Redescription, Phylogenetic Placement, and Taxonomic Reassignment of Mesobdella lineata (Sciacchitano, 1959) (Hirudinida: Arhynchobdellida)

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Redescription, phylogenetic placement, and taxonomic reassignment of *Mesobdella lineata* (Sciacchitano, 1959) (Hirudinida: Arhynchobdellida)

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ABSTRACT

Mesobdella lineata, a small terrestrial species of leech from southern Africa, originally placed in the family Haemadipsidae, is redescribed based on internal and external morphological characters of the holotype and of additional material collected in 1975. The placement of this species in the South American genus *Mesobdella* on the basis of seemingly triannulate midbody somites is found to be erroneous as midbody somites are five-annulate. *Mesobdella lineata* has neither the midventral nephridial pore, a synapomorphy of Xerobdellidae, nor the posteriolateral auricles of Haemadipsidae. With a caudal sucker that is wider than the four most posterior somites of the body, eight teeth per jaw, micromorphic median reproductive structures, and no postanal annuli, this species is placed in the mammalophilic family Praobdellidae. A morphological matrix of 32 characters was analyzed with parsimony and implied weighting. The new genus *Parapraobdella* is warranted to accommodate the unique combination of characters of the species that is morphologically similar to Neotropical representatives of the family.

INTRODUCTION

Terrestrial leeches have been recorded on all continents except Antarctica (Borda et al., 2008; Sawyer, 1986), with only one trignathous species with teeth described from Africa:

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Mesobella lineata Sciacchitano, 1959. *Mesobdella lineata* was placed in the genus *Mesobdella*, and in the family Haemadipsidae, with consideration of its terrestrial habit and Sciacchitano's (1959) observation of triannulate midbody somites. Leech taxonomists active at the time and since have repudiated much of Sciacchitano's work (Moore, 1938, 1958; Oosthuizen, 1978, 1979, 1982, 1989; Sawyer, 1986), in which he described numerous species and genera without sufficient diagnostic characters (Sciacchitano, 1935, 1936, 1941, 1952, 1960). Many of Sciacchitano's available names, particularly of the family Hirudinidae, have subsequently been synonomized with other taxa or are considered species inquirendae (Soós, 1969; Sawyer, 1986). Sciacchitanos' (1959) description of *M. lineata* (1959) was based upon mostly external morphological characters observed in specimens of the Museum of Zoology at the University of Lund, Sweden, that were collected during a university sponsored expedition in 1950–1951. Aside from a trivial diagram of the external characters (fig. 1; shown here for clarification), very little was known about the morphology and natural history of this leech when described.

Since its description, *M. lineata* has been passively carried along through taxonomic recategorizations of the genus, yet without morphological examination (Ringuelet, 1972; Sawyer, 1986; Borda et al., 2008). Even though it was an exception in geographic distribution and several morphological characters, Blanchard (1849) placed *Mesobdella* within the family Haemadipsidae. Moore (1946) found *Mesobdella gemmata* (Blanchard, 1849) to be morphologically similar to *Xerobdella lecomtei* (Frauenfeld, 1868) and *Diestecostoma* species, but the report of haemadipsine reproductive structures by Ringuelet (1943) caused Moore to hesitate in suggesting the subfamily Xerobdellinae should include *Xerobdella* and *Diestecostoma,* but not *Mesobdella*. Ringuelet (1972) placed *Mesobdella* into its own family, Mesobdellidae. Disregarding previous taxonomy, Sawyer (1986) returned all blood-feeding terrestrial leeches to Haemadipsidae and separated the taxa into duognathous and trignathous series, the latter of which included *Mesobdella*.

The systematics of both haemadipsoid and hirudinoid leeches has been substantially altered in consideration of molecular phylogenetic work and the recognition of various morphological synapomorphies (Apakupakul et al., 1999; Borda and Siddall, 2004; Phillips and Siddall, 2005; Borda et al., 2008). With the addition of molecular data, Trontelj et al. (1999) and Borda and Siddall (2004) found *Xerobdella lecomtei* and *Mesobdella gemmata* not to be sisters to the blood-feeding terrestrial leeches of the IndoPacific (i.e., Haemadipsidae). *Mesobdella* was returned to the subfamily Xerobdellinae, which was at the same time elevated to family Xerobdellidae, with additional morphological and molecular examinations of more taxa by Borda et al. (2008).

Until now, morphological and molecular investigations of *Mesobdella* have focused primarily on *M. gemmata* while *M. lineata* has received little attention. *Mesobdella lineata* stands apart as the sole African species in Xerobdellidae, yet inhabiting similar temperate latitudes as its South American counterpart. Reexaminations of internal and external morphological characters of the holotype as well as additional specimens of *M. lineata* were performed. Phylogenetic methods were used to analyze morphological characters and taxonomic reassignment is made.

MATERIALS AND METHODS

Specimens examined include the holotype (Museum of Zoology, University of Lund, Sweden; catalog number L951/4421) and a paratype specimen (Museum of Zoology, University of Lund; catalog number L951/3643). On 7 March 1975 three specimens of *Mesobdella lineata* were collected from moist vegetation near streams at Dap Naude Dam (23°48′30.84″S 29°58′12.18″E), Limpopo Province, South Africa, 6.7 km west of the type locality, and an additional five specimens were collected between 27 December and 31 December 1975 from the same locality (all deposited in the collections of the American Museum of Natural History, catalog numbers 4502, 4503, 4726, 4728, 4729, 4730, 4731, 4733). Leeches were either relaxed in 30% ethanol and fixed and preserved in 70% ethanol or fixed in 10% formalin and preserved in 5% formalin. Examination of external and internal morphology was accomplished with a Nikon® SMZ645 stereomicroscope on whole and dissected specimens. Roman numerals in all cases indicate body somites (e.g., prostomium and peristomium are I and II) and annuli receive alphanumeric designations as per Sawyer (1986). Photographs were taken with a Nikon Coolpix® 5000 digital camera and drawings were made by hand. Illustrations were digitized using Adobe Illustrator® 10.

Table 1: Taxa included in the phylogenetic analyses.

Americobdellidae	*Americobdella valdiviana* (outgroup)
Cylicobdellidae	*Cylicobdella coccinea*
Haemadipsidae	*Haemadipsa sylvestris*
Hirudinidae	*Haemopis terrestris*
	Aliolimnatis michaelseni
	Hirudo medicinalis
	Hirudinaria manillensis
Macrobdellidae	*Oxyptypchus striatus*
	Macrobdella decora
	Philobdella floridana
Praobdellidae	*Limnatis paluda*
	Tyrannobdella rex
	Myxobdella annandalei
	Dinobdella ferox
	Limnobdella mexicana
Semiscolecidae	*Semiscolex similes*
	Patagoniobdella variabilis
Xerobdellidae	*Xerobdella lecomtei*
	Mesobdella gemmata

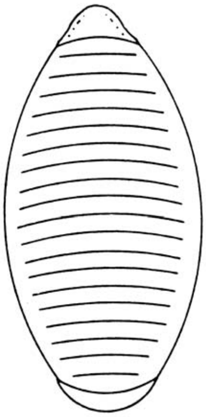


FIGURE 1. Sciacchitano's (1959) illustration of *Mesobdella lineata* from the original description.

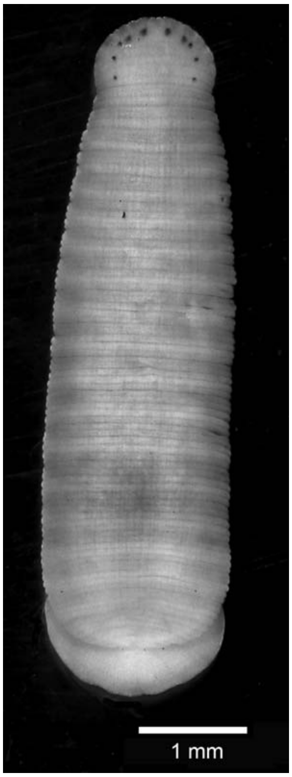
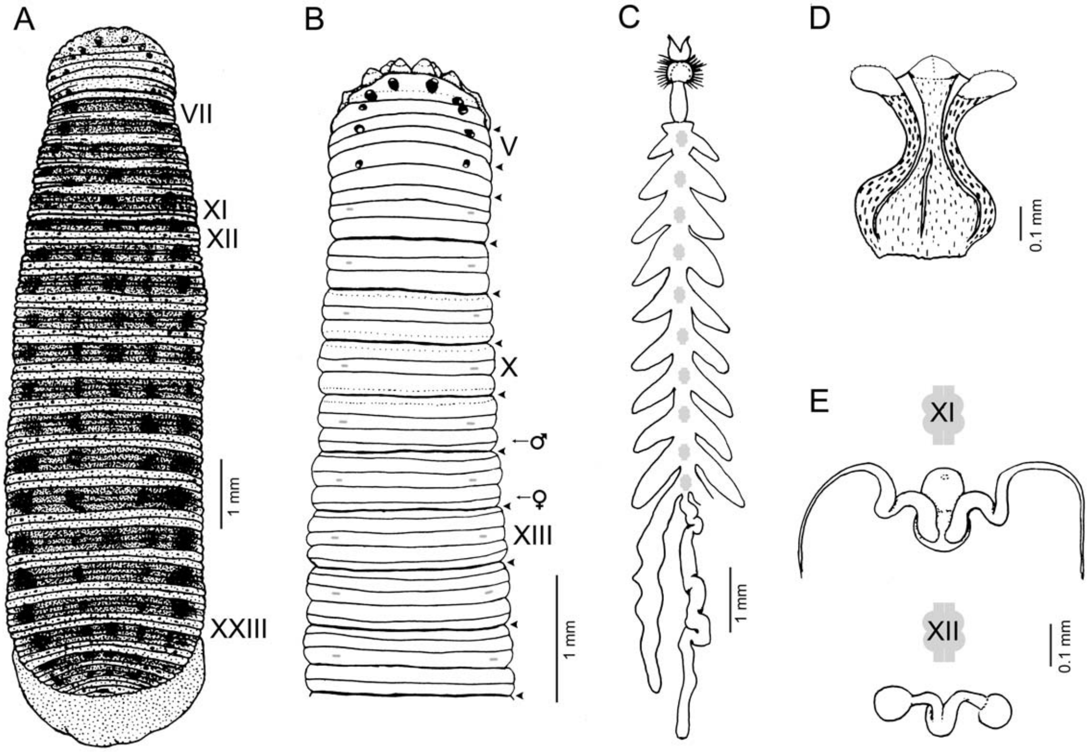


FIGURE 2. Whole-body photograph including the color pattern in a preserved specimen.

FIGURE 3 (*below*). *Parapraobdella lineata*, n. gen. **A.** Dorsal surface of body with somites indicated by Roman numerals. **B.** Dorsal view of the head showing five pairs of eyespots, position of the first nine pairs of nephridia on the ventral side, sensillae around the oral opening, and location of male and female gonopores on the ventral side. Intersegmental furrows indicated with small black arrows. **C.** Internal gastric system. **D.** Jaws with eight small teeth and pharynx. **E.** Internal male and female reproductive organs relative to somatic ganglia XI through XII.



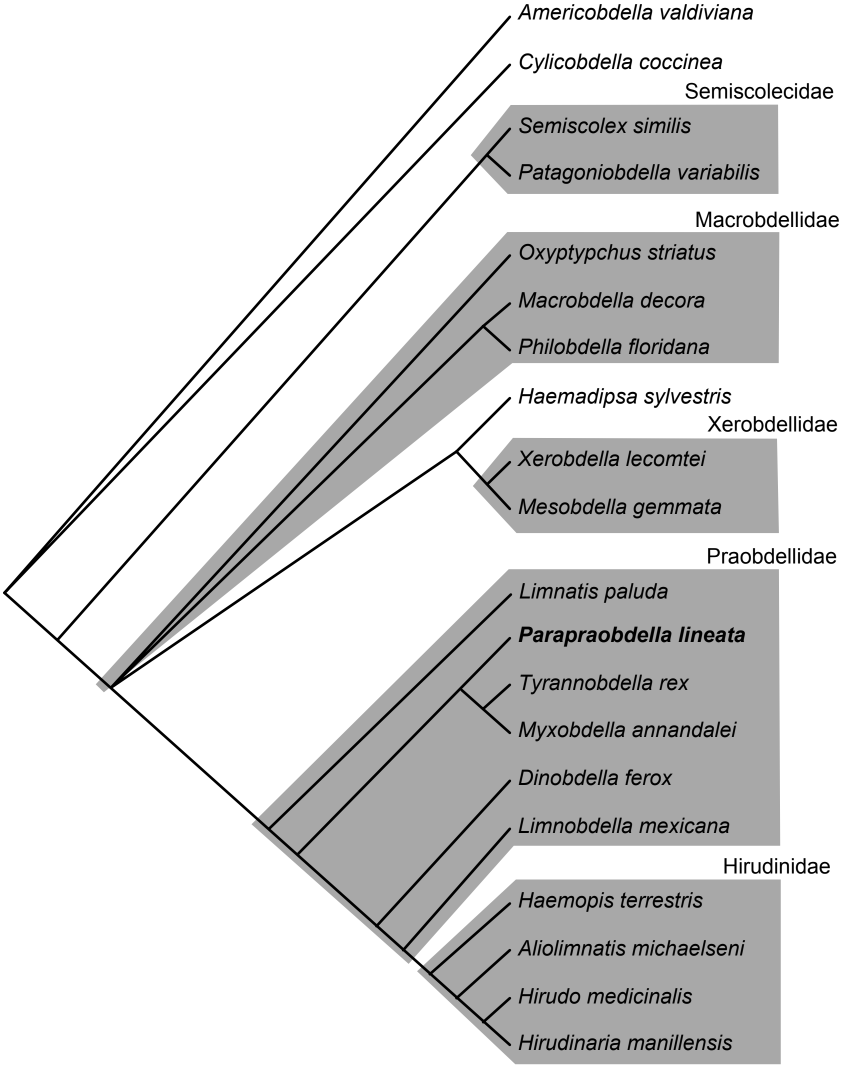


FIGURE 4. Strict consensus of 12 equally parsimonious trees obtained from 32 morphological characters with implied weighting.

Representative taxa (table 1) of the families Haemadipsidae, Xerobdellidae, Semiscolecidae, Macrobdellidae, Hirudinidae, and Praobdellidae were included with *M. lineata* in a morphological matrix of 32 characters (appendix 1) adapted from Borda and Siddall (2004). Parsimony analyses of the morphological matrix employed PAUP* 4.0b10 (Swofford, 2002). Heuristic searches used 500 replicates of the data set with random taxon addition and tree bisection-reconnection branch swapping. Parsimony jackknife (jac) values were obtained using random taxon addition and tree bisection-reconnection branch swapping with 36% deletion and 100 pseudoreplicates. All characters initially were weighted equally and were nonadditive. Additional searches were performed with implied weighting (Goloboff, 1993) varying values of *k* from 1 to 20.

RESULTS

The morphological dataset analyzed under implied weighting yielded 12 equally parsimonious trees with a best score of -23.59329. The strict consensus tree (fig. 4) remained unchanged for values of *k* ranging from 1 to 20. *Parapraobdella lineata* was in a clade with *Tyrannobdella rex* and *Myxobdella annandalei* (Oka, 1917) among a paraphyletic Praobdellidae.

SUBORDER ARHYNCHOBDELLIDA BLANCHARD, 1894

FAMILY PRAOBDELLIDAE (SAWYER, 1986)

Parapraobdella, new genus

Figures 1–3

Description: Trignathous, monostichodont. Longitudinal furrow in dorsal lip of oral sucker. Complete somite five-annulate. Eyespots dorsal, five pair in broad arch. Crop ceca simple with one pair of ceca per somite, postceca extending bilaterally. Intestine simple, acecate. Anus between last annulus and caudal sucker. Caudal sucker wider than four most posterior somites of body. Reproductive organs micromorphic. Nephridia ventral and bilateral in all cases.

Type Species: *Parapraobdella lineata* (Sciacchitano, 1959)

Etymology: From *para* (Greek for "alongside"), because it is close to the genus *Praobdella.*

Parapraobdella lineata (Sciacchitano, 1959)

Figures 1–3

Redescription: Holotype, body length 6.4 mm, maximal width 3.7 mm; dissected. Body muscular. Dorsal surface with transversal bands of light olive green on two annuli and dark olive green on the following three annuli, repeated along the length of the body (figs. 2, 3A). Fifteen five-annulate midbody somites from X to XXIV; b1 and b6 diminutive falsely leading toward a triannulate appearance. Somites: I–III uniannulate, IV and V biannulate, VI biannulate with anterior annulus subdivided dorsally, VII triannulate with annulus b6 subdivided ventrally, VIII quadrannulate, IX quadrannulate with annulus a3 subdivided dorsally, X–XXIV five-annulate, XXV triannulate, XXVI biannulate, and XXVII uniannulate. Eyespots arranged dorsally in five pairs in a broad arch. Pair 1 anterior on somite III, remaining eyespots situated laterally on contiguous annuli of a pair on each annulus of somite IV and anterior annulus of somite V. Pairs 4 and 5 separated by one annulus (IVa3; fig. 3B). First two pairs of eyespots with pigment concentrated anterolaterally in eyespot, last three pairs with pigment concentrated posterolaterally in eyespot. Sensillae obvious in live condition, mostly obscure in preserved specimens. Nephropores 17 pairs on ventral surface situated bilaterally from somite VII to somite XXIII; in complete somites, just posterior to b2/a2 furrow and 17th pair in same position as others. Caudal sucker round, wider than the four most posterior somites without friction rays. Male gonopore at XI b5/b6 in furrow, female gonopore at XII b5/b6 in furrow, five annuli between gonopores.

Jaws trignathous, monostichodont, no salivary papillae (fig. 3D). Jaws moderate in size, low, rounded. Teeth located in shallow open grooves, eight teeth per jaw. Dorsal lip of oral sucker with medial longitudinal furrow and nine sensillae, which are more pronounced in some specimens (fig. 3B). Oral velum absent. Pharynx short, terminating in somite VIII (fig. 3D). Internal muscular ridges, six arranged in dorsomedial and ventrolateral pairs, each pair fusing at base of each jaw. Esophagus narrow, lumen wide, tubular, tapering posteriorly to junction with crop. Pharynx terminating in somite VIII followed by an acecate compartment, which reaches up to the middle of somite IX. Crop from somite IX to somite XX, first 10 pairs of crop ceca simple and equal size, postceca not foliaceous extending bilaterally posterior to somite XVI. Intestine tubular, acecate, joining rectum at somite XXIV (fig. 3C). Rectum thin walled, tubular. Anus in furrow between last annulus and caudal sucker.

Internal male and female reproductive organs micromorphic. Male atrium bulbous, not extended into elongated penis or sheath (fig. 3E). Epididymis and ejaculatory bulbs absent. Vasa deferentia insert into dorsal median of male atrium. Vasa deferentia pass anterolaterally with two bends in an S-like shape before descending to testisacs. Vagina short. Common oviduct absent. Ovaries simple, bulbous.

Habitat: Terrestrial. Associated with moist surroundings, such as vegetation by streams (Oosthuizen, personal obs.).

Type Locality: Debegeni Falls (23°48′49.71″S 30°01′44.87″E), Limpopo Province, South Africa (previously Transvaal).

Remarks: *Mesobdella lineata* is not consistent with any other described genus and warrants the creation of a new genus. The species does not belong in the genus *Mesobdella* within Xerobdellidae: it is five-annulate, not three-annulate; it lacks the xerobdellid midventral nephridial pore; it does not have friction rays on the caudal sucker; the male atrium does not extend into a penis or sheath; it lacks epididymes (Sawyer, 1986; Borda et al., 2008). *Parapraobdella lineata* differs from *X. lecomtei*: it does not have epididymes or defined ejaculatory bulbs, and it lacks a seminal receptacle and the associated accessory pore (Borda et al., 2008). The species does not belong in the family Haemadipsidae: it lacks respiratory auricles; the eyespots are not arranged in the "haemadipsine" ocular arch; it has a caudal sucker that is round and lacks friction rays; the median reproductive apparatus is small compared to the highly robust apparatus typical of haemadipsids (Sawyer, 1986; Borda et al., 2008). The species also does not belong in the family Hirudinidae: it does not have muscular ejaculatory bulbs adjacent to the epididymes; the male atrium is not extended into an elongated penis and sheath; it has eight teeth compared to 60–150 teeth seen in Hirudinidae (Harding and Moore, 1927; Moore, 1938; Richardson, 1969). The species is not a macrobdellid: it does not have accessory glands, muscular ejaculatory bulbs, or annuli between the anus and the caudal sucker; it has one rather than two crop ceca per somite; it has eight teeth compared to the 30–60 teeth observed in macrobdellids (Richardson, 1969; Phillips and Siddall, 2005).

The caudal sucker wider than the four most posterior somites of the body, possessing only eight teeth, micromorphic reproductive structures, and no postanal annuli all point to a placement of this genus and species within the family Praobdellidae along with, yet distinct from, the genera *Praobdella, Myxobdella, Dinobdella, Limnatis, Limnobdella, Pintobdella,* and *Tyrannobdella* (Phillips et al., 2010). Members of the genus *Praobdella* have more than five annuli between the gonopores, while *P. lineata* has exactly five annuli between the gonopores (Sawyer, 1986). Whereas *P. lineata* has three jaws armed with eight small teeth and does not have a velar mouth, it is unlike *Pintobdella chiapasensis* (Caballero, 1958), which has three jaws with six large teeth without a velum, and unlike *Tyrannobdella rex* (Phillips et al., 2010), which has only a single jaw with eight large teeth and a velum (Caballero, 1958; Phillips et al., 2010). The new genus *Parapraobdella* is distinct from *Dinobdella ferox* (Moore, 1927), which does not possess teeth, and from the distichodont genera *Myxobdella* and *Praobdella* (Moore, 1927, 1938; Sawyer, 1986).

In Sciacchitano's (1959) original description, he noted the presence of red papillae along the dorsal surface of the body. No such coloration of the papillae was observed in this study, and although the specimens examined here were preserved, several have retained their pigmentation. In addition, Sciacchitano (1959) described 40 black longitudinal lines on the ventral surface of the specimens he examined, but it seems that he was describing the internal longitudinal muscles of the body wall.

DISCUSSION

This redescription based on morphological characters indicates that the species formerly known as *Mesobdella lineata* requires a new genus, *Parapraobdella*. Sciacchitano (1959) placed this species in the genus *Mesobdella* on the basis of its terrestrial habitat and apparent possession of three annuli per midbody somite. Examination of Sciacchitanos' (1959) types and the Dap Naude Dam material revealed five annuli per midbody somite, not three. In complete somites, b1 and b6 annuli are smaller than annuli b2, a2, and b5 leading to a triannulate appearance.

Praobdellidae is the best family to accommodate this genus and species when considering the wide caudal sucker, eight teeth per jaw, internal reproductive morphology, and lack of postanal annuli of *Parapraobdella lineata*. When first proposed by Sawyer (1986) as a subfamily within the distichodont series, Praobdellinae was distinguished as having a velar mouth, mesomorphic reproductive structures, most species with a large caudal sucker, typically parasitic in nasal passages in mammals, and distributed in Africa and southeast Asia. The subfamily was elevated to family Praobdellidae and expanded by Phillips et al. (2010) to include *Praobdella, Myxobdella,* and *Dinobdella* (sensu Sawyer, 1986), with the addition of *Limnobdella, Limnatis, Pintobdella*, and *Tyrannobdella* strongly supported by molecular data. This expansion was supported by morphological and behavioral observations: 0–12 teeth per jaw in most members of the group but 30–40 teeth per jaw in *Limnatis* and *Limnobdella*, the caudal sucker being wider than the four most posterior somites of the body, a lack of postanal annuli, and primarily feeding from mammalian mucous membranes (Phillips et al., 2010). This unique combination of morphological and behavioral characters encompasses the diversity of morphologies seen across these eight genera as well as defines the family.

Phylogenetic analyses of the morphological data while inconclusive when left unweighted, are shown to carry more information in favor of *P. lineata*'s place among the Praobdellidae than against it. While the family is not supported as monophyletic here, the clade is well supported with DNA sequence data (Phillips et al., 2010). The feeding preference of *P. lineata* has not yet been observed, yet the crop is cecate and several specimens were filled with what appears to be blood. The teeth and jaws are also equipped to allow blood feeding although host preference cannot be determined from these structures. It is more similar in teeth morphology, lacking a velar mouth, the number of annuli between gonopores, and micromorphic reproductive structures to the Neotropical members of Praobdellidae (*Pintobdella* and *Tyrannobdella*) than those with geographic distributions in the Old World.

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APPENDIX 1

MORPHOLOGICAL CHARACTERS ADAPTED FROM BORDA AND SIDDALL (2004) WITH EIGHT ADDITIONAL CHARACTERS

Character 1: Muscular jaws (0) absent, (1) present.
Character 2: Teeth arrangement (0) astichodont, (1) monostichiodont, (2) distichodont.
Character 3: Number of jaws (0) agnathous, (1) monognathous, (2) duognathous, (3) trignathous.
Character 4: Feeding habit (0) macrophagous, (1) hematophagous/sanguivorous, (2) omnivorous.
Character 5: Salivary papillae (0) absent, (1) present.
Character 6: Number of annuli with eyespots (0) none, (1) five.
Character 7: Vaginal duct (0) absent, (1) present.
Character 8: Vaginal cecum (0) absent, (1) present.
Character 9: Ovisac shape (0) absent, (1) present.
Character 10: Common oviduct (0) absent, (1) present.
Character 11: Male atrium extended into elongated penis and sheath (0) absent, (1) present.
Character 12: Penis shape (0) straight, (1) recurved.
Character 13: Ejaculatory ducts (0) U-shaped, (1) S-shaped.
Character 14: Accessory glands (0) absent, (1) present.
Character 15: Intergonadal conducting tissue (0) absent, (1) present.
Character 16: Testisacs per body somite (0) one pair, (1) two pairs.
Character 17: Cocoons (0) brooded, (1) cemented, (2) spongy and deposited on land.
Character 18: Midbody nephropore(s) (0) ventromedial (1) ventrolateral.
Character 19: Nephridia (0) single funnel apparatus, (1) multiple funnels in a ciliated organ.
Character 20: Friction rays on caudal sucker (0) absent, (1) present.

Character 21: Respiratory auricles (0) absent, (1) present.
Character 22: Muscular ejaculatory bulbs (0) absent, (1) present.
Character 23: Number of teeth per jaw (0) none, (1) 1–12, (2) 13–50, (3) 50 or more.
Character 24: Number of postanal annuli (0) none, (1) one.
Character 25: Number of crop ceca per midbody somite (0) none, (1) one, (2) two.
Character 26: Number of annuli between third and fourth pairs of eyespots (0) none, (1) one, (2) two.
Character 27: Number of annuli between fourth and fifth pairs of eyespots (0) none, (1) one, (2) two.
Character 28: Number of annuli between gonopores (0) none, (1) one, (2) two, (3) three, (4) four, (5) five, (6) six [species with gonopores falling on the annulus rather than in the furrow resulting in nonwhole numbers of annuli between gonopores are scored as the next highest whole number].
Character 29: Longitudinal furrow in upper lip (0) absent, (1) present.
Character 30: Velar mouth (0) absent (1) present.
Character 31: Seventeenth pair of nephropores (0) fused into midventral pore (1) two pores situated bilaterally on venter.
Character 32: Caudal sucker (0) narrower than the width of the four most posterior body somites (1) wider than the width of the four most posterior body somites.

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