

## Probable Mesozoic vicariance in the biogeography of Euphausiacea

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**Keywords:** Euphausiacea, biogeography, vicariance

### Abstract

The worldwide distribution of Euphausiacea is related to differences in character states found in the genera belonging to this order. An area cladogram is composed. The vicariant events postulated in this study made it possible to distinguish between different "hydroplates" of the "hydrotectonic (cf. Nelson, 1986) system" on the basis of general trends in distribution of these genera.

### Résumé

La distribution mondiale des Euphausiacea est en relation avec les différences dans les états des caractères, trouvées chez les genres appartenant à cet ordre. Un "area cladogram" est construit. Les événements vicariants postulés dans la présente étude permettent – en se basant sur les tendances générales dans la distribution de ces genres – de distinguer entre différentes "hydroplaques" du "système hydrotectonique" (cf. Nelson, 1986).

### Introduction

To understand the distribution of species on earth the geological past has to be known. But, distribution patterns can also contribute to our understanding of the history of geological events. Although nowadays different methods are available to the taxonomist to tackle the problems of evolution and biogeography, many questions are still open. In the pelagic environment the relation between present day distribution and that in the past is even more complicated than those in the terrestrial realm.

Croizat (1958, 1964) stressed that "earth and life evolve together, that taxonomic differentiation is life's response to a dynamic geology". This so pointedly put citation was quoted by Nelson (1986), who discussed various aspects of historical biogeography. Nelson continued: "Croizat did not deal with pelagic distribution, which is complicated by a second level of tectonics – the structured water mass, the boundaries of which frequently limit the geography of taxa." However, water masses are far less stable than tectonic plates and the use of the term "hydrotectonics" does not seem very promising.

When, however, systems of water masses that belong to a current system and that are characterized by pelagic communities as defined by Beklemishev (1971) are considered, things become more prospective. Especially the cyclical water mass, comprising cyclonic and anticyclonic gyral systems with primary pelagic communities, may have been relatively stable through geological times (Van der Spoel & Heyman, 1983). An attempt can be made to consider Equatorial, Central and Subpolar cyclical water masses in terms of hydrotectonics. The ocean basins themselves are entirely dependent on tectonics and distributions restricted by ocean-basin limits may be taken as subjects for vicariance biogeography. The pelagic of the neritic, bound to continents and thus to plate borders, can also bear the traces of vicariance in the past.

It should principally be possible to identify and isolate historical factors from pelagic biogeog-

graphy. Nelson (1986) already mentioned bipolarity, trans-Pacific and amphi-American patterns as bearing strong historical components. Geologically relatively young patterns around Indo-Malaya and Antarctica, developed from one area of endemism, have been discussed for Hydromedusae (Van der Spoel, in press). In the present paper possible vicariance and dispersal for closely related groups of probably different geological age will be discussed, based on some phylogenetic trends and on the distribution of euphausiids. The concept "hydroplates" (Nelson, 1986) will be further defined.

### Vicariance biogeography in the pelagic

Together with the dispersal explanation, vicariance biogeography of plankton and nekton has to be studied; especially when biogeography and phylogeny reflect (1) the separation or deformation of ocean basins, (2) the separation, displacement or deformation of water mass systems, especially of Central Waters and Equatorial Waters.

Dispersal by migrations from the (sub)polar into (sub)tropical water masses is very well possible; examples of this phenomenon in recent periods are found in the Southeast Pacific Ocean (*Sagitta tasmanica* Thomson, 1947 cold water populations occurring north of 50°S), due to influences of the Humboldt Current (Pierrot-Bults, 1974). Dispersal from (sub)tropical into North Atlantic (sub)polar waters is known for example in *Clio pyramidata* Linnaeus, 1767 and *Salpa fusiformis* Cuvier, 1804 (cf. Van der Spoel & Heyman, 1983), but these species do not migrate into the North Pacific (sub)polar waters (McGowan, 1971; McGowan & Williams, 1973). Penetration is not occurring everywhere at random; in some areas it may happen, in others it is not possible. Dispersal is not expected in cases where the phylogeny of higher taxa parallels the occurrence of specific polar patterns as shown for Hydromedusae (Van der Spoel, in press). In this group all genera seem to have the same ecological and behavioural abilities to reach the (sub)antarctic by dispersal, but still the development of (sub)antarctic taxa is restricted to a few definite higher taxa.

The Hydromedusae consist of a group of holoplanktonic species with direct development, a group of holoplanktonic species with parasitic larvae, and a group of meroplanktonic species with a sessile polyp stage. These different groups parallel the subdivision into separate subclasses (sensu Bouillon, 1985).

It is a commonly accepted idea that the Hydromedusae form a phylogenetically old group derived from the Cubomedusae. Though this assumption may be correct, it does not mean that the recent Hydromedusae reflect the link with Cubomedusae, since Cretaceous and older representatives of Hydromedusae and of some other planktonic groups nearly completely disappeared at the border between Mesozoic and Cenozoic. The absence of old distribution patterns like Central Water, Equatorial, and circumglobal tropical distribution points to a recent origin (cf. Van der Spoel, 1983) of the present day Hydromedusae taxa. Explaining phylogeny and distribution of recent Hydromedusae therefore means explaining the development of post-Cretaceous lineages derived from Cretaceous ancestors.

The Tethys Sea is here considered the ocean lying over southern Europe and South Asia being a remnant, after the northward drifting of India, of the large basin mentioned below as "Prototethys" found in the Cretaceous and older periods between S.E. Asia in the north and Australia with Antarctica and India in the south. It is proposed (Van der Spoel, in press) that open ocean ancestors of Hydromedusae disappeared during the Mesozoic/Cenozoic transition. The remaining representatives along the coast of the "Prototethys Basin" were first isolated into a northern group (around Indo-Malaya) and a southern group (around Antarctica). In this southern group indirect development was lost as the biotope of the polyp stage became unsuitable by ice coverage. This resulted in a northern group with indirect development: the Anthomedusae, Leptomedusae and Limnomedusae, mainly distributed around Indo-Malaya, and a southern group with direct development or an entirely planktonic life cycle by parasitism: the Narcomedusae and Trachymedusae found mainly around Antarctica (Van der Spoel, in press). Some of the euphausiids

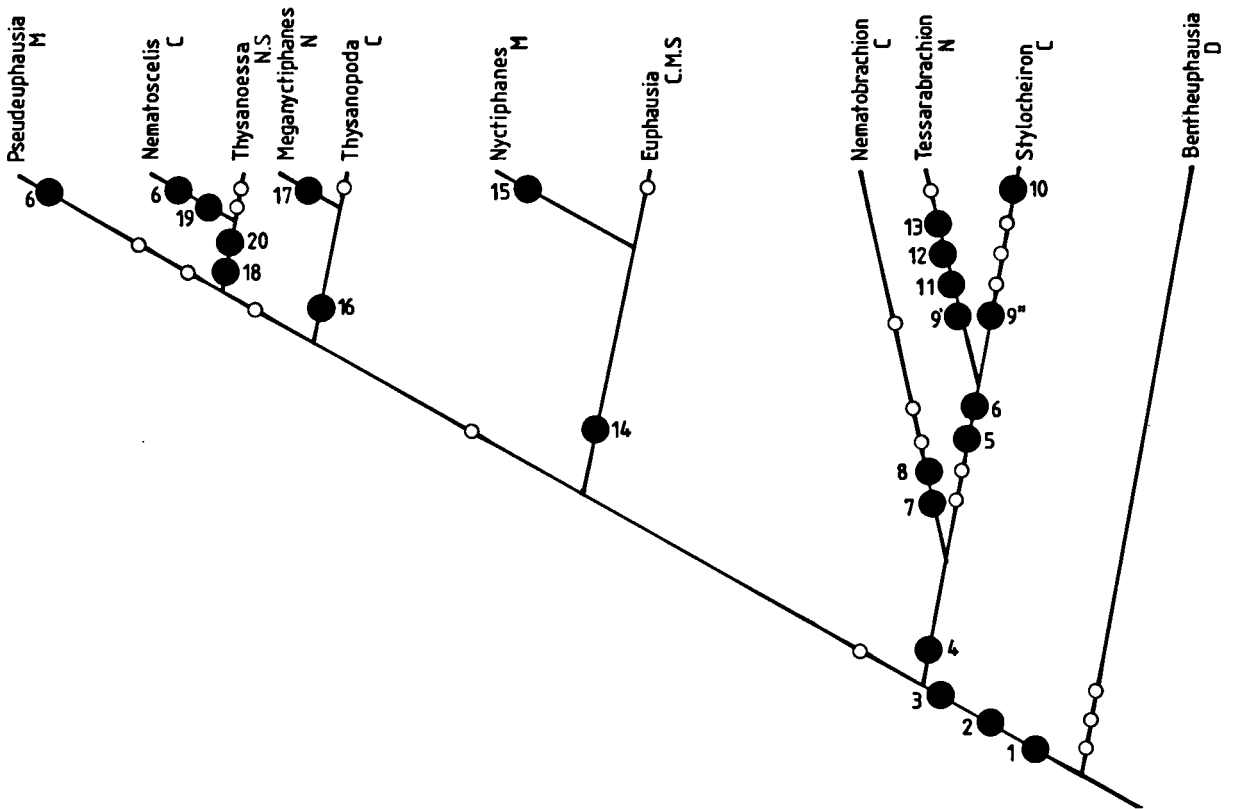


Fig. 1. Area cladogram of euphausiids based on the distribution and the characters listed with the same numbers as in Table I: C = distribution in Central Water masses; D = deepwater distribution; M = distribution around Indo-Malaya; N = distribution around Arctic centres in the northern ocean; S = distribution around Antarctic centres in the southern ocean.

siid taxa show parallels in phylogeny and distribution with the Hydromedusae and further strengthen the basis for mesozoic vicariance in the pelagic realm.

**Relation of some phylogenetic trends and distribution**

The order Euphausiacea comprises eleven genera: two monotypic genera restricted to the northern hemisphere, two genera with representatives in polar and warm waters and seven genera endemic to the warm water belt. Two proposals for a phylogeny of the genera have been published, one by Colosi (1917) and another by Zimmer & Gruner (1956). The main difference between the two proposals concerns the position of *Nematobranchion* Calman,

1896, *Nematoscelis* G.O. Sars, 1883 and *Pseudeuphausia* Hansen, 1910. A tentative cladistic approach (Fig. 1) gives a result almost similar to the phylogeny proposed by Colosi; only *Pseudeuphausia* is placed differently again. In the present paper the approach has to stay “tentative” as the biogeographic study forms the basis of the present discussion and more characters have to be investigated to properly document all splitting points in the area cladogram.

The area cladogram (Fig. 1) is based on the phylogenetic characters listed in Table I. Outgroup comparison, with the Decapoda, the sister group of the Euphausiacea in the Eucarida, shows the petasma to be newly developed in the euphausiids, only in the Penaeidae a comparable, but not similar, structure is found. The modification of the anterior thoracopods into maxillipedes and the exposed

Table 1. List of character states as used in the cladogram of Fig. 1.

Apomorph	Plesiomorph
1 petasma developed	no petasma
2 reduction of thoracal legs 7 and 8	eight subequal thoracal legs
3 10 photophores present	no photophores present
4 thoracal leg 3 elongated	thoracal leg 3 not longer (see also 2)
5 lower eye lobe larger than upper one	eye not bilobate
6 thoracal leg 6 reduced	thoracal leg 6 not reduced (see also 2)
7 upper eye lobe larger than lower one	eye not bilobate (see also 5)
8 median petasma lobe with one additional process	median lobe with one normal process (see also 1)
9 upper eye lobe strongly elongated; 9' and 9'' represent probably different apomorphic states	eye bilobed with small upper lobe (see also 5)
10 6 photophores secondarily lost	10 photophores (see also 3)
11 all petasma processes reduced	at least three well developed processes (see also 1)
12 rostrum lost	rostrum present
13 two segments of second thoracal leg elongated	all segments of subequal length (see also 2)
14 spinal petasma process secondarily lost	spinal petasma process present (see also 1)
15 proximal petasma process secondarily lost	proximal process present (see 1)
16 median petasma lobe with 2 or 1 additional process	no additional process (see also 1 & 8)
17 rostrum reduced	rostrum long
18 three or more segments of second thoracal leg elongated	segments of subequal size (see also 2)
19 last segment of endopodite of second thoracal leg slender with apical bristle	no isolated apical bristle
20 morphologically bilobated eye	round eye (see also 5, 7, 9)

thoracopodal gills are apomorphic in Euphausiacea, indicating the monophyly of Bentheuphausiidae (*Bentheuphausia*) and Euphausiidae (the other genera mentioned).

The use of the first and second swimmeret in sperm transfer can be considered a synapomorphy indicating monophyly of the Eucarida. The basic structure of the petasma of euphausiids consists of

three lobes each with a process, modifications in the different genera of this structure are considered apomorphic.

The eight subequal thoracal legs in fossil ancestors of euphausiids like *Paechella strongi* (Brooks, 1962) are considered plesiomorphous (cf. Brooks, 1962; Schram, 1974). Reduction and elongation of thoracal legs are apomorphic characters. The elongation of the second thoracopod in *Nematoscelis* and *Thysanoessa* Brandt, 1851 is similar. In *Tessarabrachion* Hansen, 1911 it is, however, another character state, as different segments are involved in the elongation. The reduction of thoracal leg 6 is found in more lineages as apomorphic parallelisms.

The benthic ancestors of euphausiids had normal round eyes. In some genera of the euphausiids a bilobed, sometimes elongated, eye developed as an adaptation to the pelagic way of life to enable multidirectional vision, as also found in pelagic fishes, and heteropod molluscs (Charles, 1966). The bilobed and elongated eyes are considered apomorphic. Parallelism in the character bilobate seems to exist, but this is not true. There is no homology as in the group of *Thysanoessa* and *Nematoscelis*; the morphology is bilobate due to deformation without differentiation in the ommatidea. In the *Tessarabrachion* and *Stylocheiron* G.O. Sars, 1883 group a differentiation in the ommatidea occurs which induces the external visible bilobation (cf. Mauchline & Fisher, 1969). For this reason character state 20 is considered a separate, though analogous, apomorphy.

The ancestors of the Euphausiacea were in all probability benthic animals in which no photophores are expected to occur, so that photophores are considered apomorphic in the Euphausiidae; in *Bentheuphausia* they are absent. In *Stylocheiron* secondary loss of some photophores is hypothesized.

In the cladogram (Fig. 1) the genus *Bentheuphausia* forms the oldest clade, *Stylocheiron*, *Tessarabrachion* and *Nematoscelis* form a second clade. In the other seven genera of more recent origin three lineages can be distinguished. In two of these clades a genus with Antarctic elements (*Euphausia* Dana, 1852, and *Thysanoessa*, respectively) has a sister genus with Indo-Malayan elements

Table II. Recent distribution of euphausiids. A = present in Atlantic Ocean; I = present in Indian Ocean; P = present in Pacific Ocean; – = absent; + = present by migration; (+) = incidentally present by migration.

	Deep sea	Central water	Equatorial	Cold water	Neritic water	Indo-Malaya	Mediterranean	Red sea	East Pacific
<i>Pseudeuphausia</i>	–	–	–	–	IP	IP	–	+	–
<i>Nematoscelis</i>	–	AIP	+ AIP	(+)	–	–	+	–	(+)
<i>Thysanoessa</i>	–	–	–	AIP	–	AIP	+	–	–
<i>Meganyctiphanes</i>	–	–	–	A	–	A	+	–	–
<i>Thysanopoda</i>	–	AIP	+ AIP	–	–	–	+	+	(+)
<i>Nyctiphanes</i>	–	–	–	(+)	AIP	AIP	+	–	+
<i>Euphausia</i>	–	AIP	–	AIP	AIP	AIP	+	+	+
<i>Nematobranchion</i>	–	AIP	–	(+)	–	–	–	–	(+)
<i>Tessarabrachion</i>	–	–	–	P	–	P	–	–	–
<i>Stylocheiron</i>	–	AIP	+ AIP	–	–	–	+	+	(+)
<i>Bentheuphausia</i>	AIP	–	–	–	–	–	–	–	–

(*Nyctiphanes* G.O. Sars, 1883, and *Pseudeuphausia* respectively).

### The euphausiid distribution

When the phylogeny of the more recent clades in Euphausiacea is related to Late Cretaceous or younger events, the older clades should be related to Mid Cretaceous or older events. For this assumption no proof can be given with present day knowledge of paleoceanography. The fact that these older genera, except for *Tessarabrachion*, show distributions all closely correlated to tropical and central water systems makes it at least possible to accept their presence already before the Late Cretaceous, as these water masses already existed in these period.

As fossil euphausiids are known from long before the Cretaceous (Brooks, 1962) it is postulated here that they occurred in all marine areas in the beginning of the Cretaceous. For the recent distribution one is referred to Table II.

If deep-sea euphausiids did primarily adapt to cold conditions they should be, like deep-sea Hydromedusae, related to (sub)polar taxa. In euphausiids cold water taxa are of a younger origin than *Bentheuphausia*. Not primarily cold adapted taxa can have penetrated the deep-sea before its cooling after the Mid Cretaceous; they immediately populated the deep-sea when it developed by rifting in the North Atlantic. *Bentheuphausia*, not related

to cold water taxa and phylogenetically old, is considered to belong to this type. Its origin is therefore placed in the North Atlantic (D in Figs. 2 & 3) in early Cretaceous times. Dispersal into the other oceans (7 in Fig. 3) followed.

After development of *Bentheuphausia* the ancestral group did split off taxa adapted to anticyclonic gyral current systems. Two warm Central Water (area C in Figs. 2 & 3) genera *Stylocheiron* and *Nematobranchion* and one cold gyral (area N in Figs. 2 & 3) genus (*Tessarabrachion*) developed. These Central Water genera reached the Indian Ocean (arrow 1 in Fig. 3) and Atlantic Ocean (arrows 2 & 3 in Fig. 3) in later periods.

The next step in phylogeny is the splitting into a (Proto)tethys Sea group (*Euphausia* and *Nyctiphanes*) and a Central Water group, the latter in turn splitted off a North Atlantic genus *Meganyctiphanes* Holt & Tattersall, 1905 and probably in recent time a genus (*Pseudeuphausia*) developed in the border regions of the Indo-Malayan Archipelago, indicated as M2 in Figs. 2 & 3. The two Atlantic genera and especially *Thysanoessa* may be derived from an Antarctic stock (arrow 10 in Fig. 3).

That one of the two northern hemisphere genera belongs to the group of young and one to the group of older genera is acceptable as the northern Atlantic (with the younger *Meganyctiphanes*) is considered, in tectonic theory, usually as of a more recent origin than the northern Pacific Ocean (with the phylogenetically older genus *Tessarabrachion*). Moreover, penetration into the North Atlantic in

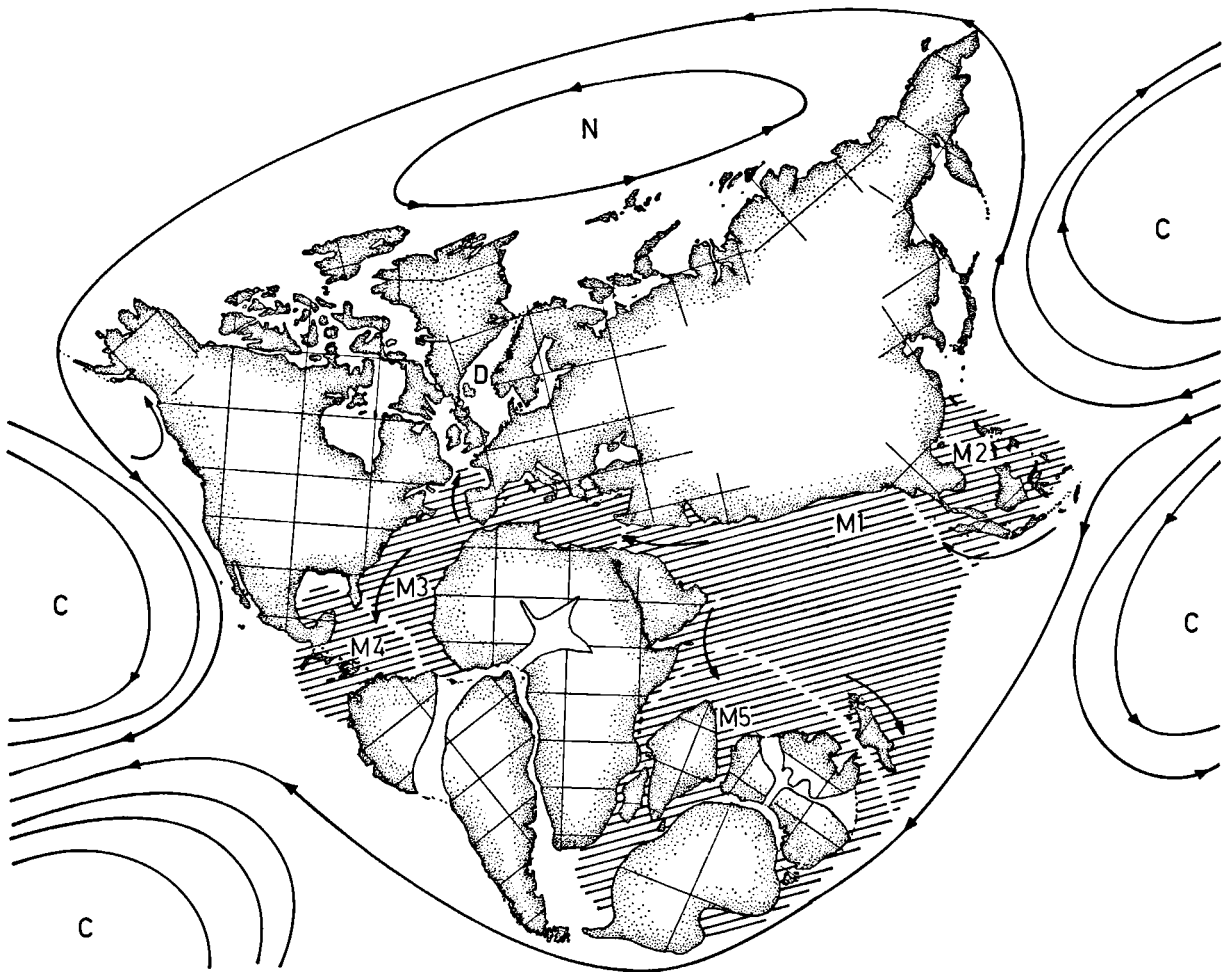


Fig. 2. Reconstructed biotopes of euphausiids in the Late Cretaceous: C = Central Water biotope; D = centre of deep-sea dispersal; M<sub>1</sub> = northern Tethys Sea centre; M<sub>2</sub> = northeastern Tethys Sea centre; M<sub>3</sub> = eastern Tethys Sea centre; M<sub>4</sub> = western Tethys Sea centre; M<sub>5</sub> = Antarctic Tethys Sea centre (the neritic Prototethys area is hatched); N = northern ocean centre.

recent times is easy while the North Pacific is more isolated in recent times (see above). *Tessarabrachion* may once have migrated also into the North Atlantic (arrow 5 in Fig. 3) after which it has disappeared during Ice Age cooling.

Part of this euphausiid phylogeny, as far as the genera *Euphausia* and *Nyctiphanes* are concerned, resembles the phylogeny of recent Hydromedusae.

The Prototethys component was in the Late Cretaceous supposedly distributed over the centres M<sub>1</sub>–M<sub>5</sub> (Figs. 2 & 3). In Post Cretaceous periods, M<sub>3</sub> and M<sub>4</sub> became isolated from the other centres indicated. M<sub>1</sub>+2 and M<sub>5</sub> became isolated from

each other by widening of the Prototethys Sea and M<sub>4</sub> and M<sub>3</sub> were separated likewise by widening of the Atlantic. *Nyctiphanes* developed in centre M<sub>1</sub> as an offshoot from *Euphausia* that itself formed endemic species or species-groups in the West Atlantic (centre M<sub>4</sub>), the East Atlantic (centre M<sub>3</sub>), the Antarctic (centre M<sub>5</sub>) and in the Indo-Malayan region (centre M<sub>1</sub>+2). In *Euphausia* and especially *Thysanoessa* bi-antitropical, arctic and antarctic elements are found. According to McGowan (1971), during Pleistocene temperature changes the Arctic and Antarctic faunas may have exchanged elements so that either the northern or the southern

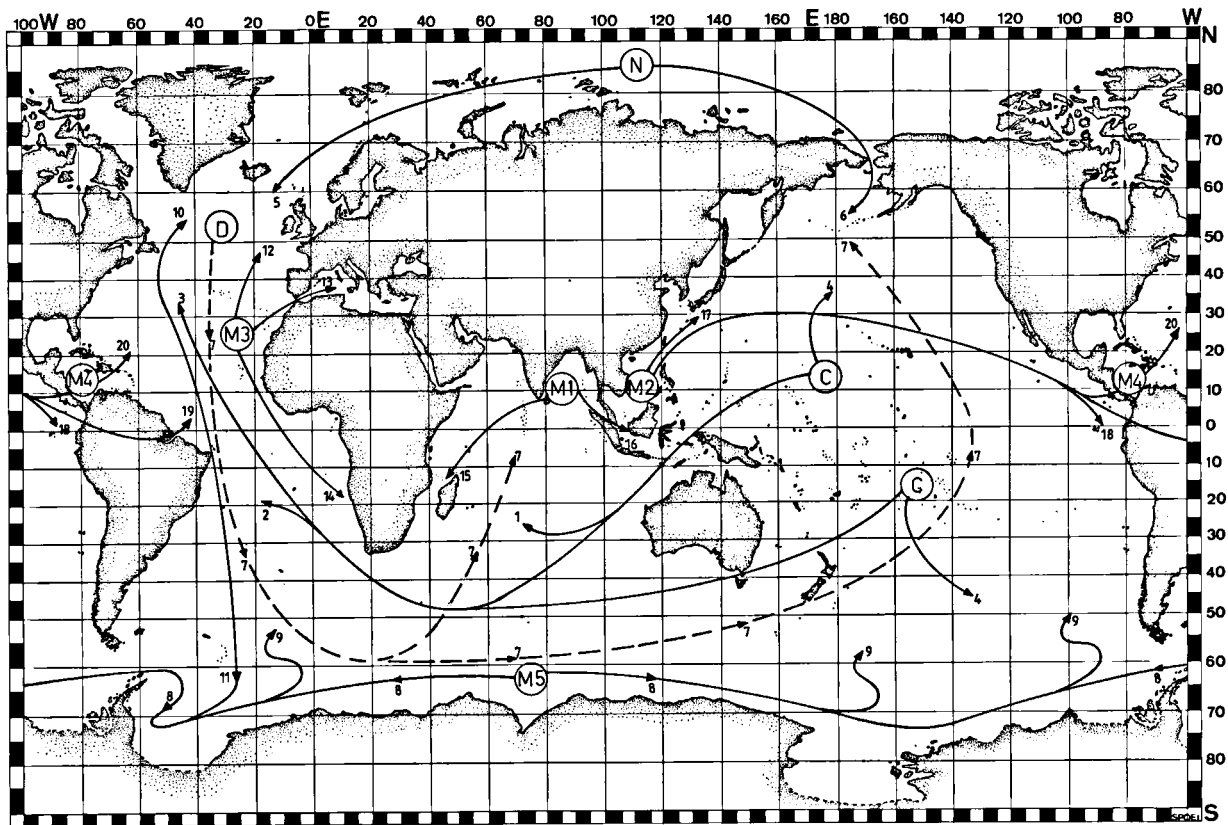


Fig. 3. Proposed historical and recent dispersal forming the basis of the recent distribution of euphausiids, with "migration routes" for: 1–4, Central Water species (C); 5–6, northern cold water species (N); 7–10, Antarctic Tethys Sea species (M5); 11–14, eastern Tethys Sea species (M3); 15–16, northern Tethys Sea species (M1) and 17–20, northeastern Tethys Sea species (M2).

ranges in these two genera may be of more recent age, and to conclude from the higher diversity in the south, it seems to be the northern range.

Two species groups of recent *Euphausia* in Central Waters recognized by Brinton (1975): the *brevis*, *diomedea*, *mutica*, *recurva* and the *hemigibba*, *gibba*, *pseudogibba*, *paragibba* group may have existed already before the other representatives of the *Euphausia/Nyctiphanes* complex became isolated in the Tethys Sea basin. The neritic taxa then were endemic to the Tethys. This neritic character also explains the vicariance into an Indo-Malayan and Antarctic group as found in the Hydromedusae by Van der Spoel (in press).

The populations in the Prototethys Sea with neritic preference presumably lived in the Late Cretaceous mainly near S.E. Asia, East of Australia

and off Antarctica where evaporites and crests (cf. Frakes, 1979) demonstrated the presence of shallow, nutrient rich, neritic habitats. When Australia drifted in a northeastern direction in the Eocene its coasts became surrounded by less shallow and nutrient poor waters, while the shallow area around Antarctica seems to have enlarged. As a result the populations near S.E. Asia became isolated from the populations around Antarctica.

When these biogeographic assumptions are correct, the global extinctions at the end of the Cretaceous have influenced Euphausiacea less seriously than Hydromedusae. This was, however, already clear from the present existence of the phylogenetically older Central Water taxa in the euphausiids that are absent in the Hydromedusae.

## Conclusions

The distribution and evolution of euphausiids discussed above suggests that, if “hydrotectonics” is accepted, the concept of “hydroplates” can be defined as “the original oceanic areas present before the continental rifting with current and water mass systems that did not change principally in circulation pattern”. The following “hydroplates” should be considered: (1) the Central Water hydroplate, (2) the northern gyral hydroplate, (3) the Equatorial Water hydroplate, (4) the southern Tethys hydroplate around Antarctica, (5) the northern Tethys hydroplate in the northern Indian Ocean with probably a subplate: (5a) the Indo-Malayan hydroplate, (6) the small North Atlantic hydroplate, and (7) the Caribbean hydroplate that nearly disappeared in recent times.

Hydroplates can not be defined as special geological or climatological structures. Physical and chemical parameters can neither be used as these changed in the geological past. The definition thus can only be based on a combined current water mass and ocean basin concept.

In some intercontinental areas the ocean configuration and currents will have changed so strongly that no continuity of any kind can be expected. Other intercontinental oceanic areas, however, changed in position and peripheral shape but maintained, unchanged, a wide central range with a stable basic current and water mass configuration.

All recent continents are situated on original continental plates. The oceans do not parallel this as the Atlantic and major part of the Indian Ocean are only of Cretaceous age, though there will have been an Atlantic and Indian Ocean hydroplate before the Cretaceous; these have disappeared by continental drift. Most of the recent Atlantic and part of the recent Indian Ocean are thus no hydroplates, as they occurred later in history and are populated by dispersal out of other hydroplates. These ocean parts can theoretically be compared to oceanic islands.

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Received: 30 March 1990