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Riser and Morse (Editors): Biology of the Turbellaria

Libbie H. Hyman Memorial Volume

# Biology of the Turbellaria

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## Biology of the Turbellaria

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- . 1966. Report on the Ecological Survey of Freshwater Planarians in the Teshio Mountains and Its Adjacent Seaboard District on the Sea of Japan. *Japan. J. Ecol.*, **16**:129–133. (In Japanese with English summary.)
- and H. Tanji. 1964. On the Distribution of Freshwater Planarians Found in the Ushubetsu and Antaroma River Systems in the Mts. Daisetsu District, Hokkaidô. *Rept. Taisetsuzan Inst. Sci. Hokkaidô Gakugei Univ. Asahigawa*, no. 3, 24–42. (In Japanese with English summary.)
- Young, J. O., and T. B. Reynoldson. 1965. A Laboratory Study of Predation on Lake-dwelling Triclad. *Hydrobiologia*, **26**:307–313.
- Zabusova-Zudanova, Z. I. 1956. Planarii Nyeryestilishch Lososyevuix ruib zapadnogo poberez'ya Kamchatki. *Tr. Obshch. Estestvoisp., Uchenye Zapiski Kazan Gosud. Univ.* V. I. Ul'ianova-Lenina, **116**(14):25–39. (In Russian.)
- . 1960. Planarii Daljinyego Vostoka. *Tr. Obshch. Estestvoisp.* 63, *Kazan Gosud. Univ.*, **120**(6):112–121. (In Russian.)
- . 1970. Rasselenie planarii po Cobetskemu soiuzu. *Boprosy Evoliutsionnoi Morforologii i Biotseologii*: 164–172. Izdatel'stvo Kazanskogo Univ., Kazan. (In Russian.)

## Chapter 15

# A Contribution to the Phylogeny and Biogeography of the Freshwater Triclad (Platyhelminthes: Turbellaria)

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Hitherto the supraspecific classification of the freshwater triclads has had little to say concerning the history of the group. The following paper, which concentrates on a single family, is intended partly to alleviate this situation. That biological classification consists of the assembling of organisms into groups that are similar as a result of their common descent (Mayr, 1969, p. 121) would be denied by few, if any, taxonomists. Common descent, however, is not enough. It follows from the theory of evolution that all organisms are phylogenetically related; it is the degree of this relationship, the recency of common ancestry, which is important. The diversity that taxonomists at-

tempt to classify is a product of organic evolution, and any classificatory system must take cognizance of this fact. This implies that the system must be based on phylogeny, and not vice versa. Therefore, I have attempted to tackle the numerous problems of the classification of freshwater triclads, as I see them, by taking the phylogenetic approach so ably advocated by Hennig (1966), Brundin (1966), and Crowson (1970). This does not imply that existing classifications are of no value, but the traditional phenetic taxonomists frequently do produce classifications which are at variance with their phylogenetic trees for the very reason that their systems are based primarily upon phenetic distance and not recency of common ancestry. The phylogeny and classification of the Paludicola proposed by Kawakatsu (1968) provides an example of this. I also believe that a true phylogenetic system is a necessary prerequisite for biogeographical analysis. This is a view which has been ably demonstrated by Nelson (1969), who also lays to rest the erroneous idea that biogeographical inquiry is meaningless in the absence of a fossil record.

Since phylogenetic relationship, or cladistic affinity, is best determined on the basis of synapomorphies, or the sharing of derived characters, it is always necessary to make distinctions between the primitive (plesiomorph) and derived (apomorph) states of given characters or character correlations. Frequently the trends are clear, but the direction is equivocal. In the absence of other evidence the principle of parsimony must decide the issue.

There is rarely, if ever, empirical proof for a given phylogenetic system, and certainly not for that developed for the Paludicola in the present paper. The probability of its correctness will be a product of the quality of the data available, and the skill of the taxonomist, and it is its heuristic value over a long period of time that will determine its worth. That there remains a great deal of work to be done before we shall fully understand evolutionary and biogeographical relationships within the Paludicola will be apparent from that which follows.

## THE HIGHER CLASSIFICATION OF FRESHWATER TRICLADS

### Historical

The classification of the Turbellaria has been in a state of flux for many years, and the categorical ranking of its subdivisions has been altered frequently. For present purposes I follow the arrangement by Ax (1956) in which the order Seriata Westblad, 1935 is divided into two suborders, viz., Proseriata Meixner, 1938 and Tricladida Lang, 1884 (= Euseriata Westblad, 1952). Within the latter the Maricola, Paludicola, and Terricola (Hallez, 1894) are given the status of infraorders, which is a well-used category in vertebrate

zoology, and which will avoid the ambiguities of the categories "section" and "series," which have diverse meanings in the zoological and botanical literature.

Steinböck (1925) divided the Tricladida into two groups based primarily on the nervous system. These were the Diploneura, containing the terrestrial forms, and the Haploneura. The latter were further subdivided into the Vaginalia (Uteriporidae, Bdellouridae), Retrobursalia (Procerodidae, Cercyridae, Micropharyngidae), and the Probursalia (= Paludicola). Both Kenk (1930a) and Hyman (1931a) in their revisions opted for this nomenclature.

The exact relationships of the Terricola to the other triclads are not clear, but it does seem that the most primitive family is the Rhynchodemidae, which may be derived from the Maricola (Meixner, 1928; Marcus, 1953). Also, the aptness of Steinböck's name for the Paludicola was lost with the discovery of marine triclads with an anterior bursa (Probursidae Hyman, 1944) and of a freshwater triclad with a posterior bursa (*Rhodax* Marcus, 1946). For these reasons I agree with Marcus (1963) that Hallez's division of the triclads into three groups with equal rank is the most useful on present knowledge.

Hallez (1894, p. 187) recognized nine genera of Tricladida Paludicola and divided them into two families. These were the Planariidae, without anterior adhesive organs, and the Dendrocoelidae, with such organs. Later, von Graff (1912-1917) increased the number of families to five, again basing their definitions on the adhesive and creeping organs, a procedure which has been considered unreliable (Hyman, 1931a; Mitchell, 1968). Three of von Graff's families were erected for the peculiar Lake Baikal triclads, which show a great diversity of size and form, and which possess many gradations of adhesive organs and suckers. It is now accepted that these forms belong to the Dendrocoelidae (Livanov, 1962; Kozhov, 1963).

A precise definition of the families of Paludicola was not attained until the revision of Kenk (1930a). He defined two families by the arrangement of the inner muscle layers of the pharynx. In the Planariidae the circular and longitudinal muscles of the inner muscle zone of the pharynx form two separate layers, whereas in the Dendrocoelidae the circular and longitudinal muscle fibers are intermingled. Kenk's scheme, based on a definite morphological character, confirmed the earlier arrangement of Hallez (1894), which was based on external features. The distribution of the genera was the same in both schemes, although many more genera had been described by the time Kenk proposed his revision.

The correlation between external form and internal morphology in the two families of freshwater triclads was upset by the detailed study and description of an unusual cave triclad from North America (de Beauchamp, 1931). Packard (1879) placed this species in the genus *Dendrocoelum* on the



basis of its external appearance. De Beauchamp (1931) was able to show, however, that the musculature of the pharynx was that of a planariid and not of a dendrocoelid, despite the presence of an anterior adhesive organ. For this and other reasons, he erected the new genus *Sphalloplana* for this species. Hyman (1931a) had also noticed the incorrect assignment of the species by Packard, but she felt that it fell naturally into the planariid genus *Fonticola*. Later, however, she described a number of new cave planarians, and in so doing not only recognized the genus *Sphalloplana* but also erected two new ones, *Kenkia* and *Speophila*, together with a new family, the Kenkiidae, to contain them (Hyman, 1937).

As more species of Kenkiidae became known, it became increasingly apparent that Hyman's original definition of the family could not be maintained. On morphological grounds de Beauchamp (1961) had not accepted it, but for purely pragmatic reasons I had retained the family in a checklist of the freshwater triclads of Nearctic and Neotropica (Ball, 1969a). Mitchell (1968), in a detailed review, synonymized the genera *Sphalloplana* and *Speophila* and presented evidence suggesting that the family could no longer be satisfactorily delimited. He regarded the genera *Sphalloplana* and *Kenkia* as merely planariids with an anterior glandulomuscular adhesive organ. He therefore proposed the elimination of the family Kenkiidae, a proposition with which Kawakatsu (1969a) disagreed.

The thirty or so genera of Tricladida Paludicola which are recognized today are distributed generally among two families as follows:

Family Planariidae: *Planaria* Müller, 1776; *Fonticola* Komarek, 1926 (inc. *Penecurva*); *Atrioplanaria* de Beauchamp, 1932; *Phagocata* Leidy, 1847; *Polycelis* Ehrenberg, 1831 (inc. *Seidlia*, *Polycelidia*, *Ijimia*); *Plagnolia* de Beauchamp and Goubault, 1964; *Crenobia* Kenk, 1930; *Sphalloplana* de Beauchamp, 1932; *Kenkia* Hyman, 1937; *Hymanella* Castle, 1941; *Rhodax* Marcus, 1946; *Bopsula* Marcus, 1946; *Cura* Strand, 1942; *Dugesia* Girard, 1850 (inc. *Spathula*).

Family Dendrocoelidae: *Dendrocoelum* Oersted, 1844; *Bdellocephala* de Man, 1874; *Rectocephala* Hyman, 1953; *Dendrocoelopsis* Kenk, 1930 (inc. *Amyadenium*); *Acromyadenium* de Beauchamp, 1931; *Thysanoplana* von Graff, 1916; *Hyperbulbina* Livanov and Porfirjeva, 1962; *Procotyla* Leidy, 1857; *Macrocotyla* Hyman, 1956; *Rimacephalus* Korotneff, 1901; *Protocotylus* Korotneff, 1912; *Polycotylus* Korotneff, 1912; *Monocotylus* Korotneff, 1912; *Armilla* Livanov, 1961; *Sorocelis* Grube, 1872; *Baikalobia* Livanov, 1962. *Caspioplana* Zabusova, 1951 is unique in its possession of pharyngeal muscles converse to those of the Planariidae. Its reproductive apparatus is closest to that of the Dendrocoelidae.

The unusual genus *Bdellasimilis*, ectoconsortic on Australian *Chelonia*, was originally, but tentatively, assigned to the Paludicola (Richardson, 1968,

1970). Since its occurrence in freshwater is paralleled by other *Maricola* (Ball, 1974), and since an anterior bursa is known in the marine Probursidae, I find the numerous morphological similarities with the *Maricola* more convincing, and have no hesitation in classifying it with this group. Richardson (1971, pers. comm.) agrees that it is probably maricolous but finds the criteria separating the Paludicola and the *Maricola* somewhat inadequate. Recent work is confirming his opinion.

### Evolutionary Trends

The most important contribution to the study of evolutionary trends within the Tricladida is undoubtedly that of Meixner (1928). Recognizing the taxonomic importance of the reproductive organs, he divided the aquatic triclads into a number of types on the basis of the female reproductive system. In summary, these types were:

- I Atrium undivided. Oviducts and shell glands open into the bursal stalk (*Maricola* and *Paludicola*).
- II Atrium undivided. Oviducts unite to form a common oviduct which opens into the posterior part of the bursal stalk or the atrium.
  - A Common oviduct and shell glands open into the bursal stalk (*Maricola* and *Paludicola*).
  - B Common oviduct opens into the bursal stalk, the shell glands into the common oviduct (*Maricola* only).
  - C Common oviduct opens into the mouth of the bursal stalk or below it into the atrium; the shell glands open chiefly into the common oviduct (*Paludicola* only).
- III Atrium divided. Common oviduct opens independently of, and anterior to, the bursal stalk into the atrium. Shell glands open into the oviduct (*Paludicola* only).

All the genera and subgenera of aquatic triclads recognized by Meixner were assigned to one or the other of these categories, together with notes on their distribution. Meixner forbore to erect any new systematic categories but went on to compare other characters and organ systems with his scheme and found many correlations in their categorical distribution. He considered that the *Maricola* and *Paludicola* showed independent evolutionary lines, that the *Maricola* were more primitive than the *Paludicola*, and that the *Paludicola* of type III were the most advanced. Many of the details of Meixner's arrangement are now questionable, but the broad principles seem to be eminently sound.

The genera *Cura* and *Dugesia* share many features in common, such as their triangular head shape and the production of stalked cocoons, which are

not found in other genera (Kenk, 1930a); they are the only Paludicola widely distributed in the Southern Hemisphere. Meixner's types I and II contain all the known species of these genera, and some species with variable oviducts could be assigned to either type. On the other hand the Dendrocoelidae, which are unique in their possession of intermingled inner pharyngeal muscles, are wholly contained in type III, as are the remainder of the Planariidae.

The principal dichotomy in Meixner's scheme seems to be between type I-II, in which the oviducts are closely associated with the bursal stalk, and type III, in which they are associated with the atrium. In their morphology and ontogeny the Proseriata form the phylogenetic precursors of the triclads (Ax, 1963), and in this group the oviducts are usually associated with the bursal stalk or the equivalent female genital canal (Meixner, 1938; Ax, 1956), as they are in the Paludicola of type I-II and all Maricola with the exception of the aberrant commensal genus *Nexilis*, in which they enter the penis bulb (Holleman and Hand, 1962). In this respect type I-II is undoubtedly more primitive than type III, and the first evolutionary advance made by the Paludicola over the Maricola appears to be the shifting of the course and position of the oviducts, and the associated shell glands.

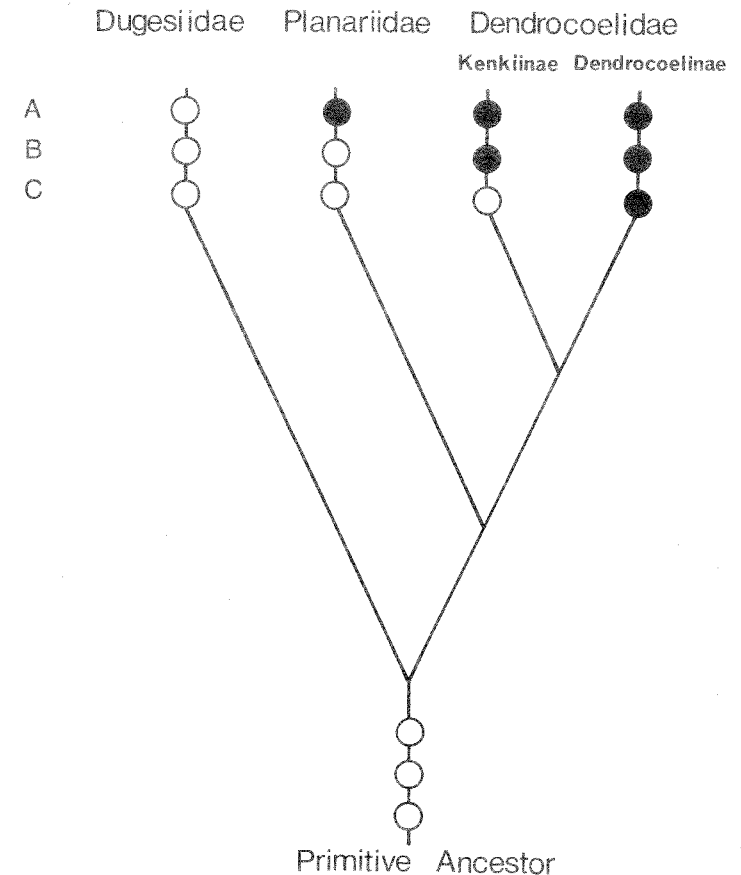
Kenk (1930a) is probably correct in saying that the Planariidae are more primitive than the Dendrocoelidae, but it follows from this that the Planariidae of type III must occupy an intermediate position between type I-II and the Dendrocoelidae. The latter could be separated by the adhesive organs (Hallez, 1894) or by their pharyngeal muscles (Kenk, 1930a).

Anterior glandulomuscular organs are not found in the Proseriata or the free-living Maricola, but they are usual in the Dendrocoelidae and thus represent an apomorph (derived) character state when considering the Tricladida as a whole. Similarly, the organization of the pharyngeal muscles of the Proseriata, Maricola, and Planariidae is basically the same. Consequently the arrangement in the Dendrocoelidae must be derived.

It seems to me that there are three principal grades of organization within the Paludicola which need to be distinguished. The most advanced of these are the Dendrocoelidae, followed by the Planariidae of type III, and then finally the Planariidae of type I-II, and I propose that the latter should be separated as a distinct family, with the name Dugesidae. This follows logically if on the basis of the characters discussed above we attempt to reconstruct the most probable evolutionary sequence.

Although the functional significances of the arrangement of the pharyngeal muscles and the courses of the oviducts are not fully understood, it is very unlikely that these two characters are functionally related. It is difficult to conceive of either of these characters being necessary correlates of the presence or absence of an adhesive organ. The congruence of the apomorph grades of all these characters in the Dendrocoelidae, and of the plesiomorph grades in the Dugesidae is, therefore, surely of phylogenetic significance.

If it is accepted that the most primitive freshwater triclad possessed oviducts which emptied into the bursal stalk, possessed a pharynx in which the inner muscles formed a distinct inner circular and outer longitudinal layer, and lacked an adhesive organ, as is the case only in the Dugesidae, then the most probable sequence leading to the other groups is that presented as Fig. 1, if a monophyletic origin for the Paludicola is assumed. The four combinations of the three characters shown are the only ones known in living Paludicola, and it follows from the scheme presented that the Dugesidae are phylogenetically equivalent to the Planariidae + Dendrocoelidae. This could be recognized by using the superfamily category.



**Figure 1** Phylogenetic relationships of the families of Tricladida Paludicola. Open circles are the plesiomorph (p), and solid circles the apomorph (a), grades of given characters. A, oviducts open to bursal stalk (p) or atrium (a). B, adhesive organs absent (p) or present (a). C, inner pharyngeal muscles layered (p) or intermingled (a). For further discussion, see text.

Kawakatsu's (1968) valuable discussion of the phylogeny of the Paludicola is summarized in his figure IV-1, and although I disagree with him in many details, the principal dichotomies in his phylogenetic tree are similar to those given here. It is encouraging that to this degree we have reached the same conclusions. However, he maintains the old threefold classification of Planariidae, Kenkiidae, and Dendrocoelidae. This is totally at variance with his phylogenetic tree since his Planariidae become a paraphyletic group, as they would if the Dugesiidae were united with them in Fig. 1. This is the more surprising inasmuch as Kawakatsu has placed his categories on a time scale which clearly indicates that at the familial level there are three major phyletic lines equivalent to those of Fig. 1, the significance of which he appears to have overlooked.

The principal difficulty of the scheme presented in Fig. 1 is that only the Dendrocoelidae are defined by true synapomorphy. It is true that the Dugesiidae are symplesiomorphic by analysis rather than by synthesis, which somewhat lessens the danger of their being a paraphyletic or polyphyletic group, but it is desirable that they should also be defined by further apomorph characters. The only such character I have been able to recognize is the triangular head so characteristic of *Dugesia* and *Cura*, which is an apomorph character within the Paludicola (p. 355). Even this, however, is absent in a few Southern Hemisphere forms which, on other grounds, must be classified with these genera. Nearly all Dugesiidae produce stalked cocoons, in contrast to the other families, but whether this is a primitive retention or a secondary (apomorph) acquisition is impossible to say.

The problem is compounded by current difficulties in adequately separating the marine and freshwater triclads, and thus, by implication, in deciding on the exact origins of the Dugesiidae. Precise definitions of the Maricola and Paludicola based on ecological and morphological (reproductive) criteria can no longer be put forward. In this connection the Probursidae (Maricola) and *Rhodax* (Paludicola) have already been discussed. One *Dinizia* species (Maricola) lacks a bursa copulatrix but has an anteriorly directed bursal stalk, and is found in freshwaters (Ball, 1974), as is *Bdellasimilis* (Maricola), which has an anterior bursa copulatrix. It has long been known that certain Paludicola may invade brackish habitats (Wilhelmi, 1909; Meixner, 1928), and that some Maricola can adapt to almost completely fresh water (Meixner, 1928; Pantin, 1931). It was this ecological overlap which led Steinböck (1925) to drop the ecological names. The genus *Caspioplana* (Paludicola) is endemic to the saline waters of the Caspian Sea, and although it shows many unusual morphological features, it is undoubtedly derived from the Dendrocoelidae (Zabusova, 1951), even though it coexists with the maricole *Pentacoelem* (de Beauchamp, 1961). More important, however, is the fact that a number of Procerodidae have been recorded from freshwaters, most frequently on South-

ern Hemisphere oceanic islands where, it is assumed, the historical absence of freshwater triclads has enabled the Maricola to invade the freshwater habitat in the face of reduced competition (Ball, 1974). New types of "freshwater triclads" may be expected to arise from these forms, and it would be difficult to distinguish them from the Dugesiidae.

The fact that the Paludicola (Dugesiidae) cannot be separated from the Maricola except by a constellation of characters which, taken individually, could pertain to either group, is a fine example of the Non-Congruence Principle discussed by Crowson (1970). As characters do evolve both concurrently and successively, this may indicate in the case of the aquatic triclads that a great many primitive types, intermediate between the major phyletic lines, have persisted to the present day, possibly with the added complications of convergence. If so, their elucidation remains a formidable task. It could also mean that the assumption of a monophyletic origin of the Paludicola from marine ancestors is erroneous. Possibly the Dugesiidae and the Dendrocoelidae + Planariidae have arisen independently from marine ancestors in the Southern and Northern Hemispheres respectively. There can be little doubt that the evolutionary relationships between the Maricola and the Paludicola are far more complex than is generally realized, and I suspect that a hypothesis of a polyphyletic origin of the higher aquatic triclads from marine ancestors may lead to a better understanding of their systematic and biogeographical relationships. I am unable to finalize such a hypothesis at the present time, for a great deal of fundamental taxonomic research is necessary before this could be attempted. It is only right, however, that one of the main difficulties derived from the present approach should be emphasized, and this is the major reason why the present study is restricted to the systematic and biogeographical relationships of the Dugesiidae.

The status of the newly restricted Planariidae requires further study which is outside the scope of the present paper. As regards the Kenkiidae, Kawakatsu clearly considers them to be a monophyletic group, and upon this we are agreed. I concur with Mitchell (1968), however, in that they cannot be awarded family rank, though I am dubious about merging them with the Planariidae. For the present they may be considered a distinct subfamily, the Kenkiinae, but their precise position in my proposed phylogenetic scheme is problematical.

If the Kenkiinae are derived from the Planariidae, it is necessary to postulate that they have acquired their adhesive organs independently of the acquisition of apparently homologous organs in the Dendrocoelidae. Mitchell (1968) does indeed argue that there is no reason to suppose that adhesive organs have arisen only once within the Paludicola and states that the wide occurrence of glandulomuscular organs in the Turbellaria suggests a multiple origin for these structures. This may well be true if the character occurs spo-

radically, and in related groups, as is the case with adenodactyls, but the suggestion is unreasonable when the organ appears within a subtaxon which shows other evidence of uniformity or monophyly, which is the case with the Kenkiinae. Hyman (1937) derived the Kenkiinae from the genus *Phagocata* (= *Fonticola*), with which both Mitchell (1968) and Kawakatsu (1968) seem to concur, and there appears to be little disagreement concerning the "naturalness" of the group.

Their association with this genus has been based largely upon the planariid pharynx and on the possession of a copulatory complex of the *Fonticola* type. In fact, the copulatory complex is typical of Meixner's type III and is found in other Planariidae and Dendrocoelidae. It has also been inferred (Mitchell, 1968) that support for the *Fonticola* origin of the Kenkiinae is forthcoming from the fact that *F. albata* is described as possessing an incipient adhesive organ (Ichikawa and Kawakatsu, 1962), although this lacks any muscular differentiation. I am of the opinion, however, that this feature has been overemphasized since adhesive depressions of this type are known in other planariid species such as *Planaria torva* (Ball *et al.*, 1969, p. 111), and modifications of the epithelium of this ventral anterior region, which presumably are of sensory function, are found in *Planaria occulta* and *P. dactyligera* (Kenk, 1970), and probably other species.

There are further difficulties in classifying the Kenkiinae with the Planariidae. Hyman (1937) and Carpenter (MS1970) have shown that fundamentally there are two types of adhesive organ: that typical of the Dendrocoelidae and one typical of the Kenkiinae. Hyman (1956) considered that of the dendrocoelid genus *Macrocotyla* to be structurally closer to that of the Kenkiinae than to the other Dendrocoelidae. The supposed derivation of the Kenkiinae from the Planariidae as a group quite independent of the Dendrocoelidae thus requires two assumptions: the independent acquisition of an anterior adhesive organ and convergence in the same organ in *Macrocotyla*.

If, however, the phylogenetic arrangement presented in Fig. 1 is accepted, neither of these assumptions is necessary, and the classificatory system is more parsimonious. The Kenkiinae are considered to be the most primitive subfamily of the Dendrocoelidae, whose sporadic occurrence in caves, subterranean waters, and deep lakes in central Asia, the Far East, and North America represents the remnants of a formerly much wider distribution, and which results in part from the evolutionary success of the more recent Dendrocoelinae (= Dendrocoelidae *sensu* Kenk, 1930a). The relict nature of cave faunas in general is well known (Vandel, 1965). It may also be noted that Carpenter (MS1970) has been unable to find any significant function related to the cave habit for the adhesive organ of the Kenkiinae, which is surprising if these are to be regarded as a specialized group of planariids

(Hyman, 1937, 1960). However, its occurrence is perfectly consistent with the hypothesis proposed here that they are plesiomorph dendrocoelids.

There are, of course, difficulties in proposing a major classificatory division on the basis of the presence or absence of adhesive organs. It could certainly be considered a retrograde step when compared with Kenk's (1930a) redefinition of the families used by Hallez (1894). But as we have seen, Kenk's reclassification on the basis of pharyngeal musculature did not alter Hallez's disposition of the genera into families on the basis of adhesive organs; it merely provided a more "acceptable" morphological criterion. Hyman (1931a) criticized the use of adhesive organs in the higher taxonomy of the group, but later she recognized that they must be of some taxonomic importance since they are absent in the Planariidae and usually present in the Dendrocoelidae (Hyman, 1937, p. 472).

The fact that adhesive organs exhibit different grades of development in the Dendrocoelinae (Kenk, 1930a) is irrelevant to their use in phylogenetic classification, though it might make diagnosis difficult. However, the only known genera of Kenkiinae are clearly defined (Mitchell, 1968; Carpenter, MS1970), and the dendrocoelids most likely to show secondary reduction of the anterior adhesive organ, as, for example, some species of *Sorocelis*, are all members of the subfamily Dendrocoelinae, which is clearly identifiable by its pharyngeal musculature.

It must be assumed that polypharyngeal Kenkiinae have acquired this character independently of its occurrence in the Planariidae. Polypharyngy is found in the eastern North American genus *Phagocata* and in the European *Crenobia*, two planariid genera which do not show particularly close relationships. The feature is undoubtedly independently acquired in each, as far as we can tell from present evidence. An alternative hypothesis would be that the Kenkiinae had a polypharyngeal ancestor, presumably close to *Phagocata*, and that polypharyngy has been secondarily lost in many species.

The Kenkiinae are also uniform in that the testes are prepharyngeal. Restriction of the testes to the anterior part of the body is frequent in both the Dugesiidae and the Planariidae, but until comparatively recently was not known in the Dendrocoelinae. However, *Macrocotyla*, which possesses a kenkiinid-like adhesive organ, also has testes which are restricted to the prepharyngeal region (Hyman, 1956). It is also interesting to note that the Kenkiinae are restricted to Asia and North America, achieving their greatest diversity in the latter, and *Macrocotyla* is endemic to North America. It is quite possible that the unpigmented, eyeless *Macrocotyla* forms a link between the Kenkiinae and the Dendrocoelinae.

From the knowledge we possess at present it is unnecessary to postulate independent acquisition of an adhesive organ in the Kenkiinae, and conver-



gence in *Macrocotyla*, in order to fit them into a satisfactory phylogenetic scheme of the Paludicola, since they can be classified satisfactorily with the phyletic lineage leading to the Dendrocoelinae.

#### A Revised Classification

I propose, therefore, a revision of the higher classification of the Paludicola, as follows:

##### Family Dugesiidae fam. n.

Paludicola in which the oviducts, separately or combined, empty into the bursal stalk, or rarely into the atrium very close to, and posterior to, the entrance of the bursal stalk. Type genus: *Dugesia* Girard, 1850. Usually pigmented. With eyes, and typically with a triangular head. Adhesive organs absent. Adenodactyls rarely present. Inner pharyngeal muscles in two distinct layers. Shell glands usually open into the bursal stalk. Cocoons spherical and stalked (exceptions *Rhodax*, *D. montana*, *D. fontinalis*). Genera: *Dugesia*, *Cura*, *Bopsula*, and possibly *Rhodax*. Distribution: Worldwide.

##### Family Planariidae Stimpson, 1857, emend.

Paludicola in which the oviducts unite to a common oviduct which empties into the roof of the atrium, independently of the bursal stalk. Anterior glandulomuscular organ absent. Type genus: *Planaria* Müller, 1776. Pigmented or white. Typically with eyes, never with a triangular head. Inner pharyngeal muscles in two distinct layers. Adenodactyls sometimes present. Shell glands open into the common oviduct. Cocoons spherical or ovoid, without a stalk. Genera: *Planaria*, *Fonticola*, *Phagocata*, *Hymanella*, *Atrio-planaria*, *Polycelis*, *Plagnolia*, and *Crenobia*. Distribution: Holarctis and parts of Orientalis.

##### Family Dendrocoelidae Hallez, 1894

Paludicola in which the oviducts unite to a common oviduct which empties into the roof of the atrium, independently of the bursal stalk. Shell glands open into the common oviduct. Anterior glandulomuscular organ present (but secondarily lost in a few species). Type genus: *Dendrocoelum* Oersted, 1844.

##### Subfamily Kenkiinae nom. n.

Inner pharyngeal muscles in two distinct layers. Usually blind, unpig-

mented cave dwellers. Adenodactyls absent, testes prepharyngeal. Genera: *Kenkia* and *Sphalloplana*. Distribution: Central and east Asia, North America.

##### Subfamily Dendrocoelinae nom. n.

Inner pharyngeal muscles intermingled. Usually with eyes and usually unpigmented. Adenodactyls frequently present. Testes usually distributed throughout the body length. Genera: *Dendrocoelum*, *Bdellocephala*, *Rectocephala*, *Dendrocoelopsis*, *Acromyadenium*, *Thysanoplana*, *Hyperbulbina*, *Procotyla*, *Macrocotyla*, *Rimacephalus*, *Protocotylus*, *Polycotylus*, *Monocotylus*, *Armilla*, *Sorocelis*, *Baikalobia*, (and *Caspioplana*?). Distribution: Holarctis.

A word on the nomenclature of the new family is necessary at this point. Of the five families recognized by von Graff (1912–1917) one, the Curtisiidae, was founded for the American species *Cura foremanii* (olim *Curtisia foremanii*), the only species of the genus known at that time. Since von Graff's classification of this triclad was based on a misinterpretation of the description by Curtis (1900), the family was unnecessary and unjustified (Meixner, 1928; Hyman, 1931a), although its retention was favored by Poche (1926). However, it would be misleading to use this name when Poche's concept of the family is so vastly different from that presented here. In addition, the name Curtisiidae was based on the generic name *Curtisia* von Graff, 1916, which has been shown to be a junior homonym, and for which the name *Cura* has been substituted (Strand, 1942). Finally, the genus *Cura* is unusual in a number of respects and the genus *Dugesia* is more typical of the family as it is at present conceived. Consequently it has been selected as the type genus of the new family.

The systematic position of the unusual Brazilian genus *Rhodax* is problematical. According to the original definition it would fall into the family Planariidae, as the common oviduct opens into the genital atrium, more particularly into the part called the common atrium (Marcus, 1946, pp. 133–134). Both the Planariidae and the Dendrocoelidae are restricted to the Northern Hemisphere (with one exception), and it is my contention that the Southern Hemisphere triclads all belong to the Dugesiidae. A careful reexamination of *Rhodax* therefore is necessary.

Marcus describes the genus as being a "collective morphological type" showing affinities with both the Proseriata and with *Phagocata* (= *Fonticola*) of the Planariidae. I hope to show later that the relationships with *Fonticola*, which also are accepted by Kawakatsu (1968), are not very strong and that the genus is indeed primitive. Its assignment in my phylogenetic scheme depends, however, solely on the course of the oviducts and associated shell glands.

In the only known species, *R. evelinae*, there is a bursa-intestinal duct posterior to the penis. The posteriorly directed bursal canal is histologically well differentiated from the atrium, and into its dorsal wall, very near to the junction with the atrium, opens what Marcus terms a common oviduct (Marcus, 1946, fig. 149). The shell glands open into this "common oviduct." According to Marcus's figure 152 the bursal stalk first assumes its typical histological structure at the level of the gonopore, and according to his figures 149 and 150 the "common oviduct" opens into the bursal stalk posterior to the level of the gonopore. From his figures I would infer that that part of the duct anterior to the gonopore is atrium, and that posterior must be considered to be bursal stalk. It may also be noted that the oviducts do not unite to form the usual slender common oviduct, but rather open separately from the sides into a broad saclike structure (Marcus, 1946, fig. 149).

For these reasons I consider the "common oviduct" of *Rhodax evelinae* to be a diverticulum of the bursal stalk into which open the shell glands. It is not homologous with the common oviduct of the Planariidae and the Dendrocoelidae. These views are supported by examination of a number of specimens of *Rhodax* kindly sent to me by Mrs. Eveline Marcus. Regrettably, only two specimens showed traces of copulatory organs, but these are consistent with the above interpretation. The similarity of this diverticulum of the bursal stalk of *Rhodax* to the "glandular duct" of the Procerodidae (Maricola) of Meixner's type IIB is very striking, and may be taken as evidence of the close relationship of *Rhodax* with the Maricola. Moreover, this genus possesses vitellaria which are anterior to the germaria, which is usual in the Maricola, but not in the Paludicola. A good case could be made for *Rhodax* having evolved from marine ancestors independently of the other Paludicola, especially as there are other features linking this genus with the Proseriata (Marcus, 1946). In this case a distinct family for the genus would be necessitated, but I decline to take this step until I have had the opportunity to study more material. Consequently, I provisionally assign *Rhodax* to the Dugesiidae and express doubt concerning any close relationships with *Fonticola*.

#### THE FAMILY DUGESIIDAE fam. n.

It is my purpose here to provide an overall synopsis and preliminary phylogenetic analysis of the family Dugesiidae. It is well known that the Paludicola are a difficult group to study taxonomically. Their lack of definite measurable characters, together with the difficulty of proper preservation, is probably responsible for this. Consequently, attempts to determine their relationships by cytological (Dahm, 1958, 1963) and cytogenetic (Benazzi, 1960, 1963, 1966) studies must be applauded, even if the full fruits of such studies have yet to be reaped. That studies of the Paludicola have for a long time remained

at the  $\alpha$ -taxonomy level is a fact that cannot be avoided, and any attempt at revision or synthesis must still be based largely upon comparative morphological data.

Our lack of knowledge concerning the functional significances of many of the characters which appear to be useful, such as the musculature of the pharynx or of the bursal stalk, is a considerable drawback. As regards phylogenetic analysis a further complicating factor is the extreme conservatism of the group. As Brundin (1966) has pointed out, morphologically uniform groups are likely to be difficult subjects for phylogenetic analysis. Such groups yield few adequate characters for analysis, and parallelism and convergence occur frequently because there are a limited number of evolutionary pathways open. Thus, strict phylogenetic analysis involving the rule of dichotomy as proposed by Brundin (1966) is difficult, if not impossible. Darlington (1970) too has drawn attention to the difficulties caused by the oversimplifications of the rule of dichotomy. The analysis of characters not considered here, and not available in most species descriptions, possibly would alleviate this situation. The areas presenting the greatest diversity, and the greatest difficulty, all lie in the Southern Hemisphere, particularly in South Africa and Australasia.

In the analysis that follows I have elected to study, by the methods of Camin and Sokal (1965), several sets of characters from the Dugesiidae so that the conclusions may be compared between sets. Where adjustments of the resulting cladograms have been necessary, for reasons to be given, I have followed in general the principle that groupings are best based on synapomorphies. I have relied heavily on the detailed descriptions of many species given by such authors as Ijima (1884), Böhmig (1902), Weiss (1910), Lang (1913), Hyman (1925), Marcus (1946, 1948, 1953, 1954, 1955), de Beauchamp (1939, 1959), Kenk (1930b, 1935, 1944), Ichikawa and Kawakatsu (1964), and Ball (1970, 1971). Owing to the kindness of many colleagues I have also been able to examine directly many specimens of *Dugesia* and *Cura* from most parts of the world.

#### Taxonomic Characters and Their Correlation

Taxonomic characters may function as diagnostic characters for a particular species or as indicators of relationship (Mayr, 1969). Failure to recognize these two principal functions of a taxonomic character has led to much sterile discussion by taxonomists on the relative values of given characters. It follows that a species description which provides only the minimum of diagnostic characters is of little value to the evolutionist and the biogeographer, even though the description is adequate for the recognition of the species.

In attempting to reconstruct the probable phylogenies of characters and character correlations, the level of plesiomorphy or apomorphy of these must

be decided. At present genetic and fossil data are insufficient to be of real value. The criteria I have relied upon are outlined below; my indebtedness to Marx and Rabb (1970) will be apparent.

1 Uniqueness: A decision concerning the phylogenetic relationships of the families of Paludicola having been made, a character state unique to a derived family is thereby inferred to be apomorph.

2 Relative abundance: A character state which is widely distributed in divergent taxa of the group under study is likely to be plesiomorph.

3 Morphological specialization: If a character state is predominant in some particular adaptive specialization, it is likely to be apomorph.

4 Ecological specialization: A character state is likely to be apomorph if it is relatively much more abundant in taxa with a particular mode of life.

5 Geographical restriction: Limitation of a character state to most taxa of a particular geographical area suggests that it is apomorph.

6 Related taxa: A character state which occurs in forms closely related to, but outside of, and not directly descended from, the group under consideration is likely to be plesiomorph.

Of course it is not possible to apply all these criteria to each of the characters discussed below, but the probability that a decision on the apomorphy or plesiomorphy of a character state is correct will be increased in proportion to the number of criteria used. A further aid to determining the direction of change is Dollo's law, in that a complex character once lost in the course of evolution is unlikely to be reacquired in exactly the same form (Crowson, 1970). This criterion must be used cautiously, however, since exceptions are known (Mayr, 1969). The correlation of given character states in a single taxon is not always useful in the absence of other data. They could be necessary correlates, and there is certainly no reason why plesiomorph and apomorph characters should not sometimes be statistically correlated. Nonetheless, the statistical correlation of apomorph characters which cannot be shown to be necessary correlates is likely to result from common genetic history of the taxa.

**Habitus** A general increase in body size often accompanies evolutionary advancement (Meixner, 1928; Bonner, 1965). The largest Paludicola known belong to the most advanced group, the Dendrocoelinae, the Lake Baikal representatives of which attain lengths of 40 cm and more (Kozhov, 1963). The other Palaearctic and Nearctic Dendrocoelinae rarely exceed 40 mm. It is slightly paradoxical, from the points of view put forward in this paper, that the Dugesiidae in general are larger than the Planariidae, but there are many exceptions and an explanation may be sought in their ecology and reproductive biology.

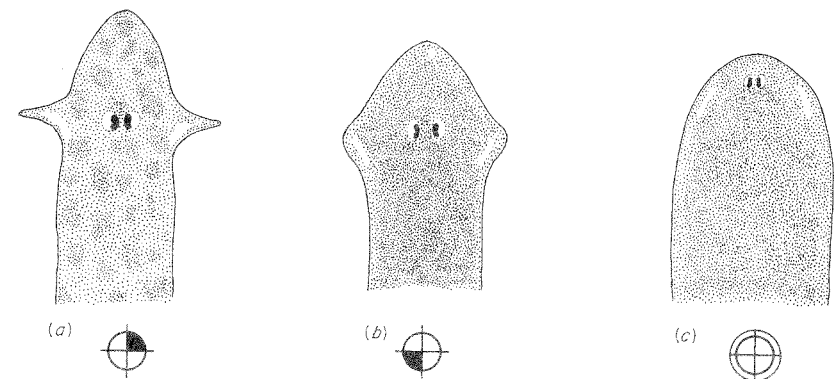
Meixner (1928) notes that the more primitive Paludicola are generally

uniformly colored or mottled, and longitudinally striped and white forms occur only in the Planariidae and Dendrocoelidae. We know now of an unpigmented *Dugesia* species, *D. batuensis*, but the absence of pigment is almost certainly related to its cave-dwelling habit (Ball, 1970).

All the Dugesiidae possess two eyes, but supernumerary eyes occasionally occur. Multiocularity occurs in both the Planariidae and Dendrocoelidae, as do eyeless forms. The usual two-eyed condition is almost certainly the ancestral condition in the Paludicola.

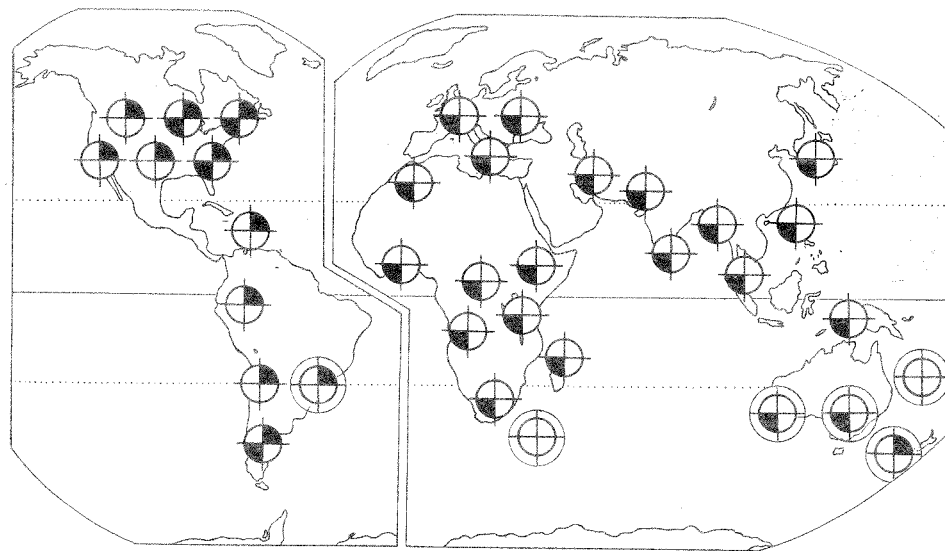
Meixner (1928) and Marcus (1946) infer that the sagittate head is the primitive condition, but more recent data lead me to question this opinion. Most, but not all, Dugesiidae possess a triangular head with projecting auricles, as do a few Maricola (Meixner, 1928). In the higher Paludicola truncate or rounded heads are usual, sometimes with the development of tentacles, as in *Polycelis felina*, *Fonticola bursaperforata*, *Crenobia*, and some Dendrocoelidae. Head shape in the Dugesiidae is illustrated in Fig. 2, and the geographical distribution of this character is shown in Fig. 3. Most Proseriata have a rounded or spatulate anterior end (Meixner, 1938; Ax, 1956; Luther, 1960), and there can be little doubt that this condition is primitive within the Turbellaria as a whole. A rounded or spatulate head is rare in the Dugesiidae but is found in some forms from Australasia, the Crozet Archipelago, and South America. The high triangular form characteristic of *D. tigrina* occurs in all the New World species of the genus, and elsewhere in only one species, *D. montana* from New Zealand. The subtriangular shape is typical of the genus *Cura* and of all *Dugesia* species from Palaearctis and Orientalis, and some from Australasia.

I conclude that the ancestral Dugesiidae were pigmented, with two eyes,



**Figure 2** Range of head shape in the Dugesiidae. (a) High triangular, *Dugesia tigrina*; (b) subtriangular, *D. gonocephala* (after de Beauchamp, 1961); (c) rounded, *Cura pinguis* (after Nurse, 1950). The symbols beneath the sketches form the key to Fig. 3.





**Figure 3** Distribution of the Dugesiidae possessing the different types of head shape. See Fig. 2 for key. Symbols on this, and subsequent maps, are composites of those given in the key. For further discussion see text.

and with a rounded or spatulate anterior end. Such forms are represented today by *Rhodax* (South America), *D. seclusa* (Crozet Islands), *C. pinguis*, *D. schauinslandi*, *D. fontinalis*, and probably most other Australian *Dugesia* species (Weiss, 1910).

**Pharynx** The relative thicknesses of the various pharyngeal muscles may well have phylogenetic significance. In many Maricola, for example, the circular layers are exceptionally well developed. In certain cases the thickness of the layers may be of diagnostic significance (Ball, 1971).

The phylogenetic significance of the inner pharyngeal muscles has been discussed. The outer pharyngeal musculature of most Dugesiidae consists of two layers, a subepithelial layer of longitudinal fibers underlain by a circular layer. This is the condition found in the Maricola and Proseriata. A few Dugesiidae have developed a third layer, consisting of longitudinal fibers beneath the outer circular layer. This extra layer is found in *Dugesia gonocephala*, *D. congolensis*, *D. ectophysa*, *D. colapha*, *Cura paeta*, and *C. jeanneli*. All these species are from west, central, and south Africa. *D. gonocephala* is also widespread in Europe.

The spatial and taxonomic distribution of this character leaves little doubt that it is an apomorph condition.

**Male Reproductive System—Penis** De Beauchamp (1939) divided the genus *Dugesia* into a number of types on the basis of penis morphology. The New World species belonged to his simplest type in their possession of a short penis and a nonmuscular bifid seminal vesicle. The Old World forms were divided into two further groups. The *D. gonocephala* group was characterized by a large folded seminal vesicle and by the diaphragm (often accompanied by extensive eosinophil glands), which separates the vesicle from the ejaculatory duct. The last type was that of *D. lugubris* with a large penis and two very muscular seminal vesicles, one behind the other. Marcus (1953) added two further types, the simple one of *D. neumanni*, *D. glandulosa*, and *D. seclusa*, and the more complicated one represented by the other Australian species described by Weiss (1910).

Hyman (1931a) considered the male sexual apparatus unsatisfactory in general for taxonomic purposes. She did consider, however, the form and presence or absence of the seminal vesicles (bulbar cavities) to be of importance. Certainly such characters as the size and shape of the penis must be disqualified since they vary greatly with maturity and method of fixation. Nevertheless there are a number of other definite morphological features which are of significance.

The form of the seminal vesicle is related to the course of the vasa deferentia, and within the Dugesiidae there are a number of possibilities. The most primitive form would seem to be in those cases where the vasa deferentia unite to a common duct which enters the penis bulb. This is found in *Rhodax*, *Bopsula*, and *Cura pinguis*, and it is also characteristic of the Bothrioplanidae and some Cercyrinae, as well as the Probursidae. The next stage may be represented by the separate entrance of the vasa deferentia into the penis bulb without enlargement to form vesicles. Such is the case in *Dugesia seclusa*, and some other South American and Australian species of *Dugesia*. Enlargement of the ducts within the penis bulb gives the characteristic bifid seminal vesicle of most New World species, and the most advanced stage is represented by the enormous and very muscular vesicle of *D. gonocephala* and its allies, from which, no doubt, the double vesicle of *D. lugubris* is derived. The single enlarged vesicle of some New World *Dugesia* species is undoubtedly a secondary acquisition (Ball, 1971), and in some of these species either condition occurs.

The ejaculatory duct may be straight, and open from the tip of the penis papilla. This is the usual state in the Proseriata and Maricola, and also in the Paludicola, and thus probably is the plesiomorph condition. In a few Dugesiidae it is highly convoluted, and occasionally it may open dorsally or ventrally from the tip of the papilla. These represent different apomorph grades.

The glandular diaphragm separating the seminal vesicle and the ejaculatory duct in *D. gonocephala* and its allies is a new structure in the triclads

and is undoubtedly apomorph. So, too, the adenodactyl of *D. cretica*, *D. iranica*, and others is a new and apomorph character in the Paludicola. This type of adenodactyl, which projects from the penis bulb alongside the penis papilla, is quite different from the type found in *D. bactriana* and some Planariidae and Dendrocoelidae, as emphasized by de Beauchamp (1959). In the latter the adenodactyl is a discrete muscular-gland organ projecting into the atrium quite independently of the penis. The atrial adenodactyls of some Australasian forms (Weiss, 1910; Meixner, 1928) appear to present a third type in that they lack a true papilla. Only the first-mentioned type of adenodactyl is considered here.

These various character states may be coded as follows, lowercase letters representing the plesiomorph, and capitals the apomorph, grade:

- a Common vas deferens.
- A1 Separate vasa deferentia without enlargement to form a vesicle.
- A2 Vasa deferentia enlarge to form a bifid vesicle that is not very muscular.
- A3 Single large, usually round vesicle, which is very muscular.
- A4 Two large, muscular vesicles, one behind the other.
- b Ejaculatory duct straight and narrow.
- B Ejaculatory duct dilated and convoluted.
- c Ejaculatory duct opens terminally.
- C1 Ejaculatory duct opens subterminally.
- C-1 Ejaculatory duct opens supraterminally.
- d No diaphragm in the ejaculatory duct.
- D Diaphragm present.
- e Adenodactyls associated with the penis bulb not present.
- E1 One adenodactyl present.
- E2 Two adenodactyls present.

Of the possible character combinations the known Dugesiiidae have utilized thirteen, as shown in Table 1. Using the methods of Camin and Sokal (1965), I have constructed a cladogram treating these thirteen types as Operational Taxonomic Units (OTU) irrespective of their present taxonomic status. The result is shown in Fig. 4.

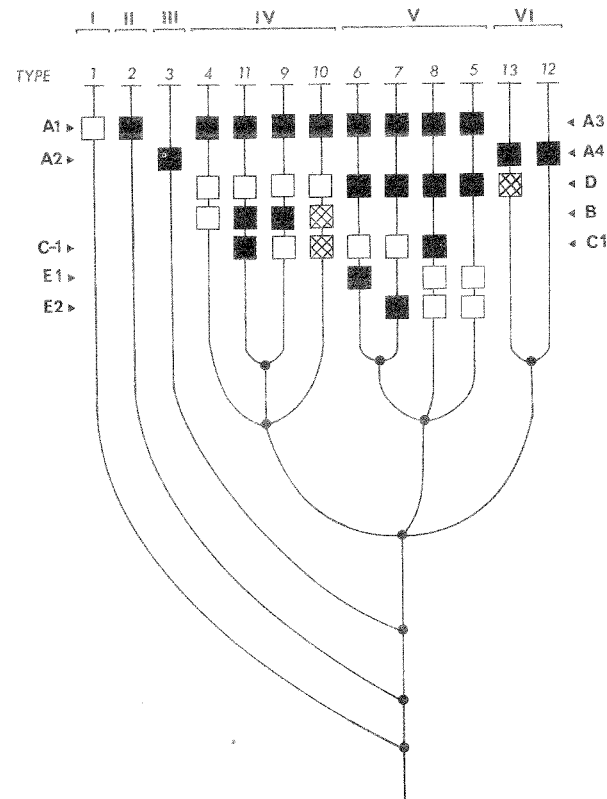
On the basis of this cladogram the Dugesiiidae may be divided into six groups as indicated, and it may be noted that Groups II to VI correspond closely to the divisions of de Beauchamp (1939) and Marcus (1953). However, this division does create some difficulties. In particular the position of *Cura paeta* (type 10) is equivocal since in terms of the characters presented by the ejaculatory duct (B and C1) it shows relationships with both Group IV and Group V. However, classifying it with Group V would involve not only convergence in character B but also secondary loss of character D. Similarly, the

**Table 1** The Thirteen Types of Male Copulatory Organ Found in the Dugesiiidae Defined on the Basis of Five Characters Discussed in the Text

Type	Characters	Examples
1	abcde	<i>Rhodax</i> , <i>Bopsula</i> , <i>C. pinguis</i>
2	A1bcde	<i>C. patagonica</i> , <i>D. arimana</i> , <i>seclusa</i> , <i>rincona</i> , <i>hoernesii</i> , <i>glandulosa</i> , <i>graffi</i>
3	A2bcde	<i>D. tigrina</i>
4	A3bcde	<i>C. foremanii</i> , <i>tinga</i> , <i>D. mertonii</i> , <i>fontinalis</i> , <i>schauinslandi</i>
5	A3bcDe	<i>C. evelinae</i> , <i>D. gonocephala</i>
6	A3bcDE1	<i>D. cretica</i> , <i>iranica</i>
7	A3bcDE2	<i>D. ilvana</i> , <i>transcaucasica</i>
8	A3bC1De	<i>D. japonica</i> , <i>nannophallus</i>
9	A3Bcde	<i>D. boehmigi</i>
10	A3BC1de	<i>C. paeta</i>
11	A3BC-1de	<i>D. montana</i>
12	A4bcde	<i>D. lugubris</i> , <i>polychroa</i>
13	A4bcDe	<i>D. ectophysa</i>

status of *D. ectophysa* (type 13) remains uncertain by virtue of its possessing a diaphragm (D) indicating relationship with Group V. Marcus (1953) has drawn attention to the similarity in the male copulatory organ between *D. ectophysa* and *D. lugubris* (type 12), but he also pointed out a number of organizational differences. There are also some important differences in the female apparatus, and it is thus possible that type 13 is best derived directly from type 5, and type 12 independently as given in the cladogram. This would also fit with their disjunct distribution (Fig. 5).

Of the groups delimited, Group I is confined to South America (Brazil) and Australasia. The geographical distributions of the remaining Groups II to VI are shown in Fig. 5. The following broad patterns may be discerned. The most primitive Groups I to III are confined to the Southern Hemisphere and North America. The most advanced types of Group V are spread throughout Africa and the Old World only, and Group IV shows possible relationships between Africa, Australasia, and possibly also the New World. However, the American representative of this Group, *C. foremanii* and *C. michaelsoni*, are probably examples of convergence or parallelism since they show so many other close relationships with *C. pinguis* and *C. patagonica* of Group II. Certainly the crenate vesicle of *C. michaelsoni* is quite different from the seminal vesicle of the *D. gonocephala* group (Böhmig, 1902, plate II, fig. 37). It may also be noted that there are no close connections between Europe and North America, and Asia and North America.



**Figure 4** Cladogram representing the evolutionary relationships of the thirteen types of male copulatory organ found in the Dugesiidae, and listed in Table 1. Open squares represent the plesiomorph, solid squares the apomorph, character state. Cross-hatching indicates noncongruent apomorph character states.

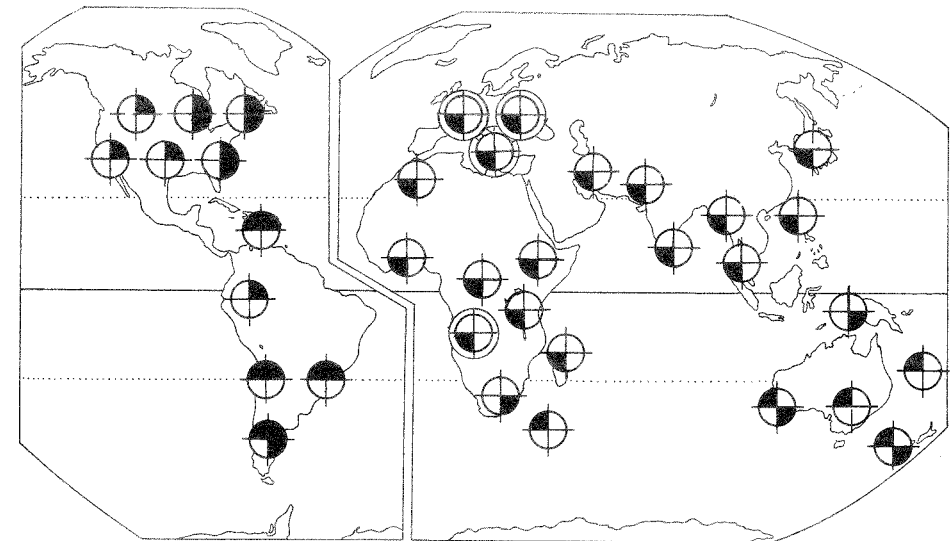
**Male Reproductive System—Testes** The male gonads present a number of character states for consideration, viz., their form, position, number, and distribution. Unfortunately, it is not easy to decide which of these various character states represents the plesiomorph, and which the apomorph, condition.

In most Paludicola, and all Maricola and Proseriata, the testes are basically round or oval follicles. Partially fused testes have been described in some Planariidae, as *Crenobia alpina* (Chichkoff, 1892, as *Planaria montana*), *Fonticola opisthogona* (Kenk, 1936), and *Fonticola velata* (Ball, 1972). As these species show few other close relationships, it is likely that the condition is secondarily acquired in each.

Fully fused testes are known only in *Hymanella retenuova* (Kenk, 1944,

as *Phagocata vernalis*?; see Ball, 1973) of the Planariidae, and in *Rhodax evelinae*. The latter species exhibits a number of other primitive features (Marcus, 1946) whereas *Hymanella* is clearly a specialized form closely related to *Fonticola*, and especially *F. velata*, with which it is easily confused (Ball, 1973). It is my opinion that the fusion of the testes is a secondarily acquired character, attained independently in each genus, follicular testes representing the primitive, and still general, condition.

The position of the testes, whether dorsal or ventral, is variable. Within the Turbellaria as a whole the original condition is probably represented by the dorsal follicles of the Acoela (Ax, 1963; Beklemishev, 1969). At the proseriate level of organization, however, they may be ventral, lateral, or dorsal (Meixner, 1928, p. 586), such variation occurring even within a single family. In *Bothrioplana* they are dorsal (Luther, 1960) or dorsolateral (Marcus, 1946), and in the Otomesostomidae they may be ventral or ventrolateral, as in the Monocelidae with the exception of *Monocelis anta* Marcus, 1954. In the Otoplanidae they are lateral or dorsolateral according to Meixner (1928), or lateral or ventrolateral according to Ax (1956, p. 601), who considers the latter condition to be primitive.



**Figure 5** The distribution of the Dugesiidae grouped according to the male copulatory organ, as shown in Fig. 4.

● Group II      ● Group III      ● Group IV  
● Group V      ● Group VI

Group I occurs in Brazil and Australasia.

Meixner (1928) considered that within the Maricola there is a relatively constant arrangement of the testes. Thus, in the primitive Stummerinae, Micropharynginae, and Uteriporidae, as in the Procerodidae of type IIA, they were described as ventral, in the Bdellouridae as lateral, and dorsal or dorsolateral in the Cercyrinae (type I) and the Procerodidae of type IIB. More recently, however, *Leucolesma corderoi*, a procerodid of type IIB, has been described with ventral testes (Marcus, 1948), which condition is also found in *Miava evelinae* Marcus, 1954, a member of the Bdellouridae. *Vatapa gabrielae* Marcus, 1948 of the Cercyrinae is also described with ventral testes. The recently defined Nesionidae, close to both the Bdellouridae and the Uteriporidae, possess ventral testes (Marcus, 1963), and in the Probursidae they are dorsal (Corrêa, 1960). Clearly the variation is greater than was suspected by Meixner.

So, too, with the Paludicola species with dorsal, and others with ventral, testes are found distributed within the three principal families. Even species which are otherwise very closely related show divergence in this character, as, for example, in the Australasian forms *Dugesia fontinalis* (dorsal) and *D. schauinslandi* (dorsal and ventral).

The systematic importance of the position of the testes has been denied by de Beauchamp (1939), but there can be little doubt that it has some value since within the Dugesiidae forms with ventral testes show a well-defined distribution pattern in that they are confined to the Southern Hemisphere and Nearctic, and they also possess other morphological features in common (Ball, 1971). The position of the testes thus may be useful for delimiting groups, but it would be difficult to use it alone for inferring phylogeny.

The number and distribution of the testes also show considerable variation. In most Paludicola they are very numerous and distributed over the whole length of the body. In the genus *Cura*, as defined by Marcus (1955), they are restricted to the prepharyngeal region. *C. schubarti* was an exception in that they extended to the bursa copulatrix, but this species belongs more properly in the genus *Dugesia* (Ball, 1971). In some species the number of testes is very small, perhaps two or three follicles on each side of the midline. Among the proseriates, very few, prepharyngeal testes are characteristic of the Bothrioplanidae and Otomesostomidae. In the Monocelidae the testes tend to be more numerous, although they are still prepharyngeal, and this is also the case in the Otoplanidae. The Maricola, too, show great variation in the number of testes (Marcus and Marcus, 1951).

Reference to the freshwater Proseriata would thus suggest that the primitive condition is represented by the few prepharyngeal follicles present in the species of *Cura* from Australasia and North and South America. On the other hand this condition is rare in the Dugesiidae and there is very great variation in the Maricola. This arrangement of the testes is not found in the

Planariidae or in the Dendrocoelidae, although there are species in these families in which the numerous testes are restricted to the prepharyngeal region.

On the basis of the three characters afforded by the male gonads, the Dugesiidae may be divided into six types, as in Table 2. The geographical distribution of the various types is shown in Fig. 6. The restriction of type 2 to the New World and New Zealand is especially noteworthy, as is the predominance of type 1 in Palaearctic and Aethiopia. Type 5 shows a curious disjunction in the New World which, possibly, will be dispelled by further collecting in northern South America.

As there is little evidence upon which to base judgments concerning the plesiomorphy or apomorphy of these types, their evolutionary relationships can be inferred only by reference to the cladogram (Fig. 4).

Superimposition of the various testis types on the penis morphology cladogram can be achieved with a fair degree of success. The principal difficulties lie with the African species of *Cura*. I have suggested elsewhere that the genus is not a uniform assemblage (Ball, 1971), and it is no longer accepted by de Beauchamp (1968). Under Marcus's (1955) definition of the genus the principal character is the restriction of the testes to the prepharyngeal region. However, he included *C. schubarti*, in which they extend to the bursa, as already mentioned. It may also be noted that in *D. montana* (Fig. 4, type 11) the testes do not extend beyond the copulatory apparatus, and this species shows closer relationships with the African *Cura* species than with the New World and Australasian *Cura* species. The latter forms are additionally characterized by the fact that the number of testes is reduced to a few discrete

Table 2 The Six Types of Testis Arrangement Found in the Dugesiidae

Type	Characters	Examples
1	Testes numerous, dorsal, pre- and postpharyngeal	<i>D. gonocephala</i> group, some New World and Australasian forms
2	Testes numerous, ventral, pre- and postpharyngeal	<i>D. tigrina</i> group, <i>D. schauinslandi</i>
3	Testes numerous, dorsal, prepharyngeal	<i>C. paeta</i> , <i>evelinae</i>
4	Testes numerous, ventral, prepharyngeal	<i>C. tinga</i>
5	Testes very few, dorsal, prepharyngeal	<i>C. foremanii</i> , <i>patagonica</i>
6	Testes very few, ventral, prepharyngeal	<i>C. pinguis</i>

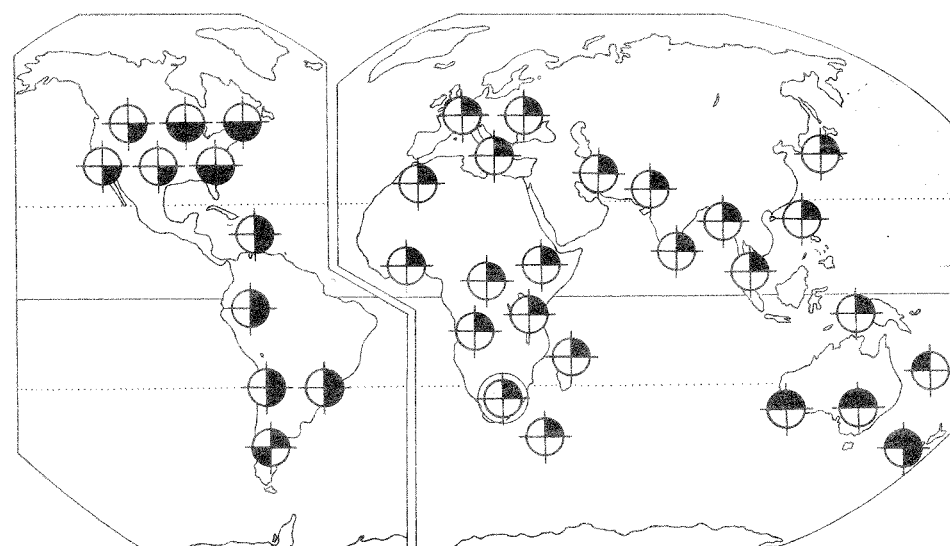


Figure 6 The distribution of the Dugesiidae possessing the different types of testis arrangement listed in Table 2.

- Type 1      ● Type 2      ● Type 5  
 ⊖ Type 6      ⊕ Types 3 and 4

follicles, which lie anterior to the pharynx. As will become apparent later, these forms also show some remarkable similarities in the female reproductive system. On the other hand, Dugesiidae which possess numerous testes have them distributed to the pharynx, copulatory apparatus, or the tail.

Rejecting the distribution of the testes as a phylogenetic character, we may recognize the following four groups of triclads:

- Group I Testes numerous and dorsal
- Group II Testes numerous and ventral
- Group III Testes very few and dorsal
- Group IV Testes very few and ventral

Of course the distribution of the testes in African forms remains a useful discriminatory character.

These groups are superimposed on the penis morphology cladogram in Fig. 7. The phyletic lines leading to types 2 and 4 clearly require further resolution. The numerous ventral testes of line 4 are exemplified only in *Cura tinga*, one of the most problematical species in many respects, and *D. schauin-*

*slandi*. As the latter species has been described as having either dorsal or ventral testes (Neppi, 1904; Nurse, 1950), its taxonomic position with respect to this character can be resolved without invoking parallelism or convergence. Considering *Cura tinga*, we may note that it is the only African species reported with ventral testes, and this condition seems likely to have been secondarily acquired. The analysis of the female system supports this conclusion. I have suggested earlier (p. 359) that *C. foremanii* and *C. michaelsoni* belong more properly in type 2 than in type 4, which also will be confirmed by the female system, and thus the phyletic line leading to type 4 becomes homogeneous.

It is not clear whether the dorsal testes of the New World *Dugesia*

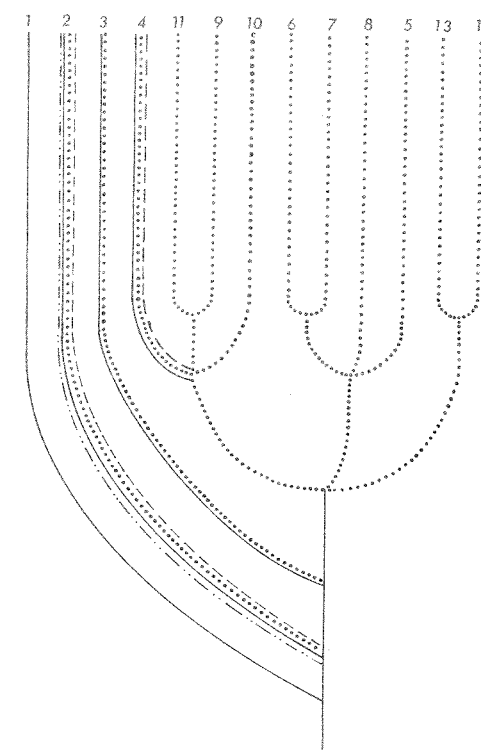


Figure 7 The various testis types found in the Dugesiidae superimposed on the cladogram of Fig. 4.

- Testes numerous and ventral
- ..... Testes numerous and dorsal
- Testes very few and dorsal
- · — · — Testes very few and ventral



species (types 2 and 3) have been derived independently of those of the Old World species. Certainly the testes of New World forms differ in that they are usually discrete, and large dorsoventrally, whereas those of the *D. gonocephala*-like forms (types 5 to 8) are usually small and aggregated into clusters. As the integrity of these two large subgroups is also supported by their external features (p. 355) and by the female system (p. 370), we may suspect this possibility.

These data suggest that the primitive condition is represented by ventral testes, but whether numerous (*Rhodax*, *Bopsula*) or few (*Cura pinguis*) cannot be stated with certainty. The most apomorph condition appears to be represented by the very numerous and small dorsal follicular groups of *D. gonocephala* and its allies.

**Female Reproductive System** Although the female reproductive system is generally acknowledged as being of great taxonomic importance (Meixner, 1928; Kenk, 1930a; Hyman, 1931a), it has been little used other than in generic definitions. Yet, it possesses many characters which are of diagnostic and phylogenetic significance.

A bursa copulatrix is usually present in the Paludicola, but it is greatly reduced in *Dugesia microbursalis* and absent in *Cura foremanii*. In my material of *C. pinguis* it is absent; Kawakatsu (1969b) found it present but reduced in size. Both Weiss (1910) and Nurse (1950) found a relatively large bursa in their material. Kenk (1935) considers the absence of a bursa in *C. foremanii* to be a primitive feature, and he is supported by my findings for *C. pinguis*. On the other hand it has been shown that the former species self-fertilizes, and does not cross-copulate, so that a well-developed bursa is unnecessary (Anderson, 1952; Anderson and Johann, 1958). Consequently it is unwise initially to place too much phylogenetic significance on this character.

Likewise, the presence of a bursa-intestinal duct is of little phylogenetic significance. Such a duct is found in divergent species in the DugesIIDae, Planariidae, and Dendrocoelidae (Steinböck, 1924; Marcus, 1946) and in a few Maricola (Corrêa, 1960), and possibly represents a recurrent ancestral character. Frequently its occurrence is constant within a species, and is thus a diagnostic character, but in other species such as *Polycelis tenuis*, it may or may not occur.

Of greater phylogenetic significance is the position of the bursa copulatrix. The Paludicola differ from the Terricola and most of the Maricola with a single genital pore in that the bursa is usually anterior to the penis. The posterior position of this organ in *Rhodax* is, therefore, yet another primitive feature retained by this genus.

The possible taxonomic importance of the musculature of the bursal

stalk has not always been recognized, with the result that in many species descriptions there are no data concerning this point. In most Paludicola, as in nearly all Maricola for which data are available, the musculature of the bursal stalk consists of two layers. In most Paludicola the inner layer is of circular fibers and the outer layer is of longitudinal fibers, and thus the sequence of muscle layers found in the body wall and atrium continues to the bursal stalk. However, in some DugesIIDae the sequence of muscles in the bursal stalk is reversed so that the circular layer is on the outside. That this situation is restricted to some species from Australasia and most from Africa, Orientalis, and Palaearctis suggests that it is an apomorph condition. It also appears that most Maricola have the longitudinal layer on the outside, an exception being *Procerodes ohlini*, in which the muscle layers of the bursal stalk are intermingled (Böhmig, 1906), a condition which may exist also in *Probursa veneris* Hyman, 1944, although I have found the available slides of the latter difficult to interpret in this respect. Regrettably, more recent descriptions of the Maricola do not include the bursal stalk musculature, but I have studied as yet undetermined species of Procerodidae from eastern Canada, and from Saint Helena, together with original slides of *Procerodes pacifica* Hyman, 1954 and *Nesion arcticum* Hyman, 1956 and in all but one of these the outer of the two muscle layers is longitudinal. The exception, from Saint Helena, has lost the outer layer of longitudinal musculature. It may be noted, however, that in *Nesion* the circular layer is extraordinarily well developed, and less so in *Probursa veneris*, but in most *Procerodes* species the bursal musculature is very weak. These data are consistent with the suggestion that a bursal stalk musculature of two layers, the outer being longitudinal, is plesiomorph, and it is relevant to note that the musculature of the atrium femininum of the proseriate *Otomesostoma auditivum* is similar in this respect (Hofsten, 1907).

Most variation in the bursal stalk musculature occurs in those species in which the inner layer is longitudinal. Some species, viz., *D. astrocheta* and *D. burmaensis*, have developed an extra layer of longitudinal fibers outside the circular layer, and in many others there is an outer layer of longitudinal fibers reinforcing the ectal region of the bursal stalk. These are undoubtedly apomorph conditions, as is the unusual and very strong sphincter composed of circular fibers which is found in the ectal region of the bursal stalk of *D. fontinalis*.

In a few DugesIIDae there is an extraordinary thickening of the outer circular layer, so that this equals or exceeds the diameter of the rest of the bursal stalk as in *Cura paeta* and *tinga* from South Africa, and in *Dugesia montana* from New Zealand. A tendency in this direction is also noticeable in a number of other African and Australian *Dugesia* species. This excessive thickening is unknown in the other Paludicola, and is almost certainly apomorph, but is

paralleled by the marine form *Nesion*, although here it is bounded by the outer longitudinal fibers.

The interpretation of the bursal stalk musculature of some species has proved to be difficult. Kawakatsu's (1969b) description of *Cura pinguis*, for example, conflicts with that of de Beauchamp (1968) and Weiss (1910), who indicate clearly that the outer layer is circular. Since drawing attention to this (Ball, 1970), I have had the opportunity to examine this species and find the bursal stalk to be very similar to that of *Cura foremanii* in that the circular muscle fibers are quite prominent whereas the longitudinal fibers are very difficult to discern. However, I am of the opinion that in both species there are scattered, not continuous, longitudinal fibers outside the circular muscles. The entire musculature, however, is very weak, and the histology of the bursal stalk is very reminiscent of the Procerodidae of Meixner's type IIA which I have examined.

A further difficulty is presented by *Dugesia schauinslandi*. Neppi (1904) indicates that the outer muscle layer of the bursal stalk is longitudinal, whereas my own observations on this species indicate the opposite. The probability of an error by Neppi is supported by the fact that in the same paper she also described *D. neumanni* as having an outer layer of longitudinal muscles, which conflicts with the more recent description of Marcus (1955), who had better-preserved material.

The bursal stalk is usually a smoothly curved duct of relatively uniform diameter, which appears to be the primitive condition, and in some cases the thickness of the duct may be of diagnostic significance (Ball, 1970, 1971) at the species level. In two species, however, *Dugesia montana* and *Cura tinga*, the bursal stalk is exceptionally dilated and its walls are thrown into folds or creases. It is of more than passing interest to note that these are two of the three species which are characterized by excessive thickening of the circular muscle layer (Fig. 9).

The course of the oviducts and shell glands is an important taxonomic character which has been discussed previously. It was concluded that the primitive condition was that in which the oviducts and shell glands open into the bursal stalk. In Meixner's type IIC, comprising the Australian species *D. hoernesii* and *D. boehmigi* of Weiss (1910), a condition apparently intermediate between the Dugesiidae and the Planariidae occurs. A long common oviduct, receiving the shell glands, opens into the atrium at the base of the bursal stalk. A common oviduct occurs in other Dugesiidae, but it opens into the bursal stalk, as do the shell glands. However, in many species there is variation in this character, and in some individuals there is a common oviduct, and in others not (see Ball, 1971), and so it is of little phylogenetic significance. Similarly, I attach little phylogenetic importance to the position of the openings of the oviducts into the bursal stalk, whether proximal or distal to the atrium, although it is a useful diagnostic character.

The caudal dichotomy in the oviducts of some species has been a controversial character. Neppi (1904) was the first to observe this peculiarity when she described *Dugesia schauinslandi* from New Zealand, and noted that the oviducts dispatched a caudal dichotomy to the vitellaria of the posterior part of the body. Meixner (1928, p. 576, note 5), however, intimated that Neppi had mistaken a simple doubling back of the oviducts, or recurvature, for a true dichotomy, and consequently Marcus (1946) considered that *Rhodax* was unique in its possession of branched oviducts. In her study of the New Zealand triclads Nurse (1950) redescribed *D. schauinslandi* under the name *Spathula limicola* (see de Beauchamp, 1951a) and described a new and closely related species as *Spathula fontinalis*. She found that both species possessed branched oviducts, thus confirming the findings of Neppi (1904). Unfortunately, de Beauchamp (1951a) misunderstood Nurse's descriptions and believed that she was erecting her new genus *Spathula* on the presence of a common oviduct, rather than on the branching of each oviduct, an error which was carried over into later papers (de Beauchamp 1959, 1961). However, I have examined specimens of both *D. schauinslandi* and *D. fontinalis* and can confirm the accuracy of Nurse's and Neppi's descriptions in this respect.

The question may now be raised as to whether the branched oviducts of *Rhodax* and the two Australian species represent a plesiomorph or apomorph condition. The only other Seriata with branched oviducts are *Otomesostoma* and *Bothrioplana* (Marcus, 1946), and this link with the freshwater Proseriata indicates that the condition is most likely a primitive retention. It is also relevant to note that *Rhodax* is one of the few Paludicola known which reproduces paratomically; whether or not *D. schauinslandi* and *D. fontinalis* possess this capability is not known. In some Dugesiidae it has proved possible to induce the formation of supernumerary reproductive organs artificially, and in such cases branching of the oviducts has been observed (Okugawa, 1955, p. 7). Further, I have slides of an undescribed species of *Dugesia* from South Africa which show evidence of both paratomy and branching of the oviducts. It is possible, therefore, that branched oviducts are related to the phenomenon of paratomy, but this does not invalidate the conclusion concerning the plesiomorphy of the character since paratomy is primitive within the Turbellaria as a whole, it being the normal method of reproduction in many Macrostomida and Catenulida (Beklemishev, 1969).

The nine characters afforded by the female system, as discussed above, may be coded as follows. As previously, lowercase letters indicate the plesiomorph condition.

- a Bursa copulatrix posterior to penis.
- A Bursa copulatrix anterior to penis.
- b Bursal stalk with two muscle layers.
- B Bursal stalk with three muscle layers.

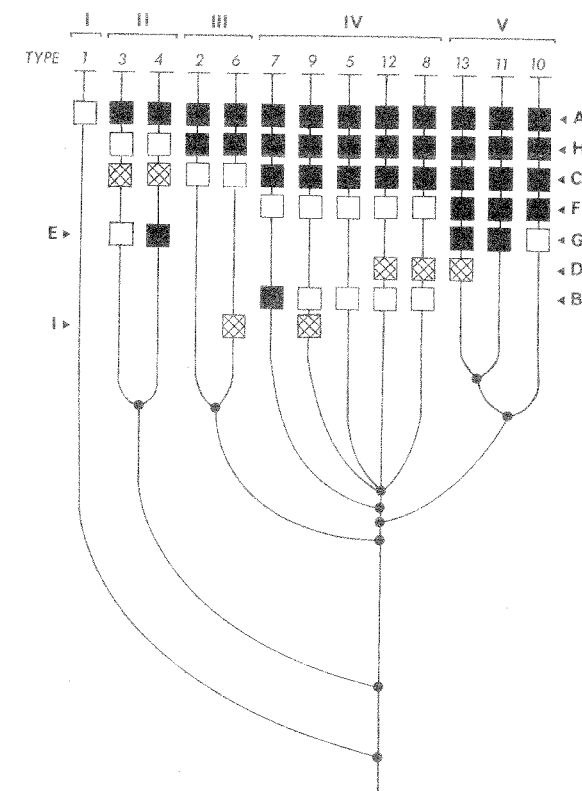


- c Inner muscle layer of the bursal stalk circular.
- C Inner layer longitudinal.
- d Ectal reinforcement absent.
- D Ectal reinforcement present.
- e Bursal stalk without strong sphincter.
- E Bursal stalk with strong sphincter.
- f Circular muscles of bursal stalk normal.
- F Circular muscle layer greatly thickened.
- g Bursal stalk relatively uniform.
- G Bursal stalk dilated and convoluted.
- h Oviducts with caudal dichotomy.
- H Oviducts without caudal dichotomy.
- i Oviducts and shell glands enter bursal stalk.
- I Oviduct enters atrium, shell glands enter common oviduct.

Of the numerous possible character combinations the known Dugesiidae have utilized thirteen, as shown in Table 3, and a cladogram of these types has been constructed (Fig. 8). In this scheme all characters were coded as two state characters, and consequently *D. polychroa* is not included since it could not be coded for characters B, C, and F. In this species the muscle layers of the bursal stalk are intermingled and it is impossible to say whether this was derived from Group II or from Groups III and IV (Fig. 8, character C).

**Table 3 The Thirteen Types of Female Reproductive Apparatus Found in the Dugesiidae, Defined on the Basis of Nine Characters Discussed in the Text**

Type	Characters	Examples
1	a(b) (c)defghi	<i>Rhodax</i>
2	AbcdefgHi	<i>Bopsula</i> , <i>C. foremanii</i> , <i>pinguis</i> , <i>patagonica</i> , <i>D. tigrina</i> , <i>annandalei</i> , <i>seclusa</i> , <i>glandulosa</i> , <i>graffi</i>
3	AbCdefghi	<i>D. schauinslandi</i>
4	AbCdEfgHi	<i>D. fontinalis</i>
5	AbCdefgHi	<i>D. indica</i> , <i>nannophallus</i> , <i>izuensis</i> , <i>batuensis</i> , <i>gonocephala</i> , <i>monomyoda</i> , <i>ectophysa</i>
6	AbcdefgHI	<i>D. hoernesi</i>
7	ABCdefgHi	<i>D. burmaensis</i> , <i>astrocheta</i>
8	AbCDefgHi	<i>D. japonica</i> , <i>gonocephala</i> , <i>lindbergi</i> , <i>iranica</i> , <i>bactriana</i> , <i>neumanni</i>
9	AbCdefgHI	<i>D. boehmigi</i>
10	AbCdeFgHi	<i>C. paeta</i>
11	AbCdeFGHi	<i>D. montana</i>
12	AbCDefgHi	<i>C. evelinae</i>
13	AbCDeFGHi	<i>C. tinga</i>



**Figure 8** Cladogram representing the evolutionary relationships of thirteen types of female reproductive apparatus found in the Dugesiidae, and listed in Table 3. Open squares represent the plesiomorph, solid squares the apomorph, character state. Cross-hatching indicates noncongruent apomorph character states.

Further consideration of characters D (ectal reinforcement of the bursal stalk) and I (common oviduct enters atrium) is necessary. Character D is clearly incompatible with character F (exceptionally thick circular muscles of the bursal stalk), and I have had to reach a decision as to which is the most useful character. I have selected F on the basis that it brings together *Cura paeta*, *C. tinga*, and *D. montana*, three species which show close relationships in the male copulatory organ and the distribution of the testes. Further, the stability of character D is open to question. *Dugesia gonocephala* has been described by de Beauchamp (1961, p. 82, fig. 39) as possessing a third muscle layer reinforcing the ectal region of the bursal stalk, whereas Marcus (1953)

does not indicate this. Therefore I have accepted character F as being the most reliable.

Meixner's (1928) reproductive apparatus type IIC comprises those Australian species of *Dugesia* which possess character I—a common oviduct into which the shell glands open, and which itself enters the atrium at the base of, and posterior to, the bursal stalk. This would seem to be a good apomorph character uniting *D. hoernesii* (Fig. 8, type 6) and *D. boehmigi* (type 9), but there are good reasons for not placing too much weight on it. In the first place the apparent position of the oviduct may depend upon the degree of contraction of the preserved specimen. It is quite obvious, for example, that Weiss based her description of *D. hoernesii* on a contracted animal (Weiss, 1910, fig. 21). There are other species in which the oviducts open into the bursal stalk extremely close to its junction with the atrium (e.g., *D. nannophallus*), and it is easy to see how misinterpretation could occur.

A second, more important, factor results from my examination of paratypical material of *D. montana* from New Zealand. Nurse's (1950) description of this species is perfectly adequate for its recognition, and there can be no doubt of the identity of the material examined by me. Nevertheless, there are some minor points which need clarification. My own interpretation of the reproductive apparatus of *D. montana* is shown in Fig. 9; it may be compared with that of Nurse (1950, plate 46, fig. 1). The blind posterior diverticulum of the atrium, not described by Nurse, receives many eosinophil glands, presumably the shell glands, and could easily be mistaken for a common oviduct. In some respects it is comparable with the nonglandular diverticulum of *D. tigrina* (Ball, 1971). The problem is compounded by the fact that the oviducts do not extend beyond the bursal stalk and recurve to it in the usual way. On the contrary they run directly to the stalk and enter it on its frontal, rather than lateral, face. This course of the oviducts is difficult to trace, but it shows on both sets of sections I have examined, and it is curiously reminiscent of the condition in *Probursa* (Corrêa, 1960). A third Australasian species, *D. mertoni* of the Kai Islands, is figured in the original description as having a common oviduct which enters the atrium at the base of the bursal stalk (Steinmann, 1914, p. 116, fig. 3: the labels for "Ovidukt" and "Drüsensack" have been transposed); the shell glands are not described. Meixner (1928) does not place this species in his type IIC, but allies it with *D. tigrina*, *D. glandulosa*, and others in type IIA.

A reexamination of the course of the oviducts in these Australian species is certainly warranted. From the data outlined above I am unable, for the present, to accept Meixner's type IIC as representing a natural grouping, and prefer to base decisions concerning the relationships of *D. hoernesii* and *D. boehmigi* on less equivocal characters. On the basis of the male apparatus and of the musculature of the bursal stalk I consider *D. hoernesii* to be much closer to the *D. tigrina* group than *D. boehmigi* is.

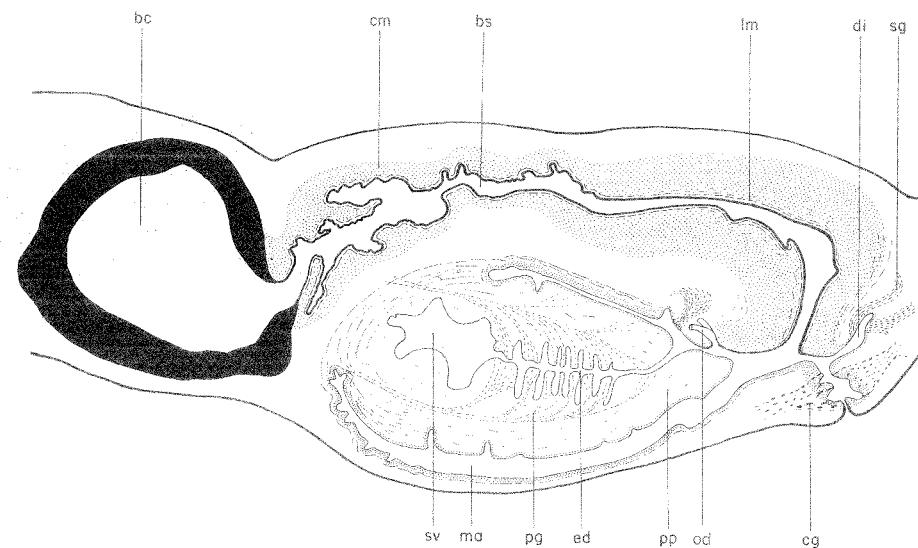


Figure 9 *Dugesia montana*. Paratype. Reconstructed sagittal section of the copulatory organs, viewed from the left side. Diagrammatic. bc, bursa copulatrix; bs, bursal stalk; cg, cement glands; cm, circular muscle; di, diverticulum; ed, ejaculatory duct; lm, longitudinal muscle; ma, male atrium; od, left oviduct; pg, penis glands; pp, penis papilla; sg, shell glands; sv, seminal vesicle.

Returning to the cladogram of the female reproductive system (Fig. 8), I have divided the various types into six Groups, as shown. The sixth Group is formed by *D. lugubris*. The geographical distribution of these Groups is shown in Fig. 10, which may be compared with Fig. 5. Again it is noteworthy that the most primitive Groups, I to III, are confined to the Southern Hemisphere and North America. The most advanced types of Groups IV and VI are spread throughout Africa and Palaearctis and Orientalis, and possibly Australia. Group V shows possible relationships between South Africa and Australasia. These data compare well with the broad patterns obtained from the analysis of the male system (p. 359), and once more the absence of Europe–North America and Asia–North America relationships is prominent.

In comparing the female reproductive system (F Groups) with the male system shown in Fig. 4 (M Groups), a number of similarities and differences become apparent. M Group VI and F Group VI are identical, with the qualification concerning *D. ectophysa* discussed earlier (p. 359). M Group V is equivalent to F Group IV, with the exception of *D. boehmigi*, whose position appears equivocal. M Groups II and III are equivalent to F Group III with the exceptions of *Cura pinguis* and *Bopsula*, which appear in M Group I. The association of these forms with other members of M Group II is, however,

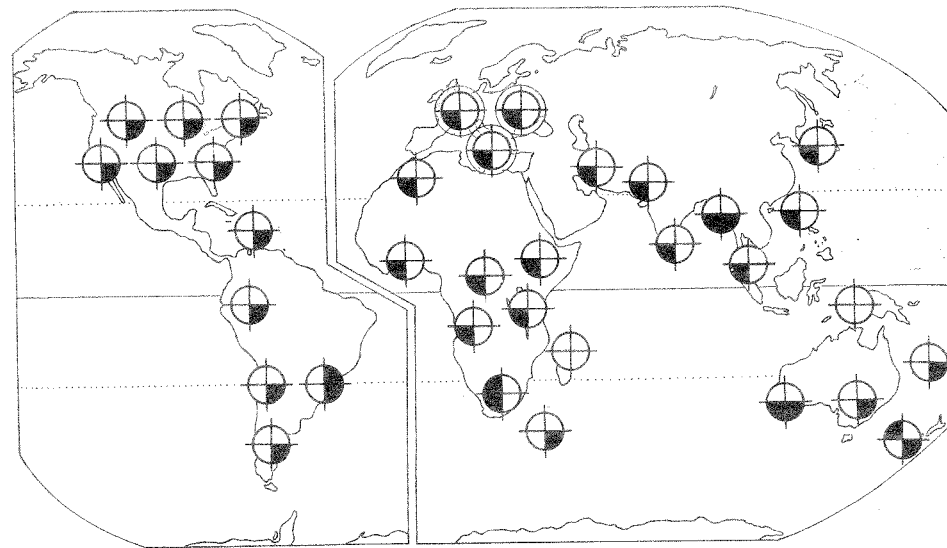


Figure 10 The distribution of the Dugesiidae grouped according to the female reproductive apparatus, as shown in Fig. 8.

- Group I      ◐ Group III      ⊕ Group IV  
 ◑ Group V      ⊕ Group VI (*D. polychroa*)

Group II is confined to New Zealand.

justifiable. *Bopsula* is known from only one specimen, and Marcus (1946) considers it to be derivable from a *Dugesia* of the *D. tigrina* type, which it resembles in outward appearance. However, *Bopsula* is so aberrant in a number of respects that its exact placing in my phylogenetic scheme is best deferred until further specimens are found. The unusual duct between the bursal stalk and the penis bulb is paralleled by the unusual oviducts of the marine form *Nexilis*. The close relationships of *C. pinguis* and *C. foremanii* are confirmed by other characters relating to the testes and the female reproductive apparatus, and these carry more classificatory weight than the primitive retention of a common vas deferens in *C. pinguis*. M Group IV is equivalent, with the exception of *D. boehmigi*, to F Groups II and IV, and since the differences between the latter two Groups are so marked, their separation seems justified.

With these limitations the correlations between the three cladograms of Figs. 4, 7, and 8 and between the character maps of Figs. 3, 5, 6, and 10 are remarkably good, so much so that it appears both useful and justifiable to propose a classification of the Dugesiidae based on the major groupings

demonstrated. *Rhodax* would be representative of the most plesiomorph form, and *D. gonocephala* of the most apomorph.

The interrelationships of the more plesiomorph forms are difficult to determine; this is often the case for primitive groups. If *Rhodax* is considered to be closest to the ancestral freshwater triclad, then its phylogenetically closest relatives would appear to be within either the *D. tigrina*- or *C. foremanii*-like forms. On the basis of head shape, the male copulatory organ, and the female reproductive apparatus either group could qualify as closest relative by virtue of some of their members. What does seem clear is that the *D. tigrina* group has not given rise to any of the higher forms and has diversified in isolation in the New World, and to a lesser extent across the Southern Hemisphere. The independent derivation of the *D. gonocephala*-like (and subsequently *D. lugubris*-like) forms and the *D. montana*-like forms from the *Cura pinguis* group not only fits the biogeographical data rather well (see below), but also agrees with the suggestion made earlier (p. 365) that the dorsal testes of these higher groups are derived independently of the dorsal testes of some members of the *D. tigrina* group.

It remains to be seen, from future work, whether other characters are confirmatory of the groupings proposed here. Some preliminary comments may be made on the basis of limited data from the literature, but to clarify discussion, it seems advisable to define these groupings formally.

### Revision and Synopsis

In view of the difficulties resulting from parallelism and convergence of producing a phylogenetically based classification of the Dugesiidae, I have adopted a conservative approach to the nomenclature of the group. Recognizing that this preliminary attempt is open to considerable refinement in the future, I have kept nomenclatural changes to a minimum and given the new categories the rank of subgenera. This permits discussion and argument without affecting the established binominal nomenclature. One change, however, has been unavoidable. The genus *Cura* clearly cannot be allowed to stand as recognized by Marcus (1955) and Kawakatsu (1969b). According to the analyses performed here *C. paeta*, *C. tinga*, *C. wimbimba*, and *C. evelinae* are far removed from *C. pinguis*, *C. patagonica*, and *C. foremanii*, and their association in the same genus, distinct from *Dugesia*, does not reflect their phylogenetic relationships. Thus, I have restricted *Cura*, as a subgenus, to the American and Australasian forms. The genus *Cura* has previously been abandoned by de Beauchamp (1951a, 1968), although other workers have declined to follow him. It will be noted that the principal subgenera proposed below are similar to the divisions of the genus *Dugesia* proposed by de Beauchamp (1939) on the basis of the male copulatory organ.

**A Synopsis of the Dugesiliidae** In the list which follows, species marked with an asterisk have been studied by me. A series of notes dealing with problematical taxa follows the list.

Genus *Rhodax* Marcus, 1946

\**Rhodax evelinae* Marcus, 1946

Genus *Bopsula* Marcus, 1946

*Bopsula evelinae* Marcus, 1946

Genus *Dugesia* Girard, 1850

Subgenus *Dugesia* Girard, 1850

Head of low triangular form. Seminal vesicle an enlarged muscular cavity. Diaphragm present. Bursal stalk musculature of inner longitudinal fibers surrounded by circular muscles. Testes numerous, forming dorsal clusters scattered throughout the body length (Note 1).

*D. (D.) gonocephala* (Dugès, 1830); \**D. (D.) cretica* (Meixner, 1928; Kenk, 1930); \**D. (D.) iranica* Livanov, 1951 (= *Euplanaria cretica*: de Beauchamp, 1936); *D. (D.) transcaucasica* Livanov, 1951; *D. (D.) taurocaucasica* Livanov, 1951; *D. (D.) praecaucasica* Livanov, 1951; *D. (D.) etrusca* Benazzi, 1946; *D. (D.) ilvana* Lepori, 1948; *D. (D.) sicula* Lepori, 1948; *D. (D.) benazzii* Lepori, 1951; *D. (D.) neumanni* (Neppi, 1904) (Note 2); *D. (D.) congolensis* de Beauchamp, 1951; *D. (D.) milloti* de Beauchamp, 1953; *D. (D.) machadoi* de Beauchamp, 1953; *D. (D.) lamottei* de Beauchamp, 1953; \**D. (D.) monomyoda* Marcus, 1953; *D. (D.) astrocheta* Marcus, 1953; *D. (D.) colapha* Dahm, 1967; *D. (D.) ectophysa* Marcus, 1953 (Note 3); \**D. (D.) japonica* Ichikawa and Kawakatsu, 1964; *D. (D.) indica* Kawakatsu, 1969; \**D. (D.) nannophallus* Ball, 1970; \**D. (D.) batuensis* Ball, 1970; ?*D. (D.) annandalei* (Kaburaki, 1918) (Note 4); ?*D. (D.) izuensis* Kato, 1950; ?*D. (D.) mertoni* (Steinmann, 1914); ?*D. (D.) jeanneli* (de Beauchamp, 1913); \*?*D. (D.) evelinae* (Marcus, 1953); \*?*D. (D.) lindbergi* de Beauchamp, 1959; \*?*D. (D.) bactriana* de Beauchamp, 1959.

Subgenus *Girardia* nom. n.

Head typically high triangular, but may be truncate. Seminal vesicle absent or of the bifid nonmuscular type. Diaphragm absent. Bursal stalk musculature of inner circular muscles surrounded by longitudinal fibers. Testes numerous, distributed throughout the body length (exception *schubarti*), and usually ventral.

\**D. (G.) tigrina* (Girard, 1850); *D. (G.) microbursalis* (Hyman, 1931b); \**D. (G.) dorotocephala* (Woodworth, 1897); *D. (G.) aurita* (Kennel, 1888); *D. (G.) festai* (Borelli, 1898); *D. (G.) polyorchis* (Fuhrmann, 1914); \**D. (G.) anceps* (Kenk, 1930) (= *dubia* Borelli, 1895); *D. (G.) nonatoi* Marcus, 1946; *D. (G.) arndti* Marcus, 1946; *D. (G.) rincona* Marcus, 1954; *D. (G.) sanchezi* Hyman, 1959; *D. (G.) jimi* Martins, 1970 (doubtfully distinct from *D. tigrina*);

*D. (G.) dimorpha* (Böhmgig, 1902); \**D. (G.) antillana* Kenk, 1941; *D. (G.) schubarti* (Marcus, 1946); *D. (G.) hypoglauca* Marcus, 1948; \**D. (G.) arimana* Hyman, 1957; *D. (G.) paramensis* (Fuhrmann, 1914); *D. (G.) andina* (Borelli, 1895); \**D. (G.) chilla* Marcus, 1954; *D. (G.) veneranda* Martins, 1970 (doubtfully distinct from *D. chilla*); *D. (G.) seclusa* (de Beauchamp, 1940); *D. (G.) graffi* (Weiss, 1910); *D. (G.) glandulosa* (Kenk, 1930) (= *striata* Weiss, 1910); *D. (G.) hoernesi* (Weiss, 1910) (Note 5).

Subgenus *Cura* Strand, 1942

Head truncate, or of the low triangular form. Seminal vesicle primitively absent, but enlarged form present in two species (*foremanii*, *azteca*). Bursal stalk musculature of inner circular muscles surrounded by a fine layer of longitudinal fibers. Testes very few, prepharyngeal. Bursal stalk frequently expanded at entrance into roof of male atrium to form a female atrium, which receives the shell glands.

\**D. (C.) foremanii* (Girard, 1852); *D. (C.) patagonica* (Borelli, 1901); *D. (C.) michaelseni* (Böhmgig, 1902); \**D. (C.) pinguis* (Weiss, 1910); *D. (C.) azteca* (Benazzi and Giannini, 1971); ?*D. (C.) falklandica* (Westblad, 1952) (Note 6).

Subgenus *Neppia* nom. n.

Head typically of low triangular form. Seminal vesicle a single muscular cavity, diaphragm absent. Bursal stalk musculature of inner longitudinal fibers surrounded by an exceptionally thick layer of circular fibers. Testes numerous, dorsal (exception *tinga*), not extending beyond the copulatory apparatus. Ejaculatory duct typically convoluted.

\**D. (N.) montana* Nurse, 1950; \**D. (N.) paeta* (Marcus, 1955); \**D. (N.) tinga* (Marcus, 1955); *D. (N.) wimbimba* (Marcus, 1970); ?*D. (N.) boehmigi* (Weiss, 1910) (Note 7).

Subgenus *Spathula* Nurse, 1950

Head rounded or spathulate, or of the low triangular form. Seminal vesicle a single cavity. Diaphragm absent. Bursal stalk musculature of inner longitudinal muscles surrounded by circular fibers. Testes numerous, dorsal or ventral, and extending throughout the body length. Oviducts branched caudally (Note 8).

\**D. (S.) schauinslandi* (Neppi, 1904); \**D. (S.) fontinalis* (Nurse, 1950).

Subgenus *Schmidtea* nom. n.

Head of the low triangular form. Seminal vesicle consisting of an intrabulbar muscular cavity and an extrabulbar muscular cavity. Diaphragm absent. Bursal stalk musculature of intermingled circular and longitudinal fibers. Testes numerous, dorsal, extending throughout the body length.

*D. (S.) lugubris* (Schmidt, 1862) *sensu* Reynoldson and Bellamy, 1970;  
 \**D. (S.) polychroa* (Schmidt, 1862) *sensu* Reynoldson and Bellamy, 1970.

The following species, described under the name *Planaria*, but presumably of the genus *Dugesia*, are inadequately described and are here considered to be *taxa dubia*.

*P. aborensis* Whitehouse, 1913a; *P. tiberiensis* Whitehouse, 1913b; *P. salina* Whitehouse, 1913b; *P. barroisi* Whitehouse, 1913b; *P. fissipara* Kennel, 1888 (possibly identical with *Rhodax*); *P. similis* Böhmig, 1902; *P. ambigua* Böhmig, 1902; *P. laurentiana* Borelli, 1897; *P. hymanae* Sivickis, 1928; *P. bilineata* Kaburaki, 1918; *P. andamanensis* Kaburaki, 1925; *P. rava* Weiss, 1910; *P. tanganyikae* Laidlaw, 1906; *P. venusta* Böhmig, 1897; *P. brachycephala* Böhmig, 1897; *P. iheringii* Böhmig, 1887.

Concerning *D. aberana* Neppi, I can find no mention of this species other than in de Beauchamp (1951b). Similarly, a species of *Dugesia* belonging to Meixner's type IIC seems never to have been described (see Meixner, 1928, p. 583). It is characterized by the strengthening of the musculature of the ectal part of the bursal stalk, which is a distinctive feature of *D. fontinalis*.

#### Notes to the List

1 A number of species which one would expect to fall into the subgenus *Dugesia* appear to be excluded by virtue of certain characters. *D. izuensis*, *annandalei*, and *lindbergi* all lack a diaphragm in the ejaculatory duct. The first two species are known only from the types, now lost, as described by the original authors, and so cannot be considered further. I have specimens from Malaya of a species which I assign to *D. lindbergi* on the basis of penis morphology and the distribution of the muscles covering the bursal stalk. These latter are weak entally and become stronger ectally (de Beauchamp 1959, p. 35). The histological condition of my material is poor, but a diaphragm is discernible. There can be little doubt of the close relationship of *D. lindbergi* to the other Oriental species of the subgenus (Ball, 1970). It may also be noted that in the specimens of *D. bactriana* available to me I cannot recognize a diaphragm, although this is described and figured by de Beauchamp (1959).

The exact status of *D. jeanneli* is also problematical. Originally described by de Beauchamp (1913) with later corrections (de Beauchamp, 1939), it was placed in the genus *Cura* by Marcus (1955). Of the subgenera recognized here it certainly cannot be assigned to either *Cura* or *Neppia*, and de Beauchamp (1939) considers its affinities to be with the *D. gonocephala*-like forms, in which case the reduced musculature of the bursal stalk, and the restriction of the testes to the prepharyngeal region must be considered secondary. Similarly, the diaphragm and bursal stalk musculature lead me to place *D. evelinae* in this group for the present, though its status needs clarification. In the slides available to me a diaphragm is not apparent.

*D. burmaensis* and *D. astrocheta* are unusual in that they possess a three-layered musculature of the bursal stalk, but as in all other respects they approach the *D. gonocephala*-like forms, notably in the possession of a distinct diaphragm in the ejaculatory duct, I consider the acquisition of the third, outer longitudinal layer to be secondary.

*Dugesia mertoni* (Steinmann, 1914) is inadequately described for its proper placement. I assume it belongs in this subgenus.

*Dugesia absoloni* (Komarek, 1919) regrettably is known only from not fully mature material (Meixner, 1928, p. 577, note 8), and so its exact relationships cannot be determined. It was originally described as a terrestrial triclad, under the name *Geopaludicola*, which name Kenk (1930) retains with subgeneric rank.

2 Both de Beauchamp (1939) and Marcus (1953) refer to *D. neumanni* as having a simple type of male copulatory organ. It seems to me that the presence of a diaphragm, the musculature of the bursal stalk, the arrangement of the testes, and the head shape, all justify its placement in this subgenus.

3 Placed in this subgenus, and not *Schmidtea* on the basis of the presence of a diaphragm, the bursal stalk musculature, and the comparative remarks of Marcus (1953).

4 *Dugesia annandalei* separates with the *D. tigrina* group according to the analysis of the female system (Fig. 8). I consider such a relationship unlikely. The original description is based on a single specimen, now lost. De Beauchamp (1951a), however, has suggested that this species is identical with *D. glandulosa*, which would be of great biogeographical interest.

5 *Dugesia hoernesii* belongs to Meixner's unusual type IIC, which I do not accept in this revision. The folds and contractions of the penis as figured by Weiss (1910, plate XIX, fig. 21) are very reminiscent of the condition figured in *D. festai* by Hyman (1939) and in *D. tigrina* by Kenk (1935). The muscular gland organ, or adenodactyl, missed by Weiss but recognized in the original sections by Meixner (1928, p. 577, note 10), similar to the one found in *D. boehmigi*, is in my opinion without phylogenetic significance. I disagree with Meixner's view that the two species are closely related; penis morphology and the histology of the bursal stalk argue strongly against this.

6 The description of *Cura falklandica* is inadequate for its proper placement. I assume it belongs in this subgenus.

7 The relatively strong circular musculature of the bursal stalk and the convoluted or dilated ejaculatory duct are the principal reasons for tentatively assigning this problematical species to the subgenus *Neppia* (compare Fig. 9 with Weiss, 1910, plate XXI, fig. 28).

8 Contrary to the philosophy stated earlier in this paper this category is defined largely by plesiomorph characters. However, only two species are involved, and their peculiarities are such that their separation seems to be both justifiable and useful at the present.

The proposed subgenera could, of course, be divided into further sub-



units, perhaps with the rank of "species groups"; I have already, for example, separated off some Caribbean and South American forms of the subgenus *Girardia* into a *Dugesia antillana* species group (Ball, 1971). Other possible species groups within this subgenus may be exemplified by *Dugesia tigrina*, *D. chilla*, and *D. glandulosa*, which differ among themselves in small ways in the morphology of the penis and atrium, and in the course of the bursal stalk and the position of the testes. Within the subgenus *Dugesia* there are two large subgroups evident, the *D. gonocephala* group with a terminal opening of the ejaculatory duct, and a more apomorph *D. japonica* group with a subterminal opening of the ejaculatory duct. It is possible that *D. burmaensis* and *D. astrocheta* form a third group (Fig. 8, type 7) or even another subgenus. Also, it is mainly within the subgenus *Dugesia* that we find species with a three-layered outer musculature of the pharynx. However, despite the success that this type of approach has had in elucidating systematic and evolutionary relationships in other groups (e.g., Vuilleumier, 1969), I feel that it would be premature to continue this line of inquiry in the Paludicola at present. It seems advisable to test and refine the revision here proposed first, and to leave further detailed analyses of the new taxa to the revisers of regional faunas.

On the basis of the characters used in the subgeneric definitions I have constructed a further cladogram to suggest the phylogenetic relationships of the genera and subgenera of Dugesiidae (Fig. 11). It will be seen that this differs from Meixner's (1928) scheme not only in the number of divisions, but also in the distribution of many of the species. Thus, Meixner type I is composed principally of primitive elements, but it also contains forms such as *D. gonocephala*, *D. lugubris*, and *D. burmaensis*, which are here considered to be the most advanced of the Dugesiidae.

Meixner placed more emphasis on the morphology of the atrium than is done here (see p. 343). His more primitive types I and II are described as having an undivided atrium. In fact, it is characteristic of a number of species of *Girardia*, and of *Cura*, that the bursal stalk enters the roof of the male atrium and does not travel to the gonopore and, especially in *Cura*, enlarges there to form a female atrium. Steinböck (1924) has commented previously on the arrangement of the bursal stalk and oviducts in *D. (Cura) pinguis*; he considered this condition to be primitive. In the higher Dugesiidae, as in the large and diverse subgenus *Dugesia*, a divided atrium is the exception rather than the rule.

The similarities in the atrial muscles and penis morphology of *D. (C.) pinguis* and *D. (D.) evelinae* have been discussed by Marcus (1955) and Ball and Fernando (1969). The present analysis has failed to resolve the problem of their possible close relationship, and the exact systematic position of the latter species remains equivocal. It may be noted that in one important respect, the presence of a diaphragm in the ejaculatory duct of *D. evelinae*, there may

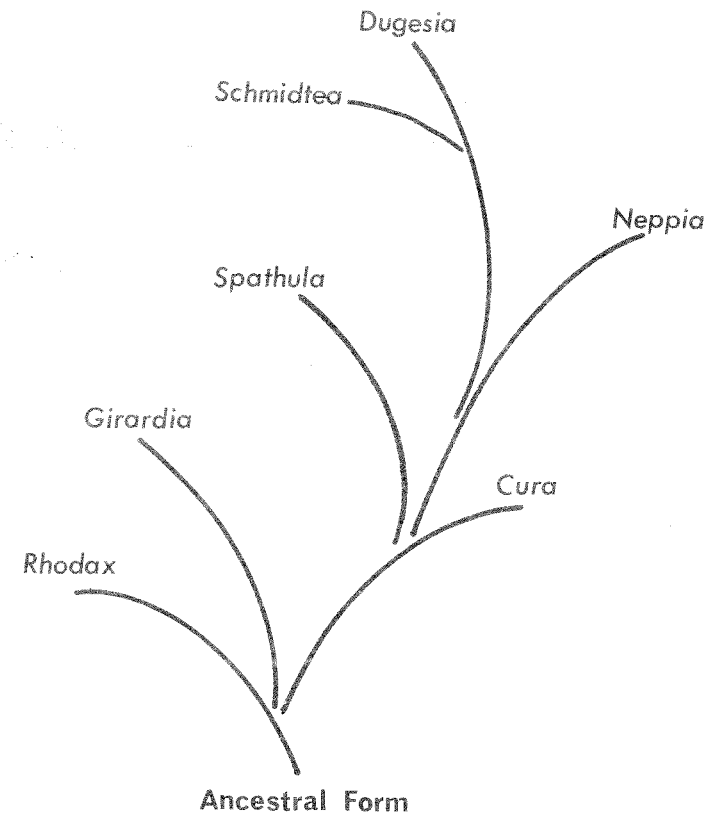


Figure 11 Suggested phylogenetic relationships of the genera and subgenera of Dugesiidae. *Bopsula* is omitted.

be good reason to reinvestigate the status of this species, since the diaphragm is not apparent in the original figure (Marcus, 1955, fig. 20) or in the original slides, although it is described. It is also of note that the atrial muscles of *D. montana* are thicker than is usual in members of the Dugesiidae (Fig. 9).

Concerning the cement glands it may be noted that in my experience these are very well developed in *Girardia* and *Cura*, and less so in *Dugesia*. Similarly, the shell glands are most extensive in the lowest forms, and in both *D. pinguis* and *D. foremanii* I have detected extensive cyanophil and eosinophil secretion of the shell glands by Mallory-Heidenhain staining. Usually the shell glands produce only an eosinophil secretion.

Pigmentation of the pharynx is rare in freshwater triclads, and it is of interest to note that it occurs only in species of the subgenus *Girardia*, but whether or not in all of them is not known.

It would certainly be of interest to have further data to compare with the proposed scheme. The structure of the anterior nervous system, for example, in the various subgenera of differing head shape may prove to be of significance. Biogeographical data, too, are of importance, and it will be the purpose of the next section of this paper to review and explain the distribution and interrelationships of the taxa.

## BIOGEOGRAPHICAL RELATIONSHIPS

### Distribution and Dispersal

All other things being equal, the area of distribution of a taxon is proportional to its age, but as Emerson (1952) has pointed out, all other things are rarely equal. The "Age and Area" theory of Willis (1922), which depends upon such space-time correlations, is now generally discredited (Croizat, 1958; Udvardy, 1969), and it is doubtful that the idea that older taxa have wider distributions is more than a loose generalization. Yet the comparative morphological evidence clearly indicates that the Dugesiidae are older and more primitive than the other families, and they are also the most widely distributed (cf. Figs. 12 and 13). The restriction of the Dendrocoelidae and the Planariidae to areas

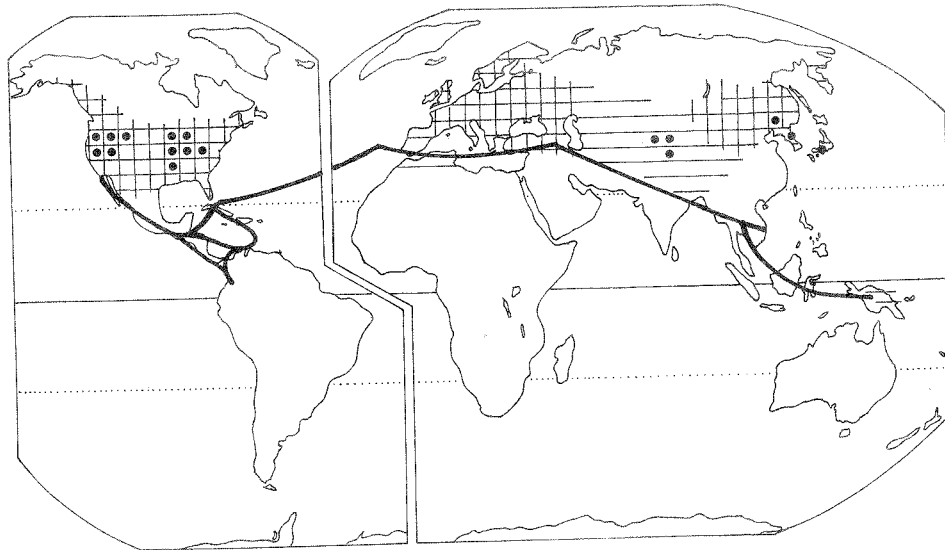


Figure 12 The distribution of the Planariidae (cross-hatching), Dendrocoelinae (vertical hatching), and Kenkiinae (dots) in relation to the Tethys and associated geosynclines (bold lines). (Basic map after Croizat, 1962.)

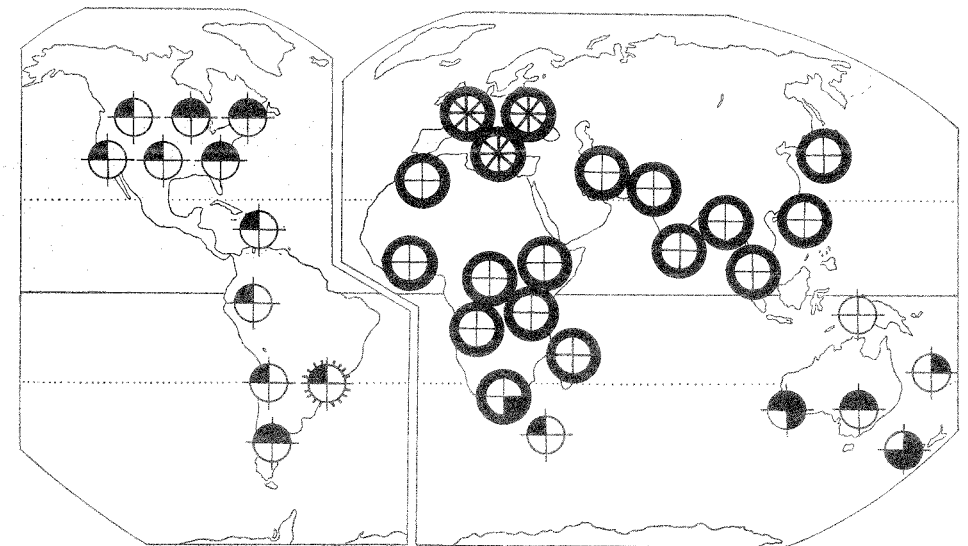


Figure 13 The distribution of the genera and subgenera of Dugesiidae.

- |             |            |           |
|-------------|------------|-----------|
| ⊙ Rhodax    | ⊙ Girardia | ⊙ Cura    |
| ⊙ Neppia    | ⊙ Spathula | ⊙ Dugesia |
| ⊙ Schmidtea |            |           |

north of the Tethys geosyncline, and the curious Europe–east Asia disjunction in the distribution of the Dendrocoelinae (Porfirjeva, 1960), are interesting facts which may be noted (Fig. 12), but a detailed explanation is as yet not possible, and an attempt is outside the scope of the present paper.

An explanation of the distribution patterns of the Dugesiidae first requires a consideration of their capacity for active and passive dispersal. The efficacy of passive dispersal as a means of extending range in many freshwater organisms cannot be denied, and there are many such organisms which may be considered cosmopolitan (Carpenter, 1928; Macan, 1963). This, however, is not true of the Paludicola; each species appears to be restricted to a particular geographical area, with two notable exceptions to be discussed further below.

Ulliyott (1936) is quite adamant in maintaining that Paludicola disperse only by their own activity and that passive dispersal is impossible, and Leloup (1944) is right in saying that most authors have taken this view. It is important to remember that freshwater triclads do not possess any resting stages which are resistant to extremes of temperature, or to desiccation, that the adults are



very fragile, and that they spend their entire life cycle in an aquatic environment. An exception is *Hymanella retenuova*, which inhabits temporary ponds and produces a thick-shelled cocoon capable of withstanding the dry periods. Nonetheless, this species has a fairly restricted distribution in eastern North America (Ball, 1969a). For these reasons anemochore dispersal would seem to be of little importance for the dispersal of these organisms, especially as they have not been recorded in the aerial plankton (Gislén, 1948). Zimmerman (1963), however, has made the point that in considering transoceanic dispersal it is the abnormal conditions, such as hurricanes, which play the most important role. Bousfield (1961) has also considered the role of hurricanes in the dispersal of littoral marine arthropods in eastern North America, but concluded that a hypothesis of chance influx alone would scarcely account for the complexity of the established fauna and for the amphiatlantic distributions of many of the species. Experimental or observational evidence relating to the transport of freshwater triclads in this way is impossible to obtain, but their structure, habits, and present-day distributions argue strongly against their having been so dispersed.

About the only agents for biochore dispersal of freshwater triclads which have been proposed are birds. Although there is some evidence that birds may have aided the dispersal of *Crenobia alpina* and *Polycelis felina* over short distances in northwestern Europe (Dahm, 1958; Reynoldson, 1966), such dispersal seems to have been of little significance on a wider scale. The studies of Maguire (1963) on biochore dispersal do not afford much evidence for the transport of triclads by other animals, and in a recent review Reynoldson (1966) concludes that birds have not been an important factor in long-range dispersal. The biochore dispersal of cocoons is a possibility, but those of the Dugesiidae are attached to the substratum, as are many of those of the Planariidae and Dendrocoelidae. Certain stream-dwelling forms produce free, unattached cocoons, but according to Voigt (1904), they are so placed in the streams as to exclude the probability of transport by birds or other animals. I have found a trichopteran larva which had incorporated a single cocoon of *Phagocata woodworthi* into its case structure, but this is unlikely to be of any significance other than in dispersing the cocoon within the lake.

The occurrence of freshwater triclads in the invertebrate drift of streams is a rare event (Minshall and Winger, 1968), but the hydrochore dispersal of cocoons or adults, either in floodwaters or on floating objects, is well established (Leloup, 1944). Their resistance to salinity, however, is low and transoceanic hydrochore dispersal is improbable, if not impossible. There is no evidence to indicate that hydrochore dispersal has played any important role in the determination of present-day distribution patterns.

Two species of *Dugesia* appear to present exceptions to what has been said above. *D. tigrina*, the most widespread North American species, occurs

in scattered localities in Europe, where it appears to be extending its range (Gourbault, 1969). In the other direction the common European form *D. polychroa* has established itself in the Saint Lawrence River and environs in North America. There can be no doubt, however, that these species have been introduced within the last 60 years or so, *D. tigrina* via the trade in aquarium plants, and *D. polychroa* probably with shipping (Ball, 1969b). Anthropochore dispersal is also probably responsible for the occurrence of triclads on Anticosti Island (Ball and Fernando, 1970) and of *Rectocephala* in Washington, D.C. (Hyman, 1953). That such accidental dispersal is a rare event is demonstrated by studies of the Paludicola of the Canadian Maritime Provinces, which show that the reduced fauna is typical of eastern North America (Ball, 1973) and that no European elements occur here, despite the activities which have been responsible for the accidental introduction of many other types of organisms (Lindroth, 1957) by European traders in this area for two or three hundred years.

Perhaps the best evidence against passive dispersal as a general phenomenon is afforded by the comparisons of the triclad faunas on opposite sides of narrow sea straits which were subject to Pleistocene glaciations. Such comparisons have been made in northwestern Europe (Ulliyott, 1936; Reynoldson, 1966) and the Gulf of Saint Lawrence (Ball and Fernando, 1970). The dissimilarities in the faunas argue very strongly against passive dispersal.

The difficulty of disproving a hypothesis of chance dispersal is, of course, great. Schopf (1970, p. 658) has made this point in saying that "the stochastic hypothesis is expressly designed to take advantage of the impossibility of providing a negative and in nullifying systematic methods of explanation by emphasizing the improbable." Strong words, but containing much truth.

It is likely that triclads disperse mainly by their own activities. It is true that the speed or ease of locomotion of organisms is in no direct relation to the speed or ability of dispersal (Udvardy, 1969), but nevertheless the Paludicola are generally slow to colonize new areas. Reynoldson (1966), for example, notes that in the north of Great Britain they are generally underdispersed, and presumably are still extending their range northwards following the last glaciation. A recent study of the distribution of triclads in eastern Canada indicates that this may also be true here (Ball, 1973). The freshwater triclads of Anticosti Island have not succeeded in crossing to the northern watershed since their presumed introduction into the Port Menier area 70 years ago (Ball and Fernando, 1970).

If freshwater triclads disperse principally by their own activities, and only through contiguous freshwater bodies, and perhaps the groundwater where soil conditions are suitable, then a causal explanation of their distribution must take careful consideration of historical events. Further, since the history of a taxon in nature is reflected by both its morphology and its dis-

tribution, a causal explanation of distribution is intimately concerned with the evolutionary relationships of its members. Using the systematic data elucidated previously, and taking cognizance of the data on vagility just discussed, a biogeographical analysis of the Dugesiidae must provide a reasonable explanation of the distribution patterns exhibited by the various genera and subgenera (Fig. 13).

### Historical Biogeography

The problem of the "center of origin" of the Dugesiidae, and thus of the Paludicola as a whole, is a difficult one to solve in the absence of a fossil record. It is a corollary of Brundin's biogeographical methods that "within the total distribution area of a group the species possessing the most primitive characters are found within the earliest, those with the most derivative characters within the latest occupied part of the area" (Brundin, 1966, p. 56), but this concept has been criticized severely by Darlington (1970), who considers it a rule of thumb to expect most primitive forms to be in distant-peripheral areas (1957), an idea which dates back to the work of Matthew (1915). The idea that the center of origin of a taxon is indicated by the point of occurrence of the greatest number of its members is also an old one (Wulff, 1950), and it is one of the important factors in the geographical-morphological method used by many botanical taxonomists (Davis and Heywood, 1963). However, Cain (1944) has justified the view that to equate center of diversity with center of origin, without supporting evidence, is a dangerous policy. Such coincidence is only to be expected in those cases where the area of the taxon has not been subjected to later influences, such as glaciations.

It must be accepted, therefore, that any conclusion concerning the center of origin, or of dispersal, of the freshwater triclads must be considered as hypothesis, open to rejection, acceptance, or modification according to the weight of evidence available. If, however, it can be shown that the criterion of diversity agrees with the conclusions reached from an examination of the distribution of a phylogenetic series, then the likelihood of attaining a correct solution is increased.

Kawakatsu (1968, figs. III-12 and IV-1) unequivocally places the origin of the Dugesiidae in the Balkan Peninsula, from where they have dispersed to most parts of the world (Fig. 14). The merits of this scheme are that it places the center of dispersal of the Dugesiidae in an area well known as an evolutionary center (Stankovic, 1960) and provides an adequate explanation of the broad distribution of the subgenus *Dugesia*. Further, the heterogeneity of the triclad fauna of Australasia is explained in that it results from three distinct immigration sources, viz., south Africa, South America, and southeastern Asia.

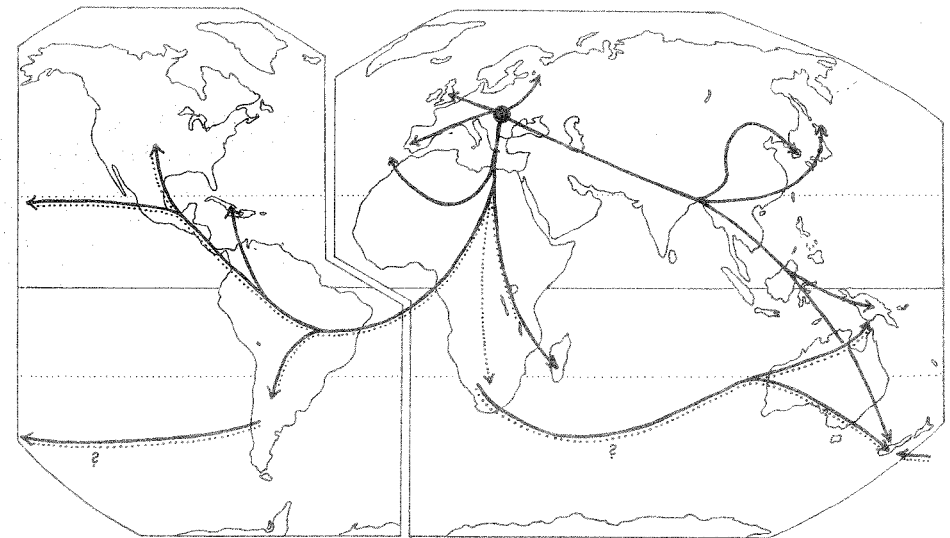


Figure 14 The distribution and dispersal of the Dugesiidae according to Kawakatsu. Solid lines represent the genus *Dugesia* s. l., broken lines the genus *Cura* s. l. (Redrawn from Kawakatsu, 1968.)

There are, however, considerable drawbacks to this proposal. In the first place the Dugesiidae are represented by only two or three species in the Balkan area, and these are apomorph species. The diversity and endemism of the Planariidae and Dendrocoelidae in Lake Ohrid (Stankovic, 1960, 1969) clearly indicate a center of diversification, and possibly dispersal, for these forms, but this does not appear to be true for the older and more primitive Dugesiidae. On the other hand, if the apomorph (and therefore specialized?) subgenus *Dugesia* is a more recent arrival in this area, diversification to the degree exhibited by the other families would not be expected.

Kawakatsu notes, correctly, the absence of amphiatlantic relations in the Northern Hemisphere. He shows the main migratory routes of the Dugesiidae as being southwards through Africa, westwards across the Atlantic Ocean to South America and then North America, and across the Pacific to New Zealand, and also eastwards from south Africa across the Indian Ocean to Australasia. The genus *Cura* s. l. arises in central Africa and follows these routes. Again the difficulties here are that the migratory routes run contrary to the phylogenetic series (cf. Figs. 11 and 13). Thus the African species of *Cura* (here referred to a distinct subgenus *Neppia*) are evolutionarily more recent than the American and Australasian species; and the same applies to *Dugesia*. What is more, Kawakatsu's scheme suggests that there should be close rela-

tionships between the Dugesidae of south Africa and South America, relationships which I cannot detect.

A further contradictory feature of this hypothesis is that it fails to account for the lack of amphiatlantic connections. The route from the Balkans to North America is circuitous, to say the least, and it would appear that the Dugesidae should have had ample time to migrate directly from Europe to North America, or even from Asia to North America. Yet it is apparent, and Kawakatsu seems to agree, that the Dugesidae of North America have been derived entirely from the south. The fact that most primitive forms are found in the Southern Hemisphere, and that here, too, is found the greatest diversity in numbers of both species and subgenera, suggests to me that the center of dispersal, and probably the center of origin, of the Dugesidae lies south of the present-day equator.

Before taking this conception further, it is desirable to consider in more detail the transoceanic migratory routes followed by the Paludicola. Since I have rejected hypotheses of chance dispersal, which I agree with Brundin (1966) are an admission of defeat, there appear to be only two alternatives left—former land (freshwater?) bridges, now sunken, and continental drift.

The general question of land bridges has been reviewed in detail by van Steenis (1962), Illies (1965a), Hallam (1967), and Udvardy (1969). It is the proponents of continental stability who continue to make most use of them. Croizat, for example, in his valuable discussion of the origin and dispersal of the angiosperms, proposes several land bridges and considers the world now to be the disconnections of the Jurassic-Cretaceous period (Croizat, 1952, fig. 98). Later, Croizat (1962) makes the point that the biogeographer must look to his own data when considering transoceanic relationships and not trouble himself with detailed problems of disintegrated land bridges versus drifting continents. This is not entirely responsible although the point concerning the validity and independence of biogeographical data is well taken. Van Steenis (1963) considers that for a satisfactory explanation of the major features of spermatophytan plant geography a minimum of five major land bridges is required. He does not find the zoogeographical data to be in conflict with these ideas, and they are largely consistent with the distribution patterns exhibited by the Paludicola.

Hallam (1967) has pointed out that the major difficulty in the transoceanic land bridge hypothesis is the isostatic problem involved in sinking an extensive sialic continent without trace. One solution would be to reduce the size of the required land bridges so that they become isthmian links, and Croizat (1952) has emphasized that a continuous land bridge at any one time is unnecessary. The geological evidence, however, does not favor hypotheses involving sunken bridges or continents (Hallam, 1967). The rejection of such hypotheses does not mean that land bridges have played no part on a smaller scale. It is quite

evident, for example, that there has been a bridge across the Bering Strait (Moore, 1961; Stegman, 1963; Hopkins, 1967), and biogeographical evidence suggests the possibility, which is not in conflict with geological data, of such a bridge, or land mass, in the Caribbean area (Ball, 1971).

The alternative to transoceanic land bridges is the hypothesis of continental drift. This is not the place to review all the evidence in favor of this hypothesis; this has already been done for the geological evidence by Runcorn (1962), Blackett *et al.* (1965), Garland (1966), Phinney (1968), Kay (1969), and Dietz and Holden (1970); for the zoological evidence by Jeannel (1961), Brundin (1966), Illies (1965a), and Hallam (1967); and for the botanical evidence by Schuster (1969) and Schopf (1970). It suffices to say that the evidence from paleoclimatology, paleomagnetism, oceanic rift structures, and the excellence of fit of the continents overwhelmingly corroborates the hypothesis.

The most recent evidence favors the idea of a single supercontinent, Pangaea, in Permian times, about 200 to 250 million years ago (Schopf, 1970; Dietz and Holden, 1970). By the end of the Triassic period, 180 million years ago, the northern part of the supercontinent, Laurasia, had split away from the southern part, Gondwanaland, and was drifting northwards, the two parts being separated by the Tethys Sea. There are excellent summaries of the timing of breakup by Heirtzler (1968) and Dietz and Holden (1970), the latter providing a particularly graphic account.

I have suggested that the center of origin of the Dugesidae is an austral one, and I further suggest that this was in Gondwanaland, probably in what is now Antarctica. I postulate that by the commencement of the Mesozoic, some 220 million years ago, the early diversification of the Dugesidae was complete, with a main massing of *Girardia* in the west, and of *Neppia* and *Spathula* in the east. The northwards dispersal of these elements coincided with the early stages of Gondwanaland breakup, leading to a concentration of *Girardia* in the Americas, with relatives across the South Atlantic to Australasia, and a main massing of *Neppia* in the east. *Cura* seems to have been particularly widespread, and perhaps it was ancestral to both the above subgenera, though this cannot be demonstrated at present. After separation was well under way, the subgenus *Dugesia* arose in Africa, and after closure of the Tethys Sea, of which the Mediterranean is a remnant, it spread northwards into Palaearctis, and eastwards to India and southeastern Asia. In general, therefore, these migratory routes are the opposite of those proposed by Kawakatsu (1968).

Additional to the fact that the proposed austral center of dispersal is near the present center of frequency and diversity, this scheme has the advantages of explaining most of the disjunctions and continuous distributions. The relatively early separation of Africa from South America fits with the quite different triclad faunas which these continents have, and the relatively late

separation of Madagascar from Africa explains why its triclad fauna consists mostly, if not entirely, of the subgenus *Dugesia*. India was probably populated entirely from the north, which again explains why its triclads belong almost exclusively to the *D. japonica* species group of the subgenus *Dugesia*. The possibly close connections between *D. astrocheta* of Africa and *D. burmaensis* (p. 380) are of interest here, but need further elucidation. The present distributions of *Neppia* and *Spathula* are the remnants of a former and probably wider distribution in eastern Gondwanaland. It may also be noted that until the Tethys Sea was closed, and the junction of North and South America accomplished, late in the Cretaceous, there was no possibility of exchange between North America and Europe. It is probable, therefore, that the Dugesiidae were not distributed in the northern continents in time to take advantage of the Laurasian supercontinent as a migratory route to North America. Heirtzler (1968), for example, dates the separation of North America at about 230 million years ago, very much earlier than Dietz and Holden (1970) do. The freshwater triclads of the Cape Verde Islands (Luther, 1956) and the Azores (Marcus and Marcus, 1959) may be expected to throw some light on these problems, but unfortunately their affinities are unknown.

It thus seems possible, even likely, that the Dugesiidae diversified rapidly early in Mesozoic times, or even earlier in the aftermath of the Permian-carboniferous glaciations, which both Croizat (1965, p. 609) and Brundin (1966) consider to be of great importance to the history of biotas. During the early stages of breakup of Gondwanaland, they dispersed northwards in the main land masses, without the possibility of interchange between Australasia and southeastern Asia. The final patterns of distribution in the Northern Hemisphere were probably achieved in the Cenozoic, when the continents had attained their present form and position.

Views similar in many ways to those proposed here have been put forward for the Plecoptera (Illies, 1965b), Chironomidae (Brundin, 1966), and Dermaptera (Popham and Manly, 1969). It is encouraging that study of such diverse groups should lead to broadly similar hypotheses. The continental drift hypothesis has also been invoked in biogeographical studies of freshwater Ostracoda (McKenzie and Hussainy, 1968), freshwater fishes (Gery, 1969), and marsupials (Cox, 1970). In addition Besch (1969) has concluded that the distributions and relationships of South American Arachnida support the concept of southern land connections. The recent discovery of Triassic tetrapods in Antarctica provides further confirmatory evidence (Elliot *et al.*, 1970).

The main objections to the proposals will probably concern the origin and history of the insular faunas (e.g., de Beauchamp, 1940b), such as those of the Crozet Islands, New Caledonia, and Hawaii, especially as stratigraphical studies have shown these islands to be relatively young. Croizat (1962, p. 258), however, has made the point that the marriage between geology and

biogeography should involve tectonics and not stratigraphy, and he criticizes the distinction between "oceanic" and "continental" islands from a biogeographical standpoint. For the present it may be noted that the triclads of Crozet [*D. (Girardia) seclusa*] and New Caledonia [*D. (Cura) pinguis*] belong to primitive groups; those of Hawaii have not yet been described.

It should be emphasized that I have presented here only a hypothesis. Considerable reservations concerning the idea of continental drift are being expressed by biologists (Croizat, 1952; van Steenis, 1962) and geologists (Meyerhoff, 1970a, 1970b; Meyerhoff and Teichert, 1971), and the data discussed in this paper are not proof for the drift hypothesis. They are consistent with it, however, and indeed are best explained with its aid, unless the land bridge theory is to be resurrected. A hypothesis of Palaearctic origins for the Dugesiidae, coupled with continental stability and permanence of the oceans is incompatible with the known facts of their distribution and phylogenetic relationships. The systematic and biogeographical scheme presented here is not intended, however, as the last word, which clearly it cannot be, but as a stimulus to future thought and research, and is presented in the hope that it soon will be replaced by a scheme based on additional and new data, and of greater refinement.

Thus, the task is not so much to see what no one has seen yet, but to think what nobody has thought yet, about that which everybody sees. [Schopenhauer]

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## BIBLIOGRAPHY

\*References not seen in the original.

†English translations of these articles will be deposited in the Library of the National Museum of Natural Sciences, Ottawa, Canada.

- Anderson, J. M. 1952. Sexual Reproduction without Cross-copulation in the Freshwater Triclad Turbellarian, *Curtisia foremanii*. *Biol. Bull.*, 102:1-8.
- and J. C. Johann. 1958. Some Aspects of Reproductive Biology in the Freshwater Triclad Turbellarian, *Cura foremanii*. *Biol. Bull.*, 115:375-383.
- Ax, P. 1956. Monographie der Otoplanidae (Turbellaria). *Akad. Wiss. Lit. Mainz Abhandl. Math. Nat. Kl.*, 1955, 13:499-796.
- . 1963. "Relationships and Phylogeny of the Turbellaria." In E. C. Dougherty (ed.), *The Lower Metazoa*, pp. 191-224. Berkeley and Los Angeles: University of California Press.
- Ball, I. R. 1969a. An Annotated Checklist of the Freshwater Tricladida of the Nearctic and Neotropical Regions. *Can. J. Zool.*, 47:59-64.
- . 1969b. *Dugesia lugubris* (Tricladida: Paludicola), a European Immigrant into North American Freshwaters. *J. Fisheries Res. Board Can.*, 26:221-228.
- . 1970. Freshwater Triclad from the Oriental Region. *Zool. J. Linnean Soc.*, 49:271-294.
- . 1971. The Systematic and Biogeographical Relationships of Some *Dugesia* Species (Turbellaria, Tricladida) from Central and South America. *Am. Museum Novitates*, no. 2472, 1-25.
- . 1973. The Haploneura of Eastern Canada (in preparation).
- . 1974. La Faune Terrestre de l'Île de Sainte Hélène: Turbellaria Tricladida. *Ann. Mus. Roy. Afr. Centrale*, in 8°, Zool. (in press).
- and C. H. Fernando. 1969. Freshwater Triclad (Platyhelminthes, Turbellaria) and Continental Drift. *Nature*, 221:1143-1144.
- and — . 1970. Freshwater Triclad (Platyhelminthes, Turbellaria) from Anticosti Island. *Naturaliste Can.*, 97:331-336.
- , T. B. Reynoldson, and T. Warwick, 1969. The Taxonomy, Habitat and Distribution of the Freshwater Triclad *Planaria torva* (Platyhelminthes: Turbellaria) in Britain. *J. Zool. London*, 157:99-123.
- Beauchamp, P. de. 1913. Turbellariés, Trématodes et Gordiacés. *Voy. Alluaud et Jeannel en Afr. Orient. Res. Scient.* Paris: Librairie Albert Schulz., 22 pp.
- . 1931. Biospéologie 56(2). Campagne spéologique de C. Bolívar et R. Jeannel dans l'Amérique du Nord (1928). Turbellariés triclades. *Arch. Zool. Exptl. Gen.*, 71:317-331.
- . 1936. A Propos d' *Euplanaria cretica* Meixner. *Bull. Soc. Zool. Fr.*, 66:433-440.
- . 1939. Results of the Percy Sladen Trust Expedition to Lake Titicaca V. Rotifères et Turbellariés. *Trans. Linnean Soc. London*, 1:51-79.
- . 1940a. Croisière du Bougainville aux Îles australes Françaises XII. Turbellariés et Rotifères. *Mem. Museum Natl. Hist. Nat. Paris*, 14:313-326.
- . 1940b. Sur les triclades paludicoles de l'hémisphère sud. *Compt. Rend. Soc. Biogéog.*, 17:7-9.
- . 1951a. A propos d'une planaire du Congo Belge. *Rev. Zool. Bot. Afr.*, 45:90-97.
- . 1951b. Turbellariés de l'Angola. *Publ. Cult. Comp. Diamantes de Angola, Museo do Dundo, Lisboa*, no. 11, 79-84.
- . 1953. Sur les *Dugesia* (Turbellariés Triclades) d'Afrique tropicale et de Madagascar. *Bull. Soc. Zool. Fr.*, 77:362-370.
- . 1959. Tricladés paludicoles d'Afghanistan. *Kgl. Fysiograf. Sällskap. Lund Forh.*, 29:27-43.
- . 1961. "Classe des Turbellariés." In P. P. Grassé (ed.), *Traité de Zoologie*, vol. IV, pp. 35-212. Paris: Masson et Cie.
- . 1968. Turbellariés d'eau douce de Nouvelle-Calédonie. *Cah. O.R.S.T.O.M., sér. Hydrobiologia*, 11:67-68.
- Beklemishev, W. N. 1969. *Principles of Comparative Anatomy of Invertebrates*. Edinburgh: Oliver & Boyd. 2 vols., xxx + 490, vii + 529.
- Benazzi, M. 1946. Sopra una nuova planaria di acqua dolce. *Arch. Zool. Ital.*, 31:93-102.
- . 1960. Evoluzione cromosomica e differenziamento razziale e specifico nei tricladi. *R. C. Accad. Lincei, Quaderno*, 47:273-296.
- . 1963. "Genetics of Reproductive Mechanisms and Chromosome Behaviour in Some Freshwater Triclad." In E. C. Dougherty (ed.), *The Lower Metazoa*, pp. 405-422. Berkeley and Los Angeles: University of California Press.
- . 1966. Cariologia della planaria americana *Dugesia dorotocephala*. *Lincei Rend. Sci. Fis. Mat. Nat.*, 40:999-1005.
- and E. Giannini. 1971. *Cura azteca*, nuova specie di planaria del Messico. *Lincei Rend. Sci. Fis. Mat. Nat.*, (VIII)50:477-481.
- Besch, W. 1969. "South American Arachnida." In Fittkau, Illies, Klinge, Schwabe, and Sioli (eds.), *Biogeography and Ecology in South America*, pp. 723-740. The Hague: W. Junk.
- Blackett, P. M., E. Bullard, and S. K. Runcorn. 1965. A Symposium on Continental Drift. *Phil. Trans. Roy. Soc. London*, A258:1-323.
- Böhmig, L. 1887. *Planaria Iheringii*, eine neue Triclade aus Brasilien. *Zool. Anz.*, 10:482-484.
- . 1897. Die Turbellarien Ost-Afrikas. K. Mobius, *Die Thierwelt Ost-Afrikas*, 4:1-15. Berlin.
- . 1902. Turbellarien, Rhabdocoeliden und Tricladiden. *Ergeb. Hamburg. Magalh. Sammelreise*, 3:1-30.
- . 1906. Tricladenstudien I. Tricladida Maricola. *Z. Wiss. Zool.*, 81:344-504.
- Bonner, J. T. 1965. *Size and Cycle*. Princeton, N.J.: Princeton University Press. vii + 219 pp.
- Borelli, A. 1895. Viaggio del Dott. Alfredo Borelli nella Repubblica Argentina e nel Paraguay. 13. Planarie d'acqua dolce. *Boll. Museo Zool. Anat. Comp. Torino*, 10:1-6.

- . 1897. Viaggio del Dott. Alfredo Borelli nel Chaco Boliviano, etc. V. Planarie d'acqua dolce. *Boll. Museo Zool. Anat. Comp. Torino*, 12:1-4.
- . 1898. Viaggio del Dr Enrico Festa nell'Ecuador etc. IX. Planarie d'acqua dolce. *Boll. Museo Zool. Anat. Comp. Torino*, 13:1-6.
- . 1901. Di una nova Planaria d'acqua dolce della Republica Argentina. *Boll. Museo Zool. Anat. Comp. Torino*, 16:1-5.
- Bousfield, E. L. 1961. Studies on Littoral Marine Arthropods from the Bay of Fundy Region. *Bull. Nat. Museum Canada*, 183:42-62.
- Brundin, L. 1966. Transantarctic Relationships and Their Significance, as Evidenced by Chironomid Midges, with a Monograph of the Subfamilies Podonominae and Aphroteniinae and the Austral Heptagylae. *Kgl. Svenska Vetenskapsakad. Handl.*, 11:1-472.
- Cain, S. A. 1944. *Foundations of Plant Geography*. New York: Harper, xiv + 556 pp.
- Camin, J. T., and R. R. Sokal. 1965. A Method for Deducing Branching Sequences in Phylogeny. *Evolution*, 19:311-326.
- Carpenter, J. H. MS1970. "Systematics and Ecology of Cave Planarians of the United States." Ph. D. thesis, University of Kentucky, 212 pp.
- Carpenter, K. 1928. *Life in Inland Waters*. London: Sidgwick & Jackson, xviii + 267 pp.
- \*Chickkoff, G. D. 1892. Recherches sur les dendrocoeles d'eau douce (Tricladés). *Arch. Biol.*, 12:435-568.
- Corrêa, D. D. 1960. Two New Marine Turbellaria from Florida. *Bull. Marine Sci. Gulf Caribbean*, 10:208-216.
- Cox, C. B. 1970. Migrating Marsupials and Drifting Continents. *Nature*, 226: 767-770.
- Croizat, L. 1952. *Manual of Phytogeography*. The Hague: W. Junk, viii + 587 pp.
- . 1958. An Essay on the Biogeographic Thinking of J. C. Willis. *Arch. Bot. Biogeogr. Ital.*, 34:1-27 (4 série, vol. III: 90-116).
- . 1962. *Space, Time, Form: The Biological Synthesis*. Caracas: The Author, xix + 881 pp.
- . 1965. An Introduction to the Subgeneric Classification of "Euphorbia" L., with Stress on the South African and Malagasy Species. I. *Webbia*, 20:573-706.
- Crowson, R. A. 1970. *Classification and Biology*. London: Heinemann, vii + 350 pp.
- Curtis, W. C. 1900. On the Reproductive System of *Planaria simplissima*, a New Species. *Zool. Jahrb. (Anat.)*, 13:447-466.
- Dahm, A. G. 1958. *Taxonomy and Ecology of Five Species Groups in the Family Planariidae*. Malmö: Nya Litografen, 241 pp.
- . 1963. The Karyotypes of Some Freshwater Tricladés from Europe and Japan. *Arkiv Zool.*, 16:41-67.
- . 1967. A New *Dugesia* "Microspecies" from Ghana Belonging to the *Dugesia gonocephala* Group. *Arkiv Zool.*, 19:309-321.
- Darlington, P. J. 1957. *Zoogeography: The Geographical Distribution of Animals*. New York: Wiley, xi + 675 pp.
- . 1970. A Practical Criticism of Hennig-Brundin "Phylogenetic Systematics" and Antarctic Biogeography. *Systematic Zool.*, 19:1-18.

- Davis, P. H., and V. H. Heywood. 1963. *Principles of Angiosperm Taxonomy*. Edinburgh: Oliver & Boyd, xvi + 558 pp.
- Dietz, R. S., and J. C. Holden. 1970. Reconstruction of Pangaea: Breakup and Dispersion of Continents, Permian to Present. *J. Geophys. Res.*, 75:4939-4956. (Also in *Sci. Am.*, 223:30-41.)
- \*Dugès, A. 1830. Aperçu de quelques observations nouvelles sur les planaires et plusieurs genres voisins. *Ann. Sci. Nat.*, 21:72-90.
- Elliot, D. H., E. H. Colbert, W. J. Breed, J. A. Jensen, and J. S. Powell. 1970. Triassic Tetrapods from Antarctica: Evidence for Continental Drift. *Science*, 169: 1197-1201.
- Emerson, A. E. 1952. The Biogeography of Termites. *Bull. Am. Museum Nat. Hist.*, 99:217-225.
- Fuhrmann, O. 1914. Turbellariés de Colombie. *Mem. Soc. Neuchâtel Sci. Nat.*, 5:748-804.
- Garland, G. D. (ed.). 1966. *Continental Drift*. Toronto: University of Toronto Press, ix + 140 pp.
- Gery, J. 1969. "The Freshwater Fishes of South America." In Fittkau, Illies, Klinge, Schwabe, and Sioli (eds.), *Biogeography and Ecology in South America*, pp. 828-848. The Hague: W. Junk.
- Girard, C. 1850. A Brief Account of the Freshwater Planariae of the United States. *Proc. Boston Soc. Nat. Hist.*, 3:264-265.
- . 1852. Descriptions of Two New Genera and Two New Species of Planaria. *Proc. Boston Soc. Nat. Hist.*, 4:210-212.
- Gislèn, T. 1948. Aerial Plankton and Its Conditions of Life. *Biol. Rev.*, 23:109-126.
- Gourbault, N. 1969. Expansion de *Dugesia tigrina* (Girard), planaire américaine introduite en Europe. *Ann. Limnol.*, 5:3-7.
- Graff, L. von. 1912-1917. "Tricladida." In Bronn, H. G. (ed.), *Klassen und Ordnungen des Tierreichs*. Bd. IV. Abt. 1c. III. Leipzig.
- Hallam, A. 1967. The Bearing of Certain Palaeozoogeographical Data on Continental Drift. *Palaeogeography, Palaeoclimatol., Palaeoecol.*, 3:201-241.
- Hallez, P. 1894. *Catalogue des Rhabdocoelides, Tricladés et Polycladés du Nord de la France*, 2d ed. Lille: L. Danel, 240 pp.
- Heirtzler, J. R. 1968. Sea Floor Spreading. *Sci. Am.*, 219:60-70.
- Hennig, W. 1966. *Phylogenetic Systematics*. Urbana: University of Illinois Press, 263 pp.
- Hofsten, N. von. 1907. Studien über Turbellarien aus dem Berner Oberland. *Z. Wiss. Zool.*, 85:391-654.
- Holleman, J. T., and C. Hand. 1962. A New Species, Genus, and Family of Marine Flatworms (Turbellaria: Tricladida, Maricola) Commensal with Mollusks. *Veliger*, 5:20-22.
- Hopkins, D. M. (ed.). 1967. *The Bering Land Bridge*. Stanford, Calif.: Stanford University Press, ix + 495 pp.
- Hyman, L. H. 1925. The Reproductive System and Other Characters of *Planaria dorotocephala* Woodworth. *Trans. Am. Microscop. Soc.*, 44:51-89.
- . 1931a. Studies on the Morphology, Taxonomy, and Distribution of North American Triclad Turbellaria. IV. Recent European Revisions of the Tricladés,

- and Their Application to the American Forms, with a Key to the Latter and New Notes on Distribution. *Trans. Am. Microscop. Soc.*, **50**:316-335.
- . 1931b. Ibid. V. Descriptions of Two New Species. *Trans. Am. Microscop. Soc.*, **50**:336-343.
- . 1937. Ibid. VIII. Some Cave Planarians of the United States. *Trans. Am. Microscop. Soc.*, **56**:457-477.
- . 1939. New Species of Flatworms from North, Central and South America. *Proc. U.S. Natl. Museum*, **86**:419-439.
- . 1944. Marine Turbellaria from the Atlantic Coast of North America. *Am. Museum Novitates*, no. 1266, 1-15.
- . 1951. *The Invertebrates*, vol. II. New York: McGraw-Hill. vii + 550 pp.
- . 1953. North American Triclad Turbellaria. 14. A New, Probably Exotic, Dendrocoelid. *Am. Museum Novitates*, no. 1629, 1-5.
- . 1954. A New Marine Triclad from the Coast of California. *Am. Museum Novitates*, no. 1679, 1-5.
- . 1956. North American Triclad Turbellaria. 15. Three New Species. *Am. Museum Novitates*, no. 1808, 1-14.
- . 1957. A Few Turbellarians from Trinidad and the Canal Zone, with Corrective Remarks. *Am. Museum Novitates*, no. 1862, 1-8.
- . 1959. On Two Freshwater Planarians from Chile. *Am. Museum Novitates*, no. 1932, 1-11.
- . 1960. Cave Planarians in the United States. *Am. Midland Naturalist*, **64**: 10-12.
- Ichikawa, A., and M. Kawakatsu. 1962. *Phagocata albata*, a New Probably Subterranean Freshwater Planarian, from Hokkaidô. *Annotationes Zool. Japon.*, **35**:29-37.
- and ———. 1964. A New Freshwater Planarian, *Dugesia japonica*, Commonly but Erroneously Known as *Dugesia gonocephala* (Dugès). *Annotationes Zool. Japon.*, **37**:185-194.
- Ijima, I. 1884. Untersuchungen über den Bau und die Entwicklungsgeschichte der Süsswasserdendrocoelen (Tricladen). *Z. Wiss. Zool.*, **40**:359-464.
- Illies, J. 1965a. Die Wegenersche Kontinentalverschiebungstheorie im Lichte der modernen Biogeographie. *Naturwissenschaften*, **18**:505-511.
- . 1965b. Phylogeny and Zoogeography of the Plecoptera. *Ann. Rev. Entomol.*, **10**:117-140.
- Jeannel, R. 1961. La Gondwanie et le peuplement de l'Afrique. *Ann. Mus. Roy. Afr. Centrale, Tervuren*, **102**:1-161.
- Kaburaki, T. 1918. Freshwater Triclad from the Basin of the Inlé Lake. *Rec. Indian Museum*, **14**:187-194.
- . 1925. Planarians from the Andamans. *Rec. Indian Museum*, **27**:29-32.
- Kato, K. 1950. A New Freshwater Triclad from Japan. *Annotationes Zool. Japon.*, **24**:45-48.
- †Kawakatsu, M. 1968. On the Origin and Phylogeny of Turbellarians: Suborder Paludicola. *Japan. Soc. Systematic Zool. Circ.*, nos. 38-41: 11-22.
- . 1969a. An Illustrated List of Japanese Freshwater Planarians in Color. *Bull. Fuji Women's College*, no. 7, 45-91.

- . 1969b. Report on Freshwater and Land Planarians from New Caledonia. *Bull. Osaka Museum Nat. Hist.*, **22**:1-14.
- . 1969c. Report on Freshwater Planaria from India. *Annotationes Zool. Japon.*, **42**:210-215.
- Kay, M. (ed.). 1969. *North Atlantic Geology and Continental Drift*. Memoir 12. The American Association of Petroleum Geologists. ix + 1082 pp.
- Kenk, R. 1930a. Beiträge zum System der Probursalier. *Zool. Anz.*, **89**:145-162, 289-302.
- . 1930b. *Euplanaria cretica* Meixner, eine Triklade mit eigentümlichen Drüsenorgan. *Zool. Anz.*, **92**:247-253.
- . 1935. Studies on Virginian Triclad. *J. Elisha Mitchell Sci. Soc.*, **51**:79-125.
- . 1936. Eine neue Hohlentriklade. *Fonticola opisthogona* n. sp. *Zool. Anz.*, **113**:305-311.
- . 1941. A Freshwater Triclad from Puerto Rico, *Dugesia antillana* New Species. *Occasional Papers Museum Zool. Univ. Mich.*, **436**:1-9.
- . 1944. The Freshwater Triclad of Michigan. *Misc. Publ. Museum Zool. Univ. Mich.*, **60**:1-44.
- . 1970. Freshwater Triclad (Turbellaria) of North America. I. The Genus *Planaria*. *Proc. Biol. Soc. Wash.*, **82**:539-558.
- Kennel, J. 1888. Untersuchungen an neuen Turbellarien. *Zool. Jahrb. (Anat.)*, **3**:447-486.
- Komarek, J. 1920. Über hohlenbewohnende Tricladen der balkanischen Karste. *Arch. Hydrobiol.*, **20**:822-828. (German translation of the original Czech paper of 1919.)
- Kozhov, M. 1963. *Lake Baikal and Its Life*. The Hague: W. Junk. vii + 344 pp.
- \*Laidlaw, F. F. 1906. Report on the Turbellaria. Zoological Results of the Third Tanganyika Expedition. *Proc. Zool. Soc. London*, 1906, 777-779.
- \*Lang, A. 1884. "Polycladen." *Fauna und Flora des Golfes von Neapel*, **11**: ix + 688 pp. W. Engelmann, Leipzig.
- Lang, P. 1913. Beiträge zur Anatomie und Histologie von *Planaria polychroa*. *Z. Wiss. Zool.*, **105**:136-155.
- Leloup, E. 1944. Recherches sur les triclades dulcicoles épigés de la Forêt de Soignes. *Mem. Mus. Roy. Hist. Nat. Belge*, **102**:1-112.
- Lepori, N. G. 1948a. Descrizione di *Dugesia sicula* n. sp. di tricladi di acqua dolce dei dintorni di Catania. *Arch. Zool. Ital.*, **33**:461-472.
- . 1948b. Descrizione di *Dugesia ilvana* n. sp. di planaria di acqua dolce dei dintorni di Catania. *Arch. Zool. Ital.*, **33**:183-193.
- . 1951. Sulle caratteristiche morfologiche e sulla posizione sistematica della planaria di Sardegna e Corsica già ascritta a *Dugesia (Euplanaria) gonocephala* (Dugès). *Atti Soc. Toscana Sci. Nat.*, **58B**:28-47.
- Lindroth, C. H. 1957. *The Faunal Connections between Europe and North America*. Stockholm: Almqvist and Wiksell. 344 pp.
- †Livanov, N. A. 1951. Planarians of Kopet-Dag and Related Species of Crimea, Caucasasia and Transcaucasias. *Tr. Murgabsk. Gidrobiol. St.*, **1**:103-114. (In Russian.)
- . 1962. "Report on Triclad in Lake Baikal." In G. I. Galazy (ed.), *Oligochaeta*



- and Planarians of Lake Baikal, pp. 152–188. Moscow: Proc. Limnol. Inst. (In Russian.)
- Luther, A. 1956. Turbellaria Tricladida von den Cap Verde-Inseln. *Soc. Sci. Fennica Commentationes Biol.*, 15:1–8.
- . 1960. Die Turbellarien Ostfennoskandiens. I. Acoela, Catenulida, Macro-stomida, Lecithoepitheliata, Prolecithophora, und Proseriata. *Soc. F. Fl. Fenn., F. F.*, 7:1–155.
- Macan, T. T. 1963. *Freshwater Ecology*. London: Longmans. x + 338 pp.
- McKenzie, K., and S. U. Hussainy, 1968. Relevance of a Freshwater Cytherid (Crustacea, Ostracoda) to the Continental Drift Hypothesis. *Nature*, 220: 806–808.
- Maguire, B. 1963. The Passive Dispersal of Small Aquatic Organisms and Their Colonization of Isolated Bodies of Water. *Ecol. Monographs*, 33:161–185.
- Marcus, E. 1946. Sobre Turbellaria brasileiros. *Bol. Fac. Filosof. Ciências Letras Univ. São Paulo, Zool.*, 11:5–254.
- . 1948. Turbellaria do Brasil. *Bol. Fac. Filosof. Ciências Letras Univ. São Paulo, Zool.*, 13:111–243.
- . 1953. *Turbellaria Tricladida*. Exploration du Parc National de l'Upemba, Fascicule 21: 1–62. Brussel: Institut des Parcs Nationaux du Congo Belge.
- . 1954. Reports of the Lund University Chile Expedition 1948–49. 11. Turbellaria. *Lunds Univ. Årsskr.*, 49:3–115.
- . 1955. "Turbellaria." In Hanström, Brinck, and Rudebeck (eds.), *South African Animal Life*, vol. 1, pp. 101–151. Stockholm.
- †———. 1963. Eine neue Meerestriklade von São Paulo. *Zool. Beitr.*, 9:441–446.
- . 1970. "Turbellaria (Addenda)." In Hanström, Brinck, and Rudebeck (eds.), *South African Animal Life*, vol. 14, pp. 9–18. Stockholm.
- and E. Marcus. 1951. Contributions to the Natural History of Brazilian Turbellaria. *Com. Zool. Museo Hist. Nat. Montevideo*, 3:1–25.
- and ———. 1959. Turbellaria from Madeira and the Azores. *Bol. Mus. Mun. Funchal*, 12:15–42.
- Martins, M. E. Q. P. 1970. Two New Species of *Dugesia* (Tricladida Paludicola) from the State of São Paulo, Brazil. *Anais Acad. Brasil. Ciênc.*, 42:113–118.
- Marx, H., and G. B. Rabb. 1970. Character Analysis: an Empirical Approach Applied to Advanced Snakes. *J. Zool. London*, 161:525–548.
- Matthew, W. D. 1915. Climate and Evolution. *Ann. N.Y. Acad. Sci.*, 24:171–318. (Reprinted 1939, *Spec. Publ. N.Y. Acad. Sci.*, 1:1–223.)
- Mayr, E. 1969. *Principles of Systematic Zoology*. New York: McGraw-Hill. xi + 428 pp.
- Meixner, J. 1928. Der Genitalapparat der Tricladen und seine Beziehungen zu ihrer allgemeinen Morphologie, Phylogenie, Ökologie und Verbreitung. *Z. Morphol. Ökol. Tiere*, 11:570–612.
- . 1938. "Turbellaria (Strudelwürmer) I." In G. Grimpe and E. Wagler (eds.), *Die Tierwelt der Nord-und Ostsee*, IVb:1–146.
- Meyerhoff, A. A. 1970a. Continental Drift: Implications of Palaeomagnetic Studies, Meteorology, Physical Oceanography, and Climatology. *J. Geol.*, 78:1–51.

- . 1970b. Continental Drift, II: High Latitude Evaporite Deposits and Geologic History of Arctic and North Atlantic Oceans. *J. Geol.*, 78:406–444.
- and C. Teichert. 1971. Continental Drift, III: Late Paleozoic Glacial Centers, and Devonian-Eocene Coal Distribution. *J. Geol.*, 79:285–321.
- Minshall, G. W., and P. V. Winger. 1968. The Effect of Reduction in Stream Flow on Invertebrate Drift. *Ecology*, 49:580–582.
- Mitchell, R. W. 1968. New Species of *Sphalloplana* (Turbellaria: Paludicola) from the Caves of Texas, and a Re-examination of the Genus *Speophila* and the Family Kenkiidae. *Ann. Speleol.*, 23:597–620.
- Moore, J. 1961. The Spread of Existing Diurnal Squirrels across the Bering and Panamanian Land Bridges. *Am. Museum Novitates*, no. 2044, 1–26.
- Nelson, G. J. 1969. The Problem of Historical Biogeography. *Systematic Zool.*, 18:243–246.
- Neppi, V. 1904. Über einige exotische Turbellarien. *Zool. Jahrb. (Syst.)*, 21:303–326.
- Nurse, F. R. 1950. Freshwater Triclads New to the Fauna of New Zealand. *Trans. Roy. Soc. New Zealand*, 78:410–417.
- Okugawa, K. I. 1955. On the Supernumerary Sexual Organs of *Dugesia gonocephala* (Dugès) Induced by the Low Temperature. *Bull. Kyoto Gakuhei Univ.*, B6: 1–14.
- Packard, A. S. 1879. *Zoology for Students and General Readers*. New York: Henry Holt. 719 pp.
- Pantin, C. F. A. 1931. The Adaptation of *Gunda ulvae* to Salinity. *J. Exptl. Biol.*, 8:63–94.
- Phinney, R. A. (ed.). 1968. *The History of the Earth's Crust*. Princeton N.J.: Princeton University Press. viii + 244 pp.
- \*Poche, F. 1926. Das System der Platoreria. *Arch. Naturgeschichte*, 91, Abt. A:1–459.
- Popham, E. J., and B. F. Manly. 1969. Geographical Distribution of the Dermoptera and the Continental Drift Hypothesis. *Nature*, 222:981–982.
- †Porfirjeva, N. A. 1960. On the Zoogeography of Planarians in the U.S.S.R. *Zool. Zh.*, 40:454–456. (In Russian, English summary.)
- Reynoldson, T. B. 1966. The Distribution and Abundance of Lake-dwelling Triclads—towards a Hypothesis. *Advances Ecol. Res.*, 3:1–71.
- and L. S. Bellamy. 1970. The Status of *Dugesia lugubris* and *D. polychroa* (Turbellaria, Tricladida) in Britain. *J. Zool. London*, 162:157–177.
- Richardson, L. R. 1968. A New Bdellourid-like Triclad Turbellarian Ectoconsortic on Murray River Chelonia. *Proc. Linnean Soc. N.S. Wales*, 93:90–97.
- . 1970. A Note on *Bdellasimilis barwicki* and an Indication of a Second Species (Turbellaria: Tricladida). *Australian Zool.*, 15:400–402.
- Runcorn, S. K. (ed.). 1962. *Continental Drift*. Int. Geophysical Series 3: 1–140. New York: Academic Press.
- Schopf, T. M. 1970. Relations of Floras of the Southern Hemisphere to Continental Drift. *Taxon*, 19:657–674.

- Schuster, R. M. 1969. Problems of Antipodal Distribution of Lower Land Plants. *Taxon*, 18:46-91.
- Sivickis, P. B. 1928. The Freshwater Planarians of the Philippines. *Trans. Am. Microscop. Soc.*, 47:356-365.
- Stankovic, S. 1960. *The Balkan Lake Ohrid and Its Living World*. The Hague: W. Junk. 357 pp.
- . 1969. Turbellariés triclades endémiques nouveaux du Lac d'Ohrid. *Arch. Hydrobiol.*, 65:413-435.
- Steenis, C. G. G. van. 1962. The Land-bridge Theory in Botany. *Blumea*, 11:235-372.
- . 1963. "Transpacific Floristic Affinities, Particularly in the Tropical Zone." In J. L. Gressitt (ed.), *Pacific Basin Biogeography*, pp. 219-231. Bishop Museum Press, Hawaii.
- Stegman, B. 1963. "The Problem of the Beringian Continental Land Connection in the Light of Ornithogeography." In J. L. Gressitt (ed.), *Pacific Basin Biogeography*, pp. 65-78. Bishop Museum Press, Hawaii.
- Steinböck, O. 1924. Untersuchungen über die Geschlechtstrakt-Darmverbindung bei Turbellarien nebst einem Beitrag zur Morphologie des Trikladendarmes. *Z. Morphol. Ökol. Tiere*, 2:461-504.
- . 1925. Zur Systematik der Turbellaria Metamerata. *Zool. Anz.*, 64:165-192.
- Steinmann, P. 1914. Beschreibung einer neuen Susswasserticlade von den Kei-Inseln. *Abk. Senck. Naturf. Ges.* 35:111-121.
- Strand, E. 1942. Miscellanea nomenclatoria zoologica et palaeontologica. X. *Folia Zool. Hydrobiol.*, 11:386-402.
- Udvardy, M. F. 1969. *Dynamic Zoogeography with Special Reference to Land Animals*. Toronto: Van Nostrand Reinhold. xviii + 445 pp.
- Ulllyott, P. 1936. A Note on the Zoogeographical History of North-western Europe. *Proc. Prehist. Soc.*, 2:169-177.
- Vandel, A. 1965. *Biospeleology*. Oxford: Pergamon Press. xxiv + 524 pp.
- \*Voigt, W. 1904. Ueber die Wanderungen der Strudelwürmer in unseren Gebirgs-bachen. *Verhandl. Naturh. Ver. Rheinl.*, 61.
- Vuilleumier, F. 1969. Systematics and Evolution in *Diglossa* (Aves, Coerebidae). *Am. Museum Novitates*, no. 2381, 1-44.
- Weiss, A. 1910. Beiträge zur Kenntniss der australischen Turbellarien I. Tricladen. *Z. Wiss. Zool.*, 94:541-604.
- Westblad, E. 1935. *Pentacoelum fucoideum*, ein neuer Typ der Turbellaria metamerata. *Zool. Anz.*, 111:65-82.
- . 1952. Turbellaria (excl. Kalyptrorhynchia). *Further Zool. Results Swed. Antarctic Expedition, 1901-1903*, 4:1-55.
- Whitehouse, R. H. 1913a. Freshwater Planaria (Zoological Records of the Abor Expedition 1911-1912, Part III, No. 22). *Rec. Indian Museum*, 8:317-321.
- . 1913b. The Planarians of the Lake of Tiberias. *J. Proc. Asiatic Soc. Bengal*, 9:459-463.
- Wilhelmi, J. 1909. "Tricladen." *Fauna und Flora des Golfes von Neapel* 32. xii + 405 pp. R. Friedlander, Berlin.

- Willis, J. C. 1922. *Age and Area*. Cambridge: Cambridge University Press. 259 pp.
- Woodworth, W. McM. 1897. Contributions to the Morphology of the Turbellaria II. On Some Turbellaria from Illinois. *Bull. Museum Comp. Zool. Harvard Coll.*, 31:1-16.
- Wulff, E. V. 1950. *An Introduction to Historical Plant Geography*. Waltham, Mass.: Chronica Botanica Co. xi + 223 pp.
- †Zabusova, Z. 1951. A New Species of Planarian from the Caspian Sea. *Tr. Murgabsk. Gidrobiol. St.*, 1:115-126. (In Russian.)
- Zimmerman, E. C. 1963. "Summary Discussion." In J. L. Gressitt (ed.), *Pacific Basin Biogeography*, pp. 477-481. Bishop Museum Press, Hawaii.