BIOGEOGRAPHICAL RELATIONSHIPS OF THE ORIENTAL AND ETHIOPIAN MAYFLIES

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Faunal interchanges of *Ephemeroptera* between the Ethiopian realm (Africa and Madagascar) and the Oriental realm generally have been assumed to be primarily through Asia Minor, largely from Oriental to Ethiopian and much less frequently from Ethiopian to Oriental. It appears, however, that several families of *Ephemeroptera* have had their primary evolutionary development on the Gondwanaland supercontinent. Subsequently these southern groups have dispersed to the temperate areas of the northern Hemisphere. In the western hemisphere, at least, when these are tropical groups invading temperate regions they have not become truly adapted to temperate conditions, but the eggs hatch only at "tropical" or "subtropical" temperatures of midsummer, emerging in late August or September. Probably the same invasion mode is common in the Old World.

Gondwanaland forms that have entered the Nearctic from South America are mostly, if not all, congeneric with their South American ancestors. This is consistent with the drift of South America so as to arrive near North America rather late in geological time, South America contacting and forming a land bridge to North America only 5.7 million years ago.

Africa has had various contacts and near contacts with Europe, Asia and the Oriental Region, at various times and with varying climates, therefore, the invasion and exchange pattern is complex. Thus we see various levels of evolutionary divergence between the Ethiopian realm forms and their Holarctic or Oriental relatives. An important transport of *Ephemeroptera* of Gondwanaland origin, especially to the Oriental realm was the detachment of Madagascar and India from Africa at least 100 million years ago and the later splitting off of the Indian plate and its subsequent collision with Asia about 45 million years ago. The leading edge of the Indian plate probably started to form mountains early in its movement. Thus the Indian plate could readily have served to deliver a variety of plants and animals, including *Ephemeroptera*, to Asia where subsequently they could have spread to Southeast Asia and Asia Minor (and possibly to Europe or North Africa). With subsequent changes in climate much of the area would have become uninhabitable for these austral groups. The best habitats for such groups would now be in Ceylon and the highlands of southwestern India and in Southeast Asia, while isolated populations might occur in Asia Minor or North Africa and some might have spread to Europe. There seems to be no biological reason to assume that Borneo or any other part of Southeast Asia was part of Gondwanaland.

The confidence that one can apply in reconstructing the history of groups spreading to Asia from Gondwanaland is highly variable and is greatly handicapped by an inadequate kn owledge of the real total distribution and details of relationships of the mayflies involved. As yet the mayflies do not provide phylogenetic sequences of Africa — Madagascar — India distribution to dete rmine whether

or not India and Madagascar remained together after separating from Africa. However, the evidence suggests that this was the case.

The genus *Prosopistoma* (the sole representative of the family *Prosopistomatidae*) appears to have originally had a Gondwanaland distribution in Africa and Madagascar and India. At present there are several species in Africa, one in Madagascar, and another on Comores Archipelago, one in Europe and a series of closely related species stretching from Ceylon east to the Philippine Islands and New Guinea. A careful analysis of the evolutionary pattern of the species relationships is essential to clarify the details, but it appears that India carried the genus *Prosopistoma* to Asia.

It is probable that the family *Oligoneuriidae* evolved in Gondwanaland. *Lachlania* and *Homoeoneuria* are geologically recent immigrants into North America. *Oligoneuriella* apparently entered Eurasia from Africa (probably not via India). The European *Oligoneurisca* is a sister-group of *Homoeoneuria* (distributed from Brazil to central North America). One must presume that *Oligoneurisca* is either undiscovered or extinct in Africa to maintain the hypothesis that *Oligoneurisca* came from Gondwanaland. If the *Oligoneuriidae* evolved primarily in Gondwanaland, then how can one explain the distribution of *Chromarcys* in China and Sumatra? *Chromarcys* has the most generalized adult characters of the *Oligoneuriidae* and in the larvae gill one is in the primitive dorsal position. *Elassoneuria* is also primitive in that the behaviour and general appearance of the larvae are similar to those of *Isonychia*. *Chromarcys* occurs also in Ceylon and Thailand. I hypothesize that the *Oligoneuriidae* occupied primarily tropical South America and Africa and Madagascar and India with the more primitive genera on the eastern edge. Thus *Chromarcys* probably was carried to the Asian continent as suggested by its present occurrence in Ceylon.

The *Tricorythidae* also appear to have evolved primarily in Gondwanaland. All of the subfamilies occur in Africa. The genus *Tricorythus* (sensu lato, including *Neurocaenis*) is found in Madagascar, Ceylon, and Southeast Asia. The distribution pattern is consistent with the transport of the genus by the drift of India to Asia.

The *Euthyplociidae* also seems to have had their major evolution in Gondwanaland with genera in South America (now extending to Central America and Mexico), Africa and Madagascar. The only genus outside the Gondwanaland remnants is *Polyplocia* known from Burma to Borneo. This genus was probably transported to Asia via India, but it is not known to occur now in Ceylon or India. The family relationships have not been studied in detail.

The distribution of the *Palingeniidae* is rather unusual in that the nearest ancestor-like relative of the *Palingeniidae*, *Pentagenia*, is in North America. *Cheirogenesia*, whose larvae I collected in Madagascar appears to be one of the most primitive forms presently assigned to the family. The larvae of *Anagenesia robusta* with similar development of the mandibles occurs in India (GRAVELY, 1920). It is not possible to suggest the distributional history of the *Palingeniidae* from the present knowledge, *Cheirogenesia* and *Anagenesia* are closely related.

From the known distribution of the *Heptageniidae*, it seems most probable that the family evolved in Laurentia and dispersed in the geologically more recent time to Africa. However, Madagascar, which has been separated from Africa for a long period of time, has two genera of *Heptageniidae*. *Thalerosphyrus* is widespread and relatively abundant. This genus could have spread via India to southeast Asia and Asia Minor. It is not reported from Africa. *Compsoneuriella* is found widespread in Africa, in some areas of Madagascar, in Ceylon and Southeast Asia. The geographic history of *Afronurus*, *Thalerosphyrus* and *Compsoneuriella* is very uncertain but it is possible that *Thalerosphyrus* and *Compsoneuriella* owe their presence in Asia to transport by the drift of India.

The *Leptophlebiidae* are in great need of study in the area. In India and Ceylon the genus *Kimminsula* and undescribed related genera are reported (PETERS and EDMUNDS, 1970). In Madagascar there are several genera closely related to the *Kimminsula* complex and unknown elsewhere. The genus *Choroterpides* of India or a very close relative is found also in Madagascar. *Choroterpes* and *Thraulus* are common to Africa, Madagascar, India and Asia but their presence on some islands near Madagascar is suggestive that drifting India may have played a significant role. Species studies here will be critical to proper evaluation.

It is my opinion that the *Baetidae* had their principal evolutionary development in Gondwanaland

with South America as the prime center of evolution, and Africa as a secondary evolutionary center. The fauna of *Baetidae* in Africa, Madagascar, India and Southeast Asia is diverse. There are suggestions from baetid specimens that I have examined, but not carefully studied, of transport from Gondwanaland to Asia via drifting India. The baetids, however are such reduced and simplified forms as adults, and frequently so conservative as large that any evaluation of their biogeographic history in the areas being considered is premature.

Obviously a number of groups of *Ephemeroptera* have moved from the Oriental region to the Ethiopian realm. Almost certainly the *Caenidae* have spread from the Oriental realm to much of the world. Some *Leptophlebiidae*, many *Baetidae*, certain *Ephemeridae* (e.g., *Ephemera*, subgenus *Ephemera* and subgenus *Dicrephemera*), and *Ephoron* have probably dispersed from the Oriental to the Ethiopian.

The main purpose of the present paper is to point out the significance of drifting India to the Oriental fauna and the subsequent spread to other parts of Eurasia. The high concentration of eastern Gondwanian elements surviving in the Oriental realm almost certainly results from the fact that there is a large area of suitable climate in the Oriental region (while many other areas are unsuitable either because of the dry seasons or of cool periods). It is also recognized that the Oriental region serves as a refugium for the subtropical Laurasian fauna and flora that was more widespread during most of the Tertiary period.

A meaningful analysis of the biogeography of Oriental-Ethiopian interchanges at the present time is severely handicapped by gross inadequacies in knowledge of present distribution. In fact, the current, inadequate analysis, is based in large part on unpublished data from my collections in Madagascar, collections by W. L. and J. G. PETERS in India and from largely unstudied collections from Ceylon by a cooperative project with the U. S. Smithsonian Institution. Ecological and life history studies have also been neglected in the region, but are essential to meaningful biogeography.

SUMMARY

Biogeographical relationships of the Oriental and Ethiopian mayflies

Faunal interchanges between the Ethiopian Realm (Africa and Madagascar) and the Oriental Realm have generally been assumed to have been via the Middle East. The drift of the Indian plate from Madagascar must have carried with it a substantial fauna of *Ephemeroptera*. Such faunal elements would have subsequently spread from the Indian plate area, and Southeast Asia is the area where this fauna most likely survived. Among the groups that are most likely to have entered the Oriental Realm by this means is *Prosopistoma*, a palingeniid related to *Cheirogenesia*, *Povilla*, *Tricorythus* (including *Neurocaenis*), *Chromarcys*, probably *Compsoneuriella* (=*Notonurus*), *Thalerosphyrus*, and several genera of *Leptophlebiidae*.

Groups such as the *Caenidae*, *Ephemerellidae* (*Teloganodinae*), most *Baetidae*, some *Leptophlebiidae* and *Ephemera* (*Dicrephemera*) apparently used the route through the Middle East. The most convincing examples of dispersal through the drift of India are the cases where lineages are found in Madagascar, Ceylon and/or South India and Southeast Asia, but not Africa. Lineages in Africa and the Oriental Realm that are absent in Madagascar probably dispersed through the Middle East. Incomplete knowledge of the mayflies of the area makes the interpretation of a complicated problem difficult.

REFERENCES

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