fusion usually is apparent. The secondary conus may be rather short or exceed half the gladius length (Fig. 36).

Secondary eyelid – An eyelid fold that covers the ventral part of the cornea in cuttlefishes.

Secondary fin – A non-muscular fin-shaped structure found in some oegopsid squids, located posterior to the true or primary fin (Fig. 37). The secondary fin may act as a buoyancy organ. **Vampire** juveniles also have secondary fins, which, however, are lost with growth.

Fig. 36 Secondary conus



Grimalditeuthis bomplandii

Fig. 37 Secondary fin

Secondary web – The narrow membrane that connects the primary web to the arms in some cirrate octopods; e.g. **Cirroteuthidae**.

Sepion (= **cuttlebone**) – The calcareous, laminate, dorsal supportive buoyancy structure in the mantle of cuttlefishes (Fig. 18).

Semelparous – A reproductive strategy in which females spawn once then die. Sometimes called terminal or 'big-bang' spawners. Many cephalopods are semelparous but in some species reproduction is prolonged (up to 50% of the ontogenesis). **Nautiluses** are iteroparous and spawn repeatedly over a period of years.

Sepioid gills – Gills of some cirrate octopods that look superficially like gills of sepioids.

Sepioidea – A high-level taxon within the **Decapodiformes**. Typically, this taxon includes the **Sepiidae**, **Idiosepiidae**, **Sepiolidae**, **Sepiadariidae** and **Spirulidae**, but the monophyletic nature of the group has been questioned. At present the phylogenetic relationships and classification within the **Decapodiformes** are unresolved.

Shell sac – The sac that secretes the shell in the **Coleoidea**, composed of ectodermal epithelium that invaginates during embryonic development to form an internal sac.

Side pockets – Small membranous folds of the integument that form small, shallow pockets lateral to the foveola in the funnel groove (Fig. 22) (see **Foveola**).

Siphuncle – The tube-like posterior extension of the body wall, coelom and covering sheath that penetrates into the phragmocone chambers in cephalopods with a chambered shell (*Spirula*, **nautiluses** and **cuttlefishes**). It regulates gas exchange into the phragmocone chambers.

Spadex – Male reproductive structure used to transfer spermatophores to the female in **nautiluses**. It is formed by the fusion of 4 circumoral tentacles.

Species – Populations of animals that interbreed or are potentially capable of interbreeding in nature. Considerable debate exists over the general definition of a species and how the theoretical definition should be applied in practice. With regard to the latter problem, cephalopod species generally are defined by distinct morphological traits not exhibited by any other species. This practice is valid if interbreeding does not occur. However, the amount of interbreeding (i.e. hybridization) that actually occurs in nature and contributes to or diminishes speciation is virtually unknown in cephalopods.

Sperm cord – The coiled rope of sperm that lies within the spermatophore (Fig. 38).

Sperm duct (= **seminal duct**) – The duct of males which joins the testis with the spermatophoric organ (Fig. 29).

Sperm groove – Sulcus along the ventral side of the hectocotylus used to transfer the spermatophores (Fig. 11).

Sperm mass – The mass of sperm held within the spermatangia of everted spermatophores.

Sperm receptacle – A bulbous structure in the buccal region or at the openings of the oviducts in females of certain cephalopods for deposition of spermatangia.

Spermatangium (pl. **spermatangia**) – Extruded, exploded, evaginated spermatophore/s, often in the form of a round bulb.

Spermathecae – Specialized sperm-storage structures found in the skin of some female **decapodiformes** or as pockets of the oviducal gland in **octopods**.

Spermatophore – A tubular structure manufactured by male cephalopods for packaging sperm; capable of holding millions of sperm, it is transferred and attached to the female until fertilization begins (Fig. 38). It forms a spermatangium after the spermatophoric reaction occurs and the spermatophore has everted.

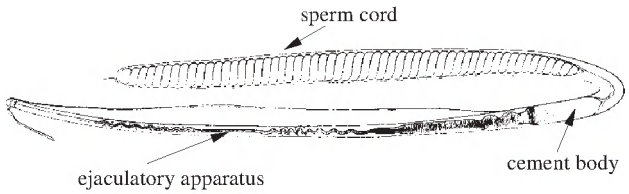


Fig. 38 Spermatophore

Spermatophore pad – A fleshy patch of tissue, usually in the mantle cavity of some female cephalopods (e.g. loliginids), to which spermatangia adhere after mating and remain until fertilization occurs.

Spermatophoric complex – The unit formed by the sperm duct, the spermatophoric organ, the spermatophoric sac, the spermatophoric duct and the penis (Fig. 29).

Spermatophoric duct – The duct of males through which the spermatophores, once formed, pass from the spermatophoric organ to the spermatophoric sac (Fig. 29).

Spermatophoric organ – Male organ where the spermatophores are formed (Fig. 29).

Spermatophoric reaction – The evagination of a spermatophore with the extrusion of the sperm mass, caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher.

Spermatophoric sac – See **Needham's sac** (Fig. 29).

Spine – See **Rostrum** (Fig. 18).

Squid – Common name given to members of the **Teuthoidea** and some members of the Sepiolidae.

Squid, general terminology – Diagrammatic drawing with external features labelled, ventral view (Fig. 17).

Stalk of tentacle – See **Tentacle stalk**.

Stalked eyes – See **Eye** (position and size).

Statocyst – A sense-organ that detects gravity, angular accelerations and low-frequency sound. The statocyst is embedded within the cephalic cartilage and contains the statoliths.

Statolith – A calcareous stone in the statocyst that detects linear acceleration, angular acceleration and orientation (Fig. 39). Statoliths of many species can be used to estimate age.

Stellate ganglion – Major ganglion of the peripheral nervous system of neocoleoid cephalopods that controls nerves to the mantle muscles.

Stomach – The muscular organ of the digestive system where primary digestion occurs (Fig. 19). The stomach generally is lined with cuticular ridges to aid in grinding food, and is supplied with digestive enzymes from the digestive gland. The stomach may be greatly expandable in size and serve as a storage area until food can be fully processed.

Striae – Numerous thin septa visible in the ventroposterior end of cuttlebone, making the cuttlebone appear as if transversely striated (Fig. 18).

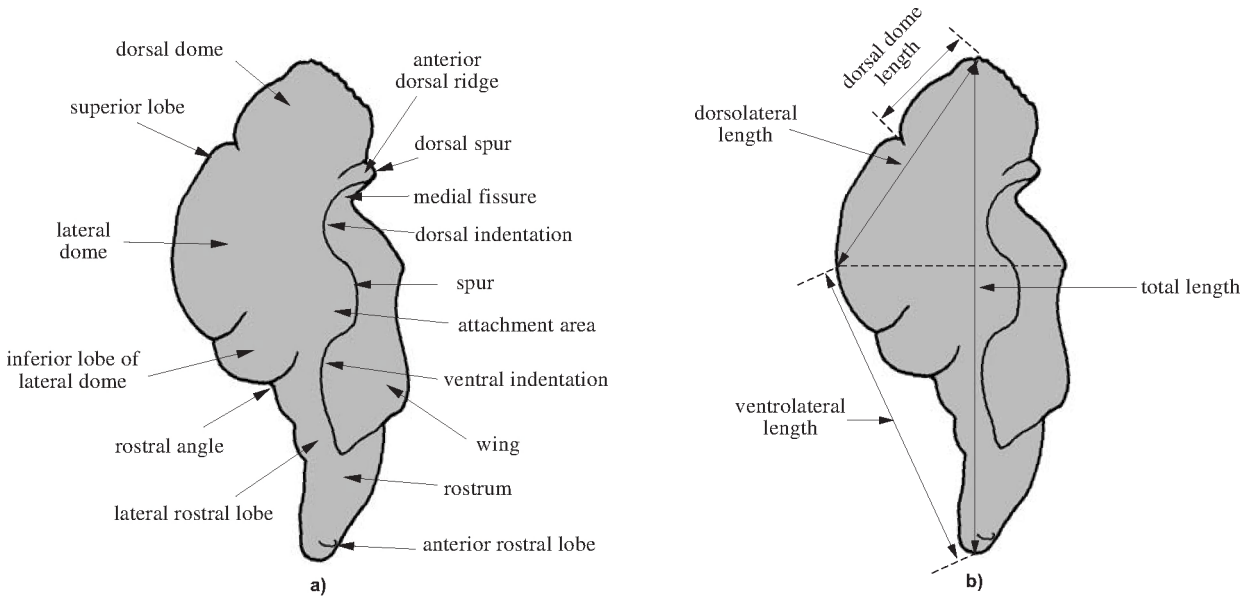


Fig. 39 Diagrams of a generalized teuthoid statolith (anterior view) with a) basic terms and b) basic dimensions labelled
(after Clarke, 1978)

Stylets – A pair of rod-like structures considered remnants of the molluscan shell in incirrate octopods. Generally in the form of a slender, cartilage-like, pointed rod tightly surrounded by the shell sac and buried in the mantle muscle at a dorsolateral position.

Subadult – Stage at which all of the characters that typically define the species are present, but the reproductive system is not mature and functional. It follows the juvenile stage and precedes the adult stage. A subadult stage is defined in cephalopods since the adult phase frequently is abbreviated.

Subequal – Nearly equal. Generally refers to the length of the arms when these appear to be approximately the same length. Arm lengths cannot be measured very accurately due to variation in their states of contraction.

Sucker/s – Muscular, suction-cup structure/s on the arms and tentacles (occasionally on the buccal membrane) of cephalopods. It consists of a cup-shaped portion, the **acetabulum**, and a flat, distal ring, the **infundibulum**, that contacts the substrate. Some are stalked, placed on muscular rods that contract (squids and cuttlefishes); some are sessile, embedded without stalks on the oral surface of the arms (octopuses) (Fig. 40a). They usually are counted either in longitudinal rows or in transverse (oblique) series (Fig. 40b).

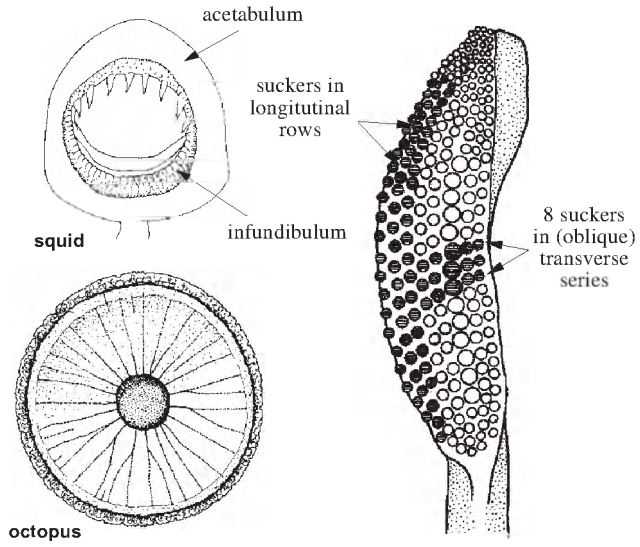


Fig. 40 Squid and octopus sucker and squid sucker orientation

Sucker ring – Chitinous, often serrated or toothed, ring that encircles the opening of suckers of squids and cuttlefishes (Fig. 41).

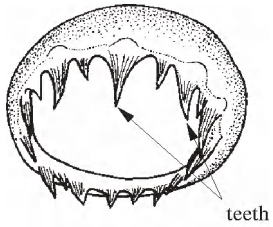


Fig. 41 Sucker ring

Sucker series – The longitudinal rows of suckers on the arms or tentacles of **decapods**. Series (= transverse rows) contrasts with **rows** (= longitudinal rows) in describing sucker arrangement. In octopods, sucker 'series' generally is synonymous with 'rows', the 'longitudinal' component of the term is implied.

Sucker stalk – The muscular support and connective structure between the sucker and the arm. In **octopods** it is a cylindrical structure about the same diameter as the sucker and in **decapods** it is constricted into a conical pillar.

Sucker teeth – Sharp, blunt, or rounded teeth on the inner horny sucker rings of some **decapods**.

Sulcus – A median longitudinal groove, sometimes flanked by two low ridges on the ventral side of the cuttlebone.

Superior buccal lobes – Lobes of the central nervous system that sit dorsal to the oesophagus where the latter enters the buccal mass.

Swimbladder – Gas-filled structure found in the dorsal region of the pelagic octopod, ***Ocythoe***.

Swimming membrane (= **keel**) – An elongate, flat, muscular vane along the aboral surface of arms and clubs of **decapods** that functions to streamline and supports the appendages during swimming (Figs 12 and 17).

Synonym – One of two or more names applied to the same taxon/species.

Systematics – The classification of organisms into hierarchal groups based on phylogenetic relationships.

Tail – Posterior narrow extension of the body posterior to the fins. The end of the fins and the beginning of the tail often overlap. An operational definition for point of demarcation for the purposes of measurement is: the point where a hypothetical line, continuous with the broad posterior edge of the fin, crosses the midline of the body (Fig. 17).

Taxa, taxon – A taxonomic group of any rank. A taxonomic unit.

Tentacles – Modified fourth pair of appendages in **decapods**, used for prey capture and capable of considerable extension and contraction. Distal ends contain clubs with suckers and/or hooks; stalks are frequently devoid of suckers. Tentacles can retract into pockets, or merely contract (Figs 17 and 33). Although the tentacles are derived evolutionarily from the fourth pair of arms, the term 'arms IV' is reserved for the subsequent arm pair, the ventral arms, which are evolutionarily the fifth pair of arms.

Tentacle absence – Tentacles can be absent because the species lacks tentacles, they are accidentally lost during capture, or they are naturally lost at a particular stage of development.

Tentacle pads – Poorly understood and complex pad-like photophores that are found on the tentacular stalks of some squids of the family **Chiroteuthidae**.

Tentacle stalk – Region of the tentacle proximal to the club.

Tentacle terminology – See Figs 17 and 33.

Tentacular club – The distal, terminal, usually expanded, part of the tentacle that bears suckers and/or hooks. Used for capturing prey (Figs 12, 17 and 33).

Tentacular retractor muscles – Muscles that serve to coil the tentacle when retracted, in contrast with those muscles that serve to shorten (contract) the tentacle.

Tentacular sheath – **(1)** The keels of arms IV are off-set laterally and often enlarged to fully or partially conceal, protect or encase the adjacent tentacles. The latter function is most fully developed in the chiroteuthids and mastigoteuthids; **(2)** tubular muscular sheaths of **nautiluses** into which the tentacles can be retracted.

Terminal fins – Fins with more than 50% of their length posterior to the muscular mantle. These fins, therefore, are at the 'terminal' or posterior end of the body and generally are supported by an elongate secondary conus of the gladius.

Terminal organ – Alternative name for penis, as true definition of a penis is 'organ of insertion'. In most cephalopods, the hectocotylized arm is used for spermatophore insertion, or placement, in the females.

Terminal pad (of tentacular club) – A small, distinct pad or circlet of small terminate suckers at the distal tip of the club.

Teuthoidea – The higher taxon that includes all squid-like **decapods**; now archaic. The monophyly of this taxon is questionable.

Total length (**TL**) – Length measured from the posterior tip of the mantle to the anterior tip of the outstretched tentacles (squids and cuttlefishes) or arms (octopuses) (Fig. 6).

Trabeculae – Muscular rods that support the protective membranes on the arms and clubs of cephalopods (Fig. 34). Occasionally membranes are reduced and/or trabeculae are elongated, so they extend beyond the edge of the membrane, papilla-like.

Tragus – Particular inward projecting knob in the funnel-locking apparatus of some squids. It is the knob found on the medial surface of the central depression (Fig. 8).

Truncate teeth – Teeth on the inner chitinous rings of decapod suckers that do not terminate in a point but rather in a broad, flat tip.

Umbilicus – The central core of the chambered nautilus shell, representing the juvenile shell with its initial coils; often a depression (Fig. 42). It can be open, so as to show the inner most coils, or closed, often covered by a thickened layer, the callus.

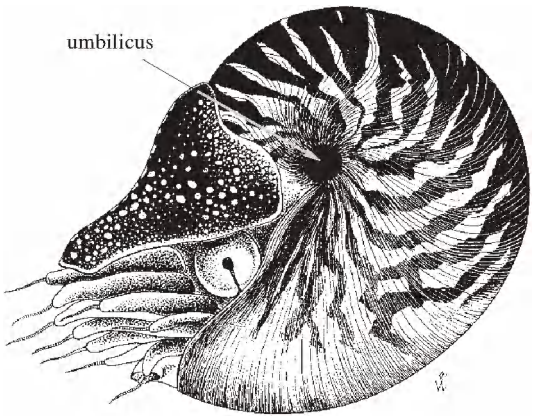


Fig. 42 ***Nautilus*** **(lateral view)**

Vane – Thin, lateral expansion of the gladius that arises from the rachis (Fig. 16) (see **Rachis**).

Ventral – The lowermost or belly surface of a cephalopod, the surface on which the funnel is located. Opposite the dorsal surface (Figs 17 and 20).

Visceral sac – The body region posterior to the head surrounded by the mantle. The body wall in this region that encases the viscera usually is rather thin-walled, hence the name 'visceral sac'. The visceral sac is also called the 'visceral dome'.

Visceropericardial coelom – The largest coelom in all cephalopods, except in the incirrate and cirrate octopods, where it is greatly reduced. Generally it encloses the gonad, and partially encapsulates the stomach, caecum and ventricle, among other structures. The visceropericardial coelom also communicates with the other cephalopodan coelom, the nephridial coelom, and the mantle cavity via a pair of ducts that open at the bases of the nephridial papillae.

Water pores – **(1)** Large cephalic orifices at base arms of some pelagic octopods, e.g. ***Tremoctopus*** (Fig. 43); **(2)** 8 small openings to the water pouches located at the base of the arms on the ventral web of the benthic octopod ***Cistopus***.

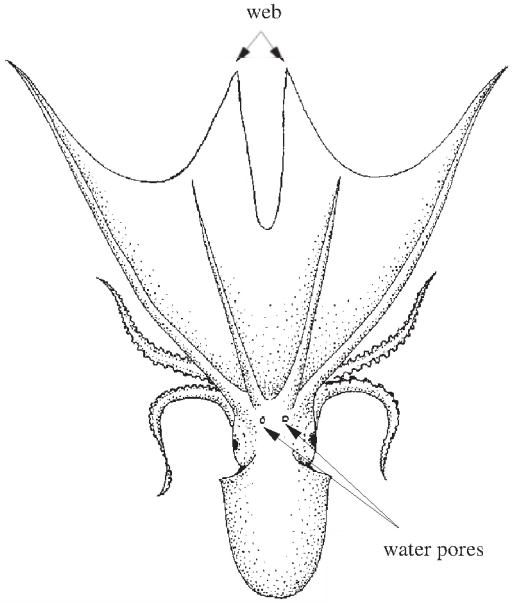


Fig. 43 ***Tremoctopus*** **(dorsal view)**

Water pouches – Glandular pouches with muscular pore openings situated in the oral webs between the base of each arm in the incirrate octopus genus ***Cistopus***.

Web – A membranous sheet of greater or lesser extent that extends between the arms of many **octopods**, giving an umbrella-like appearance when the arms are spread out, e.g. on cirroteuthids (Figs 20 and 43). It is reduced or absent in most **decapods**.

NEXT PAGE

1.5 Key to Recent Cephalopod Groups and Families

1a. More than ten (63 to 94) circumoral appendages; suckers absent; chambered, coiled external shell . . . **Nautiloidea**
Family Nautilidae (Fig. 44)

1b. Eight or ten circumoral appendages; suckers (and/or hooks) present; no external shell . . . . . **Coleoidea → 2**

2a. Suckers stalked with chitinous rings; 10 circumoral appendages, 8 arms and 2 ventrolateral tentacles (tentacles may be lost in some species). Mantle cavity communicates with the exterior via 3 openings . . . . . **Cuttlefishes, Bobtail squids, Bottletail squids, Pigmy squids, Ram's Horn squid, Myopsid squids, Oegopsid squids → 3**

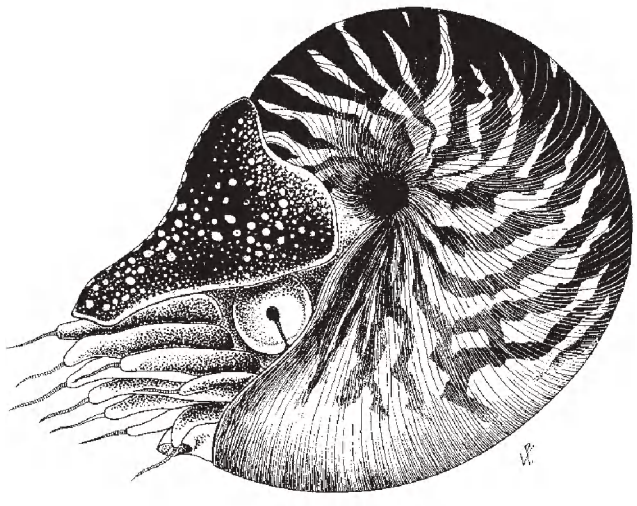
2b. Suckers without stalks, bases sometimes constricted in finned (cirrate) octopods and vampires, without chitinous rings; 8 arms, no ventrolateral tentacles. Mantle cavity communicates with the exterior via one opening, rarely 2 . . . . . **Octopods and Vampires → 4**

3a. Internal shell straight, laminate, calcified (**Sepiidae**), coiled, chambered (**Spirulidae**), rudimentary, straight and chitinous (**Sepiolidae**) or absent (**Sepiadariidae**, **Idiosepiidae**); tentacles contractile and retractile into pockets between arms III and IV; fins not joined posteriorly; mantle edge near mantle cartilages straight . . . . . **Cuttlefishes, Bobtail squids, Bottletail squids, Pigmy squids, Ram's Horn squid → 5**

3b. Internal shell straight, feather- or rod-shaped, chitinous; tentacles contractile, not retractile, no pockets; fins usually joined posteriorly; mantle edge near mantle cartilages with small projections or 'angles' . . . . . **Myopsid squids, Oegopsid squids → 7**

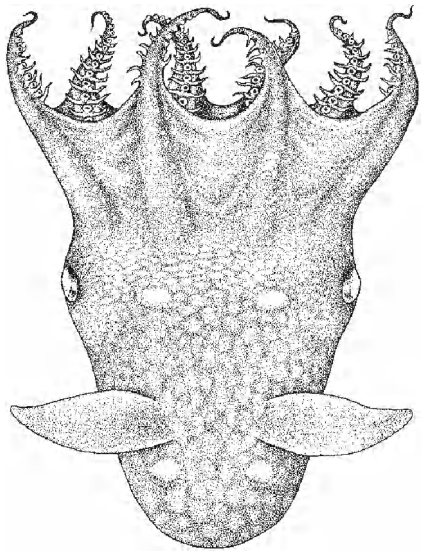
4a. Internal shell a chitinous, thin, broad plate; a pair of small filamentous appendages in pouches between bases of arms I and II; light organ (photophore) present at base of each fin and medial to each eye dorsally; colour black to dark red or brown . . . . . **Vampires** (monotypic)
Family Vampyroteuthidae (Fig. 45)

4b. Internal shell vestige either small cartilaginous rods or a U-shaped support or absent; secondary filamentous appendages absent; suckers sessile, without stalks and without chitinous rings; colour extremely variable but never black . . . . . **Octopods → 36**



lateral view

Fig. 44 Nautilidae (*Nautilus*)



dorsal view

Fig. 45 Vampyroteuthidae (*Vampyroteuthis*)

5a. Internal shell calcified, coiled, chambered . . . . . **Family Spirulidae** (Fig. 46)
5b. Internal shell calcified, straight, laminate, chalky . . . . . **Family Sepiidae** (Fig. 47)
5c. Internal shell (gladius) chitinous (except ***Euprymna***); one only or both dorsal arms or one dorsolateral arm hectocotylized . . . . . **Family Sepiolidae** (Fig. 48)
5d. Internal shell (gladius) absent . . . . . → **6**

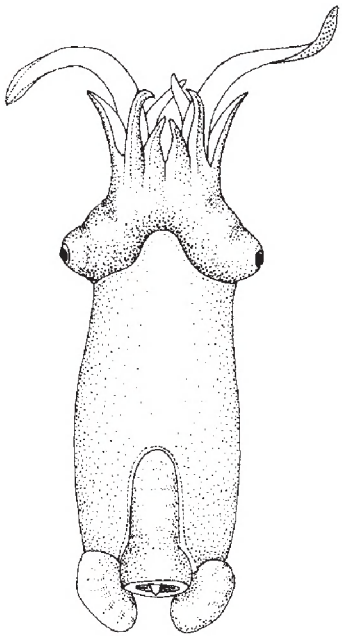


Fig. 46 Spirulidae (*Spirula*)

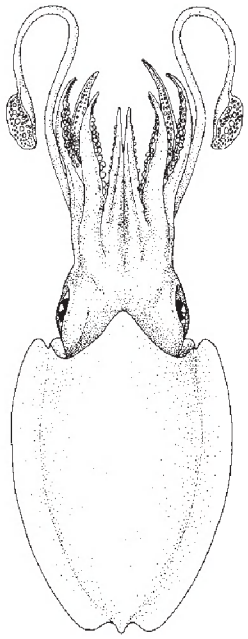


Fig. 47 Sepiidae (*Sepia*)

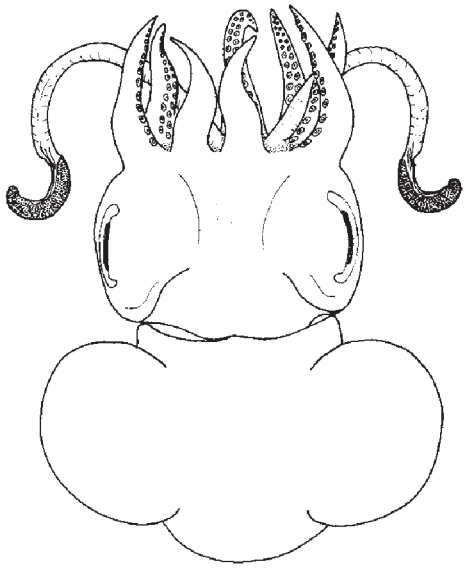


Fig. 48 Sepiolidae (*Rossia*)

6a. Left ventral arm hectocotylized; dorsal border of mantle fused with head . . . . . **Family Sepiadariidae** (Fig. 49)
6b. Both ventral arms hectocotylized; dorsal border of mantle free (unfused) from head . . . . . **Family Idiosepiidae** (Fig. 50)

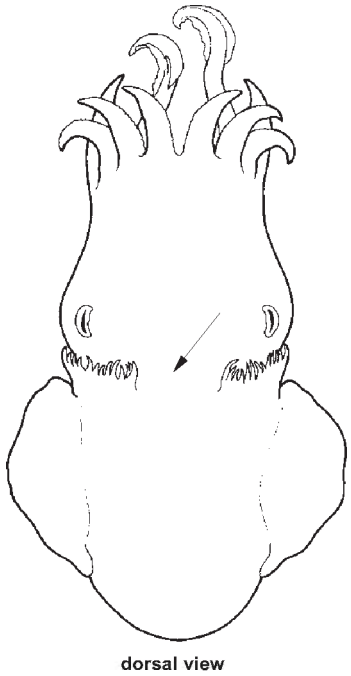


Fig. 49 Sepiadariidae (Sepioloidea)

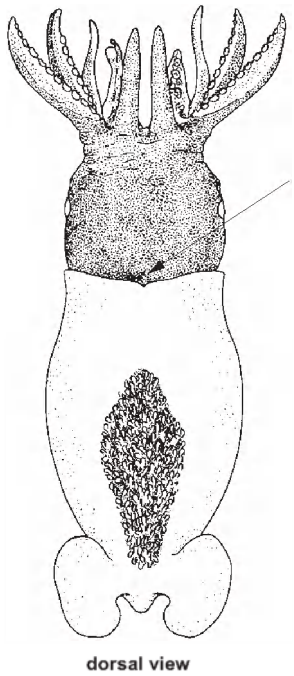


Fig. 50 Idiosepiidae (*Idiosepius*)

7a. Eye covered by transparent membrane (cornea) (Fig. 51a) . . . . . **Myopsid squids → 8**

7b. Eye without cornea; lens in open contact with seawater (Fig. 51b) . . . . . **Oegopsids squids**[1/] **→ 9**

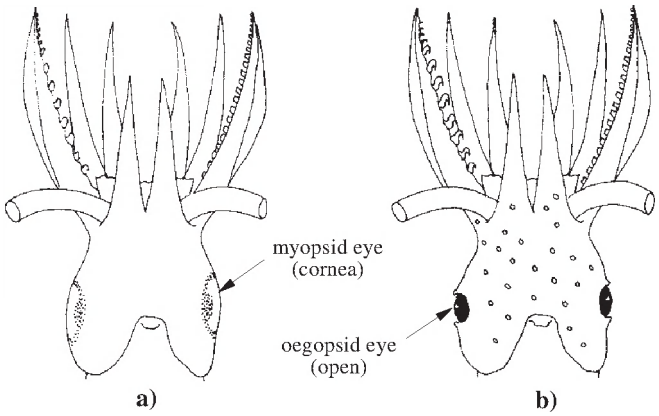


Fig. 51

8a. Four longitudinal rows (series) of suckers on manus of tentacular clubs; fins united at posterior end of mantle; medial posterior border of fins concave (Fig. 52) . . . . . **Family Loliginidae**

8b. Two longitudinal rows (series) off suckers on manus of tentacular clubs; fins not united at posterior end of mantle; medial posterior borders of fins convex (Fig. 53) . . . . . ***Pickfordiateuthis***[2/]

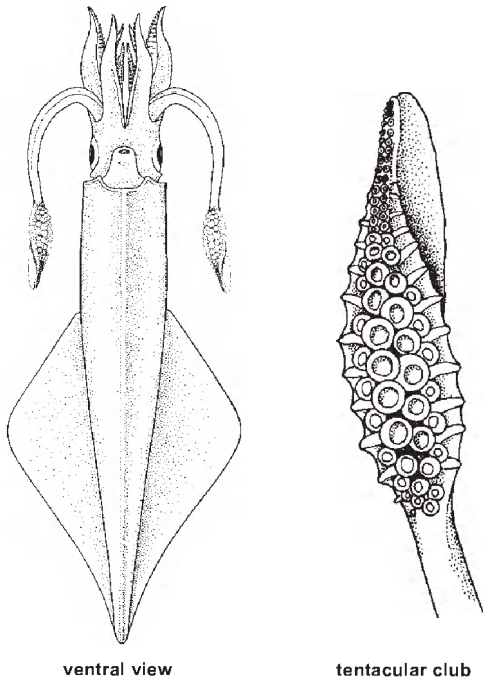


Fig. 52 Loliginidae (*Loligo*)

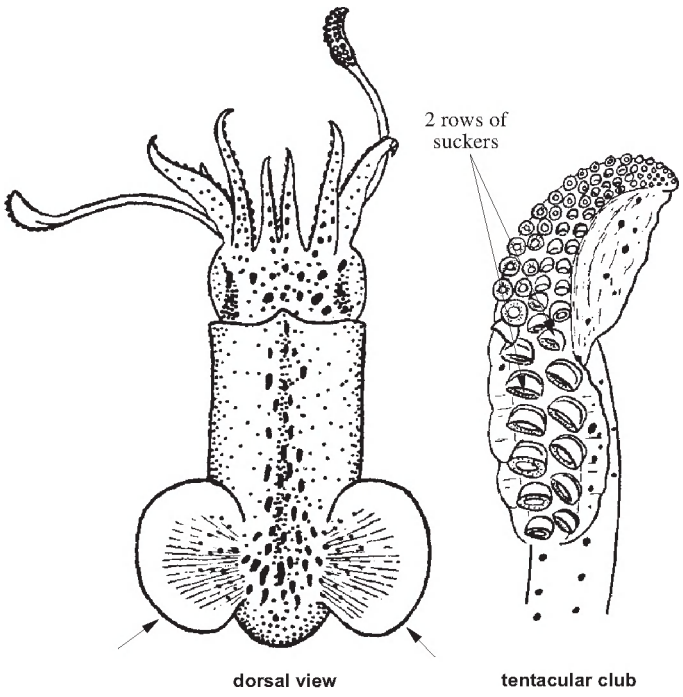


Fig. 53 Pickfordiateuthidae (*Pickfordiateuthis*)

9a. Funnel free from mantle; funnel-mantle locking apparatus present . . . . . **→ 10**

9b. Funnel fused to mantle on each side[3/]; no funnel-mantle locking apparatus present . . . . . **→ 35**

[1/] A new family of oegopsid squid has been recognized from Australian waters by C.C. Lu (personal communication). The description for publication is currently in press.

[2/] *Pickfordiateuthis*, the sole genus in a formally recognized family, recently has been placed in the family Loliginidae; it is included in the Key to indicate its unique characters within the Loliginids.

[3/] Fusion of the mantle to the funnel also occurs in adults of two Ommastrephid species: *Sthenoteuthis oualaniensis* and *Eucleoteuthis luminosa*.

10a. Funnel-locking apparatus a simple, straight groove and ridge[1/] (Fig. 54) . . . . . → **11**
10b. Funnel-locking apparatus not a simple, straight groove and ridge . . . . . → **28**

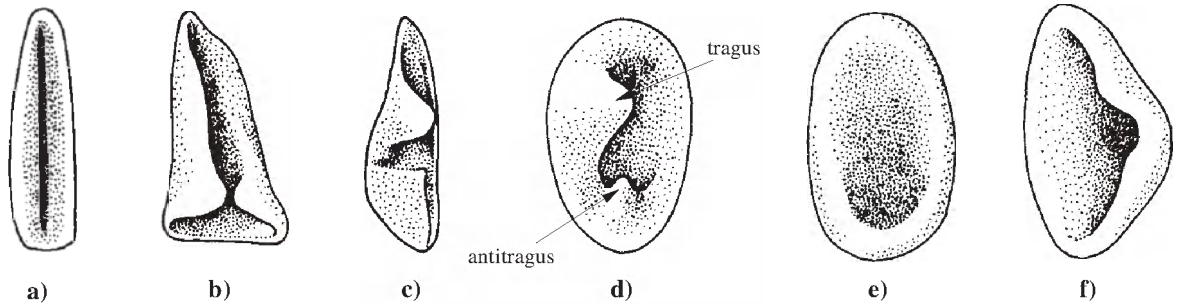


Fig. 54 Funnel-locking apparatus

11a. Arms with hooks or with suckers in 4 longitudinal rows on proximal half of ventral arms . . . . . → **12**
11b. Arms without hooks and with suckers in 2 longitudinal rows on proximal half of ventral arms . . . . . → **16**

12a. Armature (suckers, hooks) of arms in 2 rows . . . . . → **13**
12b. Armature (suckers, hooks) of arms in 4 rows (Fig. 55) . . . . . **Family Gonatidae**

13a. Tentacles and clubs absent in adults although present in larvae or occasionally in juveniles (***Taningia***) but, when present, always with rudimentary clubs armed with few suckers (Fig. 56) . . . . . **Family Octopoteuthidae**
13b. Tentacles present; fully developed clubs present (Fig. 57) . . . . . → **14**

14a. Photophores on viscera and on mantle or surface of head or arms . . . . . **Family Pyroteuthidae** (Fig. 57)
14b. Photophores on mantle and surface of head and arms but not on viscera . . . . . → **15**

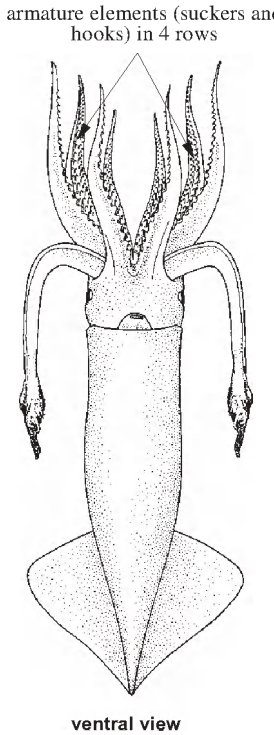


Fig. 55 Gonatidae (*Gonatus*)

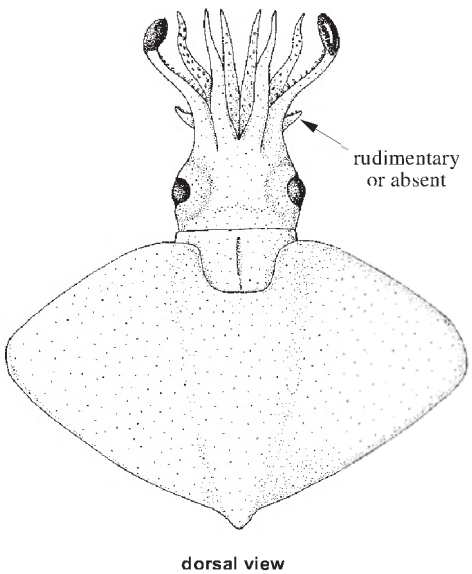


Fig. 56 Octopoteuthidae (*Taningia*)

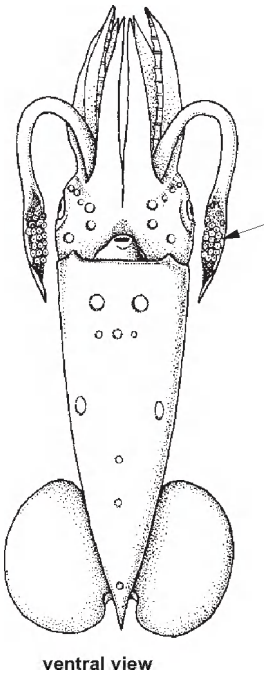


Fig. 57 Pyroteuthidae (*Pterygioteuthis*)

[1/] The classification 'simple and straight' includes some locking apparatuses that show considerable variation. For example, in the Octopoteuthidae and the Histioteuthidae the central groove is fairly broad and may curve slightly. The homogeneity of this classification becomes apparent when this type of locking cartilage is compared to the more highly specialized types (Fig. 54).

15a. Photophores on tentacles but not on eyeballs . . . . . **Family Ancistrocheiridae** (Fig. 58)
15b. Photophores on ventral eyeballs but not on tentacles . . . . . **Family Enoploteuthidae** (Fig. 59)

16a. Buccal membrane connectives attach to ventral sides of arms IV (Fig. 60b) . . . . . → **17**
16b. Buccal membrane connectives attach to dorsal sides of arms IV[1/] (Fig. 60a) . . . . . → **23**

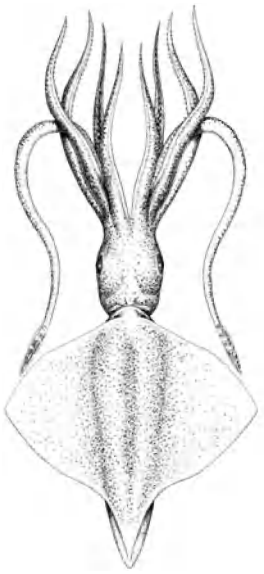


Fig. 58 Ancistrocheiridae (*Ancistrocheirus*)

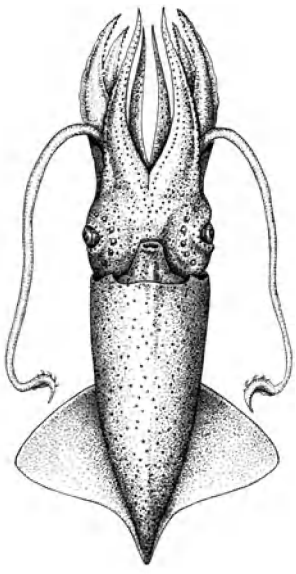


Fig. 59 Enoploteuthidae (*Abralia*)

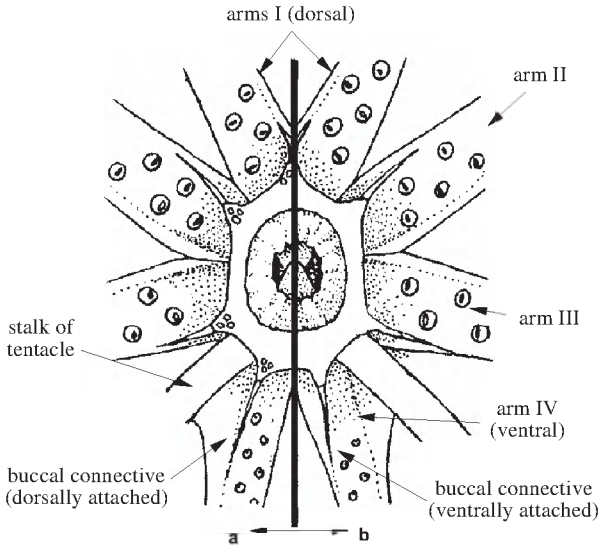


Fig. 60 Oral view

17a. Hooks present on tentacular clubs (Fig. 61a and b); tentacles and clubs are lost in mature females (Fig. 61c) . . . . . **Family Onychoteuthidae**
17b. Hooks lacking on tentacular clubs . . . . . → **18**

18a. Cartilaginous scales present on mantle (may be minute); tentacular clubs with 4 longitudinal rows of suckers . . . . . → **19**
18b. Cartilaginous scales lacking; tentacular clubs with more than 4 longitudinal rows of suckers on some areas . . . . . → **20**

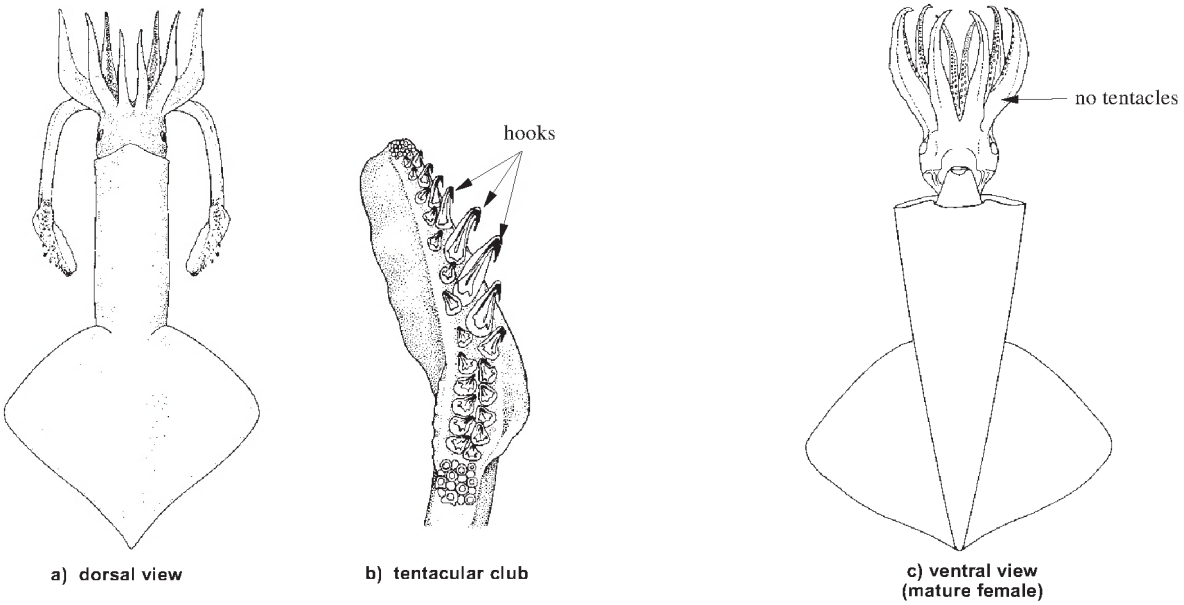


Fig. 61 Onychoteuthidae (*Onychoteuthis*)

[1/] This character is difficult to detect in some histioteuthids that have secondary modifications to the buccal membrane connectives.

19a. Tentacles present with numerous laterally compressed club suckers . . . . . **Family Pholidoteuthidae** (Fig. 62)
19b. Tentacles lost in adults; tentacles in juveniles small and weak, with a few (about 6) poorly differentiated suckers . . . . . **Family Lepidoteuthidae** (Fig. 63)

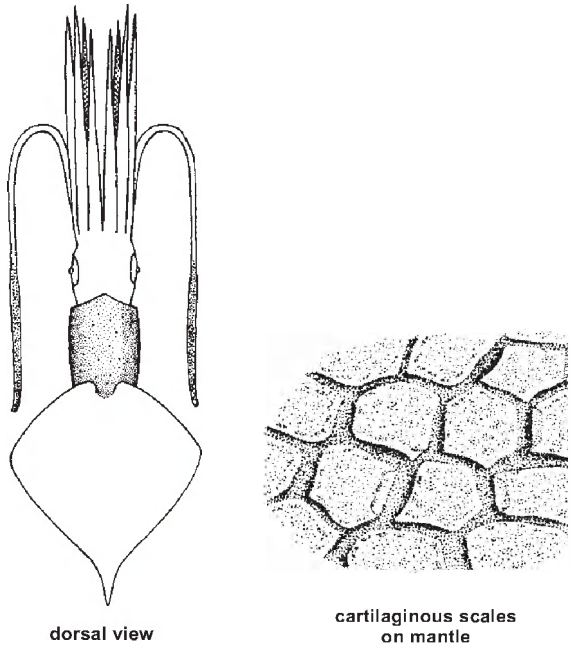


Fig. 62 Pholidoteuthidae (*Pholidoteuthis*)

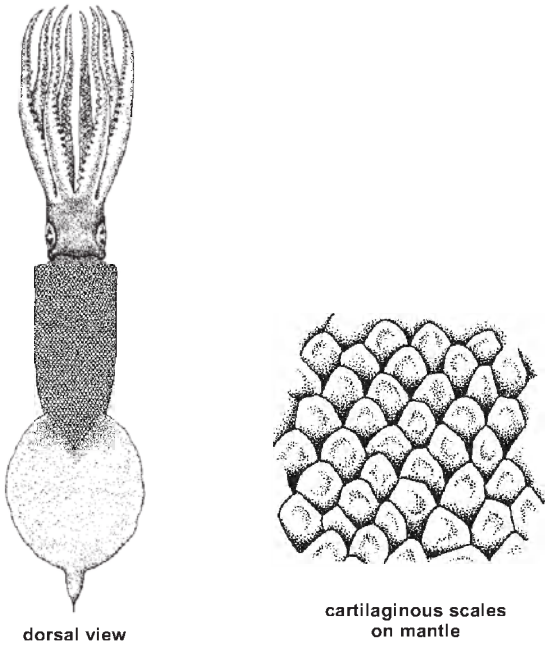


Fig. 63 Lepidoteuthidae (*Lepidoteuthis*)

20a. Fin nearly as long as mantle, supported by strong, transverse, muscular ribs; minute suckers present on oral surface of buccal lappets (Fig. 64) . . . . . **Family Chtenopterygidae**
20b. Fins less than half the body length and without supporting ribs; no suckers on buccal lappets . . . . . → **21**

21a. Tentacular clubs with 6 uniform longitudinal rows of suckers; a long, spike-like tail present greater than fin length (Fig. 65) . . . . . **Family Batoteuthidae**
21b. Tentacular clubs with 2 or 4 longitudinal rows of suckers . . . . . → **22**

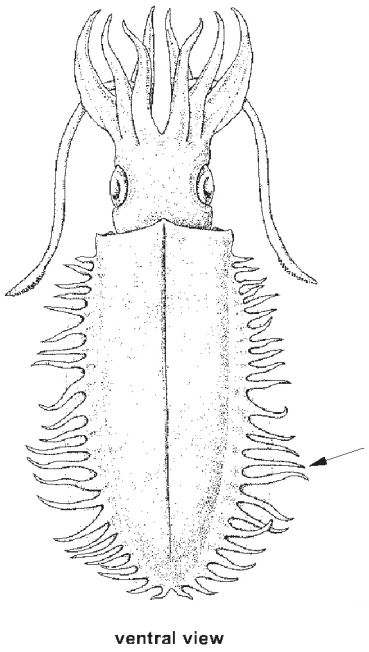


Fig. 64 Chtenopterygidae (*Chtenopteryx*)

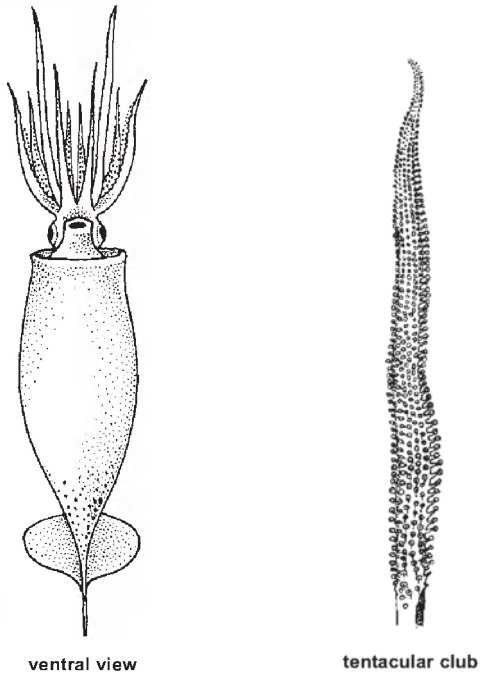


Fig. 65 Batoteuthidae (*Batoteuthis*)

22a. Tentacular clubs with 4 longitudinal rows of suckers on distal portion, numerous rows on proximal portion; no long, spike-like tail (Fig. 66) . . . . . **Family Brachioteuthidae**

22b. Tentacular clubs with 2 longitudinal rows of very widely spaced, tiny suckers; mantle broad, bluntly rounded posteriorly; fin short, wide, transversely oval (Fig. 67) . . . . . **Family Walvisteuthidae**

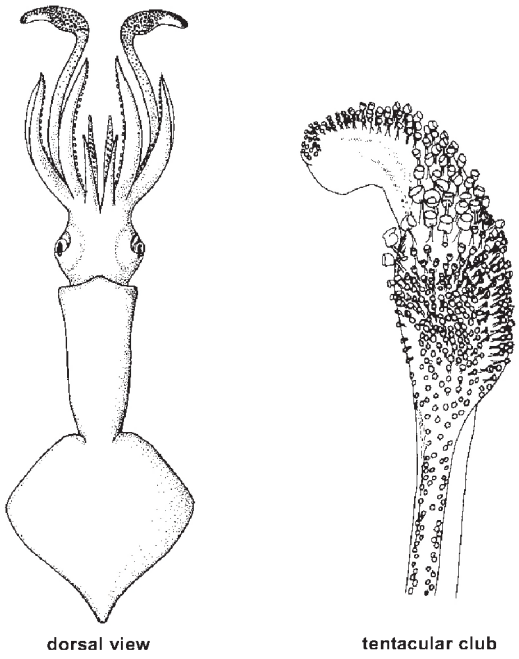


Fig. 66 Brachioteuthidae (*Brachioteuthis*)

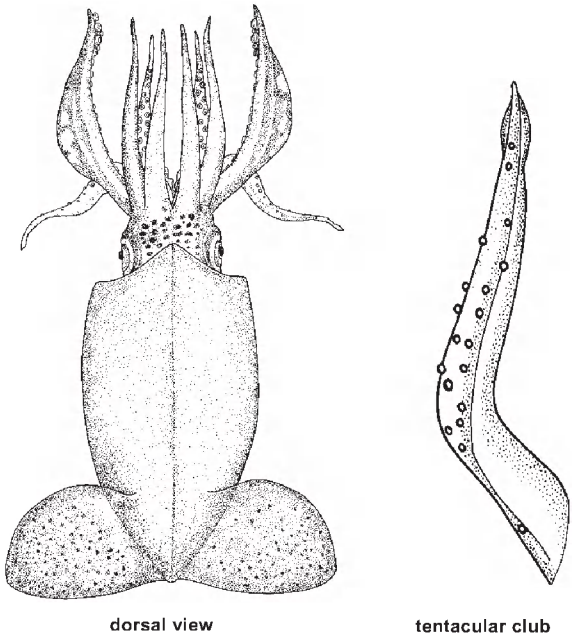


Fig. 67 Walvisteuthidae (*Walvisteuthis*)

23a. Ventral surface of eye with a row of photophores; buccal membrane with 8 separate lappets (Fig. 68) . . . . . **Family Lycoteuthidae**

23b. No photophores on eyes; buccal membrane with 7 lappets or less . . . . . → **24**

24a. Surface of mantle, head and arms covered with numerous photophores (usually large and distinct) (Fig. 69) . . . . . **Family Histioteuthidae**

24b. Surface of mantle and head without photophores (arms may have a few photophores) . . . . . → **25**

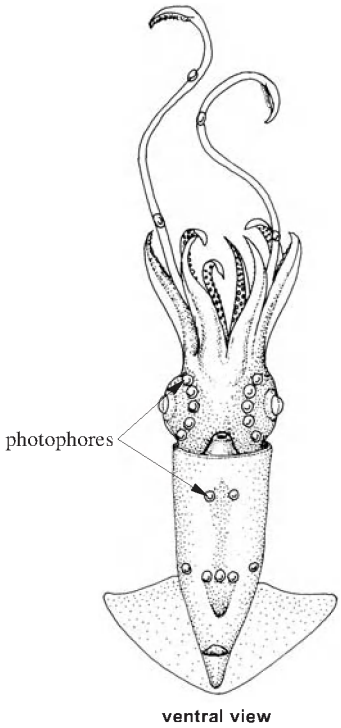


Fig. 68 Lycoteuthidae (*Lycoteuthis*)

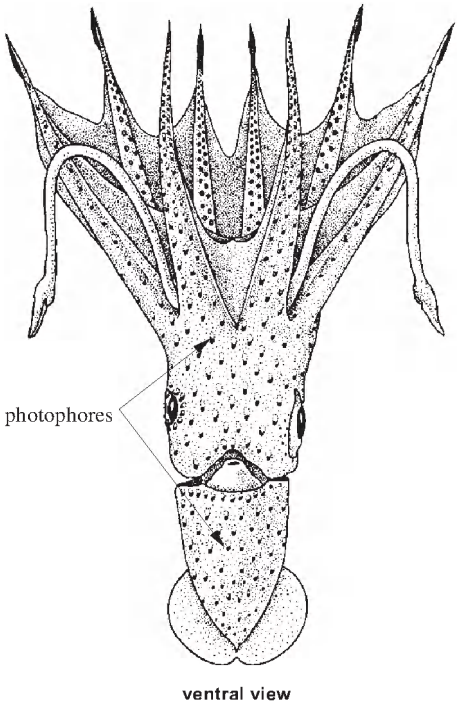


Fig. 69 Histioteuthidae (*Histioteuthis*)

25a. Minute suckers present on oral surface of buccal membrane (Fig. 70) . . . . . **Family Bathyteuthidae**
25b. No suckers on oral surface of buccal lappets . . . . . → **26**

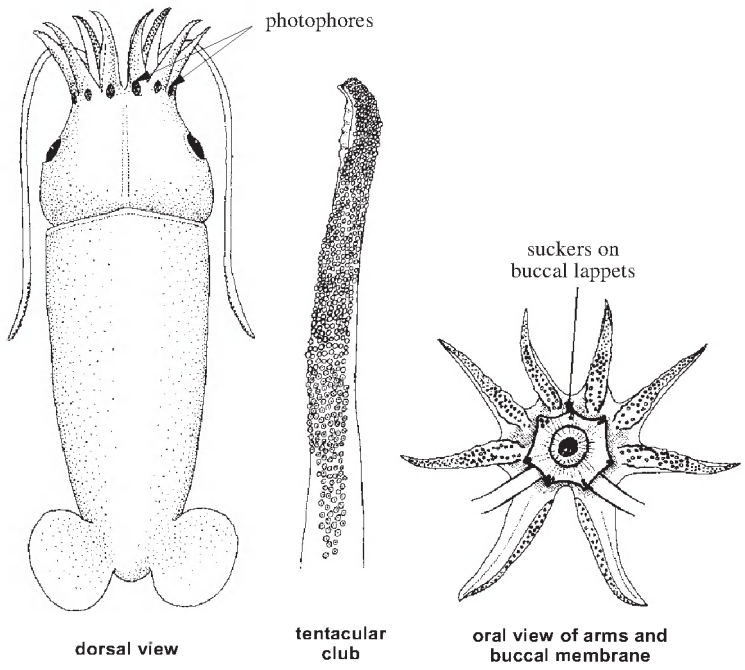


Fig. 70 Bathyteuthidae (*Bathyteuthis*)

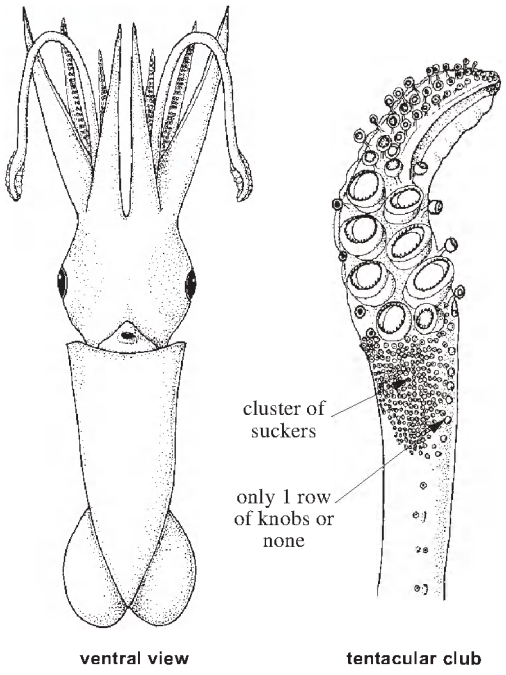


Fig. 71 Neoteuthidae (*Alluroteuthis*)

26a. Many small to minute suckers (or suckers and knobs) at proximal end of manus (Figs 71 and 72) . . . . . → **27**
26b. No cluster of small suckers at proximal end of manus (Fig. 73) . . . . . **Family Psychroteuthidae**

27a. Posterior borders of fins slightly convex; carpal knobs in a single dorsal row or absent; adults attain small size (Fig. 71) . . . . . **Family Neoteuthidae**
27b. Posterior borders of fins concave; carpal knobs in a cluster alternating with carpal suckers; adults attain gigantic size (Fig. 72) . . . . . **Family Architeuthidae**

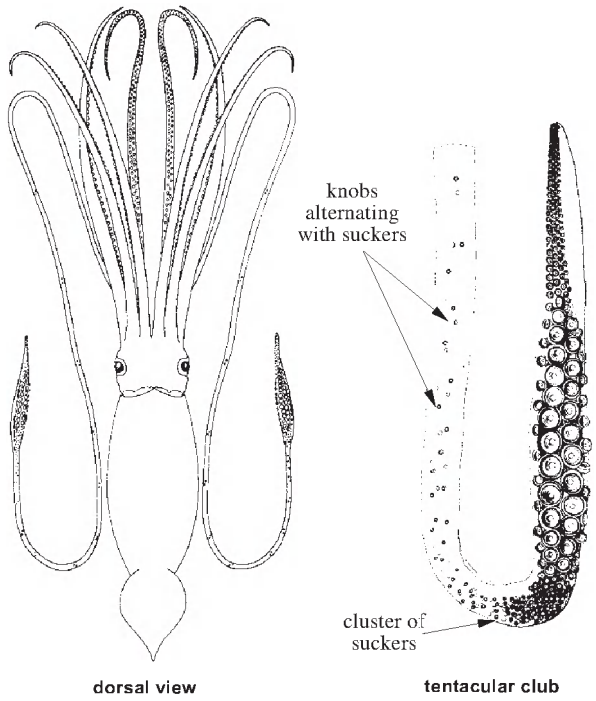


Fig. 72 Architeuthidae (*Architeuthis*)

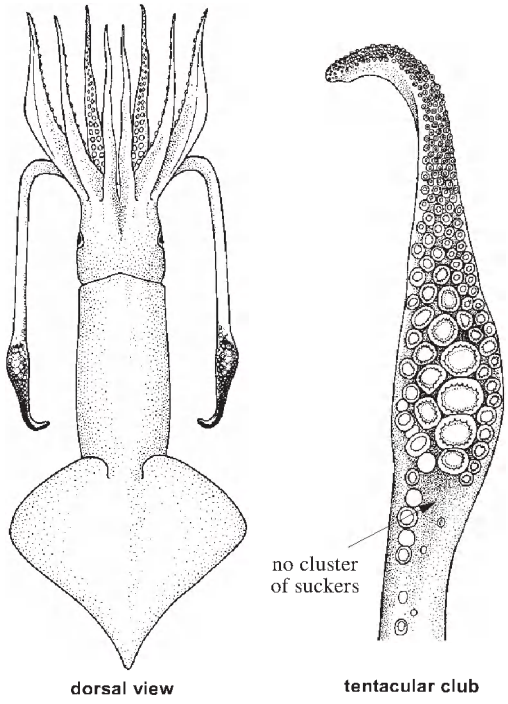


Fig. 73 Psychroteuthidae (*Psychroteuthis*)

28a. Funnel-locking cartilage with a longitudinal and a transverse groove ⊥-shaped or ⊣-shaped (Fig. 54b and c) . . . . . → **29**

28b. Funnel-locking cartilage oval, triangular, or oval with inward projecting knobs (Fig. 54d, e and f) . . . . . → **30**

29a. Funnel-locking cartilage with a longitudinal groove crossed by a transverse groove at its posterior end, ⊥-shaped; fins less than 60% of mantle length (Fig. 74) . . . . . **Family Ommastrephidae**

29b. Funnel-locking cartilage with a longitudinal groove from which a shorter groove branches medially, ⊣-shaped; fins more than 80% of mantle length (Fig. 75) . . . . . **Family Thysanoteuthidae**

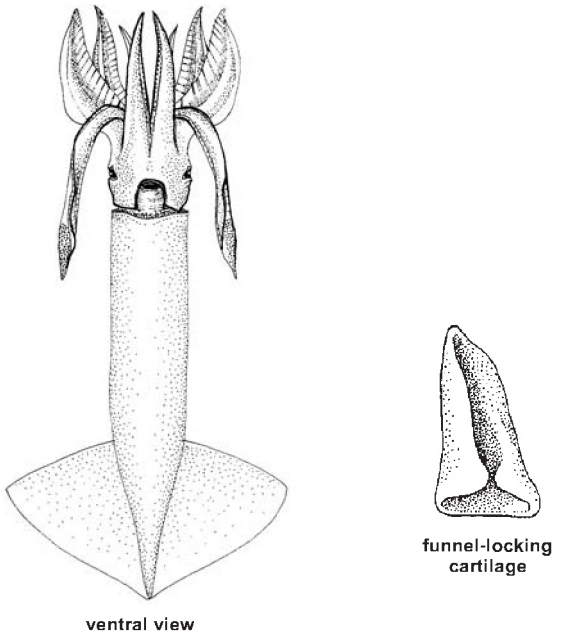


Fig. 74 Ommastrephidae (*Ommastrephes*)

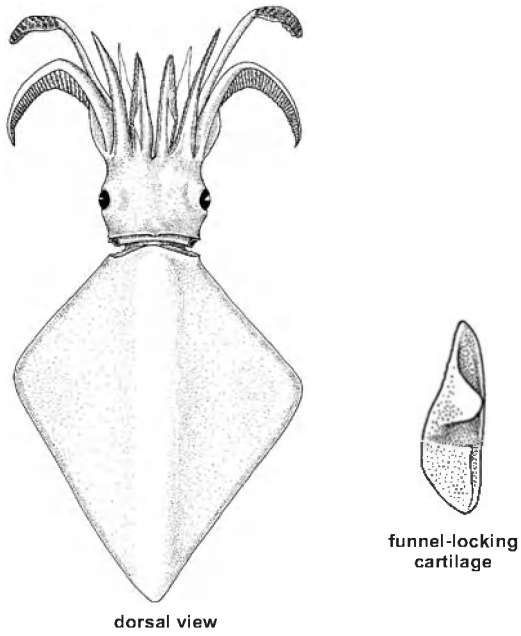


Fig. 75 Thysanoteuthidae (*Thysanoteuthis*)

30a. Funnel-locking cartilage oval with 1 or 2 knobs directed toward the centre of the concavity (Fig. 54d) . . . . . → **31**

30b. Funnel-locking cartilage oval or subtriangular, without knobs (Fig. 54e and f) . . . . . → **32**

31a. Club with only 4 longitudinal rows (series) of suckers (Fig. 76) . . . . . **Family Chiroteuthidae**

31b. Club with many (more than 15) longitudinal rows (series) of minute suckers (Fig. 77) . **Family Mastigoteuthidae**

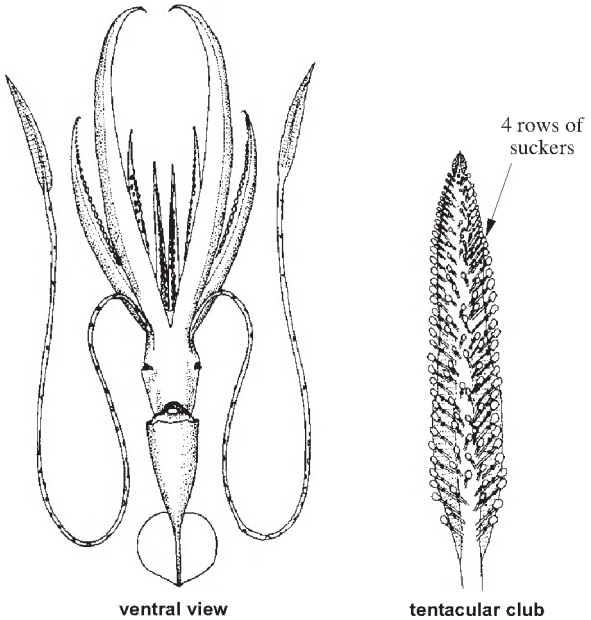


Fig. 76 Chiroteuthidae (*Chiroteuthis*)

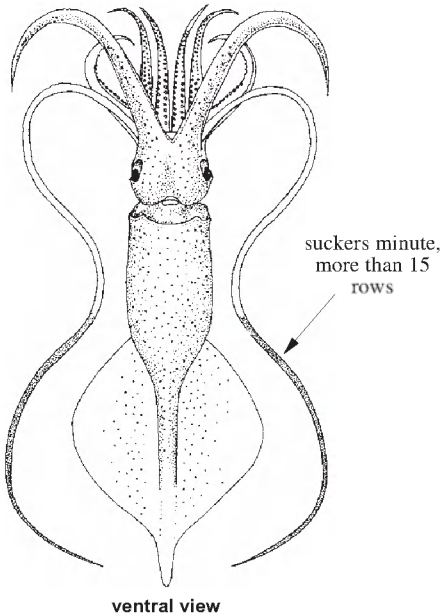


Fig. 77 Mastigoteuthidae (*Mastigoteuthis*)

32a. Suckers on arms in 4 to 6 longitudinal rows (series) . . . . . → **33**

32b. Suckers on arms in 2 rows; tail short (less than half of mantle length) or absent . . . . . → **34**

33a. Six longitudinal rows of suckers on arms I to III, 4 longitudinal rows of suckers on arms IV; tail extremely long (greater than mantle length), as a spike-like extension of the gladius; no fins on tail (Fig. 78) . . . . . **Family Joubiniteuthidae**

33b. Three or 4 longitudinal rows of suckers proximally on all arms; fins terminal, extremely long and broad, extend far posterior to mantle; gladius incorporated in fins to posterior tip (Fig. 79) . . . . . **Family Magnapinnidae**

34a. Suckers on tentacular club in 4 longitudinal rows (series); mantle free dorsally (Fig. 80). . **Family Cycloteuthidae**

34b. Suckers on tentacular club in 8 or more longitudinal rows (series); mantle fused dorsally to head (Fig. 81) . . . . . **Family Promachoteuthidae**

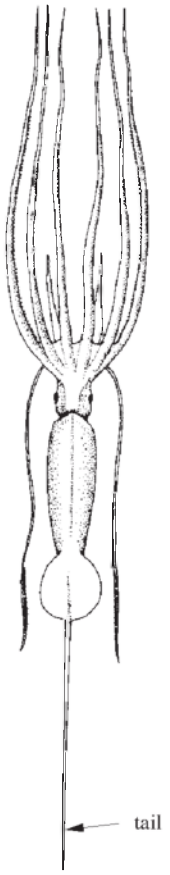


Fig. 78 Joubiniteuthidae (*Joubiniteuthis*)

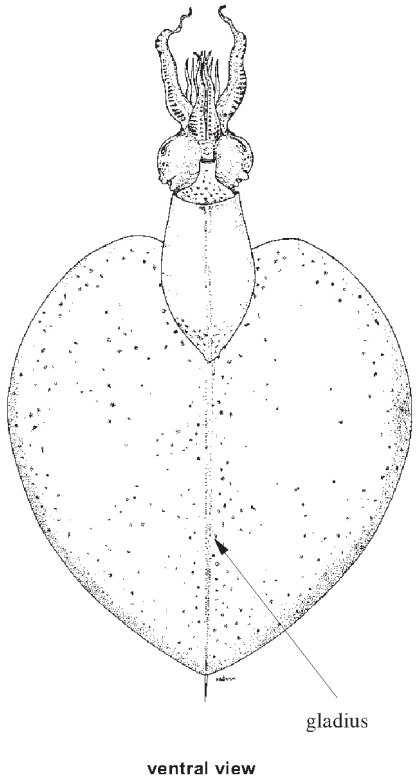


Fig. 79 Magnapinnidae (*Magnapinna*)

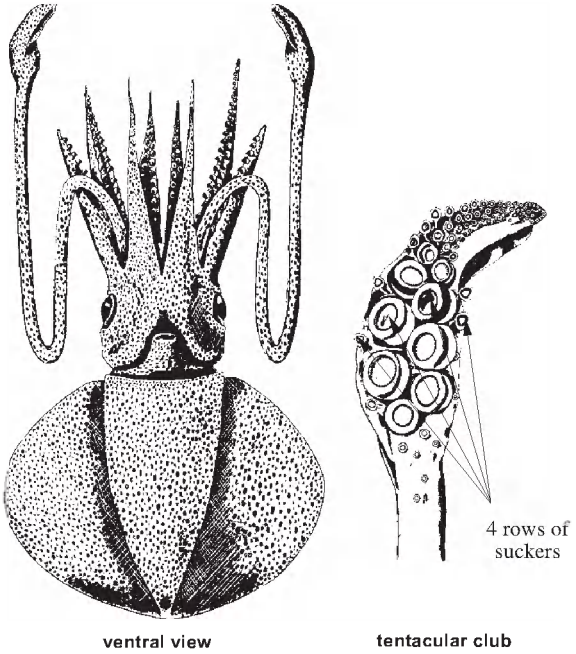


Fig. 80 Cycloteuthidae (*Discoteuthis*)

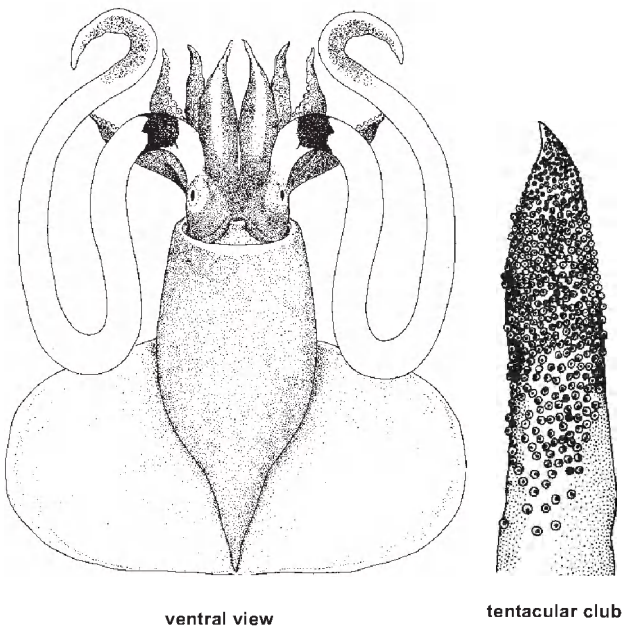


Fig. 81 Promachoteuthidae (*Promachoteuthis*)

35a. Mantle free dorsally, articulates with head by ridge and groove (Fig. 82) . . . . . **Family Grimalditeuthidae**
35b. Mantle fused dorsally with head (Fig. 83) . . . . . **Family Cranchiidae**

36a. Fins present on mantle; cirri on arms . . . . . **Cirrate Octopods → 37**
36b. Fins absent and cirri absent . . . . . **Incirrate Octopods → 39**

37a. Web attaches directly to arms . . . . . **Family Opisthoteuthidae** (Fig. 84)
37b. Contractile intermediate membrane ('secondary web') present between each arm and the primary web . . . . . **→ 38**

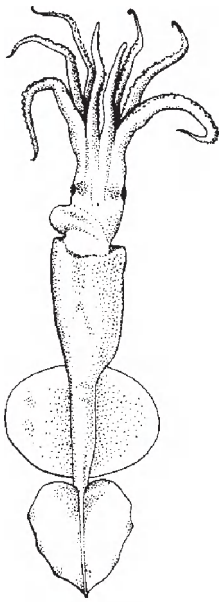


Fig. 82 Grimalditeuthidae (*Grimalditeuthis*)

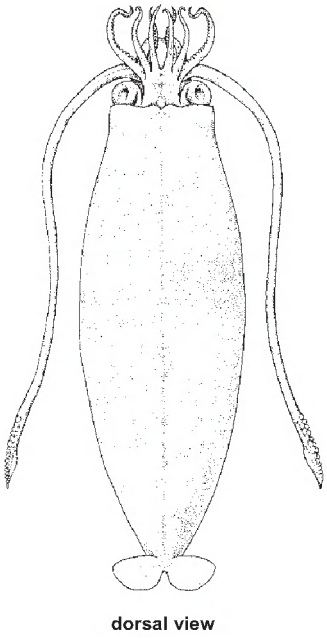


Fig. 83 Cranchiidae (*Helicocranchia*)

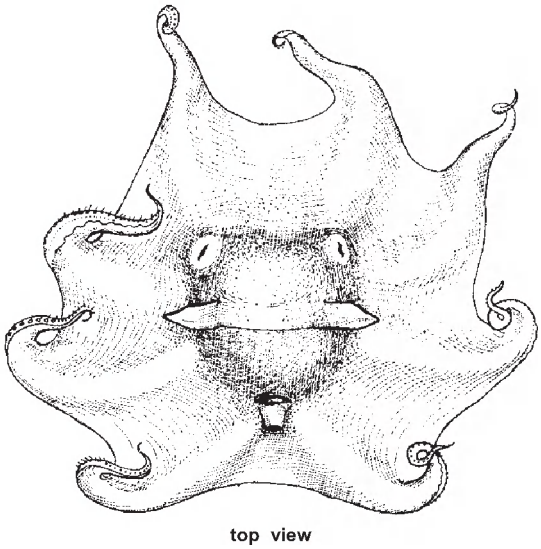


Fig. 84 Opisthoteuthidae (*Opisthoteuthis*)

38a. Shell (cartilaginous fin support) simple, U-shaped . . . . . **Family Stauroteuthidae** (Fig. 85)
38b. Shell more complex, with expanded fin-attachment areas . . . . . **Family Cirroteuthidae** (Fig. 86)

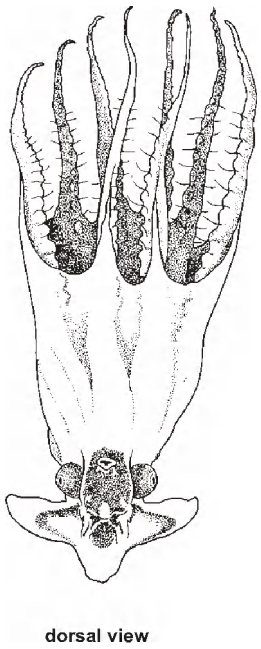


Fig. 85 Stauroteuthidae (*Stauroteuthis*)

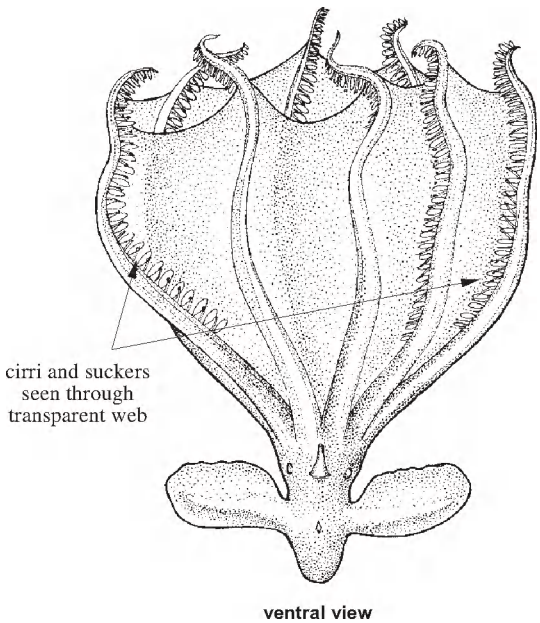


Fig. 86 Cirroteuthidae (*Cirrothauma*)

39a. Muscle tissue of body gelatinous, often transparent in life . . . . . → **40**
39b. Muscle tissue of body firm (may be covered by gelatinous subdermal layer) . . . . . → **43**

40a. Suckers biserial distal to edge of web (Fig. 87) . . . . . **Family Alloposidae**
40b. Suckers uniserial along entire length of arms (Fig. 88) . . . . . → **41**

41a. Eyes tubular, mantle fused to funnel base forming 2 openings to mantle cavity (Fig. 89) . **Family Amphitretidae**
41b. Eyes not tubular, though not necessarily round, single opening to mantle cavity . . . . . → **42**

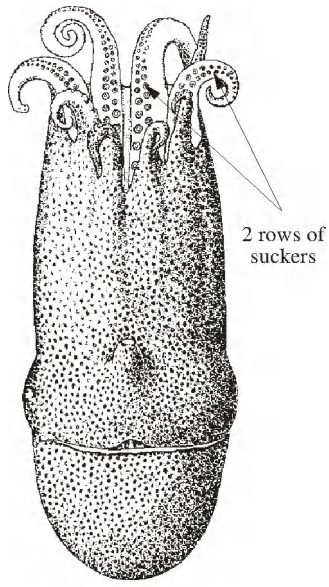


Fig. 87 Alloposidae (*Alloposus*)

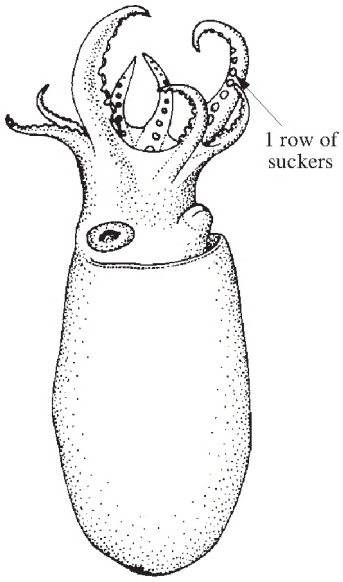


Fig. 88 Bolitaenidae (*Japetella*)

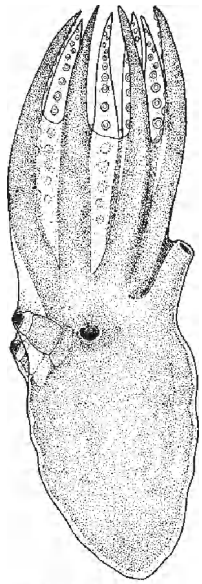


Fig. 89 Amphitretidae (*Amphitretus*)

42a. Digestive gland very elongate, spindle-shaped, pointed at one end . . . . . **Family Vitreledonellidae** (Fig. 90)
42b. Digestive gland oblong, not pointed at end . . . . . **Family Bolitenidae** (Fig. 88)

43a. Funnel-locking apparatus absent; water pores on head absent; males not very much smaller than females, with left or right ventrolateral arm hectocotylized (never in pocket), with spoon-shaped, non-filamentous tip; females without dorsal arm flaps or permanent reticulate sculpturing of ventral mantle . . . . . **Family Octopodidae** (Fig. 91)
43b. Funnel-locking apparatus present; dwarf males very much smaller than females; hectocotylus (left or right ventrolateral arm) temporarily coiled in sac below eye, with extremely long filamentous tip . . . . . → **44**

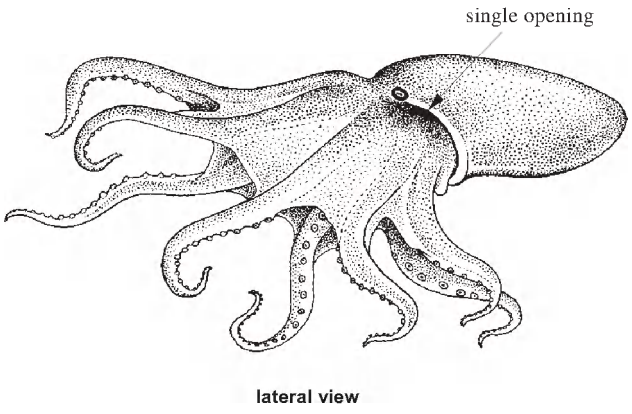


Fig. 90 Vitreledonellidae (*Vitreledonella*)

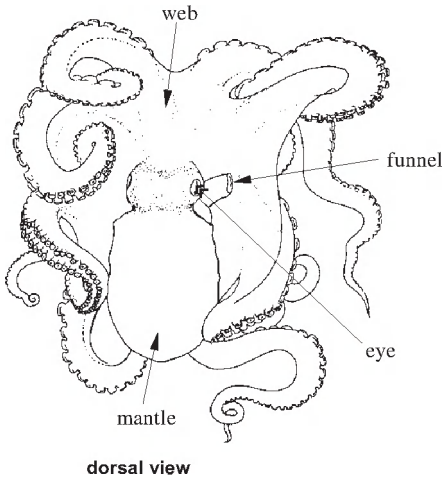


Fig. 91 Octopodidae (*Octopus*)

44a. Water pores present on head at bases of both dorsal and ventral arms; dorsal and dorsolateral arms of females joined by very deep, thin web . . . . . **Family Tremoctopodidae** (Fig. 92)

44b. Dorsal water pores absent; web, when present, not as above . . . . . → **45**

45a. Females with broad, membranous flap that secretes and holds a thin, shell-like egg case; males with hectocotylus in non-stalked sac beneath eye . . . . . **Family Argonautidae** (Fig. 93)

45b. Females with permanent reticulate sculpturing on ventral mantle; dorsal (first) arms of females lack broad, membranous flap; no shell-like egg case; males with hectocotylus in stalked sac beneath eye (Fig. 94) . . . **Family Ocythoidae**

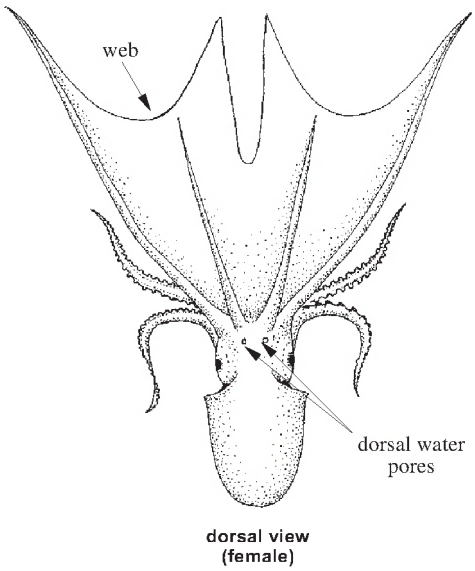


Fig. 92 Tremoctopodidae (*Tremoctopus*)

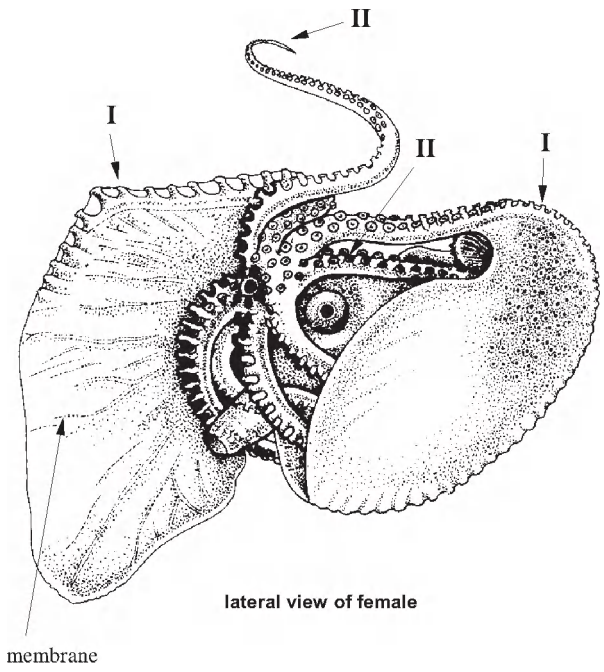


Fig. 93 Argonautidae (*Argonauta*)

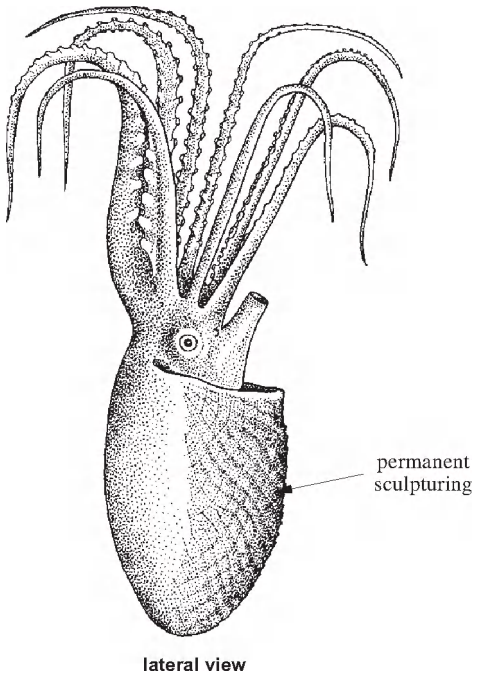


Fig. 94 Ocythoidae (*Ocythoe*)

2. CHAMBERED NAUTILUSES

by Patrizia Jereb

Living nautiluses are limited to a few species belonging to 1 family and 2 genera: the sole survivors of a once extremely specious subclass. They are unique among living cephalopods in possessing a coiled, pearly, external shell (Fig. 95). This is punctuated with chambers and the animal lives in the outermost chamber with its body attached to the sides of the chamber by the adductor muscles. This outermost chamber is connected to the innermost (apical) chamber by a tube (ectosiphuncle or siphuncular tube) which contains a core of tissue (endosiphuncle). Together, the tube and the internal tissue form the *siphuncle*, which serves as a wick to remove the fluid from the chambers. This enables the animal to regulate its buoyancy through control of fluid and gas in the chambers. Nautiluses have up to 47 pairs of circumoral arm-like appendages, also called 'tentacles', arranged in 2 rings around the mouth and 2 pairs lateral to the eyes. These appendages lack suckers and have several different sensory functions. Above the tentacles is a large fleshy wedge, called the 'hood'. This is used as a trapdoor to seal the shell closed if the animal is attacked. On each side, between the hood and the tentacles, are the eyes, which are simple and lack lenses, so that seawater flows in and out. Below the tentacles is a rolled flap of skin which acts as a funnel, enabling jet propulsion powered by the large adductor muscles that contract, pulling the body into the shell like a piston.

Until recently, our knowledge of these 'living fossils' was limited. They were thought to be rare animals occurring at only a few remote Pacific island sites. Now they are known to occur through much of the tropical Indo-Pacific region, where they live close to the bottom, primarily over reef slopes, from near the surface to about 500 m depth. Scavengers and opportunistic predators, they seem to compete successfully with deep-water crustaceans and fishes.

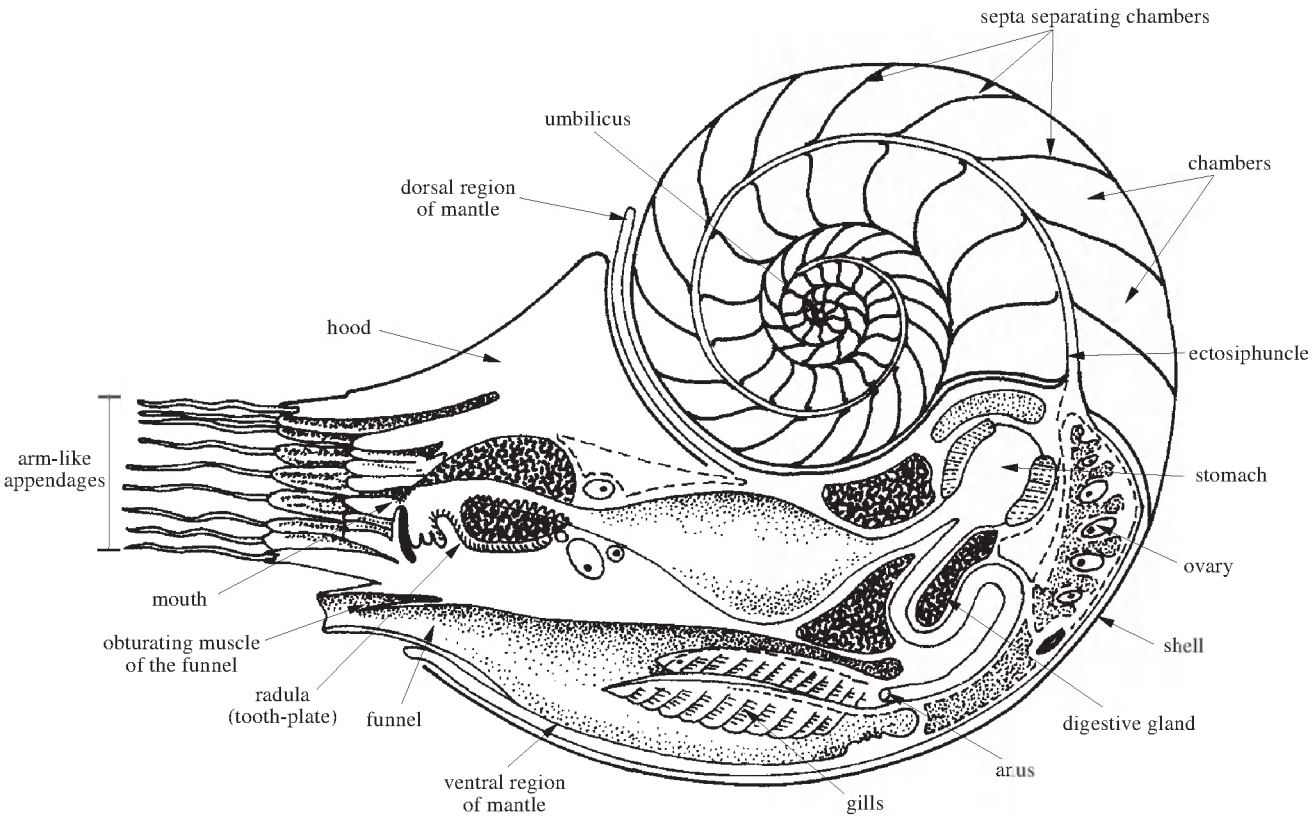


Fig. 95 Schematic cross-section of a *Nautilus*

2.1 Family NAUTILIDAE de Blainville, 1825

Nautilidae de Blainville, 1825, *Manuel de Malacologie et de Conchologie*, 647 pages, Paris, 386.

FAO Names: En – Chambered nautiluses; **Fr** – Nautiles; **Sp** – Nautilos.

Diagnostic Features: Coiled, pearly, external shell punctuated with chambers; **2 pairs** of gills; **up to 47 pairs of arm-like appendages** around mouth; **suckers and hooks lacking**; eyes simple, without lenses; funnel (or infundibulum) consisting of 2 lobes which fold together to form a tube-like structure. Chromatophores and ink sac absent. Shell compressed and involute to umbilicate and even perforate. An umbilical callus may be present. Shell sculpture of sinuous growth lines and possibly fine spiral ridges in some species. Shell coloration variable by species. Irregular red to yellow-brown stripes typically radiate from the umbilicus; they cover the entire shell in juveniles, but are restricted to the dorsal, chambered, portion of shell in adults. Shell broader and larger in mature males than in mature females. Radula with 13 elements, including 2 lateral teeth and 2 inner marginal support plates not seen in coleoids; jaws with calcite denticulation. Four tentacles in males fused to form the spadix, used to transfer spermatophores to females during copulation. Males are larger than females.

Size: Shell up to 229 mm in diameter, average animal weight up to 1 675 g. Shell size varies depending on species and geography.

Habitat and Biology: Nautiluses are primarily mobile benthic bottom dwellers, associated with coral reefs, ranging from near the surface to about 500 m depth, but their optimal range seems to be from 150 to 300 m. Factors controlling the upper limits include predation by fishes and temperature: temperatures exceeding 25°C may be lethal for these animals. This explains why most shallow water sightings of nautiluses occur at night and during cold seasons. Maximum depth limits are determined by shell implosion (about 800 m) and chamber flooding (about 300 to 400 m). Males outnumber females and both live for many years after maturity is reached at an estimated age of 5 to 15 years. Recent mark-recapture studies indicate that nautiluses may live for more than 20 years. Growth is slow and no more somatic growth occurs after the animals reach sexual maturity. Egg capsules have not been seen in natural habitats, but in captivity eggs are laid singly, attached to hard substrates and take up to 14 months to hatch in warm water (21° to 24°C). It is hypothesized that in nature they are laid in relatively shallow water (80 to 100 m) and that after hatching the young move to deeper, colder waters. The egg, similar in shape and size to a whole garlic, is equipped with 1 or 2 capsules, separated by a narrow space full of seawater. The outer shell is white, tough but flexible, and provided with a series of small holes that allow seawater to circulate between the 2 capsules. In aquaria, young hatchlings feed almost immediately on shrimp or other food items. Decapod crustaceans seem to be a standard food for adults, but echinoid fragments, fish bones, coleoid beaks and nautilus tentacles have also been observed in the crops of examined animals. Nautiluses are highly mobile; tagged animals have been seen to move over 150 km in one year. They also move to shallow waters at night and return to deeper waters during the day, where, however, they remain active.

Interest to Fisheries: At least 2 of these species are of commercial value as food, largely at the artisanal and subsistence levels, and nautilus shells are sold commercially in the shell trade (e.g. in Indonesia, Fiji, New Caledonia, and the Philippines). Nautiluses are also collected alive for public display and home aquaria and for research. They are caught using baited fish traps.

Remarks: Although 11 species have been named within the genus ***Nautilus***, only 4 are well established and can be distinguished by differences in shell and (in some instances) soft part morphology: ***Nautilus belauensis***, ***N. macromphalus***, ***N. pompilius*** and ***N. stenomphalus***. One species, ***N. repertus***, has questionable status. Recently, Ward and Saunders (1997) erected a new genus, ***Allonautilus***, for the most unusual member of the group, ***A. scrobiculatus***, and one morphologically similar, but extremely rare, and not well known form, ***A. perforatus***.

Literature: Flower (1964), Solem and Roper (1975), Saunders (1981a), Roper *et al.* (1984), Saunders (1987), Saunders and Landman (1987), Saunders (1998), Ward and Saunders (1997), Norman (2000).

Key to genera in the family Nautilidae

1a. Umbilicus small, or moderate, i.e. from 5 to about 16% of shell diameter; whorl cross-section oval (Fig. 96) . . . ***Nautilus***

1b. Umbilicus larger, approximately 20% of shell diameter; whorl cross-section quadrate (Fig. 97) . . . . . ***Allonautilus***

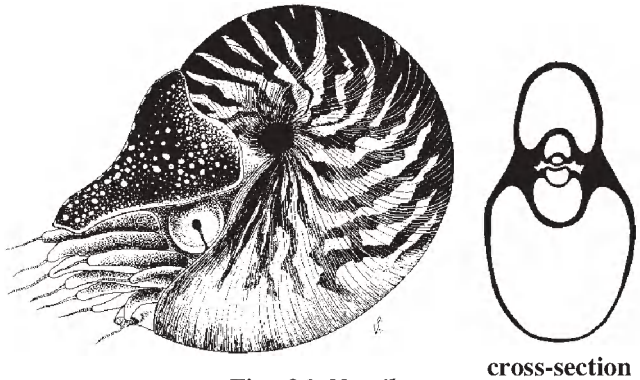


Fig. 96 *Nautilus*

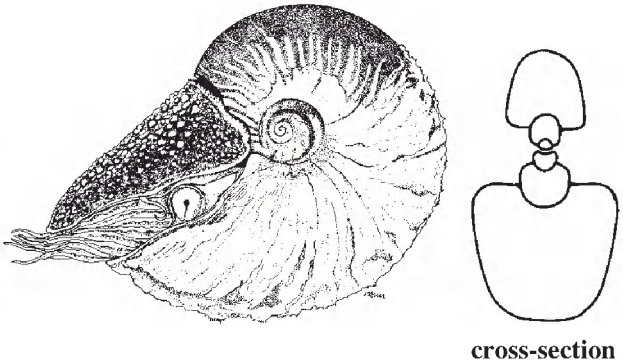


Fig. 97 *Allonautilus*

Nautilus macromphalus Sowerby, 1849 **Fig. 98**

Nautilus macromphalus Sowerby, 1849. Monograph of the genus *Nautilus*. *In*: *Thesaurus Conchyliorum*, 2: 463–465 [type locality: unknown].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Bellybutton nautilus; **Fr** – Nautile bouton; **Sp** – Nautilo ombligo.

Diagnostic Features: Umbilicus open, a deep, round shouldered concavity, approximately 15 to 16% of shell diameter at its widest point; inner coils of the shell visible. No thickened layer (callus) present.

Size: Maximum shell diameter around 160 mm.

Geographic Distribution: Southwestern Pacific Ocean; live animals known only from off northeastern Australia, New Caledonia and Loyalty Islands, while drift shells have been recorded as far south as Lizard Island, Queensland (eastern Australia) (Fig. 99).

Habitat and Biology: *Nautilus macromphalus* inhabits continental shelf and slope waters associated with coral reefs, from the surface to a depth of about 500 m. In some areas of southern New Caledonia, this species rises to very shallow waters at night (i.e. less than 20 m depth), so divers can observe animals foraging.

Interest to Fisheries: Consumed locally, it is object of artisanal fishery. It also supports a small fishery for public and private aquaria and research trade. Collected alive at a depth of about 65 m on the outer slope of the barrier reef in New Caledonia; in the Coral Sea it is caught by traps, at depths between 300 and 400 m.

Literature: Dunning (1998), Saunders (1987), Norman (2000).

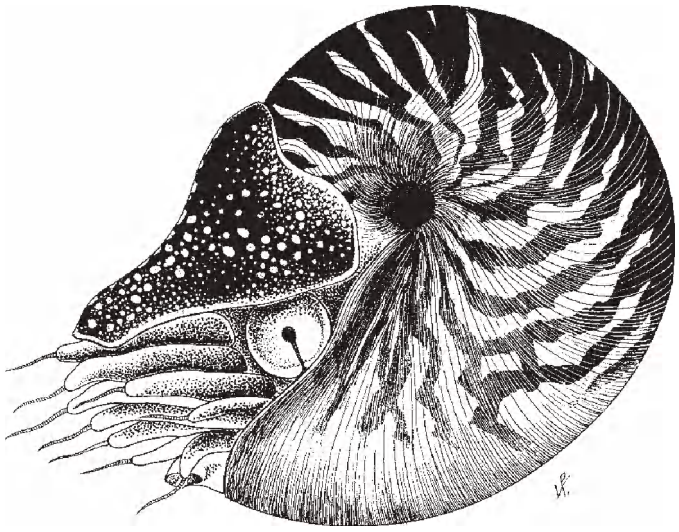


Fig. 98 *Nautilus macromphalus*

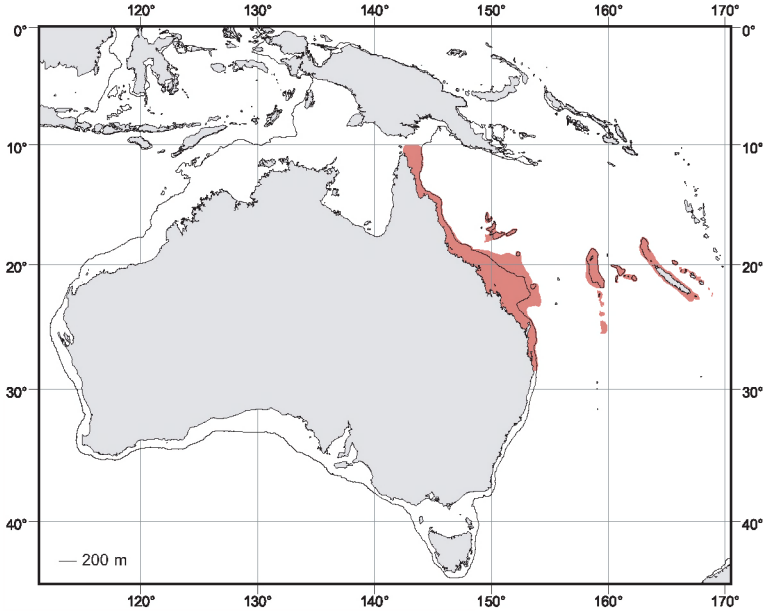


Fig. 99 *Nautilus macromphalus*
Known distribution

Nautilus pompilius Linnaeus, 1758 — Fig. 100; Plate I, 1–5

Nautilus pompilius Linnaeus, (1758). 'Systema Naturae.' 10 (1): 709. (Holmiae.) [=Stockholm] [Reprint Leipzig, 1894] [type locality: Ambon, Indonesia].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Emperor nautilus; **Fr** – Nautile flammé; **Sp** – Nautilo común.

Diagnostic Features: Umbilicus small, visible as shiny silver and black patch, closed; callus usually present (with rare exceptions). No inner coils visible. Shell colour patterns variable: irregular brown to reddish brown stripes radiate from the umbilicus to venter in the usual coloration, but this striping can be reduced to various degrees, leaving the umbilicus and even much of the flanks white.

Size: Shell diameters typically between 170 and 180 mm around Fiji and the Philippines, larger in the Western Australian population (i.e. mean diameter up to 222 mm).

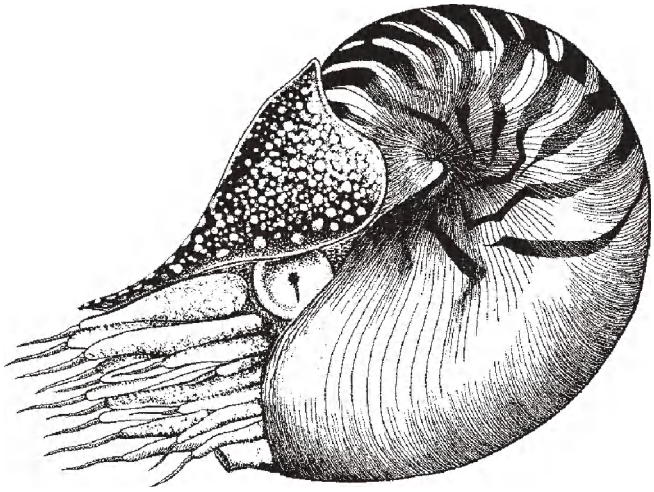


Fig. 100 *Nautilus pompilius*

Geographical Distribution: Indo-West Pacific; Andaman Islands, Ambon, the Philippines, New Guinea to Fiji; northeastern and northwestern Australia. Absent from around New Caledonia, where it is replaced by ***Nautilus macromphalus***. Sympatric with ***Allonautilus scrobiculatus*** off New Guinea and ***Nautilus stenomphalus*** off northeastern Australia. Replaced by ***Nautilus belauensis*** around Palau (Fig. 101).

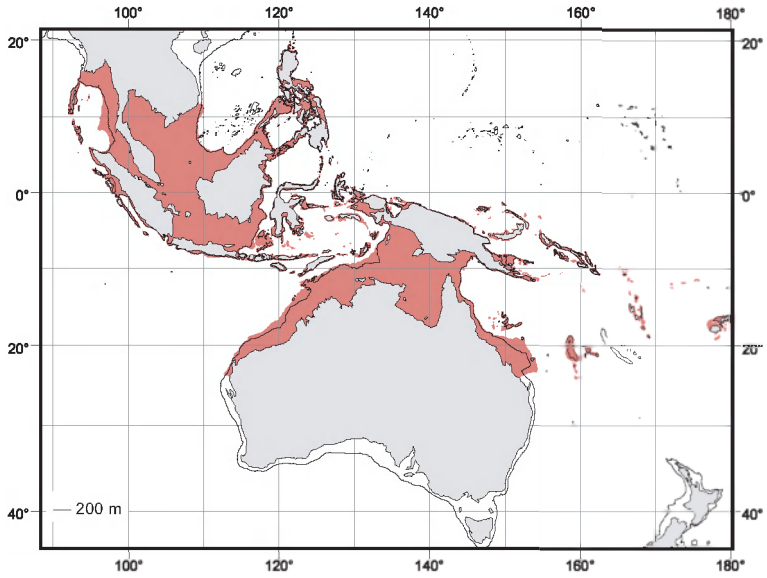


Fig. 101 *Nautilus pompilius*
Known distribution

Habitat and Biology: ***Nautilus pompilius*** is the most widely distributed and best known ***Nautilus*** species. It inhabits deeper continental shelf and slope waters around coral reefs, from near the surface to a depth of about 750 m. The species has been bred in captivity and animals are frequently kept in public aquaria.

Interest to Fisheries: This species supports a substantial shell trade, mostly from beach-drift specimens, and subsistence and artisanal fisheries. Captured in bamboo fish traps at depths from 60 to 240 m, the meat is sold in local markets and the shells go to the shell trade. The outer layers of the shells are sometimes removed, leaving the outer surface a silvery mother-of-pearl layer.

Remarks: The Western Australian population includes the largest specimens known, with a mean shell diameter of 222 mm and mean weight of 1 675 g. Here, shell striping varies from the typical form to reduced yellowish stripes that leave the umbilicus and flanks white. The questionable species ***N. repertus*** was described by Iredale (1944) on the basis of its large size (about 228 mm shell diameter) and the reduced orange-brown coloration observed on 2 drifted specimens from Western Australia. Historically, this has not generally been considered adequate to distinguish the species, given the considerable range in variation in both shell size and colour pattern in ***N. pompilius***. However, increasing documented evidence of variation in shell colour pattern and dimensions between different regions, suggests that ***Nautilus pompilius*** populations are isolated from each other, and may, at least, represent distinct subspecies. The application of recently developed biochemical and genetic analysis may shed light on the validity of ***N. repertus*** and on the possible existence of ***N. pompilius*** subspecies. Northern Australian records of animals with shells up to 240 mm in diameter may represent an additional related species.

Literature: Saunders and Davis (1985), Saunders (1987), Saunders and Ward (1987a), Swan and Saunders (1987), Dunning (1998), Saunders (1998).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Nautilus belauensis Saunders, 1981

Plates I, 6 and II, 7–9

Nautilus belauensis Saunders, 1981, A new species of *Nautilus* from Palau, *The Veliger*, 24(1): 1–7, 3 plts, 2 text figs [type locality: Palau, Western Caroline Islands].

Size: Shell diameter to 226 mm, animal weight to around 1308 g. The second largest species of ***Nautilus***.

Geographical Distribution: Palau, Western Caroline Islands.

Remarks: The first species bred in aquaria.

Literature: Saunders,1981b, Saunders and Spinosa (1978, 1979), Norman (2000).

Nautilus repertus Iredale, 1944

Nautilus repertus Iredale, 1944, Australian pearly *Nautilus*. *Australian Zoologist*, 10(3): 294–298 [type locality: Rottnest Island and Pelsart Island, Western Australia].

Size: Shell diameter up to 228 mm.

Geographical Distribution: Type locality and General distribution: Rottnest Island and Pelsart Island, Western Australia.

Remarks: Doubtful species. See Remarks in ***Nautilus pompilius***.

Literature: Dunning (1998), Saunders (1998), Norman (2000).

Nautilus stenomphalus Sowerby, 1849

Plate II, 10

Nautilus stenomphalus Sowerby, 1849. Monograph of the genus *Nautilus*. *In*: *Thesaurus Concyliorum*, 2: 463–465 [type locality: Great Barrier Reef, eastern Australia].

Size: Shell diameter to around 170 mm.

Geographical Distribution: Great Barrier Reef, eastern Australia.

Remarks: Very similar in size and weight to ***Nautilus pompilius***, from which it can be distinguished by the absence of the callus and the reduced coloration, lacking in the umbilicus region. The hood is covered by elevated papillae, in a very characteristic pattern. The first live captures were reported by Saunders and Ward (1987b).

Literature: Saunders and Ward (1987b), Saunders (1998), Norman, 2000.

Allonautilus scrobiculatus (Lightfoot, 1786) **Plate I, 4–5**

Nautilus scrobiculatus Lightfoot, 1786, A catalogue of the Portland Museum, lately the property of the Duchess Dowager of Portland, Deceased. London, 194 p. [Type locality: Ndrova Island, Manus, Papua New Guinea].

Size: Shell diameter to around 180 mm.

Geographical Distribution: Tropical western Pacific: Papua New Guinea, Manus Province, Bismark Archipelago and Milne Bay. Drift shells are known as far south as the Solomon Islands.

Remarks: The rarest and most distinctive species among nautiluses. Other than for the larger umbilicus, ***Allonautilus scrobiculatus*** differs from the other nautiluses in the very peculiar features of the shell, including creases and encrusting layer on the periostracum (see Fig. 97). Gills and male reproductive system also differ from those of ***Nautilus*** species.

Literature: Ward and Saunders (1997), Norman (2000).

Allonautilus perforatus (Conrad, 1847)

Nautilus perforatus Conrad, 1847, Notes on shells, with description of new genera and species. *Journal of the Academy of Natural Sciences*, Philadelphia, *Second Series*, 1: 210–214 [type locality: unknown].

Size: Shell diameter to around 180 mm.

Geographical Distribution: Bali, Indonesia.

Remarks: Very rare form of questionable validity, only known from shells. Shell very similar to that of ***Allonautilus scrobiculatus***.

Literature: Ward and Saunders (1997).

3. CUTTLEFISHES

by Amanda Reid, Patrizia Jereb and Clyde F.E. Roper

The families formerly referred to as belonging to the Order Sepioidea (Roper *et al.*, 1984), include the **Sepiidae**, which are of significant commercial value to artisanal and industrial fisheries; the **Sepiolidae**, which are exploited by many artisanal and subsistence fisheries; the **Sepiadariidae**, which are not fished at present (one species might be of potential interest); the **Idiosepiidae** and the **Spirulidae**, which are of no commercial interest. These families are treated herein as separate entities.[1/]

Cuttlefishes *sensu lato* are characterized by the following features: shell calcareous (***Sepia***, ***Spirula***) or chitinous (sepiolids); 10 circumoral appendages; 2 tentacles retractile into pockets; suckers with chitinous rings; posterior fin lobes free, not connected at midline; eye covered with a transparent membrane, false eyelids present (except ***Spirula***); 1 pair of gills, without branchial canal between afferent and efferent branchial blood vessels; digestive gland (liver) divided or bilobed; each tooth of radula with a single projection; buccal membrane present; olfactory organ a ciliated pit.

The combined catch of the exploited cuttlefishes made up about 12 to 16% of total cephalopod catches in the last 10 years, roughly fluctuating between 300 000 and over 500 000 metric tonnes (FAO, 2000). The most important genus exploited is ***Sepia***.

Table 6 summarizes the catch data available for the most important world fishing areas and identifies the major cuttlefish-harvesting countries, which also are the primary consumers and traders. These are mainly the southeast Asian countries, the northwest Indian Ocean regions and the nations that border the Mediterranean Sea. In spite of the progress made in the last decade to ensure the quality of data and information collected, many of the figures above should still be considered as very conservative, because the general tendency is to underestimate the artisanal component of landings, which in fact supports a conspicuous fraction of the fishery but usually is not properly recorded in national statistics.

In the industrial fisheries, cuttlefishes usually are taken only as bycatch to other target species in bottom trawls, even in cases where they make up a sizeable portion of the catch. In the artisanal fisheries, on the other hand, they are actively sought with highly selective gear and fishing techniques based on knowledge of the biology and behaviour of the species. Such techniques include the use of aggregation devices (e.g. light, substrates for egg deposition), live or artificial lures (for example, live sexually mature females are used to attract males), and a variety of fishing gear, such as harpoons, spears, trammel nets, pound nets, hoop nets, lines, jigs, baited pots, etc.

The flesh of most cuttlefishes is tender and excellent for human consumption, as well as in terms of nutrients and protein quality. It is marketed fresh, frozen, canned and dried ('surume').

Table 6
Cuttlefishes and bobtail squids captured in 2001 by FAO areas, showing the three leading countries in that year and their share of total area capture

Area	Country	2001	%
Atlantic, Eastern Central	Morocco	17 544	39
	China	8 238	18
	Mauritania	4 744	10
	Area 51 total	45 553	–
Atlantic, Northeast	France	13 814	72
	United Kingdom	2 705	14
	Portugal	1 348	7
	Area 27 total	19 310	–
Atlantic, Southeast	Spain	26	84
	Russian Federation	5	16
	Angola		0
	Area 47 total	31	–
Indian Ocean, Eastern	Thailand	20 819	57
	Malaysia	9 810	27
	Indonesia	5 360	15
	Area 57 total	36 516	–
Indian Ocean, Western	Yemen	9 330	42
	Pakistan	5 256	24
	Oman	3 854	17
	Area 51 total	22 086	–
Mediterranean and Black Sea	Tunisia	7 148	38
	Italy	6 131	32
	Greece	1 623	9
	Area 37 total	18 904	–
Pacific, Northwest	China	310 129	95
	Japan	8 297	3
	Taiwan Province of China	4 546	1
	Area 61 total	324 915	–
Pacific, Southwest	Australia	219	100
	Area 81 total	219	–
Pacific, Western Central	Thailand	44 122	67
	Malaysia	11 657	18
	Indonesia	7 850	12
	Area 71 total	65 766	–
Cuttlefishes and bobtail squids	**World Total**	**533 300**	

(Source: FAO, 2000)

[1/] The order of presentation of the sepioid families, *sensu lato*, in the text does not necessarily reflect phylogenetic or other systemic sequence.

3.1 Family SEPIIDAE Keferstein, 1866

by Amanda Reid, Patrizia Jereb and Clyde F.E. Roper

Sepiidae Keferstein, 1866, *Bronn's Klass. Ordn., Thierreichs*, 1862–66: 1441.

FAO Names : En – Cuttlefishes; **Fr** – Seiches; **Sp** – Sepias, Jíbias, Chocos, Choquitos.

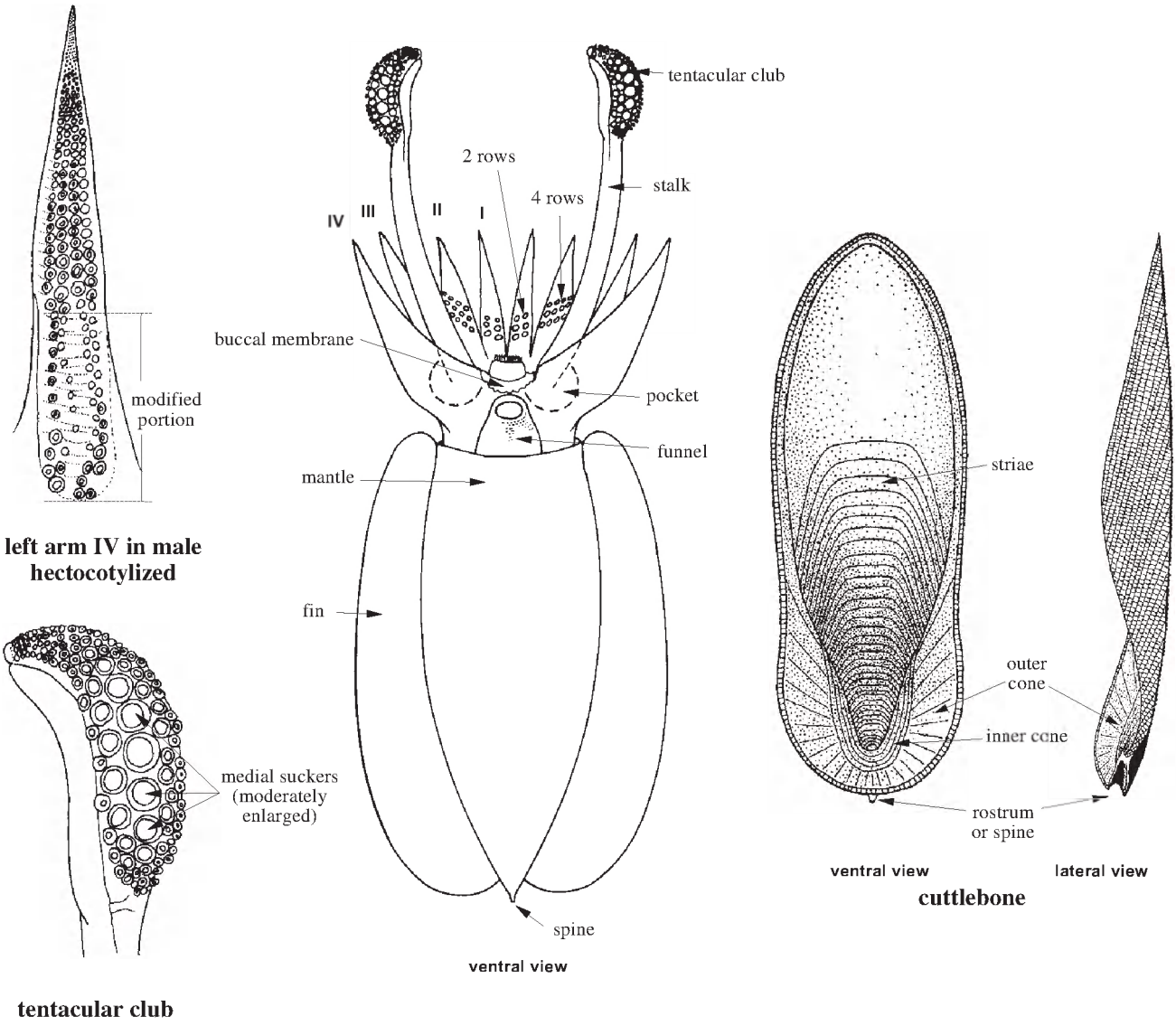


Fig. 102 Diagram of basic cuttlefish features

Diagnostic Features: Small to medium-sized cephalopods. Mantle robust, slightly flattened dorsoventrally, may be broad or slender; oval, oblong or nearly circular in outline; anterior dorsal mantle margin projected forward, not fused with head. Fins narrow, located dorsolaterally on mantle, approximately equal to mantle length; **posterior fin lobes free**, not connected to each other. Head robust, slightly narrower than mantle; eyes prominent, covered by a transparent membrane and a conspicuous secondary fold on the eyelid. Mouth surrounded by 10 appendages (8 arms and 2 tentacles). Arms with 2 to 4 suckers in transverse rows. Males of some species with hectocotylized ventral arm(s) IV for holding and transferring spermatophores; when present, the hectocotylus usually consists of a region of reduced suckers; hectocotylized region also may be swollen and crenulated by transverse folds. Tentacular clubs with 4 or more suckers in transverse rows; **tentacles retractile into pockets on the ventrolateral sides of the head between arms III and IV.** Arm and club suckers with chitinous rings. Mantle-locking apparatus angular or curved in shape. Internal **calcareous cuttlebone** located dorsally in the mantle underneath the skin; cuttlebone length usually equal to mantle length (***Metasepia*** is an exception); cuttlebone shape ranges from lanceolate to oval or diamond-shaped; dorsal side a calcareous plate (dorsal shield); ventral side finely laminate, porous, and comprised of thin, transverse septa supported by transverse calcareous rods. One pair of gills; no branchial canal between afferent and efferent branchial blood vessels. 'Liver' (digestive gland) divided or bilobed. Buccal membrane present, with or without suckers; each radula tooth unicuspid (with a single projection). Olfactory organ a ciliated pit.

Size: Up to 500 mm mantle length, and 12 kg in weight.

Habitat and Biology: Cuttlefishes inhabit the continental shelf and upper slope to a maximum depth of approximately 1000 m. They are primarily bottom-dwellers over a range of habitats, including rocky, sandy, and muddy substrates, seagrass, seaweed and coral reefs. They are slower swimmers than the more streamlined squids. Cuttlefishes are able to attain neutral buoyancy by regulating the relative amounts of gas and fluid in the chambers of the cuttlebone, and they are able to hover in midwater, with fins acting as stabilizers. The cuttlebone length, width, septal spacing and structural morphology are correlated to maximum habitat depth: the deepest living species known, including ***Sepia australis, S. elegans***, ***S. orbignyana*** and ***S. hieronis***, all are capable of descending to depths in excess of 400 m; all share the characteristics of cuttlebones with closely packed septa and modified sutures. Large species such as ***Sepia latimanus***, ***S. officinalis*** and ***S. pharaonis*** are restricted to much shallower depths, usually less than 200 m, and show very different septal spacing and sutures than the deeper water species. Some species migrate seasonally in response to temperature changes and aggregate, usually in shallow water, at spawning time. Within a species, individuals may attain sexual maturity at very different sizes, depending upon the combined effects of a number of factors including temperature, light and diet. Eggs, relatively few in number, are individually attached to various substrates in clusters; the time required for development depends upon temperature. The lifespan is between 18 and 24 months, although males of some species may live longer. Post-spawning mortality is high in females. Cuttlefishes feed on a wide range of invertebrates and bony fishes.

Literature: Hoyle (1886), Adam (1939a), Adam and Rees (1966), Roeleveld (1972), Adam (1979), Nesis (1987), Ward (1991), Oka *et al.* (1989), Okutani (1995), Khromov *et al.* (1998) and Lu (1998a).

Key to genera in the family Sepiidae

1a. Cuttlebone diamond-shaped in outline (Fig. 103); cuttlebone much shorter than mantle, located in the anterior 1/2 to 2/3 of mantle; dorsal anterior edge of mantle without tongue-like projection (Fig. 104a) . . . . . ***Metasepia***

1b. Cuttlebone outline elliptical to lanceolate; cuttlebone length approximately equal to mantle length; dorsal anterior edge of mantle usually with tongue-like projection (Fig. 104b) . . . . . → ***2***

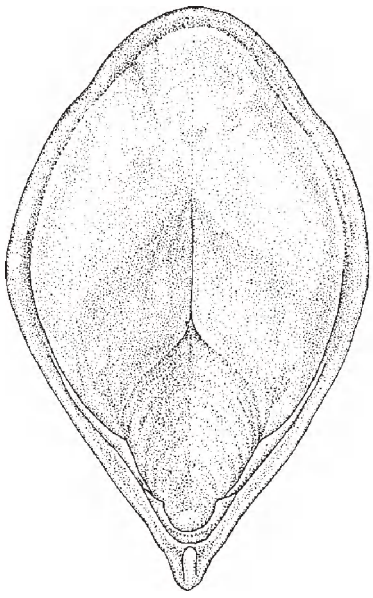
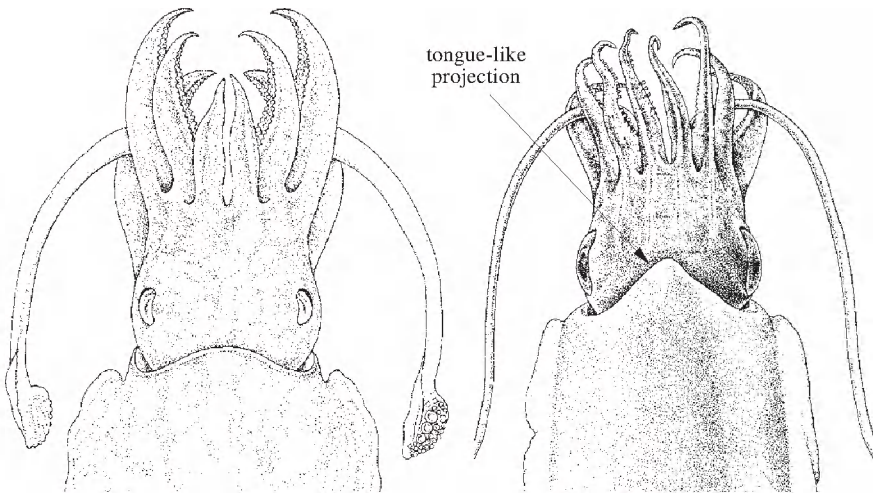


Fig. 103 *Metasepia pfefferi*
(illustration: K. Hollis/ABRS)



a) *Metasepia pfefferi* b) *Sepia, Sepiella*

Fig. 104 Head and anterior mantle (dorsal view)
(illustrations: K. Hollis/ABRS)

2a. A gland and gland pore located on the ventral side of the posterior end of the mantle (Fig. 105); mantle-locking apparatus with triangular projection (Fig. 106a); cuttlebone inner cone with very short limbs; outer cone a wide, spatulate, chitinized border around posterior end of cuttlebone (Fig. 107a) . . . . . ***Sepiella***

2b. Gland and gland pore absent; mantle-locking apparatus semicircular, without triangular projection (Fig. 106b); cuttlebone inner cone with relatively long limbs; outer cone usually calcareous, not obviously spatulate posteriorly (Fig. 107b) . . . . . ***Sepia***

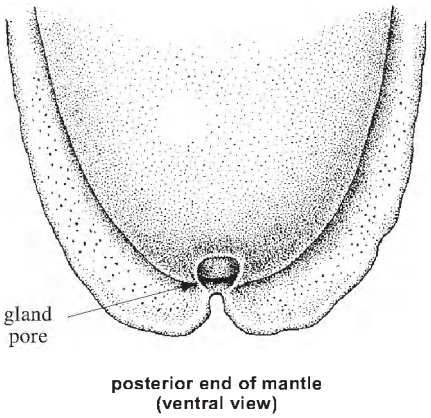


Fig. 105 *Sepiella*
(illustration: K. Hollis/ABRS)

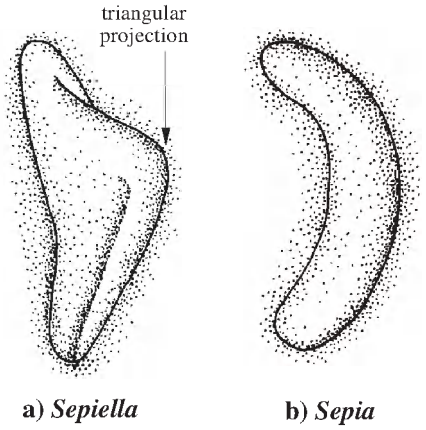


Fig. 106 Mantle-locking apparatus

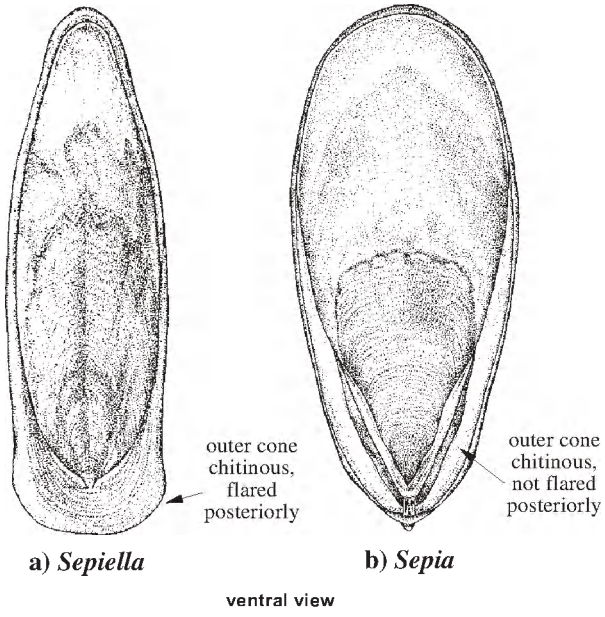


Fig. 107 Cuttlebones
(illustrations: K. Hollis/ABRS)

Metasepia pfefferi (Hoyle, 1885) **Fig. 108; Plate II, 11**

Sepia (Metasepia) pfefferi Hoyle, 1885, *Annals and Magazine of Natural History*, Series 5, 16: 199 [type locality: Challenger Stn. 188, 09°59'S 139°42'E, South of Papua, Arafura Sea].

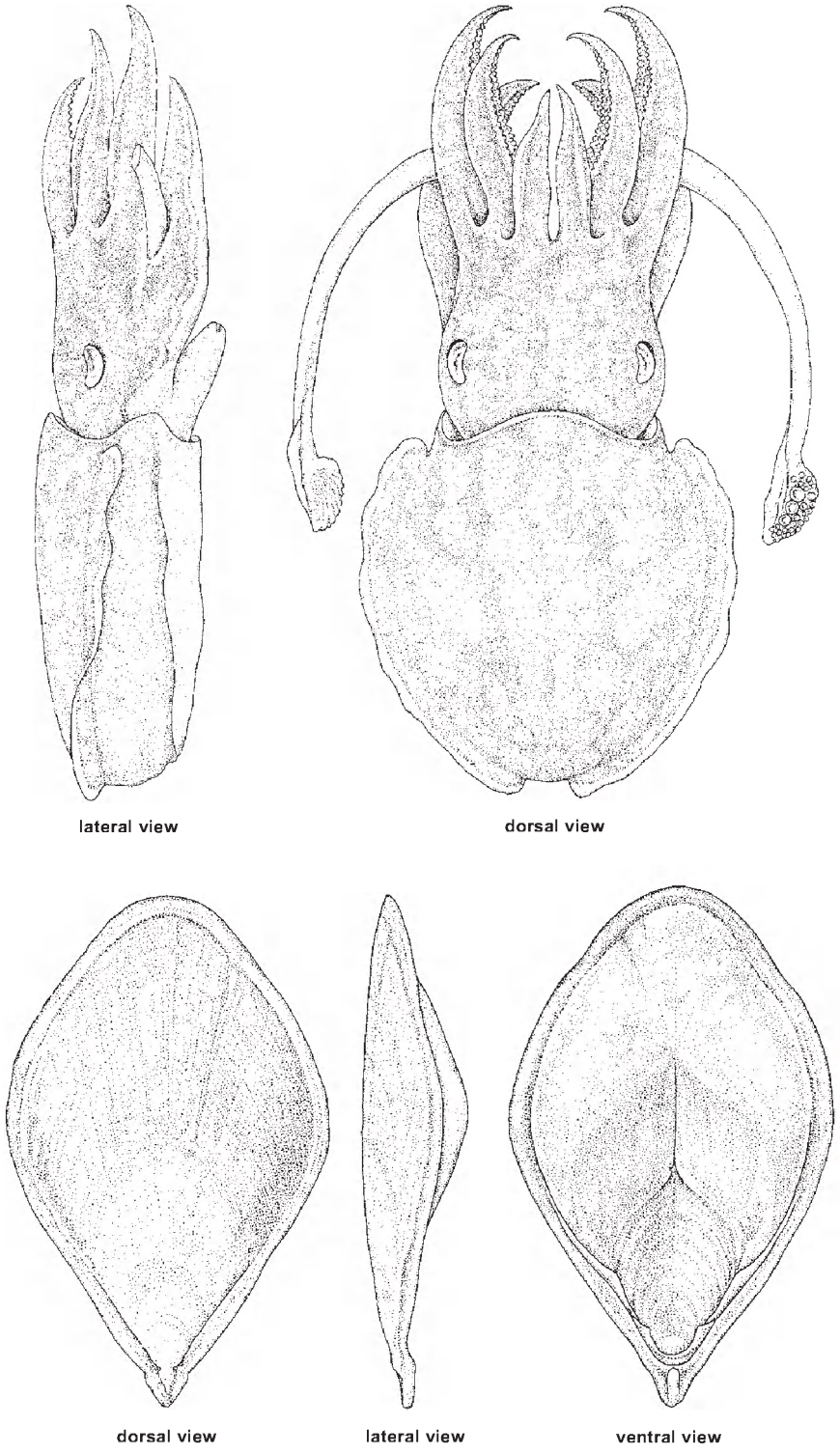
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Flamboyant cuttlefish; **Fr** – Seiche flamboyante; **Sp** – Sepia llamativa.

Diagnostic Features: Mantle oval, very broad. Arms **broad, blade-like; arms I shorter than rest**. Protective membranes in both sexes narrow. Arm suckers tetraserial. Hectocotylus present on left ventral arm: oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges and deep median furrow. Club sucker-bearing surface flattened, with **5 or 6 suckers in transverse rows**; suckers differ markedly in size: **3 or 4 median suckers greatly enlarged, occupying most of median portion of club**. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes **not joined at base of club** but fused to tentacular stalk. Dorsal and ventral membranes **differ in length**; extend proximal to carpus along stalk. Dorsal membrane forms shallow cleft at junction with stalk. Cuttlebone much shorter than mantle, located **in anterior 2/3 to 3/4 of mantle**; outline **rhomboidal**; acuminate, **acute, anteriorly and posteriorly**; dorsal surface yellowish, evenly convex; texture smooth, not pustulose; dorsal median rib absent. Chitin present as a **thin film over entire dorsal surface of cuttlebone**. Spine **absent, or small, chitinous**. Striated zone concave; last loculus strongly convex, thick in anterior third; sulcus deep, wide, extends along striated zone only. Anterior striae are inverted V-shape; limbs of inner cone are very short, uniform width, narrow, U-shape thickened slightly posteriorly; outer cone absent. Dorsal mantle has **3 pairs of large, flat, flap-like papillae**. Head with **papillae over eyes**. **Colour:** Base colour of dark brown with mobile patterns of white and yellow; purple-pink along arms.

Size: Up to 60 mm mantle length.



cuttlebone

(illustrations: K. Hollis/ABRS)

Fig. 108 ***Metasepia pfefferi***

Geographical Distribution: Tropical Indo-Pacific: northern Australia from Mandurah, Western Australia, 32°33'S 115°04'E, northeastward to Moreton Bay, southern Queensland, 27°25'S 151°43'E. New Guinea (Fig. 109).

Habitat and Biology: Depth range from 3 to 86 m. Sand and muddy substrate. Active during the day, hunting fishes and crustaceans. Capable of excellent camouflage while stalking prey. If disturbed or attacked, it quickly changes to a dramatic colour pattern of dark brown, black, white and yellow patches and may show bright red on the arm tips. It has been observed to 'amble' along the sea floor in this colour pattern, rhythmically waving the wide protective membranes on the arms. Eggs are laid singly in crevices or ledges in coral, rock or wood. One female has been observed squeezing her eggs through the hole of a coconut husk. The round white eggs turn clear as they develop. Juveniles are capable of the same bright colour pattern as adults from birth.

Interest to Fisheries: None as food. But this species is spectacular in its colour and textural displays and would make an excellent aquarium species.

Literature: Adam and Rees (1966), Roper and Hochberg (1987), Roper and Hochberg (1988), Lu (1998a).

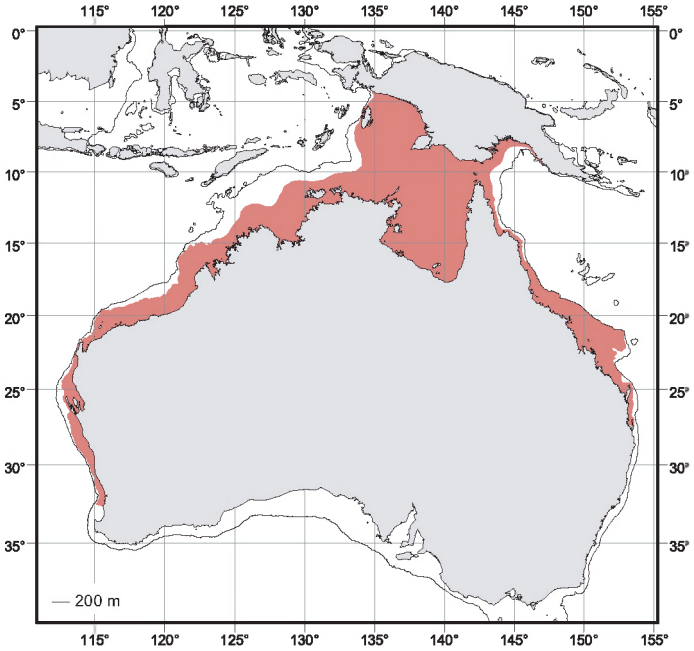


Fig. 109 ***Metasepia pfefferi***
Known distribution

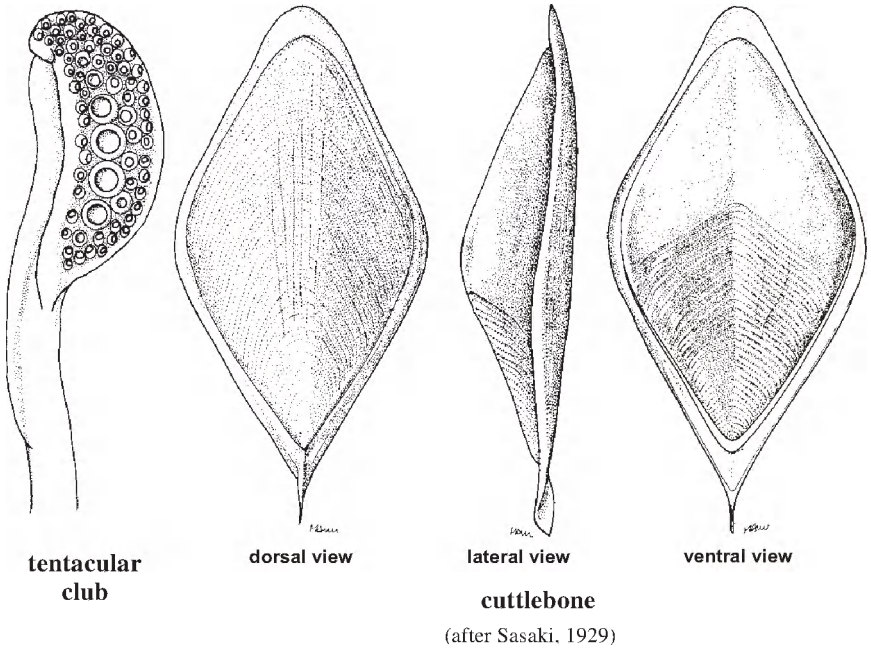
Metasepia tullbergi (Appellöf, 1886) **Fig. 110**

Sepia tullbergi Appellöf, 1886, *Svenska Vetenskaps-Akademiens Handlingar*, 21(13): 26 [type locality: Japan, Nagasaki].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Paintpot cuttlefish; **Fr** – Seiche encrier; **Sp** – Sepia tintero.



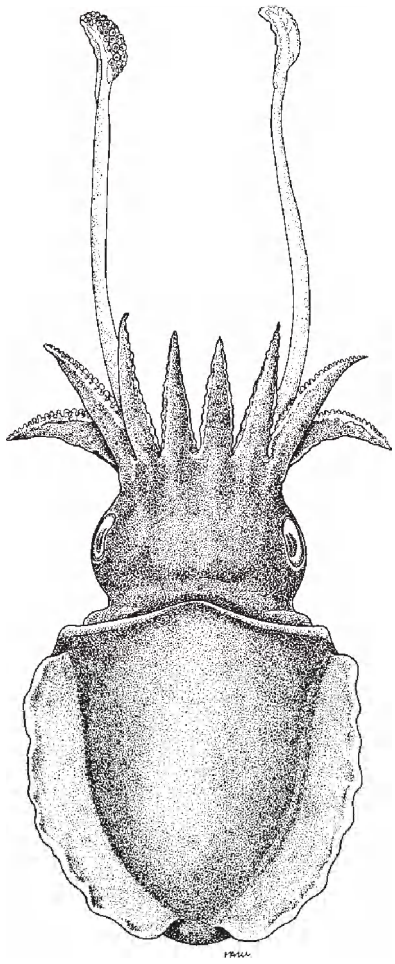


Fig. 110 ***Metasepia tullbergi***

Diagnostic Features: Mantle broad, oval. Ventral surface of mantle with 10 to 13 pores on each ventrolateral surface. Fins joined posteriorly. Arm suckers tetraserial. Hectocotylus present on left ventral arm: suckers normal proximally, 10 to 12 rows reduced suckers medially, followed by some enlarged suckers, then reduced suckers to arm tip; reduced suckers much smaller than normal arm suckers. Oral surface of modified region is wide, swollen, fleshy, and has transversely-grooved ridges. Suckers of hectocotylus in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Club crescent-shaped, sucker-bearing surface flattened, with 4 to 6 suckers in transverse rows; suckers differ markedly in size: **4 or 5 suckers in second dorsal series enlarged and 3 or 4 suckers in third series from dorsal side slightly enlarged**. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes not joined at base of club; dorsal membrane broad, much wider than ventral membrane. Cuttlebone much shorter than mantle, located in anterior 2/3 to 3/4 of mantle; outline rhomboidal, broad; bone strongly convex in lateral view; acuminate, acute, anteriorly and posteriorly; dorsal surface evenly convex. Chitin present as a thin film over entire dorsal surface of cuttlebone; bone extends posteriorly into **sharp spine with chitinous plate on dorsal side**. Cuttlebone nearly completely chitinized anteriorly, calcareous posteriorly; sulcus shallow, narrow, extends along striated zone only; limbs of inner cone are very short; outer cone absent. Head and dorsal and lateral mantle rugose with numerous papillae and tubercles; pair of broken longitudinal ridges on dorsum. Dorsum dark in colour lateral to fleshy ridges, with **bright yellow patches on head**, dorsal mantle and arms. Protective membranes on arms red.

Size: Up to 70 mm mantle length, from 30 to 40 g total weight.

Geographical Distribution: Indo-Pacific: Japan from southern Honshu, Sea of Japan, Yellow Sea, East China Sea to Taiwan Province of China and Hong Kong, South China Sea, Philippines, Gulf of Thailand (Fig. 111).

Habitat and Biology: Depth range from 20 to 100 m. This neritic demersal species occurs on the continental shelf on sandy to muddy substrate; it also has been collected from among sea pens on rocky substrate. Eggs hatch in summer in rocky areas at about 20 m depth. Hatchlings migrate to deeper, sandy-mud areas (down to 80 m) in August to September; mature individuals migrate to shallower rocky areas from March to May to spawn.

Interest to Fisheries: Currently there is no known fishery for this small, colourful species, but it does occur occasionally as bycatch. Its relevance in artisanal fisheries is undetermined. If its supply were steady, it undoubtedly would be a popular, colourful aquarium species.

Local Names: CHINA: Mak dau; JAPAN: Hana-ika.

Literature: Okutani *et al.* (1987), Nomura *et al.* (1997).

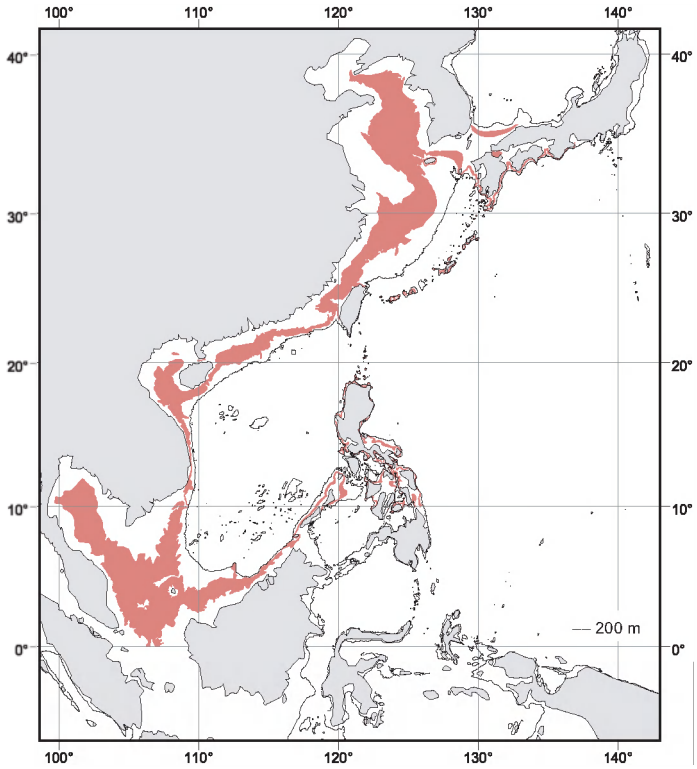


Fig. 111 *Metasepia tullbergi*
Known distribution

NEXT PAGE

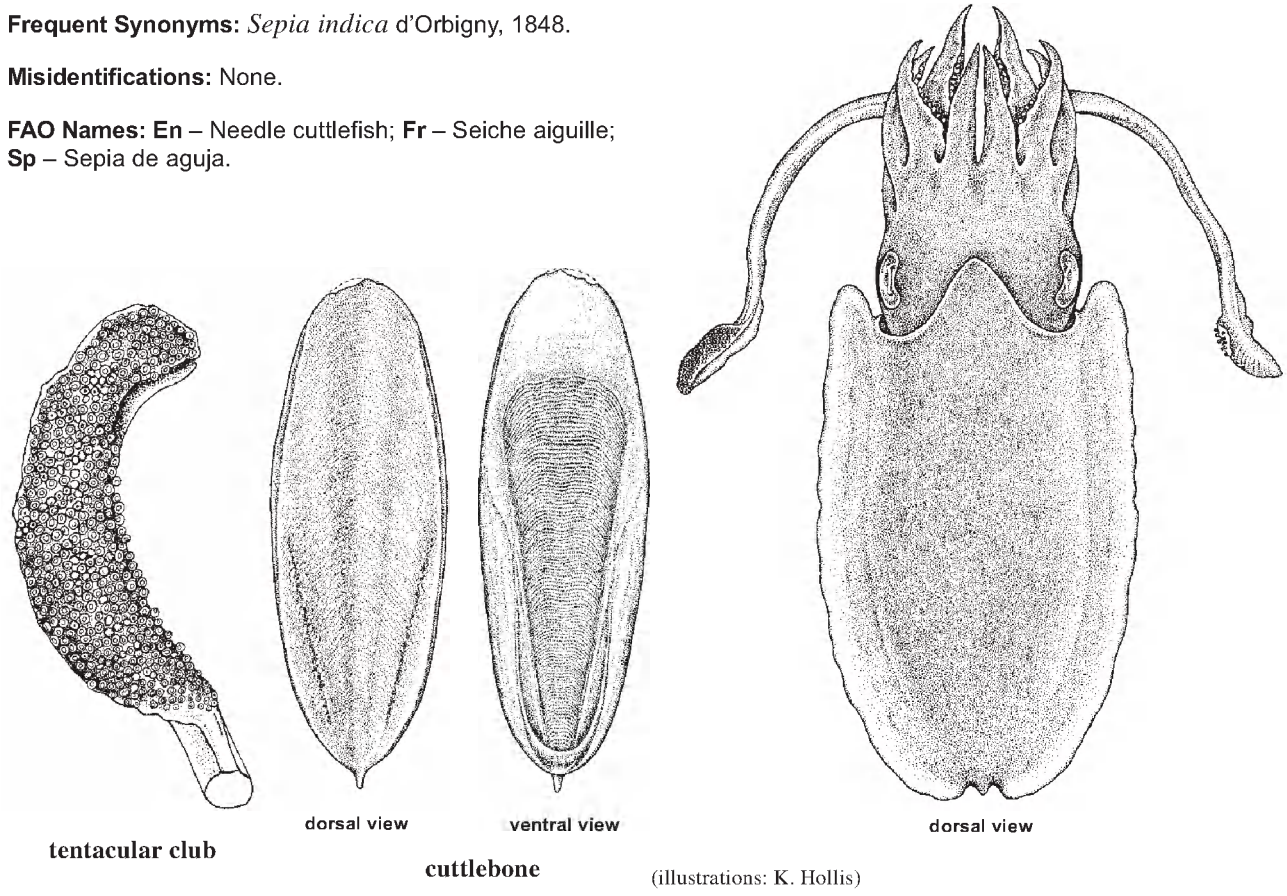
Sepia aculeata Van Hasselt, 1835 (*in* Férussac and d'Orbigny, 1834–1848) **Fig. 112; Plate II, 12–14**

Sepia aculeata Van Hasselt, 1835, pl. 5 bis (*in* Férussac and d'Orbigny 1834–1848), *Histoire naturelle générale et particulière des Céphalopodes Acétabuliferes vivants et fossiles* [type locality: Java].

Frequent Synonyms: *Sepia indica* d'Orbigny, 1848.

Misidentifications: None.

FAO Names: En – Needle cuttlefish; **Fr** – Seiche aiguille; **Sp** – Sepia de aguja.



(illustrations: K. Hollis)

Fig. 112 ***Sepia aculeata***

Diagnostic Features: Mantle oblong. Male and female arm lengths subequal. Hectocotylus present on left ventral arm: 3 rows of normal size suckers proximally, 5 or 6 rows of reduced suckers medially, then normal size suckers to arm tip. Suckers of hectocotylus in **the 2 dorsal series are much smaller than those in the 2 ventral series**; suckers in both dorsal and ventral series displaced laterally, with gap between; arm with deep median furrow in adults. Club sucker-bearing surface convex; **males with 10 to 12, females with 13 or 14** club suckers in transverse rows; all club suckers of **similar, minute, size**. Dorsal and ventral protective membranes not joined at base of club, extend proximal to carpus along stalk. Buccal membrane with a few minute suckers. Cuttlebone with distinct dorsal median and lateral ribs. Chitin present as wide glaze-like patch posteriorly; a narrow chitinous rim borders lateral margins of cuttlebone. Spine long, pointed, without keel. Anterior striae are **inverted U-shape**. Inner cone limbs are **narrow anteriorly, broaden posteriorly, then are raised into a thick, round ledge**; outer cone narrow anteriorly, broadens posteriorly. Dorsal mantle with longitudinal row of up to 8 ridge-like papillae and associated, numerous, large papillae along each side, adjacent to base of each fin. Head and arms with scattered, small tubercles. Colour of preserved specimens pale brownish. Dorsal mantle has white blotches, spots or patches, or it has a transverse saddle mark, or a fine, darkly pigmented, transverse reticulate pattern. Fins with **pale reflective line along base**. Live animals are light brown. Arms I to III have a longitudinal orange-red pigmented stripe along their aboral surfaces. Dorsal mantle with pale transverse saddle mark and pattern of bold, broad, zebra stripes during the spawning season; 3 circular, white patches occur mid-dorsally within transverse saddle mark; posteriormost patch composed of a ring of white spots.

Size: Maximum mantle length 230 mm; weight 1.3 kg.

Geographical Distribution: Indo-Pacific: India (Arabian Sea north to off the Gulf of Kutch) to the Andaman Sea and Gulf of Thailand, South China Sea, Taiwan Province of China, East China Sea, Indonesia and possibly the Timor Sea (Fig. 113).

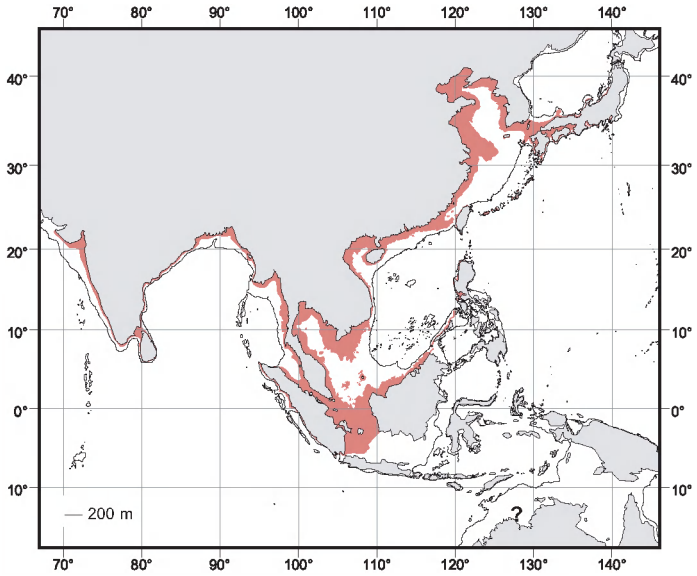


Fig. 113 ***Sepia aculeata***

Habitat and Biology: ***Sepia aculeata*** is a demersal, neritic species that occurs to 60 m depth. Along the Indian coasts maturing and mature animals are present throughout the year, which indicates a prolonged spawning and breeding season; activity peaks occur from January to April and in the second half of the year in the eastern waters, and in April, July and December in the southwestern waters, off Cochin. In the Hong Kong area, a prespawning concentration occurs on the continental shelf, followed by movement inshore to spawn at depths of 5 to 20 m from March to May at water temperatures of 18° to 24°C. In the Gulf of Thailand, spawning occurs all year at depths of 10 to 50 m, with March to April and July to September the peak months. Smallest mature individuals in this region and in the Bay of Bengal (eastern Indian Ocean) were found at 70 mm mantle length, while size at 50% maturity varies between 75 and 100 mm for males and 100 and 120 mm for females, respectively. In the Arabian Sea (western Indian Ocean) the size at 50% maturity is a little higher, i.e. over 120 and 130 mm for males and females, respectively. Growth rates are similar in females and males and the sex ratio is 1:1. Commercially caught animals from the Gulf of Thailand and the Andaman Sea range between 60 and 130 mm mantle length, those caught from the east coast of India range between 50 and 190 mm and on the west coast females of 200 mm mantle length also are captured.

Interest to Fisheries: This species is the thirdmost important commercial cuttlefish around Hong Kong where it is caught with setnets and seines during the spawning season. It is also one of the most important commercial cuttlefish in southwest India, where is mainly caught by trawl, with peak landings in October and November. The species is fished commercially in southern China, Taiwan Province of China, Sri Lanka and Thailand, where it is caught by otter trawl, pair trawl, squid light-lures, traps and push nets. Captures by traps in Thai waters are most abundant in January and February, when most animals are fully mature and females are predominantly caught.

Local Names: CHINA: Jam Mak Yue; JAPAN: Ami-mom-nkouika.

Literature: Adam and Rees (1966), Silas *et al.* (1986), Siraimeetan (1990), Chotiyaputta (1993), Rao *et al.* (1993), Chantawong and Suksawat (1997), Chotiyaputta and Yamrungreung (1998), Nateewathana (1999).

Sepia andreana Steenstrup, 1875 — Fig. 114

Sepia andreana Steenstrup, 1875, *Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 10(7): 473 [type locality: Japan, Hakodate].

Frequent Synonyms: None.

Misidentifications: *Sepia kobiensis* Hoyle, 1885.

FAO Names: En – Andrea cuttlefish; **Fr** – Seiche andreana; **Sp** – Sepia andreana.

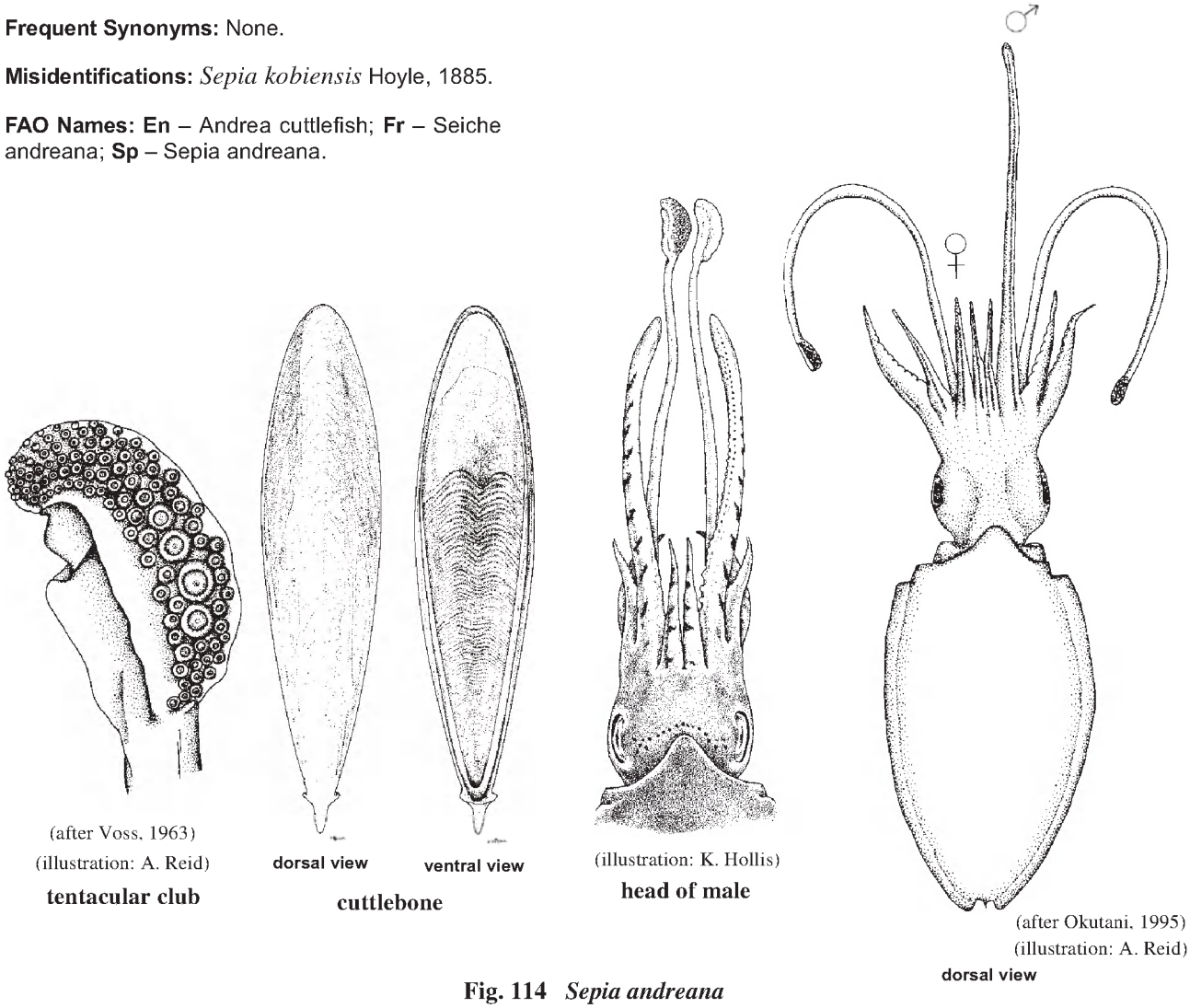


Fig. 114 *Sepia andreana*

Diagnostic Features: Mantle oblong; dorsal anterior margin triangular, acute; ventral mantle margin emarginate. Fins narrow, end in small, auriculate lobes posteriorly, with a small V-shape interstice where posterior spine is located. Male arms II **greatly elongate, 3 times longer than other arms** (except in young specimens), and **bluntly rounded distally**, not tapered. Female arm lengths subequal. Arm sucker arrangement differs between sexes. In males, sucker rows on modified arms II tetraserial on proximal third, biserial distally, becoming rudimentary and sparse at tips; arms I and III tetraserial proximally, biserial only on extreme distal arm tips; arms IV suckers tetraserial. In females, suckers on arms I tetraserial proximally, biserial on slightly expanded distal tips; arms II and III tetraserial proximally, distal third with biserial suckers, arms IV suckers tetraserial; female distal biserial suckers minute, displaced laterally, with gap between, and with distinct medial gap between rows. Hectocotylus present on left ventral arm: 10 rows of normal size suckers proximally, **distal half of arm with rudimentary suckers** on swollen peduncular bases. Club crescent-shaped, sucker-bearing surface convex with **5 or 6 suckers in transverse rows**; suckers differ in size: **4 or 5 slightly enlarged suckers** in longitudinal series towards posterior end of club. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club** but fused to tentacular stalk, terminate at posterior end of carpus. Dorsal membrane forms deep cleft at junction with stalk. Buccal membrane without suckers; in females extends ventrally with 2 spermathecae. Cuttlebone outline **lanceolate**; dorsal median rib indistinct; spine straight; striated zone and last loculus convex; sulcus shallow, narrow, extends entire length of cuttlebone. Anterior striae **shallow m-shape**; inner cone narrow, U-shape; outer cone limbs are expanded posteriorly into 2 short 'wings', directed ventrally, to form a recurved cup-like structure. Dorsal mantle with a longitudinal row of approximately 6 ridge-like papillae along each side, adjacent to base of each fin. **Colour:** Pale brownish. Arms II have oblique bands of chromatophores, **arms I to III have a longitudinal orange-red pigmented stripe along their aboral surfaces**. Dorsal mantle has yellow spots and chromatophores concentrated medially above cuttlebone. Ventral mantle pale with a narrow, longitudinal, iridescent band on each side adjacent to fins.

Size: Up to 120 mm mantle length, 200 g total weight.

Geographical Distribution: Western Pacific: Japan (Pacific coasts of southern Hokkaido, Tsugaru Strait, northern and central Honshu), Japan Sea, Yellow Sea, along south China coast, South China and East China Seas to northern Philippines. (Fig. 115).

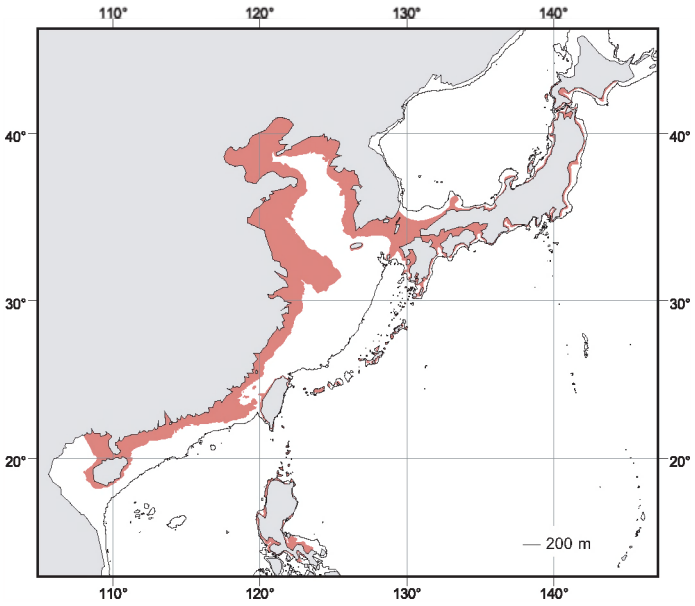


Fig. 115 ***Sepia andreana***
Known distribution

Habitat and Biology: Depth to 50 m. This demersal species occurs in coastal waters. In the Yellow Sea the spawning season is very long, with two spawning peaks, one in spring and one in autumn, the main spawning occurring in March and April. It feeds on fishes and small crustaceans.

Interest to Fisheries: Taken as bycatch in trawl and setnet fisheries. It consistently supports a fishery in the Yellow Sea.

Remarks: ***Sepia andreana*** may be confused with ***S. kobiensis*** Hoyle, 1885. Mature male ***S. andreana*** can be distinguished by the greatly elongate second arm pair, with biserial, rather than tetraserial, suckers on the distal half. All arms are of similar length in ***S. kobiensis*** and suckers on all arms are tetraserial. The hectocotylus sucker arrangement differs between the two species: ***Sepia andreana*** has 10 proximal rows of normal size suckers, and the remainder of the arm has rudimentary suckers on swollen peduncular bases; ***Sepia kobiensis*** has 6 to 12 series of normal suckers proximally, 7 to 10 series medially are reduced, with those on the distal remainder of the arm normal in size. The club suckers differ only slightly in size in ***S. kobiensis***, while in ***S. andreana*** they differ markedly in size. Adult ***Sepia kobiensis*** are also slightly smaller. ***Sepia andreana*** was misidentified in Voss (1963) and Roper *et al.* (1984). The species referred to in those works could be ***S. kobiensis***. ***Sepia andreana*** lives in cooler water than the distributions in these publications would suggest.

Literature: Okutani *et al.* (1987), Cheng (1997), Kubodera and Yamada (1998).

Sepia apama Gray, 1849 **Fig. 116; Plate III, 15–20**

Sepia apama Gray, 1849, *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Antepedia*, 103 [type locality: South Australia, Port Adelaide, 34°50'S 138°30'E].

Frequent Synonyms: *Sepia palmata* Owen, 1881; *Amplisepia verreaux* (non Rochebrune, 1884) Iredale, 1926; *Amplisepia parysatis* Iredale, 1954.

Misidentifications: None.

FAO Names: En – Giant Australian cuttlefish; **Fr** – Seiche géante australienne; **Sp** – Sepia gigante australiana.

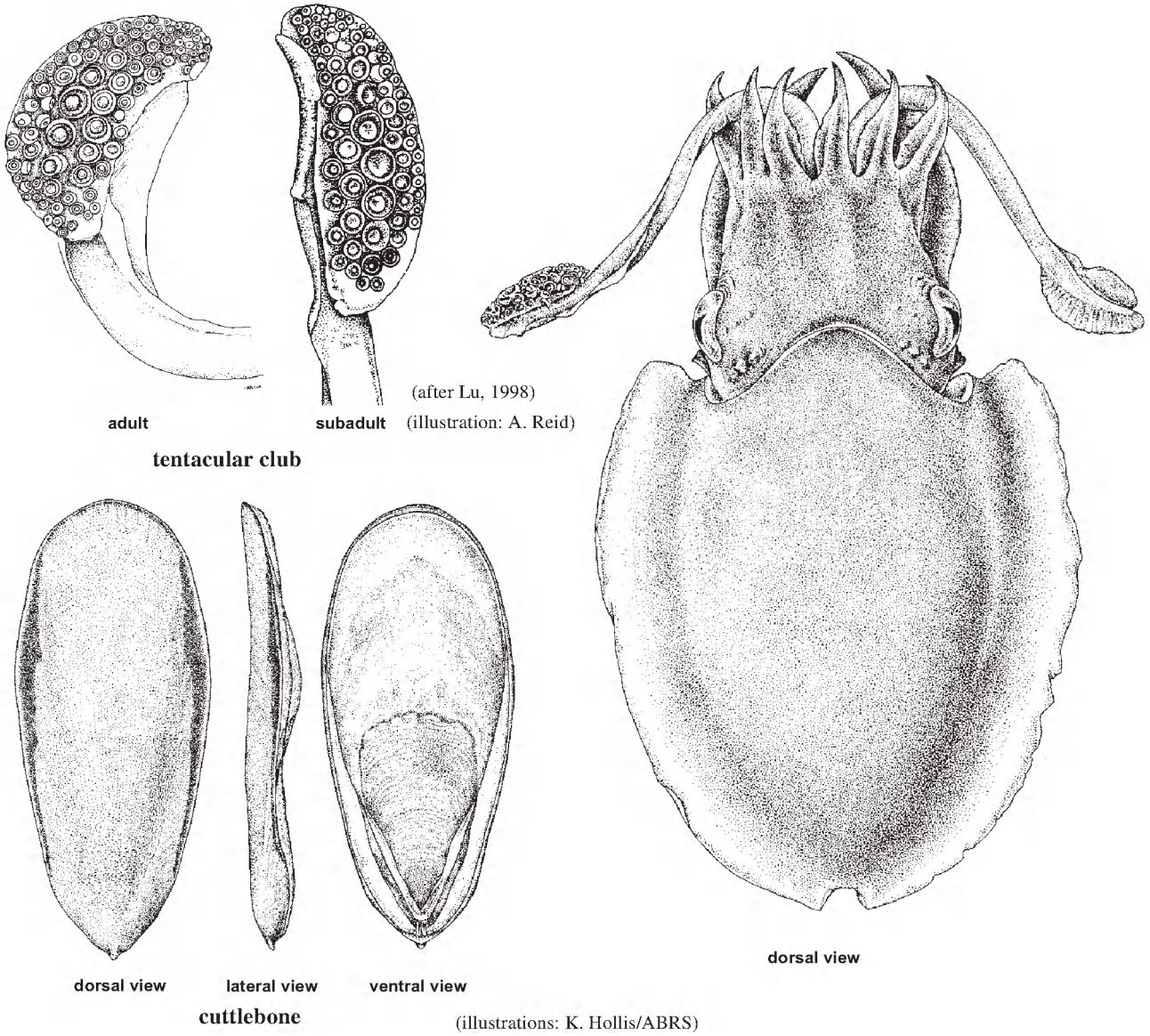


Fig. 116 ***Sepia apama***

Diagnostic Features: Very large, robust species. Mantle broadly oval. Fins wide, extend anteriorly slightly beyond mantle margin, rounded posteriorly, with wide gap between them. Funnel long, broad-based, extends to level of anterior rim of eye. Funnel organ dorsal elements inverted V-shape, with a small anterior papilla; ventral elements oval with acute anterior tips. Head short, broad, narrower than mantle. Male and female arms subequal in length; protective membranes wide, well developed. Arm suckers tetraserial. Hectocotylus present on left ventral arm: proximal end of arm with **6 to 10 rows of slightly reduced, equal sized suckers**; oral surface of modified region not wide, fleshy, but normal, as on opposite arm. Club crescent-shaped, moderate length; sucker-bearing surface flattened, with **4 or 5 suckers in transverse rows**; suckers differ markedly in size: **some median suckers greatly enlarged**; dorsal marginal longitudinal series of suckers slightly larger than those in ventral marginal series. Swimming keel of club very broad, extends well proximal to carpus; dorsal and ventral protective membranes joined at base of club; separated from stalk by membrane; dorsal membrane

forms shallow cleft at junction with stalk. Buccal membrane without suckers; in females with single median spermathecae in ventral part. Eggs spherical. Cuttlebone outline oval, or oblong (juveniles broadly oval, wider in anterior half, becoming elongate in adults); bone bluntly rounded anteriorly; acuminate, rounded posteriorly; dorsal surface creamy white, evenly convex posteriorly, flat anteriorly; dorsal surface slightly granulose with irregular longitudinal ridges; indistinct dorsal median rib present in large specimens, broadens anteriorly, bordered laterally by indistinct grooves; lateral ribs indistinct. Chitin borders lateral and anterior margins of cuttlebone. Spine present in juveniles, lost in adults. Striated zone flat, or slightly concave; last loculus flat in large animals, or convex in smaller ones; shallow, wide, sulcus extends along striated zone only, or sulcus absent. Anterior striae are **inverted U-shape in smaller specimens, becoming straight in large specimens**. Inner cone limbs are narrow anteriorly, broaden slightly posteriorly; in large specimens **thickened into rough callus** on inner margin of outer cone, which narrows anteriorly, broadens posteriorly. **Three flat, semicircular, flap-like papillae** posterior to eyes. **Colour:** Reddish brown. All arms have whitish transverse bars and spots bordered by darker pigment. Dorsal mantle with fine, irregular, reticulate, white bands and spots, some fused to form irregular transverse bands; bands joined laterally into longitudinal broken white band adjacent to fins. Fins pale, with narrow white band along outer margin.

Size: Maximum size up to 500 mm mantle length and weight in excess of 10.5 kg. This is the worlds' largest cuttlefish.

Geographical Distribution: Southern Indo-Pacific: southern Australia from Moreton Bay 27°25'S 153°20'E, possibly as far north as Shoalwater Bay, Queensland (22°30'S) to Point Cloates, Western Australia (22°43'S 113°40'E). Lord Howe and Norfolk Islands. Australian endemic (Fig. 117).

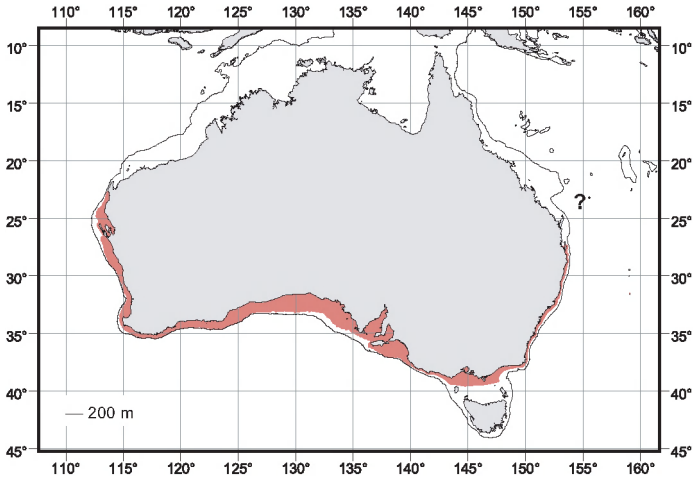


Fig. 117 ***Sepia apama***
Known distribution

Habitat and Biology: Depth range from 1 to 100 m. ***Sepia apama*** is a neritic demersal species with cryptic habits; it occurs in coral areas, seagrass beds and on open trawl grounds. It feeds on fishes, crabs and other crustaceans. During a highly ritualized and stereotyped courtship, males display broad bands of dark chromatophores that pulsate across the dorsal mantle as part of their visual display. Males often guard females to ward off other males. Small males have been observed to mimic the coloration and behaviour of females, using this diversion to sneak close to females to mate with them without the awareness of the larger aggressive males. Mating takes place head-to-head and spermatophores are placed in the female's spermathecae on the buccal membrane ventral to the mouth. Southern Australian animals spawn from April to September. Mass spawning occurs in the Spencer Gulf from April to June, with peak spawning during May to June. The lemon-shaped eggs are laid in subtidal crevices and hatch after 3 to 5 months. Low incubation temperatures around 12°C (which mitigate potential problems of diffusive gas exchanges) may be a factor that limits the distribution of the species to cool southern waters.

Interest to Fisheries: The species is taken as bycatch in prawn and mixed species trawl fisheries, by hook-and-lines or speared by divers. It is commonly available in fish markets along the southern coast of Australia, sold for human consumption and as bait. Few details on quantities or origin of catches are available.

Local Names: AUSTRALIA: Giant Australian cuttlefish.

Remarks: Recent morphological and molecular analyses have shown that specimens of ***Sepia apama*** from the east coast and southern Australia comprise two very divergent populations. However, these populations are not geographically isolated. The data suggests that populations of ***S. apama*** may have been geographically isolated in the past and have come into secondary contact.

Literature: Adam and Rees (1966), Lu (1998a), Cronin and Seymour (2000), Norman (2000), Kassahn *et al.* (2003).

Sepia arabica Massy, 1916 **Fig. 118**

Sepia arabica Massy, 1916, *Records of the Indian Museum*, 12(part 5)(16): 228 [type locality: Laccadive Sea, 11°14'30"N 74°57'15"E and Persian Gulf, 26°20'N 53°54'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Arabian cuttlefish; **Fr** – Seiche d'Arabie; **Sp** – Sepia arábiga.

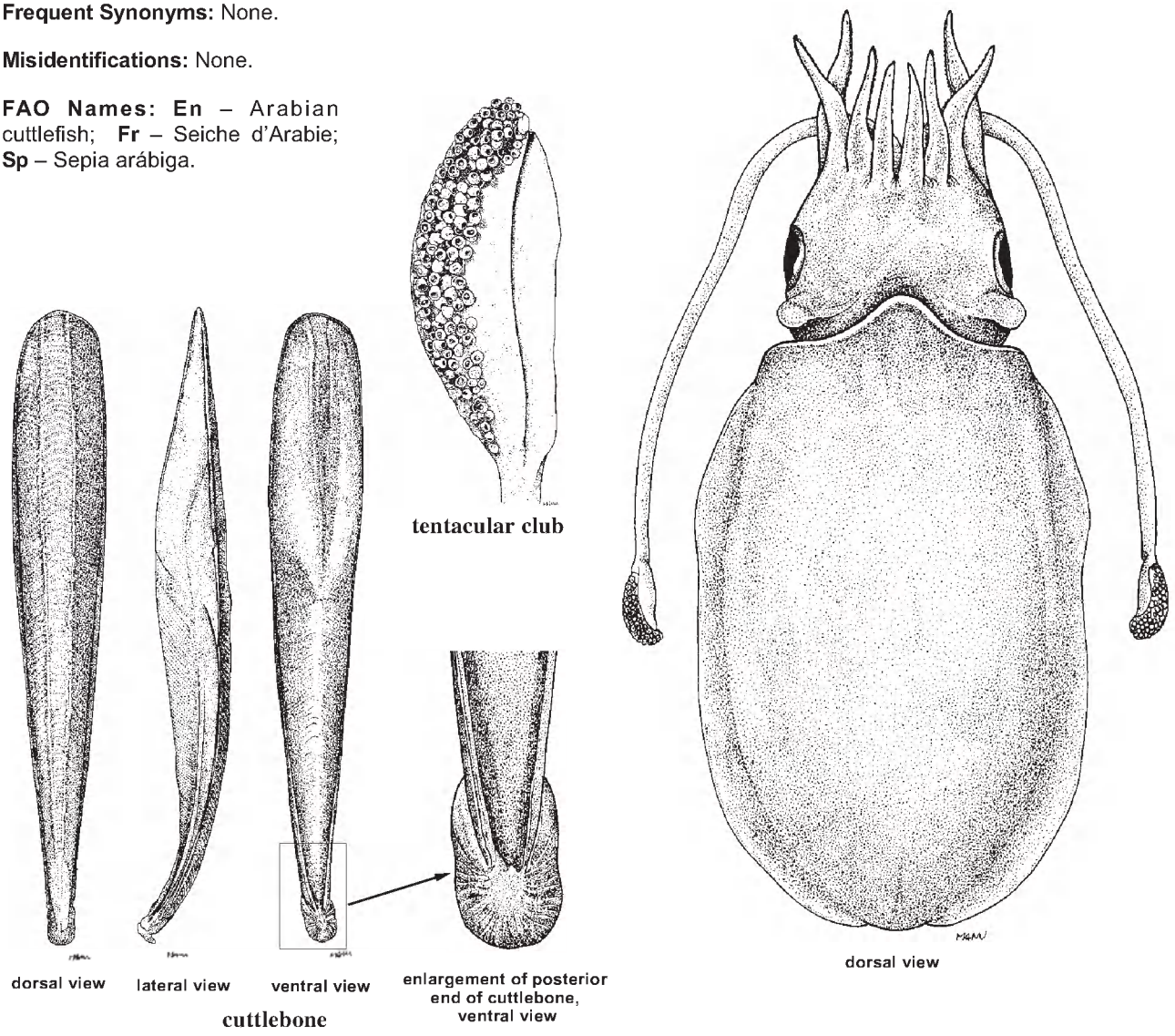


Fig. 118 *Sepia arabica*

Diagnostic Features: Mantle oval. Fins widest in posterior third; anterior origin posterior to mantle margin, posteriorly with wide gap between them. Head slender, narrower than mantle. Male and female arms subequal in length. Arm suckers tetraserial in both sexes, suckers small and widely spaced. Arm sucker rims smooth. Hectocotylus present on left ventral arm: with **greatly reduced suckers**, much smaller than normal arm suckers; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Both ventral arms of males with sucker-bearing surfaces folded together and nearly completely covered by the protective membranes. Club crescent-shaped, small; with **5 or 6 small, similar sized suckers** in transverse rows. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined** at base of club; dorsal membrane much wider than ventral membrane. Cuttlebone **outline lanceolate**; bone bluntly rounded anteriorly, **very narrow, strongly tapered posteriorly**; **recurved ventrally**; granulose dorsally; dorsal median rib indistinct, broadens anteriorly. Chitin present as wide bands bordering lateral sides of cuttlebone, extending to median rib. Spine absent; dorsoposterior end of cuttlebone with **short median longitudinal ridge**. Striated zone and last loculus convex; sulcus shallow, narrow, extends entire length of cuttlebone. Anterior striae **V-shape**; inner cone lateral limbs are separated from outer cone by smooth zones; inner cone limbs are uniform width, narrow V-shape posteriorly; slightly raised into rounded posterior ridge; inner cone posteriorly with irregular ribs radiating into outer cone (ribs calcareous medially and chitinous toward margin of outer cone); outer cone narrow anteriorly, broadens posteriorly; outer cone limbs are expanded into **2 rounded 'wings'**, directed ventrally, to form a recurved cup-like structure. Dorsal mantle has pale circular tubercles between median row of dark patches dorsal to base of fins and has a series of elongate papillae along each side, adjacent

to base of each fin. Head with **large, fleshy ear-shaped projections posterior to eyes**. **Colour:** Reddish purple. Head with chromatophores concentrated over eye orbits. Dorsal mantle chromatophores are irregularly distributed in patches; base of fins on posterior half with 10 to 12 patches of concentrated reddish purple chromatophores.

Size: Up to 88 mm mantle length.

Geographical Distribution: Indian Ocean: Red Sea, Gulf of Aden, Persian Gulf, western and southern India, Laccadive Islands (Fig. 119).

Habitat and Biology: Depth range from 80 to 272 m.

Interest to Fisheries: Presently undetermined. The species has been reported from bottom trawl resource surveys.

Literature: Adam and Rees (1966), Filippova *et al.* (1995), Nateewathana (1996).

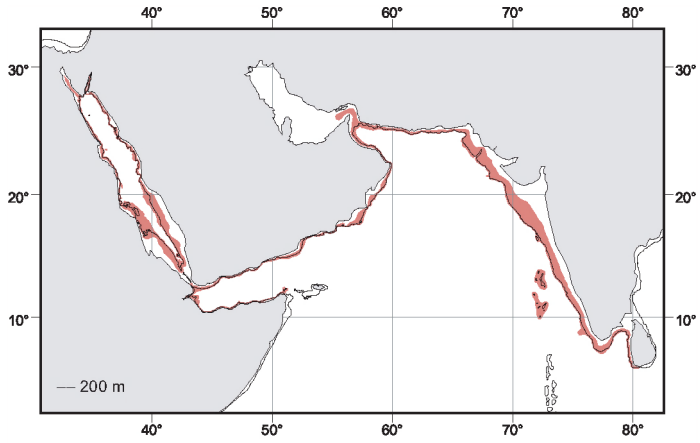


Fig. 119 ***Sepia arabica***
Known distribution

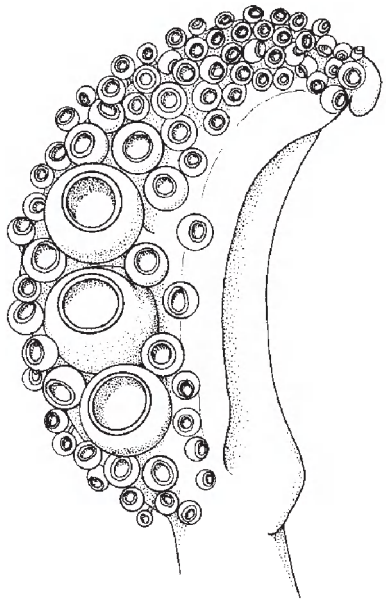
Sepia australis Quoy and Gaimard, 1832 — Fig. 120

Sepia australis Quoy and Gaimard, 1832. *Voyage de découvertes de l'Astrolabe pendant les annees 1826–1827–1828–1829, Zoologie*, 2(1): 70 [Type locality: Agulhas Bank, South Africa].

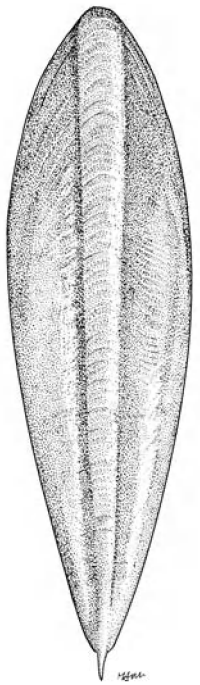
Frequent Synonyms: *Sepia capensis* d'Orbigny, 1845; *Sepia sinope* Gray, 1849.

Misidentifications: None.

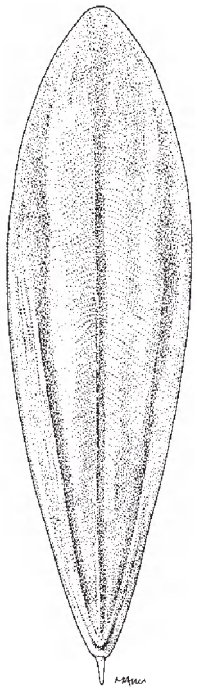
FAO Names: En – Southern cuttlefish; **Fr** – Seiche australe; **Sp** – Sepia austral.



tentacular club



dorsal view



ventral view

cuttlebone

Fig. 120 ***Sepia australis***

Diagnostic Features: Fins rounded posteriorly, with wide gap between them. Arm suckers tetraserial; median suckers larger than marginal suckers (more so in males). Hectocotylus present on left ventral arm: **2 rows of normal size suckers proximally, 6 or 7 rows of greatly reduced suckers medially**, then normal size suckers to arm tip; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Club crescent-shaped, short, with **5 suckers in transverse rows**; suckers differ markedly in size with **3 greatly enlarged suckers** towards proximal end of club. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club**. Cuttlebone outline oval; bone bluntly rounded anteriorly; tapers abruptly posteriorly, **acuminate, acute, sharply pointed**; strongly recurved ventrally; dorsal surface creamy white; evenly convex; texture smooth. Spine and posterior end (approximately one quarter) of bone covered with ochre-coloured, smooth, glaze-like substance. Dorsal median rib indistinct; broadens slightly anteriorly; ribs bordered laterally by distinct grooves; lateral ribs distinct. Chitin surrounds entire margin of cuttlebone. Spine long, straight, directed dorsally; dorsoposterior end of cuttlebone with **short, median longitudinal ridge anterior to, and separate from spine**. Striated zone and last loculus convex; sulcus **deep, narrow, flanked by rounded ribs**, extends entire length of cuttlebone. Anterior striae are **inverted U-shape**. Inner cone limbs are uniform width, narrow, U-shape posteriorly; slightly raised into rounded posterior ledge; thickened slightly; dull, not shiny; outer cone chitinous, not calcified, narrow. **Colour:** Purplish brown. Fins pale with **broad orange-pink band along base dorsally**; ventral pigment present; chromatophores concentrated near fins as for dorsum.

Size: Up to 85 mm mantle length, 50 g total weight.

Geographical Distribution: Southeastern Atlantic and western Indian Ocean: from Namibia (27ºS) to Port Elizabeth, South Africa (few records east of Port Elizabeth). Possibly Red Sea, Gulf of Aden and Somalia. Occurrence in China (as ***S. sinope*** Gray 1849), is extremely doubtful (Fig. 121).

Habitat and Biology: Depth range from 45 to 345 m (most abundant from 60 to 190 m). ***Sepia australis*** is able to thrive in areas of depleted oxygen concentrations (to as low as 1.5 ml l^{-1}) as is found in shallow northern waters of the west coast of southern Africa; here the best catches are associated with oxygen concentrations between 1.5 ml l^{-1} to 3.5 ml l^{-1} and temperatures around 9ºC. Off the south coast of South Africa, mature animals occur in early winter and the main spawning grounds are likely to be located in deeper water on the western side of the Agulhas Bank. ***Sepia australis*** is an important prey item of fur seals, hake, skates and other groundfishes. It preys mostly upon stomatopod crustaceans. On the west coast of South Africa, the largest recorded female measured 85 mm (weight 50 g) and the largest recorded male was 62 mm (weight 23 g), while on the south coast, the largest recorded female measured 67 mm (weight 15 g) and the largest recorded male 57 mm (weight 11 g).

Interest to Fisheries: This is one of the most common sepiid species found off the South African coast. The importance of the species, defined on the basis of 'survey abundance' (including commercial fisheries) and its trophic links with other organisms, indicate that ***Sepia australis*** is sufficiently abundant to be exploited by fisheries. This, along with its tasty flesh, gives it excellent commercial potential. Unknown factors are dispersal, availability and market considerations.

Literature: Adam and Rees (1966), Roeleveld (1972), Lipinski *et al.* (1991), Sánchez and Villanueva (1991), Lipinski (1992), Lipinski *et al.* (1992a), Lipinski *et al.* (1992b), Roeleveld *et al.* (1993), Augustyn *et al.* (1995).

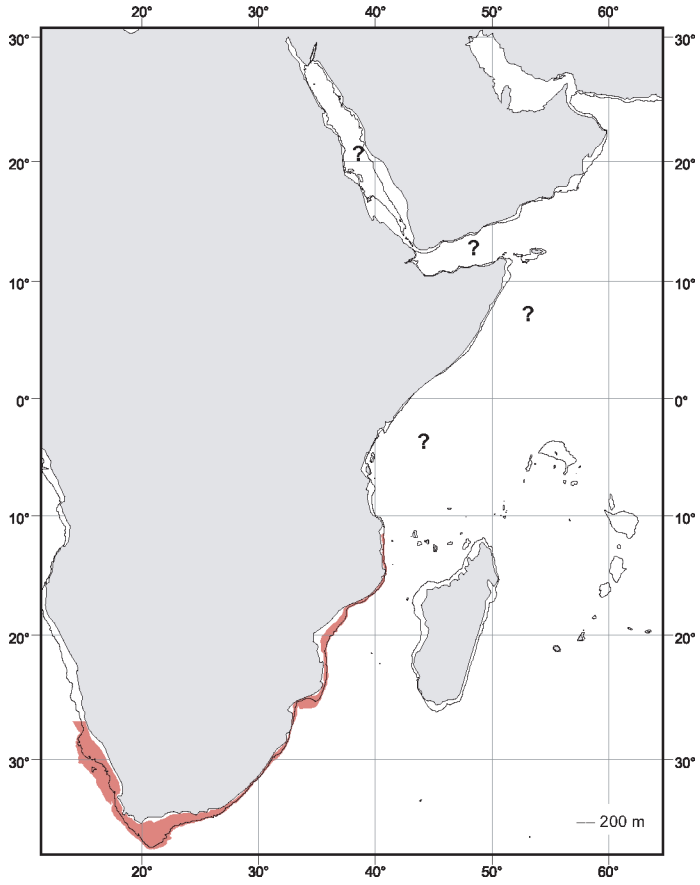


Fig. 121 ***Sepia australis***
Known distribution

NEXT PAGE

Sepia bandensis Adam, 1939

Fig. 122; Plate IV, 21–22

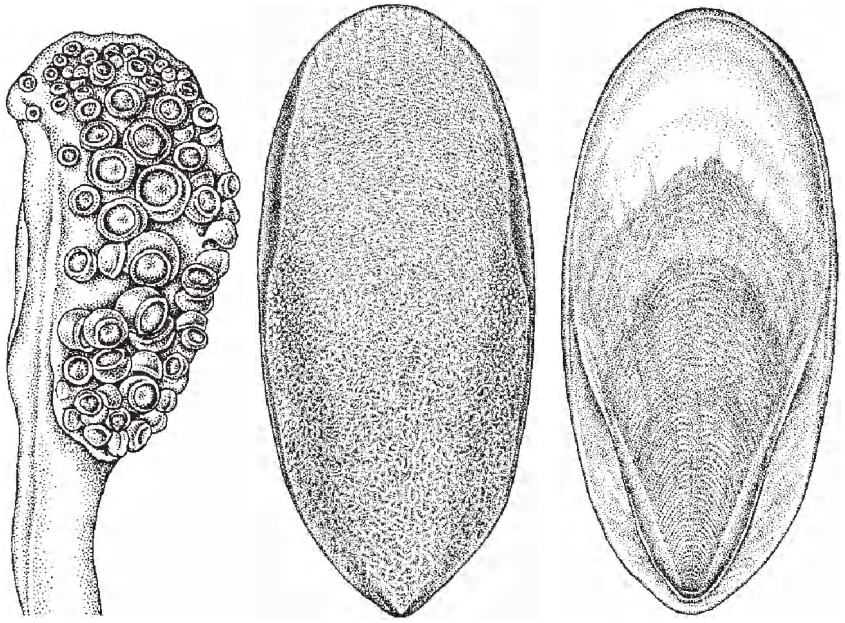
Sepia bandensis Adam, 1939b. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 15(18): 1 [type locality: Indonesia: Banda Sea, Banda Neira].

Frequent Synonyms: *Sepia baxteri* (Iredale, 1940) and *Sepia bartletti* (Iredale, 1954) are possible synonyms.

Misidentifications: None.

FAO Names: En – Stumpy cuttlefish; **Fr** – Seiche trapue; **Sp** – Sepia achaparrada.

Diagnostic Features: Club with **5 suckers in transverse rows**, central 3 suckers enlarged. Swimming keel extends beyond base of club. Dorsal and ventral protective membranes **joined at base of club**, separated from stalk by a membrane. Cuttlebone outline broad, oval; bone bluntly rounded anteriorly and posteriorly; dorsal surface evenly convex; calcified with reticulate sculpture; dorsal median and lateral ribs absent. Spine **reduced to tiny, blunt tubercle**. Sulcus shallow, narrow, extends along striated zone only. Anterior striae are **inverted U-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly, slightly convex; outer cone narrow anteriorly, broadens posteriorly. Dorsal mantle has longitudinal row of ridge-like papillae along each side, adjacent to base of each fin and scattered short ridges dorsal to cuttlebone (corresponding to whitish bars). Head and arms with short, scattered, bar-like papillae positioned dorsally and laterally. **Colour:** Light brown, or greenish yellow-brown when fresh, and with whitish mottle. Head with scattered white spots. Dorsal mantle has white blotches concentrated into short, longitudinal bars. It often shows a pair of brown patches on the posterior end of the mantle, often accompanied by white patches over the eye orbits. Fins pale with **row of small luminescent blue spots** at base.



(illustrations: K. Hollis)

Fig. 122 ***Sepia bandensis***

Size: Up to 70 mm mantle length. Animals from the Alas Strait, Indonesia reported at about 40 g (males) and 45 g (females).

Geographical Distribution: Tropical Indo-Pacific: Philippines, Malaysian Borneo, Java, Sulawesi, Alas Strait, eastern Indonesia, New Guinea. Possibly northern Australia and Marshall Islands (Fig. 123).

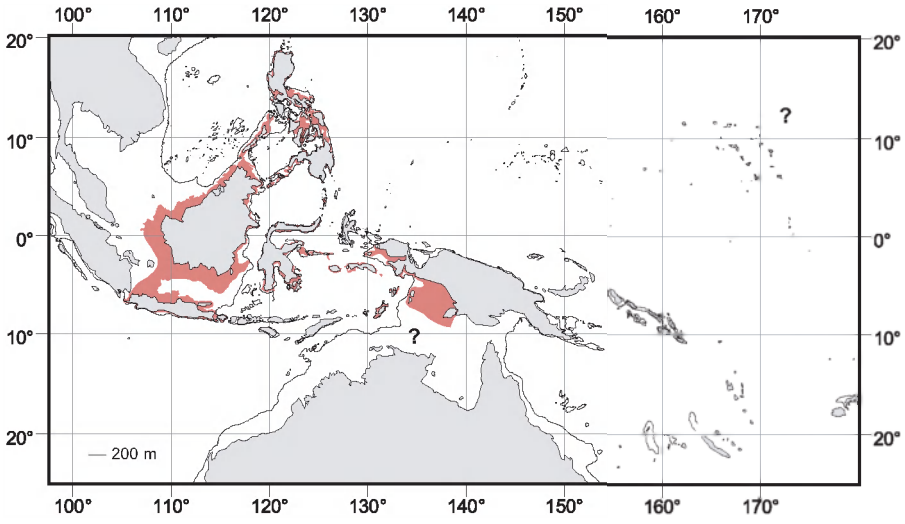


Fig. 123 ***Sepia bandensis***
Known distribution

Habitat and Biology: Coastal shallow waters. Found over coral reefs and sand. Night active. This species has been observed 'walking', rather than swimming, using arms III [or IV] and a pair of raised flaps on the ventral mantle. It is often found in association with sea cucumbers and sea stars.

Literature: Adam and Rees (1966), Gofhar (1989).

Sepia bertheloti d'Orbigny, 1835 (*in* Férussac and d'Orbigny 1834–1848) **Fig. 124**

Sepia bertheloti d'Orbigny, 1835. *Histoire naturelle générale et particulière des Céphalopodes Acétabuliferes vivants et fossiles*, pl. 11 [type locality: Canary Islands: Tenerife].

Frequent Synonyms: *Sepia verrucosa* Lönnberg, 1896; *Sepia mercatoris* Adam, 1937.

Misidentifications: None.

FAO Names: En – African cuttlefish; **Fr** – Seiche africaine; **Sp** – Sepia africana

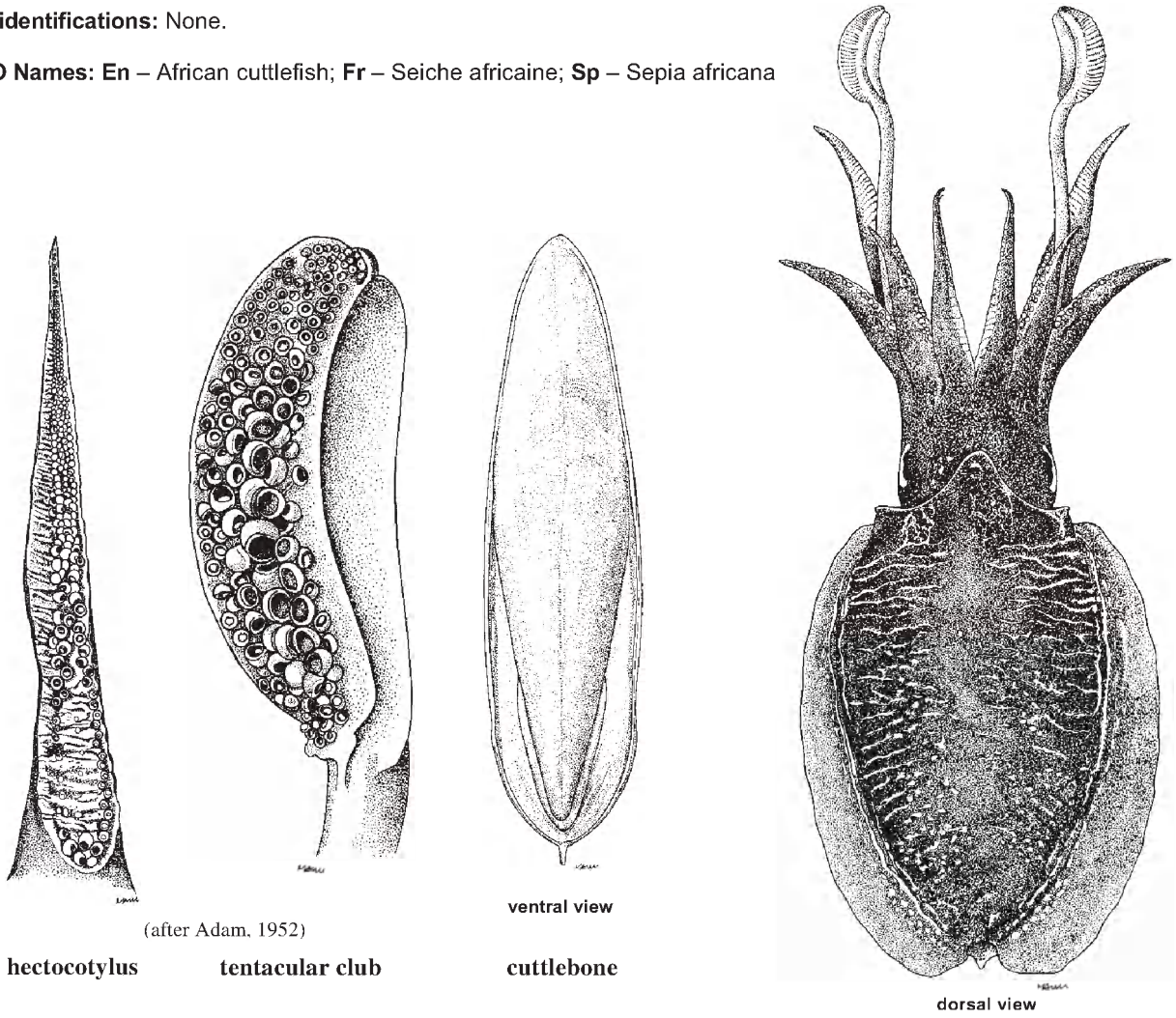


Fig. 124 ***Sepia bertheloti***

(after Adam, 1952)

Diagnostic Features: Dorsal anterior mantle margin triangular, acute; ventral mantle margin emarginate. Fins wide, with wide gap between them posteriorly. Arms IV **elongate**, particularly in males. Arm suckers tetraserial. Male median arm suckers with greater diameter than marginal ones. Hectocotylus present on left ventral arm: **1 or 2 rows of normal size suckers proximally, 9 to 13 rows of greatly reduced suckers medially**; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Dorsal protective membranes **well developed on hectocotylized arm, covering suckers**. Club straight, slender, with **5 or 6 suckers in transverse rows**; suckers differ in size: **several suckers of inner 2 or 3 rows larger than rest**. Swimming keel of club **terminates at posterior end of carpus**. Dorsal and ventral protective membranes **not joined at base of club** but fused to tentacular stalk. Dorsal and ventral membranes **same length**, terminate at posterior end of carpus. Buccal membrane in females extends ventrally with 2 spermathecae. Cuttlebone outline oblong; acuminate, acute, anteriorly; bluntly rounded posteriorly; dorsal surface evenly convex; entire surface calcified with reticulate granulose sculpture concentrated medially and on lateral margins in irregular longitudinal ridges; calcification thickest posteriorly; dorsal median rib indistinct; broadens slightly anteriorly; lateral ribs absent. Chitin borders lateral and anterior margins of cuttlebone. Spine moderate length, keel(s) absent. Striated zone and last loculus convex; sulcus shallow, narrow, extends entire length of cuttlebone. Anterior striae shallow m-shape, or inverted U-shape. Inner cone limbs are narrow, strap-like anteriorly, broaden slightly posteriorly; outer cone **chitinous, spatulate, expanded**. Dorsal mantle with series of elongate papillae along each side, medial to base of each fin. **Colour:** Purplish brown. Arms have a transverse zebra-stripe pattern and a **longitudinal orange-red pigmented stripe along their aboral surfaces**. Dorsal mantle has small spots (predominantly posteriorly) and narrow, cream-coloured, broken transverse lines. Fins pale with **narrow lustrous orange-pink band along base in males bordered by purplish band and 1 or 2 longitudinal rows of numerous short bars**.

Size: Males up to 175 mm mantle length; females to 134 mm mantle length.

Geographical Distribution: Eastern Atlantic: off northwestern Africa, from Canary Islands and off Western Sahara, to Angola (southwestern Africa), 14ºS. Endeavour Bank (Fig. 125).

Habitat and Biology: Depth range from 20 to 156 m. On the Endeavour Bank, ***Sepia bertheloti*** migrates to shallow waters to spawn during summer and autumn. The size distribution observed in the captures shows a larger range for this species than for the co-occurring ***S. officinalis*** Linnaeus, 1758 in summer.

Interest to Fisheries: ***Sepia bertheloti*** is trawled off the Canary Islands, where greatest concentrations are encountered between 70 and 140 m depth. It is commonly captured off the western Endeavour Bank, where it shares the same depth distribution with the co-occurring species ***S. hierredda*** Rang, 1835. Separate statistics are difficult to obtain because the two species are often marketed together, but information from the Spanish fishery in Saharan waters indicate that it represented 11% of cuttlefishes captured over the last decade, with ***S. hierredda*** comprising the remaining 89%. It is also a sizeable component of cephalopod catches in Mauritania waters, where it represented about 35% of the cuttlefishes captured in recent years (the remaining 65% again made up by ***S. hierredda***). Off Senegal, it is reported to represent a minor portion of the total cuttlefish catch taken by trawls. It is marketed fresh or deep-frozen for export.

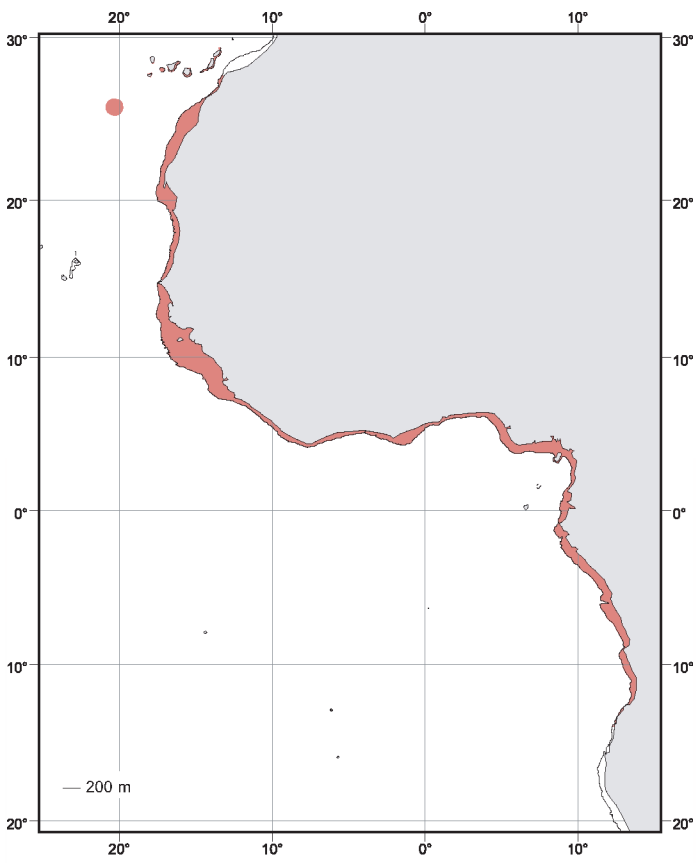


Fig. 125 ***Sepia bertheloti***
Known distribution

Remarks: Sexual dimorphism is pronounced: the mantle is relatively wider in females and the arms are much longer in males, especially the ventral pair. The soft parts are very similar to those of ***S. officinalis***, although the ventral arms of the males are much longer and the largest tentacular suckers relatively smaller. However, the cuttlebone differs markedly between the two species. Recent genetic studies show the distinctiveness of this species in relation to ***S. officinalis*** and ***S. hierredda***.

Literature: Adam and Rees (1966), Delgado de Molina *et al*. (1993), Hernandez-Garcia and Castro (1994).

Sepia braggi Verco, 1907

Fig. 126

Sepia braggi Verco, 1907, *Transactions of the Royal Society of South Australia*, 31: 213 [type locality: South Australia, Glenelg, 34°58'S 138°32'E].

Frequent Synonyms: None.

Misidentifications: *Sepia bidhaia* Reid, 2000; *Sepia cottoni* Adam, 1979; *Sepia limata* (Iredale, 1926); *Sepia rhoda* (Iredale, 1954); *Sepia vercoi* Adam, 1979.

FAO Names: En – Slender cuttlefish; **Fr** – Seiche gracile; **Sp** – Sepia grácil.

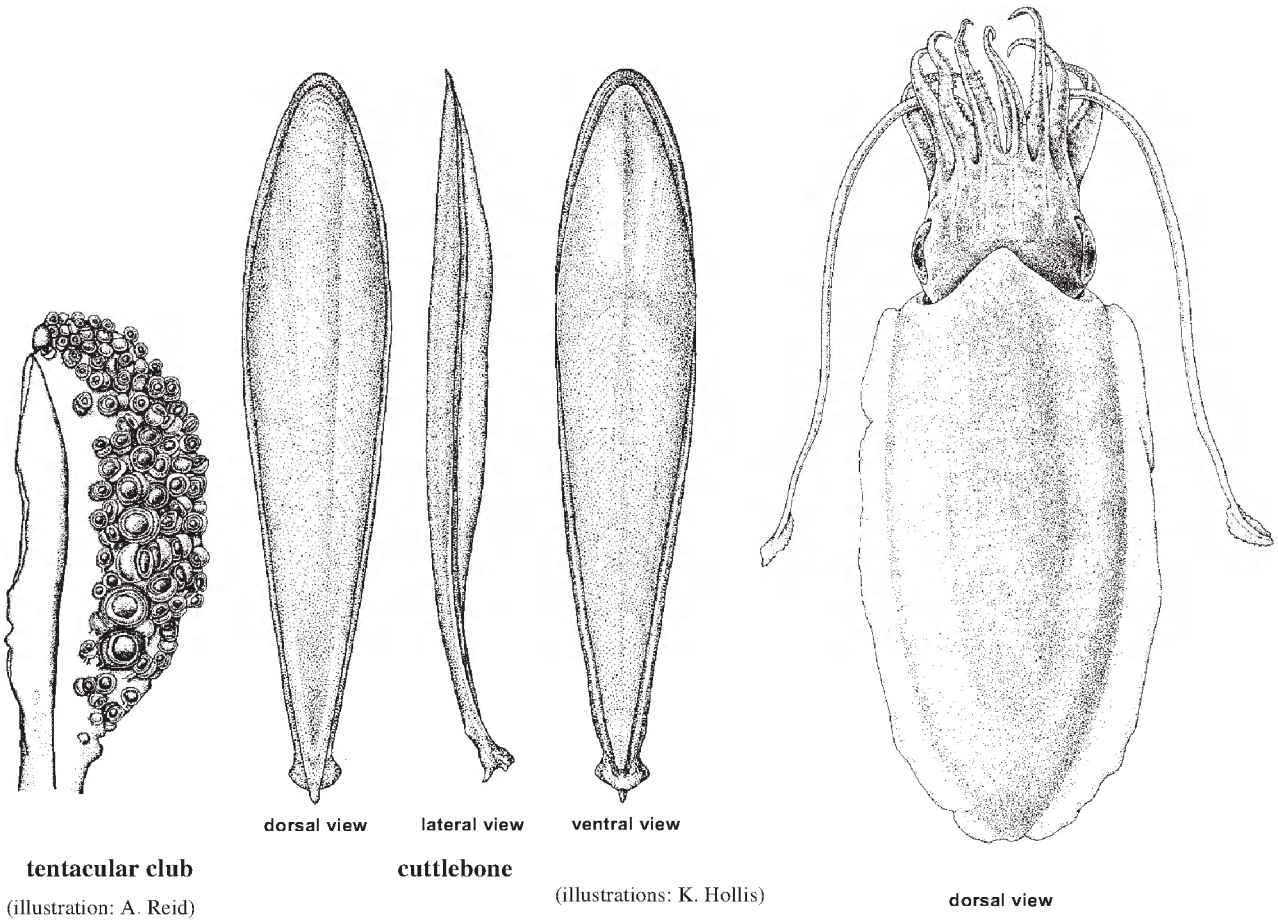


Fig. 126 ***Sepia braggi***

Diagnostic Features: Dorsal anterior mantle margin triangular, acute. Fins widest in posterior third, rounded posteriorly, with wide gap between them. Head short, slender, narrower than mantle. Male and female arms differ in relative lengths; male (mature) **arms III elongate**; female arms **II and III longer than arms I and IV** (arms II usually longer than arms III). Distal arm tips **strongly attenuate** in both sexes, suckers enclosed by protective membranes. Arm suckers **tetraserial proximally, biserial at distal arm tips** (biserial region over greater proportion of arms II and III than of arms I and IV); biserial suckers reduced and displaced laterally, with gap between them on arms II of females and arms III of males. **Hectocotylus absent**. Club slightly recurved, short, sucker-bearing surface flattened, with **4 to 6 suckers in transverse rows**; suckers differ in size: 5 or 6 median suckers twice diameter of rest. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes not joined at base of club but fused to tentacular stalk. Dorsal and ventral membranes **same length**, extend proximal to carpus along stalk. Dorsal membrane broad, much wider than ventral membrane and forms shallow cleft at junction with stalk. Gills with 26 to 30 lamellae per demibranch. Buccal membrane without suckers. Buccal membrane in females without spermathecae. Spermatophores 2.4 to 4.4 mm long; smallest male recorded with well-developed spermatophores in spermatophoric sac was 24.1 mm mantle length. Eggs oval, up to 9.4 mm long, 5.5 mm wide. Cuttlebone outline lanceolate, broadest in anterior third at anterior end of striated zone; acuminate, acute, anteriorly and posteriorly; strongly recurved ventrally; dorsal surface pinkish; evenly convex; calcified medially, slightly granulose with irregular longitudinal ridges (particularly posteriorly). Spine and posterior end (approximately one quarter) of bone covered with ochre-coloured, smooth, glaze-like substance. Dorsal median rib distinct anteriorly, indistinct posteriorly; rib broadens anteriorly; lateral ribs absent. Chitin present as wide bands bordering lateral margins of cuttlebone (covers about half of dorsal surface of cuttlebone). Spine short, pointed, curves dorsally; keel(s) absent; fine, radiating ribs between outer cone and spine. Striated zone and last loculus convex; sulcus deep, narrow,

flanked by rounded ribs, extends entire length of cuttlebone. Anterior striae are **inverted U-shape, incurved medially, slightly V-shape following sulcus**. Inner cone limbs are strap-like anteriorly, narrower posteriorly, U-shape; slightly raised into rounded posterior ridge; thickened, shiny (yellowish), inner cone posteriorly with irregular calcareous ribs radiating into outer cone; outer cone calcified, narrow, limbs are **expanded posteriorly into 2 short 'wings'**, directed ventrally, to form a recurved cup-like structure. Dorsal mantle has scattered short ridges dorsal to cuttlebone and up to five orange-pink ridges at base of each fin. Head with short, scattered papillose bars posterior to eyes; arm papillae present; same as those on head. **Colour:** In preserved specimens pale buff to pinkish brown. Arms I have a **darkly pigmented purplish band on each side of dorsal midline**. Arms II to IV have a **median longitudinal purplish band along their aboral surfaces**. All arms have short transverse bars and blotches lateral to these longitudinal bands. Arm and club sucker rims midbrown. Fins without markings along base.

Size: Males up to 49 mm mantle length; females up to 80 mm mantle length.

Geographical distribution: Southern Indo-Pacific: southern Australia from southern New South Wales, 36°23'S 150°07'E, to Western Australia, 31°51'S 115° 35'E. Australian endemic (Fig. 127).

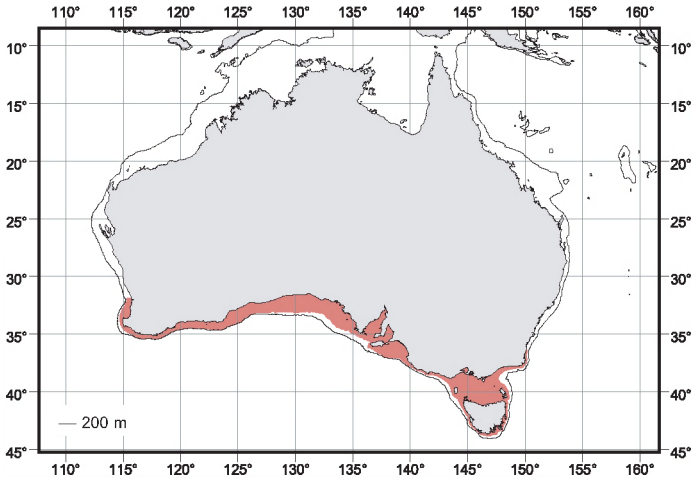


Fig. 127 ***Sepia braggi***
Known distribution

Habitat and Biology: Depth range from 30 to 86 m. ***Sepia braggi*** is a demersal species. A report of many fresh bones washed up on Gunnamatta Beach (Victoria) 26–27 May 2001, is perhaps is indicative of a spawning event.

Interest to Fisheries: Taken as bycatch with other cuttlefishes along southern Australia, then used locally as bait and food.

Remarks: The pigmentation on the arms is very distinctive and clearly visible even in small specimens. While arms III are obviously elongate in adult males, they are similar in length to the remaining arms in immature males (less than approximately 30 mm mantle length). ***Sepia braggi*** males differ from ***S. limata*** Iredale, 1926 and ***S. rhoda*** (Iredale, 1954) males in having elongate third arms. ***Sepia braggi*** does not have a hectocotylus; the left ventral arms are hectocotylized in ***S. limata*** and ***S. rhoda***. The arrangement of the arm suckers differs among these three species. Female ***S. rhoda*** have elongate second arms. While the second and third arms of ***S. braggi*** females are slightly longer than the other arms, they do not differ to the same extent as those of mature ***S. rhoda*** females. The anterior striae on cuttlebones are M-shape in ***S. rhoda*** and the posterior inner cone is very broad, while in ***S. braggi*** the anterior striae are an inverted U-shape and the inner cone narrow. The cuttlebone is broader in ***S. limata*** than the ***S. braggi*** cuttlebone. ***Sepia braggi*** of both sexes differ from all other Australian narrow-boned species in its distinctive arm pigmentation.

Literature: Adam and Rees (1966), Lu (1998a), Reid (2000).

Sepia brevimana Steenstrup, 1875 Fig. 128

Sepia brevimana Steenstrup, 1875, *Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 10(7): 475 [type locality: Indian Ocean].

Frequent Synonyms: *Sepia rostrata* (in part) Férussac and d'Orbigny, 1848.

Misidentifications: *Sepia esculenta* Hoyle, 1885; *Sepia stellifera* Homenko and Khromov, 1984.

FAO Names: En – Shortclub cuttlefish; **Fr** – Seiche petites mains; **Sp** – Sepia mazicorta.

Diagnostic Features: Mantle broad, oval; dorsal anterior margin triangular, acute. Arm suckers tetraserial. **Club small, with 6 to 8 suckers in transverse rows**; all club suckers of similar small size. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes **not joined at base of club; dorsal membrane much wider than ventral membrane**. Cuttlebone outline oval; bone very angular, **V-shape anteriorly**; dorsal surface flat, texture rough, with irregular calcified projections. Spine long, pointed, with dorsal and ventral keels. Sulcus shallow, narrow, extends along striated zone only, flanked by rounded ribs. Anterior striae are inverted blunt V-shape. Inner cone limbs **broaden posteriorly, thickened, rose-coloured or yellowish orange**; **outer margin of inner cone raised into a flattened ledge posteriorly**; outer cone calcified, narrow anteriorly, broadens posteriorly.

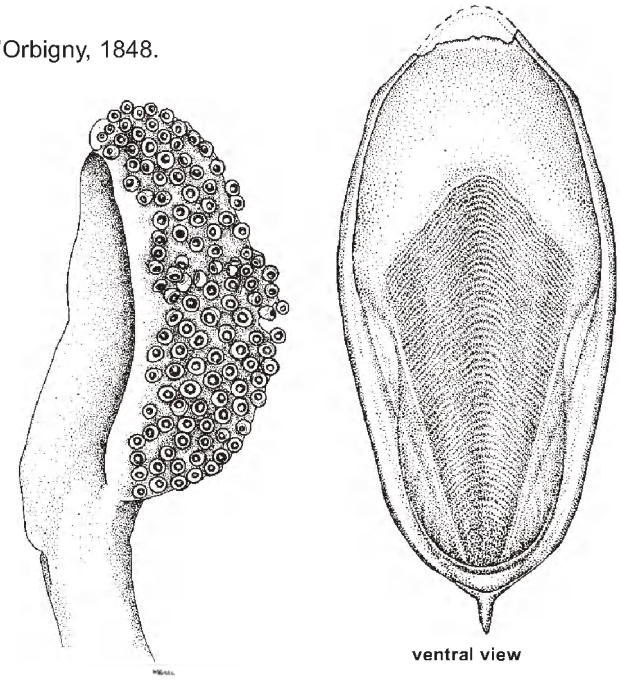


Fig. 128 *Sepia brevimana*

Size: Up to 110 mm mantle length.

Geographical Distribution: Indo-Pacific: northern Indian Ocean, Andaman Sea, Andaman and Maldive Islands, Singapore to the Gulf of Tonkin, South China Sea, Hong Kong, Java, Sulu and Celebes Seas. Possibly Saya-de-Malha Bank (Fig. 129).

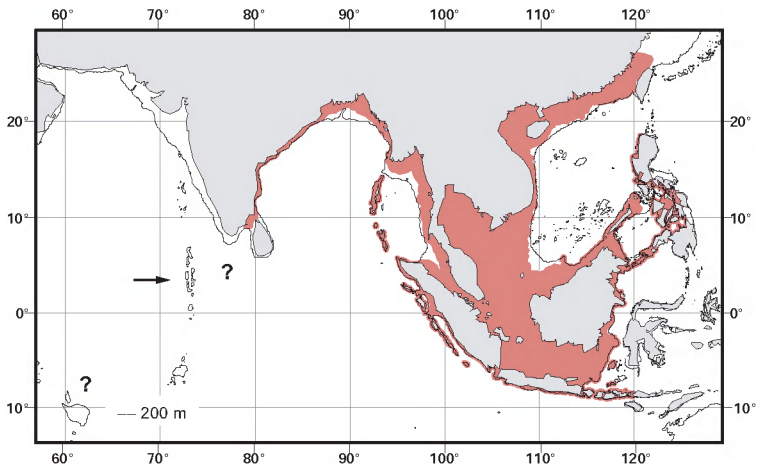


Fig. 129 *Sepia brevimana*
Known distribution

Habitat and Biology: Depth range from 10 to 100 m. ***Sepia brevimana*** is a shelf species, restricted to coastal waters. Around India, spawning occurs throughout the year. Several spawning peaks have been observed between July and February in eastern Indian waters. Hatchlings grow to adult size in 11 to 13 months, depending on temperature conditions. Off Chennai (Madras), animals attain 29 to 34 mm within 6 months, 56 to 58 mm at the end of 12 months and about 75 mm after 18 months. Length at 50% maturity for males is 56 mm off Madras and 62 mm off Waltair, and for females, 59 and 63 mm, respectively. Maximum length in the Indian trawl fishery is 85 mm off Madras, and 95 mm off Waltair (northeast India), with common size ranges from about 40 to 70 mm. In the Gulf of Thailand, 40 to 60 mm mantle length animals are caught commonly, with the maximum size attained 90 mm mantle length. The sex ratio of males to females caught is 1:2.

Interest to Fisheries: This species appears as a bycatch in the eastern Indian trawl fishery off Chennai and Waltair, but separate catch data are not reported. ***Sepia brevimana*** is important to the commercial fishery of Thailand. Most cuttlefishes in this area are caught using otter trawl, some using pair trawl, and small catches are made using squid light-lures, traps and push nets; bottom otter and pair trawls are used offshore, while push nets and lift nets are used in inshore and coastal waters. It is also fished in the South China Sea.

Remarks: This species may be confused with ***S. stellifera*** Homenko and Khromov, 1984, but differs in having 6 to 8, rather than 10, oblique rows of suckers on the club. The sulcus of the cuttlebone in ***S. brevimana*** is shallow and narrow. In ***S. stellifera***, the sulcus is deep and wide. ***Sepia brevimana*** is similar to ***S. esculenta*** Hoyle, 1885, but differs in having fewer

club suckers (there are 10 to 16 suckers in transverse rows in ***S. esculenta***), no fleshy papillae along the base of the fins, and by the coloured inner cone.

Literature: Adam and Rees (1966), Voss and Williamson (1971), Silas *et al.* (1982), Silas *et al.* (1986), Chantawong and Suksawat (1997).

Sepia cultrata Hoyle, 1885

Fig. 130

Sepia cultrata Hoyle, 1885, *Annals and Magazine of Natural History*, (series 5)16: 198 [type locality: Australia, Twofold Bay, 36°59'S 150°20'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: **En** – Knifebone cuttlefish; **Fr** – Seiche à os en couteau; **Sp** – Sepia de sepión de cuchillo.

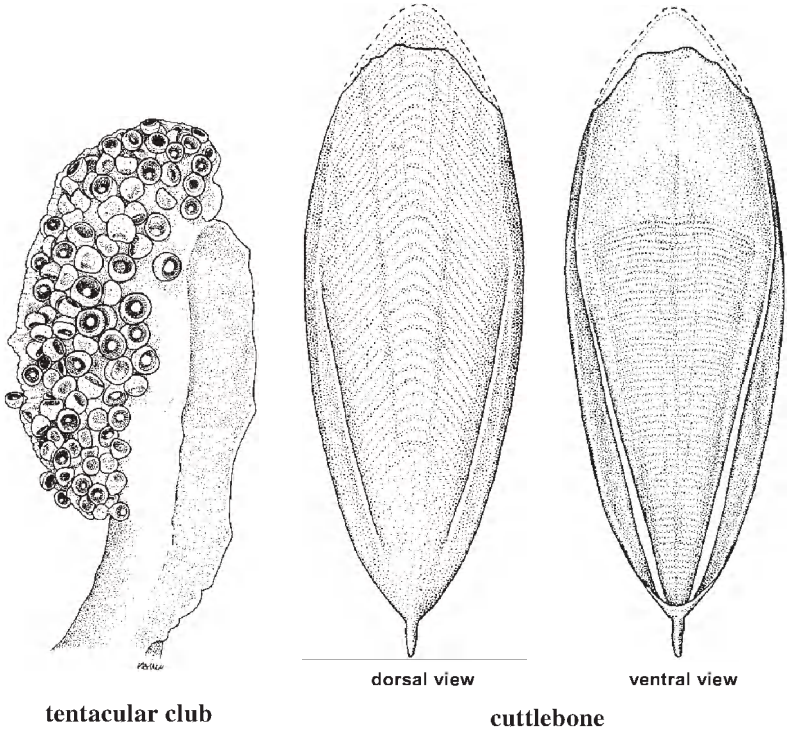


Fig. 130 ***Sepia cultrata***

Diagnostic Features: Male and female arm lengths subequal. Arm suckers tetraserial. Hectocotylus present on left ventral arm: approximately **7 rows of normal size suckers proximally**; **5 or 6 rows of greatly reduced suckers medially**. Suckers of hectocotylus in **2 dorsal series are smaller than those in 2 ventral series** (in some specimens, 2 dorsal rows appear merged as if in a single row); oral surface of modified region swollen; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Club crescent-shaped, sucker-bearing surface flattened, with **5 or 6 small suckers** in transverse rows. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes **not joined at base of club**; **dorsal and ventral membranes differ in length**; dorsal membrane **extends proximal to carpus along stalk**, ventral membrane **terminates at proximal end of carpus**. Buccal membrane without suckers. Cuttlebone outline oval; bone triangular, obtuse anteriorly; acuminate, acute, posteriorly; **dorsal surface pinkish**; dorsal surface convex posteriorly, flat anteriorly; some granulation on lateroposterior margins bordered by a longitudinal ridge; dorsal median rib present; rib broadens anteriorly; lateral ribs indistinct. Spine straight. Striated zone **concave in extreme posterior part, slightly convex in anterior part**; last loculus slightly concave; sulcus absent. Anterior striae **slightly convex to straight**. Inner cone limbs are **uniform width, very narrow, U-shape posteriorly**; thickened. Dorsal mantle with scattered short papillae along each side close to fins and with longitudinal row of ridge-like papillae adjacent to base of each fin; ventral mantle with longitudinal row of 4 or 5 narrow ridges along each side close to fins. **Colour:** Pale buff pinkish brown.

Size: Up to 120 mm mantle length.

Geographic Distribution: Southern Indo-Pacific: southern Australia from southern Queensland, 26°35'S 153°45'E, southwestward to Western Australia, Houtman Abrolhos, 28°49'S 114°04'E, including Tasmania, 42°43'S 148°22'E (Fig. 131).

Habitat and Biology: Depth range from 132 to 803 m with the majority of catches from 300 to 500 m; outer shelf and upper bathyl.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries. Possibly more than one species is identified under this name. This requires further investigation.

Literature: Adam and Rees (1966), Lu (1998a).

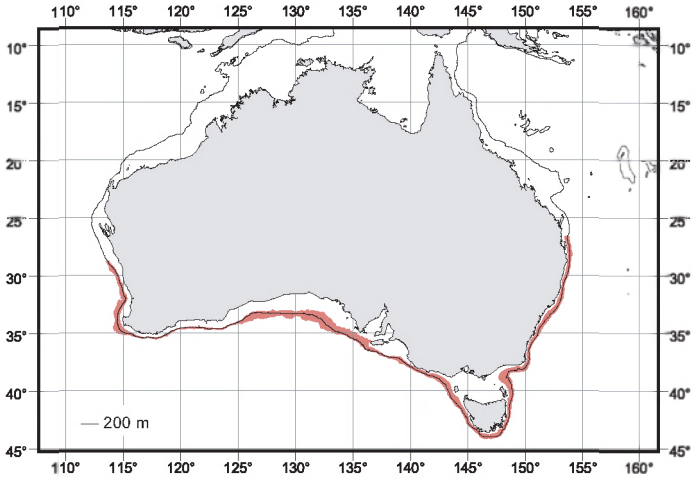


Fig. 131 ***Sepia cultrata***
Known distribution

NEXT PAGE

Sepia elegans Blainville, 1827

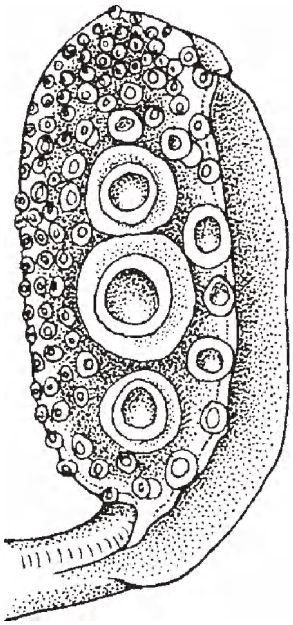
Fig. 132

Sepia elegans Blainville, 1827, *Dictionnaire des Sciences Naturelles*, 48: 284 [type locality: Sicily (*S. elegans*); Mediterranean Sea (as *S. biserialis* and *S. italica*); Island of Noirmoutiers and La Rochelle (as *S. rupellaria*).

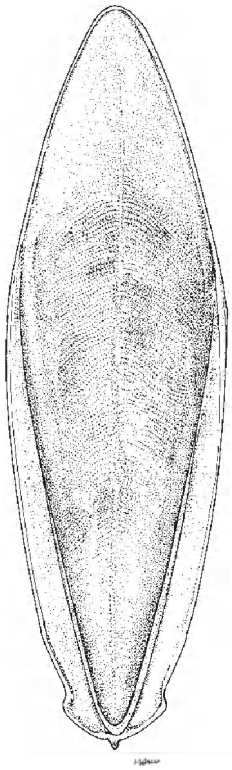
Frequent Synonyms: *Sepia rupellaria* Férussac and d'Orbigny, 1835–1848; *Sepia biserialis* Blainville, 1827; *Sepia italica* Risso, 1854.

Misidentifications: *Sepia bertheloti* d'Orbigny, 1835.

FAO Names: En – Elegant cuttlefish; **Fr** – Seiche élégante; **Sp** – Sepia elegante.

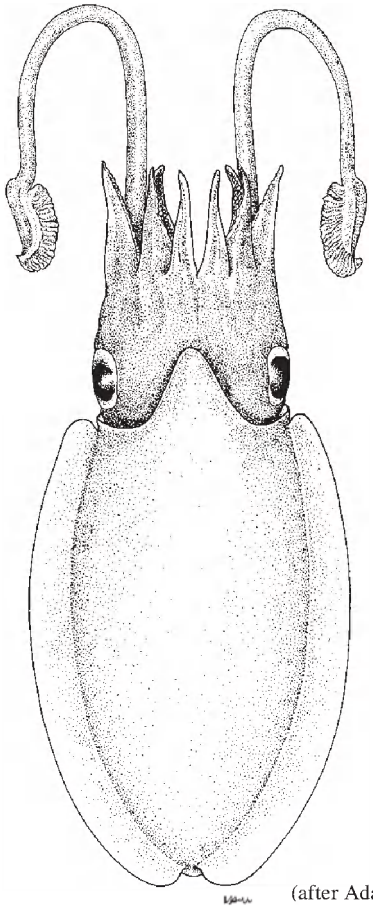


tentacular club



ventral view

cuttlebone



dorsal view

(after Adam, 1952)

Fig. 132 *Sepia elegans*

Diagnostic Features: Small species. Mantle oblong; dorsal anterior margin triangular, acute; ventral mantle margin emarginate. Male and female arms subequal in length. Arm sucker arrangement differs between sexes: in males, arm I suckers **biserial for a few rows, rest tetraserial**; arms II and III **suckers tetraserial proximally, biserial at extreme distal tips**; arm IV suckers variously arranged (approximately 10 pairs biserial suckers on arms I to III, arms IV with 2 to 4 rows biserial suckers); in females, suckers biserial proximally, tetraserial distally (5 rows biserial suckers arms I to III, 2 to 4 rows biserial suckers arms IV). Male non-hectocotylized median arm suckers with greater diameter than marginal ones. Hectocotylus present on left ventral arm: **1 or 2 rows of normal size suckers proximally, 9 to 11 rows of reduced minute suckers medially**, then normal size suckers to arm tip; suckers in 2 dorsal and 2 ventral series displaced laterally. Club short, oval; sucker-bearing surface flattened, with **6 to 8 suckers in transverse rows**; suckers differ markedly in size: **3 or 4 greatly enlarged suckers** toward posterior end of club and several dorsal suckers enlarged, but not as large as medial suckers. Buccal membrane in females with single median spermathecae in ventral part. Cuttlebone outline oblong; convex in lateral view; acuminate, acute, anteriorly and posteriorly; recurved ventrally; dorsal surface evenly convex; last loculus convex. Anterior striae are inverted U-shape. Inner cone limbs are uniform width, **narrow V-shape posteriorly**; outer cone narrow throughout; outer cone limbs are **expanded posteriorly into 2 curved 'wings'**, directed ventrally, to form a recurved cup-like structure. **Spine very short**. Dorsoposterior end of cuttlebone with short, rugose, calcareous keel. Ventral mantle with longitudinal row of 6 narrow ridges along each side close to fins; anteriormost pair and posterior 2 pairs shorter than rest. **Colour: Reddish brown**. Head with a few scattered chromatophores. Arms without markings. Dorsal mantle pale, peppered with scattered purple-black chromatophores. Fins and ventral mantle pale. Ridges whitish.

Size: Males up to 72 mm mantle length; females up to 89 mm mantle length. Total weight between 50 and 60 g.

Geographical Distribution: Eastern Atlantic and Mediterranean Sea: around British Isles, western Scotland, Ireland, Dingle Bay, Co. Kerry and the English Channel, from 50°N through the Mediterranean (including Ligurian Sea, Tyrrhenian Sea, Aegean Sea, Sea of Marmara and Levantine Sea), west Africa: Endeavour Bank to 15°S, and possibly Agulhas Bank (Fig. 133).

Habitat and Biology: Depth to 500 m, although records below 450 m are sporadic. ***Sepia elegans*** is a sublittoral species. It spends the winter in deep water (200–400 m), then migrates into the shallows in spring and summer to spawn. It feeds mainly on molluscs, small crustaceans, fishes and polychaetes. In the Sea of Marmara (Mediterranean Sea), this species has been found in brackish waters (salinity between 18 and 25‰), which indicates a high degree of tolerance. In the Mediterranean Sea, mature males and females are present throughout the year, which suggests a continuous spawning period. As a consequence of this, a continuous recruitment also occurs, with observed peaks in several Mediterranean areas. Smallest mature males have been observed at 20 mm, and females at 30 mm mantle length. The eggs are laid in clusters of 12 to 25 (diameter 5 mm) attached to alcyonarians (sea fans), shells, etc., on muddy bottoms. After hatching, juveniles immediately adopt a benthic lifestyle. A rough estimate of growth in mantle length of 2.8 mm per month for males and 3.0 mm for females is reported for animals in the Sicilian Channel. A negative allometric length–weight relationship has been found for both sexes in all seasons and different locations, with females heavier than males at any given mantle length. Females also have longer tentacular clubs and heavier stomach contents than males. Off west Africa, spawning extends almost throughout the year in shallow inshore waters, with peaks in summer and autumn. Maturity is attained at about 1 year of age. Males may carry about 95 spermatophores and females about 250 eggs. Spawning occurs at temperatures of 13° to 18°C. In Portuguese waters mature animals are also present throughout the year, but with minimum numbers in summer. The lifespan of this species is about 12 to 18 months.

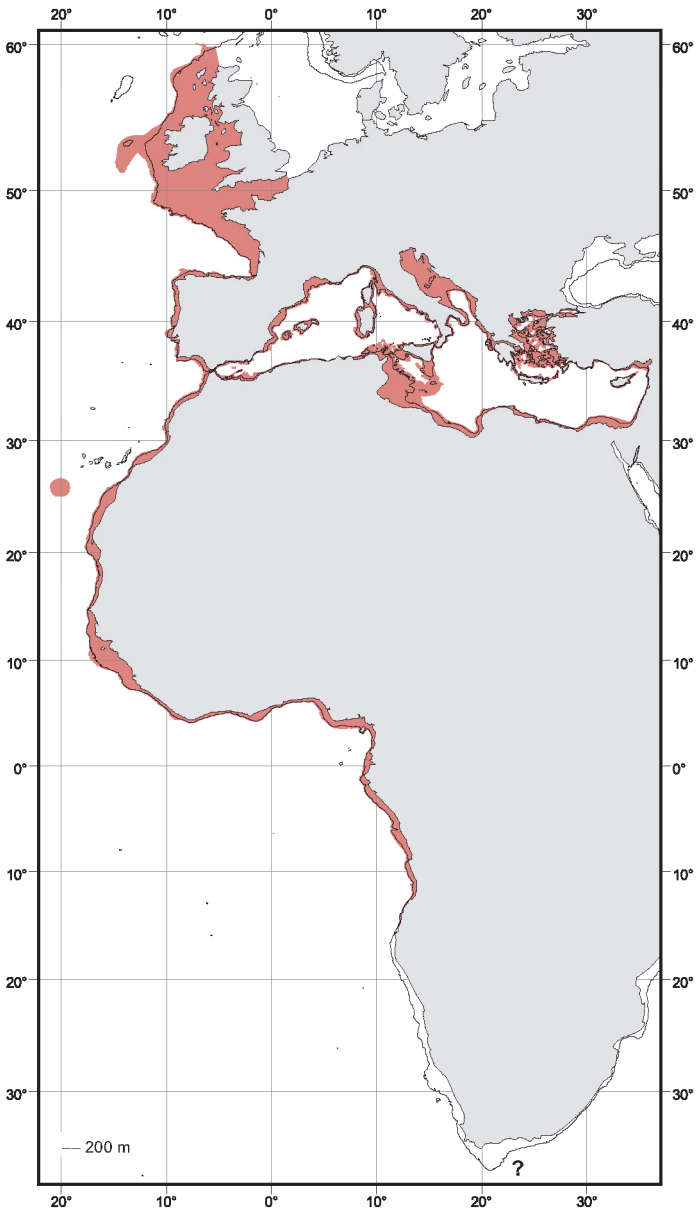


Fig. 133 ***Sepia elegans***
Known distribution

Interest to Fisheries: ***Sepia elegans*** is taken mainly as a bycatch in Mediterranean and west African trawl fisheries. It is most abundant at about 150 m depth, hence a little deeper than ***S. officinalis*** Linnaeus, 1758 and ***S. bertheloti*** d'Orbigny, 1835. Separate statistics are not reported for this species, which, however, represent a very significant percentage of the catches in some areas of its distributional range. In the Mediterranean Sea it is marketed along with ***S. orbignyana*** Férussac *in* d'Orbigny, 1826 and small ***S. officinalis*** and constitutes a valuable resource locally. In the Sicilian Channel, research studies showed an exploitation rate of 0.73 for the species, which suggests a very intense fishing pressure on this resource. It is marketed fresh and frozen.

Local Names: ITALY: Seppia elegante, Castagnola; SPAIN: Castaño.

Remarks: This species resembles ***S. australis*** Quoy and Gaimard, 1832, but differs in the arrangement of arm suckers, club and hectocotylus. ***Sepia elegans*** differs from ***S. officinalis*** in having a reddish, rather than brown, coloration and because it generally inhabits deeper water and does not bury in the sand during the day.

Literature: Mangold-Wirz (1963), Adam and Rees (1966), Guerra and Castro (1989), Bello (1990a), Jereb and Ragonese (1991), Ragonese and Jereb (1991), Wurtz *et al.* (1991), Guerra (1992), Filippova *et al.* (1995), Sanjuan *et al.* (1996), Neige and Boletzky (1997), Sanchez *et al.* (1998), Belcari (1999a), Unsal *et al.* (1999), Salman *et al.* (2002), Sobral (2002).

Sepia elliptica Hoyle, 1885

Fig. 134

Sepia elliptica Hoyle, 1885, *Annals and Magazine of Natural History*, (series 5)16: 189 [type locality: Arafura Sea, south of Papua, 09°59'S 139°42'E, and 08°56'S 136°05'E].

Frequent Synonyms: None.

Misidentifications: *Sepia esculenta* Hoyle, 1885; *Sepia madokai* Adam, 1939a; *Sepia stellifera* Homenko and Khromov, 1984.

FAO Names: En – Ovalbone cuttlefish; **Fr** – Seiche à sepion ovale; **Sp** – Sepia de sepión oval.

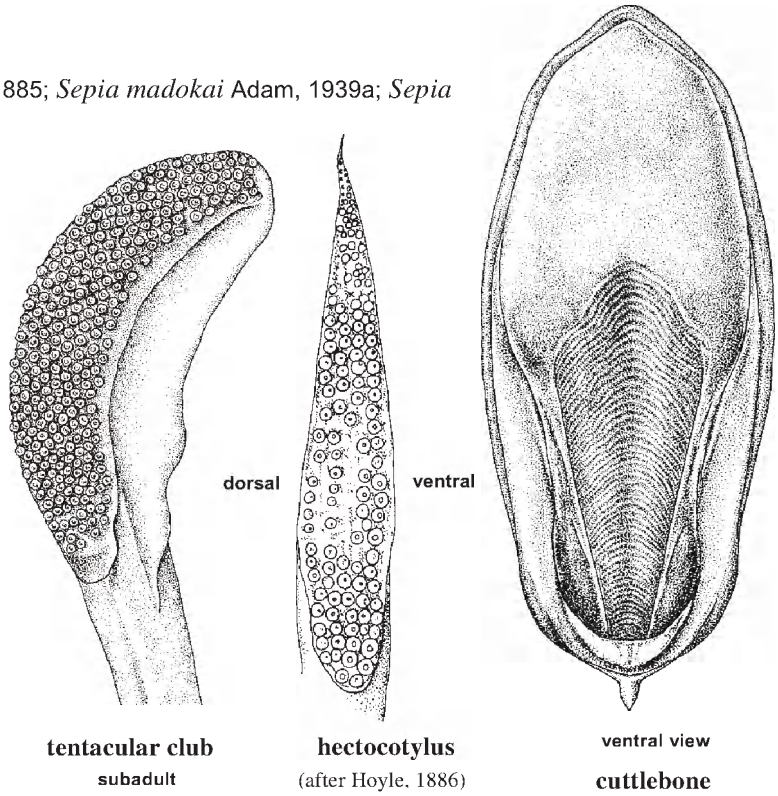


Fig. 134 *Sepia elliptica*

Diagnostic Features: Mantle oval; dorsal anterior margin triangular, acute. Male and female arm lengths subequal; protective membranes narrow. Arm suckers tetraserial. Hectocotylus present on left ventral arm: **7 or 8 rows of normal size suckers proximally**; **7 rows of reduced suckers medially**, then normal size suckers distally to arm tip. Suckers of hectocotylus in **2 dorsal series are smaller than ventral reduced suckers**; reduced suckers only slightly smaller than normal arm suckers; oral surface of modified region not wide, fleshy, but normal, as on opposite arm. Club sucker-bearing surface flattened, with **10 to 12 minute suckers in transverse rows**; suckers all similar size. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes joined at base of club; dorsal membrane forms shallow cleft at junction with stalk. Cuttlebone outline **oval**; bone **very angular, V-shape anteriorly**; bluntly rounded posteriorly; dorsal surface creamy white; dorsal surface evenly convex; texture smooth, not pustulose; dorsal median rib indistinct, broadens anteriorly; lateral ribs indistinct. Chitin surrounds entire margin of cuttlebone. Spine short, pointed, curves dorsally, keel(s) absent. Striated zone concave; last loculus convex; sulcus deep, wide. Anterior striae are **inverted U-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly; outer margin of inner cone **raised into flat posterior ledge**; ledge whitish (sometimes with a thin rim of chitin on outer margin); **ledge not thickened**; outer cone calcified.

Size: Up to 175 mm mantle length.

Geographical Distribution: Tropical Indo-Pacific: northern Australia from Western Australia, Exmouth Gulf, 22°23'S 114°06'E, to Queensland, Capricorn Island Group, 23°30'S 152°00'E, including Gulf of Carpentaria. Viet Nam and India (doubtful records) (Fig. 135)

Habitat and Biology: Depth range from 16 to 142 m. ***Sepia elliptica*** occurs mainly in coastal waters. This species was collected between 10 and 62 m in Gulf of Carpentaria surveys. A broad size range of both sexes was found to occur in the Gulf over most of the year, indicative of an extended spawning season. Several experimental studies were carried out on growth of this species in captivity; results showed that both water temperature and feeding levels affect somatic growth but with different effects on the muscular tissue development and protein composition. No direct relationship was found between individual growth rates and food availability.

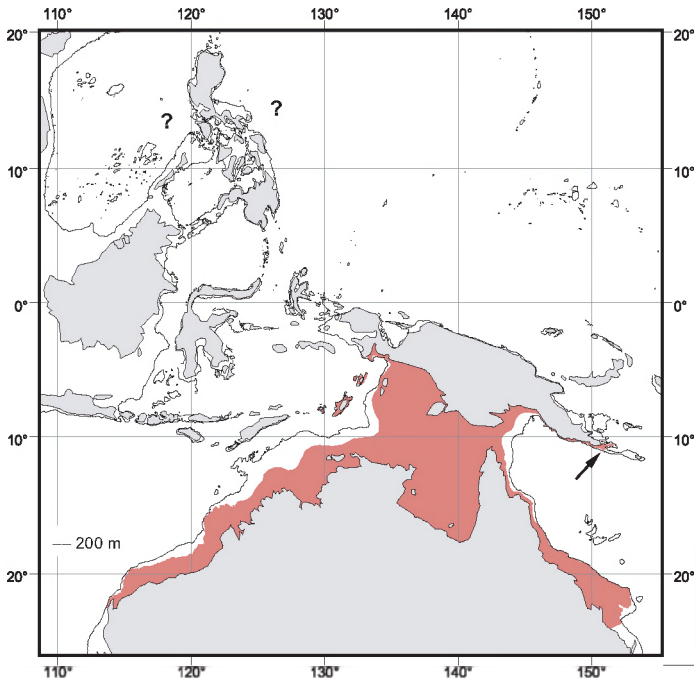


Fig. 135 *Sepia elliptica*
Known distribution

Interest to Fisheries: ***Sepia elliptica*** is taken as bycatch of prawn and mixed species trawl fisheries in most of its distributional area. The observed population structure in the Gulf of Carpentaria (Australia) by experimental trawl surveys and the relative high catch rates of trawlers in some areas suggest that ***S. elliptica*** is a promising resource for fishery there.

Remarks: This species may be confused with ***S. esculenta*** Hoyle, 1885 but it can be distinguished by the following characters: the hectocotylus of ***S. esculenta*** has 5 or 6 series of normal size-suckers, followed by 6 series of reduced suckers; in ***S. esculenta*** the dorsal and ventral protective membranes are not joined at the base of the club; in ***S. esculenta***, the cuttlebone is bluntly rounded anteriorly, the striae are inverted V-shape and the inner cone limbs are thickened posteriorly. Duc (1978, 1993) refers to ***S. elliptica*** in Vietnamese waters; however, this probably is a misidentification of ***S. esculenta***. The occurrence of ***S. elliptica*** in Indian waters is yet to be confirmed.

Literature: Adam and Rees (1966), Dunning *et al.* (1994), Lu (1998a), Moltschaniwskyj and Martinez (1998), Martinez *et al.* (2000), Moltschaniwskyj and Jackson (2000).

Sepia elobyana Adam, 1941 **Fig. 136**

Sepia elobyana Adam, 1941a, *Memoires du Musée royal d'Histoire naturelle de Belgique*, (2)21: 121 [type locality: Africa: west Africa, Gulf of Guinea, Eloby Island, 01°01'N 09°29'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Guinean cuttlefish; **Fr** – Seiche de Guinée; **Sp** – Sepia guineana.

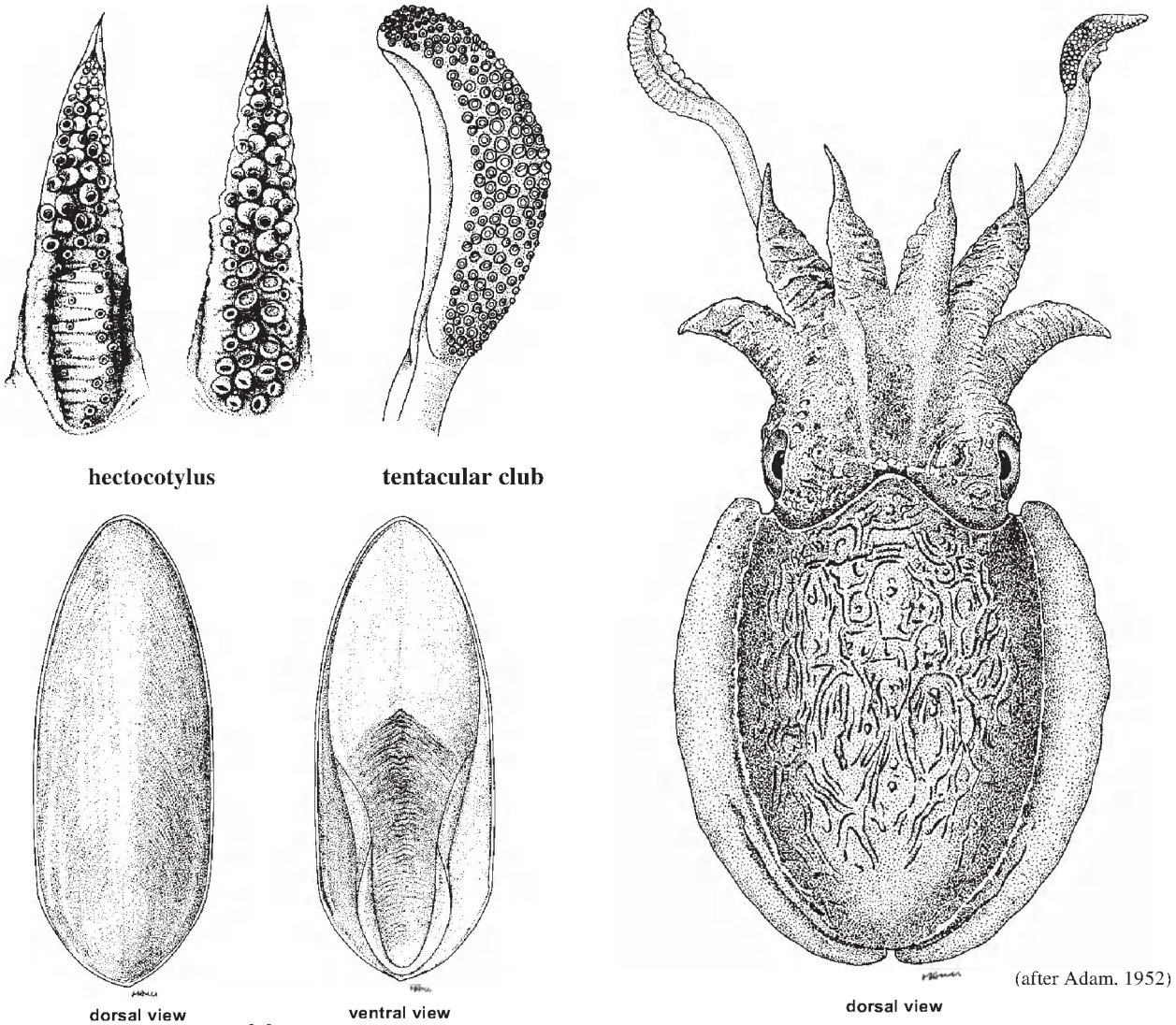


Fig. 136 ***Sepia elobyana***

Diagnostic Features: Small species. Mantle broad, oval; ventral mantle margin emarginate, with distinct lateral angles. Fins wide. Male and female arms subequal in length; protective membranes wide, well developed, particularly on modified portions of arms I and II in males. Distal tips of arms I and II **attenuate in both sexes**, with about 20 rows of globular suckers in males. Arm sucker arrangement differs between sexes: in males, **arms I to III suckers tetraserial proximally, biserial distally**; in females, **arms I and II suckers tetraserial proximally, biserial distally**. Male median arm suckers larger than dorsal and ventral marginal series on proximal end of arms. Hectocotylus present; **both ventral arms modified**. Left ventral arm with **7 or 8 rows of greatly reduced suckers** proximally, suckers normal size distally with suckers in **2 dorsal series smaller than 2 ventral rows** on modified portion of arm. Suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between, 2 ventral series close together, rows alternate, dorsal and ventral marginal suckers at base of protective membranes. Male right ventral arm suckers normal proximally for 2 transverse rows, followed distally by **4 or 5 rows of transformed suckers: median and sometimes lateral sucker rings wide (covering whole diameter of sucker) and thick**; teeth and infundibulum absent from these suckers. Club with **8 suckers in transverse rows**; suckers all of similar, small, size. Cuttlebone outline oval; acuminate, acute, anteriorly; bluntly rounded posteriorly; dorsal surface evenly convex; calcified with reticulate sculpture; dorsal median rib and lateral ribs absent. Spine a **blunt knob**. Striated zone separated from outer cone by broad, smooth, marginal zones; sulcus shallow, wide, bordered by some irregular grooves, extends along striated zone only. Anterior striae are **inverted U-shape** (slightly irregular due to grooves); limbs of inner cone extend anteriorly to end of striated zone. Inner cone limbs are narrow anteriorly, broaden posteriorly. Dorsal mantle has **scattered tubercles and reticulate pattern of ridges**.

Size: Up to 53 mm mantle length.

Geographical Distribution: Eastern Atlantic: along west African coast from Senegal to Gulf of Guinea and Gabon (southern limit undetermined) (Fig. 137).

Habitat and Biology: Unknown.

Interest to Fisheries: Possibly taken with other cuttlefishes off west Africa, but not distinguished from similar species.

Remarks: Very rarely reported species.

Literature: Adam and Rees (1966).

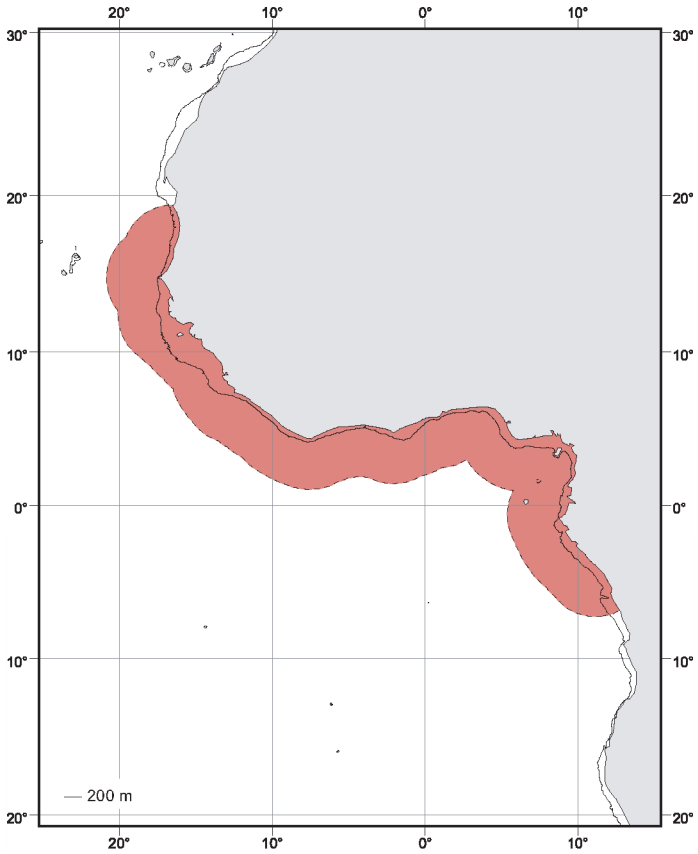


Fig. 137 *Sepia elobyana*
Known distribution

Sepia esculenta Hoyle, 1885 **Fig. 138**

Sepia esculenta Hoyle, 1885, *Annals and Magazine of Natural History*, (series 5)16: 188 [type locality: Japan].

Frequent Synonyms: None.

Misidentifications: *Sepia elliptica* Hoyle, 1885; *S. hoylei* Ortmann, 1888.

FAO Names: En – Golden cuttlefish; **Fr** – Seiche dorée; **Sp** – Sepia dorada.

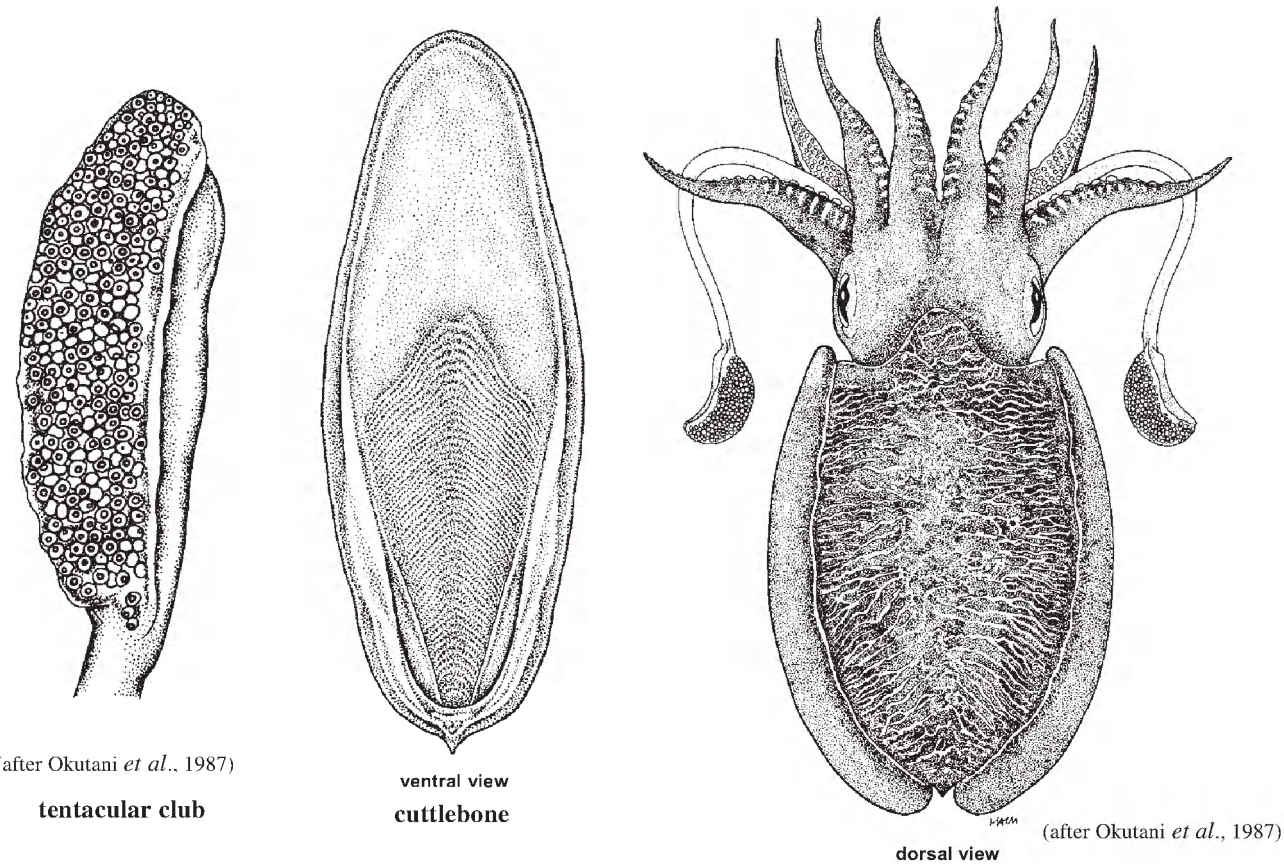


Fig. 138 ***Sepia esculenta***

Diagnostic Features: Mantle broadly oval; dorsal anterior margin triangular, obtuse; ventral mantle margin emarginate. Arm suckers tetraserial. Hectocotylus present on left ventral arm: **5 or 6 rows of normal size suckers proximally, 6 rows of reduced suckers medially**, then normal size suckers to arm tip. Club sucker-bearing surface flattened, with **10 to 16 suckers in transverse rows**; all club suckers of **similar, minute, size** (except for 2 enlarged suckers in anteriodorsal corner). Dorsal and ventral protective membranes **not joined** at base of club, extend proximal to carpus along stalk. Buccal membrane without suckers. Cuttlebone outline elliptical; bone bluntly rounded anteriorly and posteriorly; dorsal surface convex posteriorly, flat anteriorly; dorsal median and lateral ribs indistinct. Chitin present as wide patch posteriorly and a narrow chitinous rim borders lateral margins of cuttlebone. Spine present. Striated zone concave; last loculus flat; sulcus **deep, wide**. Anterior striae are **inverted V-shape**. Inner cone limbs are **narrow anteriorly, broaden posteriorly**; **raised into flat, thickened posterior ledge**; outer cone calcified, narrow anteriorly, broadens posteriorly. Dorsal mantle with longitudinal row of **6 or 7 yellowish, fleshy tubercles** at base of each fin. **Colour:** Light brown with whitish mottle. Dorsal mantle has faint light-coloured wavy transverse stripes and dark spots or blotches, sometimes studded with yellowish tubercles. Arms I to III have spots and a longitudinal orange-red pigmented stripe along their aboral surfaces. Fins with **pale golden** iridescent line along base, both dorsally and ventrally.

Size: Up to 180 mm mantle length, 600 g total weight.

Geographical Distribution: Indo-Pacific: East China Sea, Japan from central Honshu (Sea of Japan and Pacific sides) south to China and Hong Kong, Taiwan Province of China, South China Sea (north of central Philippines), Viet Nam and possibly Singapore and western Indonesia. The southernmost extent of its range is yet to be determined (Fig. 139).

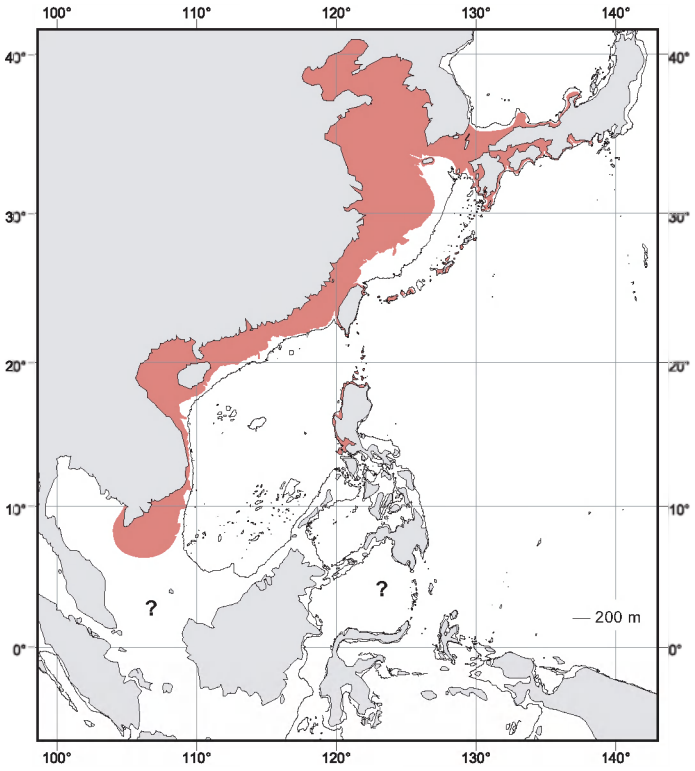


Fig. 139 ***Sepia esculenta***
Known distribution

Habitat and Biology: Depth range from 10 to 100 m, mainly inner shelf. This is a demersal neritic species found on sand, sometimes burrowing into the substrate. After overwintering in deeper water, animals migrate into shallower coastal waters where they spawn when the water temperature increases in spring. Males often guard females to ward off competing males. Before mating begins, the brilliance of the body colours of males increases dramatically, with coloration changing rhythmically from green to red and gold and the iridescent lines along the base of the fins appear to be fluorescent. Mating takes place head-to-head and spermatophores are placed in the female's buccal membrane ventral to the mouth. The eggs are of an amber colour immediately after laying, covered by a pear-shaped egg case, milky white and translucent. They are deposited on macrophytic algae and other substrates, such as sunken branches. The sticky, clear, outermost layer of the egg cases accumulates sand and other debris for camouflage as the embryonic development proceeds. Studies in captivity indicate that females prefer long, fine, and immobile materials as spawning substrates. The spawning season extends from spring to early summer. Hatching occurs after about 30 to 80 days, depending on the water temperature. Newly hatched animals already have schooling and benthic tendencies and bury themselves in the sand. ***Sepia esculenta*** feeds mainly on crustaceans and small fishes.

Interest to Fisheries: ***Sepia esculenta*** supports localized and subsistence fisheries in the Philippines, with animals collected in waters including the Visayan and Samar Seas, the Lingayen Gulf and Carigara Bay. It is the dominant ***Sepia*** species landed around the Shantung and Kiangsu provinces of China and off western Japan (East China Sea). Studies off Korea determined that maximum fishing conditions were characterized by a temperature range from 10° to 15°C and bottom salinity between 33.2 and 34.45‰. The principal capture techniques are otter trawls, pound nets, hoop nets and hook-and-line. The flesh is highly prized as food, especially in Japan, South Korea and China. In Japan, large-sized animals are consumed as sashimi, while smaller animals are marketed packed and frozen ready for cooking. This species has been reared to market size in experiments under laboratory conditions, at growth rates well above those in natural populations.

Local Names: CHINA: Gam woo chak, Jam mak yue; JAPAN: Hariika, Kouika, Maika, Sumiika.

Remarks: ***Sepia esculenta*** can be confused with ***S. elliptica*** Hoyle, 1885. In ***S. esculenta***, the inner cone ledge is thick and directed anterioventrally. In ***S. elliptica***, the ledge is much thinner, flatter and it points anteriorly, covering the posterior end of the phragmocone. The cuttlebone striae of ***S. elliptica*** are U-shaped and the bone is very angular, V-shaped anteriorly. The hectocotylus of ***S. elliptica*** differs in having 7 or 8 series of normal sized suckers, followed by 7 series of reduced suckers.

Literature: Adam and Rees (1966), Choe (1966), Baik and Park (1985), Fujita *et al.* (1997), Okutani *et al.* (1987), Natsukari and Tashiro (1991), Watanuki *et al.* (1993).

Sepia grahami Reid, 2001

Sepia grahami Reid, 2001b, *Proceedings of the Linnean Society of New South Wales*, 123: 160 [type locality: Australia: New South Wales, 29°33'S 153°25'E to 29°32'S 153°25'E].

Frequent Synonyms: None.

Misidentifications: *Sepia mestus* Gray, 1849; *Sepia rozella* (Iredale, 1926).

FAO Names: En – Ken's cuttlefish; **Fr** – Seiche de Ken; **Sp** – Sepia de Ken.

Diagnostic Features: Mantle oval. Fins wide, rounded posteriorly. Male and female arms **subequal in length**; protective membranes narrow; distal arm tips not attenuate. Arm suckers **tetraserial**. **Hectocotylus absent**. Club short, slightly recurved, sucker-bearing surface flattened, with **4 or 5 suckers in transverse rows (usually 4, rarely 5)**; suckers differ only slightly in size: **3 or 4 suckers slightly enlarged**. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes not joined at base of club; dorsal membrane extends proximal to carpus along stalk, ventral membrane terminates at proximal end of carpus. Gills with 23 to 26 lamellae per demibranch. Cuttlebone oval; dorsal surface creamy white, with slight pinkish tinge; dorsal median rib absent, lateral ribs indistinct. Spine with **ventral keel**. Striated zone concave, sulcus **shallow, narrow, indistinct**. Anterior striae are **inverted U-shape**; last loculus flat. Inner cone limbs are narrow strap-like anteriorly, broaden posteriorly. Inner cone limbs are **raised into rounded ledge posteriorly, ledge thickened, yellowish or ochre coloured**. Dorsal mantle with longitudinal rows of up to 6 ridges along each side, close to fins; prominent ear-shape lobe dorsal to eye and 2 lobes ventral to eye, anteriormost lobe largest. **Colour:** Pinkish brown. Mantle with **dorsal 'eyespots'**.

Size: Males up to 66 mm mantle length; females up to 82 mm mantle length.

Geographical Distribution: Southwestern Pacific: Australia, New South Wales, from southeast of Yamba area (29°32' 153°25'E) to off Tathra (36°44'S 150°05'E) (Fig. 141).

Habitat and Biology: Depth range from 2 to 84 m.

Interest to Fisheries: There is no official information on this species but it is commonly confused with *S. rozella* (Iredale, 1926) and *S. mestus* Gray, 1849. *Sepia rozella* commonly appears in fish markets in Sydney.

Literature: Reid (2001b).

Fig. 140

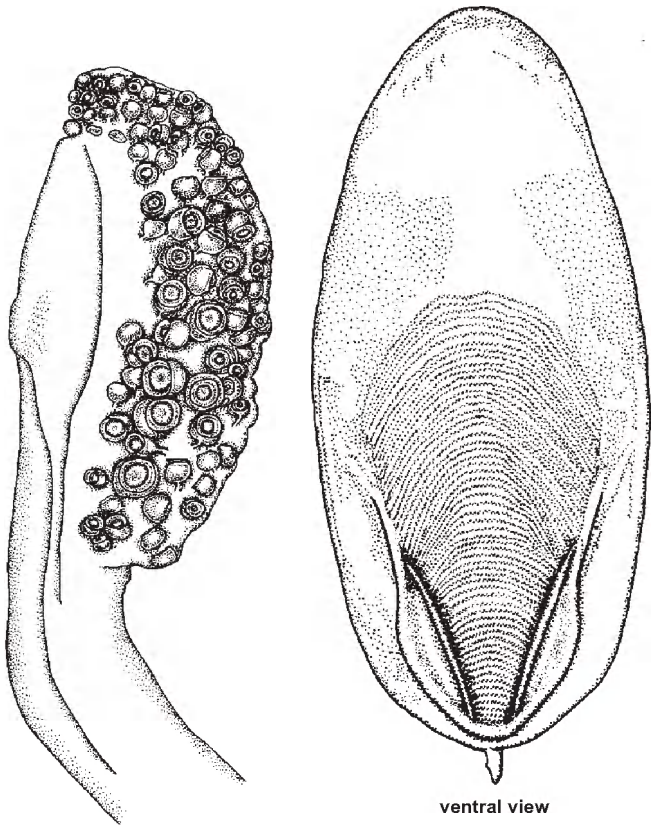


Fig. 140 *Sepia grahami*

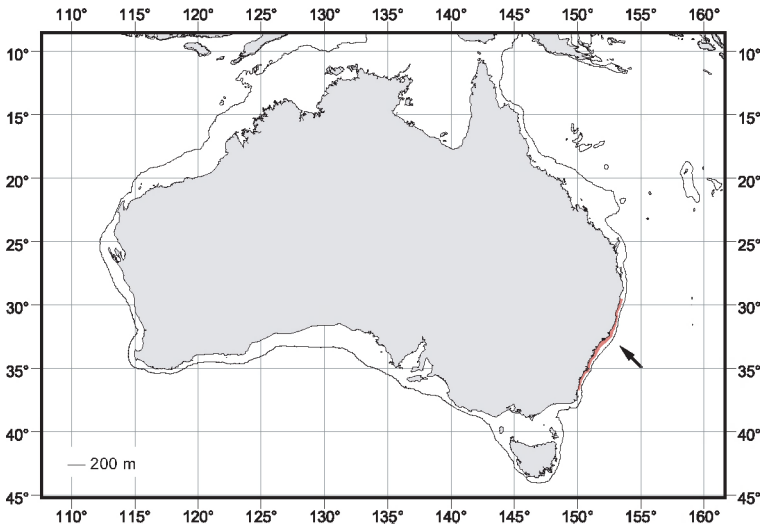


Fig. 141 *Sepia grahami*
Known distribution

Sepia hedleyi Berry, 1918

Fig. 142

Sepia hedleyi Berry, 1918, *Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour"* 1909–14, 4(5): 258 [type locality: South Australia, Investigator Strait area (35°25'S 137°22'E), south of Kangaroo Island (35°50'S 137°15'E)].

Frequent Synonyms: *Sepia dannevigi* Berry, 1918; *Decorisepia rex* Iredale, 1926.

Misidentifications: *Sepia vossi* Khromov, 1996 (as *S. rex*).

FAO Names: En – Hedley's cuttlefish; **Fr** – Seiche d'Hedley; **Sp** – Sepia de Hedley.

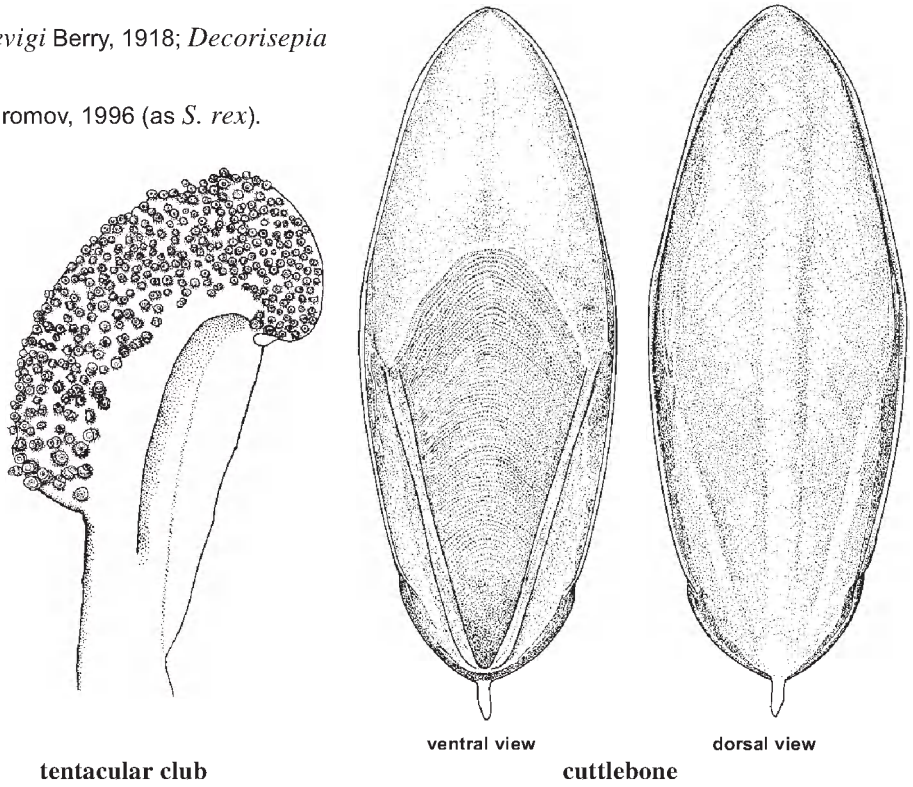


Fig. 142 *Sepia hedleyi*

Diagnostic Features: Mantle broad, oval. Fins widest in posterior third, rounded posteriorly, with narrow gap between them. Head short, broad, narrower than mantle. Male and female **arms subequal in length**; protective membranes narrow. Arm suckers **tetraserial**; male non-hectocotylized arm suckers smaller than female arm suckers in diameter. Hectocotylus present on left ventral arm: **6 to 8 rows of normal size suckers proximally, 9 or 10 rows of reduced suckers medially**. Suckers of hectocotylus in **2 dorsal series are much smaller than those in 2 ventral series**; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; 2 dorsal and 2 ventral series of suckers **displaced laterally**, with gap between; **suckers in 2 ventral series aligned in a single row**. Club crescent-shaped, moderate length, sucker-bearing surface flattened, with **9 to 12 suckers** in transverse rows; all club suckers of similar, small, size. Swimming keel of club **extends well proximal to carpus**; dorsal and ventral protective membranes **not joined at base of club** but are fused to tentacular stalk. Dorsal and ventral membranes same length; extend proximal to carpus along stalk. Gills with 29 or 30 lamellae per demibranch. Buccal membrane without suckers; in females extends ventrally with 2 spermathecae. Spermatophores 5.8 to 7.9 mm long. Eggs spherical, 2.5 to 3.1 mm diameter. Cuttlebone outline oblong; acuminate, **acute**, anteriorly and posteriorly; dorsal surface creamy white; dorsal surface evenly convex; granulose; spine and posterior tip of bone covered with smooth glaze-like substance. Dorsal median rib **distinct**; sides approximately parallel; ribs bordered laterally by distinct grooves; lateral ribs indistinct. Chitin surrounds entire margin of cuttlebone. Spine short, pointed, straight, parallel to bone, **keel(s) absent**. Striated zone flat; last loculus convex; sulcus shallow, narrow, extends entire length of cuttlebone. Anterior striae are **inverted U-shape**. Inner cone limbs are **uniform width, narrow V-shape** posteriorly, thickened, shiny; outer cone calcified, narrow anteriorly, broadens posteriorly. Dorsal mantle has longitudinal row of up to 6 ridge-like papillae along each side, adjacent to base of each fin. **Colour:** Buff pinkish brown. Arms without markings. Dorsal ridges orange-pink in colour.

Size: Males up to 83 mm mantle length; females up to 108 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: Australia, Queensland, from off the Great Barrier Reef, 22°35.3'S 153°46.7'E, southwards around southern Australia to Western Australia, southwest of Shark Bay, 27°07'S 112°49'E. Australian endemic (Fig. 143).

Habitat and Biology: Depth range from 47 to 1 092 m.

Interest to Fisheries: ***Sepia hedleyi*** is taken as bycatch of prawn and mixed species trawl fisheries.

Literature: Lu (1998a), Reid (2001a).

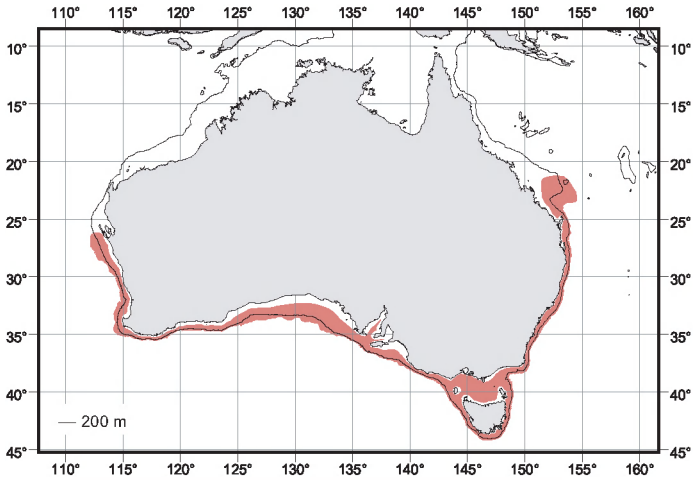


Fig. 143 *Sepia hedleyi*

Sepia hierredda Rang, 1835

Fig. 144

Sepia hierredda Rang, 1835, (*in* Férussac and d'Orbigny 1834–1848), *Histoire naturelle générale et particulière des Céphalopodes Acétabuliferes vivants et fossiles*, pl. 13 [type locality: western Africa].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Giant African cuttlefish; **Fr** – Seiche géante africaine; **Sp** – Sepia gigante africana.

Diagnostic Features: Hectocotylus present on left ventral arm: **6 rows of normal size suckers proximally, 8 to 14 rows of reduced suckers distally**. Club long, slightly recurved, with **5 or 6 suckers in transverse rows**; suckers differ in size: **5 or 6 median suckers twice diameter of rest**; club swimming keel extends slightly proximal to sucker-bearing surface. Cuttlebone outline oblong, lateral margins concave in anterior third; acuminate, acute, anteriorly; bluntly rounded posteriorly; dorsal median rib present, broadens anteriorly; median rib bordered laterally by distinct grooves; lateral ribs present. Spine present. Anterior striae **shallow m-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly; outer cone broadens posteriorly. **Colour:** Pattern very similar to that of ***Sepia officinalis***.

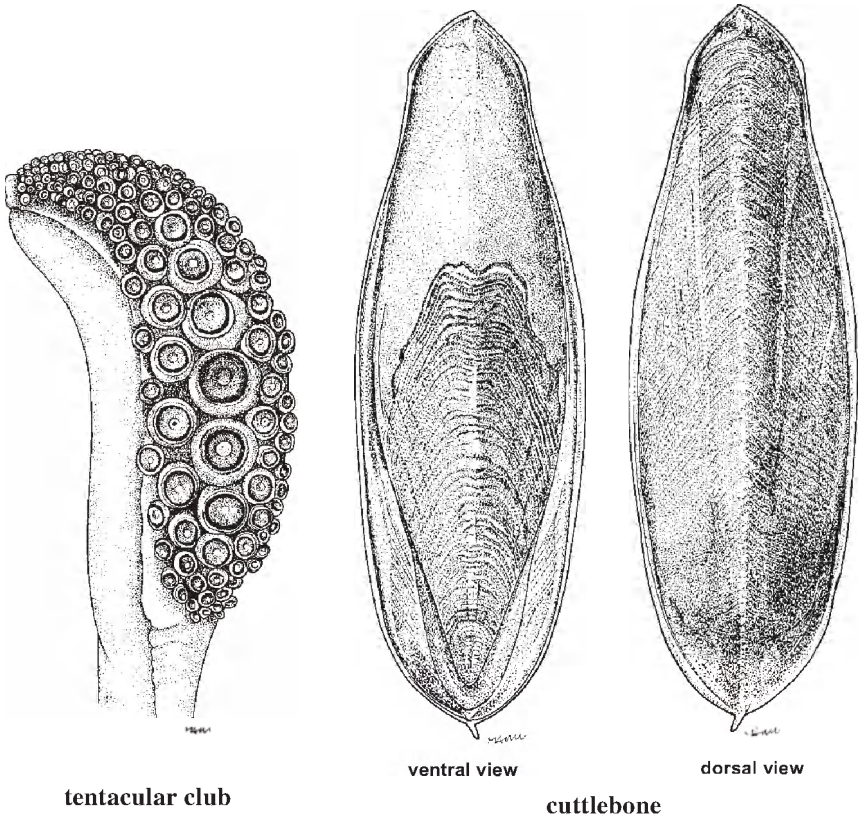


Fig. 144 ***Sepia hierredda***

Size: Up to nearly 500 mm mantle length; total weight over 7 500 g.

Geographical Distribution: Southeastern Atlantic: Africa, Cape Blanc (21°N), Mauritania (19°N) to Tigres Bay, Angola (16°30'S). Endeavour Bank (Fig. 145).

Habitat and Biology: Spawning occurs from February to September and the lifespan is 24 months. Migrations of ***S. hierredda*** occur off the west African coast. Females mature at 130 mm mantle length. In those areas where the distribution of ***S. hierredda*** overlaps that of ***S. officinalis***, the former species tends to be restricted to waters shallower than 50 m, while the distribution of ***S. officinalis*** extends to depths in excess of 100 m.

Interest to Fisheries: ***Sepia hierredda*** is the most commercially important cuttlefish in the east central Atlantic waters (from Cape Blanc, 21°N, to Cape Bojador, 26°N). It represents the dominant cuttlefish caught off Western Sahara and in Mauritania waters. Specific statistics are not available, but ***S. hierredda*** made up 90 and 65%, respectively, of the cuttlefishes caught in these areas by the Spanish fishery in recent years.

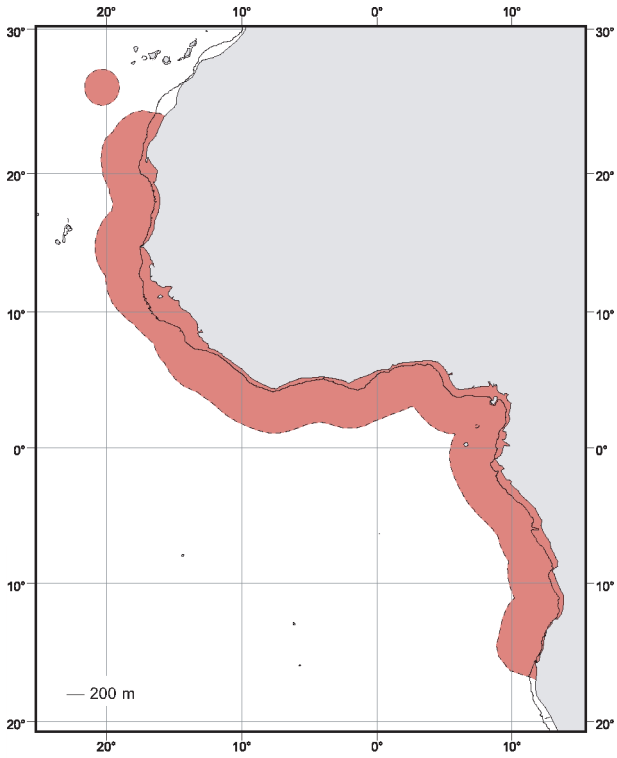


Fig. 145 ***Sepia hierredda***

Remarks: ***Sepia hierredda*** often was considered to be a subspecies of ***S. officinalis*** Linnaeus, 1758. However, the results of recent morphological and allozyme analyses strongly support the fact that ***S. officinalis*** and ***S. hierredda*** are different species. The 2 species can be distinguished as follows: the number of transverse rows of suckers is higher in ***S. hierredda*** than in ***S. officinalis***; for animals with the same mantle length, the length of the striated zone on the cuttlebone is shorter in ***S. officinalis*** from the northeastern Atlantic than in ***S. hierredda*** (for animals from the Canary Islands (central eastern Atlantic), however, this character is not useful since the striated zone is of the same length in both species); the mantle is narrower and the arms are shorter in ***S. hierredda*** than in ***S. officinalis***. The 2 species also differ at 13 allozyme loci. ***Sepia hierredda*** and ***S. officinalis*** are sympatric off the northwestern coast of Africa.

Literature: Hatanaka (1979), Bakhayokho (1983), Khromov *et al.* (1998), Guerra *et al.* (2001).

Sepia kobiensis Hoyle, 1885 — Fig. 146

Sepia kobiensis Hoyle, 1885, *Annals and Magazine of Natural History*, (series 5)16: 195 [type locality: Japan: Yokohama market (as var. *S. andreanoides*) and Bay of Kobe for *S. kobiensis*; Toyama Bay (as var. *toyamensis*); Beppu, Oita Prefecture (as var. *beppuana*); Enoura, Shizuoka Prefecture (as var. *crassa*); Korea Strait (as var. *albatrossi*)].

Frequent Synonyms: *Sepia andreanoides* Hoyle, 1885.

Misidentifications: *Sepia andreana* Steenstrup, 1875.

FAO Names: En – Kobi cuttlefish; **Fr** – Seiche kobi; **Sp** – Sepia kobi.

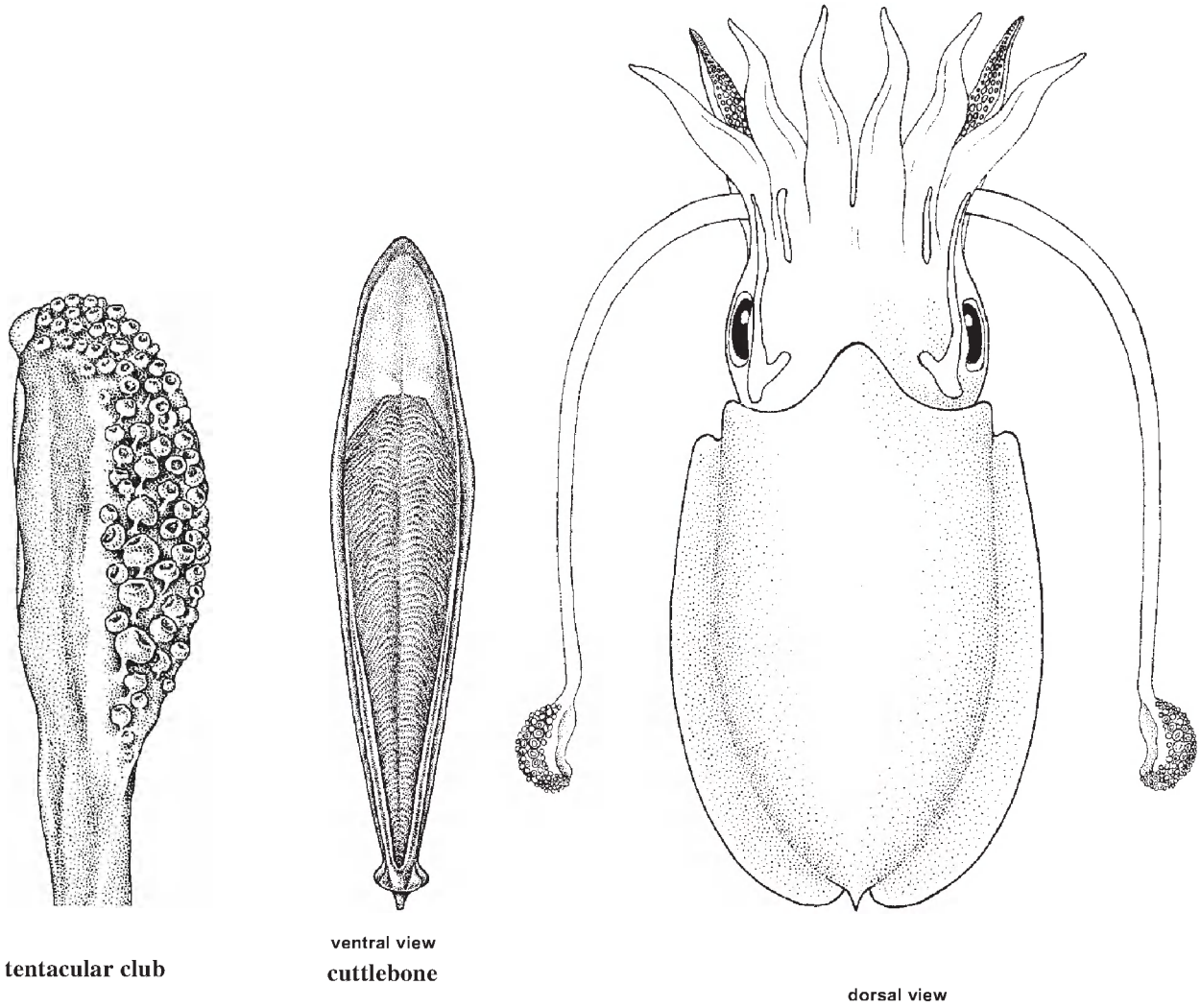


Fig. 146 ***Sepia kobiensis***

Diagnostic Features: Small species. Mantle oblong; dorsal anterior margin triangular, acute. Male and female arm lengths subequal, short. Arm suckers tetraserial, median rows larger than marginal rows; **suckers displaced laterally, with gap between on arms I to III**. Hectocotylus present on left ventral arm: **6 to 12 rows of normal size suckers proximally, 7 to 10 rows of greatly reduced suckers medially**, then normal size suckers to arm tip; oral surface of modified region **wide, swollen, fleshy, with transversely grooved ridges and deep median furrow**; suckers in **2 dorsal and 2 ventral series displaced laterally**, with gap between them. Club crescent-shaped, narrow; with **4 or 5 suckers in transverse rows**; suckers differ slightly in size: 4 or 5 suckers toward proximal end of club slightly larger than others. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes not joined at base of club. Cuttlebone **outline lanceolate**; acuminate anteriorly and posteriorly; dorsal surface pinkish, or yellowish; entire surface calcified with very fine granulose sculpture partly arranged in irregular longitudinal ridges and bordered laterally by 2 narrow calcareous ridges; dorsal median rib indistinct, broadens anteriorly. Chitin (trace only) borders lateral margins of cuttlebone. Spine long, pointed, directed dorsally. Striated zone and last loculus convex; sulcus shallow, narrow, extends entire length of cuttlebone. Anterior striae are inverted **m-shape**. Inner cone limbs are uniform width, narrow, U-shape posteriorly, thickened; outer cone calcified; limbs are **expanded posteriorly into 2 short 'wings'**, directed ventrally, to form a recurved cup-like structure. **Colour:** Reddish brown. Head with **V-shape reddish stripe on dorsal margins of eye orbits** and with **orange stripes extending from posterior end of head to basal portions of arms I to III**. Dorsal mantle has reddish spots.

Size: Up to 90 mm mantle length (usually 70 mm mantle length) and 80 g total weight.

Geographical Distribution: Indo-Pacific: off Japan, from southern part of Hokkaido, south to Kyushu (both coasts), Yellow Sea, East China Sea, Taiwan Province of China, Gulf of Tonkin, South China Sea, Philippines, Gulf of Thailand and the northern part of the Indian Ocean from the Persian Gulf, Arabian Sea and Bay of Bengal, Myanmar. Possibly the Banda Sea (Fig. 147).

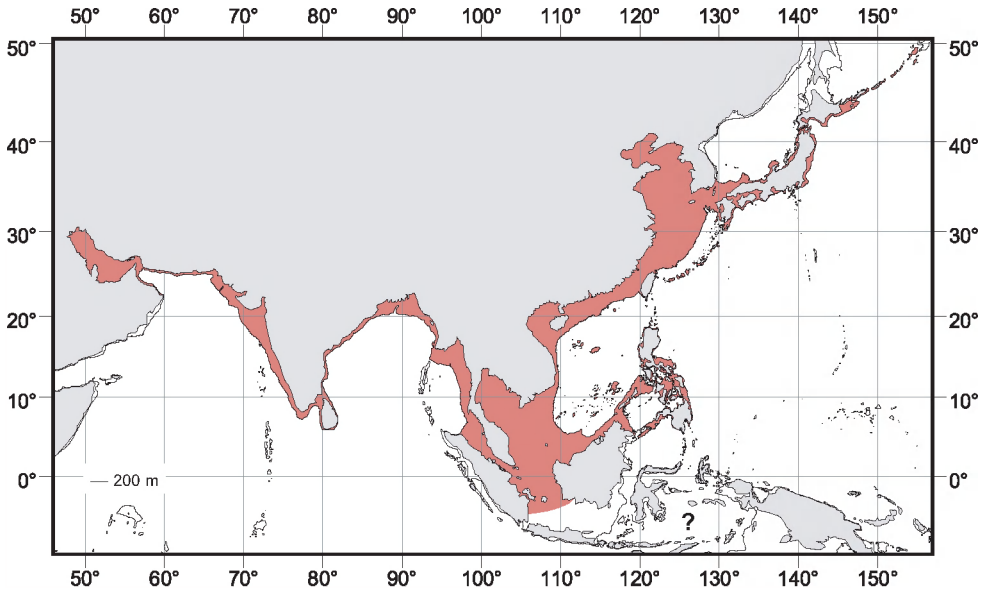


Fig. 147 ***Sepia kobiensis***
Known distribution

Habitat and Biology: Depth range subtidal to 200 m.

Interest to Fisheries: ***Sepia kobiensis*** is taken in small quantities between 80 and 160 m in the Hong Kong area, and it is also taken as bycatch in small- scale fisheries off southern Japan and in the Inland Sea, mainly with fixed nets, trawls and beach seines. It is an object of fisheries in China where it is abundant in shallow waters and locally utilized.

Local Names: JAPAN: Hime-kouika.

Remarks: ***Sepia kobiensis*** is probably a species complex. This requires investigation, particularly considering its significance in fisheries. This species has been confused with ***S. andreana*** Steenstrup, 1875, from which it is distinguished by several characters. All arms in adult ***S. kobiensis*** are similar in length, while in adult male ***S. andreana***, the second pair of arms is greatly elongate and bears biserial, rather than tetraserial suckers. The hectocotylus sucker arrangement in ***Sepia kobiensis*** follows a pattern of normal, reduced, then normal-sized suckers from the proximal to distal end of the arm, while in ***S. andreana***, some normal-sized suckers occur at the base of the hectocotylus, and the rest are reduced and very rudimentary. The club suckers differ markedly in size in ***S. andreana***, while those of ***S. kobiensis*** differ only slightly in size.

Literature: Adam and Rees (1966), Okutani *et al.* (1987).

Sepia latimanus Quoy and Gaimard, 1832

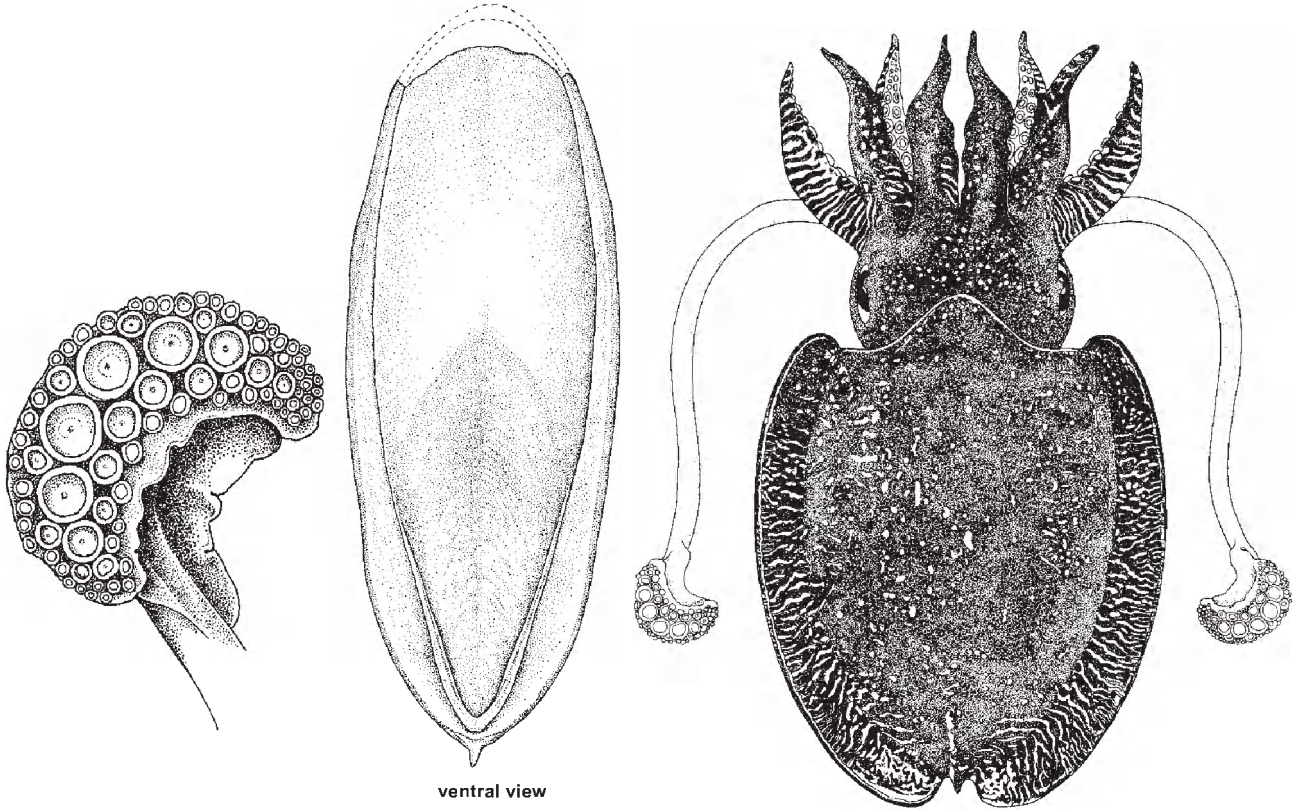
Fig. 148; Plate IV, 23–27

Sepia latimanus Quoy and Gaimard, 1832, *Voyage de découvertes de l'Astrolabe pendant les annees 1826–1827–1828–1829, Zoologie*, 2(1): 68 [type locality: New Guinea, Port Dorey, 00°51'S 134°01'E].

Frequent Synonyms: *Ponderisepia eclogaria* Iredale, 1926; *Sepia harmeri* Robson, 1928; *Sepia rappiana* Férussac, 1834 *in* Férussac and d'Orbigny (1834–1848); *Sepia mozambica* Rochebrune, 1884; *Sepia hercules* Pilsbry, 1894.

Misidentifications: None.

FAO Names: En – Broadclub cuttlefish; **Fr** – Seiche grandes mains; **Sp** – Sepia mazuda.



tentacular club

ventral view

cuttlebone

(illustration: K. Hollis)

dorsal view

(after Okutani *et al.*, 1987)

Fig. 148 ***Sepia latimanus***

Diagnostic Features: Mantle oval. Arm suckers tetraserial. **Hectocotylus absent**. Club crescent-shaped, **sucker-bearing surface flattened**, with **5 or 6 suckers in transverse rows**; suckers differ markedly in size: **some greatly enlarged**. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes **joined at base of club**; **separated from stalk by membrane**; dorsal membrane forms shallow cleft at junction with stalk. Buccal membrane without suckers. Cuttlebone bluntly rounded anteriorly and posteriorly; dorsal surface convex posteriorly, flat anteriorly; granulose (texture loosely arranged along growth lines); dorsal median rib and lateral ribs indistinct, or absent. Spine short, pointed, stout, keels absent. Striated zone concave; last loculus convex; sulcus **shallow, narrow**, extends entire length of cuttlebone. Anterior striae are **inverted V-shape**. Inner cone limbs are uniform width, narrow, U-shape posteriorly; thickened into a rounded, shiny ridge; outer cone calcified, narrow anteriorly, broadens posteriorly, deep cup-like. Dorsal mantle covered with numerous large papillae and with series of elongate papillae along each side, adjacent to base of each fin. Head papillose. **Colour:** Light brown, yellowish or dark brown (dark in males during courtship and breeding), with whitish mottle, blotches or spots. Arms have **longitudinal white bands on their margins** that appear as broad white blotches when the arms are extended, and arms I to III have broad, longitudinal brownish bands medially, extending onto head. Dorsal mantle has transverse saddle mark, small white and brown spots, narrow brown transverse bands, and bold, white, transverse stripes and spots dorsally (spots and blotches are present in most colour patterns; saddle-mark shown only occasionally; transverse stripes shown by males during the breeding season). In live animals, the eyes are typically yellow around the ventral margins. Fins pale with **white, transverse stripes** extending onto mantle and narrow, white, band along outer margin.

Size: Up to 500 mm mantle length and weight to 10 kg.

Geographical Distribution: Indo-Pacific: from southern Mozambique, throughout the periphery of the Indian Ocean, Malacca Strait, Melanesian Islands, South China Sea, Philippine Sea and East China Sea, Taiwan Province of China and Japan to southern Kyushu. Indonesia to northwestern and northeastern Australia (from Western Australia, Shark Bay, 25°25'S 113°35'E, across northern Australian waters to southern Great Barrier Reef, about 23°S, Queensland), the Coral Sea, Palau, Guam, New Caledonia, Fiji and Cocos (Keeling) Islands. Records from Madagascar and southeastern Australia doubtful (Fig. 149).

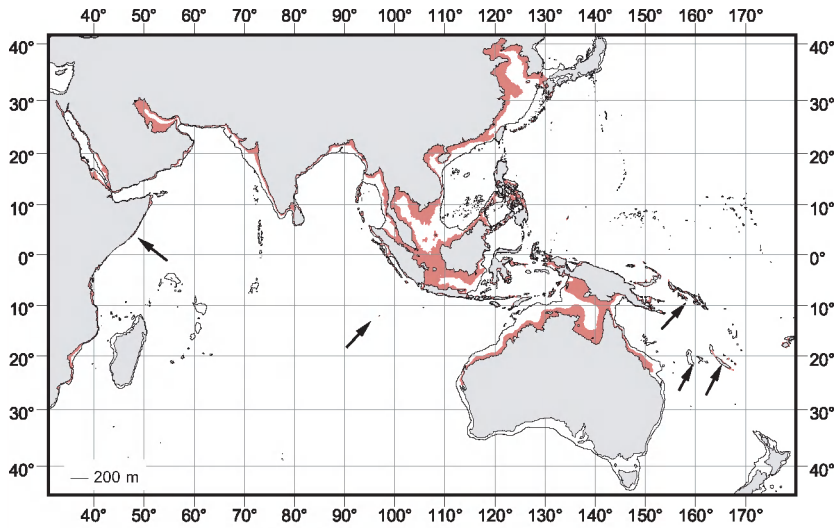


Fig. 149 ***Sepia latimanus***

Habitat and Biology: Depth to 30 m, weight to 10 kg. This shallow water species inhabits tropical coral reefs. Mating occurs on the west coast of Guam and off Okinawa in shallow water (30 m) from January to May, and the eggs hatch in 38 to 40 days. In the Alas Strait, Indonesia, males grow up to 170 mm (500 g), females 240 mm (1.3 kg) mantle length. ***Sepia latimanus*** is day active. During hunting it appears to mesmerize prey by displaying rhythmic colour bands along the body. It feeds on fishes and crustaceans. During the breeding season, males establish a territory, defending a coral head (typically *Porites*) among which females lay eggs following mating. Courtship is highly ritualized and stereotyped, and it incorporates striking visual displays. Males often guard females to ward off other males. Mating takes place head-to-head and spermatophores are placed in the females' buccal membrane ventral to the mouth. The eggs harden after laying and are very difficult to extract from the coral. They hatch after 4 to 6 weeks, and the young immediately hide among the coral and coral rubble. Juveniles often mimic mangrove leaves, their coloration and posture complete with the stem, ribs and scattered black spots.

Interest to Fisheries: ***Sepia latimanus*** is an important fisheries species throughout its range, taken by trawl, setnet, jig, handline and spear. It supports local fisheries in western Japan and the Philippines where it is caught with jigs, handlines, setnets and spears and it is common as bycatch in southeast Asian trawl fisheries. ***Sepia latimanus*** is fished in small quantities in the Ryukyus, China, near Taiwan Province of China and in the waters of Indo-China. In the Philippines, the large cuttlefishes, ***S. pharaonis*** Ehrenberg, 1831 and ***S. latimanus***, are split open dorsally, the cuttlebone and viscera removed, and the animals are dried in the sun without salt.

Local Names: INDONESIA: Sotong-besar; JAPAN: Kobushime, Kubushime.

Remarks: ***Sepia latimanus*** probably comprises a species complex. This requires investigation, particularly considering its fisheries significance. Khromov (1996) suggests that Duc's (1978) record of ***S. hercules*** Pilsbry, 1894 (a junior synonym of ***S. latimanus***) from Viet Nam actually is ***S. pharaonis***.

Literature: Adam and Rees (1966), Okutani *et al.* (1987), Hanlon and Messenger (1996).

Sepia longipes Sasaki, 1913 **Fig. 150**

Sepia longipes Sasaki, 1913, *Doubutsugaku Zasshi* [Zoological Magazine, Tokyo] 25(292): 78 [type locality: Japan: Choshi, Ibaraki Prefecture (Chiba Peninsula)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Longarm cuttlefish; **Fr** – Seiche pieuvre; **Sp** – Sepia brazolargo.

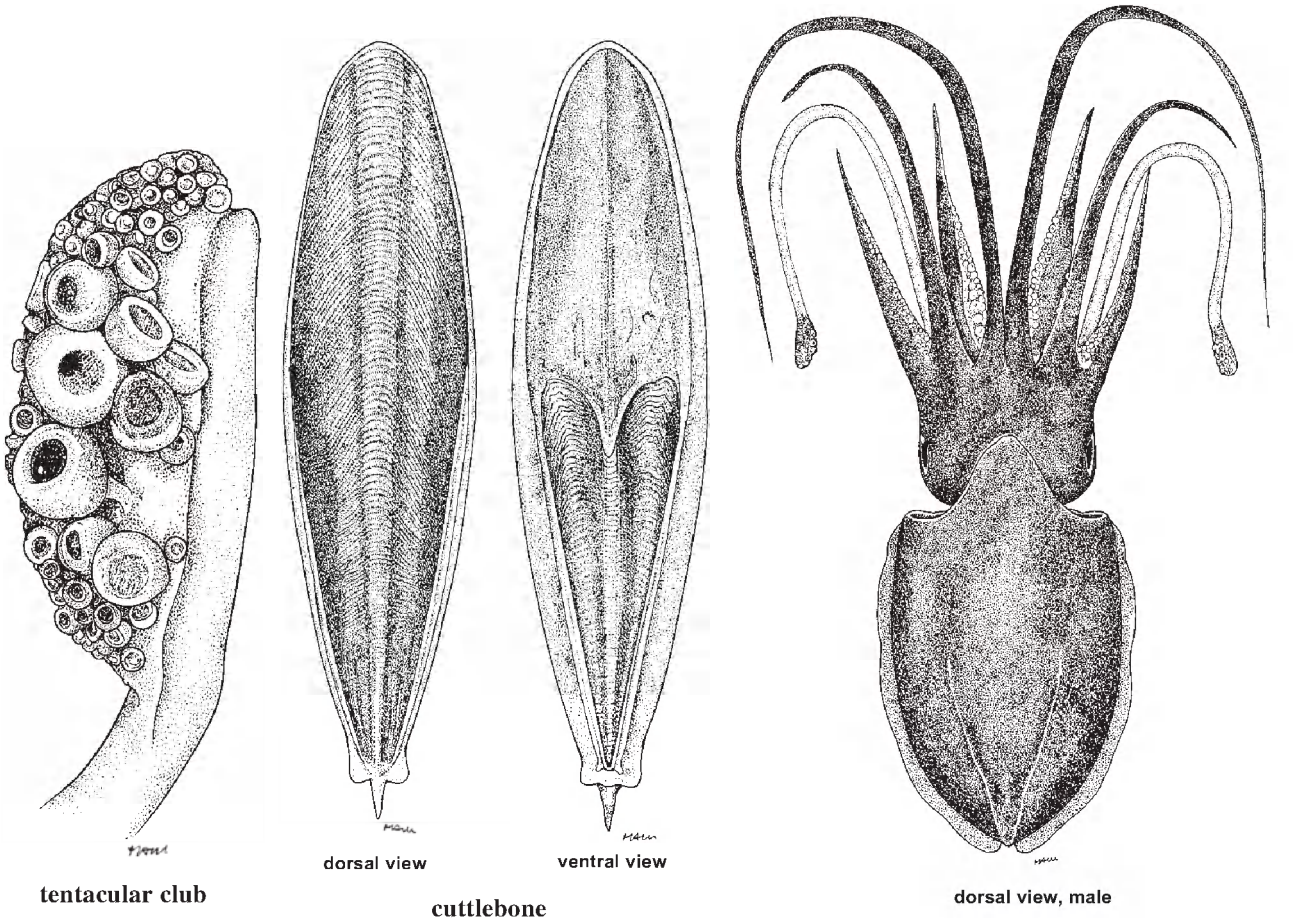


Fig. 150 *Sepia longipes*

Diagnostic Features: Dorsal anterior mantle margin triangular, acute; ventral mantle margin weakly convex. Fins wide, with very narrow gap between them. Male arms **I greatly elongate**, attenuate, whip-like, **about twice as long as other arms**, and arms II slightly elongate (relative lengths greater in large specimens); arms I with **biserial suckers on attenuated section**. Distal part of arms I thickened, bordered with long, broad trabeculae; protective membranes demarcated from proximal part by strong constriction; pedicels enlarged on distal portion of arm. Female arm lengths subequal (mostly shorter than mantle length). In males, suckers **on arms I tetraserial proximally, biserial distally, arms II to IV tetraserial**. Female arm suckers tetraserial. Sucker rings mainly smooth. Hectocotylus present; **both ventral arms modified**. Left ventral arm: sucker size normal proximally, **distal 40% of arm length with reduced suckers**; distal 40% furrowed longitudinally. Right ventral arm: **suckers reduced distally** after fourteenth row (not as much as on the left); oral surface of modified region (both ventral arms) wide, swollen, fleshy, with transversely grooved ridges. Club with **3 or 4 suckers in transverse rows**; suckers differ markedly in size: **4 or 5 greatly enlarged suckers** in longitudinal series towards posterior end of club. Cuttlebone outline **lanceolate**; bone bluntly rounded anteriorly; acuminate posteriorly; dorsal surface pinkish, granulose; dorsal median rib distinct, continuing to longitudinal groove on last loculus, rib broadens anteriorly. Spine moderate length, pointed, spindle-shape, pale pinkish. Striated zone convex, with a **high median ridge**; sulcus shallow, narrow, extends entire length of cuttlebone; **sulcus flanked by rounded ribs bordered laterally by shallow grooves**. Anterior striae **shallow m-shape**. Inner cone limbs are uniform width, narrow V-shape posteriorly; slightly raised into rounded, shiny posterior ridge; outer cone chitinous laterally, calcareous in expanded posterior part; outer cone limbs are **expanded posteriorly into 2 short 'wings'**, directed ventrally, to form a recurved cup-like structure. **Colour:** Pale brownish or purplish brown. Arms I to III have a **longitudinal orange-red pigmented stripe along their aboral surfaces**. Dorsal mantle has chromatophores concentrated medially above cuttlebone and scattered reddish spots.

Size: Up to 250 mm mantle length; 1 kg total weight.

Geographical Distribution: Northwestern Pacific: Japan, Chiba Peninsula to southern Kyushu and East China Sea (Fig. 151).

Habitat and Biology: Depth range from 100 to 300 m.

Interest to Fisheries: Occasionally trawled in southwestern Japan.

Local Names: JAPAN: Tenaga-kouika.

Remarks: This species is similar to ***S. lorigera*** Wülker, 1910, but differs in having a broader body, the first arm pair attenuate, whip-like and the cuttlebone with a high median ridge and a moderate spine.

Literature: Okutani *et al*. (1987).

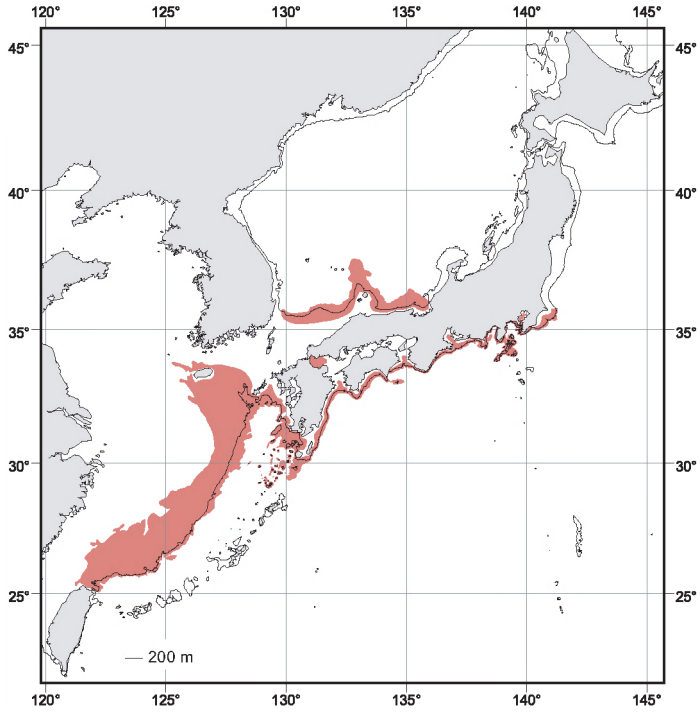


Fig. 151 ***Sepia longipes***
Known distribution

Sepia lorigera Wülker, 1910

Fig. 152

Sepia lorigera Wülker, 1910, *Abhandlungen der mathematische-physikalische Klasse der Köeniglich Bayerischen Akademie der Wissenschaften*, 3(Suppl. 1): 12 [type locality: Japan: Misaki].

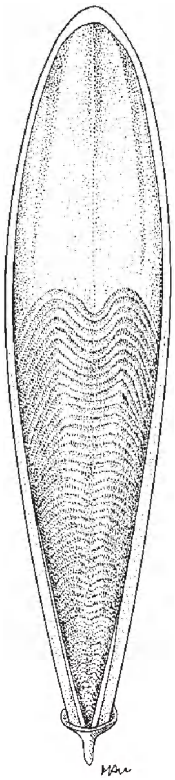
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Spider cuttlefish; **Fr** – Seiche araignée; **Sp** – Sepia loriga.

Diagnostic Features: Mantle oval (width about 40% of mantle length); dorsal anterior margin triangular, acute. Fins narrow, equal in width throughout. Male **arms I greatly elongate** (more than 1 1/2 times longer than mantle length, 3 times as long as other arms); arms I **narrow proximally, flared distally, protective membranes broad**; middle portion of arm I slender with enlarged protective membrane supported by trabeculae. Female arm lengths subequal. Non-hectocotylized arm sucker arrangement same in both sexes: suckers on **arms I to III tetraserial proximally, biserial at distal tips**; **arms IV suckers tetraserial** (in males, distal suckers arms I and II rudimentary, minute, on swollen pedicels). Hectocotylus present on left ventral arm: sucker size normal proximally, suckers **reduced in size on distal 1/3 and sucker pedicels swollen**. Club with 4 suckers in transverse rows; suckers **differ markedly in size**: 3 or 4 extremely large suckers surrounded by several moderately large suckers. Swimming keel of club extends proximally slightly beyond carpus. Cuttlebone **outline lanceolate**; acuminate, acute, anteriorly and posteriorly; dorsal surface pinkish; dorsal median rib indistinct, sides approximately parallel, bordered by grooves. Spine long, pointed. Anterior striae **shallow m-shape**. Inner cone limbs are uniform width, narrow, U-shape posteriorly; slightly raised into wide, V-shape, slightly thickened ridge; outer cone limbs are expanded posteriorly into 2 short 'wings', directed ventrally, to form small recurved cup-like structure. **Colour:** Reddish brown. Head with scattered red spots and chromatophores concentrated medially and over eye orbits. Arms have reddish spots. Ventral mantle pale, with **narrow longitudinal bands of brownish pigment with curved teardrop-shape ends on each side, adjacent to fins**.

Size: Up to 250 mm mantle length; 1 kg total weight.



ventral view

cuttlebone

Fig. 152 ***Sepia lorigera***

Geographical Distribution: Northwestern Pacific: southern and southwestern Japan from Sagami Bay to the East China Sea via the Pacific coast of Shikoku. South China Sea, Viet Nam (Fig. 153).

Habitat and Biology: Depth range from 100 to 300 m.

Interest to Fisheries: Object of minor fishery, occasionally caught by trawlers off southwestern Japan.

Local Names: JAPAN: Usubeni-kouika.

Remarks: The relative lengths of the attenuated arms increase with the size of the animal. This species is similar to the Australian species ***S. tanybracheia*** Reid, 2000, but in ***S. tanybracheia*** the dorsal arms are not as proportionally elongate and the enlarged club suckers are not as large as those of ***S. lorigera***. The distinctive ventral pigment bands are not present in the Australian species.

Literature: Okutani *et al.* (1987).

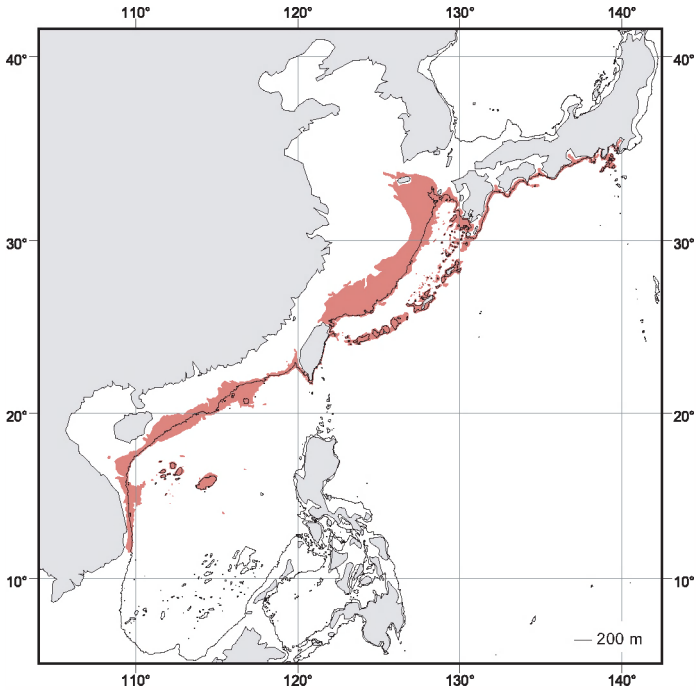


Fig. 153 ***Sepia lorigera***
Known distribution

Sepia lycidas Gray, 1849

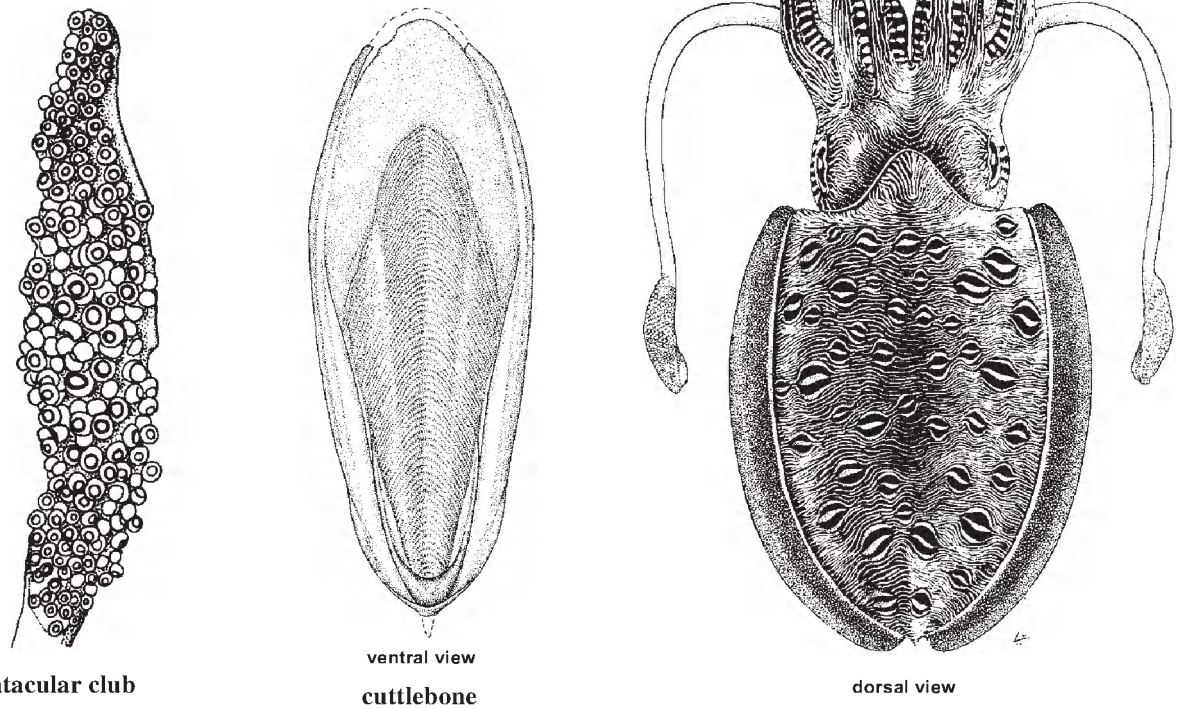
Fig. 154

Sepia lycidas Gray, 1849. *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Antepedia*, 103 [type locality: Guangzhou (China)].

Frequent Synonyms: *Sepia subaculeata* Sasaki, 1914.

Misidentifications: None.

FAO Names: En – Kisslip cuttlefish; **Fr** – Seiche baisers; **Sp** – Sepia labiada.



tentacular club
(after Okutani *et al.*, 1987)

cuttlebone

Fig. 154 ***Sepia lycidas***

Diagnostic Features: Mantle elliptical; dorsal anterior margin triangular, acute; ventral mantle margin emarginate. Fins end posteriorly in lobes, with only a small slit between them. Arm suckers tetraserial. Hectocotylus present on left ventral arm: 6 rows of normal size suckers proximally, 4 rows of reduced suckers distally. Club with **8 suckers in transverse rows** (more than 200 in number), all club suckers of similar, small size. Swimming keel of club shorter than carpus, extends from proximal 1/3 to distal tip of club. Dorsal and ventral protective **membranes not joined at base of club**, extend as membranous ridges along entire stalk. Buccal membrane with a **few, minute suckers** (single sucker on most lobes). Cuttlebone outline oblong; bone bluntly rounded anteriorly and posteriorly; dorsal surface evenly convex; dorsal median rib absent. Chitin present as wide patch posteriorly and a narrow chitinous rim borders lateral margins of cuttlebone. Spine short, pointed. Sulcus **deep, wide**. Anterior striae are **inverted V-shape**. Inner cone limbs are **thickened posteriorly, broaden into a rounded ridge**; outer cone calcified; narrow anteriorly, broadens posteriorly. **Colour:** Reddish brown or purple. Dorsal mantle has **scattered ocellate patches** and narrow, irregular, light-coloured, transverse stripes (pattern more prominent in males than females). Wide stripe adjacent to fins.

Size: Up to 380 mm mantle length. Maximum weight 5 kg.

Geographical Distribution: Indo-Pacific: southwestern Japan, south of Boso Peninsula from southern Honshu and Chingtao, Korea, to East China Sea, Taiwan Province of China and South China Sea, Philippine Sea, Viet Nam and Borneo. In the Gulf of Thailand it occurs south of 10ºN, but never appears in the inner and eastern coasts. Commonly distributed in the Andaman Sea. Western limit of range unknown (Fig. 155).

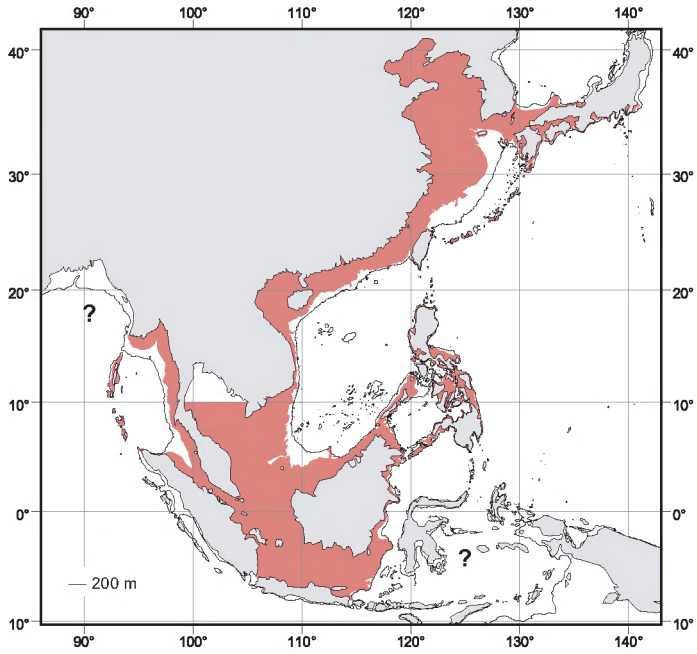


Fig. 155 ***Sepia lycidas***
Known distribution

Habitat and Biology: ***Sepia lycidas*** is a neritic demersal species with a depth range of 15 to 100 m. In the Gulf of Thailand and the Andaman Sea, most animals are caught between 20 and 40 m. The sex ratio of male to female animals caught in the Gulf of Thailand is 1:2. ***Sepia lycidas*** spends the winter at around 60 to 100 m, then moves into shallow waters to spawn in spring and early summer. In the South China Sea, it is abundant between 60 and 100 m depth in the prespawning period (November–February), then it migrates inshore to spawn in depths of 15 to 30 m from March to May. Immediately after laying, the eggs are shaped like hen eggs, and are amber coloured, like those of ***S. esculenta*** Hoyle, 1885. The egg case is pear-shaped and one of its pointed ends is bifurcated, to attach the egg to small twigs and other solid substrates. The newly hatched young individuals already show the adult benthic tendencies and bury themselves into the sand, but no schooling behaviour has been observed.

Interest to Fisheries: ***Sepia lycidas*** is an important commercial species in Japan, China, South Korea, Viet Nam and Thailand. Most cuttlefishes are caught off Thailand using otter trawl, with smaller catches made using pair trawl and to a lesser extent, squid light-lures, traps and push nets; bottom otter and pair trawls are used offshore, while push nets and lift nets are used in inshore and coastal waters. This species is the secondmost important commercial cuttlefish in Hong Kong and Japan, caught as bycatch in trawls and with setnets and jigs, or by using live cuttlefishes as lures during the spawning season, and by hook, baited with live prawns or crabs, in other seasons. The mantle flesh is thick and tasty and is, therefore, highly esteemed. The species has been reared successfully in aquaculture experiments under the name ***Sepia subaculeata***. Research indicates that waste materials obtained during the processing of this species have potential in supplementing the skin of land vertebrates as a source of collagen.

Local Names: CHINA: Fa gai na, Mak gung, Yi muk woo chak; JAPAN: Kaminari-ika, Mongouika.

Literature: Adam and Rees (1966), Choe (1966), Voss and Williamson (1971), Okutani *et al.* (1987), Natsukari and Tashiro (1991), Nagai *et al.* (2001).

Sepia madokai Adam, 1939

Fig. 156

Sepia madokai Adam, 1939a, *Siboga - Expeditie. Resultats des expeditiones zoologiques, botaniques, oceanographiques et entreprises aux Indes Neerlandaises Orientales en 1899–1900*, 55b: 77 [type locality: Japan, Tokyo Bay and Kagoshima].

Frequent Synonyms: *Sepia robsoni* Sasaki, 1929 (non *S. robsoni* Massy, 1927).

Misidentifications: *Sepia acuminata* Smith, 1916; *Sepia hedleyi* Berry, 1918.

FAO Names: En – Madokai's cuttlefish; **Fr** – Seiche madokai; **Sp** – Sepia madokai.

Diagnostic Features: Mantle elliptical; dorsal anterior margin triangular, acute; ventral mantle margin emarginate, without distinct lateral angles. Hectocotylus present on left ventral arm: sucker size normal proximally, **10 rows reduced suckers medially**, then normal size suckers to arm tip. Suckers of hectocotylus in **2 dorsal series are smaller than those in 2 ventral series**. Club crescent-shaped, sucker-bearing surface flattened, with **8 to 10 equal-sized, small suckers in transverse rows**. Cuttlebone length approximately equal to mantle length; outline oblong, nearly rhomboidal; acuminate, acute, anteriorly; bluntly rounded posteriorly; dorsal surface pinkish; dorsal median and lateral ribs indistinct. Spine present, keel(s) absent. Anterior striae are **inverted U-shape**. Inner cone limbs are of **uniform width, narrow, U-shape posteriorly**, thickened, very slender; not raised into ledge posteriorly; outer cone calcified, narrow anteriorly, broadens posteriorly. **Colour:** Pale brownish. Dorsal mantle has white blotches or spots.

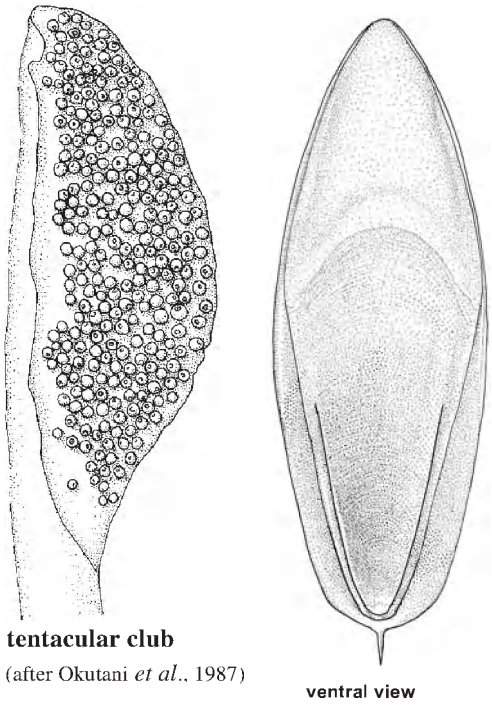


Fig. 156 ***Sepia madokai***

Size: Up to 100 mm mantle length, 100 g total weight.

Geographical Distribution: Northwestern Pacific: southwestern Japan, south of Tokyo Bay on the Pacific Coast and south of Noto Peninsula on the Japan Sea side to Kyushu. Tsushima Strait, East and South China Seas, Taiwan Province of China and Viet Nam (Fig. 157).

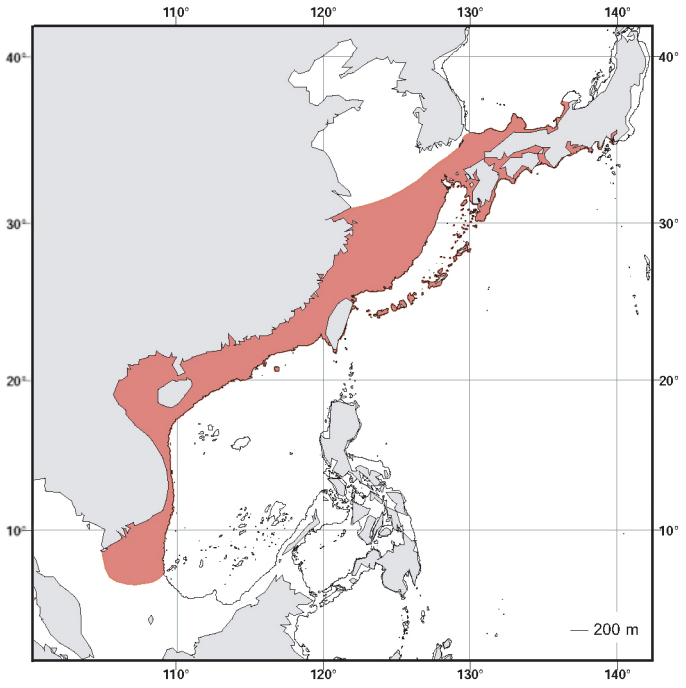


Fig. 157 ***Sepia madokai***
Known distribution

Habitat and Biology: Depth range from 20 to 200 m. ***Sepia madokai*** is a demersal species, most common in bays. It is believed that in years characterized by intensification of warm currents and high temperatures in coastal waters this thermophilic cuttlefish may migrate to areas in the northern Sea of Japan.

Interest to Fisheries: This species is common in the inland sea area of Japan, where it is fished with bottom drift nets and trawls. Due to its small size, it has limited commercial value. It often is caught with ***Sepia esculenta***, particularly in inland seas and bays off Japan. It is a minor object of fisheries in Japan and China (e.g. Peter the Great Bay).

Local Names: JAPAN: Kouika-modoki, Hari-ika.

Remarks: ***Sepia madokai*** has been confused with ***S. acuminata*** Smith, 1916 and as ***S. rex*** (a synonym of ***S. hedleyi*** Berry, 1918). In ***S. madokai***, the reduced suckers of the hectocotylus differ in size, with those of the 2 dorsal rows much smaller than those of the 2 ventral rows. In ***S. hedleyi*** all reduced hectocotylus suckers are similar in size. The club has 8 oblique rows of suckers in ***S. madokai***, rather than 9 to 12 as seen in ***S. hedleyi***. The cuttlebone is bluntly rounded posteriorly, the dorsal median ribs faint and the inner cone limbs broaden posteriorly in ***S. madokai***; in ***S. hedleyi***, the cuttlebone is acuminate posteriorly, the median ribs are distinct, and the inner cone limbs are uniform width along the length of the cuttlebone.

Literature: Adam and Rees (1966), Okutani *et al.* (1987), Shevtsov (1996), Kubodera and Yamada (1998), Lu (1998b).

Sepia murrayi Adam and Rees, 1966 — Fig. 158

Sepia murrayi Adam and Rees, 1966, *John Murray Expedition 1933–34, Scientific Reports*, 11(1): 63 [type locality: Gulf of Oman, 25°35'00"N 56°42'18"E to 25°43'00"N 56°39'18"E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Frog cuttlefish; **Fr** – Seiche grenouille; **Sp** – Sepia rana.

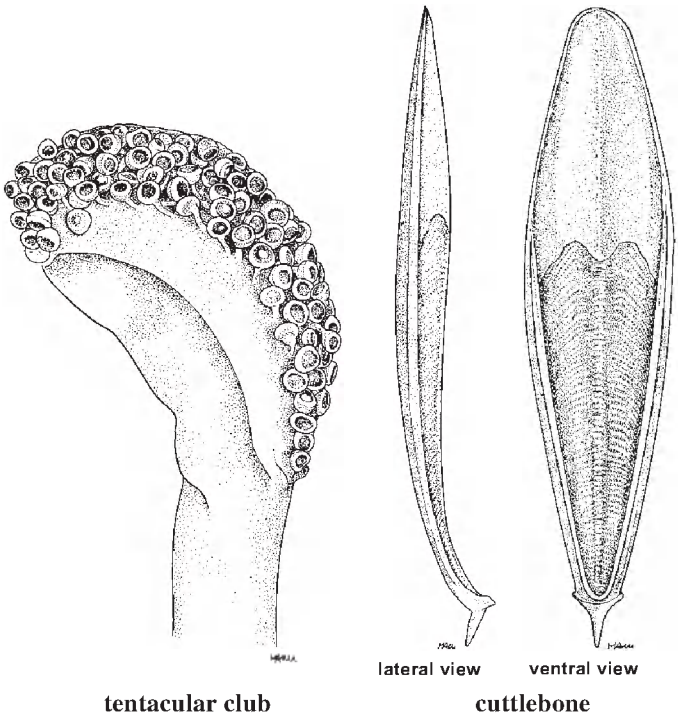


Fig. 158 *Sepia murrayi*

Diagnostic Features: Mantle oblong; dorsal anterior margin triangular, acute. Fins wide, ending in lobes posteriorly, with a narrow gap between them. Protective membranes in both sexes wide, well developed. Distal arm tips bluntly pointed in females, suckers enclosed by protective membranes. In females, suckers on arms I and II **biserial**, suckers arms III and IV **tetraserial proximally, biserial distally** (arms III may be biserial throughout); female distal biserial suckers **minute and displaced laterally, with distinct gap between**. Club crescent-shaped, short, curved posteriorly; with **5 suckers in transverse rows**; all club suckers of **similar, small, size**. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club** but fused to tentacular stalk, extend proximal to carpus along stalk as narrow ridges; **dorsal membrane much wider than ventral membrane** (nearly as wide as sucker-bearing surface). Cuttlebone outline lanceolate; strongly recurved ventrally; entire surface calcified with reticulate granulose sculpture concentrated posteriolaterally and posteriorly in irregular longitudinal ridges; dorsal median rib indistinct, flanked by shallow grooves; lateral ribs distinct. Chitin borders lateral margins of cuttlebone. Spine straight, directed dorsally, keels absent. Sulcus shallow, narrow, flanked by rounded ribs, extends **entire length of cuttlebone**. Anterior striae **shallow m-shape**; inner cone lateral limbs are separated from outer cone by smooth zones. Inner cone limbs are narrow anteriorly, broaden posteriorly, U-shape, raised into **flat posterior V-shape ledge**; inner cone posteriorly with irregular calcareous ribs radiating into outer cone; outer cone calcified, narrow, limbs are expanded posteriorly into 2 very short 'wings', directed ventrally, to form a recurved cup-like structure.

Size: Up to 41 mm mantle length.

Geographical Distribution: Northwestern Indian Ocean: Gulf of Oman, Gulf of Aden, Somalia (Fig. 159).

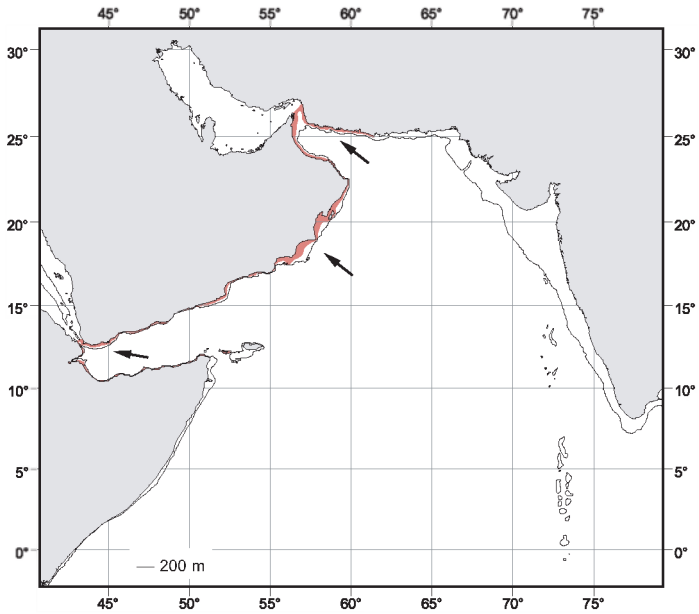


Fig. 159 *Sepia murrayi*
Known distribution

Habitat and Biology: A neritic demersal species; depth range still undetermined (the only record is 106 m).

Interest to Fisheries: Reported from a bottom trawl resource survey in the Gulf of Aden; its relevance to artisanal or industrial fisheries is undetermined.

Remarks: The males of this species are unknown. ***Sepia murrayi*** differs from ***S. kobiensis*** Hoyle, 1885 in having subequal rather than variously-sized suckers. The dorsal calcareous granules are also more pronounced in ***S. kobiensis***. The inner cone does not have a ventral ledge in ***S. kobiensis*** and the bone lacks the radiating calcareous ribs on the outer cone. The cuttlebone is similar to ***S. burnupi*** Hoyle, 1904 and ***S. trygonina*** (Rochebrune, 1884), but in ***S. murrayi*** the striae differ and the limbs of the inner cone are more divergent and with much sharper edges. The inner cone of ***S. murrayi*** is similar to that of ***S. omani*** Adam and Rees, 1966, but in ***S. omani*** the spine is keeled and the soft parts differ.

Literature: Adam and Rees, 1966.

Sepia officinalis Linnaeus, 1758

Fig. 160; Plates IV, 28 and V, 29–30

Sepia officinalis Linné, 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis*, 658 [type locality: eastern North Atlantic].

Frequent Synonyms: *Sepia filliouxi* Lafont, 1869; *Sepia mediterranea* Ninni, 1884.

Misidentifications: None.

FAO Names: En – Common cuttlefish; **Fr** – Seiche commune; **Sp** – Sepia común.

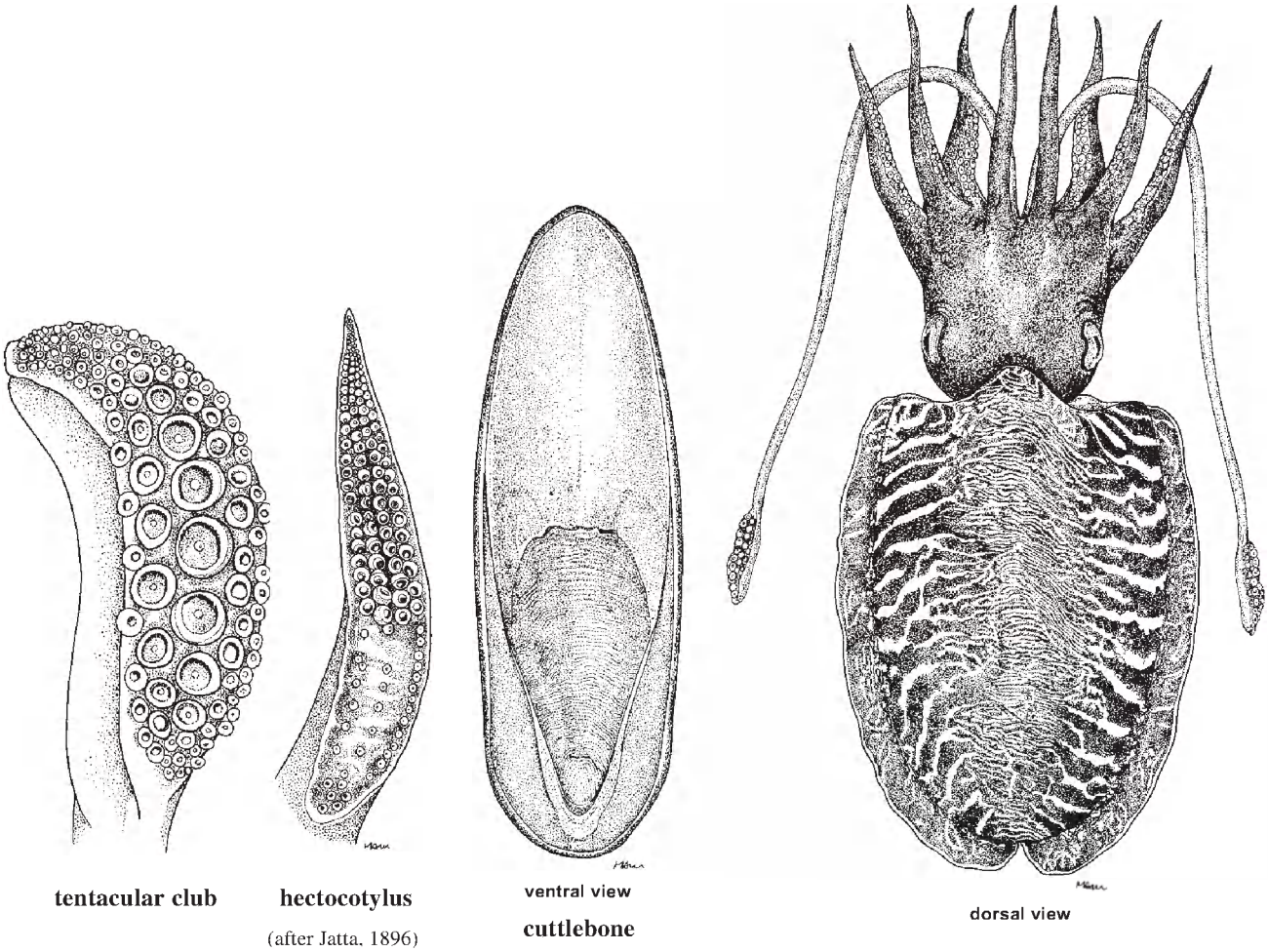


Fig. 160 *Sepia officinalis*

Diagnostic Features: Fins wide, extend anteriorly slightly beyond mantle margin. Arm suckers tetraserial. Hectocotylus present on left ventral arm: **6 rows of normal size suckers proximally**; **4 to 8 rows of reduced suckers medially**. Club with **5 or 6 suckers in transverse rows**; suckers differ in size: **5 or 6 median suckers twice diameter of rest**. Cuttlebone outline oblong; acuminate, acute, anteriorly; bluntly rounded posteriorly. Spine short, pointed, surrounded by chitinous shield. Sulcus present on last loculus only, absent from striated zone; sulcus shallow, narrow. Anterior striae are **inverted U-shape, or shallow m-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly; outer cone chitinous; outer cone narrow anteriorly, **broadens posteriorly, spatulate**, lateral limbs are flared ventrolaterally. **Colour: Light brown**. Head with scattered white spots and with dark pigment around eye orbits. Arms I to III have a broad, longitudinal brownish band medially, extending onto head. Dorsal mantle has **bold transverse zebra stripe pattern during the breeding season**; paired dorsal eye spots absent. Fins with narrow white band along outer margin and with small white spots, becoming larger toward junction of mantle and fins. Mature males with **arms IV emboldened by white and black zebra bands and white arm spots**.

Size: Up 490 mm mantle length, weight up to 4 kg in temperate waters and to 300 mm mantle length and 2 kg in the subtropics.

Geographical Distribution: Eastern Atlantic and Mediterranean Sea: eastern North Atlantic, from the Shetland Islands and southern Norway (not present in the Baltic Sea, except for occasional incursions with the northeasternmost Atlantic waters) south through the Mediterranean Sea (including Aegean Sea, Sea of Marmara and Levantine Sea) to northwestern Africa, with the southern boundary coinciding approximately with the border between Mauritania and Senegal (16ºN). Endeavour Bank (Fig. 161).

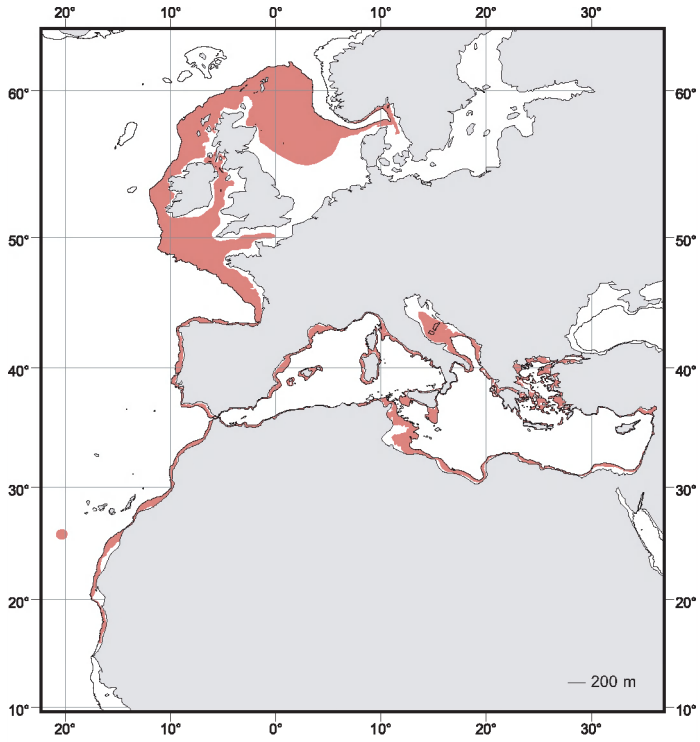


Fig. 161 ***Sepia officinalis***
Known distribution

Habitat and Biology: Depth range from subtidal waters to 200 m, most abundant in upper 100 m, with larger animals found at greater depths. ***Sepia officinalis*** is a neritic, demersal species, found on the continental shelf, predominantly on sandy or muddy substrates. The species undergoes seasonal migrations between inshore waters during spring and summer and medium shelf grounds (about 100 m depth) during autumn and winter. For example, in the Mediterranean, large individuals leave deeper water early in spring to migrate to shallower water, with males preceding females. This group is followed by a succession of smaller animals throughout the summer. In autumn, gradual decent to deeper water begins. Following an elaborate and ritualized courtship, which incorporates stereotyped visual displays and 'mate guarding', spawning occurs in shallow water, with peaks at water temperatures from 13° to 15ºC. In the western Mediterranean, this occurs between April and July; off Senegal and on the Endeavour Bank, spawning occurs between January and April. Males carry up to 1 400 spermatophores and females (depending on their size) between 150 and 4 000 eggs. Mating takes place head-to-head and spermatophores are placed in the females' buccal membrane ventral to the mouth. Eggs, 8 to 10 mm in diameter and blackened with ink, are attached in grape-like clusters to seaweed, shells, debris and other substrates. They hatch after 30 to 90 days depending upon water temperature. The total length of hatchlings is between 7 and 8 mm. The growth rate varies directly with temperature and inversely with size. Very young animals cannot live at depths much greater than about 50 to 80 m, because their cuttlebones cannot withstand water pressures higher than about 6 to 9 atmospheres. From hatchlings to adults, ***S. officinalis*** exhibits a light-induced burying behaviour; most individuals spend the daytime hidden in sand. The life cycle under natural conditions covers 12 to 24 months, varying with environmental conditions. Young hatched in early summer from the spring brood usually spawn in the autumn of the following year; those from the autumn brood spawn in the spring of their second year of life. Adult males may predominate because of massive postspawning mortality among large females. Food consists of small molluscs, crabs, shrimps, polychaetes, other cuttlefishes and juvenile demersal fishes. Prey is often ambushed when these cuttlefishes are partially buried and hidden in sand. The first and second arm pairs commonly protrude from the substrate and are darkened, perhaps acting as lures. Cannibalism is common and may be a strategy to overcome temporary prey shortages. The growth rate is rapid, given their short lifespan. Predators include sharks, sparids and other demersal fishes and cephalopods. ***Sepia officinalis*** has been reared successfully in aquaria and has aquaculture potential if live prey can be substituted by cheaper food items. Recent information on the distribution of this species in Portuguese waters (i.e. Ria de Aveiro and adjacent coasts) indicates that ***Sepia officinalis*** can tolerate brackish waters. The age and mantle length of specimens distributed in brackish areas decrease with decreasing salinity. Younger specimens have greater ecophysiological plasticity and tolerate greater environmental instability: this allows them to colonize the upper zones of the lagunar system, thus avoiding intraspecific competition.

Interest to Fisheries: ***Sepia officinalis*** is one of the most important species for cephalopod fisheries in many countries. It is probably close to its maximum sustainable production in several areas of its distribution since negative trends in captures have been observed in recent years in some heavily fished areas (e.g. in the Mediterranean). Separate official statistics for this species indicate that the main producer country in the year 2001 was Tunisia in the Mediterranean Sea, followed by Greece; Spain and Portugal were also important producers, fishing ***S. officinalis*** in the northeastern Atlantic. However, the species is also known to contribute extensively to the 'cuttlefishes' *sensu lato* official figures both in the Mediterranean (where Italy is the main producer for this category) and in Atlantic waters. In the English Channel, the value of cuttlefish landings increased greatly during recent decades, such that cuttlefishes have become a consistent component of earnings both for French and United Kingdom fishermen. This has focused attention toward a managed exploitation of the resource. Highest catches are recorded for Tunisia in the Mediterranean and off west Africa by Spanish and Moroccan fleets. In the industrial fisheries, ***S. officinalis*** is primarily trawled, either as a target species, or as bycatch to demersal finfishes. The artisanal fisheries, however, utilize a variety of selective gear, such as spears, pots and traps, often combined with the use of light. Sometimes mature females are used as lures to attract males. Trammel nets are also efficient gear to catch cuttlefishes and they are frequently used inshore in many Mediterranean fishing areas. Common cuttlefish usually is marketed fresh or frozen and it is a highly valued food item, especially in Japan, Korea, Italy and Spain.

Remarks: Five subspecies along the European–African coast were designated by Adam (1940). Khromov *et al.* (1998) recognized ***S. o. hierredda*** Rang, 1837 and ***S. o. vermiculata*** Quoy and Gaimard, 1832 as valid, but consider ***S. o. filliouxi*** Lafont, 1868 and ***S. o. mediterranea*** Ninni, 1884 as indistinct from ***S. officinalis*** (this designation restricts the distribution of the species to the subtropical and temperate waters of the eastern Atlantic in the northern hemisphere). ***Sepia officinalis*** and ***S. hierredda*** now are known to be distinct species (see Remarks ***S. hierredda***). In the Mediterranean, young ***S. officinalis*** can be distinguished from ***S. orbignyana*** Férussac, 1826 and ***S. elegans*** Blainville, 1827 by their brown, rather than red, skin colour, the shape of the bone and the club sucker arrangement. The biology of ***S. officinalis*** is well known. It has been the most extensively studied of all cuttlefish species.

Local Names: ALGERIA: Choubai, Chouebí, Seiba, Seich, Sepia, Seppio; Soupia; EGYPT: Sobbeit; FINLAND: Mustekala, Sepia; BULGARIA: Sepija; CYPRUS: Corsica: Seppia; FRANCE: Casseron, Chakod, Chibia, Margade, Seiche; GERMANY: Gemeiner Tintenfisch, Sepie; GREECE: Soupia; ISRAEL: Dyonon refui; ITALY: Seppia comune; Scarpetta, Scarpitta; Scarpitelle, Seccetella, (juveniles), Secce, Seppa, Seppia, Siccia, Sepa, Sepia imperiale; JAPAN: Mongo-ika, Yoroppa kouika; LEBANON: Sabbidije; LIBYA: Shoubia; MADEIRA: Choco; MALTA: Sicca; MONACO: Supia; MOROCCO: Chubei, Seiche; NETHERLANDS: Gewone Inktvis, Zeekat; PORTUGAL: Checo, Choco; ROMANIA: Sepia; RUSSIAN FEDERATION: Kora katitza; SENEGAL: Seiche; SPAIN: Aluda, Choco, Coca, Jibia, Jibión, Luda, Rellena, Relleno, Sipia, Sipionet; TUNISIA: Choubei, Chouebi, Seche, Sibia, Sipia, Soubia; TURKEY: Sübye; UK: Cuttlefish; YUGOSLAVIA: Sipa.

Literature: Tompsett (1939), Mangold-Wirz (1963), Boletzky (1983a), Guerra and Castro (1988), Hanlon and Messenger (1988), Guerra (1992), Augustyn *et al.* (1995), Hanlon and Messenger (1996), Sanjuan *et al.* (1996), Neige and Boletzky (1997), Khromov *et al.* (1998), Belcari (1999b), Pérez-Losada *et al.* (1999), Denis and Robin (2001), Guerra *et al.* (2001), Belcari *et al.* (2002), Jereb (2002), Salman *et al.* (2002), Sobral (2002), Vrgoč *et al.* (2004). Numerous other references pertaining to this species are available.

Sepia omani Adam and Rees, 1966

Sepia omani Adam and Rees, 1966. *The John Murray Expedition*, 11(1): 92 [type locality: Gulf of Oman].

Frequent Synonyms: None.

Misidentifications: *Sepia vossi* Khromov, 1996.

FAO Names: En – Oman cuttlefish; **Fr** – Seiche d'Oman; **Sp** – Sepia de Oman.

Diagnostic Features: Mantle oval. Arm suckers tetraserial; webs wide between dorsal and dorsolateral arms. Hectocotylus present on left ventral arm: 2 or 3 rows of normal size **suckers** proximally, suckers reduced medially for 40% of arm length, then normal size suckers to arm tip; reduced suckers much smaller than normal arm suckers; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between; 2 ventral series crowded together. Club sucker-bearing surface flattened, with **3 or 4 suckers in transverse rows**; **suckers differ markedly in size: 3 to 5 suckers in middle of third longitudinal row extremely enlarged**. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club**, do not continue along stalk. Dorsal membrane forms deep cleft at junction with stalk. Cuttlebone acuminate, acute, anteriorly and posteriorly; dorsal median rib present, sides almost parallel, flanked by shallow grooves; lateral ribs distinct. Spine long, pointed. Anterior striae **shallow m-shape**; sulcus shallow, narrow, extends entire length of cuttlebone. Inner cone limbs are uniform width, narrow, U-shape posteriorly, thickened; inner cone posteriorly with **irregular calcareous ribs radiating into outer cone**; outer cone calcified, narrow anteriorly, broadens posteriorly. **Colour:** Light brown. Dorsal mantle has dark brown transverse stripes.

Fig. 162

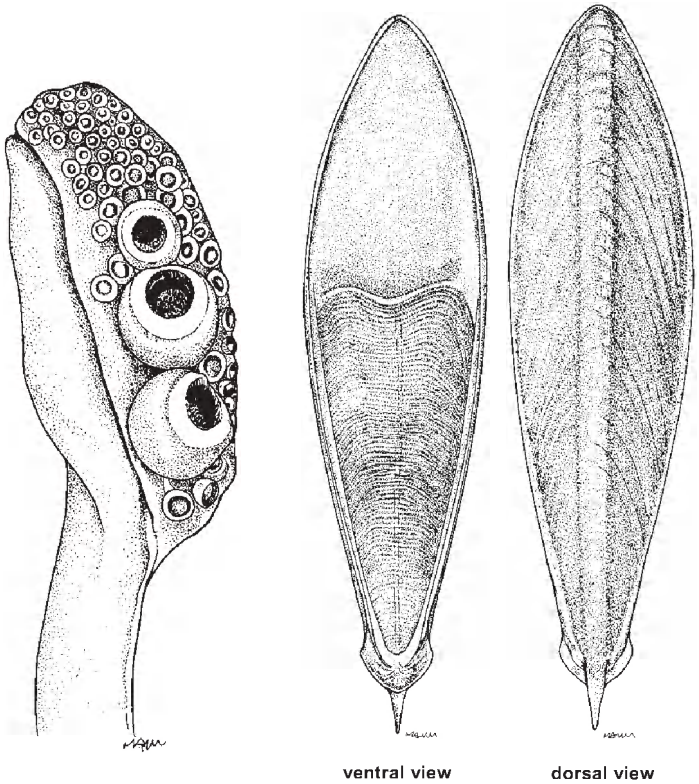


Fig. 162 ***Sepia omani***

Size: Up to 100 mm mantle length.

Geographical Distribution: Northern Indian Ocean: Gulf of Oman, off Pakistan and western India. Limits of range unknown (Fig.163).

Habitat and Biology: This is a neritic demersal species. Depth range from 50 to 210 m.

Interest to Fisheries: At present still undetermined. Probably the species occurs in mixed species trawls, where it is not separated from other sepiids.

Remarks: Records from the Indo-Pacific refer to *S. vossi* Khromov (1996).

Literature: Filippova *et al.* (1995).

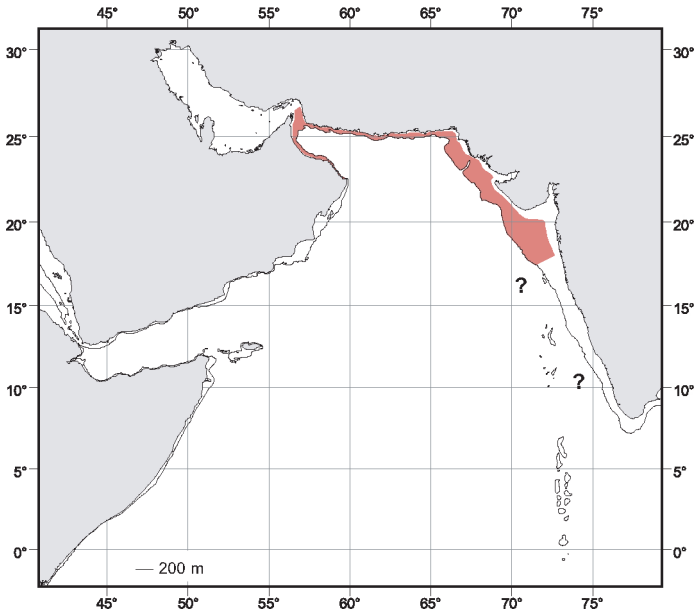


Fig. 163 *Sepia omani*
Known distribution

Sepia opipara (Iredale, 1926)

Fig. 164

Glyptosepia opipara Iredale, 1926, *The Australian Zoologist*, 4(3): 191 [type locality: Australia: Queensland, Masthead Island, Capricorn Group, 23°32'S 151°44'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Magnificent cuttlefish; **Fr** – Seiche magnifique; **Sp** – Sepia magnífica.

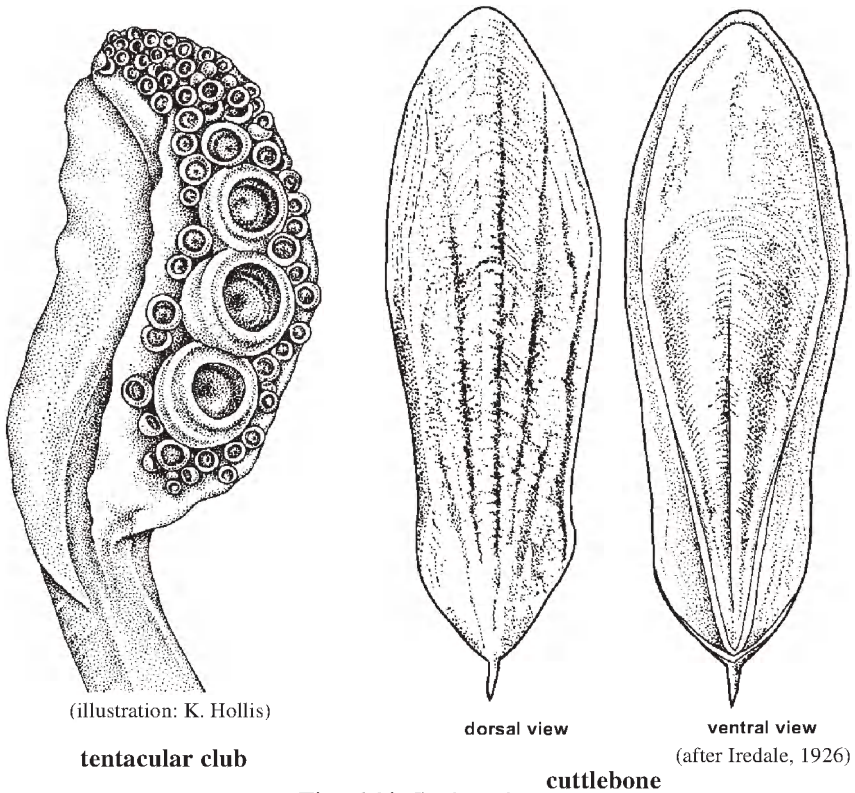


Fig. 164 *Sepia opipara*

Diagnostic Features: Mantle broad, oval. Male and female arm lengths subequal; protective membranes narrow. Arm suckers tetraserial. Hectocotylus present on left ventral arm: **5 or 6 rows of normal size suckers proximally, 6 or 7 rows of reduced suckers medially**, then normal size suckers distally to arm tip; oral surface of modified region not wide, fleshy, but normal, as on opposite arm. Club sucker-bearing surface flattened, with **3 or 4 suckers in transverse rows**; suckers differ markedly in size: middle of club with **4 or 5 greatly enlarged suckers**, second proximal one the largest, obliquely 1 small lateral sucker and 1 minute marginal sucker dorsal to the big sucker, 1 small lateral and 4 minute marginal suckers ventral to it; suckers proximal and distal to the big suckers are small. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes not joined at base of club but **fused to tentacular stalk**. Dorsal and ventral membranes **of equal length**; extend proximal to carpus along stalk. Dorsal membrane forms deep cleft at junction with stalk. Cuttlebone outline oblong; bone bluntly rounded anteriorly; acuminate, acute, posteriorly; **dorsal surface pinkish**; dorsal surface **flat medially and laterally**; texture rough, with irregular calcified projections; dorsal median rib **distinct**; **sides approximately parallel**, flanked by broad grooves; **lateral ribs distinct**. Chitin borders lateral and anterior margins of cuttlebone. Spine

short, pointed, curves dorsally, with **ventral keel**. Striated zone flat; last loculus convex; sulcus shallow, narrow. Anterior striae are **inverted U-shape**; limbs of inner cone extend anteriorly to end of striated zone. Inner cone limbs are uniform width, narrow, **U-shape posteriorly**, thickened; outer cone calcified, narrow anteriorly, broadens posteriorly.

Size: Up to approximately 150 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: northern Australia from Dirk Hartog Island, 25°45'S 113°03'E (Western Australia), to southern Queensland, 36°57'S 151°45'E (Fig. 165).

Habitat and Biology: Depth range from 83 to 184 m.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries. The size of this species and its broad distribution indicate that it has potential for exploitation.

Literature: Lu (1998a).

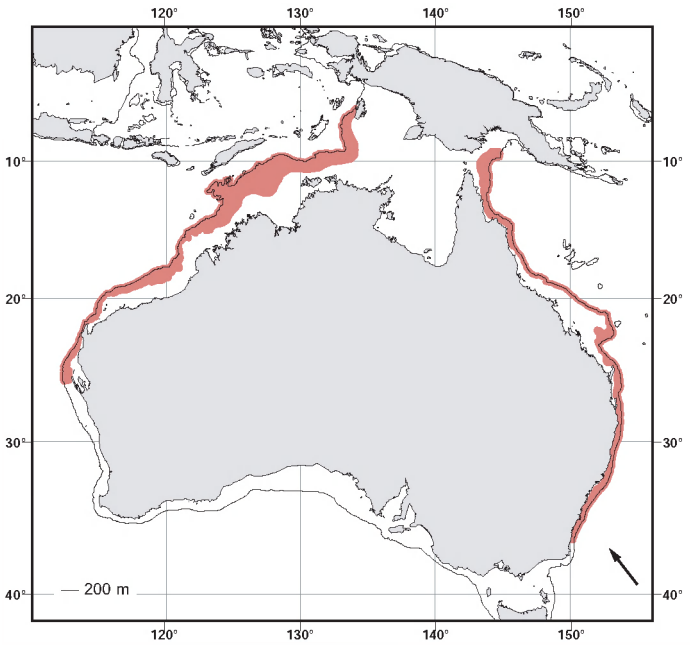


Fig. 165 *Sepia opipara*
Known distribution

Sepia orbignyana Férussac *in* d'Orbigny, 1826 — Fig. 166

Sepia orbignyana Férussac *in* d'Orbigny, 1826, *Annales des Sciences Naturelles, Paris*, series 1, 7: 156 [type locality: France: La Rochelle].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Pink cuttlefish; **Fr** – Seiche rosée; **Sp** – Sepia con punta.

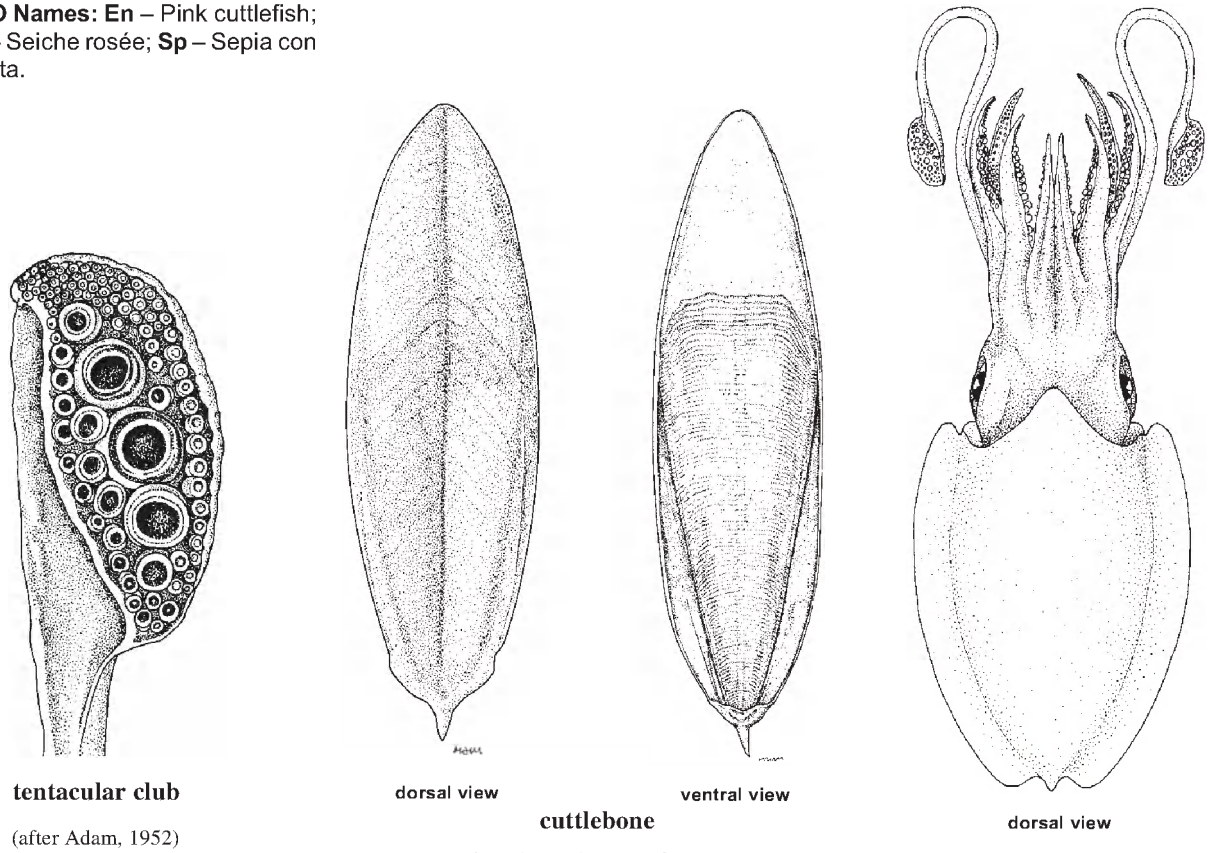


Fig. 166 *Sepia orbignyana*

Diagnostic Features: Mantle oval. Male and female arms subequal in length. Arm suckers tetraserial. Male medial non-hectocotylized arm suckers with greater diameter than marginal ones. Hectocotylus present on left ventral arm: 1 or 2 rows of normal size suckers proximally, greatly reduced suckers medially, then normal size suckers distally to arm tip. Suckers of hectocotylus in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Club **short, oval**, with **5 or 6 suckers in transverse rows**; suckers differ markedly in size: **3 large suckers medially with one slightly smaller sucker on each side of these**. Swimming keel of club extends proximal to carpus; dorsal and ventral protective membranes **joined at base of club**. Buccal membrane in females with single median spermathecae in ventral part. Cuttlebone outline oblong; acuminate, acute, anteriorly; bluntly rounded posteriorly; **strongly recurved ventrally**; dorsal surface pinkish; dorsal surface flat medially, curved, convex laterally; granulose; dorsal median rib absent; bone with **dorsal median groove present**, shallow, narrow, extending full length of cuttlebone. Spine long, pointed (prominent), straight, directed dorsally, with **ventral keel**. Striated zone and last loculus convex; sulcus **shallow, narrow, extends** entire length of cuttlebone; **sulcus flanked by rounded ribs bordered laterally by shallow grooves**. Anterior striae **shallow m-shape,** or wavy. Inner cone limbs are uniform width, narrow V-shape posteriorly, thickened slightly; outer cone limbs are slightly expanded posteriorly, directed ventrally to form a recurved cup-like structure. **Colour:** Reddish brown.

Size: Males up to 96 mm mantle length; females up to 120 mm mantle length.

Geographical Distribution: General distribution: eastern Atlantic and Mediterranean Sea: from the Irish Sea, English Channel and Bay of Biscay to southern Angola (17°S), and throughout the Mediterranean Sea (including the Adriatic and Aegean Seas, Sea of Marmara and Levantine Sea). Saharan Bank (Fig. 167).

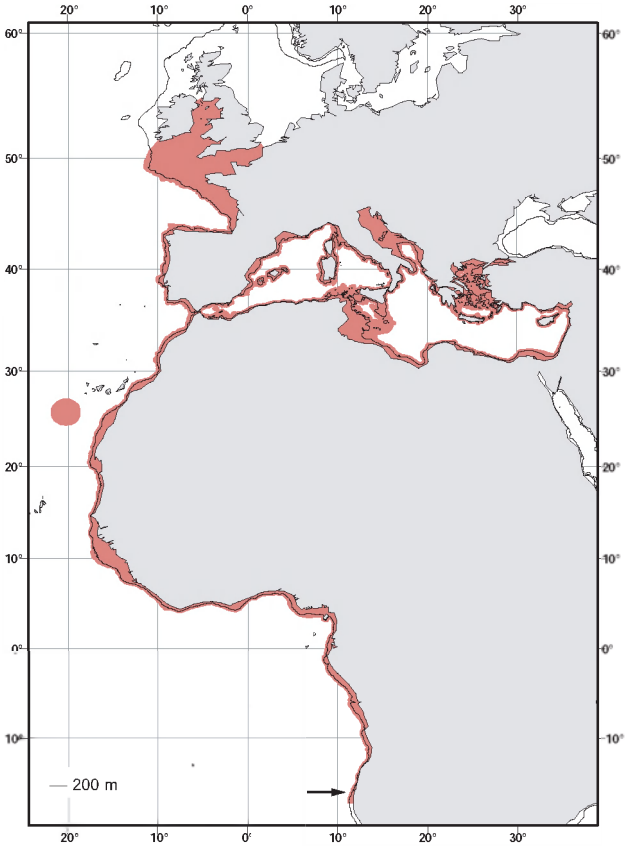


Fig. 167 ***Sepia orbignyana***
Known distribution

Habitat and Biology: The depth range for this species is from 15 to 570 m, and it is most abundant between 50 and 250 m. ***Sepia orbignyana*** is a demersal species that lives mainly on sandy and sandy-muddy bottoms. It is frequently sympatric (and confused) with ***S. elegans*** Blainville, 1827. In the Sea of Marmara the species can occur in brackish waters. In Mediterranean waters, males and females are usually found together throughout the year and the spawning period is probably continuous, with peaks of activity from spring to autumn. A predominance of mature individuals in spring is also reported for the species in Portuguese waters. No onshore spawning migrations have been reported. Due to the extended reproductive period, recruitment is also continuous but variable, with seasonal density peaks. Growth rates of females are higher than those of males, and females also attain larger sizes. In the Mediterranean, the smallest mature males are 35 mm, and the smallest females 65 mm mantle length. Mature males, aged 6 or 7 months, carry about 100 spermatophores; females of 9 or 10 months of age, carry around 400 eggs. Egg diameter increases with the size of the females. The eggs (maximum size 7 to 8.5 mm diameter) are laid in clusters of 30 to 40 and are attached to sponges on muddy bottoms. Diet consists mainly of crustaceans, but fish and cephalopods make up a minor component.

Interest to Fisheries: ***Sepia orbignyana*** is one of the most abundant cephalopod species in some areas of its distributional range (e.g. within the Mediterranean: Aegean, southern Adriatic and Tyrrhenian Seas and in the Sicilian Channel). It is taken mainly as a bycatch throughout the Mediterranean and in the west African trawl fisheries. Separate statistics are not reported, but ***S. orbignyana*** represents a very significant percentage of the catches in some areas. In the Mediterranean Sea it is marketed along with ***S. elegans*** and small ***S. officinalis*** and constitutes a valuable resource locally. In the Sicilian Channel, research studies showed an exploitation rate of 0.60 for this species, which suggests an intense fishing pressure on this resource. It is marketed fresh and frozen.

Local Names: ITALY: Seppia pizzuta; SPAIN: Sepia puntiaguda, Chopito.

Remarks: ***Sepia orbignyana*** differs from ***S. elegans*** in having more than 100 suckers on the club. The 2 species also differ in the cuttlebone form and structure. ***Sepia elegans*** lacks a cuttlebone spine, while a spine is present in ***S. orbignyana***. In addition, ***Sepia orbignyana*** differs from ***S. officinalis*** Linnaeus, 1758 in having a reddish, rather than brown coloration, it generally inhabits deeper water and does not bury in the sand during the day.

Literature: Mangold-Wirz (1963), Adam and Rees (1966), Bello (1990a), Jereb and Ragonese (1991), Ragonese and Jereb (1991), Wurtz *et al.* (1991), Guerra (1992), D'Onghia *et al.* (1996), Sanjuan *et al.* (1996), Neige and Boletzky (1997), Belcari (1999c), Salman *et al.* (2002).

Sepia papuensis Hoyle, 1885

Fig. 168; Plate V, 31

Sepia papuensis Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 16: 197 [type locality: Challenger Station 188, 09°59'S 139°42'E, Arafura Sea, South of Papua].

Frequent Synonyms: ?*Sepia galei* Meyer, 1909; *Solitosepia submestus* Iredale, 1926; *Solitosepia occidua* Cotton, 1929; *Solitosepia genista* Iredale, 1954; *Solitosepia lana* Iredale, 1954; *S. prionota* Voss, 1962a.

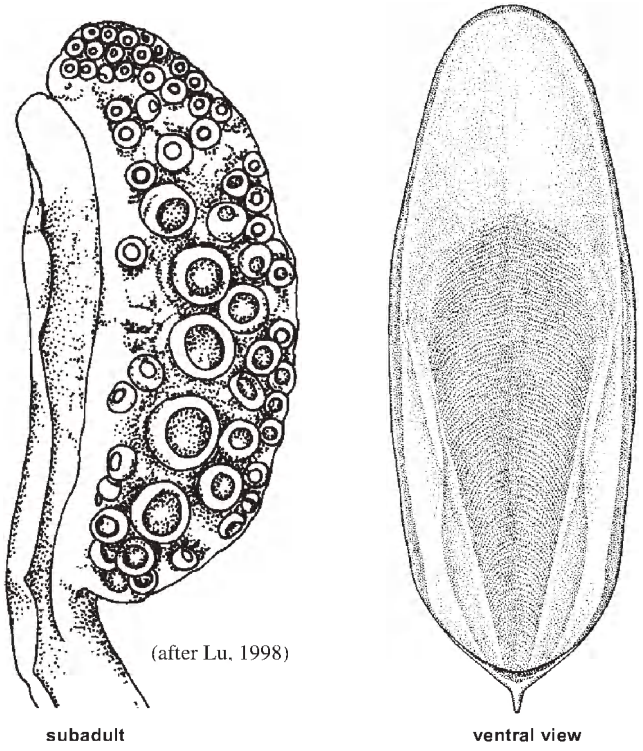
Misidentifications: None.

FAO Names: En – Papuan cuttlefish; **Fr** – Seiche de Papouasie; **Sp** – Sepia de Papua.

Diagnostic Features: Mantle oval. Male and female arm lengths subequal; protective membranes wide, well developed as a series of semicircular lappets. Arm sucker arrangement differs between sexes: in males, sucker rows on arms I to III **tetraserial proximally, biserial at distal tips**, arms IV **suckers tetraserial**; in females, arm **suckers tetraserial. Hectocotylus absent**. Club sucker-bearing surface flattened, with **5 or 6 suckers in transverse rows**; **suckers differ markedly in size**. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes not joined in small specimens, joined at base of club in large specimens; dorsal protective membrane **much longer than ventral protective membrane**, extending proximal to carpus along stalk. Dorsal membrane forms deep cleft at junction with stalk. Cuttlebone length approximately equal to mantle length; outline oblong; bone bluntly rounded anteriorly and posteriorly; dorsal surface creamy white; dorsal surface convex medially, flat laterally; texture smooth, not pustulose; dorsal median and lateral ribs distinct; **median rib broadens anteriorly**. Chitin borders lateral and anterior margins of cuttlebone. Spine long, pointed, curves dorsally, with **ventral keel**. Striated zone and last loculus concave; sulcus shallow, wide, extends entire length of cuttlebone. Anterior striae are **inverted U-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly, **thin**; outer cone calcified; narrow anteriorly, broadens posteriorly. Dorsal mantle with series of elongate papillae along each side, adjacent to base of each fin, rest of mantle covered with numerous small papillae. Papillae in 2 series: i) a conspicuous series that consists of a pair of large, triangular, flattened primary papillae that emerge from mantle white spots; ii) just posterior and lateral to mantle white spots lies a pair of papillate ridges located along the boundary between a white midline stripe and darker lateral fields. Head with 2 pairs large papillae located over anterior and posterior ends of each eye, numerous scattered, small papillae and one on each eyelid. Arms I to III with papillae. **Colour:** Light brown. Dorsal mantle has white blotches or spots. Paired dorsal eye spots present.

Size: Up to 110 mm mantle length.

Geographical Distribution: Indo-West Pacific: Philippine Islands, Indonesia, Bali, Ternate, Arafura and Coral Seas, northern Australia from southern Western Australia (Freemantle, 32°03'S 115°44'E) to southern NSW (36°35'S 150°16'E), including Gulf of Carpentaria (Fig. 169).



(illustration: K. Hollis)

Fig. 168 *Sepia papuensis*

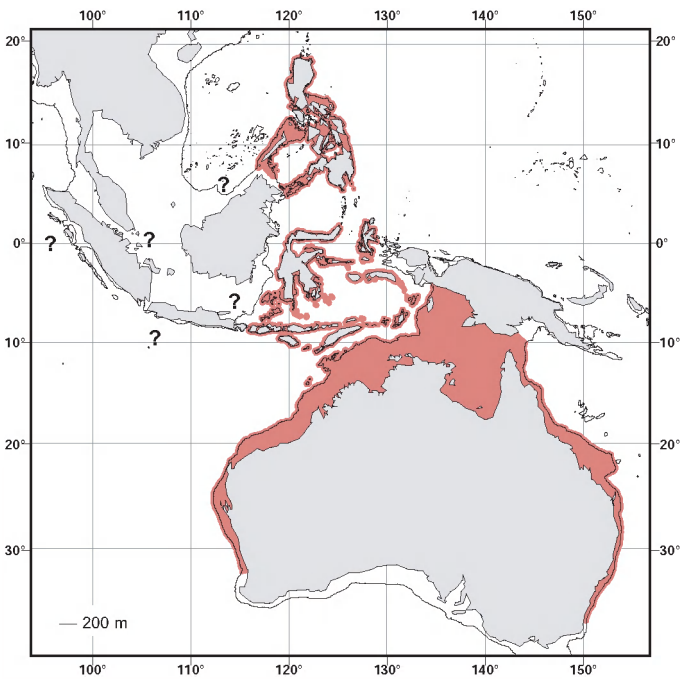


Fig. 169 *Sepia papuensis*
Known distribution

Habitat and Biology: Depth range from 10 to 155 m. ***Sepia papuensis*** is a shelf species found on silt, sand or muddy substrates. This species appears to be night-active and has been observed foraging in beds of seaweed and seagrass. Small individuals have been observed to extend flattened arms to mimic the shape of the seaweed *Halimeda* as camouflage. Behavioural studies have shown that the species exhibits a very wide range of colour patterns associated with substrate colour and texture, and in response to potential attack by predators.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries. This species was collected in small numbers in demersal trawl and dredge surveys in the Gulf of Carpentaria, Australia, in 1990 and 1991 and probably forms part of the bycatch of Taiwanese trawl fisheries in the region.

Literature: Adam and Rees (1966), Roper and Hochberg (1987), Lu (1998a).

Sepia pharaonis Ehrenberg, 1831

Fig. 170; Plate V, 32–34

Sepia pharaonis Ehrenberg, 1831, *In*: Ehrenberg, C.G. (1831). Cephalopoda in Mare Rubro viventia. In 'Symbolae Physicae, seu Icones et descriptiones Corporum Nauralium...quae ex itineribus per Libyan, Aegyptum... Habessiniam...Pars Zoologica'. (P.C. Hemprich and C.G. Ehrenberg, eds) [4]: 4 [type locality: Massaouah, Gulf of Suez].

Frequent Synonyms: *Sepia torosa* Ortmann, 1888; *Sepia rouxii* d'Orbigny, 1839–1842; *Sepia formosana* Berry, 1912a; *Crumenasepia hulliana* Iredale, 1926; *Crumenasepia ursulae* Cotton, 1929; *Sepia rouxi* d'Orbigny, 1841; *Sepia formosana* Berry, 1912; *Sepia formosana* Sasaki, 1929; *Sepia tigris* Sasaki, 1929.

Misidentification: None.

FAO Names: En – Pharaoh cuttlefish; **Fr** – Seiche pharaon; **Sp** – Sepia faraón.

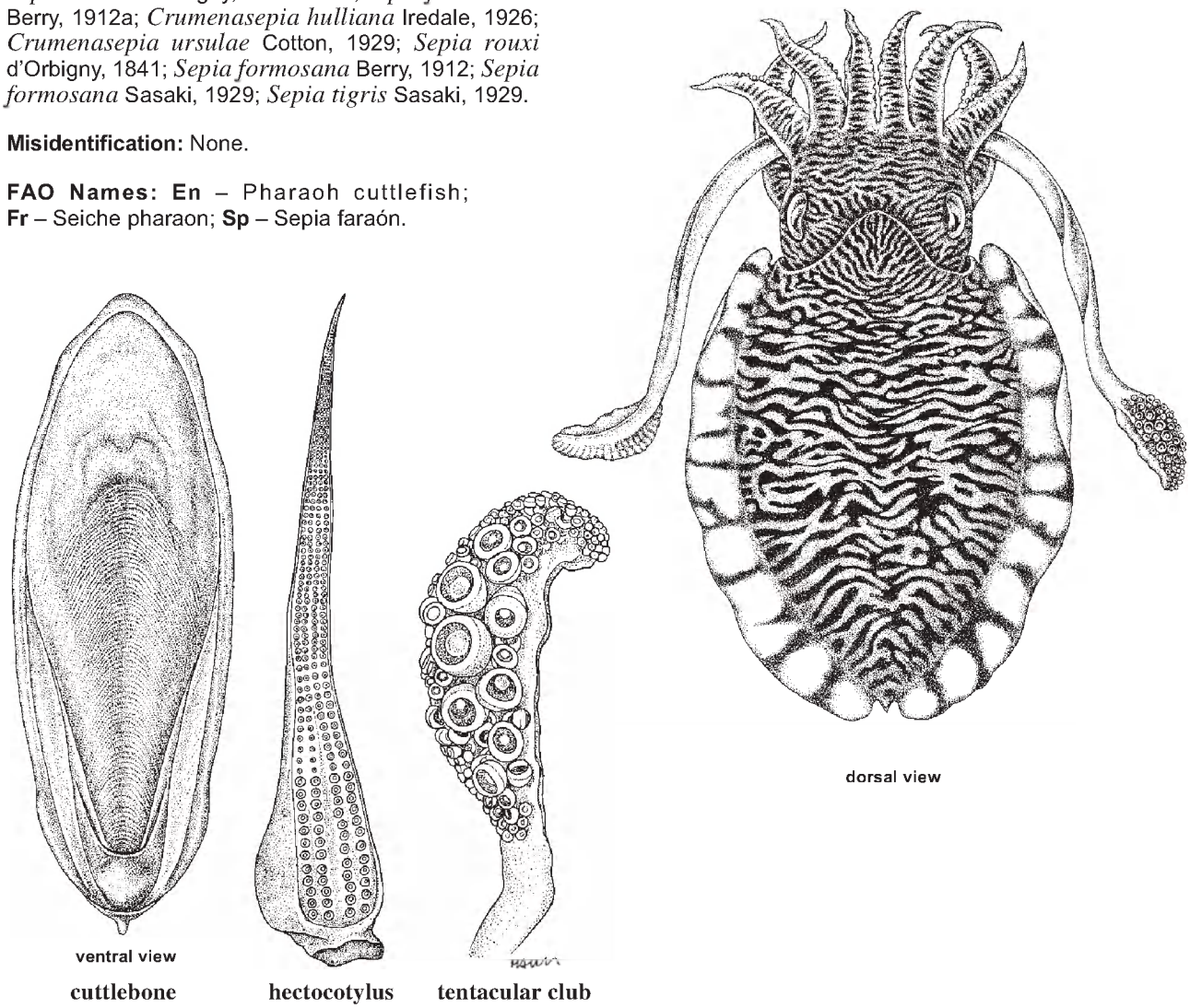


Fig. 170 ***Sepia pharaonis***

Diagnostic Features: Mantle oval. Male and female arm lengths subequal. Arm suckers tetraserial. Hectocotylus present on left ventral arm: **10 to 12 rows of normal size suckers proximally, 6 rows of reduced suckers medially**, then normal size suckers distally to arm tip. Suckers of hectocotylus in **2 dorsal series are much smaller than those in 2 ventral series**; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; with shallow median furrow; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Club sucker-bearing surface flattened, with **8 suckers in transverse rows**; suckers differ markedly in size: 5 or 6 median suckers enlarged (3 or 4 of these are greatly enlarged). Swimming keel of club terminates at proximal end of carpus. Dorsal and ventral protective membranes **not joined at base of club**; dorsal and ventral membranes same length; extend proximal to carpus along stalk. Dorsal membrane forms shallow cleft at junction with stalk. Buccal membrane with **a few, minute suckers** (each lappet bearing 1 or 2 small suckers). Cuttlebone outline oblong; bone bluntly rounded anteriorly; acuminate, acute, posteriorly; dorsal surface creamy white; dorsal surface evenly convex; texture smooth; dorsal median rib distinct, rib broadens anteriorly; lateral ribs indistinct. Chitin borders lateral and anterior margins of cuttlebone. Spine short, pointed, curves dorsally, keel(s) absent. Striated zone concave; last loculus flat; sulcus **deep, wide, extends** entire length of cuttlebone; sulcus **flanked by rounded ribs**. Anterior striae are **inverted U-shape**; limbs of inner cone extend anteriorly to end of striated zone. Inner cone limbs are narrow anteriorly, broaden posteriorly with **distinctive thick bulbous swelling**; outer cone calcified; narrow anteriorly, broadens posteriorly. Dorsal mantle with series of elongate papillae along each side, adjacent to base of each fin, or covered with numerous small papillae. **Colour:** Pale brownish or reddish purple. Head and arms with transverse zebra-stripe pattern. Dorsal mantle has white blotches or spots, transverse saddle mark, and has a transverse zebra-stripe pattern (saddle mark in females; stripes especially in males; small specimens may show stripe markings or few markings). Fins with longitudinal white band at base, bordered by narrow band of ground-coloured pigment along each side; white stripe solid on anterior 3/4 of body, interrupted by blocks of ground-coloured pigment on posterior 1/4 of mantle.

Size: Up to 420 mm mantle length; weight to 5 kg.

Geographical Distribution: Indian Ocean and western Pacific: including the Red Sea and Arabian Sea south to Zanzibar and Madagascar, Andaman Sea to South China Sea, East China Sea, Taiwan Province of China, Japan (Kyushu and possibly southern Honshu), eastern Indonesia and northern Australia (from Monte Bello Island, Western Australia, 20°26'S 115°37'E, to at least Townsville, Queensland, 19°16'S 146°41'E, including Gulf of Carpentaria). Wadge Bank (Fig. 171).

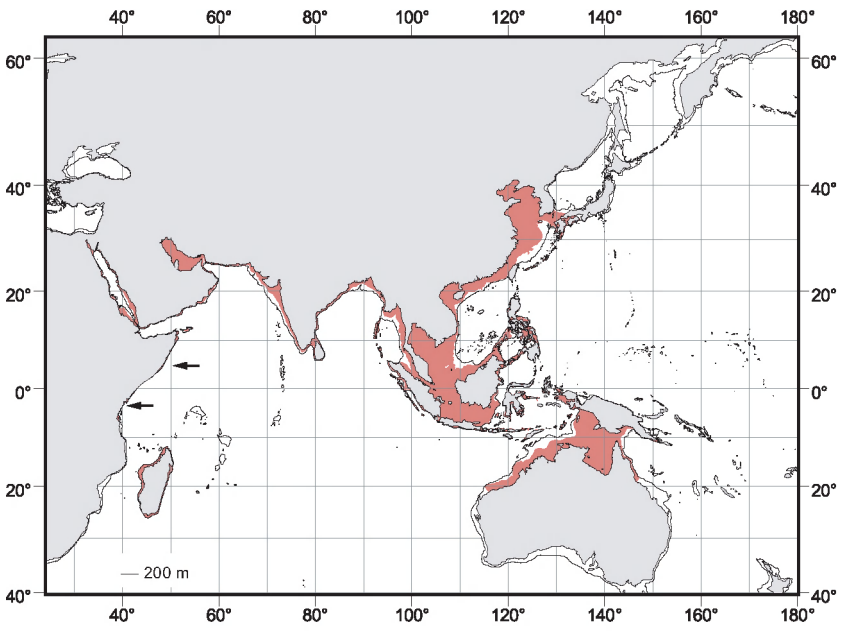


Fig. 171 ***Sepia pharaonis***
Known distribution

Habitat and Biology: ***Sepia pharaonis*** is a neritic demersal species which occurs down to 130 m. In the Gulf of Thailand and the Andaman Seas, animals are found from the coastal shallows to 100 m depth, with most caught between 10 and 40 m. Around Hong Kong, animals migrate to shallower waters during the mating season, where large numbers of adults congregate in 40 to 80 m on the continental shelf from November to February. During February and March, they move to the coast where spawning takes place from April to May in water temperatures between 18 and 24°C. Eggs are laid in clusters and attached to plants, shells and other hard substrates in approximately 5 to 20 m depth.

In the Gulf of Thailand, spawning occurs all year round, with peak months during January and February and from July to September. The ratio of males to females is 1:3. During the spawning season, 4 or 5 adults congregate, sometimes near a boulder. During mating, the males adopt a very bold striped pattern. Both males and females raise their dorsal arms vertically and the female elevates lappets on her mantle: 6 on the base of each fin and 2 over each eye. The males approach either head on, or with ventral arms spread, they swim from behind and over her back. Mating takes place head on, each holding the other with the arms. Mating may occur more than once with a single pair. Females lay white eggs that are attached singly to hard surfaces.

In Iranian waters, ***S. pharaonis*** is the dominant cephalopod species. The main spawning season occurs between the southwest and northeast monsoon periods in November and December. In Yemen, ***S. pharaonis*** is one of the species with greatest commercial value; experts have estimated the standing stocks and an annual exploitable yield has been recommended.

Sepia pharaonis rises to the lower part of the water column to feed at night, mainly on crustaceans and a variety of small demersal fishes. During maturation, there is a shift of emphasis from somatic growth to gonadal development and vitellogenesis. Research observations suggest that energy and nutrients for maturation are supplied mainly by diet rather than stored resources: the species does not use protein from muscle tissue for developing and growing its reproductive tissues. ***Sepia pharaonis*** appears to be an intermittent multiple spawner. In captive animals, the life cycle is less than 10 months. Estimated growth rates for wild animals show higher values for females than for males.

Interest to Fisheries: This species supports industrial or artisanal fisheries throughout its range. With ***S. esculenta*** Hoyle, 1885, it is the most abundant cuttlefish species caught in the Philippines and the Samar and Visayan Seas, with the highest catches reported in the Lingayen Gulf and Carigara Bay. In Iran, the fishing activity occurs during the spawning season, when adults migrate from deeper waters to shallower waters in the littoral zone. ***Sepia pharaonis*** is caught by bottom trawlers in the Oman Sea, and by traps in the Persian Gulf and is one of the most important cuttlefish species fished in both areas. The species is important to the commercial cephalopod fishery of Thailand, being highly abundant in the Gulf and the Andaman Sea, where it is the most common species of cuttlefish caught. The species contributes about 90% of the cuttlefishes caught off Australia by Chinese pair trawlers. Off the North West Shelf and Timor Seas, sepiids (mainly ***S. pharaonis***) tend to replace squids as the dominant cephalopods caught. Domestic fisheries in these waters take this species as bycatch of prawn and mixed species trawl fisheries. In the Hong Kong area, it is the most abundant cuttlefish species and it is of greatest commercial importance in this area and along the whole coast of Kwangtung and Fukien, with about 400 tonnes landed annually in Hong Kong. Animals in this region are caught by spearing, lure-hooking and trawling. In southern Thailand, in addition to otter and pair trawls, the trammel net and hook-and-line are commonly used for catching ***S. pharaonis***, with bottom otter and pair trawls used offshore, and push nets and lift nets used in inshore and coastal waters. Squid traps, in which egg clusters are placed to entice squids to enter, are also widely used and cuttlefishes, all mature animals ready to spawn, are a major bycatch. These traps accounted for 5% of total Thai cephalopod catch in 1994 (i.e. over 7 000 tonnes). Off the southwest coast of India, a modified type of hook, a baited hand-jig, is used to catch this species. ***Sepia pharaonis*** has been grown successfully in culture, and techniques are currently being improved in Thailand to culture these animals commercially. The flesh is thick, tender and excellent for human consumption.

Local Names: CHINA: Mak mo, Foo baan woo chack; JAPAN: Torafu-kouika, Mongouika.

Remarks: The diagnostic features given above were obtained from a range of sources and examination of Australian specimens. They should be treated with caution because animals currently referred to as ***S. pharaonis*** are probably representatives of a species complex. One species from southeast India, ***S. ramani*** Neethiselvan, 2001, has been described recently. ***Sepia ramani*** differs from ***S. pharaonis*** in having a longer club with 15 to 24 subequal enlarged suckers. ***Sepia pharaonis*** has 6 enlarged medial club suckers, 3 or 4 of which are much larger than the rest. ***Sepia ramani*** has 14 to 16 transverse rows of normal size suckers on the proximal end of the hectocotylized arm, instead of 10 to 12 rows, as in ***S. pharaonis***. In other traits, these 2 species are very similar. The hectocotylus differs between ***S. pharaonis*** from Japan and Australia. Given its fisheries importance, the status of this putative species needs to be examined and specimens from throughout its range compared with those from the type locality to accurately determine its population structure and/or species boundaries.

Literature: Adam and Rees (1966), Silas *et al.* (1982), Valinassab (1983), Nair (1986), Okutani *et al.* (1987), Gutsal (1989) Chu *et al.* (1992), Kukharev *et al.* (1993), Khaliluddin (1995), Chantawong and Suksawat (1997), Chotiyaputta and Yamrungreung (1998), Lu (1998a), Rocha *et al.* (1998), Gabr *et al.* (1999).

Sepia plangon Gray, 1849

Fig. 172; Plate V, 35

Sepia plangon Gray, 1849, *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Antepedia*: 104 [type locality: Australia, New South Wales, Port Jackson, 33°51'S 151°16'E].

Frequent Synonyms: *Solitosepia plangon adhaesa* Iredale, 1926.

Misidentifications: None.

FAO Names: En – Striking cuttlefish; **Fr** – Seiche impressionnante; **Sp** – Sepia impresionante.

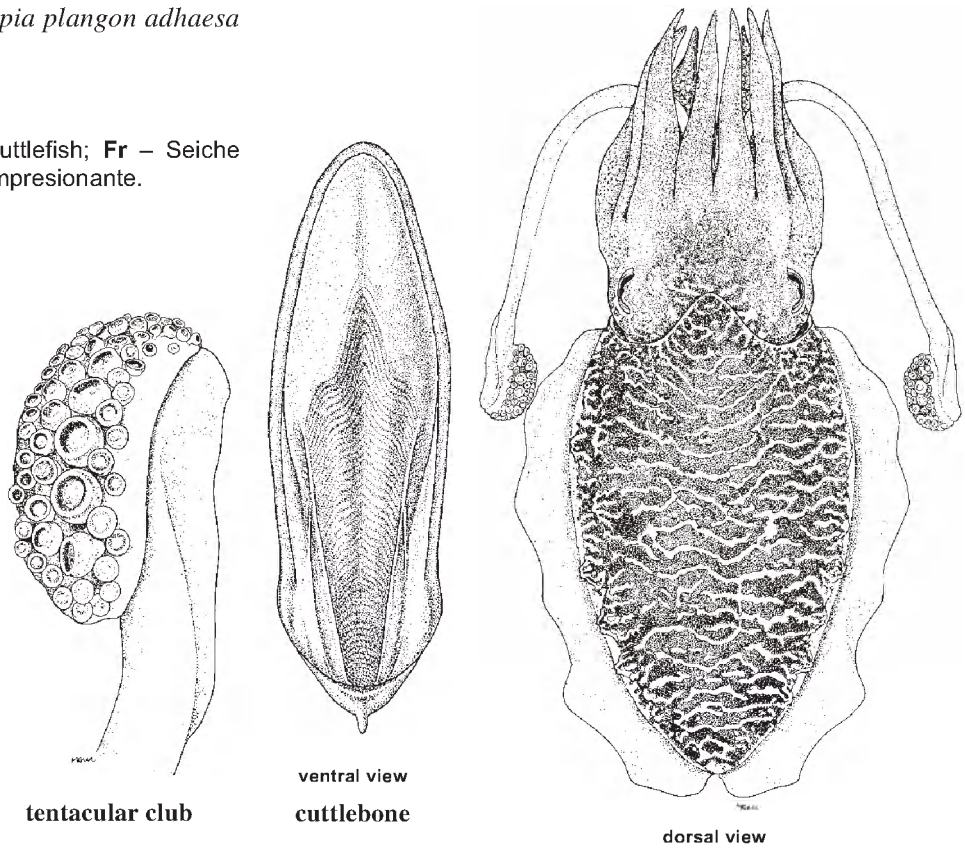


Fig. 172 *Sepia plangon*

Diagnostic Features: Mantle broad, oval. Male and female Arm lengths subequal; protective membranes narrow. Arm suckers tetraserial. Hectocotylus present on left ventral arm: 5 rows of normal size suckers proximally, **5 rows of reduced suckers medially**, then normal size suckers distally to arm tip. Suckers **equal in size**, reduced suckers only slightly smaller than normal arm suckers; oral surface of modified region not wide, fleshy, but normal, as on opposite arm. Club sucker-bearing surface flattened, with **5 suckers in transverse rows**; suckers differ markedly in size: some greatly enlarged (median series largest followed by those immediately bordering ventral series). Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes **joined at base of club** but fused to tentacular stalk. Dorsal and ventral membranes **same length**; extend proximal to carpus along stalk. Dorsal membrane forms **deep cleft at junction with stalk**. Cuttlebone outline oblong; acuminate, acute, anteriorly; bluntly rounded posteriorly; dorsal surface pinkish; dorsal surface convex medially, flat laterally; granulose; dorsal median rib distinct; sides approximately parallel; lateral ribs indistinct. Chitin borders lateral and anterior margins of cuttlebone. Spine long, pointed, straight, parallel to bone, **with ventral keel**. Striated zone concave; last loculus flat; sulcus **deep, narrow**, extends entire length of cuttlebone; **sulcus flanked by rounded ribs** (giving striae a wavy appearance). Anterior striae are **inverted V-shape**. Inner cone limbs are **uniform width**, narrow, U-shape posteriorly; outer cone calcified; narrow anteriorly, broadens posteriorly. **Colour:** Reddish purple, light brown, or dark brown, or sometimes with whitish mottle. During the breeding season, the head and dorsal mantle of males have narrow, irregular light-coloured transverse stripes. Fins pale with broad light greenish band along base.

Size: Up to 135 mm mantle length.

Geographical Distribution: Southwestern Pacific: eastern Australia from Gulf of Carpentaria to Sydney, NSW 33°53'S 151°13'E (Fig. 173).

Habitat and Biology: Depth range intertidal to 83 m. *Sepia plangon* frequently is found among seaweed and seagrass. It is active during the day, foraging for crustaceans and fishes. It often can be seen resting on the sea floor, raising the anterior end of the body by using its arms as stilts. Females are plain coloured, without pattern, during courtship.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries.

Literature: Adam and Rees (1966), Lu (1998a).

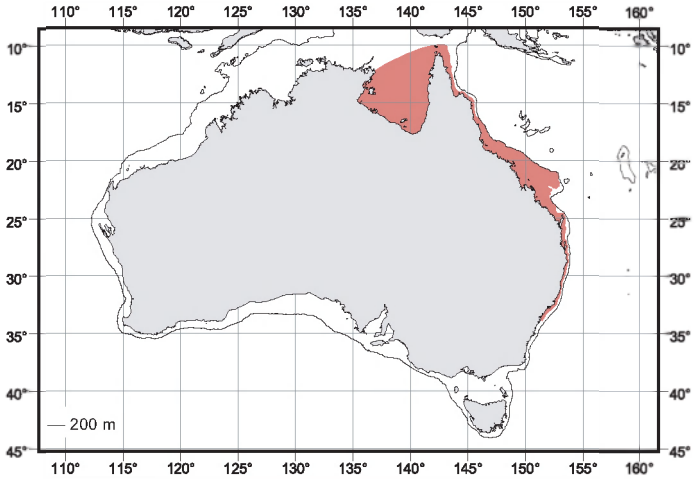


Fig. 173 *Sepia plangon*
Known distribution

NEXT PAGE

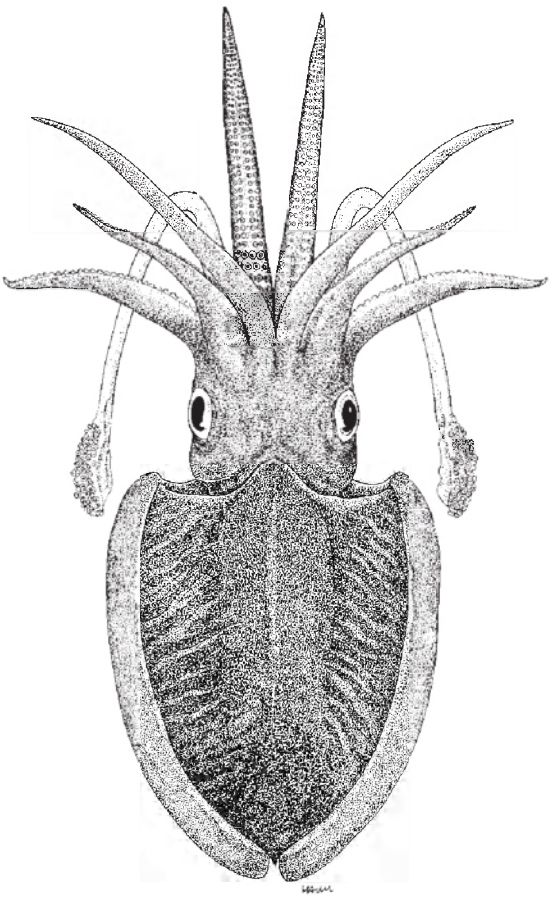
Sepia prabahari Neethiselvan and Venkataramani, 2002 — Fig. 174

Sepia prabahari Neethiselvan and Venkataramani, 2002, *Indian Journal of Marine Sciences*, 31(1): 45 [type locality: southeast coast of India, Tuticorin, 08°47'N 78°9'E].

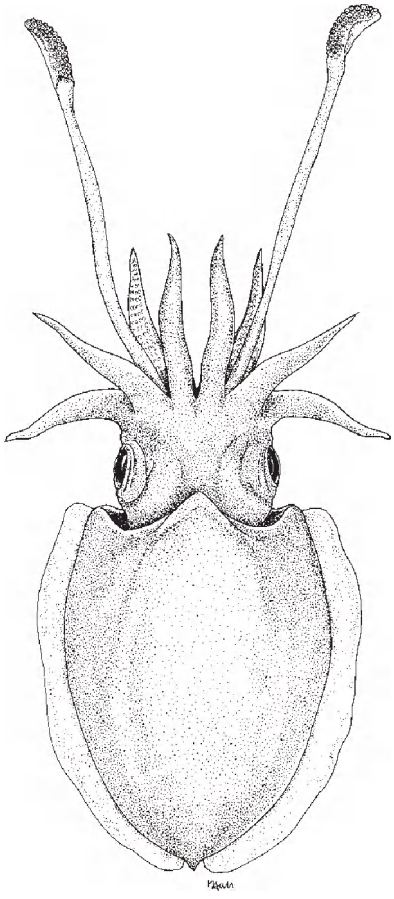
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Small striped cuttlefish; **Fr** – Petite seiche rayée; **Sp** – Sepia listada pequeña.



male



female

Diagnostic Features: Male arms elongate, robust; **arms I and IV elongate, whip-like** (more pronounced in mature males); in females arms approximately subequal in length; arm formula in both sexes IV, I, III, II; arm suckers tetraserial. Hectocotylus present on left arm IV: 8 transverse rows of normal size suckers proximally, followed by 7 rows of modified suckers, then rest normal to arm tip. Suckers in **2 dorsal series greatly reduced, suckers in 2 ventral series normal in size** on modified portion of arm; 2 dorsal and 2 ventral series displaced laterally, with fleshy ridge between. Club short, with **6 suckers in transverse rows**; **suckers all of similar minute size**. Swimming keel terminates at posterior end of carpus. Dorsal protective membrane broader than ventral protective membrane. Dorsal and ventral protective membranes extend slightly beyond carpus, **not joined at base of club**. Cuttlebone elliptical; broader in females than males; rugose dorsally, with indistinct median and lateral ribs. Spine curved dorsally, without keels. Sulcus deep, broad, extends length of striated zone. Anterior striae are inverted V-shape. Inner cone limbs are **narrow anteriorly, broaden posteriorly, then are raised into a thick, round ledge**; outer cone

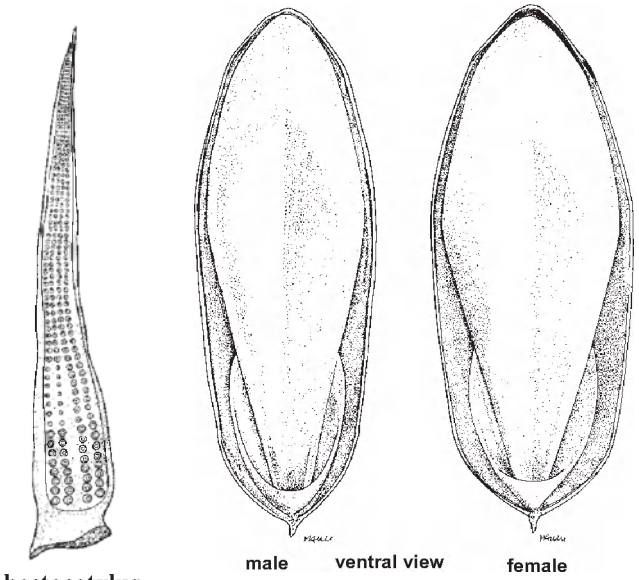


Fig. 174 *Sepia prabahari*

narrow anteriorly, broadens posteriorly, fused to inner cone. **Colour:** Dorsal mantle, head and arms dark brown with transverse zebra-stripe pattern (more prominent in males than females, and more obvious in fresh animals). Fins with pale, narrow, longitudinal line along base. Golden yellow nidamental glands visible in mantle cavity of female over 60 mm mantle length. Cuttlebone inner cone white.

Size: Up to 130 mm mantle length.

Geographical Distribution: Indian Ocean: Indian Coast, Gulf of Mannar. Depth ranges up to 100 m (Fig. 175).

Habitat and Biology: No detailed information is available yet for this newly described species.

Interest to Fisheries: *Sepia prabahari* is fished year round along the Thoothukkudi southeast coast (India).

Remarks: *Sepia prabahari* appears to breed continuously throughout the year.

Local Names: INDIA: Chinna vari kanavai.

Literature: Neethiselvan and Venkataramani, 2002.

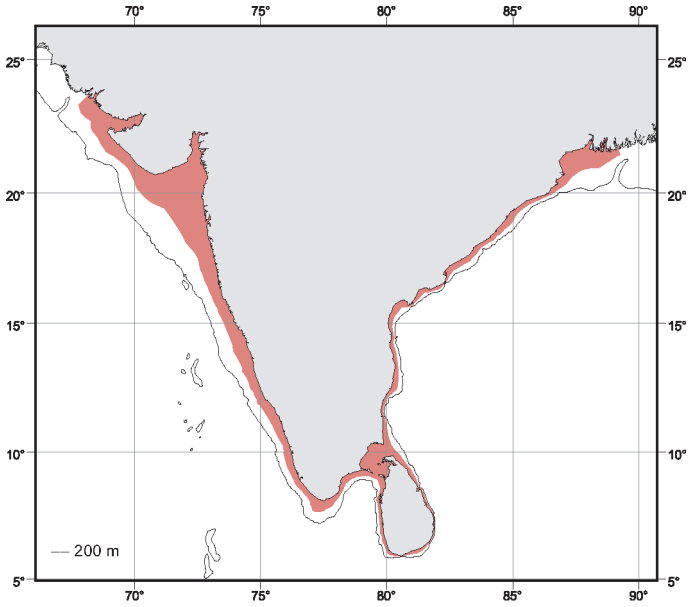


Fig. 175 *Sepia prabahari*
Known distribution

Sepia prashadi Winckworth, 1936 **Fig. 176**

Sepia prashadi Winckworth, 1936, *Proceedings of the Malacological Society of London*, 22(1): 16 [type locality: India, Chennai (Madras), Bay of Bengal].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Hooded cuttlefish; **Fr** – Seiche capuchon; **Sp** – Sepia caperuza.

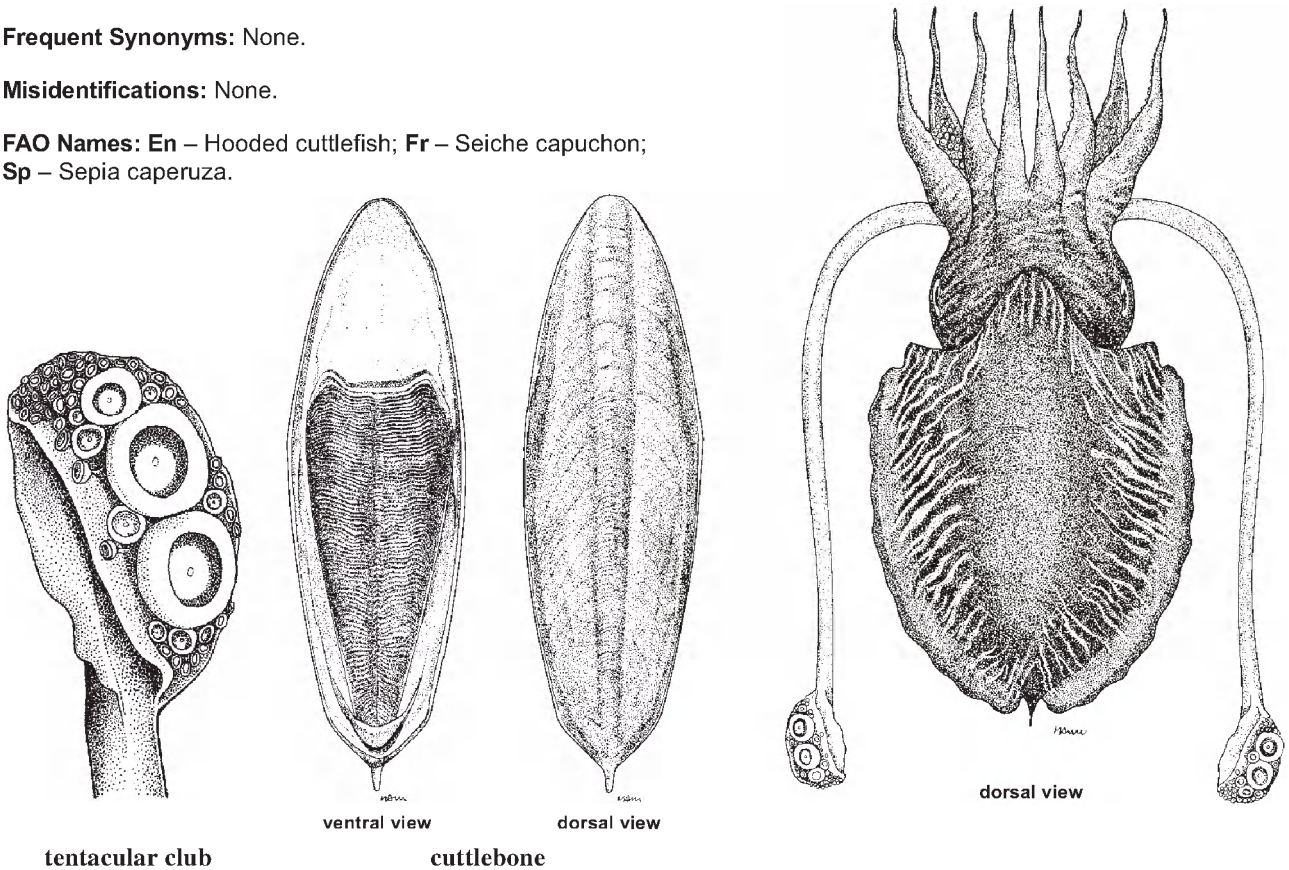


Fig. 176 *Sepia prashadi*

Diagnostic Features: Male and female arms subequal in length; protective membranes narrow. Arm suckers tetraserial. Male median arm suckers with **greater diameter than marginal ones** over most of arm length. Hectocotylus present on left ventral arm: **4 rows of normal size suckers proximally, 12 to 14 rows of reduced suckers medially**, then normal size suckers to arm tip; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges. Suckers of hectocotylus in 2 ventral series are displaced laterally, with gap between on proximal part of modified region, becoming closer together distally. Club short, oval; sucker-bearing surface flattened, with **3 to 5 suckers in transverse rows**; suckers differ markedly in size: **median 4 suckers extremely large**, surrounded by moderately large suckers. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club**. Cuttlebone outline oblong; bone triangular, obtuse anteriorly; bluntly rounded posteriorly; granulose; **dorsal median rib distinct**, broadens slightly anteriorly; ribs **bordered laterally by distinct grooves**; lateral ribs distinct. Chitin borders lateral and anterior margins of cuttlebone. Spine long, pointed, straight, directed dorsally, with dorsal and ventral keel. Striated zone convex; striated zone separated from outer cone by narrow, smooth marginal zones; sulcus shallow, narrow, **flanked by rounded ribs**, extends entire length of cuttlebone. Anterior striae **shallow m-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly; **raised into rounded, thickened ledge**; outer cone chitinous laterally, calcareous in expanded posterior part. Dorsal mantle has transverse zebra stripe pattern in breeding males.

Size: Up to 140 mm mantle length.

Geographical Distribution: Indian Ocean: from off northeastern India (Calcutta) to the Gulf of Oman, Red Sea, Gulf of Suez, southern Mozambique, Madagascar, Mauritius, Andaman–Nicobar Seas (Fig. 177).

Habitat and Biology: A demersal, shallow water, small-sized species ranging in depth from the coastline to 200 m. Off Waltair (northeastern coast of India), the species occurs throughout the year, even though sporadically. For this area, preliminary studies reported mature individuals at 72 and 67 mm mantle length for females and males, respectively. In the waters off Madras (southeast India), ***S. prashadi*** is found from January to April, along with upwelled deeper water fishes. In the Gulf of Suez a life span of 18 months was estimated.

Interest to Fisheries: Taken by trawls in the Red Sea and along the Indian east coast off Waltair and Madras (northeast India), ***S. prashadi*** is most abundant from the beginning of the year to June and in some years, from October to December. Off Madras, it is taken in small quantities in local upwelling areas as bycatch to finfishes normally occurring in deeper waters. Separate catch statistics are not reported for this species. Exploratory surveys in the Andaman–Nicobar Seas indicate a wide distribution of cephalopod resources both in the coastal and oceanic waters. It was suggested that suitable techniques, such as light fishing with lift nets, would result in better exploitation of demersal species, among which ***S. prashadi*** is well represented. Based on stock assessment studies in the Gulf of Suez, ***S. prashadi*** was underexploited in the mid-1990s.

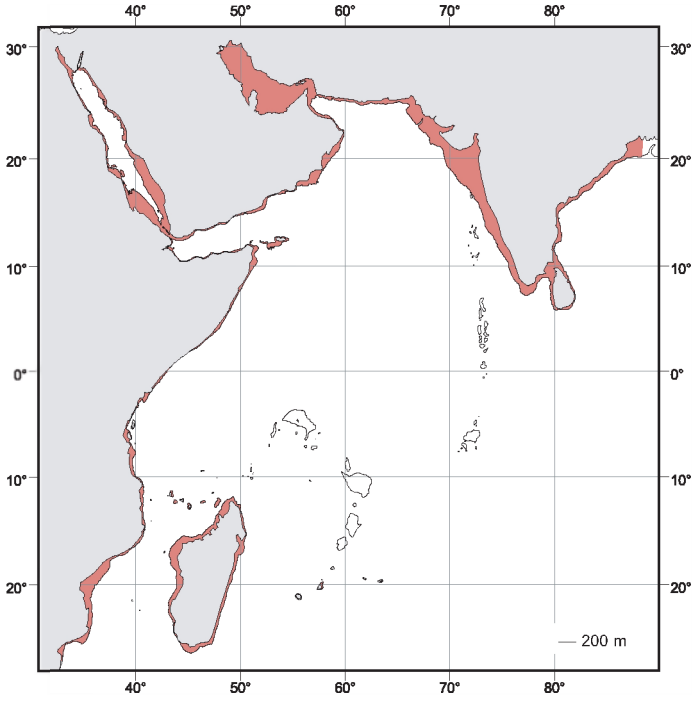


Fig. 177 ***Sepia prashadi***
Known distribution

Literature: Adam and Rees (1966), Silas *et al.* (1982), Silas *et al.* (1986), Okutani *et al.* (1987), Sreenivasan and Sarvesan (1990), Emam (1994), Filippova *et al.* (1995), Khaliluddin (1995), Nateewathana (1999).

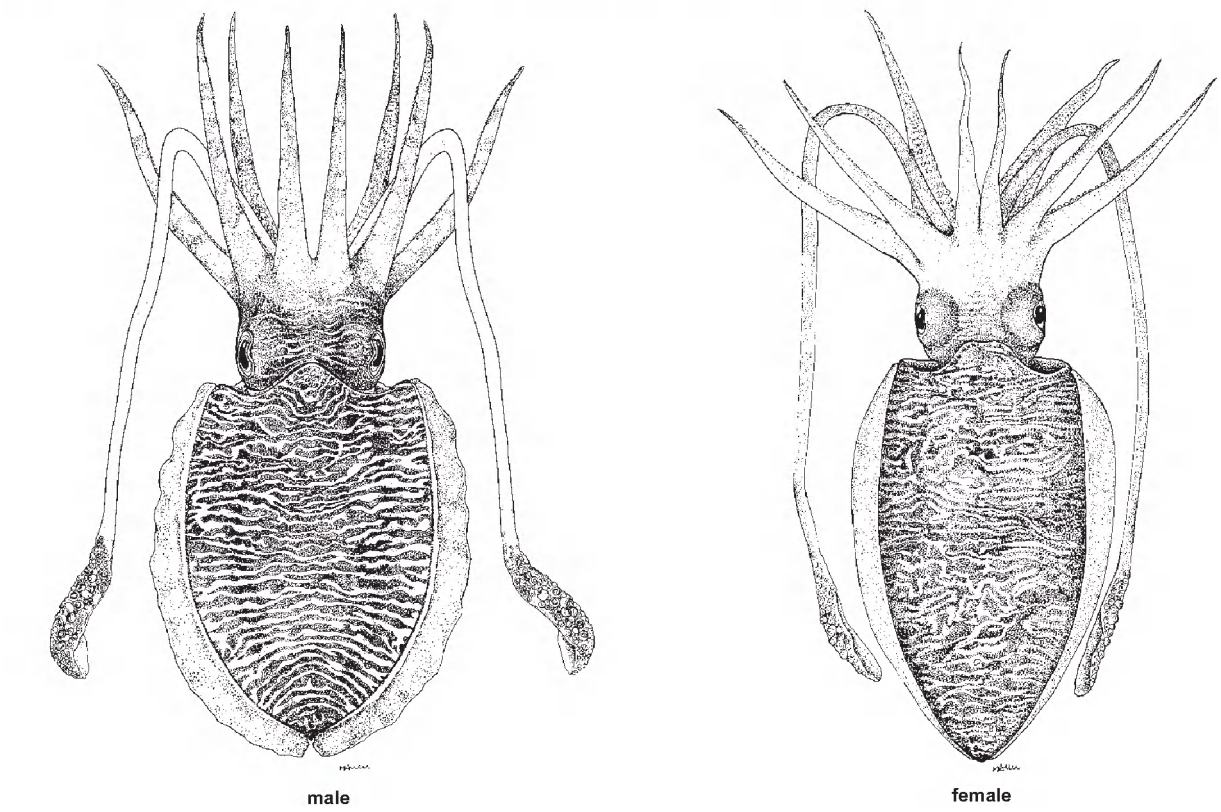
Sepia ramani Neethiselvan, 2001 **Fig. 178**

Sepia ramani Neethiselvan, 2001, *Indian Journal of Marine Sciences*, 30: 82 [type locality: southeast coast of India, Tuticorin, 08°47'N 78°09'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Large striped cuttlefish; **Fr** – Grande seiche rayée; **Sp** – Sepia listada grande.



Diagnostic Features: Male and female arms approximately subequal in length; arm formula in both sexes IV, III, II, I; arm suckers tetraserial. Hectocotylus present on left arm IV: 14 to 16 transverse rows of normal size suckers proximally, followed by 7 to 10 rows of modified suckers, then rest normal to arm tip. Suckers in **2 dorsal series minute, suckers in 2 ventral series normal in size** on modified portion of arm; 2 dorsal and 2 ventral series displaced laterally, with fleshy ridge between. Club long; **15 to 24 suckers enlarged, all enlarged suckers similar in size**. Swimming keel narrow, terminates at posterior end of carpus. Dorsal and ventral protective membranes extend slightly beyond carpus, **not joined at base of club**. Buccal membrane with minute suckers. Cuttlebone slender, elliptical; rugose dorsally, with indistinct median and lateral ribs. Spine short, stout, without keels. Sulcus deep, broad, extends length of striated zone. Anterior striae are inverted V-shape. Inner cone relatively short, limbs are **narrow anteriorly, broaden posteriorly, with distinctive, thick, bulbous swelling**; outer cone narrow anteriorly, broadens posteriorly. **Colour:** Dorsal mantle, head and arms dark brown with transverse zebra stripe pattern (more prominent in males than females, and more obvious in fresh animals). Fins with pale, narrow, longitudinal line along base.

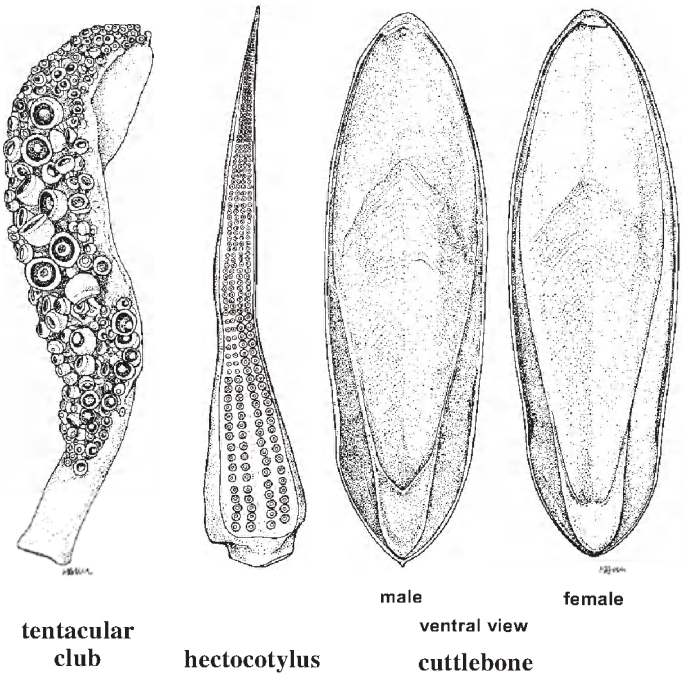


Fig. 178 *Sepia ramani*

Size: Up to 375 mm mantle length.

Geographical Distribution: Indian Ocean: southern Indian Coast, Gulf of Mannar. Depth ranges up to 100 m (Fig. 179).

Habitat and Biology: No detailed information is available yet for this recently described species.

Interest to Fisheries: ***Sepia ramani*** is a component of the commercial fishery throughout the year along the Thoothukkudi coast (southeast India).

Remarks: ***Sepia ramani*** is morphologically very similar to ***Sepia pharaonis*** Ehrenberg, 1831. ***Sepia pharaonis*** has 5 or 6 enlarged club suckers, of which 3 or 4 suckers are greatly enlarged, in contrast to ***S. ramani*** with 15 to 24 enlarged suckers that are all of similar size. In addition, there are 10 to 12 transverse rows of normal suckers on the base of the hectocotylus in ***S. pharaonis***, and 14 to 16 transverse rows of normal suckers in ***S. ramani***. The spawning season of ***S. ramani*** seems to extend from September to December.

Local Names: INDIA: Periya vari kanavai.

Literature: Neethiselvan, 2001.

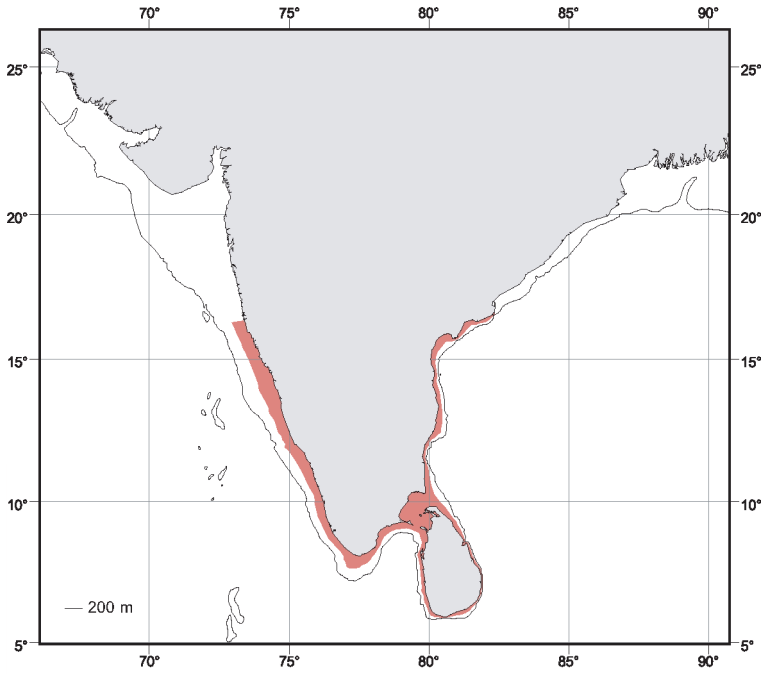


Fig. 179 ***Sepia ramani***
Known distribution

Sepia recurvirostra Steenstrup, 1875 — Fig. 180

Sepia recurvirostra Steenstrup, 1875, *Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 10(7): 479 [type locality: South China Sea].

Frequent Synonyms: *Sepia singaporensis* Pfeffer, 1884.

Misidentifications: None.

FAO Names: En – Curvespine cuttlefish; **Fr** – Seiche hameçon; **Sp** – Sepia ganchuda.

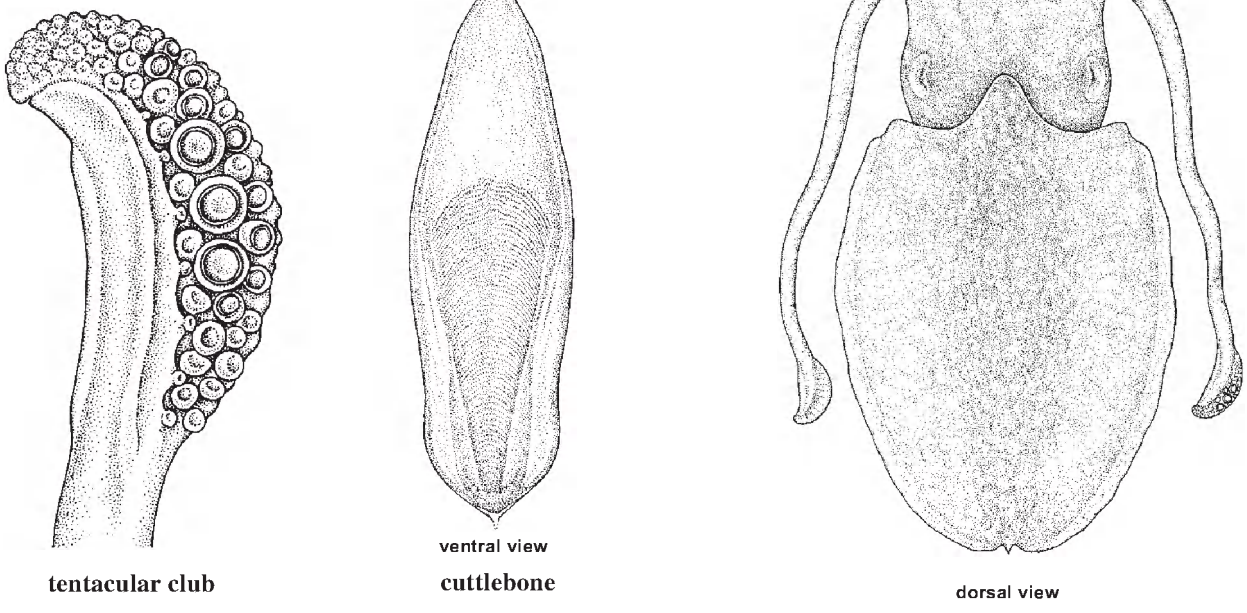


Fig. 180 ***Sepia recurvirostra***

Diagnostic Features: Mantle broad, oval. Non-hectocotylized arm sucker arrangement same in both sexes: suckers arms I to III **tetraserial proximally, biserial at distal tips**; arms IV **suckers tetraserial**. Hectocotylus present on left ventral arm: sucker size normal proximally, reduced medially, then normal size suckers to arm tip. Suckers of hectocotylus in **2 dorsal series smaller than those in 2 ventral series**; reduced suckers much smaller than normal arm suckers; suckers evenly spaced on modified portion of arm. Club sucker-bearing surface flattened, with **5 or 6 suckers in transverse rows**; suckers differ markedly in size: **5 or 6 median suckers enlarged**. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes not joined at base of club; dorsal membrane forms deep cleft at junction with stalk. Buccal membrane without suckers. Cuttlebone outline oblong; **bone very angular, V-shape anteriorly**; bluntly rounded posteriorly; dorsal median and lateral ribs present. Chitin present as wide patch posteriorly and a narrow chitinous rim borders lateral margins of cuttlebone. Spine curves ventrally. Last loculus concave; sulcus shallow, narrow, extends along striated zone only. Anterior striae are **inverted U-shape**. Inner cone limbs are uniform width, narrow, U-shape posteriorly, **thickened posteriorly into a rough chitinous callus**; outer cone calcified, narrow anteriorly, broadens posteriorly. Dorsal mantle pale with opalescent blue transverse stripes. Fins with **pale reflective opalescent blue line along base**.

Size: Up to 170 mm mantle length and 0.4 kg weight.

Geographical Distribution: Western Pacific: Yellow Sea, China, Hong Kong, East China Sea, Taiwan Province of China, South China Sea, Philippines, Celebes Sea, Java Sea, Gulf of Thailand, Singapore. Indian Ocean: Andaman Sea and Myanmar, Bay of Bengal (Fig. 181).

Habitat and Biology: Depth range from 10 to 140 m. ***Sepia recurvirostra*** is a demersal species that inhabits the continental shelf. In the Gulf of Thailand, spawning occurs all year, with peak times from November to February and July to September. The ratio of males to females caught in the Gulf is 1:3.

Interest to Fisheries: The species has some commercial importance in Hong Kong, where it is caught in multispecies trawls. It is a commercial species in the Gulf of Thailand, South and East China Seas, and Japan. In Thailand, most cuttlefishes are caught using otter trawl, with smaller catches reported from pair trawl, squid light-lures, traps and push nets, with bottom otter and pair trawls used offshore, and push nets and lift nets used in inshore and coastal waters. A few cuttlefishes are caught using purse seine and hook and line. In the Gulf of Thailand, most captured animals are between 40 and 130 mm mantle length.

Local Names: CHINA: Jam mak yue; JAPAN: Ajia-kouika.

Literature: Adam and Rees (1966), Chantawong and Suksawat (1997).

Fig. 181 ***Sepia recurvirostra***
Known distribution

NEXT PAGE

Sepia rozella (Iredale, 1926) Fig. 182

Solitosepia rozella Iredale, 1926, *The Australian Zoologist*, 4(3): 190 [type locality: New South Wales, Manly Beach, 33°48'S 151°17'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Rosecone cuttlefish; **Fr** – Seiche au cône rosé; **Sp** – Sepia de cono rosado.

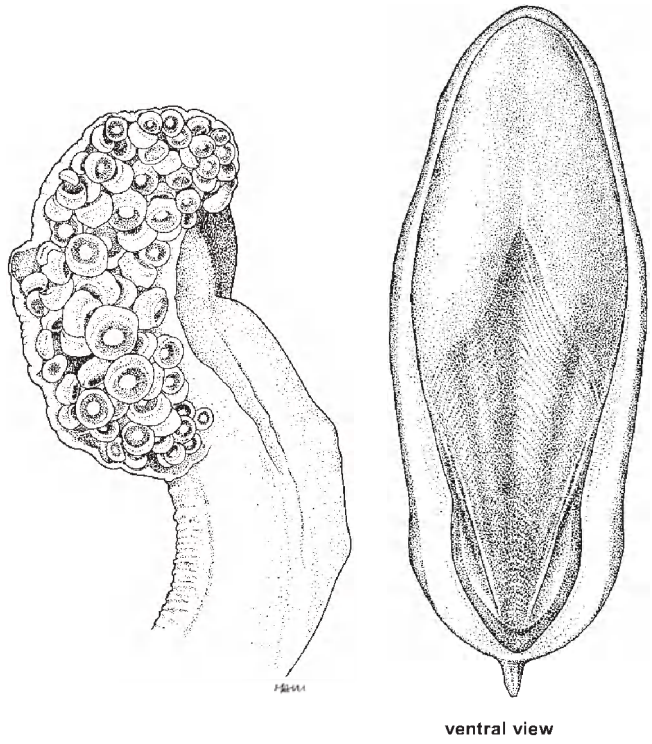


Fig. 182 *Sepia rozella*

Diagnostic Features: Mantle oval; dorsal anterior margin triangular, acute. Fins wide, rounded posteriorly, with narrow gap between them. Head elongate; slender, narrower than mantle. Male and female arm lengths subequal. Arm suckers tetraserial; female arms I protective membranes well developed, enveloping suckers; arm tips attenuate. Male non-hectocotylized arm suckers normal in size (not greatly enlarged). **Hectocotylus absent**; the only modification being the basal 40% of the left ventral arm is slightly thicker and the oral surface of arm is wider than the corresponding portion of the right ventral arm, with a shallow median furrow. Club short, oval; sucker-bearing surface flattened, with **4 or 5 suckers in transverse rows**; suckers differ slightly in size: **4 or 5 enlarged** suckers in longitudinal series towards posterior end of club. Swimming keel of club extends well proximal to carpus; dorsal and ventral protective membranes **joined at base of club** (V-shape); separated from tentacular stalk by membrane; dorsal and ventral membranes same length; dorsal membrane much wider than ventral membrane; dorsal membrane forms deep cleft at junction with stalk. Buccal membrane without suckers. Eggs spherical. Cuttlebone oblong in outline; bone bluntly rounded anteriorly and posteriorly; recurved ventrally; dorsal surface creamy white; dorsal surface evenly convex; entire surface calcified, granulose, sculpture reticulate on posterolateral half of bone. Spine and posterior tip of bone covered with smooth glaze-like substance. Dorsal median rib and lateral ribs indistinct. Chitin borders lateral margins of cuttlebone. Spine long, pointed, straight, directed dorsally, with **ventral keel** and ventral notch at base. Striated zone concave; last loculus flat; sulcus **deep, wide, distinct V-shape medially, flanked by rounded ribs**. Anterior striae are **inverted V-shape**. Inner cone limbs are narrow anteriorly, broaden posteriorly, **rose coloured**; outer margin of inner cone raised into **rounded, thickened posterior ledge**; outer cone calcified; narrow anteriorly, broadens posteriorly; outer cone lateral limbs are flared ventrolaterally. Dorsal mantle covered with numerous small papillae; ventral mantle with longitudinal row of 6 narrow ridges along each side close to fins; anteriormost pair and posterior 2 pairs shorter than rest. Head papillose dorsally and laterally. **Colour:** Purplish brown. Head with chromatophores concentrated over eye orbits. Arms without markings. Paired dorsal eye spots absent. Fins pale, without markings at base. Dorsal ridges reddish purple.

Size: Up to 140 mm mantle length.

Geographical Distribution: Southwestern Pacific: northeastern Australia, from southern Queensland, 27°42'S 153°35'E, to New South Wales, northeast of Tathra, 36°41'S 150°02'E (Fig. 183).

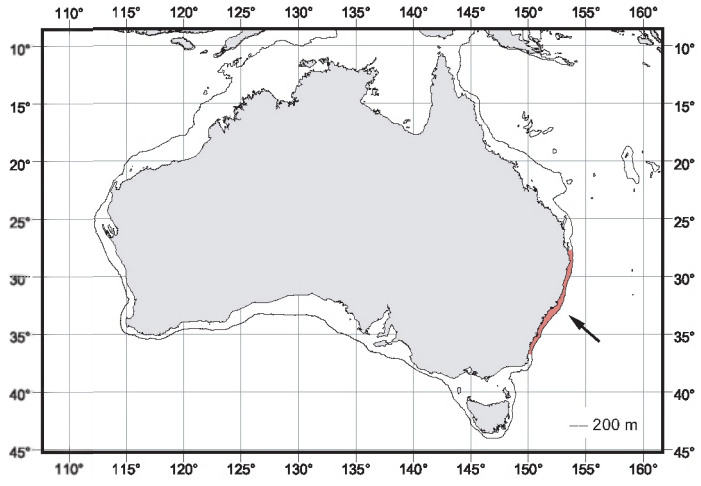


Fig. 183 *Sepia rozella*
Known distribution

Habitat and Biology: Depth range from 5 to 183 m.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries.

Literature: Lu (1998a).

Sepia savignyi Blainville, 1827

Fig. 184

Sepia savignyi Blainville, 1827, *Dictionnaire des Sciences Naturelles*, 48: 285 [type locality: Red Sea].

Frequent Synonyms: None.

Misidentifications: *Sepia plathyconchalis* Filippova and Khromov, 1991.

FAO Names: En – Broadback cuttlefish; **Fr** – Seiche gros dos; **Sp** – Sepia robusta.

Diagnostic Features: Mantle broad, oval; ventral mantle margin emarginate. Fins wide. Male and female arms subequal in length. Arm suckers tetraserial. Club straight, slender; sucker-bearing surface convex, with **8 suckers in transverse rows**; suckers differ slightly in size; **several suckers of inner 2 or 3 rows very slightly larger than rest**. Swimming keel of club terminates at proximal end of carpus (approximately). Dorsal and ventral protective membranes **not joined at base of club**, extend proximal to carpus along stalk. Buccal membrane with a few minute suckers. Cuttlebone outline oval; bone slightly acuminate, acute, anteriorly; bluntly rounded posteriorly; calcified with reticulate sculpture; dorsal median rib and lateral ribs indistinct; median rib broadens anteriorly. Chitin borders lateral and anterior margins of cuttlebone. Spine **short**, pointed. Striated zone flat, or slightly concave posteriorly; slightly convex anteriorly on each side of sulcus; striated zone separated from outer cone by broad, smooth marginal zones; last loculus flat; sulcus shallow, wide, extends along striated zone only. Anterior striae are **inverted U-shape**; limbs of inner cone extend anteriorly to approximately two-thirds length of striated zone. Inner cone limbs are narrow anteriorly, broaden posteriorly; outer margin of inner cone slightly raised as a slightly rounded ridge; not thickened; dull, not shiny; outer cone calcified, narrow anteriorly, broadens posteriorly. **Colour:** Light brown.

Size: Up to 190 mm mantle length.

Geographical Distribution: Western Indian Ocean: Red Sea, Gulf of Aden, Arabian Sea, Persian Gulf and Saya-de-Malha Bank. Not recorded south of Socotra Island (Fig. 185).

Habitat and Biology: Depth range from 20 to 50 m.

Interest to Fisheries: Not determined at present, but the size and distribution of the species indicate that ***S. savignyi*** is probably harvested in mixed species fisheries even though not specifically targeted.

Remarks: This species can be confused with ***S. plathyconchalis*** Filippova and Khromov, 1991, from which it differs by having a ventral median sulcus and a normal striated zone in the cuttlebone. The striated zone is very narrow in ***S. plathyconchalis***.

Literature: Adam and Rees (1966), Filippova *et al.* (1995).

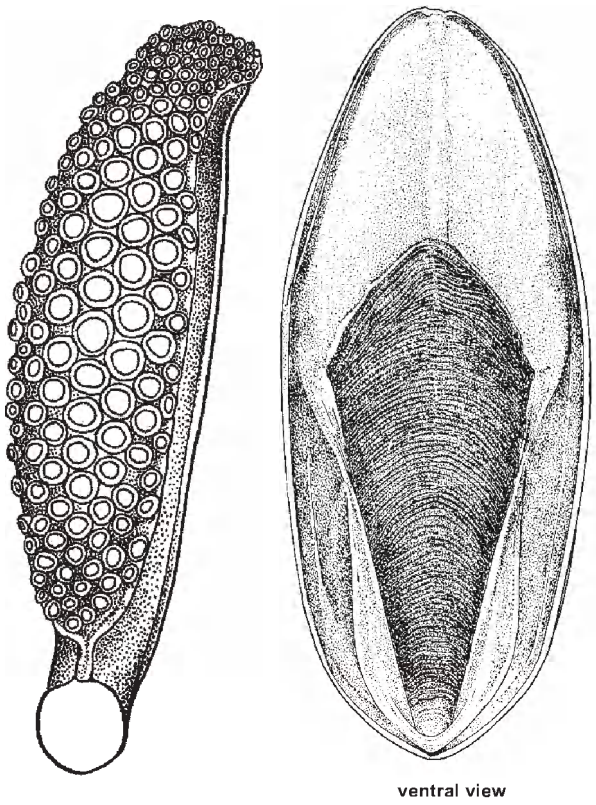


Fig. 184 ***Sepia savignyi***

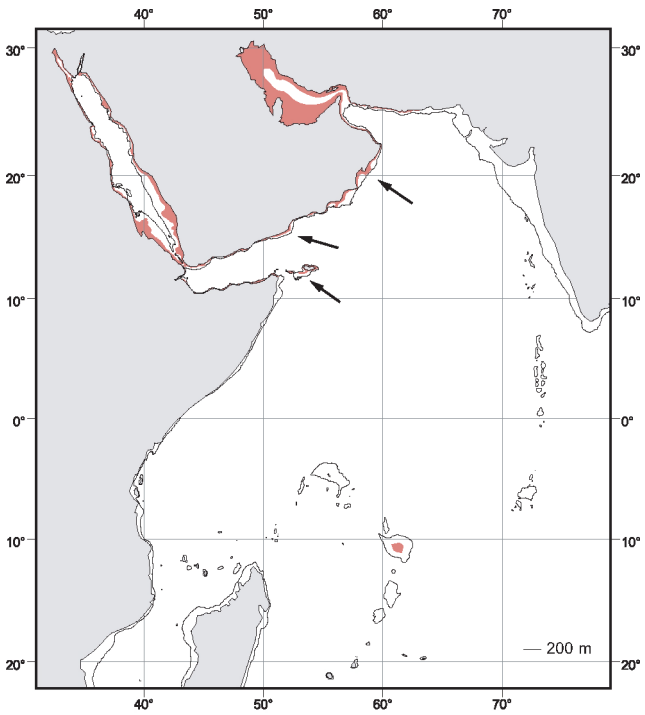


Fig. 185 ***Sepia savignyi***
Known distribution

Sepia smithi Hoyle, 1885 **Fig. 186; Plate V, 36**

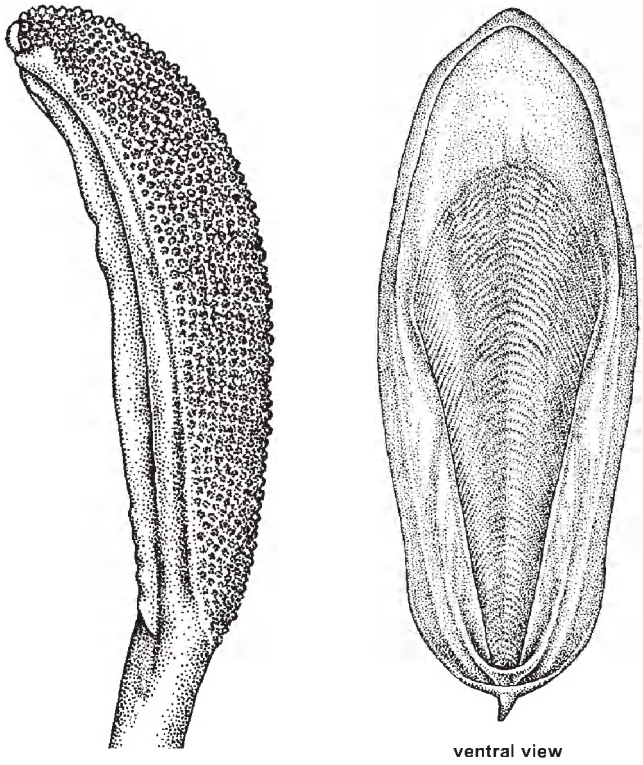
Sepia smithi Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 16: 190 [type locality: Arafura Sea, South of Papua, 09°59'S 139°42'E].

Frequent Synonyms: *Acanthosepion pageorum* Iredale, 1954.

Misidentifications: *Sepia whitleyana* (Iredale, 1926).

FAO Names: En – Smith's cuttlefish; **Fr** – Seiche de Smith; **Sp** – Sepia de Smith.

Diagnostic Features: Mantle broad, oval. Fins wide, anterior origin almost at mantle margin, rounded posteriorly, with narrow gap between them. Head elongate; slender, narrower than mantle. Male and female arms subequal in length. Arm suckers tetraserial. Hectocotylus present; **both ventral arms modified**. Left ventral arm: **8 rows of normal size suckers** (approximately) **proximally, 5 to 8 rows of greatly reduced suckers medially**, then normal size suckers distally to arm tip. Suckers of hectocotylus in **2 ventral series are smaller than those in 2 dorsal series**; oral surface of modified region not wide, fleshy, but normal; without distinct median furrow. Male right ventral arm: approximately **6 to 8 rows normal size suckers proximally, 5 rows reduced suckers medially**, then normal size suckers to arm tip. Suckers of hectocotylus in **dorsal row are smaller than those in 2 ventral series** in modified region; oral surface of modified region very **wide, fleshy, sponge-like in texture with pronounced median depression**; suckers in 2 dorsal series aligned in a single row. Both ventral arms of males: suckers in 2 ventral series are displaced laterally, with gap between, widely spaced (more obviously so on right ventral arm). Club straight, slender, or slightly recurved, long, sucker-bearing surface convex, with **13 to 22 suckers in transverse rows**; all club suckers of **similar, minute, size**. Swimming keel of club terminates at proximal end of carpus. Dorsal and ventral protective membranes **not joined at base of club** but fused to tentacular stalk. Dorsal and ventral membranes same length, terminate at posterior end of carpus. Dorsal membrane forms shallow cleft at junction with stalk. Buccal membrane without suckers; in females with single median spermathecae in ventral part. Eggs spherical. Cuttlebone outline oblong; **bone triangular, obtuse anteriorly**; bluntly rounded posteriorly; dorsal surface creamy white, or yellowish; dorsal surface evenly convex; entire surface calcified, granulose with sculpture arranged in series of blunt, transverse, inverted V-shape ridges. Spine and posterior end (approximately one quarter) of bone covered with **ochre-coloured smooth glaze-like substance**. Dorsal median rib and lateral ribs indistinct; median rib broadens slightly anteriorly, bordered laterally by indistinct grooves. Chitin surrounds entire margin of cuttlebone. Spine short, pointed, straight, directed dorsally, **keel(s) absent**. Striated zone concave; last loculus flat; sulcus shallow, wide, extends along striated zone only. Anterior striae are inverted U-shape. Inner cone limbs are broad, strap-like anteriorly, U-shape posteriorly; outer margin of inner cone **raised into rounded, thickened, shiny, posterior ledge**. Dorsal mantle covered with numerous small papillae and with series of 7 or 8 elongate orange-pink papillae along each side, adjacent to base of each fin. Head papillose dorsally and laterally. **Colour:** Pale buff pinkish brown, light brown, or greyish brown with white blotches and spots, sometimes joined to form irregular transverse bands. Arms I to III have a **longitudinal band of orange-red pigment along their aboral surfaces**. Arm and club sucker rims pale brown, or yellow brown. Dorsal mantle has pinkish spots, or blotches and scattered purplish spots and blotches. **Paired dorsal eye spots are present (both sexes)**. Fins in both sexes with **longitudinal whitish band lateral to series of orange-pink ridges overlain with regularly spaced transverse purplish blotches**.



(illustrations: K. Hollis)

Fig. 186 ***Sepia smithi***

Size: Males up to 140 mm mantle length; females up to 150 mm mantle length.

Geographical Distribution: Indo-Pacific: northern Australia from Shark Bay, Western Australia, 25°25'S 113°35'E, along the northern coast, then southward to Moreton Bay, Queensland, 27°25'S 153°20'E. Timor, Arafura and Coral Seas (Fig. 187).

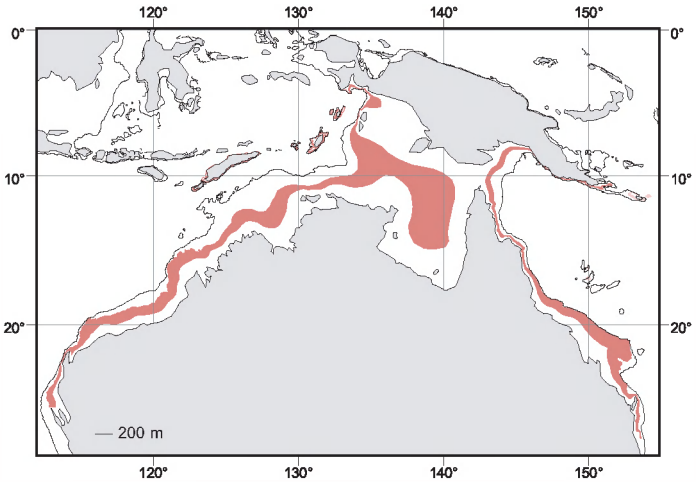


Fig. 187 ***Sepia smithi***
Known distribution

Habitat and Biology: Depth range from 33 to 138 m. In the Gulf of Carpentaria, ***S. smithi*** has been caught where bottom depths varied between 7 and 55 m, typically on sand and mud. ***Sepia smithi*** has been observed at night lying on the sea floor or burying into the sand, its pale colours and skin textures matching the sand surface. This lack of nocturnal activity suggests the species may be day-active.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries.

Remarks: ***Sepia smithi*** often is confused with ***S. whitleyana*** (Iredale, 1926). The 2 species differ in the nature of the cuttlebone inner cone, which is round, shiny and thickened in ***S. smithi*** and thin, narrow and not shiny in ***S. whitleyana***. The bases of the fins of ***S. whitleyana*** lack the longitudinal whitish bands that are present in ***S. smithi***. Male ***S. smithi*** lack the distinctive longitudinal white bars that are present in male ***S. whitleyana***. The cuttlebone is wider in ***S. whitleyana*** than in ***S. smithi***, particularly in the anterior third of the bone

Literature: Lu (1998a).

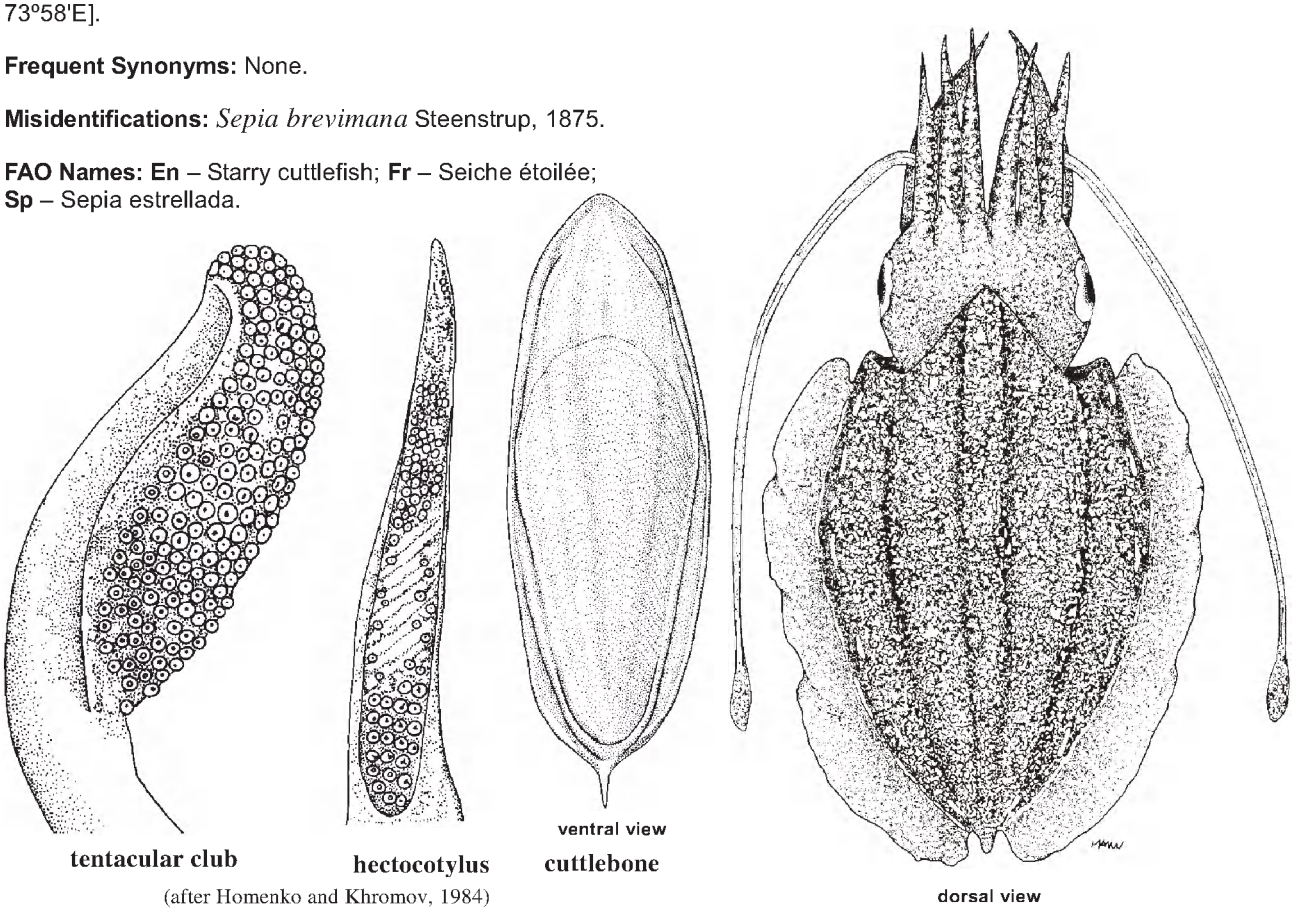
Sepia stellifera Homenko and Khromov, 1984 **Fig. 188**

Sepia stellifera Homenko and Khromov, 1984, *Zoologicheskii Zhurnal*, 63: 1150 [type locality: east Arabian Sea, 13º59'N 73º58'E].

Frequent Synonyms: None.

Misidentifications: *Sepia brevimana* Steenstrup, 1875.

FAO Names: En – Starry cuttlefish; **Fr** – Seiche étoilée; **Sp** – Sepia estrellada.



(after Homenko and Khromov, 1984)

(after Homenko and Khromov, 1984)

Fig. 188 ***Sepia stellifera***

Diagnostic Features: Club with **10 suckers in transverse rows**; all club suckers of similar, small size. Dorsal and ventral protective membranes not joined at base of club. Hectocotylus present; **left ventral arm modified**: suckers normal proximally, reduced medially, then normal size suckers proximally to arm tip. Suckers of hectocotylus in 2 ventral series are displaced laterally, with gap between; oral surface of hectocotylus with transversely grooved ridges. Cuttlebone outline oval; bone very angular, V-shape anteriorly (subrhomboidal in anterior fourth); **dorsal median rib very pronounced**; **lateral ribs present.** Spine long, pointed, with **dorsal and ventral keel**. Sulcus deep, wide, extends along striated zone only; sulcus with **3 deep, broad grooves and 2 ribs between them**; limbs of inner cone extend anteriorly to end of striated zone; outer cone present. **Colour:** Dorsal mantle with many small, bright, brown-pink spots, encircled with green-blue rings, the whole pattern resembling a starry sky.

Size: Up to 120 mm mantle length.

Geographical Distribution: Indian Ocean: Arabian Sea and west coast of India to Cape Comorin, Bay of Bengal, Andaman Sea, Gulf of Thailand. Possibly Saya-de-Malha Bank. Eastern extent of range unknown (Fig. 189).

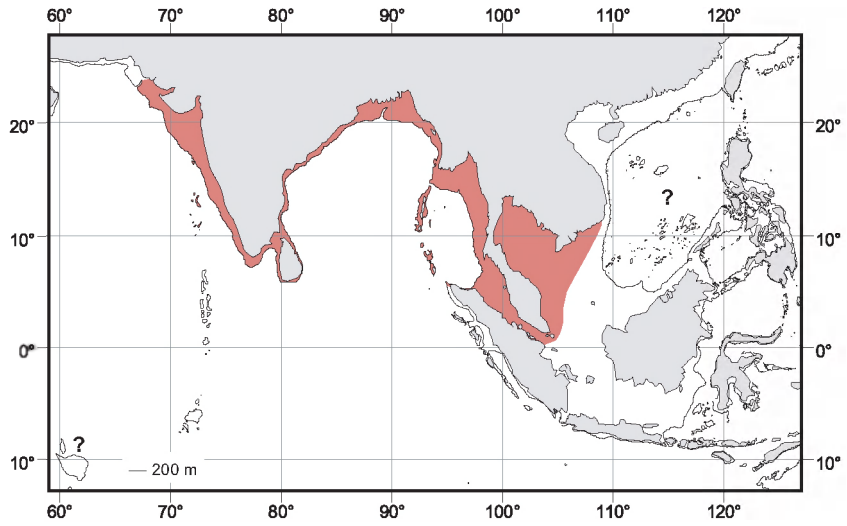


Fig. 189 *Sepia stellifera*
Known distribution

Habitat and Biology: Depth to 200 m.

Interest to Fisheries: This species is fished commercially in India and may figure in statistical data with ***Sepia brevimana*** Steenstrup, 1875.

Remarks: ***Sepia stellifera*** is similar to ***S. brevimana*** Steenstrup, 1875. It differs from ***S. brevimana*** in having 10 oblique club sucker rows, rather than 6 to 8, and the sulcus is deep and wide, rather than narrow and shallow as seen in ***S. brevimana***.

Literature: Homenko and Khromov, 1984.

Sepia sulcata Hoyle, 1885

Sepia sulcata Hoyle, 1885, *Annales and Magazine of Natural History*, (5)16: 192 [type locality: Indonesia: Arafura Sea, off Kai Island, 05°49'15"S 132°14'15"E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Grooved cuttlefish; **Fr** – Seiche striée; **Sp** – Sepia estriada.

Diagnostic Features: Sucker rows on arms I and III in males **biserial proximally, tetraserial distally** (approximately 8 to 11 rows biserial suckers arms I, 6 to 8 rows biserial suckers arms II and III); suckers on arms IV biserial at base (approximately 2 rows), tetraserial distally. Sucker rows on arms I to III in females **biserial proximally for 6 or 7 rows, tetraserial distally**, suckers on arms IV biserial proximally for 2 or 3 rows, rest tetraserial. Distal arm tips strongly attenuate. Left ventral arm hectocotylized: proximally 14 rows (approximately) of greatly reduced suckers; **2 dorsal series smaller than 2 ventral series**; 2 dorsal and 2 ventral series widely spaced in mature males. Oral surface wide, fleshy with deep longitudinal furrow between swollen protective membranes. Club with **5 to 7 small, subequal**

Fig. 190

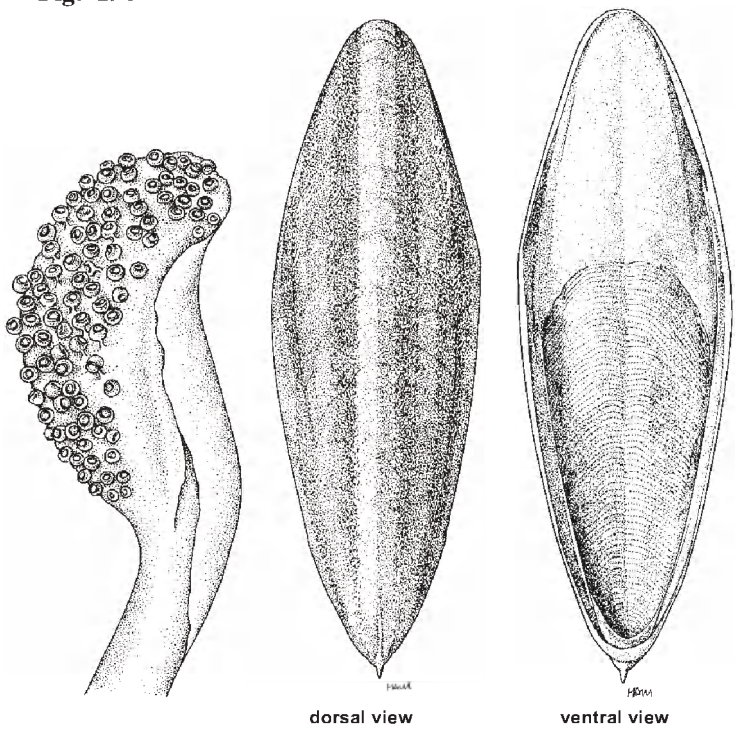


Fig. 190 *Sepia sulcata*

suckers in transverse rows. Dorsal and ventral protective membranes not joined at base of club. Cuttlebone oblong, strongly acuminate, acute, anteriorly and posteriorly. A **thick, cartilaginous subdermal layer** adheres closely to dorsal side of cuttlebone. Dorsal median and lateral ribs distinct; sulcus shallow, narrow, flanked by **prominent rounded ribs** bordered laterally by shallow grooves. **Inner cone** limbs form **narrow, raised ledge posteriorly**. Dorsal mantle with up to **10 short, longitudinal, orange-pink ridges** along each side close to fins; ventral mantle with 6 longitudinal ridges along each side close to fins.

Size: Males up to 68 mm mantle length; females up to 97 mm mantle length.

Geographical Distribution: Indo-Pacific: Indonesia, Arafura Sea, off Kai Islands, 05°49'15"S 132°14'15"E, to Australia: Western Australia, North West Shelf, 19°58'S 115°13'E (Fig. 191).

Habitat and Biology: Depth range from 150 to 404 m. Habitat mud, silt, rock.

Interest to Fisheries: Due to its size and distribution, this species may occur in multispecies trawl catches.

Remarks: The depth range occupied by this species is broad. There is some evidence to suggest that there might be a migration into relatively shallower waters for spawning. The cuttlebone of this species shows some similarities with that of ***S. australis*** Quoy and Gaimard, 1832 from South Africa. In both species, the cuttlebone is narrow and oblong, distinctly pointed anteriorly, with pronounced dorsal median and lateral ribs and, on the ventral side, the lateral ribs in both species are bordered by grooves. The ventral grooves, and sulcus are much deeper and more pronounced in ***S. australis*** than in ***S. sulcata***, with the sulcus extending along the last loculus in ***S. australis,*** unlike that of ***S. sulcata*** that is present only in the striated zone. Both species have a short, median ridge on the dorsal side of the cuttlebone, anterior to the spine. The posterior end of the cuttlebone is broader in ***S. sulcata***; in ***S. australis*** the outer cone is poorly developed and the inner cone is not raised into a ledge. ***Sepia australis*** is darkly pigmented, unlike ***S. sulcata,*** and it has a distinctive, unbroken longitudinal ridge at the base of the fins. The arm suckers in ***S. australis*** are arranged in four series, unlike those seen in ***S. sulcata***.

Literature: Adam and Rees (1966), Reid (2000).

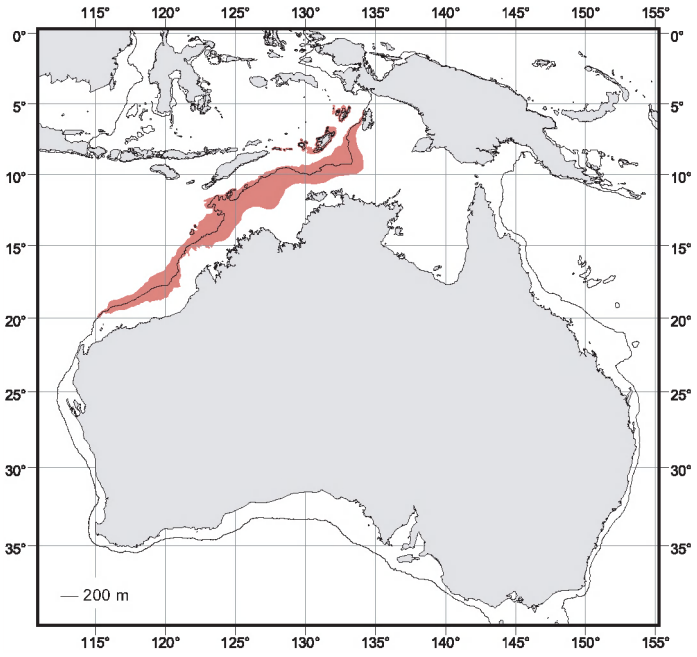


Fig. 191 ***Sepia sulcata***
Known distribution

NEXT PAGE

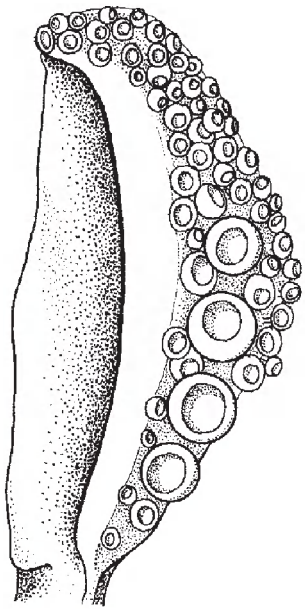
Sepia trygonina (Rochebrune, 1884) Fig. 192

Doratosepion trygoninum Rochebrune, 1884, *Bulletin des Sciences par la Societe Philomatique de Paris*, 7(8): 97 [type locality: Red Sea].

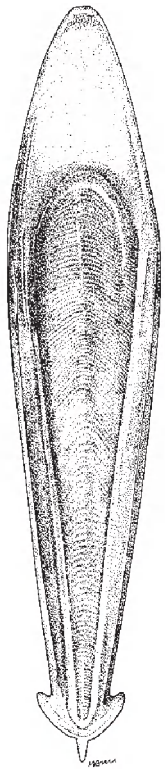
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Trident cuttlefish; **Fr** – Seiche trident; **Sp** – Sepia tridente.

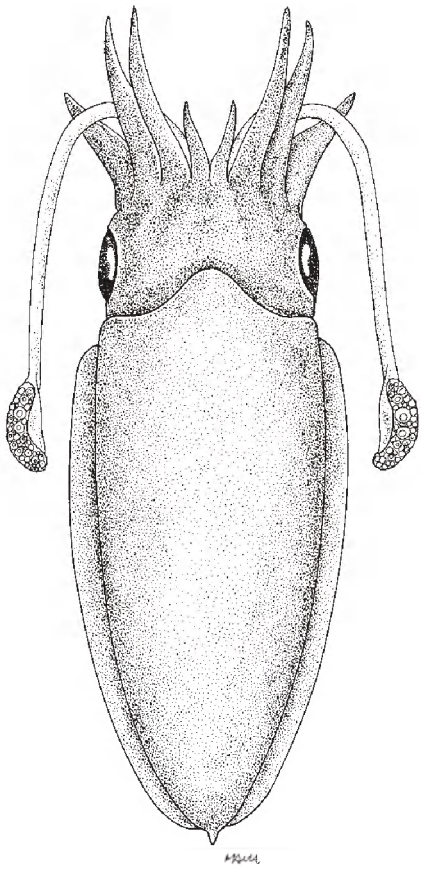


tentacular club



ventral view

cuttlebone



dorsal view, male

Fig. 192 *Sepia trygonina*

Diagnostic Features: Mantle oblong, acuminate posteriorly. Male and female arms differ in relative lengths: male arms I **shorter than rest**, female arm lengths **subequal**. Arm sucker arrangement differs between sexes: in males, arm suckers **tetraserial**; in females, suckers on arms I and IV **tetraserial**, suckers arms II and III **tetraserial proximally, biserial on distal third** of arms; **suckers displaced laterally, with gap between, on distal ends of female arms II and III**. Hectocotylus present on left ventral arm: 6 rows normal size suckers proximally, **suckers absent medially**, then normal size suckers to arm tip. Oral surface of modified region of hectocotylus **concave and covered by large transversely grooved protective membranes**; **ventral membrane wider than dorsal membrane**, thick and curved inwards (similar to *S. elongata*). Club short, oval; with 5 suckers in transverse rows; suckers differ markedly in size: **4 or 5 greatly enlarged suckers** in longitudinal series towards posterior end of club. Dorsal and ventral protective membranes not joined at base of club. Swimming keel of club extends proximally slightly beyond carpus. Buccal membrane in females without spermathecae. Cuttlebone outline **lanceolate**; strongly recurved ventrally; **dorsal surface pinkish**; calcified medially, thickest posteriorly, slightly granulose with irregular longitudinal ridges; dorsal median rib indistinct. Chitin present as wide bands bordering lateral margins of cuttlebone. Spine curves dorsally, **keel(s) absent**. Sulcus **shallow, wide**, extends entire length of cuttlebone; **sulcus flanked by rounded ribs**. Anterior striae are inverted U-shape; inner cone lateral limbs overlie calcareous striated zone, anteriorly bordered and separated from outer cone by striated zone. Inner cone limbs are uniform width, narrow, **U-shape posteriorly**; slightly raised into rounded posterior ridge; outer cone limbs are expanded into 2 short 'wings', directed ventrally, to form a recurved cup-like structure. **Colour:** Purplish brown. Base of fins in males with **dark purple band**; adjacent to band (or partially on it) is a series of small oval or circular cream-coloured patches, often raised as low tubercles.

Size: Up to 140 mm mantle length.

Geographical Distribution: Indian Ocean: from Saya-de-Malha Bank, 15°35'N–11°30'S, region of Mascarene Ridge and Zanzibar to Red Sea, Persian Gulf and southern India (Fig. 193).

Habitat and Biology: Depth from 20 to 410 m.

Interest to Fisheries: The fishery potential of the species is presently undetermined. However, the size and distribution of ***S. trygonina*** suggest that it probably occurs in the local fisheries catches.

Remarks: The female of this species is very similar to ***Sepia sokotriensis*** Khromov, 1988. The cuttlebone is very similar to ***S. burnupi*** Hoyle 1904, but differs in having a less well-defined dorsomedial rib. There is sexual dimorphism in the relative lengths and armament of the arms. In ***S. trygonina***, the arms of males are not as modified as in ***S. burnupi***, and females differ in having widely spaced suckers on the distal ends of the lateral arms. The club and hectocotylus resemble that of ***S. elongata*** d'Orbigny, 1839-1842, but the cuttlebone of ***S. elongata*** is thicker and the inner cone and the striae differ.

Literature: Adam and Rees (1966), Filippova and Khromov (1991), Filippova *et al.* (1995).

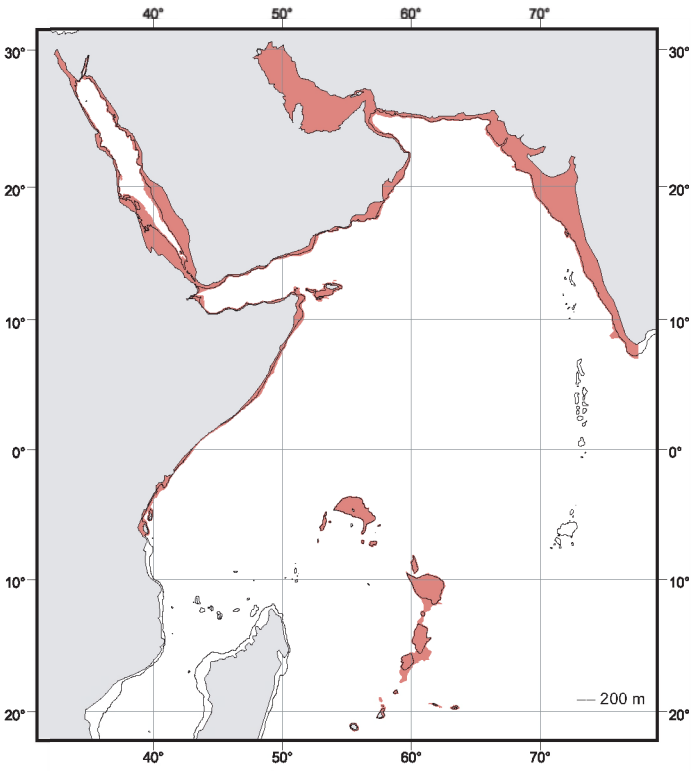


Fig. 193 ***Sepia trygonina***
Known distribution

Sepia vermiculata Quoy and Gaimard, 1832 **Fig. 194**

Sepia vermiculata Quoy and Gaimard, 1832, *Voyage de decouvertes de l'Astrolabe pendant les annees 1826–1827–1828–1829, Zoologie*, 2(1): 64 [type locality: Africa: South Africa, Cape of Good Hope].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Patchwork cuttlefish; **Fr** – Seiche réticulée; **Sp** – Sepia reticulada.

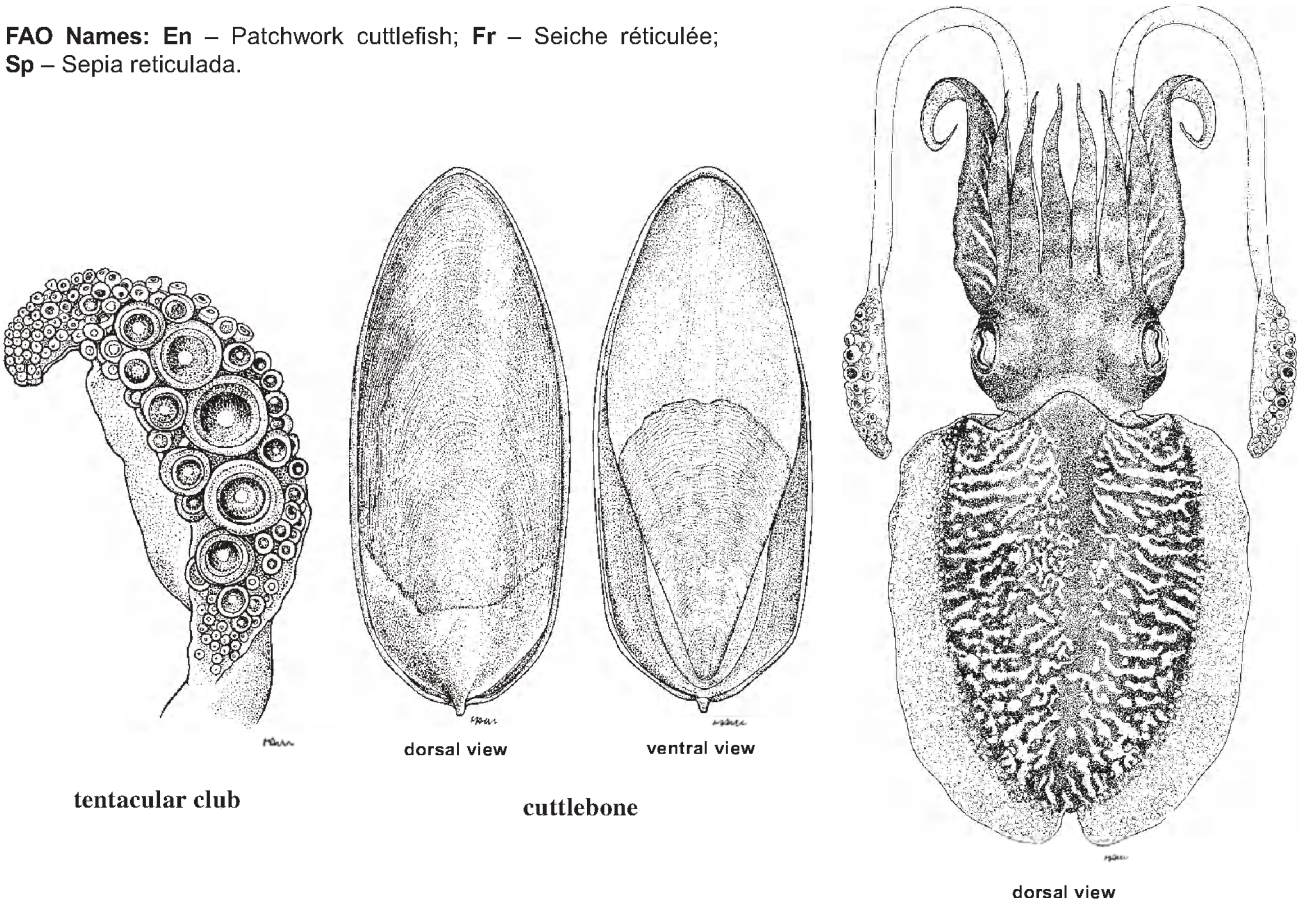


Fig. 194 *Sepia vermiculata*

Diagnostic Features: Mantle broadly oval, anterior margin somewhat produced dorsally. Fins broad and rounded, well separated posteriorly. Head short and broad. Arms joined by a shallow web, ventral arms longer than dorsal arms. Arms III and IV keeled, arms II sometimes keeled, arms I usually not keeled; arm tips somewhat attenuated. Arm suckers tetraserial; all suckers with finely toothed rings, distal teeth longer than proximal ones. Protective membranes well developed. Hectocotylus present on left ventral arm: approximately **6 normal suckers basally, followed by 8 to 13 rows of modified suckers**, modified suckers much smaller and separated by transverse ridges on arm; distal portion of arm normal. Tentacular club length approximately 1/3 of mantle length, **with 3 or 4 suckers in** transverse rows, small distally; **median suckers** of proximal part **variously enlarged**, 1 1/2 to 3 times as large as marginal suckers. Rings of large club suckers smooth. Swimming keel slightly shorter than club. Cuttlebone broadly oval, tapering slightly anteriorly and posteriorly; spine present, surrounded by chitinous covering; dorsal surface tuberculate, with fairly broad chitinous margins; no marked dorsal ridge. Striated zone about half of total cuttlebone length, with shallow sulcus; **anterior border of striated zone convex on either side of median ridge**.

Size: Up to 287 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: South Africa, 30°42'S 15°59'E, to central Mozambique, 19°S; Saya-de-Malha Bank and region of Mascarene Ridge (Fig. 195).

Habitat and Biology: Little information is available at present, but the species deserves investigation, due to its potential to fisheries and aquaculture. This is the only ***Sepia*** in southern Africa that enters lagoons and river mouths (e.g. Langebaan and Kysna lagoons, Kowie River), and it is found from very shallow waters (few metres) to 290 m.

Interest to Fisheries: No separate information is available at present, but the species is believed to have potential to fisheries, due to its size and distribution.

Literature: Adam and Rees (1966), Roeleveld (1972), Sanchez (1998), Filippova and Khromov (1991), Filippova *et al.* (1995).

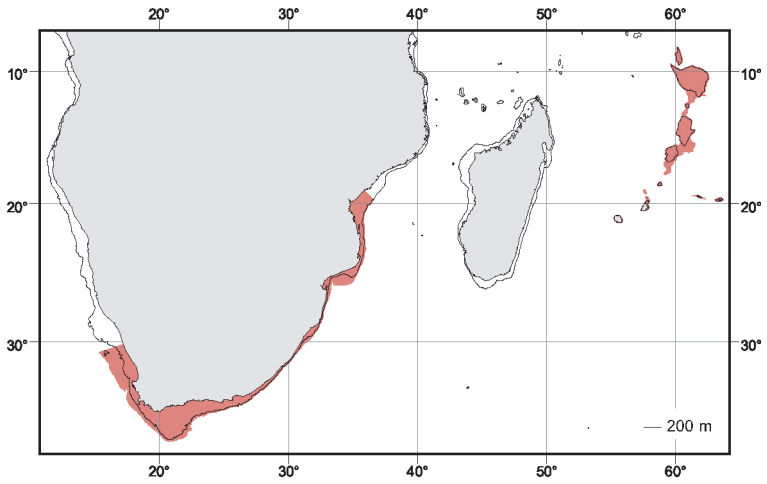


Fig. 195 ***Sepia vermiculata***
Known distribution

Sepia vietnamica Khromov, 1987

Fig. 196

Sepia vietnamica Khromov, 1987, *Asian Marine Biology*, 4: 35 [type locality: South China Sea, Gulf of Tonkin, 18°00'N 107°08'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Viet Nam cuttlefish; **Fr** – Seiche du Viet Nam; **Sp** – Sepia de Viet Nam.

Diagnostic Features: Mantle broad, oval, dorsoventrally compressed. Fins wide, anterior origin almost at mantle margin, rounded posteriorly. Male and female arms subequal in length; ventral arms slightly longer than rest. Arm suckers **tetraserial proximally, biserial at extreme distal tips**, medial suckers larger than lateral suckers on ventral arms. Hectocotylus present on left ventral arm: sucker size **normal proximally for 8 to 11 rows**, followed by **2 or 3 rows reduced suckers**, suckers of normal size medially, then distal third with reduced suckers to tip. Suckers of hectocotylus in **2 dorsal series are smaller than those in 2 ventral series**; dorsal suckers partially covered by wide protective membrane; reduced suckers much smaller than normal arm suckers; arm with deep median furrow; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between them. Club crescent-shaped, small; sucker-bearing surface flattened, with **5 suckers in transverse rows**; suckers differ slightly in size: 4 or 5 suckers enlarged in second ventral row, with suckers decreasing in size from this row to margins. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club**. Buccal membrane without suckers. Cuttlebone outline lanceolate, widest in anterior 1/3; bone bluntly rounded anteriorly; acuminate, acute, posteriorly; dorsal surface creamy white; dorsal surface evenly convex; dorsal median rib indistinct;

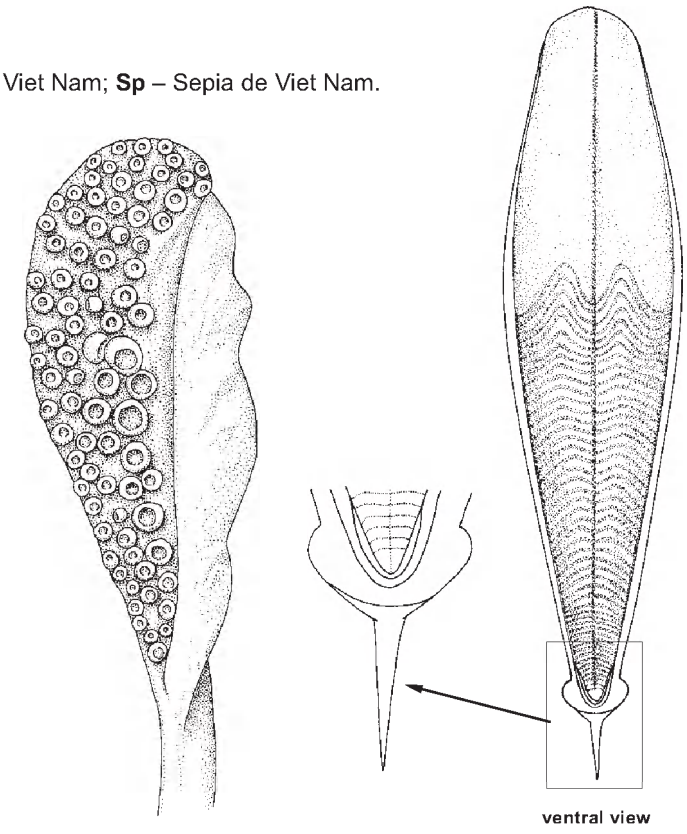


Fig. 196 ***Sepia vietnamica***
(after Khromov, 1987)

lateral ribs absent. Chitin (trace only) borders lateral margins of cuttlebone. Spine long, pointed, straight, keel(s) absent. Striated zone and last loculus convex; sulcus **deep, narrow, extends** entire length of cuttlebone. Anterior striae **M-, or m-shape**; limbs of inner cone are very short. Inner cone limbs are uniform width, narrow V-shape posteriorly, thickened; **slightly raised into rounded posterior ridge**; outer cone narrow throughout; outer **cone limbs are expanded posteriorly into 2 short 'wings', directed ventrally, to form a recurved cup-like structure**. Dorsal mantle with longitudinal row of ridge-like papillae along each side, adjacent to base of each fin (males only?); up to 6 fin papillae (approximately) in each row; papillae present on aboral surfaces of arms I to III. **Colour:** Dark brown. Head with **2 small, crescent-shaped orange spots near dorsal projection of mantle margin and above eyes**. Arms I to III have spots on aboral surface as for mantle. Fins pale with rows of large wine-coloured spots (in males and only at certain times).

Size: Up to 70 mm mantle length.

Geographical Distribution: Indo-Pacific: northwestern South China Sea, off Viet Nam and Taiwan Province of China. From original description, type specimens were collected off Viet Nam between 11°34'N and 20°00'N. The northern and southern extents of the range of this species have yet to be determined (Fig. 197).

Habitat and Biology: Depth range from 23 to 104 m. Type specimens were collected between 33 and 70 m.

Interest to Fisheries: No separate information is available at present, but the species is likely to occur in the catches within its distributional range.

Remarks: This species differs from ***Sepia lorigera***, Wülker 1910 in having subequal arms, while the 2 dorsal arms of ***S. lorigera*** are long in males. The posterior region of the inner cone of the cuttlebone is expanded in ***S. lorigera***, and is an unexpanded furrow in this species. There is no hectocotylus in ***S. lorigera***.

Literature: Lu (1998b).

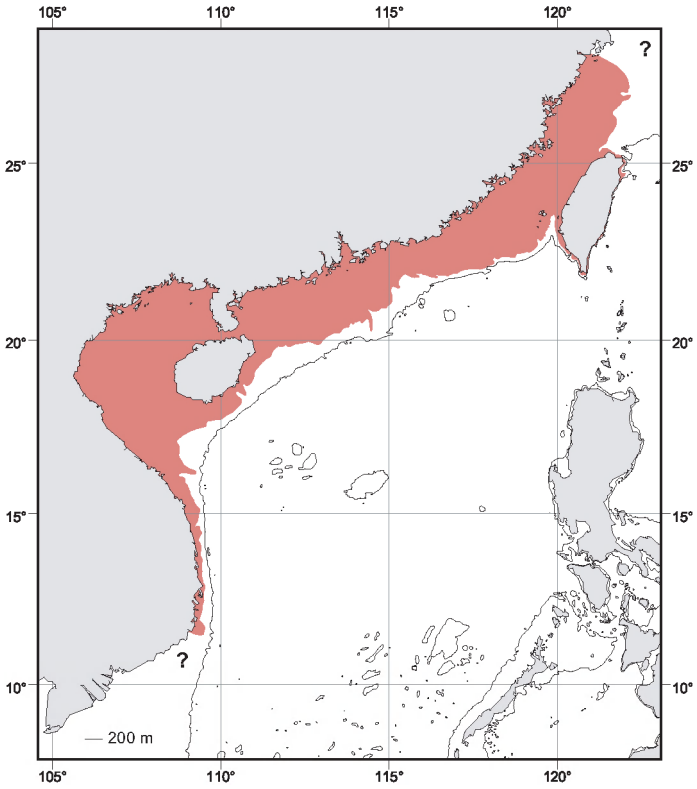


Fig. 197 ***Sepia vietnamica***
Known distribution

Sepia vossi Khromov, 1996

Fig. 198

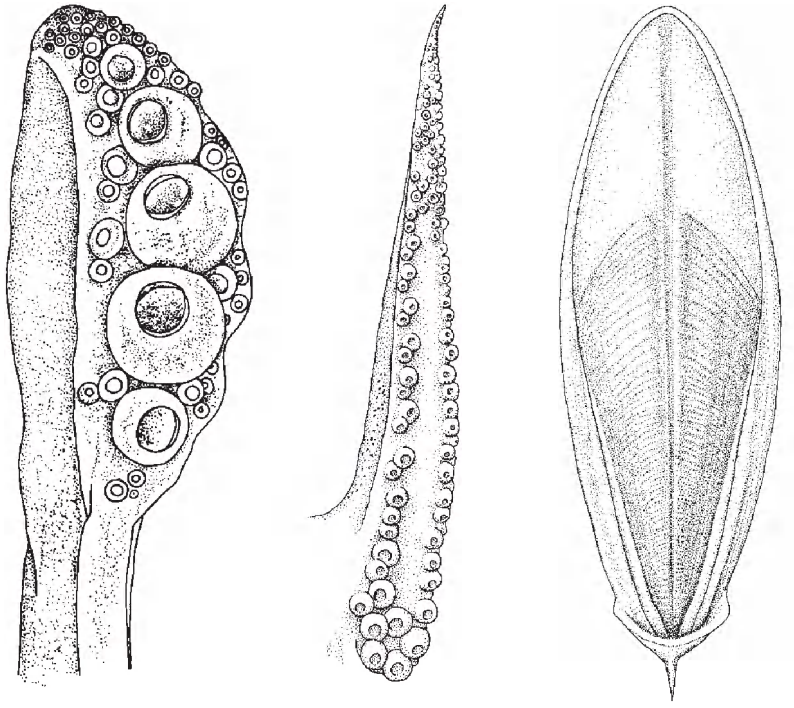
Sepia vossi Khromov, 1996, *Ruthenica*, 5(2): 143 [type locality: east coast of Viet Nam].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Voss' cuttlefish; **Fr** – Seiche de Voss; **Sp** – Sepia de Voss.

Diagnostic Features: Arms short, subequal in length; arm suckers tetraserial. Hectocotylus present on left arm IV: 3 rows of normal size suckers proximally, followed by greatly reduced suckers, then rest normal to arm tip. Suckers in **2 dorsal and 2 ventral series displaced laterally, with gap between, widely spaced**, crowded together; oral surface wide, fleshy with transversely grooved ridges. Club short, broad with **3 to 5 suckers in transverse rows**; suckers differ markedly in size: **3 to 5 suckers in middle of third longitudinal row extremely large**. Swimming keel extends slightly beyond club sucker-bearing surface. Dorsal and ventral protective membranes **not joined at base of club**. Cuttlebone pinkish, blunt-pointed anteriorly and posteriorly; median rib distinct, lateral ribs indistinct. Spine with dorsal and ventral keels. Sulcus shallow, narrow, extends entire length of cuttlebone; sulcus flanked by shallow furrows. Anterior striae are inverted U-shape. Inner cone limbs are uniform width, narrow, rounded, into V-shape posterior ledge; outer cone recurved, cup-like. **Colour:** Dorsal mantle light brown with dark brown transverse stripes.



(after Voss and Williamson, 1971)

Fig. 198 ***Sepia vossi***

Size: Up to 100 mm mantle length.

Geographical Distribution: Indo-Pacific: Hong Kong to southern Viet Nam. Depth range from 2 to 140 m. Neritic demersal species (Fig. 199).

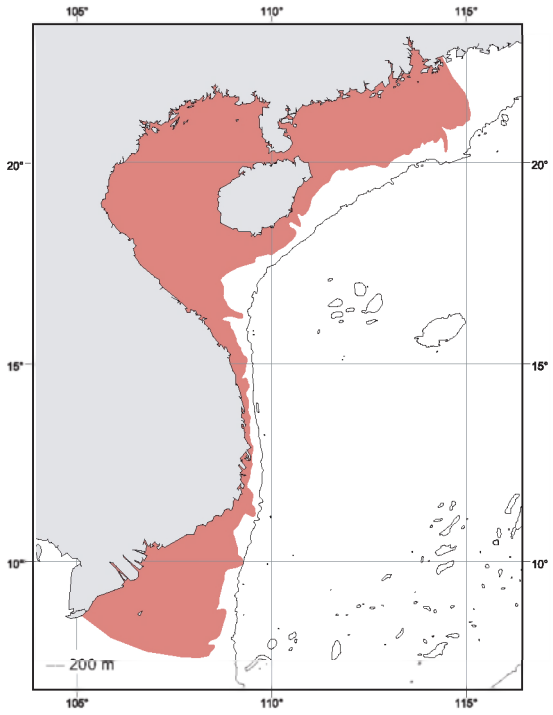


Fig. 199 ***Sepia vossi***
Known distribution

Interest to Fisheries: Separate statistics are not available, but the species is probably captured along with other demersal species.

Remarks: Treated under ***Sepia omani*** Adam and Rees, 1966, *in* Voss and Williamson (1971) and ***S. rex*** (a synonym of ***S. hedleyi*** Berry, 1918) *in* Khromov (1988).

Literature: Khromov, 1996.

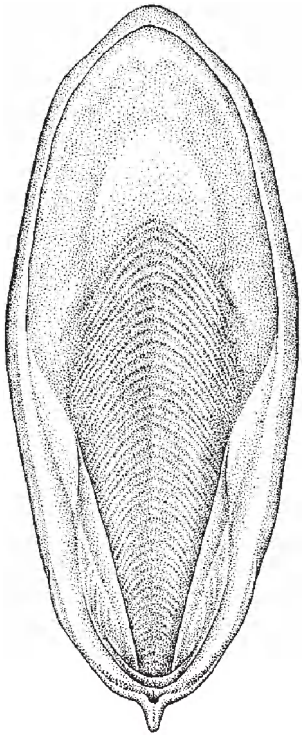
Sepia whitleyana (Iredale, 1926) Fig. 200

Acanthosepion whitleyana Iredale, 1926, *The Australian Zoologist*, 4(3): 195 [type locality: New South Wales, Port Macquarie, 31°27'S 152°55'E].

Frequent Synonyms: None.

Misidentifications: *Sepia smithi* Hoyle, 1885.

FAO Names: En – Whitley's cuttlefish; **Fr** – Seiche de Whitley; **Sp** – Sepia de Whitley.



ventral view

cuttlebone

Fig. 200 *Sepia whitleyana*

Diagnostic Features: Mantle broad, oval. Fins rounded posteriorly, with narrow gap between them. Male and female arms subequal in length. Arm suckers tetraserial. Hectocotylus present; **both ventral arms modified**. Male left ventral arm: **6 to 8 rows of normal size suckers proximally, 5 or 6 rows of reduced suckers medially**, then normal size suckers to arm tip. Suckers of hectocotylus in **2 dorsal series are much smaller than those in 2 ventral series**; oral surface of modified region wide, slightly fleshy (but not to same extent as right ventral arm). Male right ventral arm: **5 to 7 rows normal size suckers proximally, 5 or 6 rows reduced suckers medially**, then normal size suckers to arm tip; oral surface of modified region **wide, fleshy, sponge-like in texture with distinct median furrow**; suckers in **2 dorsal and 2 ventral series displaced laterally, with wide gap between them**; reduced suckers all approximately same size or dorsal and ventralmost rows may be smaller than median 2 rows on proximal end of modified region. Club long; sucker-bearing surface flattened, with **12 to 21 small suckers in transverse rows**. Swimming keel of club terminates at proximal end of carpus. Dorsal and ventral protective membranes not joined at base of club but fused to tentacular stalk. Dorsal and ventral membranes same length, terminate at proximal end of carpus; approximately equal width; dorsal membrane forms shallow cleft at junction with stalk. Buccal membrane without suckers; females have single, median spermathecae in ventral part. Cuttlebone outline oblong; **acuminate, acute, anteriorly**; bluntly rounded posteriorly; dorsal surface creamy white; dorsal surface convex medially, flat laterally; granulose, or calcified medially. Spine and posterior tip of bone covered with **smooth glaze-like substance**. Dorsal median rib and lateral ribs absent or indistinct; sides of median rib approximately parallel. Chitin surrounds entire margin of cuttlebone. Spine short, pointed, straight, directed dorsally. Spine **keel(s) absent**. Striated zone deeply concave; last loculus convex; sulcus deep, wide, extends along striated zone only; sulcus flanked by rounded ribs. Anterior striae are inverted U-shape; limbs of inner cone short, extend anteriorly to approximately one-third the length of the striated zone. Inner cone limbs are narrow anteriorly, broad U-shape posteriorly; **slightly raised into flat, very narrow, posterior ledge; ledge not thickened, dull, not shiny**; outer cone calcified, narrow anteriorly, broadens posteriorly. Dorsal mantle with longitudinal row of up to 9 ridge-like papillae along each side, adjacent to base of each fin. **Colour:** Bluish grey. Head with a few scattered chromatophores. Arms I to III have a **longitudinal band of pale pigment along their aboral surfaces**. Arm and club sucker rims pale brown, or yellow brown. Dorsal mantle has pinkish spots, or blotches and narrow longitudinal whitish bands in males only. Paired dorsal eye spots present. Fins **without markings at base**, or with approximately six short, dark transverse bars along each side.

Size: Up to 174 mm mantle length (both sexes).

Geographical Distribution: Southwestern Pacific: eastern Australia from the Gulf of Carpentaria, 16°51'S 139°51'E, southward to off Port Stephens, 32°37'S 152°25'E. Western extent of range unknown (Fig. 201).

Habitat and Biology: Depth range from 0 to 128 m.

Interest to Fisheries: Species taken as bycatch of prawn and mixed species trawl fisheries.

Remarks: ***Sepia whitleyana*** is often confused with ***S. smithi*** Hoyle, 1885. See ***S. smithi*** Remarks for differences.

Literature: Lu (1998a).

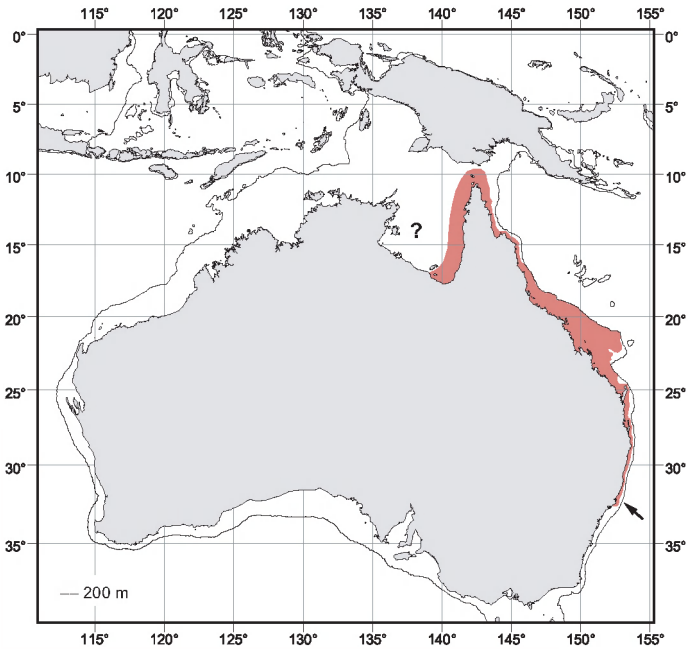


Fig. 201 *Sepia whitleyana*
Known distribution

Sepia zanzibarica Pfeffer, 1884

Fig. 202

Sepia zanzibarica Pfeffer, 1884, *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 9 [type locality: east Africa, Zanzibar].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Zanzibar cuttlefish; **Fr** – Seiche de Zanzibar; **Sp** – Sepia de Zanzibar.

Diagnostic Features: Arm suckers tetraserial. Hectocotylus present on left ventral arm: **6 rows of reduced suckers medially**, then normal size suckers distally to arm tip; reduced suckers much smaller than normal arm suckers; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; suckers in 2 dorsal and 2 ventral series displaced laterally, with gap between; **2 ventral series close together, rows alternate**. Club short, oval; with **6 suckers in transverse rows**; suckers differ slightly in size; several suckers of inner 2 or 3 rows slightly larger than rest. Swimming keel of club extends proximally slightly beyond carpus; dorsal and ventral protective membranes **not joined at base of club**. Buccal membrane with a few, minute suckers. Cuttlebone outline oblong; bone bluntly rounded anteriorly and posteriorly; strongly recurved ventrally; dorsal surface evenly convex; entire surface calcified, granulose, sculpture reticulate on posterolateral half of bone; dorsal median rib indistinct; rib broadens anteriorly; lateral ribs indistinct. Chitin borders lateral and anterior margins of cuttlebone. Spine short, pointed, curves dorsally, keel(s) absent. Striated zone concave; last loculus convex; sulcus **deep, wide**, extends along striated zone only. Anterior striae are **inverted V-shape**; limbs of inner cone extend anteriorly to approximately halfway along striated zone; inner cone lateral limbs are separated from outer cone by smooth zones. Inner cone limbs are narrow anteriorly, broaden slightly posteriorly; **raised into rounded posteriorly thickened ledge**; outer cone calcified; narrow anteriorly, broadens posteriorly.

Size: Up to 250 mm mantle length.

Geographical Distribution: Western Indian Ocean: from the Gulf of Aden to South Africa, Port Elizabeth. Common in open regions of the Indian Ocean, near islands including Madagascar, Saya-de-Malha Bank, region of Mascarene Ridge and Socotra (Fig. 203).

Habitat and Biology: Depth range from 20 to 125 m.

Interest to Fisheries: This species is commercially important in the Gulf of Aden and is likely to constitute a sizeable component of mixed species fisheries along the eastern African coastal and open oceanic waters.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova and Khromov (1991), Filippova *et al.* (1995).

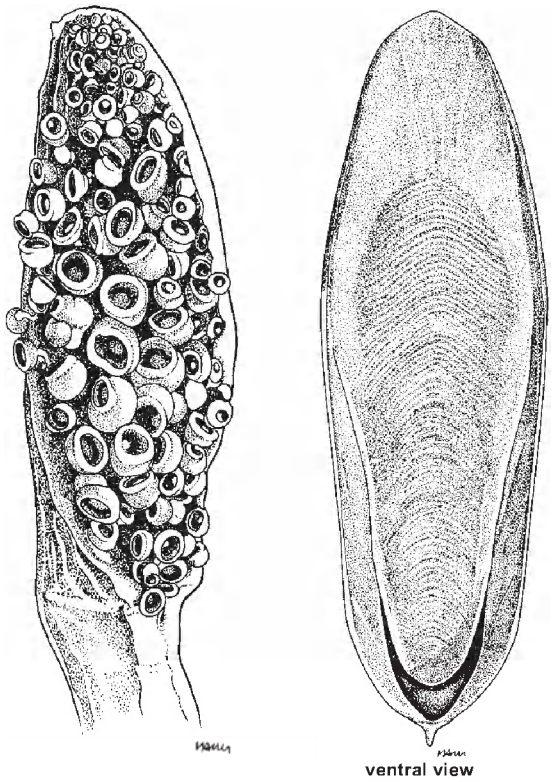


Fig. 202 *Sepia zanzibarica*

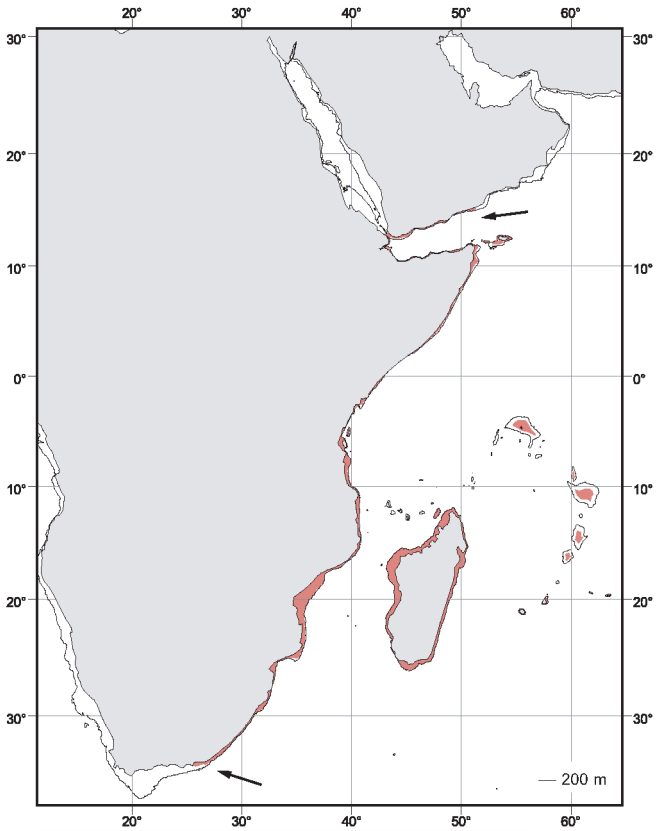


Fig. 203 *Sepia zanzibarica*
Known distribution

NEXT PAGE

Sepiella inermis (Van Hasselt, 1835) (*in* Férussac and d'Orbigny, 1834–1848) **Fig. 204; Plate VI, 37**

Sepia inermis Van Hasselt, 1835 (*in* Férussac and d'Orbigny 1834–1848). *Histoire naturelle générale et particulière Céphalopodes Acétabuliferes vivants et fossiles*, pl. 6bis [type locality: Indian Ocean].

Frequent Synonyms: *Sepia (Sepiella) microcheirus* Gray, 1849; *Sepia affinis* Eydoux and Souleyet, 1852; *Sepiella maindroni* de Rochebrune, 1884.

Misidentifications: None.

FAO Names: En – Spineless cuttlefish; **Fr** – Sépia inerme; **Sp** – Sepia inerme.

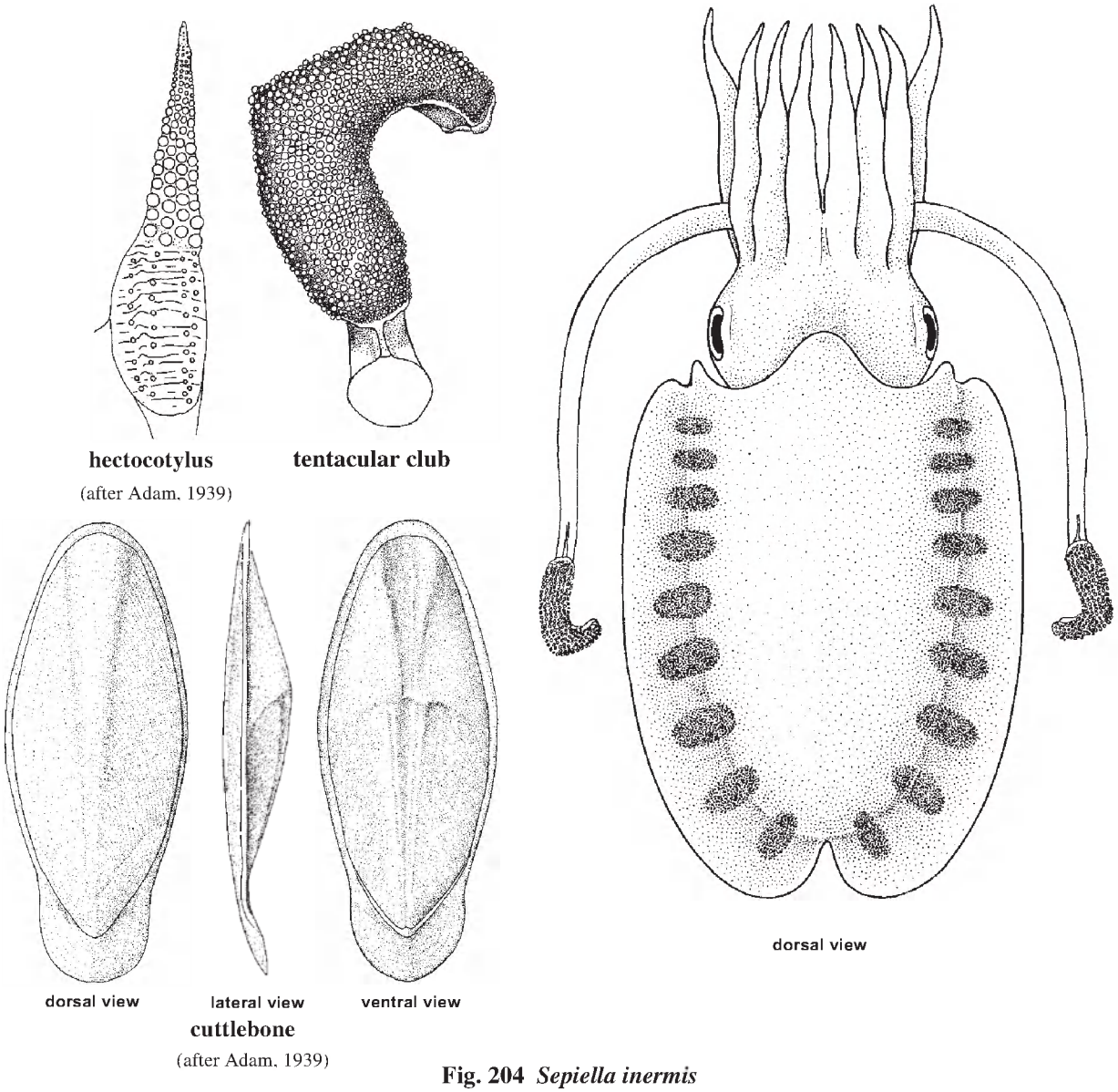


Fig. 204 ***Sepiella inermis***

Diagnostic Features: Mantle oblong. Posterior gland and gland pore pigmented reddish. Protective membranes on arms in both sexes wide, well-developed. Arm suckers tetraserial. Hectocotylus present on left ventral arm: 10 rows of reduced suckers proximally. Club with **12 to 24 suckers in transverse rows** (very variable depending upon geographic area). Swimming keel of club **slightly shorter than carpus**; dorsal and ventral protective membranes not joined at base of club; extend proximal to carpus along stalk as low ridges. Cuttlebone outline oval, broad; cuttlebone **width 33 to 43% cuttlebone length**; **strongly convex in lateral view**; granulose dorsally; dorsal median rib distinct. Spine absent. Striated zone and last loculus convex; sulcus extends entire length of cuttlebone. Inner cone limbs are uniform width, narrow, inner cone U-shape posteriorly, thickened, raised in the centre as a rounded knob; outer cone chitinous, spatulate, expanded. **Colour:** Greyish brown. Dorsal mantle has **more than 7 reddish patches** adjacent to base of fins.

Size: Maximum mantle length about 125 mm.

Geographical Distribution: Indian Ocean: mouth of Zambezi River, southern Red Sea, Gulf of Aden, Persian Gulf, to Andaman Sea and southern South China Sea, Gulf of Tonkin and eastern Indonesia. The northern and eastern extent of the distribution of this species is not known (Fig. 205).

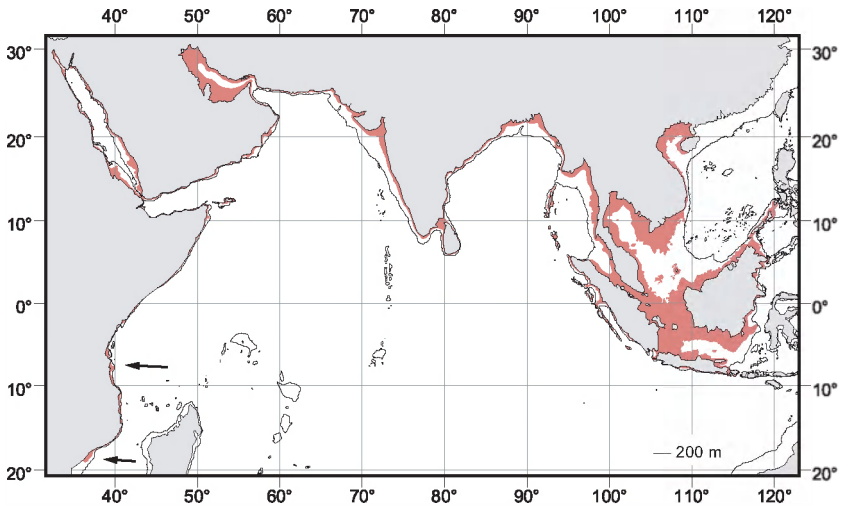


Fig. 205 ***Sepiella inermis***
Known distribution

Habitat and Biology: ***Sepiella inermis*** is a demersal, shallow water species found to 40 m depth. Length at maturity varies with stocks: on the east coast, off Waltair, it is about 53 mm for males and 52 mm for females and off Madras, about 56 mm and 60 mm; off Cochin, however, on the west coast, animals mature at larger sizes: 81 mm and 83 mm, for males and females, respectively. Females grow larger than males and growth is allometric in both sexes. Spawning extends almost throughout the year, with seasonal peaks correlating with environmental conditions. Off Kakinada and Waltair (northeast India) spawning occurs from June to September and from November to December; off Madras, in September, December and March; off Portonovo from March to October; off Cochin (southwest coast) in April and from September through October. The majority of spawning cuttlefishes are aged 9 to 12 months on the east coast and about 18 months on the west coast. Capsules containing several eggs are attached to various substrates in very shallow waters. Growth varies according to environmental conditions. Hatchlings may attain 29 to 35 mm mantle length after 6 months. At the end of one year, they can grow to sizes ranging from 53 mm (Kakinada) to 61 mm (Cochin), while after 18 months they reach 74 mm (Waltair and Kakinada) to 82 mm (Madras). Longevity on the east coast is estimated at 24 months, while on the west coast it is believed to be over 24 months. The diet of spineless cuttlefish consists primarily of small demersal fishes and crustaceans; cephalopods are a minor food component. This species has been reared successfully in aquaculture experiments conducted in Thailand since 1978 with the objective to develop commercial mass culture techniques. Three generations have been reared in culture, fed on live mysids and postlarval penaeid shrimp. The eggs are laid singly, are black and round, and have an incubation period that averages 12.6 days at 28ºC. In culture, hatchlings were planktonic for 5 days before changing to a benthic stage. Females mature at 60 days, spawn at 87 days and produce about 500 eggs. Both sexes die after spawning, at an average age of 116 days. Maximum observed life span was 149 days, with size of around 80 mm and weight around 65 grams. Size at first maturity was 50 mm for males and 31 mm for females in experimental cultures in India.

Interest to Fisheries: The species is an object of several small fisheries and is caught in quantities in the Arabian Sea near southern India and in the waters of Indo-China. Maximum lengths in the Indian trawl catches are around 110 mm on the east coast and over 120 mm on the west coast off Cochin. ***Sepiella inermis*** is important to the commercial cuttlefish fishery in Thailand, where it is highly abundant in the Gulf and in the Andaman Sea. In the Gulf of Thailand, most animals caught commercially range between 20 and 80 mm mantle length, with the maximum size recorded at 105 mm mantle length. Cuttlefishes in this region usually are caught using otter trawl or pair trawl, but squid light lures, traps, and to a lesser extent, push nets, purse seines and hook-and-line also are used, with bottom otter and pair trawls used offshore, and push nets and lift nets used in inshore and coastal waters. ***Sepiella inermis*** is one of the main commercial species in India and Sri Lanka. In the Andaman Sea it is collected using push nets. Off East Java, in Probolinggo waters, this species has been collected using bagan (lift net) in inshore areas. In shallow Saurashtra waters off Veraval (Gujarat, India), a continuous decline in the annual landings and average annual stock observed from trawl fishery operations (1979–1983) was attributed to high fishing pressure. This led to proposals to develop suitable regulatory measures for this fishery.

Remarks: ***Sepiella inermis*** is possibly a species complex; this should be examined given its fisheries significance. It is very similar to ***S. cyanea*** Robson, 1924b.

Literature: Adam and Rees (1966), Silas *et al.* (1982), Unnithan (1982), Silas *et al.* (1986), Sudjoko (1987), Kasim (1988), Appannasastry (1989), Filippova *et al.* (1995), Khaliluddin (1995), Chantawong and Suksawat (1997), Nabhitabhata (1997).

Sepiella japonica Sasaki, 1929 **Fig. 206**

Sepiella japonica Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University*, 20 (suppl.): 219 [type locality: Japan Sea, Toyama Bay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Japanese spineless cuttlefish; **Fr** – Sépia inerme japonaise; **Sp** – Sepia inerme japonesa.

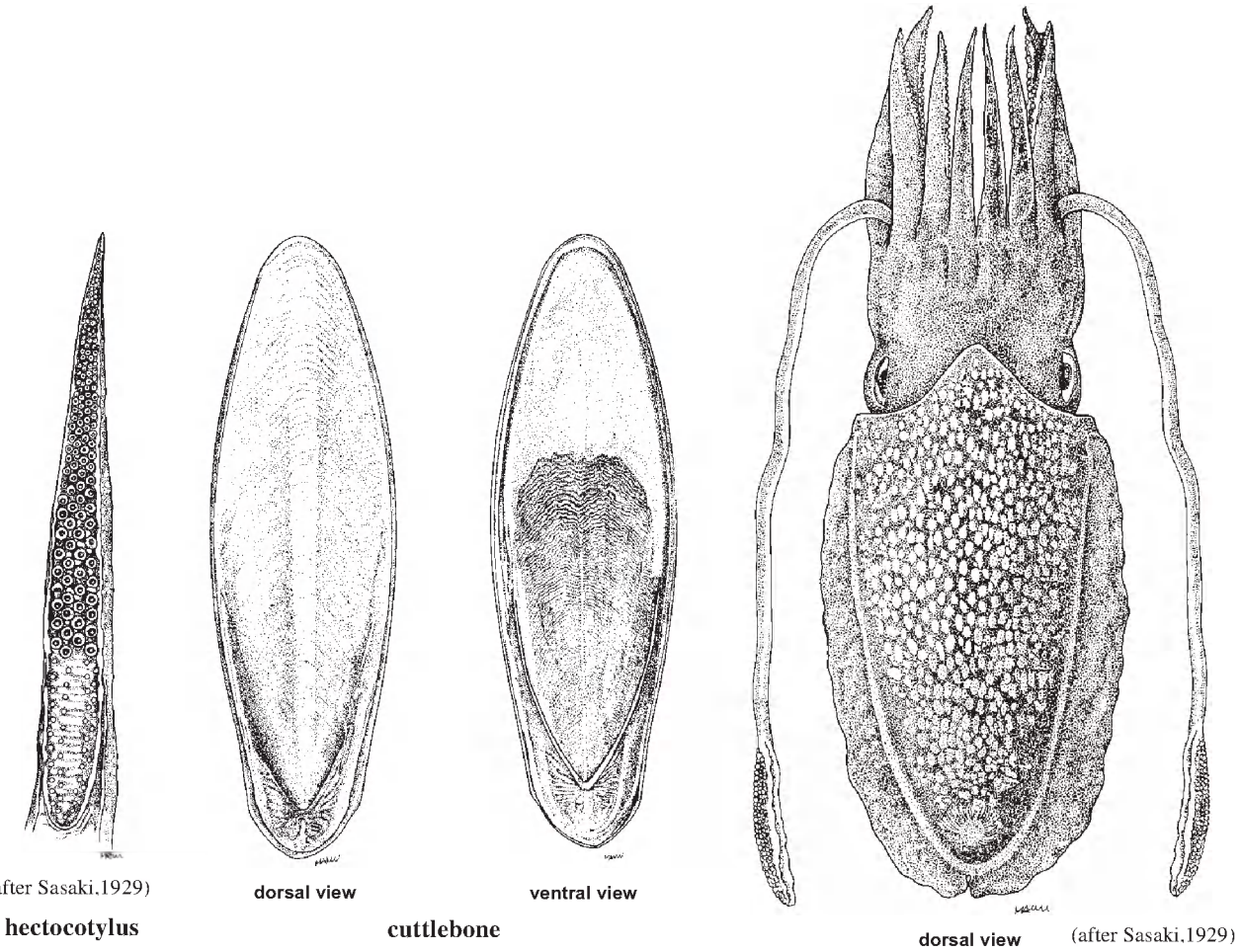


Fig. 206 ***Sepiella japonica***

Diagnostic Features: Mantle oval; dorsal anterior margin triangular, obtuse. Posterior gland and gland pore present between, and just below, the posterior fin lobes. Posterior half of ventral mantle sometimes stained brown with secretion from pore. Fins widen gradually posteriorly. Arms relatively short. Arm suckers tetraserial. Hectocotylus present on left ventral arm: **12 rows of reduced suckers proximally**; reduced suckers much smaller than normal arm suckers, ventral 2 rows of suckers close together, dorsal 2 rows separated. Suckers of hectocotylus in 2 dorsal and 2 ventral series are displaced laterally, with gap between them. Club with **16 to 32 suckers in transverse rows** (usually >20); all club suckers of similar, minute, size. Cuttlebone outline broad, oval; cuttlebone **width 30 to 35% cuttlebone length**; bone **strongly convex** in lateral view; dorsal surface evenly convex; granulose; dorsal median rib and lateral ribs indistinct. Spine absent. Striated zone and last loculus convex; sulcus shallow, narrow, extends entire length of cuttlebone. Anterior striae are inverted U-shape striated zone with faint, radiating grooves, the median groove is more pronounced than the others. Inner cone limbs are uniform width, narrow, U-shape posteriorly (rudimentary); inner cone with rounded posterior knob; outer cone chitinous, spatulate, expanded. **Colour:** Greyish brown. Dorsal mantle has white blotches or spots. Fins with **pale reflective line along base**. **No spots or wine-coloured patches** at base of fins. Ventral mantle pale but usually stained pale red.

Size: Up to 180 mm mantle length, 600 g total weight.

Geographical Distribution: Northwestern Pacific: Russian Federation, Possiet Bay in southern Primorye; Japan, from the Kanto region of Honshu, to South Korea, East China Sea, South China Sea, Taiwan Province of China, Kwang-chow (Canton), Hong Kong (Fig. 207).

Habitat and Biology: Depth to 50 m. In the Hong Kong area, the species is present in low numbers to the 50 m contour, but peak occurrences, when huge numbers of this species occur, have been reported. It spawns in May off Japan, and February to March around Hong Kong, varying with temperature. It is believed that in years characterized by intensification of warm currents this species migrates to areas in the northern Sea of Japan (up to Vostok Bay and Peter the Great Bay, Russian Federation).

Interest to Fisheries: ***Sepiella japonica*** is important in the fisheries of Japan, South Korea, Taiwan Province of China and China, caught in large numbers in bottom trawls. In Japan, most of the catch is dried and marketed as 'surume'. It is the dominant species of cuttlefishes caught around the Chekiang and Kiangsu provinces of China, with over 10 000 tonnes caught annually, and is a component of the fishery in the waters around Jiaozhou Bay. Around Hong Kong it is normally not important for the fishery, except when infrequent population peaks occur.

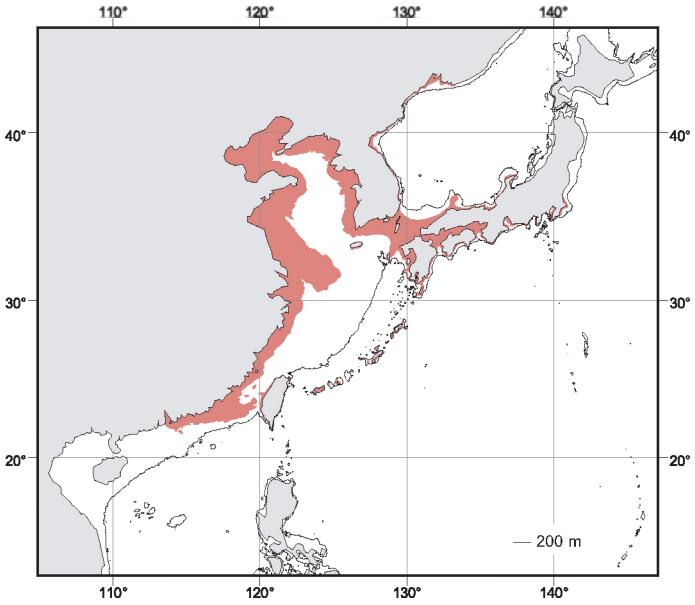


Fig. 207 ***Sepiella japonica***
Known distribution

Local Names: CHINA: Ngor Huet Mak, Mo Jam Woo Chak; JAPAN: Harinashi-kouika, Shirikusari, Shiriyakeika.

Remarks: According to Khromov (1996), Duc's (1978, 1993, 1997) records from Viet Nam possibly refer to ***S. inermis*** Van Hasselt, 1835. The species has been reared successfully in aquaculture experiments under the name ***Sepiella maindroni*** (Choe, 1966).

Literature: Adam and Rees (1966), Choe (1966), Ueda (1985), Okutani *et al.* (1987), Natsukari and Tashiro (1991), Morozov (1997), Zhang *et al.* (1997).

Sepiella ornata (Rang, 1837) **Fig. 208**

Sepia ornata Rang, 1837, *Magasin de Zoologie*, 7(Cl.V.): 76 [type locality: Gulf of Guinea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Ornate cuttlefish; **Fr** – Sépia ornée; **Sp** – Sepia ornada.

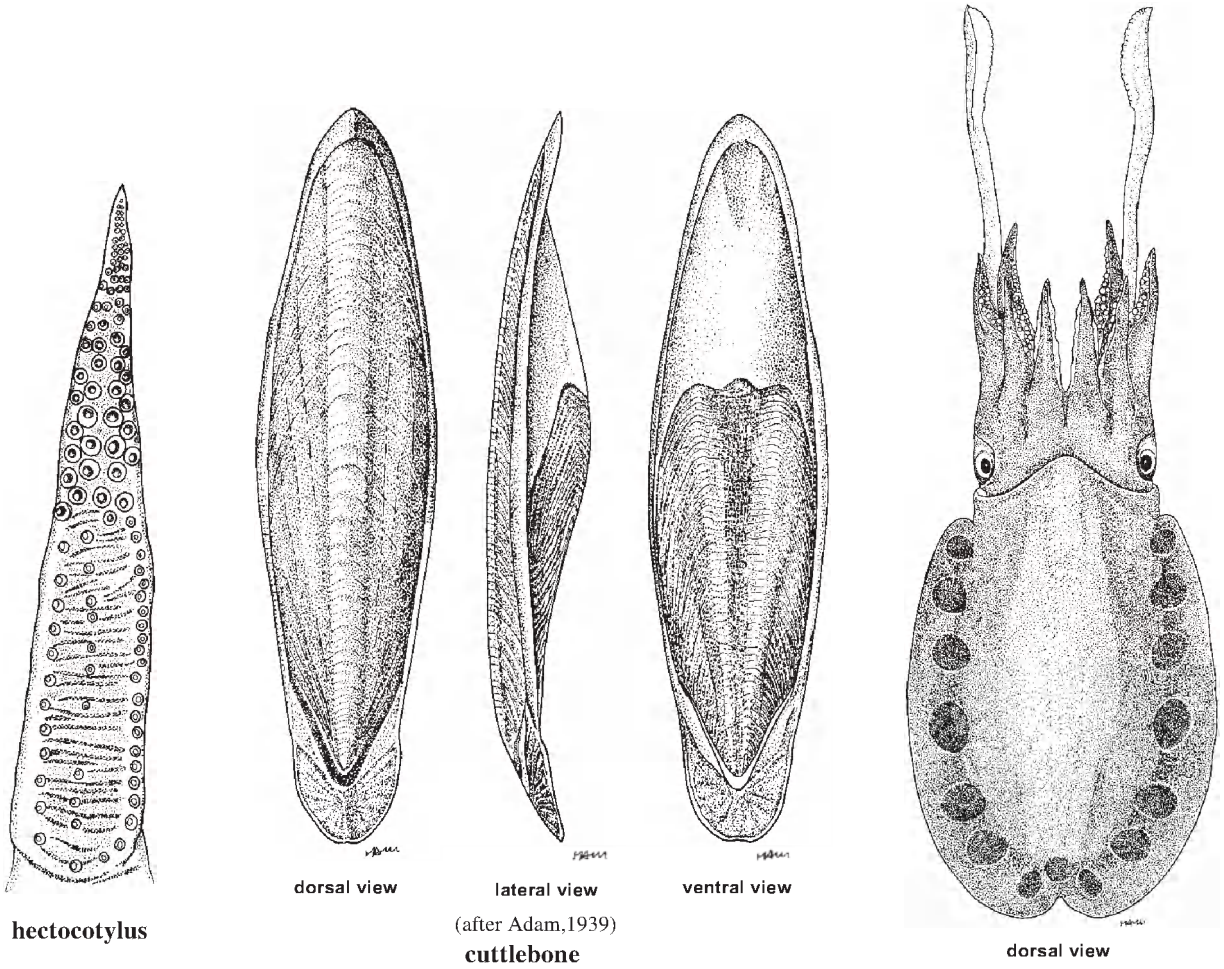


Fig. 208 ***Sepiella ornata***

Diagnostic Features: Mantle oblong. Arm suckers tetraserial. Hectocotylus present on left ventral arm: 10 rows of greatly reduced suckers proximally; suckers equal in size across rows; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges. Suckers of hectocotylus in 2 dorsal and 2 ventral series are displaced laterally, with gap between them. Club with **10 to 14 suckers in transverse rows**. Cuttlebone much shorter than mantle, located in anterior 2/3 to 3/4 of mantle; outline oblong; cuttlebone **width 24 to 27% cuttlebone length in males** and **27 to 30% cuttlebone length in females**; bone **strongly convex in lateral view**; acuminate, acute, anteriorly; bluntly rounded posteriorly. Spine absent. Sulcus shallow, narrow, extends along striated zone only, flanked by rounded ribs; limbs of inner cone are short, extend anteriorly to junction of striated zone and posterior termination of last loculus. Inner cone limbs are uniform width, narrow V-shape posteriorly; outer cone chitinous, spatulate, expanded, recurved ventrally. **Colour:** Fin bases with **row of large wine coloured spots**.

Size: Up to 100 mm mantle length.

Geographical Distribution: Eastern Atlantic: off west Africa from Cape Blanco to Cape Frio (Fig. 209).

Habitat and Biology: Depth range from 20 to 150 m, but most abundant in waters deeper than 50 m.

Interest to Fisheries: It is taken mostly as bycatch in bottom trawls mixed with ***Sepia*** species, the highest yields coming from waters deeper than 50 m.

Local Names: JAPAN: Hana-ika.

Literature: Okutani (1980), Roper and Sweeney (1981).

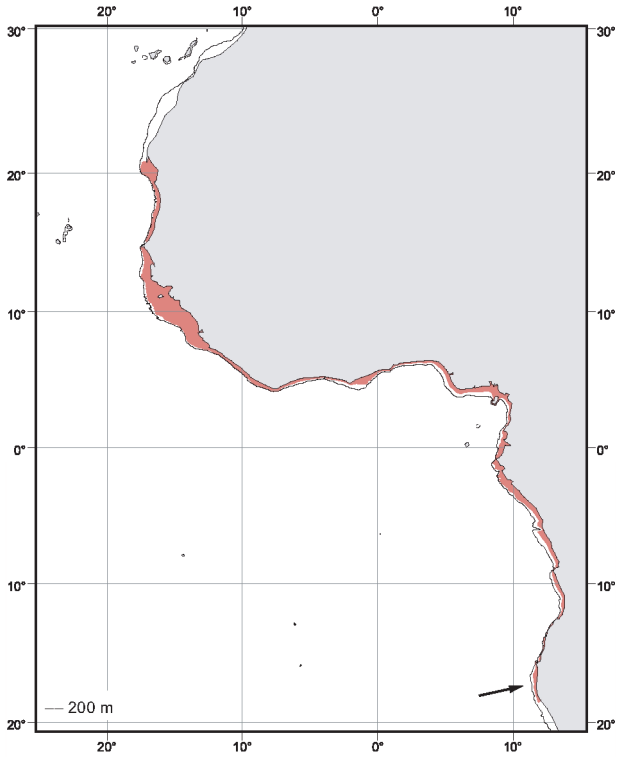


Fig. 209 ***Sepiella ornata***
Known distribution

Sepiella weberi Adam, 1939

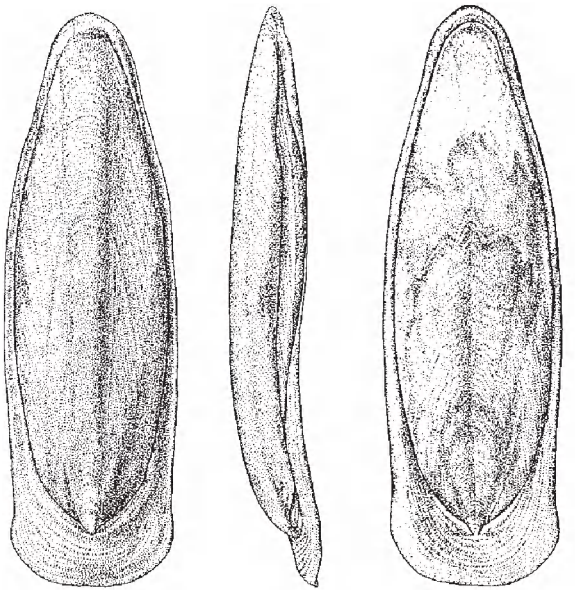
Fig. 210

Sepiella weberi Adam, 1939a, *Part III. Revision du Genre Sepiella (Gray) Steenstrup, 1880. Siboga-Expeditie*, 556: 98 [type locality: Timor, 8°35'S 126°00'E, and Soemba, 10°S 119°56'E, eastern Indonesia].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Web's cuttlefish; **Fr** – Sépia de Web; **Sp** – Sepia de Web.



(illustrations: K. Hollis/ABRS)

cuttlebone

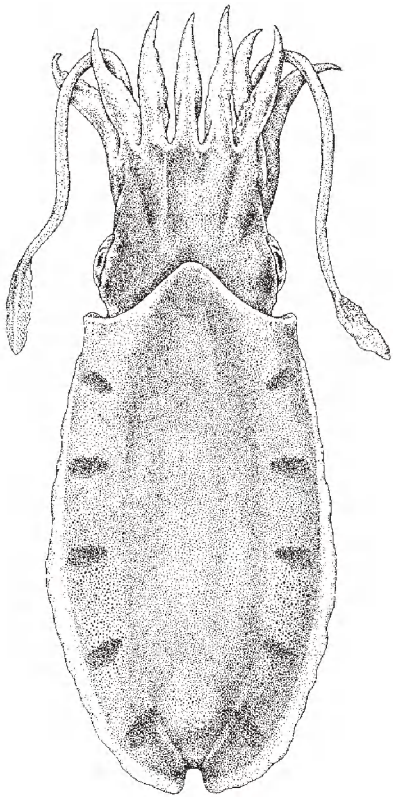


Fig. 210 ***Sepiella weberi***

Diagnostic Features: Male and female arms subequal in length. Arm suckers tetraserial; 2 median series of suckers in males are larger than dorsal and ventral marginal series, and larger than female arm suckers. Hectocotylus present on left ventral arm: **11 or 12 rows of reduced suckers proximally**; suckers in 2 dorsal series smaller than those in 2 ventral series; reduced suckers much smaller than normal arm suckers; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges. Suckers of hectocotylus in 2 dorsal and 2 ventral series are displaced laterally, with gap between, 2 ventral series close together, rows alternate. Club crescent-shaped, sucker-bearing surface convex, with **7 to 10 suckers in transverse rows**. Dorsal and ventral protective membranes not joined at base of club. Swimming keel and club protective membranes are **equal in length to sucker-bearing surface of club**. Gills with 27 or 28 lamellae per demibranch. Buccal membrane without suckers. Cuttlebone outline oblong; cuttlebone width 21 to 31% cuttlebone length in males, 30 to 33% in females; bone strongly recurved ventrally; dorsal median rib indistinct; rib broadens anteriorly; lateral ribs absent. Striated zone and last loculus convex; sulcus shallow, narrow, flanked by rounded ribs, extends entire length of cuttlebone. Anterior striae are inverted U-shape, or wavy; limbs of the inner cone are short, thickened slightly; shiny; outer cone chitinous, spatulate, expanded; **without indentation on posterolateral margin**. **Colour:** Purplish brown. Dorsal mantle pale, peppered with scattered purple-black chromatophores. Fins with **5 or 6 oval orange-pink spots** at base in both sexes, spots slightly larger in males.

Size: Males up to 60 mm mantle length; females up to 70 mm mantle length.

Geographical Distribution: Indo-Pacific: Indonesia (Timor–Soemba), 08º35'S 126°00'E to 10°S 119°56'E, to northwestern Australia, 12°39'S 127°03'E to 19°35'S 117°14'E. South China Sea: Viet Nam (unconfirmed records) (Fig. 211).

Habitat and Biology: Depth range from shallow waters to 88 m (Australia). In contrast all other *Sepiella* species, the ventral side of the cuttlebone is not strongly convex medially in *S. weberi*.

Interest to Fisheries: Specific reports are not available, but the species may occur in multispecies trawl catches due to its size and distribution.

Literature: Lu (1998a), Reid and Lu (1998).

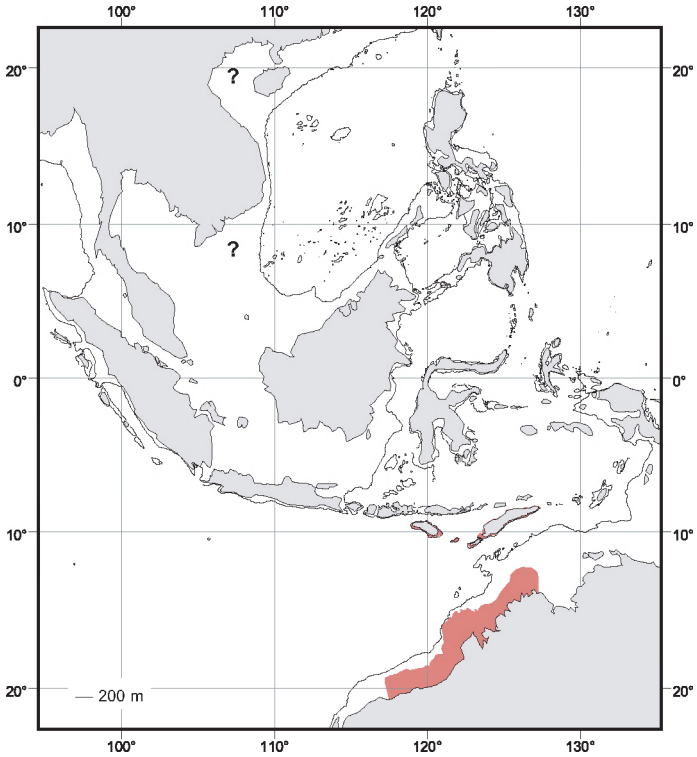


Fig. 211 *Sepiella weberi*
Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Sepia acuminata Smith, 1916

Sepia acuminata Smith, 1916, *Proceedings of the Malacological Society of London*, 12(1): 21 [type locality: South Africa: Port Elizabeth and Natal, Tongaat Beach].

Size: Males up to 100 mm mantle length; females up to 120 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: southeast Africa from South Africa, Port Elizabeth–Somalia, 01º30'N–30ºS, and Madagascar. Depth range from 44 to 369 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova *et al.* (1995).

Sepia adami Roeleveld, 1972

Sepia adami Roeleveld, 1972, *Annals of the South African Museum*, 59(10): 224 [type locality: South Africa: S 79ºE off Cape Natal].

Size: Females up to 59 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: known only from the type locality. Depth to 99 m.

Literature: Roeleveld (1972).

Sepia angulata Roeleveld, 1972

Sepia angulata Roeleveld, 1972, *Annals of the South African Museum*, 59(10): 242 [type locality: Africa: South Africa, Bloubergstrand, 33º48'S 18°27'E].

Size: Up to 75 mm cuttlebone length.

Geographical Distribution: Southeastern Atlantic: Bloubergstrand, 33º48'S 18°27'E, to Still Bay, 34°23'S 21°25'E. Known only from cuttlebones.

Literature: Roeleveld (1972).

Sepia appellofi Wülker, 1910

Sepia appellofi Wülker, 1910, *Abhandlungen der mathematische-physikalische Klasse der Köeniglich Bayerischen Akademie der Wissenschaften*, 3(Suppl. 1): 14 [type locality: Japan: Misaki].

Size: Up to 90 mm mantle length.

Geographical Distribution: Northwestern Pacific: Japan, Kyushu to south Honshu, Tsushima Strait. Depth to 350 m.

Literature: Adam and Rees (1966).

Sepia aureomaculata Okutani and Horikawa, 1987

Sepia aureomaculata Okutani and Horikawa, 1987. *In*: T. Okutani, M. Tagawa and H. Horikawa, *Cephalopods from continental shelf and slope around Japan*: 62 [type locality: Japan: Tosa Bay].

Size: Up to 160 mm mantle length.

Geographical Distribution: Northwestern Pacific: Japan, Kii Channel, Tosa Bay, Hyuga-Nada and East China Sea. Depth range from 190 to 350 m.

Literature: Okutani *et al*. (1987).

Sepia bartletti (Iredale, 1954)

Blandosepia bartletti Iredale, 1954, *Australian Zoologist*, 12(1): 67 [type locality: Misima and the Conflict Group, Louisiade Archipelago (southeast of Papua New Guinea)].

Size: Up to 74 mm mantle length.

Geographical Distribution: Western Pacific: known only from the type locality.

Remarks: Depth range unknown. Status uncertain, known only from type and six other specimens (all cuttlebones) reported by Iredale, 1954. Possible synonym of ***Sepia bandensis*** Adam, 1939b.

Literature: Iredale (1954).

Sepia bathyalis Khromov, Nikitina and Nesis, 1991

Sepia bathyalis Khromov, Nikitina and Nesis, 1991, *Zoologicheskii Zhurnal*, 70(6): 13 [type locality: Madagascar, 22º19' to 22º23'S 43º06'E].

Size: Up to 80 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: northwestern and southwestern Madagascar. Depth range from 300 to 500 m.

Literature: Khromov *et al*. (1991).

Sepia baxteri (Iredale, 1940)

Blandosepia baxteri Iredale, 1940, *Australian Zoologist*, 9(4): 442 [type locality: Lord Howe Island, 31°33'S 159°05'E].

Size: Up to 74 mm mantle length.

Geographical Distribution: Southwestern Pacific: Lord Howe Island, 31°33'S 159°05'E. Known only from type cuttlebones. Depth range unknown. Possible synonym of ***Sepia bandensis*** Adam, 1939b.

Literature: Adam and Rees (1966).

Sepia bidhaia Reid, 2000

Sepia bidhaia Reid, 2000, *Invertebrate Taxonomy*, 14: 4 [type locality: Australia: Queensland, 17°55.8'S 146°58.2'E].

Size: Males up to 37 mm mantle length; females up to 57 mm mantle length.

Geographical Distribution: Southwestern Pacific: Australia, Queensland, off the Great Barrier Reef, 17°20'S 146°41.5'E to 22°07'S 153°19'E. Depth range from 200 to 304 m.

Literature: Reid (2000).

Sepia burnupi Hoyle, 1904

Sepia burnupi Hoyle, 1904, *Journal of Conchology*, 11(1): 27 [type locality: South Africa: Natal, Umkomaas].

Size: Up to 90 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: southeast Africa, from Port Elizabeth to southern Mozambique. Saya-de-Malha Bank. Depth range from 40 to 240 m. Rare species.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova *et al.* (1995).

Sepia carinata Sasaki, 1920

Sepia carinata Sasaki, 1920, *Proceedings of the United States National Museum*, 57(2310): 192 [type locality: Japan: Sagami Sea, 35°04'50"N 139°38'18"E].

Size: Up to 60 mm mantle length.

Geographical Distribution: Western Pacific: southern Japan, Sagami Bay, South China Sea, Viet Nam. Depth range lower sublittoral, to 128 m.

Remarks: This is likely to be a very rare species as it has not been recorded from Japanese waters since its original description.

Literature: Sasaki (1920).

Sepia chirotrema Berry, 1918

Sepia chirotrema Berry, 1918. *Biological Results Fishing Experiments 'Endeavour' 1909–1914*, 4(5): 268 [type locality: South Australia, Investigator Strait area, 35°25'S 137°22'E, south of Kangaroo Island, 35°50'S 137°15'E].

Size: Up to approximately 200 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: Southern Australia from Investigator Strait, 35°25'S 137°22'E, to Western Australia, Dirk Hartog Island, 25°45'S 113°03'E. Depth range from 120 to 210 m.

Literature: Lu (1998a).

Sepia confusa Smith, 1916

Sepia confusa Smith, 1916, *Proceedings of the Malacological Society of London*, 12(1): 24 [type locality: South Africa: Natal, Port Elizabeth, Tongaat Beach].

Size: Up to 150 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: southeastern Africa from Port Elizabeth to south Mozambique, Zanzibar and Pemba, 5° to 30ºS. Saya-de-Malha Bank. Madagascar. Record from the Arabian Sea (Zuev, 1971) erroneous, while record from Saya-de-Malha Bank (Nesis, 1993) has not been confirmed by more recent expeditions. Depth range from 53 to 352 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova *et al.* (1995).

Sepia cottoni Adam, 1979

Sepia cottoni Adam, 1979, *Records of the Western Australian Museum*, 7(2): 193 [type locality: Australia: Western Australia, west of Lancelin, 31°54'S 114°55'E].

Size: Up to 55 mm mantle length.

Geographical Distribution: Southeastern Indian Ocean: Australia, Western Australia, northwest of Broome, 17°31.5'S 121°27'E, to Rottnest Island, Armstrong Point, 32°S 115°30'E. Depth range from 83 to 183 m.

Literature: Reid (2000).

Sepia dollfusi Adam, 1941

Sepia dollfusi Adam, 1941b, *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 17(62): 12 [type locality: southern Red Sea: Périm Island].

Size: Up to 110 mm mantle length.

Geographical Distribution: Red Sea and southern part of Suez Canal. Depth range unknown.

Literature: Adam and Rees (1966), Gabr (1999).

Sepia dubia Adam and Rees, 1966

Sepia dubia Adam and Rees, 1966, *John Murray Expedition 1933–34, Scientific Reports*, 11(1): 119 [type locality: Africa: South Africa, False Bay, 34°11'S 18°27'E].

Size: Up to 17 mm mantle length.

Geographical Distribution: Southeastern Atlantic: known only from the type locality. Depth 25 m.

Literature: Roeleveld (1972).

Sepia elongata d'Orbigny, 1839–1842 (*in* Férussac and d'Orbigny 1834–1848)

Sepia elongata d'Orbigny, 1839–1842 (*in* Férussac and d'Orbigny), *Histoire naturelle générale et particulière Céphalopodes Acétabuliferes vivants et fossiles*, pl. 24 [type locality: Red Sea, near Cossier].

Size: Up to 97 mm mantle length.

Geographical Distribution: Northwestern Indian Ocean: Red Sea to Somalia. Depth range unknown.

Literature: Adam and Rees (1966).

Sepia erostrata Sasaki, 1929

Sepia erostrata Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University*, 20(supplement): 183 [type locality: Japan: Manazuru, Kanagawa Prefecture].

Size: Up to 90 mm mantle length.

Geographical Distribution: Northwestern Pacific: off western mainland Japan, Sagami Bay to Kii Peninsula. Subtidal, inshore.

Literature: Okutani *et al*. (1987).

Sepia faurei Roeleveld, 1972

Sepia faurei Roeleveld, 1972, *Annals of the South African Museum*, 59(10): 251 [type locality: South Africa, 88 km southeast of Cape Seal, 35°00'S 23°07'E].

Size: Up to 21 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: South Africa, S 14°E(?) of Cape Seal 88 km, 35°00'S 23°07'E (to the east of the Cape of Good Hope). Depth to 168 m.

Literature: Roeleveld (1972).

Sepia foliopeza Okutani and Tagawa, 1987

Sepia foliopeza Okutani and Tagawa, 1987, *In*: T. Okutani, M. Tagawa and H. Horikawa, Cephalopods from continental shelf and slope around Japan: 66 [type locality: East China Sea].

Size: Up to 110 mm mantle length.

Geographical Distribution: Western Pacific: East China Sea and Taiwan Province of China. Depth range unknown.

Literature: Okutani *et al*. (1987), Lu (1998b).

Sepia gibba Ehrenberg, 1831

Sepia gibba Ehrenberg, 1831, *In*: C.G. Ehrenberg, 1828–1845. *Symbolae Physicae, seu Icones et descriptiones Corporum Nauralium novorum aut minus cognitorum, P.C. Hemprich et C.G. Ehrenberg, Pars Zoologica*: 5 [type locality: Red Sea].

Size: Up to 100 mm mantle length.

Geographical Distribution: Red Sea. Depth range unknown, at least as shallow as 1 m.

Literature: Adam and Rees (1966).

Sepia hieronis (Robson, 1924)

Rhombosepion hieronis Robson, 1924a, *Proceedings of the Zoological Society of London*, 1924(2): 645 [type locality: South Africa, Cape Town, 32°32' to 33°03'S 17°29' to 17°42'E].

Size: Up to 70 mm mantle length.

Geographical Distribution: Southeastern Atlantic and southwestern Indian Ocean: west Africa, southern Namibia, from approximately 27°S to Port Alfred, South Africa, and east Africa from 17°S to Kenya and Mozambique. Saya-de-Malha Bank. Depth range from 43 to 500 m (most abundant at 110 to 250 m).

Literature: Adam and Rees (1966), Augustyn *et al*. (1995), Filippova *et al*. (1995).

Sepia incerta Smith, 1916

Sepia incerta Smith, 1916, *Proceedings of the Malacological Society, London*, 12: 23 [type locality: South Africa: Tongaat Beach, Natal; Port Elizabeth, Cape Province].

Size: Up to 150 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: south and east Africa, from Port Elizabeth to Mozambique (north to 18ºS). Saya-de-Malha Bank. Depth range from 90 to 345 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova *et al*. (1995).

Sepia insignis Smith, 1916

Sepia insignis Smith, 1916, *Proceedings of the Malacological Society, London*, 12: 25 [type locality: Africa: South Africa, Natal, Tongaat, on beach, 29°35'S 31°07'E (cuttlebones only)].

Size: Up to 60 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: Africa, south Africa, from Cape of Good Hope to Natal. Depth to 42 m.

Literature: Adam and Rees (1966), Roeleveld (1972).

Sepia irvingi Meyer, 1909

Sepia irvingi Meyer, 1909, *Die Fauna Südwest-Australiens*, 2(19): 333 [type locality: Western Australia, Cockburn Sound, Garden Island, 32°11'S 115°43'E, Port Royal (King George Sound), 35°03'S 117°58'E, and Warnbro Sound, 32°20'S 115°43'E].

Size: Up to 100 mm mantle length.

Geographical Distribution: Southeastern Indian Ocean: Western Australia, from Cockburn Sound to North West Shelf, 18°49'S 118°29'E. Depth range from 130 to 170 m.

Literature: Lu (1998a).

Sepia ivanovi Khromov, 1982

Sepia ivanovi Khromov, 1982, *Zoologichesky Zhurnal*, 61(1): 137 [type locality: southeast Africa: Kenya, Mombasa, 04°03'S 40°00'E].

Size: Up to 70 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: probably throughout southeast Africa, Kenya, Mozambique to mouth of Zambezi River. Depth to 50 m.

Literature: Khromov (1982).

Sepia joubini Massy, 1927

Sepia joubini Massy, 1927, *Annals of the South African Museum*, 25: 161 [type locality: Cape Natal, Tugela River Mouth, Cape Natal, The Bluff, Durban].

Size: Females up to 64 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: South Africa, off Tugela River Mouth, 29º11'S 31º25'E, to Cape Natal. Off southern Mozambique, 24ºS to 25ºS. Saya-de-Malha Bank. Depth range from 66 to 170 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova *et al.* (1995).

Sepia kiensis Hoyle, 1885

Sepia kiensis Hoyle, 1885, *Annals and Magazine of Natural History*, (series 5)16: 194 [type locality: Arafura Sea, off Kai Island].

Size: Up to 37 mm mantle length

Geographical Distribution: Indo-Pacific: Kai Islands, possibly to Timor and northern Australia. Depth up to 256 m.

Literature: Adam and Rees (1966).

Sepia koilados Reid, 2000

Sepia koilados Reid, 2000, *Invertebrate Taxonomy*, 14: 24.

Size: Males up to 68 mm mantle length; females up to 58 mm mantle length.

Geographical Distribution: Type locality: Australia: Western Australia, North West Shelf, 18°36'S 118°2'E to 18°39'S 118°4'E. General distribution: southeastern Indian Ocean: Western Australia, North West Shelf: 18°31'S 118°09'E to 19°12.6'S 116°25.8'E. Depth range from 182 to 203 m.

Literature: Reid (2000).

Sepia limata (Iredale, 1926)

Arctosepia limata Iredale, 1926, *The Australian Zoologist*, 4: 193 [type locality: Australia: New South Wales, Manly Beach, 33°48'S 151°17'E].

Size: Males up to 35 mm mantle length; females up to 42 mm mantle length.

Geographical Distribution: Southwestern Pacific: Australia, southern Queensland to New South Wales, 26°30'S 153°44'E to 34°40'S 150°51'E. Depth range from 17 to 183 m.

Literature: Reid (2000).

Sepia mascarensis Filippova and Khromov, 1991

Sepia mascarensis Filippova and Khromov, 1991, *Zoologichesky Zhurnal*, 70(8): 63 [type locality: Indian Ocean, Saya-de-Malha Bank].

Size: From 67 to 124 mm mantle length.

Geographical Distribution: Western Indian Ocean: Saya-de-Malha Bank, 11°31'S 61°00'E, Mascarene Ridge, Cargados-Carajos Shoals. Depth range from 87 to 325 m.

Literature: Khromov *et al.* (1991), Filippova *et al.* (1995).

Sepia mestus Gray, 1849

Sepia mestus Gray, 1849. *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Antepedia*, 108 [type locality: Australia].

Size: Males up to 77 mm mantle length; females up to 124 mm mantle length.

Geographical Distribution: Southwestern Pacific: Queensland: Escape Reef, 15º47'S 145º47'E to New South Wales, Jervis Bay, Murrays Beach, 35º08'S 150º46'E. Records from China and Viet Nam are now known to be misidentifications. ***Sepia mestus*** is an Australian endemic. Depth range from 0 to 22 m.

Literature: Lu (1998a), Reid and Lu (2005).

Sepia mira (Cotton, 1932)

Tenuisepia mira Cotton, 1932, *Records of the South Australian Museum*, 4(4): 546 [type locality: Queensland, North-West Islet, Capricorn Group, 23°18'S 151°42'E].

Size: Up to 55 mm mantle length.

Geographical Distribution: Southwestern Pacific: Australia, New South Wales, Clarence R., 29°19'S 153°29'E, to off Wooli, 29°49'S 153°27'E. Depth range from 20 to 72 m.

Literature: Lu (1998a), Reid (1998).

Sepia mirabilis Khromov, 1988

Sepia mirabilis Khromov, 1988, *Zoologicheskii Zhurnal*, 67: 785 [type locality: Arabian Sea, 12°22'N 54°28'E].

Size: Up to 70 mm mantle length.

Geographical Distribution: Western Indian Ocean: near Sokotra Island, probably to east Africa. Depth to 50 m.

Literature: Khromov (1988).

Sepia novaehollandiae Hoyle, 1909

Sepia novaehollandiae Hoyle, 1909, *Proceedings of the Royal Physical Society of Edinburgh*, 17(6): 266 [type locality: South Australia, Kangaroo Island, 35°50'S 138°03'E].

Size: Up to 77 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: Australia from Shellharbour, NSW, 34°35'S 150°52'E to Western Australia, North West Shelf, 18°57'S 118°45'E. Depth range from 15 to 348 m.

Literature: Adam and Rees (1966), Lu (1998a).

Sepia papillata Quoy and Gaimard, 1832

Sepia papillata Quoy and Gaimard, 1832, *Voyage de decouvertes de l'Astrolabe pendant les annees 1826–1827–1828–1829, Zoologie*, 2(1): 61 [type locality: Africa: South Africa, Cape of Good Hope].

Size: Up to 140 mm mantle length.

Geographical Distribution: Southeastern Atlantic and southwestern Indian Ocean: South Africa, from Lüderitz Bay, 26°11'S 15°10'E, to Natal coast off Tugela and Umvoti Rivers, 29°11'S 31°25'E. Mascarene Ridge. Depth range from 26 to 210 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova and Khromov (1991), Augustyn *et al.* (1995), Filippova *et al.* (1995).

Sepia pardex Sasaki, 1913

Sepia pardex Sasaki, 1913, *Doubutsugaku Zasshi [Zoological Magazine, Tokyo]*, 25(292): 74 [type locality: Japan: Chiba Prefecture, Kajiyama].

Size: Up to 230 mm mantle length.

Geographical Distribution: Western Pacific: Japan, along the Pacific coast from the Chiba Peninsula and along the Japan Sea coast from Toyama Bay to South Korea, Taiwan Province of China and the East China Sea. Depth range unknown.

Literature: Okutani *et al*. (1987), Lu (1998b). Also cited as ***Sepia pardalis*** Sasaki, 1914.

Sepia peterseni Appellöf, 1886

Sepia peterseni Appellöf, 1886, *Svenska Vetenskaps-Akademiens Handlingar*, 21(13): 23 [type locality: Japan].

Size: Up to 120 mm mantle length.

Geographical Distribution: Western Pacific: Japan, south of central Honshu to southern Kyushu, South Korea. Depth range from 20 to 100 m; inner shelf.

Literature: Okutani *et al*. (1987).

Sepia plana Lu and Reid, 1997

Sepia plana Lu and Reid, 1997, *Records of the Western Australian Museum*, 18: 279 [type locality: southeastern Indian Ocean: Australia: Western Australia, North West Shelf, 14°15'S 121°59'E].

Size: Males up to 99 mm mantle length; females up to 151 mm mantle length.

Geographical Distribution: Australia: Western Australia, North West Shelf, 12°04'S 122°59'E to 17°55.5'S 118°16.0'E. Depth range from 396 to 505 m. Cuttlebones found off eastern Australia.

Literature: Lu and Reid (1997).

Sepia plathyconchalis Filippova and Khromov, 1991

Sepia plathyconchalis Filippova and Khromov, 1991, *Zoologichesky Zhurnal*, 70(8): 66 [type locality: Indian Ocean, Saya-de-Malha Bank, 09°42'S 61°08'E].

Size: From 8 to 63 mm mantle length.

Geographical Distribution: Western Indian Ocean: Saya-de-Malha Bank; Cargados-Carajos Shoals; St Brandon Shoals. Shallow water species, depth range from 25 to 63 m.

Literature: Filippova and Khromov (1991).

Sepia pulchra Roeleveld and Liltved, 1985

Sepia pulchra Roeleveld and Liltved, 1985, *Annals of the South African Museum*, 96(1): 2 [type locality: Africa: South Africa, Cape Peninsula, Llandudno].

Size: Up to 22 mm mantle length.

Geographical Distribution: Southeastern Atlantic: South Africa, Cape Peninsula. Depth range from 15 to 50 m.

Literature: Boletzky and Roeleveld (2000).

Sepia reesi Adam, 1979

Sepia reesi Adam, 1979, *Records of the Western Australian Museum*, 7(2): 200 [type locality: Western Australia, Rottnest Island, Salmon Bay].

Size: Up to 45 mm mantle length.

Geographical Distribution: Southeastern Indian Ocean: cuttlebone known only from the type locality.

Literature: Adam (1979).

Sepia rhoda (Iredale, 1954)

Arctosepia rhoda Iredale, 1954, *Australian Zoologist*, 12(1): 75 [type locality: Australia: Western Australia, Point Cloates, 22°43'S 113°40'E].

Size: Males up to 61 mm mantle length; females up to 58 mm mantle length.

Geographical Distribution: Indo-Pacific: Australia, Northern Territory, Arafura Sea, 10°24'S 130°23'E to Western Australia, NW Shelf, 20°47'S 114°48'E. Depth range from 64 to 184 m.

Literature: Reid (2000).

Sepia robsoni (Massy, 1927)

Rhombosepion robsoni Massy, 1927, *Annals of the South African Museum*, 25(4): 159 [type locality: Africa: South Africa, Hout Bay].

Size: Up to 20 mm mantle length.

Geographical Distribution: Southeastern Atlantic: South Africa, Hout Bay. Known only from the type locality. Depth range from 17 to 37 m.

Literature: Adam and Rees (1966), Roeleveld (1972).

Sepia saya Khromov, Nikitina and Nesis, 1991

Sepia saya Khomov, Nikitina and Nesis, 1991, *Zoologicheskii Zhurnal*, 70(6): 13 [type locality: western Indian Ocean, Saya-de-Malha Bank, 10°30'S 61°10'E to 10°32'S 61°11'E].

Size: Up to 90 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: known only from the type locality. Depth range from 87 to 117 m.

Literature: Khromov *et al.* (1991).

Sepia senta Lu and Reid, 1997

Sepia senta Lu and Reid, 1997, *Records of the Western Australian Museum*, 18: 286 [type locality: Australia: Western Australia, 14º07'S 122º06'E].

Size: Males up to 62 mm mantle length; females up to 83 mm mantle length.

Geographical Distribution: Southeastern Indian Ocean: Western Australia, North West Shelf, 12°04'S 122°51'E to 18°44'S 116°59'E. Possibly Indonesia. A very similar, probably closely related animal has been found in the Philippines. Depth range from 256 to 426 m.

Literature: Lu and Reid (1997).

Sepia sewelli Adam and Rees, 1966

Sepia sewelli Adam and Rees, 1966. *Scientific Reports. The John Murray Expedition*, 11(1): 61 [type locality: Africa: near Cape Guardafui, Somalia, 11°57'12"N 50°35'00"E to 11°56'42"N 50°39'12"E].

Size: Up to 30 mm mantle length.

Geographical Distribution: Western Indian Ocean: from Cape Guardafui, Somalia, 11º57'N 50º35'E to 05º40'S 39º17'E, to Zanzibar and probably Madagascar. Depth range from 37 to 238 m.

Literature: Adam and Rees (1966).

Sepia simoniana Thiele, 1920

Sepia simoniana Thiele, 1920, *Deutsche Sudpolar-Expedition 1901–1903*, 16(Zoology 8): 436 [type locality: Africa: South Africa Simon's Bay].

Size: Up to 185 mm mantle length.

Geographical Distribution: Western Indian Ocean: from Cape Town to Agulhas Bank, north to northern Kenya and southern Mozambique. Saya-de-Malha Bank. Depth to 190 m (usually less than 100 m).

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova and Khromov (1991), Augustyn *et al.* (1995), Filippova *et al.* (1995).

Sepia sokotriensis Khromov, 1988

Sepia sokotriensis Khromov, 1988, *Zoologichesky Zhurnal*, 67(5): 788 [type locality: Peoples' Democratic Republic of Yemen, Arabian Sea, Sokotra Island, 12°10'N 54°25'E].

Size: Up to 80 mm mantle length.

Geographical Distribution: Western Indian Ocean: near Sokotra Island, probably east Africa. Depth to 100 m.

Literature: Khromov (1988).

Sepia subplana Lu and Boucher-Rodoni, 2001

Sepia subplana Lu and Boucher-Rodoni, 2001, *Mémoires du Muséum National d'Histoire Naturelle*, 185: 370 [type locality: southwest Pacific, Bayonnaise Bank, 11°54'S 179°32'W].

Size: Male 60 mm mantle length; female 55 mm mantle length (known only from types).

Geographical Distribution: Southwestern Pacific: known only from the type locality. Depth range from 400 to 600 m.

Literature: Lu and Boucher-Rodoni (2001).

Sepia subtenuipes Okutani and Horikawa, 1987

Sepia subtenuipes Okutani and Horikawa, 1987. *In*: T. Okutani, M. Tagawa and H. Horikawa, 1987, *Cephalopods from continental shelf and slope around Japan*: 57 [type locality: Japan].

Size: Up to 94 mm mantle length.

Geographical Distribution: Western Pacific: southwestern Japan: Tosa Bay, Shikoku, Kii Channel. East China Sea. Depth range from 90 to 300 m.

Literature: Okutani *et al.* (1987).

Sepia tala Khromov, Nikitina and Nesis, 1991

Sepia tala Khromov, Nikitina and Nesis, 1991, *Zoologischesky Zhurnal*, 70(6): 17 [type locality: southwest Madagascar: off Cape Tala, 22°19'S to 22°23'S, 43°06'E].

Size: Up to 80 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: southwestern Madagascar off Cape Tala. Known only from the type locality. Depth range from 325 to 332 m.

Literature: Khromov *et al.* (1991).

Sepia tanybracheia Reid, 2000

Sepia tanybracheia Reid, 2000, *Invertebrate Taxonomy*, 14: 47 [type locality: Australia: Western Australia, 12°36'S 123°45'E].

Size: Males up to 51 mm mantle length.

Geographical Distribution: Southeastern Indian Ocean: known only from type locality. Depth range from 200 to 205 m.

Literature: Reid (2000).

Sepia tenuipes Sasaki, 1929

Sepia tenuipes Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University*, 20(supplement): 193 [type locality: Japan: Ibaraki Prefecture, Isohama].

Size: Up to 105 mm mantle length.

Geographical Distribution: Western Pacific: southwestern Japan, eastern Honshu and western Japan Sea to south of Kyushu, Korea and East China Sea. Depth range from 100 to 250 m.

Literature: Okutani *et al*. (1987), Kubodera and Yamada (1998).

Sepia thurstoni Adam and Rees, 1966

Sepia thurstoni Adam and Rees, 1966, *John Murray Expedition 1933–34, Scientific Reports*, 11(1): 2 [type locality: India, Madras, Ramesvaram Island, 09°18'N 79°19'E].

Size: Up to 110 mm mantle length.

Geographical Distribution: Indian Ocean: India, off Madras. Sri Lanka: off Negombo and Hambantota. Depth range from 20 to 40 m.

Literature: Adam and Rees (1966).

Sepia tokioensis Ortmann, 1888

Sepia tokioensis Ortmann, 1888, *Zoologische Jahrbucher, (Systematik)*, 3: 653 [type locality: Japan: Tokyo Bay].

Size: Up to 90 mm mantle length.

Geographical Distribution: Western Pacific: Japan, from Tsugaru Strait to Kyushu and the Ohsumi Islands including Sagami Bay, Suruga Bay, western Japan Sea and Shimane Prefecture. Shelf.

Literature: Okutani *et al*. (1987) (as ***Sepia (Doratosepion) misakiensis***).

Sepia tuberculata Lamarck, 1798

Sepia tuberculata Lamarck, 1798, *Bulletin des Sciences, par la Societe Philomatique*, 2(5): 130 [type locality: unknown].

Size: Up to 82 mm mantle length.

Geographical Distribution: Africa: South Africa, Melbosstrand, 33°43'S 18°26'E to Knysna, 34°03'S 23°03'E. Depth to 3 m.

Literature: Adam and Rees (1966), Roeleveld (1972).

Sepia typica (Steenstrup, 1875)

Hemisepius typicus Steenstrup, 1875, *Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 10(7): 468 [type locality: Africa: South Africa, Table Bay, 33°50'S 18°27'E].

Size: Up to 26 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean and southeastern Atlantic: South Africa, from Saldanha Bay, 33°00'S 17°56'E, to southern Mozambique. Depth range from 2 to 290 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Augustyn *et al*. (1995), Filippova *et al*. (1995).

Sepia vercoi Adam, 1979

Sepia vercoi Adam, 1979, *Records of the Western Australian Museum*, 7(3): 190 [type locality: Western Australia, west of Shark Bay, 25°31'S 112°29'E].

Size: Up to 46 mm mantle length (both sexes).

Geographical Distribution: Southeastern Indian Ocean: Western Australia, 18°31'S 118°09'E to 25°31'S 112°29'E. Depth range from 76 to 201 m.

Literature: Reid (2000).

Sepiella cyanea Robson, 1924

Sepiella cyanea Robson, 1924b, *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 3: 13 [type locality: South Africa, Natal].

Size: Up to 80 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: Port Elizabeth and Durban, north to central Mozambique, 26ºN and Madagascar. Depth range from 13 to 73 m.

Literature: Adam and Rees (1966), Roeleveld (1972), Filippova *et al*. (1995).

Sepiella mangkangunga Reid and Lu, 1998

Sepiella mangkangunga Reid and Lu, 1998, *The Beagle, Records of the Museums and Art Galleries of the Northern Territory*, 14: 74 [type locality: Australia: Northern Territory, Stingray Head, 12°48'S 130°21'E].

Size: Males up to 58 mm mantle length; females up to 59 mm mantle length.

Geographical Distribution: Indo-Pacific: Australia, Northern Territory, 12°48'S 130°21'E to 13°14'S 130°57'E. Depth from 1.1 to 3.3 m.

Literature: Reid and Lu (1998).

Sepiella ocellata Pfeffer, 1884

Sepiella ocellata Pfeffer, 1884, *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 13 [type locality: Java].

Size: Up to 50 mm mantle length.

Geographical Distribution: Indo-Pacific: Known only from the type locality. Depth range unknown. Known from a single male specimen only. The status of this species is questionable.

Literature: Reid and Lu (1998).

Note:

As this catalogue was being printed, the description of a new species of ***Sepia*** became available (Reid and Lu, 2005). It is hereby reported (in synthesis) for sake of completeness.

Sepia filibrachia Reid and Lu, 2005

Sepia filibrachia Reid and Lu, 2005, *Zootaxa*, 911: 13 [type locality: Taiwan: Kaohsiung, Ling Yuan, 22°28'N 120°24'E].

Size: Males up to 62 mm, females up to 70 mm mantle length.

Geographical Distribution: Taiwan Province of China, Mu-Do-Yu, 23°44'N 119°35'E, Peng-Hu and Wu-chi, Taichung 24°17'N 120°30'E. South China Sea, Hainan Island, Haikou. 20°40'N 107°56'E; 18°40'N 106°47'E; 11°25'N 109°15'E. Viet Nam, Gulf of Tonkin, Guryanova. Depth range 34–95 m.

Interest to Fisheries: The species is marketed in Taiwan Province of China.

Literature: Reid and Lu (2005).

3.2 Family SEPIOLIDAE Leach, 1817

by Amanda Reid and Patrizia Jereb

Sepiolidae Leach, 1817, *Synopsis of the Orders, Families and Genera of the Class Cephalopoda*, *In*: Leach and Nodder, The Zoological Miscellany, 3(30):137–141.

FAO Names: En – Bobtail squids; **Fr** – Sépioles; **Sp** – Globitos, Sepietas, Sepiolas, Sepiolinas.

Diagnostic Features: Mantle broad, oval; posterior mantle margin rounded. Dorsal mantle fused to head, or free from head. Mantle cavity divided by thin septum. Fins wide; rounded, semicircular, or kidney-shaped, with pronounced anterior lobes, or 'earlets'; attached about midway along mantle; fin attachment short, fin length exceeds attachment length. Head slightly broader than, or as wide as, mantle. Large eyes covered by corneal membranes. Mantle-locking cartilage simple, linear. Arms short; protective membranes absent in both sexes. Webs between arms III and IV envelop tentacle bases on outside only, without forming sac. Hectocotylus present: left dorsal arm, both dorsal arms, or dorsolateral arms modified. Tentacles retractable, each bears a well defined club. Only the left oviduct is developed. Eggs large, development direct. Internal gladius present, rudimentary, chitinous, or absent.

Size: Small, up to 80 mm, rarely 100 mm, mantle length.

Habitat and Biology: Benthic or neritic. Represented in tropical, temperate and subpolar waters of all oceans.

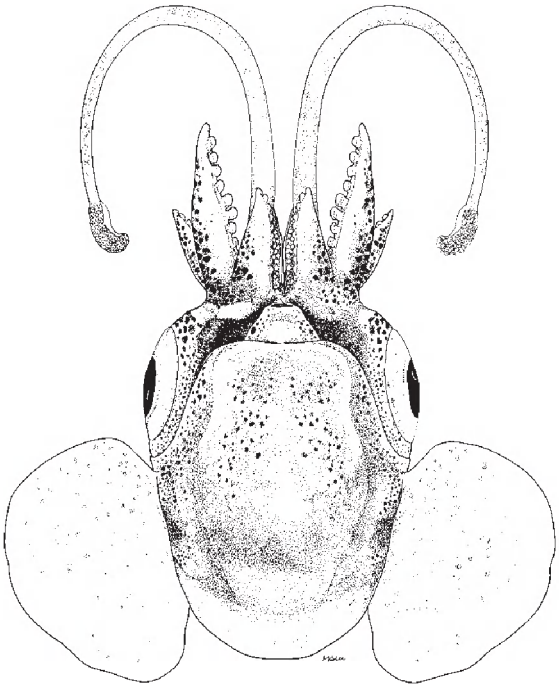
Interest to Fisheries: Separate statistics are not reported for this group, but many species are utilized locally as food even though not commercially exploited. The flesh is generally very tasty though difficult to preserve. Currently of low commercial value; in some areas of their distribution catches are very abundant and the resource is valued as a delicacy (i.e. some areas of the Mediterranean Sea).

Literature: Fioroni (1981), Boletzky (1995).

Key to subfamilies and genera in the family Sepiolidae

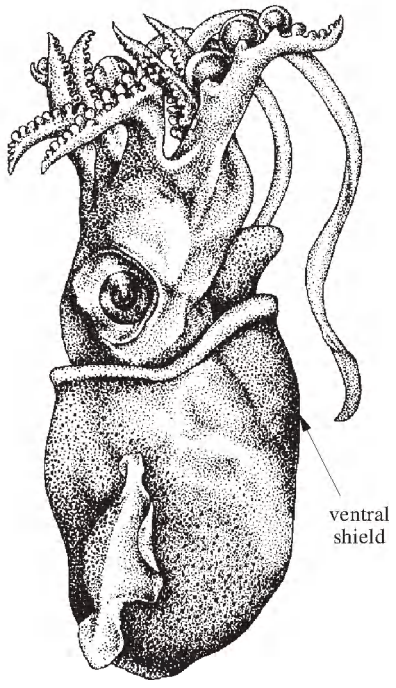
1a. All arms except the fourth pair united by a broad web (Fig. 212); anterior edge of ventral mantle extended into extensive ventral shield anteriorly, covering funnel and sometimes reaching eye level (Fig. 213) . . . . . **(subfamily Heteroteuthinae) → 3**

1b. Arms not united by a broad web, or only third and fourth arms united by a broad web; anterior edge of ventral mantle not forming a ventral shield . . . . . **→ 2**



ventral view

Fig. 212 *Iridoteuthis iris*

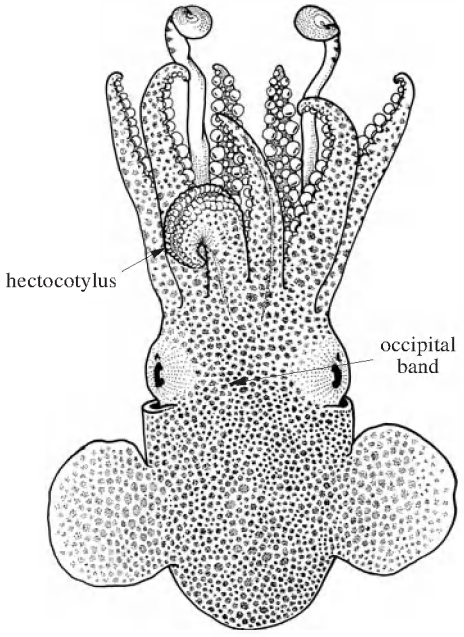


lateral view of male

Fig. 213 *Heteroteuthis serventyi*

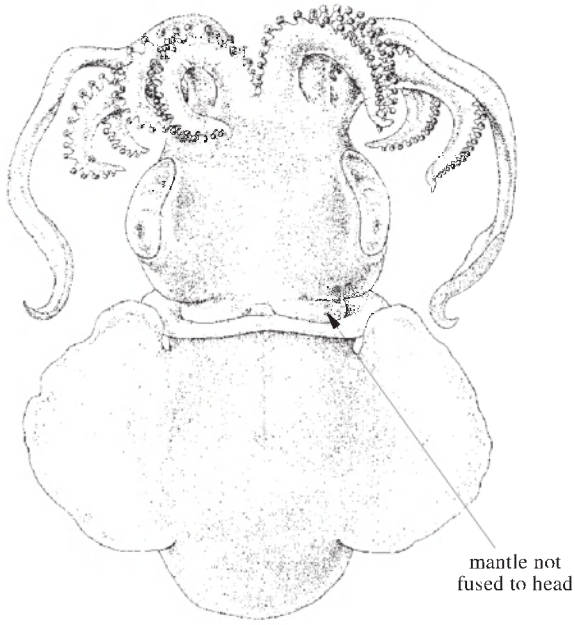
2a. Dorsal mantle fused to head by cutaneous occipital band (Fig. 214); nuchal cartilage absent; left dorsal arm hectocotylized; internal gladius rudimentary, or absent . . . . . **(subfamily Sepiolinae) → 7**

2b. Dorsal mantle not fused to head (Fig. 215); nuchal cartilage present; left or both dorsal arms hectocotylized; gladius present . . . . . **(subfamily Rossiinae) → 11**



dorsal view

Fig. 214 *Euprymna tasmanica*



dorsal view of female

(illustration: K. Hollis/ABRS)

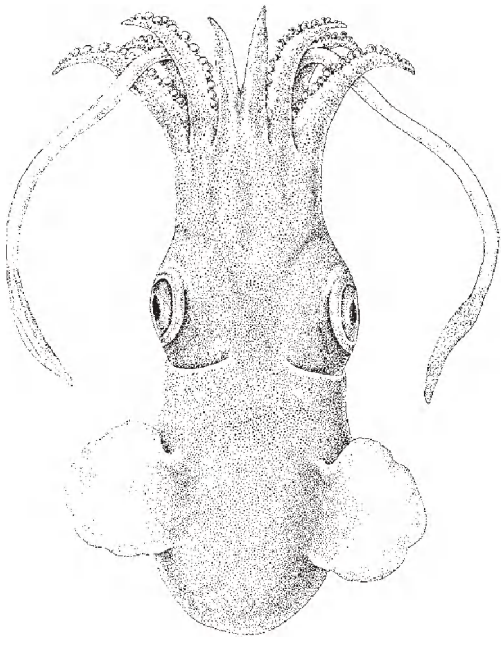
Fig. 215 *Austrorossia australis*

3a. Dorsal mantle fused to head (Fig. 216) . . . . . **→ 4**

3b. Dorsal mantle not fused to head . . . . . **→ 6**

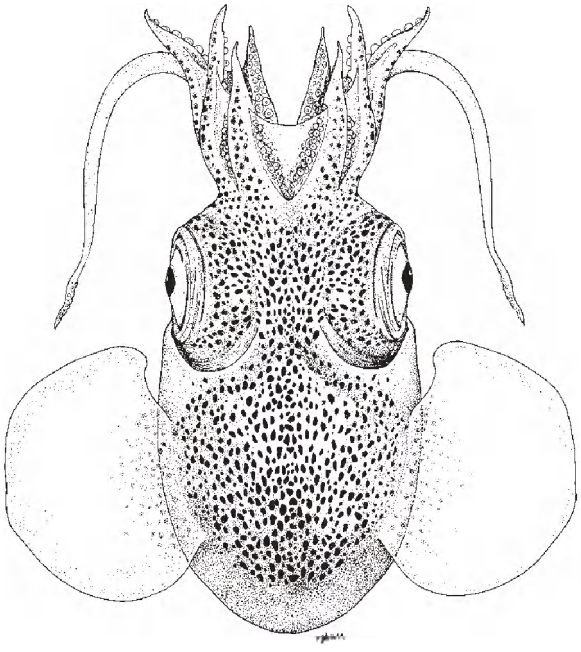
4a. Body slightly flattened dorsoventrally; fins from 60 to 80% mantle length (Fig. 216) . . . . . ***Sepiolina***

4b. Body broad, not flattened dorsoventrally; fin length usually >80% mantle length (Fig. 217) . . . . . **→ 5**



dorsal view

Fig. 216 *Sepiolina nipponensis*

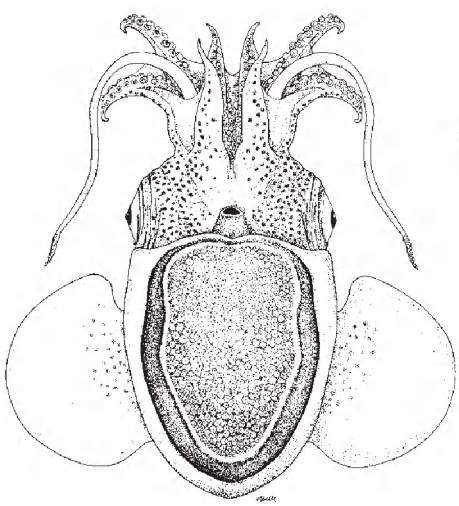


dorsal view

Fig. 217 *Stolotheutis leucoptera*

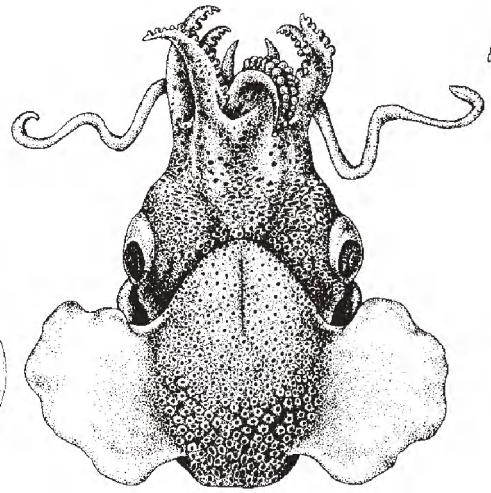
5a. Occipital band (joining mantle to head) from 40 to 50% head width (Fig. 217); ventral shield extending only to level of eyes (Fig. 218); fins attach to anterior part of mantle; posterior-fin margins do not reach end of body; eyes small (Fig. 218) . . . . . ***Stoloteuthis***

5b. Occipital band almost equal to head width (Fig. 219); ventral shield exceeds level of anterior margin of eye, reaching proximal end of arms (Fig. 220); fins attached to mantle at level of midline; posterior fin margins reach, or extend posteriorly beyond mantle margin; eyes very large (Fig. 220) . . . . . ***Iridoteuthis***



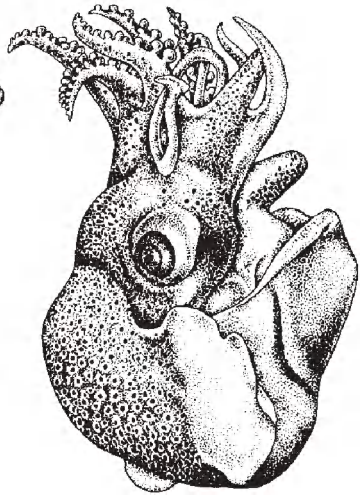
ventral view

Fig. 218 *Stolotheutis leucoptera*



dorsal view

Fig. 219 *Iridoteuthis* **sp.**

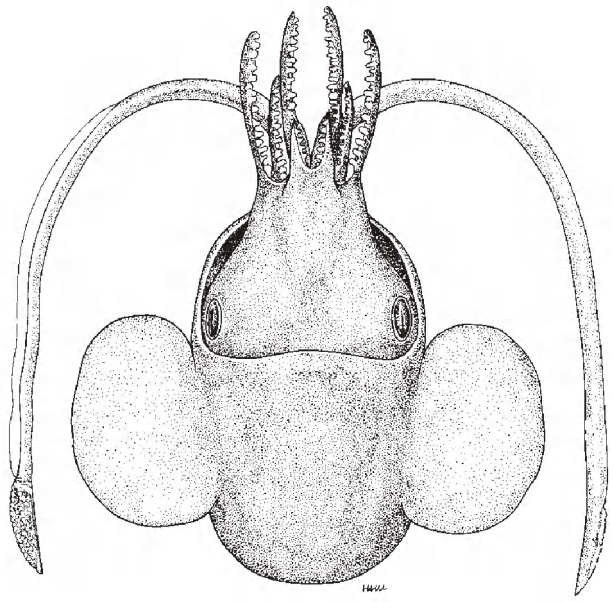


lateral view

Fig. 220 *Iridoteuthis* **sp.**

6a. Fins attached close to mantle midline; anterior fin margins extend beyond anterior edge of mantle (Fig. 221a); distal arm suckers with elongate, thick pedicels (Fig. 221b) . . . . . ***Nectoteuthis***

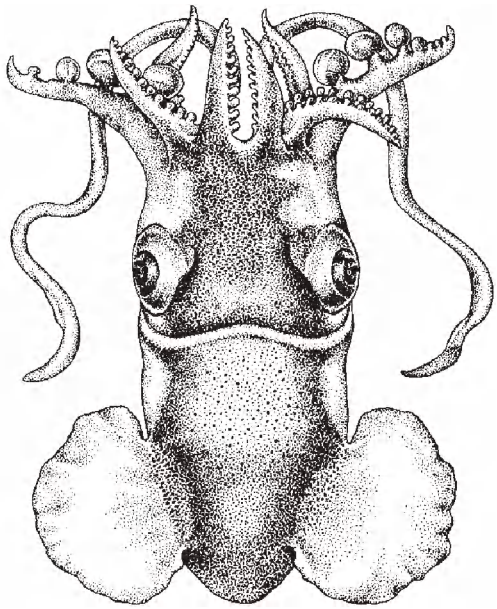
6b. Fins attached to posterior half of mantle, not reaching anterior edge (Fig. 222); sucker pedicels normal, not thick, elongate . . . . . ***Heteroteuthis***



a) dorsal view

b) distal tip of arm

Fig. 221 *Nectoteuthis pourtalesi*

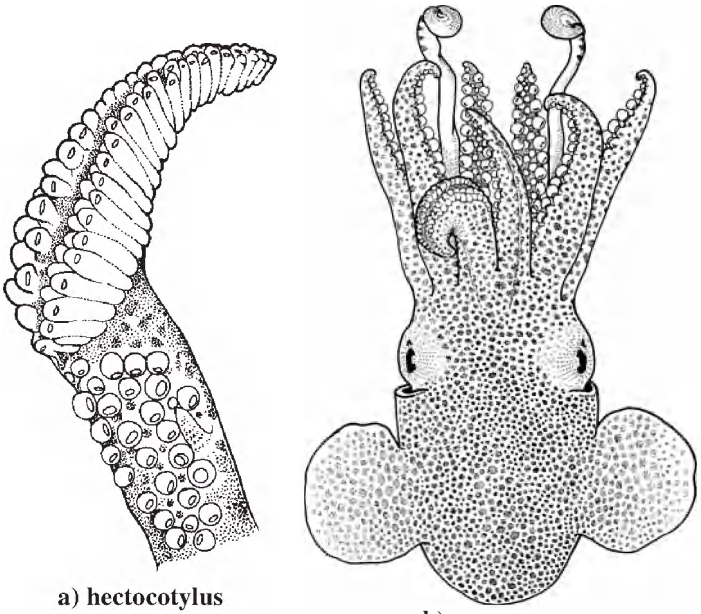


dorsal view

Fig. 222 *Heteroteuthis serventyi*

7a. Arm suckers usually tetraserial (biserial only in *E. phenax*); distal suckers on male hectocotylized arm greatly modified, with closely packed fleshy papillae formed from enlarged and elongate swollen sucker pedicels (Fig. 223a); male third arms not bent inward (Fig. 223b) . . . . . ***Euprymna***

7b. Proximal arm suckers biserial; hectocotylus modified as copulatory apparatus with recesses and projections, not as above; male third arms bent toward mouth (Fig. 224) . . . . . → **8**

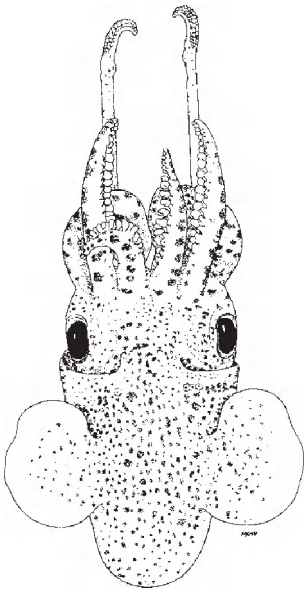


a) hectocotylus

b) dorsal view

(after Norman and Lu, 1997)

Fig. 223 ***Euprymna tasmanica***



dorsal view

(after Okutani, *et al.*, 1987)

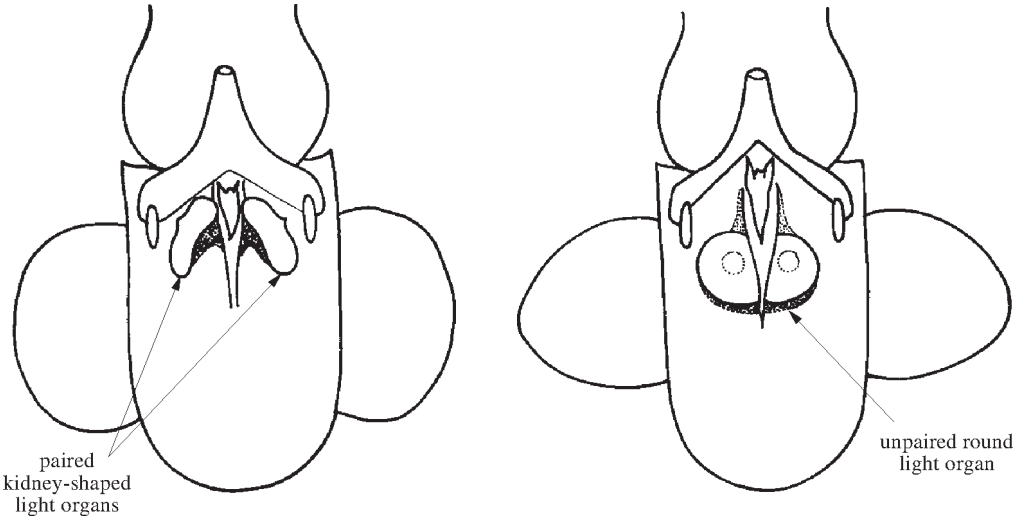
Fig. 224 ***Sepiola birostrata***

8a. Occiptal band wide, from 33 to 50% head width; light organ on ink sac . . . . . → **9**

8b. Occipital band narrow, usually <33% head width; inc sac without light organs . . . . . → **10**

9a. Paired, kidney-shaped light organs on anterior surface of ink sac (Fig. 225a); tentacular club suckers usually in 4 to 8 transverse rows. . . . . ***Sepiola***

9b. Unpaired, round light organ (Fig. 225b) deeply embedded in tissue on ventral side of ink sac; tentacular club suckers in 16 transverse rows . . . . . ***Rondeletiola***



a) *Sepiola*

b) *Rondeletiola*

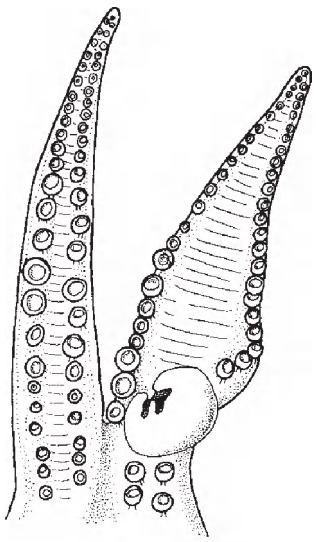
Fig. 225 Mantle cavity

10a. Both dorsal arms of males fused proximally; hectocotylized arm broad, spoon-like distal to copulatory apparatus (Fig. 226); tentacular-club suckers in >10 transverse rows . . . . . ***Sepietta***

10b. Hectocotylized arm not broad distal to copulatory apparatus (may be slightly broad in region of copulatory apparatus); tentacular club suckers in 8 to 10 rows . . . . . ***Inioteuthis***

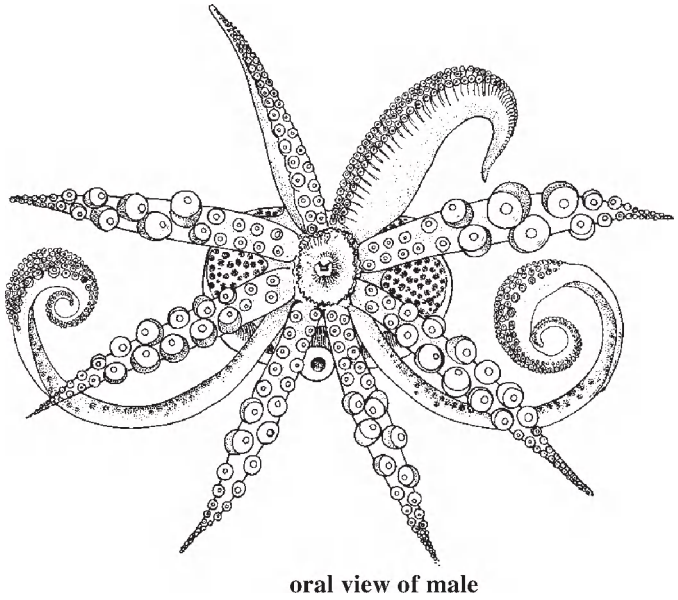
11a. Light organ present on ink sac; left dorsal arm of male hectocotylized (Fig. 227) . . . . . ***Semirossia***

11b. No light organ on ink sac; both dorsal arms of males hectocotylized . . . . . → **12**



hectocotylus

Fig. 226 *Sepietta oweniana*



oral view of male

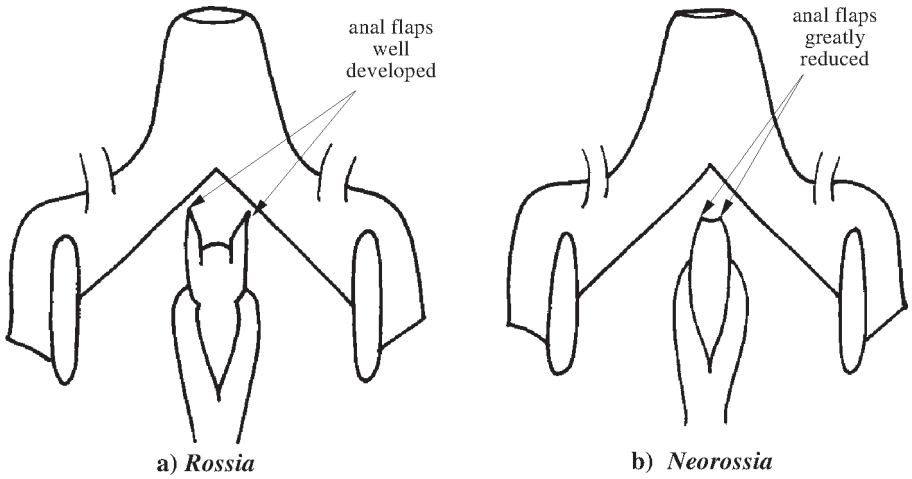
Fig. 227 *Semirossia tenera*

12a. Anal flaps present, well developed (Fig. 228a); ink sac well developed . . . . . → **13**

12b. Anal flaps reduced, or absent (Fig. 228b); ink sac greatly reduced . . . . . ***Neorossia***

13a. Male with both dorsal arms hectocotylized by an expanded ventral membrane or thickened fold (*R. moelleri*); arm suckers of males not greatly enlarged; tentacular clubs expanded with 5 to 16 transverse rows of medium-sized suckers . . . . . ***Rossia***

13b. Males with both dorsal arms hectocotylized by an expanded swollen membrane or fold on the proximal ventral margin; some suckers of all male arms enlarged; tentacular clubs not expanded, with 24 to 40 transverse rows of minute suckers . . . . . ***Austrorossia***



a) *Rossia* b) *Neorossia*

Fig. 228 anus (inside mantle cavity)

3.2.1 Subfamily SEPIOLINAE Appellöf, 1898

Sepiola affinis Naef, 1912 **Fig. 229**

Sepiola affinis Naef, 1912b, *Zoologischer Anzeiger*, 40(2): 81 [type locality: Tyrrhenian Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Analogous bobtail squid; **Fr** – Sépiole analogue; **Sp** – Sepiola análoga.

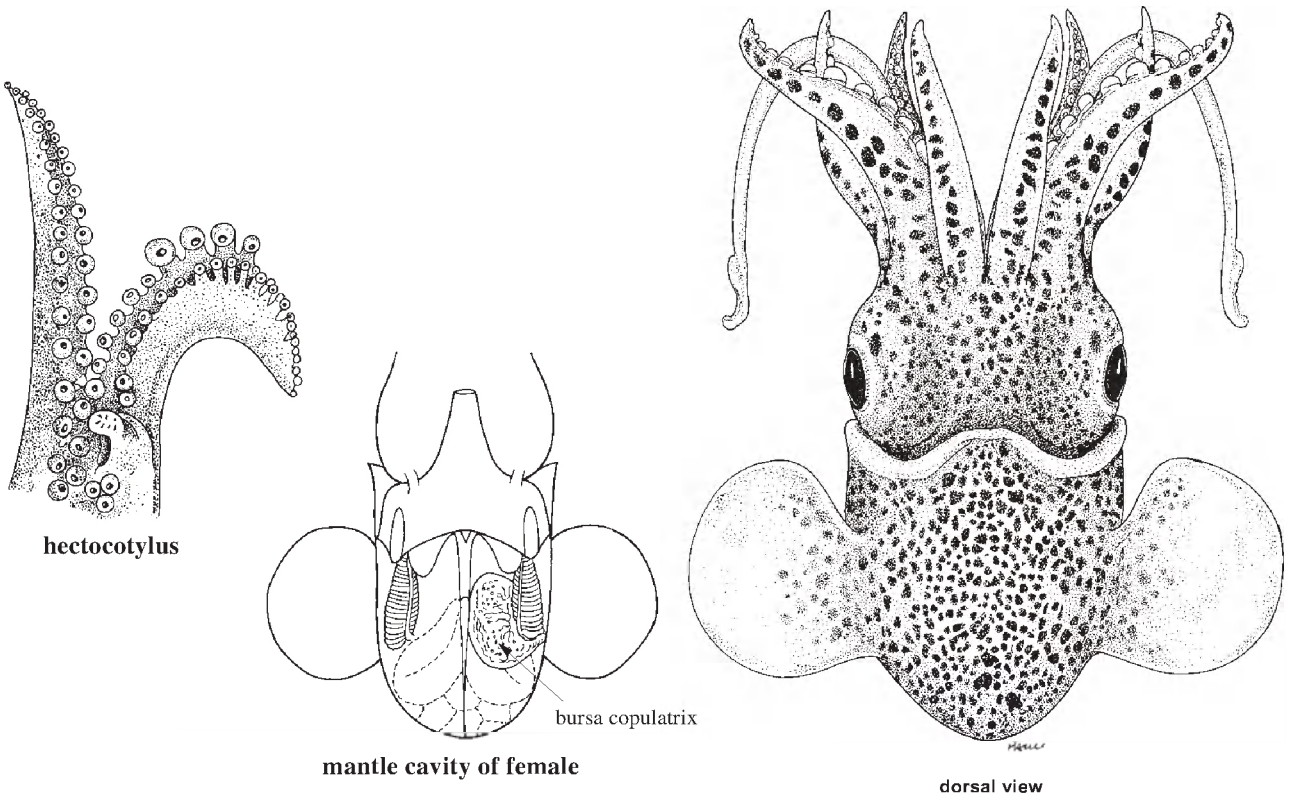


Fig. 229 *Sepiola affinis*

Diagnostic Features: Mantle slightly conical, head robust with prominent eyes; fins wide; rounded, semicircular; do not exceed length of mantle anteriorly or posteriorly; arm suckers biserial; tentacles delicate, club with 6 transverse rows of very small suckers; a few of the dorsal sucker rows close to the stalk slightly enlarged. Hectocotylus present, left dorsal arm modified: **3 small suckers** at the base, followed distally by the swollen lobe of the copulatory apparatus consisting of a primary lobe followed by a smaller lobe and a wrinkled tubercle; suckers biserial distal to copulatory apparatus, the dorsal ones differing in size: **first 4 to 6 small suckers are followed by 3 or 4 very large ones**, remaining suckers small, decreasing regularly in size to distal tip of arm; ventral rows of suckers uniformly small. Paired, kidney-shaped light organs present inside mantle cavity on each side of ink sac. **Bursa copulatrix small**. **Colour:** Dark brown, chromatophores large, violet brownish, dense.

Size: Up to 25 mm mantle length (both sexes).

Geographical Distribution: Mediterranean Sea, including Strait of Sicily, Adriatic Sea and north Aegean Sea. Depth range from 20 to 178 m (Fig. 230).

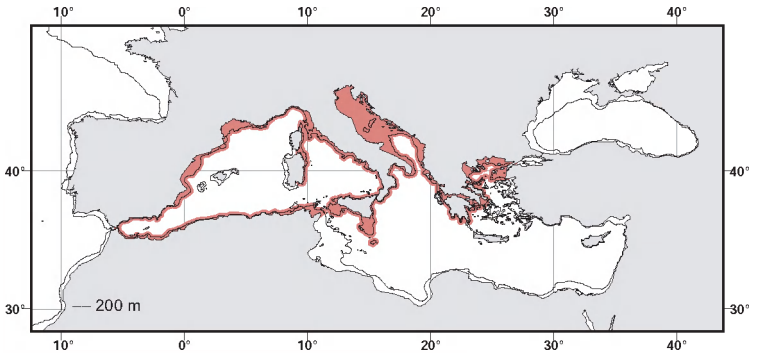


Fig. 230 *Sepiola affinis*
Known distribution

Habitat and Biology: A Mediterranean endemic, ***Sepiola affinis*** has been found at depths slightly over 150 m, but it is typically abundant in shallow waters (15–30 m), mostly on sandy or sandy-muddy substrates. It is often associated with ***S. intermedia*** Naef, 1912, from which young females are very difficult to distinguish. The smallest mature males are 12 mm, and the smallest mature females are 18 mm mantle length. Eggs are relatively large (2.2 × 1.8 mm) and experimental observations indicate that spawning may occur in one single event as well as being continuous or intermittent. The maximum observed spawning duration is 2 months and all animals die after spawning. During prey capture the species exhibits a great variety of colour patterns, with rapid colour changes.

Interest to Fisheries: It is commonly caught by small-scale and artisanal fisheries and consumed locally together with other species of the group. Separate statistics are not available.

Local Names: ITALY: Seppiola affine, Cappuccetto.

Literature: Naef (1923), Mauris (1989), Bello (1990b), Guerra (1992), Bello (1995), Gabel-Deickert (1995), D'Onghia *et al.* (1996), Jereb *et al.* (1997), Salman *et al.* (2002).

Sepiola atlantica Orbigny, 1839–1842 **Fig. 231**

Sepiola atlantica Orbigny, 1839–1842 (*in* Férussac and d'Orbigny, 1834–1848), *Histoire Naturelle Générale et Particulière Céphalopodes Acétabulifères Vivants et Fossiles*, pl. 4 [type locality: France: Bay of Biscay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: **En** – Atlantic bobtail squid; **Fr** – Sépiole grandes oreilles; **Sp** – Sepiola atlántica.

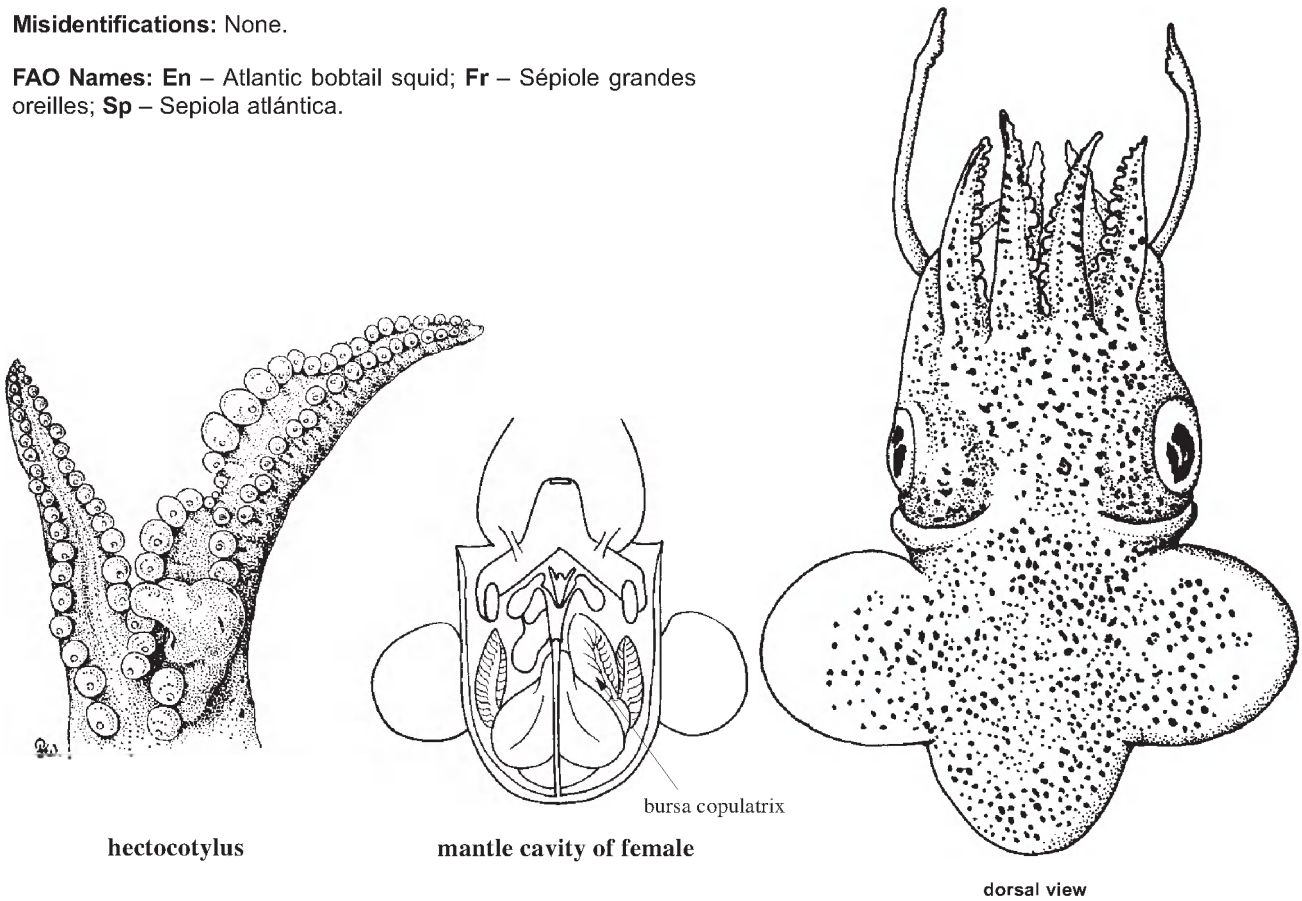


Fig. 231 ***Sepiola atlantica***

Diagnostic Features: Fins short, do not exceed length of mantle anteriorly or posteriorly. Arms IV with biserial suckers proximally, **4 to 8 rows of minute suckers at distal tips**; remaining arms with biserial suckers. Hectocotylus present; left dorsal arm modified: proximal end with fleshy pad formed from enlarged and fused sucker pedicels; copulatory apparatus a large swollen horn, with secondary lobes basally; dorsal row of suckers distal to copulatory apparatus with **3 or 4 slightly enlarged suckers with swollen pedicels, 3 or 4 greatly reduced suckers, then 3 to 5 greatly enlarged suckers** approximately halfway along arm. Hectocotylized arm strongly bent in distal half. Club with 8 suckers in transverse rows. Paired, kidney-shaped light organs (photophores) present inside mantle cavity on each side of ink sac.

Size: Up to 21 mm mantle length (mature males and females similar in size).

Geographical Distribution: Northeastern Atlantic: 65°N to 35°N, from Iceland, Faeroe Islands and western Norway to Morocco. Mediterranean Sea (single record only) (Fig. 232).

Habitat and Biology: Continental shelf to edge of slope. Epibenthic, but has been collected in midwater during both night and day. The ecology of the species in Firemore Bay, Loch Ewe, Scotland has been well studied. The resident population has a variable age composition, which suggests an extended reproductive season. Juveniles occur throughout the year, with peak recruitment in April and July to August.

Interest to Fisheries: Specific records are not available, but the species is likely to occur in local fisheries, due to its wide distribution and fairly common occurrence on the north European continental shelf.

Remarks: According to Naef (1916), Grimpe (1925), Bello (1986), Mangold and Boletzky (1988) and Bello (1992) ***Sepiola atlantica*** is absent from the Mediterranean Sea. However, Wurtz *et al.* (1995) referred to one mature male captured in the Tyrrhenian Sea at 90 m depth. ***Sepiola atlantica*** is distinguished from other sepiolid species in the northeastern Atlantic by the 4 to 8 rows of minute suckers at the distal tips of arms IV and the presence of the internal, ventrally positioned, bilobed light organs.

Literature: Joubin (1902a), Naef (1912b), Herring *et al.* (1981), Roper *et al.* (1984), Guerra (1986), Nesis (1987), Guerra (1992), Yau and Boyle (1996), Collins *et al.* (2001).

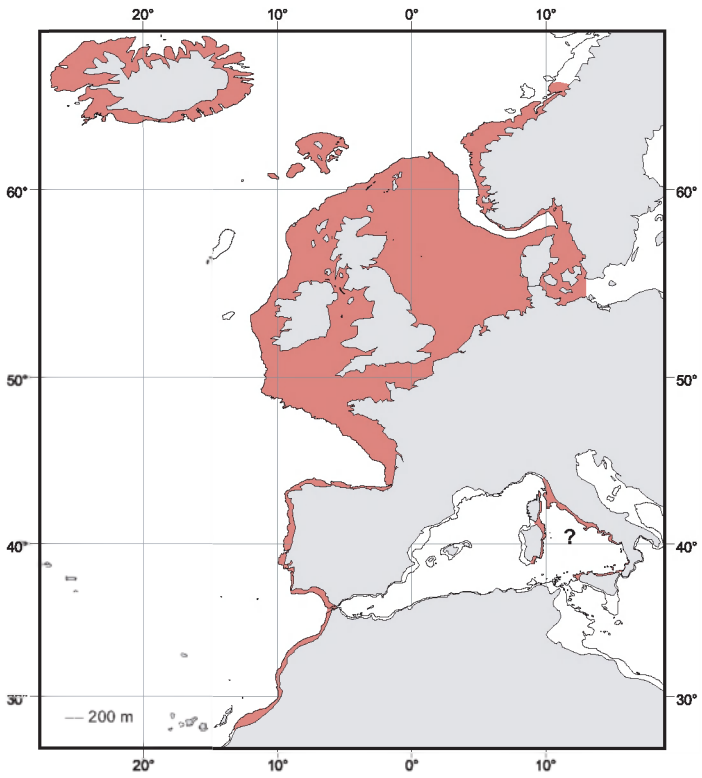


Fig. 232 ***Sepiola atlantica***
Known distribution

Sepiola birostrata Sasaki, 1918 Fig. 233

Sepiola birostrata Sasaki, 1918, *Doubutsugaku Zasshi* [Zoological Magazine Tokyo], 30: 235. [In Japanese] [type locality: Japan Sea, Toyama Bay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Butterfly bobtail squid; **Fr** – Sépiole papillon; **Sp** – Sepiola mariposa.

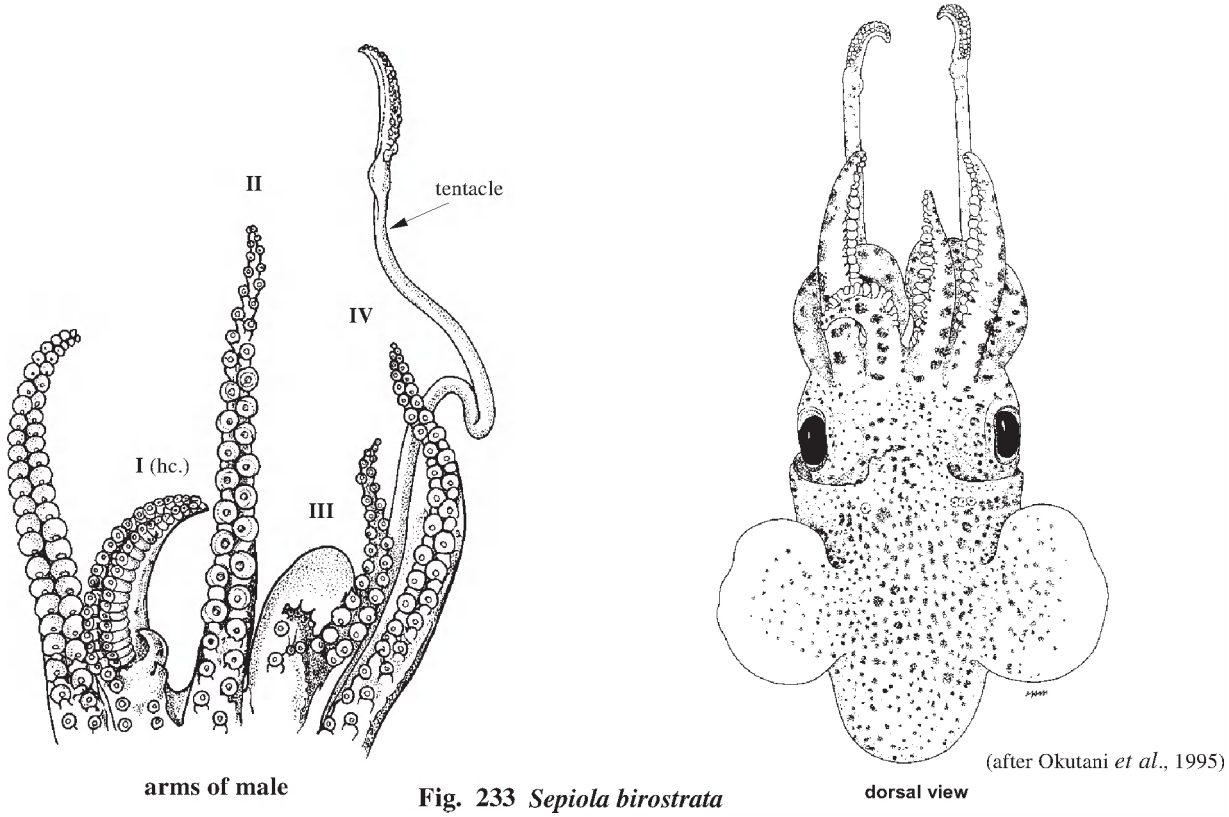


Fig. 233 *Sepiola birostrata*

Diagnostic Features: Mantle dome-shaped, half as wide as long. Dorsal mantle fused to head. Fins wide, ovate, short, do not exceed length of mantle anteriorly or posteriorly; attached slightly anterior to mantle midline. Arms III in both sexes stout and strongly curved inward (more obviously so in males). Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial. Dorsal and ventral rows of suckers on arms I and II of males equal in size, larger than suckers on arms III and IV. Hectocotylus present, left dorsal arm modified: proximal end with **2 slender, fleshy, papillae formed from enlarged and elongate sucker pedicels**; anteriormost papilla longest and thickest, posterior papilla fleshy; both papillae blunt distally. Club slightly recurved; short; with 4 suckers in proximal transverse rows, up to 16 rows distally; suckers small, dorsal marginal longitudinal series of suckers slightly larger than those in ventral marginal series. Paired, kidney-shaped light organs present inside mantle cavity on each side of ink sac. **Colour:** Mantle and head with many minute brown or black chromatophores; arms III deep pink, arms I to III each with single longitudinal row of large chromatophores, arms IV with double row of small chromatophores.

Size: Up to 22 mm mantle length.

Geographical Distribution: Northwestern Pacific: Sea of Okhotsk, southern Sakhalin, south Kurile Islands, Primorye (Russian Federation), North and South Korea, Japan, East China Sea (Fig. 234).

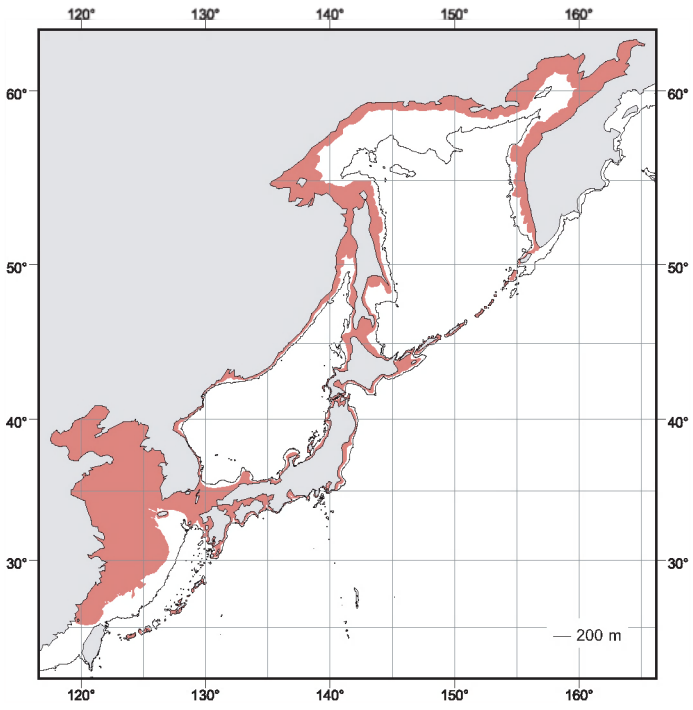


Fig. 234 *Sepiola birostrata*
Known distribution

Habitat and Biology: Neritic. Depth range to approximately 100 m.

Interest to Fisheries: No specific information is available, but the species is likely to occur, occasionally, in multispecies fisheries.

Remarks: ***Sepiola birostrata*** usually differs from ***S. trirostrata*** Voss, 1962, by the absence of a third blunt, fleshy lobe at the base of the pair of elongate papillae on hectocotylized arm. However, there appears to be some intraspecific variability in ***S. birostrata***: 3 lobes have been reported to occur in some specimens. All papillae on the hectocotylized arm of ***S. birostrata*** arise from a common mound-like base. In contrast, the third lobe-like papilla of ***S. trirostrata*** does not arise from the same base as the other two papillae. See Remarks under ***Sepiola parva*** Sasaki, 1913 for differences between ***S. birostrata*** and ***S. parva***.

Literature: Roper *et al.* (1984), Nesis (1987), Takayama and Okutani (1992), Okutani (1995), Kubodera and Yamada (1998).

Sepiola intermedia Naef, 1912 **Fig. 235**

Sepiola intermedia Naef, 1912a, *Zoologischer Anzeiger*, 39(7): 270 [type locality: Tyrrhenian Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: **En** – Intermediate bobtail squid; **Fr** – Sépiole intermédiaire; **Sp** – Sepiola intermedia.

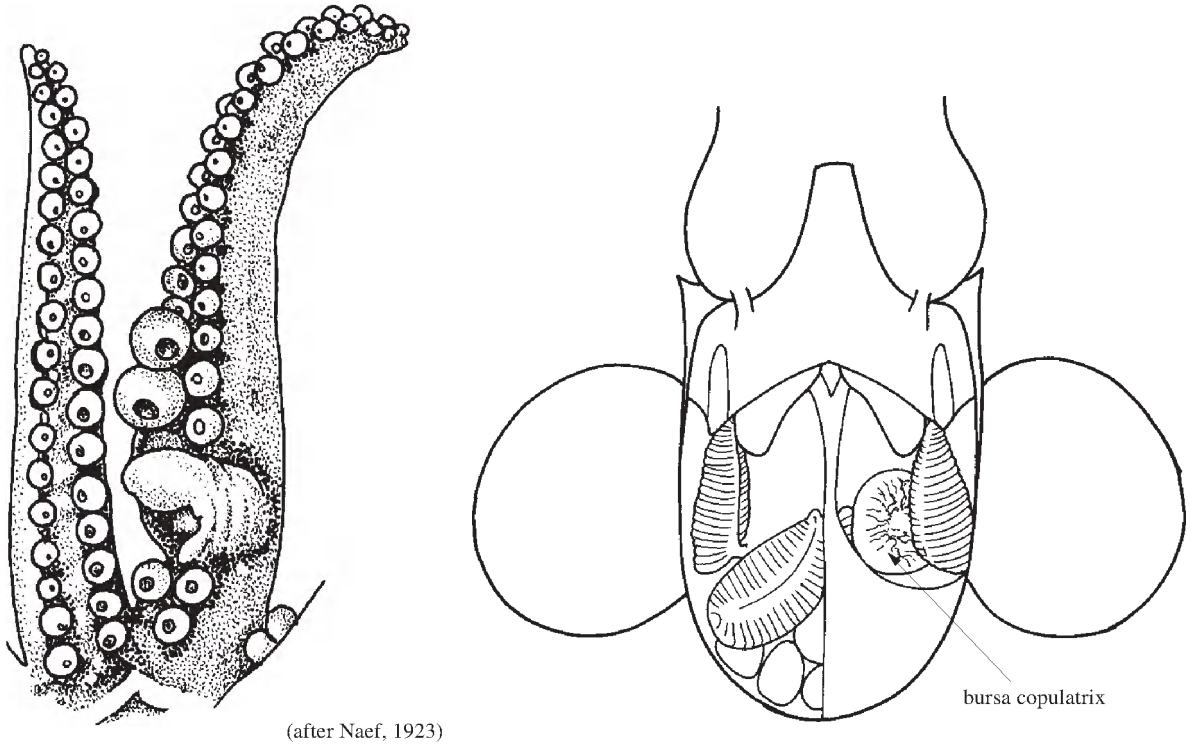


Fig. 235 ***Sepiola intermedia***

Diagnostic Features: Fins short, rounded, do not exceed length of mantle anteriorly or posteriorly. **Arms II and IV in males with a few enlarged suckers**. Tentacles very delicate, tentacle clubs with 6 transverse rows of small suckers. Hectocotylus present; left dorsal arm modified: **3 normal suckers at the base** (only slightly enlarged); copulatory apparatus consisting of a swollen and wrinkled tubercle, curved inward, with the markedly enlarged lobe projecting free; dorsal row of suckers distal to copulatory apparatus very variable in size: **2 markedly enlarged** (of which the proximal is slightly larger); or **3 enlarged**, of which the median is the largest; or **1 very small** followed by **1 very large** then **1 moderately large** sucker distal to the basal apparatus; left dorsal arm much longer than the right one. **Colour:** Dark coffee brown, with a strong shade of reddish brown; large chromatophores loosely scattered all over the mantle surface.

Size: Males up to 26 mm mantle length; females up to 28 mm mantle length.

Geographical Distribution: Northeastern Atlantic and Mediterranean Sea: including Ligurian Sea, Strait of Sicily, Adriatic Sea and northern Aegean Sea. Possibly Gulf of Cádiz. Continental shelf, depth range from 8 to 110 m (Fig. 236).

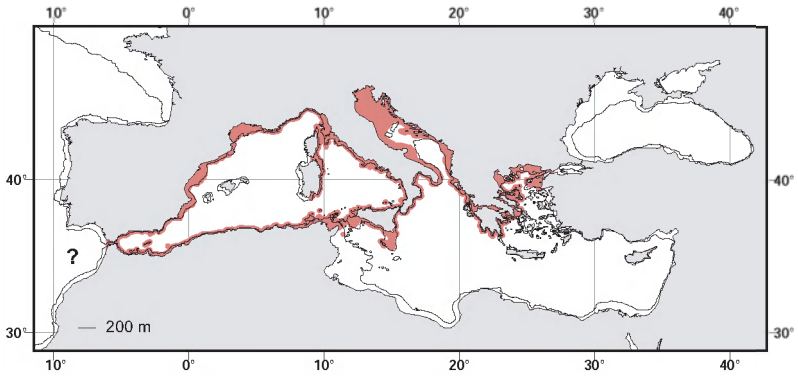


Fig. 236 ***Sepiola intermedia***
Known distribution

Habitat and Biology: ***Sepiola intermedia*** lives mainly on muddy bottoms between 60 and 200 m depth throughout its distributional range. In Italian waters, a preference for shallower, coastal and sandy bottoms has been observed both in the Adriatic and the Tyrrhenian Seas, where the species can be very abundant and is often found associated with *Turritella communis*, *Astropecten bispinosus* and *Ophiura texturata*. The biology of the species is poorly known, but the presence of mature individuals throughout the year suggests there may be a prolonged spawning period. Adult ***Sepiola intermedia*** have been collected in midwater, at night, by purse seine for blue fishes, confirming the strong swimming ability of this small bobtail squid (as observed in other species of the group).

Interest to Fisheries: No separate statistics are available, but the species is collected by local small-scale fisheries throughout its distributional range and represents a component of the bobtail squids captured in many Mediterranean areas.

Local Names: ITALY: Seppiola intermedia, Cappuccetto.

Literature: Naef (1912b), Naef (1923), Belcari *et al.* (1989), Orsi Relini and Bertuletti (1989), Guerra (1992), Bello (1995), Volpi *et al.* (1995), D'Onghia *et al.* (1996), Jereb *et al.* (1997), Salman *et al.* (1997).

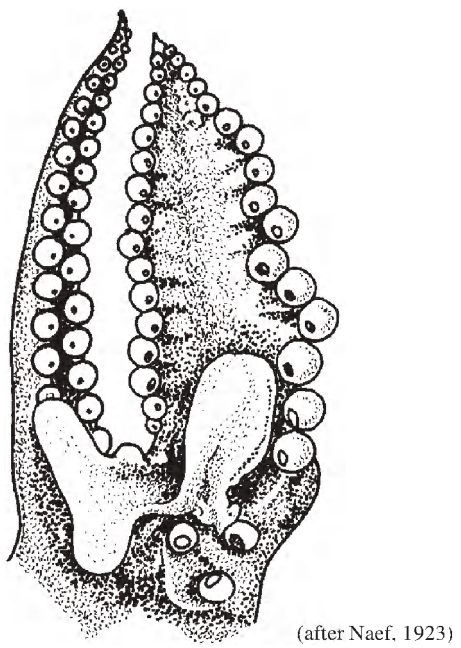
Sepiola ligulata Naef, 1912 — **Fig. 237**

Sepiola ligulata Naef, 1912a, *Zoologischer Anzeiger*, 39(7): 271 [type locality: Tyrrhenian Sea].

Frequent Synonyms: None.

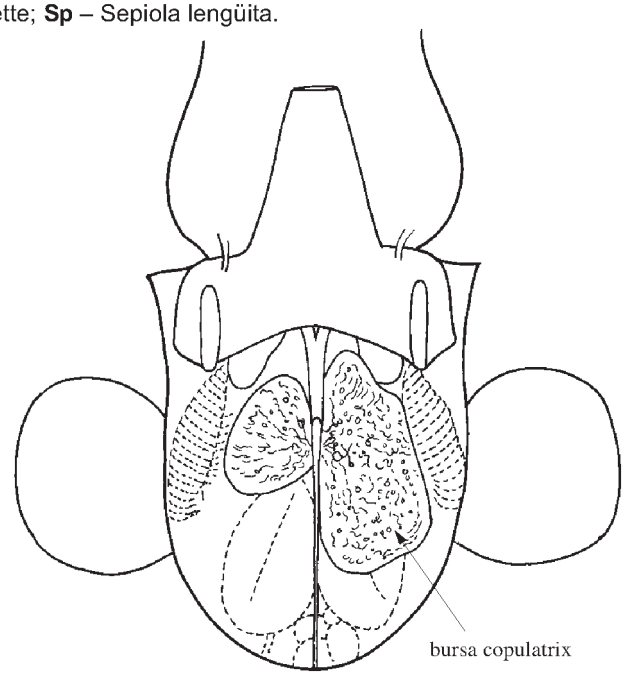
Misidentifications: None.

FAO Names: En – Tongue bobtail squid; **Fr** – Sépiole languette; **Sp** – Sepiola lengüita.



(after Naef, 1923)

hectocotylus



mantle cavity of female

Fig. 237 ***Sepiola ligulata***

Diagnostic Features: Mantle ventral margin may be markedly produced, with a deep median indentation. Fins relatively small, with a round lateral corner and relatively straight posterior margin. Tentacles delicate; club with 8 dense transverse rows of minute suckers. Hectocotylus present, left dorsal arm modified; **3 small normal suckers** at the base followed distally by the copulatory apparatus: **spatula-like thick and large lobe** extending towards the distal part of the arm and an **adjacent appendage forming a stalked plate or shovel-like structure that extends toward the right arm**; distal to copulatory apparatus, first suckers of the ventral row enlarged, with long, robust stalks. Bursa copulatrix large, extending anteriorly to cover renal papillae and genital opening and extends through the mantle septum over a large part of the right side of the mantle cavity. **Colour:** Bright, almost golden yellow, with yellowish orange, brownish red tones.

Size: Up to 25 mm mantle length.

Geographical Distribution: Mediterranean Sea: including Ligurian Sea, Tyrrhenian Sea, Strait of Sicily, Adriatic Sea and northern Aegean Sea. Possibly eastern Atlantic around Portugal and Spain. Depth range from 44 to 380 m (Fig. 238).

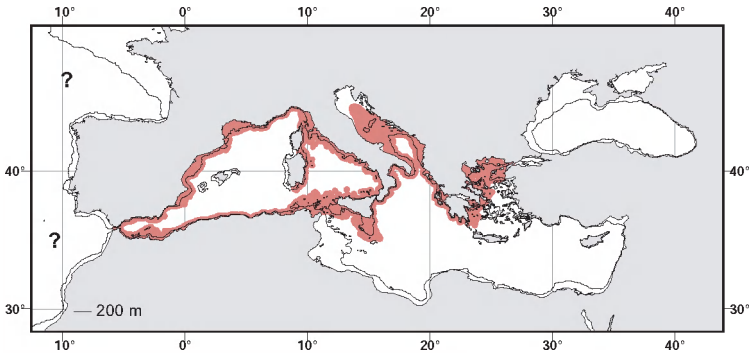


Fig. 238 ***Sepiola ligulata***
Known distribution

Habitat and Biology: The male copulatory apparatus and the female bursa copulatrix are very distinctive in ***S. ligulata***, enabling it to be readily distinguished from other species in the genus. It is one of the smallest species of the genus and is reported to be common throughout its range, though never abundant. ***Sepiola ligulata*** is an epibenthic species, living on muddy bottoms and mainly on the continental shelf, although it has also been found on the slope. It is often captured with ***Sepietta oweniana*** (Orbigny, 1839–1841) and ***Rondeletiola minor*** Naef, 1912. Information on the biology of ***S. ligulata*** is scarce, and is mostly derived from aquarium observations. Eggs are red and relatively large (3.5 mm diameter) and growth is rapid with water temperatures between 12° and 20°C, allowing newly hatched individuals (1.8 to 2.5 mm mantle length) to reach 9 mm mantle length in about six months. The smallest mature males are 11 mm, and the smallest females 14 mm mantle length.

Interest to Fisheries: Never abundant, but often present in captures with the other species of the group, it is used as food locally.

Local Names: ITALY: Seppiola linguetta.

Literature: Naef (1912b), Naef (1923), Boletzky *et al.* (1971), Orsi Relini and Bertuletti (1989), Bello (1990b), Guerra (1992), Bello (1995), Sartor and Belcari (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995), D'Onghia *et al.* (1996), Jereb *et al.* (1997), Salman *et al.* (2002).

Sepiola parva Sasaki, 1913 Fig. 239

Sepiola parva Sasaki, 1913, *Dobutsugaku Zasshi* [Zoological Magazine Tokyo], 25: 252. [In Japanese] [type locality: Japan, Tokyo Bay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Spotty bobtail squid; **Fr** – Sépiole mouchetée; **Sp** – Sepiola manchada.

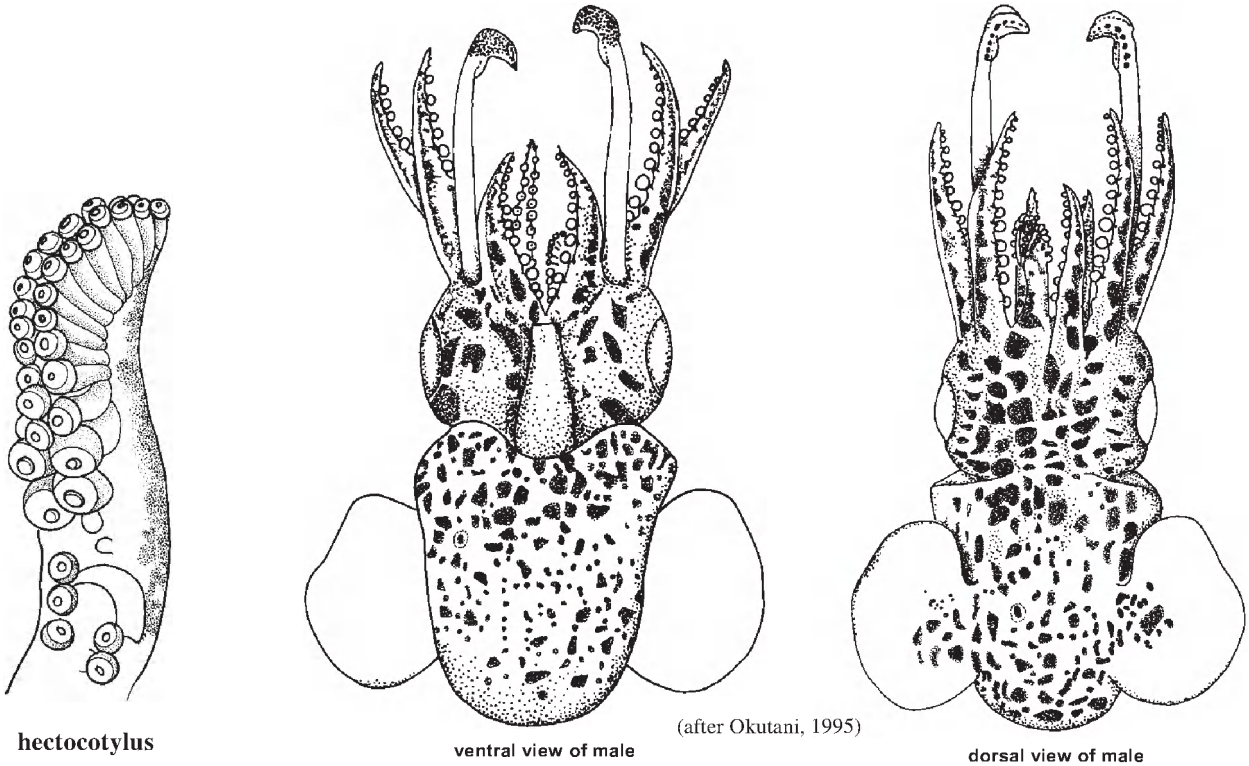


Fig. 239 *Sepiola parva*

Diagnostic Features: Mantle dome-shaped. Dorsal mantle fused to head. Fins narrow, ear-shaped, short; do not exceed length of mantle anteriorly or posteriorly. Head broad, narrower than mantle. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial. Hectocotylus present, left dorsal arm modified: proximal end with **fleshy hook-like papilla** formed from enlarged sucker pedicel; 2 rows of suckers on arm proximal to hook-like papilla; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed forming two double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings. Club with 8 suckers in transverse rows; dorsal and ventral marginal longitudinal series of suckers smaller than medial suckers (medial suckers 1.6 times larger than marginal ones). Internal gladius absent. Paired, kidney-shaped light organs present inside mantle cavity on each side of ink sac.

Size: Up to 10 mm mantle length.

Geographical Distribution: Northwestern Pacific: southern Japan to northern Philippines (Fig. 240).

Habitat and Biology: Upper sublittoral. This species seems to prefer the subtidal zone with hard substrates, unlike *S. birostrata* Sasaki, 1918, which is abundant in shallow water with sandy or muddy substrates.

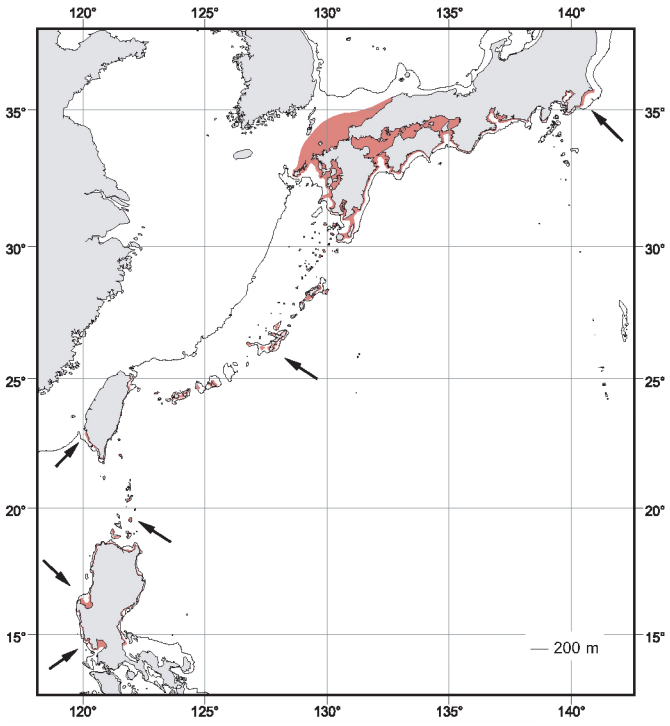


Fig. 240 *Sepiola parva*
Known distribution

Interest to Fisheries: The species is occasionally caught and consumed locally.

Remarks: This species closely resembles ***S. birostrata***. The 2 species, however, can be distinguished by differences in the dentition of the chitinous rings on the tentacle-club suckers, regardless of maturity and sex. In ***Sepiola parva,*** the club-sucker rings have three rows of polygonal processes bearing bush-like papillae. ***Sepiola birostrata*** Sasaki, 1913 has 4 rows of polygonal processes; the inner 2 rows bear blunt, flat-topped pegs. The 2 or 3 hook-like processes on the hectocotylized arm arise from a common elevated base in ***S. birostrata***, unlike that of ***S. parva***, in which a single process arises directly from the arm flesh.

Literature: Takayama and Okutani (1992), Okutani (1995), Reid and Norman (1998).

Sepiola robusta Naef, 1912 — Fig. 241

Sepiola robusta Naef, 1912a, *Zoologischer Anzeiger*, 39(7): 271 [type locality: Tyrrhenian Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Robust bobtail squid; **Fr** – Sépiole robuste; **Sp** – Sepiola robusta.

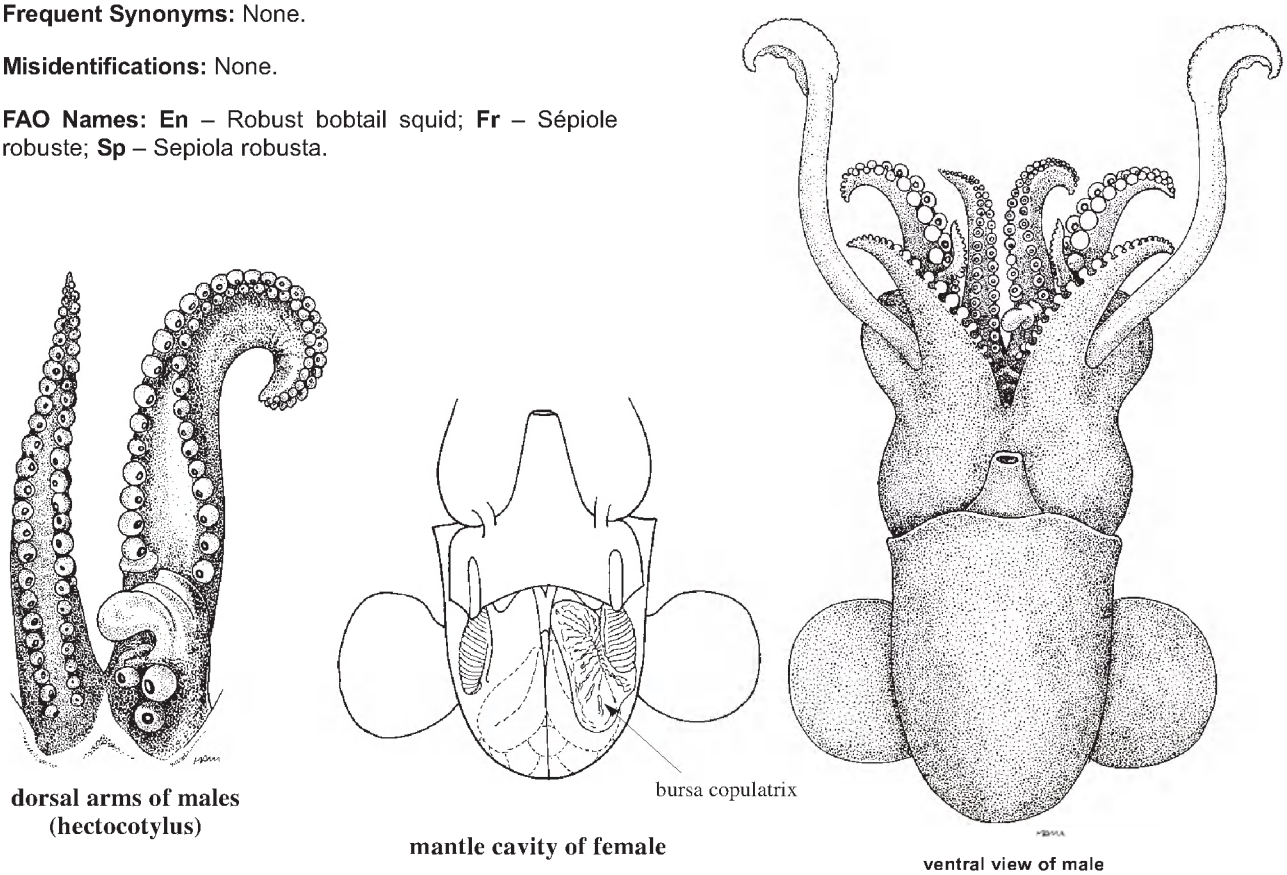


Fig. 241 *Sepiola robusta*

Diagnostic Features: Ventral mantle normal, **not strongly produced anteriorly**. Fins short, do not exceed length of mantle anteriorly or posteriorly. Hectocotylus present, left dorsal arm modified: proximal end with fleshy pad formed from enlarged and fused sucker pedicels; copulatory apparatus a **complexly twisted lobe (very variable) consisting of 3 hook-like structures**; horn of copulatory apparatus slightly recurved, but does not form a small hole; base of hectocotylus with one sucker of ventral row markedly enlarged; distal end of hectocotylized arm with normal suckers (not enlarged or modified); arm slightly widened distal to copulatory apparatus and sharply bent distally; arm without groove on inner side. Arm often narrower at level of fifth and sixth sucker rows distal to copulatory apparatus. **Club large with 8 suckers in transverse rows; suckers in dorsal rows in widest part of club markedly enlarged. Female bursa copulatrix moderately large (exceeds length of gill insertion posteriorly)**; caecum absent; posterior left side of mantle cavity in females without mantle constrictor muscle (cutaneous muscle extending from mantle septum to base of left gill). Paired, kidney-shaped light organs (photophores) present inside mantle cavity on each side of ink sac.

Size: Males up to 25 mm mantle length; females up to 28 mm mantle length.

Geographical Distribution: Mediterranean Sea: absent in Marmara and Black Sea (Fig. 242).

Habitat and Biology: Outer shelf. Depth range from 26 to 498 m. Mating takes place when the male grasps the female's 'neck' region, and spermatophores are placed in the females' bursa copulatrix. Males have been observed to guard females during courtship.

Interest to Fisheries: ***Sepiola robusta*** is one of the most frequently captured Mediterranean ***Sepiola***, where it contributes (although in low numbers) to the bobtail squid catches by local trawlers.

Local Names: ITALY: Seppiola robusta, Cappuccetto.

Remarks: The doubtful record from Galizia (Spain, northeastern Atlantic) noted by Guerra (1984) has not subsequently been confirmed; the species is considered to be a Mediterranean endemic (Guerra, 1992).

Literature: Naef (1923), Boletzky *et al.* (1971), Boletzky (1983b), Nesis (1987), Guerra (1984), Belcari *et al.* (1989), Orsi Relini and Bertuletti (1989), Guerra (1992), Bello (1995), Jereb and Di Stefano (1995), Volpi *et al.* (1995), Jereb *et al.* (1997).

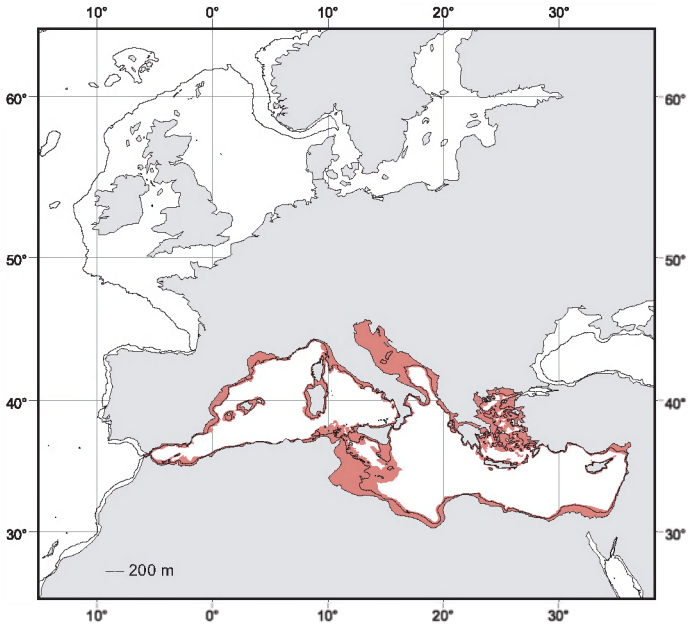


Fig. 242 ***Sepiola robusta***
Known distribution

Sepiola rondeleti Leach, 1834 — **Fig. 243**

Sepiola rondeleti Leach, 1834 (*in* Férussac and d'Orbigny, 1834–1848), *Histoire Naturelle Générale et Particulière Céphalopodes Acétabuliferes Vivants et Fossiles*, 230 [type locality: Mediterranean Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Dwarf bobtail squid; **Fr** – Sépiole naine; **Sp** – Sepiola enana.

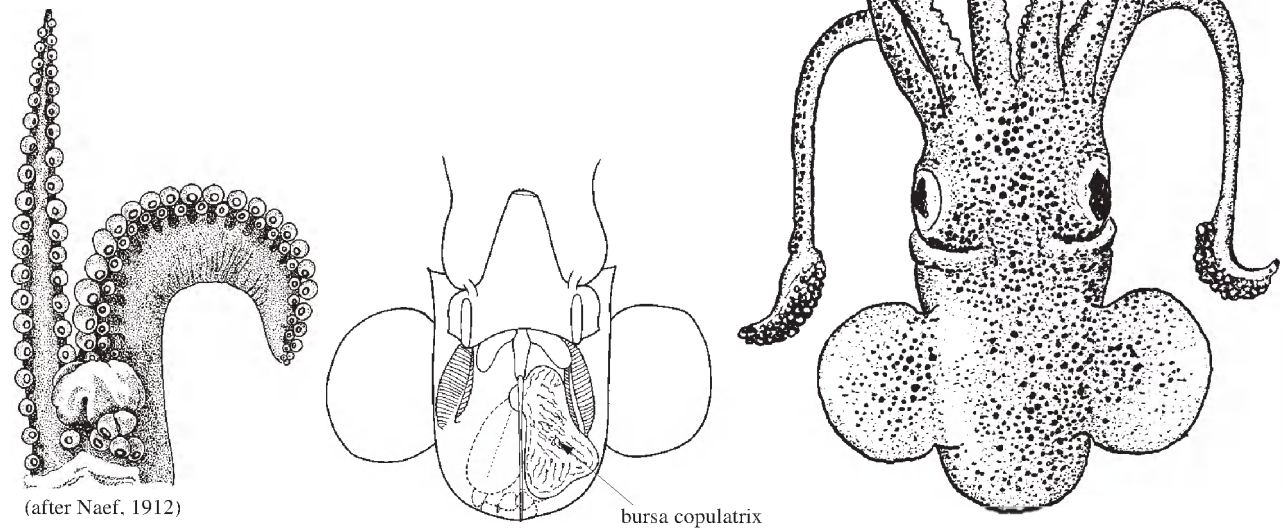


Fig. 243 ***Sepiola rondeleti***

Diagnostic Features: Ventral mantle margin **projects markedly anteriorly**. Fins short, do not exceed length of mantle anteriorly or posteriorly. Hectocotylus present, left dorsal arm modified: proximal end with fleshy pad formed from enlarged and fused sucker pedicels; **horn of copulatory apparatus recurved to form a small hole**; base of hectocotylus with equal sized suckers; distal end of hectocotylized arm with some enlarged suckers; ventral row of suckers distal to copulatory apparatus much smaller than those in dorsal row; arm without groove on inner side. **Club with 8 suckers in transverse rows; dorsal marginal series of suckers enlarged on proximal end of club**. Female bursa copulatrix large; extends posteriorly beyond gill insertion; caecum present, small; barely protrudes into right half of mantle cavity. Posterior left side of mantle cavity in females without mantle constrictor muscle (cutaneous muscle extends from mantle septum to base of left gill). Internal gladius present, rudimentary, chitinous. Paired, kidney-shaped light organs present inside mantle cavity, on each side of ink sac. Anterior ventral mantle margin with dense border of chromatophores. Outer surface of tentacular clubs heavily pigmented with chromatophores.

Size: Males up to 25 mm mantle length; females up to 60 mm mantle length (but most commonly from 40 to 50 mm mantle length).

Geographical Distribution: Northeastern Atlantic and Mediterranean Sea: including Strait of Sicily, Aegean Sea, Adriatic Sea, Sea of Marmara and Levantine Sea. In the northeastern Atlantic it extends from the North Sea to Senegal (Fig. 244).

Habitat and Biology: Sandy and muddy substrates, common in *Posidonia* seagrass beds down to 35 m. Epibenthic, or mesobenthic, ***Sepiola rondeleti*** has been recorded from very shallow waters down to around 450 m. Mating takes place when males grasp the female's 'neck' region, and spermatophores are placed in her bursa copulatrix. In the western Mediterranean, the spawning season extends from March to November, with longevity estimated at 18 months. The species feeds on crustacea and small fishes. All females over 30 mm mantle length are mature.

Interest to Fisheries: Captured during bottom trawls and occasionally with purse seines and drift nets. It is consumed locally; the flesh is very tasty, though difficult to preserve.

Local Names: ITALY: Seppiola di Rondelet, Cappuccetto.

Remarks: ***Sepiola rondeleti*** is known to preferentially inhabit waters shallower than 50 m throughout the year. Deeper records from the Mediterranean were long considered doubtful (Mangold-Wirtz 1963, Bello 1983–84). However, more recent evidence has confirmed a greater depth distribution for this species than previously thought, verifying the maximum recorded depth of 450 m (Dieuzeide, 1955).

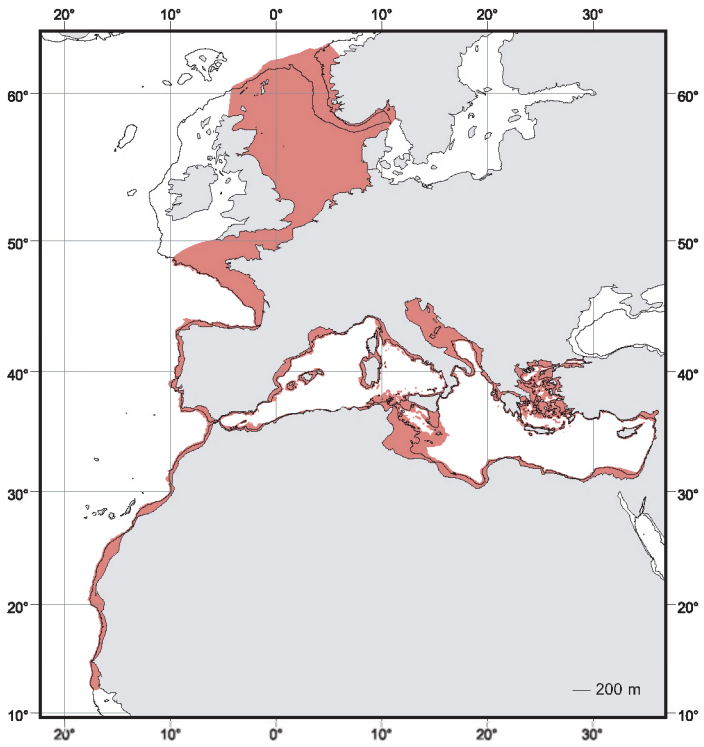


Fig. 244 ***Sepiola rondeleti***
Known distribution

Literature: Joubin (1895, 1902a), Naef (1912b), Naef (1923), Boletzky *et al.* (1971), Bello (1983–84), Roper *et al.* (1984), Guerra (1992), Bello (1995), Orsi Relini and Bertuletti (1989), D'Onghia *et al.* (1996), Jereb *et al.* (1997).

Sepiola trirostrata Voss, 1962 — Fig. 245

Sepiola trirostrata Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 172 [type locality: Philippines].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Knobby bobtail squid; **Fr** – Sépiole bosselée; **Sp** – Sepiola nudosa.

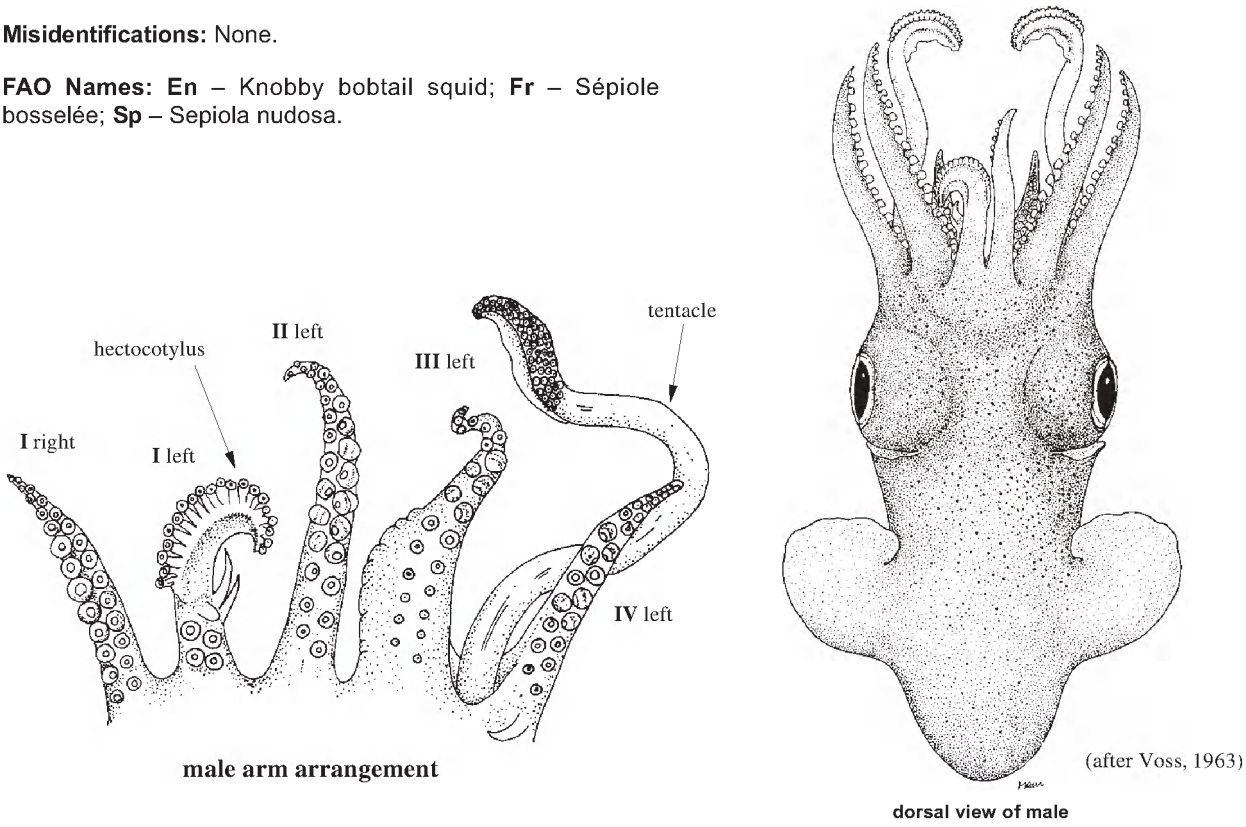


Fig. 245 *Sepiola trirostrata*

Diagnostic Features: Fins short, do not exceed length of mantle anteriorly or posteriorly. Arms III in both sexes stout and strongly curved inward, more obviously so in males. Suckers in ventral series of right arm I and arms II of males larger than dorsal suckers. Hectocotylus present, left dorsal arm modified: proximal end with **2 slender fleshy papillae** (anteriormost papilla longest) and dorsolateral to these a **blunt tongue-like lobe**, all formed from enlarged and elongate sucker pedicels; 2 rows of suckers on arm proximal to fleshy pad; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed to form 2 double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings. Club with 4 large suckers in transverse rows; suckers differ in size; dorsal marginal longitudinal series of suckers larger than those in ventral marginal series. Paired kidney-shaped light organs present inside mantle cavity on each side of ink sac. **Colour:** Mantle and head with many minute brown or black chromatophores; arms III deep pink, arms I to III each with single longitudinal row of large chromatophores, arms IV with double row of small chromatophores.

Size: Up to 12.5 mm mantle length.

Geographical Distribution: Indo-Pacific: Philippines, Singapore (Fig. 246).

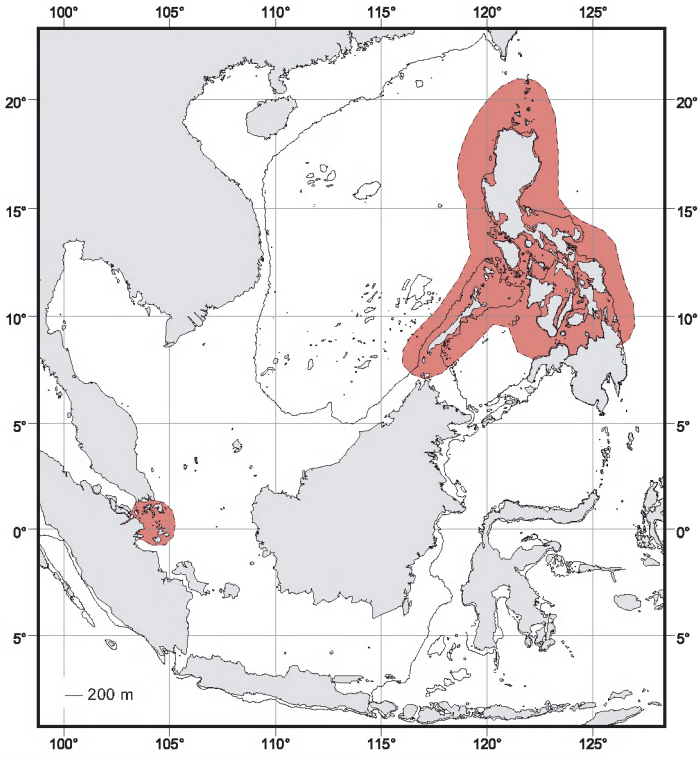


Fig. 246 *Sepiola trirostrata*
Known distribution

Interest to Fisheries: Presently undetermined.

Remarks: Differs from ***S. birostrata*** Sasaki, 1918 in the presence of the blunt, fleshy papilla, in addition to the 2 slender papillae on the hectocotylus. The slender papillae arise from a common mound-like base, while the third lobe arises separately. In this trait, ***S. trirostrata*** differs from those ***S. birostrata*** specimens that bear a third lobe on the hectocotylus.

Literature: Voss (1963).

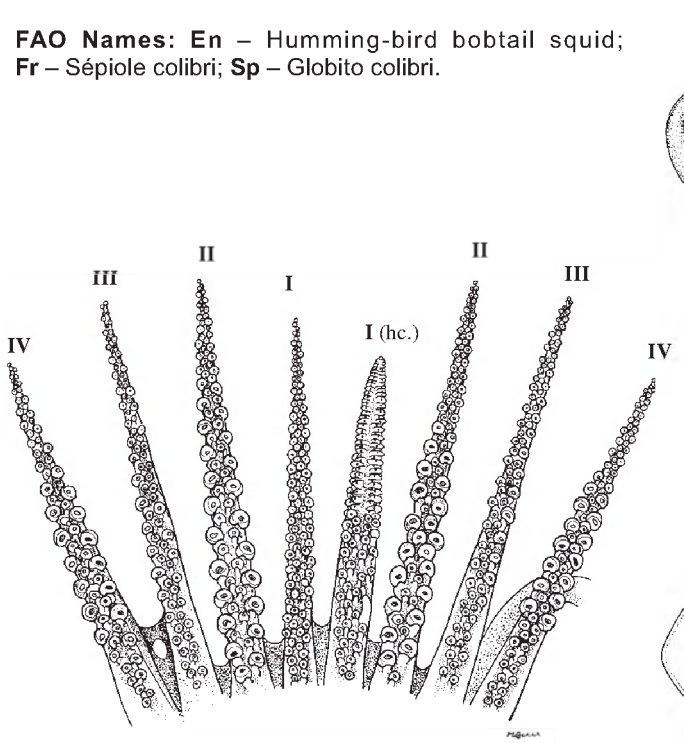
Euprymna berryi Sasaki, 1929 — Fig. 247

Euprymna berryi Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University*, 20(supplement): 143 [type locality: Japan, Honshu].

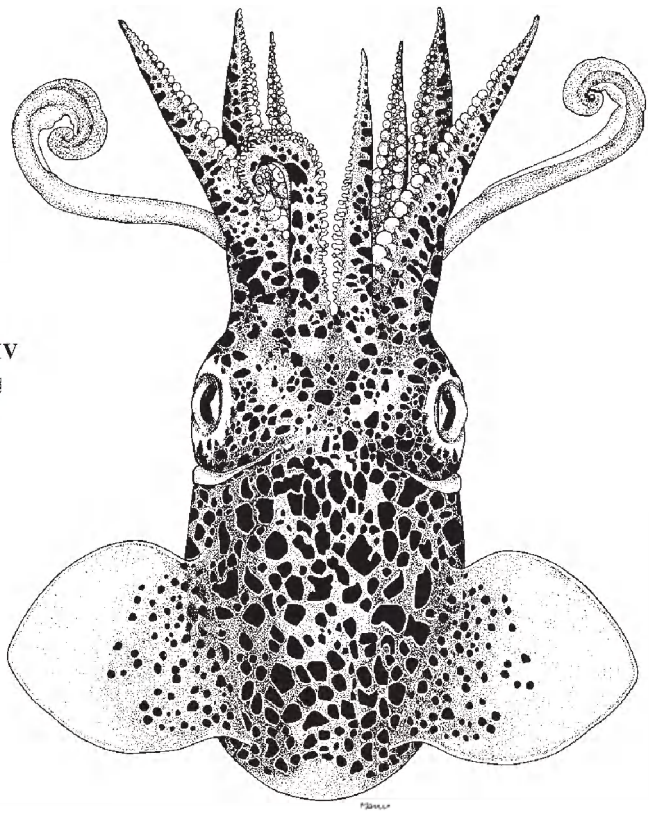
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Humming-bird bobtail squid; **Fr** – Sépiole colibri; **Sp** – Globito colibri.



arms of male
(oral view)



(after Okutani *et al.*, 1995)

dorsal view of male

Fig. 247 ***Euprymna berryi***

Diagnostic Features: Fins short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial. Male non-hectocotylized arm suckers enlarged on some arms: **arms II and IV with approximately 10 moderately enlarged suckers in dorsal and ventral rows from proximal second to fourth suckers; approximately 8 slightly enlarged suckers in ventral row of arm III from proximal fifth to eighth sucker.** Hectocotylus present; left dorsal arm modified: arm thick, short, and blunt; proximal end with 2 fleshy papillae formed from enlarged, or elongate sucker pedicels; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed forming 2 double rows of 70 to 80 columnar structures; suckers reduced with tiny, fleshy, slit-like openings. Marginal suckers on dorsal arms I are slightly larger than medial ones. Tentacular club suckers goblet-shaped. Swimming keel of club extends well beyond carpus.

Size: Males up to 30 mm mantle length; females up to 50 mm mantle length.

Geographical Distribution: Indo-Pacific: Along coasts of China, south to Hong Kong and Japan (but not in Hokkaido), Taiwan Province of China, possibly Andaman Islands and Sri Lanka (Fig. 248).

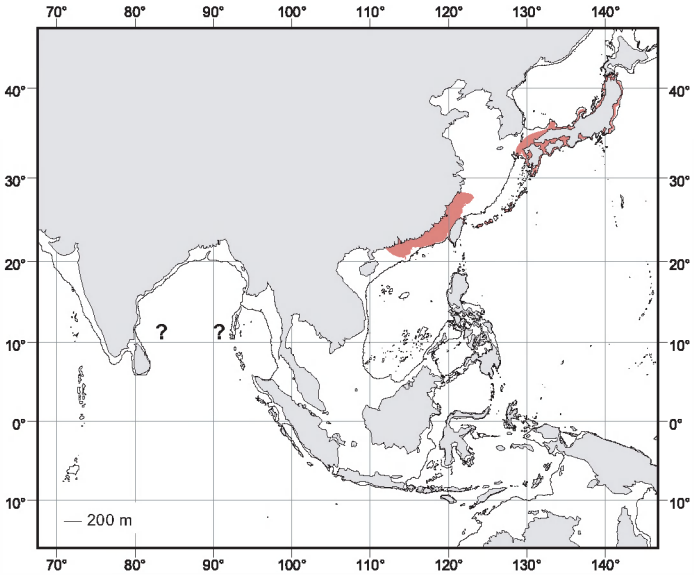


Fig. 248 ***Euprymna berryi***
Known distribution

Habitat and Biology: Upper sublittoral and pelagic in warm temperate waters; depth range to 107 m. This species has been reared successfully in aquaculture experiments. Females lay clumps of round, pale orange eggs.

Interest to Fisheries: Consumed locally in China and Taiwan Province of China, where this species is abundant and sustains local small fisheries; currently not commercially exploited in Hong Kong.

Local Names: CHINA: Leung yee jai; JAPAN: Niyori-mimi-ika.

Remarks: The taxonomic status of members of this genus is largely unresolved (Norman and Lu 1997). ***Euprymna berryi*** is sympatric with, and very similar to ***E. morsei*** Verrill (1881). Non-quantitative differences between the 2 species include: among 4 rows of arm suckers, only the ventral rows are enlarged in ***E. morsei*** (particularly from third to fourth suckers on arms II to IV), but both dorsal and ventral arms have enlarged suckers in ***E. berryi***; the club suckers are spherical, or cup-shaped in ***E. morsei***, but goblet-shaped in ***E. berryi***. The club suckers have an indistinct proximal border in ***E. berryi***, while those in ***E. morsei*** have distinct borders.

Literature: Roper *et al*. (1984), Okutani and Horita (1987), Okutani (1995), Norman and Lu (1997), Kubodera and Yamada (1998), Lu (1998b).

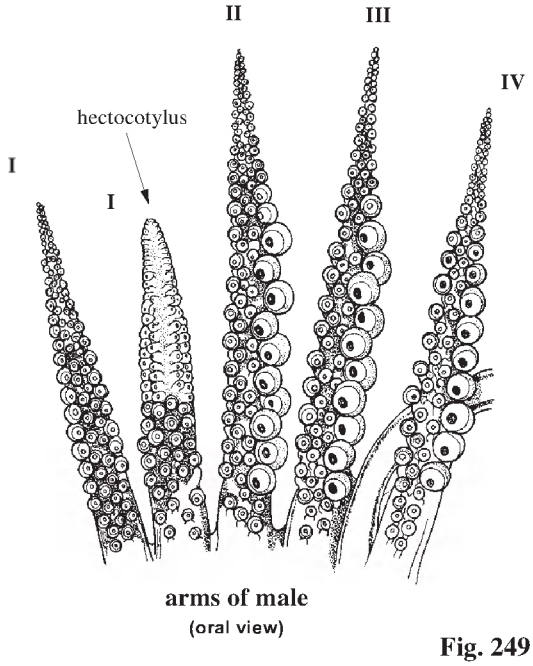
Euprymna morsei (Verrill, 1881) **Fig. 249**

Inioteuthis morsei Verrill, 1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 417 [type locality: Japan, Tokyo Bay].

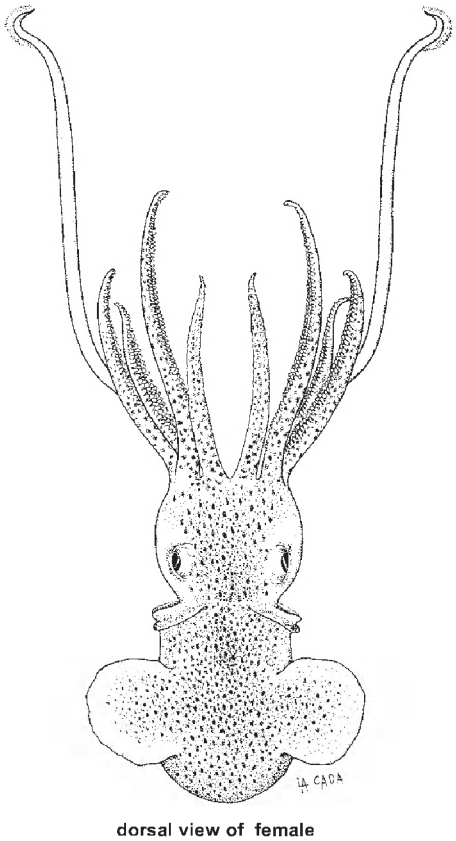
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Mimika bobtail squid; **Fr** – Sépiole mimika; **Sp** – Globito mimika.



arms of male
(oral view)



dorsal view of female

Fig. 249 ***Euprymna morsei***

Diagnostic Features: Mantle dome-shaped, plump. Dorsal mantle fused to head. Fins wide, rounded, semicircular; short, do not exceed length of mantle anteriorly or posteriorly; posteriorly with wide gap between fins; anterior origin posterior to mantle margin. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial. **Ventral rows of arms II to IV in males with enlarged suckers, approximately 10 on each arm from proximal third or fourth suckers.** Hectocotylus present; distal half of left dorsal arm modified: sucker pedicels enlarged and tightly packed to form 2 double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings; proximal end of arm with single nipple-like papilla. Marginal suckers arms I slightly larger than medial suckers. Tentacular-club suckers cup-shaped or spherical. Internal gladius absent. Paired saddle-shaped light organs present inside mantle cavity on ink sac. **Colour:** Iridescent gold to purple with large black chromatophores.

Size: Up to 40 mm mantle length.

Geographical Distribution: Indo-Pacific: southern Japan (sympatric with ***E. berryi*** Sasaki, 1929), East China Sea and the Philippines, south at least to Indonesia. Possibly Bay of Bengal, India (record based on females only) and Maldive Islands (Fig. 250).

Habitat and Biology: This neritic species has been reported from the stomach contents of lancet fishes, *Alepisaurus ferox*, captured in the Solomon Sea.

Interest to Fisheries: Harvested on a minor scale, primarily as trawl bycatch. Low economic value, but utilized locally.

Remarks: The taxonomic status of members of this genus is largely unresolved (Norman and Lu 1997).

Literature: Joubin (1902a), Raj and Kalyani (1971), Okutani *et al.* (1987), Okutani and Tsukada (1988), Okutani (1995), Norman and Lu (1997), Kubodera and Yamada (1998), Reid and Norman (1998).

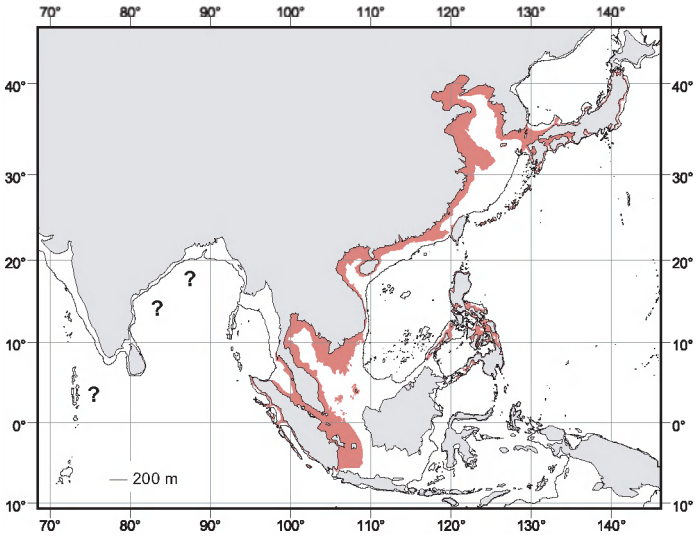


Fig. 250 ***Euprymna morsei***
Known distribution

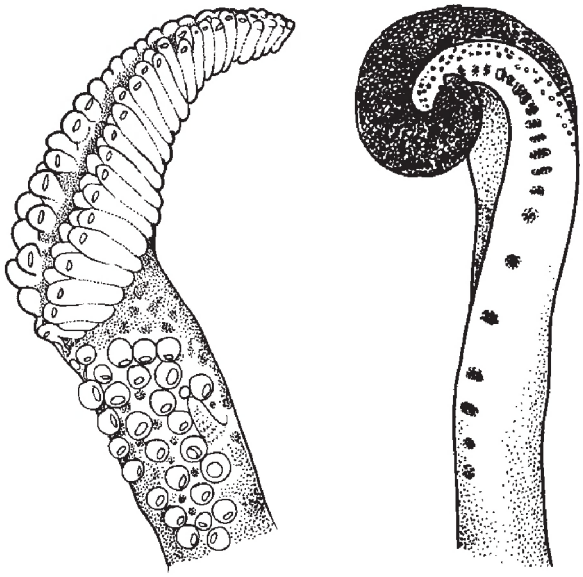
Euprymna tasmanica (Pfeffer, 1884) Fig. 251; Plate VI, 39–41

Sepiola tasmanica Pfeffer, 1884, *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 6 [type locality: Australia: Bass Strait].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Southern bobtail squid; **Fr** – Sépiole du Tasmanie; **Sp** – Globito de Tasmania.



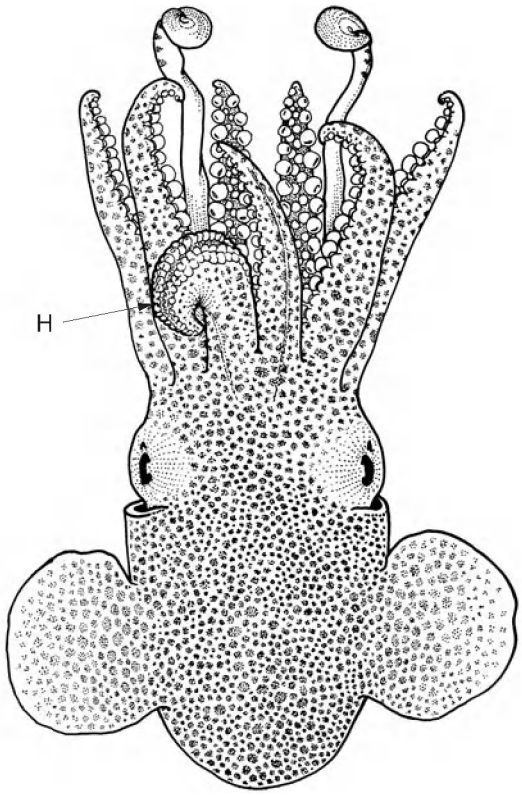


Fig. 251 *Euprymna tasmanica*

Diagnostic Features: Dorsal mantle fused to head. Fins wide, rounded, semicircular; short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial. **Dorsal and ventral rows of suckers on arms II to IV in males enlarged; ventral marginal rows of arms II and III with 1 to 3 greatly enlarged suckers basally** (8 to 11% mantle length); **dorsal and ventral marginal rows of arms II to IV with more than 10 enlarged suckers** (diameter 4 to 7% mantle length). Hectocotylus present, distal half of left dorsal arm modified: third and/or fourth proximal suckers in ventral row elongated into long papilla(e), each bearing a tiny sucker; base of hectocotylus with 29 to 38 normal suckers; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed to form 2 double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings (30 to 38 in dorsal rows, 29 to 38 in ventral rows). Tentacular club suckers (many hundreds) all of similar minute size. Saddle-shaped bacterial light organ inside mantle cavity.

Size: Up to 40 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: eastern and southeastern Australia, from Brisbane to Shark Bay, Western Australia (Fig. 252).

Habitat and Biology: This species lives in sandy and muddy areas, often in association with seagrass beds. It remains buried in sand during the day, and emerges at night to forage for small crustaceans and fishes. It can 'glue' sand grains to its dorsal body surface to aid in camouflage. Spawning occurs in spring and summer. Females lay pale orange eggs in loose clumps, usually at the base of seaweed or seagrass.

Interest to Fisheries: Undetermined, but the species is likely to be utilized on a local basis.

Remarks: The taxonomic status of members of this genus is largely unresolved.

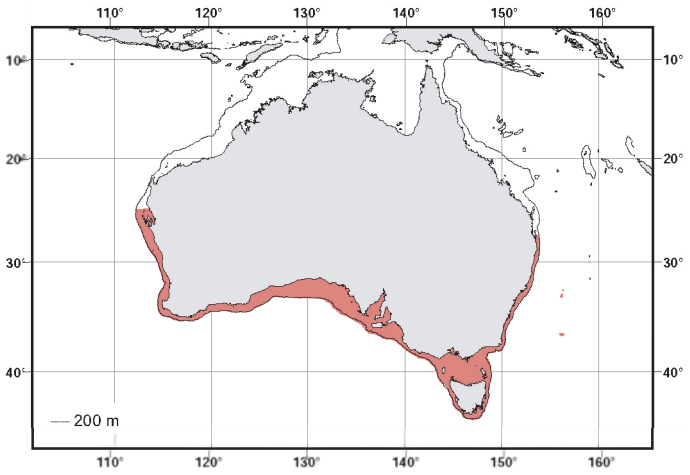


Fig. 252 *Euprymna tasmanica*
Known distribution

Literature: Norman and Lu (1997), Reid and Norman (1998).

Rondeletiola minor (Naef, 1912) **Fig. 253**

Sepietta minor Naef, 1912a, *Zoologischer Anzeiger*, 39(7): 267 [type locality: Tyrrhenian Sea].

Frequent Synonyms: *Sepietta minor* Naef, 1912.

Misidentifications: None.

FAO Names: En – Lentil bobtail squid; **Fr** – Sépiole bobie; **Sp** – Globito pequeño.

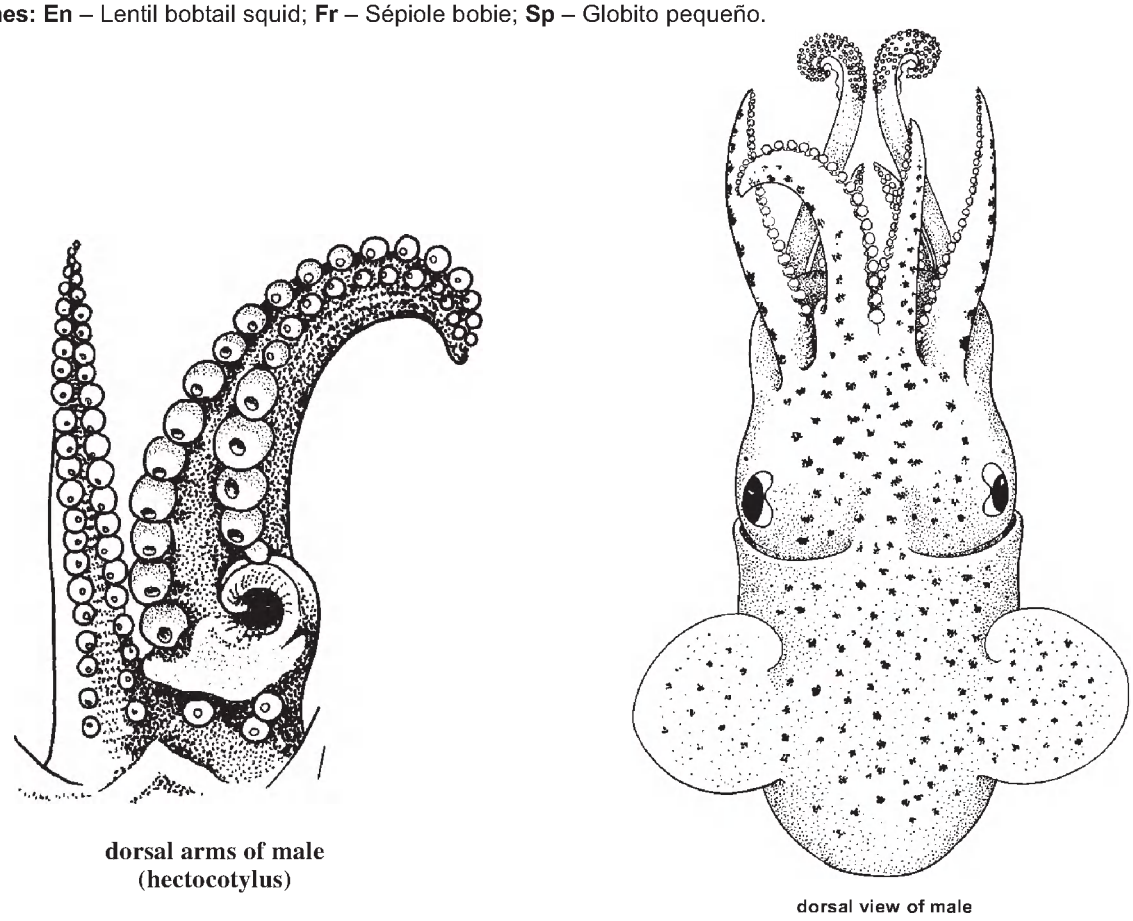


Fig. 253 ***Rondeletiola minor***

Diagnostic Features: Mantle bullet-shaped, **delicate consistency**. Fins small, bluntly pointed laterally rather than curved; short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial. Hectocotylus present; left dorsal arm modified: proximal end with fleshy pad formed from enlarged and fused sucker pedicels; **copulatory apparatus a large, swollen, transverse, hood-shaped horn with small accessory papilla**; 3 small suckers proximal to fleshy pad; proximal half of ventral row of suckers distal to copulatory apparatus with enlarged suckers; oral surface of modified region as for remaining arms, not wide, fleshy; suckers evenly spaced on modified portion of arm, rows not widely separated. Club with 16 suckers in transverse rows. Paired, roundish light organs present inside mantle cavity on ventral side of ink sac, deeply embedded in its tissue; closely connected to nidamental gland in female. **Base of right gill of female separated from median and posterior part of mantle cavity by a septum**.

Size: Up to 23 mm mantle length.

Geographical Distribution: Eastern Altantic and Mediterranean Sea: northwest of Spain, Portugal and the eastern, central and western Mediterranean Sea (including Ligurian Sea, northern and southern Tyrrhenian Sea, Strait of Sicily, Gulf of Taranto, Adriatic Sea, north Aegean Sea, Sea of Marmara and Levantine Sea) to the southeastern Atlantic Beguela Current off Namibia (Fig. 254).

Habitat and Biology: ***Rondeletiola minor*** lives on muddy bottoms. It is a sublittoral, demersal, or upper bathyal species, with depth a range between 76 and 496 m. In the Sea of Marmara (Mediterranean Sea) the species was found in brackish waters (salinity between 18 and 25‰), which indicates a high degree of tolerance to fresh water. Recent studies confirm a common reproductive pattern for the species in the western and eastern Mediterranean (Aegean Sea): an extended spawning period is likely to occur, since mature animals are found throughout the year. ***Rondeletiola minor*** may ascend to the surface during the reproductive period and has been collected at the surface at night using artificial light.

Interest to Fisheries: Caught throughout its range and consumed locally.

Local Names: ITALY: Seppiola minore, Cappuccetto.

Remarks: This species, often reported as rare in some areas of its distributional range, has recently proved to be fairly common in several areas of the western Mediterranean and in the Aegean Sea.

Literature: Naef (1923), Guerra (1982), Roper *et al.* (1984), Bello (1990b), Guerra (1992), Villanueva and Sánchez (1993), Bello (1995), Jereb and DiStefano (1995), Sartor and Belcari (1995), Villanueva (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995), D'Onghia *et al.* (1996), Salman and Katagan (1996), Jereb *et al.* (1997), Unsal *et al.* (1999).

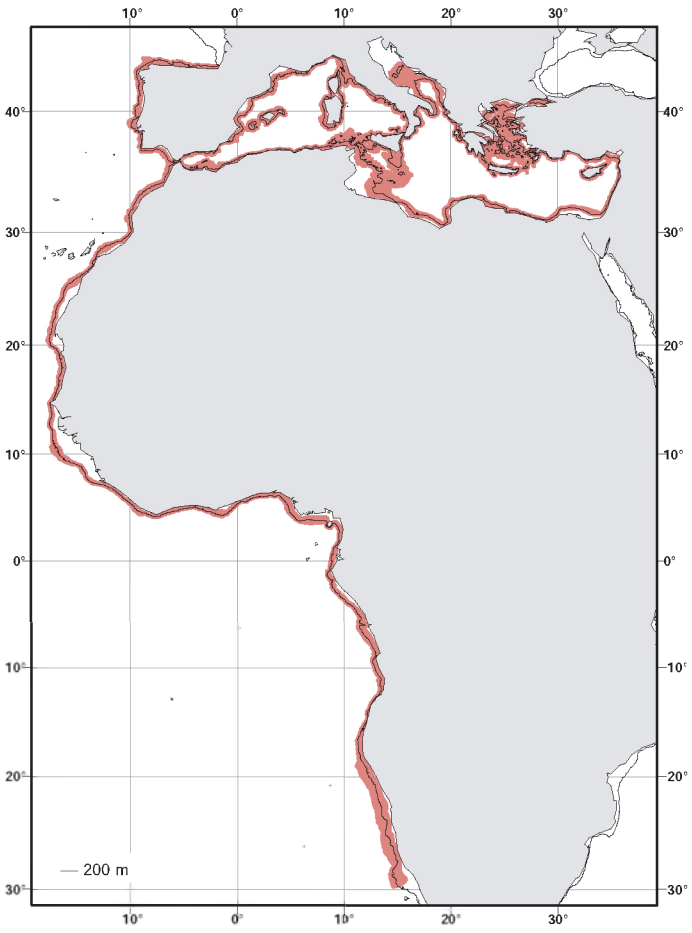


Fig. 254 ***Rondeletiola minor***
Known distribution

Sepiola trirostrata Voss, 1962 — Fig. 245

Sepiola trirostrata Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 172 [type locality: Philippines].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Knobby bobtail squid; **Fr** – Sépiole bosselée; **Sp** – Sepiola nudosa.

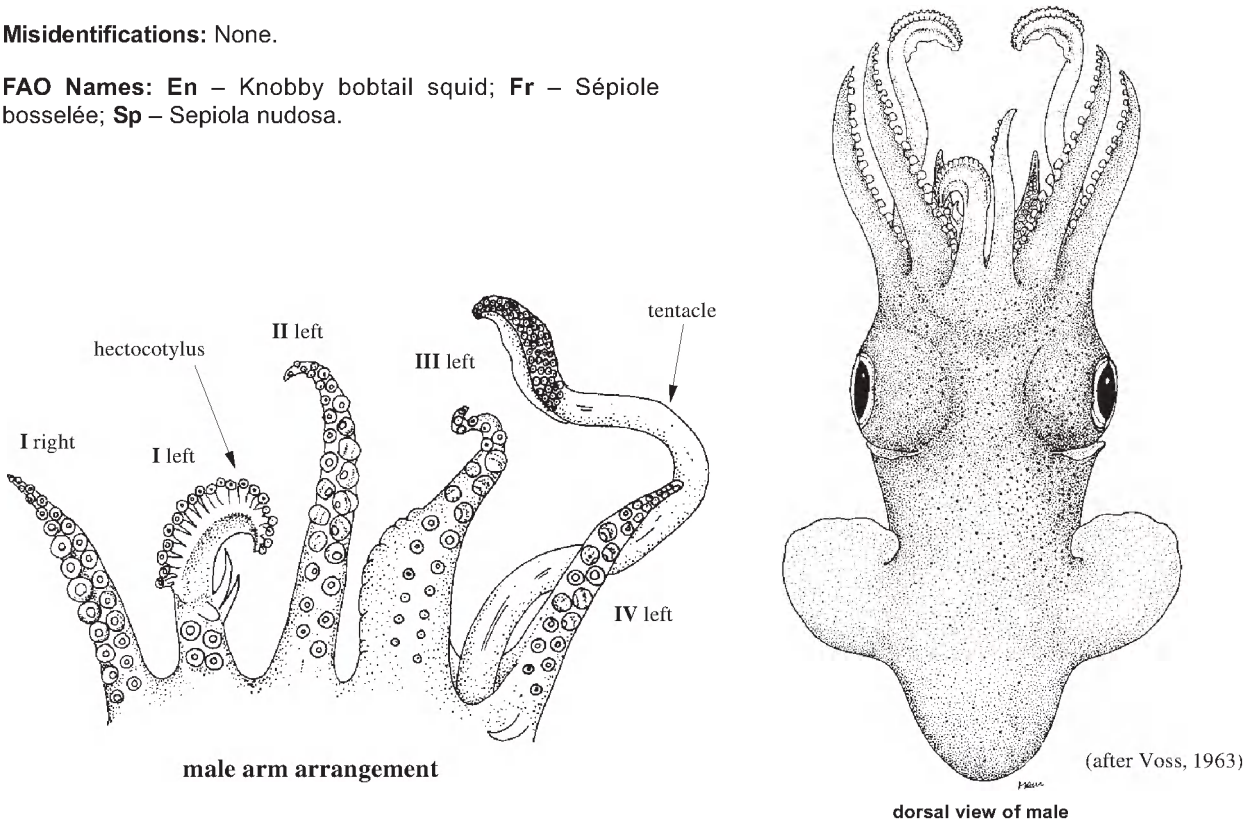


Fig. 245 *Sepiola trirostrata*

Diagnostic Features: Fins short, do not exceed length of mantle anteriorly or posteriorly. Arms III in both sexes stout and strongly curved inward, more obviously so in males. Suckers in ventral series of right arm I and arms II of males larger than dorsal suckers. Hectocotylus present, left dorsal arm modified: proximal end with **2 slender fleshy papillae** (anteriormost papilla longest) and dorsolateral to these a **blunt tongue-like lobe**, all formed from enlarged and elongate sucker pedicels; 2 rows of suckers on arm proximal to fleshy pad; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed to form 2 double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings. Club with 4 large suckers in transverse rows; suckers differ in size; dorsal marginal longitudinal series of suckers larger than those in ventral marginal series. Paired kidney-shaped light organs present inside mantle cavity on each side of ink sac. **Colour:** Mantle and head with many minute brown or black chromatophores; arms III deep pink, arms I to III each with single longitudinal row of large chromatophores, arms IV with double row of small chromatophores.

Size: Up to 12.5 mm mantle length.

Geographical Distribution: Indo-Pacific: Philippines, Singapore (Fig. 246).

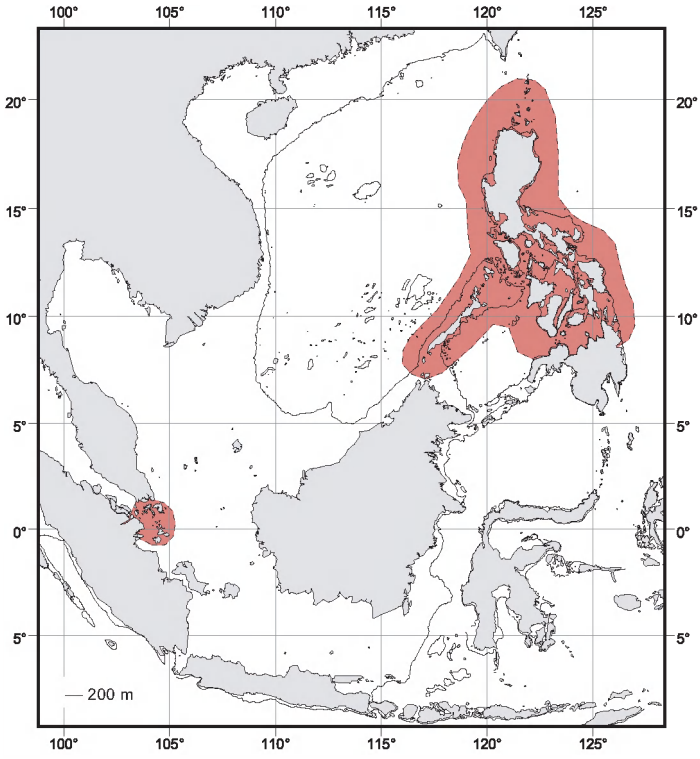


Fig. 246 *Sepiola trirostrata*
Known distribution

Interest to Fisheries: Presently undetermined.

Remarks: Differs from ***S. birostrata*** Sasaki, 1918 in the presence of the blunt, fleshy papilla, in addition to the 2 slender papillae on the hectocotylus. The slender papillae arise from a common mound-like base, while the third lobe arises separately. In this trait, ***S. trirostrata*** differs from those ***S. birostrata*** specimens that bear a third lobe on the hectocotylus.

Literature: Voss (1963).

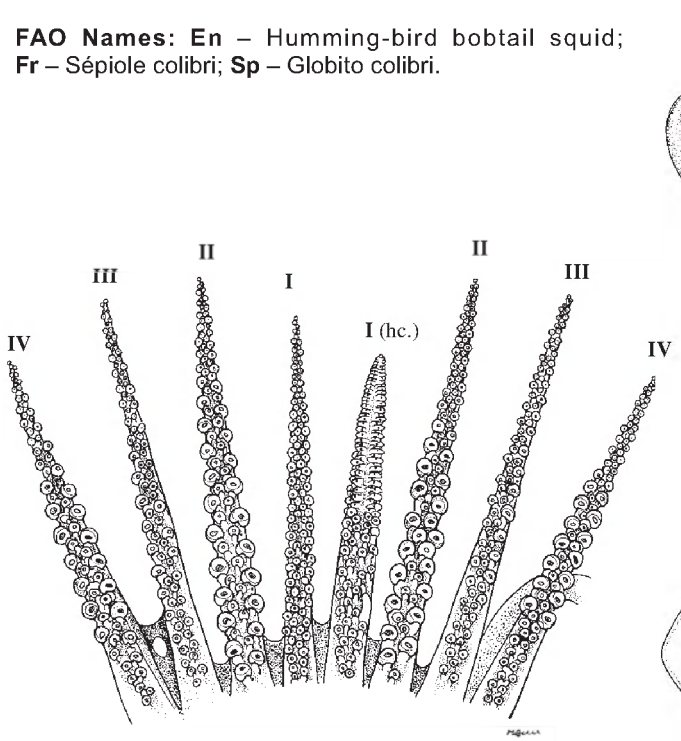
Euprymna berryi Sasaki, 1929 — Fig. 247

Euprymna berryi Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University*, 20(supplement): 143 [type locality: Japan, Honshu].

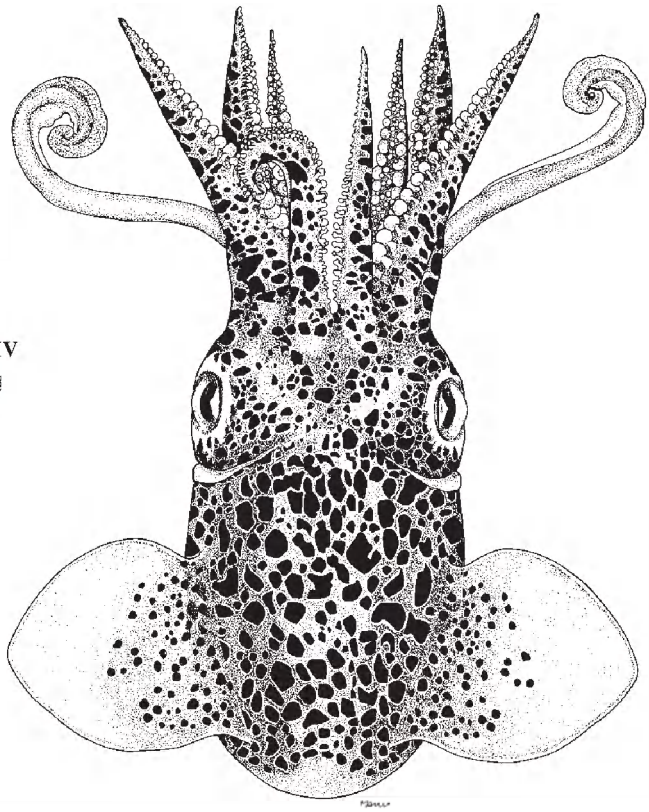
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Humming-bird bobtail squid; **Fr** – Sépiole colibri; **Sp** – Globito colibri.



arms of male
(oral view)



(after Okutani *et al.*, 1995)

dorsal view of male

Fig. 247 ***Euprymna berryi***

Diagnostic Features: Fins short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial. Male non-hectocotylized arm suckers enlarged on some arms: **arms II and IV with approximately 10 moderately enlarged suckers in dorsal and ventral rows from proximal second to fourth suckers; approximately 8 slightly enlarged suckers in ventral row of arm III from proximal fifth to eighth sucker.** Hectocotylus present; left dorsal arm modified: arm thick, short, and blunt; proximal end with 2 fleshy papillae formed from enlarged, or elongate sucker pedicels; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed forming 2 double rows of 70 to 80 columnar structures; suckers reduced with tiny, fleshy, slit-like openings. Marginal suckers on dorsal arms I are slightly larger than medial ones. Tentacular club suckers goblet-shaped. Swimming keel of club extends well beyond carpus.

Size: Males up to 30 mm mantle length; females up to 50 mm mantle length.

Geographical Distribution: Indo-Pacific: Along coasts of China, south to Hong Kong and Japan (but not in Hokkaido), Taiwan Province of China, possibly Andaman Islands and Sri Lanka (Fig. 248).

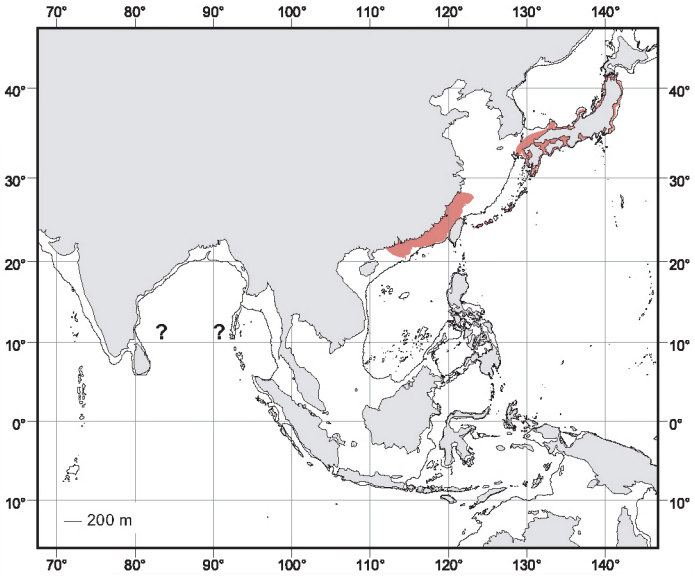


Fig. 248 ***Euprymna berryi***
Known distribution

Habitat and Biology: Upper sublittoral and pelagic in warm temperate waters; depth range to 107 m. This species has been reared successfully in aquaculture experiments. Females lay clumps of round, pale orange eggs.

Interest to Fisheries: Consumed locally in China and Taiwan Province of China, where this species is abundant and sustains local small fisheries; currently not commercially exploited in Hong Kong.

Local Names: CHINA: Leung yee jai; JAPAN: Niyori-mimi-ika.

Remarks: The taxonomic status of members of this genus is largely unresolved (Norman and Lu 1997). ***Euprymna berryi*** is sympatric with, and very similar to ***E. morsei*** Verrill (1881). Non-quantitative differences between the 2 species include: among 4 rows of arm suckers, only the ventral rows are enlarged in ***E. morsei*** (particularly from third to fourth suckers on arms II to IV), but both dorsal and ventral arms have enlarged suckers in ***E. berryi***; the club suckers are spherical, or cup-shaped in ***E. morsei***, but goblet-shaped in ***E. berryi***. The club suckers have an indistinct proximal border in ***E. berryi***, while those in ***E. morsei*** have distinct borders.

Literature: Roper *et al*. (1984), Okutani and Horita (1987), Okutani (1995), Norman and Lu (1997), Kubodera and Yamada (1998), Lu (1998b).

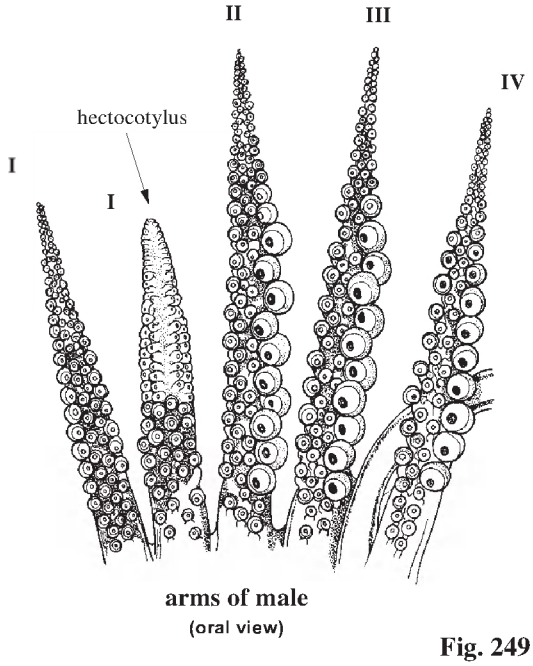
Euprymna morsei (Verrill, 1881) **Fig. 249**

Inioteuthis morsei Verrill, 1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 417 [type locality: Japan, Tokyo Bay].

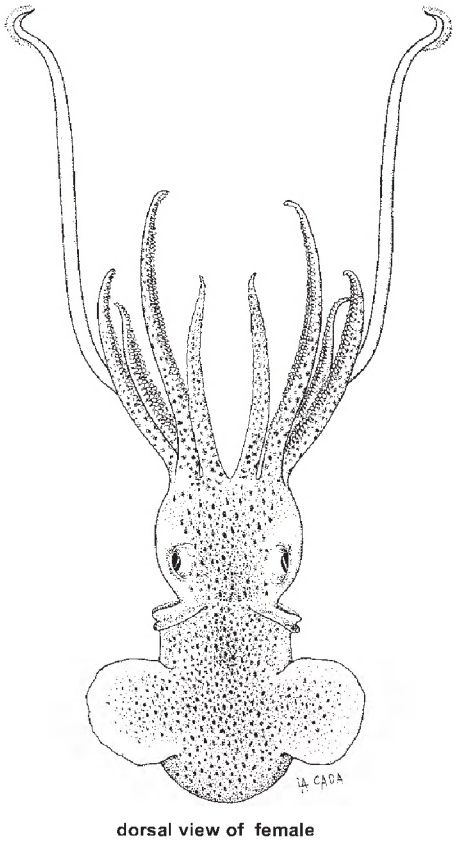
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Mimika bobtail squid; **Fr** – Sépiole mimika; **Sp** – Globito mimika.



arms of male
(oral view)



dorsal view of female

Fig. 249 ***Euprymna morsei***

Diagnostic Features: Mantle dome-shaped, plump. Dorsal mantle fused to head. Fins wide, rounded, semicircular; short, do not exceed length of mantle anteriorly or posteriorly; posteriorly with wide gap between fins; anterior origin posterior to mantle margin. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial. **Ventral rows of arms II to IV in males with enlarged suckers, approximately 10 on each arm from proximal third or fourth suckers.** Hectocotylus present; distal half of left dorsal arm modified: sucker pedicels enlarged and tightly packed to form 2 double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings; proximal end of arm with single nipple-like papilla. Marginal suckers arms I slightly larger than medial suckers. Tentacular-club suckers cup-shaped or spherical. Internal gladius absent. Paired saddle-shaped light organs present inside mantle cavity on ink sac. **Colour:** Iridescent gold to purple with large black chromatophores.

Size: Up to 40 mm mantle length.

Geographical Distribution: Indo-Pacific: southern Japan (sympatric with ***E. berryi*** Sasaki, 1929), East China Sea and the Philippines, south at least to Indonesia. Possibly Bay of Bengal, India (record based on females only) and Maldive Islands (Fig. 250).

Habitat and Biology: This neritic species has been reported from the stomach contents of lancet fishes, *Alepisaurus ferox*, captured in the Solomon Sea.

Interest to Fisheries: Harvested on a minor scale, primarily as trawl bycatch. Low economic value, but utilized locally.

Remarks: The taxonomic status of members of this genus is largely unresolved (Norman and Lu 1997).

Literature: Joubin (1902a), Raj and Kalyani (1971), Okutani *et al.* (1987), Okutani and Tsukada (1988), Okutani (1995), Norman and Lu (1997), Kubodera and Yamada (1998), Reid and Norman (1998).

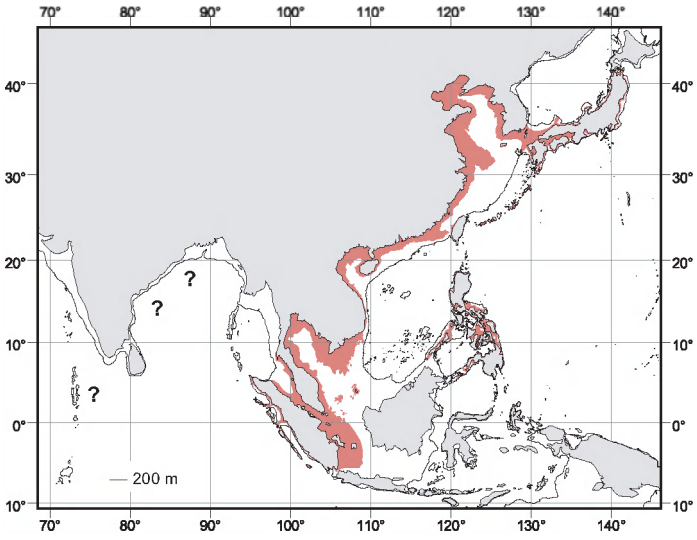


Fig. 250 ***Euprymna morsei***
Known distribution

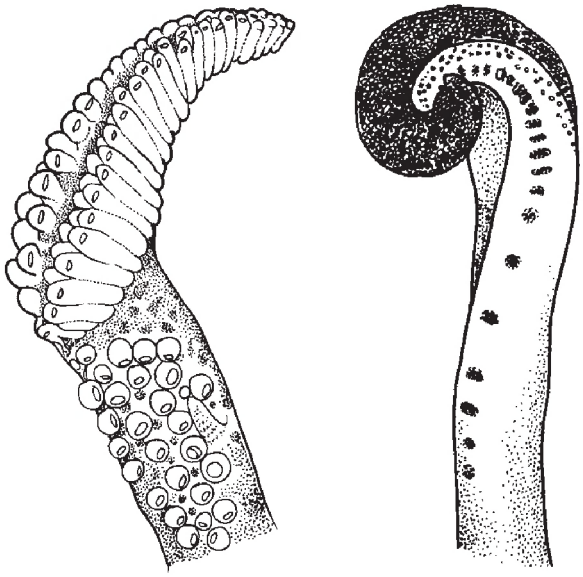
Euprymna tasmanica (Pfeffer, 1884) Fig. 251; Plate VI, 39–41

Sepiola tasmanica Pfeffer, 1884, *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 6 [type locality: Australia: Bass Strait].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Southern bobtail squid; **Fr** – Sépiole du Tasmanie; **Sp** – Globito de Tasmania.



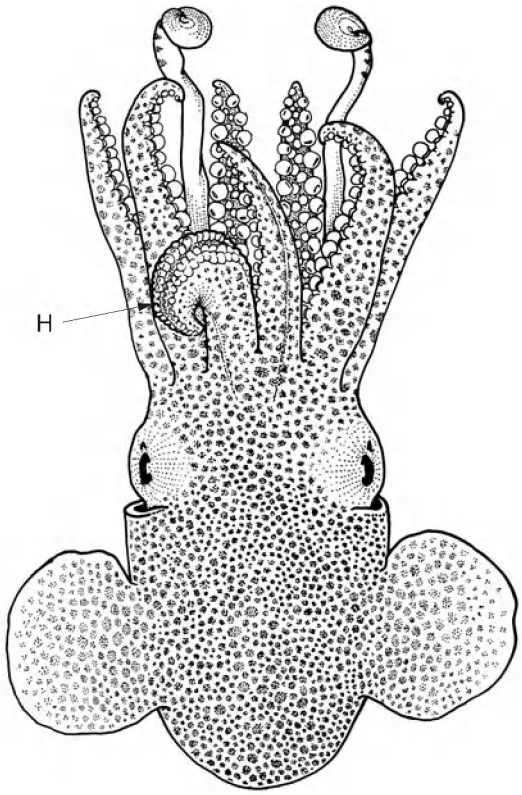


Fig. 251 *Euprymna tasmanica*

Diagnostic Features: Dorsal mantle fused to head. Fins wide, rounded, semicircular; short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial. **Dorsal and ventral rows of suckers on arms II to IV in males enlarged; ventral marginal rows of arms II and III with 1 to 3 greatly enlarged suckers basally** (8 to 11% mantle length); **dorsal and ventral marginal rows of arms II to IV with more than 10 enlarged suckers** (diameter 4 to 7% mantle length). Hectocotylus present, distal half of left dorsal arm modified: third and/or fourth proximal suckers in ventral row elongated into long papilla(e), each bearing a tiny sucker; base of hectocotylus with 29 to 38 normal suckers; distal end of hectocotylized arm with sucker pedicels enlarged and tightly packed to form 2 double rows of columnar structures; suckers reduced with tiny, fleshy, slit-like openings (30 to 38 in dorsal rows, 29 to 38 in ventral rows). Tentacular club suckers (many hundreds) all of similar minute size. Saddle-shaped bacterial light organ inside mantle cavity.

Size: Up to 40 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: eastern and southeastern Australia, from Brisbane to Shark Bay, Western Australia (Fig. 252).

Habitat and Biology: This species lives in sandy and muddy areas, often in association with seagrass beds. It remains buried in sand during the day, and emerges at night to forage for small crustaceans and fishes. It can 'glue' sand grains to its dorsal body surface to aid in camouflage. Spawning occurs in spring and summer. Females lay pale orange eggs in loose clumps, usually at the base of seaweed or seagrass.

Interest to Fisheries: Undetermined, but the species is likely to be utilized on a local basis.

Remarks: The taxonomic status of members of this genus is largely unresolved.

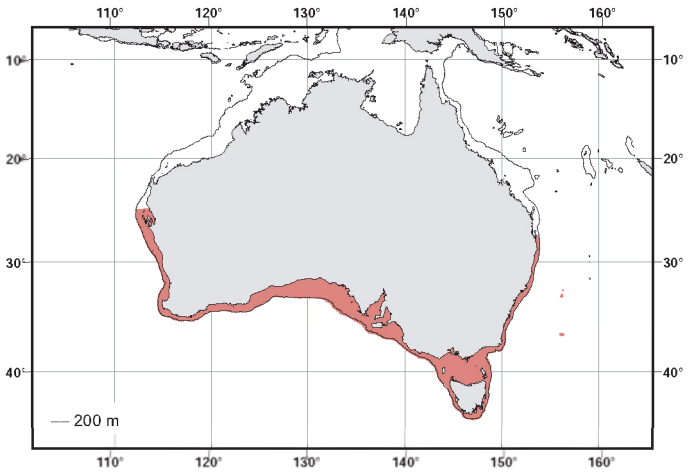


Fig. 252 *Euprymna tasmanica*
Known distribution

Literature: Norman and Lu (1997), Reid and Norman (1998).

Rondeletiola minor (Naef, 1912) **Fig. 253**

Sepietta minor Naef, 1912a, *Zoologischer Anzeiger*, 39(7): 267 [type locality: Tyrrhenian Sea].

Frequent Synonyms: *Sepietta minor* Naef, 1912.

Misidentifications: None.

FAO Names: En – Lentil bobtail squid; **Fr** – Sépiole bobie; **Sp** – Globito pequeño.

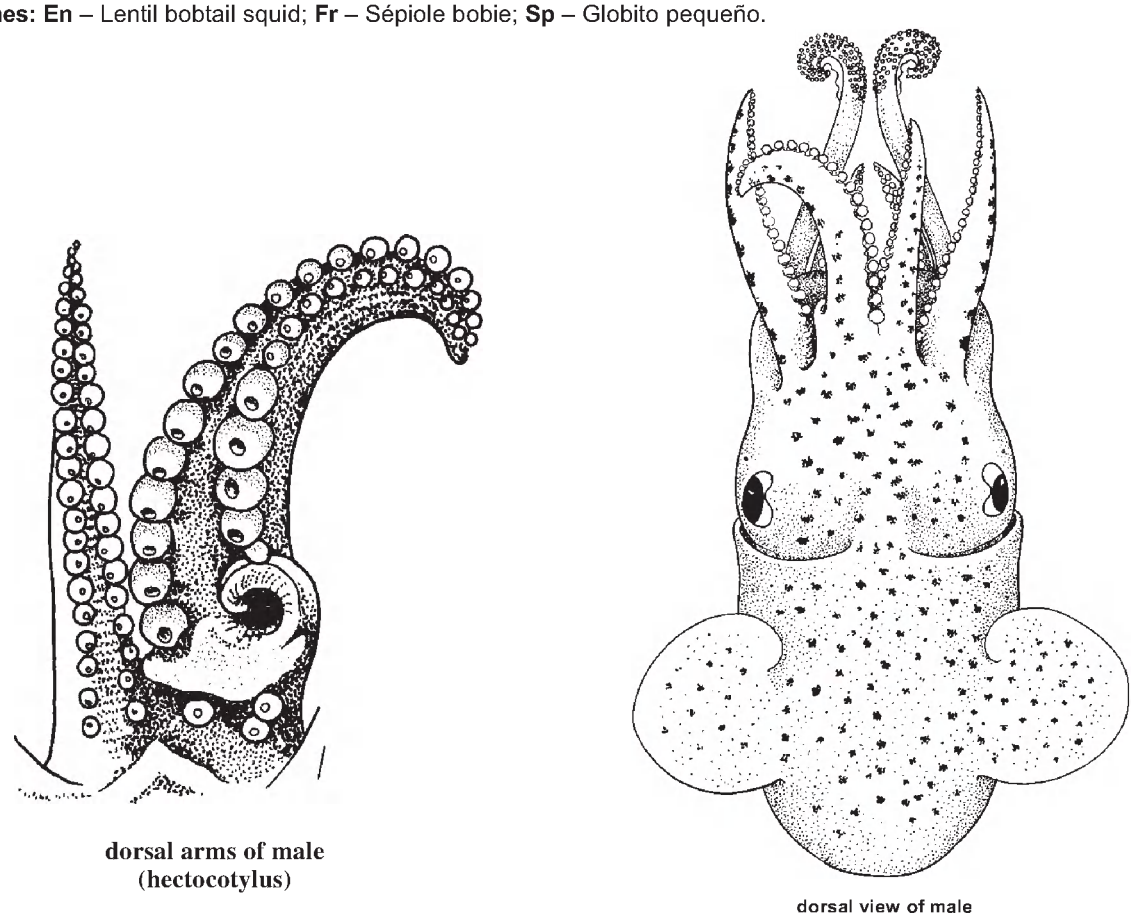


Fig. 253 ***Rondeletiola minor***

Diagnostic Features: Mantle bullet-shaped, **delicate consistency**. Fins small, bluntly pointed laterally rather than curved; short, do not exceed length of mantle anteriorly or posteriorly. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial. Hectocotylus present; left dorsal arm modified: proximal end with fleshy pad formed from enlarged and fused sucker pedicels; **copulatory apparatus a large, swollen, transverse, hood-shaped horn with small accessory papilla**; 3 small suckers proximal to fleshy pad; proximal half of ventral row of suckers distal to copulatory apparatus with enlarged suckers; oral surface of modified region as for remaining arms, not wide, fleshy; suckers evenly spaced on modified portion of arm, rows not widely separated. Club with 16 suckers in transverse rows. Paired, roundish light organs present inside mantle cavity on ventral side of ink sac, deeply embedded in its tissue; closely connected to nidamental gland in female. **Base of right gill of female separated from median and posterior part of mantle cavity by a septum**.

Size: Up to 23 mm mantle length.

Geographical Distribution: Eastern Altantic and Mediterranean Sea: northwest of Spain, Portugal and the eastern, central and western Mediterranean Sea (including Ligurian Sea, northern and southern Tyrrhenian Sea, Strait of Sicily, Gulf of Taranto, Adriatic Sea, north Aegean Sea, Sea of Marmara and Levantine Sea) to the southeastern Atlantic Beguela Current off Namibia (Fig. 254).

Habitat and Biology: ***Rondeletiola minor*** lives on muddy bottoms. It is a sublittoral, demersal, or upper bathyal species, with depth a range between 76 and 496 m. In the Sea of Marmara (Mediterranean Sea) the species was found in brackish waters (salinity between 18 and 25‰), which indicates a high degree of tolerance to fresh water. Recent studies confirm a common reproductive pattern for the species in the western and eastern Mediterranean (Aegean Sea): an extended spawning period is likely to occur, since mature animals are found throughout the year. ***Rondeletiola minor*** may ascend to the surface during the reproductive period and has been collected at the surface at night using artificial light.

Interest to Fisheries: Caught throughout its range and consumed locally.

Local Names: ITALY: Seppiola minore, Cappuccetto.

Remarks: This species, often reported as rare in some areas of its distributional range, has recently proved to be fairly common in several areas of the western Mediterranean and in the Aegean Sea.

Literature: Naef (1923), Guerra (1982), Roper *et al.* (1984), Bello (1990b), Guerra (1992), Villanueva and Sánchez (1993), Bello (1995), Jereb and DiStefano (1995), Sartor and Belcari (1995), Villanueva (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995), D'Onghia *et al.* (1996), Salman and Katagan (1996), Jereb *et al.* (1997), Unsal *et al.* (1999).

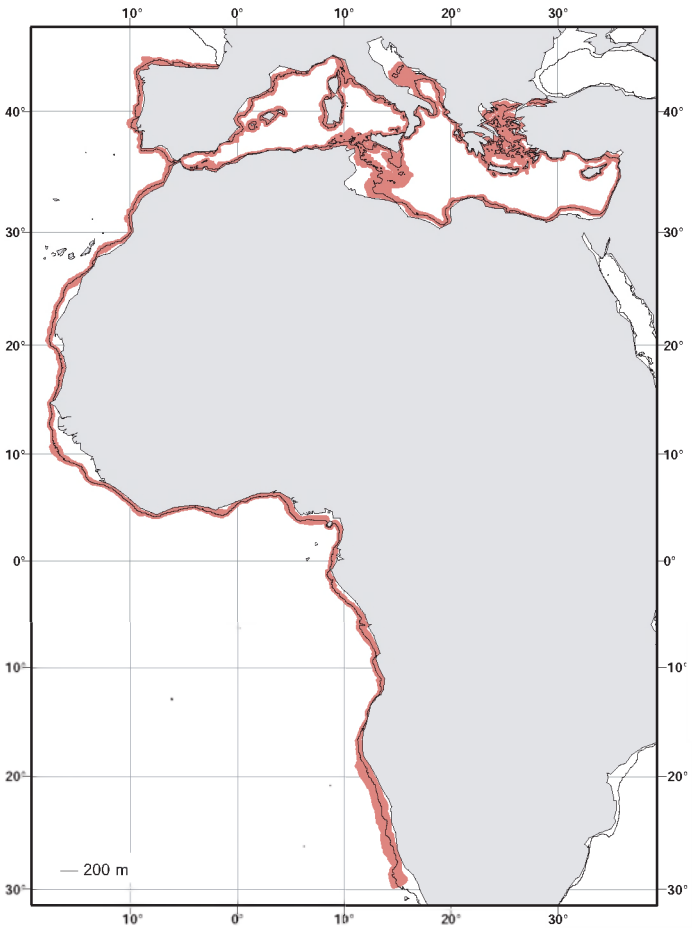


Fig. 254 ***Rondeletiola minor***
Known distribution

Sepietta neglecta Naef, 1916

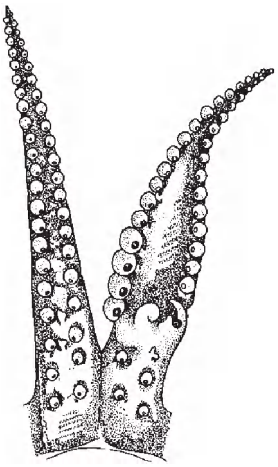
Fig. 255

Sepietta neglecta Naef, 1916, *Pubblicazioni della Stazione Zoologica di Napoli*, 1: 9 [type locality: Tyrrhenian Sea].

Frequent Synonyms: None.

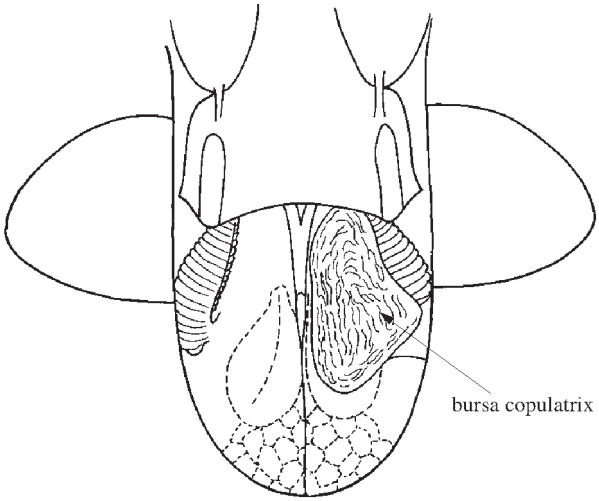
Misidentifications: None.

FAO Names: En – Elegant bobtail squid; **Fr** – Sépiole élégante; **Sp** – Sepieta elegante.



(after Naef, 1923)

dorsal arms of male (hectocotylus)



mantle cavity of female

Fig. 255 ***Sepietta neglecta***

Diagnostic Features: Fins rounded, **bluntly pointed laterally** rather than curved; short, do not exceed length of mantle anteriorly or posteriorly. Hectocotylus present, left dorsal arm modified: proximal end with fleshy pad formed from enlarged and/or fused sucker pedicels; copulatory apparatus a dome-shaped lobe medially and short, pointed, horn with smaller papilla between these; horn of copulatory apparatus slightly recurved, but does not form a small hole; base of hectocotylus proximal to fleshy pad with **4 normal suckers** (not modified); dorsal row of suckers distal to copulatory apparatus with first **3 or 4 suckers markedly enlarged**; arm broad, spoon-like. Tentacles very thin, delicate. **Club with 16 uniform-sized suckers in transverse rows**. Female bursa copulatrix large (extends posteriorly beyond gill insertion). Light organs absent.

Size: Up to 33 mm mantle length.

Geographical Distribution: Northeastern Atlantic and Mediterranean Sea: southern coast of Norway and Orkney Islands to Morocco; eastern and western Mediterranean Sea (Ligurian Sea, Strait of Sicily, Adriatic Sea, north Aegan Sea, Sea of Marmara and Levantine Sea) (Fig. 256).

Habitat and Biology: ***Sepietta neglecta*** lives preferentially on muddy substrates at depths ranging between 25 and 475 m. It is often associated with ***Rossia macrosoma*** and ***Sepietta oweniana***. It spawns continuously throughout the year.

Interest to Fisheries: Even though less common, ***S. neglecta*** is caught along with other species of the genus and is sold and consumed locally.

Remarks: This species closely resembles ***S. oweniana*** (Orbigny, 1839–1841) and it can be difficult to distinguish females of the 2 species under a certain size (i.e. ***S. oweniana*** is larger). This is particularly true when the tentacle clubs are damaged or lost during fisheries operations. The clubs differ between the 2 species: the club is shorter, more delicate and bears smaller suckers in ***S. neglecta***, than in ***S. oweniana***. Males are easily identified by the structure of the hectocotylus.

Literature: Naef (1923), Boletzky *et al.* (1971), Guescini and Manfrin (1986), Orsi Relini and Bertuletti (1989), Bello (1990b), Guerra (1992), Bello (1995), Jereb and Di Stefano (1995), Volpi *et al.* (1995), Jereb *et al.* (1997), Lefkaditou and Kaspiris (1998).

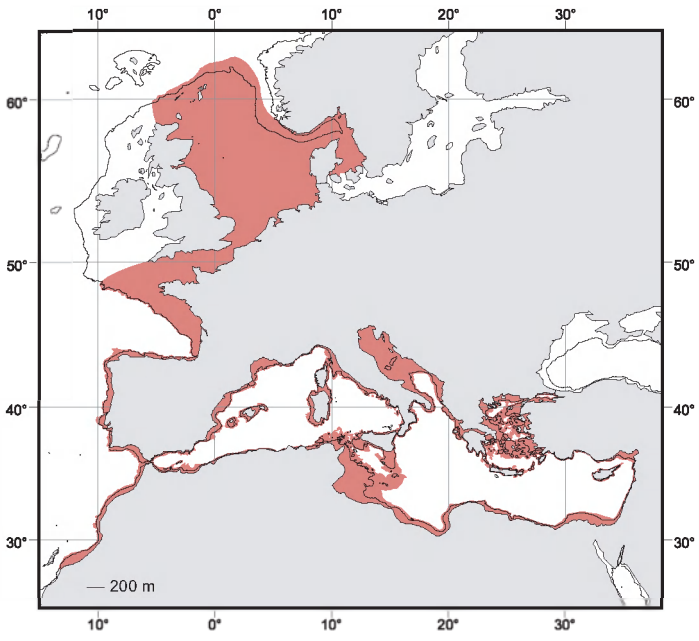


Fig. 256 ***Sepietta neglecta***
Known distribution

Sepietta obscura Naef, 1916

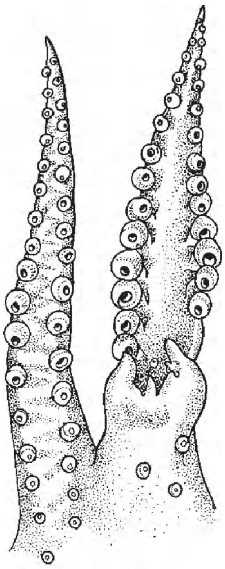
Fig. 257

Sepietta obscura Naef, 1916, *Pubblicazioni della Stazione Zoologica di Napoli*, 1: 4 [type locality: Gulf of Naples].

Frequent Synonyms: None.

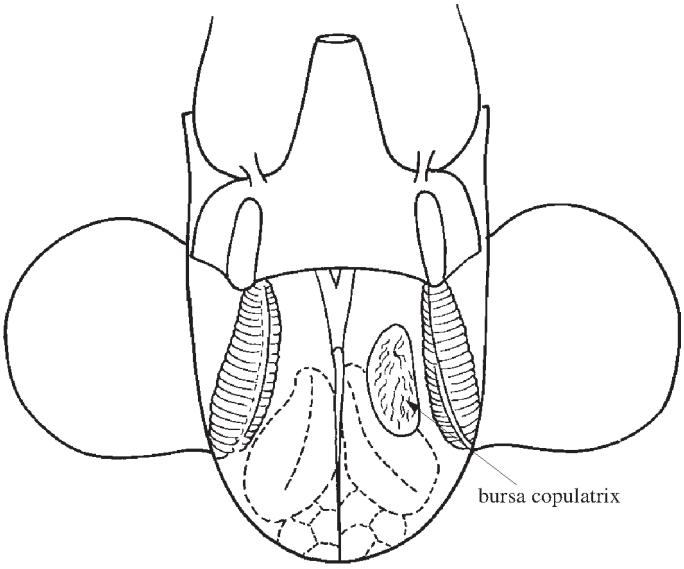
Misidentifications: *Sepietta oweniana* (Orbigny, 1839–1841); *Sepiola rondeleti* Leach, 1834.

FAO Names: En – Mysterious bobtail squid; **Fr** – Sépiole mystérieuse; **Sp** – Sepieta misteriosa.



(after Naef, 1923)

hectocotylus



mantle cavity of female

Fig. 257 ***Sepietta obscura***

Diagnostic Features: Fins small, short, almost circular, margin broadly rounded. Tentacles relatively robust; club with 12 suckers in transverse rows, dorsalmost suckers markedly enlarged. Arms II and III with 3 to 5 normal suckers proximally, followed by 2 larger suckers distally, then smaller ones continuously decreasing in size towards distal tip of the arm. Hectocotylus present, left dorsal arm modified: 3 normal suckers at base of the arm, followed distally by the copulatory apparatus: apparatus consists of a transverse 'crest' with four elevations, differing in development and outline, **the outer one usually more prominent, forming a separate, inward curved lobe**, the inner one with a simple edge. Distal to the copulatory apparatus, the first 2 suckers of the dorsal row are markedly enlarged, followed distally by smaller suckers decreasing in size; stalks of first suckers of ventral rows are elongate and often connected with each other. Distal part of the arm widened and spoon-shaped. Bursa copulatrix small, not extending beyond gill insertion. **Colour:** Reddish to dark brown.

Size: Males up to 19 mm mantle length; females up to 30 mm mantle length.

Geographical Distribution: Mediterranean Sea, including Ligurian Sea, Tyrrhenian Sea, Strait of Sicily, Adriatic Sea, northern Aegean Sea and Levantine Sea. Northeastern Atlantic (off Portugal) (Fig. 258).

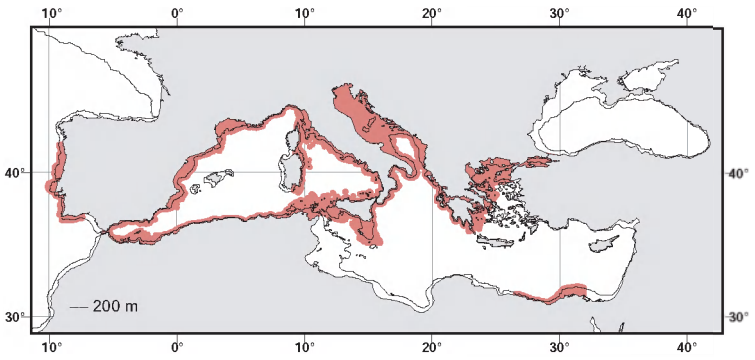


Fig. 258 ***Sepietta obscura***
Known distribution

Habitat and Biology: ***Sepietta obscura*** lives preferentially on sandy and muddy bottoms, often colonized by *Posidonia oceanica* in coastal areas. Its depth range is 27 to 376 m. It is often associated with ***Sepiola affinis*** Naef, 1912, and both species seem to have gregarious habits. A benthic species, ***Sepietta obscura*** has, however, been captured by pelagic nets, confirming its capacity to leave the bottom and undergo significant vertical migrations. The smallest mature individuals measure 12 mm mantle length. The spawning season extends at least from spring to autumn in the Mediterranean. Females in aquaria were observed to spawn intermittently over a period of 2 weeks, and the animals died afterwards. The eggs are relatively large (3.7–4.5 mm diameter) but young hatchlings measure about 2 mm mantle length.

Interest to Fisheries: No statistics are available, but the species is frequently captured as a bycatch of trawl and purse seine fisheries, and can be a relatively abundant component of the bobtails marketed locally.

Local Names: ITALY: Seppiola misteriosa.

Remarks: Nesis (1987), in his world review, considered ***Sepietta obscura*** a junior name for ***S. petersi*** (Steenstrup, 1887). However, Naef did not mention Steenstrup's work in his original description of ***S. obscura*** (Naef, 1916). This is very unusual considering Naef's accuracy and his otherwise detailed and very numerous references to previous workers. It is possible that he may have overlooked the description of ***S. petersi*** when determining the status of his supposed new ***Sepietta*** species. However, considering the current need for a revision of this group, including a proper (re)description of ***Sepietta petersi***, ***S. obscura*** is here retained as the valid name for the species. Long considered a Mediterranean endemic, recent records of 2 specimens of ***Sepietta obscura*** from the waters off Portugal extend the distributional range of this small bobtail squid.

Literature: Naef (1923), Boletzky *et al.* (1971), Orsi Relini and Bertuletti (1989), Guerra (1992), Bello and Biagi (1995), Gabel Deickert (1995), Wurtz *et al.* (1995), Pereira (1996), Jereb *et al.* (1997), Salman *et al.* (2002).

Sepietta oweniana (Orbigny, 1839–1841) **Fig. 259**

Sepiola oweniana Orbigny, 1839–1841 (*in* Férussac and d'Orbigny, 1834–1848), *Histoire Naturelle Générale et Particulière Céphalopodes Acétabuliferes Vivants et Fossiles*, pl. 3 [type locality: Tyrrhenian Sea (uncertain)].

Frequent Synonyms: *Sepiola oweniana* d'Orbigny, 1840.

Misidentifications: None.

FAO Names: En – Common bobtail squid; **Fr** – Sépiole commune; **Sp** – Sepieta común.

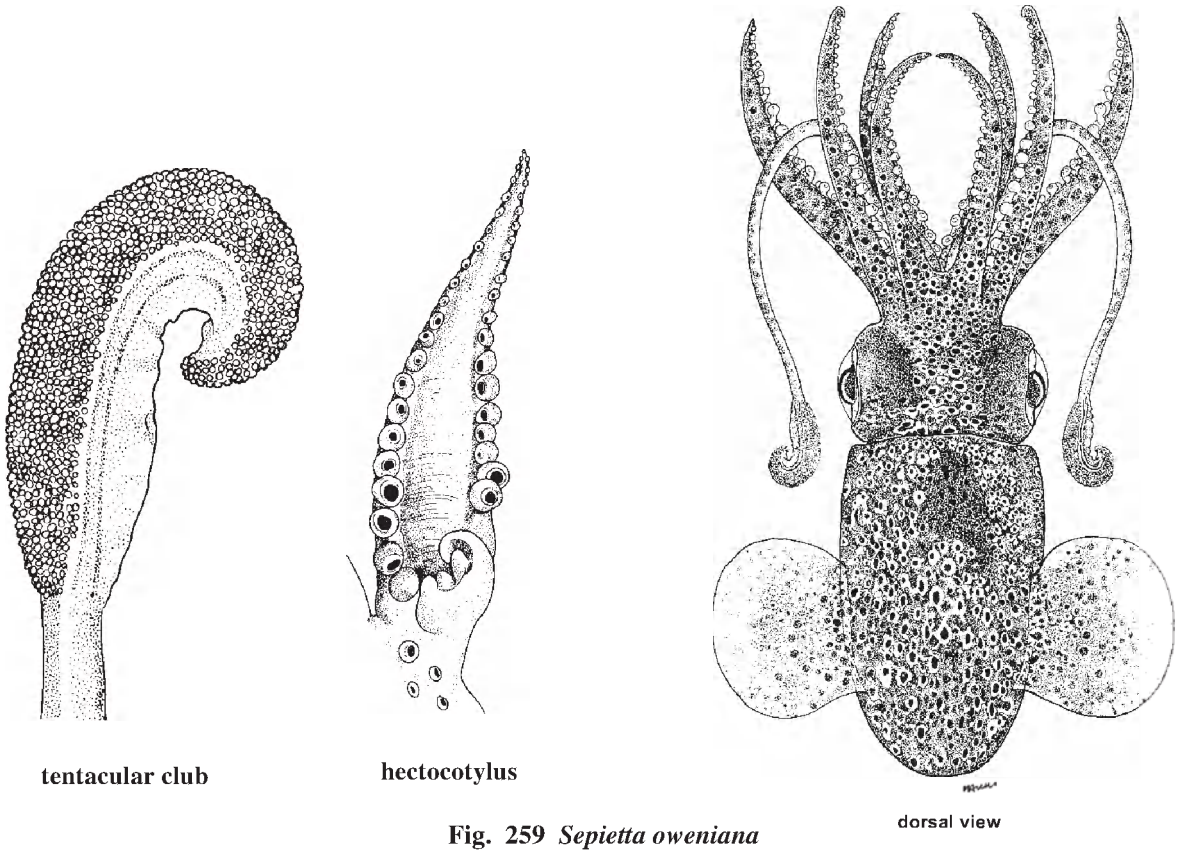


Fig. 259 ***Sepietta oweniana***

Diagnostic Features: Mantle dome-shaped; posteriorly more rounded in females. Fins wide; rounded, semicircular; **with pronounced anterior lobes, or 'earlets'**; short, do not exceed length of mantle anteriorly or posteriorly; attached slightly obliquely at mantle midline. Arm suckers biserial. Proximal end of arms I fused in males. Hectocotylus present; left dorsal arm modified: proximal end with fleshy pad formed from enlarged and fused sucker pedicels; copulatory apparatus a fleshy transverse swelling with long, hook-like inwardly curved horn, deep cleft medially, flask-like rugose bulb, and swelling at dorsal edge; 2 rows of normal suckers on arm proximal to fleshy pad (usually 2 rows, sometimes 3, 5 or 6 suckers); **first 2 or 3 suckers in dorsal row distal to copulatory apparatus greatly enlarged, followed by 2 to 4 smaller suckers, then 2 enlarged**, then remaining suckers decrease in size to distal tip of arm; ventral rows with moderately enlarged suckers; oral surface of modified region broad; concave. **Club long, well developed, with 32 suckers in transverse rows; all suckers of similar minute size, giving velvety appearance. Female bursa copulatrix large (extends posteriorly beyond gill insertion).** Light organs absent.

Size: Up to 50 mm mantle length in the North Sea; males up to 35 mm, females up to 40 mm mantle length in the Mediterranean Sea.

Geographical Distribution: Eastern Atlantic and Mediterranean Sea: from Norway to the Faeroe Islands; Morocco and Madeira Islands south to Mauritania; Mediterranean Sea, including Ligurian Sea, Strait of Sicily, Aegean Sea, Adriatic Sea, Sea of Marmara and Levantine Sea. Indian Ocean: Visakhapatam (single record only) (Fig. 260).

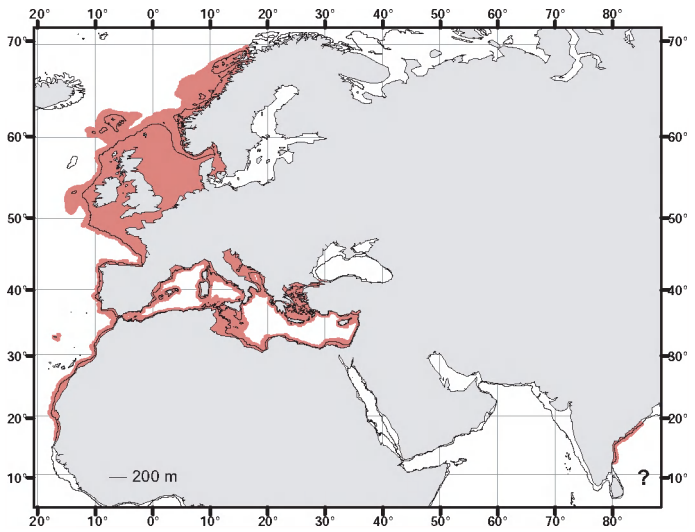


Fig. 260 ***Sepietta oweniana***
Known distribution

Habitat and Biology: ***Sepietta oweniana*** is an epipelagic–mesopelagic species, occurring within a wide depth range, i.e. from close to the surface (8 m) down to over 1 000 m. In the North Atlantic it is most common between 50 and 300 m and in the Mediterranean between 100 to 200 and 400 m. It prefers soft, muddy substrates throughout its distributional range, and it is often found on shrimp fishing grounds. Tolerance to salinity variations seems lower than that observed in other bobtail squids and ***S. oweniana*** has never been found in brackish waters. Seasonal movements, related to reproduction, and vertical movements, mostly linked to trophic relationships, have been reported for this species, both in the North Atlantic and in the Mediterranean. In the Mediterranean Sea, mature animals are found throughout the year, suggesting an almost continuous spawning season. Peaks in reproductive activity, however, are reported for several different areas of the Mediterranean. In the western Mediterranean, for example, onshore migrations of large individuals occur in late winter to early spring, followed by spawning in spring and early summer. In the Tyrrhenian Sea, summer spawning peaks have been observed, while in the Aegean Sea, peaks of spawning occur in April to May and October to November. Mating takes place head-to-head and spermatophores are placed in the female's bursa copulatrix. Spawning usually occurs in relatively shallow coastal waters, though records of egg masses in deeper waters (i.e. down to 200 m) do exist. Several subsequent laying events have been observed in aquaria. The eggs, spherical to lemon-shaped and greyish white in colour, are deposited on various solid substrates, both living and dead, with an interesting preference for ascidians (*Microcosmus*). The duration of egg development depends upon the water temperature: at 20°C they take about 30 days to hatch, while at 10°C this time range extends to about 2 months. Growth after hatching, however, seems relatively independent of water temperature, and quite rapid. Studies in the laboratory indicate that animals grow and mature within 6 months following hatching. The whole life cycle is, therefore, rather short and may range between 6 and 9 months, depending mainly on the time of embryonic development. Field data indicates that the mantle length at 50% maturity varies between the Atlantic and the Mediterranean female populations, and is greater in the Atlantic (i.e. 33 mm versus less than, or equal to, 30 mm). Within the Mediterranean populations, females from the eastern and central basin are mature at a slightly smaller size compared with those from the western basin (i.e. 28 and 26 mm respectively, versus 30 mm). Similar differences were not apparent in males, where the size at 50% maturity varies between 20 and 24 mm both in the Atlantic and in the Mediterranean. ***Sepietta oweniana*** has been cultured successfully in aquaria. Juveniles were fed on mysids (*Praunus flexuosus* and *P. inermis*), amphipods (*Ericthonius*) and large copepods. Adults fed on *Pranus flexuosus* and the shrimps *Palaemon elegans*, *Thoralus cranchii* and *Crangon crangon*. Animals in wild populations feed mainly upon crustaceans; a specific preference for the euphasiid *Maganyctiphanes norvegica* in north Atlantic waters and the decapod *Pasiphaea sivado* in the northern Tyrrhenian Sea has been observed, supporting hypothesized trophic migrations of ***S. oweniana*** in response to prey abundance and distribution. Feeding occurs primarily from dusk to dawn, with adult animals spending the day buried in the bottom substrate. ***Sepietta oweniana*** is preyed upon by several demersal fish and occasionally by cetaceans.

Interest to Fisheries: This is one of the most abundant bobtail squids throughout its distributional range and one of the most abundant cephalopods caught in some Mediterranean areas. It represents an important bycatch of many trawl fisheries, both multispecific and shrimp targeting. Specific statistics are not available, but the species is commonly sold on Mediterranean markets and it is valued as a delicacy in some areas (e.g. in southern Sicily). In the Mediterranean, catches are generally most abundant in summer and a marked seasonality has been observed in some areas (e.g. the northern Tyrrhenian Sea).

Local names: ITALY: Seppiola comune, Cappuccetto.

Remarks: Six specimens were recorded from Visakhapatam in the Indian Ocean (off the northeastern Indian coasts, in the Bay of Bengal) by Mohan and Rao in 1978. However, no subsequent records exist for the area, or in other parts of the Indian Ocean.

Literature: Joubin (1902a), Naef (1912b), Naef (1923), Mangold and Froesh (1977), Mohan and Rao (1978), Bergstrom and Summers (1983), Bergstrom (1985), Roper *et al.* (1984), Orsi Relini and Massi (1988), Orsi Relini and Bertuletti (1989), Guerra (1992), Bello (1995), Blanco *et al.* (1995) Jereb and Di Stefano (1995), Santos *et al.* (1995), Volpi *et al.* (1995), D'Onghia *et al.* (1996), Bello (1997), Jereb *et al.* (1997), Salman (1998), Sartor *et al.* (1998), Belcari and Sartor (1999a).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Sepiola aurantiaca Jatta, 1896

Sepiola aurantiaca Jatta, 1896, *Fauna und Flora des Golfes von Neapel*, 23: 130 [type locality: Tyrrhenian Sea.]

Size: Up to 20 mm mantle length (both sexes).

Geographical Distribution: Northeastern Atlantic, from southern Norway, and western Mediterranean Sea. Outer shelf and upper bathyal. Depth range possibly from 200 to 400 m. Rare.

Literature: Naef (1912b), Naef (1923), Guerra (1992), Bello (1995).

Sepiola knudseni Adam, 1984

Sepiola knudseni Adam, 1984, *Atlantide Report*, 13: 157 [type locality: Atlantic Ocean: 06°17'N 03°27'E].

Size: Males up to 8.5 mm mantle length; females up to 18 mm mantle length.

Geographical Distribution: Eastern Atlantic: northwest and west Africa, from the Canary Islands to the Gulf of Guinea. Inner continental shelf. Depth range from 32 to 90 m.

Literature: Adam (1984).

Sepiola pfefferi Grimpe, 1921

Sepiola pfefferi Grimpe, 1921, *Zoologischer Anzeiger*, 53(1–2): 4 [type locality: northeastern Atlantic: 53°53'N 00°32'E].

Size: Males up to 12 mm mantle length; females up to 13 mm mantle length.

Geographical Distribution: Northeastern Atlantic: Faeroe Islands and southern Norway to Brittany, France. Continental shelf. Depth range unknown.

Literature: Grimpe (1921).

Sepiola rossiaeformis Pfeffer, 1884

Sepiola rossiaeformis Pfeffer, 1884, *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 8 [type locality: Java].

Size: Type 6.0 mm mantle length.

Geographical Distribution: Indo-Pacific: unknown.

Literature: Pfeffer (1884).

Sepiola steenstrupiana Levy, 1912

Sepiola steenstrupiana Levy, 1912, *Archives de Zoologie Experimentale et Générale, (series 5)9, Notes et Revue*, 3: LVI [type locality : "Villafranca".].

Size: Up to 30 mm mantle length.

Geographical Distribution: Mediterranean Sea: including central Tyrrhenian Sea, Adriatic Sea, Aegean Sea and Levantine Sea. Red Sea, Gulf of Aden. Indian Ocean: Somalia.

Literature: Naef (1923), Guerra (1992), Bello (1995), Rocha *et al*. (1998).

Euprymna albatrossae Voss, 1962

Euprymna albatrossae Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 171 [type locality: Philippines].

Size: Up to 24 mm mantle length.

Geographical Distribution: Western Pacific: Philippines. Depth range unknown. Types collected using nightlight.

Literature: Voss (1963).

Euprymna hoylei Adam, 1986

Euprymna hoylei Adam, 1986, *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 56: 133 [type locality: Sulu Archipelago].

Geographical Distribution: Tropical Indo-Pacific: western tropical Pacific and northwestern Australia.

Literature: Norman and Lu (1997).

Euprymna hyllebergi Nateewathana, 1997

Euprymna hyllebergi Nateewathana, 1997, *Phuket Marine Biological Center Special Publication*, 17(2): 466 [type locality: Thailand: Andaman Sea, Trang Province, Kantang Fish Landing].

Size: Up to 35 mm mantle length.

Geographical Distribution: Eastern Indian Ocean: Thailand, Andaman Sea. Depth to 74 m.

Literature: Nateewathana (1997).

Euprymna penares (Gray, 1849)

Fidenas penares Gray, 1849, *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Antepedia*, 95 [type locality: Singapore].

Geographical Distribution: Indo-Pacific: unknown.

Literature: Gray (1849).

Euprymna phenax Voss, 1962

Euprymna phenax Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 171 [type locality: Philippines].

Size: Type 11 mm mantle length.

Geographical Distribution: Indo-Pacific: Philippines, possibly East China Sea. Depth range unknown (collected at nightlight).

Literature: Kubodera and Yamada (1998).

Euprymna scolopes Berry, 1913

Euprymna scolopes Berry, 1913, *Proceedings of the United States National Museum*, 45(1996): 564 [type locality: Hawaiian Islands].

Size: Up to 30 mm mantle length.

Geographical Distribution: Central Pacific: Hawaiian Islands. Shallow coastal waters.

Literature: Arnold (1972), Moynihan (1983a), Shears (1988), McFall-Ngai and Montgomery (1990), McFall-Ngai (1994), Fleisher and Case (1995), Montgomery and McFall-Ngai (1995), Anderson and Mather (1996), Hanlon *et al.* (1997), Norman and Lu (1997), Claes and Dunlap (1999).

Euprymna stenodactyla (Grant, 1833)

Euprymna stenodactyla Grant, 1833, *Transactions of the Zoological Society of London*, 1: 85 [type locality: Mauritius].

Geographical Distribution: Indian Ocean: known with certainty only from Mauritius. Records from the Indo-west Pacific (Mascarene Islands to Queensland, Australia and Polynesia) are doubtful.

Literature: Joubin (1902a), Okutani (1995), Norman and Lu (2000).

Sepietta petersi (Steenstrup, 1887)

Sepiola petersi Steenstrup, 1887, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1887: 58 [type locality: Adriatic Sea].

Geographical Distribution: Mediterranean Sea and Atlantic coast of Morocco (doubtful).

Remarks: Doubtful species, that has been considered the senior name for ***S. obscura*** Naef, 1916 (see remarks in ***S. obscura***). A detailed redescription of all the anatomical features of this purported species is needed to solve the problem.

Literature: Steenstrup (1887).

Inioteuthis capensis Voss, 1962

Inioteuthis capensis Voss, 1962b, *Transactions of the Royal Society of South Africa*, 36(4): 255 [type locality: South Africa].

Geographical Distribution: Southeastern Atlantic: South Africa, from Lüderitz Bay to Mossel Bay.

Literature: Voss (1962b).

Inioteuthis japonica (Orbigny, 1845)

Sepiola japonica Orbigny, 1845 (*in* Férussac and d'Orbigny, 1834–1848), *Histoire Naturelle Générale et Particulière Céphalopodes Acétabuliferes Vivants et Fossiles*, 234 [type locality: Japan].

Size: Up to 20 mm mantle length.

Geographical Distribution: Western Pacific: Southern Japan, China and Taiwan Province of China.

Literature: Joubin (1902a).

Inioteuthis maculosa Goodrich, 1896

Inioteuthis maculosa Goodrich, 1896, *Transactions of the Linnaean Society of London*, (series 2, Zoology), 7(1): 2 [type locality: Andaman Islands].

Size: Males up to 13 mm mantle length; females up to 14 mm mantle length.

Geographical Distribution: Indo-Pacific: northern Indian Ocean, Persian Gulf, India, Arabian Sea, Bay of Bengal, Andaman Sea, Taiwan Province of China, Philippines, Indonesia.

Literature: Nateewathana (1997).

NEXT PAGE

3.2.2 Subfamily ROSSIINAE Appellöf, 1898

Rossia macrosoma (Delle Chiaie, 1830) Fig. 261

Sepiola macrosoma Delle Chiaie, 1830, *Memoire sulla storia e notomia degli Animali senza vertebre del Regno di Napoli*. 4 volumes, atlas. Napoli, pl. 17 [type locality: Tyrrhenian Sea].

Frequent Synonyms: *Sepiola macrosoma* Delle Chiaie, 1829.

Misidentifications: None.

FAO Names: En – Stout bobtail squid; **Fr** – Sépiole melon; **Sp** – Globito robusto.

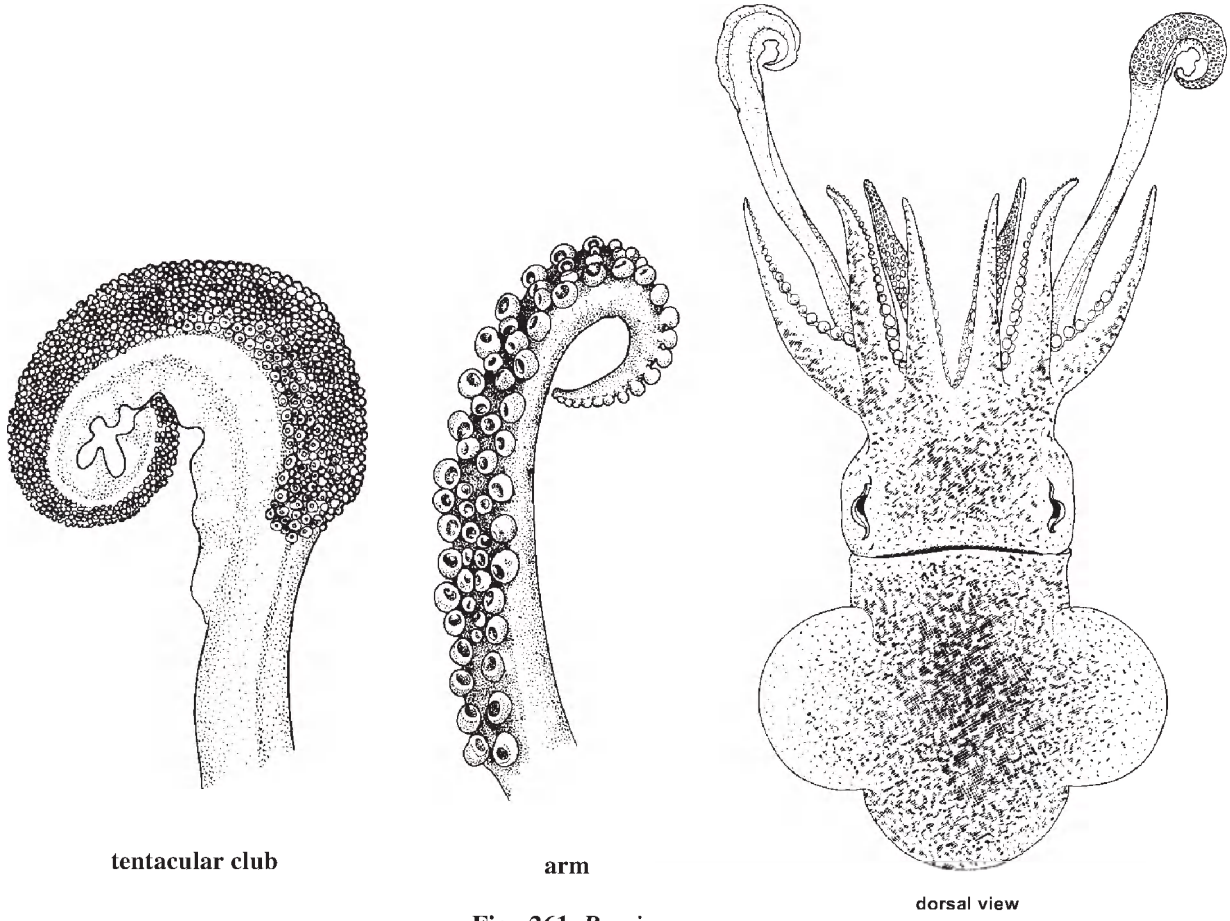


Fig. 261 *Rossia macrosoma*

Diagnostic Features: Body smooth, soft. Males mature at smaller sizes and do not grow as large as females. Mantle dome-shaped. Dorsal mantle free from head (not fused to head). **Nuchal cartilage oval, broad**. Fins short, do not exceed length of mantle anteriorly or posteriorly. Arm webs broad between arms III and IV. Non-hectocotylized arm sucker arrangement same in both sexes: **arm suckers biserial basally, tetraserial medially and distally**. Dorsal and ventral sucker rows of arms II to IV of males enlarged; ventral marginal rows of arms II and III with 1 to 3 greatly enlarged suckers basally (diameter 8 to 11% mantle length); dorsal and ventral marginal sucker rows of arms II to IV with more than 10 enlarged suckers (diameter 4 to 7% mantle length); suckers on median rows in males smaller than female arm suckers in size. Hectocotylus present; both dorsal arms modified: ventrolateral edge of proximal oral surface of hectocotylized arms bordered by swollen glandular crest, inner edge of which forms a deep furrow; glandular crest extends over entire arm length; suckers decrease in size from proximal to distal end of arms; biserial proximally, tetraserial distally (marginal and medial suckers similar in size, smaller than on rest of arm); arms with deep median furrow and with transversely grooved ridges. Tentacular club expanded, broader than stalk, with **8 to 12 suckers in transverse rows**; suckers small, **very similar in size**; protective membrane borders entire club; **swimming keel equal to club length**. Anal flaps well developed. Ink sac well developed. **Epirenal bodies absent; anal pads absent**. **Colour:** Light yellowish brown with greenish tinge to dark reddish brown.

Size: Up to 85 mm mantle length, usually between 20 to 60 mm mantle length.

Geographical Distribution: Eastern Atlantic and Mediterranean Sea: Greenland Sea, off Greenland and Iceland, Norway, Faeroe Islands, North Sea, Britain to the Azores, Morocco and Senegal; Mediterranean Sea except northern Adriatic Sea and southeastern Levantine Sea (Fig. 262).

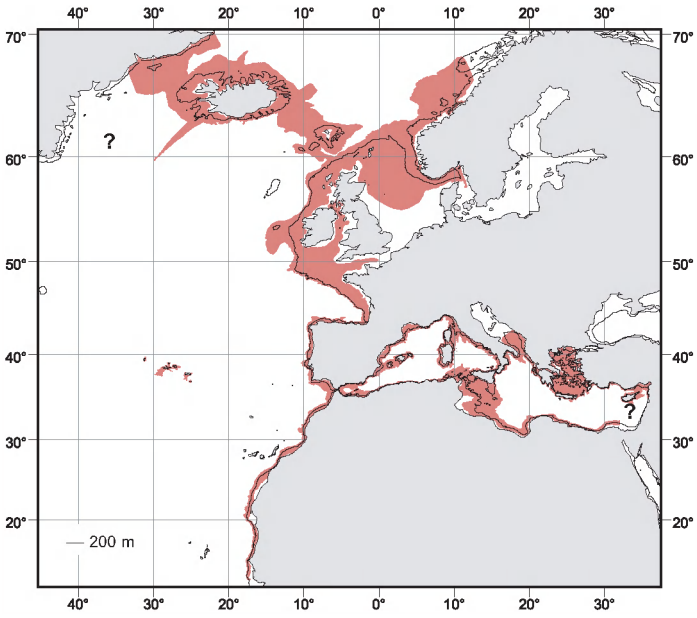


Fig. 262 ***Rossia macrosoma***
Known distribution

Habitat and Biology: Sandy and muddy substrate. Demersal, depth range 32 to 899 m; animals have been collected between the surface and 500 m at night. This species is common at depths between 200 and 400 m in the Mediterranean Sea, where it is associated with the wide transitional zone (100–600 m) representing a region of overlapping shelf and slope faunas. It usually prefers deeper waters, especially in winter, ascending to shallower waters to spawn. It is fairly frequent in catches but generally never abundant, thus information on its biology and ecology is still poor. Most of the present knowledge is based on the observations made in the western Mediterranean and studies in the laboratory. In the western Mediterranean ***Rossia macrosoma*** carries out seasonal migrations between deeper offshore waters in winter and shallower coastal zones for the rest of the year. This migration is partitioned by size such that the largest individuals arrive first in spring, followed by smaller animals in summer. Mature males, aged 7 to 8 months carry 85 to 100 spermatophores; females, 8 to 11 months, have about 120 to 150 eggs in their ovaries. The spawning season probably extends throughout the year throughout the whole Mediterranean, with peaks in spring and autumn. Mating takes place when the male grasps the female's 'neck' region and then inserts the hectocotylus into her mantle cavity. Spermatophores have been found attached to the oviducal openings in this species. ***Rossia macrosoma*** is polytelic, each individual spawning several times. Eggs, measuring 7 to 8 mm in diameter, are laid in small clusters of 30 to 40, and covered by a violet-red hard coat. They are deposited on bivalve shells e.g. of *Pinna* sp., or other solid substrates. Hatching occurs after 45 days at temperatures of about 16°C. Females grow larger than males, and longevity is about 12 months. Smallest mature males are 30 mm mantle length; smallest females 35 mm mantle length.

Interest to Fisheries: ***Rossia macrosoma*** is a species of relatively minor commercial importance, taken as bycatch in bottom trawls, mostly between 200 and 400 m. Its commercial value varies among Mediterranean countries. The flesh is tasty but difficult to preserve. Separate statistics are not reported for this species, which, however, is rather common in fish markets and sold fresh and frozen.

Local Names: FRANCE: Sépiole; ITALY: Seppiola grossa, Babbunedda, Cape e chiuove, Capo di chiodo, Purpo seccia, Vurpascele; MOROCCO: Sepiole; SPAIN: Choco, Chopito, Globito.

Literature: Joubin (1895, 1902b), Naef (1923), Mangold-Wirtz (1963), Boletzky and Boletzky (1973), Roper *et al.* (1984), Bello (1990b), Guerra (1992), Bello (1995), Jereb and Di Stefano (1995), Okutani (1995), Sartor and Belcari (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995), D'Onghia *et al.* (1996), Jereb *et al.* (1998), Belcari and Sartor (1999b), Quetglas *et al.* (2000).

Rossia pacifica pacifica Berry, 1911 **Fig. 263**

Rossia pacifica pacifica Berry, 1911a, *Proceedings of the United States National Museum*, 40(1838): 591 [type locality: Alaska].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – North Pacific bobtail squid; **Fr** – Sépiole du Pacifique boréal; **Sp** – Globito del Pacífico boreal.

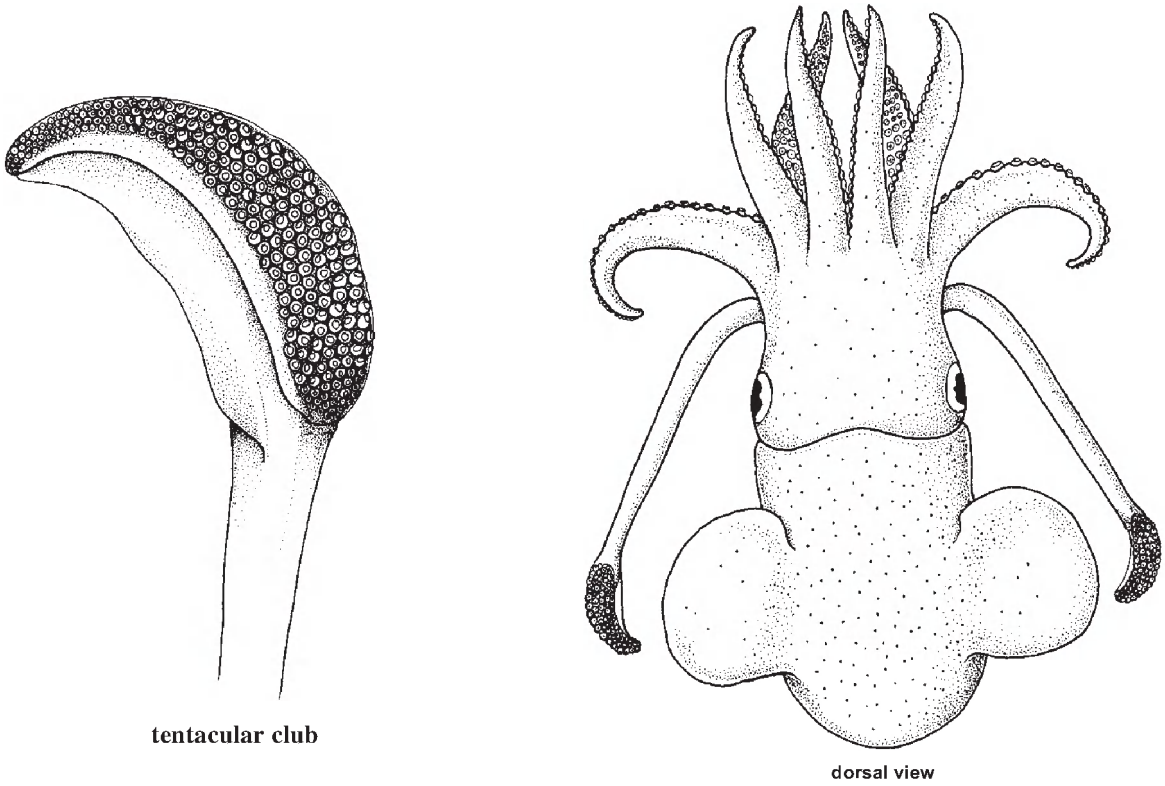


Fig. 263 *Rossia pacifica pacifica*

Diagnostic Features: Body smooth, soft. Males mature at smaller sizes and do not grow as large as females. Mantle dome-shaped. Dorsal mantle free from head (not fused to head). **Nuchal cartilage oval, narrow**. Fins ear-shaped. Male and female arms short, stout; not united by deep webs. Non-hectocotylized arm sucker arrangement same in both sexes: suckers biserial basally, tetraserial medially and distally; male arm suckers enlarged on arms II to IV, larger than female arm suckers. Hectocotylus present; both dorsal arms modified: ventrolateral edge of proximal oral surface of hectocotylized arms bordered by swollen glandular crest, inner edge of which forms a deep furrow; **glandular crest extends over 2/3 arm length**; suckers smaller than on sessile arms (about 1/3 the size of those on lateral arms). Tentacular club expanded, broader than stalk; sucker-bearing face flattened, with **6 to 8 suckers in transverse rows proximally**, 4 rows distally; suckers differ slightly in size, dorsal suckers largest; protective membrane borders entire club. Lower beak with tooth on shoulder. Anal flaps well developed. Ink sac well developed. **Epirenal bodies and anal pads absent**. Internal gladius present, chitinous; gladius spoon-shaped, short.

Size: Males up to 45 mm mantle length; females up to 90 mm mantle length.

Geographical Distribution: Northern Pacific: Bering Sea, Sea of Okhotsk, Kamchatka, Kuril Islands, Japan to Korea, Aleutian Islands and Gulf of Alaska south to British Columbia, San Diego and California (to about 28°N off Baja California) (Fig. 264).

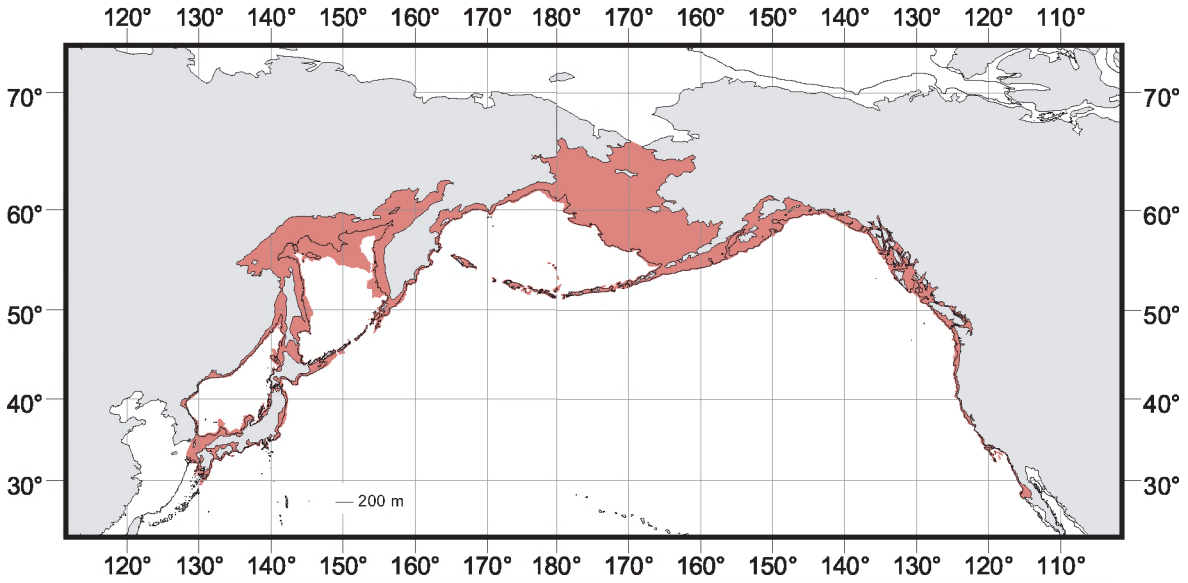


Fig. 264 ***Rossia pacifica pacifica***
Known distribution

Habitat and Biology: Neritic; depth range 30 to 310 m (possibly to 550 m) in the western Pacific; 10 m and deeper in the eastern Pacific (maximum depth undetermined). This species is night active; it remains buried in sand and mud during the day, then emerges at night to forage. Shrimps, crabs, small fishes and cephalopods comprise over 80% of the diet of this species in its natural environment. Females are polytelic: ova ripen in small clusters, each individual spawning several times, probably throughout the year. In the northeastern Pacific, eggs are attached singly, or in small groups, to seaweed and other objects on the sea floor. Egg masses are found in the Greater Puget Sound Region in calm water, with little tidal flow, attached to smooth, hard, surfaces protected from siltation by overhanging rocks. The eggs are about 1 cm in diameter and ovoid, with a flattened area of attachment; they are usually found at depths from 15 to 30 m, but are reported from 250 m depth (1.6°C) in the Bering Sea. This species has been reared successfully in captivity; egg development took nearly 5 months both in an open seawater system, with temperatures ranging between 6° and 15°C reflecting the ambient temperature, and in a temperature controlled environment at 10°C (± 1°C). The time of embryonic development, however, seems linked to the lunar cycle. Because this species is known to occur over a wide depth range and lacks a planktonic juvenile stage, hatching of eggs laid far below the photic zone would be out of synchrony with those laid at shallow depths based on light effects alone. Growth in captivity is strongly dimorphic, with females growing much faster than males after a first phase of rather slow growth common to both sexes. The lifespan from hatching to death is 18 to 19 months. Accordingly, the time taken for embryonic development was recently estimated to be about 5 months for animals of the Bering, Okhotsk (Russia) and northern seas of Russia and the Polar Basin. However, results obtained from statolith microstructure in a few specimens of ***Rossia pacifica*** from the northwest Bering Sea, would suggest a much shorter lifespan (i.e. 4–5 months).

Interest to Fisheries: ***Rossia pacifica*** often is trawled in large quantities off the Sanriku-Hokkaido coasts of Japan and other subarctic Pacific regions. It is believed to have inferior meat quality and therefore has low economic value, even though the resource is large. Separate statistics are not reported for this species.

Local Names: JAPAN: Bouzuika.

Remarks: This species seems most closely related to the Arctic ***R. moelleri*** Steenstrup, 1856, suggesting its possible origin by isolation during the Tertiary elevations of the Bering Strait. ***Rossia pacifica diegensis*** Berry, 1912 is found at greater depths than ***R. pacifica pacifica***; it is smaller and more delicate in structure, and it has relatively larger fins and arm suckers, predominantly in 2 rows. Some large ***Rossia*** eggs (14–18 mm) have been found in 1 204 to 1 222 m (4.1°C) depth in Santa Catalina Basin. These may belong to ***R. pacifica diegensis,*** or it may be that ***R. pacifica pacifica*** produces larger eggs at lower temperature in this location. Alternatively, another ***Rossia*** taxon may exist in these waters, and ***R. pacifica pacifica*** may actually be a cold water, large-egged form, with the second taxon an unnamed smaller-egged species found in shallower water.

Literature: Sasaki (1920), Sasaki (1929), Mercer (1968), Boletzky (1970), Brocco (1971), Hochberg and Fields (1980), Roper *et al.* (1984), Okutani *et al.* (1987), Summers and Colvin (1989), Summers (1992), Anderson and Shimek (1994), Arkhipkin (1995), Okutani (1995), Mangold *et al.* (1998), Nesis (1999).

Rossia tortugaensis Voss, 1956

Fig. 265

Rossia tortugaensis Voss, 1956, *Bulletin of Marine Science of the Gulf and Caribbean*, 6(2): 103 [type locality: Caribbean Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Tortuga bobtail squid; **Fr** – Sépiole de la Tortue; **Sp** – Globito de Tortugas.

Diagnostic Features: Body soft, fleshy. Males mature at smaller sizes and do not grow as large as females. Dorsal mantle free from head (not fused to head). Fins ovate, short. Male and female arms long. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial. Suckers elongated, barrel-shaped, without dentition. Hectocotylus present, both dorsal arms modified: **glandular crest extends over entire arm length**. Club large; sucker-bearing face flattened; tentacular club expanded, broader than stalk, with **10 suckers in transverse rows**; suckers finely toothed; swimming keel of club extends slightly proximal to carpus. Anal flaps reduced. Ink sac well developed. **Epirenal bodies and anal pads absent**.

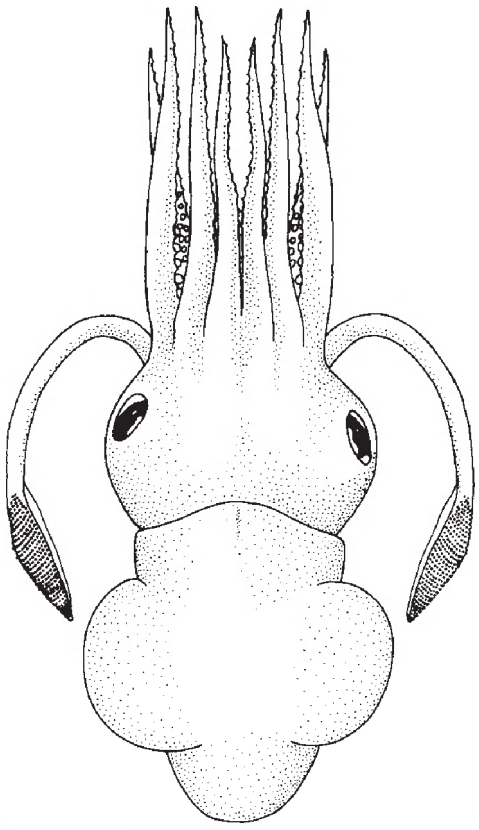
Size: Up to 50 mm mantle length.

Geographical Distribution: Tropical western Atlantic: Gulf of Mexico, Dry Tortugas, Florida and off Suriname (Fig. 266).

Habitat and Biology: Depth range 520 m (Dry Tortugas) to 760 m (Suriname). These are the only known records. This species is polytelic: ova ripen in small clusters, each individual spawning several times, probably throughout the year.

Interest to Fisheries: Undetermined.

Literature: Roper *et al*. (1984), Okutani (1995).



dorsal view

Fig. 265 *Rossia tortugaensis*

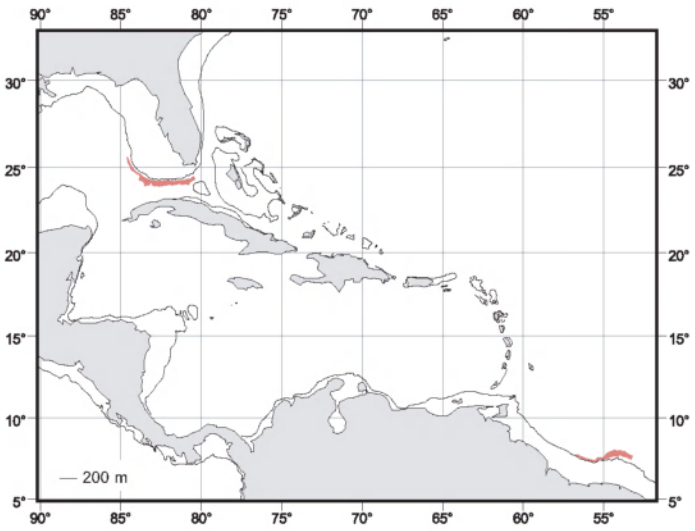


Fig. 266 *Rossia tortugaensis*
Known distribution

Semirossia equalis (Voss, 1950) Fig. 267

Rossia (Semirossia) equalis Voss, 1950, *Revista de la Sociedad Malacológica "Carlos de la Tarre"*, 7(2): 73 [type locality: Caribbean Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Greater shining bobtail squid; **Fr** – Sépiole cracheuse; **Sp** – Globito reluciente.

Diagnostic Features: Fins wide, ovate, short, do not exceed length of mantle anteriorly or posteriorly; anterior fin lobes prominent. Male and female arms long, slender. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial, widely spaced; median arm suckers enlarged. Suckers globular, barrel-shaped with untoothed rings. Hectocotylus present, left dorsal arm modified: suckers normal proximally, reduced distally; broad lateral membrane present, extending from **third sucker pair for about 3/4 of arm length**; sucker arrangement from proximal to distal end of arm: **10 series of normal suckers, 4 series of reduced suckers**; oral surface of modified region swollen, fleshy, sucker pedicels form palisade effect, with transversely grooved ridges. Club moderate length, expanded, broader than stalk, with **7 or 8 suckers in transverse rows**; suckers differ in size, dorsal suckers largest, those in two dorsalmost rows larger than rest; length of swimming keel of club equal to length of carpus. Light organs present inside mantle cavity on ink sac. **Colour:** Deep purple; fins pigmented over basal half.

Size: Up to 50 mm mantle length.

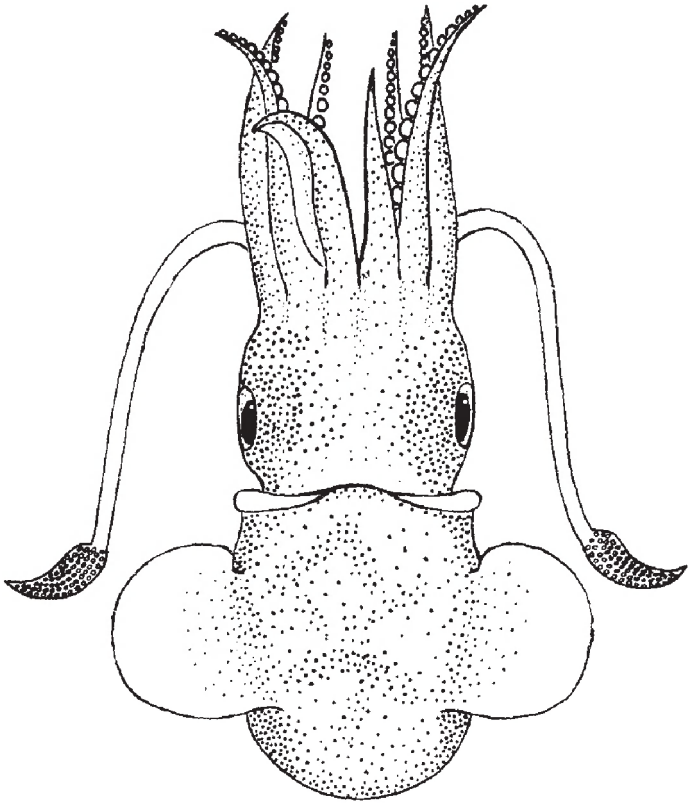
Geographical Distribution: Tropical western Atlantic: eastern Gulf of Mexico to Florida, Cuba, the Caribbean Sea and Suriname (Fig. 268).

Habitat and Biology: Muddy substrates. Benthic; depth range from 130 to 260 m, but specimens have been collected in the water column between the surface and 115 m at night.

Interest to Fisheries: No specific information available, but it is likely to be used as food locally.

Remarks: Differs from *S. tenera* (Verrill 1880) in its larger size, smaller arm suckers and slightly enlarged suckers on the dorsal side of the club.

Literature: Roper *et al.* (1984), Okutani (1995).



dorsal view

Fig. 267 *Semirossia equalis*

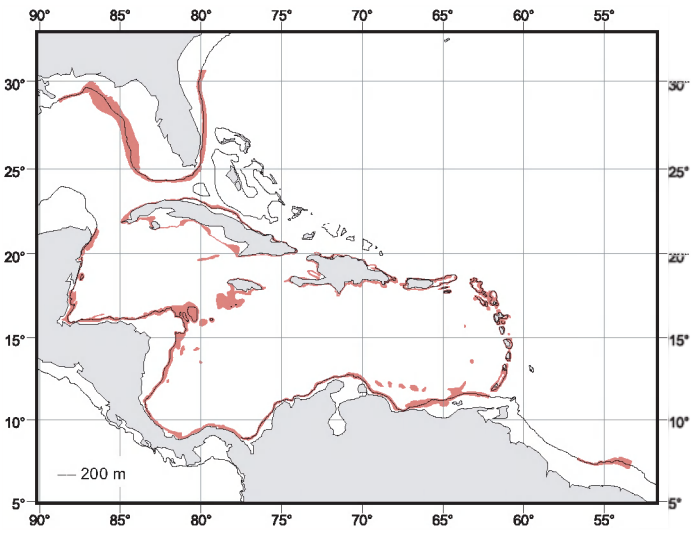


Fig. 268 *Semirossia equalis*
Known distribution

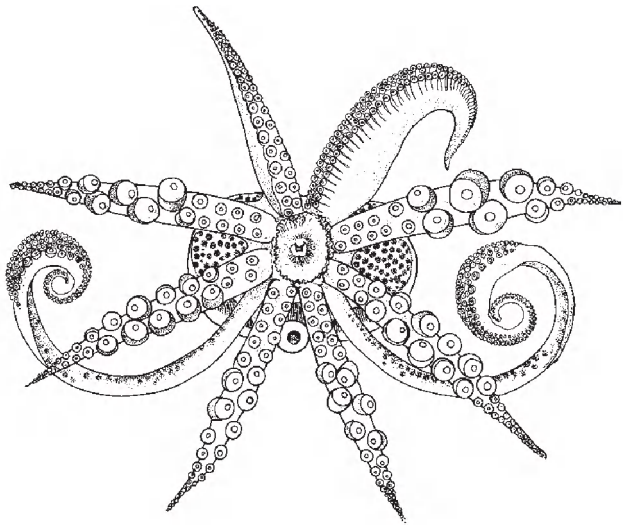
Semirossia tenera (Verrill, 1880) Fig. 269

Heteroteuthis tenera Verrill, 1880, *American Journal of Science*, (series 3) 20(41): 392 [type locality: northwestern Atlantic Ocean].

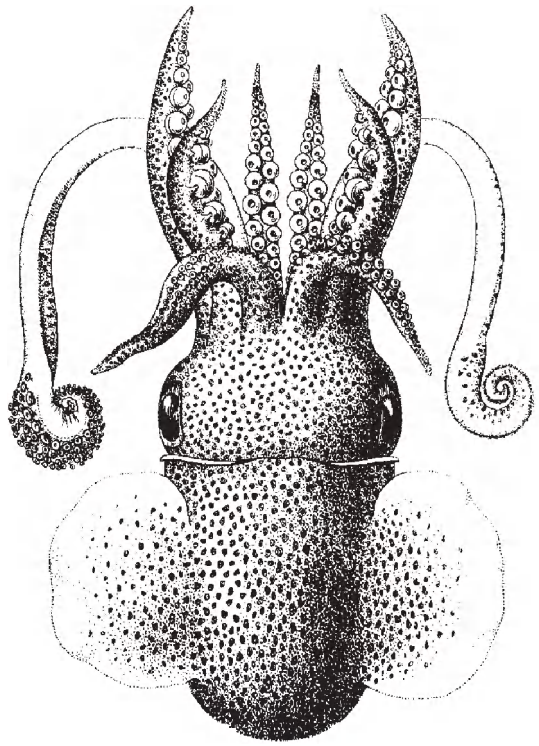
Frequent Synonyms: *Rossia tenera* (Verrill, 1880); *Heteroteuthis tenera* Verrill, 1880.

Misidentifications: None.

FAO Names: En – Lesser shining bobtail squid; **Fr** – Sépiole calamarette; **Sp** – Globito tierno.



oral view of male



dorsal view, male

Fig. 269 *Semirossia tenera*

Diagnostic Features: Small; body soft, fleshy. Mantle dome-shaped, broad. Dorsal mantle free from head (not fused to head). Fins ovate. Male and female arms moderate length. **Arms III and IV united by a web**. Arm suckers greatly enlarged in middle section of arms in males, abruptly decrease in size distally near arm tip. Hectocotylus present; left dorsal arm modified: suckers normal proximally, reduced distally; broad lateral membrane present ventrally, and extends distally for about **3/4 of arm length from third basal pair of suckers**; sucker arrangement from proximal to distal end of arm: **7 series of normal suckers, 4 series of reduced suckers**; oral surface of modified region swollen, fleshy, sucker pedicels form a pallisade effect, with transversely grooved ridges. Tentacular club moderately expanded, broader than stalk; club with **6 or 7 suckers in transverse rows**; suckers differ in size, **dorsal suckers twice as large as rest**; suckers toothed around entire margin; length of club swimming keel equal to length of carpus. Light organs present inside mantle cavity, on ink sac.

Size: Up to 50 mm mantle length.

Geographical Distribution: Western North Atlantic: widespread around the eastern coast of North America, from Nova Scotia, the northern Gulf of Maine to the Gulf of Mexico and the Caribbean Sea; possibly also present in the southwestern Atlantic, along the coasts of Suriname, French Guiana, Brazil and Uruguay (latter records questionable). (Fig. 270).

Habitat and Biology: Sandy and muddy substrates. Demersal; depth range from 85 to 135 m in New England area (USA).

Fig. 270 *Semirossia tenera*
Known distribution

Interest to Fisheries: Reported to be fished in the Gulf of San Matias and some localities on the south coast of Argentina (though species identification needs to be verified).

Local Names: ARGENTINA: Calamarcito.

Literature: Joubin (1902b), Voss (1956), Roper *et al.* (1984), Okutani (1995).

Neorossia caroli (Joubin, 1902) Fig. 271

Rossia caroli Joubin, 1902b, *Bulletin de la Société Zoologique de France*, 27: 138 [type locality: Eastern Atlantic: Azores Islands].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Carol bobtail squid; **Fr** – Sépiole de Carol; **Sp** – Globito de Carol.

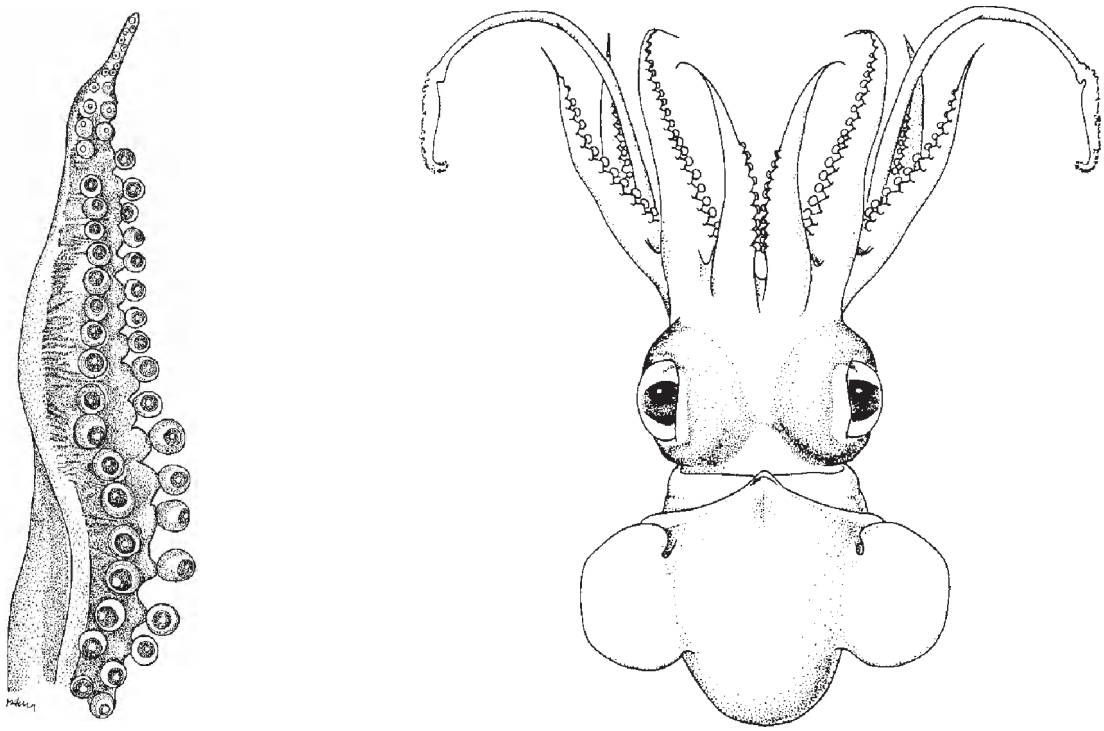


Fig. 271 *Neorossia caroli*

Diagnostic Features: (Based on type and specimens from the eastern Atlantic.) Body soft, fleshy. Mantle broad, oval; dorsal anterior margin slightly convex; posterior mantle margin rounded. Dorsal mantle free from head (not fused to head). **Nuchal cartilage oval**. Fins wide, rounded, semicircular; anterior origin almost at mantle margin. Funnel organ dorsal elements inverted V-shaped with small anterior papilla, median limbs with broad, blunt lobes; ventral elements oval with acute anterior tips. Mantle-locking cartilage a simple straight ridge; funnel-locking cartilage a simple, straight depression. Head slightly broader than mantle; eyes large. Male and female arms similar in relative lengths; arm formula 3,4,2,1, or 3,2,4,1. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial; **largest suckers on arms II and III larger than those on arms I and IV in both sexes**. Hectocotylus present, both dorsal arms modified: ventrolateral edge of proximal oral surface of hectocotylized arms bordered by swollen glandular crest, inner edge of which forms a deep furrow; inside crest fleshy, with transverse grooves; oral surface broad, fleshy; suckers smaller than on remaining arms; glandular **crest extends over sucker rows 3 to 18**. Club slightly recurved, sucker-bearing face convex with 8 to 11 suckers in transverse rows; all suckers of similar size; swimming keel of club extends well proximal to carpus. Anal flaps present, reduced. Ink sac greatly reduced, non functional. **Epirenal bodies present in males only**. Internal gladius present, chitinous; gladius elongate, slender, diamond-shaped anteriorly, tapers posteriorly; length approximately equal to mantle length; rachis extends posteriorly for 2/3 length of vane; **vane present only on posterior half of gladius**.

Size: Males up to 51 mm mantle length; females up to 83 mm mantle length.

Geographical Distribution: Eastern Atlantic and Mediterranean Sea: from southwestern Iceland and Ireland southward to the Gulf of Guinea and Namibian coast of southern Africa; in the Mediterranean Sea, from the northwestern Mediterranean eastward to the Ligurian Sea, northern and southern Tyrrhenian Sea, Strait of Sicily, Adriatic Sea, northern Aegean Sea, Levantine Sea and Algerian Sea. Doubtful records from the southern slope of the Great Newfoundland Bank, the slope off Nova Scotia, and the Gulf of Mexico. Southwestern Atlantic: (subspecies ***N. c. jeannae*** Nesis *et al.* (2001)) Patagonian slope north of Falkland Islands (Fig. 272).

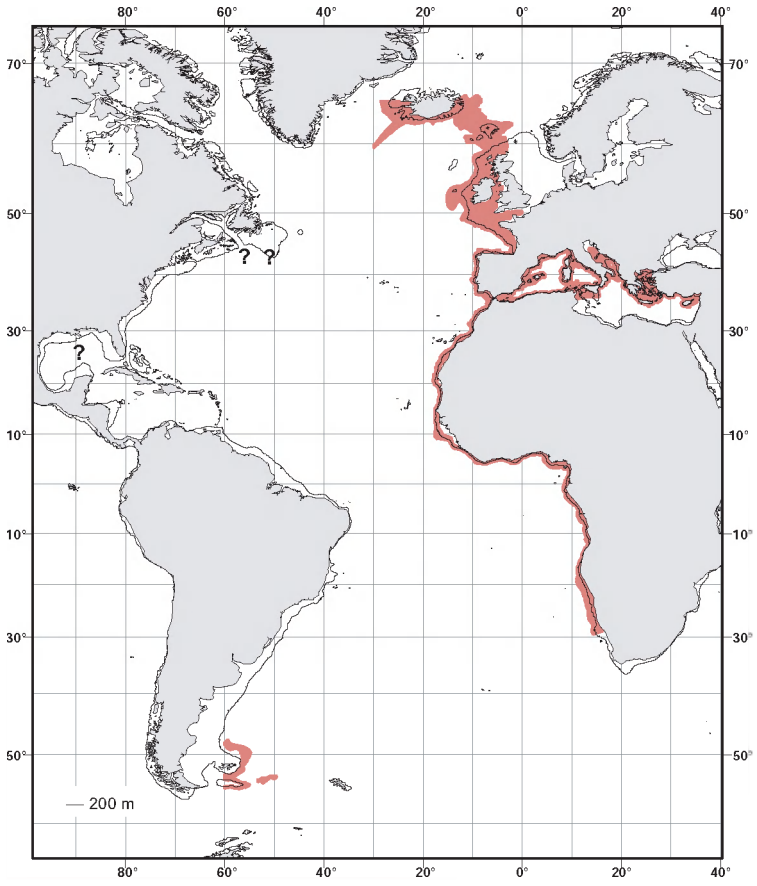


Fig. 272 ***Neorossia caroli***
Known distribution

Habitat and Biology: Depth range from 40 to 1 744 m. ***Neorossia caroli*** is the most bathyal among the species belonging to the family Sepiolidae, collected down to the greatest depths in the western Mediterranean basin (1 744 m) and in the eastern Atlantic (1 535 m). It is a demersal species living preferentially on deep muddy bottoms characterized by *Isidella elongata* populations, often overlapping with ***Rossia macrosoma*** in the upper level of its distributional range and frequently associated with ***Sepietta oweniana*** and ***Rondeletiola minor***. In the western Mediterranean, it is the most common cephalopod captured between 1 000 and 2 000 m, along with ***Bathypolypus sponsalis***. The occurrence of small individuals of both ***N. caroli*** and ***B. sponsalis*** at greater depths than larger individuals, suggests there may be an upslope ontogenetic migration. ***Neorossia caroli*** is most abundant between 400 and 600 to 700 m both in the western and eastern Mediterranean, although it is also present on the upper slope (200–400 m), and there are sporadic records of its occurrence in shallower waters (less than 100 m). ***Neorossia c. jeannae*** has been collected between 474 and 670 m. Mature individuals are found throughout the year, suggesting an extended spawning season, probably with peaks in summer and/or autumn. The smallest mature males are 35 mm, and the smallest mature females 50 mm mantle length. Lower sizes at first maturity have, however, been reported for specimens from the central Mediterranean (i.e. Strait of Sicily: 30.5 mm for males and 35 mm for females). Eggs are large (8–10 mm diameter), covered by a hard violet-coloured coating and are attached to hard substrates at various depths. The lifespan is probably between 12 and 24 months.

Interest to Fisheries: Of minor commercial importance, it is taken usually as trawl fishery bycatch. Separate statistics are not reported for this species. It is sold fresh and frozen in fish markets with ***Rossia macrosoma*** and other bobtail squids.

Local names: ITALY: Seppiola grossa di fondo.

Remarks: Differs from its congener, ***N. leptodons*** Reid, 1992, in the shape of the radula teeth. The rhachidian teeth and first lateral teeth have broad, rather than narrow, bases and the base usually is strongly indented. ***Neorossia c. jeannae*** differs from ***N. c. caroli*** only in the shape of the size of the fins and nuchal cartilage (smaller in ***N. c. jeannae***) and shape of the nuchal cartilage. Future study and comparison of specimens from the entire range of ***N. caroli*** will determine the status of the two subspecies, and (possibly) help in revaluating the genus.

Literature: Joubin (1902b), Chun (1913), Joubin (1924), Mercer (1968), Boletzky (1971), Bello (1990b), Salcedo-Vargas (1991), Guerra (1992), Reid (1992), Villanueva (1992), Bello (1995), Jereb and Di Stefano (1995), Sartor and Belcari (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995), D'Onghia *et al.* (1996), Jereb *et al.* (1998), Collins *et al.* (2001), Nesis *et al.* (2001).

NEXT PAGE

Austrorossia antillensis (Voss, 1955) Fig. 273

Rossia antillensis Voss, 1955, *Bulletin of Marine Science of the Gulf and Caribbean*, 5(2): 86 [type locality: Cuba].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Antilles bobtail squid; **Fr** – Sépiole mignonne; **Sp** – Globito antillano.

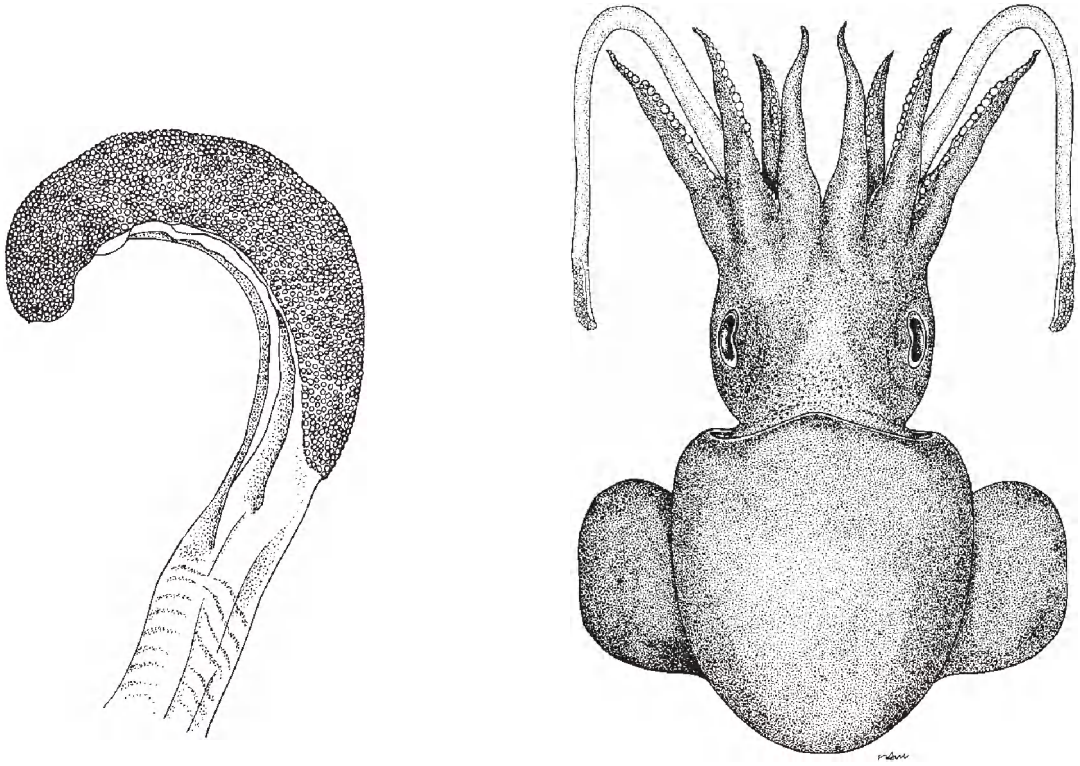


Fig. 273 *Austrorossia antillensis*

Diagnostic Features: Body soft, fleshy. Males mature at smaller sizes and do not grow as large as females. Mantle oval, short, saccular. Dorsal mantle free from head (not fused to head). Fins wide; ovate; short, do not exceed length of mantle anteriorly or posteriorly. Head slightly broader than mantle; eyes large. Male and female arms moderate length. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial, suckers sparsely arranged; median arm suckers enlarged in males; larger than female arm suckers. Hectocotylus present, both dorsal arms modified: ventrolateral edge of proximal oral surface of hectocotylized arms bordered by swollen glandular crest, inner edge of which forms a deep furrow; **glandular crest extends over sucker rows 3 to 8**. Club slightly recurved, short; sucker-bearing face convex; tentacular club not expanded, same width as stalk; with **30 to 40 suckers in transverse rows**; all suckers of similar minute size; swimming keel of club extends slightly proximal to carpus. Anal flaps well developed. **Epirenal bodies and anal pads absent**. Ink sac well developed. **Colour:** Pinkish brown, with scattered dark purple chromatophores; fins pigmented the same as the mantle; dorsal pigmentation extends to ventral surface of fins.

Size: Up to 90 mm mantle length.

Geographical Distribution: Tropical western Atlantic: Caribbean Sea, Cuba, Dry Tortugas, and the Gulf of Mexico northward to the latitude of Tampa, Florida. Suriname (Fig. 274).

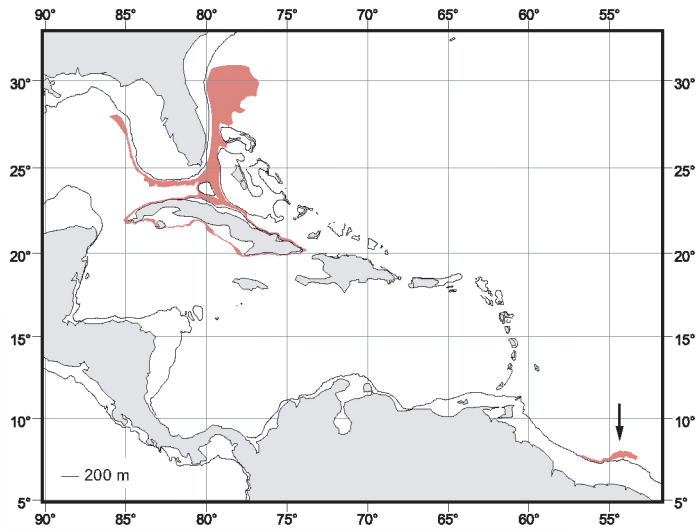


Fig. 274 *Austrorossia antillensis*
Known distribution

Habitat and Biology: Demersal; depth range from 540 to 700 m. This species is polytelic: ova ripen in small clusters, each individual spawning several times, probably throughout the year.

Interest to Fisheries: Undetermined, but it is likely to be consumed locally when captured as a bycatch of demersal trawl fisheries.

Remarks: ***Austrorossia antillensis*** is a large species in the genus. It is replaced by ***Rossia bullisi*** Voss, 1956 in more northerly waters.

Literature: Boletzky (1970), Roper *et al.* (1984), Okutani (1995).

Austrorossia australis Berry, 1918 **Fig. 275**

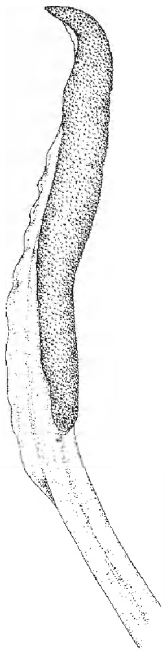
Rossia (Austrorossia) australis Berry, 1918, *Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour," 1909–14*, 4(5): 253 [type locality: southwestern Australia: Great Australian Bight southwest of Eucla, Western Australia].

Frequent Synonyms: None.

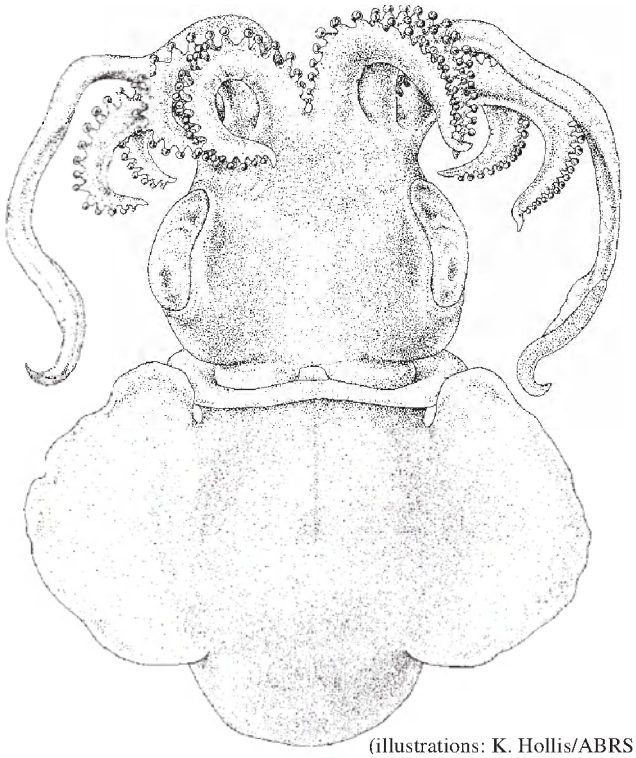
Misidentification: None.

FAO Names: En – Big bottom bobtail squid; **Fr** – Sépiole australe; **Sp** – Globito austral.

nuchal-locking cartilage



tentacular club



dorsal view of female

(illustrations: K. Hollis/ABRS)

Fig. 275 ***Austrorossia australis***

Diagnostic Features: Body smooth, soft. Males mature at smaller sizes and do not grow as large as females. Dorsal mantle free from head (not fused to head). Nuchal cartilage oblong, rounded anteriorly, tapers to slightly narrower posteriorly. Fins wide, ovate, short, do not exceed length of mantle anteriorly or posteriorly; attached within anterior 2/3 of mantle. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial; largest suckers on arms II and III larger than those on arms I and IV in both sexes. Hectocotylus present, both dorsal arms modified: ventrolateral edge of proximal oral surface of hectocotylized arms bordered by swollen glandular crest, inner edge of which forms a deep furrow; glandular crest **extends from sucker rows 4–6 to 8–11**. Club straight, slender, long; sucker-bearing face convex; **males 18 to 26 suckers in transverse rows; females 25 to 33 suckers in transverse rows**; all suckers of similar minute size. Anal flaps well developed. Ink sac well developed. **Epirenal bodies present in males only; anal pads present in both sexes**. Internal gladius present, chitinous; length approximately equal to mantle length; rachis extends almost to posterior tip of vane; **vane extends entire length of gladius**; shape lanceolate. **Colour:** Uniform pinkish to purplish brown.

Size: Males up to 34 mm mantle length; females up to 63 mm mantle length.

Geographical Distribution: Indo-Pacific: Australia, Queensland, Raine Island, 11°35'S 144°04'E, to Western Australia, Great Australian Bight, 34°S 130°50'E (Fig. 276).

Habitat and Biology: Sandy and muddy substrates. Benthic; depth range from 131 to 665 m. This species is polytelic: ova ripen in small clusters, each individual female spawns several times, probably throughout the year.

Interest to Fisheries: Possibly minor fishery potential.

Remarks: A second ***Rossia*** species is found on the northwest shelf of Western Australia. While it has been shown to differ from ***R. australis***, primarily in quantitative characters, it cannot be distinguished from the African ***Austrorossia mastigophora*** (Chun, 1915). Further work is needed to clarify the status of this species.

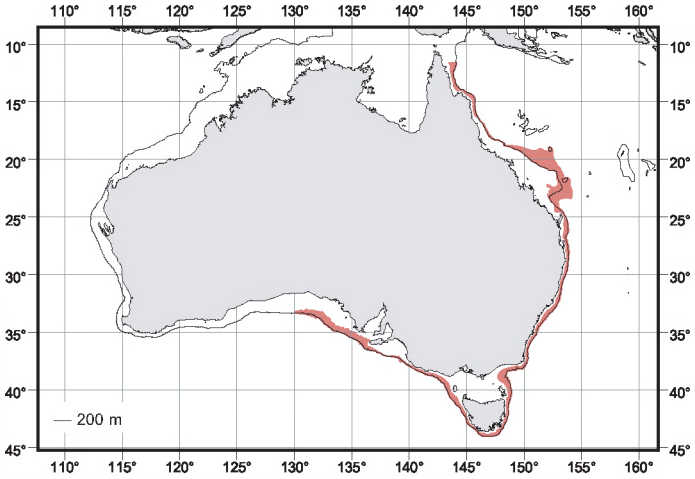


Fig. 276 ***Austrorossia australis***
Known distribution

Literature: Reid (1992), Okutani (1995), Reid and Norman (1998).

Austrorossia bipapillata (Sasaki, 1920) **Fig. 277**

Rossia bipapillata Sasaki, 1920, *Proceedings of the United States National Museum*, 57(2310): 190 [type locality: Japan, Suruga Bay, Shizuoka Prefecture].

Frequent synonyms: None.

Misidentifications: None.

FAO Names: En – Big-eyed bobtail squid; **Fr** – Sépiole à gros yeux; **Sp** – Globito ojos grandes.

Diagnostic Features: Body smooth, soft. Males mature at smaller sizes and do not grow as large as females. Dorsal anterior margin of mantle triangular, acute, blunt. Dorsal mantle free from head (not fused to head). **Nuchal cartilage oval**. Fins rounded, semicircular, short, do not exceed length of mantle anteriorly or posteriorly. Funnel organ strongly shouldered, with long extensions; ventral elements oval with acute anterior tips. Male and female arms subequal in length and long; female arm formula 3:2:1=4. Dorsal and lateroventral arms with low, but distinct keels. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial, globular. Club straight, slender, or coiled; with **25 to 30 suckers in transverse rows**; all suckers of similar minute size. Anal flaps well developed. Ink sac well developed. **Epirenal bodies and anal pads present in both sexes**.

Size: Up to 57 mm mantle length.

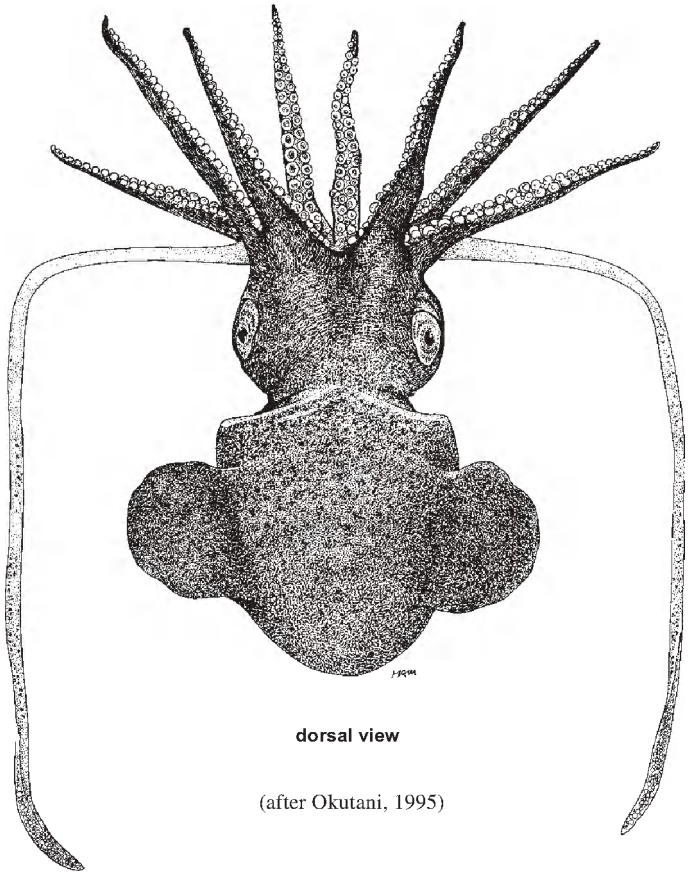


Fig. 277 ***Austrorossia bipapillata***

Geographical Distribution: Western Pacific: East China Sea, Japan (common on the lower shelf in Suruga Bay to Tosa Bay), Taiwan Province of China, Philippines (Fig. 278).

Habitat and Biology: Depth range 240 m in Suruga Bay, 432 m in the East China Sea. A polytelic species: ova ripen in small clusters and each individual female spawns several times, probably throughout the year.

Interest to Fisheries: Of minor interest to fisheries, it is usually caught as bycatch and is marketed fresh and frozen.

Remarks: This species differs from ***Austrorossia mastigophora*** (Chun, 1915) in the shape of the funnel organ, which is not so sharply angled in ***A. mastigophora***, and in the arm formula (***Rossia mastigophora***: 3:4:2:1). ***Austrorossia bipapillata*** differs from ***R. mollicella*** Sasaki, 1920 in possessing anal pads and in the number of tentacle-club suckers (8 in each transverse row in ***R. mollicella***). It differs from ***R. pacifica*** Berry, 1912 in having an oval, rather than elongate, parrallel-sided, nuchal-locking cartilage, and in the number of club suckers; the club suckers are arranged in 8 to 10 rows, and anal pads are lacking in ***R. pacifica***.

Literature: Sasaki (1929), Voss (1963), Okutani *et al.* (1987), Okutani (1995), Kubodera and Yamada (1998), Lu (1998b), Reid and Norman (1998).

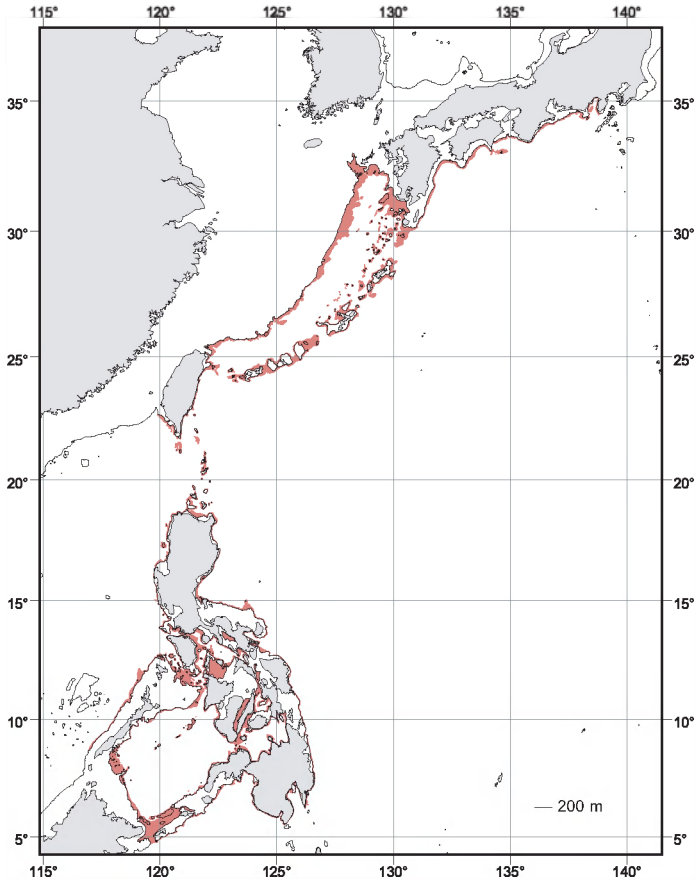


Fig. 278 ***Austrorossia bipapillata***
Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Rossia brachyura Verrill, 1883

Rossia brachyura Verrill, 1883, *Bulletin of the Museum of Comparative Zoology*, 11(5): 110 [type locality: Caribbean Sea].

Geographical Distribution: Tropical western Atlantic: Greater and Lesser Antilles.

Literature: Joubin (1902b).

Rossia bullisi Voss, 1956

Rossia bullisi Voss, 1956, *Bulletin of Marine Science of the Gulf and Caribbean*, 6(2): 101 [type locality: Gulf of Mexico].

Size: Up to 45 mm mantle length.

Geographical Distribution: Tropical western Atlantic: northern Gulf of Mexico and Straits of Florida.

Literature: Roper *et al*. (1984).

Rossia glaucopis Loven, 1845

Rossia glaucopis Loven, 1845, *Ofversigt af Kongl. Vetenskaps-Akademiens Forhandlingar*, 2(5): 121 [type locality: Chile].

Geographical Distribution: Southeastern Pacific, Chile.

Literature: Joubin (1902b), Rocha (1997).

Rossia megaptera Verrill, 1881

Rossia megaptera Verrill, 1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 349 [type locality: northwest Atlantic Ocean].

Size: Up to 40 mm mantle length.

Geographical Distribution: Northwestern Atlantic: Davis Strait and western Greenland, Hudson Canyon, off New York. Depth range from 179 to 1 536 m.

Literature: Mercer (1968), Joubin (1902b), Okutani (1995).

Rossia moelleri Steenstrup, 1856

Rossia moelleri Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4: 198 [type locality: Greenland].

Geographical Distribution: North Atlantic and Arctic Ocean: eastward to the Laptev Sea, westward to Amundsen Bay, western and northeastern Greenland, northeastern Canada, Labrador, Spitzbergen, Jan Mayen and Kara Seas. Depth range from 17 to 250 m.

Literature: Mercer (1968), Joubin (1902b), Okutani (1995), Nesis (1999).

Rossia mollicella Sasaki, 1920

Rossia mollicella Sasaki, 1920, *Proceedings of the United States National Museum*, 57(2310): 189 [type locality: Japan, Wakayama Prefecture].

Size: Up to approximately 36 mm mantle length.

Geographical Distribution: Western Pacific: Japan, Pacific coast, south from Sendai Bay. Outer shelf and upper bathyal. Depth range from 729 to 805 m.

Literature: Sasaki (1929), Okutani (1995).

Rossia pacifica diegensis Berry, 1912

Rossia pacifica diegensis Berry, 1912b, *Bulletin of the Bureau of Fisheries*, 30(1910): 292 [type locality: California].

Geographical Distribution: Eastern Pacific: USA, California, Santa Catalina Basin(?) (see Remarks in ***R. pacifica pacifica***).

Literature: Mangold *et al*. (1998).

Rossia palpebrosa Owen, 1834

Rossia palpebrosa Owen, 1834, *In* J. Ross, *Narrative of a second voyage in search of a North West Passage, 1829–1833. (Volume II, Appendix, Natural History)*, xcii [type locality: "Arctic Regions"].

Size: Up to approximately 45 mm mantle length.

Geographical Distribution: Amphi-North Atlantic: from the Canadian Arctic, Baffin Bay, Greenland south to South Carolina (32°N) in the western Atlantic; from Iceland, Spitzbergen, Scotland, Berents Sea and Kara Sea to the North Sea and off Ireland (51°N) in the eastern Atlantic. Depth range from 75 to 549 m.

Literature: Joubin (1902b), Akimushkin (1963), Aldrich and Lu (1968), Mercer (1968), Boletzky (1970).

Austrorossia enigmatica (Robson, 1924)

Rossia enigmatica Robson, 1924a, *Proceedings of the Zoological Society of London*, 1924(2): 635 [type locality: South Africa].

Size: Types up to 27 mm mantle length.

Geographical Distribution: Southeastern Atlantic: South Africa, Namibia to Cape Province. Depth range from 276 to 400 m.

Literature: Voss (1962b), Roeleveld *et al*. (1992), Augustyn *et al*. (1995).

Austrorossia mastigophora (Chun, 1915)

Rossia mastigophora Chun, 1915. *Wissebschaftliche Ergebnisse der Deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 1898–1899*, 18(2): 405 [type locality: northwestern Indian Ocean, 0°27'S 42°47'E, near East African coast].

Size: Males up to approximately 31 mm mantle length; females up to 46 mm mantle length.

Geographical Distribution: Western, southern and eastern Africa: from Guinea and Somalia to the Cape of Good Hope. Chile (doubtful). Depth up to approximately 640 m.

Literature: Voss (1962b), Rocha (1997).

Semirossia patagonica (Smith, 1881)

Rossia patagonica Smith, 1881, *Proceedings of the Zoological Society of London*, 1881(1): 22 [type locality: Argentina: Patagonia].

Geographical Distribution: Southwestern Atlantic and southeastern Pacific: southern part of South America from Chile, Anegada Bay, Tierra del Fuego, Argentina, Falkland Islands.

Literature: Joubin (1902b), Rodhouse *et al*. (1992), Rocha (1997).

Neorossia leptodons Reid, 1992

Neorossia leptodons Reid, 1992, *Bulletin of Marine Science*, 49(3): 797 [type locality: South Australia: Great Australian Bight, 37°18.81'S 138°36.3'E to 37°17.76'S 138°35.01'E].

Size: Males up to 42 mm mantle length; females up to 77.5 mm mantle length.

Geographical Distribution: Southwestern Pacific: Australia, New South Wales, 32°08'S 153°07'E to South Australia, 33°58'S 131°22'E. Depth range from 130 to 1 110 m.

Literature: Reid (1992).

3.2.3 Subfamily HETEROTEUTHINAE Appellöf, 1898

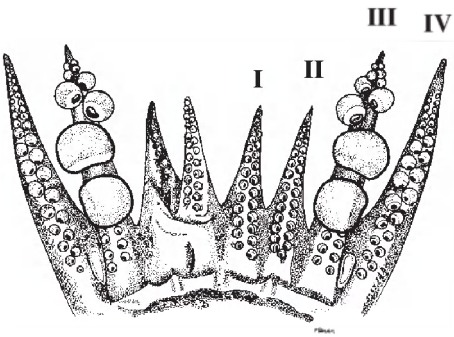
Heteroteuthis (Heteroteuthis) dispar (Rüppell, 1844) Fig. 279

Sepiola dispar Rüppell, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 133 [type locality: Italy: Sicily].

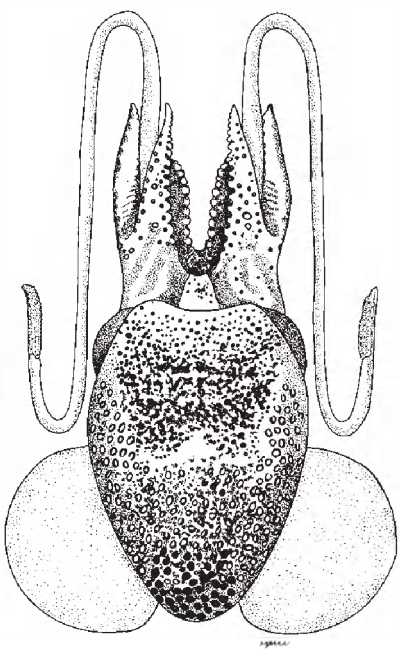
Frequent Synonyms: None.

Misidentifications: None.

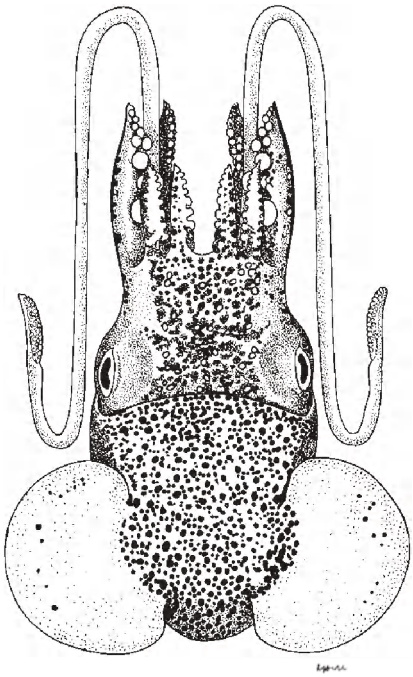
FAO Names: En – Odd bobtail squid; **Fr** – Sépiole différente; **Sp** – Globito aberrante.



arms of mature male



ventral view of male



dorsal view of male

(after Naef, 1923 [1972])

Fig. 279 *Heteroteuthis (Heteroteuthis) dispar*

Diagnostic Features: Dorsal mantle free from head (not fused to head). Ventral mantle strongly produced anteriorly, nearly covers funnel. Fins long; positioned posterior to the dorsal mid-point; anterior edge approximately at level of middle of ventral side of mantle. **Male and female arms differ in relative lengths: arms I and II equal in length and shorter than arms III and IV.** Right arms I and II connected from inner side by muscular band for half their length, depth of web between first arms in mature males 33 to 50% of arm length. Distal tips of arms I and II in mature females without suckers, tip of arm II slightly thickened with keel on oral side; **mature male arms III with enlarged suckers: 2 very large suckers (several times larger than rest)** attached at angle of 90° to each other, followed distally by three smaller suckers. **Tentacles very long** with more than 8 transverse rows of club suckers. Rounded light organ present inside mantle cavity on ink sac.

Size: Up to 25 mm mantle length.

Geographical Distribution: Amphi-Atlantic and Mediterranean Sea: from the Bermuda Islands, Caribbean Sea, to La Plata in the western Atlantic; from southwestern Ireland southward to the Azores Islands, Madeira Islands, Canary Islands and Guinea, in the eastern Atlantic; throughout the Mediterranean Sea, including Ligurian Sea, northern and southern Tyrrhenian Sea, Adriatic Sea, Aegean Sea and Levantine Sea. Also reported from Walters Shoals (southwestern Indian Ocean) and the Nazca and Sala y Gomez submarine ridges (eastern Pacific) (Fig. 280).

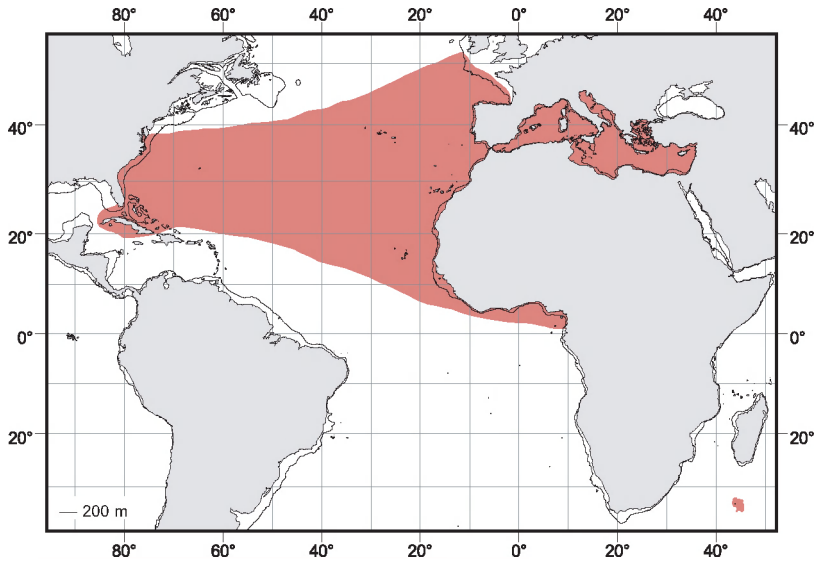


Fig. 280 *Heteroteuthis (Heteroteuthis) dispar*
Known distribution

Habitat and Biology: Mesopelagic, or benthopelagic, but has also been collected on the bottom; depth range to 1 588 m. Spawning occurs on the bottom, on the slope. The paralarvae live in the mesopelagic and bathypelagic zones, often far from the coasts, with bottom depths ranging between 1 500 and 3 000 m. Adults live frequently in groups in the lower epipelagic and mesopelagic zones, most commonly in depths between 200 and 300 m. This is one of the most common pelagic species in the Mediterranean Sea, where it is often found in areas inhabited by populations of red shrimps. ***Heteroteuthis dispar*** represent a sizeable component of the diet of several predators at the top of the food web, including dolphins (e.g. *Grampus griseus*) sharks (*Etmopterux spinax*, *Galeus melastomus*, *Scyliorhinus canicula*), swordfish (*Xiphias gladius*) and tunas (*Thunnus alalunga*). Populations from the eastern and western Atlantic are probably isolated from each other.

Interest to Fisheries: Of no commercial interest because of the low quantities available to fisheries, ***Heteroteuthis dispar*** is caught by pelagic nets as well as by trawlers, mainly targeting shrimp, and it is marketed along with other bobtail squids.

Remarks: Another species, ***Heteroteuthis atlantis***, was described by Voss (1955). Nesis (1987) records ***H. atlantis*** as a synonym of ***H. dispar***, but other authors disagree (e.g. Guerra, 1992) and the name ***H. atlantis*** is still used in some publications. Until the taxonomy of the genus is studied in detail, the validity of ***H. atlantis*** remains questionable.

Literature: Joubin (1902a), Naef (1923), Nesis (1987), Bello (1990), Guerra (1992), Nesis (1994), Bello (1995, 1996, 1997, 1999), Orsi Relini (1995), Sartor and Belcari (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995), Parin *et al.* (1997), Lefkaditou *et al.* (1999).

Stoloteuthis leucoptera (Verrill, 1878) **Fig. 281**

Sepiola leucoptera Verrill, 1878, *American Journal of Science and Arts*, (series 3) 16(46): 378 [type locality: USA: Gulf of Maine].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Leucoptera bobtail squid; **Fr** – Sépiole leucoptère; **Sp** – Globito leucóptero.

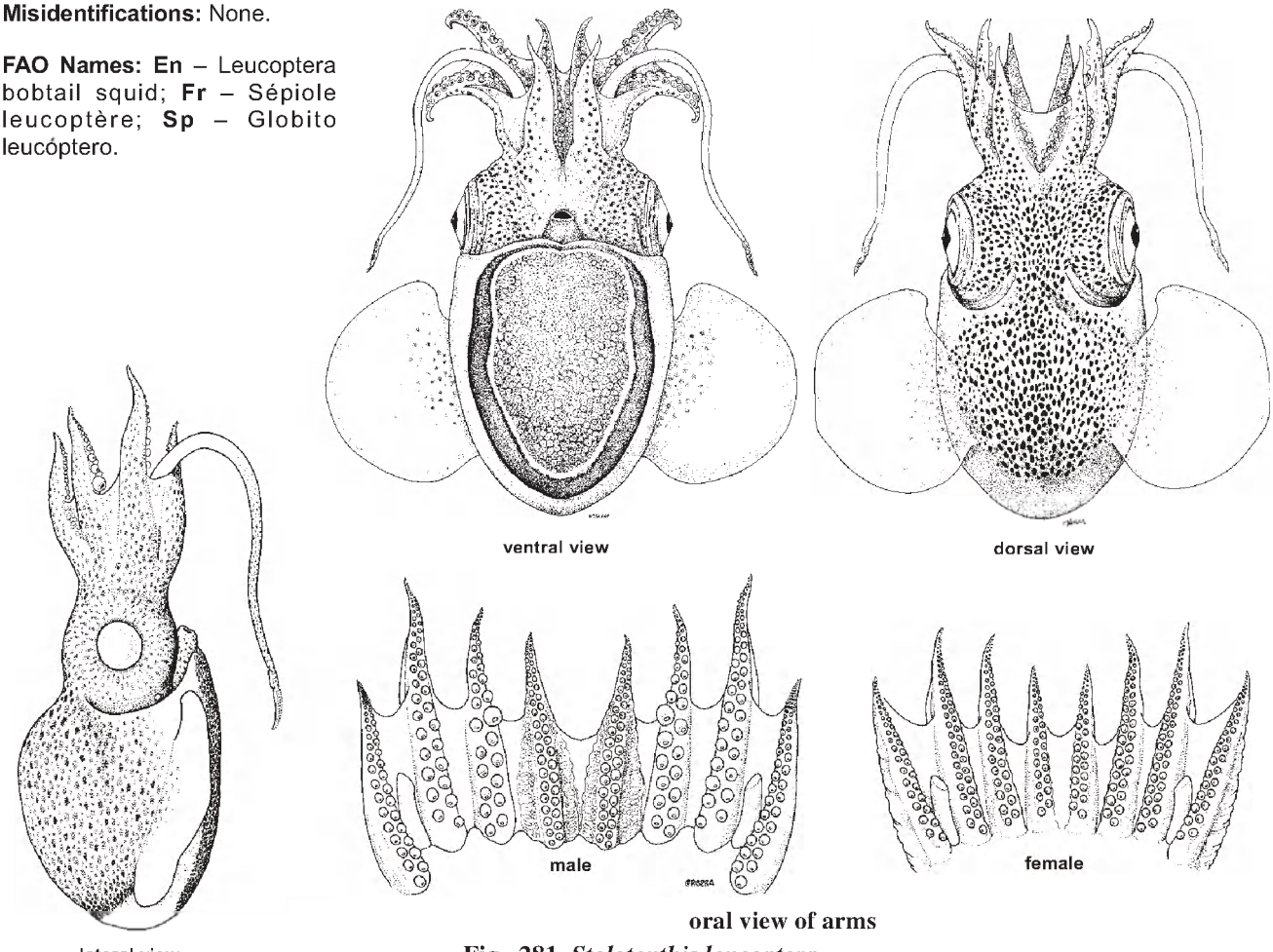


Fig. 281 ***Stoloteuthis leucoptera***

Diagnostic Features: Mantle with **marked median bulge dorsally**. Dorsal mantle fused to head, junction of mantle and head broad, **40 to 50% head width**; site of fusion lies considerably more dorsally than middle of eye level. Ventral mantle projects anteriorly only slightly, to about level of eyes. Ventral mantle broadly flattened into **dark shield-like structure**, with median anterior indentation. Fins long; positioned about midway along mantle; fin attachment short, fin length exceeds attachment length. Mantle-locking cartilage a simple straight ridge; funnel-locking cartilage a simple, straight narrow depression. Eyes small. Male and female arms short, muscular. All arms except ventral pair united by broad web. **First arm pair in males with thickened, cushion-like lateral membranes for 2/3 arm length and transverse bundles of finger-like structures adjacent to these** (function unknown). Arm sucker arrangement differs between sexes: in males, suckers biserial proximally, tetraserial at distal tips; in females, arm suckers biserial. Male **arms II with pair (3 rarely) of enlarged suckers at level of fifth and sixth sucker rows**. Club with 12 to 14 suckers in transverse rows. Club with lateral crest at base. Anal flaps well developed. Rounded light organ on ink sac, with 2 pores medially. **Colour:** In life brown on dorsal side of head, arms IV, central mantle and ventral shield, silvery laterally and posteriorly. **Blue along margin of shield, head and dorsum**. Fins large, almost transparent.

Size: Males up to 17 mm mantle length; females up to 18 mm mantle length.

Geographical Distribution: Amphi-Atlantic and the Mediterranean Sea: from the Gulf of St Lawrence to the Straits of Florida in the western Atlantic and in the Bay of Biscay in the Eastern Atlantic; Mediterranean Sea, including the northern and southern Tyrrhenian Sea, Ligurian Sea and Gorgona Island. Also recorded from the Benguela Current off Namibia. Possibly off eastern Tasmania (Fig. 282).

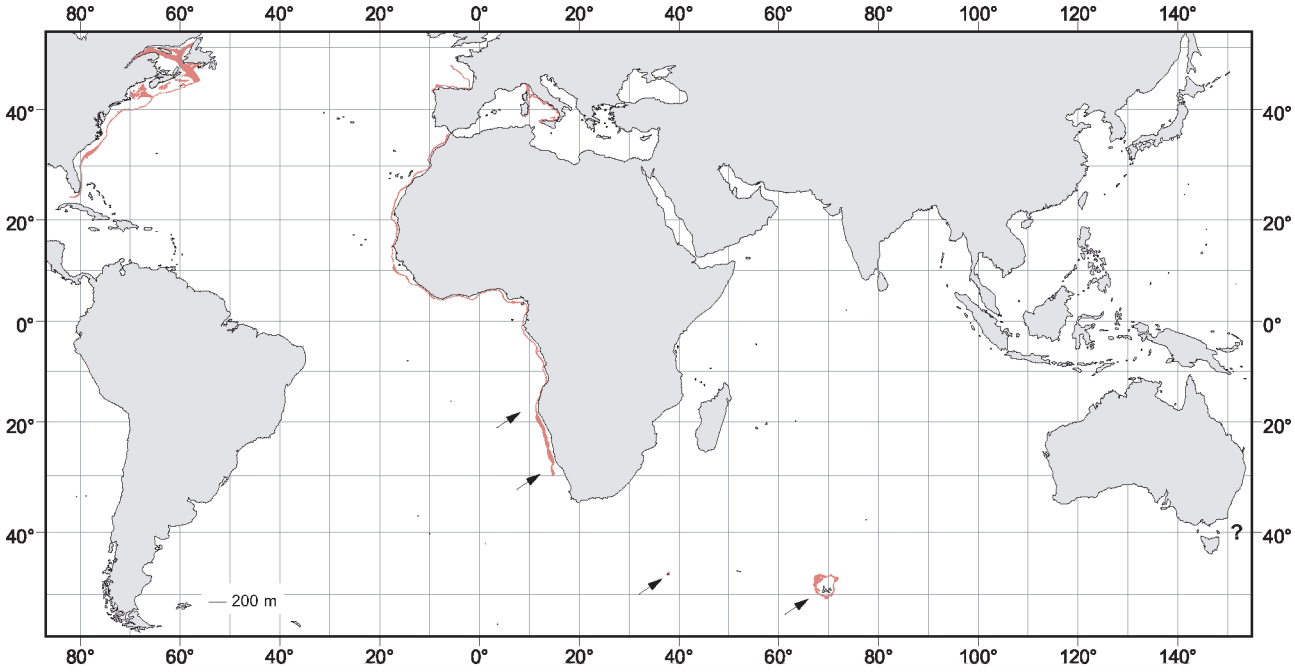


Fig. 282 ***Stoloteuthis leucoptera***
Known distribution

Habitat and Biology: Lower sublittoral and upper bathyal; depth range from 160 to 700 m. Possible diurnal activity in the upper mesopelagic.

Interest to Fisheries: Undetermined.

Remarks: Whether all recorded specimens of this widely distributed taxon are conspecific is unknown and needs to be investigated. A related, possibly identical, form has been found in the upper bathyal near the Kerguelens, Prince Edward Islands and on the Discovery Bank (southern Indian Ocean). There are only a few records of this species from the Mediterranean; it may be a recent introduction.

Literature: Joubin (1902a), Nesis (1987), Orsi Relini and Massi (1991), Guerra (1992), Villanueva and Sánchez (1993), Bello (1995), Volpi *et al.* (1995), Wurtz *et al.* (1995).

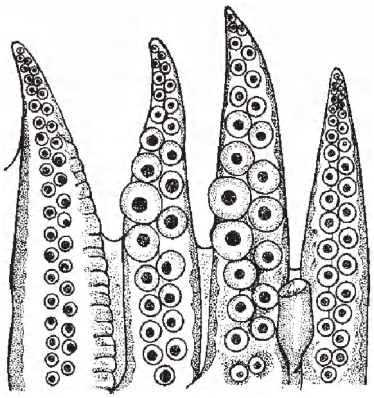
Sepiolina nipponensis (Berry, 1911) Fig. 283

Stoloteuthis nipponensis Berry, 1911b, *Zoologischer Anzeiger*, 37(2): 39 [type locality: Japan].

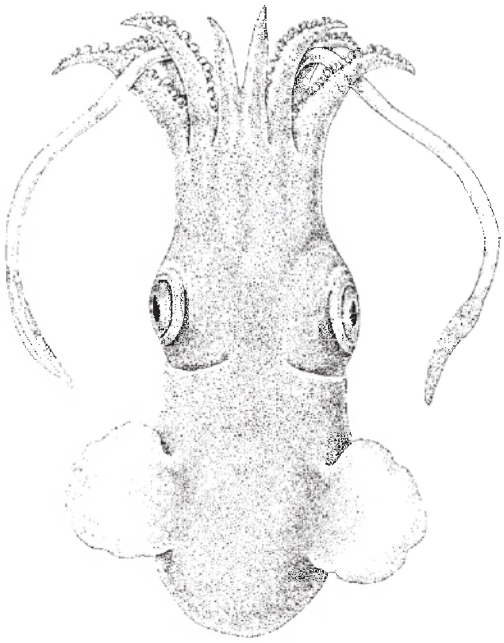
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Japanese bobtail squid; **Fr** – Sépiole japonaise; **Sp** – Sepiolina japonesa.

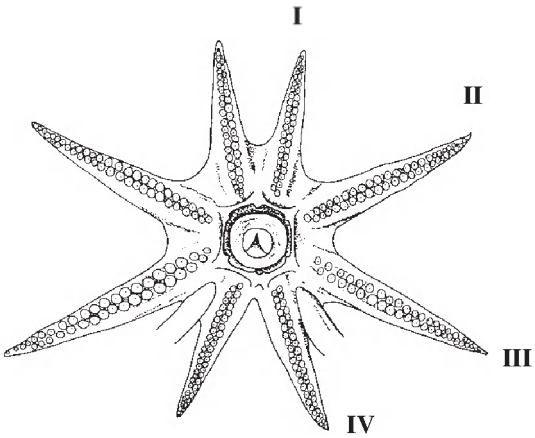


oral view of arms of male

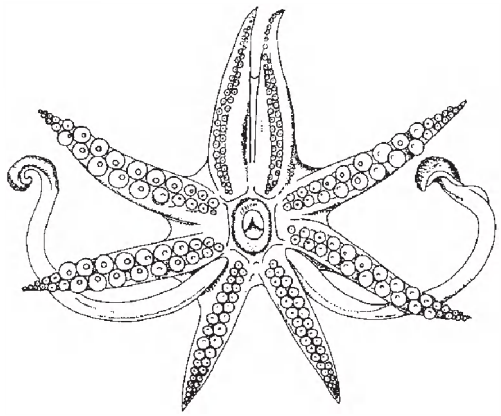


dorsal view

(illustration: K. Hollis/ABRS)



arms of female (oral view)



arms of male (oral view)

Fig. 283 *Sepiolina nipponensis*

Diagnostic Features: Mantle oval, or dome-shaped. Dorsal mantle fused to head; junction of dorsal mantle and head narrow, approximately 3 mm. Fins wide, ovate, short, lobe approximately 60% mantle length. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers biserial; female arm suckers numerous, small throughout; **male suckers enlarged on arms II and III** and to a lesser extent on arms IV. Females with higher average sucker counts than males. Hectocotylus present, both dorsal arms modified: oral surface of modified region swollen, fleshy; with transversely grooved ridges; suckers in dorsal and ventral series widely spaced, small. Club straight, slender; sucker-bearing face convex; with **13 to 16 suckers in transverse rows**; all suckers of similar minute size; swimming keel of club extends slightly proximal to carpus. Rounded light organ inside mantle cavity, on ink sac, visible through mantle in fresh specimens; light organ secretes a luminous cloud instead of ink. **Colour:** Body with numerous small chromatophores; ventral pigment present, dark; **ventral mantle margin encircled by silvery iridescent band, approximately 5 mm wide**, chromatophores peppered over band.

Size: Up to 25 mm mantle length.

Geographical Distribution: Western Pacific: southern Japan, Taiwan Province of China, the Philippines and the Great Australian Bight (southern Australia) (Fig. 284).

Habitat and Biology: Neritic.

Interest to Fisheries: Undetermined.

Remarks: Based on its distribution, it seems likely that more than a single species is present. This requires investigation.

Literature: Roper *et al.* (1984), Okutani *et al.* (1987), Okutani (1995), Lu (1998b), Reid and Norman (1998).

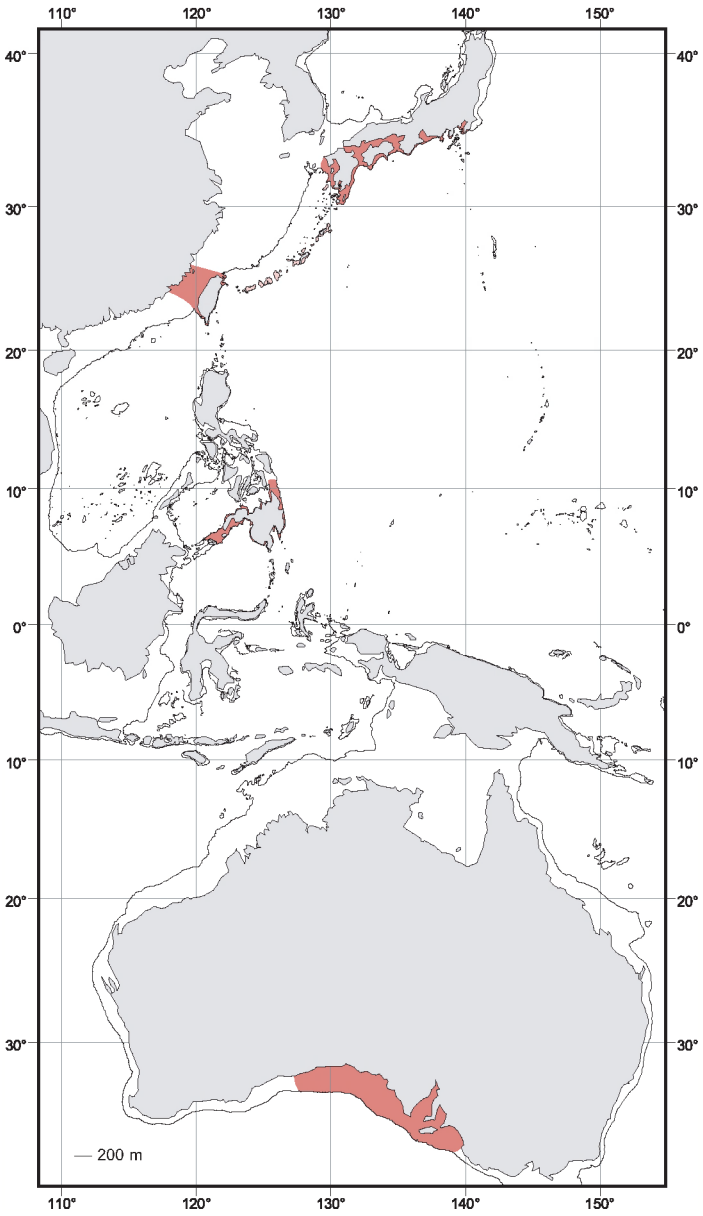


Fig. 284 ***Sepiolina nipponensis***
Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Heteroteuthis (Heteroteuthis) weberi Joubin, 1902

Heteroteuthis weberi Joubin, 1902a, *Bulletin de la Societe scientifique et medicale de l'Ouest*, 11: 401 [type locality: Indonesia].

Geographical Distribution: Indo-Pacific: central Indonesia.

Literature: Joubin (1902c), Nesis (1987), Reid and Norman (1998).

Heteroteuthis (Stephanoteuthis) dagamensis Robson, 1924

Heteroteuthis hawaiiensis var. *dagamensis* Robson, 1924b, *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 3: 11 [type locality: South Africa].

Geographical Distribution: Southeastern Atlantic and southwestern Indian Ocean: western, southern and southeastern Africa.

Literature: Robson (1924b).

Heteroteuthis (Stephanoteuthis) hawaiiensis (Berry, 1909)

Stephanoteuthis hawaiiensis Berry, 1909, *Proceedings of the United States National Museum*, 37(1713): 409 [type locality: Hawaiian Islands: near Kauai Island].

Size: Up to approximately 30 mm mantle length.

Geographical Distribution: Central and western Pacific: Hawaii, Bonin, Ryukyu Islands, Indonesia, Great Australian Bight. Possibly southwest Pacific, Banc Combe, 12º14'S 177º28'W, 795 to 820 m.

Literature: Young (1995), Lu and Boucher-Rodoni (2001).

Heteroteuthis (Stephanoteuthis) serventyi Allan, 1945

Heteroteuthis serventyi Allan, 1945, *Records of the Australian Museum*, 21(6): 340 [type locality: Australia: New South Wales, Jervis Bay].

Geographical Distribution: Southwestern Pacific: southeastern Australia.

Literature: Allan (1945).

Nectoteuthis pourtalesi Verrill, 1883

Nectoteuthis pourtalesi Verrill, 1883, *Bulletin of the Museum of Comparative Zoology*, 11(5): 108 [type locality: Barbados Island].

Geographical Distribution: Tropical western Atlantic: Florida and the Antilles. Bathybenthic.

Literature: Joubin (1902a).

Iridoteuthis iris (Berry, 1909)

Stoloteuthis iris Berry, 1909, *Proceedings of the United States National Museum*, 37(1713): 410 [type locality: Hawaiian Islands: off south coast of Molokai Island].

Size: Males up to 24 mm mantle length; females up to 28 mm mantle length.

Geographical Distribution: Northern central Pacific: Hawaiian Islands; southeast and northwest Hancock, Colahan and Kammu seamounts, Ceram Sea (doubtful). Pelagic, found in the open ocean.

Literature: Harman and Seki (1990), Young (1995).

Iridoteuthis maoria Dell, 1959

Iridoteuthis maoria Dell, 1959, *Zoology Publications from Victoria University of Wellington*, 25: 410 [type locality: New Zealand].

Geographical Distribution: Southwestern Pacific: New Zealand, North Island, Cook Strait, Chatham Rise. Nazca and Sala y Gomez submarine ridges (eastern Pacific).

Literature: Parin *et al.* (1997).

NEXT PAGE

3.3 Family SEPIADARIIDAE Fischer, 1882 *in* 1880–1887

by Amanda Reid

Sepiadariidae Fischer, 1882, *Manuel de Conchyliologie et de Paléontologie Conchyliologique ou histoire naturelle des Mollusques vivants et fossiles*, 1369 pages, 23 plates, London.

FAO names: En – Bottletail squids, bottle squids; **Fr** – Sépiolettes; **Sp** – Sepiolillas.

Diagnostic Features: Small. Dorsal mantle fused to head. Nuchal cartilage absent. Fins narrow, or short; ear-shaped, with pronounced anterior lobes, or 'earlets'; fin attachment long. Mantle and funnel-locking cartilages absent in ***Sepiadarium*** (mantle and funnel permanently fused) or with 2 components in ***Sepioloidea***. Non-hectocotylized arm sucker arrangement same in both sexes: biserial, sometimes tetraserial at middle and distal tips of arms. Hectocotylus present, left ventral arm modified: distal end of hectocotylus without suckers, pedicels modified forming series of transverse lamellae. Tentacle stalk held in deep sheath or web between bases of arms III and IV, web encircles base of tentacles on outside and inside forming cutaneous sac. Internal gladius absent. Light organs absent. Dorsal mantle surface covered with large, white leucophores surrounded by smaller red-brown chromatophores.

Size: Up to 40 mm mantle length.

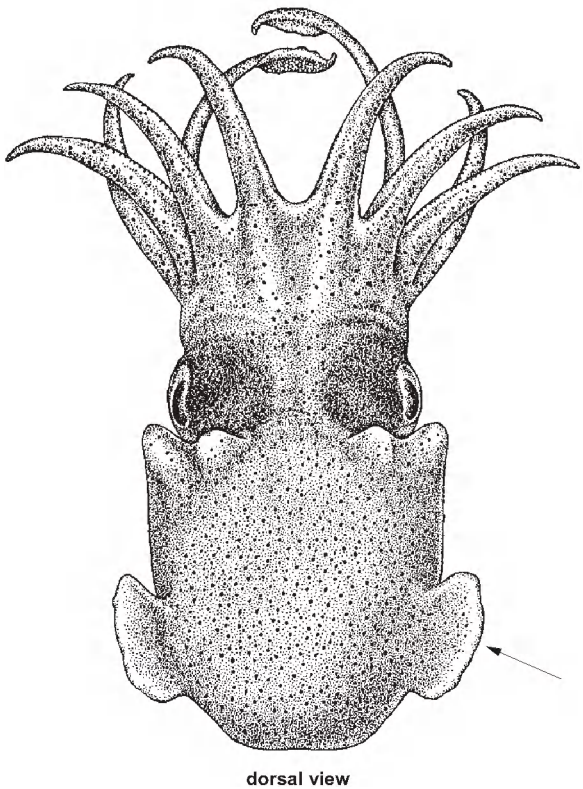
General Distribution: Found only in the western central Pacific, including Australia and New Zealand.

Habitat and Biology: Benthic. All species bury in the sand during the day and emerge at night to feed. All produce mucous from the underside of the body when disturbed.

Key to genera in the family Sepiadariidae

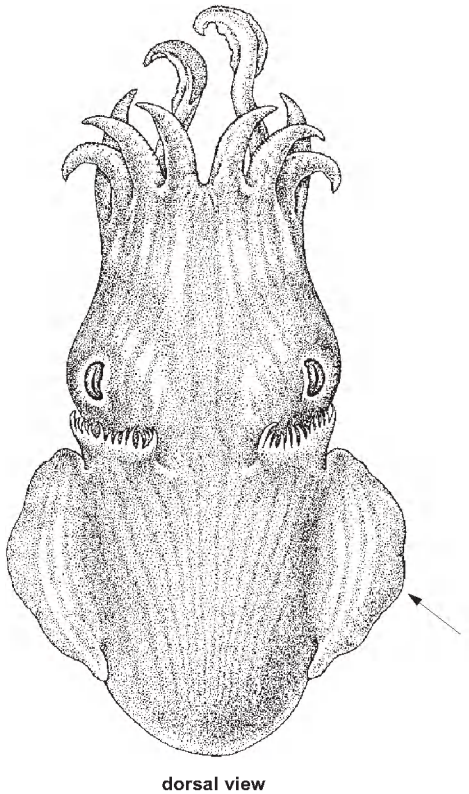
1a. Ventral mantle permanently connected to funnel by wide muscular band, funnel-locking apparatus absent; fins positioned in posterior half of mantle (Fig. 285) . . . . . ***Sepiadarium***

1b. Ventral mantle not permanently connected to funnel, funnel-locking apparatus present; fins extend along most of mantle length (Fig. 286) . . . . . ***Sepioloidea***



dorsal view

Fig. 285 *Sepiadarium*



dorsal view

Fig. 286 *Sepioloidea*

Sepiadarium austrinum Berry, 1921

Fig. 287; Plate VII, 42–44

Sepiadarium austrinum Berry, 1921, *Records of the South Australian Museum*, 1(4): 354 [type locality: South Australia: St Vincent Gulf].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Southern bottletail squid; **Fr** – Sépiolette du sud; **Sp** – Sepiolilla sureña.

Diagnostic Features: Dorsal mantle fused to head. Mantle cavity divided by thin septum. Ventral mantle fused to each side of proximal end of funnel. Fins short, do not exceed length of mantle anteriorly or posteriorly; attached within posterior half of mantle. Head broad, as wide as mantle. Male and female arms differ in relative lengths: arms I and II longer than III and IV. Non-hectocotylized arm sucker arrangement same in both sexes: **biserial, sometimes tetraserial at middle and distal tips of arms**. Hectocotylus present, left ventral arm modified: base of hectocotylus with **9 or 10 pairs of normal suckers; suckers replaced by single series of conical lamellae on distal end of hectocotylized arm**; arm grooved at distal tip, recurved dorsally, without protective membrane. Club with **6 suckers in transverse rows**; club with wide keel, not bound by distinct folds or continuous membranes. **Colour: Body transparent, yellow or orange, with large ovoid leucophores**.

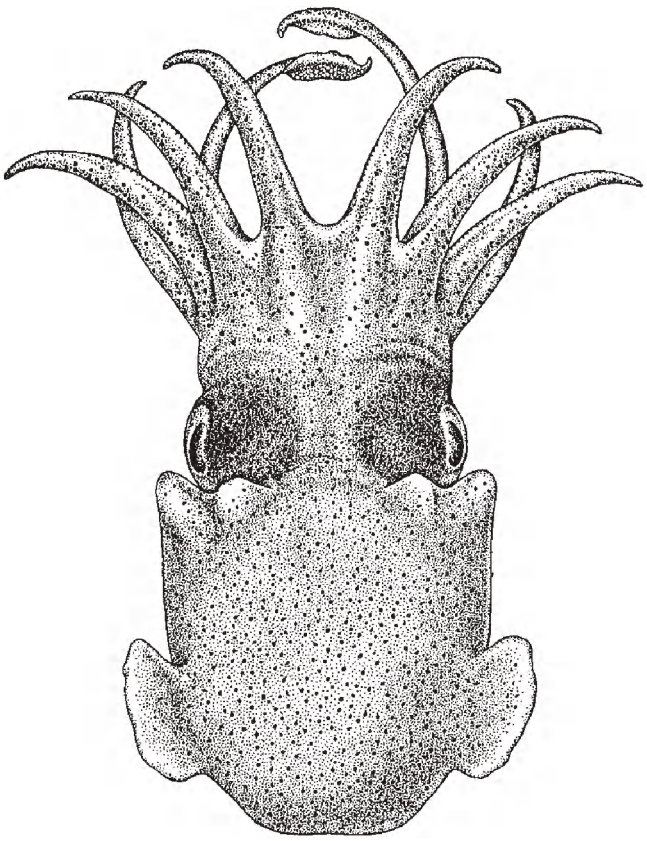
Size: Up to 30 mm mantle length.

Geographical Distribution: Southern Indo-Pacific: southern Australia (Fig. 288).

Habitat and Biology: This species is found in sandy habitats in sheltered waters. They bury in the sand during the day, with only the eyes showing; they emerge at night to feed over the sand and near seagrass beds. They can be maintained easily in aquaria, fed on amphipods, isopods and other small crustaceans. They are able to produce slime from glands on the ventral surface of the body. Both sexes mate from an early age, with immature females able to store sperm in a buccal pouch. Sand-coated eggs are attached to the base of seaweed or seagrass. The young settle soon after hatching.

Interest to Fisheries: Undetermined. This species may have a certain economic interest due to its easy survival in aquaria.

Literature: Lu and Dunning (1998), Norman (2000).



dorsal view

(illustration: K. Hollis)

Fig. 287 ***Sepiadarium austrinum***

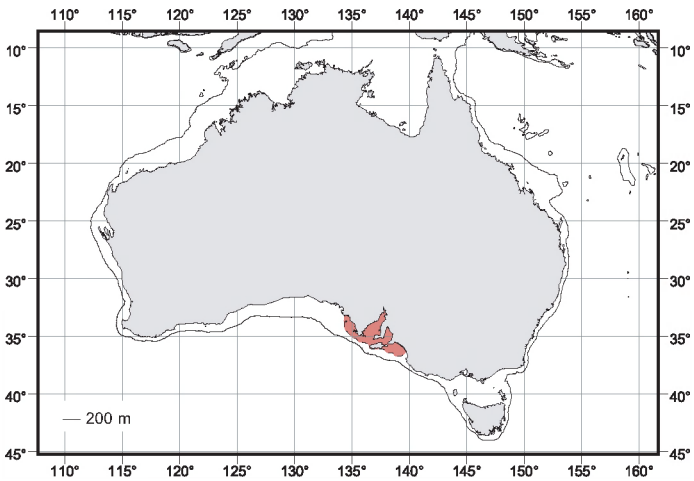


Fig. 288 ***Sepiadarium austrinum***
Known distribution

Sepiadarium kochii Steenstrup, 1881 **Fig. 289**

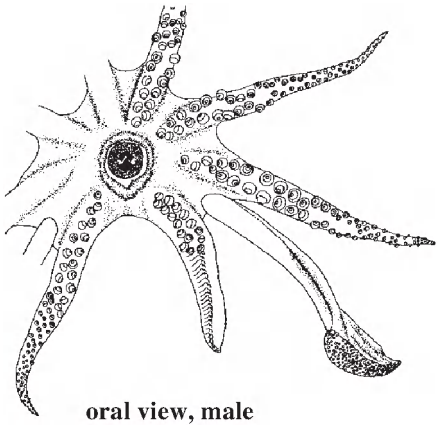
Sepiadarium kochii Steenstrup, 1881, *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 218 [type locality: Hong Kong, probably Deepwater Bay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Koch's bottletail squid; **Fr** – Sépiolette de Koch; **Sp** – Sepiolilla de Koch.

Diagnostic Features: Small, mantle dome-shaped. Dorsal mantle fused to head; length of fused portion approximately 1/4 mantle length. Mantle cavity divided by thin septum. Ventral mantle fused to each side of proximal end of funnel. Fins narrow; oblong; short, do not exceed length of mantle anteriorly or posteriorly; posteriorly with wide gap between them; attached along posterior half of mantle. Male and female arms subequal in length; arms I and II longer than III and IV. Non-hectocotylized arm sucker arrangement same in both sexes: **biserial basally, tetraserial over distal 20 transverse rows**. Hectocotylus present; left ventral arm modified: base of hectocotylus suckers normal, not modified; **18 to 20 fleshy lamellae over distal 2/3 of arm**, bordered by fold-like membrane; lamellae thick, longitudinally grooved transverse pads. Club with **8 suckers in transverse rows**; all suckers of similar minute size; very densely set. **Colour:** Dorsal mantle surface covered with **large, white leucophores surrounded by smaller red-brown chromatophores**.



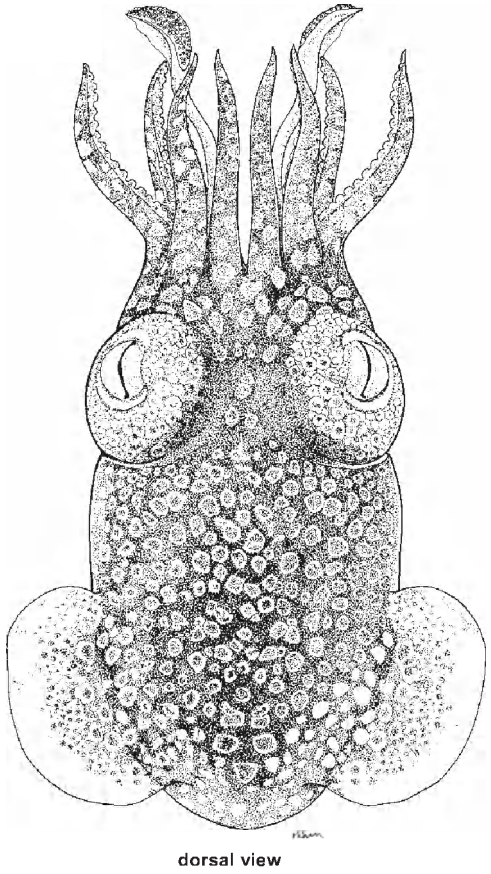


Fig. 289 *Sepiadarium kochii*

Size: Up to 30 mm mantle length.

Geographical Distribution: Indo-Pacific: throughout Indo-Malayan waters from Japan (Tokyo Bay, Pacific side and Toyama Bay (Japan Sea side), Taiwan Province of China and the South China Sea to India; southern Indonesia to New Guinea and northern Australia. The species has been reported from South Australia, though this record is unconfirmed (Fig. 290).

Habitat and Biology: Upper sublittoral; depth range to 60 m. Inhabits soft sediments. Remains buried during the day, then emerges at night to feed, primarily on small crustacea.

Interest to Fisheries: Undetermined.

Literature: Roper *et al.* (1984), Okutani *et al.* (1987), Okutani (1995), Lu (1998), Lu and Dunning (1998), Norman and Reid (1998).

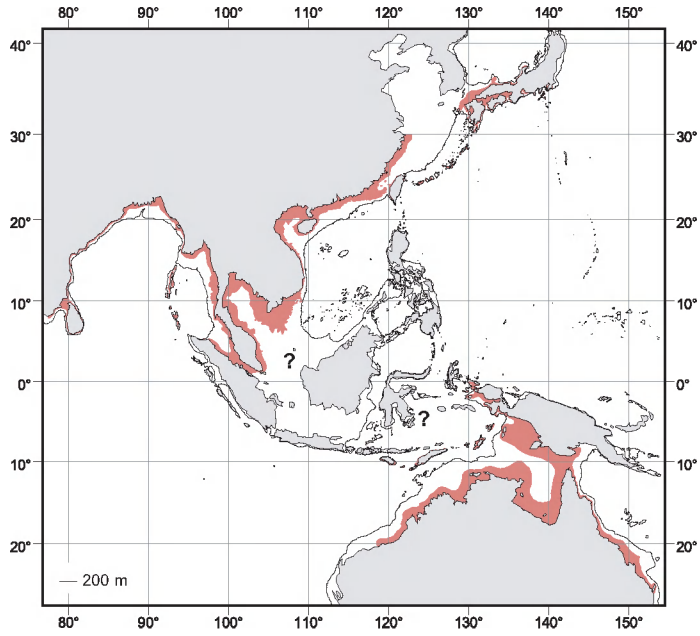


Fig. 290 *Sepiadarium kochii*
Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Sepiadarium auritum Robson, 1914

Sepiadarium auritum Robson, 1914, *Proceedings of the Zoological Society of London*, 1814: 678 [type locality: Western Australia: Monte Bello Islands, Hermite Island].

Size: Type specimen, 11 mm mantle length.

Geographical Distribution: Eastern Indian Ocean: northwestern Australia.

Literature: Robson (1914).

Sepiadarium gracilis Voss, 1962

Sepiadarium gracilis Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 170 [type locality: Philippines].

Geographical Distribution: Indo-Pacific: South China Sea, Western Philippines.

Literature: Voss (1962a).

Sepiadarium nipponianum Berry, 1932

Sepiadarium nipponianum Berry, 1932, *The Philippine Journal of Science*, 47(1): 42 [type locality: Japan].

Geographical Distribution: Western Pacific: Japan, southern Honshu, Shikoku, Kyushu.

Literature: Berry (1932).

Sepioloidea lineolata (Quoy and Gaimard, 1832) **Plate VII, 45–46**

Sepiola lineolata Quoy and Gaimard 1832, *Mollusques. Voyage de decouvertes de l'Astrolabe pendant les annees 1826–1827–1828–1829, Zoologie*, 2(1): 82 [type locality: southeastern Australia: Jervis Bay].

Size: Up to 50 mm mantle length.

Geographical Distribution:. Southern Indo-Pacific: eastern, southern and western Australia.

Literature: Norman and Reid (1998), Okutani (1995) Norman (2000).

Sepioloidea pacifica (Kirk, 1882)

Sepiola pacifica Kirk, 1882, *Transactions and Proceedings of the New Zealand Institute*, 14(42): 283 [type locality: New Zealand].

Geographical Distribution: Southern Pacific: New Zealand (western Pacific) and the Nazca and Sala y Gomez submarine ridges (eastern Pacific).

Literature: Parin *et al.* (1997), Lu and Dunning (1998).

3.4 Family IDIOSEPIIDAE Appellöf, 1898

Fig. 291 by Amanda Reid

Idiosepiidae Appellöf, 1898, Cephalopoden von Ternate, 2: Untersuchungen über *Idiosepius*, *Sepiadarium* und verwandte Formen. Ein Beitrag zur Beleuchtung der Hektokotylisation und ihrer systematischen Bedeutung. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 24(4): 570–637.

FAO names: En – Pygmy cuttlefishes; **Fr** – Seiches pygmées; **Sp** – Sepias pigmeas.

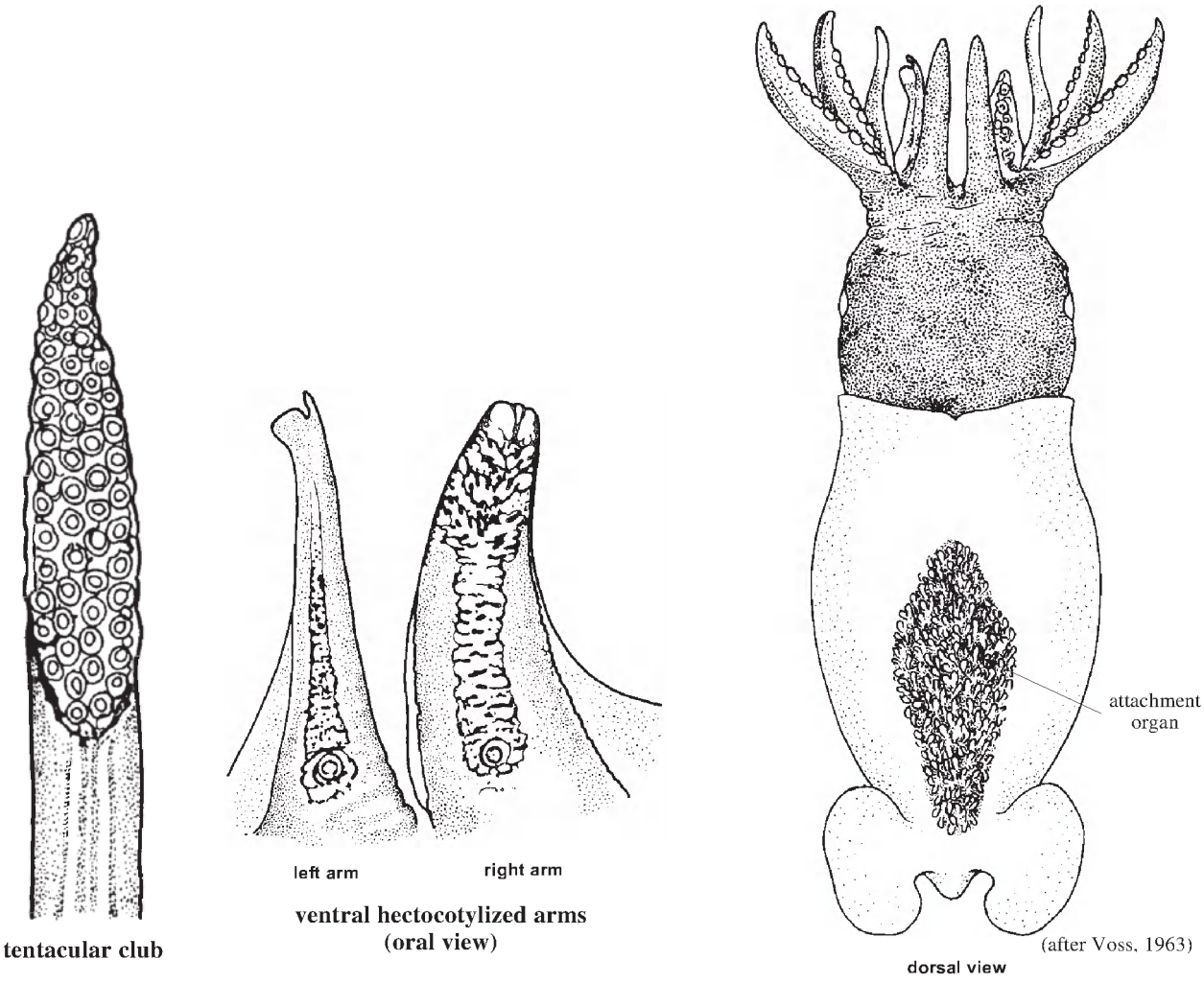


Fig. 291 Idiosepiidae

Diagnostic Features: Small animals (less than 25 mm mantle length). Mantle elongate, obovate; posterior mantle margin bluntly pointed at distal tip. Fins small, kidney-shaped, attached laterally to posterior end of mantle. Dorsal mantle not fused to head. Nuchal cartilage absent. Glandular oval attachment organ on dorsal posterior end of mantle. Arms short; arm suckers biserial. Arm suckers enlarged in males. Hectocotylus present, both ventral arms modified: right arm flattened, wide, with protective membranes, sometimes with transverse ridges and grooves, distal tip of left ventral arm bilobed; both arms mainly without suckers. Club with 2 to 4 suckers in transverse rows. Gladius absent. In females, right oviduct non-functional; eggs small, benthic. Development includes pelagic stage, but no metamorphosis occurs. All live near the coasts in shallow beds of seagrass or algae.

Interest to Fisheries: None.

Literature: Nesis (1987).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Idiosepius biserialis Voss, 1962

Idiosepius biserialis Voss, 1962b, *Transactions of the Royal Society of South Africa*, 36(4): 258 [type locality: South Africa].

Size: Females up to 10.5 mm mantle length.

Geographical Distribution: Southwestern Indian Ocean: southern Africa. Records from Andaman Sea, Thailand probably refer to ***I. thailandicus*** Chotiyaputta *et al.* (1991). Shallow waters inshore.

Literature: Hylleberg and Nateewathana (1991a), Okutani (1995), Norman and Lu (2000).

Idiosepius macrocheir Voss, 1962

Idiosepius macrocheir Voss, 1962b, *Transactions of the Royal Society of South Africa*, 36(4): 259 [type locality: South Africa].

Geographical Distribution: Southwestern Indian Ocean: Southern Africa. Shallow waters inshore.

Literature: Voss (1962b).

Idiosepius minimus (Orbigny, 1835)

Cranchia minimus Orbigny, 1835 (*in* Férussac and d'Orbigny, 1834–1848), Histoire Naturelle Générale et Particulière Céphalopodes Acétabuliferes Vivants et Fossiles, pl. 1, figs 4–5 [type locality: unreported].

Size: Up to 15 mm mantle length.

Geographical Distribution: 'Coast of Africa' fide (Berry 1932). Shallow, inshore waters.

Literature: Berry (1932).

Idiosepius notoides Berry, 1921

Idiosepius notoides Berry, 1921, *Records of the South Australian Museum*, 1(4): 361 [type locality: South Australia: Goolwa].

Size: Males up to 15.8 mm mantle length; females up to 25 mm mantle length.

Geographical Distribution: Southwestern Pacific: southern and eastern Australia. Shallow, inshore waters.

Literature: Burn (1959), Norman (2000).

Idiosepius paradoxus (Ortmann, 1888)

Microteuthis paradoxus Ortmann, 1888, *Japanische Cephalopoden. Zoologische Jahrbucher, (Systematik)*, 3: 649 [type locality: Japan: Bay of Tokyo, Kadsiyama].

Size: Up to 16 mm mantle length.

Geographical Distribution: Western Pacific: Japan, southern Hokkaido, Honshu, Kyushu. South Korea, northern Australia. Shallow, inshore waters.

Literature: Joubin (1902a), Natsukari (1970), Dong (1992), Okutani (1995), Norman and Lu (2000).

Idiosepius picteti (Joubin, 1894)

Loligo picteti Joubin, 1894, *Revue Suisse de Zoologie et Annales du Museum d'Historie Naturelle de Genève*, 2: 60 [type locality: Indonesia: Amboina].

Size: Up to 17 mm mantle length.

Geographical Distribution: Indo-Pacific: eastern Indonesia.

Literature: Joubin (1894).

Idiosepius pygmaeus Steenstrup, 1881

Idiosepius pygmaeus Steenstrup, 1881, *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 219 [type locality: South China Sea and 04°20'N 107°20'E].

Size: Up to 20 mm mantle length.

Geographical Distribution: Indo-Pacific: Japan, South China Sea, Philippines, Palau Islands, Indonesia, northern and northeastern Australia. Shallow, inshore waters.

Literature: Allan (1945), Moynihan (1983b), Jackson (1986, 1989), Yamamoto (1988), Hylleberg and Nateewathana (1991b), Lewis and Choat (1993), Okutani (1995), Semmens *et al.* (1995), Pecl and Moltschaniwshyj (1997), Reid and Norman (1998), Norman and Lu (2000).

Idiosepius thailandicus Chotiyaputta, Okutani and Chaitiamvong, 1991

Idiosepius thailandicus Chotiyaputta *et al.*, 1991, Venus, 50(3): 167 [type locality: Gulf of Thailand].

Geographical Distribution: Indo-Pacific: Thailand.

Literature: Okutani (1995), Nabhitabhata (1998).

3.5 Family SPIRULIDAE Owen, 1836

by Amanda Reid

Spirulidae, Owen 1836, Descriptions of some new and rare Cephalopoda, collected by Mr. George Bennet, Corr. Memb. Z. S. *Proceedings of the Zoological Society of London*, 37: 19–24

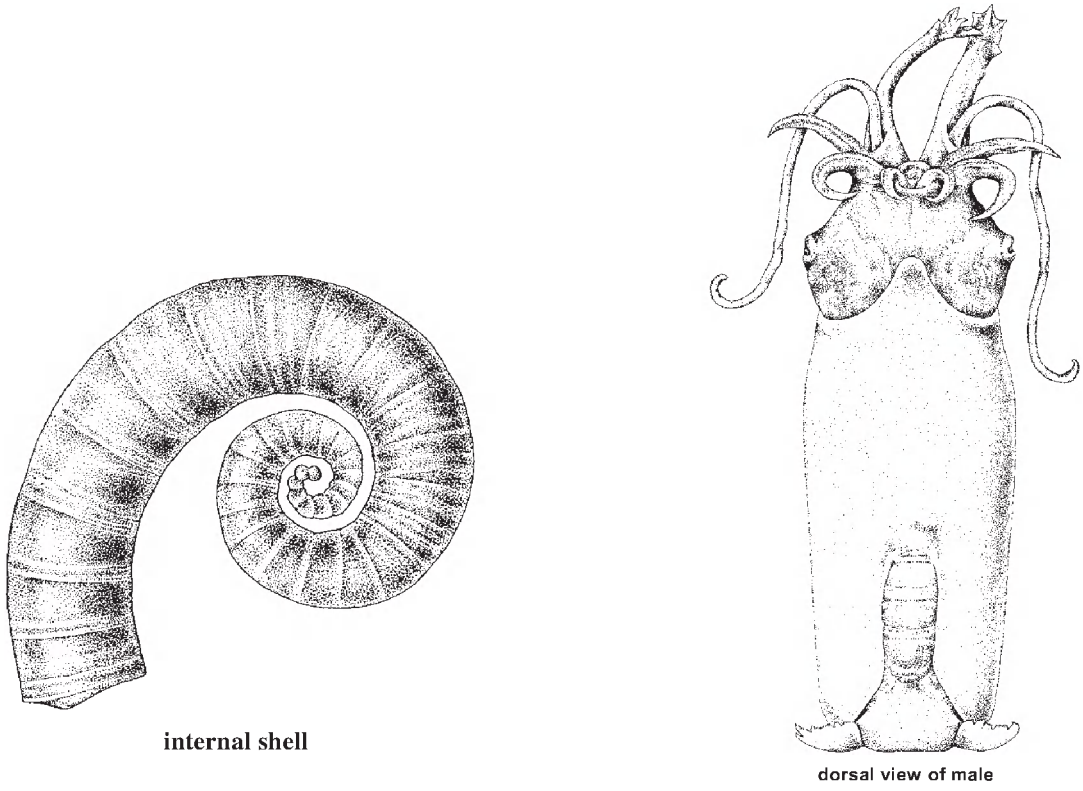
Spirula spirula (Linnaeus, 1758) Fig. 292

Nautilus spirula Linnaeus, 1758, *Systema Naturae per Regna tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis*, 710.

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Ram's horn squid; **Fr** – Spirule; **Sp** – Espírula.



(illustration: K. Hollis/ABRS)

Fig. 292 ***Spirula spirula***

Diagnostic Features: Mantle cylindrical, thin, muscular; dorsal anterior margin triangular, acute, free from head (not fused to head). Ventral mantle with 2 tongue-like projections from between which funnel protrudes. Fins narrow, ovate, with fringed anterior margins; short, do not exceed length of mantle anteriorly or posteriorly; attached dorsolaterally on posterior end of mantle (almost perpendicular to longitudinal axis of body). Mantle-locking cartilage a simple straight ridge; funnel-locking cartilage a simple, straight depression. Eyes large; ventral eyelids present. Arms increase in length dorsally to ventrally, with arms I short, arms IV longest. All arms except fourth pair united by broad webs. Non-hectocotylized arm sucker arrangement same in both sexes: arm suckers tetraserial, or in 6 rows. Hectocotylus present, both ventral arms modified: **right hectocotylized arm grooved, concave, with spoon-like expansion, pointed tip and 2 finger-like outgrowths; left hectocotylized arm round in cross-section with 2 spoon-like and one finger-like outgrowth with soft papillae at distal tip**. Tentacular club straight, slender; not expanded, same width as stalk; with 12 to 16 suckers in transverse rows; all suckers of similar small size. Radula absent. Buccal membrane in females with spermathecae. **Spirally coiled internal shell** present, located in posterior end of animal; shell comprised of over 30 chambers in adults. Large photophore present between fins, surrounded by annular fold of skin. **Colour:** Dark reddish brown. Luminescent.

Size: Rarely exceeds 45 mm mantle length.

Geographical Distribution: Tropical and subtropical oceanic waters worldwide, where the water temperature at 400 m is 10ºC or warmer (Fig. 293).

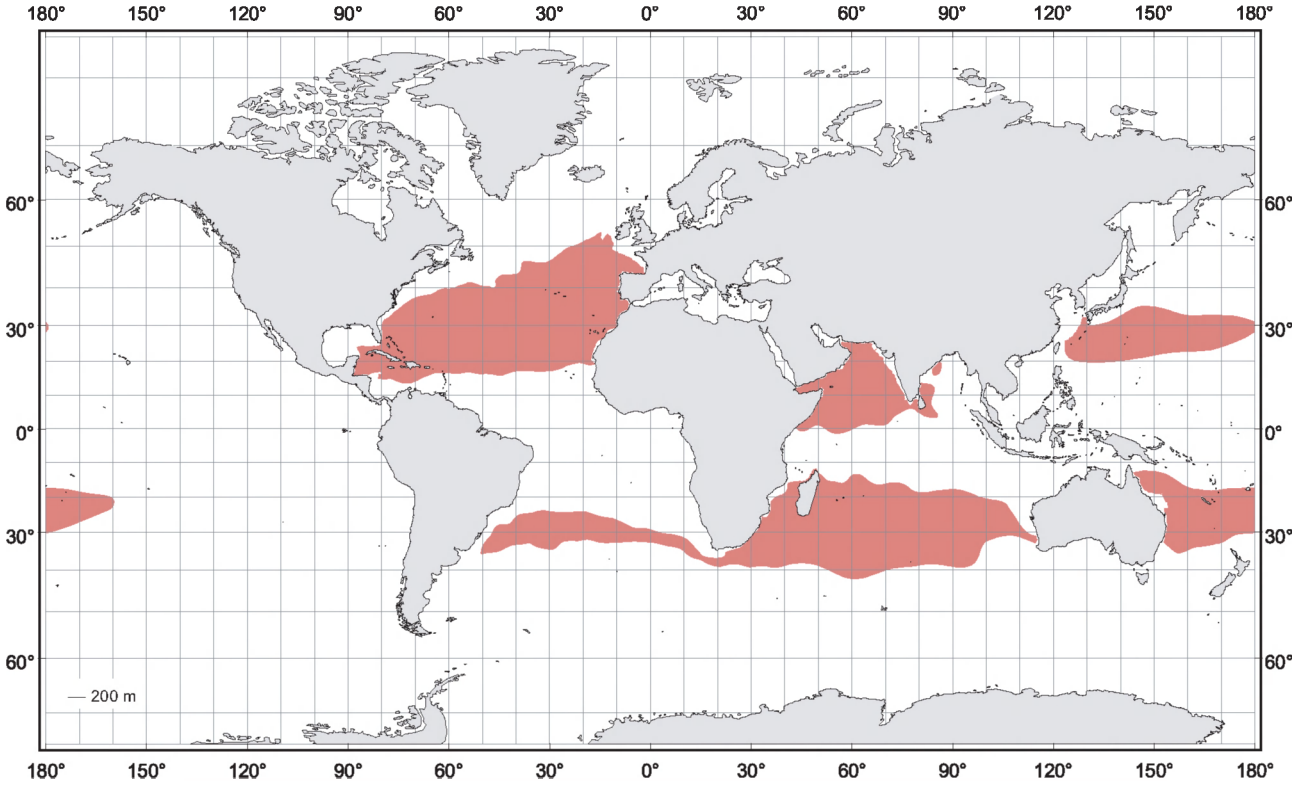


Fig. 293 ***Spirula spirula***
Known distribution

Habitat and Biology: This is a mesopelagic species, inhabiting from 600 to 700 m during the day and found in depths less than 300 m at night. Its common name is derived from the coiled shell, numbers of which are frequently washed ashore. The capture of young at depths between 1 000 and 1 750 m suggests that females possibly lay eggs on the bottom of continental slopes. Eggs are small and the smallest known paralarva has a 1.5 mm mantle length with two shell chambers. The species attains sexual maturity at about 30 mm mantle length (after 12 to 15 months of life), and the life span is estimated to be about 18 to 20 months. ***Spirula spirula*** is normally covered in a red-brown to silvery skin, which is often lost in trawled animals. Live animals have been seen to retract their head and arms into their mantle and close the opening with the pointed 'flaps' formed by the mantle. They take up a vertical position, head downwards, when at rest.

Interest to Fisheries: No direct interest to fishery exists, but the shells collected on the beach are sold in the shell trade.

Literature: Bruun (1943, 1955), Clarke (1970), Nesis (1987), Lu *et al.* (1992), Reid and Norman (1998).

NEXT PAGE

4. LIST OF NOMINAL SPECIES

The following list gives information (horizontally) in the order (i) the scientific name as it originally appeared, in alphabetical order according to the specific name; (ii) the author(s); (iii) date of publication; and (iv) present allocation.

NOMINAL SPECIES	PRESENT ALLOCATION
NAUTILIDAE	
Nautilus belauensis Saunders, 1981	*Nautilus belauensis*
Nautilus macromphalus Sowerby, 1849	*Nautilus macromphalus*
Nautilus perforatus Conrad, 1847	*Allonautilus perforatus*
Nautilus pompilius Linnaeus (1758)	*Nautilus pompilius*
Nautilus repertus Iredale, 1944	*Nautilus repertus*
Nautilus scrobiculatus Lightfoot, 1786	*Allonautilus scrobiculatus*
Nautilus stenomphalus Sowerby, 1849	*Nautilus stenomphalus*
SEPIIDAE	
Acanthosepion whitleyana Iredale, 1926	*Sepia whitleyana*
Arctosepia limata Iredale, 1926	*Sepia limata*
Arctosepia rhoda Iredale, 1954	*Sepia rhoda*
Blandosepia bartletti Iredale, 1954	*Sepia bartletti*
Blandosepia baxteri Iredale, 1940	*Sepia baxteri*
Doratosepion trygoninum Rochebrune, 1884	*Sepia trygonina*
Glyptosepia opipara Iredale, 1926	*Sepia opipara*
Hemisepius typicus Steenstrup, 1875	*Sepia typica*
Rhombosepion hieronis Robson, 1924a	*Sepia hieronis*
Rhombosepion robsoni Massy, 1927	*Sepia robsoni*
Sepia aculeata Van Hasselt, 1835	*Sepia aculeata*
Sepia acuminata Smith, 1916	*Sepia acuminata*
Sepia adami Roeleveld, 1972	*Sepia adami*
Sepia andreana Steenstrup, 1875	*Sepia andreana*
Sepia angulata Roeleveld, 1972	*Sepia angulata*
Sepia apama Gray, 1849	*Sepia apama*
Sepia appellofi Wülker, 1910	*Sepia appellofi*
Sepia arabica Massy, 1916	*Sepia arabica*
Sepia aureomaculata Okutani and Horikawa, 1987	*Sepia aureomaculata*
Sepia australis Quoy and Gaimard, 1832	*Sepia australis*
Sepia bandensis Adam, 1939b	*Sepia bandensis*
Sepia bathyalis Khromov, Nikitina and Nesis, 1991	*Sepia bathyalis*
Sepia bertheloti d'Orbigny, 1835	*Sepia bertheloti*
Sepia bidhaia Reid, 2000	*Sepia bidhaia*
Sepia braggi Verco, 1907	*Sepia braggi*
Sepia brevimana Steenstrup, 1875	*Sepia brevimana*
Sepia burnupi Hoyle, 1904	*Sepia burnupi*
Sepia carinata Sasaki, 1920	*Sepia carinata*
Sepia chirotrema Berry, 1918	*Sepia chirotrema*
Sepia confusa Smith, 1916	*Sepia confusa*
Sepia cottoni Adam, 1979	*Sepia cottoni*
Sepia cultrata Hoyle, 1885	*Sepia cultrata*
Sepia dollfusi Adam, 1941b	*Sepia dollfusi*
Sepia dubia Adam and Rees, 1966	*Sepia dubia*

Sepia elegans Blainville, 1827	*Sepia elegans*
Sepia elliptica Hoyle, 1885	*Sepia elliptica*
Sepia elobyana Adam, 1941a	*Sepia elobyana*
Sepia elongata d'Orbigny, 1839–1842	*Sepia elongata*
Sepia erostrata Sasaki, 1929	*Sepia erostrata*
Sepia esculenta Hoyle, 1885	*Sepia esculenta*
Sepia faurei Roeleveld, 1972	*Sepia faurei*
Sepia filibrachia Reid and Lu, 2005	*Sepia filibrachia*
Sepia foliopeza Okutani and Tagawa, 1987	*Sepia foliopeza*
Sepia gibba Ehrenberg, 1831	*Sepia gibba*
Sepia grahami Reid, 2001b	*Sepia grahami*
Sepia hedleyi Berry, 1918	*Sepia hedleyi*
Sepia hierredda Rang, 1835	*Sepia hierredda*
Sepia incerta Smith, 1916	*Sepia incerta*
Sepia inermis Van Hasselt, 1835	*Sepiella inermis*
Sepia insignis Smith, 1916	*Sepia insignis*
Sepia irvingi Meyer, 1909	*Sepia irvingi*
Sepia ivanovi Khromov, 1982	*Sepia ivanovi*
Sepia joubini Massy, 1927	*Sepia joubini*
Sepia kiensis Hoyle, 1885	*Sepia kiensis*
Sepia kobiensis Hoyle, 1885	*Sepia kobiensis*
Sepia koilados Reid, 2000	*Sepia koilados*
Sepia latimanus Quoy and Gaimard, 1832	*Sepia latimanus*
Sepia longipes Sasaki, 1913	*Sepia longipes*
Sepia lorigera Wülker, 1910	*Sepia lorigera*
Sepia lycidas Gray, 1849	*Sepia lycidas*
Sepia madokai Adam, 1939a	*Sepia madokai*
Sepia mascarensis Filippova and Khromov, 1991	*Sepia mascarensis*
Sepia mestus Gray, 1849	*Sepia mestus*
Sepia mirabilis Khromov, 1988	*Sepia mirabilis*
Sepia murrayi Adam and Rees, 1966	*Sepia murrayi*
Sepia novaehollandiae Hoyle, 1909	*Sepia novaehollandiae*
Sepia officinalis Linné, 1758	*Sepia officinalis*
Sepia omani Adam and Rees, 1966	*Sepia omani*
Sepia orbignyana Férussac *in* d'Orbigny, 1826	*Sepia orbignyana*
Sepia ornata Rang, 1837	*Sepiella ornata*
Sepia papillata Quoy and Gaimard, 1832	*Sepia papillata*
Sepia papuensis Hoyle, 1885	*Sepia papuensis*
Sepia pardex Sasaki, 1913	*Sepia pardex*
Sepia peterseni Appellöf, 1886	*Sepia peterseni*
Sepia (Metasepia) pfefferi Hoyle, 1885	*Metasepia pfefferi*
Sepia pharaonis Ehrenberg, 1831	*Sepia pharaonis*
Sepia plana Lu and Reid, 1997	*Sepia plana*
Sepia plangon Gray, 1849	*Sepia plangon*
Sepia plathyconchalis Filippova and Khromov, 1991	*Sepia plathyconchalis*
Sepia prabahari Neethiselvan and Venkataramani, 2002	*Sepia prabahari*
Sepia prashadi Winckworth, 1936	*Sepia prashadi*
Sepia pulchra Roeleveld and Liltved, 1985	*Sepia pulchra*

Sepia ramani Neethiselvan, 2001	*Sepia ramani*
Sepia recurvirostra Steenstrup, 1875	*Sepia recurvirostra*
Sepia reesi Adam, 1979	*Sepia reesi*
Sepia savignyi Blainville, 1827	*Sepia savignyi*
Sepia saya Khomov, Nikitina and Nesis 1991	*Sepia saya*
Sepia senta Lu and Reid, 1997	*Sepia senta*
Sepia sewelli Adam and Rees, 1966	*Sepia sewelli*
Sepia simoniana Thiele, 1920	*Sepia simoniana*
Sepia smithi Hoyle, 1885	*Sepia smithi*
Sepia sokotriensis Khromov, 1988	*Sepia sokotriensis*
Sepia stellifera Homenko and Khromov, 1984	*Sepia stellifera*
Sepia subplana Lu and Boucher-Rodoni, 2001	*Sepia subplana*
Sepia subtenuipes Okutani and Horikawa, 1987	*Sepia subtenuipes*
Sepia sulcata Hoyle, 1885	*Sepia sulcata*
Sepia tala Khromov, Nikitina and Nesis, 1991	*Sepia tala*
Sepia tanybracheia Reid, 2000	*Sepia tanybracheia*
Sepia tenuipes Sasaki, 1929	*Sepia tenuipes*
Sepia thurstoni Adam and Rees, 1966	*Sepia thurstoni*
Sepia tokioensis Ortmann, 1888	*Sepia tokioensis*
Sepia tuberculata Lamarck, 1798	*Sepia tuberculata*
Sepia tullbergi Appellöf, 1886	*Metasepia tullbergi*
Sepia vercoi Adam, 1979	*Sepia vercoi*
Sepia vermiculata Quoy and Gaimard, 1832	*Sepia vermiculata*
Sepia vietnamica Khromov, 1987	*Sepia vietnamica*
Sepia vossi Khromov, 1987	*Sepia vossi*
Sepia zanzibarica Pfeffer, 1884	*Sepia zanzibarica*
Sepiella cyanea Robson, 1924b	*Sepiella cyanea*
Sepiella japonica Sasaki, 1929	*Sepiella japonica*
Sepiella mangkangunga Reid and Lu, 1998	*Sepiella mangkangunga*
Sepiella ocellata Pfeffer, 1884	*Sepiella ocellata*
Sepiella weberi Adam, 1939a	*Sepiella weberi*
Solitosepia plagon adhaesa Iredale, 1926	*Sepia plagon*
Solitosepia rozella Iredale, 1926	*Sepia rozella*
Tenuisepia mira Cotton, 1932	*Sepia mira*
SEPIOLIDAE	
Euprymna albatrossae Voss, 1962a	*Euprymna albatrossae*
Euprymna berryi Sasaki, 1929	*Euprymna berryi*
Euprymna hoylei Adam, 1986	*Euprymna hoylei*
Euprymna hyllebergi Nateewathana, 1997	*Euprymna hyllebergi*
Euprymna phenax Voss, 1962a	*Euprymna phenax*
Euprymna scolopes Berry, 1913	*Euprymna scolopes*
Euprymna stenodactyla Grant, 1833	*Euprymna stenodactyla*
Fidenas penares Gray, 1849	*Euprymna penares*
Inioteuthis capensis Voss, 1962	*Inioteuthis capensis*
Inioteuthis maculosa Goodrich, 1896	*Inioteuthis maculosa*
Inioteuthis morsei Verrill, 1881	*Euprymna morsei*
Sepietta minor Naef, 1912a	*Rondeletiola minor*
Sepietta neglecta Naef, 1916	*Sepietta neglecta*

Sepietta obscura Naef, 1916	*Sepietta obscura*
Sepiola affinis Naef, 1912b	*Sepiola affinis*
Sepiola atlantica Orbigny, 1839–1842	*Sepiola atlantica*
Sepiola aurantiaca Jatta, 1896	*Sepiola aurantiaca*
Sepiola birostrata Sasaki, 1918	*Sepiola birostrata*
Sepiola intermedia Naef, 1912a	*Sepiola intermedia*
Sepiola japonica Orbigny, 1845	*Inioteuthis japonica*
Sepiola knudseni Adam, 1984	*Sepiola knudseni*
Sepiola ligulata Naef, 1912a	*Sepiola ligulata*
Sepiola oweniana Orbigny, 1839–1841	*Sepietta oweniana*
Sepiola parva Sasaki, 1913	*Sepiola parva*
Sepiola petersi Steenstrup, 1887	*Sepietta petersi*
Sepiola pfefferi Grimpe, 1921	*Sepiola pfefferi*
Sepiola robusta Naef, 1912a	*Sepiola robusta*
Sepiola rondeleti Leach, 1834	*Sepiola rondeleti*
Sepiola rossiaeformis Pfeffer, 1884	*Sepiola rossiaeformis*
Sepiola steenstrupiana Levy, 1912	*Sepiola steenstrupiana*
Sepiola tasmanica Pfeffer, 1884	*Euprymna tasmanica*
Sepiola trirostrata Voss, 1962a	*Sepiola trirostrata*
Subfamily ROSSIINAE	
Heteroteuthis tenera Verrill, 1880	*Semirossia tenera*
Neorossia leptodons Reid, 1992	*Neorossia leptodons*
Sepiola macrosoma Delle Chiaie, 1830	*Rossia macrosoma*
Rossia antillensis Voss, 1955	*Austrorossia antillensis*
Rossia (Austrorossia) australis Berry, 1918	*Austrorossia australis*
Rossia bipapillata Sasaki, 1920	*Austrorossia bipapillata*
Rossia brachyura Verrill, 1883	*Rossia brachyura*
Rossia bullisi Voss, 1956	*Rossia bullisi*
Rossia caroli Joubin, 1902b	*Neorossia caroli*
Rossia enigmatica Robson, 1924a	*Austrorossia enigmatica*
Rossia (Semirossia) equalis Voss, 1950	*Semirossia equalis*
Rossia glaucopis Loven, 1845	*Rossia glaucopis*
Rossia mastigophora Chun, 1915	*Austrorossia mastigophora*
Rossia megaptera Verrill, 1881	*Rossia megaptera*
Rossia moelleri Steenstrup, 1856	*Rossia moelleri*
Rossia mollicella Sasaki, 1920	*Rossia mollicella*
Rossia pacifica diegensis Berry, 1912b	*Rossia pacifica diegensis*
Rossia pacifica pacifica Berry, 1911a	*Rossia pacifica pacifica*
Rossia palpebrosa Owen, 1834	*Rossia palpebrosa*
Rossia patagonica Smith, 1881	*Semirossia patagonica*
Rossia tortugaensis Voss, 1956	*Rossia tortugaensis*
Subfamily HETEROTEUTHINAE	
Heteroteuthis hawaiiensis var. *dagamensis* Robson, 1924b	*Heteroteuthis (Stephanoteuthis) dagamensis*
Heteroteuthis serventyi Allan, 1945	*Heteroteuthis (Stephanoteuthis) serventyi*
Heteroteuthis weberi Joubin, 1902a	*Heteroteuthis (Heteroteuthis) weberi*
Iridoteuthis maoria Dell, 1959	*Iridoteuthis maoria*
Nectoteuthis pourtalesi Verrill, 1883	*Nectoteuthis pourtalesi*
Sepiola leucoptera Verrill, 1878	*Stoloteuthis leucoptera*

Sepiola dispar Rüppell, 1844	*Heteroteuthis (Heteroteuthis) dispar*
Stephanoteuthis hawaiiensis Berry, 1909	*Heteroteuthis (Stephanoteuthis) hawaiiensis*
Stoloteuthis nipponensis Berry, 1911b	*Sepiolina nipponensis*
Stoloteuthis iris Berry, 1909	*Iridoteuthis iris*
SEPIADARIIDAE	
Sepiadarium auritum Robson, 1914	*Sepiadarium auritum*
Sepiadarium austrinum Berry, 1921	*Sepiadarium austrinum*
Sepiadarium gracilis Voss, 1962a	*Sepiadarium gracilis*
Sepiadarium kochii Steenstrup, 1881	*Sepiadarium kochii*
Sepiadarium nipponianum Berry, 1932	*Sepiadarium nipponianum*
Sepiola lineolata Quoy and Gaimard, 1832	*Sepioloidea lineolata*
Sepiola pacifica Kirk, 1882	*Sepioloidea pacifica*
IDIOSEPIIDAE	
Cranchia minimus Orbigny, 1835	*Idiosepius minimus*
Idiosepius biserialis Voss, 1962b	*Idiosepius biserialis*
Idiosepius macrocheir Voss, 1962b	*Idiosepius macrocheir*
Idiosepius notoides Berry, 1921	*Idiosepius notoides*
Idiosepius pygmaeus Steenstrup, 1881	*Idiosepius pygmaeus*
Idiosepius thailandicus Chotiyaputta *et al*., 1991	*Idiosepius thailandicus*
Loligo picteti Joubin, 1894	*Idiosepius picteti*
Microteuthis paradoxus Ortmann, 1888	*Idiosepius paradoxus*
SPIRULIDAE	
Nautilus spirula Linnaeus, 1758	*Spirula spirula*

5. LIST OF SPECIES BY MAJOR FISHING AREAS

SPECIES	page	GEOGRAPHICAL DISTRIBUTION — MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Nautilus macromphalus	52															●				
Nautilus pompilius	53											●				●				
Nautilus belauensis	54															●				
Nautilus repertus	54											●								
Nautilus stenomphalus	54															●				
Allonautilus scrobiculatus	55															●				
Allonautilus perforatus	55											(?)				●				
Metasepia pfefferi	60											●				●				
Metasepia tullbergi	61													●		●				
Sepia aculeata	63										●	●		●		●				
Sepia andreana	65													●		●				
Sepia apama	67											●				●		●		
Sepia arabica	69										●									
Sepia australis	70								●		●									
Sepia bandensis	72											●				●				
Sepia bertheloti	73					●			●											
Sepia braggi	75											●						●		
Sepia brevimana	77										●	●				●				
Sepia cultrata	78											●				●		●		
Sepia elegans	79			●		●	●		●											
Sepia elliptica	81											●				●				
Sepia elobyana	82					●														
Sepia esculenta	84													●		●				
Sepia grahami	86															●		●		
Sepia hedleyi	87											●				●		●		
Sepia hierredda	88					●			●											
Sepia kobiensis	89										●	●		●		●				
Sepia latimanus	91										●	●		●		●				
Sepia longipes	93													●						
Sepia lorigera	94													●		●				
Sepia lycidas	95											●		●		●				
Sepia madokai	97													●		●				
Sepia murrayi	98										●									
Sepia officinalis	99			●		●	●													
Sepia omani	101										●									
Sepia opipara	102										●					●		●		

SPECIES	page	GEOGRAPHICAL DISTRIBUTION MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																	
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Sepia orbignyana	103			●		●	●		●											
Sepia papuensis	105											●				●		●		
Sepia pharaonis	106										●	●		●		●				
Sepia plangon	109															●		●		
Sepia prabahari	110										●	●								
Sepia prashadi	111										●	●								
Sepia ramani	113										●	●								
Sepia recurvirostra	114											●		●		●				
Sepia rozella	116															●		●		
Sepia savignyi	117										●									
Sepia smithi	118											●				●				
Sepia stellifera	119										●	●				●				
Sepia sulcata	120											●				●				
Sepia trygonina	122										●									
Sepia vermiculata	124								●		●									
Sepia vietnamica	125													●		●				
Sepia vossi	127													●		●				
Sepia whitleyana	128															●		●		
Sepia zanzibarica	129								●		●									
Sepiella inermis	130										●	●		●		●				
Sepiella japonica	132													●						
Sepiella ornata	134					●			●											
Sepiella weberi	135											●								
Sepia acuminata	137								●		●									
Sepia adami	137										●									
Sepia angulata	137								●											
Sepia appellofi	137													●						
Sepia aureomaculata	138													●						
Sepia bartletti	138															●				
Sepia bathyalis	138										●									
Sepia baxteri	138																	●		
Sepia bidhaia	139															●				
Sepia burnupi	139								●		●									
Sepia carinata	139													●		●				
Sepia chirotrema	139											●								
Sepia confusa	140								●		●									
Sepia cottoni	140											●								
Sepia dollfusi	140										●									

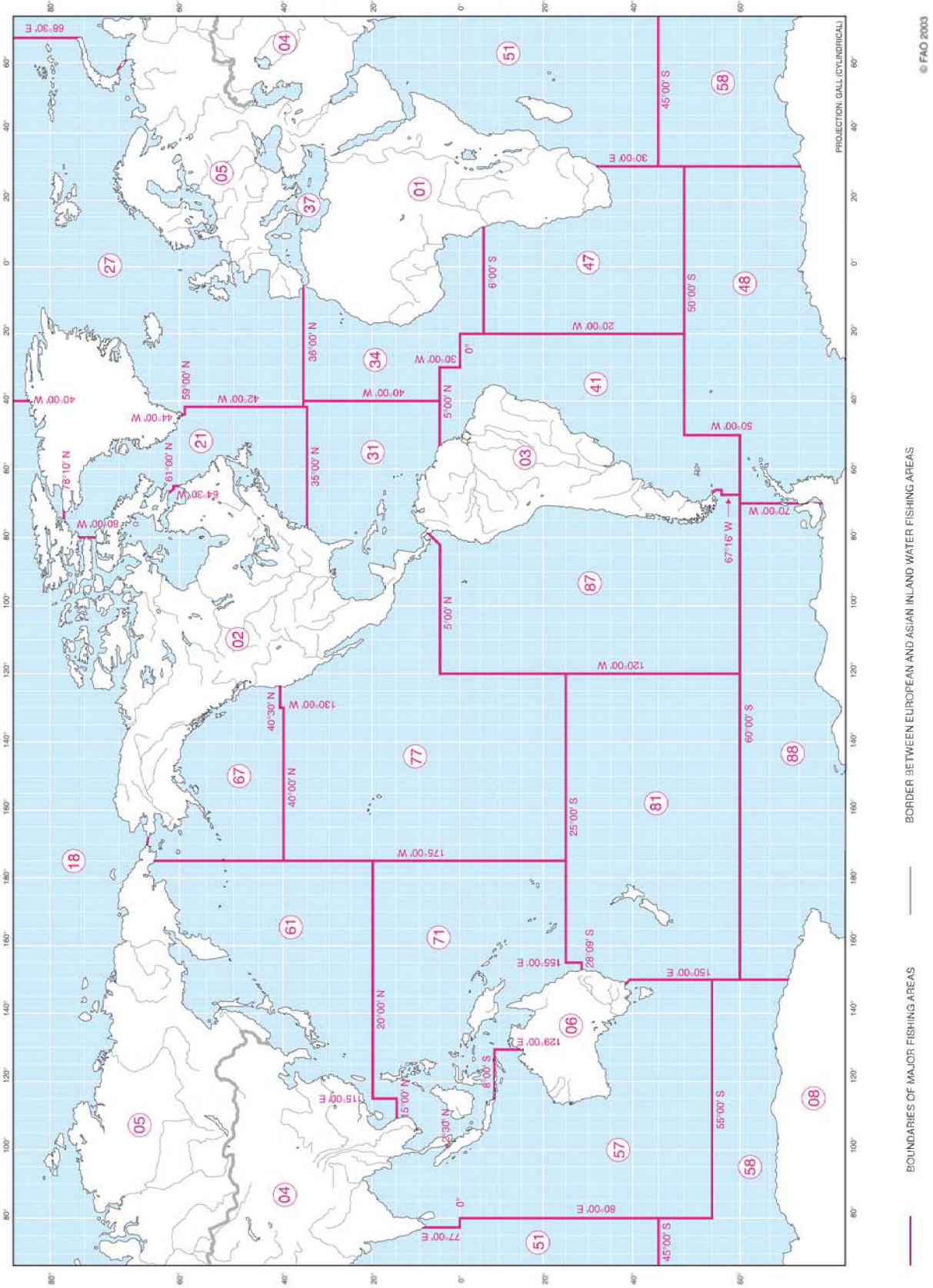
SPECIES	page	GEOGRAPHICAL DISTRIBUTION — MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																	
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Sepia dubia	140								●											
Sepia elongata	141										●									
Sepia erostrata	141													●						
Sepia faurei	141								●											
Sepia foliopeza	141													●		●				
Sepia gibba	142										●									
Sepia hieronis	142								●		●									
Sepia incerta	142								●		●									
Sepia insignis	142								●		●									
Sepia irvingi	143											●								
Sepia ivanovi	143										●									
Sepia joubini	143								●		●									
Sepia kiensis	143											●				●				
Sepia koilados	144											●								
Sepia limata	144															●		●		
Sepia mascarensis	144										●									
Sepia mestus	144															●		●		
Sepia mira	145																	●		
Sepia mirabilis	145										●									
Sepia novaehollandiae	145											●						●		
Sepia papillata	145								●		●									
Sepia pardex	146													●						
Sepia peterseni	146													●						
Sepia plana	146											●								
Sepia plathyconchalis	146										●									
Sepia pulchra	147								●											
Sepia reesi	147											●								
Sepia rhoda	147											●				●				
Sepia robsoni	147								●											
Sepia saya	148										●									
Sepia senta	148											●								
Sepia sewelli	148										●									
Sepia simoniana	148								●		●									
Sepia sokotriensis	149										●									
Sepia subplana	149																●			
Sepia subtenuipes	149													●						
Sepia tala	149										●									
Sepia tanybracheia	150											●								

SPECIES	page	GEOGRAPHICAL DISTRIBUTION MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																	
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Sepia tenuipes	150													●						
Sepia thurstoni	150											●								
Sepia tokioensis	150													●						
Sepia tuberculata	151								●											
Sepia typica	151								●		●									
Sepia vercoi	151											●								
Sepiella cyanea	151								●		●									
Sepiella mangkangunga	152										●					●				
Sepiella ocellata	152											●				●				
Sepia filibrachia	152													●		●				
Sepiola affinis	158						●													
Sepiola atlantica	159			●		●	●													
Sepiola birostrata	161													●						
Sepiola intermedia	162						●													
Sepiola ligulata	163						●													
Sepiola parva	165													●		●				
Sepiola robusta	166						●													
Sepiola rondeleti	167			●		●	●													
Sepiola trirostrata	169															●				
Euprymna berryi	170													●						
Euprymna morsei	171											●		●		●				
Euprymna tasmanica	173											●				●		●		
Rondeletiola minor	174			●		●	●		●											
Sepietta neglecta	176			●		●	●													
Sepietta obscura	177			●			●													
Sepietta oweniana	178			●		●	●													
Sepiola aurantiaca	180			●			●													
Sepiola knudseni	180			●		●														
Sepiola pfefferi	180			●																
Sepiola rossiaeformis	180											(?)				(?)				
Sepiola steenstrupiana	180						●				●									
Euprymna albatrossae	181															●				
Euprymna hoylei	181											●				●				
Euprymna hyllebergi	181											●								
Euprymna penares	181											(?)				(?)				
Euprymna phenax	181													(?)		●				
Euprymna scolopes	181																●			
Euprymna stenodactyla	182										●									

SPECIES	page	GEOGRAPHICAL DISTRIBUTION — MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																	
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Sepietta petersi	182					●	●													
Inioteuthis capensis	182								●											
Inioteuthis japonica	182													●						
Inioteuthis maculosa	182										●	●		●		●				
Rossia macrosoma	183			●		●	●													
Rossia pacifica pacifica	185													●	●		●			
Rossia tortugaensis	187				●															
Semirossia equalis	188				●															
Semirossia tenera	189		●		●															
Neorossia caroli	190			●		●	●													
Austrorossia antillensis	192				●															
Austrorossia australis	193											●				●		●		
Austrorossia bipapillata	194													●		●				
Rossia brachyura	196				●															
Rossia bullisi	196				●															
Rossia glaucopis	196																		●	
Rossia megaptera	196		●																	
Rossia moelleri	196	●	●	●																
Rossia mollicella	196													●						
Rossia pacifica diegensis	197																●			
Rossia palpebrosa	197		●	●																
Austrorossia enigmatica	197								●											
Austrorossia mastigophora	197					●			●		●									
Semirossia patagonica	197							●											●	
Neorossia leptodons	197											●						●		
Heteroteuthis (Heteroteuthis) dispar	198		●	●	●	●	●													
Stoloteuthis leucoptera	199		●	●	●	●	●		●				●					(?)		
Sepiolina nipponensis	201											●		●		●				
Heteroteuthis (Heteroteuthis) weberi	203											●				●				
Heteroteuthis (Stephanoteuthis) dagamensis	203								●		●									
Heteroteuthis (Stephanoteuthis) hawaiiensis	203											●				●	●			
Heteroteuthis (Stephanoteuthis) serventyi	203																	●		
Nectoteuthis pourtalesi	203				●															
Iridoteuthis iris	203															●	●			
Iridoteuthis maoria	203																	●	●	

SPECIES	page	GEOGRAPHICAL DISTRIBUTION MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																	
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Sepiadarium austrinum	205											●								
Sepiadarium kochii	206											●		●		●				
Sepiadarium auritum	207											●								
Sepiadarium gracilis	207															●				
Sepiadarium nipponianum	207													●						
Sepioloidea lineolata	207											●						●		
Sepioloidea pacifica	207																	●	●	
Idiosepius biserialis	209										●									
Idiosepius macrocheir	209										●									
Idiosepius minimus	209					(?)	(?)		(?)		(?)									
Idiosepius notoides	209											●								
Idiosepius paradoxus	209													●		●				
Idiosepius picteti	210															●				
Idiosepius pygmaeus	210													●		●				
Idiosepius thailandicus	210											●				●				
Spirula spirula	211			●	●	●		●	●		●	●	●			●		●		

MAJOR FISHING AREAS FOR STATISTICAL PURPOSES



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Tree of Life (Cephalopods): http://tolweb.org/tree?group=Cephalopoda&contgroup=Mollusca

NEXT PAGE

7. INDEX OF SCIENTIFIC AND VERNACULAR NAMES

Explanation of the System

Italics : Valid scientific names (double entry by genera and species)

Italics : Synonyms, misidentifications and subspecies (double entry by genera and species)

ROMAN : Family names

ROMAN : Scientific names of divisions, classes, subclasses, orders, suborders and subfamilies

Roman : FAO names

Roman : Local names

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8. LIST OF COLOUR PLATES

PLATE I

1. *Nautilus pompilius*
2. *Nautilus pompilius* male
3. *Nautilus pompilius* adult
4. *Allonautilus scrobiculatus* and *Nautilus pompilius*
5. *Allonautilus scrobiculatus* and *Nautilus pompilius*
6. *Nautilus belauensis* mature animal

PLATE II

7. *Nautilus belauensis* juvenile
8. *Nautilus belauensis*
9. *Nautilus belauensis*
10. *Nautilus stenomphalus*
11. *Metasepia pfefferi*
12. *Sepia aculeata* juvenile
13. *Sepia aculeata*
14. *Sepia aculeata*

PLATE III

15. *Sepia apama*
16. *Sepia apama*
17. *Sepia apama*
18. *Sepia apama*
19. *Sepia apama*
20. *Sepia apama*

PLATE IV

21. *Sepia bandensis*
22. *Sepia bandensis*
23. *Sepia latimanus*
24. *Sepia latimanus* large adult
25. *Sepia latimanus*
26. *Sepia latimanus* frontal view
27. *Sepia latimanus* juvenile
28. *Sepia officinalis* mature male

PLATE V

29. *Sepia officinalis* mature male
30. *Sepia officinalis* juvenile
31. *Sepia papuensis*
32. *Sepia pharaonis*
33. *Sepia pharaonis* female
34. *Sepia pharaonis* male
35. *Sepia plangon*
36. *Sepia smithi*

PLATE VI

37. *Sepiella inermis*
38. *Sepiola*
39. *Euprymna tasmanica*
40. *Euprymna tasmanica* adult
41. *Euprymna tasmanica*

PLATE VII

42. *Sepiadarium austrinum*
43. *Sepiadarium austrinum*
44. *Sepiadarium austrinum*
45. *Sepioloidea lineolata*
46. *Sepioloidea lineolata*

PLATE VIII

47. Beach seine and seine boat - India
48. Lift nets and fish market - India
48. *Octopus maya* catch from pots - Venezuela
50. Squid jigging machines at night - Japan
51. Trawl catch of squid - New England
52. Traditional waterwheel clay scoops recycled for *Octopus vulgaris* fishery - Sant Carles de la Ràpita, Catalonia
53. Clay octopus pots linked by a line - Farwah Lagoon, Libya
54. PVC pipe pots linked by a line for *Octopus vulgaris* fishery - Deltebre, Catalonia

PLATE IX

55. Clay pots for *Octopus vulgaris* fishery - L'Ampolla, Catalonia
56. Squid catch on deck - Western North Atlantic
57. Squid drying in sun - Japan
58. Squid drying in sun - Japan
59. Closing up purse seine with squid - Japan
60. Soft body (green) and hard body (black) squid jigging hooks on reel - Japan

ADDITIONAL INFORMATION

Plate I

Fig. 3: This animal was caught in a baited trap set at 330 m which was then brought slowly to the surface. Milne Bay, Papua New Guinea.

Fig 4: Photographed in shallow water off Ndrova Island, Manus, Admiralty Islands, Papua New Guinea, after being trapped at about 270 m depth.

Fig. 5: Photographed at about 270 m off Ndrova Island, Manus, Admiralty Islands, Papua New Guinea. Large red snapper *Etelis carbunculus* was also attracted to bait and entered trap.

Fig. 6: Mature animal trapped at about 30 m depth off Mutremdiu Point, Palau Islands, South Pacific.

Plate II

Fig. 7: Juvenile trapped at about 300 m depth off Mutremdiu Point, Palau Islands, South Pacific.

Fig. 8: Two specimens attracted to tuna bait at 217 m depth off Mutremdiu Point, Palau Islands, South Pacific.

Fig. 9: Two adults approaching exterior foreground with tentacles extended in typical search posture. Six other nautilus are within trap; one pair is mating (lower left). Photo taken at 274 m depth off Mutremdiu Point, Palau Islands, South Pacific.

Fig. 10: Specimen captured at about 250 m off Lizard Island, Great Barrier Reef, Australia.

Fig. 11: Specimen 'walking' on substrate with ventral arms and abdominal flaps at 20 m. Lizard Island, Great Barrier Reef, Australia.

Fig. 12: Juvenile hovering above the substrate. Total length 15 cm. Papua New Guinea.

Fig. 13: Specimen sitting on bottom in highly cryptic body pattern. Milne Bay, Papua New Guinea.

Plate III

Fig. 15: Photographed in south Australia.

Fig. 16: Sneaker male (above right) in mottled colour pattern with egg-laying female (below) and mate-guarding male.

Fig. 17: Two males in combat display over an egg-laying female (visible bottom left).

Fig. 18: Three males compete to mate with a small female (far left).

Fig. 19: Frontal 'spade' display of male, often used to flip an oppenent over.

Fig. 20: Photographed in south Australia.

Plate IV

Fig. 21: North Sulawesi, Indonesia.

Fig. 23: Great Barrier Reef, Australia

Fig. 24: Large adult hanging beneath a tabletop coral head. Total length about 50 cm. Palau Islands, South Pacific.

Fig. 25: A somewhat cryptic body pattern. Palau Islands, South Pacific.

Fig. 26: Frontal view illustrates how a cuttlefish can literally hide its body behind its own head and arms. Photo taken in the laboratory (represents a wild population from Palau Islands, South Pacific).

Fig. 27: Photo of juvenile taken in the laboratory (represents a wild population from Palau Islands, South Pacific).

Fig. 28: Photo of mature male taken in the laboratory (represents a wild population from eastern Atlantic, UK or France).

Plate V

Fig. 29: Mature male showing intense zebra display. Photo taken in the laboratory (represents a wild population from the eastern Atlantic).

Fig. 30: Juvenile showing the green iridescence on the ventral mantle in contrast to the pattern on the dorsal mantle. Photo was taken in the laboratory (represents a wild population from the eastern Atlantic).

Fig. 31: Western Australia.

Fig. 32: Male on top of female being guarded. Photo taken in the laboratory (represents a wild population of Gulf of Thailand).

Fig. 33: Female swimming in large culture tank in general mottled body pattern with an iridescent blue stripe along fin base. Photo was taken in the laboratory (represents a wild population from the Gulf of Thailand, western Pacific).

Fig. 34: Male in dramatic zebra stripe body pattern with arms spread as he postures toward other males nearby. Photo taken in the laboratory.

Fig. 35: New South Wales, Australia.

Plate VI

Fig. 37: Singapore.

Fig. 40: Adult with fully developed light organ.

Fig. 41: Victoria, Australia.

Plate VII

Fig. 43: Victoria, Australia.

Fig. 44: Pair mating face-to-face (female stores sperm in a pouch around her mouth).

Fig. 46: Specimen using both eyes to take aim at a passing shrimp. Western Australia.

COLOUR PLATES

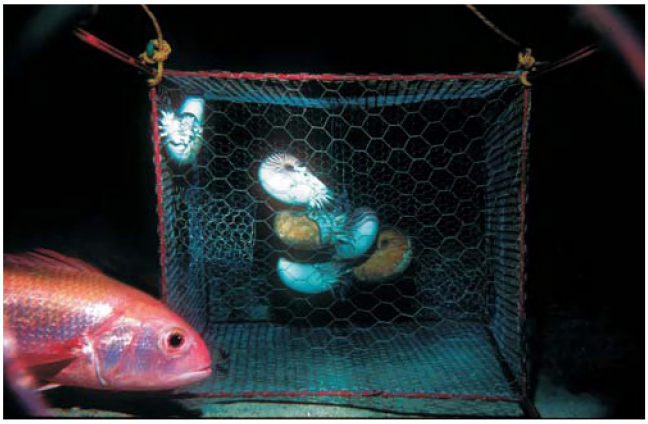
PLATE I

1. *Nautilus pompilius*
(M. Norman)

2. *Nautilus pompilius* male
(M. Norman)

3. *Nautilus pompilius* adult
(J.W. Forsythe)

4. *Allonautilus scrobiculatus* (left) and *Nautilus pompilius* (right)
(W.B. Saunders)

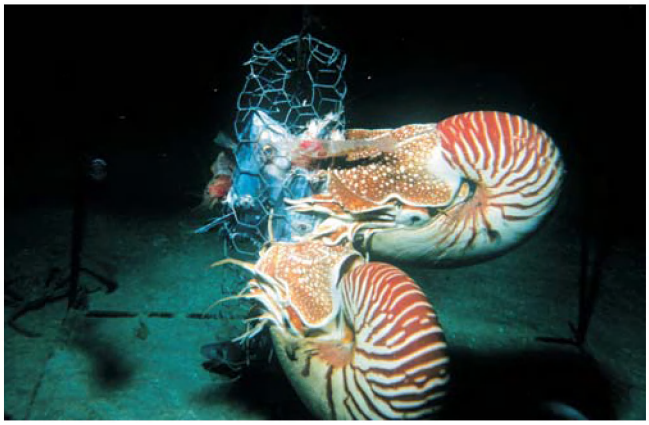


5. *2 Allonautilus scrobiculatus* and 3 *Nautilus pompilius*
(W.B. Saunders)

6. *Nautilus belauensis* mature animal
(W.B. Saunders)

PLATE II

7. *Nautilus belauensis* juvenile
(W.B. Saunders)



8. *Nautilus belauensis*
(W.B. Saunders)

9. *Nautilus belauensis*
(W.B. Saunders)

10. *Nautilus stenomphalus*
(W.B. Saunders)

11. *Metasepia pfefferi*
(C.F.E. Roper)

12. *Sepia aculeata* juvenile
(J.W. Forsythe)

13. *Sepia aculeata*
(J.W. Forsythe)

14. *Sepia aculeata*
(J.W. Forsythe)

PLATE III

15. *Sepia apama*
(M. Norman)

16. *Sepia apama*
(M. Norman)

17. *Sepia apama*
(M. Norman)

18. *Sepia apama*
(M. Norman)

19. *Sepia apama*
(M. Norman)

20. *Sepia apama*
(M. Norman)

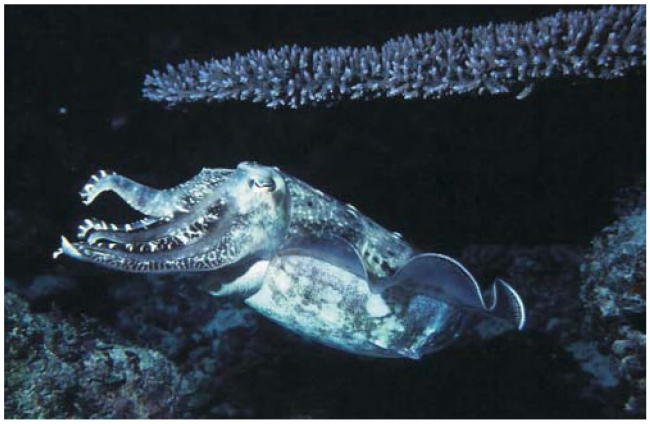
NEXT PAGE

PLATE IV

21. *Sepia bandensis*
(M. Norman)

22. *Sepia bandensis*
(M. Norman)

23. *Sepia latimanus*
(M. Norman)

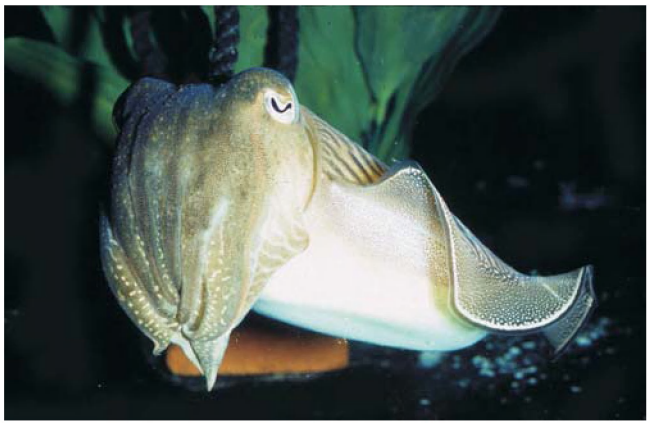


24. *Sepia latimanus* large adult
(J.W. Forsythe)

25. *Sepia latimanus*
(J.W. Forsythe)

26. *Sepia latimanus* frontal view
(J.W. Forsythe)

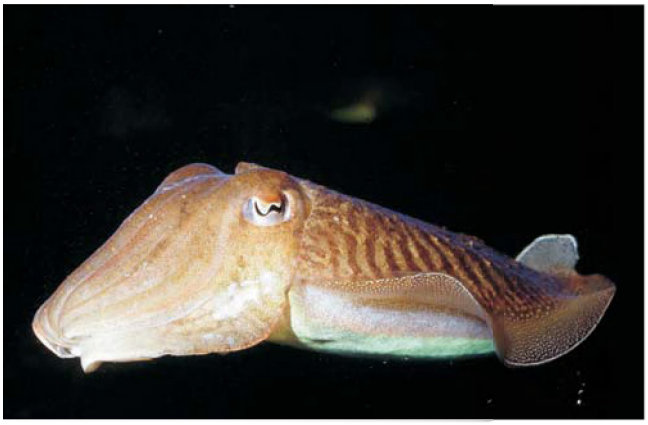
27. *Sepia latimanus* juvenile
(J.W. Forsythe)



28. *Sepia officinalis* mature male
(J.W. Forsythe)

PLATE V

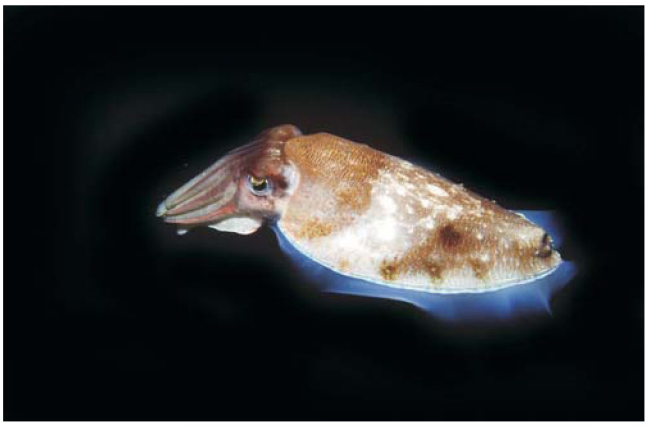
29. *Sepia officinalis* mature male
(J.W. Forsythe)



30. *Sepia officinalis* juvenile
(J.W. Forsythe)

31. *Sepia papuensis*
(M. Norman)

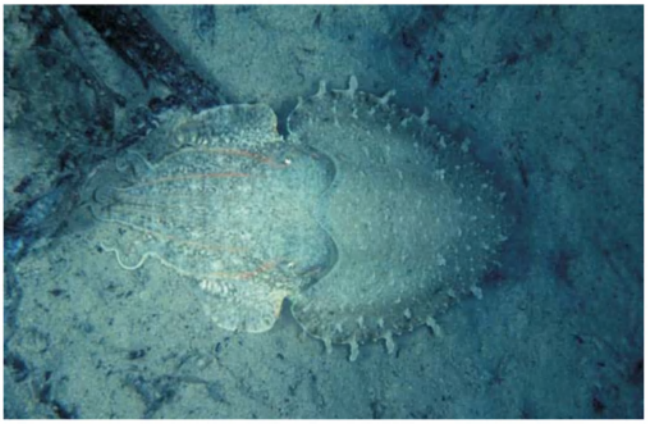
32. *Sepia pharaonis*
(J.W. Forsythe)



33. *Sepia pharaonis* female
(J.W. Forsythe)

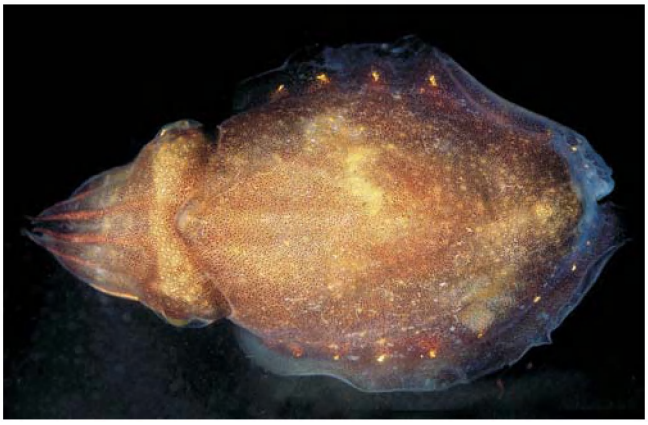
34. *Sepia pharaonis* male
(J.W. Forsythe)

35. *Sepia plangon*
(M. Norman)



36. *Sepia smithi*
(M. Norman)

PLATE VI



37. *Sepiella inermis*
(M. Norman)

38. *Sepiola*
(J.W. Forsythe)

39. *Euprymna tasmanica*
(M. Norman)

40. *Euprymna tasmanica* adult
(M. Norman)

41. *Euprymna tasmanica*
(M. Norman)

PLATE VII

42. *Sepiadarium austrinum*
(M. Norman)

43. *Sepiadarium austrinum*
(M. Norman)

44. *Sepiadarium austrinum*
(M. Norman)

45. *Sepioloidea lineolata*
(M. Norman)

46. *Sepioloidea lineolata*
(M. Norman)

NEXT PAGE

PLATE VIII

47) Beach seine and seine boat - India
(C.F.E. Roper)

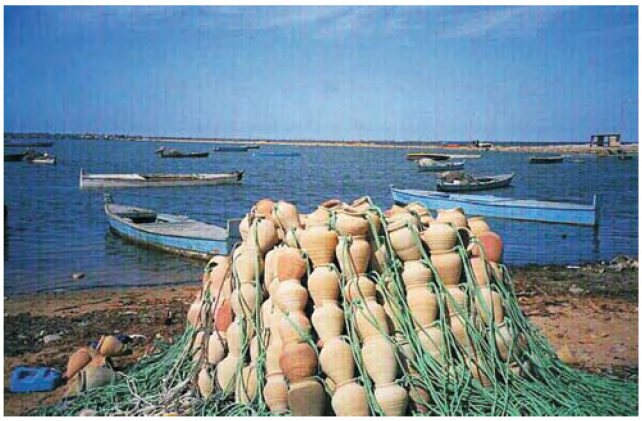
48) Lift nets and fish market - India
(C.F.E. Roper)

49) *Octopus maya* catch from pots - Venezuela
(W.F. Rathjen)

50) Squid jigging machines at night - Japan
(W.F. Rathjen)

51) Trawl catch of squid - New England
(W.F. Rathjen)

52) Traditional waterwheel clay scoops recycled for *Octopus vulgaris* fishery - Sant Carles de la Ràpita, Catalonia
(P. Sánchez)



53) Clay octopus pots linked by a line - Farwah Lagoon, Libya
(M. Lamboeuf)

54) PVC pipe pots linked by a line for *Octopus vulgaris* fishery - Deltebre, Catalonia
(M. Demestre)

PLATE IX

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(J. Lleonart)

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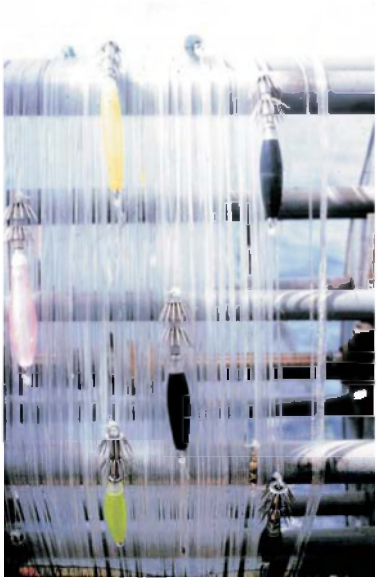
(W.F. Rathjen)

57) Squid drying in sun - Japan
(C.F.E. Roper)

58) Squid drying in sun - Japan
(C.F.E. Roper)

59) Closing up purse seine with squid - Japan
(C.F.E. Roper)



60) Soft body (green) and hard body (black) squid jigging hooks on reel - Japan
(C.F.E. Roper)

This is the first volume of the entirely rewritten, revised and updated version of the original FAO Catalogue of Cephalopods of the World (1984). The present volume is a multiauthored compilation that reviews six families: Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae, with 23 genera and the 201 species known to the date of the completion of the volume. It provides accounts for all families and genera, as well as illustrated keys to all taxa. Information under each species account includes: valid modern systematic name and original citation of the species (or subspecies); main synonyms; English, French and Spanish FAO names for the species; illustrations of dorsal and ventral aspect of the whole animal (as necessary) and other distinguishing illustrations; field characteristics; diagnostic features; geographic and vertical distribution, including GIS map; size; habitat; biology; interest to fishery; local names when available; a remarks section (as necessary) and literature. The volume is fully indexed and also includes sections on terminology and measurements, an extensive glossary, an introduction with an updated review of the existing biological knowledge on cephalopods (including fisheries information and catch data for recent years) and a dedicated bibliography.

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