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A Revision of the Malagabdellinae (Arhynchobdellida: Domanibdellidae), with a Description of a New Species, *Malagabdella niarchosorum,* from Ranomafana National Park, Madagascar

ELIZABETH BORDA

ABSTRACT

This study provides the first photo-documentation of some of the sanguivorous terrestrial leeches of Madagascar, including the characterization of the male and female reproductive systems that were previously considered to be "monotonous" in land leeches. Three species of *Malagabdella* are redescribed and one new haemadipsoid species, *Malagabdella niarchosorum*, n.sp., is described. *M. niarchosorum*, n.sp. is the second species described from Madagascar that possesses four complete annuli between the gonopores. The only other Malagasy leech with these same characteristics, *Malagabdella dussumieri* (Blanchard, 1917), has an unknown type locality, and the examination of the type specimen reveals characteristics suggesting that this leech was not from Madagascar. A revised and restricted provisional key for the Malagabdellinae is provided.

INTRODUCTION

Other than being known as tiny vampires of the eastern rainforests, little is known about the natural and evolutionary history of the terrestrial leeches of Madagascar. There have been three major contributions toward the classification of Malagasy leeches. In his *Monographie des Hémadipsines*, Blanchard (1917) described four new species from Madagascar, assigning three to the only five-annulate genus at the time, *Haemadipsa* Tennet, 1859: *Haemadipsa fallax* Blanchard, 1917, *Haemadipsa vagans* Blanchard, 1917,

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and *Haemadipsa morsitans* Blanchard, 1917, and one species to the four-annulate genus *Philaemon* Lambert, 1898: *Philaemon grandidieri* Blanchard, 1917.

Richardson (1975) revised previous classifications (e.g., Blanchard, 1917; Moore, 1927; Augner, 1931; Soos, 1967, 1970) that placed all terrestrial leeches under a single subfamily, Haemadipsinae Blanchard, 1893, or family Haemadipsidae Blanchard, 1893, by roughly dividing the group based on geographic region and jaw morphology. He also elevated the land leeches to superfamily Haemadipsoidea Richardson, 1975. Richardson (1975) redefined and restricted the Haemadipsidae for the trignathous leeches of India, East Asia, and Southeast Asia and erected two families: Domanibdellidae Richardson, 1975 for the duognathous leeches from the Australasian region (including Oceana, with limited extensions into Wallacea) and Idiobdellidae Richardson, 1975 for the duognathous leeches found in the Seychelles and Madagascar. Richardson (1975) also erected the genera *Malagabdella* Richardson, 1975 and *Tristabdella* Richardson, 1975 for the five-annulate and four-annulate Malagasy leeches, respectively.

In his erratum, Richardson (1978) admitted to having been premature in his previous classification of the Malagasy leeches within the Idiobdellidae (see Richardson, 1975). His original classification (Richardson, 1975) was based only on the dissection of one specimen of *Idiobdella seychellensis* Harding, 1913 from the Seychelles, wherein his "experience of the monotony of the internal morphology in land leeches elsewhere led me to assume that the morphology of the reproductive systems in the species of Madagascar would be similar to *seychellensis*, and on this assumption I placed all in the Idiobdellidae" (Richardson, 1978: 838). Richardson (1978) amended his initial conclusions based on differences found in the median male reproductive region resulting from his examination of *Malagabdella vagans* (Blanchard, 1917). As a result, Richardson (1978) restricted Idiobdellidae to include only the leeches from the Seychelles and erected the subfamily Malagabdellinae Richardson, 1978, and placed it under the Domanibdellidae.

In February and March of 2002, as part of an American Museum of Natural History expedition team, I attempted to rediscover the blood-feeding terrestrial leeches of Madagascar, even though these were well known by locals, tourists, and visiting field biologists as mere nuisances. The collection of these leeches would allow their incorporation into ongoing phylogenetic work and permit photo-documentation of the Malagasy leeches for the first time. During this expedition, efforts were focused in humid rainforests in three principal localities throughout the east coast of Madagascar: Fort Dauphin (southeastern Toliara Province), Ranomafana National Park (Fianarantsoa Province), and Andasibe (Taomasina Province). These collections allowed a better insight into the diversity of yet another group of endemic organisms from Madagascar in the face of a changing and disappearing environment.

MATERIALS AND METHODS

Terrestrial leeches were collected from exposed skin prior to or while they were blood-feeding. Collection strategies involved walking along forest trails and through the damp undergrowth, especially after rain, to attract leeches. Other methods included walking barefoot through the forest to increase skin exposure for leeches found in the undergrowth. Coordinates for localities were estimated using a Garmin eTrex GPS unit, when signal was available. After collection, leeches were relaxed using an ethanol gradient, starting with an ~10% ethanol solution and gradually adding 95% ethanol until the leeches were relaxed (and dead). Leeches were fixed either in 10% buffered ($CaCl_2$) formalin to use for dissection and/or scanning electron microscopy or in 95% ethanol to use for DNA extraction. Formalin-fixed specimens were later transferred to and stored in 70% ethanol. Examination and dissection of specimens were done using a Nikon SMZ-U stereomicroscope. Photo-documentation of leeches was done using a SPOT-RT (Diagnostic Instruments, Inc.) digital camera.

In the most recent classification of leeches, Sawyer (1986) placed all blood-feeding terrestrial leeches in the Haemadipsidae and divided the leeches based on jaw and pharynx morphology into series (i.e., *duognathous* series and *trignathous* series). Therefore, the Malagasy leeches were classified under the *duognathous* series of the Haemadipsidae. Until a more complete revision of the systematics of blood-feeding terrestrial leeches is available, Richardson's (1975, 1978) classification for the leeches of Madagascar will be followed, in part. Species redescriptions are based on the somital limits and morphology used by Richardson (1975, 1978), which were adapted from Moore (1927). Richardson's (1975, 1978) classification scheme represents the diversity of the leeches of the IndoPacific, which, otherwise, is lost in the more recent treatments of this group (i.e., Sawyer, 1986). The superfamily Haeamdipsoidea proposed by Richardson (1975) for the land leeches will not be considered here based on the results from Borda and Siddall (2004) and unpublished data showing that leeches from the IndoPacific are monophyletic and are a derived group within a monophyletic hirudiniform clade. Therefore, the IndoPacific land leeches are considered to be of equal family ranking to other groups of hirudiniform leeches (Borda and Siddall, 2004).

Type specimens from the Muséum National d'Histoire Naturelle (Paris, France) were also examined and include: *Haemadipsa dussumieri* Blanchard, 1917 (MNHN 802; no. 198), *Haemadipsa fallax* Blanchard, 1917 (MNHN 751; no. 143 and no. 146A), *Haemadipsa moristans* Blanchard, 1917 (MNHN 802; no. 198) and *Haemadipsa vagans* Blanchard, 1917 (MNHN 751; no. 145). MNHN numbers are lot numbers, not catalog numbers. The Hirudinea collection is stored in lots, with type and non-type specimens stored together. Therefore, the scientific name is used to locate the specimen within a lot. Richardson (1975) designated *Haemadipsa fallax* as the type species for the genus *Malagabdella* based on page priority in Blanchard (1917).

RESULTS

Three endemic species from the terrestrial blood-feeding genus *Malagabdella* were collected from the east coast of Madagascar; one species is new to science. These include the species described below.

ORDER HIRUDINIDA

SUBORDER ARHYNCHBODELLIDA BLANCHARD, 1894

HIRUDINIFORMES CABALLERO, 1952

FAMILY DOMANIBDELLIDAE RICHARDSON, 1975

SUBFAMILY MALAGABDELLINAE RICHARDSON, 1978

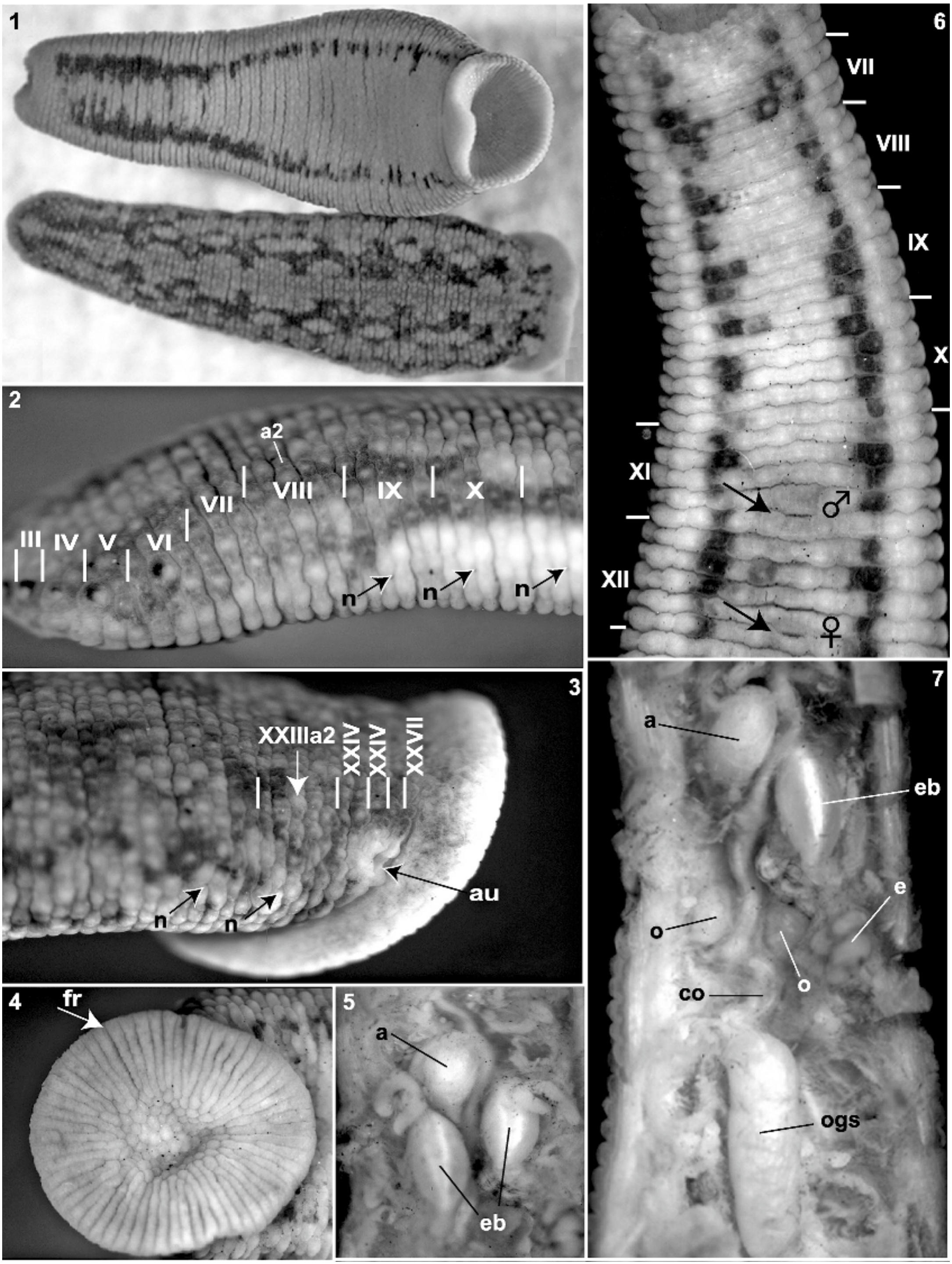
GENUS MALAGABDELLA RICHARDSON, 1975 (REVISED AND RESTRICTED)

TYPE SPECIES: *Haemadipsa fallax* Blanchard, 1917.

DIAGNOSIS: Duognathous; Cephalic somites II, III, and IV uni-annulate; V two-annulate, VI and VII three-annulate; VIII to XXIII five-annulate; XXIV two-annulate (incomplete three-annulate or incomplete four-annulate); XXV to XXVII uni-annulate; Male gonopore in XI b5/b6 (or XI/XII); female gonopore in XII b5/b6 (anterior in b5 or anterior in XIII); 57 (or 58) friction rays, ventral, on caudal sucker; respiratory auricles bilobed.

REMARKS: Richardson (1978) recognized four species in the genus *Malagabdella*: *M. fallax*, *M. dussumieri*, *M. morsitans*, and *M. vagans*. After the type specimens of *Malagabdella* species were examined, it became questionable whether *M. dussumieri* was actually a leech from Madagascar.

First, Blanchard's (1917) description of *Haemadipsa dussumieri* was based on a single specimen (length: 36 mm; MNHN 802; no. 198; $N = 1$) collected by Dussumier from an unknown type locality. Blanchard (1917) never suggested that *H. dussumieri* was from Madagascar and actually proposed that this leech was from the south of Hindustan (Madras). When Richardson (1975) transferred *H. dussumieri* into the genus *Malagabdella*, he referred to having read Dussumier's letter (1827) written to the administrators of the Muséum National d'Histoire Naturelle. In it he (Dussumier) said that most of his collections were from the Malabar Coast, with some additional collections of vertebrates in the Seychelles Islands and Madagascar. There is no mention of leeches having been collected specifically from Madagascar. Based on the latter and the fact that the somital annulation patterns appeared



Figs. 1–7. *Malagabdella fallax*. **1.** Dorsal and ventral views of color patterns showing "chain-link" patterns on the dorsum. **2.** View of the cephalic somites and anterior somital series, showing the position of

to deviate from *Haemadipsa* species, Richardson (1975) accepted this as evidence and merely guessed that *H. dussumieri* was from Madagascar. Second, domanibdellid leeches are duognathous. When the type specimen of *M. dussumieri* was examined, widening of the oral cavity exposed a dorsomedial slit for the presence of a jaw, indicating that this leech is trignathous. Third, Sawyer (1986) showed the systematic utility of counting the number of friction rays found on the caudal sucker in *Haemadipsa* species. According to Sawyer (1986), most species of *Haemadipsa* are described as having more than 80 friction rays on the ventral side of the sucker. The total number of friction rays for *M. dussumieri* is 86, which suggests that this leech actually may have been from India, as originally speculated by Blanchard (1917). *Malagabdella* species only have 57 (or 58) friction rays on the ventral side of the caudal sucker.

M. dussumieri should be removed from the genus *Malagabdella*, as well as from the family Domanibdellidae, and returned to the Haemadipsidae sensu stricto under its original name, *Haemadipsa dussumieri*, until a more thorough evaluation of the Haemadipsidae is available.

Malagabdella fallax (Blanchard, 1917)
Figures 1–7

Haemadipsa fallax Blanchard, 1917: 664.
Chtonobdella fallax — Augener, 1931: 9; Soos, 1967: 423.
Malagabdella fallax — Richardson, 1975: 142; Richardson, 1978: 859–860; Sawyer, 1986: 762.

TYPE MATERIAL: *Syntype*, Madagascar—east coast forests, 1882, Lantz (MNHN 751; no. 143; $N = 1$). *Syntype*, Madagascar—east coast forests, 1890, Dr. Catat (MNHN 751; no. 146A; $N = 1$).

ADDITIONAL MATERIAL ($N = 134$): Eight specimens (AMNH 5277, Annelida) fixed in 95% ethanol and three specimens (AMNH 5278, Annelida) fixed in formalin, 196 m, Domaine de la Cascade, Taolagnaro (Fort Dauphin) (MG02-01), 24°59.34′S, 46°55.43′E, February 21, 2002, southeast rainforest, 10 km west from Hotel Dauphin. Ten specimens (AMNH 5279, Annelida), fixed in 95% ethanol and seven specimens (AMNH 5280, Annelida) fixed in formalin, Parc National d'Andohahela (MG02-03) in "Manangotry forest", February 27, 2002. Twenty-eight specimens (AMNH 5281, Annelida) fixed in 95% ethanol and thirty-two specimens (AMNH 5282, Annelida) fixed in formalin, Talatakely (selectively logged, low montane forest), Parc National Ranomafana (MG02-05), March 5, 2002. Eighteen specimens (AMNH 5283, Annelida) fixed in 95% ethanol, on trail between Talatakely and Vatoharanana, Parc National Ranomafana (MG02-06), March 5, 2002. Twenty-eight specimens (AMNH 5284, Annelida) fixed in 95% ethanol, near campsite in Vatoharanana (undisturbed, low montane forest) ~4 km south of Talatakely, Parc National Ranomafana (MG02-07), March 5, 2002. All specimens collected by Mark Siddall, Elizabeth Borda, Evon Hekkala, Clara Imboule, and Raina Rakotondriany.

DESCRIPTION: Dorsum with beige background and a wide dorsal band, beige, with light brown mid-dorsal line. Paramedial dark mottling with "chain-link" pattern, dark brown to black on borders of each "link" of chain; beige color within "link". Venter with beige background and a pair of dark brown to black paramedial lines, each thick anteriorly,

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the nephropores (n) at b2/a2 of each somite. **3.** Dorso-lateral view of the posterior somital annulation series, the nephropores (n) and respiratory auricle (au). **4.** Ventral view of caudal sucker showing 57 friction rays (fr). **5.** Median male reproductive system showing micromorphic atrium (a) and large ejaculatory bulbs (eb). **6.** Ventral view of the anterior somital annulation series and positions of the male (♂) and female (♀) gonopores, showing five complete annuli between gonopores. **7.** Male and female reproductive systems, showing the male atrium (a), the right ejaculatory bulb (eb) and the right epididymes (e); left male ejaculatory bulb moved to expose paired female ovaries (o), the common oviduct (co) and the haemadipsoid oviducal glandular sac (ogs).

becoming thinner or less pigmented posteriorly (fig. 1).

Duognathous, monostichodont jaws. Cephalic somites with five pairs of eyespots, one on each of II, III, IV, V, and VI (fig. 2). Somites II, III, and IV uni-annulate, V and VI two-annulate (incomplete three-annulate, ventrally) and three-annulate, respectively, VII three-annulate. Midbody somites, VIII–XXIII, five-annulate. Nephropores lateral in furrow of b2/a2 of each somite (fig. 2), with first nephropore observed in VIII b2/a2. Posterior series, XXIV two-annulate, XXV–XXVII uni-annulate (fig. 3). Seven annuli between XXIII a2 and anus (fig. 3). Posterio-lateral respiratory auricles bilobed and formed along the lateral margins of XXIV a2 to XXVII (fig. 3). Caudal sucker, ventral, with 57 friction rays ventrally on sucker. Prehensile lobe absent (fig. 4).

General organization and regional morphology of male and female reproductive systems haemadipsoid (figs. 5–7). Male genital pore opens at furrow of XI b5/b6 and female genital pore opens at furrow of XII b5/b6 (or anteriorly in b6) (fig. 6). Gonopores separated by five complete annuli. Median male reproductive system in XI and XII (fig. 5). Male atrium found in XI, micromorphic, bulbous, and conical. Ejaculatory ducts exit male atrium anteriorly at XI. Ejaculatory ducts run lateral to atrium, posteriorly directed, giving rise to large ejaculatory bulbs at XI/XII. Ejaculatory bulbs approximately twice the size of male atrium and observed within XI and XII. Small tightly coiled epididymes in XII and XIII, each recurving anteriad at XIII. Single pair of globular ovaries in XII, each with thin oviducts that converge at XII/XIII into a common oviduct (fig. 7). The long, thin, common oviduct enters anterior face of oviducal glandular sac at XIII. Oviducal glandular sac extends posteriorly to XVI.

Remarks: The posterior annulation series of this species does not match that designated by Richardson (1975, 1978) for *M. fallax*. According to Richardson (1975, 1978), XXIV is three-annulate, with eight annuli between XXIII a2 and the anus. The posterior series for these specimens collected for this study is consistent, in part, with that described for *M. morsitans* (Richardson, 1978) (i.e., seven annuli between XXIIIa2 and the anus). However, the position of the gonopores appears to be consistent with Blanchard (1917) and Richardson (1975, 1978) for *M. fallax*. Richardson (1975) noted that the only differences between *M. fallax* and *M. morsitans* were limited to the latter having somite XXIII being four-annulate and with genital pores being found in the furrows of XI/XII and XII/XIII. Some have proposed that these two species be synonymized (Augener, 1931).

In describing *H. fallax*, Blanchard (1917) examined two specimens from Le Muséum de Paris: no. 143 (MNHN 751; Lantz, 1882) and no. 146A (MNHN 751; Catat, 1890). With the opportunity to examine these specimens, I found that both were in very poor condition, and this prohibited the verification of the annulation pattern described by Blanchard (1917) and Richardson (1975, 1978). Of the two, Blanchard's specimen no. 146A was intact, but engorged with blood. The somites are visible on the specimen, but the annuli within somites are not, making it impossible to corroborate Richardson's (1978) claim regarding the posterior annulation series. The gonopores on the type specimen are also visible and are found within somites, confirming the gonopore position of *M. fallax* and for the specimens detailed here.

Richardson's (1978) redescription of *M. morsitans* was based on a specimen that was identified by Moore (U.S. Nat. Mus. 37970, Montagne d'Amor, Madagascar, Shickenburg Coll.—Acc. No. 259718), not based on Blanchard's specimen (MNHN 802; No. 198). Richardson (1978) reported that the gonopores of *M. morsitans* were located at XI/XII and XII/XIII and illustrated the posterior series with XXIII complete four-annulate and XXIV incomplete three-annulate. The intersomital position of gonopores and the posterior annulation series are evident from the types (MNHN 802; $N = 7$), rendering them distinct from *M. fallax* and the specimens detailed here.

Malagabdella morsitans (Blanchard, 1917)

Haemadipsa morsitans Blanchard, 1917: 664, fig. 13.

Malagabdella morsitans — Richardson, 1975: 142; Richardson, 1978: 864, fig. 4E; Sawyer, 1986: 761.

TYPE MATERIAL: *Syntypes*, Madagascar—Moramonga, east coast forests, 1893, Sikora? (MNHN 802; *N* = 7).

DESCRIPTION: Duognathous, monostichodont jaws. Cephalic somites with five pairs eyespots, one on each of II, III, IV, V, and VI. Somites II, III, and IV uni-annulate, V and VI two-annulate and three-annulate, respectively, VII three-annulate. Midbody somites VIII–XXII five-annulate. Nephropores lateral in furrow of b2/a2 in each somite. XXIII incomplete five-annulate (four annuli dorsally). XXIV incomplete three-annulate, XXV–XXVII uni-annulate. Seven (eight) annuli between XXIII a2 and anus. Male genital pore at furrow of XI/XII and the female genital pore at furrow of XII/XIII. Gonopores separated by five complete annuli.

REMARKS: Because I did not have access to fresh material of *M. morsitans* for dissection, the characteristics of the reproductive systems remain a mystery. Richardson's (1978) redescription of this species was solely based on the somital annulation patterns and based on the position of the gonopores. The specimen Richardson (1978) examined (USNM 37970) was dried out and with a strongly compressed body. He also mentioned that the male pore was not obvious, but that the female pore was found in XII/XIII (i.e., "two full annuli to a weakly defined end of the clitellum"; p. 864). The position of the gonopores has been confirmed based on the examination of the type specimen (see also *M. fallax*: REMARKS). Based on the latter and based on the annulation patterns renders *M. morsitans* distinct from other *Malagabdella* species, although the comparison of the reproductive systems to other species of *Malagabdella* is pending for a redescription of this species.

Malagabdella niarchosorum, new species

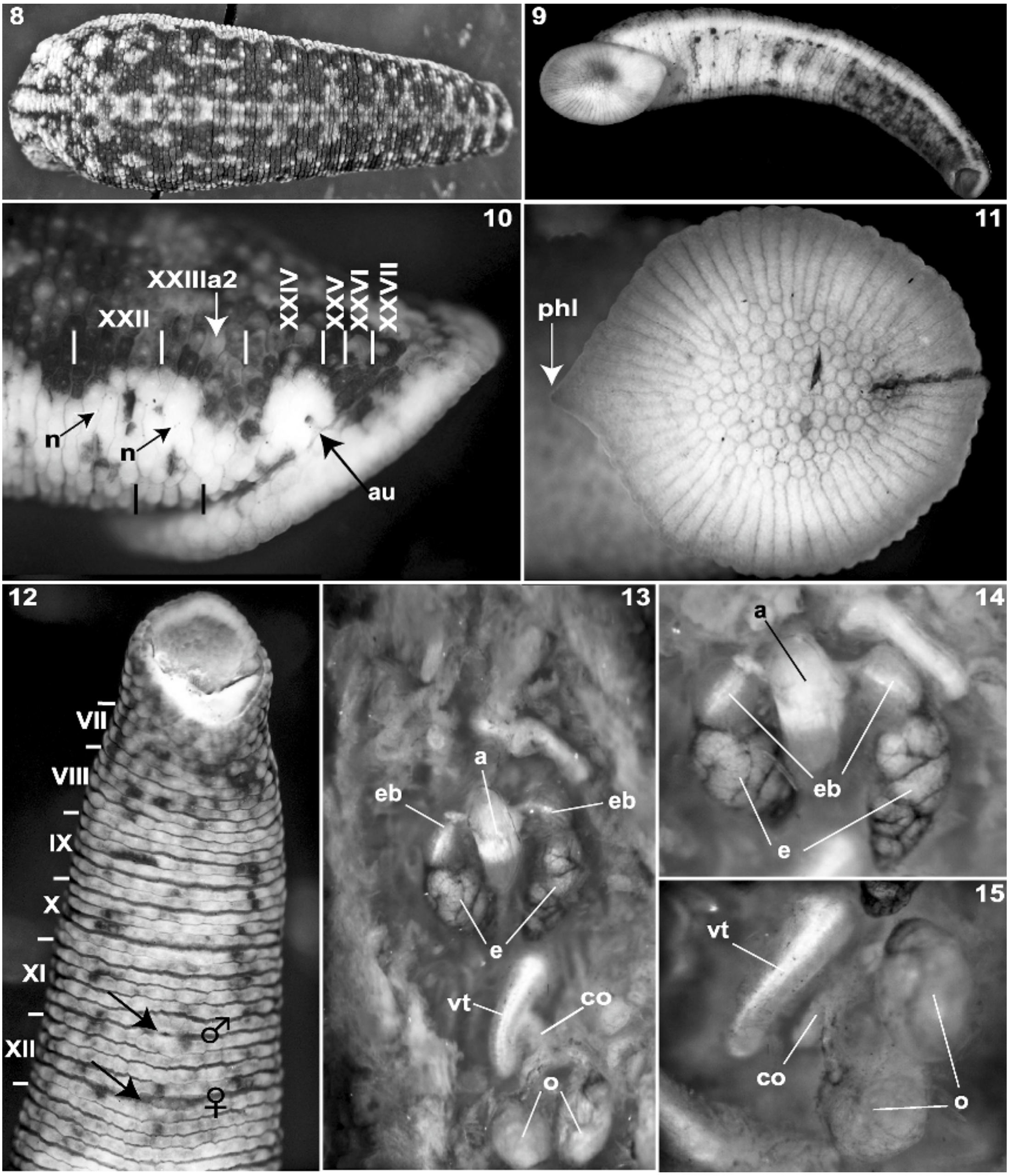
Figures 8–15

TYPE MATERIAL: *Holotype*, specimen fixed in 95% ethanol, Madagascar—Parc National Ranomafana in Talatakely (selectively logged, low montane forest; MG02-05), March 5, 2002. Collected by Mark Siddall, Elizabeth Borda, Evon Hekkala, Clara Imboule, and Raina Rakotondriany (AMNH 5285, Annelida). *Paratypes* (*N* = 2), one specimen fixed in formalin, dissected, same collection data as holotype (AMNH 5287, Annelida). One specimen fixed in 95% ethanol, Parc National Ranomafana, on trail between Talatakely and Vatoharanana (MG02-06), March 5, 2002, collected by Mark Siddall and Elizabeth Borda, (AMNH 5286, Annelida).

DIAGNOSIS: Male pore in XI b5/b6; Female pore XII b5 (anterior); four complete annuli between gonopores; XXIV incomplete four-annulate; nine annuli between XXIII a2 and anus; oviducal glandular sac absent; muscular vaginal tube present. Prehensile lobe present.

DESCRIPTION: Dorsum with dark brown to black background field, wide beige medial chain-link band, each link with darker field at center, approximately five annuli per link. Medial chain becomes continuous light field bordered with dark brown to black paramedial lines in posterior series. Paramedial dorsal light brown to white diamond-shaped patches at approximately the same position of every other chain-link of medial band. Dorsolateral light spots on sensillae of a2. Dark spots found along lateral margins, against light background that continues ventrally. Venter, light background with dark brown to black mottling. Annular papillae, present (figs. 8, 9).

Duognathous, monostichodont jaws. Cephalic somites with five pairs eyespots, one on each of II, III, IV, V, and VI. Somites II, III, and IV uni-annulate, V and VI two-annulate and three-annulate, respectively, VII three-annulate. Midbody somites, VIII–XXIII, five-annulate. Nephropores, lateral, in furrow of b2/a2 of each somite, first nephropore observed at IX b2/a2. Posterior somites, XXIV incomplete four-annulate (b6 converges with b5 along the anterio-lateral margin of the respiratory auricle) and XXV–XXVII uni-annulate (fig. 10). Nine annuli (dorsally) between XXIII a2 and anus. Posteriolateral respiratory auricles, bilobed, and formed along the lateral margins of XXIV b5 to XXII (fig. 10). Caudal sucker, ventral, with 57 friction rays ventral on sucker. Prehensile lobe, present (fig. 11).



Figs. 8–15. *Malagabdella niarchosorum*, n.sp. **8.** Dorsal view of color patterns showing mid-dorsal "chain-link" band and dark brown to black background field with light brown to white diamond-shaped patches (paratype). **9.** Ventral view showing light background field with dark brown to black mottling, especially in the anterior region. **10.** Dorso-lateral view of the posterior somital annulation series, position of the nephropores (n) and the respiratory auricle (au). **11.** Ventral view of the caudal sucker showing 57 friction rays and prehensile lobe (phl). **12.** Ventral view of the anterior somital annulation series and the positions of the male (♂) and female (♀) gonopores, with four complete annuli between gonopores. **13.** Male and female reproductive systems showing the male atrium (a), ejaculatory bulbs (eb), epididymes (e), female paired ovaries (o), common oviduct and vaginal tube (vt). **14.** Male reproductive system exhibiting a narrow

General organization and regional morphology of male and female reproductive systems, not typical haemadipsoid (figs. 12–15). Male genital pore opens at the furrow of XI b5/b6 and female genital pore opens anteriorly in XII b5 (or a2/b5) (fig. 12). Gonopores separated by four complete annuli. Median reproductive system micromorphic (fig. 13). Median male reproductive system found entirely in XI (fig. 14). Male atrium, narrow, recurves anteriorly at XII. Short ejaculatory ducts exit the male atrium laterally in XI and give rise to small, globular ejaculatory bulbs in XI. Tightly coiled epididymes arise from ejaculatory bulbs, each twice the size of an ejaculatory bulb and recurved anteriad at XII. Median female reproductive system found entirely in XII (fig. 15). Single pair of globular ovaries, posteriorly directed in XII, with thin-walled oviducts that converge into common oviduct. Common oviduct is tightly coiled ventrally and inserts into a simple, muscular, vaginal tube. Vaginal tube recurves anteriad at approximately XIII, with tube widening anteriorly and terminating in bulb at the insertion point of the gonopore at XII b5. Haemadipsoid oviducal glandular sac absent.

REMARKS: When Richardson (1975, 1978) included *Haemadipsa dussumieri* as a member of the genus *Malagabdella*, it was the only species that possessed four complete annuli between the gonopores. This was initially consistent with *M. niarchosorum*, n.sp. However, after the examination of the type specimen, it became obvious that *M. dussumieri* was distinct from *M. niarchosorum*, n.sp. (and from the genus *Malagabdella*). For example, the position of the female pore for the type specimen of *H. dussumieri* is on an obviously ventrally subdivided annulus of XII b5, whereas in *M. niarchosorum*, n.sp., it is not subdivided. In addition, as detailed above, *M. dussumieri* possesses characters that deviate from domanibdellid leeches. Therefore, with the exclusion of *M. dussumieri* from the Malagabdellinae, *M. niarchosorum*, n.sp. is distinct from all other members of the genus based on external coloration and patterns, the characteristics of the male and female reproductive systems, the position of the gonopores, and the posterior annulation series, but inclusive in the Malagabdellinae based on somital annulation pattern and the possession of 57 friction rays ventrally on the caudal sucker.

ETYMOLOGY: This species is named after the Niarchos family in light of their generosity in funding this expedition. Without their support, the rediscovery of known species from Madagascar and the opportunity to describe another endemic species would not have been possible.

Malagabdella vagans (Blanchard, 1917)

Figures 16–23

Haemadipsa vagans Blanchard, 1917: 665, fig. 14.

Haemadipsa vagans — Soos, 1967: 426.

Malagabdella vagans — Richardson, 1975: 142; Richardson, 1978: 860–863, fig. 4 A–D); Sawyer, 1986: 762.

TYPE MATERIAL: *Syntype*, Madagascar—east coast forests, 1882, Lantz (MNHN 751; no. 143; *N* =1). *Syntype*, Madagascar—Montagne d'Ambre, Diego-Suarez, 1890, Dr. Catat? (MNHN 802; *N* =3).

ADDITIONAL MATERIAL: Six specimens (AMNH 5288, Annelida) fixed in 95% ethanol and six specimens (AMNH 5289, Annelida) fixed in formalin (two specimens used for SEM), in forest adjacent to town of Andasibe, ~3 km from entrance of Analamazoatra (Perinet Special Reserve) (MG02-04), near the Antananarivo–Taomasina railroad, March 3, 2002.

Brilliant green or orange when alive. Pale in color, almost neutral when fixed. Only markings found dorsally are paramedial wavy lines that become faded posteriorly. Dorsal and ventral papillae present (fig. 16).

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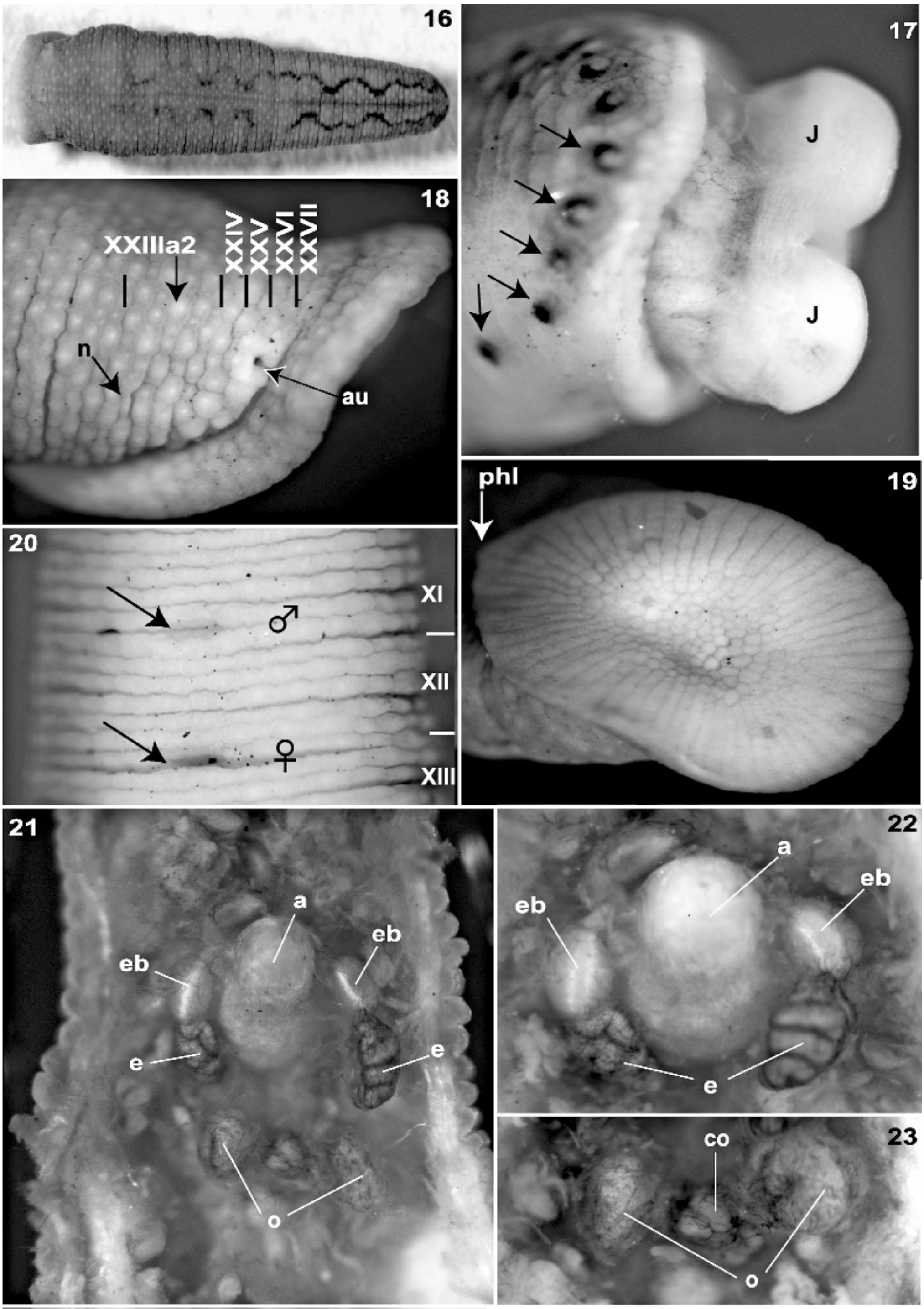
male atrium (a), small bulbous ejaculatory bulbs (eb) and coiled epididymes (e). **15.** Female reproductive system showing paired globular ovaries, each with independent oviducts that converge into the common oviduct (co) that inserts into a simple vaginal tube (vt).



Figs. 16–23. *Malagabdella vagans*. **16.** Dorsal view showing beige background field with paramedial wavy lines that fade posteriorly. **17.** Anterior view of cephalic somites, with partial view of the right five eyespots (arrows) and a set of producible duognathous jaws (j). **18.** Lateral view of the posterior somital

Duognathous, monostichodont jaws armed with serrated edge of minute teeth (fig. 17). Cephalic somites with five pairs of eyespots, one on each of II, III, IV, V, and VI. Somites II, III, and IV uni-annulate, V and VI two-annulate and three-annulate, respectively, VII three-annulate. Midbody somites VIII–XXIII five-annulate. Nephropores lateral in furrow of b2/a2 in each somite, with first nephropore observed in IX b2/a2. XXIV– XXVII uni-annulate (fig. 18). Six annuli between XXIII a2 and anus. Respiratory auricles present, bilobed, and formed along the lateral margins of XXIV a2 to XXVII. Caudal sucker, ventral, with 58 friction rays ventral on sucker. Small prehensile lobe present (fig. 19).

General organization and regional morphology of male and female reproductive systems not typical haemadipsoid (figs. 20–23). Male genital pore opens at the furrow of XI b5/b6 and the female genital pore opens at the furrow of XIII b1/b2 (fig. 20). Gonopores separated by seven complete annuli. Median reproductive system micromorphic and entirely in XI (figs. 21, 22). Male atrium bulbous. Short ejaculatory ducts exit the atrium ventrally in anterior XI and run laterally, posteriorly directed, giving rise to small ovoid ejaculatory bulbs. Epididymes, small, approximately the size of the ejaculatory bulbs, tightly coiled, and recurve anteriad at XII. Median female reproductive system micromorphic (fig. 23). Single pair of globular ovaries in XII, with short thin walled oviducts that coil and converge into the common oviduct. The common oviduct is tightly coiled in the median and exits in XIII. Oviducal glandular sac and muscular vaginal tube absent.

REMARKS: Richardson (1975) noted a resemblance in the somital annulation pattern of *H. vagans* to *Idiobdella seychellensis* and, therefore, originally included *H. vagans* as a member of the genus *Idiobdella*. Richardson (1978) revised his previous classification of the leeches of Madagascar based on a specimen from the collection of the National Museum of Natural History that he identified as *Malagabdella vagans* (U.S. Nat. Mus. Cat. No. 55386; Acc. 242082; 2 km east of Perinet, Tamatave Province; off human skin). This resulted in the revision of the genus *Malagabdella*, the removal of the genus from Idiobdellidae, and the establishment of the Malagabdellinae (Richardson, 1978).

Interestingly, Richardson (1978) reported that the specimen of *M. vagans* was engorged with blood and with the "annulation obliterated". Furthermore, it does not appear that he examined any type material for this species. Therefore, it is difficult to imagine that the annulation patterns he described and illustrated for this species came from this specimen (see also *M. fallax* REMARKS), but rather a conversion of the annulation patterns described by Blanchard (1917). In his revision, Richardson (1978) described the male reproductive system for Malagasy leeches based on this USNM specimen of *M. vagans*. This resulted in an overgeneralization for the characteristics of male reproductive systems for the *Malagabdella* species. It should be mentioned that the observation of the male system was facilitated by the USNM specimen having been "split through transversely at XII/XIII providing access to the anterior portion of the male paired system and the male median region" (Richardson, 1978: 863), yet he illustrates the majority of male system (i.e., atrium and ejaculatory bulbs and epididymes) found within XI.

DISCUSSION

Richardson (1969a) showed that the male and female reproductive systems had important diagnostic characters for hirudinid

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annulation series and the respiratory auricle (au). **19.** Ventral view of the caudal sucker showing 58 friction rays and a small prehensile lobe (phl). **20.** Ventral view of the positions of the male (♂) and female (♀) gonopores, with seven complete annuli between gonopores. **21.** Medial male and female reproductive systems, showing the male atrium (a), ejaculatory bulbs (eb), epididymes (e), and paired ovaries (o). **22.** Male reproductive system showing a bulbous male atrium (a), small ejaculatory bulbs (eb), and small epididymes (e). **23.** Female reproductive system showing a pair globular ovaries (o) with short independent oviducts that converge into a coiled common oviduct (co) before insertion into gonopore.

leeches, from the family level down to the species level. However, Richardson (1969b, 1975, 1978) repeatedly referred to the characteristics of the reproductive systems for land leeches as being "monotonous" and seemed to overvalue the somital annulation patterns, above all else.

Before this study, descriptions of the male and female reproductive systems for Malagasy leeches were incomplete, other than what was described for the male anatomy for *M. vagans* (Richardson, 1978). Resulting from this study was the opportunity to rediscover some of the known five-annulate species from Madagascar and to include a new species of terrestrial leech. This study has shed some light toward the classification of Malagasy leeches, but more specifically, it has shown that the "monotony" of male and female reproductive systems may have been overestimated by Richardson (1978). Of these species, only *M. fallax* appears to possess the typical haemadipsoid reproductive system—micromorphic male median region and the female region with a large oviducal glandular sac—whereas the remaining species observed here deviate from this form. Therefore, a better characterization of the reproductive morphologies across all land leeches is still warranted, as there may be a greater diversity and taxonomic value in these systems than previously thought (Richardson 1975, 1978). In addition, the position of the gonopores and the posterior annulation series appear to be good diagnostic characters for species, as they were distinct among the species examined here.

The endemism of continental landmasses associated with the breakup of Gondwanaland has been well documented across various leech taxa (Moore, 1927; Soos, 1967; Richardson, 1975, 1978; Sawyer, 1986; Westergren and Siddall, 2004). An example is Madagascar, the world's fourth largest island, having been isolated from Africa and India for approximately 160 million years and 84–88 million years, respectively (Storey et al., 1995; Briggs, 2003). This may suggest that the hirudinifauna of Madagascar, which are found nowhere else, may have originated ~160 mya or earlier.

There are five described species of terrestrial blood-feeding leeches from Madagascar and a single record of a freshwater leech (i.e., *Linta be* Westergren and Siddall, 2004). Our collection efforts were limited to three localities along the east coast forests of Madagascar, possibly resulting in an underestimation of the species diversity of leeches, although successful in the discovery of two new species (i.e., *L. be* and *M. niarchosorum*). The lack of knowledge of the Malagasy hirudinifauna is attributed to our limited collection and that of previous workers. Additionally, because terrestrial leeches are seasonal (Sawyer, 1986), former collections may have been made during times of the year when leeches were least abundant (i.e., the dry season). Finally, such practices as slash-and-burn agriculture and deforestation of the eastern rainforests of Madagascar threaten the habitats of many of its endemic species. Therefore, expeditions such as this one are key to better assess species diversity of invertebrates, whose loss may go unnoticed in an ever-changing landscape.

Provisional Key to Terrestrial Blood-Feeding Leeches of the Malagabdellinae (revised)

1. Cephalic somites, II–IV uni-annulate, V two-annulate, VI three-annulate, XXV–XXVII uni-annulate.................................. 2
2. VII three-annulate; somites of middle series, VIII–XXIII complete five-annulate; XXV–XXVII uni-annulate: genus *Malagabdella* 3

— VII four-annulate; somites of middle series, VIII–XXIII complete four-annulate; XXIV two-annulate: genus *Tristabdella* Richardson, 1975.................. 8

3. Male pore XI b5/b6 4

— Male pore XI/XII 7

4. Prehensile lobe absent.................................. 5

— Prehensile lobe present 6

5. Female pore XII b5/b6; five complete annuli between gonopores; XXIV two-annulate; seven annuli between XXIII a2 and anus; XXIV two-annulate; 57 friction rays; oviducal glandular sac present to XV .... *Malagabdella fallax*
6. Female pore XII b5; four complete annuli between gonopores; XXIV incomplete four-annulate; nine annuli between XXIII a2 and anus; 57 friction rays; oviducal glandular sac absent; muscular

vaginal tube present ....
.... *Malagabdella niarchosurum*

– Female pore XIII b1/b2; seven complete annuli between gonopores; XXIV uniannulate; six dorsal annuli between XXIII a2 and anus; 58 friction rays; simple coiled common oviduct inserts into gonopore; oviducal glandular sac absent; muscular tube absent................ *Malagabdella vagans*

7. Female pore XII/XIII; five complete annuli between gonopores; XXIII incomplete five-annulate (four annuli dorsally); XXIV incomplete three-annulate; seven (eight) annuli between XXIII a2 and anus .... *Malagabdella morsitans*
8. Seven annuli between XXIII a2 and anus; male pore XI b5, female pore XII b5/b6; four complete annuli between gonopores .... *Tristabdella grandidieri* (Blanchard, 1917)

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