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Importance of Polydesmidean Millipedes for the Reconstruction of the Palaeogeographic Evolution of Eastern Gondwanaland in the Permo-Triassic

by

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Abstract: The position of Indochina, the Malayan peninsula and the Indonesian archipelago during the Mesozoic has been debated. Their grouping with Gondwana, rather than with Laurasia is more consistent with the historical biogeography of Polydesmida as well as with distributional data from other millipedes. An area cladogram for the families inside the suborder Polydesmidea has been worked out, and distributional data from the different families are discussed. A divide informational analysis based on the distribution of the families inside the order Polydesmida gave the same conclusion as the area cladogram.

1. Introduction:

Palaeomagnetic and many palaeogeographical papers have demonstrated that the World total land mass was made up of two gigantic continents in the Mesozoic period, viz. Laurasia and Gondwana. Laurasia encompassed what was eventually to be North America and Eurasia. Gondwana in the course of time split into Antarctica, Australia, South America, Africa and India. Central and southern New Guinea is part of the same continent as Australia, and northern New Guinea was accreted during the Cenozoic. As regards Indochina, the Malayan peninsula and the Indonesian archipelago, most scholars have been of the opinion that they were parts of Laurasia during the late Palaeozoic and Mesozoic. In this article I will try to show that their grouping with Gondwana is more consistent with some key biogeographical facts as we know them. Palaeogeographic and other data indicate that Australia and New Guinea were located in the southern latitudes during the Mesozoic, when south Australia was still attached to Antarctica. During most of the Mesozoic (pre-late Cretaceous) the position of the Indo-Malayan zone is uncertain.

It is generally believed that the faunal interchange between the different Sunda islands took place across land-bridges in the Pleistocene period. At the same time, there were extensive areas of contact between Australia and New Guinea. New Guinea contains Australian faunal elements and a large number of Oriental species. It is believed that these oriental species reached New Guinea in a strong wave of migration which took place during the Quaternary period. The birds and mammals of New Guinea have close counterparts in the Australian fauna. On account of this, most authors group New Guinea and Australia together in the same biogeographic realm (Notogaea). On the other hand, GRESSITT (1961) found that, in contrast to the extensive Notogaeian vertebrate fauna, New Guinean insects are closely related to their oriental equivalents. GRESSITT therefore considered New Guinea an Oriental subregion. This raises a number of interesting biogeographic and related migratoric problems.

2. Method:

Figure 1 shows a biogeographic division of the geographical areas under consideration (eastern parts of Gondwanaland) in terms of the diplopod families in the order Polydesmida (mainly based on HOFFMAN 1980). The method used is the divisive information analysis employed by KIKKAWA & PEARSE (1969) to divide Australia into biogeographic subareas:

$$I = s \log n - \sum \{a_j \cdot \log a_j + (n - a_j) \cdot \log(n - a_j)\}$$

where s is the total number of families, n the number of places (lands/areas) where they occur and a_j the number of places containing the j th family. The families are analyzed for monophyly to ensure that only natural and real groups will be considered.

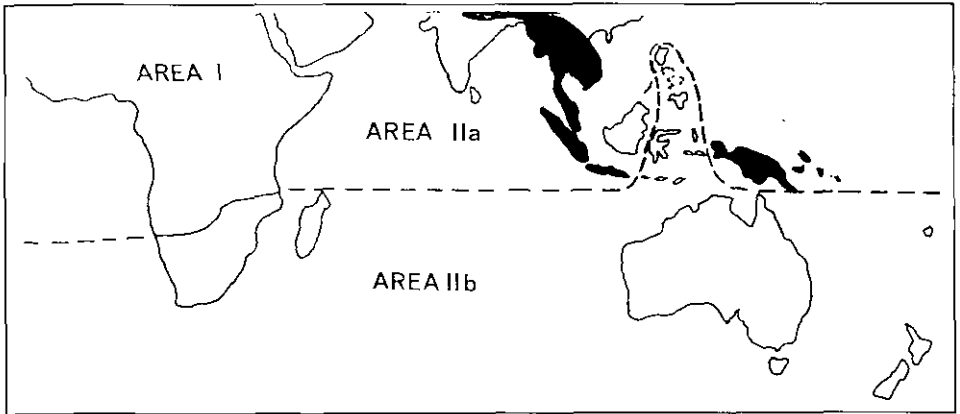


Fig. 1: Biogeographical classification of eastern Gondwanaland based on a divisive information analysis (see text) of Polydesmidan families.

I is low if the n area family lists resemble each other, and high if they differ. The areas are divided into two classes for each family: $A+$ contains all the areas where family A occurs, and $A-$ all the areas from which family A is absent. Area diversities $IA+$ and $IA-$ are calculated, for these classes treated separately. The diversity drop IA (the loss of information content) is: $IA = I - (IA+ + IA-)$. I is calculated for all families. One can see which dichotomy yields the largest diversity drop, and this fixes the first division to be made in classifying the data. Next, each class itself is divided by a repetition of the method, and so on.

3. Results:

The result shows that the largest diversity drop score occurs between tropical Africa (area I) and the remainder of the area (area II). A further division partitions area II into a southern region (IIb) consisting of Australia, South Africa, New Zealand, New Caledonia, Madagascar, Celebes and the Philippines, and a northern region (IIa). From Indonesia the line dividing the regions runs along the Wallace line to enclose the Philippines (apart from Palawan) in the southern region and New Guinea in Orientalis. A further subdivision of the Oriental realm shows Nepal, Bhutan, Indochina, Sumatra, Java and New Guinea to make up a homogeneous subarea of IIa (black area).

The grouping of New Guinea with Orientalis rather than Australia is strengthened by the distribution of the various diplopod families; Doratodesmidae (Malaya, Japan, Indochina, Java, Sumatra, New Guinea); Pyrgodesmidae (South America, West Africa, India, China, Indochina, Loyalty Islands, Java, New Guinea); the Cryptodesmidae subfamily Otodesminae (Borneo, Burma, Assam, Japan, Southeast Asia, Sumatra, Indochina, Sri Lanka, China, New Guinea); the Paradoxosomatidea tribe Eustrongylosomatini (New Guinea, Micronesia, Mindanao, Solomon Islands)

and the Platyrhacidae tribe Psaphodesmini (Halmahera, Moluccas, New Britain, Solomon Islands, Celebes, New Guinea). The presence of 21 known endemic diplopod genera on New Guinea (a level of endemism of about 80 %) indicates a fauna older than the presumed age of contact between Indonesia and New Guinea (about 15 my.). In light of this, the hypothesis that the diplopods spread from Orientalis to New Guinea during the Quaternary period, and only subsequently diverged to such a high number of species and genera, seems quite inconvincing.

JEEKEL (1985) carried out an analysis of the families in the diplopod superorder Diplocheta. He suggested a sister-group relation between Cambalopsidae, which is endemic to Southeast Asia (Southern India, India, Sri Lanka, Burma, Malaya, Java, Southern China, Indochina, Borneo, Sumatra) and all the rest of the families of the superorder. This sister-group to Cambalopsidae has a world-wide distribution. Contrary to the prevailing opinion among geologists, JEEKEL concluded that the evidence of diplopod distribution entails a close link between India, Farther India and the Sunda area prior to the collision of India and Central Asia.

This view is corroborated by the phylogeny of the superfamily Polydesmoidea (Fig. 2) (SIMONSEN, in press). Opisotretidae, which is found in Nepal, Bhutan, Indochina, Java, Sumatra, Ryu-kyu Islands and New Guinea turns out to be the sister-group of a family group with a world-wide distribution. The only plausible interpretation of this pattern is that the distribution area of Opisotretidae must have been isolated from the rest of Pangaea in the later Perm and early Triassic period. The occurrence of Opisotretidae in New Guinea suggests a link between New Guinea and the rest of the distribution area during the same period (i.e. Southeastern Asia and Indonesia must have been adjacent to New Guinea and Australia on Gondwanaland in the later Perm or early Triassic period).

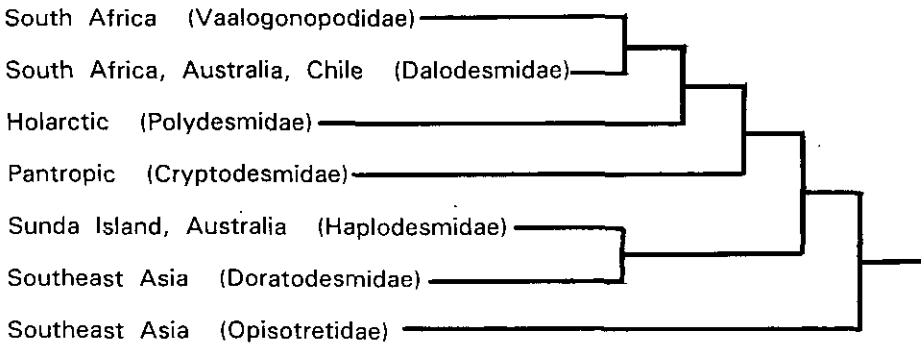


Fig. 2: Area cladogram for the families inside the suborder Polydesmoidea (Polydesmida, Diplopoda), from SIMONSEN (1990)

As indicated by the phylogenetic diagram (area cladogram, Fig. 2), Haplodesmidae and Doratodesmidae seem to be sister-families. Their distribution (Fig. 3) exhibits a vicariance pattern in Southeast Asia and Australia. Haplodesmidae is found in Sumatra, Java, the Philippines, Australia and Tasmania whereas the sister-family is endemic to Japan, Indochina, Malaya, Sumatra, Western Java and New Guinea. Since the general features of modern biotic distribution are determined by the subdivision of ancestral biotas in response to a changing geography (CROIZAT, NELSON & ROSEN 1974), and the splitting of populations, that is a prerequisite for evolutionary divergence, results from the fragmentation of landmasses and the rafting apart of their biotas, this distributional pattern can hardly be explained in any other way than by postulating a configuration of adjacent subareas in the Permian and Triassic periods.

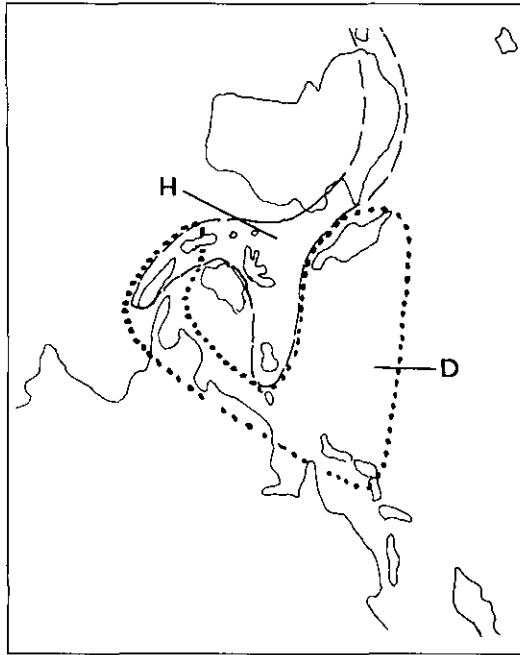


Fig. 3: Distribution of the sister-families Haplodesmidae (H) and Doratodesmidae (D).

Another cogent piece of evidence linking the origin of parts of Orientalis to Gondwanaland is the distribution of Cryptodesmidae (Polydesmida) (Fig. 4). This pantropical family is divided (HOFFMAN 1973) into four subfamilies: Cryptodesminae KARSCH, 1881 in South and Central America; Pterodesminae COOK, 1895 in tropical Africa and in Malaya, Java, Sumatra and Palawan; Thelydesminae COOK, 1896 in Cameroon, Liberia and Zaire and Otodesminae COOK, 1896 with representatives in Orientalis (Borneo, Burma, Japan, Southeast Asia, Sumatra, Indochina, Sri Lanka, China, New Guinea). The most significant point, however, is the distribution pattern within Pterodesminae. There are three distinct tribes. Two of them are endemic to Africa, whereas the third, Ophrydesmini HOFFMAN, 1973, which contains about eight species, is found exclusively in Malaya, Java, Sumatra and Palawan. This pattern links the Sunda area directly to Africa.

The phylogeny and biogeography of polydesmoid diplopods dovetails well with AUDLEY-CHARLES' (1983) reconstruction of eastern Gondwanaland (Fig. 5). AUDLEY-CHARLES hypothesized the existence of continental fragments that split off from northern Australia – New Guinea during the Jurassic period and that later came to form south Tibet – Burma – Thailand – Malaya and Sumatra. His claims rested on similarities in stratigraphy and what he regarded as key invertebrate fossil faunas, as well as the identification of a major suite of calc-alkaline and acid volcanic and granite intrusions of mid-late Triassic age that united eastern Australia, Central New Guinea, Sumatra, Borneo, Malaya, Thailand, Burma and South Tibet in an active continental margin from the late Permian to the late Triassic.

The dichotomy between Nepal, Bhutan, Java, Sumatra, Indochina and New Guinea on the one hand and the rest of Orientalis on the other, resulting from the divisive information analysis appears to be in broad agreement with palaeogeographical reconstruction put forward by AUDLEY-CHARLES.

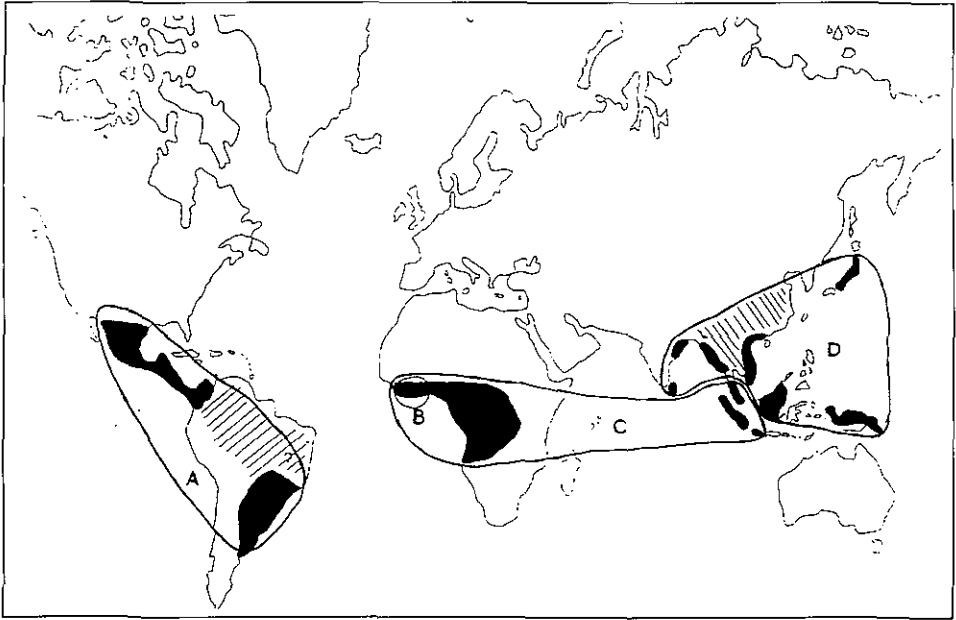


Fig. 4: Distribution of the family Cryptodesmidae. A Subfamily Cryptodesminae, B Subfamily Thelydesminae, C Subfamily Pterodesminae, D Subfamily Otodesminae.



Fig. 5: AUDLEY-CHARLES' qualitative reconstruction of eastern Gondwanaland during late Triassic (220 myr.) with the distribution of the family Opisotretidae (Polydesmida, Diplopoda), from AUDLEY-CHARLES (1983). I Indochina, J Java, B Borneo, NG New Guinea.

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