

TREATISE ONLINE

Number 14

Part M, Chapter 6:
Biogeography of Recent Forms

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2010

KU PALEONTOLOGICAL
INSTITUTE

The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART M, CHAPTER 6: BIOGEOGRAPHY OF RECENT FORMS

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INTRODUCTION

Biogeography is the study of the geographical distribution of organisms through space and time, but such a definition masks the complexity of plotting the distribution of marine organisms and especially of the fast-moving members of the Cephalopoda. Biogeography has mostly followed two paths, historical biogeography and ecological geography (MYERS & GILLER, 1988), to which cladistic biogeography has been added (HUMPHRIES & PARENTI, 1986). The first path attempts to reconstruct the origin, dispersal, and extinctions of taxa over long periods of time; the second follows dispersal and movements of extant or recently extinct organisms over short periods of time; and the third has the search for patterns of relationships among areas of endemism as its basic premise (HUMPHRIES & PARENTI, 1986). To follow the sequence of historical processes, the phylogeny of taxa must be known. To obtain some precision in historical reconstruction, an understanding of the age of endemic forms will help, as isolation, both temporal and spatial, is important in the emergence of such forms (MYERS & GILLER, 1988).

A description of the distribution of cephalopods across space and short periods of time poses some considerable difficulties. Members of the Coleoidea vary widely in their habits and habitats. Oceanic forms range from strong swimmers moving at speeds of up to 1.4 m/sec (O'DOR & WEBBER, 1991) to others that are close to neutral buoyancy and subjected to the movements of currents. There are numerous species inhabiting the shelf waters, some of which are capable of migrating more than 2000 km, traveling at 20 km/day (O'DOR, 1983). The coastal waters provide habitats for swimming and benthic forms, some

of the latter remaining in restricted areas for their lifetime. Our knowledge of the distribution of cephalopods has increased considerably during the past few decades; nevertheless, it is mostly coastal species, notably those of commercial importance, of which we have most details of geographic distributions.

Description of the geographic distribution of any species depends on its identification, and as the refinement of conventional taxonomy reveals the existence of sibling species and multispecies complexes, so the determination of a species will provide the geographic boundaries and species richness in any given area (MYERS, 1997). In order to determine the geographic distribution of a species throughout its life cycle, its habits, including the habitats occupied at every stage of its life, its migratory habits (vertical, horizontal, diel, seasonal, ontogenetic), and its reproductive habits must be ascertained. The abiotic factors of the oceans and seas include currents, turbulent mixing, water-column stability, light intensity, temperature, salinity, and such climatic factors such as storms and variation in local weather patterns. Water masses can be traced over many thousands of kilometers and form large regions of the oceans, and they have particular temperature and salinity characteristics. Biotic factors, such as productivity, which is often seasonal, also have an important role in distribution. Some or many of these factors ensure that the environment is one of complex patterns and may bring about changes in distribution during the life cycle of an animal. The distribution of one deep-ocean coleoid, *Vampyroteuthis infernalis*, the only member of the order Vampyromorpha, was attributed to water masses by PICKFORD (1946); she was probably the first to recognize such a distribution in a marine animal (ANGEL, 1992). Any attempt

to describe the geographic distribution of Coleoidea is somewhat premature, because there are many areas for which we have little or no information of the species inhabiting them. Furthermore, our knowledge of the life cycle of most species is incomplete, particularly the early posthatching and mature adult stages, the exceptions being a small number of common coastal species, notably members of the three most speciose genera of Cephalopoda, namely *Octopus*, *Sepia*, and *Loligo* (BOYLE, 1983a).

The progress of the captures and descriptions of species of Cephalopoda was traced by G. L. VOSS (1977) from 1848, when 16 genera and 129 species had been described, until 1974, by which time, a further 190 genera and 854 species had been added. Since the late 1940s, there has been an upsurge of interest in these animals, and besides descriptions of new species, numerous critical revisions and monographs have been published. This research has, in some instances, resulted in synonymy and consequent reduction in the number of species and genera; in other instances, new species and genera have been described; and reexamination of existing material has also revealed new species. In 1977, G. L. VOSS considered that there were about 150 genera and some 650 species of living cephalopods, since which time new species and genera have been added to the list (SWEENEY & ROPER, 1998).

The Minoans and Mycenaeans were familiar with cuttlefish, squid, paper nautilus, and especially the octopus, as is evident from the numerous illustrations on pottery and other artifacts dating from 1500 BCE (HIGGINS, 1981). As early as the fourth century BCE, Aristotle described the habits and anatomical features of the common coastal coleoids of the Mediterranean Sea (translation by THOMPSON, 1910). In 1851, VÉRANY published the first part of *Mollusques Méditerranéens*, which was devoted to cephalopods. The inauguration of marine stations occurred toward the end of the 19th century; the first was in Naples,

Italy, where the fauna, including Coleoidea, were studied extensively and resulted in a series of significant contributions, including monographs by JATTA (1896) and NAEF (1921, 1923, 1928).

The last quarter of the 19th century saw an era of national oceanographic expeditions, followed by research on the collections (MURRAY & HJORT, 1912). Knowledge of the geographic and bathymetric distribution of the marine fauna, including the oceanic coleoids, greatly expanded as a result. One of the first surveys of the geographic distribution of coleoids was by HOYLE (1886), based on his study of the collections of these animals made during the expedition of HMS *Challenger*. HOYLE was aware of the incompleteness of the material, as the ship had spent little time in shallow waters, so he also searched the literature for further information. PFEFFER's (1912) monograph concentrated on the paralarval and juvenile stages of oceanic squids, and he summarized the geographic distribution of Oegopsida. ADAM and REES (1966) discussed the geographic distribution of members of the Sepiidae, and so too did ROELEVELD (1972), after studying the species of *Sepia* living along the coast of South Africa. ROBSON (1932) gave a brief outline of the distribution of the Octopodinae. The geographic distributions of the families of oceanic squids were reviewed by CLARKE (1966). Two catalogs, published by the Food and Agricultural Organisation, mapped the geographic distribution of each species of coleoid described (ROPER, SWEENEY, & NAUEN, 1984; ROPER, SWEENEY, & CLARKE, 1985). Monographs and revisions often include distribution maps (for example, THORE, 1949; R. E. YOUNG & ROPER, 1968; ROPER, 1969; TOLL, 1981; N. A. VOSS, 1985), and one was given for each of the species reviewed in *Cephalopod Life Cycles* (BOYLE, 1983a). NESIS (1982) gave the geographical distributions of most cephalopods in his book, *Cephalopods of the World*, and of oceanic cephalopods in a later book (NESIS, 1985). The systematics and zoogeography of coleoids were reviewed by

N. A. VOSS (1988), the deep-sea Octopoda by G. L. VOSS (1988a), and the geographical distribution of each family by NESIS (1985) and MANGOLD and VON BOLETZKY (1989). The biogeography of some groups of Recent coleoids has been reviewed; they include the Sepiida (KHROMOV, 1998); the squid families Onychoteuthidae (KUBODERA & others, 1998), Histioteuthidae (N. A. VOSS, NESIS, & RODHOUSE, 1998), and Ommastrephidae (DUNNING, 1998); and some of the octopods (VOIGHT, 1998).

Most cephalopods have excellent vision and are agile and capable of rapid escape movements; these features enable many of them to avoid nets. Various capture techniques are available, including nets, trawls, and jigs from ships (RATHJEN, 1991), to which light as an attractant can be added and which increases the numbers and sometimes the sizes of the species captured (CLARKE & PASCOE, 1998). Information about distribution can be obtained from examining the stomachs of such predators as sperm whales, porpoises, seals, sharks, teleosts, penguins, albatrosses, and other sea birds, as the lower beaks of coleoids possess features that are characteristic, so that the genera and even the species consumed can be identified (CLARKE, 1962, 1980, 1986, 1996). Other hard-tissue structures, such as the statolith (CLARKE, 1978; CLARKE & MADDOCK, 1988b), gladius, dermal tubercles, and mantle locking apparatus (HESS & TOLL, 1981), may be helpful in the identification of coleoids eaten. The species and families in any sample are found in different proportions, depending on the method of collection. CLARKE (1977) compared captures in nets with large and small area mouth openings with those made by a variety of predators and convincingly demonstrated the inefficiency of the capturing techniques developed by man. Nets with a large mouth opening catch a greater number of species and larger specimens than those with a small mouth opening (ROPER, 1977). Research nets usually collect small species as well as the young of larger species. Commercial nets

have a bias toward catching members of the family Eupoloteuthidae and cephalopods of a size not captured by research nets or by sperm whales (Fig. 1). The largest of the specimens caught in nets are nearly always smaller than those eaten by large predators such as the sperm whale (CLARKE, 1980). These mammals can also provide a survey of the cephalopods in oceanic waters, as they feed on different species of squids in various regions of the world during their long migrations (CLARKE, 1980, 1983) (Fig. 2). Underwater cameras, submersibles, and remote operating vehicles allow observations of coleoids in their natural habitats; some of the underwater vehicles can capture the individuals observed for subsequent examination.

It is apparent that different and complementary views of the geographic distribution and diversity of the cephalopod fauna are obtained from captures by their natural predators and from the various methods devised by man. CLARKE (1966, p. 93–94) emphasized the need for information from as many sources as possible in order “to obtain anything approaching a realistic picture of the cephalopods of a region” and stressed that the “taxonomic tangle prevents any but the most limited analysis” and the “impression one has of distribution is also influenced by the number of samples taken in different areas of the globe.” The now more numerous and diverse methods of capture and observation of coleoids available will perhaps make it possible to fill some of the gaps in our knowledge.

The biomass of coleoids is considerable, as the total weight eaten per year in one region (Southern Ocean) by one species of predator, the sperm whale, has been estimated as 35 million tons (CLARKE, 1983), and as much as 100 million tons in one year by this mammal worldwide (CLARKE, 1977). These figures represent huge numbers of coleoids around the world, including both polar regions. The total biomass of coleoids in open waters is clearly large, but as yet, it is not possible to make any direct comparison with the biomass of those inhabiting the continental

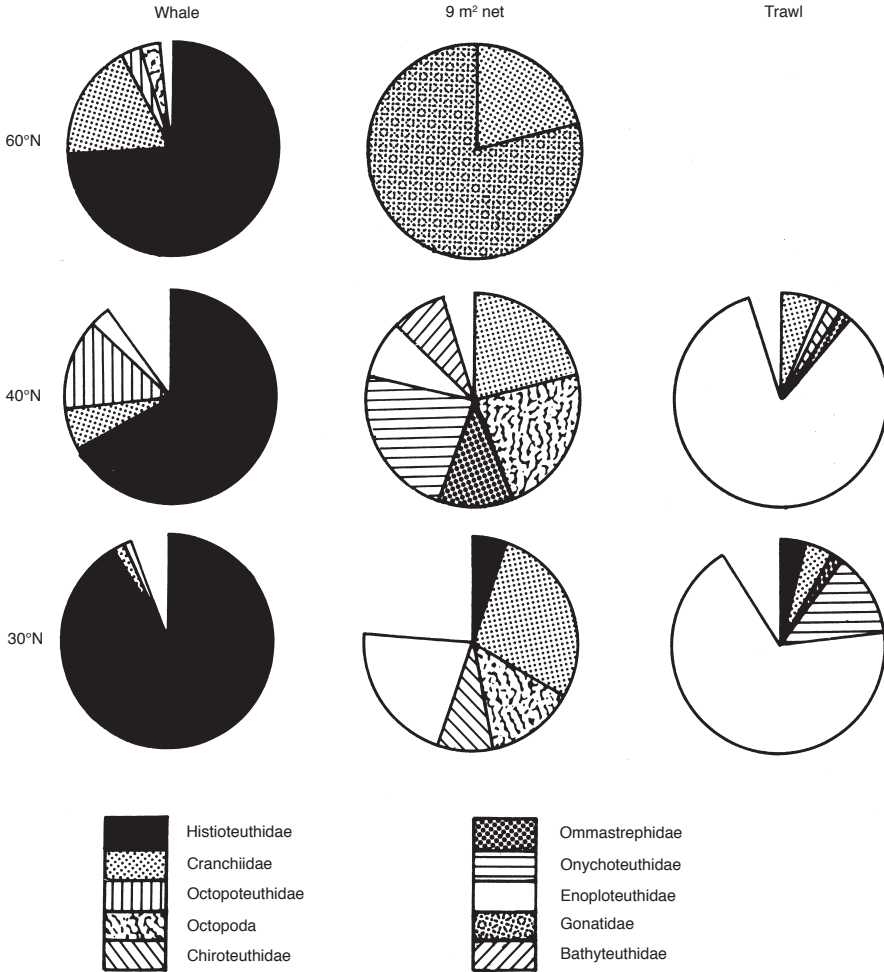


FIG. 1. Families of oceanic coleoids, mostly squids, shown as proportions taken by sperm whales, research nets (9 m² mouth opening area) or commercial trawls in three areas of the North Atlantic Ocean (Clarke, 1983).

margins and forming the basis of fisheries in many areas. Open waters account for 79 percent of the total area of the world's oceans and seas and coastal waters 21 percent, the former being inhabited by 43 percent and the latter by 57 percent of the species of extant Coleoidea.

GEOGRAPHIC DISTRIBUTION

OCEANS AND SEAS

The cephalopod fauna has been investigated in the far eastern seas and adjacent Pacific Ocean (AKIMUSHKIN, 1963), the

eastern part of the Pacific Ocean (OKUTANI & MCGOWAN, 1969; R. E. YOUNG 1972a; OKUTANI, 1974), the central part (R. E. YOUNG, 1978), the Mediterranean Sea, especially the European area (NAEF, 1921, 1923; MANGOLD-WIRZ, 1963; ROPER, 1972; MANGOLD & VON BOLETZKY, 1988), the northeastern Atlantic Ocean (CLARKE & LU, 1974, 1975; LU & CLARKE, 1975a, 1975b; HAYWARD, 1990) and the Iberian peninsula (GUERRA, 1992), and the Southern Ocean (ROPER, SWEENEY, & CLARKE, 1985). In the review that follows, the sampling sites included have been the subject of detailed

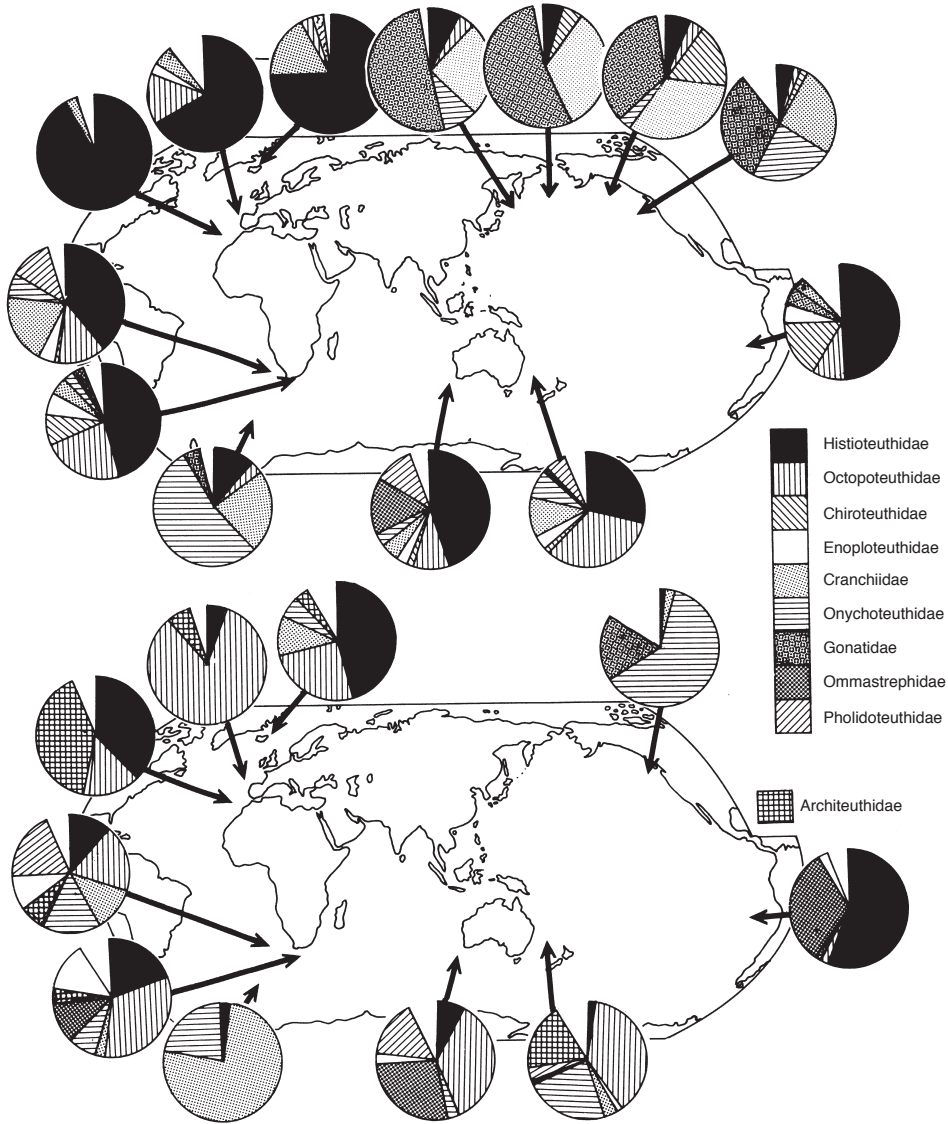


FIG. 2. Composition of families of oceanic squids in diet of sperm whales captured in various parts of the world, based upon identification of their lower beaks (*upper diagram*); composition by weight of squids consumed and estimated from number and size of beaks present (*lower diagram*) (Clarke, 1983).

studies, mostly in the past three decades, as these have benefited from taxonomic revisions published during the same period.

THE ATLANTIC OCEAN

In the open waters of the northeastern Atlantic Ocean, the RRS *Discovery* made a series of cruises to capture cephalopods

at a similar longitude (20°W–25°W) but at six different latitudes; discrete depth horizons were sampled between the surface and 2000 m, day and night, with opening-closing nets (CLARKE & LU, 1974, 1975; LU & CLARKE, 1975a, 1975b). The number of coleoid species was observed to increase from only 3 at 60°N to 40 at 18°N (Fig. 3).

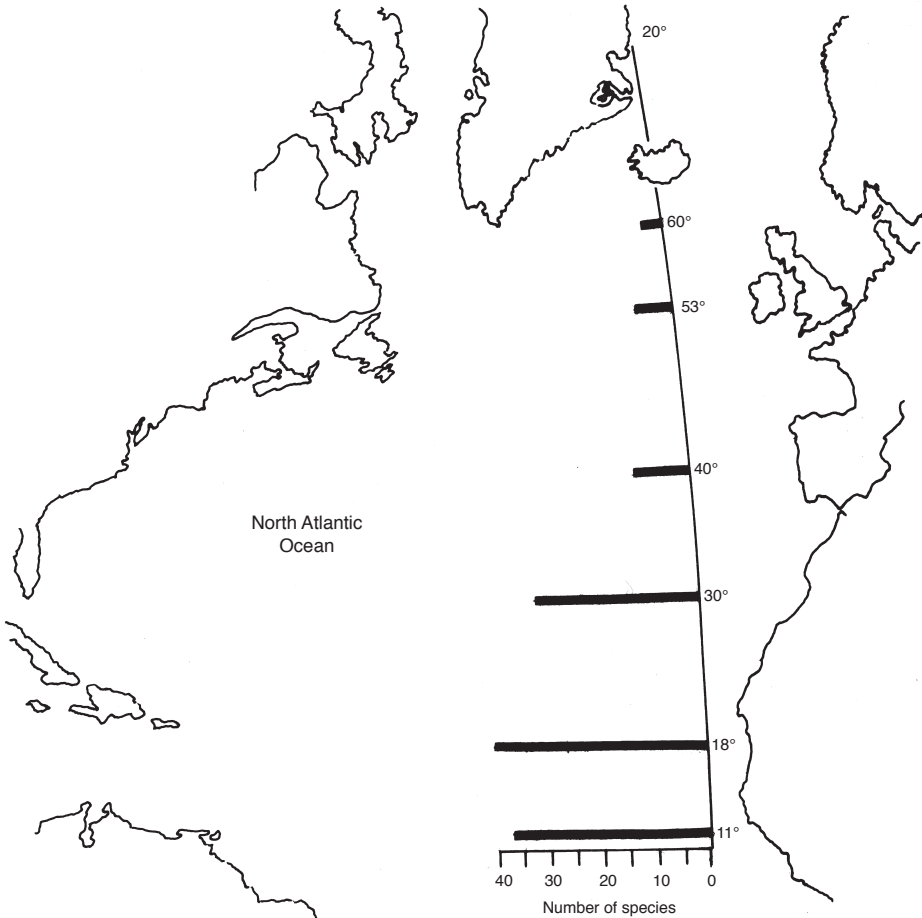


FIG. 3. Numbers of species of coleoids captured from same longitude, 20°W–25°W, but at different latitudes in North Atlantic Ocean (data from Clarke & Lu, 1974, 1975; Lu & Clarke, 1975a, 1975b).

At the three most northerly sampling sites, the species caught belonged to different genera, but farther south, several species of some genera were recorded. *Mastigoteuthis* was represented at all six sampling sites; representatives of the genera *Pterygoteuthis*, *Onychoteuthis*, *Leachia*, *Galiteuthis*, *Bathothauma*, *Vampyroteuthis*, *Japetella*, and *Vitreledonella* were caught only between 40°N and 11°N.

Farther east are the waters around the British Isles, the North Sea, and the Norwegian Sea (Table 1) (HAYWARD, 1990). Coleoids occur only rarely around the Danish islands and in Kiel Bay in the western Baltic

Sea, and then only as a result of strong influxes of water masses from the North Sea (JAECKEL, 1937, 1958; UWE PIATKOWSKI, personal communication, 1985); most are loliginids.

Off the Canary Islands, one cruise went close to the southern end of Fuerteventura (27°N 13°W); all the coleoids collected were oceanic forms and represented 16 genera and 10 families (Table 1) (CLARKE, 1969). Twelve of the genera found there were also represented at 30°N 23°W in open oceanic waters (CLARKE & LU, 1974).

The Madeiran archipelago (33°N 170°W) is surrounded by deep water, and the cole-

TABLE 1. Number of genera belonging to each of the coleoid orders found in some areas of oceans, seas, coastal regions, and continental and coastal islands; the number of families is given in parentheses; order Octopoda includes oceanic and coastal forms, and the paralarvae (P) of some coastal forms are planktonic and sometimes found in open waters (sources of data given in text).

	Spirulida	Sepiida	Sepiolida	Myopsida (coastal)	Oegopsida (oceanic)	Vampyromorpha	Cirroctopoda	Octopoda (coastal)	Octopoda (oceanic)
Northeastern Atlantic 20°W 60°N					3 (3)				
Northeastern Atlantic 20°W 53°N					6 (6)				1 (1)
Northeastern Atlantic 20°W 40°N					8 (5)	1 (1)			2 (2)
Northeastern Atlantic 23°W 30°N	1 (1)				25 (16)	1 (1)		P (1)	3 (3)
Northeastern Atlantic 25°W 18°N					35 (15)	1 (1)		P (1)	3 (3)
Northeastern Atlantic 20°W 11°N			1 (1)		31 (13)	1 (1)		2 (1)	2 (2)
Madeiran waters 17°W 33°N	1 (1)	1 (1)	1 (1)	1 (1)	14 (8)			3 (1)	6 (6)
Canary Islands 13°W 27°N	1 (1)		1 (1)		13 (6)			1 (1)	
British Isles, North Sea, Norway		2 (1)	7 (1)	4 (1)	16 (8)		1 (1)	4 (1)	1 (1)
Bermuda Islands 64°W 33°N	1 (1)			3 (1)	22 (10)		1 (1)	2 (1)	4 (3)
Gulf of Mexico, Caribbean, Florida Straits	1 (1)		11 (1)	6 (2)	63 (24)	1 (1)	2 (2)	16 (1)	6 (4)
Cuba 79°W 20°N			5 (1)	3 (1)	8 (4)		2 (2)	4 (1)	2 (2)
Australian waters 110–155°E 10–40°S		34 (2)	11 (2)	7 (1)	75 (18)	1 (1)	3 (2)	24 (1)	8 (4)
Hong Kong 14°W 22°N		12 (2)	2 (1)	6 (1)	4 (2)	1 (1)	2 (2)	11 (2)	8 (5)
Japan 125–145°E 25–45°N		22 (2)	4 (1)	7 (1)	22 (9)		1 (1)	7 (1)	3 (3)
Hawaiian waters 158°W 21°N			1 (1)		43 (14)	1 (1)		7 (1)	6 (5)
Californian waters 116–120°W 28–34°N			1 (1)	1 (1)	35 (13)	1 (1)	1 (1)	9 (1)	6 (4)
Southern Ocean 20°W 60°N					27 (18)		3 (2)	15 (1)	

oids recorded include littoral, shelf, and slope forms, as well as pelagic, bathypelagic, and abyssal oceanic species (Table 1) (REES & MAUL, 1956).

The Mediterranean Sea was once linked to both the Atlantic and Indian Oceans. Communication with the Indian Ocean ceased in the early Miocene, and communication with the Atlantic Ocean became

reduced to one channel, the South Rif Strait, which was itself constricted by the end of the Miocene (RUGGIERI, 1967). The Mediterranean was transformed into a series of lagoons that dried up, and RUGGIERI, on p. 286, commented, "It is possible that the marine Miocene fauna was able to survive in some parts of the Mediterranean, but it seems much more likely that it was totally

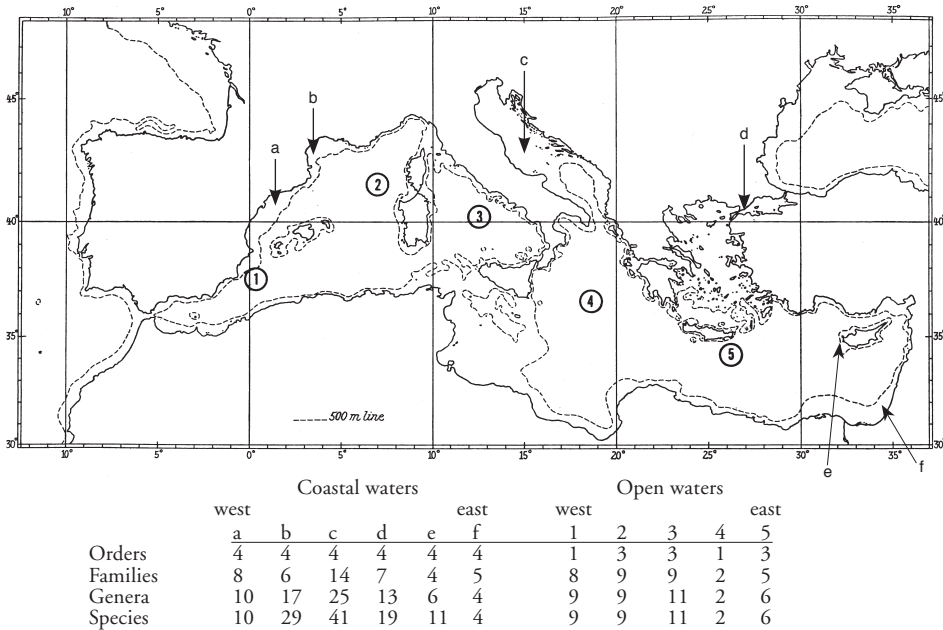


FIG. 4. Outline map of Mediterranean Sea showing sampling sites in open waters (numbers 1–5) and coastal sites (letters a–f); numbers of species, genera, families, and orders of coleoids recorded at each site shown in key above (data from Mangold-Wirz, 1963; Roper, 1972, 1974; Ruby & Knudsen, 1972; Knudsen, 1981; Mangold & Boletzky, 1988; Bello, 1990, 1992; Villanueva, 1992a; Katagan, Salman, & Benli, 1993).

destroyed by the adverse environmental conditions.” Results from deep-sea drilling suggest that approximately 6 myr ago, the Mediterranean basin was a desert 3000 m deep (Hsü, 1972). These dry conditions were followed by a deluge, as sea water flooded in from the Atlantic Ocean over a gigantic waterfall at the beginning of the Pliocene; the normal-marine circulation has prevailed ever since (Hsü & others, 1977). The Mediterranean remains today as a land-locked sea, connected to oceanic water only through the Strait of Gibraltar, which is 14 km wide and 260 m deep. It has two basins, eastern and western, with communication between them across sills in the Straits of Messina and Sicily. Geological evidence indicates that invasions have taken place since the Pliocene but only from the western entrance, so that most coleoid species now living in the Mediterranean Sea occur in the Atlantic Ocean. A temporary contact

between the eastern Mediterranean and the Red Sea occurred during the Pleistocene, but it is considered that little or no faunal addition took place from the nearby Red Sea during the whole Pleistocene, and no traces of coleoids have been found in the fossil record (MANGOLD & VON BOLETZKY, 1988).

In their review of the coleoids inhabiting the Mediterranean Sea, MANGOLD and VON BOLETZKY (1988) commented that they are best known along the European coast where marine stations have been established longest. There is some suggestion of a decrease in the number of families, genera, and species from the west to the east in the Mediterranean, but the areas sampled also diminish in size and number in the same direction. Captures in open waters reflect a similar situation, with the western half of the Mediterranean being richer in species than the eastern half (Fig. 4) (ROPER, 1972, 1974). In the Adriatic Sea,

which is somewhat isolated, the distribution is not uniform, and the teuthofauna is more diverse in the southern part than in the northwestern basin (BELLO, 1986, 1990, 1992). In the Sea of Marmara, 19 species have been recorded (KATAGAN, SALMAN, & BENLI, 1993). Endemic species found in the Mediterranean all belong to the subfamily Sepiolinae, which is also the most speciose in this sea (MANGOLD & VON BOLETZKY, 1988; VOLPI, BORRI, & VON BOLETZKY, 1995). The apparently higher number of species in the western Mediterranean is consistent with invasion from oceanic waters at the western end.

The Bermuda Islands, with coral sand beaches surrounded by reefs, lie some 1100 km from the nearest mainland and are more isolated than the Canary Islands. The coleoids found within a radius of 300 km of these islands are mostly oceanic, but shelf and coastal forms are present (Table 1) (G. L. VOSS, 1960). Two of the oegopsid squids, *Onykia carriboea* and *Ommastrephes pteropus*, and two of the myopsid squids, *Loligo plei* and *Sepioteuthis sepioidea*, occur here (G. L. VOSS, 1956a) and also quite widely along the coasts of the western Atlantic (see Table 7). Two species of *Octopus* live in the coastal waters. Empty shells of the oceanic spirulid, *Spirula spirula*, and occasionally the paper-thin shells of *Argonauta argo* are washed onto the beaches (ROPER, 1986). Sixty-nine species have been found recently around these islands (STERRER, 1998).

The Gulf of Mexico and Caribbean Sea, an embayment of the western Atlantic Ocean, have areas of very deep water to a maximum of 3850 m. From the Caribbean Sea, water enters the Gulf of Mexico through the Yucatan Channel and leaves in the fast-flowing waters of the Straits of Florida. Numerous studies in this region have recorded more than 100 genera, almost a quarter of which occur around Cuba, the largest of the chain of islands (Table 1) (G. L. VOSS, 1955, 1956a, 1956b; HOCHBERG & COUCH, 1971; CAIRNS, 1976; PASSERELLA & HOPKINS, 1991; SALCEDO-VARGAS, 1991).

THE PACIFIC OCEAN

The Pacific is the largest, deepest, and possibly the oldest of the oceans. Here the cephalopod fauna has been studied in a number of areas, but most especially in the waters of the isolated oceanic islands of Hawaii (BERRY, 1912; R. E. YOUNG, 1978) and the waters around Japan (OKUTANI, TAGAWA, & HORIKAWA, 1987).

The Hawaiian Islands are isolated in the middle of the Pacific Ocean and are volcanic in origin. Cruises to the south of the island of Oahu have captured more than 3300 coleoid specimens representing 58 genera, 43 of which belong to 14 of the 23 families of the Oegopsida (Table 1) (R. E. YOUNG, 1978; HARMAN & YOUNG, 1985; R. E. YOUNG, HARMAN, & MANGOLD, 1985a; R. E. YOUNG & HARMAN, 1987; R. E. YOUNG, HARMAN, & HOCHBERG, 1989). Coleoids inhabiting the coastal waters include several octopuses, *Octopus cyanea*, *O. ornatus*, and *O. sp.*, some sepiolids, and loliginids (BERRY, 1912; HOUCK, 1982). A study in progress has recorded 73 species around these islands (STERRER, 1998). This number is similar to that of the Bermuda Islands (69 species), which lie somewhat farther north in the Atlantic Ocean.

The islands of Japan form a crescent-shaped archipelago partly encircling the Japan Sea. The cephalopods caught within a radius of 370 km of these islands belong to 27 genera (Table 1) (OKUTANI, TAGAWA, & HORIKAWA, 1987). Others have been recorded from the stomachs of predatory fish and from strandings (NISHIMURA, 1968).

The Philippine Islands, an archipelago consisting of some 7000 islands, have a rich cephalopod fauna. Specimens obtained early in the 20th century were identified and described by G. L. VOSS (1963); they include 54 species belonging to 47 genera, of which 6 were benthic octopuses. Recently 20 species of shallow water octopuses have been recognized, 18 of which belong to the genus *Octopus* and 1 species each in the

genera *Hapalochlaena* and *Cistopus* (NORMAN & SWEENEY, 1997).

In the eastern Pacific Ocean, in a region extending from 28°N to 34°N off the coast of southern California, more than 5000 cephalopods were captured in midwater trawls (R. E. YOUNG, 1972a) belonging to 33 genera (Table 1). Off the coast of Mexico, between latitudes 20°N and 20°S and as far west as longitude 126°W, a series of micronekton tows collected more than 6000 specimens belonging to 20 genera (OKUTANI, 1974).

The waters within a radius of 320 km of Hong Kong yielded species belonging to 43 genera of coleoids (Table 1) (G. L. VOSS & WILLIAMSON, 1971). These authors commented that plankton and midwater hauls alone would add many further species to the list. Recently, further species of shallow-water octopodids have been described from these waters (NORMAN & HOCHBERG, 1994).

In New Zealand waters, some 41 species have been recorded (DELL, 1952, 1959; FÖRCH & UOZUMI, 1990); they belong to 23 genera, and of these, 6 are coastal in habit.

In Australian waters, within 300 km of the coast, 163 species belonging to 68 genera have been identified (LU & PHILLIPS, 1985; ZEIDLER, 1989), and most are oceanic (Table 1). Several new species of octopods (STRANKS, 1990; LU & STRANKS, 1991; NORMAN, HOCHBERG, & LU, 1997) and a new genus, *Ameloctopus* (NORMAN, 1992), have been recorded recently from these waters. *Octopus* and *Sepia* are especially richly represented in the coastal waters, and it is now considered that the diversity of octopod species is greater here than in any other region of the world (NORMAN, 1997 in 1997–1998).

In the southern Indian Ocean, trawls collected cephalopods around four separate island groups, and these were identified by LU and MANGOLD (1978). Prince Edward Islands consist of two sub-Antarctic islands between 40°S and 50°S, close to the Prince Edward–Crozet Ridge. One specimen of the

subfamily Heteroteuthinae and a number of specimens of *Octopus* sp. were captured in the surrounding waters (LU & MANGOLD, 1978). On Marion Island, during one year, the diet of a breeding colony of King Penguins consisted mainly of oceanic squids belonging to seven different families (ADAMS & KLAGES, 1987). The Crozet Islands lie at the eastern end of the Prince Edward–Crozet Ridge, and here five species were recorded, most belonging to the same species of *Octopus* found at Prince Edward Islands. The Kerguelen Islands form an archipelago of some 300 islands lying close to the Southern Ocean. Their shores are washed by tempestuous seas. Here *Benthooctopus levis* and *Graneledone* sp. were caught with five other species. Heard Island lies farther south and is almost always completely covered with ice, and here too *Graneledone* sp. and *Benthooctopus levis* were captured, as well as the deep-living squid *Bathyteuthis abyssicola* (LU & MANGOLD, 1978); all are Southern Ocean forms.

In the Southern Ocean, 45 species belonging to 45 genera have been recorded (Table 1) (TAKI, 1961; DELL, 1972; ROPER, 1981; ROPER, SWEENEY, & CLARKE, 1985; KUBODERA & OKUTANI, 1986, 1994; KUEHL, 1988; G. L. VOSS, 1988a; LU & WILLIAMS, 1994a, 1994b). Two squids are abundant, *Bathyteuthis abyssicola* and *Galiteuthis glacialis*, and both are circumpolar in distribution (ROPER, 1969), as are *Mesonychoteuthis hamiltoni*, *Alluroteuthis antarcticus*, and *Todarodes filippova* (ROPER, SWEENEY, & CLARKE, 1985). The genus *Pareledone* predominates among the octopods living in these waters, with eight species; several species of *Graneledone* and also *Megaleledone senoi*, *Thaumeledone*, *Benthooctopus* sp., and *Grimptoteuthis* sp. occur here (KUBODERA & OKUTANI, 1994).

COASTAL WATERS

The coleoids inhabiting the continental margins belong mainly to the orders Sepiida, Sepiolida, and Octopoda, and to the suborder Myopsida. Four of their

families are rich in species, the Sepiidae, Sepiolidae, Loliginidae, and Octopodidae; the last of these includes the most speciose genus of Recent Coleoidea. Most species belonging to these genera have been arranged in geographical regions by NESIS (1982). Distribution maps for commercially important species of coastal waters were given by ROPER, SWEENEY, and NAUEN (1984).

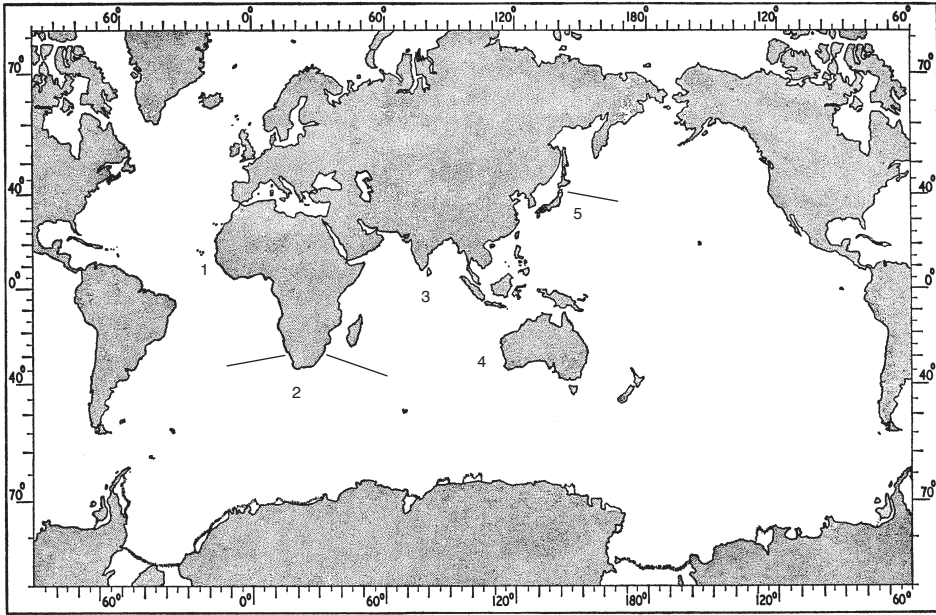
The genus *Sepia* includes almost 100 species found between latitudes 55°N and 40°S and longitudes 20°W and 170°E, most being found east of longitude 10°E (G. L. VOSS, 1977; NESIS, 1980, 1982; SWEENEY & ROPER, 1998). Sepiids inhabit the continental shelf and slope and even the intertidal zone (Fig. 5.1; Table 2) (ROPER, SWEENEY, & NAUEN, 1984). The most striking feature of the geographic distribution of *Sepia* is the complete absence of any representative around the coasts of the Americas (HOYLE, 1886). In their monograph of the family, ADAM and REES (1966, p. 145) stated that "no Sepiidae have ever been found on the coasts of the American continent or on those of New Zealand, except as stranded cuttlebones." G. L. VOSS (1974) confirmed these observations when he demonstrated clearly that the cuttlebones from various localities in the Americas came from known European or African species and commented that not one whole *Sepia*, living or dead, has ever been seen in the western Atlantic. He also noted the absence of *Sepia* from Greenland and Iceland. ROELEVELD (1972) suggested that the absence of *Sepia* from the Americas and from New Zealand was due to the separation of these land masses by deep oceans or the presence of very cold water in areas where migration might have taken place. Several species are widespread, notably *S. phaeonion* and *S. latimanus*, followed by *S. elliptica*, *S. zanzibarica*, and *S. kobiensis* (Fig. 5; Table 2). Off the coast of South Africa, the distribution of species of *Sepia* between Walvis Bay and Punta Zavora have been indicated in Figure 6: many have quite narrow distributions, and none is widespread (ROELEVELD, 1972; ROELEVELD & LILTVED, 1985). In

contrast, only a few species of *Sepia* inhabit the edge of the Mediterranean Sea or the coasts of the eastern Atlantic Ocean north of 20°S. A review of the biogeography of the Sepiidae (KHROMOV, 1998) shows the coasts of the eastern Pacific and Indian Oceans to be rich in species (Fig. 5.2).

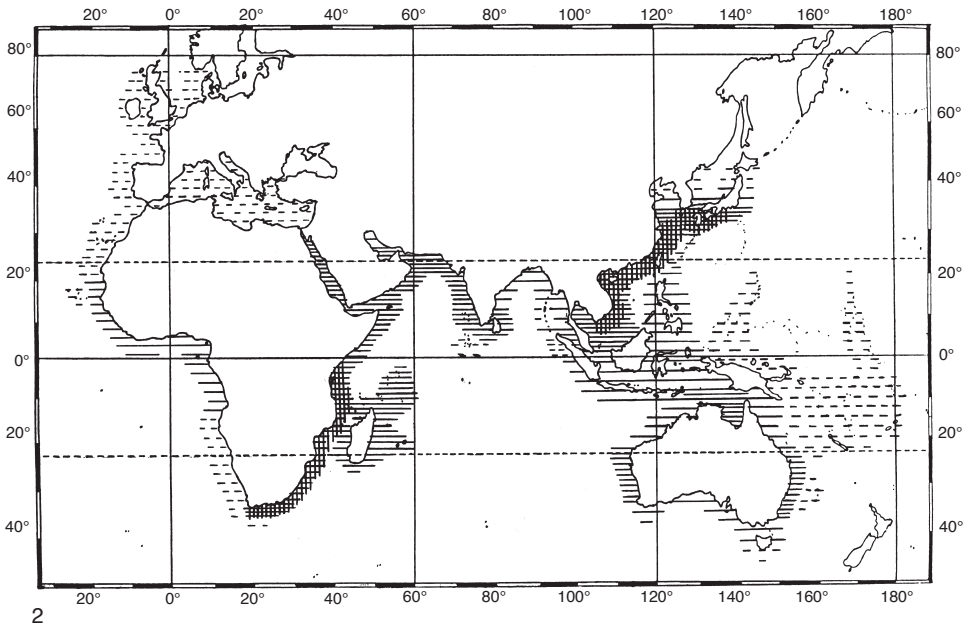
There are ten or more species in three genera, *Sepiola*, *Euprymna*, and *Rossia*, of the family Sepiolidae. They are widely distributed, but those of the Mediterranean are currently the best known (VOLPI, BORRI, & VON BOLETZKY, 1995).

The genus *Loligo* includes 13 species (SWEENEY & ROPER, 1998) that live in coastal and neritic waters between latitudes 60°N and 60°S, but their distribution is uneven, with few species being present on the eastern coasts of the Atlantic and Pacific Oceans (Fig. 7; Table 3). The coasts of the Indian and the western Pacific Oceans are relatively rich in species (NESIS, 1980), followed by the coasts of the western Atlantic (COHEN, 1976). One species, *Loligo gahi*, is found in both the Atlantic and Pacific Oceans, as it lives along the coasts of South America (Fig. 7; Table 3). The most widespread species include *L. duvauceli*, *L. vulgaris*, and *L. forbesi* (ROPER, SWEENEY, & NAUEN, 1984). Unusual physical events, such as El Niño, can extend the horizontal range of coleoids; *Loligo opalescens* penetrates farther north in years of warm temperatures, but this migration is temporary. Although adults in spawning condition were captured, their young did not appear in later captures (WING & MERCER, 1990).

The genus *Octopus* is the most speciose of all extant Cephalopoda (G. L. VOSS, 1977; VOIGHT, 1994; SWEENEY & ROPER, 1998) and currently includes more than 100 species. Its members inhabit coastal waters between latitudes 60°N and 55°S, but few species are found along the eastern coasts of either the Pacific or the Atlantic Oceans. The coasts bordering the western Pacific Ocean are rich in species of this genus, those of Australia perhaps being the richest of all (Table 4).



1



2

FIG. 5. 1, Outline map of the world divided artificially into areas (1–5), and the species of Recent *Sepia* recorded in each is listed in Table 2; note complete absence of representatives of this genus around coasts of the Americas; 2, outline map to show the Recent distribution range of Sepiidae; lines or hatching represents number of species present, as a percentage of total number of species in family, as follows: broken lines, <5%; sparse hatch lines, 5%–10%; dense hatch lines, 11%–15%; crosshatched lines, >15% (Khromov, 1998).

TABLE 2. *Sepia* inhabits coastal waters, and species listed in columns 1–5 correspond to areas 1–5 of Figure 5. Species occurring in more than one area are shown above dashed line; those below are restricted to one area, and some may be endemic (data compiled from Nesis, 1987).

1	2	3	4	5
Eastern Atlantic, North Sea to Angola, Mediterranean	South Africa, Namibia to southern Mozambique	Northern Indian Ocean, Indonesia and Indo-China Peninsula, Red and Arabian Seas, Persian Gulf, eastern Africa to Mozambique	Australian waters	Japanese waters, Sea of Japan, Yellow, East, and China Seas
		<i>S. pharonis</i> <i>S. latimanus</i>	<i>S. pharonis</i> <i>S. latimanus</i>	<i>S. pharonis</i> <i>S. latimanus</i>
<i>S. officinalis</i>	<i>S. officinalis</i> <i>S. zanzibarica</i>	<i>S. zanzibarica</i> <i>S. elliptica</i> <i>S. papuensis</i> <i>S. aculeata</i> <i>S. kobiensis</i>	<i>S. elliptica</i> <i>S. papuensis</i>	<i>S. aculeata</i> <i>S. kobiensis</i>
<i>S. bertheloti</i>	<i>S. acuminata</i>	<i>S. arabica</i>	<i>S. apama</i>	<i>S. andreana</i>
<i>S. elegans</i>	<i>S. adami</i>	<i>S. bandensis</i>	<i>S. baxteri</i>	<i>S. appelloefi</i>
<i>S. elobyana</i>	<i>S. angulata</i>	<i>S. dollfusi</i>	<i>S. braggi</i>	<i>S. carinata</i>
<i>S. orbignyana</i>	<i>S. apillata</i>	<i>S. elongata</i>	<i>S. chirostrema</i>	<i>S. erostrata</i>
	<i>S. australis</i>	<i>S. gibba</i>	<i>S. cottoni</i>	<i>S. esculenta</i>
	<i>S. burnupi</i>	<i>S. ivanovi</i>	<i>S. cultrata</i>	<i>S. longipes</i>
	<i>S. confusus</i>	<i>S. murrayi</i>	<i>S. irvingi</i>	<i>S. lycidas</i>
	<i>S. dubia</i>	<i>S. omani</i>	<i>S. mestus</i>	<i>S. madokai</i>
	<i>S. faurei</i>	<i>S. prashada</i>	<i>S. mira</i>	<i>S. origera</i>
	<i>S. hieronis</i>	<i>S. recurvirostris</i>	<i>S. novaehollandiae</i>	<i>S. pardalis</i>
	<i>S. incerta</i>	<i>S. savignyi</i>	<i>S. pfefferi</i>	<i>S. peterseni</i>
	<i>S. insignis</i>	<i>S. sewelli</i>	<i>S. plangon</i>	<i>S. tenuipes</i>
	<i>S. joubini</i>	<i>S. stellifera</i>	<i>S. reesi</i>	<i>S. tokioensis</i>
	<i>S. pulchra</i>	<i>S. suleata</i>	<i>S. rex</i>	<i>S. tullbergi</i>
	<i>S. robsoni</i>	<i>S. thurstoni</i>	<i>S. rhoda</i>	
	<i>S. simoniana</i>	<i>S. trygonina</i>	<i>S. rozella</i>	
	<i>S. tuberculata</i>		<i>S. smithi</i>	
	<i>S. typica</i>		<i>S. vercoi</i>	

The geographic distribution of species of *Sepia*, *Loligo*, and *Octopus* is uneven, and it is notable that the coasts of the eastern Atlantic and the eastern Pacific Oceans are inhabited by the smallest number of species of each genus, when compared with other coasts (Fig. 5, Fig. 7; Tables 2–4). The greatest number of species live in the indo-western Pacific region, followed by the Gulf of Mexico and Caribbean Sea. These two areas are both relatively shallow and are also richest in coastal macrobenthos (VALENTINE & MOORES, 1974), as well as being rich in coral reefs and highly productive. Apart from those living in the Mediterranean Sea, little is known of the biogeography of the sepiolids.

ESTUARIES

A very small number of species, mostly loliginids, are now known to enter estuarine waters; the migration is usually temporary, although it may last for some months. *Loliguncula brevis* is found in major estuaries of the Gulf of Mexico, where it tolerates low salinity (DRAGOVICH & KELLY, 1967; BRAKONIECKI, 1980); its young inhabit these waters, too, and also the shelf waters (VECCHIONE, 1982). Farther south, *Loligo surinamensis* is currently known only from around the mouth of the Suriname River (ROPER, SWEENEY, & NAUEN, 1984). The brackish waters of the Gulf of Panama in the

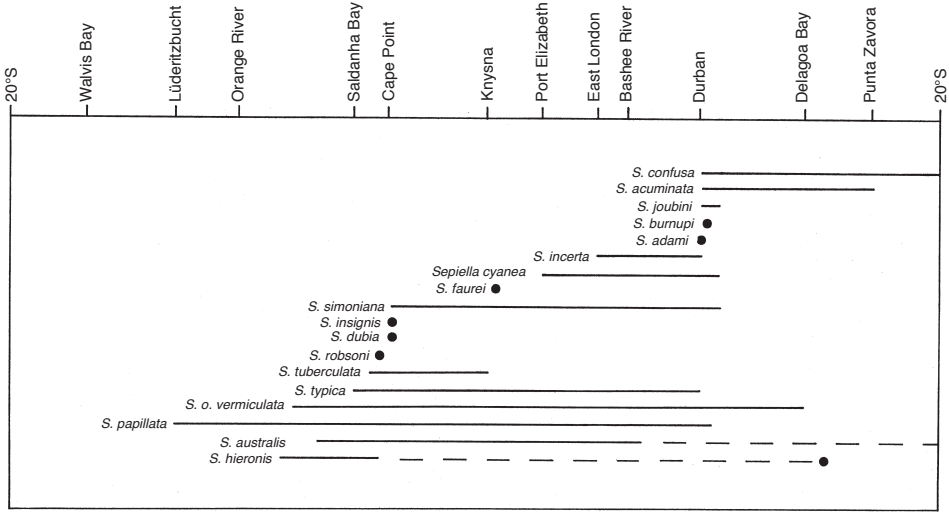


FIG. 6. Species of *Sepia* living around South Africa from West to East (below 20°South); extent of horizontal distribution of each species around this coast is represented by lengths of lines, and broken lines indicate uncertainty of distribution (Roeleveld, 1972).

TABLE 3. *Loligo* lives in costal waters, and species listed in columns 1–4a correspond to areas 1–4a indicated in Figure 7; *Loligo gabi* (areas 1a, 4a) is found around the coasts of South America and thus is present in both Pacific and Atlantic Oceans (data compiled from Nesis, 1982).

Western Atlantic Ocean	Eastern Atlantic Ocean	Indian and western Pacific Oceans: southern Africa to Japan, Australia, and Polynesia	Eastern Pacific Ocean
Areas 1, 1a	Area 2	Area 3	Area 4, 4a
<i>L. gabi</i> (area 1a, and 4a)			<i>L. gabi</i> (area 4a, and 1a)
<i>L. brasiliensis</i>	<i>L. forbesi</i>	<i>L. arabica</i>	<i>L. opalescens</i>
<i>L. ocula</i>	<i>L. vulgaris</i>	<i>L. aspersa</i>	
<i>L. patagonica</i>		<i>L. beka</i>	
<i>L. pealei</i>		<i>L. bleekeri</i>	
<i>L. plei</i>		<i>L. budo</i>	
<i>L. roperi</i>		<i>L. chinensis</i>	
<i>L. surinamensis</i>		<i>L. duvauceli</i>	
		<i>L. edulis</i>	
		<i>L. japonica</i>	
		<i>L. pickfordia</i>	
		<i>L. reesi</i>	
		<i>L. sibogae</i>	
		<i>L. singhalensis</i>	
		<i>L. spectrum</i>	
		<i>L. sumatrensis</i>	
		<i>L. uyii</i>	
		<i>L. vossi</i>	

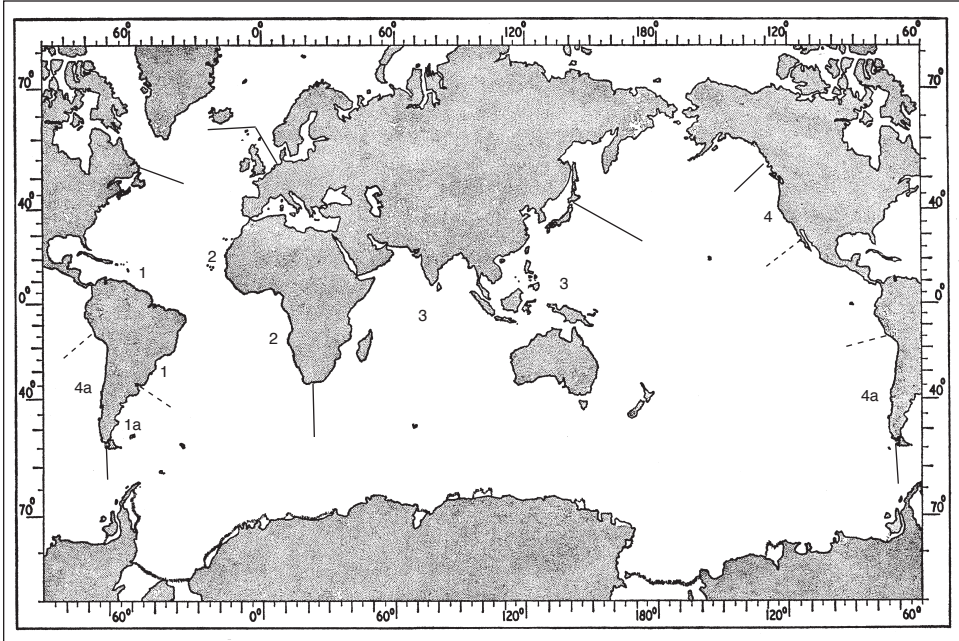


Fig. 7. Outline map of the world divided artificially into areas (1–4a); species of *Loligo* found in each is listed in Table 3.

eastern Pacific are inhabited by *Lolliguncula tydeus* (BRAKONIECKI, 1980). Other loliginids entering estuarine waters have been found in Australia and include *Loliolus noctiluca* (LU, ROPER, & TAIT, 1985) and *Sepioteuthis lessoniana* (JACKSON, 1990). A small idiopsepiid, *Idiosepius pygmaeus*, inhabits estuaries and mangrove swamps for most of the year near Townsville, Australia (JACKSON, 1989).

DISTRIBUTIONS OF COLEOIDS

WIDELY DISTRIBUTED FORMS

Some coleoids have a wide geographical distribution, mostly in tropical or temperate waters; others are less widespread; and some are restricted, even to one locality (ROPER, SWEENEY, & NAUEN, 1984; ROPER, SWEENEY, & CLARKE, 1985). Widespread species include the spirulid *Spirula spirula* (Fig. 8) (BRUUN, 1955); the oegopsid squids *Thysanoteuthis rhombus*, *Onychoteuthis banksi*, and *Ommastrephes bartrami* (ROPER, SWEENEY, & NAUEN, 1984); the vampyromorph *Vampyroteuthis*

infernalis (Fig. 9) (PICKFORD, 1940, 1952), which is restricted to the oxygen-minimum layer (SEIBEL & others, 1997); and the pelagic octopods, *Vitreledonella richardi* (Fig. 10a), *Japetella diaphana* (Fig. 10b) (THORE, 1949), *Tremoctopus violaceus*, *Ocythoë tuberculata*, *Argonauta argo*, and *Alloposus mollis* (Fig. 10c) (THORE, 1949; ROPER, SWEENEY, & NAUEN, 1984). Some cold-water teuthids have circumpolar distributions; these include *Moroteuthis ingens*, *Todarodes filippova*, *Mesonychoteuthis hamiltoni* (ROPER, SWEENEY, & CLARKE, 1985), and *Bathyteuthis abyssicola* (ROPER, 1969), but none is bipolar. These coleoids vary markedly in the size they attain as adults and in their reproductive habits, including egg size, mode of spawning, and in the presence or absence of egg care. There is, however, growing evidence to show that some of the so-called cosmopolitan species are composed of multiple species or subspecies, exhibiting a complex of individual distributional patterns (N. A. VOSS, 1988; F. G. HOCHBERG & K. MANGOLD, personal communication, 1995).

TABLE 4. *Octopus* inhabits coastal waters, and species at head of each list occur in more than one area; species below dashed line have more restricted distributions; it is noteworthy that the western coasts of both Pacific and Atlantic Oceans are richer in species than their eastern borders (data compiled from Nesis, 1982).

Western Atlantic Ocean	Eastern Atlantic Ocean	Indian Ocean	Western Pacific Ocean	Eastern Pacific Ocean
<i>O. macropus</i>	<i>O. macropus</i>	<i>O. macropus</i>	<i>O. macropus</i>	
<i>O. vulgaris</i>	<i>O. vulgaris</i>	<i>O. vulgaris</i>	<i>O. vulgaris</i>	
		<i>O. aegina</i>	<i>O. aegina</i>	
		<i>O. cyanea</i>	<i>O. cyanea</i>	
		<i>O. membranaceus</i>	<i>O. membranaceus</i>	
<i>O. burryi</i>	<i>O. burryi</i>			
<i>O. defilippi</i>	<i>O. defilippi</i>			

<i>O. fontanianus</i>	<i>O. saluti</i>	<i>O. tetricus</i>	<i>O. alpheus</i>	<i>O. pricei</i>
<i>O. hummelincki</i>	<i>O. schultzei</i>		<i>O. arenoides</i>	
<i>O. joubini</i>			<i>O. ariabilis</i>	
<i>O. lobensis</i>			<i>O. aspilosomatis</i>	
<i>O. maya</i>			<i>O. conspicadeus</i>	
<i>O. megalocyathus</i>			<i>O. dierythraeus</i>	
<i>O. tebuelus</i>			<i>O. dollfusi</i>	
<i>O. zonatus</i>			<i>O. exannulatus</i>	
		<i>O. fujitai</i>		
		<i>O. globosus</i>		
		<i>O. graptus</i>		
		<i>O. minor</i>		
		<i>O. ocellatus</i>		
		<i>O. ochotensis</i>		
		<i>O. oliveri</i>		
		<i>O. polyzenia</i>		
		<i>O. spinosus</i>		
		<i>O. tsugarensis</i>		
		<i>O. yendoi</i>		

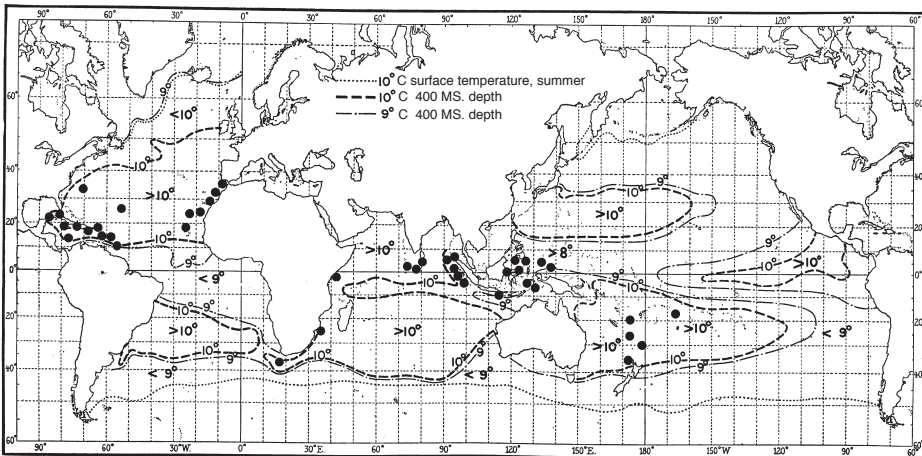


FIG. 8. Distribution of *Spirula spirula* (Bruun, 1955).

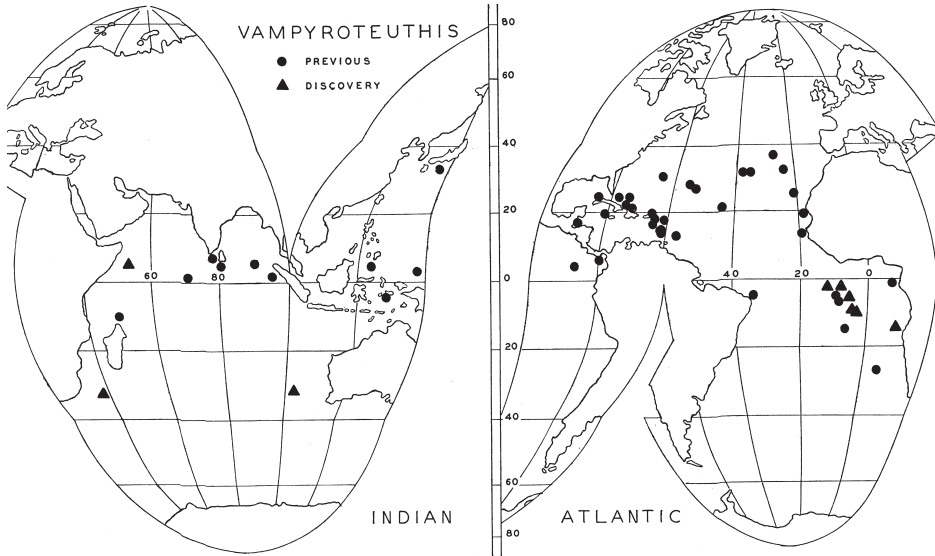


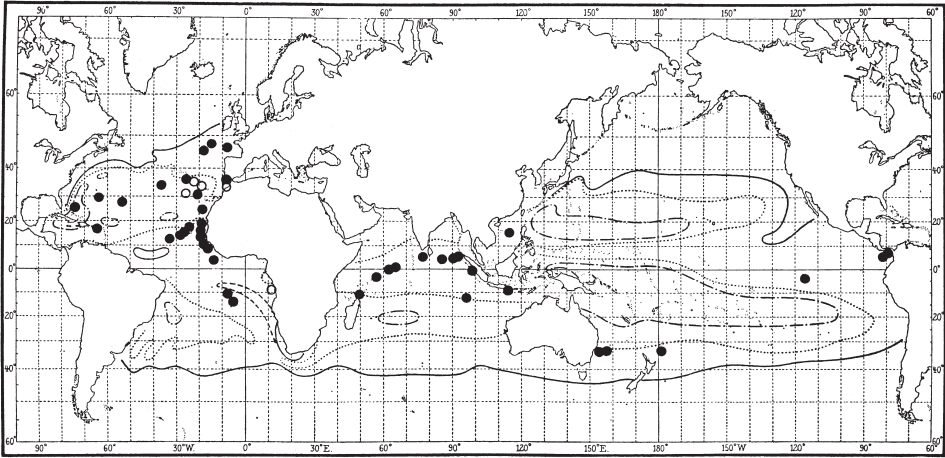
FIG. 9. Distribution of *Vampyroteuthis infernalis* (circles, earlier records; triangles, Discovery captures) (Pickford, 1952).

The success of coleoids in spreading widely around the world does not seem attributable to any single feature of their mode of life as adults or their reproductive strategies, except perhaps the presence of a planktonic phase, even if extremely brief, during the life cycle. Where the juvenile and adult stages are benthic, a post-hatching planktonic phase allows dispersal. The hatchlings of some species are found in current systems that could carry them considerable distances from the site of hatching (OKUTANI & MCGOWAN, 1969; O'DOR, 1983; DUNNING, 1985). Other factors, not as yet addressed in cephalopods, are the influences that trigger changes in habitat, such as the ontogenetic migrations, evident in some oceanic squids and octopods (CLARKE & LU, 1974, 1975; LU & CLARKE, 1975a, 1975b; ROPER & YOUNG, 1975; R. E. YOUNG, 1978), and the settlement of planktonic young to their juvenile and adult habitat on the bottom (NIXON & MANGOLD, 1996). A planktonic phase may influence the distribution of many species, especially bottom-living forms, but other species that spend their entire lives in open waters and

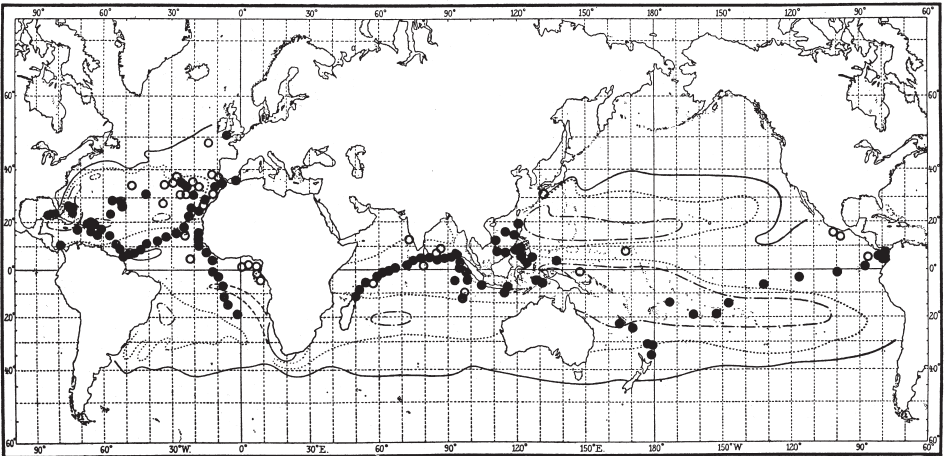
have planktonic posthatchlings are not widespread. This suggests that other factors have a role in the distribution of coleoids, and these may include light, temperature, oxygen, salinity, upwelling areas, current systems, and high productivity.

THE GONATIDAE

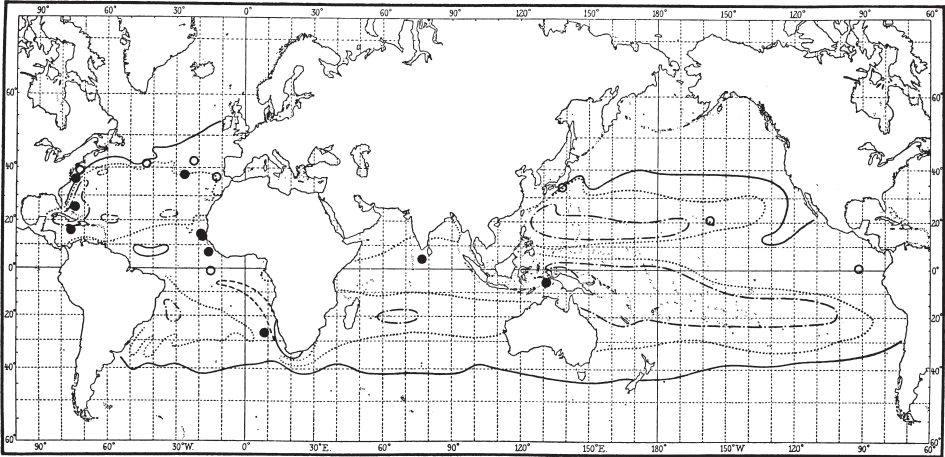
Representatives of this family of oceanic squids inhabit the cold waters of the Pacific and Atlantic Oceans. Each of its four genera has representatives in the North Pacific Ocean (Fig. 11), the most speciose being *Gonatus* with species in both oceans (KRISTENSEN, 1981; OKUTANI, KUBODERA, & JEFFERTS, 1988). The distributions of members of this genus in the North Pacific are shown in Figure 11a–b; nine species occur in the north, three are trans-Pacific, five are northeastern; and three are northwestern in distribution, two of the latter being very restricted (OKUTANI, KUBODERA, & JEFFERTS, 1988). The Atlantic Ocean is inhabited by only three species, two in the north (Fig. 12) and one isolated in Antarctic waters (KRISTENSEN, 1984). One, *G. fabricii*, is widely distributed and is the dominant



1



2



3

FIG. 10. Distribution of three octopods; 1, *Vitreledonella richardi*; 2, *Japetella diaphana*; 3, *Alloposus mollis* (open circles, earlier records; filled circles, DANA stations) (Thore, 1949).

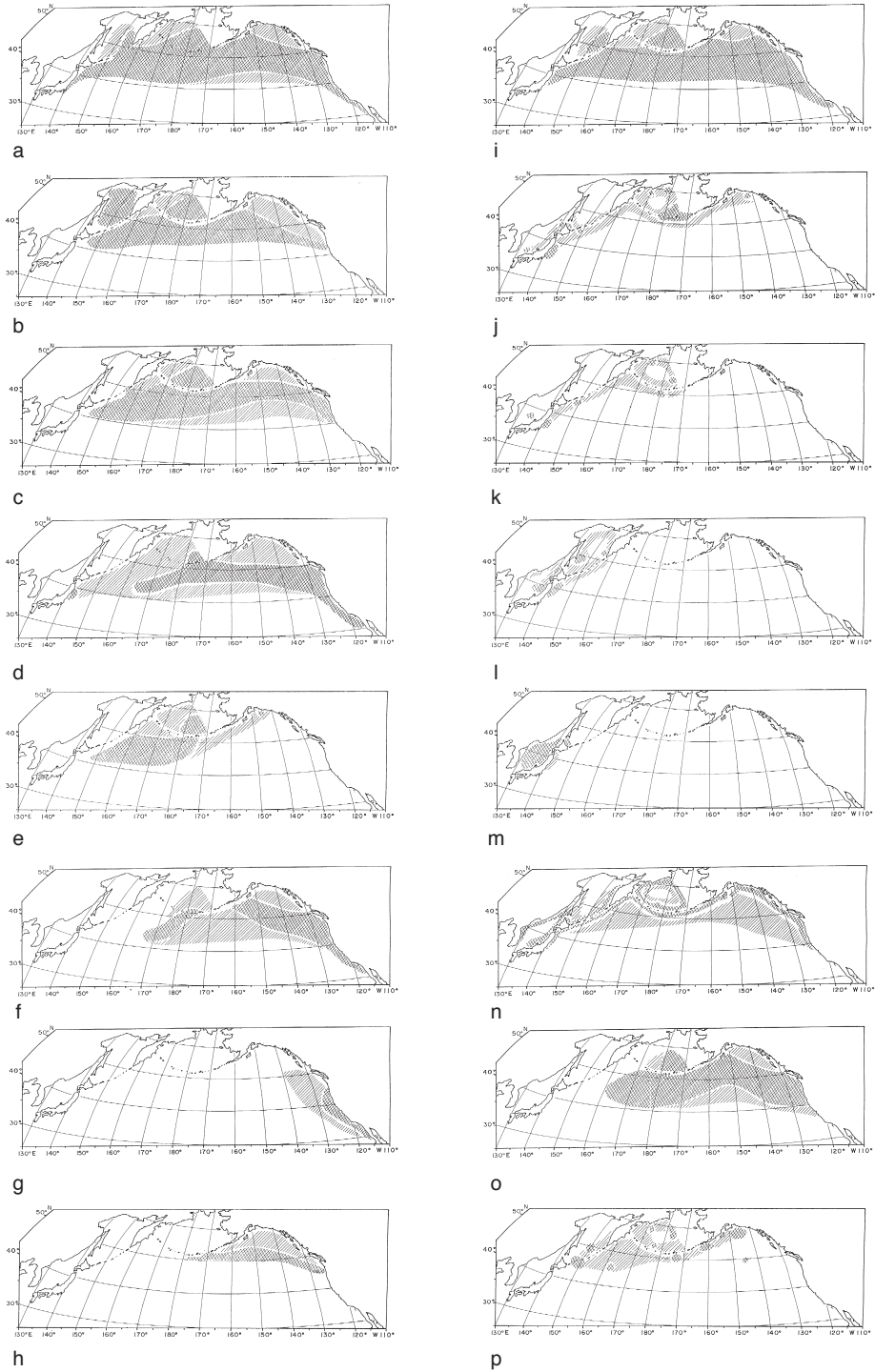


FIG. 11. Distribution of species of family Gonatidae, shown by shading, in the Pacific Ocean; *a-b*, *Gonatus*; *i-m*, *Gonatopsis*, *n-o*, *Berryteuthis*, and *p*, *Eggonatus* (Okutani, Kubodera, & Jefferts, 1988).

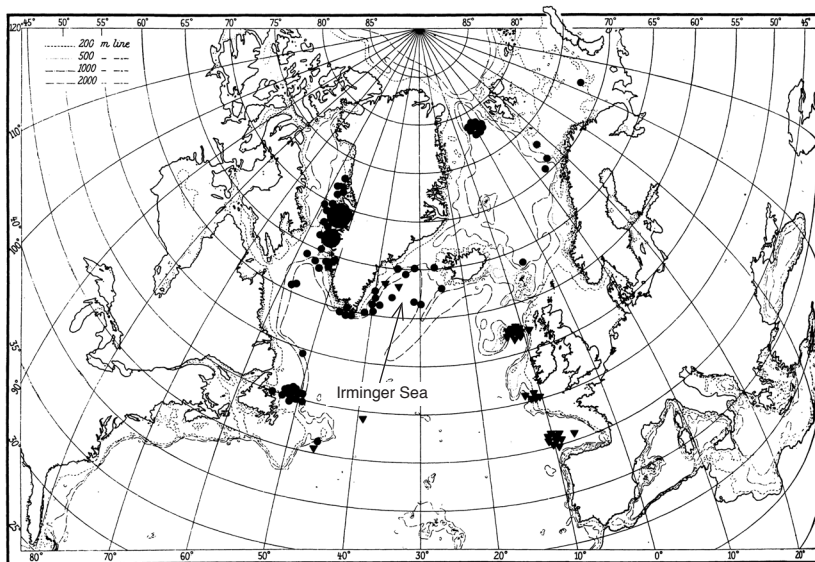


FIG. 12. Gonatidae in the North Atlantic Ocean. *Gonatus fabricii* (circles) and *G. steenstrupi* (triangles) overlap in Irminger Sea; *G. fabricii* spawns in autumn in Disko Bugt and in spring and early summer at entrance to Amerdlog Fjord (Kristensen, 1981, 1982).

squid of Arctic and sub-Arctic waters, the other, *G. steenstrupi*, is widespread in boreal waters; the two species overlap in the Irminger Sea (Fig. 12) (KRISTENSEN, 1982), and in the south, *G. antarcticus* is a circumpolar species. *Gonatopsis* is the second most speciose genus of the family, with five species living in the North Pacific (Fig. 11*i-m*). One has a wide, trans-Pacific distribution, and the others have northwestern distributions, although one extends some distance to the northeast, and another is restricted to the Sea of Japan. The genus *Berryteuthis* has two species; one is trans-Pacific in distribution, and the other lives in the northeastern Pacific and westward to 160°E (Fig. 11*n-o*). The remaining genus, *Eogonatus*, with only one species, is found widely in the North Pacific (Fig. 11*p*) (NESIS, 1982). Of the many species of the family Gonatidae living in the North Pacific Ocean, some are widely distributed and others restricted. The North Pacific Ocean is thus the center of diversity for this family.

The common ancestor of *Gonatus fabricii* and *G. steenstrupi* probably migrated

through the Bering Strait into the Arctic and North Atlantic Oceans in the early late Pliocene (during the Beringian transgression) approximately 3.5 to 3.2 Ma (NESIS, 1997). Sometime later, during the Pleistocene, the ancestor of the notalian *G. antarcticus* migrated from the northeastern Pacific Ocean into the Southern Ocean. These three species are closely related to each other and to *G. californiensis*. This author concludes that the radiation of the Gonatidae took place between the late Miocene and mid-Pliocene, that *Berryteuthis* is probably the oldest taxon, and that there is a considerable difference between this genus and the other gonatids. Such a relationship has been indicated in the structure of the statoliths and beaks (CLARKE, 1988).

OTHER GENERA

The genus *Teuthowenia* (Cranchiidae) comprises three discrete, closely related, allopatric species of oceanic oegopsid squids (N. A. VOSS, 1985). *T. megalops* lives in sub-Arctic and temperate waters of the North Atlantic Ocean, between latitudes

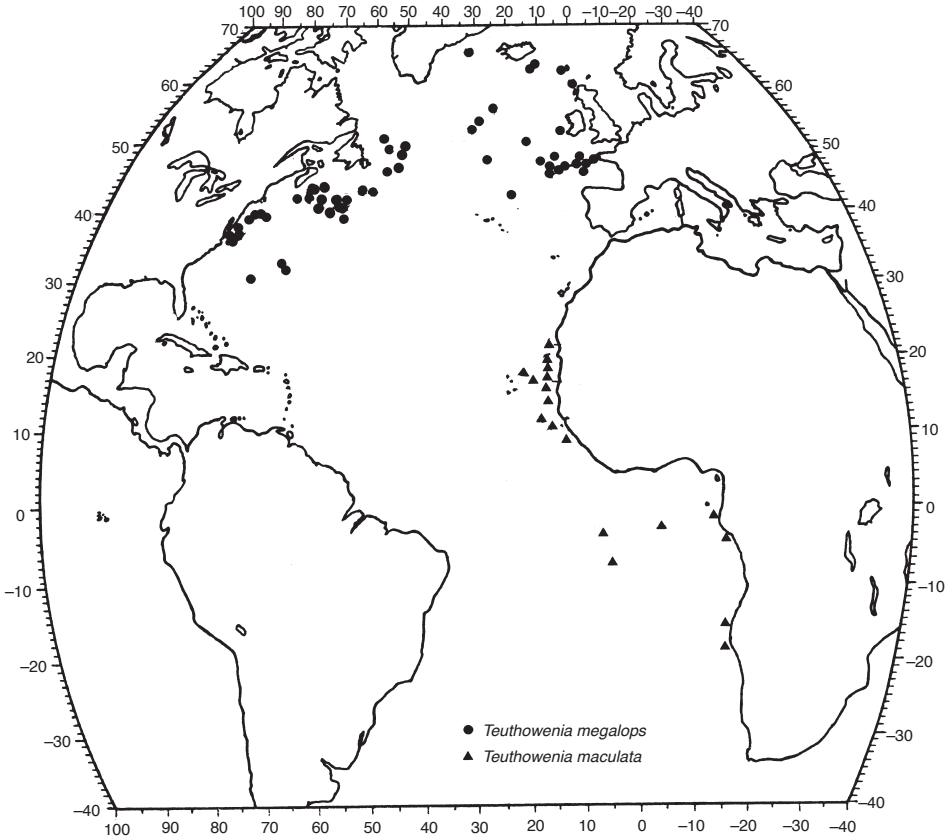


FIG. 13. Distribution of *Teuthowenia megalops* (circles) and *T. maculata* (triangles) in Atlantic Ocean (N. A. Voss, 1985).

62° to 66°N and 44° to 45°N (Fig. 13), with the main concentrations in sub-Arctic waters. *T. maculata* is restricted to the eastern tropical Atlantic Ocean, in the Mauritanian Upwelling Region and the Guinean Province (Fig. 13). *T. pellucida* has a narrow, circumglobal distribution in the Southern Subtropical Convergence, in the vicinity of 49°S (Fig. 14). The geographic isolation appears complete in these three species, and their distribution is considered to result from a combination of biological and physical factors (N. A. VOSS, 1985). Evidence suggests that these squids undergo an ontogenetic descent to breed in midwater. Breeding and spawning occurs throughout the ranges of these species and is extended, perhaps throughout the year. So far no

mature or nearly mature specimens of *T. maculata* have been captured. Paralarval stages are similar in *T. megalops* and *T. pellucida*, but in the latter, maturation occurs at a smaller size, and it produces fewer but larger eggs than *T. megalops*.

The genus *Hapalochlaena* (Octopodidae) is found in the Indo-Pacific region and is a complex of species, all bearing iridescent blue markings. *H. maculosa* lives in the shallow coastal waters of Queensland, Victoria, Tasmania, South and Western Australia, and Indonesia. When newly hatched, its young resemble the adult and are also benthic in habit (STRANKS & LU, 1991). *H. fasciata* lives in the shallow waters of southern Queensland and New South Wales and is endemic to Australia; at hatching, its

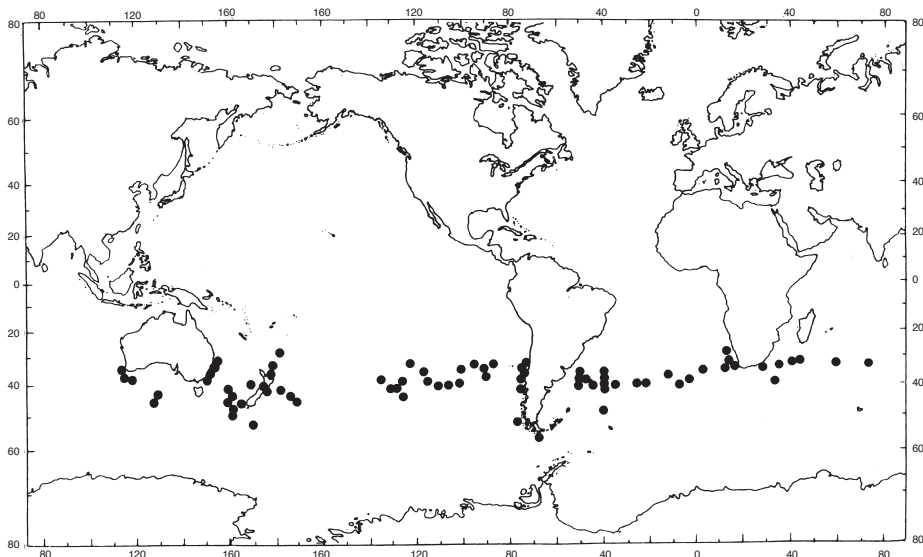


Fig. 14. Distribution of *Teuthowenia pellucida* (filled circles) (N. A. Voss, 1985).

young immediately adopt benthic habits (ROPER & HOCHBERG, 1988). *H. lunulata* is Indo-Malayan (NORMAN & SWEENEY, 1997) and has been recorded from Australia, New Zealand, Papua New Guinea, the Philippines, and Sri Lanka. On hatching, its young spend a short time in the plankton (VON BOLETZKY & HANLON, 1983). *H. lunulata* is the most widespread member of this species complex (ROPER & HOCHBERG, 1988). It is notable that the most widely distributed of these species has young that spend a short period in the plankton.

The genus *Eledone* (Octopodidae) has two species living in European waters, both of which have been studied extensively (BOYLE, 1983b; MANGOLD, 1983). *E. moschata* inhabits the coast of southern Portugal, the Gulf of Cadiz, and the Mediterranean. *E. cirrhosa* is found from the coasts of Iceland, the Faroe Islands, Norway, the British Isles, and southward into the Mediterranean Sea. The latter reaches a larger adult size and produces a larger number of smaller eggs; the hatchlings are smaller and are planktonic. This contrasts with the larger eggs and benthic hatchlings of *E. moschata* (Table 5). *E. cirrhosa*, with its planktonic phase, is

more widespread than the other without such a stage.

GEOGRAPHICAL VARIATION WITHIN SPECIES

Specimens of *Loligo pealei* (Loliginidae), caught in the western North Atlantic, consist of several morphometrically variable populations with differences in size, gill length, and the number of sucker rows at sexual maturity (COHEN, 1976). HIXON, HANLON, and HULET (1981) reviewed the recorded sizes of specimens of this species caught in different geographic locations and confirmed COHEN's findings that only the largest are found in the northern and coldest end of the range.

Eledone cirrhosa (Octopodidae) has a relatively wide geographic distribution between Norway and the Mediterranean. This permitted a simultaneous study of two populations, one in the southern and the other in the northern part of its range, to determine whether they exhibited any biological variation (BOYLE, MANGOLD, & NGOILE, 1988). These populations form parts of a continuous geographic distribution, separated by a distance of 1650 km and

TABLE 5. Two populations of *Eledone cirrhosa*, separated geographically, were subjected to various measurements and counts made simultaneously (Boyle, Mangold, & Ngoile, 1988); comparison can be made between these two populations and with *Eledone moschata*, which also lives in the Mediterranean Sea, but has a more restricted distribution (Mangold, 1983).

	<i>Eledone cirrhosa</i>		<i>E. moschata</i>
	Aberdeen 2°W 57°N	Banyuls 3°E 44°N	Banyuls 3°E 44°N
Maximum weight of mature adult			
male	600 g	400 g	
female	1450 g	900 g	
average of male and female			up to 600 g
Mantle length of newly hatched young	3.0 mm	4.5 mm	10–12 mm
Period of egg laying	Jan.–Oct.	Apr.–Aug.	Nov.–Aug.
Length of egg-laying period by single female	1 month	10–15 days	8–10 weeks
Number of eggs produced by single female	8900	5500	100–500
Length of egg	7.0 mm	7–8 mm	12–16 mm
Habits of newly hatched young	planktonic	planktonic	benthic
Life cycle, approximate duration	2 years	1 year	2 years

by the pattern of water circulation so that they are reproductively isolated. Specimens of the northern population were captured within 100 km of Aberdeen, Scotland, in the North Sea, and those of the southern one were caught from 5 to 15 km off the shore of Banyuls in the Mediterranean. Both males and females of the former population grow larger, have a greater fecundity, and a longer lifespan than those of the latter population (Table 5).

Gonatus fabricii (Gonatidae) shows variation in several morphometric characters in specimens inhabiting two geographically close areas off western Greenland (at about 69°N). There is no external sexual dimorphism in this species, but morphometric differences do separate these populations. Furthermore, the time of reproduction differs: *G. fabricii*, from Disko Bugt, spawns in autumn, and those at the entrance to the Amerdloq Fjord spawn in spring and early summer (Fig. 12) (KRISTENSEN, 1982). Temporal separation of spawning activities has been observed in other species, for example, *Alloteuthis subulata* (GRIMPE, 1925) and *Loligo opalescens* (FIELDS, 1965).

THE EFFECTS OF ISOLATION

Loligo vulgaris (Loliginidae) is common along the coasts of western Europe, the

Mediterranean Sea, and northwestern Africa; farther south, another similar species, *L. reynaudii*, occurs (ROPER, SWEENEY, & NAUEN, 1984), but both are absent from the African coast between latitudes 20°S and 28°S. Analyses of morphological measurements and meristic counts of selected characters of these two species indicate differences in most body dimensions and in the number of suckers present on the tentacular club; however, protein electrophoretic analyses showed that the genetic difference between these two nominal species was at subspecific rather than specific level (AUGUSTYN & GRANT, 1988). These authors suggested that the geographical separation of these subspecies, *L. vulgaris vulgaris* and *L. v. reynaudii*, was caused by a hydrographic barrier of cold, oxygen-deficient water separating the populations off the western coast of southern Africa. This water is turbulent due to wind-driven upwelling and occurs between latitudes 24°S and 28°S off the coast of Namibia. The circulation system probably became established about 2.5 million years ago (SHANNON, 1985).

Tropical shallow-water octopodines (Octopodidae) living on either side of the Panamanian isthmus include a number of morphologically similar species or geminate congeneric pairs (Table 6). There is a strong

TABLE 6. Shallow-water octopuses that inhabit coasts of eastern Pacific and western Atlantic Oceans; strong similarities are present in many external features between two members of each of six pairs of octopods that straddle the central American isthmus, providing evidence that each of the pairs shares a recent common ancestor (Voight, 1988).

Eastern Pacific	Western Atlantic
<i>Octopus oculifer</i>	<i>Octopus hummelincki</i>
<i>O. bimaculatus</i>	<i>O. maya</i>
<i>O. digueti</i>	<i>O. sp. A</i>
<i>O. chierchiaie</i>	<i>O. zonatus</i>
<i>O. alecto</i>	<i>O. briareus</i>
<i>Euaxoactus panamensis</i>	<i>Euaxoactus pillsburyae</i>

resemblance between six and possibly seven geminate species pairs, indicating that each of the pairs shares a recent common ancestor; the putative ancestral species must have been split by the uplift of Central America that took place some 3.0 to 3.5 million years ago (VOIGHT, 1988). This period of time has allowed speciation to take place, but the shorter separation time of *Loligo vulgaris vulgaris* and *L. v. reynaudii* appears to be sufficient to reach the subspecies level.

DIVERSITY, SPECIATION AND ENDEMICISM

The center of diversity of the family Gonatidae is in the North Pacific Ocean (see above). The greatest species and genetic

diversity of the family Loliginidae occurs in the center of the indo-western Pacific and the tropical western Atlantic (NESIS, 1985), being at their most diverse in the Caribbean Sea, especially the Panama area (Table 7). COHEN (1976) examined the morphological features of four species of *Loligo* living in this region and found *L. roperi* to be the smallest and most distinctive. The two smallest species, *L. roperi* and *L. ocula*, are both associated with islands. The number of species along the mainland coasts falls from that in the Panama area toward the north and south, but several of the species are widely distributed, including *Loligo pealei*, *L. plei*, *Lolliguncula brevis*, and *Sepioteuthis sepioidea* (HAIMOVICI, PEREZ, & COSTA, 1989). Two species, *Loligo plei* and *Sepioteuthis sepioidea*, are also found off the coasts of Bermuda (G. L. VOSS, 1960), Cuba (G. L. VOSS, 1955), the Virgin Islands (HOCHBERG & COUCH, 1971), and Florida (G. L. VOSS, 1956a).

Sepiolidae is a family of very small, mainly benthic animals inhabiting the continental shelf and slope in many parts of the world. In the Mediterranean, there are 17 species, 4 of which are endemic (VOLPI, BORRI, & VON BOLETZKY, 1995). High numbers of endemic species of *Sepia* are found along the coasts of Africa (ROLEVELD, 1972), Australia (ADAM & REES, 1966; ADAM, 1979), and the northern borders of the Indian Ocean and the northwestern Pacific Ocean (NESIS, 1985) (Fig. 5).

TABLE 7. Horizontal distribution of members of family Loliginidae along western borders of the Atlantic Ocean and in the Gulf of Mexico and Caribbean Sea (Cohen, 1976; Haimovici, 1985; Haimovici, Perez, & Costa, 1989). Of these, the most widespread species is *Loligo plei*, which is also found in Bermuda, as is *Sepioteuthis sepioidea*.

Longitude	Horizontal distribution	Species
45°N–10°S	Newfoundland to Brazil, Gulf of Venezuela	<i>Loligo pealei</i>
39°N–27°S	Delaware Bay to Rio de Janeiro	<i>Lolliguncula brevis</i>
35°N–37°S	New Jersey to Mar del Plata, Bermuda	<i>Loligo plei</i>
32°N–13°S	Cape Canaveral to Bahia, Brazil, and Bermuda	<i>Sepioteuthis sepioidea</i>
6°N–9°N	Suriname (currently only known in this area)	<i>Loligo surinamensis</i>
25°S–8°S	Caribbean Sea, associated with islands	<i>Loligo roperi</i>
25°S–20°S	Cuba	<i>Loligo ocula</i>
20°S–42°S	Espiritu Santo, Brazil, to Rio Negro, Argentina	<i>Loligo sanpaulensis</i>

Speciation has been most successful in two genera, *Sepia* and *Octopus*, each with about 100 species, and to a lesser extent *Loligo*, with some 50 species (SWEENEY & ROPER, 1998). All live in shelf and slope waters along the margins of oceans and seas, yet these areas form only one fifth of the oceanic area. Relatively few families and genera are found in coastal waters although they include the most speciose genera of the coleoids. This is in marked contrast with oceanic waters where the number of families and genera is high but the number of species is small; for example, *Histioteuthis*, *Gonatus*, and *Mastigoteuthis* are among the most speciose genera of the oegopsid squids, each with only some 10 species. The species-level richness, which is so characteristic of animals living on land, is apparent only among benthic groups in the sea (GHISELIN, 1987). This is so for cephalopods, notably those living in coastal waters where the habitat is more varied and diverse than in open waters, and it is the eastern margins of the oceans that are richest in coastal genera, especially of *Sepia*, *Loligo*, and *Octopus*.

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