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A hypothesis on Mesozoic vicariance in Hydromedusae

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Abstract. In the Hydromedusae, many species show a tendency to be less restricted to a special distribution pattern compared to most other planktonic organisms. Latitudinal belt-shaped patterns in Hydromedusae are usually broader than the comparable distributions of molluscs or crustaceans. As a rule, the bathypelagic Hydromedusae are less restricted to specific depth layers than other taxa. Taxa of Hydromedusae showing distributions correlated with water masses are less restricted to water masses than taxa of other groups. Many types of distribution, like Equatorial and Central water patterns, commonly found in most planktonic groups, are absent in Hydromedusae, and many species show a strong tendency for southward dispersal. The present-day patterns of Narcomedusae and Trachymedusae seem to originate from an Antarctic fauna, the other subclasses of Hydromedusae show distribution patterns around the Indo-Malayan Archipelago. It is presumed that the Hydromedusae reflect a post-Cretaceous dispersal from two faunal centres, one in Indo-Malaya and one in Antarctica, that already became separated in Eocene times. The two Eocene faunal centres can be derived from one continuous area in which Hydromedusae survived the period of extinction at the end of the Cretaceous. Splitting of this centre probably forms the vicariant event responsible for the development of the Narcomedusae and Trachymedusae in the Antarctic waters, and of the Anthomedusae, Leptomedusae and Limnomedusae in the Indo-Malayan waters.

Introduction

Research in the North Atlantic Ocean and Banda Sea (Bleeker and van der Spoel, 1988; van der Spoel and Bleeker, 1989) showed that distributions of Hydromedusae are less sharply limited than those of taxa in other planktonic groups. A literature survey was carried out in order to get up to date on distribution patterns. For ~400 species, the distribution was studied. Although for many species zoogeographical data are scarce and probably incomplete, some general trends in zoogeography can be recognized. The Hydromedusae consist of holoplanktonic species, holoplanktonic species with parasitic larvae and meroplanktonic species with a sessile polyp stage. These different groups, which parallel the subdivision into separate subclasses (sensu Bouillon, 1985), have to be treated separately with regard to zoogeography as the modes of dispersal are distinctly different.

When studying development of distribution patterns, one should consider the phylogeny of the taxa. It is a commonly accepted idea that the Hydromedusae are an old phylogenetic group probably derived from the Cubomedusae. Although this assumption may be correct, it does not mean that recent Hydromedusae still reflect the direct link with Cubomedusae, for Cretaceous and older representatives of the Hydromedusae and many other planktonic groups nearly disappeared completely at the transition between Mesozoic and Cenozoic (Herman, 1979). Explaining the phylogeny and distribution of recent Hydromedusae means explaining the development of post-Cretaceous lineages derived from Cretaceous ancestors.
In this paper, the proposition is made that some Cretaceous Hydromedusae with indirect development (with alternating medusa and polyp stage) are ancestral to the recent taxa and not the Cubomedusae with direct development (in which medusae directly give rise to a new generation of medusae). At least three groups with different morphology, life strategy and zoogeography, i.e. the Trachymedusae, the Narcomedusae and the remaining Hydromedusae, developed after the Cretaceous.

That the dispersal and developmental strategy of present-day Hydromedusae is of relatively recent age is deduced from the fact that many old patterns are not represented in the zoogeography of the group (cf. van der Spoel and Heyman, 1983). To illustrate the typical characteristics of the zoogeography of the Hydromedusae, a comparison is made with the types of distribution distinguished by van der Spoel and Heyman (1983).

In an earlier paper (van der Spoel, 1991), a less detailed historical biogeography was given for the group; in the present paper, an attempt is made to explain these recent patterns along the lines of vicariance biogeography (sensu Wiley, 1988).

**Horizontal patterns**

In the epi- and bathypelagic Hydromedusae, narrowly distributed circumglobal patterns are rare, and most warm-water patterns are of the 40°N–40°S type or even distinctly broader. Only a few species, like *Pegantha trilobata* Haeckel, 1879 (Figure 1) resemble the narrow pattern of the *Euphausia teneroides* type (van der Spoel and Heyman, 1983; Figure 75), a circumglobal pattern mainly between 30°N and 30°S. The local differences in abundance and spatial occurrence in many patterns of Hydromedusae, however, make it acceptable to indicate the Indo-Malayan area as the centre of dispersal, like in *Euphysora furcata* Kramp, 1948 (Figure 2). For this species, most samples and most numerous records are found at localities in and around the Indo-Malayan Archipelago.

Real Equatorial patterns are absent among Hydromedusae, so are the Central water patterns and Transitional water patterns. Examples of the ‘species-groups’ as described by van der Spoel and Heyman (1983) are likewise absent.

The patterns spreading around the Indo-Malayan region are very common in Hydromedusae. Some holoplanktonic species show patterns of the *Hydromyles globosoides* type (van der Spoel and Heyman, 1983; Figure 112), these species penetrate the warm waters of the Indian and Pacific Oceans. The meroplanktonic taxa frequently show the neritic type called *Lucifer hansenoides* type (van der Spoel and Heyman, 1983; Figure 130) characterized by a more or less disjunct distribution between the South African, Australian and Japanese coasts with Indonesia as a centre of dispersal. In the subclasses Trachymedusae and Narcomedusae, <15% of the genera seem distributed around the Indo-Mayalan area, for the remaining classes of Hydromedusae this figure is ~80%. A strong difference between the holo- and meroplanktonic groups is thus present.
Mesozoic vicariance in Hydromedusae

Fig. 1. Distribution of *Pegantha trilobata*.

Fig. 2. Distribution of *Euphysora furcata*.
Solmaris lenticula Haeckel, 1879 (Figure 3) is one of the few examples with a H.globosoides type of distribution among the Narcomedusae with parasitic life stages. This species shows a direct development that occurred secondarily in a family and genus with indirect development. In the same genus, three species—S.cora

ona (Keferstein and Ehlers, 1861), S.flavescens (Kölliker, 1853) and S.solmaris (Gegenbaur, 1856) (Figure 4)—are found to be endemic to the Atlantic Ocean, an exceptional phenomenon in the Hydromedusae.

Examples of the L.hansenoides type of distribution, such as Eutima curva Browne, 1905 (Figure 5), are very common among the meroplanktonic taxa. This pattern frequently shows a radiation, as described for Acetes (van der Spoel, 1983; van der Spoel and Heyman, 1983).

Distributions restricted to the Pacific east of 120°W, between 40°N and 40°S, comparable to the Sagitta bierioides type (van der Spoel and Heyman, 1983; Figure 117) are incidentally found. Polyorchis penicillatus (Eschscholtz, 1829), Lizzia alvarinoae Segura, 1980 and L.ferrarii Segura, 1980 (Figure 3) are representatives of this type. These patterns are considered as being developed by relatively recent migration and speciation from Indo-Malayan ancestors (van der Spoel and Heyman, 1983). This implies that the mentioned percentage of taxa with an Indo-Malayan origin is actually >80%. Also, meroplanktonic circumglobal patterns are mentioned above as having an Indo-Malayan origin so that the percentage of taxa with an Indo-Malayan origin can be considered as being as high as 85% for the Anthomedusae, Leptomedusae and Limnomedusae together.

618
Fig. 4. Distribution of Solmaris corona (1), S.flavescens (2) and S.solmaris (3).

Fig. 5. Distribution of Eutima curvata (1), Euchylotheca intermedia (2), Eutima mucosa (3), E.variabilis (4) and E.gentiana (5); continuous arrows indicate possible and interrupted arrows less possible dispersal (cf. van der Spoel and Heyman, 1983).
Arctic neritic patterns are scarce, *Cyclocanna welshi* Bigelow, 1918, *Eutonina indicans* (Romanes, 1876) (Figure 6) and probably some representatives of *Ptychogona* can be considered epipelagic Subarctic elements, *Crossota norvegica* Vanhöffen, 1902, *C. pedunculata* Bigelow, 1913 and *C. rufobrunnea* (Kramp, 1913) (Figure 7) can be considered bathypelagic Subarctic in their distributions, and *Botrynema murrayi* Günther, 1903 reaches the deep Subarctic waters from the south. *Calycopsis nematophora* Bigelow, 1913 is a north Pacific element comparable to the *Calanus pacificoides* type of distribution (van der Spoel and Heyman, 1983; Figure 79) occupying the whole North Pacific between ~30 and 60°N, but it can of course not be considered Subarctic.

The number of species restricted to the North Atlantic Ocean is very low, and only for five meroplanktonic genera may a slight indication for Atlantic origin be present. This conclusion is, however, based on negative evidence as there was no clear indication for another area of origin.

The genus *Pandaea* is the only taxon of Hydromedusae clearly showing dispersal around an Atlantic origin. This conclusion is based on the similarity between this distribution (Figure 8) and the *Peraclis reticulatoides* type (van der Spoel and Heyman, 1983; Figure 59), a distribution shared by all species of the pteropod genus *Peraclis* around the area off Dakar in the NE Atlantic.

*Psychedagastria polaris* Allmann, 1878 is the only member of the Hydromedusae with evident bipolarity.

The *Crossota* species may very well originate from the Antarctic centre of origin and not from an Atlantic centre. *Crossota brunnea* Vanhöffen, 1902 (Figure 9)
Mesozoic vicariance in Hydromedusae

Fig. 7. Distribution of *Crossota alba* (1), *C. norvegica* (2), *C. pedunculata* (3) and *C. rufobrunnea* (4).

Fig. 8. Distribution of *Pandaea conica*.
forms an indication for such an Antarctic origin. Its two northward extensions in distribution, also found in the patterns of other Hydromedusae, may well be taken as reflecting the invasions of the northern hemisphere (cf. Figure 7).

The representatives of Antarctic distribution patterns are more numerous than the Arctic ones. The typical narrow (ice-) neritic Antarctic range of the *Euphausia crystallorophoides* type (van der Spoel and Heyman, 1983; Figure 135), a belt-shaped distribution around Antarctica, is only found for species of the meroplanktonic groups and they are not common. The only two good examples of this pattern are *Calycopsis borchgrevinski* (Browne, 1910) (Figure 6) and *Zanclonia weldoni* (Browne, 1910); probably *Euphysora gigantea* Kramp, 1957 belongs equally to this distribution type. These Antarctic patterns can be derived from oceanic patterns, as is also seen in other planktonic groups. This opinion is supported by the difference in pattern shape when compared to the group of which *Crossota brunnea* forms the best example. Most Antarctic patterns of Hydromedusae are very broad with regular or incidental dispersal into tropical regions, sometimes even to the northern hemisphere. *Chromatonema rubrum* Fewkes, 1882 (Figure 10) is the only meroplanktonic Hydromedusae of this broad type of cold water distribution that is much more commonly found among the holoplanktonic subclasses. Examples of the latter are *Crossota brunnea* (Figure 8), *Haliscera conica* Vanhöffen, 1902 (Figure 11), *Arctopodema ampla* (Vanhöffen, 1902) and *Colobonema sericeum* Vanhöffen, 1902 (Figure 12). For the meroplanktonic taxa, the Antarctic seems not to be an important place of origin, but >70% of the holoplanktonic genera seem to originate from Antarctic waters.
Mesozoic vicariance in Hydromedusae

Fig. 10. Distribution of *Chromalonema rubrum*.

Fig. 11. Distribution of *Halicerea conica*. 
Comparison of distributions in the northern and southern hemisphere of the patterns mentioned above shows that in cold as well as in warm water distributions the penetration into higher latitudes is stronger on the southern than on the northern hemisphere. For meroplanktonic Hydromedusae, the difference is small (3% of the species show asymmetry to the south). For the Narcomedusae and Trachymedusae, it was found that 27% were symmetrically distributed, but 46% showed a broader distribution on the southern hemisphere and 27% showed a broader distribution on the northern hemisphere: the difference for these two subclasses is thus 19%. This difference in biogeography is a latitudinal difference and not necessarily an ecological difference. It should be taken into account that the southern hemisphere shows (sub)polar conditions at lower latitudes than the northern hemisphere the actual differences are stronger.

Tethys Sea influence on planktonic distributions is difficult to indicate (van der Spoel, 1983; van der Spoel and Heyman, 1983). Kubota (1987) recorded a Tethys Sea pattern for *Eutima* and *Eutima*-like Hydromedusae associated with bivalves. Although the relationships proposed by Kubota seem reliable, there is one objection to be made: as for most taxa, no life cycles are known, and it is not certain that all the closely related taxa are considered. The Japanese–Mediterranean distribution of *Eugymnantha i. inquilina* Palombi, 1935 and *E.i.japonica* Kubota, 1979 probably shows a very incomplete picture. Studying the distribution of all *Eutima*, *Eucheilotha* and *Eugymnanthea* (Figures 5, 13–15) taxa associated with bivalves and others shows that there is a complete series of distributions from the Indo-Malayan area via the East Pacific, West Atlantic and East Atlantic to the Mediter-
Fig. 13. Distribution of *Eutima levuca* (1), *E. japonica* (2), *E. commensalis* (3), *E. hartlaubi* (4) and *E. brownei* (5); continuous arrows indicate possible and interrupted arrows less possible dispersal (cf. van der Spoel and Heyman, 1983).

Fig. 14. Distribution of *Eutima orientalis* (1), *E. newcaledonia* (2), *E. modesta* (3), *E. gegenbauri* (4) and *E. mira* (5); continuous arrows indicate possible and interrupted arrows less possible dispersal (cf. van der Spoel and Heyman, 1983).
The classic example of tropical submergence is the Chaetognatha *Eukrohnia hamata* (Möbius, 1875); among Medusae, *Periphylla periphylla* (Peron and Lesueur, 1809) is the best known representative of this pattern. Among Hydromedusae, *Colobonema sericeum* (Figure 12) shows tropical submergence. In fish, crustaceans, molluscs and chaetognaths, subtropical submergence can be defined as an occurrence at depths below 1000–2000 m in the tropics and occurrence from the surface to depths greater than 1000 m in the colder waters with a gradual transition between 50 and 35° latitude.

The Hydromedusae studied showed a small but significant deviation from this pattern. It consists of a very shallow occurrence of this type of species, also in the high tropics, in upwelling areas, near sills, near sea mounts and in other areas with vertical mixing (Bouillon *et al.*, 1986; van der Spoel and Bleeker, 1988).

Also typically bathypelagic species of Hydromedusae show this tendency of an easy upwards shift of their upper limit in the water column in areas with vertical disturbance or unfavourable conditions in the deeper layers. When the whole deep-sea fauna occupies higher strata, the deep-sea Hydromedusae are shifted most (van der Spoel and Schalk, 1988).

It seems as if the behaviour of species to occupy broader horizontal ranges is associated with broader vertical ranges; this is also described for higher taxonomic groups (van der Spoel and Heyman, 1983).

No mention is made of the conditions affecting the shallower occurrence of deep-sea species as this problem is discussed separately (van der Spoel, 1994).

**Discussion**

'The evolutionary processes and mechanisms occurring in Hydromedusae evidently are not reducible to a single model' is the opinion of Bouillon (1987a), but he also stated that Narcomedusae are the most primitive Hydromedusae, from which the Trachymedusae evolved directly (Bouillon, 1987b). The Cubomedusae are usually considered as the ancestors of the Narcomedusae (Petersen, 1979).

Let us first of all recognize the impossibility of finding ancestors of present-day taxa among present-day groups; thus, Cubomedusae are not ancestral to Narcomedusae and Narcomedusae are not ancestral to other Hydromedusae. It is only possible to accept the hypothesis that Cubomedusae-like organisms and Narcomedusae-like organisms were ancestral. However, is it correct to assume that indirect development (in Anthomedusae, Leptomedusae and Limnomedusae) is derived from direct development (in Narcomedusae, Trachymedusae and Cubomedusae)?

Study of the distributions of Hydromedusae and of the possible main vicariance events between the groups evidently shows the reverse to have occurred. The indirect development must be accepted as ancestral to direct development, as shown below.

From the distribution patterns in Hydromedusae, it is clear that there are some remarkable phenomena to be explained. There are no Central water distributions, so that old patterns (cf. van der Spoel, 1983) found in most other planktonic groups like Copepoda, Mollusca, Chaetognatha and Euphausiidae (van der Spoel et al., 1990) are missing. The Central water patterns, completely without contacts with land masses, are also typical for truly oceanic species. Thus, the absence of Central water taxa in this group points to the fact that old, oceanic, holoplanktonic species were not present, or that older Hydromedusae did not develop Central water forms. There are no real Arctic or Subarctic patterns so that there is no reason to accept any original fauna in the Arctic or Subarctic. In many groups, and evidently in Copepoda and Pteropoda, the North Atlantic was considered the place of origin of the deep-sea taxa, but on the basis of zoogeography, the deep North Atlantic Ocean cannot be indicated as the place of origin for bathypelagic Hydromedusae.
There are no Equatorial species, in general there are no species of Hydro
medusae restricted to the warm water belts which may indicate that Equatorial
water never formed a centre of origin for the group, although it is accepted to be
the place of origin of other planktonic taxa (van der Spoel and Pierrot-Bults, 1979).

A typical high diversity with primitive taxa in the Atlantic, like that found for
Pteropoda by van der Spoel (1967), or in the Pacific, like that found for Chaetog-
natha by Pierrot-Bults (1976), is not found for Hydromedusae.

There is no good evidence from patterns of Hydromedusae to accept a Tethys
Sea dispersal.

The very great diversity of Narcomedusae and Trachymedusae in Antarctic
waters, and the more wide distribution in waters of the southern hemisphere
(Figure 16) is noticed, the highest diversity for the other Hydromedusae, the
Anthomedusae, Leptomedusae and Limnomedusae, is evidently present in the
Indo-Malayan area.

Although all of the above conclusions are based on very scattered and too lim-
ited sampling, it seems evident that the general trends reflect the presence of an
area of origin around Antarctica for the mainly recent epipelagic Narcomedusae
and the bathypelagic Trachymedusae, and an area of origin around India and
Indo-Malaya for the other recent mainly epipelagic or neritic subclasses of
Hydromedusae.

To explain this configuration, special attention should be given to post-Cre-
taceous events influencing marine dispersal since older influences cannot be recog-
nized (van der Spoel, 1983; van der Spoel and Heyman, 1983). Moreover, the great
extinction of planktonic species at the border between the Cenozoic and Mesozoic
resulted in the development of completely new lineages of species. This too holds
good for old phylogenetic groups like planktonic Foraminifera, Radiolaria and
Calareous Nannoplankton (Herman, 1979). Although the Hydromedusae are an
old group, the recent Hydromedusae can be considered as mainly of post-Cre-
taceous age and, using zoogeographical tools, we can only study post-Cretaceous
phylogeny.

The paleogeographic situation during the Cretaceous is roughly known (Frakes,
1979). Two phenomena are of special interest for the study of the zoogeography of
Hydromedusae: the circum Pangaea current and the four areas of high production
reconstructed after Frakes (1979) (A–D in Figure 17). As generally accepted,
species diversity decreased at the end of the Cretaceous (Herman, 1979; van der
Spoel and Heyman, 1983) and one should try to depict the zoogeographical
changes during extinction influenced by the two mentioned factors. In areas A and
B (Figure 17), a high frequency of evaporites (Frakes, 1979) points to the presence
of many shallow water niches and a great diversity of neritic environment. In the
productive area C, no evaporites are found and a restricted, less diverse neritic
fauna is expected to have lived there. With the prevailing westward currents, the
decrease in species diversity will have affected first and most the western coasts of
Pangaea. Along the east coast of the complex of continents, species will have per-
sisted longer and in greater numbers due to high productivity, numerous available
niches and supply (instead of loss) of populations coming from the waters in areas
C and D in the open ocean.
Mesozoic vicariance in Hydromedusae

Fig. 16. Distribution of *Pantochogon haeckeli* (interrupted lines) and *Rhopalonema velatum* (continuous lines) to show the southward extension of patterns as hatched and black, respectively.

Fig. 17. Global paleogeography during the Cretaceous period, with areas of high productivity (hatched) based on cherts and phosphorites occurrence and ocean currents (arrows) redrawn after Frakes (1979).
When continental drift proceeded at the beginning of the Cenozoic, areas A and B, that first formed a continuous range, became separated at the moment that Australia shifted northeastwards, while water mass A with high productivity kept its original position. This high-productivity area A came close to Antarctica in the Eocene. Moreover, it is the Australian continent that shows no or very few evaporites in the Eocene, pointing to a less diverse neritic environment. The productivity along the west coasts of America also decreased and it disappeared almost at the east side of the Australian continent.

The most favourable area in which Hydromedusae survived was split into the India–Indo-Malayan area (B in Figure 18) and the Antarctic area (A in Figure 18), separated by an Australian area with very unfavourable conditions. Area E (Figure 18) was still isolated from areas A and B.

The hypothesis is that during the Late Cretaceous, the Maastrichtian, the pre-recent Hydromedusae disappeared except for a few taxa persisting in the favourable areas A and B (Figure 17). The link with the neritic areas seems so strong that it is accepted that the surviving species had indirect development. If holoplanktonic taxa had survived, recent zoogeography would have shown traces of Central water, Tropical or Transitional distribution patterns (cf. van der Spoel, 1983). During the Paleocene and Eocene, areas A and B became separated, to conclude from the data given by Frakes (1979) (Figure 18), and two stocks of populations of Hydromedusae were formed. The stock of species near Antarctica (A in Figure 19) spread first around Antarctica and penetrated the world oceans to the north. The other stock (B in Figure 19) started to populate the Pacific, Indian and probably the Atlantic Oceans. Closure of the Panama isthmus made westward penetration impossible after the Miocene, only a Pliocene–Pleistocene dispersal via Brazil then remains possible (van der Spoel, 1983).

The Antarctic seas with the stock (A) of species of Hydromedusae showed paleotemperatures of 19°C in the Eocene (Douglas and Savin, 1975), but these temperatures decreased quickly (Herman, 1979) and ice formation probably occurred already in the Oligocene so that most niches for the sessile polyp life stage disappeared. The strong seasonality that developed in the Antarctic climate made a life strategy necessary that could follow the shortening periods of maximum productivity. This stress on the developmental cycle will also have favoured the suppression of the sessile life stages. The Hydromedusae in area A were thus forced to become holoplanktonic either through direct development or through the development of a parasitic larval stage.

The stock of Hydromedusae with originally indirect development in area A split off the usually epipelagic Narcomedusae with parasitic larvae living on other planktonic species. When evolution proceeded, paralleled by the glaciation of the seas around the continent far remote from the shores, the Trachymedusae developed in area A. This group is still more adapted to cold, Antarctic waters, as is shown by the present bathypelagic distribution (frequently in Antarctic intermediate waters) of most species, and by the biogeographical tendency of a wider distribution in the southern oceans. If the Trachymedusae indeed developed later than the Narcomedusae, they found the niche for parasitic larvae already occupied, which may have been another reason to develop direct development.
Fig. 18. Global paleogeography during the Late Eocene period, with areas of high productivity (hatched) based on cherts and ocean currents (arrows) redrawn after Frakes (1979).

Fig. 19. Global paleogeography during the Pliocene period, with areas of origin of Hydromedusae (hatched) derived from the productive areas in Figures 17 and 18, and with the dispersal of Narcomedusae and Trachymedusae (continuous arrows) and the other Hydromedusae (interrupted arrows).
It was mentioned that the bathypelagic behaviour in Hydromedusae is not as well developed as in other planktonic groups, many species were recorded far outside the 'normal' depth ranges. This points to a relatively small degree of specialization and adaptation, and probably to recent speciation which would also agree with the given hypothesis. In these groups, the deep occurrence is made possible by an adaptation to low temperatures (found in the post-Cretaceous deep sea) and not by an adaptation to depth with high temperatures [a (pre)Cretaceous condition].

The stock of Hydromedusae in area B did not suffer from a climatic stress, they preserved the indirect development and epipelagic, usually neritic, distribution. The subclasses Anthomedusae, Leptomedusae and Limnomedusae, distributed around area B, the Indo-Malayan water, also show a much greater species diversity than the two Antarctic subclasses. The taxa around area B had a longer uninterrupted phylogenetic history than the Narcomedusae and Trachymedusae, the latter being of an age of only 38–80 million years. Among the subclasses distributed around area B, so far characterized by the indirect development, some species also prolonged the planktonic life stage by other modes of reproduction, like budding or direct fission (Stretch and King, 1980). The distribution of these species, like Aequorea macrodactyla (Brandt, 1935), still reflects the Indo-Malayan origin. That all present-day Hydromedusae developed from Cretaceous ancestors with indirect development is not excluding the possibility that earlier development of the group started with taxa showing direct development, as proposed by Bouillon (1987b).

As mentioned, sampling of Hydromedusae is not sufficient to reconstruct the complete distribution maps of most species. However, the present conclusion of a southern origin of the Narcomedusae and Trachymedusae is not caused by insufficient sampling as the Coronata obtained from the same samples and literature clearly show an origin in the Northern hemisphere.

Conclusions

The Hydromedusae show distribution patterns with some peculiar characteristics, as follows.

(i) In most patterns, a tendency is found to occupy broader ranges than do other planktonic animal groups.
(ii) Many types of distribution, and among these especially the older ones, are not found in Hydromedusae.
(iii) The Indo-Malayan area shows an extreme high diversity in Hydromedusae.
(iv) The Antarctic waters show a high species diversity in Hydromedusae compared to other planktonic groups.

The above phenomena strongly suggest that:
(v) A vicariance forms the basis for the evolution of Narcomedusae and Trachymedusae at one side, and Anthomedusae, Leptomedusae and Limnomedusae at the other side. Thus, the best first-order explanation for the observed disjunct dis-
Mesozoic vicariance in Hydromedusae

distribution between the two groups of Hydromedusae is that it represents a fragmentation of a widespread ancestral taxon, rather than a dispersal phenomenon from a more restricted ‘centre of origin’, and as many species show this pattern the more likely the first proposition is (Wiley, 1988; p. 514).

(vi) Recent Hydromedusae reflect the dispersal and phylogeny of a post-Cretaceous age only.

(vii) The Narcomedusae originated in the Antarctic waters.

(viii) After the Narcomedusae, the Trachymedusae developed in the Antarctic waters.

(ix) The Anthomedusae, Leptomederusae and Linromedusae originated from an Indo-Malayan faunal centre.

(x) The ancestors of recent Hydromedusae had an indirect development.

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References marked with an asterisk are used for distribution data only.


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