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In the footsteps of Prof. Ernst Marcus: redescription and lectotypes/paralectotypes designations of *Aeolosoma* species (Annelida, Aeolosomatidae) from original material

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ABSTRACT

Of the 20,000 species of Annelida, most live in salt water, and the minority inhabits freshwater or terrestrial environments. Among the freshwater representatives, the family Aeolosomatidae draws attention mainly due to its enigmatic phylogenetic position. In the 1940s, Prof. Ernst Marcus was a pioneer in the study of Aeolosomatidae, mainly from collections in the state of São Paulo, Brazil. His research resulted in the description of eight species, four of which were new to science. Later, Marcus' description of *Aeolosoma headleyi* was recognized as a fifth new species by Van der Land (1971) and named *Aeolosoma marcusi* in his honor. Recently, during a visit to the Museum of Zoology of the University of São Paulo (MZUSP), we found the original material deposited by Marcus (1944), but not formally registered. Thus, the aim of this work was to redescribe and designate the lectotypes and paralectotypes of *Aeolosoma gertae* Marcus, 1944 and *Aeolosoma sawayai* Marcus, 1944. We were able to study and photograph the specimens using a light microscope with Differential Interference Contrast (DIC). We were also able to identify and redescribe many important taxonomic features. However, some structures can only be observed in living individuals (as they are not preserved in the fixed material), which reinforces the need to study live specimens. This paper contributes to understand the diversity of *Aeolosoma*, provides new morphological knowledge and lays the foundation for new approaches to the study of aeolosomatids.

Keywords: Meiofauna, Fresh water, Aphanoneura, Museum collections, Deposited type specimens

INTRODUCTION

There are currently approximately 20,000 species of Annelida (Capa and Hutchings, 2021). Approximately 9,000 of these are members of the Clitellata, and the remaining nearly 11,000 belong to the "Polychaeta", Sipuncula and Echiura (now dropped to the family rank Thalassematidae) (Goto et al., 2020; Rouse et al., 2022). Most annelids live in salt water—representing a significant proportion of the diversity and abundance of marine benthos—and a smaller proportion live in freshwater or terrestrial environments. One freshwater group that has attracted attention due to its enigmatic phylogenetic position is the family Aeolosomatidae Levinsen, 1884 (Fauchald, 1977; Glasby and Timm, 2008; Erséus et al., 2020; Rouse et al., 2022).

The taxon Aeolosomatidae contains 32 species divided into three genera: *Aeolosoma* Ehrenberg, 1828 (28 species), *Hystricosoma* Michaelsen,

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1926 (3 species) and *Rheomorpha* Ruttner-Kolisko, 1955 (1 species) (Read and Fauchald, 2023). Aeolosomatids live among sediments, on the bottom of freshwater habitats, or associated with aquatic macrophytes, occurring in rivers, lakes, lagoons and streams (Bunke, 1967, 1988; Glasby and Timm, 2008). They also inhabit moist leaf litter of forests and can live in brackish environments (estuaries), with only one species being exclusively marine, *Aeolosoma maritimum* Westheide and Bunke, 1970, found in the Gulf of Tunis (Tunisia) (Westheide and Bunke, 1970; Bunke, 1988).

In terms of morphological structures, the Aeolosomatidae are small, elongated, ventrally flattened organisms, devoid of parapodia and ranging from 0.3 to 10 mm in length (Marcus, 1944; Paxton, 2000). They have epidermal glands along the body, structures that can be reddish, yellowish, greenish, or colorless (Bunke, 1988). The prostomium is shaped like a lobe and has cilia responsible for movement on its ventral region. In addition, a pair of ciliated pits can be observed on the sides of the prostomium (Bunke, 1988; Timm, 2020). Capillary chaetae (most frequent) and sigmoid chaetae are arranged in four chaetal bundles per segment, two dorsolateral and two ventrolateral (Marcus, 1944; Van der Land, 1971; Bunke, 1988; Timm, 2020; Rouse et al., 2022;).

The Aeolosomatidae are hermaphroditic and reproduce mostly asexually by paratomy, with sexual reproduction being uncommon. The first zooid can contain up to 18 segments, but the number of segments in an individual can be higher if there is a chain of zooids. In asexual reproduction, development occurs from the fission zone, generating chains of two to eight zooids that subsequently detach from the main body (Bunke, 1988; Falconi et al., 2006; Timm, 2020). Some species of Aeolosomatidae also have the ability to encyst. In this state, they endure drought and water temperatures near 0 °C and later resume activity in water and warmer conditions (Herlant-Meewis, 1950; Stout, 1956). In addition, the presence of these organisms in a given environment can be used to assess habitat quality, that is, aeolosomatids can be used as environmental indicators (Särkkä, 1989).

Knowledge about the diversity of the Aeolosomatidae is very limited worldwide. The Palearctic realm, where *Aeolosoma* have been known for almost 190 years, is the most studied area. In contrast, the Neotropical fauna is one of the least studied (Marcus, 1944; Bunke, 1986). The first study of the diversity of Brazilian Aeolosomatidae was conducted by Prof. Ernst Gustav Gotthelf Marcus in the 1940s, using samples from the city of São Paulo and surrounding areas (Marcus, 1944). Marcus (1944) found ten species (eight currently accepted), a significant number compared to the diversity of other areas known at the time, such as the Palearctic, Neartic and Afrotropical realm (Marcus, 1944; Read and Fauchald, 2023). His study led to the description of four new species, *Aeolosoma aureum* Marcus, 1944, *Aeolosoma evelinae* Marcus, 1944, *Aeolosoma gertae* Marcus, 1944 and *Aeolosoma sawayai* Marcus, 1944, all of which are still accepted (Read and Fauchald, 2023). Later, Marcus' description of *Aeolosoma headleyi* Beddard, 1888 was recognized as a fifth new species by Van der Land (1971) and named *Aeolosoma marcusi* Van der Land, 1971 in his honor.

During a visit to the Museum of Zoology of the University of São Paulo (MZUSP), we found and examined the original material of Aeolosomatidae species deposited by Prof. Ernst Marcus, but not formally registered. This study aimed to redescribe two species described by Marcus (1944)—*A. gertae* and *A. sawayai*—and to determine their respective lectotypes and paralectotypes. This redescription is important for a better understanding of the diversity of the *Aeolosoma*, providing new morphological knowledge and laying the foundation for future studies in many different areas, such as the biogeography, ecology and phylogeny of aeolosomatids.

METHODS

We found slides of nine species of *Aeolosoma*: *A. beddardi* Michaelsen, 1900; *A. corderoi* Ev. Marcus, 1944; *A. evelinae* Marcus, 1944; *A. gertae* Marcus, 1944; *A. hemprichii* Ehrenberg, 1828; *A. marcusi* Van der Land, 1971; *A. sawayai* Marcus, 1944; *A. travancorense* Aiyer, 1926; and *A. viride* Stephenson, 1911. However, one slide of *A. beddardi* was found in a poor state of preservation and with no description by Marcus (1944), only a brief comment. In the case of *A. corderoi*, only one slide was also found, but its description was made by Du Bois-Reymond Marcus (1944), so we thought it would best fit a separate study. Unfortunately, we did not find *A. aureum*, on the other hand, we realized that the *A. headleyi* described by Marcus (1944) is actually the type material of *A. marcusi* (Van der Land, 1971).

We therefore decided to work initially with both the new species described by Marcus (1944) and *A. marcusi*. We collected new samples to study live specimens, but found only *A. evelinae* and *A. marcusi*. Thus, we decided to publish a first work only with the preserved material of Marcus (*A. gertae* and *A. sawayai*), and there is a second redescription in progress for the species for which new material was obtained (*A. evelinae* and *A. marcusi*).

The original material consists of both whole mounts and semithin sections (Figure 1). Individuals were observed using a ZEISS Axioskop 2 plus light microscope with Differential Interference Contrast (DIC) equipped with a ZEISS Axiocam 105 color video camera. The characters were photographed, analyzed and measured using the Zen 2.5 (blue edition) program, and the data obtained were tabulated (see Tables 1 and S1, S2, S3, S4, S5, S6, S7, S8, S9, S10 and S11).

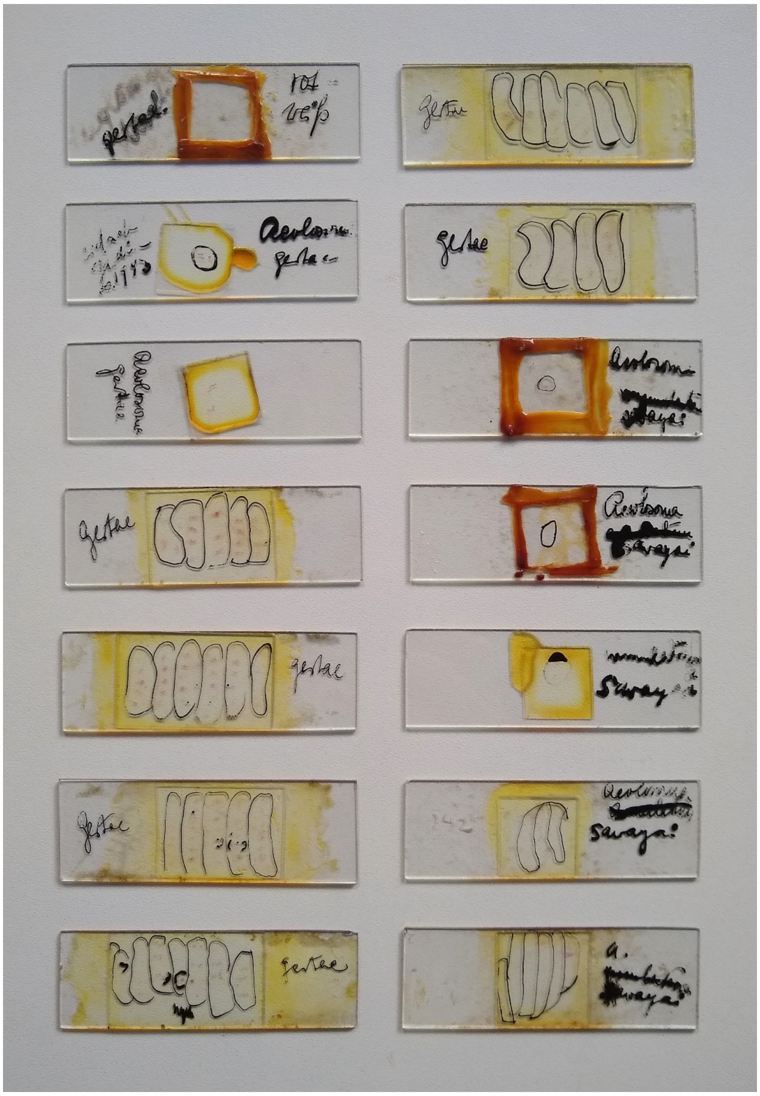

Figure 1. Whole mount slides and semithin sections. *Aeolosoma gertae* - first column and top two in the second column. *Aeolosoma sawayai* - bottom five of the second column.

Table 1. Comparison of morphological features between *Aeolosoma gertae* and *Aeolosoma sawayai* according to Marcus (1944). Our contributions are shown in bold. Nº = number, * = not observable or not applicable.

	A. gertae	**A. sawayai**
Body color	Whitish	Transparent
Color of epidermal glands	Intense red	Yellow, approximately lime
Colorless stain next to epidermal glands	Present	Absent
Epidermal glands throughout the body	Restricted to the dorsal side; few glands distributed along the body; greater concentration in the pygidium	Concentrated in the prostomium, peristomium and pygidium
Ring folds of the epidermis	Absent	Present
First zooid length (mm)	**1.6 – 2.4**	**0.5 – 0.62**
Whole body length (with all zooids) (mm)	2.0 – 4.0 (**2.1 – 2.6**)	0.6 – 2.0 (**0.9 – 1.14**)
N° of segments of the first zooid	14 – 17 or more (**15 – 24**)	6 – 9 (**6**)
Total n° of segments of all zooids	**23 - 32**	18 (**15 – 16**)
Width (µm)	150 - 200 (**101 – 216**)	60 (**69 – 112**)
Prostomium shape	The prostomium anterior zone is flattened and has only sensory cilia; the anterior edge has a cusp form; the prostomium and peristomium are nearly circular	Widens behind the ciliated pits, constricted at their level
Prostomial ciliated field	Figures 5 and 18 by Marcus (1944) suggest that it is restricted to the ventral side	Does not reach the prostomium anterior edge, but is contiguous to the ciliated pits
Sensory cilia	Present	Present, few and tenuous
Ciliated pits	Nearly spherical, laterally situated, without connection to the ciliated ventral field	Small
Transversal fold	Absent	Present
Brain	Anteriorly notched and provided with two lobules posteriorly	Longer than wide (including the posterior lobules)
Mouth	Narrow, with elliptical contour, sometimes with enlarged lower lip	Narrow, semi-lunar
Intestine dilation	III – X (**IV-VI – X-XIII**)	II – IV (**II – V**)
Intestine color	Colorless	Orange (reserves stored in the intestine)
Bundle of chaetae	4 – 8 (more frequently 5) **2 - 9 (more frequently 6)**	**2 - 4 chaetae (more frequently 4)**
N° of long capillary chaeta	**1 - 4 in a bundle (more frequently 3)**	**1 or 2 in a bundle (more frequently 1)**
Long capillary chaeta length (µm)	250 (**93 – 174**)	Up to 85 (**40 – 66**)
Long capillary chaeta ornaments	**Can be serrated at the base, in the middle, at the end or in the entire extension of the chaeta**	Absent
No. of short capillary chaeta	**1 - 5 in a bundle (more frequently 4)**	**1 - 3 in a bundle (more frequently 2)**
Short capillary chaeta length (µm)	100 – 120 (**32 – 64**)	**14 - 42**
Short capillary chaeta ornaments	**Can be serrated at the base, in the middle, at the end or in the entire extension of the chaeta**	Absent

continued

	A. gertae	**A. sawayai**
No. of sigmoid chaeta	Absent	**1 or 2 (more frequently 1)**
Sigmoid chaeta length (µm)	*	Up to 35 (**16 – 28**)
Sigmoid chaeta ornaments	*	Bifid end with 2 or 3 lateral denticles, next to the terminal bifurcation. The two ends are juxtaposed, not discernible as superior (distal) and inferior (proximal)
Septa	Incomplete, but clearly separating the segments	Undeveloped
Blood commissures	Very distinct	Vessels have no special characters
Nephridia	Begin in I or II; may be missing in some segments; the nephridial funnels are wider than the nephroducts	Begin in I
Fission zone	XIII – XV (**XV – XVIII**)	VI – VII (**VI**)
Pygidium	**Cylindrical with a rounded edge**	**Cylindrical, slightly tapered near the anus, ending in a rounded edge**

Some considerations are worth highlighting for a better understanding of the redescriptions presented below. The peristomium is considered the first segment in Oligochaeta, to which the *Aeolosoma* was counted in the time of Marcus, but is considered presegmental in most studies on Annelida, which are followed in this paper (Fauchald, 1977; Glasby et al., 2000; Verdonschot, 2015). We defined the anterior, median and posterior regions in the first zooid, according to the maximum number of segments, the dilation of the intestine and the position of the fission zone, following Marcus (1944). In *A. gertae*, the number of segments is 14 – 17, the intestine dilates from III to X and the fission zone starts in XIII – XV; thus: Anterior (I – IV); Middle (V – XII); Posterior (XIII – XVII). In *A. sawayai*, the first zooid has 6-9 segments, the intestine dilates from II to IV and the fission zone starts in VI – VII; thus: Anterior (I – III); Middle (IV – VI); Posterior (VII – IX). For standardization, the division of the body was limited to the first zooid, as not all specimens have more than one zooid. Lastly, for the measurements of the chaetae, we selected only one bundle from each region of interest (anterior, median and posterior / dorsal and ventral). In this bundle, we measured only one chaeta per type (long capillary, short capillary and sigmoid).

We do not know whether the characteristics described by Marcus (1944) were based exclusively on live specimens, at least there is no indication in the original study. We believe that he studied them in both conditions, alive and preserved, but if his measurements were made with live specimens, there may naturally be some differences from ours, since individuals tend to shrink and flatten when fixed under a coverslip (Bunke, 1988; Costa-Paiva et al., 2007).

RESULTS

TAXONOMIC ACCOUNT

Class Aphanoneura Vejdovský, 1884
Family Aeolosomatidae Levinsen, 1884
Genus *Aeolosoma* Ehrenberg, 1828
Type species *Aeolosoma hemprichii* Ehrenberg, 1828

DESCRIPTIONS

Aeolosoma gertae Marcus, 1944

Figures 1 and 2, Tables 1, S1, S2, S3, S4 and S5.

Material examined

Whole specimens: one lectotype (collection number: 5758) and six paralectotypes (collection numbers: 5759 and 5760).

Semithin sections: six slides, in no particular order and with an undetermined number of specimens (collection number: 5762).

There is also one additional slide (collection number: 5761), but it is in poor condition and therefore not suitable for study. This material was also deposited for its historical value.

Location

In the surroundings of the city of São Paulo, such as the neighborhoods of Caxingui and Cidade Jardim, among roots of *Eichhornia crassipes* (Mart.) Solms-Laubach or on the margin of clean streams, among fallen wet leaves.

Description

Description based on the fully grown lectotype and three paralectotypes, Lec (5758), Paralec 3 (5759), Paralec 1 (5760) and Paralec 3 (5760). The other three paralectotypes are considerably smaller and do not have all structures fully developed, which leads us to believe that they are juveniles.

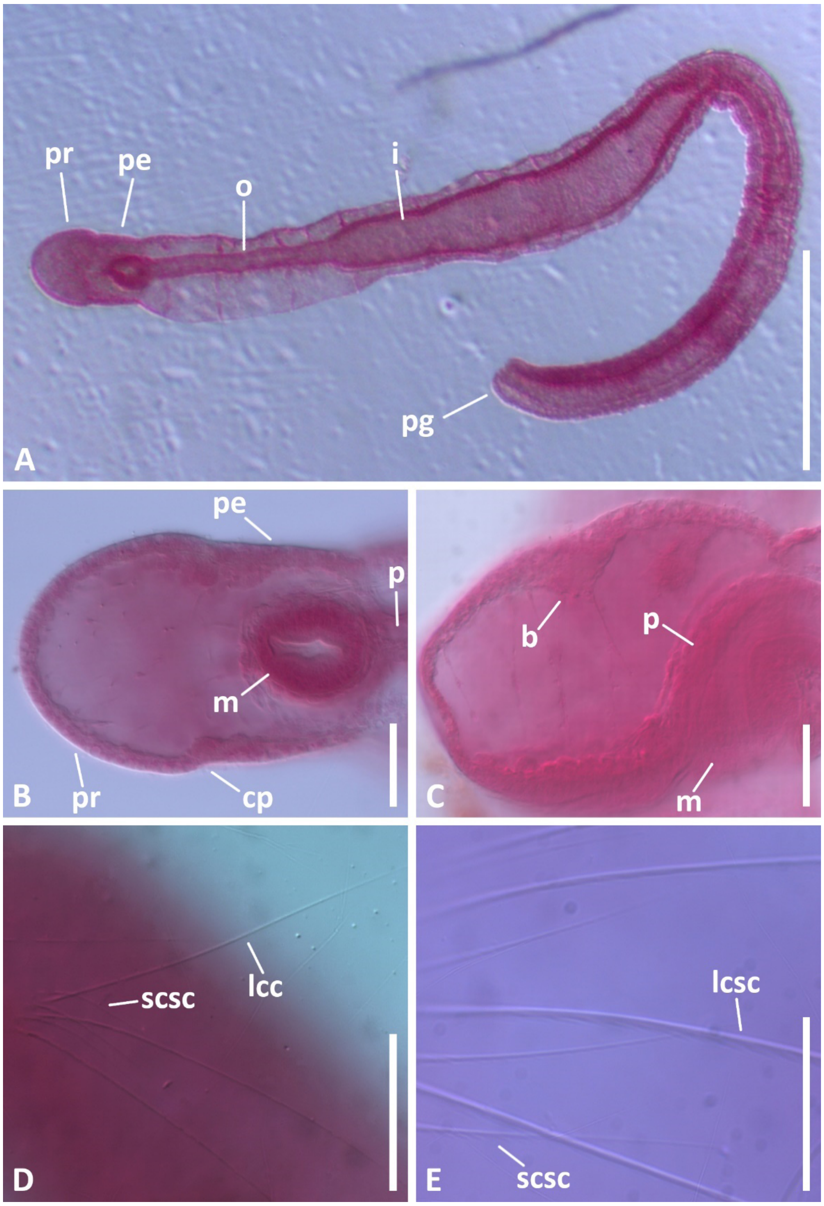

Figure 2. *Aeolosoma gertae* material in light microscope with DIC. Lectotype 5758 (A,B). Some paralectotypes from 5759, 5760 (C - E). (A) Whole individual, ventral view, single zooid. (B) Anterior region, ventral view. (C) Anterior region, lateral view. (D) Ventral chaetal bundle. (E) Dorsal chaetal bundle. Abbreviations: b = brain, cp = ciliated pit, i = intestine, lcc = long capillary chaeta, lcsc = long capillary serrated chaeta, m = mouth, o = oesophagus, p = pharynx, pe = peristomium, pg = pygidium, pr = prostomium, scsc = short capillary serrated chaeta. Scales: (A) 400 µm, (B) 50 µm, (C and D) 40 µm, (E) 20 µm.

Elongated body measuring 2,1 – 2,6 mm in length, with 23 – 32 segments and a chain of up to three individual zooids. First zooid length in the range of 1,6 – 2,4 mm with 15 – 24 segments. The body is wider in the middle region, with anterior width of 108 – 163 µm, middle width of 161 – 216 µm and posterior width of 101 – 140 µm (Figure 2A). The prostomium is wider than longer and semi-elliptical in shape, with length of 109 – 142 µm and width of 147 µm. Peristomium length of 73 – 95 µm and width of 128 µm. Ciliated pits located laterally between prostomium and peristomium. Rounded mouth, 69 µm long and 63 µm wide. Mouth opening narrow and longitudinally stretched (Figure 2B and C). Intestine dilates from IV-VI to X-XIII, throughout seven or eight segments. Bundle of chaetae consisting of 2 – 9 capillary chaetae, more frequently six, 1 – 4 being long (most often 3) and 1 – 5 being short (most often 4). Long chaetae in the range of 93 – 174 µm (mean length = 139 µm) and short chaetae in the range of 32 – 64 µm (mean length = 47 µm). Both long and short chaetae are generally smooth, but one or more per bundle may be serrated. Serrated structures may be present at the base, in the middle, at the end or throughout the extension of the chaeta. It is necessary to use a 100x oil immersion objective to verify these structures (Figure 2D and E). Fission zone begins in XV – XVIII. The pygidium is cylindrical with a rounded edge.

Remarks

The width of the prostomium, the width of the peristomium and the dimensions of the mouth were measured in only one specimen, the only one that was dorsoventrally fixed. The presence of ciliated pits was confirmed only in the dorsoventrally specimen by observation of its lateral cilia; in the laterally fixed specimens, it was not possible to observe ciliated pits, nor their shape and extent. Ciliated field boundaries were not verified.

A comparison of the above description with that of Marcus (1944) reveals some differences. In his study, the body length of *A. gertae* was 2 – 4 mm, while in the slides it was 2,1 – 2,6 mm. Regarding the segments, Marcus (1944) described the first zooid as having 14 – 17 segments, and for the chain of zooids, he only reported that there were "more". We counted 15 – 24 segments in the first zooid and 23 – 32 segments in the chain. In the original description, the body width was 150 – 200 µm, but in the preserved material, the anterior width was 108 – 163 µm, the middle width was 161 – 216 µm and the posterior width was 101 – 140 µm. The intestine should dilate from III to X, but we noticed that it went from IV-VI to X-XIII. In the original description, long capillary chaetae reached 250 µm and short capillary chaetae were in the range of 100 – 120 µm, but from the preserved specimens, we observed 93 – 174 µm for long capillary chaetae and 32 – 64 µm for short capillary chaetae. The stem base of the capillary chaeta was mentioned to resemble a bayonet, but we did not notice this similarity. The fission zone was described as starting in XIII – XV, but we observed that it started in XV – XVIII. Prof. Ernst Marcus described the pygidium as obtuse and rounded, while we prefer to describe it as cylindrical with rounded edges. Lastly, Marcus did not observe serrated chaetae in the original description of this species.

The following characteristics could not be observed by us because they were lost during slide mounting, but they were originally described by Marcus (1944) when the specimens were alive: (i) Distribution patterns of the epidermal glands (scarce, intense red and restricted to the dorsal side with greater concentration at the posterior end); (ii) Structures adjacent to the epidermal glands (colorless stain); (iii) Epidermal cells (may contain granular secretion in vacuoles, white in reflected light, gray in transmitted light); (iv) Prostomium (the anterior edge is cusp-shaped, flattened and lacks cilia except for the sensory ones); (v) Ciliated pits (nearly spherical, located laterally, without connection to the ciliated ventral field); (vi) Mouth (may have an enlarged lower lip); (vii) Septa (incomplete, but clearly separating the segments); (viii) Vessels (easily discernible, but commissure between segments II and III appears to be missing); (ix) Nephridia (begin in segment I or II, but not all subsequent segments have them; the nephridial funnels are wider than the nephroducts); (x) Brain (anteriorly notched and provided with two lobules posteriorly).

Aeolosoma sawayai **Marcus, 1944**

Figures 1 and 3, Tables 1, S6, S7, S8, S9, S10 and S11.

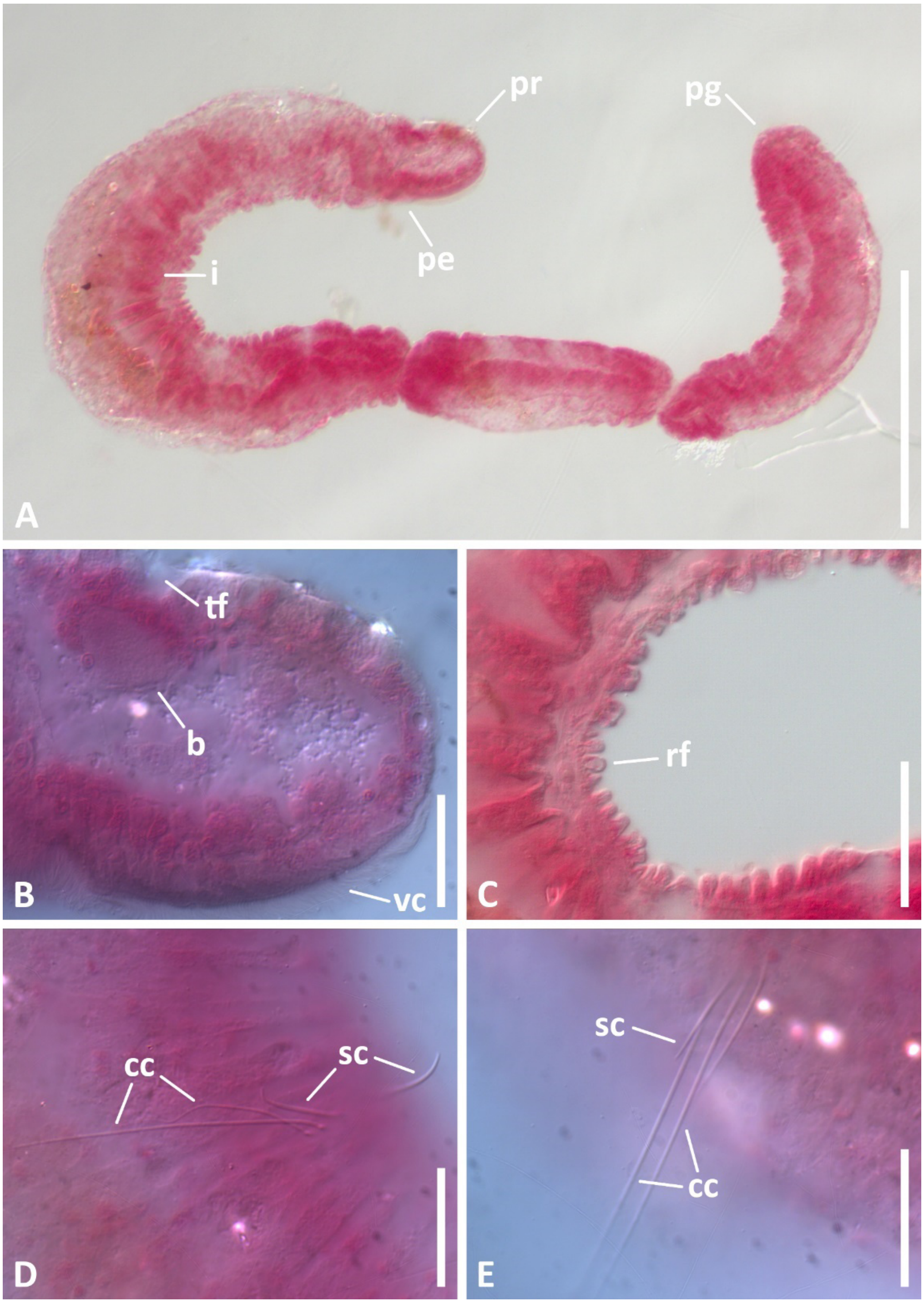

Figure 3. *Aeolosoma sawayai* material in light microscope with DIC. All images are from lectotype 5763. (A) Whole individual, lateral view, three zooids. (B) Anterior region, lateral view. (C) Middle region, ventral side, lateral view. (D) Ventral chaetal bundle. (E) Dorsal chaetal bundle. Abbreviations: b = brain, cc = capillary chaeta, i = intestine, pe = peristomium, pg = pygidium, pr = prostomium, rf = ring folds, sc = sigmoid chaeta, tf = transversal fold, vc = ventral cilia. Scales: (A) 200 µm, (B, D and E) 20 µm (C) 50 µm.

Material studied

Whole specimens: one lectotype (collection number: 5763) and three paralectotypes (collection number: 5764).

Semithin sections: two and four paralectotypes (collection numbers: 5767 and 5768, respectively).

There are also two additional slides (collection numbers: 5765 and 5766), but they are in poor condition and therefore not suitable for study. This material was also deposited for its historical value.

Location

In the surroundings of the city of Curitiba (Paraná state), several places in the countryside of the state of São Paulo (Santa Rita and Mogi das Cruzes cities etc.) and suburbs of the city of São Paulo (Pinheiros, Santo Amaro and other neighborhoods).

Description

Description based on the fully grown lectotype and one paralectotype, Lec (5763) and Paralec 3 (5764). Two other specimens are considerably smaller and do not have all structures fully developed, which leads us to believe that they are juveniles.

Body length of 0,9 – 1,14 mm, with 15 – 16 segments and a chain of zooids up to three individuals. First zooid length of 0,5 – 0,62 mm with six segments. The body enlarges in the middle region, with anterior width of 69 – 79 µm, middle width of 81 – 112 µm and posterior width of 74 – 84 µm (Figure 3A). There are ring folds of the epidermis in the segments (Figure 3C). Prostomium length of 47 – 60 µm. Peristomium length of 39 – 46 µm. Transversal fold above the brain (Figure 3B). The intestine dilates throughout segments II – V. Bundle of chaetae consisting of 2 – 4 chaetae (most often 4), with 1 – 2 long capillary chaetae (more frequently 1), 1 – 3 short capillary chaetae (more frequently 2) and 1 – 2 sigmoid chaetae (more frequently 1). In the first zooid, sigmoid chaetae are more common on the ventral side and only one was found on the dorsal side, but in the last zooids, there are more dorsal sigmoid chaetae. Long capillary chaetae of 40 – 66 µm (mean length = 54 µm). Short capillary chaetae of 14 – 42 µm (mean length = 28 µm). Sigmoid chaetae of 16 – 28 µm (mean length = 20 µm) (Figure 3D and E). The fission zone begins in VI. The pygidium is cylindrical, slightly tapered near the anus, ending in a rounded edge.

Remarks

Prostomium and peristomium widths were not measured because the specimens were mounted laterally. Ciliated pits and their connection to the transversal fold above the brain were not observed. The presence of a transversal fold was confirmed by a cleft above the brain, but it was not possible to verify its extension along the sides of the head. Prostomial ciliated field boundaries could not be determined.

A comparison of our redescription with that of Marcus (1944) reveals some divergences. In his paper, the various ring folds of the epidermis in each segment seem to occur all over the body, but in the preserved material, they were observed only on the ventral side of the middle region. This probably has to do with the position in which the specimens were fixed (with the ventral side contracted, accentuating the ring folds). In the paper of Marcus (1944), the first zooid is 530 µm long and a chain of four zooids can reach 2.0 mm. Both the single zooid and the chain of zooids are 60 µm wide. In the slides, the first zooid was also close to 530 µm long (500 and 620 µm), but in a chain of three zooids, the longest was 1.14 mm long. The width varied from 69 to 112 µm. Marcus (1944) pointed out that the first zooid has 6 – 9 segments and the chain of zooids has 18. However, we counted six segments in the first zooid and up to 16 in the chain. According to Marcus (1944), the intestine dilates from the end of II to the end of IV. In contrast, we verified that the intestine dilates from II to V. In the original description, few capillary chaetae are curved in *A. sawayai*, but we did not identify this curvature in the slide specimens. In the posterior region of the first zooid, we also did not observe a decrease in the number of capillary chaetae compared with the rest of the body. Marcus (1944) pointed out that sigmoid chaetae never occur in segment I, but in the two fully grown specimens analyzed, we did not observe sigmoid chaetae in segment II either. As there are few specimens, we cannot say that sigmoid chaetae are always missing in segment II or even in segment I. There was also some discrepancy in the length of the chaetae. In the paper of Marcus (1944), capillary chaetae are described to reach 85 µm and sigmoid chaetae are said to reach 35 µm. In our analysis, we divided capillary chaetae into long (40 – 66 µm) and short (14 – 42 µm). Sigmoid chaetae range in size from 16 to 28 µm. Marcus (1944) also pointed out that sigmoid chaetae are slightly serrated, with two or three lateral denticles near the terminal bifurcation. The two ends of the latter are juxtaposed, not discernible as superior (distal) and inferior (proximal), but we did not identify any ornaments on the sigmoid chaetae from the preserved material. In contrast to our observations, Marcus (1944) stated that the fission zone can also begin in VII. As for the shape of the pygidium, Prof. Ernst Marcus pointed out that it is conical, with few thin sensory cilia. However, we categorized it as cylindrical, slightly tapered near the anus and ending in a rounded edge.

Marcus (1944) described some other structures that were visible in live specimens but were lost during slide mounting. These characteristics are: (i) Body color (transparent); (ii) Epidermal glands (yellow, approximately lime color, in some specimens these glands are rare, always accumulated in the prostomium and in the pygidium); (iii) Prostomium (with few and tenuous sensory cilia, frequently widens behind the ciliated pits, being constricted at their level); (iv) Ciliated field (does not reach the anterior edge of the prostomium, but is contiguous with the small ciliated pits, located laterally); (v) Mouth (narrow, semilunar); (vi) Brain (unusual longitudinal extension, longer than wide—including the posterior lobules); (vii) Intestinal wall (stores orange reserve materials); viii) Septa (not developed); (ix) Vessels (have no special characters); (x) Nephridia (begin in I, with a nephridium occasionally missing in subsequent pairs); (xi) Pygidium (has few thin sensory cilia).

DISCUSSION

Because meiofaunal organisms (delimited by sieve mesh width, upper 500 µm and lower 44 µm) are neglected groups and difficult to preserve, early taxonomic studies often did not include the deposition and recording of type series (Giere, 2008; Fonseca et al., 2018; Garraffoni et al., 2019). In this paper, we are pleased to make the *Aeolosoma* material used in the paper of Marcus (1944) available to the scientific community, in appropriate conditions for study, by formally registering it in the Museum of Zoology of the University of São Paulo. This type series is not only of taxonomic importance, but also has an inestimable historical value associated with the Marcus couple.

Ernst and Eveline's contribution to the knowledge of zoological diversity was so significant that it made them one of the most influential zoologists of the 20th century (Corrêa, 1991). Some observations must be made about the authorship of the couple's manuscripts. Although their first articles were written jointly, only Ernst appeared as the author. According to Corrêa (1991), this was done to justify Ernst's full-time position as a professor and because Eveline had never accepted paid work. Eveline's contribution only becomes apparent when she is acknowledged in the first sentences of these studies, as in Marcus (1944): "In continuation of our studies on freshwater Oligochaetes, my wife, Mrs. Eveline du Bois-Reymond Marcus, and I present some observations on representatives of the families Aeolosomatidae, Naididae and Tubificidae, the first of which has not yet been reported in Brazil".

While still in Germany, Ernst and Eveline devoted themselves primarily to the study of marine fauna, publishing various papers on little-known groups such as Bryozoa and Tardigrada (Mendes, 1994). With the rise of Nazism and the persecution of Jews in the 1930s, the couple's safety was in jeopardy (Mendes, 1994). According to Eveline herself, the Society for the Protection of Science and Learning (SPSL), an organization at the time dedicated to finding work for displaced Jewish scientists, recommended Ernst for the position of Professor of Zoology at the University of São Paulo (Winston, 2002; Zimmerman, 2006). Marcus accepted, and the couple arrived in Brazil in 1936 (Corrêa, 1991).

In the early years, the two focused their efforts on studying marine diversity with materials collected on their excursions and donated by Brazilian and foreign colleagues (Mendes, 1994).

With the outbreak of World War II, they began to study freshwater and terrestrial animals, such as Oligochaeta and “Turbellaria” since as Germans, they were forbidden to visit the Brazilian coast (Corrêa, 1991; Mendes 1994; Winston, 2002). The aeolosomatids are exactly one of the freshwater oligochaetes studied during this period of restricted circulation. After the end of the war, the couple was able to explore the coast of São Paulo again, and in the course of their career they wrote more than 200 papers on Protozoa, Tardigrada, Onychophora, Pantopoda, Annelida, Nemertea, Ctenophora and Phoronida, but with an emphasis on Bryozoa, “Turbellaria” and Mollusca (Eales, 1969; Corrêa, 1991; Mendes, 1994).

Despite the enormous contribution of the couple, the majority of Aeolosomatidae descriptions still refer to the Palaearctic realm, with 18 recorded species (Van der Land, 1971; Read and Fauchald, 2023). The Neotropical realm comes second with nine species, followed by the Oriental with three, the Afrotropical with one and the Nearctic with one (Van der Land, 1971; Read and Fauchald, 2023). The number of species reports follows the same pattern, with 25 species found in the Palaearctic realm, 14 in the Neotropical, eight in the Nearctic, five in the Oriental, three in the Afrotropical, two in the Australasian and one in Pacific and oceanic islands (Glasby and Timm, 2008). As observed in many meiofauna taxa, the distribution of *Aeolosoma* may be the result of a spatial layout bias known as the “rotiferologist” effect (Fontaneto et al., 2012). According to these authors, the distribution patterns and species richness of these microscopic metazoan reflect the number, nationality and location of taxonomists’ laboratories rather than a “true” spatial distribution resulting from a “true” biogeographic process. This effect can be clearly observed in the Neotropic, where the pattern of *Aeolosoma* species distribution may reflect the location of Marcuses rather than the distribution of the taxa themselves. Only in the vicinity of the city of São Paulo, six species have been described, while three other species are known from the whole Neotropical realm (Van der Land, 1971; Read and Fauchald, 2023).

Like the biogeographical issues, the phylogenetic position of the Aeolosomatidae remains a fascinating mystery in Annelida. Some studies place them next to Clitellata, while others place them next to different “polychaete” taxa (Struck and Purschke, 2005; Rousset et al., 2007Struck et al., 2007; Erséus et al., 2020). Although this question persists, the occurrence of Aeolosomatidae in different environments can provide us with clues in an attempt to reconstruct their evolutionary history. Of the 32 species in the family, 30 are freshwater, one is brackish (*Aeolosoma litorale* Bunke, 1967) and one is exclusively marine (*Aeolosoma maritimum* Westheide and Bunke, 1970) (Glasby and Timm, 2008; Read and Fauchald, 2023). Regardless of the phylogenetic tree in question, most of the groups close to Aeolosomatidae inhabit salt water, suggesting a marine origin for the family (Rousset et al., 2008; Erséus et al., 2020). Thus, the most parsimonious hypothesis for the transition between aquatic environments is that Aeolosomatidae originated in the sea and later invaded fresh water, with *A. litorale* representing a transitional stage and *A. maritimum* remaining in salt water.

Interestingly, while most of the main lineages of Annelida appeared at the end of the Carboniferous, only a few successfully invaded continental waters (Rouse and Pleijel, 2001; Glasby and Timm, 2008). Surprisingly, Aphanoneurans is one of them, together with Clitellata, *Caobangia* Giard, 1893 (and Branditka Jones, 1974), *Namanereis* Chamberlin, 1919 and *Stratiodrilus* Haswell, 1900 (Glasby and Timm, 2008). Glasby and Timm (2008) also pointed out that the radiation of Aphanoneura may have occurred in Pangea, so it is possible that the transition to fresh water occurred at least 250 million years ago.

To occupy fresh water, a marine lineage must cope with low salt concentrations, a barrier that requires greater energy expenditure by specimens for osmotic regulation (Prosser, 1973). For example, it is hypothesized that the transition of Clitellata to fresh water coincided with duplications in a gene related to osmoregulation (Horn et al., 2019). It is also known that freshwater “Polychaeta” have a series of adaptations that protect the larvae from low salinity, including direct sperm transfer and direct development (Glasby and Timm, 2008). In the Aeolosomatidae, these adaptations include asexual reproduction by paratomy and, for sexual reproduction, copulation, sperm storage in the spermatheca and oviposition in cocoon-like envelopes (Glasby and Timm, 2008). *Aeolosoma* can even be considered an extreme case that came from the sea. Due to their ability to encyst, these animals can live in environments where the availability of water is uncertain, such as mosses, plant litter and even bromeliad tanks (Herlant-Meewis, 1950; Bunke, 1967, 1988; Céréghino et al., 2018). It is known that for several meiofaunal organisms, encystment can also contribute to passive dispersal, with transport by wind or even attachment to larger animals such as birds (Frisch, 2007; Giere, 2008; Fontaneto, 2019).

Although promising, understanding aeolosomatid diversity has not been an easy task. In addition to the difficulties inherent to the study of the group, such as the small size and fragility of the specimens, describing species based only on preserved material is challenging because some structures are naturally lost or no longer visible, reinforcing the need to study live specimens (Bunke, 1988; Garraffoni et al., 2019; Timm, 2020). New samples from the type localities would be interesting, but due to the growth of the city of São Paulo, they either no longer exist or are polluted (Barros et al., 2005; Grosso et al., 2008). Nevertheless, as unlikely as it may seem, some of the original populations may still exist. For example, marine annelids are known to persist in the polluted Gulf of Naples, in exactly the same localities where they were described a century ago (Crocetta et al., 2020).

In addition, taxonomy is currently facing an alarming crisis, with a shortage of specialists and one of the fastest growing rates of biodiversity loss in Earth’s history (Wheeler, 2020; Capa and Hutchings, 2021). The proper study of diversity requires solid basic knowledge of both the morphological and genetic variation of specimens (Dayrat, 2005; Will et al., 2005). For instance, Glasby and Timm (2008) highlight that *Aeolosoma hemprichii* Ehrenberg, 1828, the type species of the genus, has been recorded in most continents, but likely with misidentifications. In meiofaunal organisms, the first descriptions were often more concise, probably due to the technological limitations of the time; however, with the development of new methodologies, new perspectives have been added to species delimitation (Todaro et al., 1996; Fonseca et al., 2018). In this context, some species may end up being synonymized or, on the other hand, turn out to be cryptic, revealing a previously hidden diversity (Bickford et al., 2007; Glasby and Timm, 2008). Taxonomic revision thus becomes an indispensable effort to understand the multiple facets of biodiversity (Beheregaray and Caccone, 2007; Struck et al., 2018). To adequately address all these challenges, future research should use new technologies—such as scanning electron microscopy, computed nanotomography and genetic sequencing—from the perspective of integrative taxonomy (Padial et al., 2010; Fonseca et al., 2018; Garraffoni et al., 2019).

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AUTHOR CONTRIBUTIONS

N.D.G.S.: Conceptualization; Data Curation; Formal Analysis; Investigation; Methodology; Validation; Visualization; Writing – Original Draft; Writing – Review & Editing.

A.R.S.G.: Conceptualization; Formal Analysis; Funding Acquisition, Methodology; Project Administration; Resources; Supervision; Validation; Visualization; Writing – Review & Editing.

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