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A new higher classification of planarian flatworms (Platyhelminthes, Tricladida)

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This paper presents a revised classification for the higher taxa within the Tricladida. A historical sketch is provided of the higher classificatory systems of triclad flatworms. As far as possible, the new classification is based on published phylogenetic studies. A phylogenetic tree generalizing currently available hypotheses on the higher-taxon relationships of the Tricladida forms the backbone of the new classification. There is no longer any room in formal classifications for the taxon names Terricola and Paludicola, previously used to indicate the suborders of freshwater and land planarians, respectively. It is a consequence of the new classification that the taxonomic rank of the terrestrial planarians is now at the level of family. A new diagnosis of this family is provided. The taxon name Continenticola denotes a monophyletic group consisting of the freshwater planarians and the terrestrial planarians. At this stage it is difficult to find unequivocal morphological apomorphies enabling a diagnosis for the Continenticola.

Keywords: Platyhelminthes; Tricladida; Terricola; Paludicola; Continenticola; new classification

Introduction

The first major phylogenetic re-assessment of the phylum Platyhelminthes stems from 1985, when it became clear that the classical division of the group into three Classes (Turbellaria, Trematoda, Cestoda; cf. Hyman 1951) no longer corresponded with modern, cladistic analyses (cf. Ehlers 1985). Notably, the Class Turbellaria, the free-living flatworms, turned out to comprise a paraphyletic group of taxa. Over the past few years there has been a second major revolution in the taxonomy of the flatworms, mainly due to the advent of molecular systematics. It was discovered that the phylum Platyhelminthes, as classically conceived, formed a polyphyletic assemblage of taxa. Earlier, Smith et al. (1986) had already suggested that Platyhelminthes was polyphyletic in view of the lack of robust morphological synapomorphies uniting the three major clades that were at that time recognized within the phylum, *viz*. Acoelomorpha, Catenulida, and Rhabditophora. In particular, the Acoelomorpha (comprising the Acoela and Nemertodermatida) turned out to form a basal branch in the phylogeny of the Bilateria, whereas the majority of the classical Platyhelminthes grouped within the Lophotrochozoa (cf. Baguñà and Riutort 2004 and references

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therein). Most of the earlier hypotheses on the evolution of the bilaterian animals assigned the Platyhelminthes as a whole a basal position, due to their lack of a coelom, and thus considered the phylum to constitute an early-emerging branch on the phylogenetic tree of the Bilateria. Some workers developed an alternative view, postulating that the Platyhelminthes originated from coelomate ancestors by the reduction of coelomic cavities in the adult worm (Remane et al. 1980) or by progenesis from larval forms (Rieger 1985). The recent, second revolution in the taxonomy of the flatworms revealed that the basal position applies only to the Acoelomorpha and that, consequently, the classically conceived phylum of the Platyhelminthes constitutes a polyphyletic group. Recently, it was shown that the Acoelomorpha does not represent a monophyletic group but that Acoela and Nemertodermatida are two separate early lineages of the Bilateria (Wallberg et al. 2007). Workers have continued to use, mostly implicitly, the taxon name Platyhelminthes for the Catenulida + Rhabditophora (i.e. the classical Platyhelminthes minus Acoela and Nemertodermatida), which form a monophyletic clade at the base of the Lophotrochozoa. In conformity with the new diagnosis provided by Baguñà and Riutort (2004) we recommend using the name Platyhelminthes for this restricted group of lophotrochozoans.

The studies underlying the first and second revolution in the taxonomy of the flatworms also re-evaluated the phyletic position of the triclad flatworms within the Platyhelminthes, as well as the phylogenetic relationships between the various higher taxa within the Tricladida. Differences between insights resulting from the first and second revolution, contradictory results between various recent studies, as well as unresolved problems have now resulted in much confusion concerning a currently appropriate taxonomy and the assignment of taxon names and categories to various taxa of the planarian flatworms or Tricladida. For example, Baguñà and Riutort (2004: table 3), considered several taxon names that have been available for very many years to be *nomina nuda*. Tyler et al. (2006) suggested that in a modern classification a still unnamed taxon would be necessary for the Dugesiidae + Terricola, whereas such a name is already available (see later).

In this paper we present a revised classification for the higher taxa within the Tricladida. As far as possible this classification is based on published phylogenetic studies and thus truly aims to be a cladistic classification, reflecting the topology of the phylogenetic trees. In a phylogenetic taxonomy, categorical ranking reflects the topology of the underlying phylogenetic tree of the taxa. At the same time this is the reason that the classification presented later can only reflect current phylogenetic knowledge and consensus and, consequently, is at best a working hypothesis open to future refinements and corrections.

Furthermore, we review older classificatory systems of triclad flatworms and discuss recent systematic developments. We hope that the new classification presented, together with the review of the older systems and the discussion of more recent developments, will provide both flatworm specialists and general biologists with a framework that allows them to understand and appreciate the taxonomic diversity of triclads and will stimulate future thought and research.

Historical review

The current higher classification of the triclads reflects Hallez' (1892) scheme in which he recognized three main groups of planarians on the basis of their different

habitats, *viz*. Maricola (marine planarians), Paludicola (freshwater planarians), and Terricola (land planarians). Although Von Graff (1912–17: 3202, in 1916) considered this threefold division based on habitat to be a mere "Notbehelf" (stopgap), these three groups and their respective taxon names have persisted up to the present.

Within the Paludicola, Hallez (1892) recognized two families, the Planarida Stimpson, 1857 and the Dendrocoelida Hallez, 1892, the latter characterized by the presence of anterior adhesive organs. Later, Hallez (1894) used the names Planaridae (non Planariidae) and Dendrocoelidae. Von Graff (1912–17: 3212–3221, in 1916) recognized five families within the Paludicola: Curtisiidae Von Graff, 1916; Planariidae Stimpson, 1857; Procotylidae Korotneff, 1908; Podoplanidae Von Graff, 1916; Dicotylidae Zabusov, 1901. However, the type species for the Curtisiidae, *Curtisia simplicissima* (Curtis, 1900) [= *Cura foremanii* (Girard, 1852)], actually represents a member of the Dugesiidae Ball, 1974, a group formerly included in the Planariidae. The other three families, Procotylidae, Podoplanidae, and Dicotylidae, contained representatives of the peculiar Baikalian triclads that are now considered to be members of the Dendrocoelidae (cf. Kenk 1974; Porfirjeva 1977), a family that did not feature in Von Graff's (1912–17) scheme.

Within the Maricola, Hallez (1892) recognized three families, *viz*. Otoplanida Bergendal, 1890, Procerodida, Diesing, 1862 and Bdellourida Diesing, 1862. Later, Hallez (1894) used these names as Otoplanidae (later removed from the Tricladida), Procerodidae, and Bdellouridae. Böhmig (1906) employed two families and five subfamilies: Procerodidae (Euprocerodinae, Cercyrinae, Micropharynginae), and Bdellouridae (Uteriporinae, Eubdellourinae). Subsequently, Wilhelmi (1909) recognized five families in his monographic treatment of the group: Procerodidae Diesing, 1862; Uteriporidae Böhmig, 1906; Cercyridae Böhmig, 1906; Bdellouridae Diesing, 1862; Micropharyngidae Böhmig, 1908. The same taxonomic system was employed by Von Graff (1912–17: 3205–3211 in 1916). The contorted classifications within the Maricola have been reviewed by Sluys (1989a), who recognized the six well-established families, as well as the Centrovarioplanidae Westblad, 1952, based on a phylogenetic analysis of the entire group. For additions and emendations of taxonomic names of the Tricladida Maricola, see Sluys and Kawakatsu (1995).

Within the Terricola, Hallez (1892, 1893) recognized only three families, *viz*. Leimacopsida Schmarda, 1859, Geoplanida Stimpson, 1857, and Polycladida Stimpson, 1857. Only 2 years later, he employed the same classificatory system but changed the spelling of the taxon names, i.e. Leimacopsidae, Geoplanidae, Polycladidae (Hallez 1894). Von Graff (1896) only recognized two of Hallez' families and added three others: Leimacopsidae; Geoplanidae; Bipaliidae Stimpson, 1857; Cotyloplanidae Von Graff, 1896; Rhynchodemidae Von Graff, 1896. In his monograph on the land planarians Von Graff (1899) employed the same classificatory system but renamed Leimacopsidae as Limacopsidae. This system was preserved in his later work (Von Graff 1912–17: 3221–3230, in 1916).

Current classifications no longer recognize the Limacopsidae and the Cotyloplanidae as valid families and only use Bipaliidae, Rhynchodemidae and Geoplanidae (cf. Hyman 1951; Ogren and Kawakatsu 1987, 1988, 1989, 1990, 1991). However, the currently used diagnostic features of these three families are basically the same as those used by Von Graff (1899, 1912–17). The Bipaliidae are characterized by the presence of a spatulate head and multiple eyes, the Rhynchodemidae by a non-expanded head and the presence of only two eyes, and the Geoplanidae by a non-expanded head and numerous small eyes (cf. Ogren et al. 1992: 98–103, pls I–IV).

The taxonomic system of land planarians was the subject of several partial revisions over the past 60 years. These changes are reported in a serial publication, published annually since 1987 (cf. Kawakatsu et al. 2007).

Steinböck (1925) used the different structure of the nervous system in the Maricola, Terricola, and Paludicola as the basis for a new higher classification. He noted that the nervous system of the Terricola differs from that of the Maricola and the Paludicola, notably in the fact that there is only one pair of ventral nerve cords and a highly developed subepidermal nerve plexus (cf. Sluys 1989b). Steinböck called this situation the diploneuran nervous system and coined the taxon name Diploneura for the land planarians. Further he united the Maricola and the Paludicola into one group, the Haploneura. Sluys (1989b) still considered the diploneuran nervous system to represent a defining characteristic of the Terricola. In contrast, Ball (1981) noted that the Haploneura was devoid of supporting autapomorphies and, subsequently, the comprehensive analysis of Sluys (1989b) showed that it is a paraphyletic group that has thus lost its taxonomic integrity.

In addition to the Maricola, Paludicola, and Terricola, a fourth major clade was proposed by Sluys (1990), *viz*. the Cavernicola. This clade groups five enigmatic planarians (within four genera) of which four were formerly assigned to the Maricola, albeit with much reservation, and a fifth had been tentatively placed among the paludicolans. The morphological phylogenetic analysis of this group suggested that the Cavernicola should not be classified among the Maricola, Terricola or Paludicola but represents a separate, fourth lineage within the Tricladida. Sluys (1990) argued that the Cavernicola is more closely related to the Paludicola than the Terricola and suggested a possible sistergroup relationship between Cavernicola and Paludicola.

Relationships within these four major taxa or suborders have been analyzed in detail for the Cavernicola (Sluys 1990) and the Maricola (Sluys 1989a). For the Paludicola the only comprehensive morphological higher-level analysis is that of Sluys (1989b), suggesting the following relationships: ((Dugesiidae)((Planariidae) (Dendrocoelidae))). Earlier, a major step was taken in the higher classification of freshwater triclads when Ball (1974) separated the family Dugesiidae Ball, 1974 as a distinct group from the Planariidae, being defined by its unique eye structure with a multicellular pigment cup containing numerous light receptive cells.

With respect to the Paludicola, lower-level phylogenetic analyses have mostly focused on the Dugesiidae and its nominal genus, *Dugesia* Girard, 1850 (Ball 1974; Sluys et al. 1998; Sluys 2001). Phylogenetic relationships within the Planariidae and the Dendrocoelidae have generally been neglected. It was only recently that Sluys and Kawakatsu (2006) presented an exploratory analysis of presumed morphological apomorphies for some major groups within the family Dendrocoelidae.

As exponents of the second major revolution in the taxonomy of flatworms, several molecular studies radically changed our views on the phylogenetic relationships between the major taxa of the Tricladida. Basically, it was shown that the Paludicola is a paraphyletic group because the Dugesiidae has a sistergroup relationship with the Terricola, as strongly suggested by a unique 18S gene duplication shared by the two last-mentioned taxa (Carranza et al. 1998). It was suggested that the new taxon name Continenticola should be used for this new group comprising the land planarians and the freshwater planarians and, consequently, use of the now obsolete taxon names Paludicola and Terricola should be abandoned. More recent studies (Baguñà et al. 2001; Alvarez-Presas et al. 2008) on larger sets of sequences and taxa corroborated

these earlier findings but also complicated the picture: two dugesiid genera (*Spathula*, *Romankenkius*) out of the seven examined grouped within the land planarians, thus suggesting that the Dugesiidae, as currently understood, is polyphyletic. Recent unpublished results also indicate that the dugesiid genus *Reynoldsonia* falls within the land planarians and together with *Spathula* and *Romankenkius* forms the sistergroup of the Microplaninae. However, this counterintuitive result of some dugesiid genera falling within the land planarians may be due to rooting problems.

A phylogenetic tree that takes into account currently available hypotheses on the relationships between the major taxa of the Tricladida is presented in Figure 1. It is a generalized, hand-drawn supertree, reflecting current insights and consensus on the phylogenetic relationships between the major taxa within the triclads. This tree forms the backbone of the new classification presented in the following section.

New classification

Order **TRICLADIDA** Lang, 1884
  Suborder **MARICOLA** Hallez, 1892
    Superfamily CERCYROIDEA Böhmig, 1906
      Family CENTROVARIOPLANIDAE Westblad, 1952
        Genus *Centrovarioplana* Westbald, 1952
      Family CERCYRIDAE Böhmig, 1906
        Genus *Stummeria* Böhmig, 1908

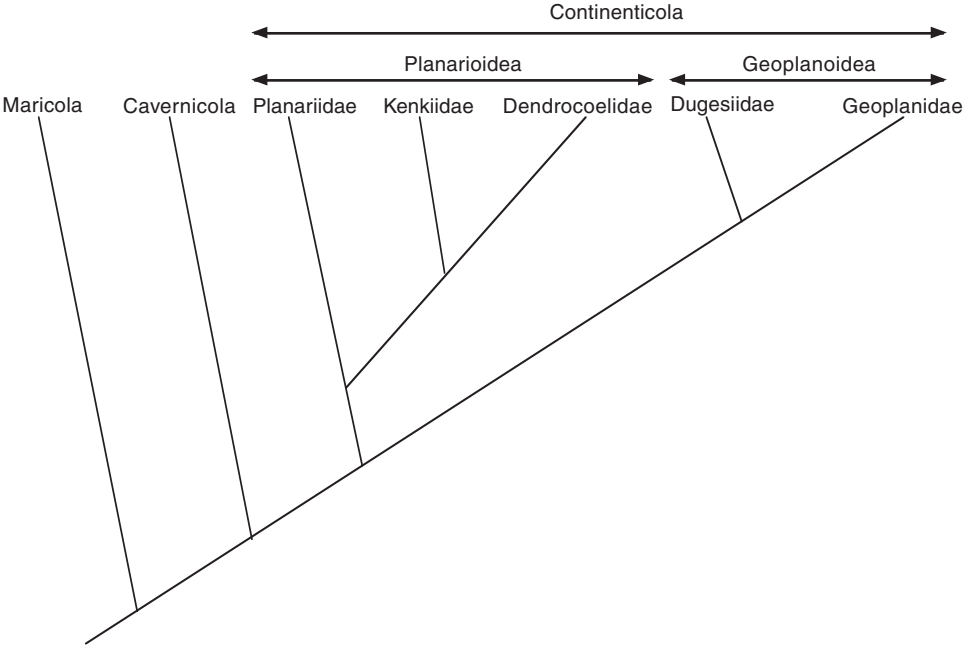

Figure 1. Phylogenetic supertree of the major taxa within the Tricladida, as generalized from various published studies, forming the backbone for the classification presented.

Genus *Oregoniplana* Holmquist and Karling, 1972
Tribe Cercyrini Böhmig, 1906
Genus *Probursa* Hyman, 1944
Genus *Pacifides* Holmquist and Karling, 1972
Genus *Puiteca* Du Bois-Reymond Marcus, 1955
Genus *Cerbussowia* Wilhelmi, 1909
Genus *Sabussowia* Böhmig, 1906
Genus *Cercyra* Schmidt, 1861
Family MEIXNERIDIDAE Westblad, 1952
Genus *Meixnerides* Westblad, 1952
Genus *Jugatovaria* Sluys and Ball, 1989
Superfamily BDELLOUROIDEA Diesing, 1862
Family UTERIPORIDAE Böhmig, 1906
Subfamily UTERIPORINAE Böhmig, 1906
Genus *Foviella* Bock, 1925
Genus *Uteriporus* Bergendal, 1890
Genus *Nexilis* Holleman and Hand, 1962
Genus *Allogenus* Sluys, 1989
Genus *Dinizia* Marcus, 1947
Genus *Leucolesma* Marcus, 1948
Genus *Vatapa* Marcus, 1948
Genus *Micaplana* Kato, 1937
Subfamily ECTOPLANINAE Bresslau, 1933
Genus *Obrimoposthia* Sluys and Ball, 1989
Genus *Nesion* Hyman, 1956
Genus *Tryssosoma* Ball, 1977
Genus *Paucumara* Sluys, 1989
Genus *Ectoplana* Kaburaki, 1917
Genus *Ostenocula* Sluys, 1989
Genus *Procerodella* Sluys, 1989
Genus *Miroplana* Kato, 1931
Family BDELLOURIDAE Diesing, 1862
Subfamily BDELLOURINAE Diesing, 1862
Genus *Nerpa* Marcus, 1948
Genus *Pentacoelum* Westblad, 1935
Genus *Syncoelidium* Wheeler, 1894
Genus *Bdelloura* Leidy, 1851
Subfamily PALOMBIELLINAE Sluys, 1989
Genus *Palombiella* Westblad, 1951
Genus *Miava* Marcus, 1954
Genus *Oahuhawaiiana* Kawakatsu and Mitchell, 1984
Genus *Synsiphonium* Hallez, 1911
Superfamily PROCERODOIDEA Diesing, 1862
Family PROCERODIDAE Diesing, 1862
Genus *Procerodes* Girard, 1850

Genera Incertae Sedis:
Genus *Micropharynx* Jägerskiöld, 1896
Genus *Tiddles* Marcus, 1963

Suborder **CAVERNICOLA** Sluys, 1990
Family DIMARCUSIDAE Mitchell and Kawakatsu, 1972
Genus *Balliania* Gourbault, 1972
Genus *Rhodax* Marcus, 1946
Genus *Opisthobursa* Benazzi, 1972
Genus *Mitchellia* Kawakatsu and Chapman, 1983

Suborder **CONTINENTICOLA** Carranza, Littlewood, Clough, Ruiz-Trillo, Baguñà and Riutort, 1998
Superfamily PLANARIOIDEA Stimpson, 1857
Family PLANARIIDAE Stimpson, 1857
Genus *Planaria* Müller, 1776
Genus *Polycelis* Ehrenberg, 1831
Genus *Phagocata* Leidy, 1847
Genus *Ijimia* Bergendal, 1890
Genus *Seidlia* Zabusov, 1911
Genus *Crenobia* Kenk, 1930
Genus *Atrioplanaria* De Beauchamp, 1932
Genus *Digonoporus* An der Lan, 1941
Genus *Hymanella* Castle, 1941
Genus *Plagnolia* De Beauchamp and Gourbault, 1964
Genus *Bdellasimilis* Richardson, 1968
Genus *Paraplanaria* Ball and Gourbault, 1978
Family DENDROCOELIDAE Hallez, 1892
Genus *Dendrocoelum* Örsted, 1844
Genus *Bdellocephala* De Man, 1875
Genus *Anocelis* Stimpson, 1857
Genus *Procotyla* Leidy, 1857
Genus *Sorocelis* Grube, 1872
Genus *Rimacephalus* Zabusov, 1901
Genus *Protocotylus* Korotnev, 1908
Genus *Polycladodes* Steinmann, 1910
Genus *Archicotylus* Korotnev, 1912
Genus *Baikaloplana* Berg, 1925
Genus *Miodendrocoelum* De Beauchamp, 1929
Genus *Dendrocoelopsis* Kenk, 1930
Genus *Baikalobia* Kenk, 1930
Genus *Acromyadenium* De Beauchamp, 1931
Genus *Caspioplana* Zabusova, 1951
Genus *Armilla* Livanov, 1961
Genus *Hyperbulbina* Livanov and Porfirjeva, 1962
Genus *Papilloplana* Kenk, 1974
Genus *Hyperpapillina* Porfirjeva, 1973
Genus *Atria* Porfirjeva, 1970
Genus *Baikalocotylus* Porfirjeva, 1977
Genus *Alaoplana* Kenk, 1974
Family KENKIIDAE Hyman, 1937
Genus *Sphalloplana* De Beauchamp, 1931
Genus *Kenkia* Hyman, 1937

- Superfamily GEOPLANOIDEA Stimpson, 1857
  - Family DUGESIIDAE Ball, 1974
    - Genus *Girardia* Ball, 1974
    - Genus *Bopsula* Marcus, 1946
    - Genus *Cura* Strand, 1942
    - Genus *Weissius* Sluys, 2007
    - Genus *Schmidtea* Ball, 1974
    - Genus *Dugesia* Girard, 1850
    - Genus *Neppia* Ball, 1974
    - Genus *Romankenkius* Ball, 1974
    - Genus *Eviella* Ball, 1977
    - Genus *Spathula* Nurse, 1950
    - Genus *Reynoldsonia* Ball, 1974
  - Family GEOPLANIDAE Stimpson, 1857
    - Subfamily BIPALIINAE Von Graff, 1896
      - Genus *Bipalium* Stimpson, 1857
      - Genus *Diversibipalium* Kawakatsu, Ogren, Froehlich and Sasaki, 2002*
      - Genus *Humbertium* Ogren and Sluys, 2001
      - Genus *Novibipalium* Kawakatsu, Ogren and Froehlich, 1998
    - Subfamily MICROPLANINAE Pantin, 1953
      - Genus *Amblyplana* Von Graff, 1896
      - Genus *Diporodemus* Hyman, 1938
      - Genus *Geobenazzia* Minelli, 1974
      - Genus *Incapora* Du Bois-Reymond Marcus, 1953
      - Genus *Microplana* Vejdovsky, 1890
      - Genus *Othelosoma* Gray, 1869
      - Genus *Pseudoartiocotylus* Ikeda, 1911
      - Genus *Statomicroplana* Kawakatsu, Froehlich, Jones, Ogren and Sasaki, 2003*
    - Subfamily RHYNCHODEMINAE Von Graff, 1896
      - Tribe Rhynchodemini Von Graff, 1896
        - Genus *Anisorhynchodemus* Kawakatsu, Froehlich, Jones, Ogren and Sasaki, 2003*
        - Genus *Cotyloplana* Spencer, 1892
        - Genus *Digonopyla* Fischer, 1926
        - Genus *Dolichoplana* Moseley, 1877
        - Genus *Platydemus* Von Graff, 1896
        - Genus *Rhynchodemus* Leidy, 1851
      - Tribe Caenoplanini Ogren and Kawakatsu, 1991
        - Genus *Arthurdendyus* Jones and Gerard, 1999
        - Genus *Artioposthia* Von Graff, 1896
        - Genus *Australopacifica* Ogren and Kawakatsu, 1991*
        - Genus *Australoplana* Winsor, 1991
        - Genus *Caenoplana* Moseley, 1877
        - Genus *Coleocephalus* Fyfe, 1953
        - Genus *Endeavouria* Ogren and Kawakatsu, 1991
        - Genus *Fletchamia* Winsor, 1991
        - Genus *Kontikia* C. G. Froehlich, 1955

Genus *Lenkunya* Winsor, 1991
Genus *Newzealandia* Ogren and Kawakatsu, 1991
Genus *Parakontikia* Winsor, 1991
Genus *Pimea* Winsor, 1990
Genus *Reomkago* Winsor, 1991
Genus *Tasmanoplana* Winsor, 1991
Genus *Timyma* E. M. Froehlich, 1978
Tribe Anzoplanini Winsor, 2006
Genus *Anzoplana* Winsor, 2006
Genus *Fyfea* Winsor, 2006
Tribe Eudoxiatopoplanini Winsor, 2009
Genus *Eudoxiatopoplana* Winsor, 2009
Tribe Pelmatoplanini Ogren and Kawakatsu, 1991
Genus *Beauchampius* Ogren and Kawakatsu, 1991
Genus *Pelmatoplana* Von Graff, 1896
Subfamily GEOPLANINAE Stimpson, 1857
Genus *Amaga* Ogren and Kawakatsu, 1990
Genus *Cephaloflexa* Carbayo and Leal-Zanchet, 2003
Genus *Choeradoplana* Von Graff, 1896
Genus *Enterosyringa* Ogren and Kawakatsu,1990
Genus *Geobia* Diesing, 1861
Genus *Geoplana* Stimpson, 1857
Subgenus *Barreirana* Ogren and Kawakatsu, 1990
Subgenus *Geoplana* Stimpson, 1857
Genus *Gigantea* Ogren and Kawakatsu, 1990
Genus *Gusana* E. M. Froehlich, 1978
Genus *Issoca* C. G. Froehlich, 1978
Genus *Liana* E. M. Froehlich, 1978
Genus *Notogynaphallia* Ogren and Kawakatsu, 1990
Genus *Pasipha* Ogren and Kawakatsu, 1990
Genus *Polycladus* Blanchard, 1845
Genus *Pseudogeoplana* Ogren and Kawakatsu, 1990*
Genus *Supramontana* Carbayo and Leal-Zanchet, 2003
Genus *Xerapoa* C. G. Froehlich, 1955

Note: *indicates collective group.

Discussion

The monophyletic status of the Tricladida is supported by at least two complex apomorphic features, *viz*. a unique embryological development, and the presence of a ventral annular zone of adhesive gland openings (cf. Sluys 1989b). Because of the presumed close relationship between the Bothrioplanida and the triclads, Sluys (1989b) suppressed the tricladoid intestine as an apomorphy for the Tricladida. However, recent molecular analyses revealed that the Bothrioplanida are not closely related to the triclads and thus have independently evolved the three-branched intestine, with the consequence that this kind of gut arrangement may again be postulated as an apomorphy for the Tricladida (cf. Littlewood et al. 2004). The morphology-based hypotheses on the monophyly of the triclads were corroborated by molecular studies

that identified the Tricladida as a monophylum with a very high degree of support (Carranza et al. 1998; Baguñà et al. 2001). The same molecular phylogenetic analyses retrieved the Maricola as a monophyletic group with high support. The morphological support for a monophyletic Maricola was less robust and based on the presence of adhesive papillae arranged into the ventral annular zone that was postulated as an autapomorphy for the entire group of triclads (Sluys 1989b). Recently, Ax (2008) argued that this marginal band with adhesive papillae is a plesiomorphic feature and therefore cannot support the presumed monophyly of the Maricola. Molecular studies consistently fail to support the earlier hypotheses on the monophyletic status of the Paludicola (see earlier) and at the same time are as yet unable to find support for a monophyletic group of land planarians (cf. Baguñà et al. 2001; Alvarez-Presas et al. 2008). However, the last-mentioned situation may be a result of rooting problems (cf. Alvarez-Presas et al. 2008), since at least three autapomorphies have been listed in support of the monophyletic status of the land planarians, *viz*. the presence of a creeping sole, diploneuran nervous system, and a complex type of pharynx musculature (Sluys 1989b).

Although molecular studies generally provide a robust hypothesis on a sister-group relationship between the Dugesiidae and the land planarians, it has remained difficult to find unambiguous morphological synapomorphies supporting this relationship. It has been argued that the multicellular eye cup with numerous photoreceptive cells, which was originally postulated as an apomorphy for the Dugesiidae (cf. Sluys 1989b and references therein), might be a synapomorphy for the Dugesiidae and the Terricola since land planarians also possess such eyes (Carranza et al. 1998). However, Sluys and Kawakatsu (2006) showed that multicellular eye cups with numerous light receptive cells are not restricted to the Dugesiidae and the Terricola but also occur in a good number of dendrocoelid species (family Dendrocoelidae) and even in a few planariid species (family Planariidae). These workers concluded that the level of universality at which eye structure may be postulated as an apomorphy remains to addressed in future and more detailed studies.

Recently, Falleni et al. (2006, forthcoming) suggested some ultrastructural features as possible synapomorphies for the Dugesiidae and the land planarians. In both taxa the female gonad possesses a small amount of yolk globules that lack cortical granules in the peripheral ooplasm, while the vitellocytes contain egg shell globules with a meandering/concentric pattern. Such yolk globules and egg shell globules do not occur in the other freshwater planarians, nor do they occur in the marine triclads and in many other flatworms; therefore, this situation is interpreted as the plesiomorphic condition.

In the new classification presented above, the taxa, notably the genera, are arranged according to their order on the available phylogenetic trees (e.g. for Maricola, Cavernicola, Dugesiidae). In cases where phylogenetic trees are not available, the taxa have been arranged alphabetically.

In our text, we have continued to use the name Terricola to indicate the presumably monophyletic group of land planarians. However, as a consequence of the phylogenetic relationships revealed by molecular studies there is no longer any room in formal classifications for the taxon name Terricola. These relationships suggest that there are three major groups of taxa, *viz*. Maricola, Cavernicola, and Continenticola (Figure 1), the latter comprising two other major taxa, *viz*. the Planarioidea and the Geoplanoidea. The land planarians merely form a subgroup of the Geoplanoidea

and therefore no longer rank taxonomically at the same level as the suborders Maricola and Cavernicola. In a similar vein, there is no longer any room for the old suborder Paludicola. Under this new system the land planarians rank as a family, the Geoplanidae Stimpson, 1857. Evidently, one may wish to continue usage of the name "Terricola" or the vernacular name terricolans to refer to the group of the land planarians. In a comparable way one has continued to use the names "Turbellaria" and turbellarians to indicate the informal grouping of the free-living flatworms (cf. Schockaert et al. 2008), albeit that the latter do not constitute a monophylum. Although the land planarians probably do form a monophyletic group, their altered taxonomic rank precludes the formal usage of the old (sub)order name Terricola. Since family names have to be based on the stem of one of the included genera, we have chosen the genus *Geoplana* as the type genus for the entire family of land planarians, i.e. the Geoplanidae. For many years this family name was employed for only a restricted group of land planarians, albeit that originally Stimpson (1857) coined it to comprise all land planarians. For the sake of clarity we present the following new diagnosis:

Family **GEOPLANIDAE** Stimpson, 1857

Triclads with an auxillary, ventral nerve plexus and a distinct creeping sole.

Since some or all characters that make up the creeping sole may be secondarily lost in some land planarian taxa, this structure requires some additional discussion. The majority of the land planarians possess creeping soles that are presently generally understood to be ciliated creeping soles or creeping ridges, albeit not always specifically referred to as being provided with cilia (Von Graff 1912–17; Hyman 1951; Ball and Reynoldson 1981; Sluys 1989b). Generally, there is no mention in the literature of the secretions that are also usually present in a ciliated creeping sole; they are taken for granted. We suggest the following definition of the creeping sole:

A flat or ridged modified strip of epithelium on the ventral surface of geoplanid triclad flatworms characterized by the presence of cilia, the relative predominance of cyanophil glands, and absence of rhabdoids of the rhammite type, and which provides propulsive forces by ciliary or muscular action, or by a combination of both.

Some taxa have secondarily lost the ciliated creeping sole, such as the genera *Geobia* and *Arthurdendyus*, together with as yet undescribed Australian taxa (L. Winsor, pers. comm.). The absence of a creeping sole in *Geobia* was already noted by Von Graff (1912–17), who postulated that these animals do not practice the creeping or sliding type of locomotion usual in triclads, but wriggle, twist and turn in the manner of nematodes.

Evidently, the new phylogenetic trees imply that the old distinction between Rhynchodeminae and Geoplaninae, based on the presence of only two or multiple eyes is no longer valid. In the new scheme (cf. Alvarez-Presas et al. 2008: fig. 4) the Rhynchodeminae is shown to be the sistergroup of a former geoplanid taxon, the Caenoplanini, with the Rhynchodeminae + Caenoplanini in turn sharing a sistergroup relationship with the Geoplaninae. The caenoplanids studied by Alvarez-Presas et al. (2008) are: three species of *Artioposthia*, *Arthurdendyus*

triangulatus, three species of *Caenoplana*, a species of *Newzealandia*, and a species of *Australoplana*. From the Geoplaninae they examined four species of *Geoplana*, and one species of *Notogynaphallia*. The new classification reflects these recently acquired phylogenetic insights.

In their paper, Carranza et al. (1998: 639) remarked that for the new grouping of the freshwater triclads plus the terrestrial planarians, "perhaps a suitable name . . . would be the Continenticola." Although the phylogenetic tree in their paper (Carranza et al. 1998: fig. 3) plots character states on several branches, they did not present an explicit discussion on the possible diagnostic features of the new clade. Furthermore, the label on the tree refers to "Continenticola". As a consequence, Baguñà and Riutort (2004: table 3) refer to this taxon as "Continenticola" *nom. nud.* (see also Tyler et al. 2006). However, since the International Code of Zoological Nomenclature (ICZN) (1985, 1999) does not regulate taxon names above the family group level a diagnosis is not required in order to make the names available. These names are simply names of groups that may be coined or replaced when deemed necessary. Therefore, we have here assigned the Continenticola to the rank of Suborder with the authorship of Carranza et al. (1998).

At this stage it is difficult to find unequivocal morphological apomorphies enabling one to provide a diagnosis for the Continenticola. One may be inclined to use the features listed by Sluys as apomorphies for this clade: loss of Haftpapillen (adhesive papillae), presence of resorptive vesicles, reduction of the number of longitudinal nerve cords (Sluys 1989b: fig. 1, characters 14, 15, 16, respectively). The same features were also presented on the tree of Baguñà et al. (2001: fig. 6.6, characters 8, 9, 10). However, these three presumed apomorphies were originally used by Sluys (1989b) without any consideration of the taxonomic status, phylogenetic position and anatomical features of the Cavernicola, a taxon that was erected one year later (Sluys 1990). Although the trees presented in Baguñà et al. (2001) and in Alvarez-Presas et al. (2008, fig. 1B) suggest that these three characters may function as apomorphies for the Continenticola, this is only due to the fact that their characters 8, 9, and 10 and 2, 3, and 4, respectively, are positioned at an incorrect level of universality. Loss of adhesive papillae, presence of resorptive vesicles, and reduction of the number of longitudinal nerve cords are features also to be found in members of the Cavernicola. Therefore, these characters should be placed as presumed apomorphies of a clade comprising Cavernicola, the freshwater planarians, and the land planarians (cf. Sluys 1990: fig. 5). As a consequence, it is presently very difficult to find unequivocal autapomorphic characters for the Continenticola. Evidently, the problem hinges on the phyletic position of the Cavernicola as a separate taxon. It is highly opportune to undertake a molecular phylogenetic analysis of all cavernicolan genera in order to determine whether they fall within or outside of the Continenticola. If they fall within the Continenticola the afore-mentioned characters are autapomorphies for the Continenticola (see also Ax 2008), if not, then apomorphies for the Continenticola remain to be discovered.

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