Platyhelminths as paleogeographical indicators

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Abstract

Turbellarians do not feature as examples in the present discussions on the theory and method of analytical biogeography. It is argued, however, that turbellarian distributional records form good examples of large-scale biogeographic patterns resulting from continental breakup. Some turbellarian taxa also indicate biogeographic links across the Pacific Ocean, which can be visualized readily by means of track construction. Amphi-pacific organismal distributions form the ingredients of trans-Pacific biogeographic tracks. Such tracks may be explained historically either as the result of dispersal or of vicariance. In the case of the flatworm examples, as well as many other organisms, dispersal explanations are the least satisfactory. However, under a vicariance paradigm the classical pre-drift reconstruction of Pangea cannot adequately explain trans-Pacific tracks. Therefore, alternative paleogeographic models may be invoked as explanatory hypotheses: the lost continent Pacifica, island integration, a new reconstruction of eastern Gondwanaland, an expanding earth. None of these alternative models is fully compatible with all geological and biogeographic data available at present. It is stressed that biogeographic data and theories should not be made subservient to geological theories. Biogeographical data on flatworms may indicate paleogeographical relations which are worthy of examination by geologists.

Introduction

Currently, the theory and practice of analytical biogeography form the subjects of an ongoing debate in the discipline of systematic biology (Myers & Giller, 1988; Brooks & McLennan, 1991; Humphries, 1992). The number of practical examples analysed in many of these theoretical papers revolves around a limited number of recurring cases, e.g. Rosen's poecilid fishes, Brundin's midges, Nothofagus (see Humphries & Parenti, 1986; Humphries, 1992). It is evident that present biogeographic theory owes much to detailed analyses of these taxa, particularly those with world-wide distributional patterns reflecting the sequence of continental breakup. Therefore, it is surprising that biogeographic patterns in such an old group as flatworms hardly ever have been used in methodological studies in analytical biogeography, either as clear examples or as interesting problematic cases. An exception is the parasitic helminths studied by Brooks (see Brooks & McLennan, 1991 and references therein), which formed the starting point for a method in historical biogeography and coevolutionary studies now known as Brooks Parsimony Analysis (Brooks, 1990). Turbellarians, however, do not feature in recent discussions on the theory and method of biogeography.

In this paper I want to draw attention to the fact (1) that turbellarians exhibit large-scale biogeographic patterns reflecting continental breakup, and (2) that some turbellarian distributional patterns require alternative vicariance explanations and suggest paleogeographic connections between areas which, according to conventional theory, never have been in proximity.

Method

At present there is no single biogeographic method all workers agree upon, but a consensus is emerging that a phylogenetic analysis of taxa and a subsequent cladistic biogeographic study form the basic ingredients for analysing and comparing biotic patterns in space and time (see Humphries, 1992 and references therein). The extent to which these two requirements are met in certain cases depends on the state of systematic knowledge of particular taxa and on the specific questions asked. It is the author's opinion that in less than ideal cases considerable insight still can be gained by applying a more 'generalized technique' (Humphries, 1992) than cladistic biogeography, i.e. track analysis. Individual tracks are drawn between sister taxa or concern an entire monophyletic group when relationships within that group have not yet been analysed. Coincident individual tracks make up a generalized track, assumed to link areas that once constituted a single ancestral biota. In one of the following sections I shall deploy track analysis in order to visualize some interesting and important biogeographic patterns in turbellarians.

Previous studies featuring planarians

In the past a number of workers have used planarians as examples of large-scale biotic relations that may have resulted from altered continental configurations.

Harrison (1928) used land planarians as one of his animal examples showing the former connections between South America, Australia, and New Zealand by way of Antarctica. According to Harrison, Wegener's hypothesis is capable of elucidating the biogeography of a large number of disparate taxa. Harrison also discussed biotic distributions that do not fit the Wegener hypothesis. In particular, he pointed to endemic distributions on Pacific islands, which he explained by postulating a 'Polynesian arc', running from Antarctica to Hawaii via Tonga and Samoa.

To the best of my knowledge, the first planarian systematist putting triclad biogeography into the perspective of continental drift was Marcus when he wrote that 'Wegener's theory or hypothesis of Continental Drift cannot be proved by the hitherto known distribution of the Terricola, but the recent maps of their distribution become more intelligible with this theory' (Marcus, 1953: 53). In similar vein, Ball & Fernando (1969) and Ball (1975) concluded some years later that the distributional patterns of southern hemisphere dugesids are best explained by the vicariance process of continental drift.

Apart from the monographic study of the marine triclads (Sluys, 1989) there have been no other studies analyzing planarian biogeography from a plate tectonic perspective. Distributional patterns in selected turbellarian taxa

Three genera of land planarians

According to the taxonomic review of Ogren & Kawakatsu (1991) the terricolan genus Kontikia contains 22 species, of which a generalized distribution map is presented in Fig. 1 [it must be noted that the taxonomy of this genus has not yet stabilized - see Winsor (1991), Ogren et al. (1993)]. It is clear from Fig. 1 that the pattern is mainly Gondwanian, with only isolated records from Laurasia and that the track bypasses the African continent (the latter most likely due to a collecting artefact). Under the assumption that the animals are poor dispersers, such a disjunct distribution only can be explained adequately by assuming that the vicariant process of plate tectonics operated during the evolution of the genus Kontikia. As it happens, the assumption of poor dispersal capacity in triclads is the least supported for land planarians. All available evidence suggests that freshwater and marine triclads have poor dispersal capacities (Ball & Fernando, 1969; Sluys, 1989), but there is ample circumstantial evidence that the situation in land planarians can be different. For example, land planarians have been recorded from greenhouses and botanic gardens all over the world. To some extent, this is the case also in the genus Kontikia. K. ventrolineata (Dendy, 1892) has been found in botanic and private gardens in Victoria, Tasmania, and southeastern Queensland (Winsor, 1979); K. orana Froehlich, 1955 has been reported from urban gardens in Queensland (Winsor, 1986) while it was already known from man-modified areas in Brazil. Passive anthropochore dispersal is invoked to account for the occurrence of these two species in Australia (Winsor, 1979; 1986).

Other records have been explained also as the result of passive dispersal. Froehlich (1955; 1967) and De Beauchamp (1961) invoked dispersal to explain the distribution of *K. kenneli* (Von Graff, 1899) and *K. orana* in the new world and Jones (1981) speculated that the occurrence of *K. andersoni* Jones, 1981 in northern Ireland resulted from introduction of the animal in pots of soil. Specimens of *K. mexicana* (Hyman, 1939) in California were presumably introduced (Hyman, 1943). The occurrence of *K. bulbosa* Sluys, 1983 on Madeira has been attributed to introduction by means of banana rhizomes (Marcus & Marcus, 1959; Sluys, 1983). A new record for *K. bulbosa* concerns the Canary Islands, where it was collected



Fig. 1. Generalized distribution and track of the land planarian genera Kontikia, Dolichoplana, and Rhynchodemus; records from greenhouses omitted.

from Las Palmas (collection Natural History Museum, London, BMNH 1965.3.16.1, Las Palmas, August 1962).

The number of *ad hoc* hypotheses postulated for the distributional records of the genus *Kontikia* obscures the fact that the major track conforms to a well founded generalized track across former parts of Gondwanaland, *viz*. South America, Africa, India, Australia, and New Zealand. Within the Terricola this track is exemplified also by the genera *Dolichoplana* and *Rhynchodemus* (Fig. 1).

Trans-Pacific tracks

For both *Kontikia* and *Rhynchodemus* species have been recorded from localities well within the Pacific basin, suggesting biogeographic links across the Pacific. On the basis of a cladistic analysis of the taxa involved, such trans-Pacific tracks have been demonstrated also for the marine triclads (Sluys, 1989). These trans-Pacific tracks have been demonstrated for many other groups of organisms (see Croizat, 1958; Sluys, 1989; Matile, 1990) and I am convinced that they hold true not only for the turbellarians mentioned above but also for many other taxa. However, other studies suggesting trans-Pacific tracks in turbellarians appear to be scarce. At present, I know only of Tajika's (1991) study of the polyclad genus *Discoplana*. *D. pacificola* (Plehn, 1896) from the East Pacific is the sister species of *D. gigas* (Schmarda, 1859), which is broadly distributed in the Indo-West Pacific region; the sister group relationship between these two species evidently suggests a trans-Pacific track within the genus *Discoplana*.

Vicariance explanations and alternative paleogeographic models

Because of the biology of some turbellarians, workers may choose dispersal hypotheses for explaining particular distributional records. Such has been the case for the genus *Kontikia* (see above). In similar vein one could try to explain the trans-Pacific sister group relationship between the polyclads *D. pacificola* and *D. gigas* as a result of allopatric speciation after dispersal of larvae. However, the larvae of *Discocelis* are of the direct type, which generally is found only among

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inshore plankton (Prudhoe, 1985). In this paper I wish to de-emphasize such quantum-dispersal explanations and to examine turbellarian distribution from the perspective of vicariance. Under a vicariance paradigm, the usual breakup sequence of Pangea can explain adequately trans-Atlantic, trans-Indian Ocean, and trans-Antarctic biogeographic tracks in turbellarians and other organisms. However, trans-Pacific tracks pose a problem because according to conventional theory the Pacific Ocean always has been present since Pangean times, its precursor being the EoPacific or Panthalassa. This has induced several workers to search for and propose alternative paleogeographical models that are more in agreement with the biogeography of the Pacific basin (for a review, see Sluys, 1994).

The most controversial alternative model concerns the theory of an expanding earth, proposing that the earth has increased in size over the ages. In the present context, the fascinating consequence of Shields' (1979) reconstruction of the supercontinent Pangea on a smaller earth at Jurassic times is that it obliterates the EoPacific. As a consequence, Shields' hypothesis shows a perfect fit between trans-Pacific tracks and breakup of the supercontinent. But this fit may in part be due to the fact that Shields' reconstruction is based on geological, paleontological, as well as biogeographic information. Other continental assemblies on a smaller earth are different (Owen, 1983) and can explain only biogeographic tracks in the Indo-West Pacific.

This alternative model involving an expanding earth, as well as others (e.g. lost continent Pacifica, new reconstruction of eastern Gondwanaland, island integration; see Sluys, 1994) are still debated among geologists. Therefore, I suggest that in our explanations of the historical biogeography of the Platyhelminthes we do not feel constrained by any geological model, either conventional or alternative. We should let the biogeographic data speak for themselves; the still developing methods of the discipline of historical biogeography shall enable us to compare biogeographic generalizations with paleogeographic hypotheses and look for mutual consistency. In this way, biogeographers may point to possible paleogeographic connections not taken into consideration by geologists and thus stimulate particular lines of geological research. It is highly likely that an evolutionarily old group as flatworms still indicate in their present-day distributional record geographic situations of old.

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