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DISTRIBUTION OF RECENT CEPHALOPODA AND IMPLICATIONS FOR PLIO-PLEISTOCENE EVENTS

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ABSTRACT

The Recent Cephalopoda include 2 subclasses, 11 orders/suborders, 50 families, 18 subfamilies, 154 genera, 35-36 subgenera, approximately 718 species (some doubtful), and 42 subspecies. The class includes both *neritic* and *oceanic* species and both assemblages include *pelagic* and *bottom-connected* species. The assemblage of *oceanic* cephalopods include 84% of all families, 73% of genera and 48% of species of recent cephalopods. *Neritic* cephalopods include species living on or near the bottom on the continental shelf, usually not far from the coast such as *Sepia* and *Octopus*. Oceanic cephalopods include *oceanic pelagic, nerito-oceanic, bathyal-pelagic* and some rare *distant-neritic* species.

There are two main principles in zoogeographic regionalization of the marine environment: *faunistic* and *zonal-geographic (latitudinal-zonal)*. The distribution of shallow-water species will be described in terms of faunistic zoogeography, that of oceanic species in terms of *zonal-geographic* zoogeography.

The maximum diversity of the cephalopod fauna is in the tropics and subtropics. The highest number of endemics is observed in the Indo-West Pacific Tropical Region, including the western Indian Ocean, in second place is the Eastern Pacific Region. There are also some bi-subtropical, bi-central, bi-peripheral, subtropical, north subtropical-boreal and south subtropical-notalian genera and species. The number of endemics in cold and temperate zones is not high, however, their rank may be high, particularly in the Antarctic. Benthic and nektobenthic shelf-living species, deep-water bottom and near-bottom inhabitants, nerito-oceanic, and oceanic species have substantially different distribution patterns.

The following types of ranges exist in oceanic and nerito-oceanic pelagic cephalopods: 1. Arctic. 2. Arctic-boreal. 3. Boreal: 3.1. Atlantic boreal: 3.1.1. Atlantic low-boreal; 3.2. Pacific boreal: 3.2.1. Pacific panboreal; 3.2.2. Pacific high-boreal; 3.2.3. Northwest Pacific (Asiatic) low-boreal; 3.2.4. Northeast Pacific (American) low-boreal. 4. Low-boreal-subtropical. 5. Peripheral. 6. Subtropical. 7. Tropical: 7.1. Tropical-boreal-notalian; 7.2. pan-tropical (tropical-subtropical); 7.3. Narrow-tropical; 7.4. Equatorial; 7.5. Equatorial-west-central (inhabiting equatorial and central waters in western and only equatorial in the eastern halves of the Atlantic and/or Pacific); 7.6. Equatorial-subtropical – avoiding central waters. 8. Central. 9. South subtropical-notalian and species of the Southern Subtropical Convergence. 10. Notalian. 11. Notalian-Antarctic. 12. Antarctic.

The following scheme of latitudinal zonality of the epipelagic and mesopelagic realms of the World Ocean is proposed based on cephalopod distribution: 1. Arctic Zone with High-Arctic and Low-Arctic subzones. 2. Boreal Zone with High-Boreal and Low-Boreal subzones. *a*. Northern peripheral ecotone. 3. North Subtropical Zone. 4. Tropical Zone with North Central, Equatorial, and South Central subzones. 5. South Subtropical Zone. *b*. Southern peripheral ecotone (the zone of the Southern Subtropical Convergence). 6. Notalian Zone. 7. Antarctic Zone with Low-Antarctic and High-Antarctic subzones. There are 30-32 centres of speciation of neritic benthic and nektobenthic cephalopods and 46 zoogeographic provinces of the shelf zone, including 3 transitional and 4 doubtful.

A scheme is presented of correlation between latitudinal zones and subzones in the pelagic realm and the zoogeographic provinces of the shelves united into 10 faunistic shelf regions: Arctic (4 provinces), Atlantic Boreal (4),

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Pacific Boreal (3), West Atlantic tropical + subtropical (4), East Atlantic (3), Indo-West Pacific (12), East Pacific tropical + subtropical (4), Magellanic notalian (2), Kerguelenian notalian (3), and Antarctic (3); 4 provinces cannot be included into any region.

Problems are discussed concerning: the opening of the Bering Strait, closure of the Central American Seaway (Panama Strait), faunistic exchange between northern and southern temperate belts through the equatorial area during the Pleistocene; and formation of faunistic disjunctions and "locked up" faunas during the Ice Ages.

The author concludes that the rate of speciation among Recent Cephalopoda caused by climatic or orogenic isolation is of the order of one or a few million years.

INTRODUCTION

The Recent Cephalopoda include 2 subclasses, 11 orders/suborders, 50 families, 18 subfamilies, 154 genera, 35-36 subgenera, approximately 718 species (some doubtful), and 42 subspecies (Nesis 1985, 1987, Voss *et al.* 1988, information from CephBase and subsequent data) (Table 1).

The study of the distribution of Recent Cephalopoda is impeded by the fact that this class includes both *neritic* and *oceanic* species and both these assemblages include *pelagic* and *bottom-connected* species with different distributional patterns.

In the assemblage of *oceanic* Cephalopoda I include orders Nautilida (the only family Nautilidae with two genera) and Spirulida (the only species *Spirula spirula*), a part of Sepiolida [Sepiolidae: Rossiinae (only the genus *Neorossia*) and all Heteroteuthinae], all Oegopsida, Vampyromorpha (the only species *Vampyroteuthis infernalis*), all Cirrata (=Cirrina) and Incirrata (=Incirrina) except 2 subfamilies of Octopodidae (Octopodinae and Eledoninae). All other Recent coleoids – all Sepiidae, Sepiadariidae, Idiosepiidae, Loliginidae, Pickfordiateuthidae, most Sepiolidae, and 2 subfamilies of Octopodidae (Octopodinae and Eledoninae) are treated as *neritic* cephalopods (Nesis 1985, 1987).

This distinction is not, of course, absolute. For example, the families Sepiidae, Loliginidae, Octopodidae are predominantly shallow-water animals, some species of *Sepia* and *Octopus* even inhabit the intertidal zone, but some others live in the bathyal zone at depths of some hundred meters. On the contrary, some oceanic squids of the family Ommastrephidae may be found at the surface very close to the shore. But as a rule oceanic species, even surface-living, do not enter waters over depths of less than about 175-300 m (Nesis 1993, Moiseev 2001). In my distinction between neritic and oceanic cephalopods those species inhabiting predominantly (although not exclusively) shelf waters are related to the *neritic* assemblage while those living either in the pelagic realm or on/near the bottom outside the outer shelf boundary are related to the *oceanic* one.

The neritic cephalopods include species living on or near the bottom but most of them may occur in midwater and many extend up to the surface, but usually not far from the coast (on/over the shelves). The oceanic cephalopods may be purely pelagic, usually never entering the bottom or near-bottom realm, while others may one way or another be connected with the bottom: they may either permanently live on the bottom, or in the near-bottom layer, or descend to the bottom only in adulthood to lay eggs, or may predominate in the areas over the slopes or underwater rises because of enhanced productivity, etc. Among these is a rather diverse assemblage of species living in the pelagic zone but predominantly over the slopes or, at least, not far oceanward from slopes. They do not cross the open ocean except where latitudinal chains of seamounts and ridges exist. They are called *nerito-oceanic* species. Some very important commercial squids are found among the nerito-oceanic species.

The assemblage of pelagic species, which do not enter the shelf (mainly mesopelagic inhabitants) but do not cross the ocean, live over the slopes and the so-called "near-shore abyss" and are in some ways connected with the bottom or near-slope areas of enhanced productivity, they are usually termed the "*bathyal-pelagic assemblage*" (Parin 1984) or "*mesopelagic boundary community*" (Reid *et al.* 1991, Vecchione 2001).

There are also some (a very limited number) of

Table 1 Taxonomic composition of Recent Cephalopoda with distinction between neritic and oceanic assemblages. Based on CephBase and K.N. Nesis' file. Doubtful species are included

Orders, suborders, families	Subfamilies	Genera	Subgenera	Species	Subspecies
Nautilida					
Nautilidae	-	2	-	5	2
Spirulida					
Spirulidae	-	1	-	1	-
Sepiida					
Sepiidae	-	3	6-7	111	-
Sepiolida s.l.					
Sepiolidae	3	14	2	55	4
Sepiadariidae	-	2	-	7	-
Idiosepiidae	-	1	-	7	-
Teuthida, Myopsida					
Loliginidae	2	11	2	45	2
Pickfordiateuthidae	-	1	-	2	-
Teuthida, Oegopsida					
Lycoteuthidae	2	4	-	5	-
Enoploteuthidae	-	4	12	40	4
Ancistrocheiridae	-	1	-	1	-
Pyroteuthidae	-	2	-	6	2
Octopoteuthidae	-	2	-	7	-
Onychoteuthidae	-	6	-	15	-
Walvisteuthidae	-	1	-	1	-
Gonatidae	-	3	4	18	3
Chtenopterygidae	-	1	-	3	-
Bathyteuthidae	-	1	-	3	-
Histioteuthidae	-	1	-	13	6
Psychroteuthidae	-	1	-	1	-
Architeuthidae	-	1	-	1	3
Neoteuthidae	-	3	-	3	-
Brachioteuthidae	-	2	-	6	-
Ommastrephidae	5	11	-	21	2
Thysanoteuthidae	-	1	-	1	-
Pholidoteuthidae	-	1	-	3	-
Lepidoteuthidae	-	1	-	1	-
Batoteuthidae	-	1	-	1	-
Cycloteuthidae	-	2	-	4	-
Chiroteuthidae	-	5	2	13	4
Mastigoteuthidae	-	3	3	19	-
Joubiniteuthidae	-	1	-	1	-
Magnapinnidae	-	1	-	1	-
Promachoteuthidae	-	1	-	1	-
Cranchiidae	2	14	2	31	-
Vampyromorpha					
Vampyroteuthidae	-	1	-	1	-
Octopoda, Cirrina					
Opisthoteuthidae	-	2	-	19	-
Grimpoteuthidae	-	2	-	11	-
Luteuthididae	-	1	-	2	-
Stauroteuthidae	-	1	-	2	-
Cirroteuthidae	-	3	-	5	-
Octopoda, Incirrina					
Boliaenidae	-	3	-	3	2
Amphitretidae	-	1	-	2	-
Idioctopodidae	-	1	-	1	-
Octopodidae	4	24	2	206	6
Vitreledonellidae	-	1	-	1	-
Alloposidae	-	1	-	1	-
Ocythoidae	-	1	-	1	-
Tremoctopodidae	-	1	-	3	2
Argonautidae	-	1	-	7	-
In general					
7 orders, 4 subord., 50 fam.	18	154	35-36	718	42
Neritic assemblage					
7 families (2 partly)	6	42	10-11	371	6
Oceanic assemblage					
43 families	12	112	25	347	36

pelagic species whose ranges stretch along the coasts over the slopes and "near-shore abyss" and do not cross the open ocean but which, according to recent information, are not connected with the bottom at all. They are called "*distant-neritic*" (Beklemishev 1969) or "*pseudo-oceanic*" (Voss 1985) species. It is believed that they are connected with coastal modifications of oceanic water masses or with "neutral zones" between main oceanic gyres.

The assemblage of *oceanic* cephalopods includes 43 families (wholly or partly), 12 subfamilies, 112 genera, 25 subgenera, approximately 347 species and 36 subspecies, i.e., 84% of all families, 73% of genera and 48% of species of recent cephalopods (Table 1). The distinction between per cent values of oceanic assemblages at familial, generic and specific level is caused by the fact that the two most speciose genera of cephalopods, *Sepia* and *Octopus*, are neritic ones.

ZOOGEOGRAPHY OF RECENT CEPHALOPODA

There are two main principles in zoogeographic regionalization of the marine environment: *faunistic* and *zonal-geographic (latitudinal-zonal)* principles (Kafanov & Nesis 1982, Nesis 1985, Kafanov & Kudryashov 2000). For analysis of the geographic distribution of a group (macro-taxon) of animals both principles must be based on the distribution of species and avoid use of data on abundance/biomass of animals, on distribution of temperature, salinity, currents and any other abiotic factors. A typification of ranges is necessary for any generalization because the individual records which make up a range must be changed into an idealized and typified unbroken (quasi-continuous) range. But the general distributional patterns are different in neritic and oceanic cephalopods: the first are better described in terms of *faunistic* zoogeography while the second in terms of *zonal-geographic (latitudinal-zonal)* zoogeography. The main unit of zoogeographic division using the faunistic principle is the *Province*; the higher unit is the *Region*, and the subordinate unit is the *District*. Using the latitudinal-zonal principle we have *Zone* and *Subzone* (Nesis 1985).

It is reasonable to correlate the system of provinces and districts along opposite coasts of an ocean (contralateral) and in different oceans. But this is hindered by the fact that the farther from the poles the smaller is the number of amphi-oceanic or inter-oceanic neritic species inhabiting both provinces under comparison. Thus the correlation of provinces and districts and their amalgamation into latitudinal zones/subzones should be objective only in near-polar regions and ever more subjective the closer to the equator they are located. Here the distributional system of oceanic species may help us. We may collate the provinces and districts of the shelves based on the ranges of shallow-water (shelf and neritic) species, having predominantly meridionally extended ranges, with latitudinal zones/subzones based on the ranges of pelagic oceanic species, having predominantly latitudinally extended ranges.

Although we do not use temperature data for the selection of latitudinal zones, only the ranges of species, the latitudinal distribution of species (as well as communities) in the ocean primarily reflects the thermal tolerance of species. As a result, the boundaries of neritic provinces and districts usually coincide with areas of strong hydrological gradients. Analogically, the boundaries of latitudinal faunistic zones in the pelagic realm coincide with areas of division between the main cells of oceanic circulation (oceanic fronts, convergences and divergences of currents). And the areas of strong hydrological gradients on shelves just coincide with areas where the boundaries of the main cells of oceanic circulation come close to the coasts. Thus, the main patterns of faunistic zonality on the shelves and in the open ocean should be alike because both reflect the general scheme of oceanic circulation. In the result we may homologize the contralateral shelf provinces with the aid of their correlation with the same latitudinal zones of the pelagic realm.

The work reported here was done by me over many years for different areas of the World Ocean as data on cephalopod distribution in these areas were accumulated. In many of my publications there were zoogeographic schemes for the Arctic Ocean, different areas of the Atlantic, Indian and Pacific oceans, for the Gulf of Mexico, the Caribbean Sea and adjacent western tropical Atlantic, for the Mediterranean Sea, the Australian-New Zealand region, and finally for the whole ocean (Nesis 1982a, 1985). The data from the last-named work, with corrections and additions, is the basis of this paper.

Maximum diversity of cephalopods, as of most other groups of marine animals, is observed in the tropics and subtropics. The ranges of 68.8% of all genera and subgenera (130 out of 189) lie, entirely or partly, in the tropics and subtropics; however, only 10.6% (20) live exclusively in the tropics. The highest number of endemics is observed in the Indo-West Pacific Tropical Region (including the western Indian Ocean): the number of endemic genera and subgenera here [17: *Nautilus, Allonautilus; Sepia (Acanthosepion), Metasepia, Sepiolina; Abralia (Abralia), Abralia (Enigmoteuthis), Heteroteuthis (Stephanoteuthis), Idioteuthis, Loliolus, Photololigo, Uroteuthis; Ameloctopus, Cistopus, Octopus (Abdopus), Teretoctopus, Velodona*] is higher than their number in the three other tropical regions taken together. In second position is the Eastern Pacific Region [4 endemic genera/subgenera: *Dosidicus, Drechselia, Lolliguncula (Loliolopsis), Vulcanoctopus*], further out is the Western Atlantic Region (*Nectoteuthis, Tetracheledone*), and in the last place is the Eastern Atlantic Region (*Rondeletiola*).

Some endemic genera exist in the subtropics too but their number is much smaller than in the Indo-West Pacific: there are 3 bi-subtropical genera [*Architeuthis, Iridoteuthis, Ommastrephes,* including 2 bi-subtropical species (*A. dux, O. bartramii*), which migrate into the boreal and notalian zones for foraging)], 2 bi-central genera (*Hyaloteuthis, Ocythoe*), three genera inhabiting peripheral belts located between the subtropical and temperate zones (2 bi-peripheral: *Eucleoteuthis*, *Lampadioteuthis,* one inhabiting the zone of the Southern Subtropical Convergence: *Notonykia*), one Pacific northern subtropical subgenus [*Abraliopsis (Boreabraliopsis)*] and one southern subtropical genus (*Nematolampas*), in total ten. To this number one Pacific north subtropical-boreal genus (*Watasenia*) and one Atlantic south subtropical-notalian genus (*Walvisteuthis*) may be added.

The number of endemics in cold and temperate zones is not high, however, their rank may be high. This particularly concerns the Antarctic where there are 2 endemic families of squid (the antarctic Psychroteuthidae and the notalian-antarctic Batoteuthidae). In general terms, the cold and temperate waters of the southern hemisphere are twice as rich in endemics than those of the northern hemisphere.

Benthic and near-benthic (*nektobenthic*) shelf-living species, deep-water bottom and near-bottom inhabitants, nerito-oceanic, and oceanic species have substantially different distributional patterns. The most important zoogeographic pattern of benthic and nektobenthic cephalopods is the predominance of meridionally extended linear ranges, covering only one Region and in some cases only one Province.

But even among nektobenthic neritic cephalopods two tropical-subtropical families – Sepiidae (true cuttlefishes) and Loliginidae (neritic squids) – have strongly different distributions. Maximum diversity of genera and species in loliginids is observed in the Indo-Malayan Province of the Indo-West Pacific Region. In the second place is the Western Atlantic Region; morphologically and ecologically aberrant forms are tropical ones. The sepiids are absent in the New World, and in the Old World their northern and southern boundaries almost coincide with those of loliginids. But maximum diversity, degree of endemism, and number of aberrant forms (such as the subgenera *Doratosepion* and *Rhombosepion* of the genus *Sepia*) are generally observed outside the Indo-Malayan Province, particularly off eastern and southern Africa, in Japanese and Chinese waters, and off western and eastern Australia. Only *Sepia (Acanthosepion)* and *Sepiella* are most diverse in the Indo-Malayan Province (Nesis 1980, 1985, Khromov 1998). These differences are controlled primarily by the difference in the evolutionary course of each of these speciose families.

The patterns of distribution of shallow-water octopodid octopods and non-sepiid cuttlefishes (Sepiolida s.l.) in general are like those of loliginids except for increased octopodid species richness in the Eastern Pacific Region and in some subtropical faunistic centres, such as southern Japan and the Gulf (and Peninsula) of California (Nesis 1985, Voight 1988, 1998).

The boreal fauna is very much poorer than the tropical one, although it is possible to distinguish between low-boreal and high-boreal faunas, particularly in the northern Pacific (for example, among gonatid squids, in which 4 out of 5 genera and subgenera and most species are boreal Pacific endemics: Nesis 1997). The notalian (subantarctic) fauna is even poorer (one endemic squid genus, *Nototeuthis*) but the Antarctic one is rather diverse (mostly among octopods) and highly endemic: 7 endemic oegopsid genera (*Alluroteuthis, Batoteuthis, Kondakovia, Martialia, Mesonychoteuthis, Psychroteuthis, Slosarczykovia*) and 2 octopod genera (*Megaleledone, Pareledone*); some of them inhabit both the Antarctic and Notalian zones.

On the contrary, the ranges of oceanic cephalopods (in some cases also nerito-oceanic ones) are extended longitudinally and many species are circumglobal. The faunas of pelagic cephalopods of the Atlantic and Indo-Pacific or Indo-West Pacific are basically the same but the Indo-West Pacific fauna is significantly richer than the Atlantic one. The faunas of oceanic cephalopods in the western and eastern tropical Atlantic are almost identical but those of nerito-oceanic cephalopods are somewhat different and the western Atlantic one is richer than the eastern Atlantic fauna. Even more pronounced are the distinctions between the nerito-oceanic faunas of different parts of the Indo-Pacific. There are almost no common species between the Indo-West Pacific and Eastern Pacific regions, however, the boundary between the West and East Pacific faunistic regions is significantly shifted to the east and located between the Sala y Gómez Islands and the South American coast (Parin *et al.* 1997). The fauna of oceanic cephalopods of the eastern Pacific is distinctly impoverished but has some endemic species.

Among tropical cephalopods it is possible to select equatorial, narrow-tropical and pan-tropical species, the latter being the most widely distributed. There are some central, subtropical, and peripheral species (the central species are those inhabiting the Central Gyres). Boreal faunas are rich in species, particularly the North Pacific boreal one. There are also some (uncommon) west- and east-Pacific, west- and east-Atlantic nerito-oceanic boreal species (particularly among gonatids: Nesis 1997). The peripheral and subtropical faunas in the Northern hemisphere are much poorer than in the Southern hemisphere. The faunas of pelagic cephalopods of the Notalian and Antarctic zones are not poorer than that of the Boreal Zone while the fauna of the Arctic Zone is extremely poor (2 species).

The pattern of distribution of bathyal and abyssal bottom and near-bottom cephalopods is poorly studied but in general features it corresponds to existing schemes of zoogeography of bathyal (Zezina 1985, 1997) and abyssal (Vinogradova 1959, 1997, Kussakin 1971) realms with only minor differences.

The following types of ranges exist in oceanic and nerito-oceanic pelagic cephalopods (some examples are included).

1. Arctic species (Fig. 1; no entirely arctic species are known among oceanic and nerito-oceanic pelagic cephalopods).

2. Arctic-boreal species (*Cirroteuthis muelleri*: Fig. 1, *Gonatus fabricii*: Fig. 2).

3. Boreal species:
  - 3.1. Atlantic low-boreal (*Gonatus steenstrupi* [NE Atlantic: Fig. 2], *Teuthowenia megalops*: Fig. 3).
  - 3.2. Pacific boreal:
    - 3.2.1. Pacific pan-boreal (*Chiroteuthis calyx, Gonatus berryi, Gonatopsis borealis*: Fig. 3*, Gonatus onyx*: Fig. 4*, Galiteuthis phyllura*).
    - 3.2.2. Pacific high-boreal (*Gonatus kamtschaticus, G. madokai*: Fig. 2*, G. tinro*].
    - 3.2.3. Northwest Pacific (Asiatic) low-boreal [*Berryteuthis magister shevtsovi*].
    - 3.2.4. Northeast Pacific (American) low-boreal [*Berryteuthis anonychus*: Fig. 5*, Gonatus californiensis*); there are also species with wide-boreal ranges in the western and high boreal in the eastern Pacific [*Berryteuthis magister magister*: Fig. 3*, Gonatopsis (G.) octopedatus*].

4. Low-boreal-subtropical species:
  - 4.1. Oceanic [*Onychoteuthis borealijaponica* in the Pacific: Fig. 6].
  - 4.2. Nerito-oceanic [*Illex illecebrosus* in northwestern Atlantic: Fig. 7, *Todarodes sagittatus* in northeastern Atlantic: Fig. 5, *Watasenia scintillans* and *Todarodes pacificus* in northwestern Pacific: Figs 5, 7].

5. Peripheral species [north peripheral, south peripheral: *Abraliopsis (Micrabralia) gilchristi*; bi-peripheral: *Eucleoteuthis luminosa*: Fig. 8, *Lampadioteuthis megaleia*].

6. Subtropical species (north subtropical, south subtropical: *Abralia* [*Astrabralia*] *astrolineata, Nototodarus gouldi* in southwestern Pacific: Fig. 7; bi-subtropical: *Architeuthis dux*: Fig. 9,

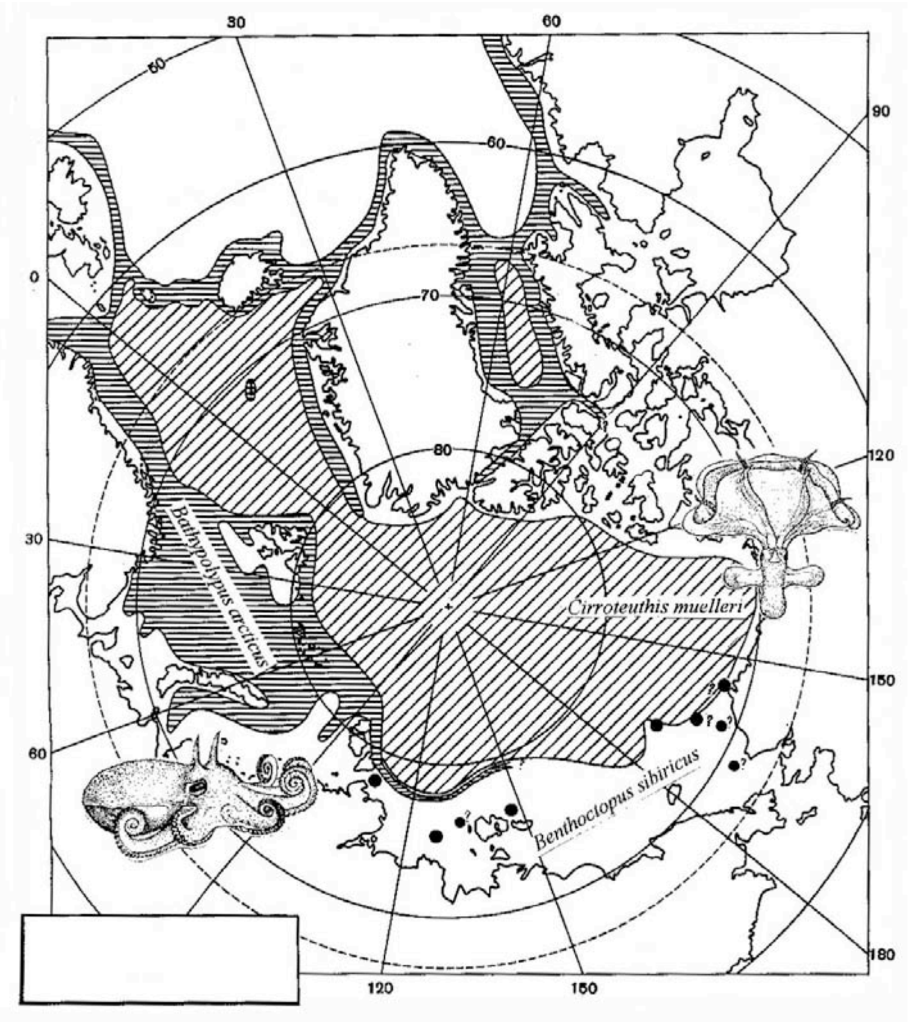

Fig. 1 Distribution of cephalopods in the Arctic Ocean: *Cirroteuthis muelleri* (arctic-boreal panarctic), *Bathypolypus arcticus* ("Atlanto-West-Arctic" arctic-boreal) and *Benthoctopus sibiricus* (East-Arctic) (from Nesis 1985, with modifications)

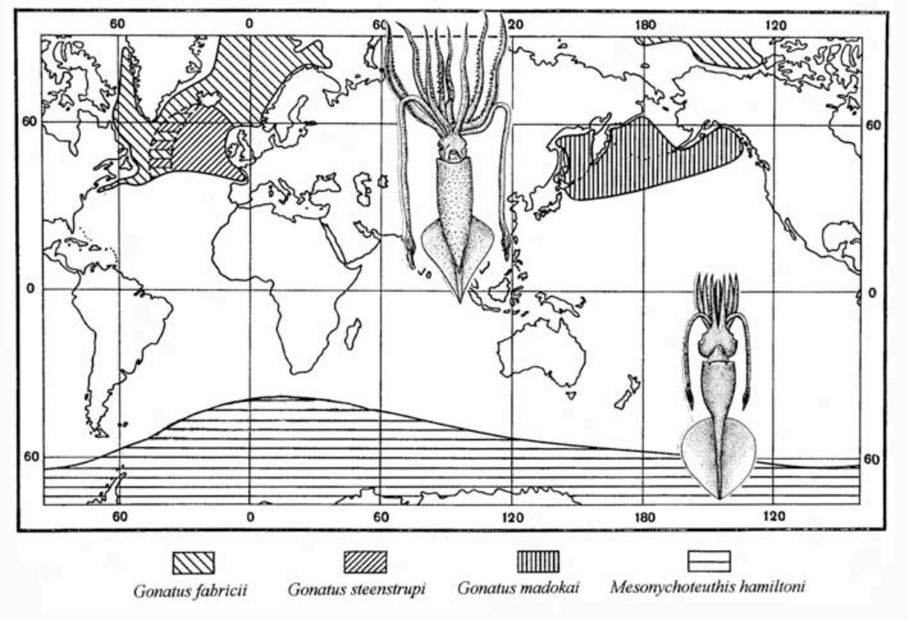

Fig. 2 Distribution of *Gonatus fabricii* (arctic-boreal panarctic), *G. steeenstrupi* (NE Atlantic boreal), *G. madokai* (Pacific high-boreal), and *Mesonychoteuthis hamiltoni* (Antarctic) (from Nesis 1985, with modifications)

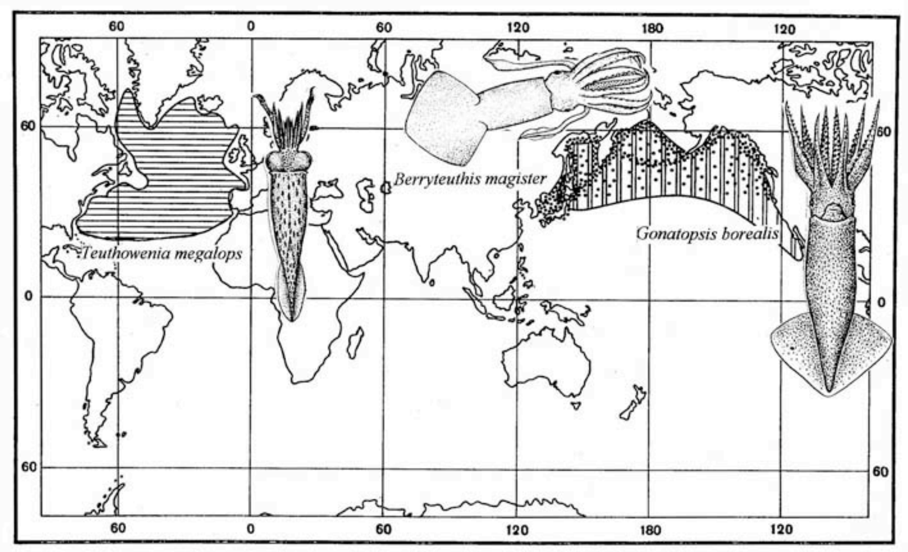

Fig. 3 Distribution of *Teuthowenia megalops* (Atlantic low-boreal oceanic), *Berryteuthis magister* (dots: pan-boreal in western and high-boreal in eastern Pacific) and *Gonatopsis borealis* (vertical ruling: Pacific pan-boreal) (from Nesis 1985 and Voss 1985, with modifications)

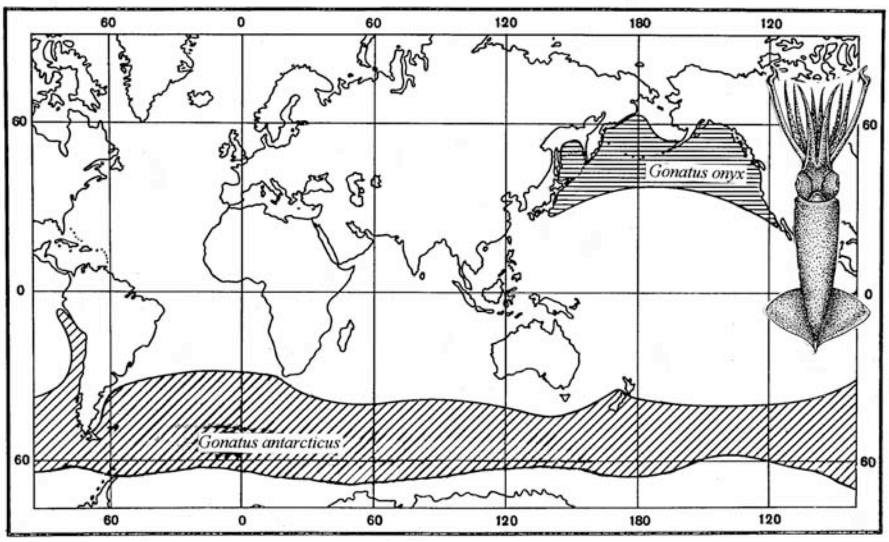

Fig. 4 Distribution of *Gonatus onyx* (Pacific pan-boreal) and *G. antarcticus* (Notalian) (from Nesis 1985, 1999, with modifications)

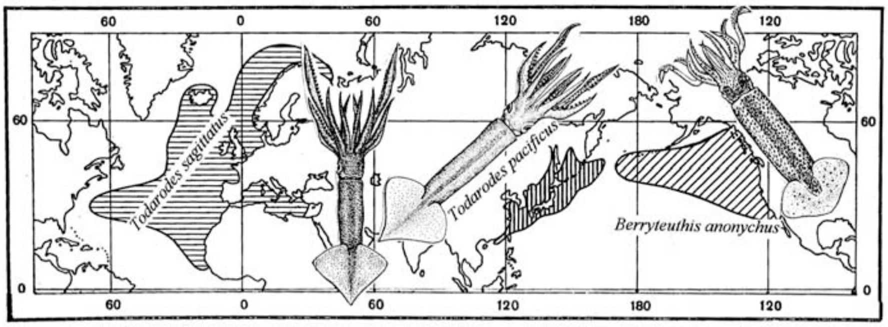

Fig. 5 Distribution of the low-boreal-subtropical nerito-oceanic species *Todarodes sagittatus* (NE Atlantic) and *T. pacificus* (NW Pacific). Distribution of the northeast-Pacific (American) low-boreal nerito-oceanic *Berryteuthis anonychus* (from Nesis 1985, with modifications)

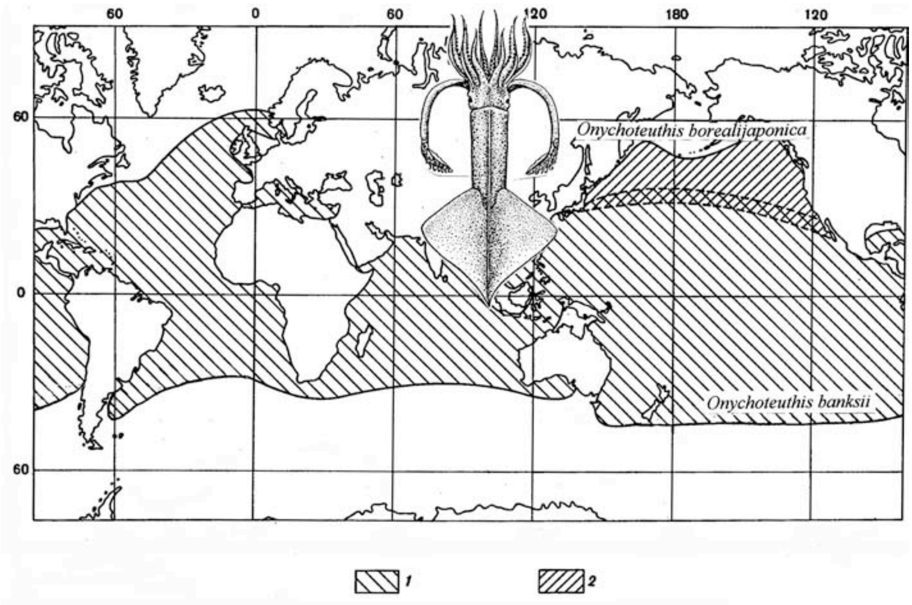

Fig. 6 Distribution of the pantropical oceanic *Onychoteuthis banksii* and the Pacific low-boreal-subtropical oceanic *O. borealijaponica* (from Nesis 1985, with modifications)

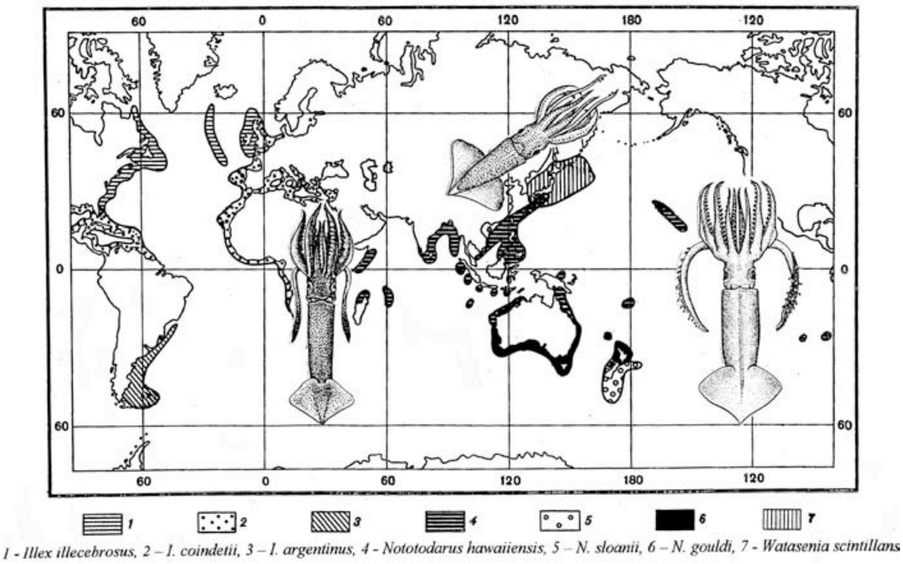

Fig. 7 Distribution of nerito-oceanic species of the genera *Illex* (low-boreal-subtropical *I. illecebrosus* mainly in NW Atlantic*, I. argentinus* in SW Atlantic and pantropical Atlantic *I. coindetii*); *Nototodarus* (south subtropical *N. gouldi* and notalian *N. sloanii* in southwestern Pacific and pantropical Indo-West Pacific *N. hawaiiensis*) and *Watasenia* (low-boreal-subtropical *W. scintillans* in NW Pacific) (from Nesis 1985, with modifications).

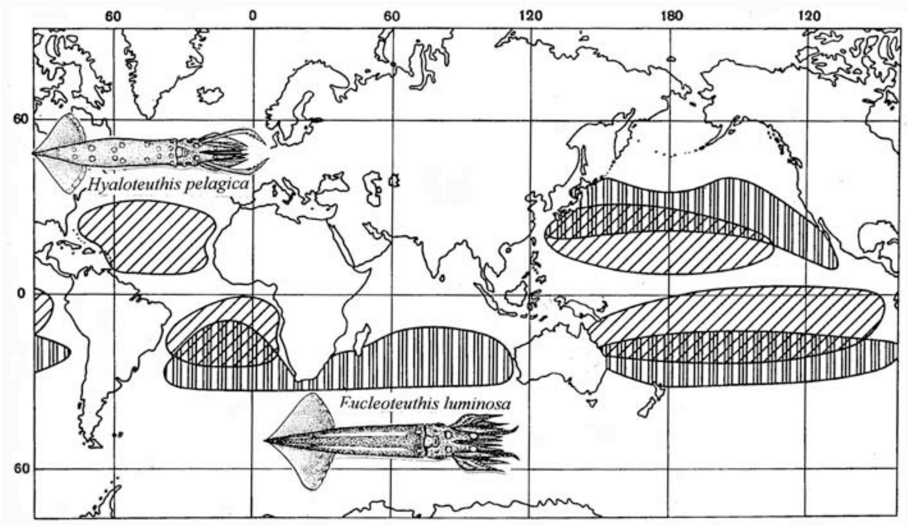

Fig. 8 Distribution of bi-central *Hyaloteuthis pelagica* and bi-peripheral *Eucleoteuthis luminosa* (from Nesis 1985, with modifications).

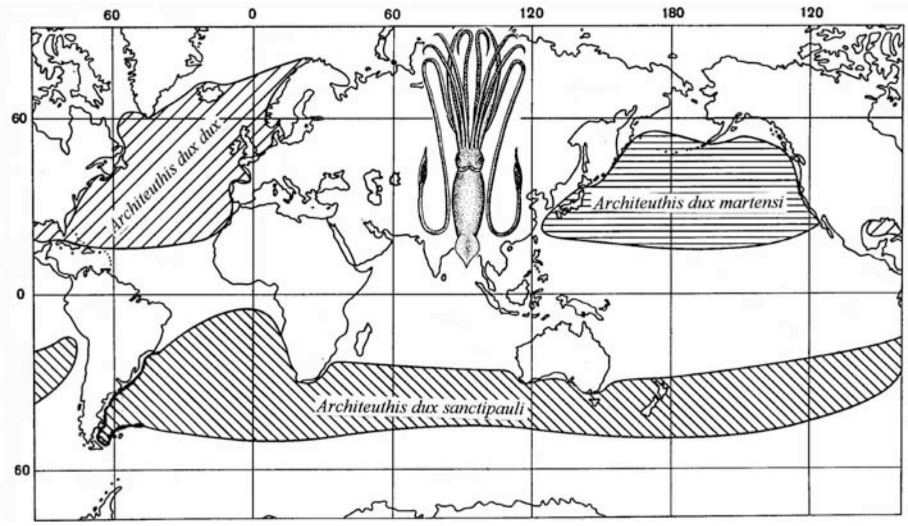

Fig. 9 Distribution of bi-subtropical species *Architeuthis dux*: *A. dux dux* in the North Atlantic, *A. dux martensi* in the North Pacific and *A. dux sanctipauli* in the Southern Ocean (from Nesis 1985, with modifications).

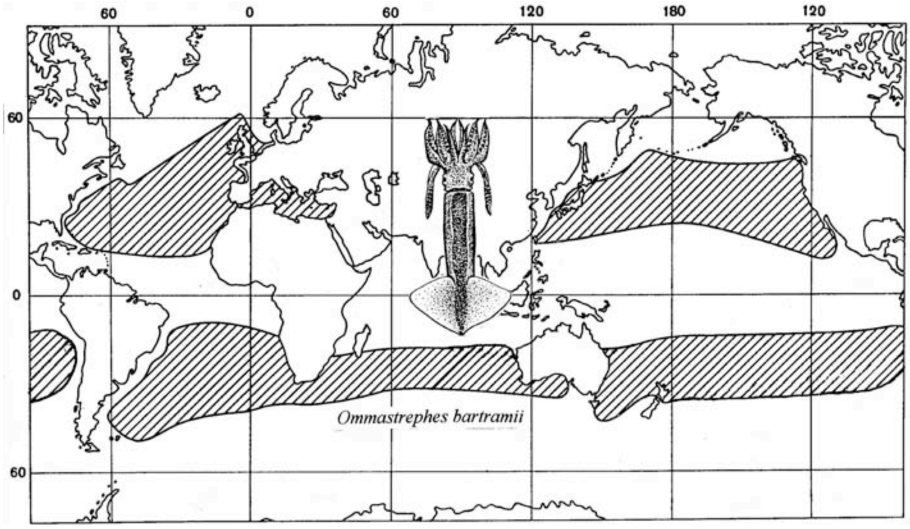

Fig. 10 Distribution of bi-subtropical *Ommastrephes bartramii* (from Nesis 1985, with modifications).

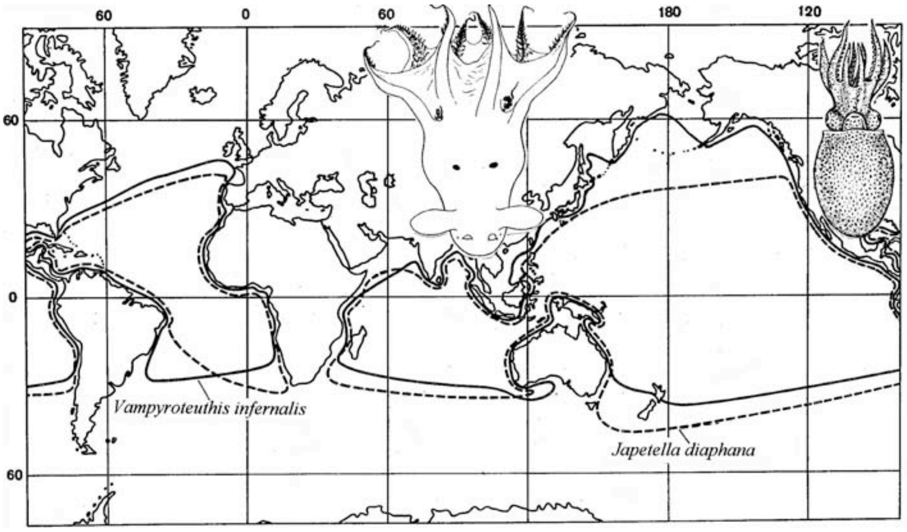

Fig. 11 Distribution of the pan-tropical cosmopolites *Vampyroteuthis infernalis* and *Japetella diaphana* (from Nesis 1985, with modifications).

Ommastrephes bartramii: Fig. 10).

7. Tropical species (cosmopolites, Atlantic, Indo-Pacific, Indo-West Pacific, West Pacific, and East Pacific tropical oceanic and nerito-oceanic):

   7.1. Tropical-boreal-notalian (*Haliphron atlanticus, Taningia danae*).

   7.2. Pan-tropical (cosmopolites: *Japetella diaphana diaphana*: Fig. 11*, Onychoteuthis banksii*: Fig. 6*, Vampyroteuthis infernalis*: Fig. 11; Atlantic: *Illex coindetii*: Fig. 7, *Ornithoteuthis antillarum*: Fig. 12; Indo-West Pacific: *Nototodarus hawaiiensis*: Fig. 7*, Ornithoteuthis volatilis*: Fig. 12; Indo-Pacific: *Pterygioteuthis giardi hoylei;* East Pacific: *Abraliopsis* [*Pfefferiteuthis*] *affinis, A. (P.) falco, Dosidicus gigas*: Fig. 12).

   7.3. Narrow-tropical (*Abraliopsis* [*Micrabralia*] *lineata, Enoploteuthis* [*E.*] *leptura leptura, Sthenoteuthis pteropus*, *S. oualaniensis*: Fig. 13).

   7.4. Equatorial (*Abralia* [*Heterabralia*] *heminuchalis, A.* [*Pygmabralia*] *similis, Enoploteuthis* [*E.*] *leptura magnoceani, E.* [*E.*] *octolineata*).

   7.5. Equatorial-west-central; the range includes equatorial and central waters in western and only equatorial in eastern halves of the Atlantic and/or Pacific (*Amphitretus pelagicus, Megalocranchia abyssicola*: Fig. 15*, Thysanoteuthis rhombus*: Fig. 14).

   7.6. Equatorial-subtropical, avoiding central waters (*Histioteuthis bonnellii*: Fig. 16*, H. meleagroteuthis*).

8. Central species:

   8.1. Bi-central (*Hyaloteuthis pelagica*: Fig. 8*, Megalocranchia oceanica*: Fig. 15*, Ocythoe tuberculata, Tremoctopus gelatus*).

   8.2. North-central (*Abraliopsis* [*A*] *pacificus, Helicocranchia papillata, Histioteuthis corona berryi*).

   8.3. South central (no south central cephalopods are known as yet).

9. South subtropical-notalian species (*Galiteuthis suhmi, Histioteuthis macrohista*: Fig. 16*, Liguriella podophthalma; Illex argentinus* in southwestern Atlantic: Fig. 7) and species of the Southern Subtropical Convergence (*Notonykia africanae*: distributional map in Nesis *et al.* [1998]; *Teuthowenia pellucida*: Fig. 17).

10. Notalian species (*Gonatus antarcticus*: Fig. 4 [Nesis 1999]*, Histioteuthis eltaninae, Nototeuthis dimegacotyle*; *Nototodarus sloanii* in southwestern Pacific: Fig. 7).

11. Notalian-Antarctic species (*Batoteuthis skolops, Martialia hyadesi, Mastigoteuthis psychrophila, Slosarczykowia circumantarctica*).

12. Antarctic species (*Alluroteuthis antarcticus, Galiteuthis glacialis, Kondakovia longimana, Mesonychoteuthis hamiltoni*: Fig. 2, *Psychroteuthis glacialis*).

The following scheme of latitudinal zonality of the epipelagic and mesopelagic realms of the World Ocean is proposed based on cephalopod distribution (Fig. 18):

1. Arctic Zone with High-Arctic and Low-Arctic subzones.
2. Boreal Zone with High-Boreal and Low-Boreal subzones.
   a. Northern peripheral ecotone.
3. North Subtropical Zone.
4. Tropical Zone with North Central, Equatorial, and South Central subzones.
5. South Subtropical Zone.
   b. Southern peripheral ecotone (the zone of the Southern Subtropical Convergence: Fig. 19).
6. Notalian Zone.
7. Antarctic Zone with Low-Antarctic and High-Antarctic subzones.

Three faunas of oceanic pelagic cephalopods exist: arcto-boreal (inhabiting the 1st and 2nd zones), tropical (zones 3-5) and notalian-antarctic (zones 6 and 7). These three latitudinal superzones are divided by two peripheral ecotonal strips (*a* and *b*).

Continental shelves

Now we may return to the shelves. The analysis of the distribution of benthic and nektobenthic shelf cephalopods and comparison of their distribution with that of other bottom animals shows that there are 30-32 centres of speciation of neritic, benthic and nektobenthic cephalopods and 46 zoogeographic provinces of the shelf zone, including three transitional

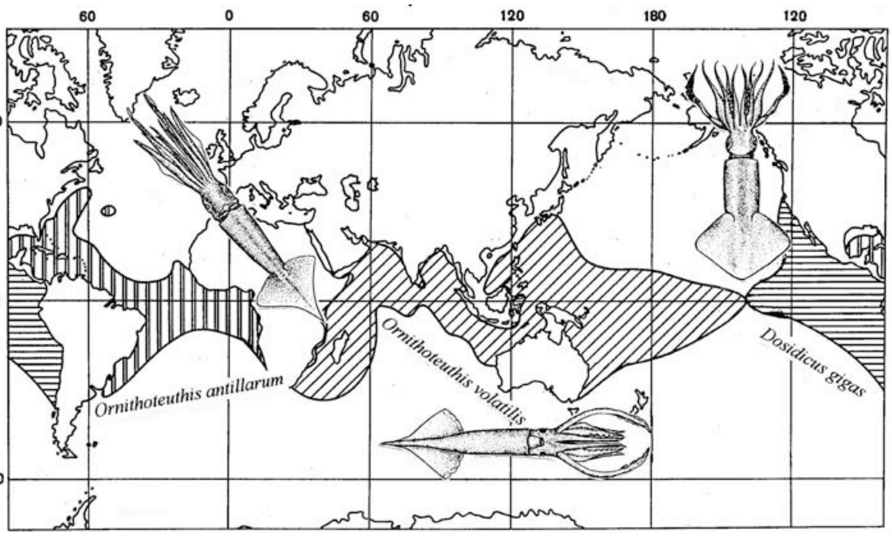

Fig. 12 Distribution of the amphi-Atlantic tropical nerito-oceanic *Ornithoteuthis antillarum*, Indo-West Pacific *O. volatilis* and the Eastern Pacific tropical-subtropical *Dosidicus gigas* (from Nesis 1985, with modifications).

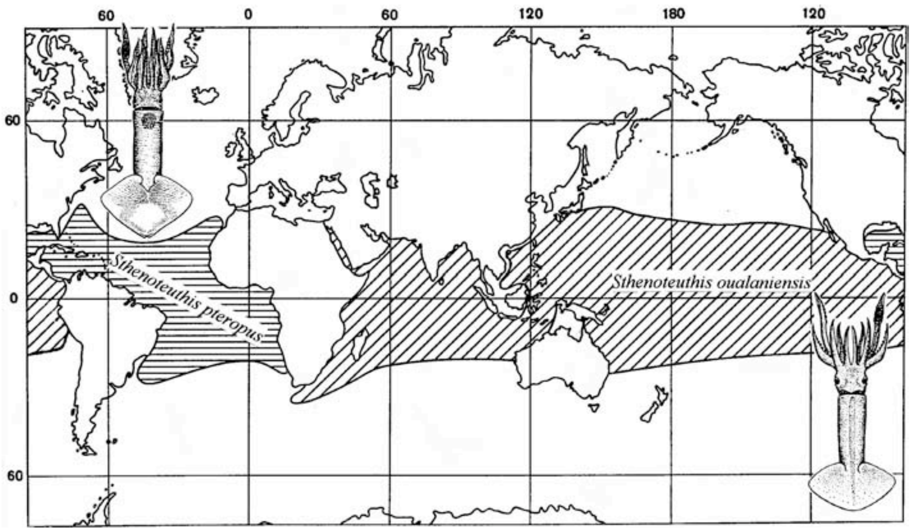

Fig. 13 Distribution of the narrow-tropical *Sthenoteuthis pteropus* (Atlantic) and *S. oualaniensis* (Indo-Pacific) (from Nesis 1985, with modifications)

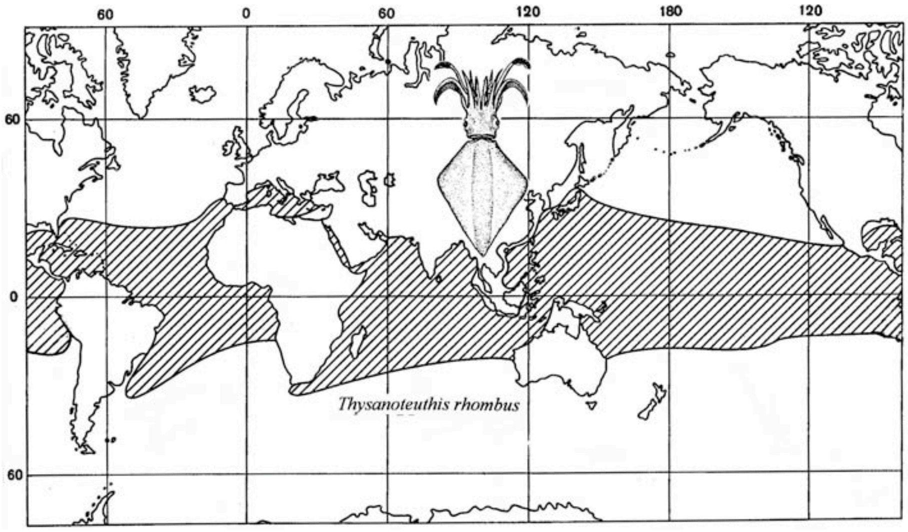

Fig. 14 Distribution of the equatorial-west-central *Thysanoteuthis rhombus* (from Nesis 1985, with modifications).

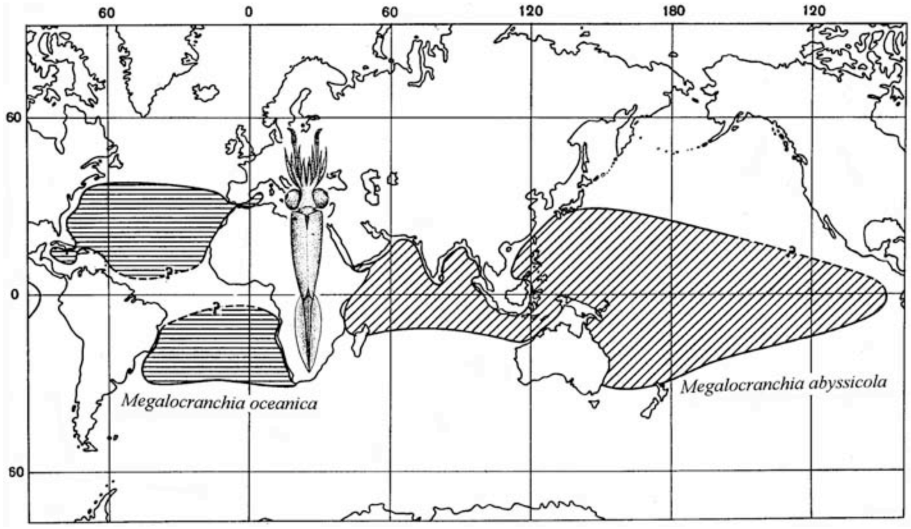

Fig. 15 Distribution of the Atlantic bi-central *Megalocranchia oceanica* and the Indo-Pacific equatorial-west-central *M. abyssicola* (from Nesis 1985, with modifications).

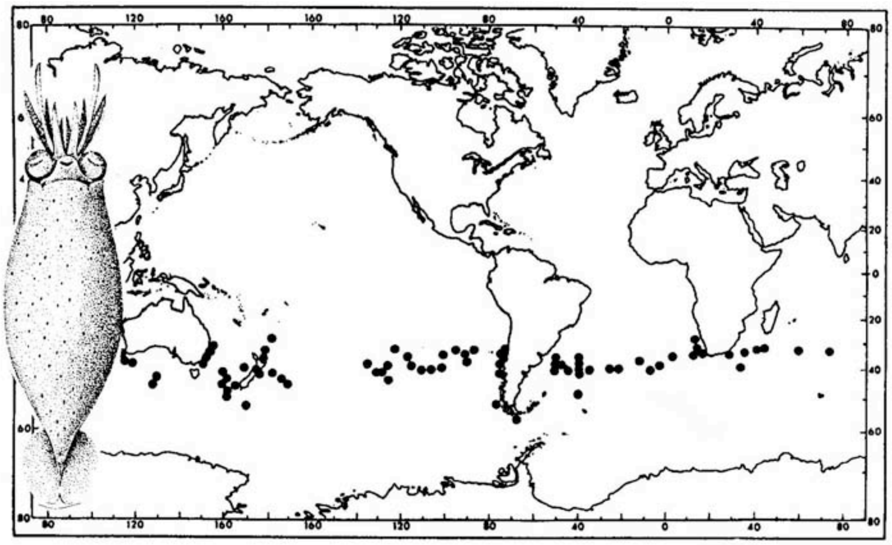

Fig. 16 Distribution of *Teuthowenia pellucida*, an example of species of the Southern Subtropical Convergence (from Voss 1985, modified).

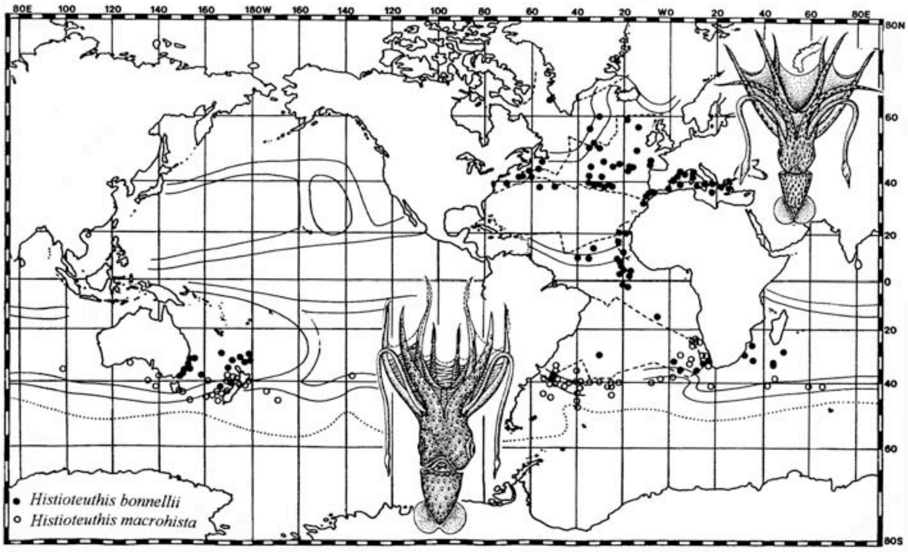

Fig. 17 Distribution of *Histioteuthis bonnellii* (equatorial-subtropical species avoiding central waters) and *H. macrohista* (southern subtropical-notalian species) (from Voss *et al* 1998, modified)

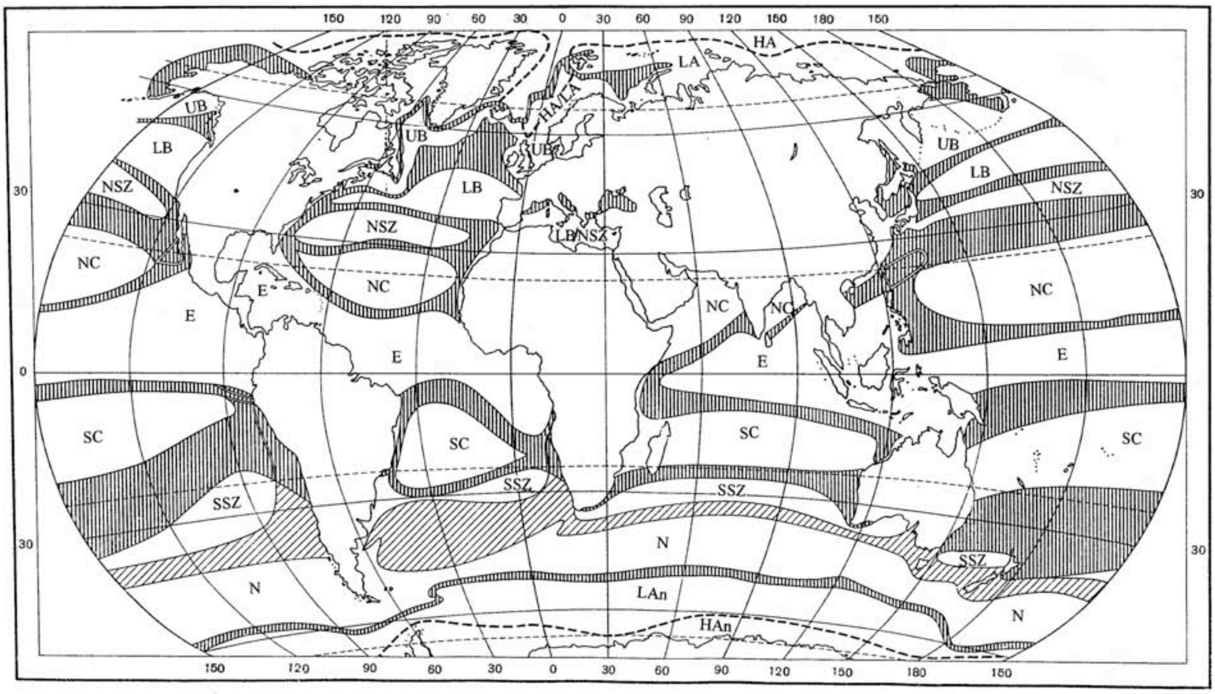

Fig. 18 Latitudinal zoogeographic zones in the pelagic realm of the World Ocean (from Nesis 1985, with modifications). HA - High-Arctic, LA - Low-Arctic subzones of the Arctic Zone; UB - High-Boreal, LB - Low-Boreal subzones of the Boreal Zone; NSZ - North Subtropical Zone; NC - North Central, E - Equatorial, SC - South Central subzones of the Tropical Zone; SSZ - South Subtropical Zone; N - Notalian Zone; LAn - Low-Antarctic, HAn - High-Antarctic subzones of the Antarctic Zone. Central parts of each zone/subzone shown in white, transitional strips shaded. Dotted lines: boundaries between subzones of the Arctic and Antarctic zones. Oblique shading: Southern peripheral ecotone (the zone of the Southern Subtropical Convergence)

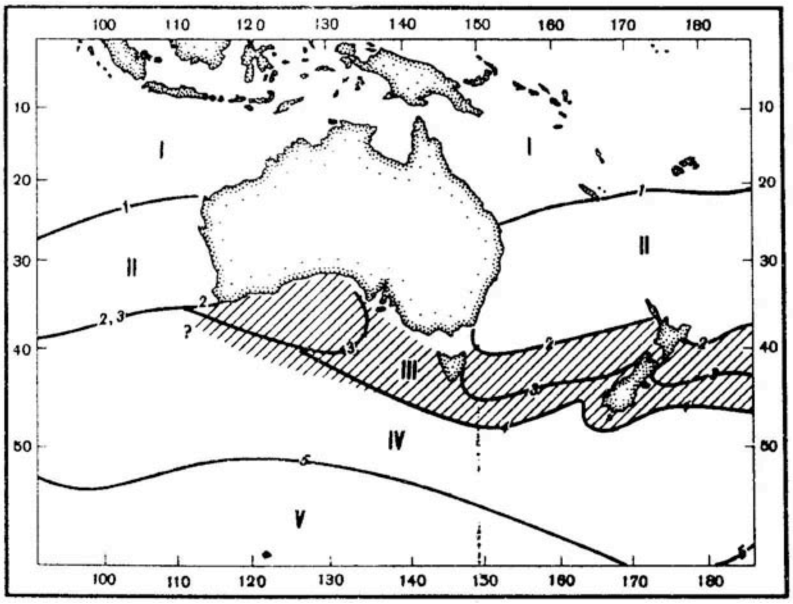

Fig. 19 Zoogeography of the Australian – New Zealand region with cephalopods (from Nesis 1979, 1985). I - Equatorial zone, II - South Subtropical Zone; III - peripheral strip (shaded), IV - Notalian Zone, V - Antarctic zone. *1* - southern boundary of the non-impoverished tropical fauna and northern boundary of south-subtropical, bi-central and peripheral species; *2* - southern boundary of the main stock of pan-tropical species and extreme northern boundary of most eurythermic notalian species; *3* - southern boundary of tropical and south-subtropical species and northern boundary of the main stock of notalian species; *4* - extreme southern boundary of some most eurythermic pan-tropical species and northern boundary of notalian-antarctic species

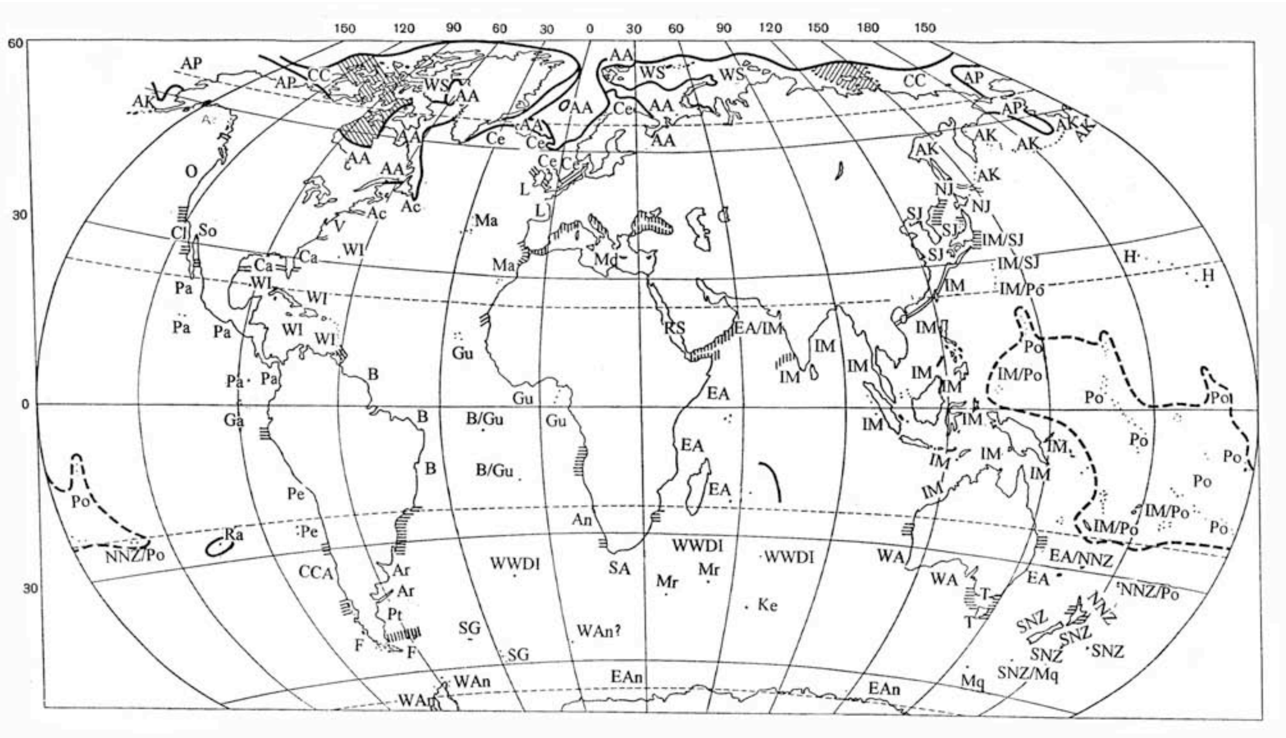

Fig. 20 Zoogeographic provinces of the World Ocean shelves; north to south and west to east; ? - doubtful provinces (from Nesis 1982a, 1985, with modifications). WS - West Siberian, CC - Chukchi-Canadian, AA - Arcto-Atlantic transitional, AP - Arcto-Pacific transitional, Ac - Acadian, Ce - Celtic (=Scandinavian), AK - Aleutian-Kamchatkan, V - Virginian, L - Lusitanian, Md - Mediterranean, NJ - North Japanese (=Ainuan), O - Oregonian, Ca - Carolinian, Ma - Mauritanian, SJ - South Japanese (=Sino-Japanese, Sino-Nipponense), Cl - Californian (So - Sonoran District), WI - West Indian, B - Brazilian, Gu - Guinean, RS - Red Sea, EA - East African, IM - Indo-Malayan, H - Hawaiian, Po - Polynesian, Pa - Panamanian, Ga - ?Galapagosian, Ar - Argentinian, An - Angolan (=Angolo-Namibian), WWDI - West Wind Drift Islands, SA - South African, WA - West Australian, EA - East Australian, T - Tasmanian (=Maugean), NNZ - North New Zealandian, SNZ - South New Zealandian, Ra - ?Rapanuiian, Pe - Peruvian, CCA - Central Chilean (=Araucanian) transitional, Pt - Patagonian, F - Fuegian, Mr - ?Marionian, Ke - Kerguelenian, Mq - Macquoriean, SG - South Georgian, WAn - West Antarctic (=Antarctandean), EAn - East Antarctic (=Antarctgondwanian)

(they have no endemic cephalopod species), and four doubtful (selected on data mainly concerning non-cephalopod fauna because their cephalopods are poorly known) (Fig. 20).

A scheme is presented here of correlation between latitudinal zones and subzones in the pelagic realm and zoogeographic provinces of the shelves (from the western Atlantic eastward to the eastern Pacific) (Fig. 21).

A special analysis of the zoogeographic position of the Mediterranean Sea (Nesis 1982b, 1985) led me to the conclusion that the Mediterranean Province is a single province, though with substantial intra-provincial faunistic differences. It combines features of the Low-Boreal Subzone and the North Subtropical Zone but cannot be included in either of these, and has no analogue in the western Atlantic or in the Pacific. It must occupy a separate place in the scheme of latitudinal zones/subzones but may be included in the Lusitano-Mediterranean Superprovince together with the low-boreal Lusitanian and subtropical Mauritanian provinces.

It has been shown (Nesis 1979, 1982a, 1985) that three provinces located in the Southern peripheral ecotone (the zone of the Southern Subtropical Convergence) – the Tasmanian (=Maugean), South New Zealandian provinces and the Central Chilean (=Araucanian) transitional province – are neither south subtropical nor notalian ones but occupy a separate place in the scheme of latitudinal zones/subzones (Fig. 21).

The West Wind Drift Islands Province recently described (Collette & Parin 1991) includes Tristan da Cunha and the Gough islands in the central south Atlantic Ocean, Vema Seamount in the southeastern Atlantic, Walters Shoals and an unnamed seamount

Zone	Subzone	Province	Province
Arctic	High-Arctic	West Siberian	Chukchi-Canadian
	Low-Arctic	Arcto-Atlantic transitional	Arcto-Pacific transitional
Boreal	Upper-Boreal	Acadian Celtic (Scandinavian)	Aleutian-Kamchatkan: Okhotsk Sea D. Kurile Sea D. Commander Aleutian D.
	Low-Boreal	Virginian Lusitanian Mediterranean	North Japanese Ainuan Oregonian
North Subtropical		Carolinian Mauritanian	South Japanese (Sino-Japanese) Californian Sonoran D.
Tropical	North Central	West Indian	Red Sea Hawaiian
	Equatorial	Brazilian Guinean	East African Indo-Malayan Polynesian Panamanian
	South Central		?Galapagosian
South Subtropical		Argentinian Angolan (Angolo-Namibian) West Wind Drift Islands	South African: Cape D. Natal D. West Australian East Australian North New Zealanidan ?Rapanuiian Peruvian West Wind Drift Islands Tasmanian South New Zealandian Central Chilean (Araucanian) transitional
Notalian		Patagonian Fuegian	?Marionian Kerguelenian Macquoriean
Antarctic	Low-Antarctic	South Georgian	
	High-Antarctic	West Antarctic (Antarctandean)	East Antarctic (Antarctgondwanian)

D. = District

Fig. 21 Comparison of latitudinal zoogeographic zones in the pelagic realm with regional (provincial) subdivisions of the shelf (from Nesis 1982a, 1985, with modifications)

UN-2 south of Madagascar, St.Paul and Amsterdam islands in the central south Indian Ocean. Briggs (1974) considered the Tristan-Gough Province as cold-temperate, an analogue of his Magellan Province (Patagonian + Fuegian provinces of our scheme), and the Amsterdam-Saint Paul Province (the doubtful St.-Paul Province of Nesis, 1985) as warm-temperate, an analogue of his Agulhas Province (Cape District of our scheme). An analysis of the cephalopod fauna of Walters Shoals (Nesis 1994) leads to the conclusion that it includes pan-tropical, south-central and southern peripheral species while notalian species are rare. The same conclusion applies to shallow water fishes of this seamount (Collette & Parin 1991, Parin *et al.* 1993). I consider Walters Shoals and the West Wind Drift Islands Province in general as lying at the southern periphery of the South Subtropical Zone but not in the Southern peripheral ecotone (the zone of the Southern Subtropical Convergence).

The 46 zoogeographic provinces of the shelf are united into 10 faunistic shelf regions (four provinces, namely Mediterranean, Tasmanian, South New Zealandian and Central Chilean, cannot be included into any faunistic region):

Arctic (4 provinces)
Atlantic Boreal (4)
Pacific Boreal (3)
West Atlantic tropical + subtropical (4)
East Atlantic (3)
Indo-West Pacific (12, including West Wind Drift Islands Province)
East Pacific tropical + subtropical (4)
Magellanic notalian (2)
Kerguelenian notalian (3)
Antarctic (3).

General patterns of cephalopod distribution are rather like those of fishes (Parin 1968, 1984).

THE HISTORY OF FORMATION OF RECENT RANGES IN SOME GROUPS OF CEPHALOPODA

Here I will discuss problems concerning the opening of the Bering Strait, closure of the Central American Seaway (Panama Strait), faunistic exchanges during the Pleistocene, including those between northern and southern temperate belts through the equatorial area, and formation of the faunistic disjunction and “locked up” faunas during the Ice Ages. The two first events were interrelated and almost coincided in time (review: Nesis 2000).

5.96 million years ago (mya) the Messinian salinity crisis began in the Mediterranean Sea. At 5.59 mya the Rif Strait in present Morocco was closed (another strait, the Betic, in present southern Spain, closed even earlier) and the Mediterranean Sea very soon dried up and was transformed into a series of isolated saline (hyperhaline) lakes. The stenohaline marine biota became extinct. The drying up of the Mediterranean marked the end of the Miocene and the beginning of the Pliocene. Then, 5.50 mya, a brackish lake (“Mare Lago”) was formed in place of the former sea but 5.33 mya the Strait of Gibraltar opened with a high marine waterfall (Krijgsman *et al.* 1999). Soon the Mediterranean Sea was restored but it was now populated by a totally different biota, an Atlantic one instead of a Tethyan one (Nesis 1982b).

Simultaneously with the opening of the Strait of Gibraltar, 5.32 mya (Gladenkov *et al.* 2002), the Bering Strait opened for the first time after 100 my (from mid-Cretaceous) of being land. The Bering Strait at that time was narrow and filled with cold water. Migration of marine fauna (e.g. the bivalve mollusk *Astarte* [*Tridonta*] *borealis*) through it proceeded mostly southward, from the Arctic to the Pacific (Marinkovich & Gladenkov 1999, Sher 1999, Gladenkov 1999, Marinkovich *et al.* 2002), although it is possible that a North Pacific bivalve *Macoma golikovi*, the ancestor of the European-Mediterranean Plio-Pleistocene species *M. obliqua,* had migrated through it from the Pacific to the Atlantic (Kafanov 1999). Soon the Strait closed, and opened again 1.5-2 my later, at the time of closure of the Central American seaway, about 3.5 mya (the Beringian Transgression). At that time it was much deeper and wider than it is today, and the Pacific boreal biota moved through it as a mighty stream, crossing the whole Polar Basin in a very short time and reaching the North Atlantic (Kafanov 1982, Nesis 1985).

Table 2 List of cephalopod species recorded in the East Pacific (including the Gulf of California) and West Atlantic (including the Gulf of Mexico and Caribbean Sea). Tropical zoogeographic regions by categories

Category	East Pacific (incl. Gulf of California)	West Atlantic (incl. Gulf of Mexico and Caribbean Sea)
Oceanic pelagic	55	71
Nerito-oceanic	9	18
Nectobenthic	6	8
Benthic	19	29
Oceanic pelagic - benthic	1	2
Totals	90	128

The Central American Isthmus

The slow but continuous elevation of the Central American Isthmus (Panama Isthmus) between the eastern Pacific and the Caribbean Sea began 4.6 mya, soon after the first opening of the Bering Strait. About 3.7-3.6 mya it accelerated, about 3.2 mya the connection between the oceanic faunas on both sides of the emerging Panama Isthmus was interrupted (Ibaraki 1997, Molina-Cruz 1997), and 1.9 mya the Central American Seaway (Panama Strait) was fully closed (Haug & Tiedemann 1998).

This event led to the reorganization of surface circulation in the tropical eastern Pacific (intensification of the Peruvian Upwelling 3.5 mya [Ibaraki 1997], onset of the Peru Countercurrent and the Costa-Rican Coastal Current about 3.2 mya [Molina-Cruz 1997]), and redirection of the warm Antilles Current from the eastern Pacific into the northwestern Atlantic and eastward to the European coasts to form the Gulf Stream. This resulted in a major warming of the climate in the North Atlantic and Arctic 3-4 mya (Burton *et al.* 1997) resulting in the second opening of the Bering Strait ~3.5 mya, and the conquering of these areas by the Pacific boreal biota[1].

But in the mid-Pliocene, 2.73 mya, the subarctic waters of the North Pacific suddenly became more brackish, a strong pycnocline was formed between the surface and subsurface water masses and conditions originated for the formation of a winter ice cover (Haug & Tiedemann 1998, Haug *et al.* 1999). This resulted in the ending of the Lower Pliocene warm period and the beginning of the glaciation of the Arctic. The Bering Strait was closed again.

We now consider the Panama Isthmus in relation to cephalopods. More than a hundred years ago it was known that there are many species of fishes, molluscs, crustaceans and other animals on both sides of the Panama Isthmus which are absent outside the tropical eastern Pacific and tropical western Atlantic including the Caribbean Sea. It was even proposed to unite the tropical eastern Pacific and the western Atlantic, including the Gulf of Mexico and the Caribbean Sea, into the Central-American Tropical Region. Now it is known (Ekman 1953, Briggs 1974) that the degree of similarity between these regions differs strongly in different animal groups, but in general is rather noticeable among shallow-water animals and quickly decreases when moving to greater depths. A comparison between the faunas of neritic, nerito-oceanic and oceanic cephalopods on both sides of central America shows (Nesis 1985) that if we analyze the areas of comparable size, for example between southern California and central Chile in the eastern Pacific and between Cape Canaveral and northeastern Brazil in the western Atlantic, the number of species of all cephalopods, neritic and oceanic, in both regions is approximately equal. But when we include in the analysis only tropical areas (much narrower in the eastern Pacific than in the western Atlantic) the number of species in the western Atlantic (including the Gulf of Mexico and Caribbean Sea) will be much greater than in the eastern Pacific (including the Gulf of California),

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[1] Incidentally, simultaneously with the final closure of the Central American Seaway, ~1.9-1.8 mya (very close to the Pliocene/Pleistocene boundary [1.87 mya (Chumakov 1993); 1.8 mya (Topinka 2001); 1.75 mya (Odin 1994)] important processes of anthropogenesis took place: the last *Australopithecus* became extinct (if *Homo habilis* was in fact an *Australopithecus*) and the first *Homo, H. erectus (= H. ergaster*), the ancestor of *H. sapiens*, appeared (~1.8 mya) and quickly began to disperse through the Old World (Lieberman 2001, Asfaw 2002).

Table 3 Closely related cephalopod species inhabiting seas along both sides of the Panama Isthmus but absent outside the Eastern Pacific (including the Gulf of California) and Western Atlantic (including the Gulf of Mexico and Caribbean)

Eastern Pacific	Western Atlantic
Lolliguncula (L.) panamensis Berry, 1911	*L. (L.) brevis* (Blainville, 1823)
Pickfordiateuthis vossi Brakoniecki, 1996	*P. pulchella* Voss, 1953
Octopus oculifer Hoyle, 1904	*O. hummelincki* Adam, 1936 (=*filosus* Howell, 1867)
O. bimaculatus Verrill, 1883	O. *maya* Voss & Solís, 1966
O. digueti Perrier & Rochebrune, 1894	*O. joubini* Robson, 1929
O. chierchiae Jatta, 1889	*O. zonatus* Voss, 1968
O. alecto Berry, 1953	*O. briareus* Robson, 1929
O. mimus Gould, 1852	*O. vulgaris* Cuvier, 1797
Euaxoctopus panamensis Voss, 1971	*E. pillsburyae* Voss, 1975

indeed 128 against 90. The number of oceanic pelagic species in the eastern Pacific is about 60% of that in the western Atlantic and the number of nerito-oceanic, nektobenthic and benthic species together represents 62% (Table 2). The same may be observed in the eastern in comparison with the western tropical Atlantic.

The impoverishment of shelf- and slope-living tropical cephalopod faunas in the eastern halves of the Atlantic and Pacific oceans is noticeable on the lists of species of the Sepiolida s.l. (Sepiolidae, Sepiadariidae, Idiosepiidae) and Myopsida (Loliginidae and Pickfordiateuthidae). In the tropical Indo-West Pacific Region (including the western Indian Ocean and the Red Sea) there are 44 species (16 sepiolids, 21 loliginids and 7 other), in the West Atlantic Region 17 (9, 7 and 1). But in the East Atlantic Tropical Region there are only 7 (5 sepiolids, including deep-water ones, and 2 loliginids), and in the East Pacific Region 4-6 (3-5 Loliginidae, 1 Pickfordiateuthidae, no Sepiolidae).

The scantiness of the eastern Pacific fauna, particularly in those benthic, nektobenthic and nerito-oceanic species which inhabit the outer shelf and slope, as well as the impoverishment of the eastern Atlantic fauna, is unequivocally explained by strengthening of Trade Winds during glacial epochs, and intensification of upwelling along the eastern margins of the Pacific and Atlantic, principally off Peru, California, Namibia and north-west Africa. Environmental conditions in upwelling zones associated with the Trade Winds are rather unfavourable for cephalopods inhabiting the outer shelves and slopes, because oxygen deficit is common there, sometimes reaching complete absence of oxygen and the appearance of hydrogen sulfide contamination. This is coupled with shortage of macroplankton in the early stages of succession and general lowering of temperature (Nesis, 1985). During the Ice Ages the conditions of existence of nektobenthic and nerito-oceanic cephalopods – inhabitants of outer shelves and slopes – were much worse in the eastern halves of the Atlantic and Pacific than in the Caribbean Sea, while in the Indo-Malayan Province the climate still provided a favourable environment. O.N. Zezina (1985) came to a similar conclusion from studies of the bottom fauna of the slope of the eastern Pacific.

It will be of interest to trace the signs of former unity of the present eastern Pacific and the Caribbean Sea in modern cephalopod faunas. Indeed, these footprints do exist! No cephalopod species are known that are distributed along both sides of Panama Isthmus and nowhere else, but there are at least nine pairs of very similar species in the eastern Pacific and western Atlantic (Nesis 1985, Voight 1988, Brakoniecki 1996, Warnke 1999) (Table 3).

The first two pairs are shallow-water nektobenthic squids, the other seven are shallow-water bottom-dwelling octopuses. Some members of the pairs in Octopodidae are very close, geminate species, particularly *Octopus chierchiae - O. zonatus, O. alecto - O. briareus, O. mimus - O. vulgaris, Euaxoctopus panamensis - E. pillsburyae* (Nesis 1985, Voight 1988, Warnke 1999). The existence of such pairs is an obvious sign of the former existence of a single trans-Panamanian fauna, now represented by different, although in some cases very close, species, and that all these species are shallow-water, i.e., they diverged at the last stages of the uplift of the Isthmus. However, there are no visible signs of the former existence of a

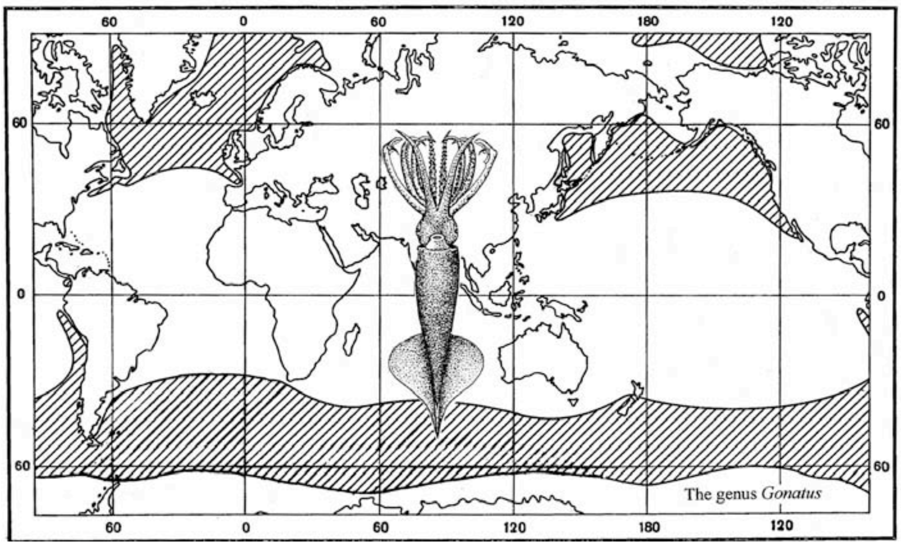


Fig. 22 Distribution of the genus *Gonatus* (from Nesis 1985, with modifications)

single fauna among pelagic oceanic and deep-water cephalopods.

The following conclusion may be formulated. The length of time since the separation of the oceanic fauna of the eastern Pacific from that of the Caribbean Sea, about 3-5 my, is too long to preserve the traces of the existence of a former unitary fauna (remember the high dispersal capabilities of cephalopods!), while the length of time since the separation of nearshore shallow-water faunas, about 2 my, is short enough for these signs to be preseved. These data indicate possible evolutionary rates among cephalopods.

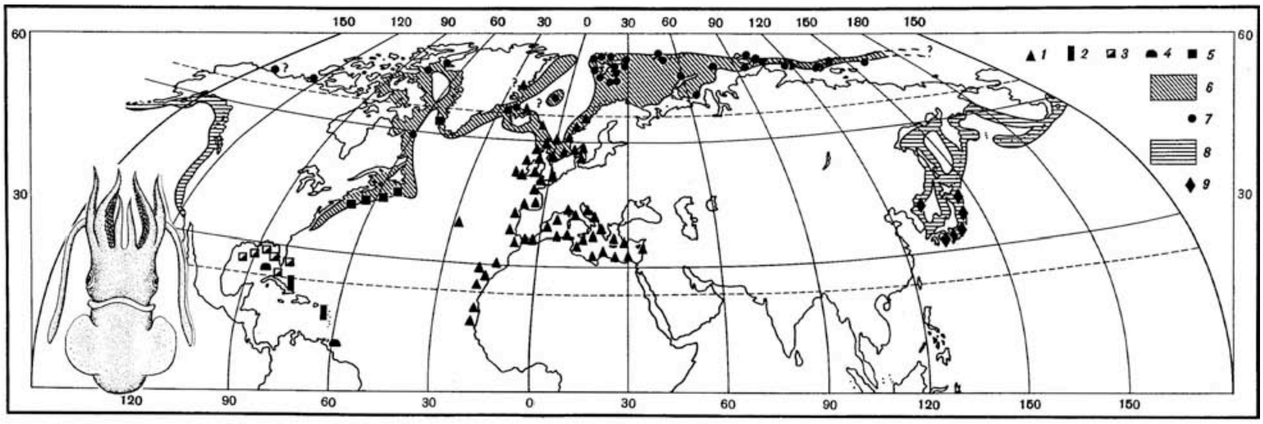
Faunal exchange through the Bering Strait

Analysis of the distribution of the genera *Rossia* (Sepiolidae), *Gonatus* (Gonatidae), and *Benthoctopus* (Octopodidae) in the north Atlantic, Arctic and north Pacific indicates that faunal exchange through the Bering Strait was possible in the time of the Beringian Transgression, about 3.5 mya, when the strait, now uninhabitable by cephalopods, was much deeper and wider than today. Almost all invertebrates and fish migrated through the strait northward, from the Pacific into the Arctic and then to the northern Atlantic (Nesis 1961, 1985, 1988). However, this is not true for all cephalopods.

The distribution of the genus *Gonatus* (Fig. 22) and the whole family Gonatidae indicates that they originated in, and radiated from the boreal North Pacific. Then, the ancestor of the epi-meso-bathypelagic species *Gonatus (Gonatus) fabricii* migrated in the mid-Pliocene from the Bering Sea northward into the Polar Basin and further into the North Atlantic. This squid is an Arcto-Atlantic circumpolar arcto-boreal species. Its distribution embraces the entire deep-water part of the Central Polar Basin, the Greenland and Norwegian seas, western and central parts of the Barents Sea, waters around Greenland, Denmark and Davis straits, Baffin, Labrador and Irminger seas, and the northwestern Atlantic from the Reykjanes Ridge to the area south of Cape Cod. *G. (G.) fabricii* probably originated in the Upper Pliocene.

A group of species inhabiting the North Pacific is rather close to *G. fabricii*. In the warmer part of the North Atlantic – the northeastern Atlantic south of the Faeroe-Iceland Ridge and east of (probably including) the Mid-Atlantic Ridge – a separate species *G. steenstrupi*, very close to *G. fabricii* (it may be a subspecies), originated in a subsequent epoch (Kristensen 1981, Nesis 1985, 1988, 2001).

At the same time of the Beringian Transgression the ancestor of the benthic octopod *Benthoctopus sibiricus* migrated in the same direction. This is an endemic East-Arctic species, found (sometimes with a question mark because of identification problems concerning females and juveniles) in the Laptev, East Siberian, Chukchi and Beaufort seas, approximately 105°E–155°W, at depths of 38 (?30) to 220 m. It is the most cold- and shallow-water adapted species of the predominantly bathyal-abyssal genus *Benthoctopus*. *B. sibiricus* is definitely of North Pacific origin. The most closely related species is *B. abruptus*, a southern Japanese lower-bathyal species (Nesis 1985, 1988, 2001). Recently an undescribed species, close to both



1 – R. macrosoma, 2 -R. brachyura, 3 - R. bullisi, 4 - R. tortugaensis, 5 - R. megaptera, 6 - R. palpebrosa, 7 - R. moelleri, 8 - R. pacifica, 9 - R. mollicella

Fig. 23 Distribution of the genus Rossia (from Nesis 1985, with modifications). 1 - Rossia macrosoma, 2 - R. brachyura, 3 - R. bullisi, 4 - R. tortugaensis, 5 - R. megaptera, 6 - R. palpebrosa, 7 - R. moelleri, 8 - R. pacifica, 9 - R. mollicella (R. pacifica diegensis is not shown]

B. abruptus and *B. sibiricus,* was recognized in the western part of the Bering Sea at depths of 200-750 m and off northeastern Honshu at 300-800 m (Kubodera 1996, Nesis & Nigmatullin 1997, Laptikhovsky 1999). It was postulated by Nesis and Nigmatullin (1997) that the ancestor of *B. sibiricus* was a rather deep-water (upper bathyal) species which migrated from the North Pacific to the eastern Arctic through the Bering Strait, probably in the mid-Pliocene, and then, during the glacial epochs, became adapted to cold, shallow-water and widely fluctuating conditions but lost the ability to live at the constant or seasonal positive temperatures characteristic of the low-Arctic areas to the west and east of its present range boundaries.

But sepiolid cuttlefishes of the genus *Rossia* migrated in the opposite direction. Analysis of distribution of this genus (Fig. 23) showed (Nesis 1985, 1988) that it is of North Atlantic origin and includes 10 species and subspecies: 3 western Atlantic and 1 eastern Atlantic-Mediterranean tropical-subtropical, 1 western Atlantic low-boreal, 1 Arcto-boreal, 1 high-Arctic, and 3 northern Pacific predominantly boreal species/subspecies (Nesis 1985) [the subspecies *R. pacifica diegensis* is not shown on the map (Fig. 23) because its taxonomic rank and distribution are unclear]. After the migration of the ancestor of those species, which now inhabit the Arctic and north Pacific, into the Arctic and through the Bering Strait into the Pacific, this ancestor radiated and formed four mostly sublittoral and upper bathyal species in the north-Pacific (Nesis 1985):

R. pacifica North Pacific (Bering Sea to Tsushima Strait and South California), probably during the Upper Pliocene.

R. palpebrosa Arcto-Atlantic (from Ellesmere Island and north Greenland to South Carolina, off Iceland, Ireland, in the northern North Sea and in the Arctic westward to Somerset Island, eastward to the East Siberian Sea).

R. mollicella northwest-Pacific low-boreal (Pacific side of Hokkaido and Honshu and Japan Sea), at the outset of the Pleistocene or during the glacial period.

R. moelleri High-Arctic (from northwestern Greenland eastward to the East Siberian Sea, westward to Franklin Bay and ?Yukon Territory), during the Pleistocene.

Ice age related events in cephalopod distribution

We begin the review of Ice Age-related events in cephalopod distribution with the question of the West-Arctic and East-Arctic distribution. Four out of the five shelf-living benthic cephalopods known in the Arctic Ocean are definitely of Atlantic origin: the above-mentioned sepiolid cuttlefishes *Rossia palpebrosa* and *R. moelleri*, and the octopods *Bathypolypus arcticus* and *Benthoctopus piscatorum*[2]. They are either Arcto-

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[2] *Bathypolypus arcticus*: Labrador to southeastern Florida, Iceland and Norway to southwestern Spain, in the Arctic to the west up to Franklin Bay, to the east to the Laptev Sea, sublittoral and bathyal: Fig. 1. *Benthoctopus piscatorum*: from Newfoundland to off New York, in the Denmark Strait, off Ireland, Hebrides, Shetland, Faeroe, and Jan Mayen islands, off Norway, and from West Svalbard to north of the eastern Kara Sea.

Atlantic arcto-boreal or high-Arctic species. They live in the sublittoral and upper (or whole) bathyal zones but predominantly deeper than 50-200 m; however, in some west-Arctic fjords some species may be found at such shallow depths as 6-8 m. But being widely eurybathic in the western Arctic they are unknown on the shelves of the eastern Arctic (East Siberian, Chukchi and Beaufort seas), where only *Benthoctopus sibiricus* (Fig. 1) is found. Our new data (Nesis 2001) indicate that the ranges of *B. arcticus* and *B. sibiricus* overlap widely longitudinally but their depth ranges overlap only marginally. The depth range of the former species in the zone of overlap is 180-360 m, of the latter species it is 38-220 m (?30-220 m).

Although gaps still exist in the known distributions of *R. palpebrosa, R. moelleri* and *B. arcticus* between the eastern boundaries of their ranges in the Asian Arctic (150° E for *R. palpebrosa,* 154° E for *R. moelleri* and 135° E for *B. arcticus*) and the western boundaries in the Canadian Arctic [approximately 95° W for *R. palpebrosa*, 126° W for *B. arcticus*, and 126° W (?140° W) for *R. moelleri*] (Figs 1, 23) (Nesis 2001) there is little doubt that these three species, previously considered as West-Arctic or Atlanto-West-Arctic (Nesis 1983, 1985, 1988), are in fact circumpolar but widely eurybathic in the western sector of the Arctic, while in the eastern sector they are distributed below 100-200 m. *B. piscatorum* may be circumpolar too, but if so, only on the slope of the central Polar Basin, being absent in shallower water of the American sector of the Arctic; however, this question cannot be resolved now.

The difference in bathymetric distribution between eurybathic "West-Arctic" species and the shallow-water *Benthoctopus sibiricus* (Figs 1, 23) can supposedly be explained by a striking difference in the conditions of the Quaternary glaciations in the western and eastern Arctic (Nesis 1983, 1988, 2001). When the shelves of the western Arctic were glaciated, the ice tongues went deep into the ocean preventing the existence of shallow-water stenobathic benthic animals. Some animals adapted to live at greater depths, others became extinct, at least in the Arctic. Species that adapted became widely eurybathic but lost the ability to live on the shallow shelf with wide fluctuations of environmental conditions, except in high-Arctic fjords where these fluctuations are rather insignificant.

In contrast, the shelves of the eastern Arctic were not glaciated and the shallow-water stenobathic benthic animals retained the ability to live on the shelves below the lowered sea-level (Nesis 1983, 1985, 2001).

Equally instructive is the analysis of the distribution of genera and species with disjunct anti-tropical or anti-equatorial ranges. Good examples are 4 monotypic genera: bi-subtropical *Architeuthis (A. dux)* (Fig. 9) and *Ommastrephes (O. bartramii)* (Fig. 10); bi-peripheral (northern Pacific and southern parts of three oceans) *Eucleoteuthis* (*E. luminosa);* bi-central (Atlantic and Pacific) *Hyaloteuthis* (*H. pelagica)* (Fig. 8)*;* and the bi-temperate subgenus *Gonatus (Gonatus)* (Fig. 22).

During glacial epochs the ranges of bi-central, bi-subtropical and bi-peripheral species had the form of eastward-convex arcs, while the strongly curtailed ranges of equatorial and narrowly-tropical species were crescent-like. At that time the now isolated north-Pacific and southern parts of the ranges of *A. dux, O. bartramii, E. luminosa* and *H. pelagica* were joined in the equatorial eastern Pacific, and the north-Atlantic and southern parts of the ranges of *A. dux, O. bartramii* and *H. pelagica* were united in the equatorial eastern Atlantic. It is unknown where these species first arose, thus we cannot judge from what part of their present ranges they were dispersed. Comparison of the substrate-specific properties of cholinestherases of the optic ganglia in the specimens of *O. bartramii* from the North Atlantic, North Pacific and Southern Ocean (Great Australian Bight) showed that the North Atlantic and Southern Ocean forms (supposedly subspecies) are closer to each other than to the North Pacific form (Shevtsova *et al.* 1977, 1979). This was treated as an indication that the ranges of the North Pacific and Southern Ocean forms may have united in the eastern Pacific only at times of maximum cooling (Riss glaciation) while those of the North Atlantic and Southern Ocean forms may have united in the eastern Atlantic even later, during the last (Würm) glaciation. At the present time these last forms are absent between approximately 12°N and 17°S (Nesis 1985). It is important to note that these forms have not diverged to the stage of full species, or even geminate ones, but still belong to the same species.

Supposedly at the time of maximum glaciation, the ranges of the now separate north-Atlantic *Todarodes sagittatus* and southeast-Atlantic *T. angolensis*, also disjunct today between approximately 12°N and 17°S, were united in the East Atlantic (Nesis 1985). In the East Pacific the ranges of the Californian *Gonatus (Gonatus) californiensis* and the Subantarctic *G. (G.) antarcticus* (Figs 4, 22), now disjunct between 25°N and 6°S,[3] may have been similarly connected.

In the southeastern Atlantic west of the Cape of Good Hope the ranges of the now vicariant, very common tropical oceanic epi-mesopelagic squids *Sthenoteuthis pteropus* (Atlantic) and *S. oualaniensis* (Indo-Pacific) (Fig. 13) were probably united during pre-glacial times (approx. 2.0-0.7 mya). Based on morphological data, *S. pteropus* is closer to the common ancestor than *S. oualaniensis*.

Similarly, the ranges of the tropical nerito-oceanic (epi-mesopelagic, lower sublittoral and bathyal) squids *Ornithoteuthis antillarum* (Atlantic) and *O. volatilis* (Indo-West Pacific) (Fig. 12) probably were formerly continuous. The relations between the species of *Ornithoteuthis* are as yet unresolved (Nesis 1985). In all these cases the divergence resulted in the formation of separate, although rather close, species.

The formation of the relatively cold-water (not subtropical but also not notalian) fauna of the Tasmanian (=Maugean) Province (Fig. 19) was also connected with the Pleistocene glaciations. This included the inception of discontinuous ranges of several rather warm-water species of cuttlefishes (some *Sepia*, *Sepiadarium austrinum, Sepioloidea lineolata*) which are absent off western Tasmania.

The formation of some endemics of the Mediterranean (such as *Sepiola affinis, S. intermedia, S. ligulata, S. robusta, S. steenstrupiana, Sepietta petersi*), the Red Sea [*Sepia (Sepia) dollfusi, S. (S.) gibba, S. (Doratosepion) elongata, Photololigo abulati, Octopus (Octopus) nanus*] and the northern part of the Gulf of California [Sonoran District of the Californian Province, for example *Octopus (Octopus) alecto, O. (O.) fitchi*] is also connected with glacial episodes when the Mediterranean and Red seas were not isolated from the Ocean as, for example, the Japan Sea, but the surface currents in the straits of Gibraltar and Bab-el-Mandeb changed. Their regime was then somewhat like that in the present Bosporus: in the upper layer the current flows outwards, into the ocean, in the intermediate layer inwards into the sea.

During the glacial period the present fauna of the northern part of the Gulf of California was part of the continuous subtropical fauna of the present-day Californian Province, but during post-glacial time it was confined to the Sea of Cortez, suboptimal for a true tropical fauna because of winter cooling, and diverged from the tropical Panamanian one, which occupied the southern part of the Gulf and the outer side of the Californian Peninsula (Nesis 1985, Voight 1988, 1998). However, the similarities between the Mediterranean, Red Sea and Sonoran faunas are caused by the similarity of their histories, while the sources and taxonomic composition of these faunas are different: the low-boreal-subtropical in the Mediterranean Sea, composed mostly of species of the sepiolid genera *Sepiola* and *Sepietta;* the tropical in the Red Sea composed mainly of *Sepia;* and the subtropical in the Sonoran District (mostly *Octopus*).

Conclusions: rates of speciation and origin of the fauna

We come to the following conclusion: the rate of speciation among Recent Cephalopoda caused by climatic or by geographical isolation is of the order of one or a few million years. Distributional data on recent cephalopods are in accordance with paleontological records. The recent cephalopod fauna was formed mainly during the Neogene. The roots of neritic cephalopods (Sepiidae, Loliginidae) reach down into the Paleogene, but the roots of oceanic forms are hardly older than the Miocene. It may be supposed that Recent species of cephalopods were formed not earlier, or at least not significantly earlier, than the Pliocene.

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[3] Although a larva of *G. (G.)* sp. aff. *californiensis* was recorded in the Gulf of Panama at approx. 7°N (Young, 1972; Nesis, 1985, 1999).

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