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THE ZOOGEOGRAPHICAL AND PALEOGEOGRAPHICAL PROBLEM OF THE INDIAN OCEAN AND THE RED SEA ACCORDING TO THE ICHTHYOFAUNA OF THE LITTORAL*

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ABSTRACT

The Red Sea is generally considered zoogeographically as an appendix of the Indian Ocean. In reality this sea has its own paleogeographic history, beginning as a bay of the Mediterranean Tethys in early Tertiary and isolated for a rather, long time during the Pleistocene.

The ichthyofauna, especially the coastal fishes there can be distinguished as three different groups of immigrants to the Red Sea. Thus the Red Sea fauna is different in many aspects from the fishes of the Indian Ocean and has numerous endemic species. The ichthyofauna of the East African coast is influenced by the fishes of the Red Sea.

The Indian Ocean is not a homogeneous unit with a uniform ichthyofauna. The eastern part till India and the Maldives is different from the western part. As the Indo-Australian Archipelago shows also different conditions the whole Indian Ocean region has to be divided into four subregions, including the Red Sea in the west and the Indo-Australian Archipelago in the east.

INTRODUCTION

WHILE Weber and Beaufort (1911-1962) as well as Fowler (1956) as ichthyologists considered the Indian Ocean with the Indo-Australian Archipelago in the East and the Red Sea in the West more or less as a unit without any greater differentiation, this zoogeographical province shows some distinctive characters from the geographical point of view. No doubt, the Indian Ocean is a typical basin, but along its borders it has some greater differentiations.

In the east, there exist a group of rather large islands between Indomalaya and Australia. The south is absolutely open. In the north, there is the coast of Asia stretched from east to the west, but with the Indian subcontinent as a large triangle-shaped block projecting southwards into the ocean. In the centre there exist several groups of islands, the Laccadive and the Maldive as well as the Chagos Archipelagos, almost as a prolongation of India. In the southwest there is the large island Madagascar surrounded by a group of smaller islands, including Mauritius. The east coast of Africa is rather homogeneous, but it has some groups of offshore islands. The north-western corner of the Indian Ocean is characterised by several large and deep bays, the Gulf of Aden, the Red Sea and the Persian Gulf with the Gulf of Oman.

It is a question whether certain fishes show, from the taxonomical and zoogeographical standpoint, some distinctive characters according to the geographic

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differentiations of the Indian Ocean. It is necessary that these fishes do belong to the fauna of the littoral zone, that they have a rather low migration rate, also as larvae, and that they show a stationary behaviour. These criteria are typical for species of the families such as Pomacentridae, Chaetodontidae, Acanthuridae, Balistidae, Ostraciontidae, Tetraodontidae.

In this study the zoogeographical realms are discussed based mainly on the distribution of the butterflyfishes (family Chaetodontidae) with the subfamilies Chaetodontinae, the true butterflyfishes, and Pomacanthinae, the angelfishes.

Distributional Data

According to Day (1878, 1888), Ahl (1923), Fraser-Brunner (1933, 1951), Weber and Beaufort (1936), Baschieri-Salvadori (1954), Munro (1955), Smith and Smith (1963), Klausewitz (1960, 1969) and my unpublished studies on the fishes of the Maldives, the species of the Chaetodontidae have the following detailed scheme of distribution :

Of the subfamily Chaetodontinae there are in all 64 species in the Indian Ocean area from the Indo-Australian Archipelago to the Red Sea, but there is only one species found in all parts of this area, while the others have restricted distribution.

Six species are found in the Indo-Australian Archipelago, the Indian Ocean, the Madagascar area, on the East African coast, in the Red Sea, but not in the Persian Gulf.

Three species occur in the Indo-Australian Archipelago, the Indian Ocean, along the East African coast, but not in the Madagascar area, the Red Sea and the Persian Gulf.

One species lives in the Indo-Australian Archipelago, the Indian Ocean and the Madagascar area, but not along the East African coast and nor in the Red Sea and Persian Gulf.

Six species are found in the Indo-Australian Archipelago and the Indian Ocean, but not in the other areas.

Twenty-three species occur only in the Indo-Australian Archipelago (without consideration of any relationship to the Pacific), but not in the Indian Ocean and the other mentioned areas.

One species lives in the Indian Ocean, including the East African coast and the Madagascar area, but is missing in the other areas.

One species is endemic for the East African coast.

One species lives along the East African coast and the Madagascar area, but is missing in the other areas.

Four species are endemic in the Madagascar area ; six species in the Red Sea ; and two species in the Persian Gulf.

Considering the subfamily Pomacanthinae, the angelfishes, the situation is similar.

There are 25 species in the Indic area with the following distribution :

Three species live in all areas.

Two species are to be found in the Indo-Australian Archipelago and the Indian Ocean, including the East African coast and the Madagascar area.

Two species live in the Indo-Australian Archipelago, the Indian Ocean and along the East African coast, but not in the other areas.

One species occurs only in the Indo-Australian Archipelago and the eastern Indian Ocean.

One species occurs in the Indian Ocean except along the East African coast and the other areas.

Ten species live in the Indo-Australian Archipelago, but not in the other sections of the Indian Ocean.

One species is found along the East African coast and in the Red Sea.

Two species are endemic along the East African coast ; and two species in the Red Sea.

These distributional patterns indicate that zoogeographically the area of the Indian Ocean is not a homogeneous unit. The existence of the following geographical areas need substantiation : the Indo-Australian Archipelago; the northern coast of the Indian Ocean ; the Laccadive-Maldive-complex ; the Madagascar-Mauritius-complex ; the East-African coast ; the Red Sea with the Gulf of Aden ; and the Persian Gulf including the Gulf of Oman.

In Schilder (1956) the Eotropical Region includes the Indo-Australian and the Indian provinces, with the last mentioned divided into an Indo-African and an Arabian or Erythraen subprovince. De Lattin (1967) distinguishes only the Malaian and the Indian provinces without any further classification. According to fish distribution both systems seem to be insufficient.

Considering the different parts of the Indian Ocean we start with the *Indo-Australian Archipelago*, which has not only most of the species of Chaetodontidae in total, but evinces greater species diversity as compared to the other parts of the Indian Ocean. This area has 26 species of the Chaetodontinae in common with parts of the Indian Ocean, while 23 species are endemic or in common with the ichthyofauna of the western Pacific. The Pomacanthinae have 8 species in common with the fauna of the Indian Ocean, 10 species are endemic or belong to the Pacific fauna. Therefore, it is absolutely legitimate to consider the Indo-Australian Archipelago as a distinct unit or as a province of the same status as the Pacific and the Indian Ocean as Ekman (1967) and the other authors did.

What needs change is the western biogeographical border of the Indo-Australian Archipelago. As Greenfield (1968) demonstrated on the genus *Myripristis*, and

Klausewitz (1969) on the fishes of the genus *Heniochus*, the Malayan Peninsula as well as the islands Sumatra and Java form a border with many different species or subspecies to the east and west of this series of islands. A good example of the genus *Heniochus* is the vicarious and nearly related species *varius*, ranging from the east coast of Java and Sumatra to the western Pacific, and *pleurotaenia*, which is distributed from the west coast of Java and Sumatra to Ceylon and the Maldives.

This fact was already recognised by Ahl (1923) who opined that ' Die Grenze gegen den Indo-Australischen Archipel läuft an der Westküste Sumatras entlang. Daher erklärt sich auch, daß wir an der Westküste Sumatras zum Teil andere, vikariierende Formen finden als an der Ostküste.' (The border of the Indo-Australian Archipelago runs along the west coast of Sumatra. Therefore it is understandable, that in some cases on the west coast there are different forms than along the east coast). Ahl mentioned as examples the following species or subspecies of the genus *Chaetodon* :

Chaetodon t. trifasciatus = east

Chaetodon trifasciatus caudifasciatus = west

Chaetodon u. unimaculatus = east

Chaetodon unimaculatus interuptus = west

Chaetodon ulietensis = east

Chaetodon falcula = west

Chaetodon triangulum baronessa = east

Chaetodon t. triangulum = west

These point to the need for a revision of the biogeographical maps based on regional system of the littoral fauna. The border between the Indo-Australian Archipelago and the Indian Ocean should not run west of Sumatra and even west of its western offshore islet as well as west of the Nicobars and Andamans, but it should run along the middle of the Malayan Peninsula, the southern part of Sumatra and the middle of Java. Biogeographically the Andamans and Nicobars are not a part of the Indo-Australian Archipelago, but belong to the Indian Ocean.

Along the coast of *India* and Ceylon there occur 18 species of the Chaetodontinae and 9 species of the Pomacanthinae. None of these are endemic for this area. But 3 species of the Chaetodontinae and one Pomacanthinae species live in the Indo-Australian Archipelago and the eastern part of the Indian Ocean. Another Chaetodontinae species lives only in the eastern half of the Indian Ocean.

This situation can be well demonstrated on the fauna of the *Maldive Archipelago*. We found there 20 species of the Chaetodontinae. Of these, the species confined to the eastern half of the Indian Ocean are the following :

Heniochus pleurotaenia (W.Sumatra to the Maldives)

Chaetodon triangulum (Pacific to the Maldives)

Chaetodon collare (W.Pacific to the Maldives)

Chaetodon citrinellus (Pacific to the Maldives)

Another species which we did not find around the Maldives, but which is also confined to the eastern half of the Indian Ocean is *Parachaetodon ocellatus* (Philippines to India).

Of the Pomacanthinae we collected in the Maldives 5 species with one species, *Arusetta xanthometopon* (W.Pacific to Maldives) lives in the eastern half of the Indian Ocean.

These indicate that the Maldives do not constitute a distinct unit, but that they are for some species the western limit of their distribution, thus dividing the Indian Ocean into two halves.

In the *Western Indian Ocean* (including the East African coast, but excluding the Red Sea and the Persian Gulf) there are 7 species of Chaetodontinae and 4 species of Pomacanthinae confined to this area and not occuring in the eastern Indian Ocean. Twenty species of Chaetodontinae and 7 species of Pomacanthinae are common to both areas. Thirty-five per cent of the butterflyfishes and Fifty-seven per cent of the angelfishes differ in both areas. These figures indicate that there are significant differences between both halves of the Indian Ocean. It is not advisable to treat both as different sub-provinces, but I would propose to call them as two sections of the Indo-African Subprovince.

The *Madagascar area* (including Mauritius and the other small islands of the neighbourhood) has 23 species of Chaetodontinae and 5 species of Pomacanthinae. Of the former subfamily, 4 species (17 per cent) are endemic. Following Ahl, this area should be treated as a distinct biogeographical 'Faunenkreis'. But on the above degree of differentiation it may not be possible to treat this area as a subprovince, as there exist a good relationship to the East African coast. However, without any doubt, the Madagascar area should also be considered as a distinct zoogeographical section.

The *East African coast*, including the Seychelles, has 21 species of Chaetodontinae with 1 species endemic for East Africa and Madagascar and 1 species endemic for East Africa. In this area live also 11 species of the Pomacanthinae, with 2 species endemic for East Africa, 1 species occuring along the East African coast, in the Red Sea and in the Persian Gulf and 1 species along East Africa and in the Red Sea.

The *Red Sea* has a significantly distinct fauna. The Chaetodontinae are very different from the fauna of the Indian Ocean. Of 14 species, only 6 are common in both seas, while 6 species and 2 subspecies (57 per cent) are endemic for the Red Sea. The Pomacanthinae are also rather significant : of 7 species 2 (28.5 per cent) are endemic for the Red Sea. Another species is typical for the Red Sea and the East African coast and a fourth one is endemic in the Red Sea, the East African coast and the Persian Gulf. These are indicative of considerable faunal differences biogeographically between the Red Sea and the Indian Ocean.

The fauna of the Gulf of Aden and the South Arabian coast shows a great similarity with that of the Red Sea, but it has also some affinities with the Persian Gulf and the East African coast (Fraser-Brunner, 1951).

In the *Persian Gulf* there seem to live only 3 species of the Chaetodontinae, 2 of which are endemic. No Pomacanthine is endemic for this area. The Chaetodontidae of the Persian Gulf are more closely related to the species of the Red Sea

than to those of other parts of the Indian Ocean. Remarkable are the differences between the ichthyofauna of the Persian Gulf and the coast of India.

There exists a near faunal connection between the Red Sea, the Gulf of Aden, the Arabian coast and the Persian Gulf. This northwestern part and extension to the Indian Ocean should be treated as a distinct zoogeographical unit, the Arabian Subprovince, which has to be divided into three sections :

1. The Erythraeen Section with the Red Sea, including the Gulf of Aqaba ;

2. The South Arabian Section with the Gulf of Aden and the South Arabian coast ; and

3. The Persian Section with the Persian Gulf and the Gulf of Oman.

It would be rather unreasonable to correct and differentiate a reliable zoogeographic system on the distribution of the species of only one family of fishes. But we have substantiated the conclusions drawn with also the help of the distribution of other fish families of the littoral zone *e.g.*, Acanthuridae, Pomacentridae, Gobiidae, Balistidae, etc.. They all show similar patterns of distribution of species in the different areas of the Indian Ocean.

In other groups of animals, the differences seem to be even more convincing. For the Red Sea, Ekman (1967) mentioned the following rates of endemic forms of invertebrates : 31 % of the Decapod Macrura and 33 % of the Brachyura.

Paleogeographical aspects and discussion

For the classical descriptive zoogeography the faunal distinctions of the different parts of the Indian Ocean are not easily understandable as there does not seem to exist real geographical or ecological barriers along the coastlines. There seem to exist no reason for any isolation which may cause specific or sub-specific radiation.

Ecologically as well as geographically there seems to exist no good reason for any disjunctive or restricted distribution of the littoral fishes. Without any difficulty they should be able to migrate from the Indo-Australian Archipelago along the northern coast line of the Indian Ocean to the Persian Gulf, to the South Arabian coast, to the Red Sea and along the East African coast to Madagascar.

Besides the abovementioned low migration rate and a stationary behaviour of those species which show significant differentiations, paleogeography will help us to understand the zoogeographical heterogeneity of the ichthyofauna of the Indian Ocean.

The Indo-Australian Archipelago as a geographical barrier is easily understandable. It is well known, that during the Pleistocene period the sea level showed several greater fluctuations. These eustatic oscillations were caused by the absorption of great water masses by the icecaps during the glacial phases and their release during the interglacials. During the second glacial the sea level showed a depression of about 200 m, what causes a full connection of almost all islands of the Indo-Australian Archipelago with farther India. There existed a broad and solid barrier

from Malaya almost to Australia, separating the faunas of the Indian Ocean and the Pacific. Even 10,000 years ago, at the end of the Pleistocene there still existed a depression of the sea level of about 60 m (Cullen, 1967). This geographical barrier could lead to the isolation of fish populations of formerly homogeneous species and cause the evolution of subspecies or even new species. All the different forms mentioned above and living on the one or the other side of Sumatra or Java are nearly related. They developed during the Pleistocene and may not be older than 500,000 years, presumably some of them are considerably younger.

Another unsolved problem is the limited distribution of the fishes along the northern coast of the Indian Ocean. Some of the littoral species range to India, they live also around the Laccadives and Maldives, but they do not reach the South-Arabian coast. For this disjunct distribution mainly two interpretations can be offered.

It was Ahl (1923) who published the hypothesis that a landbridge or at least a continuous series of islands between India and Madagascar, acted as a geographical barrier which stopped the fishes going further west along the coast of the Arabian Sea and diverted the fishfauna in a southerly direction to Mauritius and Madagascar. In fact, the fishes of India, Ceylon, the Maldives and Madagascar are nearer related than the species found in India on the one hand and South Arabia on the other.

At least the former existence of a continuous series of the islands between India and Madagascar is no more an unrealistic theory. Such a landbridge of series of islands could have existed consisting of the Laccadive-Maldive ridge system as well as the Chagos area, the latter of volcanic origin rather than a continental relic (Rao, 1971). Ecologically the lack of reefs along the west coast of the Indian sub-continent is very important. Consequently the typical reef fishes are missing and apparently are not able to migrate along the several thousands of miles long coastline.

Whatever the reasons might have been, there seems to be no doubt, that the Madagascar/Mauritius-complex as well as the East African coast were—at least partly—populated *via* the Maldives and Chagos Islands.

The Madagascar-complex is so near to the East African coast that both have many species in common, but it is also so distant, that several endemic forms have evolved.

The Red Sea has a history which is very different from that of the Indian Ocean. Originally, during the Oligocene and Miocene of the Tertiary, the northern part of this ' graben ' was an elongate bay of the Mediterranean part of the Tethys. The tropical Indo-Atlantic Tethys fauna, similar to that of the recent Indopacific, lived also in this predecessor of the Red Sea, which was populated *via* the tropical Mediterranean. During the Miocene this ' graben ' deepened to the south. At the end of this period the connection with the Mediterranean ceased (as well as the connection between the Mediterranean and the Indian Ocean). During the Pliocene the southern opening of the Red Sea, the Straits of Bab-el-Mandeb, broke through the Yemen-Ethiopian barrier making the Red Sea an extension of the Indian Ocean. The Red Sea fauna, formerly of tropical Tethys origin, became a mixture of Tethys and Indic elements. During the glacial phases several more or less complete isolations of the Red Sea were caused by eustatic depressions of the sea level. These repeated isolations of the Red Sea resulted in a high rate of evolutionary changes, with many endemic species and subspecies.

It is my opinion that in the Red Sea there are distinguishable three different paleogeographical groups of littoral fishes :

1. *Postglacial Indian Ocean immigrants* which show no differences or only minor ones in comparison to the original population of the Indian Ocean. *Borcipiger longirostris* and *Chaetodon leucopleura*, both living only in the most southern part of the Red Sea, are example for the first mentioned case, the *Heniochus acuminatus* population in the Gulf of Aqaba for the second one (Klausewitz, 1969, 1970).

2. *Pliocene or Post-Pliocene-Pleistocene immigrants from the Indian Ocean :* They show specific or subspecific differences, but their relationship to the Indic is easily recognisable. Examples are (the ancestors from the Indian Ocean are in parenthesis) : *Chaetodon austriacus* (*Ch. trifasciatus*) ; *Chaetodon auriga auriga* (*Ch. auriga setifer*) ; *Chaetodon fasciatus* (*Ch. lunula*), fam. Chaetodontidae. A few examples from other families : *Amphiprion bicinctus* (*A. allardi* from the East African coast), fam. Pomacentridae. *Sufflamen albicaudatus* (*S. chrysopterus*) and *Rhinecanthus assasi* (*R. aculeatus*), fam. Balistidae. *Oxymonacanthus halli* (*O. longirostris*), fam. Aluteridae (Clark and Gohar, 1953, Klausewitz, 1960).

3. *Miocene immigrants from the Mediterranean part of the Tethys :* These species do not show any near relationship to recent species of the Indian Ocean. Examples of the family Chaetodontidae are : *Chaetodon larvatus, Chaetodon semilarvatus, Chaetodon mesoleucus, Arusetta asfur* and perhaps *Pomacanthodes maculosus*. Examples from other families : *Acanthurus sohal*, perhaps *Zebrasoma xanthurus*, fam. Acanthuridae. *Ostracion cyanurus*, fam. Ostraciontidae. *Lotilia graciliosa*, fam. Gobiidae.

There is some faunal influence from the Red Sea as an evolutionary centre to the northwestern parts of the Indian Ocean. A number of species, endemic for the Red Sea, are also found in the Gulf of Aden (Fraser-Brunner, 1951). Examples are *Chaetodon semilarvatus, larvatus* and *mesoleucus*. They migrated from the Red Sea in a southern direction through the Bab-el-Mandeb and into the Gulf. Some species were also collected along the South-Arabian coast.

In some cases it is rather difficult to find out the original range. *Pomacanthodes maculosus* lives in the Red Sea, but also on the South-Arabian coast, along the East-African coast and in the Persian Gulf (Klausewitz, 1969). It is my opinion, that this species, which shows no near relationship to any other species of the Indian Ocean, may belong to the Pre-Pliocene immigrants from the Mediterranean Tethys. Another case is *Zebrasoma xanthurus* of the family Acanthuridae. This species has a range similar to the *Pomacanthodes semicirculatus* and has also no nearly related species in the Indopacific. Probably this species originated also from the Tethys-fauna.

In the Persian Gulf there live only very few species of the Chaetodontidae. *Chaetodon arabica* and *Chaetodon nigropunctatus* seem to be confined to this Gulf. Their relationship is not yet clear. Their restricted distribution is remarkable. It may be possible that these two species also date back to the former Tethys-fauna. It is also interesting that they are not found eastwards along the coast of India.

One species-couple makes an exceptions to the rule that the Indian and the Arabian do not have nearly related vicarious species. The exception is made by

the Pomacanthine fish *Apolemichthys, xanthurus* from the coast of India and Ceylon (Day, 1878, 1888) and *Apolemichthys xanthotis* from the South Arabian coast and the Red Sea (Fraser-Brunner, 1951 ; Klausewitz and Wongratana, 1970). Both forms are so different that they can be distinguished as two species, but both are also so similar and nearly related, that their differentiation can be interpreted as a rather young phylogenetical process. It is possible that probably the older Indian species extended its range to the west after the hypothetical landbridge from southern India to Madagascar or at least to the Chagos Island had submerged and was no more acting as a biogeographical barrier.

This landbridge is one of the great paleogeographical problems, which can only be solved by the research as of marine geologists. We hope that the results of the geological studies carried out during the International Indian Ocean Programme will produce the answer of this enigma.

Summing up the ichthyofauna of the littoral zone of the Indian Ocean is anything but a homogeneous zoogeographical unit. It shows great differentiations which are mostly the results of paleogeographical processes of the Tertiary and Pleistocene, but some are even of postglacial origin.

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