On the evolution of the so-called thalassoid molluscs of Lake Tanganyika

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With 1 figure in the text

Quite a few authors have discussed the peculiar prosobranch fauna of Lake Tanganyika and several hypotheses and theories as to the origin of this fauna have been put forward. Schwetz and Dartevelle (1948) have given an account of the various viewpoints on the problem. They conclude their survey with the following quotation: "Le problème du Tanganika reste irrésolu." It seems to me, however, that it may be possible to throw new light on the whole problem by studying the general mode of evolution in fresh water and by applying some new results concerning the physiography of Lake Tanganyika.

The so-called thalassoid or halolimnic prosobranchs of Lake Tanganyika are throughout endemical for the lake. The various species have in many instances evolved greatly diverging shell forms; and many of these forms show a striking similarity to the shapes of various marine shell types, e.g. *Trochus, Natica, Nassa, Murex*, etc. The anatomical examination of the "thalassoid" Tanganyika species, particularly as carried out by Moore and Digby, has disclosed that the species have a common origin. Pilsbry and Bequaert (1927) include the whole "thalassoid" fauna of Tanganyika in the family Melaniidae. Thiele (1931) includes all the species except those belonging to the genus *Lavigeria* in the Paramelanieae, a tribus of the subfamily Paludominae of the family Melaniidae. It is thus apparent that the similarities between the Tanganyika shells and marine shells are due to convergent evolution. Further, the complete endemism of the Tanganyika forms and the lack of fossil representation outside the area in all probability proves that they evolved within the area. The above considerations prompt two questions. Why has such a far-going evolution taken place in Lake Tanganyika? And why has this evolution lead to shell forms of a marine type?

In endeavouring to solve the first problem we must start with a discussion on organic evolution in fresh water in general. It is obvious that the fresh-water fauna is very poor in forms as compared with the marine or the terrestrial fauna. Recent investigations seem to emphasize this difference. My own studies on the Lymnaeidae show, for instance, that the number of valid species in this group is only about fifty, though at least 1 200 forms have been described. Professor Schwetz of Brussels has personally demonstrated to me his breeding experiments with some African Planorbidae. The progeny of one single form, may, when bred under different environmental conditions, give rise to forms which have previously been regarded as
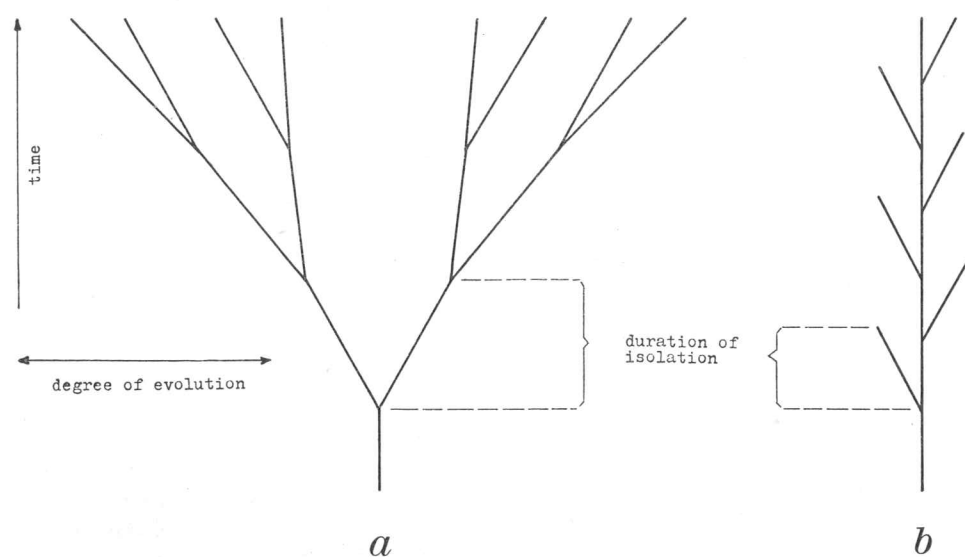
Fig. 1. A diagrammatical illustration of the principal difference between evolution in marine and terrestrial biotops (*a*) and fresh-water biotops [*b*]. The upper border of the diagram represents recent time. Each branch or section between two places of parting, represents one population. Compare the text.

different species. Critical revisions of marine and terrestrial groups often lead to a decrase too, in the number of valid species, but generally not to the same extent as among fresh-water groups. Presuming that a poorer fauna and consequently also a slower evolution are true characteristics of the fresh-water fauna (though some particular groups are exceptions) we have to search for the cause of this difference between evolution, on the one hand, in fresh water, and, on the other in the sea and on land. The different duration of the life time of the fauna types cannot give a satisfactory explanation.

When comparing the evolution of fresh-water biotops with that in other biotops there is no reason to presuppose a difference in the substantial base of the evolution, i.e. the frequency of mutation, between the two categories. The decisive qualification is rather to be searched for in the respective conditions of isolation. The general mode of evolution is demonstrated diagrammatically in Fig. 1 *a*. The geographical range of a species may become divided by a barrier. If the barrier is effective, if it prevents communication between the two populations to a sufficient extent, each population evolves independently of the other. They are then able to become two geographical races of one species. If the separating barrier breaks down at that moment, the two races will mix again and form a unitary population with an increased genotypical variation. On the other hand, if the barrier remains for a longer time, the geographic races will be transformed into two different species and remain so even if the barrier subsequently collapses.

Fresh-water biotops are generally isolated areas in a far higher degree than marine or terrestrial biotops. The pronounced shore-living aquatic species very often have a great power of passive dispersal, which diminishes the importance of the isolated

character of the biotops. But many sedentary species, particularly those living beneath the very epilimnion, have but a comparatively small power of dispersal. Particularly as regards the last group of animals, but to some extent in respect of the first-mentioned group as well, the isolating effect of the biotops is sufficient to allow some independent evolution. This evolution very often leads to microgeographic races. The isolating effect is not enough to produce real geographic races. If a barrier of geographical extent arises, a formation of geographic races in the same way as among non-limnic species may be possible. In limnic biotops however, the microgeographic and geographic races very seldom evolve into distinct species. The life-time of the isolated populations is generally too short (Fig. 1 *b*). Marine and terrestrial populations generally produce an unbroken chain of generations. Limnic populations, on the contrary, generally produce a restricted number of generations due to the geologically very short life-time of the lake basins. The limnic populations are seldom isolated long enough to promote the formation of new species. In my opinion this is the reason, or at least the main reason, for the comparatively small number of species in the limnic fauna. There is, however, one more theoretical possibility of explaining the connection between the short life-time of the lake basins and the paucity of the limnic fauna. The short life-time of the lake basins is an essential part of the environmental conditions of their fauna. Consequently, this short life-time may influence the selection value of some genes of the inhabitants. In this way the short life-time of the lake basins may favour the evolution of comparatively unspecialized and euryoic faunal elements with a comparatively high efficiency of passive dispersal. And these characteristics of the faunal elements contribute to the paucity of the limnic fauna as a whole and to its somewhat monotonous appearance. The opinion that the short life-time of the lake basins causes the comparative paucity of the limnic fauna has been expressed before, the first time probably by BELT (1874, p. 334). As far as I know, however, the causality has not been analysed before.

In some lakes, such as Baical, Ochrida, three lakes on Celebes and, above all, Tanganyika, comparatively rich endemical faunas have evolved. Even in these lakes the number of species seems to have been overestimated. Nevertheless, an extraordinarily fast production of new species has undoubtedly taken place in the lakes or the areas under consideration, that is when the evolution in fresh water in general is regarded as the standard. These exceptions from the general paucity of the freshwater fauna are quite in harmony with the above considerations. The lakes containing endemical faunas are characterized by a high geological age as compared with lakes in general. From a pure evolutionary point of view, only the extraordinarily old lakes have evolved normal faunas. From this point of view the fauna of Tanganyika is in no way strange but the poverty of limnic faunas in general is remarkable.

The degree of endemism of the Tanganyikan fauna seems quite considerably to surpass that of the other above-mentioned lakes. According to CUNNINGTON (1920) about 70 per cent of all Tanganyika animals are endemic. The endemism of the "thalassoid" snails is, however, of still greater importance, as it reaches almost the rank of subfamily. Besides among molluscs endemic genera also occur among fishes and decaped crustaceans.

Some recently discovered physiographical conditions of Lake Tanganyika (CAPART 1949) may contribute to the explanation of the exceptionally well-pronounced endemism, at least when applied to forms living below the epilimnion. CAPART has studied the bottom topography of the lake by echo sounding. He has found that the lake

comprises three different basins separated by sublimnic ridges. Across the northern ridge runs a sublimnic river valley shaped as a canyon connecting the northern and the middle basins. Across the southern ridge runs a V-shaped river valley connecting the southern and the middle basins. The existence and the shape of the valleys show that the water-level was about 500 m lower than now when the valleys were formed. Such extensive fluctuations of the level of Tanganyika correspond well with other geological data. They show that the various basins of Tanganyika must previously have been separate lakes connected only by rivers. Furthermore, the fluctuations of the water-level have probably been repeated. Most probably these temporary isolations of the basins were of very great importance for the evolution of the Tanganyikan fauna. Of course, the isolation between the basins, or the lakes at that time, cannot have been complete for shore-living aquatic animals. The "thalassoid" gastropods of Tanganyika, however, do not live in the very shore region but in deeper water. This is shown in a table given by DARTEVELLE and SCHWETZ (1948) and is confirmed by Dr CAPART, member of the Belgian exploration of Tanganyika 1946–1947 (personal communication).

The fact that the endemism in the Tanganyika fauna surpasses that of the few other geologically old lakes, for instance Lake Baical, may possibly to some degree be due to the geographical situation of the lake. Its situation in the tropical region with a comparatively even and warm temperature climate may have allowed a more rapid sequence of generations which may have favoured the evolution.

We have now arrived at the answer to our first question, why such a far-going evolution has taken place in Tanganyika. The evolution of the endemical fauna of Tanganyika seems to be due to the great age of the lake — it is at least five to ten million years old — and to the hydrographical history of the lake. The fluctuations of the water-level caused temporary (temporary in a geological sense) isolations of populations. And an isolating agency is of vital importance for the formation of species.

The second question, why have the "thalassoid" gastropods of Tanganyika adopted marine shell types, has previously been explained mainly in two different ways. Some authors believe the fauna to be a marine relic fauna, others suppose the shell features to have been influenced by the comparatively high salinity of the lake. Of course, the high salinity about 4 ‰ with magnesium compounds predominating and perhaps increasing to 18 ‰ during the low-level stages (Dr CAPART; personal communication) may influence the selection value of the genes and thus contribute to the directing of the evolution. I suppose, however, that two other viewpoints are of greater importance in this connection.

As shown above the evolution in fresh water in general is reduced. Consequently the bulk of fresh-water gastropods, particularly the Basommatophora, have a somewhat monotonous appearance. Among the Tanganyika gastropods, however, the evolution has proceeded without restraint, and the Tanganyika gastropods have had the possibility to evolve shell forms which are well fitted to aquatic life and which have also been able to evolve among marine gastropods. In addition, the marine gastropods show an enormous polymorphism, and it seems possible that most shell types which are well fitted to aquatic life and which are natural from a purely constructive point of view, and are in accordance with the startingpoint of their evolution, have already evolved. Therefore, an unrestricted evolution of a fresh-water gastropod fauna can hardly avoid parallelism or even convergency with marine shell forms.

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