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ZOOGEOGRAPHICAL STUDIES
ON RHIZOSTOMEAE (SCYPHOZOA)

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INTRODUCTION

An attempt is made in the present paper to find out, whether the geographical distribution of the systematic groups of rhizostome medusae at the present time could be explained from historical points of view in relation to the geological periods.

The ordo Rhizostomeae is a well-defined group of Scyphomedusae with numerous species. Their morphology and classification have been thoroughly studied by Stiasny in a series of papers (1920-1940); the classification introduced by this prominent author was followed in the Synopsis of the Medusae of the World (Kramp 1961) and also forms the basis of the zoogeographical discussion in the present paper.

From an ecological point of view the numerous species exhibit an interesting uniformity in two respects: their occurrence is restricted to tropical waters (exceptionally somewhat extended into temperate areas), and all of them are epipelagic and neritic, occurring in the upper water layers in coastal areas; their scyphostome larvae, where known, are littoral. The medusae may, of course, be carried along by surface-water currents, but though several species attain a considerable size and presumably have a pelagic existence of fairly long duration, they are never met with at very great distances from coastal areas; there are no "oceanic" Rhizostomeae.

In accordance herewith the zoogeography of the Rhizostomeae may be discussed in conjunction with "The warm-water fauna of the shelf" as treated by Ekman in his Zoogeography of the Sea, 1953, chapter I.

As emphasized by Ekman in the terminal sentence of his Concluding Remarks (p.374) "biogeography...must also proceed historically", and in his attempt to explain the present distribution of the living forms he has given a vivid account of the composition and distribution of the faunas during the geological periods up to the present time, which has been possible for such groups of marine animals as corals, echinoderms, molluscs, and crustaceans, where the ancient faunas are represented by fossils. As far as the medusae are concerned, however, fossil forms or "impressions", which have been found in Cambrian and Jurassic rocks, are

very few and unfit for taxonomic and zoogeographical considerations. An attempt is made here to discuss the zoogeography of the Rhizostomeae "historically" without the aid of fossils.

Ekman came to the conclusion that the "warm-water fauna of the shelf" was widely distributed in the Tethys Sea, when this constituted a circumglobal belt of water with favourable conditions for the development of a rich fauna. During the Tertiary periods the conditions were subjected to considerable changes of more or less fatal influence to the constituents of the marine fauna.

The Tethys Sea, which existed long before the commencement of the Tertiary period, surrounded the globe in its equatorial part; it was mainly divided into the same three great oceans as now, connected through more or less wide gaps across the continents, reaching southwards to the Antarctic continent, but up to Cretaceous time almost separated from the arctic seas. The gaps across the continents were all within warm areas and gave rise to the development of a rich marine fauna of predominantly tropical character. During later Tertiary periods considerable changes took place, the connection between the oceans varying in width as well as in geographical position, and connection with arctic regions was established, changes which naturally caused alterations in the composition of the marine fauna.

In the Cretaceous period the connection between the Indian and the Pacific Oceans was south of the Australian continent, but in the Palaeocene narrow gaps were formed in the area, where now the Malayan Archipelago is, and during the Tertiary period open connections of increasing width were established through the Indo-Malayan area. There was, therefore, (and still is) a possibility for the development and interchange of a rich tropical, marine fauna between the two oceans, an Indo-West-Pacific fauna, also including a fauna of rhizostome medusae.

The Atlantic-Pacific connection. The large and massive chain of mountains along the Pacific coasts of North and South America mainly arose in the Lower Tertiary and were impenetrable for the oceanic water masses. The connection between the Atlantic and the Pacific Oceans has therefore always been rather narrow, across what is now called the Isthmus of Panama. In the Eocene this connection between the two oceans was narrow, fairly wide in the Oligocene and Upper Miocene, but completely closed from the Pliocene to the present time (since the Panama Canal with its sluices, great differences in level, and predominant content of fresh water cannot be called a natural transport route). In the only other connection, south of South America, the temperature of the water was too low for rhizostome medusae, at least in the Upper Tertiary periods.

The predominant domicile of the Rhizostomeae is in the Indo-West-Pacific region. One family with only one genus and one species *Stomolophus meleagris*, is exclusively American, occurring on both sides of the Isthmus of Panama. All of the other nine families are inhabitants of the Indo-West-Pacific region, particularly in the Indo-Malayan area; a number of species occur in the East Atlantic,

a few also in the Mediterranean, and a few species have appeared on the Atlantic coasts of America, but none on the Pacific side (apart from a few specimens which undoubtedly were introduced artificially, see below). The eastward distribution of Rhizostomeae in the Pacific Ocean has been remarkably slight.

In the present investigation special interest is attached to the "shelf fauna", an expression introduced by Ekman. Our knowledge of the shelf fauna and its alterations during the Tertiary periods is derived from investigation of such groups of animals, which have left fossil remains. Rhizostome medusae may or may not have existed before the Tertiary period, but we know nothing about their relationship with recent groups; it is discussed, however, whether correlation exists between the present distribution of the various groups of Rhizostomeae and the geographical changes of the oceans.

A few remarks should be introduced on species recorded from American localities, into which specimens of these medusae were most probably introduced artificially from distant areas.

Mastigias scintillae was described as a new species by Moreira (1961). It was first observed in 1955 near São Paulo in Brazil, and in the subsequent years it was found in increasing numbers near the coast between Cananeiro and Rio de Janeiro. It is most probably identical with *Mastigias albipunctatus* Stiasny, which was recorded a few years later from Jamaica in the West-Indies by Vannucci (1964), a species previously known from Australia and the Malayan Archipelago. All other species of the family Mastigiadidae are likewise inhabitants of the Indo-West-Pacific region and have been found nowhere else. *M. albipunctatus* is a large and conspicuous medusa, up to 145 mm wide. If in former time it had existed in Brazilian and West-Indian waters, it might probably have been observed before it was secured by Moreira. It seems probable, therefore, that its occurrence in these West-Atlantic waters, very far from the range of distribution of its numerous relatives, must be due to a recent introduction, presumably in the polyp-stage attached to the bottom of a ship. It is interesting that it became an inhabitant of these waters, at least for a number of years.

The Catostylidae is a large family with many species, widely distributed in the Indo-West-Pacific region, one species of the genus *Catostylus* also recorded from East-Atlantic coastal waters. In the Pacific Ocean none of them has been observed further east than New Zealand. But two species are recorded from the Pacific coasts of Panama and Equador. *Catostylus ornatellus* was described by Vanhöffen (1888) as *Loborhiza ornatella*, by Mayer (1910) referred to *Catostylus*; two specimens were found near Guayaquil, Equador, and the species has never been observed again. Stiasny (1921 p. 142 and 1922 p. 229) has examined, what is considered the type specimen, and found several errors in the description given by Vanhöffen, and he found (in spite of its mutilated condition) that it belongs to the genus *Catostylus* (as supposed by Mayer) or at least to the same family. It seems to me that the record of this medusa from the coast of Equador is so uncertain that it is not

worth while to discuss it; the statement of the locality may even be due to a confusion of labels in those ancient times. There is no confusion, however, about the record of *Catostylus tagi* (Haeckel) from Taboga and Taboquilla in Panama, as the three specimens were collected by Th. Mortensen. The specimens are in the Zoological Museum of Copenhagen, they were examined and figured by Stiasny (1922 b p.541), who identified them as *Catostylus tagi*; I have also seen them, and the identification seems beyond doubt, at least the specimens belong to the genus *Catostylus*, which is really astonishing considering the further distribution of the medusae belonging to the family Catostylidae. Most of the species are decidedly Indo-West-Pacific, ranging from East Africa to New Zealand; but *C. tagi* is widely distributed along the Atlantic coast of Africa, it was originally described from Portugal and is also recorded from the Bay of Biscay. Dr. Th. Mortensen, however, found it on the Pacific coast of Panama; most probably it was introduced artificially, presumably by a ship, and it has not been able to settle and remain a member of the East-Pacific fauna.

SPECIAL SECTION

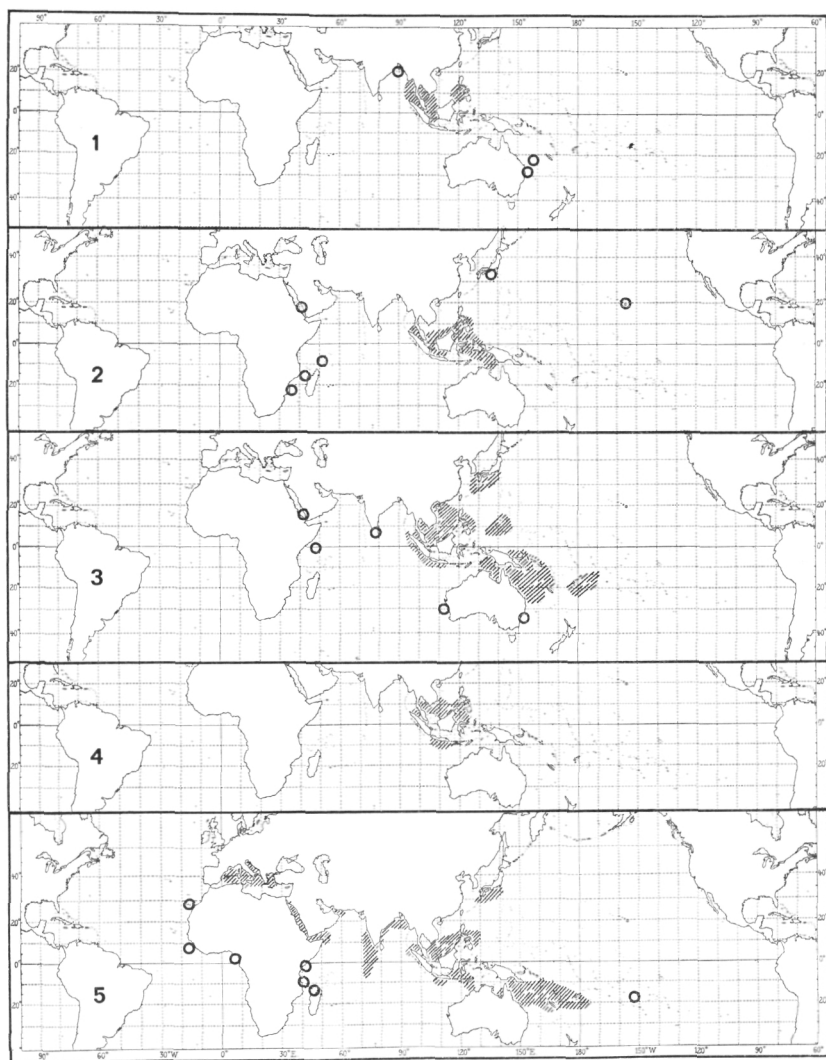
1. Occurrence restricted to the Indo-West-Pacific Region.

This applies to four of the families: Versurigidae, Thysanostomidae and Mastigiadidae among the Kolpophorae, and Lobonemidae among the Dactylophorae.

The family Versurigidae contains only one genus, *Versuriga* Kramp, 1961 (nov. nom. for *Versura* Haeckel) with only one valid species, *V. anadyoneme* (Maas); it has a rather narrow area of distribution, from the Bay of Bengal through the Malayan Archipelago to the Philippines and two localities on the east coast of Australia (see map, Fig. 1) it is a large medusa, up to 600 mm in diameter.

The family Thysanostomidae (Fig. 2) likewise consists of only one genus, *Thysanostoma* L. Agassiz, 1862, but there are three distinct species. *Th. lorifera* was described from the Red Sea by Ehrenberg, 1835; Stiasny (1923) examined the type specimen and compared it with specimens from several localities in the Malayan Archipelago and the Philippines, undoubtedly belonging to the same species. *Th. thysanura* Haeckel is recorded from several localities in the Malayan Archipelago and from the Philippines and southern Japan. *Th. flagellata* (Haeckel) has an extensive though scattered, distribution, originally described from the Hawaiian Islands and later on found there again, recorded from a few localities in the Philippines and the Malayan Archipelago, and on the Danish Galathea Expedition in 1951 it was taken in three localities near the east coast of Africa and north of Madagascar (Kramp 1968). It is the only species of Rhizostomeae which has been recorded from Hawaii. (see map, Fig. 2).

The Mastigiadidae (Fig. 3) is a somewhat more exuberant family with three genera, one of them with at least four species.



Figs. 1-5. Distribution of the families: 1. Versurigidae. 2. Thysanostomidae.
3. Mastigiadidae. 4. Lobonemidae. 5. Cepheidae.

Hatched: numerous finding places, circles: isolated finding places.

Mastigietta palmipes (Haeckel) was described from northern Australia (the type examined by Stiasny 1922a p.68); other records have been discussed and more or less rejected, but the species has been found near Crusadai Island in southern India.

The genus *Phyllorhiza* L. Agassiz, 1862 had a somewhat complicated history (see Kramp 1965 p.361); two obsolete species were recorded from the Philippines, the only valid species *Ph. punctata* (Lendenfeld) seems to be exclusively Australian, originally described from Port Jackson in New South Wales, recorded by the pre-

sent author from Cairns in northern Queensland (numerous specimens) and Swan River in South-West Australia; a record from southern Japan is uncertain.

The genus *Mastigias* L. Agassiz, 1862, contains four valid and a number of doubtful species which, however, presumably belong to this genus and may throw light on the distribution of the genus. The genotype, *Mastigias papua* (Lesson, 1829) is a very common medusa, which has been recorded from numerous localities, though within a somewhat restricted area between about 100° W. (on the coast of Sumatra and in the Gulf of Siam) and 180° (Fiji Islands in Melanesia); it is almost generally distributed in the Malayan Archipelago and the Philippines, in Micronesia, and on the coasts of Japan; further in the waters of northern Australia and in the Coral Sea as far as the Fiji Islands; but it has never been found in the central and western parts of the Indian Ocean. *M. ocellatus* (Modeer, 1791) is likewise generally distributed in the Malayan Archipelago and the Philippines and north of Australia, but not farther East in the Pacific; it is recorded from Hong-kong in China, but not from Japan. *M. albipunctatus* Stiasny, 1920, has a still more restricted distribution being repeatedly recorded from a number of localities in the Malayan Archipelago and found near Madras in south-eastern India; a record from Great Barrier Reef in North Australia is doubtful; its occurrence in Brazilian and West-Indian localities is most probably due to recent artificial introduction (see above, p. 9). *M. sidereus* Chun, 1896, was first described from the Zanzibar coast in East Africa (the original specimens examined by Stiasny, 1922a p.44), later on recorded from Singapore and Sumatra. Two of the uncertain species, most probably belonging to *Mastigias*, mark the extreme eastern and western limits of distribution of the genus: *M. pantherhinus* Haeckel from Samoa, 172° W. in the Polynesian Islands, and *M. gracilis* (Vanhöffen) from Assab, just inside the southern entrance to the Red Sea. The genus *Mastigias* thus has an extensive distribution, from the Red Sea to Samoa, absolutely dominating in the Malayan Archipelago and around northern Australia, but very rare in the central and western parts of the Indian Ocean. By *Phyllorhiza* the distribution of the entire family Mastigiadidae is extended somewhat to the south-eastern and south-western parts of Australia.

The subordo Kolpophorae is divided into three systematic groups, mainly characterized by the configuration of the subumbrellar muscles and the branching of the oral arms; two of these groups, Actinomyariae (with the family Cepheidae) and Kampylomyariae (fam. Cassiopeidae) are considered ancient, primitive groups, while the third group, the Krikomyariae (with annular subumbrellar muscles) should be regarded as more highly organized and a later developed derivative from the main line of Kolpophorae. This group consists of the three families mentioned above: the Versurigidae, the Thysanostomidae and the Mastigiadidae; they are closely related, by some authors regarded as one family.

The fourth of the families, whose occurrence is restricted to the Indo-West-Pacific region is that of the Lobonemidae (Fig. 4) with five species belonging to

two genera, *Lobonema* and *Lobonemoides*. Each of the species is found in a few localities only within a narrow area, the Philippines, Nhatrang in Vietnam, the Mergui Archipelago in Bay of Burma, and the coasts of Java. This family is regarded as derived from the Lychnorhizidae, the primary stem of the Dactylophorae.

The general result of the above investigation is that all of the four families of Rhizostomeae, the species of which have never been observed outside the Indo-West-Pacific region, are derivatives, and presumably late derivatives, of some primary stems of the Rhizostomeae.

2. Occurrence in the Indo-West-Pacific Region and eastern Atlantic.

The following three families are represented in the Indo-West-Pacific region as well as in the eastern Atlantic, partly also in the Mediterranean, but within each of the families many of the species are exclusively Indo-West-Pacific. The families are: Cepheidae, Catostylidae, and Rhizostomidae. None of them have representatives in the western Atlantic.

The family Cepheidae (Fig. 5) is regarded as the most primitive family among the Kolpophorae, most directly descended from the Aureliinae among the Semaestomeae. The musculature is radial, the oral arms dichotomous. It consists of three genera, *Cephea*, *Cotylorhiza*, and *Netrostoma*.

Netrostoma L. S. Schultze, 1898. – Three of the four species (which may be more or less uncertain) have been found in only a few localities: the Ganges estuary, Amboina, Japan, and the Fiji Islands. *N.coerulescens* Maas, 1903, however, has an almost continuous distribution from the Gulf of Oman in the Arabian Sea to Japan and northern Australia, with remarkably many records from India; this genus is not represented in the Atlantic.

Cotylorhiza L. Agassiz, 1862, has an entirely different distribution. *C.ambulacrata* Haeckel, 1880, has only been found near the Canary Islands in the Atlantic (the type was examined by Stiasny 1922); *C.erythraea* Stiasny, 1920, only in the Suez Canal. *C.tuberculata* (Macri, 1778) is a well-known medusa in the Mediterranean Sea, generally distributed along the European coasts from Spain to the Aegean Sea (no available records from the African coast). Once recorded from Assab in the southern part of the Red Sea (by Vanhöffen, 1888), according to Mayer (1910 p.661) introduced through the Suez Canal.

The genus *Cephea* Péron & Lesueur, 1809, has four valid species. *C.conifera* Haeckel is only known from the Caroline and Samoa Islands, *C.octostyla* (Forskål) from the Philippines and north-eastern Australia, besides a doubtful record from the Red Sea. *C.cephea* (Forskål), however, has an extensive distribution, originally described from the Red Sea (certified by Stiasny), recorded from Dar-es-Salam on the east coast of Africa, and from Madras in India, frequently observed in Japan and the Philippines and on the northern coasts of Australia; it is also recorded from the Melanesian Islands, and has been found as far east in the Pacific as

Marquesa, 140° W. *Cephea coerulea* Vanhöffen occurs in the Mozambique Channel east of Africa, but it has also been found off Sierra Leone and Nigeria on the Atlantic coast of Africa, which is very remarkable (see below p. 24).

The family Cepheidae thus has an extensive distribution, but the occurrence of the species is very diversified; most of the species are restricted to the Indo-West-Pacific region, from the Red Sea and East Africa and far east in Pacific waters, but two species occur in the Atlantic Ocean off the west coast of Africa, and one is an inhabitant of the Mediterranean.

The principal stem of the sub-ordo Dactylophorae remains as the family Lychnorhizidae, from which are derived the two families Lobonemidae (most probably a recent derivative, which was mentioned above) and the Catostylidae, presumably an ancient derivative, which has given rise to six genera with at least 20 species; as seen from the following account, the family Catostylidae (Fig. 6) has an extensive distribution in the Indo-West-Pacific region and the eastern Atlantic. The majority of the species, however, are exclusively Indo-West-Pacific.

Leptobrachia leptopus (Chamisso & Eysenhardt, 1821) has only been found in the Radak Chain of the Marshall Islands, and may be a species of *Catostylus*.

Acromitoides Stiasny, 1921, with two species: *A. purpureus* (Mayer) in the Philippines and North Australia, and *A. stipthropterus* (Schultze) at Ternate in the Malayan Archipelago.

Acromitus Light, 1914, contains five species, four of them found in only a few localities: *A. rabanchatu* Annandale, Chilka Lake on the east coast of India; *A. maculosus* Light in the Philippines; *A. tankahkeei* Light on the coast of China, and *A. hardenbergi* Stiasny near Borneo and on the coast of Vietnam. The fifth species *A. flagellatus* (Maas), however, has been collected in numerous localities, mainly in the Malayan Archipelago but also on the east and west coast of India, near Ceylon, and on the coasts of Vietnam, China, and Formosa. The occurrence of the five species of *Acromitus* thus are concentrated within a strictly limited Indo-West-Pacific area.

Among the three species of *Crambione* Maas, 1903, *C. cooki* Mayer is only recorded from Great Barrier Reef in North Australia, *C. bartschi* (Mayer) from Jolo in the Philippines and a single locality near Celebes. *C. mastigophora* Maas is somewhat more common, recorded from Ceylon, some localities in the Malayan Archipelago, Dinagat in the Philippines, and a locality in the Caroline Islands.

None of the four genera mentioned above occurs farther West than off the coasts of India, neither very far East in the Pacific, in contradistinction to some species of the following two genera.

Crambionella Stiasny, 1921, has three species: *C. annandalei* Rao occurs in the Bay of Bengal and on the east coast of India; *C. stuhlmanni* (Chun) has been found in a few localities in the Mozambique Channel off the east coast of Africa, and *C. orsini* (Vanhöffen) likewise belongs to the western part of the Indian Ocean, where it occurs in great abundance; it is recorded from the Travancore Coast and

Krusadai Island on the east coast of India, from the Iranian Gulf and from Assab at the southern entrance to the Red Sea; the present author saw it in great quantities floating at the surface from Mombasa in East Africa to the surroundings of the Seychelle Islands, but not much farther east in the open ocean; like all other Rhizostomeae it is a neritic medusa.

Catostylus L. Agassiz, 1862. Four of the five species occur in narrow and widely separated parts of the Indo-West-Pacific region, and the fifth species is Atlantic.

C. peresi Ranson occurs in the Iranian Gulf and neighbouring parts of the Arabian coast. *C. townsendi* Mayer is recorded from a number of localities in the Malayan Archipelago, the Gulf of Siam, and the coast of Vietnam; *C. ouwensi* Moestafa & McConnaughey was recently described (1966) from the south coast of New Guinea. *C. mosaicus* (Quoy & Gaimard) is generally distributed along the east coast of Australia from Melbourne to Cairns in northern Queensland and the south coast of New Guinea.

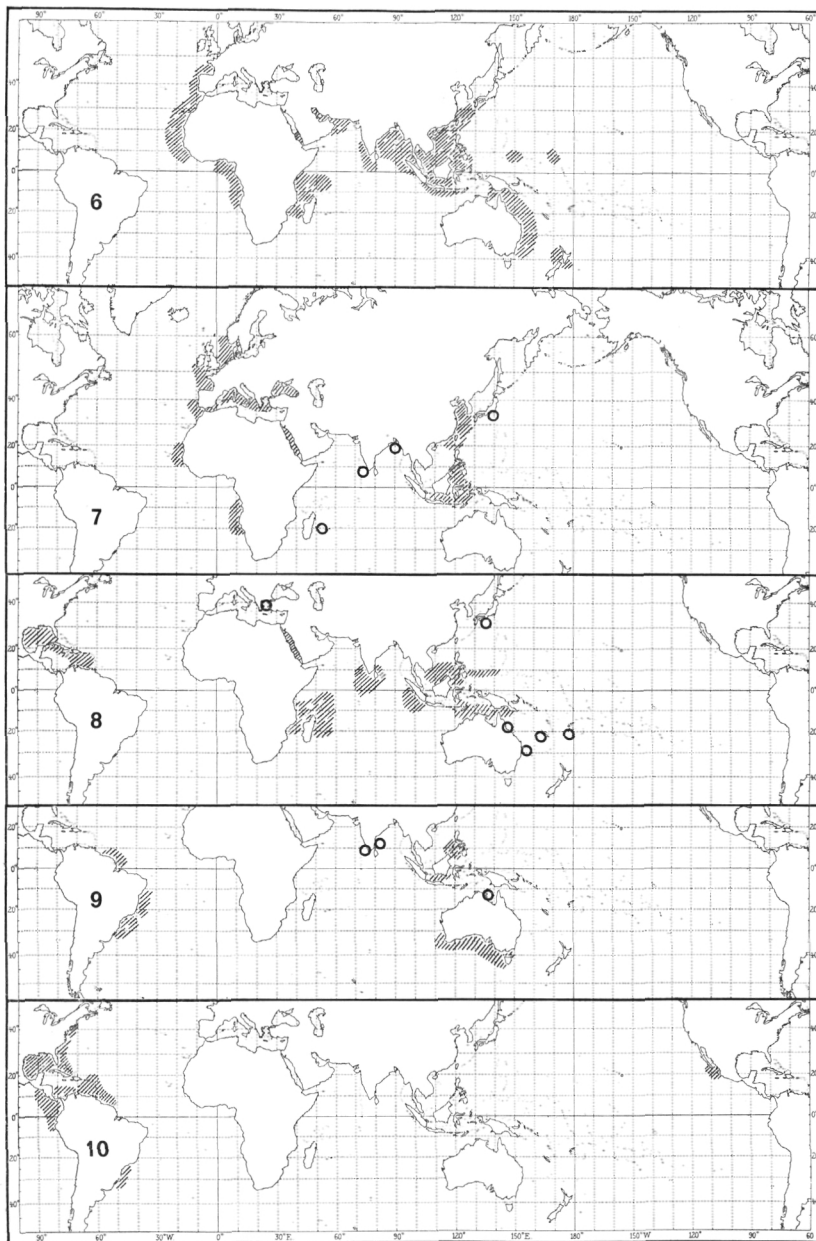
Catostylus tagi (Haeckel, 1869), on the other hand, has never been found in Indo-West-Pacific waters; it is an East-Atlantic species recorded from numerous localities along the west coast of Africa from about 15°S. in Angola and further north along the coasts of Spain and Portugal to the mouth of Loire in the Bay of Biscay. Its accidental occurrence in Panama was mentioned above (p. 10).

The family Catostylidae thus has an extensive distribution from Australia to the southern as well as the northern parts of East Africa and also along a very considerable part of the Atlantic coasts of Africa and Europe, but this applies to only one of the many species.

Undoubtedly, the distribution of the family Catostylidae was originally restricted to the Indo-West-Pacific region where, however, its distribution was extended comparatively far westward towards Africa, and one species was able to penetrate south of Africa into the Atlantic and obtained an isolated occurrence along the west coast of Africa, developing the morphological features by which, at present, it differs from the other species.

The third family, which has representatives in the Indo-West-Pacific region as well as in the East Atlantic, is that of the Rhizostomidae (Fig. 7), an ancient branch of the Dactylophorae. It has usually been connected with the Stomolophidae, the two families constituting a taxonomic group, Scapulatae, characterized by the possession of "scapulets" on the basal part of the oral arms; in his diagram of the taxonomy Stiasny (1921 p. 52) even denotes the Stomolophidae as derived from the Rhizostomidae. In my opinion, however, the two families are quite independent of each other, arisen as two separate branches of the main stem of Dactylophorae (see below, p. 19).

At an early period the family Rhizostomidae was divided into two genera, occurring in two different geographic areas, *Rhopilema* in the Indo-West-Pacific region, *Rhizostoma* in the eastern Atlantic and the Mediterranean. (A third genus *Eupilema* Haeckel (1880) is obsolete; according to Stiasny (1921) the only specim-



Figs. 6-10. Distribution of the families: 6. Catostylidae. 7. Rhizostomidae.
8. Cassiopidae. 9. Lychnorhizidae. 10. Stomolophidae.
Hatched: numerous finding places, circles: isolated finding places.

en, recorded from Japan, was probably a damaged specimen of *Rhopilema esculenta*).

The genus *Rhopilema* contains three valid species. The type-species, *Rh. rhopalophorum* Haeckel has been observed only twice, originally described from the Indian Ocean east of Madagascar, recorded and thoroughly described from Amoy in China by Stiasny (1933 pp.149-155), who maintains that it is a valid species. (*Rh. verrilli* (Fewkes) is an obsolete species, described from New Haven, Connecticut on the Atlantic coast of North America; according to Stiasny (1921 p.163) the descriptions given by Fewkes (1887) and Mayer (1910) are erroneous in several respects); it can be taken for granted, therefore, that the genus *Rhopilema* does not occur in Atlantic waters but is entirely Indo-West-Pacific. The two records of *Rh. rhopalophorum* were mentioned above. *Rh. esculentum* Kishinouye (1891) has only been observed in coastal waters of China and Japan, but is very common there. *Rh. hispidum* (Vanhöffen, 1888) has an extensive distribution: Japan, China, the Philippines, the Malayan Archipelago, India, and the Red Sea, where it was even found in the Gulf of Suez.

In contradistinction to *Rhopilema* the genus *Rhizostoma* is completely absent in the Indo-West-Pacific region, and it is remarkable that, just as the two genera of the family are geographically separated, also the two species of *Rhizostoma* occur in separate, though slightly overlapping areas.

Rhizostoma luteum (Quoy & Gaimard, 1827) is recorded from several localities along the Atlantic coast of Africa from Angola to the Strait of Gibraltar and from the coast of Portugal near Lissabon, but it has never been observed in the Mediterranean.

Rh. pulmo (Macri, 1778) is generally distributed along the European coasts from Gibraltar to the North Sea, frequently carried by the Jutland Current to the southern parts of Norway and into the Skagerrak and northern Kattegat, sometimes in great numbers. Among the rhizostomid medusae this is the only species penetrating into boreal waters. It is, however, also very common in the Mediterranean, where it seems to be generally distributed, occasionally even penetrating into the Black Sea.

The family Rhizostomidae is certainly an ancient family, probably like the majority of the Rhizostomeae originating in Indo-West-Pacific waters, where it is still represented by the genus *Rhopilema*. One of the ancestors emigrated south of Africa into the Atlantic, giving origin to the genus *Rhizostoma* and developing into two species, one being depended on tropical conditions (*Rh. luteum*), the other (*Rh. pulmo*) adapted to somewhat lower temperatures.

It is characteristic of these three families, all of which are of ancient origin, that most of the species are restricted to the Indo-West-Pacific region, while one or two species within each family emigrated south of Africa to coastal waters of the eastern Atlantic which will be further discussed in the conclusions.

3. Occurrence in the Indo-West-Pacific Region and western Atlantic

Two families, both of ancient origin, each of them with several species in the Indo-West-Pacific region and two or three in tropical West-Atlantic.

The family Cassiopeidae (Fig. 8) is a rather primitive derivative of the subordo Kolpophorae, constituting the group Kampylomyariae, with subumbrellar muscles in feather-like arcs and with the canal net issuing from the stomach. There is only one genus, *Cassiopea* Péron & Lesueur, 1809, but with several species, eight of which are considered valid, two or three more or less doubtful. Most of the species have narrowly restricted areas of occurrence, two or three of them in tropical West-Atlantic, the others in the Indo-West-Pacific region, none in both areas and none in the eastern Atlantic. Some of the species are of considerable size.

Each of the following species (*Cassiopea ndrosia* Agassiz & Mayer, 1899, *meritensi* Brandt, 1838, *medusa* Light, 1914, and *ornata* Haeckel, 1880) occur in a few localities between Japan and northern Australia, *C. ndrosia* extended eastwards to Tahiti. A gigantic medusa, 900 mm wide, was taken in the Bay of Bengal by the Galathea Expedition, 1952, belonging to *Cassiopea*, but in a damaged condition, which prevented a reliable description (Kramp 1968 p. 93). Two species are recorded from one or two localities in East-Africa, *C. depressa* Haeckel, 1880 from Madagascar and Mozambique, *C. picta* Vanhöffen, 1888 from the Red Sea. One species, however, has a very extensive distribution in Indo-West-Pacific waters, viz. *Cassiopea andromeda* (Forskål, 1775); it is generally distributed from Tahiti in the Pacific to East-Africa, also found in the Red Sea and once observed in the Aegean Sea (Schäfer 1955), evidently escaped through the Suez Canal. It is remarkable that one species has such an extensive distribution, while seven other species of the same genus are recorded from only few localities within narrow areas.

Three species of *Cassiopea* are recorded from the western Atlantic: *C. frondosa* (Pallas, 1774) and *C. xamachana* R.P. Bigelow, 1892, occur in the West-Indies (Caribbean Sea, Gulf of Mexico, Florida); *C. vanderhorsti* Stiasny, 1922, may be a variety of *xamachana* (the original specimens examined by Hummelinck 1933). *C. frondosa* is a large medusa up to 260 mm in diameter. The occurrence of *Cassiopea* in the West-Atlantic is thus restricted to an area with decidedly tropical conditions.

The family Lychnorhizidae (Fig. 9) is the most primitive family of the subordo Dactylophorae; the net of anastomosing canals issues from the primary and permanent ring canal, and there are no scapulets on the oral arms. There are three genera, but in contradistinction to the preceding family there are not many species.

Anomalorhiza shawi Light, 1921, by Uchida, 1926, elevated to a proper family, Anomalorhizidae, occurs in the Philippines, *Pseudorhiza aurosa* Lendenfeld, 1882 and *P. haeckeli* Haacke, 1884, in Australia, mainly in southern Australia; among the three species of the genus *Lychnorhiza* one, *L. malayensis* Stiasny, 1920, occurs in the Malayan Archipelago and at the Trivandrum Coast in India, the two others

in the western Atlantic. The distribution of this family in the Indo-West-Pacific region, thus, is not very extensive.

Lychnorhiza arubae Stiasny, 1920 has only been found in a single locality, near Aruba in the West-Indies and is a doubtful species, *L. lucerna* Haeckel, 1880, in several localities along the Atlantic coasts of South America from Montevideo to French Guyana, about 35°S. to 5°N., but is not recorded from the West-Indies; it sometimes penetrates into brackish-water areas. The distribution of the Lychnorhizidae, thus, is not so pronouncedly tropical as that of the Cassiopeidae.

There is hardly any doubt that these two ancient families, Cassiopeidae and Lychnorhizidae, originate in the Indo-West-Pacific region, whence they emigrated south of Africa into the Atlantic, where presumably they obtained an extensive distribution in warm areas, but during the period of deterioration in Pliocene and early Quaternary time they became extinct in the eastern Atlantic but were able to survive in the western Atlantic, where a few species of both families were differentiated and still occur at the present time. Their dispersal to the West-Atlantic, however, was not accomplished before the Isthmus of Panama was closed in the Pliocene Period, which prevented their further penetration into the East-Pacific. So here again the historical view of zoogeography could be maintained.

4. Endemic in American waters

One family, the Stomolophidae (Fig. 10), with one genus and one species, *Stomolophus meleagris*, is exclusively American, occurring on both sides of the continent, between 5°S. and 25°N. in the Pacific, 30°S. to 40°N. in the Atlantic. No representatives of this family occur in any other parts of the world.

Also in morphological respect this is an aberrant family; in the previous taxonomical classification it is classified with the Rhizostomidae as a special group of Dactylophorae, the Scapulatae, the proximal parts of the oral arms being provided with eight pairs of wing-like "scapulets", like those of the Rhizostomidae, but in some important regards *Stomolophus* differs from *Rhizostoma*; the mouth-arms are coalesced in their entire length, the lower arms are dichotomously or irregularly branched, the manubrium with reduced canal system, and in contradistinction to all other Rhizostomeae it has a permanent, central primary mouth opening, which must be regarded as a primitive feature. Evidently it is an ancient family, an early derivative of the Dactylophorae, which has not given rise to more than one genus with one species, and during the periods up to the Miocene it has been able to expand its area of distribution through the warm coastal areas on both sides of central America, when there was still an open connection between the Atlantic and the Pacific Oceans across the Isthmus of Panama. The available records are all from the neighbourhood of the coasts which is in good accordance with the prevailing currents. These medusae cannot follow the sea-going currents beyond areas with tolerable high temperatures.

CONCLUSION

In an attempt to regard the present geographical distribution of the Rhizostomeae from a historical point of view the first question, which arises, is how far back we must go in the geological periods to trace the origin of this ordo of Scyphomedusae. It is generally agreed that the ordo Rhizostomeae is derived from the Semaestomeae, especially from the Aureliinae (Uchida 1926 and 1960). A phylogenetic tree of the Scyphozoa, which seems reliable, is given by H. Thiel (1966 p.110).

Evidently, therefore, the ordo Rhizostomeae is not of very ancient origin, which also seems to appear from the geographical distribution of the families and species, particularly their complete absence in the eastern Pacific, with the only exception of *Stomolophus meleagris*, which secondarily has traversed the Isthmus of Panama from the Atlantic and is the only representative of its family, the Stomolophidae (see above, p. 19). The amphi-american occurrence of this family shows that it must have existed at least before the Miocene, when the Isthmus of Panama was closed.¹

It should be rather easy to unravel the zoogeographical problems of the Rhizostomeae, because all of them are epipelagic, neritic warm-water animals. There has never been any intermixture from arctic or antarctic regions.

As mentioned in the Introduction, the circumglobal Tethys Sea had a very rich fauna of tropical character, rather homogeneous, but in the Lower Tertiary it was possible to distinguish between an Indo-European and a central American fauna of shelf animals, though there was still a closer relationship between the eastern and western parts of the Atlantic than at present. No important climatic fluctuations have taken place in the Indo-Malayan areas, which have been able to retain their very rich faunas, and still in Tertiary times there was no "bridge" of islands in the eastern Pacific to facilitate an expansion of shelf animals from the Malayan waters to the East-Pacific.

On the other hand, there was a broad connection between the Indo-Malayan areas and the East-Atlantic waters through a Mediterranean area of considerable extension, and in the early Tertiary the Atlantic had a tropical fauna of a distinct Indo-West-Pacific character, remarkable also in the "Mediterrannic". During the Tertiary periods, however, considerable changes took place. The connection between the Mediterranean and the Indo-West-Pacific was barred, and climatic changes in the Atlantic had a fatal influence on its tropical fauna. Ekman (1953 p.68) gave a series of "Examples of animals at present confined to the Indo-West-

1. In a recent book by S. van der Spoel (1967) this author has traced the origin and evolution of the Pteropoda from historical points of view from their origin in the Tethys Sea, with reference to Wegener's theory on the drifting of the continents. No matter whether this theory is accepted or not, we need not go so far back to trace the origin of the Rhizostomeae; moreover the Pteropoda are oceanic animals, their distribution therefore quite different from that of the rhizostome medusae, which are neritic.

Pacific, but formerly existing in the East Atlantic", comprising Alcyonaria, Madreporaria, Crustacea, Xiphosura, Mollusca and Echinodermata, all represented by fossils. It applies, however, to all these, that their occurrence in "Europe" was before the Eocene, when the Mediterranean area was still extensive and in open connection with the Indian Ocean; there is no indication of a former transition of rhizostome medusae between the Atlantic and the Indo-Pacific through the "Mediterrannic"; if so, the Atlantic population of these animals might either have been completely extinguished, or their Atlantic descendants might have a distribution entirely different from that actually occurring in that ocean as described above and further discussed below. There is no doubt that all of the representatives of rhizostome medusae occurring in the Atlantic at the present time are derived from immigrants by the only available route, south of Africa, from the Indo-West-Pacific region which, presumably, was the place of origin of the entire ordo Rhizostomeae.

The very great abundance of species in the Indo-Malayan areas has induced some authors to regard this region as the principal, or even the sole center of origin and development for many groups of marine animals, while others are more or less opposed to this view. There can hardly be any doubt, however, but that the ordo of the rhizostome medusae originated in the Indo-West-Pacific region.

In zoogeographical discussions Endemism is of considerable importance. A characteristic feature of an area may be an abundance of species within certain taxonomic groups which are endemic there and have been found nowhere else, and it is obvious that in this respect endemic families are of greater importance than endemic genera or species.

Summarizing the statements in the Special Section above the following can be stated:

Among 72 existing species of Rhizostomeae no less than 61 species are endemic in the Indo-West-Pacific region.

Among the ten existing families the occurrence of four families is restricted to the Indo-West-Pacific region.

Five other families have a much greater number of representatives in the Indo-West-Pacific region than in the Atlantic.

The regional distribution in the Atlantic of the few species occurring there presents features of considerable interest.

The four families which are endemic in the Indo-West-Pacific region are the Verurigidae, Thysanostomidae, Mastigiadidae and Lobonemidae; all of them have their principal occurrence in and about the Malayan area and the western Pacific. It is very remarkable that all of these four families are derivatives, and presumably late derivatives, of some primary stems of Rhizostomeae (see above, pp. 10-12). None of them has been able to extend their distribution into the Atlantic Ocean, most of them not even to the western parts of the Indian Ocean.

Provisionally disregarding the American Stomolophidae we may discuss the Atlantic occurrence of the five other families. First and foremost they can be divided into two groups, three of the families being represented in the eastern and two in the western Atlantic. Though all of them are richly represented in the Indo-West-Pacific region no members of these families have been found on both sides of the Atlantic. It is emphasised that all of these five families are of comparatively ancient origin.

Three families are represented in the East Atlantic area. One of them is the Cepheidae (see above, p. 13-14), which belongs to the Kolpophorae and is regarded as the most primitive family of that group, directly descended from the Aureliinae; it is divided into three genera with altogether eleven species, eight of which are endemic in the Indo-West-Pacific region. This applies to all of the four species of *Netrostoma*. Among the four valid species of *Cephea* two are known from only a few localities in the western Pacific (some uncertain species likewise have a scattered occurrence), one species, *C. cephea*, however, is widely distributed from East Africa to the Marquesas Islands in central Pacific, but it has not penetrated into the Atlantic; the fourth species, *Cephea coerulea*, occurs in only two narrowly restricted areas, but they are on each side of Africa, in the surroundings of the Mozambique Channel in East Africa and in the equatorial part of West Africa; it should be noted that this is the only species of Rhizostomeae which has been recorded from both sides of Africa and has not differentiated into separate species. The distribution of the third genus of Cepheidae, *Cotylorhiza*, is interesting; one of the three species, *C. ambulacrata*, is only recorded from the Canary Islands in the Atlantic, another, *C. erythraea*, only from the Suez Canal, but the third species, *C. tuberculata* is generally distributed in the Mediterranean and has been found nowhere else, except at Assab in the Red Sea, where it may have been introduced through the Suez Canal.

It is important that *Cotylorhiza ambulacrata* has been found near the Canary Islands, and also that a species of the closely related Indo-West-Pacific genus *Cephea* occurs in the equatorial part of West Africa; it confirms my view as follows: predecessors of *Cotylorhiza*, belonging to the ancient family Cepheidae, have passed from the Indian Ocean around South Africa and spread northwards along the west coast of Africa, being isolated and differentiated into a number of species, some of which may have been extinguished during the period of deterioration in Pliocene and early Quaternary time, but some developed into the genus *Cotylorhiza*, one species, *C. tuberculata*, penetrating into the Mediterranean, being established there under favourable conditions. Secondly, *C. tuberculata* traversed the Suez Canal, which was opened in 1869, and was found in the southern part of the Red Sea; the rare species *Cotylorhiza erythraea*, described from the Suez Canal by Stiasny 1920, may also be derived from the Mediterranean. – The view expressed above is further confirmed by the distribution of species belonging to two other families.

Direct descendants from the original stem of Dactylophorae are the Lychno-rhizidae, and an ancient derivative of these is the family Catostylidae (see above p. 15); it is a great and diversified family with five genera and altogether 20 valid species, one of which occurs in the eastern Atlantic, while all the others are endemic in the Indo-West-Pacific region. Most of the species mainly occur in the eastern areas, but a few are recorded from East Africa. Among the five species of the genus *Catostylus* four have remained in the Indo-West-Pacific region, ranging from Australia to the coasts of Arabia, but one species invaded the Atlantic Ocean, and after its arrival there differentiated and developed into a separate species, *Catostylus tagi*, generally distributed along the west coast of Africa and somewhat farther north to the Bay of Biscay. This is another example of an emigrant from the Indian Ocean which has developed into a distinct Atlantic species. It is not easy to decide, whether this development took place in comparatively recent time under favourable conditions, or whether this species has been able to survive during the cold period in Pliocene and early Pleistocene; the latter supposition seems the more probable.

The Rhizostomidae likewise constitutes an ancient branch of the Dactylophorae; it differentiated, presumably at an early period, into two genera, established under the influence of natural conditions in two different geographical areas, *Rhopilema* with three species in the Indo-West-Pacific region (one of them generally distributed from Japan to the Red Sea), *Rhizostoma* in the eastern Atlantic, with two closely related, though quite distinct species, *Rhizostoma luteum* along the west coast of Africa to Gibraltar and Portugal, *Rhizostoma pulmo* in European waters, sometimes regarded as two varieties, *octopus* on the Atlantic coasts from Gibraltar to the North-Sea waters, *pulmo* in the Mediterranean and the Black Sea, thus another example of differentiation of the species when established in the East-Atlantic.

There is no reason to believe that the emigration to the Atlantic of species belonging to these three families took place in or about the Oligocene period from the Indian Ocean east and north of Arabia into the Mediterranean and from there to the Atlantic Ocean; they emigrated south of Africa to coastal waters in the eastern Atlantic, some of them obtained an extensive East-Atlantic distribution and now occur in considerable numbers, two of them penetrating into the Mediterranean; they remained in the East-Atlantic areas and were not dispersed to the western Atlantic. It is possible that in former time more species occurred off the West-African coasts but disappeared during the period of deterioration in Pliocene and early Quaternary time, when e.g. *Cotylorhiza tuberculata* was entirely extinguished in the Atlantic but obtained an exuberant occurrence in the Mediterranean. This species (or its predecessors) evidently settled in the Atlantic areas before the cold period in Pliocene and early Pleistocene, and the same most probably applies to *Catostylus tagi* and the two species of *Rhizostoma*, these being more resistant to deterioration. It is difficult to believe that the differentiation, development and ex-

tensive distribution of these exuberant species were accomplished in Quaternary time. On the other hand, *Cephea coerulea* may have arrived in the Atlantic in a comparatively recent period, since specimens of one and the same species occur on both sides of Africa, but this seems to be a unique instance (see above p. 14).

Ekman and others have frequently maintained that the early Tertiary fauna in the East Atlantic was more closely related to the Indo-West-Pacific fauna than it is at the present time, but in Miocene and Pliocene the tropical character of this Atlantic fauna was changed considerably, a substantial portion being extinguished during the period of deterioration, when the climate of West Africa was much colder than before (and also much colder than it is to-day). The disastrous reduction in the Atlantic of the tropical fauna of Indo-West-Pacific character may be an established fact for several groups of animals, which have been studied by means of fossils, and the possibility exists that also some species of rhizostome medusae became extinct during the cold period, but I am inclined to think that they have been very few. The picture given above of the differentiation and distribution of a few species belonging to three families is clear and simple; if a greater number of species had been present at the same time, more complicated circumstances could be expected; it is hardly possible that only the few species mentioned above survived. Moreover, in Tertiary time a closer relationship existed between the eastern and western parts of the Atlantic than at the present time. This problem is dealt with under the discussion of the West Atlantic fauna.

Still disregarding the purely American Stomolophidae we shall now discuss the two families occurring in the Indo-West-Pacific region and also in the West Atlantic, but unknown in the East Atlantic, the Cassiopeidae and the Lychnorhizidae, both of comparatively ancient origin (see above, pp. 18-19).

The Cassiopeidae contain only one genus, *Cassiopea*, with eight valid and a few doubtful species. Most of them are endemic in the Indo-West-Pacific region, where only one, *C. andromeda*, is generally distributed and very common in the warm waters, the others within narrowly restricted areas in the eastern portions of the region. Three species are recorded from the West Atlantic, *C. frondosa* and *xamachana*, which are rather common, and the doubtful species *C. vanderhorsti*, all of them only in the West-Indian region, and all of them undoubtedly belonging to the same genus as the many Indo-West-Pacific forms, differentiated into separate species, but not into separate genera.

The Lychnorhizidae is a primitive family with three genera and some few species known from rather few localities in the eastern parts of the Indo-West-Pacific region; one species, *Lychnorhiza lucerna*, however, is fairly common along a considerable part of the Atlantic coast of South America, but it has not been observed in West-Indian waters, in contradistinction to the species of *Cassiopea* mentioned above. *L. lucerna* does not occur in the Indo-West-Pacific region.

The few West Atlantic species of these two families certainly originated in the Indo-West-Pacific region, where closely related species still exist separated from

the West Atlantic species by extensive gaps. The first immigrants south of Africa into the Atlantic did not move against the Atlantic West Wind Drift; they may have followed the Benguela Current northwards along the coast of Africa to the equatorial parts of the ocean, but all of them were extinguished during the deterioration in Pliocene and early Pleistocene, while a few drifted towards America with the Equatorial Currents, perhaps facilitated by floating algae in the Sargasso Sea, which may have served as substratum for the polyps, but they did not reach the American coastal waters before the Isthmus of Panama was closed in the Pliocene, in contradistinction to the last of the families discussed below.

I have previously expressed my view on the systematical position of the Stomolophidae (p. 15) as an ancient family of Rhizostomeae, separating them from the Rhizostomidae with which they had been united as a group of Dactylophorae, the Scapulatae. In my opinion the "scapulets" of these two families developed independently in each of them. The Stomolophidae is an ancient lateral branch of the main stem of the Dactylophorae, their ancestors presumably, like all other Rhizostomeae, originating in the Indo-West-Pacific region but completely extinguished there as also in such parts of the Atlantic, from which one of them crossed this ocean and differentiated into the solitary American species, *Stomolophus meleagris*, which was able to extend its distribution through the Central American passage, before this was finally closed in the Pliocene period, and it obtained an extensive distribution on both sides of the American continent. There are no records from the Pacific coast south of 5°S., which may be due to the upwelling of cold water along the greater part of the South American west coast, though lack of sufficient investigations in these waters may be partly responsible. *Stomolophus* has been found as far north as California, 25°N. on the Pacific coast; in the Atlantic coastal waters it occurs from 30°S. to 40°N., including the Caribbean Sea.

A deterioration like that in the East Atlantic also occurred in the West Atlantic coastal waters but, as stated for various other groups of marine animals, the West Atlantic deterioration was not so fatal to the tropical fauna (Ekman 1953 p. 71-72, Lattin 1967 p. 133 ff); it was mainly effected as a southward displacement of the tropical elements of the fauna which, however, reappeared in the Pliocene. During the cold period the warm-water fauna along the northern parts of the American coasts was replaced by new types immigrating from the north, and many of them remained there, but rhizostomate medusae never existed in northern waters.

Representatives of the three families of Rhizostomeae now occurring in West Atlantic waters crossed the Atlantic Ocean from the coastal waters of Africa, probably in the equatorial belt, first the Stomolophidae before the time, when the Central American passage to the Pacific was closed, differentiating into one genus with one species, the predecessors of this ancient family completely disappearing in all eastern regions, the Cassiopidae and the Lychnorhizidae somewhat later, differentiating into separate West Atlantic species, but not into separate genera.

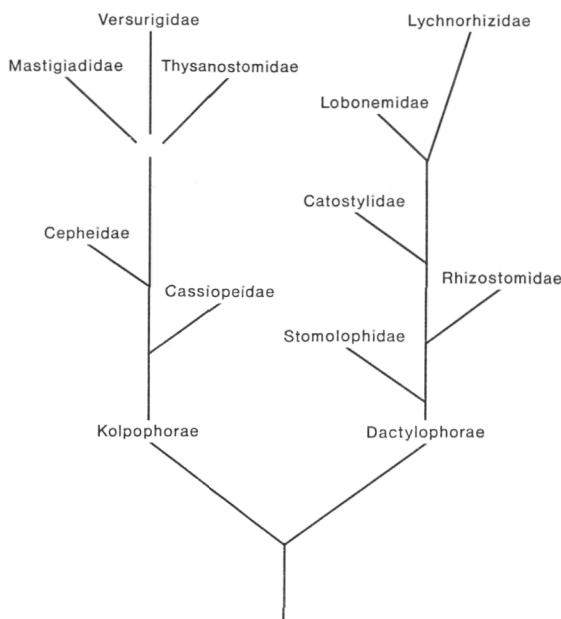
These are also rather ancient families; they evidently arrived south of Africa into the Atlantic before the cold period, they were unable to resist the deterioration in the East Atlantic, but survived the less disastrous cold period in the West Atlantic; this explains their present occurrence in the West Atlantic and their simultaneous total absence in the East Atlantic.

SUMMARY

As emphasized in the Introduction the Rhizostomeae are epipelagic and neritic, occurring in the upper water layers in coastal areas of tropical and subtropical waters. Morphologically they are highly organized, though the order is not of very ancient origin, being derived from the Aureliinae among the Semaestomeae. Their Indo-West-Pacific origin seems beyond doubt, four families and a vast majority of the species in the other families are still endemic in the Indo-West-Pacific; they have never been able to extend their distribution to the eastern Pacific, and they have never descended into deep water. If the division of the order into the systematic groups (in ten families) of the present time was accomplished in early Tertiary, a distribution from the Indo-West-Pacific via the broad passage through the "Mediterrannic" east and north of Arabia and through the large Mediterranean Sea to the Atlantic Ocean in or about the Oligocene period could be expected, which, however, is contradicted by the actual occurrence of the few Atlantic representatives; all immigration into the Atlantic undoubtedly took place south of Africa, at various times but mainly before the Atlantic deterioration, the cold period in Pliocene and early Quaternary time, when some of them were extinguished but probably not many (see above, pp. 21, 23).

The division of the order Rhizostomeae into ten families was of course, established with reference to the morphological characters, but since all of the families originated in the Indo-West-Pacific region the geographical distribution, which they have obtained, is not correlated with the morphological characters, but as pointed out above, the geographic expansion depends on the age of origin of the different families; the latest arisen families generally have a rather constricted area of distribution, while those of greater age were widely distributed and some of the species immigrated into the Atlantic; the distribution may accordingly be discussed "historically". The determination of succession of age as here employed is in accordance with the statements by Stiasny (1921 p. 52, see Fig. 11).

The most ancient of the families is evidently that of the Stomatolophidae; they are highly organized, but have retained certain primitive characters, and for geographical reasons they were presumably the first to immigrate into the Atlantic; their ancestors crossed this ocean, in American waters one genus with one single species, *Stomatolophus meleagris*, was differentiated, giving rise to a population which penetrated into the Pacific Ocean through the Central American passage, before it was finally closed in the Pliocene period, leaving an Atlantic population,



Figur 11. From Stiasny (1921 p. 52), slightly altered.

which was able to survive the cold period in the West Atlantic, while East Atlantic and Indo-West-Pacific representatives of this family were completely extinguished.

Representatives of two families, both of ancient origin, the Cassiopeidae and the Lychnorhizidae, likewise crossed the Atlantic, but not before the Central American passage to the Pacific was closed. A few separate West Atlantic species were differentiated, but no separate genera; they were able to resist the West Atlantic deterioration, but former East Atlantic members of these families were completely extinguished during the cold period in Pliocene and early Pleistocene, and no new populations have arrived from the Indo-West-Pacific region, where both families are richly represented.

Three families are represented in East Atlantic waters, the Rhizostomidae, the Catostylidae and the Cepheidae, all of them of ancient origin; it is interesting to see how differently the East Atlantic populations of these families behaved. The family Rhizostomidae (see pp. 15, 23) is differentiated morphologically as well as geographically into two genera, *Rhopilema* with three species in the Indo-West-Pacific region, *Rhizostoma* with two Atlantic species, *R. luteum* along the African coast, *R. pulmo* in European coastal waters, penetrating somewhat into boreal waters and also into the Mediterranean Sea. – The Catostylidae (see pp. 4, 23) is an exuberant family with several genera and numerous species, widely distributed in the Indo-West-Pacific region, but with only one Atlantic representative, and that even a distinct Atlantic species, *Catostylus tagi*, generally distributed along the coast of West Africa and western Europe. – The Cepheidae (see pp. 14, 23) is likewise

a family with several genera and numerous Indo-West-Pacific species; a few have immigrated into the Atlantic where, however, their occurrence is very diversified; all of them are separate species, though belonging to Indo-West-Pacific genera. One species of *Cotylorhiza*, *C. ambulacrata*, was observed only once, near the Canary Islands, but *C. tuberculata* is generally distributed in the Mediterranean. It is highly probable that some more species of Rhizostomeae have existed in the East Atlantic but have been extinct during the cold period in Pliocene and early Pleistocene; this most probably applies to an Atlantic population of *Cotylorhiza tuberculata* which, however, found favourable conditions in the warmer water of the Mediterranean. No representatives of these families traversed the Atlantic Ocean to the American waters. – Of particular interest is the occurrence of *Cephea coerulea* (see pp. 14, 22), belonging to a genus with many species widely distributed in the Indo-West-Pacific region, but only this one species has been found in the Atlantic; within the entire order of the Rhizostomeae this is the only species occurring on both sides of Africa, and since the East Atlantic population (few in number) has not been differentiated into a separate Atlantic species, it seems probable that the immigration around South Africa took place in comparatively recent time.

The four families, the Versurigidae, Thysanostomidae, Mastigiadidae and Lobonemidae, all of comparatively late origin and more or less widely distributed in the Indo-West-Pacific region, have never immigrated into the Atlantic Ocean (see pp. 10, 21).

The general result of the above considerations is that the extension of the geographical distribution of the Rhizostomeae from their common origin in the Indo-West-Pacific region was accomplished in the following succession:

1. Stomolophidae were carried to American waters before the passage through Central America was closed in the Pliocene; one species obtained an extensive distribution in warm areas on both sides of the continent, but their predecessors in the East Atlantic and Indo-West-Pacific regions were extinguished.

2. Representatives of Cassiopidae and Lychnorhizidae were established in West Atlantic waters somewhat later, when the passage to the Pacific was closed; they survived the West Atlantic deterioration, but East Atlantic representatives were extinguished.

3. Some of the Rhizostomidae, Catostylidae and Cepheidae survived the deterioration in the East Atlantic, but did not cross the ocean towards America.

4. The Versurigidae, Thysanostomidae, Mastigiadidae and Lobonemidae remained in the Indo-East-Pacific region.

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