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Clitellate evolution and leech diversity: Glossiphoniidae excl. *Helobdella* (Annelida: Hirudinea: Rhynchobdellida) from South America

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Abstract

A review of the valid species of Glossiphoniidae other than *Helobdella* produced 25 nominal species reported to date from South America. These species belong to the following taxa: Glossiphoniinae: Placobdella (4 species); Haementeriinae: Alboglossiphonia (1 species); Haementeria (16 species); Maiabdella (1 species); Trybothrynobdella (1 species); Theromyzinae (bird leeches): Theromyzon (2 species). 88% of this fauna is endemic to the South American continent. Full synonyms and detailed South American occurrences are provided. This is the first reassessment of these South American glossiphoniid leeches in 26 years. I also provide a history of ideas on clitellate phylogeny, and summarize recent results on leech evolution. Although molecular phylogenies consistently fail to indicate the sister group of the Euclitellata, the interstitial estuarine worms belonging to the Questidae share several synapomorphies with true clitellates: direct development, bifid and hair chaetae, a cocoon producing clitellum and sperm stored in spermathecae in females, as well as gonads limited to a few segments in both sexes. From an applied perspective, I suggest the use of leeches in ecological studies of environmental impact, given their unprecedented rates of endemicity among freshwater organisms.

Key words: biodiversity, ecology, evolution, indicator organisms, Neotropical region, true leeches.

Resumo

EVOLUÇÃO DOS CLITELADOS E DIVERSIDADE DOS HIRUDÍNEOS: GLOSSIPHONIIDAE EXCL. HELOBDELLA (ANNELIDA: HIRUDINEA: RHYNCHOBDELLIDA) DA AMÉRICA DO SUL. Uma revisão das espécies válidas de Glossiphoniidae exceto Helobdella produziu 25 espécies nominais registrados até hoje na América do Sul. Estas espécies pertencem aos seguintes taxa: *Placobdella* (4 espécies); Haementeriinae: *Alboglossiphonia* (1 espécie); *Haementeria* (16 espécies); *Maiabdella* (1 espécie); *Trybothrynobdella* (1 espécie); Theromyzinae: *Theromyzon* (2 espécies). 88% desta fauna é endêmica do continente sul americano. Sinonímias completas e ocorrências detalhadas na América do Sul são fornecidas. Esta é a primeira reavaliação dos Glossiphoniidae sul americanos em 26 anos. Eu também forneço um histórico das idéias de filogenia dos clitelados, e sumarizo resultados recentes sobre evolução dos hirudíneos. Embora filogenias moleculares consistentemente falhem na indicação do grupo irmão dos Euclitellata, os vermes estuarinos intersticiais pertencentes aos Questidae compartilham diversas sinapomorfias com os euclitelados: desenvolvimento direto, cerdas capilares e bífidas, um clitelo produtor de casulos e espermatozóides armazenados pelas fêmeas, além de gônadas limitadas a alguns poucos segmentos em ambos os sexos. Numa perspectiva aplicada, sugiro que hirudíneos sejam usados em estudos de impacto ambiental, dado o seu grau ímpar de endemismo entre os organismos aquáticos.

Palavras chave: biodiversidade, ecologia, evolução, organismos indicadores, região Neotropical, sanguessugas verdadeiros.

Introduction

Clitellata represents more than one third of the circa 15 000 species of segmented worms (Annelida) currently considered valid (Erséus, 2005: 357). Synapomorphies of Euclitellata are the presence of a glandular clitellum, hermaphroditism, direct development, a unique sperm morphology, and the relocation of the brain from the prostomium to a more posterior position (Rouse & Fauchald, 1997).

The Hirudinea, or leech-like annelids, have a circumoral and a posterior ventral sucker, and a fixed number of segments (Wetzel, 1992: 90). Hirudinea include acanthobdellidans, branchiobdellidans, and the true leeches. Branchiobdellida are now thougth to represent the sister group of the Euhirudinea (Siddall et al., 2001: 346).

Acanthobdellida, containing the single and rare ectoparastic species of salmon *Acanthobdella* peledina, lacks a prostomium and peristomium, has 29 true segments, and 4 pairs of hook-shaped chaetae on the five anteriormost

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segments, arranged around the mouth opening and functioning as a hooked sucker (Purschke et al., 1993: 91). A. peledina has a protrusible pharynx for feeding from the surface of fishes that it parasites. Such a proboscis-like structure is an apomorphy of leeches (Siddall & Burreson, 1998: 159). Acanthobdellids are now believed to have shared a recent common ancestor with branchiobdellidans and true leeches (Siddall et al., 2001: 346).

Branchiobdellids consist of about 150 species of small clitellates, only a few millimeters long, devoid os chaetae, with fixed number of 15 post-oral segments, and well-developed coelomic cavities (Ferragutti, 2000: 125). Paired jaws represent a synapomorphy of this taxon (Brinkhurst, 1999: 283). They are a Holarctic, freshwater monophyletic group of commensal or parasitic clitellates, mostly associated with members of the Astacidae (Timm, 1991; Brinkhurst & Gelder, 2001).

Moquin-Tandón (1846: 300) referred two new species of Branchiobdellidae for Chile, *B. auriculae* Moquin-Tandón, 1846, from the body cavity of the mollusk *Auricula dombeii*, and *B. chilensis* Moquin-Tandón, 1846, from the gills of a crustacean collected in Santiago, and later refered to as *Astacobdella chilensis* by Diesing (1850). However, descriptions of these two species were not provided, so they are listed as nomina nuda in Gelder (1996: 660). There are thus no known acanthobdellids and branchiobdellids from South America.

Knowledge of clitellate phylogeny has progressed considerably in the last decade. Evolutionary relationships of leeches have been investigated using morphological characters (Siddall & Burreson, 1995), life history data (Siddall & Burreson, 1996), nuclear and mitochondrial gene sequences (Siddall & Burreson, 1998; Trontejl et al., 1999; Siddall et al., 2001; Erséus & Källersjö, 2004), as well as combinations of these data sets at the family level (Apakupakul et al., 1999; Light & Siddall, 1999; Siddall, 2002; Borda & Siddall, 2004; Siddall et al., 2005a). These phylogenies have been reviewed by Martin et al., 2000) and Erséus (2005). The most ambitious attempt to resolve annelid relationships with molecular data has just been published (Rousset et al., 2007).

Siddall et al. (2001) demonstrated with nuclear and mitochondrial gene sequences that true leeches (Euhirudinea), branchiobdellidans and acanthobdellidans form a monophyletic clitellate group that shares a closest common ancestor with Lumbriculidae. In fact, as summarized in Siddall et al. (2005a: 394, fig. 1), there are three main phylogenetic lineages in the traditional Oligochaeta: (1) the aquatic microdrile Tubificida, (2) the oligochaete taxon Lumbriculidae plus their leech-like descendants, and (3) the mainly terrestrial earthworms, including their midrodrile sister taxon Enchytraeidae.

Erséus & Källersjö (2004) obtained similar basal clades with a cladistic analysis using 18S rDNA: The marine euclitellate Capilloventridae as the most basal clade, with the sister lineage forming a dichotomy, one clade containing the aquatic Tubificidae, Phreodrilidae, Haplotaxidae, and Propappidae, and the other clade containing two subgroups: (1) Lumbriculidae together with all leech-like taxa (*Acanthobdella, Branchiobdella* and *Euhirudinida*), and (2) Enchytraeidae together with a monophyletic group of all earthworms included in their study (Lumbricidae, Almidae and Megascolecidae).

Under phylogenetic principles ´Oligochaeta` is consistently non-monophyletic and should be substituted by the monophyletic taxon Clitellata, in order not to exclude part of the descendants of oligochaetes, the leeches. The alternative would be to expand the concept of Oligochaeta Grube (1850), which is older than Clitellata Michaelsen (1928). However, the latter was explicitly formulated to include Hirudinea, so it has priority using phylogenetic principles (Martin, 2001: 1097) and under the phylogenetic code (Cantino & De Queiroz, 2004).

The phylogenetic implication of these results for true leeches is that the proboscis-less medicinal leeches and their kin (the Arhynchobdellidae) are nested within a paraphyletic Rhynchobdellida (Siddall et al., 2005a). A character previously deemed unreliable, the possession of two pairs of compact salivary cells at the base of the proboscis, serves to unite species of *Haementeria* and *Placobdella*, placed in separate subfamilies.

Leeches exibit a remarkable scope of diversity, including ground-dwelling, ectocommensal, blood-feeding, and predatory life-history strategies. They display a variety of themes in parental care and cocoon deposition behaviors, as well as habitats that range from terrestrial to freshwater and marine environments (Siddall & Burreson, 1996: 278).

Euhirudinea, or true leeches, are predatory or ectoparasitic (carnivorous) clitellates without chaetae, having a characteristic sucker mode of locomotion, and a fixed number of segments. Near obliteration of the coelom is a synapomorphy of all euhirudineans, but not of *Acanthobdella* or branchiobdellidans (Brinkhurst, 1999: 282). An anterior sucker, specifically arranged sperm sacs, and the position of male and female openings provide other synapomorphies for the true leeches (Purschke et al., 1993; Trontelj et al., 1999: 141). The oral and caudal organs in euhirudineans are used both for locomotion and feeding, either for grasping prey by macrophagous leeches or for attachment to a host by the ectoparasitic species (Siddall & Burreson, 1995: 1048). The presence of specifically arranged crop caeca for the storage of liquid food is generally not appreciated as an euhirudinian apomorphy (Purschke et al., 1993; Siddall & Burreson, 1996; Trontelj et al., 1999: 146).

True leeches are notorious for their blood feeding habits. But leeches that are opportunistic predators of microinvertebrates are far more abundant in freshwater lakes and streams than are blood-feeders (Siddall & Burreson, 1998: 156). Many predacious species do not suck blood at all (Sawyer, 1986: 4).

There are about 650 species of leeches from freshwater, marine, and terrestrial environments. Euhirudinians transfer their sperm into the interior of the partner´s body, by means of spermatophores or a penis, and hence, have lost the spermathecae of their oligochaete ancestors. The cocoons, in fact, receive fertilized eggs (Westheide, 1999: 199).

The ancestral hirudinid leech was a blood feeder in a freshwater environment no older than frogs and turtles, on which ancestral glossiphoniids and piscicolids are known to feed on, respectively. The majority of the basal-most members of the glossiphoniids are from Africa and South America, suggesting a Gondwanan origin for this family (Siddall et al., 2005a). The Rhynchobdellida are characterized by possessing a muscular proboscis for blood-feeding. The giant Amazonian leech, *Haementeria ghiliani*, grows to a tremendous 40 cm and has a proboscis almost half the body length. They may inspire legends of horrifying attacks from hordes of terrestrial leeches that are the scourge of tropical jungles (Siddall et al., 2001: 346).

Rhynchobdellida feed on blood and other body fluids with the help of a protrusible proboscis (Trontelj et al., 1999: 141), which they insert into their hosts. The plesiomorphic condition in leech evolution was consequently a strictly aquatic life-history. While vertebrates are intermediate hosts for haemogregarine blood parasites, rhynchobdellids are the only leeches known to transmit blood parasites (Siddall & Burreson, 1996: 282).

Glossiphoniidae are dorsovantrally flattened leeches that brood their young (Siddall & Burreson, 1998: 158). Their circulatory apparatus is very simple, as in their aquatic precursors (Omodeo, 1998: 62). They have long been recognized as representing basal leeches (Selensky, 1907; Autrum, 1939). This family is also among the more species rich leech families in terms of described numbers of species (Sawyer, 1986; Ringuelet, 1985). Some species of *Glossiphonia* and *Helobdella* feed on hemolymph of aquatic oligochaetes and snails. The family is also characterized by a remarkable degree of parental care that is unmatched in the phylum Annelida (Kutschera, 1992: 74; Siddall et al., 2005b).

The cocoons of Glossiphoniidae are transparent, flexible, and thin. *Haementeria* and *Helobdella* always attach their cocoons onto the ventral surface of the parent (Kutschera & Wirtz, 2001: 133). These fragile, membranaceous cocoons are viewed as derived in relation to the hardened cocoons of their oligochaete ancestors, and which occur as a plesiomorphy in the remaining leeches. On the other hand, the unique behavior among glossiphoniids to remain with the cocoons, covering and fanning them with their ventral body surface, is closely correlated with the loss of the protective hardened cocoon (Siddall & Burreson, 1996: 282). High complexity of brooding in Glossiphoniidae probably evolved as a survival mechanism for protecting the eggs and young from heavy predation attacks (Sawyer, 1971: 202).

Theromyzon are almost exclusive parasites of the nostrils of ducks, swans and geese (Anatidae) (Sawyer, 1986: 700). *T. tesselatum* from Chile is identical to the European duck leech, and represents the first suggestion of an introduced species of leech (Siddall & Budinoff, 2005: 467).

Since the efforts of Ringuelet (1981), no species inventories of the glossiphoniid leeches from South America have been attempted.

The diverisity and endemism of neotropical hirudineans, which are a result of limited dispersal range of the majority of species, is well known (Moore, 1911; Siddall & Borda, 2004: 14). South America is especially important because of the large number of endemic species.

Ecology and biodiversity. Besides their importance for understanding the evolutionary origin of the continental hermaphroditic clitellates from marine male and female polychaete precursors, leeches represent an underexplored resource for several ecological and hydrological investigations, both continental and marine. Their incredible diversity of habitats, with marine, freshwater and terrestrial predators and ectoparasites of a diverse span of invertebrate and vertebrate aquatic and terrestrial hosts, their feeding and reproductive specializations, their ummatched diversity of parental care strategies among the Annelida, and their loss of larval forms, put the Hirudinea among the most endemic groups among the aquatic organism known to date.

The unmatched endemism of aquatic leeches make them potentially very useful as indicator species of water quality and of undisturbed environments. Their habitat specificity make them very sensitive to any forms of anthropic influences. Despite their ecological potential as bioindicator organisms, basic studies on lecch taxonomy, biology and ecology have been almost totally neglected in tropical regions, including South America.

As a starting point towards obtaining better knowledge of the more inconspicuous invertebrates in our megadiverse continent, I find it important to filter through the existing literature, inventorying the available information and weeding out synonyms and misidentifications according to previous monographic and faunistic studies.

In this paper I provide a catalogue of the glossiphoniids other than *Helobdella* cited to date from the South American continent. The most diverse glossiphoniid genus, *Helobdella*, containing almost half the known species diversity of the

South American hirodofauna, is treated in another paper. I review the phylogeny of Clitellata and state my views on the nature of its sister group. I also suggest that leeches be used as model organisms in studies of environmental impact in freshwater environments.

Material and Methods

I have used 3-letter abbreviations for South American countries (ARG, Argentina; BRA, Brazil; CHI, Chile; COL, Colombia; ECU, Ecuador; FRG, French Guyana; PAR, Paraguay; PER, Peru; SUR, Surinam; URU, Uruguay; VEN, Venezuela) and 2-letter abbreviations for sampled States in Brazil (AM, Amazonas; CE, Ceará; MG, Minas Gerais; MT, Mato Grosso; PA, Pará; PB, Paraíba; PE, Pernambuco; RJ, Rio de Janeiro; RS, Rio Grande do Sul).

Results

Species marked with an asterisk (*) are previously only reported from South America.

Subphylum EUCLITELLATA Jamieson, 1983

Class HIRUDINEA Lamarck, 1818
Syn: Hirudinoidea Soos, 1965

Subclass EUHIRUDINEA Lukin, 1956

Order RHYNCHOBDELLIDA R. Blanchard, 1894

GLOSSIPHONIIDAE Vaillant, 1890

GLOSSIPHONIINAE Autrum, 1939

Placobdella R. Blanchard, 1893
Type: *P. costata* (F. Müller, 1846)
Syn: *Microbdella* Moore, 1900; Oligobdella Moore, 1918 (Type: *Microbdella* biannulata Moore, 1900); *Trachybdella* Pinto, 1920 (Type: *T. bistriata* Pinto, 1920)

1*. *P. bistriata* (Pinto, 1920).
Syn: *Trachybdella bistriata* Pinto, 1920.
Distr: BRA: MG: ponds at km 915 and 931 of railroad (Pinto, 1920a: 624): Uberlândia: Uberabinha river, on freshwater turtle *Phrynops gefroanus* (Brites & Rantin, 2004: 273).

2*. *P. brasiliensis* (Cordero, 1937)
Syn: *Oligobdella brasiliensis* Cordero, 1937.
Distr: BRA (Cordero, 1937a: 1): PE: São Francisco river, on the toirtoise *Hydrapsis geoffroyana* Schlweigert (Ringuelet, 1981: 192).

3*. *P. cheloniae* (Ringuelet, 1978)
Syn: *Oligobdella cheloniae* Ringuelet, 1978
Distr: ARG (Ringuelet, 1978: 264).

4*. *P. columbiensis* (Ringuelet, 1972)
Syn: *Oligobdella columbiensis* Ringuelet, 1972
Distr: COL: Amazonia: Miriti-Paraná river, on the cayman *Palaeosuchus trigonatus* (Schneider) (Ringuelet, 1981: 192).

HAEMENTERINAE Autrum, 1936

Alboglossiphonia Lukin, 1976
Type: *A. heteroclita* (Linnaeus, 1761)

5*. *A. mesembrina* (Ringuelet, 1949)
Syn: *Glossiphonia mesembrina* Ringuelet, 1949
Distr: ARG (Ringuelet, 1949: 141).

Haementeria De Philippi, 1849
Type: *H. ghilianii* De Philippi, 1849
Syn: *Blennobdella* C. E. Blanchard, 1849; Hybobdella Weyenberg, 1877

6*. *H. bonaerensis* MacDonagh, 1928
Distr: ARG (MacDonagh, 1928: 233).

7*. *H. brasiliensis* (M. Weber, 1915)
Syn: *Liostomum brasiliensis* M. Weber, 1915.
Distr: CHI. ARG. PAR. BRA: RS (Pinto, 1923: 968).

8*. *H. depressa* (C. E. Blanchard, 1849)
Syn: *Blenobdella depressa* C. E. Blanchard, 1849.
Distr: CHI. ARG. URU. PAR (Ringuelet, 1981: 191). PER: Amazon (Shain et al., 2007). BRA: RS; CE (Ringuelet, 1981: 191).

9*. *H. dissimilis* Cordero, 1937
Distr: Subantarctic South America (Cordero, 1937a: 36).

10*. *H. eichhornia* Ringuelet, 1978
Distr: ARG (Ringuelet, 1978: 259).

11*. *H. ghilianii* De Philippi, 1849
Distr: SUR (Ringuelet, 1981: 191). FRG (Sawyer et al., 1982: 411). BRA; RJ: PE (Ringuelet, 1981: 191); AM: Amazonia (Perkins et al., 2005: 5219); PA (Pinto, 1923: 959).

12*. *H. gracilis* (Weyenberg, 1883)

Distr: CHI: Valdivia: Teja island: Los Lotos lagune, 13 m deep (Siddall & Borda, 2004: 8). URU: Aspinas brook (Siddall & Borda, 2003: 25). PAR (Ringuelet, 1948: 229).

13*. *H. helleri* (M. Weber, 1915)
Syn: *Liostomum helleri* M. Weber, 1915.
Distr: SUR (Pinto, 1923: 966).

14*. *H. laevis* (M. Weber, 1915)
Syn: *Liostomum laevis* M. Weber, 1915.
Distr: BRA: RS: Porto Alegre (Pinto, 1923: 971).

15*. *H. lutzi* Pinto, 1920
Distr: ECU: Pastaza river (Siddall & Borda, 2003: 25). BRA (Pinto, 1920b: 467): PR (Ringuelet, 1981: 192); PA (Lainson, 1981: 150); MG: Lassance (Pinto, 1923: 973).

16*. *H. maculata* (M. Weber, 1915)
Syn: *Placobdella maculata* M. Weber, 1915.
Distr: PER: Amazon (Shain et al., 2007). BRA (Cordero, 1937b: 19): RS: Porto Alegre; MT: Guahyba; PB: Campina Grande (Ringuelet, 1981: 192).

17*. *H. molesta* (Cordero, 1934)
Syn: *Placobdella molesta* Cordero, 1937.
Distr: South America (Cordero, 1937a: 26). URU: Aspinas brook (Siddall & Borda, 2003: 25).

18. *H. officinalis* De Philippi, 1849
Syn: *H. mexicana* De Philippi, 1849; *Clepsina tuberculifera* Grube 1871. *Glossiphonia granulosa* Jimenez, 1965.
Distr: VEN: San Fernando de Apure (Ringuelet, 1981: 192).
Furth. Distr: Mexico and United States (Ringuelet, 1981: 192).

19*. *H. paraguayensis* (M. Weber, 1915)
Syn: *Liostomum paraguayensis* M. Weber, 1915.
Distr: ARG (Ringuelet, 1944: 5). PAR: San Bernardino. VEN (Pinto, 1923: 970). BRA: RJ; PE; PB (Ringuelet, 1981: 192).

20*. *H. steineri* Hotz-Bolliger, 1981
Distr: BRA: AM (Hotz-Bolliger, 1984: 183).

21. *H. tuberculifera* (Grube, 1871)
Syn: *Clepsina tuberculifera* Grube, 1871.
Distr: ARG (Ringuelet, 1944: 5). URU: Aspina brook (Siddall & Borda, 2003: 25). PAR (Ringuelet, 1948: 230). VEN: Falcón State; Fuárico State. SUR. BRA: PE (Ringuelet, 1981: 192).
Furth. Distr: Cuba (Ringuelet, 1981: 192).

Maiabdella Ringuelet, 1980
Type: *M. batracophila* Ringuelet, 1980

22*. *M. batracophila* Ringuelet, 1980
Distr: ARG: Andean region of Jujuy (Ringuelet, 1980: 68).

Tribothrynobdella Ringuelet, 1976
Type: *T. andicola* Ringuelet, 1976

23*. *T. andicola* Ringuelet, 1976
Distr: PER: Apurimac; Mayabamba; Junín: Naticocha lake; San José (Ringuelet, 1981: 192).

THEROMIZINAE Sawyer, 1986

Theromyzon De Philippi, 1867
Type: *T. pallens* De Philippi, 1867
Syn: *Glossiphonia* (part) Johnson, 1816; *Clepsine* (part) Savigný, 1822; *Haemocharis* (part), De Philippi, 1837 (nec Savigný, 1822); Hemiclepsis (part) Vejdovský, 1883; *Protoclepsine* Moore, 1898 (Type: *P. sexoculatum* Moore, 1898); *Protoclepsis* Livanow, 1902 (Type: *P. garjaewi* Livanow, 1902).

24*. *T. propinquium* (Ringuelet, 1947)
Syn: *Protoclepsis propinquium* Ringuelet, 1947.
Distr: CHI: Neltume, Panguipuilli, Villarica, and Tinquilco lakes; Chiloé: Miraflores (Siddall & Borda, 2004: 8). ARG (Ringuelet, 1947: 217). PER: Junín: Naticocha lake; Cuzco: San Gerónimo stream (Ringuelet, 1981: 192).

25. *T. tessellatum* (O. F. Müller, 1774)
Syn: *Hirudo tessellata* O. F. Müller, 1774; *Ichthyobdella tessellata* (O. F. Müller, 1774); *Erpobdella tesselata* (O. F. Müller, 1774); *Erpobdella vulgaris* var. *tessellata* (O. F. Müller, 1774); *Hemiclepsis tessellata* (O. F. Müller, 1774); *Nephelis tessellata* (O. F. Müller, 1774); *Clepsine tessellata* (O. F. Müller, 1774); *Glossiphonia tessellata* (O. F. Müller, 1774); *Protoclepsis tesselata* (O. F. Müller, 1774); *Glossiphonia eacheana* Thompson, 1846; *Haemocharis eacheana* (Thompson, 1846); *Hirudo vitrina* Dalyell, 1853; *Protoclepsis maculosa* Rathke, 1862.
Distr: CHI (R. Blanchard, 1892: 56). ARG. PER: Víctor (Ringuelet, 1981: 192).
Furth. Distr: Nearctic and Palearctic regions (Ringuelet, 1981: 192).

Discussion

Twenty five nominal species of Glossiphonidae other than *Helobdella* have been refered in the literature for South America, 22 of which are endemic to the South

American continent. This produces an almost 90% index of endemism, a remarkable proportion for animals of aquatic origin. Of the three species that are not restricted to South America, *Haementeria tuberculifera* extends its range into the Caribbean, *H. officinalis* also occurs in Central and North America, and *Theromyzon tesselatum* extends into the Nearctic and Palearctic regions. 28% of the known species were described by the Argentinian Raul Adolfo Ringuelet (†1914-1982), who has thus contributed most to our knowledge of South American glossiphoniids treated herein.

In accordance with recent phylogenetic analyses of the Clitellata, I consider the tubificids and other microdile aquatic worms such as the Capilloventridae, which were dismembered from the Tubificidae by Harman & Loden (1984), as forming the most basal lineage of the Clitellata. The efforts of Erséus (e.g. 1976, 1992) during the last 30 years has disclosed a previouly unknown high diversity of truly marine forms of clitellates, especially of Tubificidae. Euclitellates supposedly originated from marine ¨polychaetes¨, from which the continental forms of freshwater midrodriles, the leech-like clitellates, and the primarily terrestrial earthworms have subsequently evolved. Almeida & Christoffersen (2001) and Almeida et al. (2003) have indicated the polychaete taxon Questidae as the most likely model for such a marine polychaete precursor. The Questidae are remakably tubificid-like in appearance, live in transitional marine-continental habitats (estuaries), and even possess a precursor of a the cocoon-secreting clitellum. Rouse & Fauchauld (1997) suggested that simple bodied polychaetes such as Questidae and Paraonidae were basal annelids on the basis of morphological analyses.

Almeida et al. (2003) argued that Annelida are paraphyletic and should be substituted by the monophyletic taxon Metameria. Questidae represent the sister group of clitellates in that work. For this reason, I use Euclitellata in the classification herein, introduced by Jamieson (1983) for the clitellates exclusive of Questidae. The molecular phylogenies which include Questidae (Erséus et al., 2000; Struck et al., 2002; Erséus & Källersjö, 2004; Rousset et al. 2007) do not give support to this relationship (Erséus, 2005: 357), but neither do they provide an alternative, well supported sister group for the Euclitellata among the polychaetes. There exist as many candidate sister groups to Clitellata as there are molecular studies addressing the issue (Martin, 2001: 1096). Brown et al. (1999) paired Siboglinidae with Clitellata. The sister group of Clitellata remains elusive in molecular phylogenies (Rousset et al., 2007: 42). Erséus et al. (2000) gave support for a sister relationship with Neanthes (Nereidae) and Aphrodita (Aphroditidae). These relationships are questionable on morphological grounds (Martin, 2001: 1096). Interestingly, Almeida et al. (2003) provided morphological and developmental evidence for considering Siboglinidae and Aphroditidae sister groups of the metamerian taxa Radialia and Ecdysozoa, respectively.

The Capilloventridae is now thought to represent the basal clade of the true clitellates (Erséus & Källersjö, 2004: 187). The Questidae continue to represent the most likely candidate among the polychaetes for a sister group relationship with the true clitellates, on the basis of its shared morphological apomorphies with Euclitellata. In fact, few taxa can be recognized as clearly and simply as a monophyletic group by a single autapomorphic character as the Clitellata (Purschke et al., 1993; Westheide & Müller, 1996: 263). Like feathers among vertebrates, or the chitinous exosqueleton of arthropods, I believe that the clitellum signals a complex series of unique adaptations acquired in metameric worms for life in continental habitats.

For example, the relatively smooth body surface and the absence of parapodia and other appendages in Clitellata can be interpreted as specific adaptations to the cocoon shedding process (Westheide & Müller, 1996: 263). Spermathecae are also of great interest to the interpretation of simultaneous hermaphroditism in the clitellates (Westheide, 1999: 200). Internal fertilization, direct development without primary larval stages (Sawyer, 1986: 6), the specialized genital organs, and copulation, can all be interpreted as adaptations to the rigor of the terrestrial or freshwater habitats in which most clitellates live (Lassere, 1975: 216). Finally, the evolution of hermaphroditism shoud be favoured in small species (Clark, 1978). The stem species of the clitellates was probably small-bodied (about several millimeters) and reproduced by direct sperm transfer (Westheide, 1999: 211).

Questidae are small littoral and sublittoral intestitial marine worms (Jamieson, 1983: 179). Questids are dioecious, and lack the sperm specializations which are diagnostic of true Euclitellata, such as the acrosome tube of the sperm (Jamieson, 1983). In these plesiomorphic features, the Questidae fall outside of the Euclitellata. On the other hand, the females have a clitellum and produce a cocoon, store sperm in spermathecae, and animals of both sexes have a limited number of gonadal segments, sharing hair and bifid chaetae with the aquatic clitellates (Giere & Riser, 1981). By positioning the Questidae as the sister group of the Euclitellata on all this morphological, developmental, and ecological evidence, it is possible to visualize how a large series of adaptations for a continental existence evolved in a small group of estuarine interstitial clitellate worms, the Questidae, before the actual evolution of hermaphroditism and before the more elaborate sperm specializations were acquired by the remaining Euclitellata (Jamieson, 1983; Ferragutti, 2000).

Small interstitial and estuarine worms such as the Questidae represent ideal evolutionary and ecological model organisms for reconstructing the conquest of continental habitats by the Annelida, for understanding the evolution of hermaphroditism in clitellates, and for comprehending the unparalleled behaviours of brood care that evolved in leeches.

From a more applied perspective, the use of leeches as indicator organisms in ecological studies of environmental impact should be seriously considered, given their unprecedented endemicity and niche specificity in freshwater habitats.

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References

ALMEIDA, W.O. & CHRISTOFFERSEN, M.L. 2001. Análise cladística dos grupos basais de Metameria: uma nova proposta para o posicionamento dos Arthropoda e grupos afins entre os poliquetos errantes. Second Edition. Série Teses, Dissertações e Monografias, 1. Ribeirão Preto, SP: Holos.

ALMEIDA, W.O., CHRISTOFFERSEN, M.L., AMORIM, D.S., GARRAFFONI, A.R.S. & SILVA, G.S. 2003. Polychaeta, Annelida and Articulata are not monophyletic: articulating the Metameria (Metazoa, Coelomata). Revista Brasileira de Zoologia 20: 23-57.

APAKUPAKUL, K., SIDALL, M.E. & BURRESON, E.M. 1999. Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. Molecular Phylogenetics and Evolution 12: 350-359.

AUTRUM, H. 1939. Hirudineen. Geographische Verbreitung, pp. 497-520. In: BRONNS, H.S. Klassen und Ordnung des Tierreichs. Band 4. Abt. III, Buch 4, Tiel 2. Leipzig: Akademische Verlagsgesellschaft.

BLANCHARD, R. 1892. Description de la Glossiphonia tesselata. Memoires de la Societé Zoologique de France 5: 56-88.

BORDA, E. & SIDDALL, M.E. 2004. Arhynchobdellida (Annelida: Oligochaeta: Hirudinida): phylogenetic relationships and evolution. Molecular Phylogenetica and Evolution 30: 213-225.

BRINKHURST, R.O. 1999. Lumbriculids, branchiobdellidans and leeches: a review of progress. Hydrobiologia 406: 281-290.

BRINKHURST, R.O. & GELDER, S.R. 2001. Annelida: Oligochaeta, including Branchiobdellidae, pp. 431-463. In: THORP, J.H. & COVICH, A.P. Ecology and classification of North American freshwater invertebrates. Second edition. San Diego: Academic Press.

BRITES, V.L.C. & RANTIN, F.T. 2004. The influence of agricultural and urban contamination on leech infestation of freshwater turtles, *Phrynops geoffroanus*, taken from two areas of the Uberabinha River. Environmental Moniting and Assessment 96: 273-281.

BROWN, S., ROUSE, G., HUTCHINGS, P. & COLGAN, D. 1999. Assessing the usefulness of histone H3, U2 snRNA and 28S rDNA in analyses of polychaete relationships. Australian Journal of Zoology 47: 499-516.

CANTINO, P.D. & DE QUEIROZ, K. 2004. PhyloCode: A phylogenetic code of biological nomenclature. Version 2b. http://www.ohiou.edu/phylocode (accessed 11.06.2007).

CLARK, R.B. 1978. Composition and relationships, pp. 1-32. In: MILL, P.J. Physiology of annelids. London: Academic Press.

CORDERO, E.H. 1937a. Hirudineos neotropicales y subantarcticos. Nuevos, críticos o ya conocidos del Museo Argentino de Ciências Naturales. Anales del Museu Argentino de Ciencias Naturales 39: 1-78.

CORDERO, E.H. 1937b. Los hirudineos del Nordeste del Brasil, I. Especies recogidas por Clemente Pereira en 1933 y por el autor en 1935. Anais da Academia Brasileira de Ciências 9: 13-26.

DIESING, C.M. 1850. Systema Helminthum, Vol. 1-2. Vindvonae: Braumiller, 558 pp.

ERSÉUS, C. 1976. Littoral Oligochaeta (Annelida) from Eyjafjorour, north coast of Iceland . Zoologica Scripta 5: 5-11.

ERSÉUS, C. 1992. A generic revision of the Phallodrilinae (Oligochaeta, Tubificidae). Zoologica Scripta 21: 5-48.

ERSÉUS, C. 2005. Phylogeny of oligochaetous Clitellata. Hydrobiologia 535: 357-372.

ERSÉUS, C. & KÄLLERSJÖ, M. 2004. 18S rDNA phylogeny of Clitellata (Annelida). Zoologica Scripta 33: 187-196.

ERSÉUS, C., PRESTEGAARD, T. & KÄLLERSJÖ, M. 2000. Phylogenetic analysis of Tubificidae (Annelida, Clitellata) based on 18S and rDNA sequences. Molecular Phylogenetics and Evolution 15: 381-389.

FERRAGUTTI, M. 2000. Euclitellata, pp. 125-182. In: JAMIESON, B.G.M. Reproductive biology of invertebrates. Volume IX, Part B. Progress in male gamete ultrastructure and phylogeny. Oxford: New Dehli.

GELDER, S.R. 1996. A review of the taxonomic nomenclature and a checklist of the species of the Branchiobdellae (Annelida: Clitellata). Proceedings of the Biological Society of Washington 109: 653-663.

GIERE, O.W. & RISER, N.W. 1981. Questidae - polychaetes with oligochaetoid morphology and development. Zoologica Scripta 10: 95-103.

GRUBE, A. E. 1850. Die Familien der Anneliden. Archiv für Naturgeschicht Berlin 16: 249-364.

HARMAN, W.J. & LODEN, M.S. 1984. Capilloventer atlanticus gen. et sp. n. a member of a new family of marine Oligochaeta from Brazil. Hydrobiologia 115: 51-54.

HOTZ-BOLLIGER, H. 1984. Bau und Verhalten der Hirudinee Haementeria steineri nov. spec. Vierteljahrschrift Naturforschung Gesellschaft in Zurich 129: 181-206.

JAMIESON, B.G.M. 1983. Spermiogenesis in the oligochaetoid polychaete Questa (Annelida, Questidae). Zoologica Scripta 12: 179-186.

KUTSCHERA, U. 1992. Reproductive behaviour and parental care of the leech Helobdella triserialis (Hirudinea: Glossiphoniidae). Zoologischer Anzeiger 1: 74-81.

KUTSCHERA, U. & WIRTZ, P. 2001. The evolution of parental care in freshwater leeches. Theory in Bioscience 120: 115-137.

LAINSON, R. 1981. On Cyrilia gomesi (Neiva & Pinto, 1926) gen. nov. in the fish Synbranchus marmoratus: simultaneous transmission by the leech Haementeria lutzi. Special Publication of the Society of Protozoology 1: 150-158.

LASSERE, P. 1975. Clitellata, pp. 215-272. In: GIESE, A.C. & PEARSE, J.S.P. Reproduction of marine invertebrates Vol. 3: Annelids and echiurans. New York: Academic Press.

LIGHT, J.E. & SIDDALL, M.E. 1999. Phylogeny of the leech family Glossiphoniidae based on mitochondrial gene sequences and morphological data. Journal of Parasitology 85: 815-823.

MACDONAGH, E.J. 1928. Hirudineos: *Haementeria bonaerensis* n. sp. y una *Helobdella* sp. huésped de cercarias, con una aclaración sobre el nombre ¨sanguaypé¨. Seminarios Medicos de Buenos Aires 35: 230-235.

MARTIN, P. 2001. On the origin of the Hirudinea and the demise of the Oligochaeta. Proceedings of the Royal Society of London Series B Biological Sciences 268: 1089-1098.

MARTIN, P., KAYGORODOVA, I., SHERBAKOV, D.Y. & VERHEYEN, E. 2000. Rapidly evolving lineages impede the resolution of phylogenetic relationships among Clitellata (Annelida). Molecular Phylogenetics and Evolution 15: 355-368.

MICHAELSEN, W. 1928. Miscellania oligochaetologica. Arkiv för Zoologi Series A 20(2): 1-15.

MOORE, J.P. 1911. Hirudinea of southern Patagonia. Report of the Princeton University Expediton to Patagonia 1896-1899 3: 669-689.

MOQUIN-TANDÓN, A. 1846. Monographie de la famille des hirudinées. Paris: J. B. Bail Liere.

OMODEO, P. 1998. History of Clitellata. Italian Journal of Zoology 65: 51-73.

PERKINS, S.L., BUDINOFF, R.B. & SIDDALL, M.E. 2005. New Gammaproteobacteria associated with blood-feeding leeches and a broad phylogenetic analysis of leech endosymbionts. Applied Environmental Microbiology 71: 5219-5224.

PINTO, C. 1920a. Contribuição ao estudo dos hirudíneos do Brasil (Trachybdella histriata, nov. gen., nov. sp.). Brasil-Médico 34: 624.

PINTO, C. 1920b. Contribuição ao estudo dos hirudíneos do Brasil. Brasil-Médico 34: 467.

PINTO, C. 1923. Ensaio monographico dos hirudíneos. Revista do Museu Paulista 13: 853-1118.

PURSCHKE, G., WESTHEIDE, W., ROHDE, D. & BRINKHURST, R.O. 1993. Morphological reinvestigation and phylogenetic relationships of Acanthobdella peledina (Annelida, Clitellata). Zoomorphology Berlin 113: 91-101.

RINGUELET, R.A. 1944. Los hirudineos Argentinos de los gêneros *Helobdella* R. Bl., *Batracobdella* Vig., *Cylicobdella*

Gr. y *Semioscolex* Kinb. Revista del Museo de la Plata Sección Zoologia 4: 5-94.

RINGUELET, R.A. 1947. Notas sobre hirudineos neotropicales, III: *Theromyzon propinquus* nov. sp. de la Argentina. Notas del Museo de la Plata Zoologia 12: 217-222.

RINGUELET, R.A. 1948. Notas sobre hirudineos neotropicales, V: Especies de la Republica del Paraguay. Notas del Museo de la Plata Zoologia 13: 213-244.

RINGUELET, R.A. 1949. Notas sobre hirudineos neotropicales. VI. Presencia del genero *Glossiphonia* en la Argentina y otras adiciones al conocimiento de la hirudofauna de los países del Plata. Notas del Museo de la Plata Zoologia 14: 141-159.

RINGUELET, R.A. 1978. Hirudineos nuevos o ya descritos de la Argentina y del Uruguay. Limnobios 1: 258-268.

RINGUELET, R.A. 1980. Un hirudineo con marsupio de la region andina de Jujuy, Argentina (*Maiabdella batracophila* n.g., n. sp., Glossiphoniidae). Limnobios 26: 68-71.

RINGUELET, R.A. 1981. Hirudínea, pp. 191-196. In: HURLBERT, S.H., RODRIGUEZ, G. & DOS SANTOS, N.D. Aquatic biota of tropical South America. Being a compilation of taxonomic bibliographies for the fauna and flora of inland waters of the tropical portion of South America). Part 2. Anarthropoda. San Diego, CA: San Diego University.

RINGUELET, R.A. 1985. Fauna de agua dulce de la Republica Argentina, Volumen XVII Annulata, Fasciculoi 1, Hirudínea, pp. 1-321. In: DEJOUX, C. & ILTIS, A. Lake Titicaca - A synthesis of limnological knowledge. Buenos Aires: Fundacion para la Educacion, la Ciencia y la Cultura.

ROUSE, G.W. & FAUCHALD, K. 1997. Cladistics and polychaetes. Zoologica Scripta 26: 139-204.

ROUSSET, V., PLEIJEL, F., ROUSE, G.W., ERSÉUS, C. & SIDDALL, M.E. 2007. A molecular phylogeny of annelids. Cladistics 23: 41-63.

SAWYER, R.T. 1971. Phylogenetic development of brooding behaviour in Hirudinea. Hydrobiologia 37: 197-204.

SAWYER, R.T. 1986. Leech biology and behavior. Vol. 2. Feeding biology, ecology and systematics. Oxford: Clarendon Press.

SAWYER, R.T., DAMAS, D. & TOMIC, M.T. 1982. Anatomy and histochemistry of the salivary complex of the giant leech *Haementeria ghilianii* (Hirudinea, Rhynchobdellida). Archiv für Zoologie Experimental und General 122: 411-425.

SELENSKY, W. 1907. Studien über di Anatomie von Piscicola. Travaux de la Societè Imperiale National de Petrograd Zoologie und Physiologie 36: 37-88.

SHAIN, D. H., GUAVARA, M.I.A., CORAL, A.L., CRAMPTON, G.R. & ALBERT, J.S. 2007. A survey of freshwater annelids in the Peruvian Amazon. Acta Hydrobiologica Sinica Supplement (in press).

SIDDALL, M.E. 2002. Phylogeny of the leech family Erpobdellidae (Hirudinea: Oligochaeta). Invertebrate Systematics 16: 1-6.

SIDDALL, M., APAKUPAKUL K., BURRESON E.M., COATES K.AA, ERSÉUS C., GELDER S.R., KÄLLERSJÖ M. & TRAPIDO-ROSENTHAL H. 2001. Validating Livanow: Molecular data agree that leaches, branchiobdellidans and *Acanthobdella peledina* form a monophyletic group of oligochaetes. Molecular Phylogenetics and Evolution 21: 346-351.

SIDDALL, M.E., BELY, A. & BORDA, E. 2005a. Hirudinida, pp. 393-429. In: ROUSE, G. & PLEIJEL, F. Reproductive biology and phylogeny of Annelida. Enfield, NH.

SIDDALL, M.E. & BORDA, E. 2003. Phylogeny and revision of the leech genus *Helobdella* (Glossiphoniidae) based on mitochondrial gene sequences and morphological data and a special consideration of the triserialis complex. Zoologica Scripta 32: 23-33.

SIDDALL, M.E. & BORDA, E. 2004. Leech collections from Chile including two new species of *Helobdella* (Annelida : Hirudinida). Amererican Museum Novitates 3457: 1-18.

SIDDALL, M.E & BUDINOFF, R.B. 2005. Dna-barcoding evidence for widespread introductions of a leech from the South American *Helobdella triserialis* complex. Conservation and Genetics 6: 467-472.

SIDDALL, M.E., BUDINOFF, R.B. & BORDA,E. 2005b. Phylogenetic evaluation of systematics and biogeography of the leech family Glossiphoniidae. Invertebrate Systematics 19: 105-112.

SIDDALL, M.E. & BURRESON, E.M 1995. Phylogeny of the Euhirudinea - Independent evolution of blood-feeding by leeches. Canadian Journal of Zoology 73: 1048-1064.

SIDDALL, M.E & BURRESON, E.M. 1996. Leeches (Oligochaeta?: Euhirudinea), their phylogeny and the evolution of life-history strategies. Hydrobiologia 334: 277-285.

SIDDALL, M.E. & BURRESON, E.M. 1998. Phylogeny of leeches (Hirudinea) based on mitochondrial cytochrome c oxidase subunit I. Molecular Phylogenetics and Evolution 9: 156-162.

STRUCK, T.H., HESSLING, T.R. & PÜRSCHKE, G. 2002. The phylogenetic position of the Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of the ´Polychaeta´, based on molecular data from 18S rDNA sequences. Journal of Zoological Systematics and Evolutionary Research 40: 155-163.

TIMM, T. 1991. Branchiobdellida (Oligochaeta) from the farthest South-East of the USSR. Zoologica Scripta 20: 321-331.

TRONTELJ, P., SKET, B. & STEINBRÜCK, G. 1999. Molecular phylogeny of leeches: Congruence of nuclear and mitochondrial rDNA data sets and the origin of bloodsucking. Journal of Zoological Systematics and Evolutionary Research 37: 141-147.

WESTHEIDE, W. 1999. Ultrastructural and functional significance of intestinojunctional spermathecae in enchytraeids (Oligochaeta, Annelida). Hydrobiologia 406: 199-211.

WESTHEIDE, W. & MÜLLER, M.C. 1996. Cinematographic documentation of enchytraeid morphology and reproductive biology. Hydrobiologia 334: 263-267.

WETZEL, M.J. 1992. Aquatic Annelida of Illinois: introduction and checklist of species. Transaction of the Illinois State Academy of Sciences 85: 87-101.