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## A CONTRIBUTION TO THE ZOOGEOGRAPHY OF NEOTROPICAL LAND PLANARIANS

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### RESUMO

#### Uma contribuição á zoogeografia das Planarias neotropicais da terra

Das três famílias de planárias terrestres, apenas os Bipaliidae não têm formas endêmicas na Região Neotropical, sendo representados pela espécie cosmopolita *Bipalium kewense*. Os Rhynchodemidae representam senessa Região por suas duas sub-famílias, Microplaninae e Rhynchodeminae, ambas provavelmente antigas na Região, havendo, contudo, possibilidade de alguma invasão pós-pleiocênica. O gênero *Dolichoplana* é introduzido.

A família dominante é a dos Geoplanidae, representada em sua grande maioria por formas com testículos dorsais, restritas à Região. Devem ter-se originado a partir de formas com testículos ventrais, semelhantes a *Coenoplana*, gênero essencialmente da Região Australiana. Algumas espécies do Chile assemelham-se a *Artioposthia*, também desta Região. No Chile ocorre uma espécie primitiva, relíquia talvez do tronco original. As semelhanças referidas reforçam a idéia de antiga conexão entre a América do Sul e a Região Australiana, provavelmente através da Antártida. Os Geoplanidae neotropicais pertencem, em sua grande maioria, ao gênero *Geoplana*, que apresenta alguns grupos de espécies largamente espalhados e outros restritos a áreas menores. Mostra, ainda, indícios de que se encontra num processo ativo de especiação. Os outros gêneros, nenhum deles de larga distribuição, não diferem muito de *Geoplana* e parecem ter-se diferenciado a partir dêste em época relativamente recente.

The systematics of land planarians has not yet attained a satisfactory stage, even at the family level (cf. Beauchamp, 1961, p. 117). On the other hand, the land planarian fauna of large areas, some of them very important zoogeographically, are known fragmentarily, if at all. These reasons preclude a thorough analysis of the origin and distribution of the Terricola. In the present paper some general remarks on the distribu-

tion of the various groups of land planarians are presented, and a more extended discussion on the Neotropical ones.

Three families of land planarians are currently recognized, *Rhynchodemidae* (with two subfamilies, *Microplaninae* and *Rhynchodeminae*) *Geoplanidae*, and *Bipaliidae*. The *Bipaliidae* are characterized by the broadened head plate, narrow creeping sole, numerous eyes, and a rather uniform type of copulatory apparatus. The *Rhynchodemidae* and the *Geoplanidae* are distinguished on the basis of the number of eyes, two in the first and many in the second. However, in the many-eyed genus *Pelmatoplanea* there is great diversity as regards the structure of the copulatory apparatus, some of the types resembling closely those of different *Microplana* and Oriental *Othelosoma*, while others are more *Geoplanid*-like, and one (that of *P. glandulosa* Beauchamp) approaches the *Bipaliid* type. This indicates that a multiplication of eyes has occurred in several evolutive lines, and that the number of eyes is unreliable for distinguishing those two families. New family diagnoses, however, must wait for a thorough revision of the critical genus *Pelmatoplanea*, which, as it now stands, is heterogeneous.

Land planarians probably differentiated from an old trielad stock near to *Maricola* (Meixner, 1928). Considering their restricted means of dispersal and worldwide distribution, they must be an old group. Very likely they originated, as so many terrestrial groups, in the upper Paleozoic. The following are considered primitive characters in the *Terricola*: two eyes; small body size and narrow creeping sole, the epidermal cilia perhaps restricted to the latter; weak subepidermal muscles and strongly developed longitudinal parenchymal ones: nervous system in two longitudinal cords; cylindrical pharynx; testes ventral in position and, in each side, uniserial, connecting directly or through short efferent ductules with the simple efferent duct located at the side of or above the nerve cord; penis with both bulb and papilla developed; and female copulatory apparatus comprising a bursa and a single female genital canal that opens into the male atrium near the gonopore. Small size, a nervous system in two cords, and perhaps a few other of the above characters related to size, may be secondarily reacquired. As regards the male efferent system, a very common development is the appearance of intermediate ducts which, in all forms with ventral testes, are located ventrally to the nerve cords (or plate). In this case, the ental part of the efferent ducts may also be found under the nerve cords.

The group that includes the most primitive land planarians are the *Microplaninae* and, particularly, the genus *Microplana*, in some species

of which (the *M. aberana*-group, cf. Marcus, 1953) all the primitive characters mentioned above are present. From *Microplana*-like ancestors arose the other genera of the *Microplaninae*, the *Rhynchodeminae*, and "*Pelmatoplanea*". The *Geoplanidae* arose from one of the evolutive lines of *Pelmatoplanea*, the *Bipaliidae* from another. A general zoogeographic discussion on land planarians and particularly on the *Microplaninae* is found in Marcus, 1953.

The *Microplaninae* occur in all zoogeographic regions, but are chiefly Arctogeic. They are represented in the Neotropical Region by the genera *Microplana*, *Diporodemus*, and *Incapora*. The distribution of *Microplana* is similar to that of the subfamily. This genus was divided by Marcus, 1. c., into three groups, the *M. aberana*-group, characterized by a simple, closed bursa; the *M. terrestris*-group, with genito-intestinal connection; and the transitory group (i. e., to the *Rhynchodeminae*), with simple female copulatory organs. All three groups occur in the Neogea, the *M. aberana*-group represented by *M. costaricensis* (Beauchamp), from Costa Rica; the *M. terrestris*-group by *M. yaravi* du B.-R. Marcus, Peru, *M. cockerelli* (Graff), Jamaica, and *M. montoyai* (Fuhrmann), Colombia; and the transitory group by *M. haitiensis* (Prudhoe), Haiti. *Diporodemus*, with a separate bursal-cutaneous canal, has three neotropical species, *D. yucatani* Hyman, Mexico, *D. plenus* Hyman, Panama, and a new species we have from the Territorio do Amapá, North Brazil. *Diporodemus* extends further to North America (1 species) and Europe (2 species). *Incapora*, with intestino-cutaneous ducts at the level of the copulatory apparatus, is an endemic genus known only from Peru (*I. weyrauchi* du B.-R. Marcus). The present distribution of the *Microplaninae* in the Neotropical Region apparently indicates that they are remnants of an old fauna, although a more recent, post-Pliocene invasion from the north may also have occurred. Up to the present, no *Microplaninae* is known from Chile (*M. ruca* Marcus was misidentified).

The *Rhynchodeminae* are represented in the Neotropical Region by 15 nominal species of the widely distributed genus *Rhynchodemus* and by two species of *Dolichoplanea*, probably both synonyms of *D. striata* Moseley, a cosmopolitan species. The subfamily is chiefly Oriental and Australian. The genera *Platydemus* and *Cotyloplanea* are restricted to these Regions. *Digonopyla* is known only from Celebes. *Dolichoplanea* has a sole sure species, *D. striata* Moseley (= *D. feildeni* Graff), with a rather long list of synonyms; it is Oriental in origin. *Rhynchodemus* itself occurs in all zoogeographic regions, an indication that it is an old genus, existing already before the Tertiary. The systematics of this genus is

unsatisfactory due to similar external features in several species, to the simple, homogeneous female part of the copulatory apparatus, and to the great variations, from fully developed to almost absent, shown by the male part in different phases of sexual activity. Further study may prove some names to be synonyms and, perhaps, that some of the similar forms described from various parts of the world belong to a species widely distributed through human agency, as *Bipalium kewense* and *Dolichoplana striata*.

The *Bipaliidae*, comprising a sole genus, *Bipalium*, are essentially Oriental. Two thirds of the 150-odd species described belong to this Region. About 20 species occur in the Manchurian Subregion of the Palearctic Region, 14 of them in the Japanese Island, and 24 are Malagasy. *Bipalium kewense* is cosmopolitan. *B. adventitium* Hyman has been introduced into the United States of America. *B. costaricense* Hyman, from Costa Rica, is likely an introduced species too. In fact, the description of two specimen on which the species was based makes us suspect they could be faded specimens of *B. kewense*.

The *Geoplanidae* constitute the dominant family in the Neotropical Region, as well as in the Australian Region. The family is found also in the Oriental Region (with an invasion into the Manchurian Subregion of the Palearctic Region) and in the Malagasy Subregion. There are, besides, a few records elsewhere: *Pelmatoplana buettneri* Graff, from Togo; and *Kontikia* sp. Marcus (= *Geoplana mexicana* Hyman? Beauchamp) from Madeira (Beauchamp, 1957; Marcus & Marcus, 1959).

Within the Neotropical Region, no Geoplanid is known from the Antillean Subregion. The Mexican Subregion is, on the whole, poorly known as regards land planarians, but the known Geoplanid species belong to *Geoplana*. *G. mexicana* Hyman, introduced into Texas and California from Mexico, may be a *Kontikia*; if it is really a Mexican form, or introduced from somewhere else, remains obscure. Another species, *G. vaga* Hyman, introduced into California, merits its name regarding both origin and systematic position. The discussion that follows, therefore, refers essentially to the South American fauna.

Neotropical Geoplanids, with very few exceptions, have dorsal testes and male efferent system, even when a set of intermediate ducts is present, wholly dorsal to the nerve plate. These characters distinguish them from the other land planarians, which have ventral testes, and the intermediate efferent ducts, when present (sometimes also part of the efferent ducts proper: "vasa deferentia"), ventral to the nerve plate, or cords. The chief Neotropical genus is *Geoplana* (in the strict sense, as

redefined by Froehlich, 1955), with over 200 described species, widely spread within the Region but restricted to it. Although we can recognize some species groups within *Geoplana*, it is not possible, at present, to divide it into subgenera, because most groups pass gradually to others or show only minor differences between them.

Graff (1899: 293-294), in his large monograph, recognized, for *Geoplana*, seven groups, based fundamentally on external characters, which led to heterogeneity. Goetsch, 1933, grouped Chilean species into "Formenkreise", based also on external characters, which impairs their value. A tentative grouping of the Brazilian species, taking into account both external and internal characters, is presented by E. M. Froehlich, 1955, who listed six groups, plus a few more problematical ones. These groups are utilized, in part, in the following discussion. We have not attempted here to group all species. Some (e. g., *G. pseudorhynchodemus* and *G. bergi*) are isolated, and some are hard to place. We have chosen, however, to present the larger groups and those that show different patterns of distribution. Several species from Chile, kindly sent me by Prof. Dr. F. di Castri, Santiago de Chile, together with informations on the biotopes, are considered in the present discussion, although their descriptions have not been published.

A large group comprises the large, broad, and flat species (most of the "platte und breite, meist grosse Formen", group a) of Graff; Group B of E. M. Froehlich; and which may be called the *G. applanata*-group). They are always provided with a penis papilla, there is no separation between male and female atria, and the female canal comes from the dorsal side. Their distribution covers South America, the colder southern part excepted. In four Peruvian species, *G. chalona* du B.-R. Marcus, *G. cantuta* du B.-R. Marcus, *G. gabriellae* du B.-R. Marcus, and *G. quichua* du B.-R. Marcus, the penis papilla is short and tending to the vertical. Besides these four, the following species belong to the group (Brazilian species are indicated by State): *G. apeva* Froehlich, Santa Catarina; *G. applanata* Graff, Rio de Janeiro and Minas Gerais; *G. argus* Graff, Rio de Janeiro; *G. assu* Froehlich, Santa Catarina; *G. aymara* du B. R. Marcus, Peru; *G. bimbergi* Fuhrmann, Colombia; *G. braunsi* Graff, São Paulo; *G. bresslaui*, Riester (not Schirch), Rio de Janeiro; *G. burmeisteri* M. Schultze, Rio de Janeiro, Guanabara, São Paulo, Paraná, Santa Catarina; *G. carinata* Riester, Rio de Janeiro, São Paulo, Paraná; *G. carrierei* Graff, São Paulo, Rio Grande do Sul, Paraguay, Argentina; *G. catharina* Hyman, Santa Catarina; *G. chulpa* du B.-R. Marcus, Peru; *G. dictyonota* Riester, Rio de Janeiro; *G. fryi* Graff, Rio de Janeiro; *G.*

*divae* Marcus, São Paulo; *G. glieschi* Froehlich, Rio Grande do Sul; *G. itatiayana* Schirch, Rio de Janeiro, São Paulo; *G. ladislavii* Graff, Santa Catarina, Rio Grande do Sul; *G. lareta* du B.-R. Marcus, Peru; *G. marmorata* Fritz Müller, Santa Catarina, Argentina; *G. mayori* Fuhrmann, Colombia; *G. rufiventris* Fritz Müller, Santa Catarina; *G. tamboensis* Fuhrmann, Colombia; and three undescribed species from Chile.

Similar to the *G. applanata*-group, but with a very small penis papilla, or lacking it, is a group of Andean species from Peru and Colombia, the *G. amagensis*-group: *G. amagensis* Fuhrmann, Colombia; *G. becki* Fuhrmann, Colombia; ? *G. bogotensis*, Hyman, Peru; *G. bürgeri* Busson, Colombia; *G. bussoni* Froehlich, Colombia; *G. contamanensis* Hyman, Peru; and *G. ortizi* Fuhrmann, Colombia.

Also similar to the *G. applanata*-group, but with the female canal horizontal or coming from below, most of the species provided with glandular ridges on the penis papilla, some also with a dilated female atrium, is a group—the *G. gigantea*-group—that extends from Costa Rica to Peru and to Trinidad; *G. gigantea* Graff, Trinidad; and *G. chiriquii* Hyman, Panama, both without glandular ridges on the penis papilla, and the following species provided with these structures; *G. idaia* du B.-R. Marcus, Peru; *G. montana* Hyman, Costa Rica; *G. picadoi* Beauchamp, Costa Rica; *G. sandersoni* Prudhoe, Trinidad; *G. vungunteni* Fuhrmann, Colombia; and, perhaps, *G. cameliae* Fuhrmann, Colombia.

Another large group, the distribution of which is similar to that of the *G. applanata*-group, comprises the mostly medium-sized species with the body relatively less flat than in the latter one, always provided with a penis papilla, and with the female canal coming from the dorsal side. This is Group C of E. M. Froehlich, and we call it now the *G. taxiarcha*-group, which includes *G. alterfusca* Hyman, Panama; *G. beckeri* Froehlich, Bahia; *G. caucaensis* Fuhrmann, Colombia; *G. evelinae* Marcus, São Paulo; *G. ferussaci* Graff, Rio de Janeiro, São Paulo, Minas Gerais; *G. fuhrmanni* Hyman, Panama, Trinidad; *G. fusca* Hyman, Panama; *G. hina* Marcus, São Paulo; *G. joia* Froehlich, Panama; *G. livia* E. M. Froehlich, São Paulo; *G. multipunctata* Fuhrmann, Colombia; *G. pavani* Marcus, São Paulo; *G. pichuna* du B.-R. Marcus, Peru; *G. poca* Froehlich, São Paulo; *G. polyophthalma* Graff, Paraná, Santa Catarina; *G. pseudovaginuloides* Riester, Rio de Janeiro; *G. pulla* (Darwin), Uruguay; *G. regia* E. M. Froehlich, São Paulo; *G. riesteri* Froehlich, Rio de Janeiro; *G. schubarti* Froehlich, São Paulo; *G. shapra* du B.-R. Marcus, Peru; *G. tamoia* E. M. Froehlich, Rio de Janeiro; *G. taxiarcha* Marcus, São Paulo; *G. toriba* Froehlich, São Paulo; *G. trigueira* E. M. Froeh-

lich, Rio de Janeiro; *G. vicuna* du B.-R. Marcus, Peru; *G. yara* E. M. Froehlich, Rio de Janeiro; and an undescribed species from Chile. Some species that should be located in this group have the female atrium partly or wholly filled up by a cellular mass containing lacunae. They are *G. caapora* Froehlich, São Paulo; *G. chiuna* E. M. Froehlich, São Paulo; *G. crawfordi* Beauchamp, Peru; *G. crioula* E. M. Froehlich, São Paulo; *G. fragai* Froehlich, Rio de Janeiro; *G. gaucha* Froehlich, Rio Grande do Sul; *G. goetteri* Schirch, Rio de Janeiro; *G. incognita* Riester, Rio de Janeiro; *G. multicolor* Graff, Rio de Janeiro, São Paulo, Paraná; *G. phocaica* Marcus, São Paulo; *G. preta* Riester, Rio de Janeiro, São Paulo; *G. saima* du B.-R. Marcus, Peru; *G. suva* Froehlich, Santa Catarina; *G. vaginuloides*, Prudhoe (not Darwin), Trinidad. The same cellular mass, of unknown function, is found also in some species that clearly do not belong here, e.g., *G. goetschi* Riester, Rio de Janeiro, São Paulo; and *G. pinima* E. M. Froehlich, São Paulo.

Group E of E. M. Froehlich, which may be called the *G. barreirana*-group, is very homogeneous but small. The copulatory apparatus approaches that of the *G. taxiarcha*-group, but all species are small, rounded, and the colour pattern includes transverse bands on the back. The group is composed of *G. barreirana* Riester, *G. cassula* E. M. Froehlich, *G. zebroides* Riester, all from Rio de Janeiro, and probably *G. elegans* (Darwin), Guanabara.

Group F of E. M. Froehlich is characterized by an elongate body, absence of a penis papilla, folded male atrium, and female genital canal arriving from the ventral side. The group, which we call the *G. pasipha*-group, comprises the following species; *G. astraea* Marcus, São Paulo; *G. caeruleonigra* Riester, Rio de Janeiro; *G. cafusa* Froehlich, São Paulo; *G. chimbeva* E. M. Froehlich, São Paulo; *G. hauseri* Froehlich, Rio Grande do Sul; *G. oliverioi* Froehlich, Rio de Janeiro; *G. pasipha* Marcus, São Paulo; *G. penhans* Riester, Paraíba; *G. pinima* E. M. Froehlich, São Paulo; *G. plana* Schirch, Rio de Janeiro; *G. rosea* E. M. Froehlich, São Paulo; *G. splendida* Graff, Rio de Janeiro; *G. velutina* Riester, Minas Gerais, and a species from Chile, probably *G. chilensis* Graff. *G. aphalla* Hyman, Panama, should perhaps be included here.

A group of mostly South Brazilian species are medium-sized, elongate, and muscular. They lack a penis, the male atrium is large, with folded walls, and the female canal comes from the dorsal side. We call it the *G. abundans*-group, and it comprises *G. abundans* Graff, Rio Grande do Sul; *G. albonigra* Riester, Rio de Janeiro; *G. fita* Froehlich, Santa

Catharina; *G. marginata* auct. (not Fritz Müller), São Paulo, Paraná, Rio Grande do Sul, Paraguay; and *G. mülleri* Diesing, Santa Catarina.

Two species from Chile, *G. lata* Graff and *G. cruciata* Graff, have in common a small, short but broad body (preserved), a large male atrium but a very small penis papilla, and the female genital canal arriving from below.

The genera *Polycladus*, *Geobia*, *Choeradoplana*, *Issoca*, and *Xerapoa* are all closely related to *Geoplana*, *Polycladus* (monotypic: *P. gayi*) occurs in the forest zone of Chile. *Geobia* (monotypic: *G. subterranea*), *Issoca* (5 species), and *Xerapoa* (2 species) are known only from the southern half of Brazil, while *Choeradoplana* (6 species) extends also to Argentina.

Of greater zoogeographic interest are some undescribed Chilean species, which are to be put into two new genera. One of these, comprising four species, parallels the Notogeic genus *Artioposthia* in having adeno-caetyls associated with the copulatory apparatus. They have, however, dorsal testes. One of the species comes from the arid "Norte Chico", two from the savanna zone, and one from Nahuelbuta, in the forest zone. The other genus is represented by one species from Fray Jorge, Province of Coquimbo in the Norte Chico, in a relict hygrophilous cloud-forest (dominant plant species: *Aextoxicon punctatum*) surrounded by arid terrain. This species, beside some specialized characters as a broad creeping sole, a blunt cephalic end approaching that of *Bipalium*, and absence of a definite penis papilla, has ventral testes in a single row on each side, each testes opening directly into the corresponding efferent duct, what is a very primitive condition. It may be a relict of an old Geoplanid stock akin to Notogeic and Oriental forms, replaced in the Neotropical Region by those with dorsal testes.

Two other Geoplanid genera have been recorded from South America, viz., *Pelmatoplana* and *Kontikia*, but probably both were introduced. The first genus is represented by *P. graffi* Fuhrmann, from Colombia, collected apparently in cultivated land "under stones and old tiles". This species is capable of asexual reproduction by transverse splitting, a rare phenomenon among land planarians, but occurring in two other introduced species already referred to *Bipalium kewense* and *Dolichoplana striata*. These two species are also restricted to cultivated lands, other environments altered by human activity. This similarity makes us suspect strongly that *P. graffi* is not autoctonous. Considering the number of fruit-bearing or ornamental plants which have been introduced into the Americas from the Oriental Region, it is not surprising that with them

came land planarians some of which encountered a favourable new environment. The same holds true for *Kontikia*, represented by *K. kenneli* (Graff), from Trinidad, and *K. orana* Froehlich, from Brazil.

Concluding, we are of the opinion that the Geoplanids with dorsal testes have arisen in South America, to become there the dominant land planarians. The original stock was more closely related to the Notogeic forms, especially to *Coenoplana*, while a group of Chilean species parallels *Artioposthia*. These relations strengthen the idea of an old, pre-Tertiary Antarctic connection between South America, and Australia and New Zealand. As a matter of fact, such a connection is suggested too by the distribution of several other groups of invertebrates. A primitive species, with ventral testes, found in Chile, may be a relict of the original stock.

The great majority of Neotropical Geoplanids belong to *Geoplana*, within which, as we have indicated, several groups of species are recognizable. We believe the groups presented above to be mostly natural ones, but it is still hard to judge if similarity is not the result of convergence, in which case the group would really represent a morphological type. Some of the groups are widely spread, e.g., the *G. applanata* and *G. taxiarcha*-groups. Others, e.g., the *G. amagensis*, *G. gigantea*, *G. barreriana*, and *G. abundans*-groups occupy more restricted areas, pointing to local differentiation. Besides, each species of *Geoplana*, in the great majority of cases, occupies a small area, what indicates, considering the large number of species, that they are undergoing an active process of speciation. This is further supported by the climatic fluctuations known to have taken place in large areas of South America, the southern half of Brazil included, during the Pleistocene to Recent times.

The genera that have differentiated from *Geoplana* are still close to it. *Polycladus* differs by its great size and breadth; *Geobia*, by its adaptation to subterranean life; *Choeradoplana* and *Issoca* by the glandulo-muscular structures at the anterior end; and *Xerapoa* by the sensory pits located at the tip of small papillae. All these genera occupy relatively small areas, which, in their case, suggests they are young ones.

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