POLYCLADIDA BIODIVERSITY AND SYSTEMATICS: AN INTEGRATIVE APPROACH

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München, den

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Paper I

Bahia, J., Padula, V., Correia, M.D. & Sovierzoski, H.H. (2015) First records of the order Polycladida (Platyhelminthes, Rhabditophora) from reef ecosystems of Alagoas State, north-eastern Brazil, with the description of *Thysanozoon alagoensis* sp. nov.. Journal of the Marine Biological Association of the United Kingdom, 95(8): 1-14.

Paper II

Bahia, J. (2015) First records of polyclads (Platyhelminthes, Polycladida) associated with *Nodipecten nodosus* (Linnaeus 1758) aquaculture. Marine Biodiversity, 1-5. DOI: 10.1007/s12526-015-0425-6

Paper III

Bahia, J. & Schrödl, M. (2016) *Pseudobiceros wirtzi* sp. nov. (Polycladida: Cotylea) new species from Senegal with revision of valid species of the genus. Zootaxa, 4097(1), 101-117.

Paper IV

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Paper V

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Summary of the Ph.D. candidate's contributions

	I	II	III	IV	V
Design of the study	●	●	●	●	●
Morphology	●	●	●	●	●
Molecular biology	-	-	-	-	●
Analysis	-	-	-	-	●
Manuscript drafting	●	●	●	●	●
Figure design	●	●	●	●	●

● parts of the paper in which the Ph.D. candidate was envolved.

München,

Prof. Dr. Michael Schrödl

Juliana Bahia Maceira

Summary

In face of the fact that marine biodiversity is highly threatened by human impacts on the environment, it is important to know what we want to protect. This thesis addresses the biodiversity and systematics of Polycladida, which are free-living Platyhelminthes with highly ramified intestine. Polylclads live in all types of marine environments whereas most areas of the world remain unsampled. From the around 1000 species considered valid many were described based on single or immature specimens and few have designated type material or specimens deposited in museums or research institutions. This is especially the case for Brazilian species that had no type material designated, labeled with codes in the publication or deposited. Characters used traditionally in polyclad taxonomy concern eyespots, type of pharynx, reproductive system, especially prostatic vesicle, but so far, those characters have not been tested against molecular evidence. The order Polycladida has two suborders, Cotylea and Acotylea, and their systematics is based on two conflictive classifications in use, which reflects inadequacy in characters choice. Molecular data from this group is still scarce and there is no morphological or molecular phylogeny that includes the whole order. Three gaps in knowledge are addressed in this work: biodiversity, type material and phylogeny with character evolution.

Here I contribute to fill the first one by describing some new species, and by adding novel information, such as color photographs of living animals and microscopic observations to species that are already known. Samplings were made in some previously non-assessed areas in Brazil, Senegal and Cape Verde. One new species from each area is described and distribution ranges are discussed. The genus of the African species *Pseudobiceros wirtzi* is revised based on literature records. Additionally species associated to aquaculture were sampled for the first time in Brazil.

To fill the second gap I studied species from Brazil described by Ernst Marcus and / or Eveline Du Bois-Reymond Marcus. Specimens donated by Eveline Marcus to the Swedish Museum of Natural History were analyzed and I recognized holotypes, paratypes, and designated lectotypes and paralectotypes, as required. Before this work began, most Brazilian species had unknown type material, whereas in this work type specimens of 52 species were designated or recognized. Out the 71 species reported from Brazil, ten remain without information about type material.

As a way to fill the third gap I present here a new and comprehensive set of partial 28S nuclear ribosomal DNA (rDNA) data across Polycladida families. Our phylogenetic analysis, despite being based only on a single molecular marker, is the first to test traditional morphology-based hypotheses on relationships inside the order. Remarkably, all our molecular trees were fully resolved and most nodes robustly supported. The overall topology is consistent with evidences from an updated and revised list of morphological and histological characters. Albeit largely congruent at genus and family level, our integrative phylogenetic hypothesis is not compatible with superfamilies and suborders of neither of the two conventional yet conflicting classification systems by Faubel and Prudhoe. The suborders Acotylea and Cotylea, as traditionally considered, were rejected in the hypothesis tests, thus the taxa were amended to reflect molecular monophyly. According to our trees, just two of Prudhoe's and Faubel's superfamilies were monophyletic; a novel concept of polyclad superfamily was thus proposed. Molecular results revealed that prominent characters used in previous classifications, such as the position of eyespots, the type of pharynx, and the type of prostatic vesicles were prone to homoplasy in both the Acotylea and the Cotylea branches. A novel scenario of morphological character evolution is suggested and the significance of certain features for taxonomy is discussed.

Overall, samples from areas not previously sampled resulted in several new records for Brazil and two new species in this thesis, indicating the potential for future biodiversity exploration. The re-discovery of Ernst and Eveline Marcus' type material is very important for both the contemporary and future study of Atlantic Polycladida. Our molecular results and its combination to morphological data is a unique effort in Polycladida phylogeny. Even though they are preliminary, the novel hypotheses and the data presented here provide a fresh baseline for future studies on Polycladida systematics.

INTRODUCTION

General introduction

General characteristics

Polycladida are free-living Platyhelminthes, whose name means many (poly) divisions, ramifications (clad). This reflects the main characteristic of the group: its highly ramified intestine (Hyman, 1951). The order has two suborders divided basically by the presence (suborder Cotylea) or absence (suborder Acotylea) of a ventral sucker. As the circulatory system is absent, the animal depends on the highly ramified intestine and diffusion for nutrients to reach the tissues and organs (Boyer, 1972). First, transport through diffusion from intestine ramifications and then diffusion from cell to cell. The pharynx is protractile and usually ruffled, with many or few folds, but it can also be tubular. The food is broken down mechanically, using the whole body, or enzymatically. There is no excretory system in Acotylea (Bock, 1913), but some cotyleans present openings of the main intestine: in the median line in a small dorsal pore at 2/3 of the body, or numerous short ducts on the whole dorsal surface, numerous marginal vesicles, or a dorsal pore at the hind end of body (Kato, 1943). Because of the lack of those systems, polyclads have improved their relation area / surface to effectively perform diffusion, allowing it to be one of the largest free-living flatworms (Ruppert et al., 2005).

The epidermis is formed by a single layer of columnar cells, covered by microvilli and cilia, (9+2 microtubules) on a bipartite basement membrane. Four types of glands can be found: rhabdite glands, rhabdoid glands, and two types of mucoid glands, one with flocculent material and the other with slime (Liana et al., 2012). Pigment can be on the epidermis or beneath it (Bock, 1922) and are usually as granules or cells with large pigment filled vacuoles. Those pigment cells are present in most species, except on transparent species that derive color from food items (Liana et al., 2012). Color and color pattern can be considerably important in taxonomy of genera with very uniform reproductive systems (Hyman, 1952). Definitions of groups of color pattern (Newman & Cannon, 1994) and molecular tests of color (Litvaitis & Newman, 2001; Litvaitis et al., 2010) used in species delimitation have proven effective so far.

Muscles are organized in diagonal, circular, and longitudinal layers, which are responsible for complex movements (Bolaños & Litvaitis, 2009). Beneath those layers is the parenchyma which has loosely organized cells and can be very important for transport of nutrient and other substances. Locomotion can happen by swimming through undulating movements in the dorso-ventral direction, and also by creeping through ciliary and muscular movement with anterior or antero-lateral adhesion to the substrate and muscular contraction (Child, 1904). As other groups of platyhelminthes, polyclads can also regenerate, however not as much as triclads (Egger et al., 2007). In Polylcadida, the central nervous system is necessary for complete regeneration (Child, 1904), when the brain is damaged the worm is unable to regenerate the anterior part to its previous size (Olmsted, 1922a).

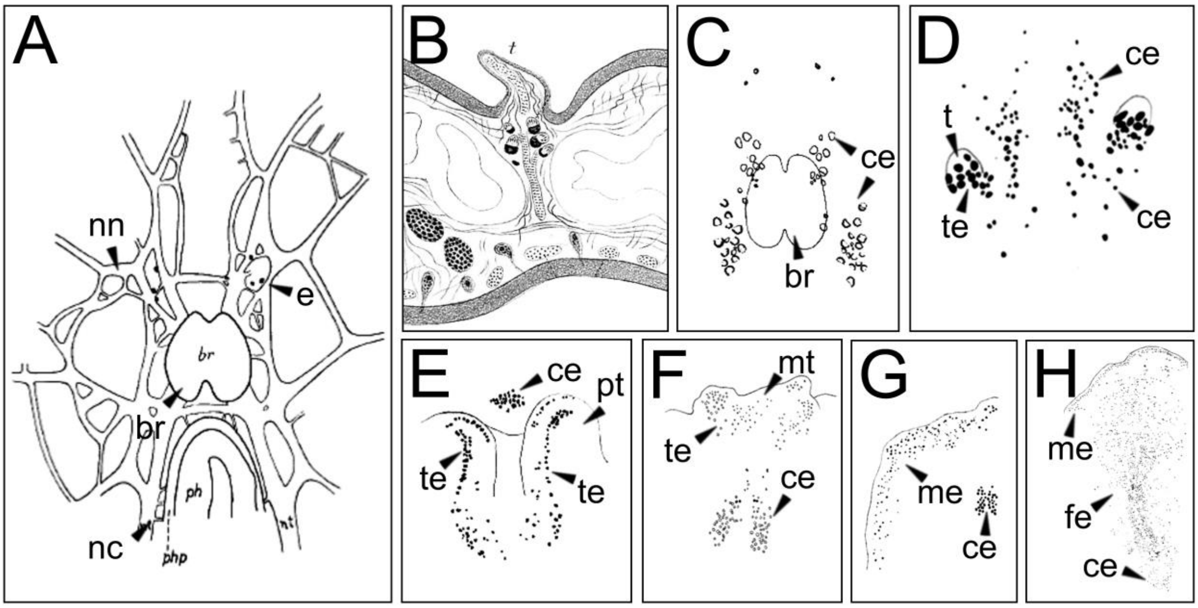


Figure 1: A- Polycladida nervous system; B- nuchal tentacle; C- cerebral eyespots; D- cerebral and nuchal tentacles and eyespots; E- cerebral eyespots, pseudotentacles and tentacular eyespots; F- cerebral eyespots, marginal tentacles and tentacular eyespots; G- cerebral and marginal eyespots; H- cerebral, frontal and marginal eyespots. Figure modified from Graff, 1893 (B), Bock, 1913 (C, D, E, G, H), Bock, 1925 (A), Bock, 1931 (F).

As ramified as the intestine is also the nervous system (Figure 1A). It is characterized by an anterior encapsulated bilobed brain, six pairs of ventral nervous branches and a finely ramified nervous net (Quiroga et al., 2015). Polyclads are one of the first groups of animals with bilateral symmetry, and the locomotory system directional capacity of noticing gradient of resources. The brain is placed at the middle line of anterior end, which can be considered the probable beginning of cephalization or at least a polarization of sensorial capacity. Polyclads lack statocysts, but most of the basic cellular level machinery found in higher metazoans, like multiple membrane channels, transmitters, cell types, non-spiking and multimodal neurons are present in polyclads (Koopowitz, 1986). Much of the behavior is controlled by the peripheral nervous system and the function of the brain and interneurons is integrating the different inputs, coordinate, and sequence reflexes (Koopowitz, 1986). Polyclads can ingest food and lay eggs without a brain (Gruber & Ewer, 1962) and also crawl through ciliary action, but they cannot swim (Olmsted, 1922b) or follow prey. In the absence of the brain, the remaining movements are made without anterior orientation (Koopowitz, 1970). Those are evidences of central nervous system control of the regeneration process and fine or complex movements, and of peripheral nervous system control of some behaviors or reactions.

These flatworms present eyespots (Figure 1C-H) that are usually located over or near the brain area (cerebral), around the margins of the body (marginal), between the brain and the margin (frontal), or associated to tentacles (tentacular). The eyespots number change with growth, but the arrangement maintains its general form (Prudhoe, 1985). Those structures do not form image, but do sense light variation, and therefore species-specific recognition must be through chemical receptors (Newman & Cannon, 1995). As the tentacles can be either located near the brain on the dorsal surface (nuchal) or in the margin (marginal tentacles and pseudotentacles), the eyespots groupings can be named accordingly (Figure 1B-H). Among the marginal eyespots there are different arrangements, some species present them all around the body margin and other have them restricted to the anterior margin. They can also be placed in one or more rows, scattered or in line (Figure 1G and H).

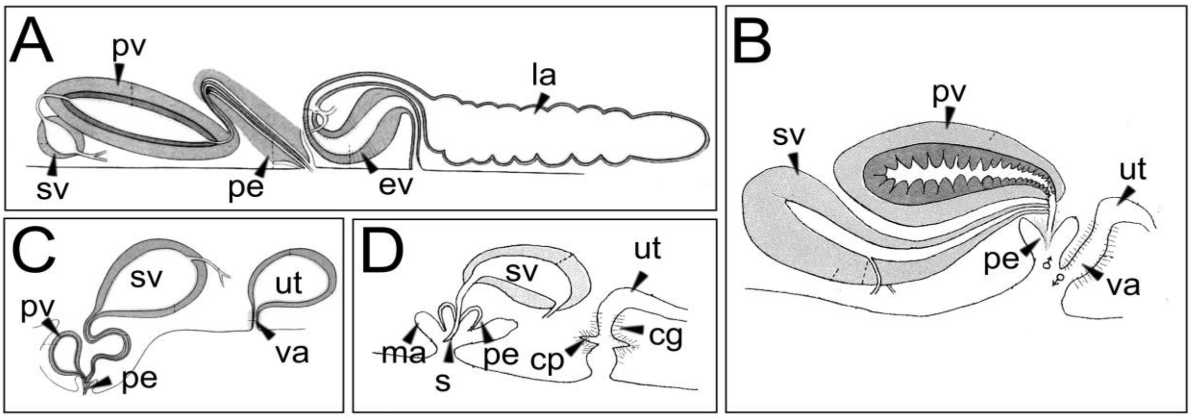


Figure 2: Polycladida reproductive system sagittal sections. A- interpolated prostatic vesicle and Lang's vesicle; B- free prostatic vesicle as seen in Acotylea; C- free prostatic vesicle as seen in Cotylea; D- short vagina and cement pouches. cg: cement glands; cp: cement pouch; ev: external vagina; la: Lang's vesicle; ma: male atrium; pe: penis; pv: prostatic vesicle; s: stylet; sv: seminal vesicle; ut: uteri; va: vagina. Figures modified from Plehn, 1896a (A and C) and Jacubowa, 1906 (B and D)

The hermaphrodite reproductive system is organized with testicular and ovarian follicles scattered in the parenchyma (Hyman, 1951). The ovaries are primitive, there are no vitellocytes, and the yolk is produced independently (Boyer, 1972) and stored in the oocyte cytoplasm, which characterize them as endolecithal eggs (Laumer & Giribet, 2014). The oviducts usually are named uteri when containing ripe eggs, and are connected to the vagina. This can be long and divided in two parts: the internal and external vagina; or be short and simple (Figure 2C and D). It is surrounded by cement glands, responsible for producing adhesive substances for the fixation of the egg masses, and can present a pouch (Figure 2D). A Lang's vesicle can also be connected posteriorly to the vagina, and is believed to store sperm (Hyman, 1951). Sperm ducts or vas deferens can be expanded into spermiducal vesicles, which can be very muscular. Usually a seminal vesicle and prostatic vesicle are present. They can be independent from each other with the prostatic duct connecting in variable points of the ejaculatory duct (Figure 2B and C); or connected with the ejaculatory duct coming from the seminal vesicle and entering the prostatic vesicle (Figure 2A). In some cases the prostatic vesicle can be incorporated in a muscular penis bulb, but usually the ejaculatory duct and prostatic duct join in the penis papilla. This can be armed with hard structures like stylet (Figure 2), spines or a penis modified in cirrus (Hyman, 1951). The spermatozoon is biflagellate and its axonemes are in 9+"1" arrangement. Multiplication of male gonopores can be found in both Acotylea (Beauchamp, 1949) and Cotylea (Faubel, 1984b). And multiplication of female gonopores is known in the suborder Cotylea (Newman & Cannon, 1996). It can be accompanied by multiplication of other reproductive structures as well, like prostatic vesicles, or the whole sexual apparat. Hermaphroditism in the group can be an adaptation to low population densities (Ruppert et al., 2005), then any encounter between individuals of the same species can result in copulation. This can be the case in marine flatworms, as most polyclad species are represented by few individuals (Rawlinson, 2008).

Ecology

Polyclads live in all type of marine environments, they inhabit hard bottom as rocky shores with boulders (Bahia et al., 2014; Aldana et al., 2016), coral reefs (Newman & Cannon, 1994), mangroves (Rawlinson, 2008), soft bottom (Bulnes & Faubel, 2003) or mesopsamic (Curini-Galletti et al., 2008), deep-sea (Quiroga et al., 2006), and can also be pelagic (Bock, 1925) or associated to pelagic environment like *Sargassum* sp. (Graff, 1893; Plehn, 1896b). From the 12 known pelagic species one is holopelagic, and not associated to drifting substrate (Faubel, 1984a). Polyclads are also found in Antarctica (Bock, 1931;

Marcus, 1954b). Three species of Polycladida are limnic or from brackish waters (Faubel, 1984a) and one was described as “semi-terrestrial”, from high intertidal zone, under woodlogs (Newman & Cannon, 1997).

Polyclads are carnivorous predators of sessile and motile invertebrates and eat nudibranchs (Bahia et al., 2014), other gastropods, chitons, bryozoans (Aldana et al., 2016), amphipods (Janiak et al., 2017), snapping shrimp and rock crabs (Wei-ban et al., 2013), cnidarians like *Velella* sp. (Bock, 1925), or corals (Hume et al., 2014), different bivalves, especially oysters (Galleni et al., 1980), compound ascidians, polychaetes, isopods and also partially decomposed material (Jennings, 1957), and can be the major cause of mortality of barnacles (Hurley, 1975). The protractile pharynx either ruffled or tubular is used to reach for the prey. For feeding on ascidians the flatworms protrude the pharynx to suck individual zooids, for motile prey they grab it by folding the anterior part and then transport the prey to the mouth region (Jennings, 1957). In bivalves and barnacles they insert the pharynx between valves or opercular plates, or do a hole in the shell (Galleni et al., 1980). Some species slide the whole body through the valves and eat the prey (Newman et al., 1993). Polyclads can also follow prey and take snails from shells (Koopowitz, 1970), some of which try to escape by running, elevating shell from substrate or clamping (Phillips & Chiarappa, 1980). Polyclads can also be associated to woodborer mollusc (Brusa & Damborena, 2013), gorgonian (Cannon, 1990) or be part of biofouling in pectinid aquaculture (Baeza et al., 1997, Bahia, 2016). Some polyclads showed species-specific relation to ascidians (Pérez-Portela & Turon, 2007).

Species of Polylcadida were shown to live in symbiosis with other animals as gastropods (Smith, 1960; Faubel et al., 2007), chitons (Kato, 1935), hermit crab (Lytwyn & McDermott, 1976) and equinoderms (Doignon et al., 2003), but no damage was yet proven and some species were also found outside the host (Smith, 1960). Some species showed preference for species of snails that live higher in the rocky shore, and ate outside the host and have planktonic larvae (Fujiwara et al., 2015). It is thought that the association is commensalism as the polyclad would benefit from shelter from predators and dissecation without damaging the other species (Smith, 1960; Faubel et al., 2007). However, usually more than one specimen is found inside the palial cavity, and could be using it for reproduction or feeding on eggs or feces (Lytwyn & McDermott, 1976; Faubel et al., 2007). One species was also found to put eggs on the margin of the pallial cavity (Kato, 1935).

Polyclads are prey to fishes (Ang & Newman, 1998; Fujiwara et al., 2015) and mammals (Newman & Cannon, 1997) and can be parasitized by protists (Anderson et al., 1993). As defense mechanisms, in the absence of hard structures, they can use other invertebrates as shelter, as mentioned, or invest on cryptic or aposematic coloration (Ang & Newman, 1998; Newman & Cannon, 1995). The aposematic coloration can be related to their own toxins (And & Newman, 1998), or related to mimicry of toxic species of nudibranchs (Newman et al., 1994) and general patterns of aposematic coloration (Newman & Cannon, 1995). As Polycladida eyespots do not form images, but only sense light, the color pattern is thought to be a sign for visual predators and not used in intra-specific recognition (Newman & Cannon, 1995). These marine flatworms were proven toxic to vertebrates (And & Newman, 1998; Newman et al., 1994) as they present tetrodotoxin, a toxin also found in puffer fish. This toxin and others can also be used to capture prey instead of protection from predators (Ritson-Williams et al., 2006; Newman et al., 1993; Wei-ban et al., 2013). As polyclads eat sessile animals with chemical defenses, and seem adapted to it, they can develop their own chemical defenses, accumulate and have prey toxins in higher concentrations (Newman & Cannon, 1995). The ability to use special traits of prey is also possible for polyclads which use zooxanthellae (Hume et al., 2014) and nematocysts (Goodheart & Bely, 2017).

Development

Reproduction in polyclads happens through true copulation (penis/vagina), dermal impregnation (deposit of spermatophores on the dorsal surface), or hypodermic impregnation (armed penis to inject sperm through epidermis) (Gammoudi et al., 2012). The latter type of copulation is called penis fencing (Michiels & Newman, 1998) as it seems to be a fight between hermaphrodite individuals. Specimens are believed to fight to increase sperm donation over sperm receipt, to father more eggs and have less injuries. The animals present strong avoidance behavior (Michiels & Newman, 1998) which might be related to avoidance of being the “mother” and having the energetic expense of producing egg masses and attaching it to the substrate. After internal fertilization, in the uterus or internal vagina, sperm is absorbed on the epidermis and transported through the mesenchymal space to reach the eggs (Gammoudi et al., 2012). Then numerous eggs are laid simultaneously and kept together by gelatinous material in plates (Domenici et al., 1975) or strings (Wheeler, 1894), in a honeycomb arrangement and secreted by cement glands and ventral wall of parent (Kato, 1940). An egg capsule can have one or multiple (2-12) embryos (Gammoudi et al., 2012; Johnston & Lee, 2008). Some species are known to present parental care, covering egg masses or undulating their bodies, whilst brooding the egg masses (for aeration/water exchange) until before hatching (Johnston & Lee, 2008; Rawlinson et al., 2008).

Polyclad species can present direct or indirect development and three types of larvae were identified so far (Figure 3) and they are similar to the pilidium of nemerteans and the trochophore (Lapraz et al., 2013) because of lobes and ciliary bands. Two of them are free-swimming and are differentiated by number of larval lobes: Götte’s larvae have 4 to 6 lobes, Müller’s larvae have 6 to 8 lobes. The third larval type develops and metamorphoses inside the egg capsule: Kato’s larvae have 10 to 12 lobes (Ballarin & Galleni, 1984; Rawlinson et al., 2011). Kato’s larvae were also found to hatch, like other larval types (Martin-Duran & Egger, 2012). Polyclad larvae are relatively insensitive to light compared to other invertebrate larvae. As young larvae they can be positively phototatic at high light intensity and negative phototatic at low intensity, which is a typical predation avoidance shadow response. Later, as older larvae, they became positive phototatic to be transported to shallow water (Johnson & Forward Jr., 2003). An apical organ, also found in other Platyhelminthes, is present in polyclad larvae and then degenerates. This organ might be used for breaking the capsule (Kato, 1940) and hatch as planktonic larvae. The larvae also present one protonephridium on each side of the body similar to triclads (Watson et al., 1992). The larval body wall has helicoid muscles, circular and longitudinal muscles, retractor muscles, and sphincter muscles around the stomodeum (Semmler & Wanninger, 2010). During the metamorphosis the larval lobes are reabsorbed, the apical organ degenerates, the body flattens, eyes are multiplied and parenchymal muscles and pharynx develop (Ruppert, 1978).

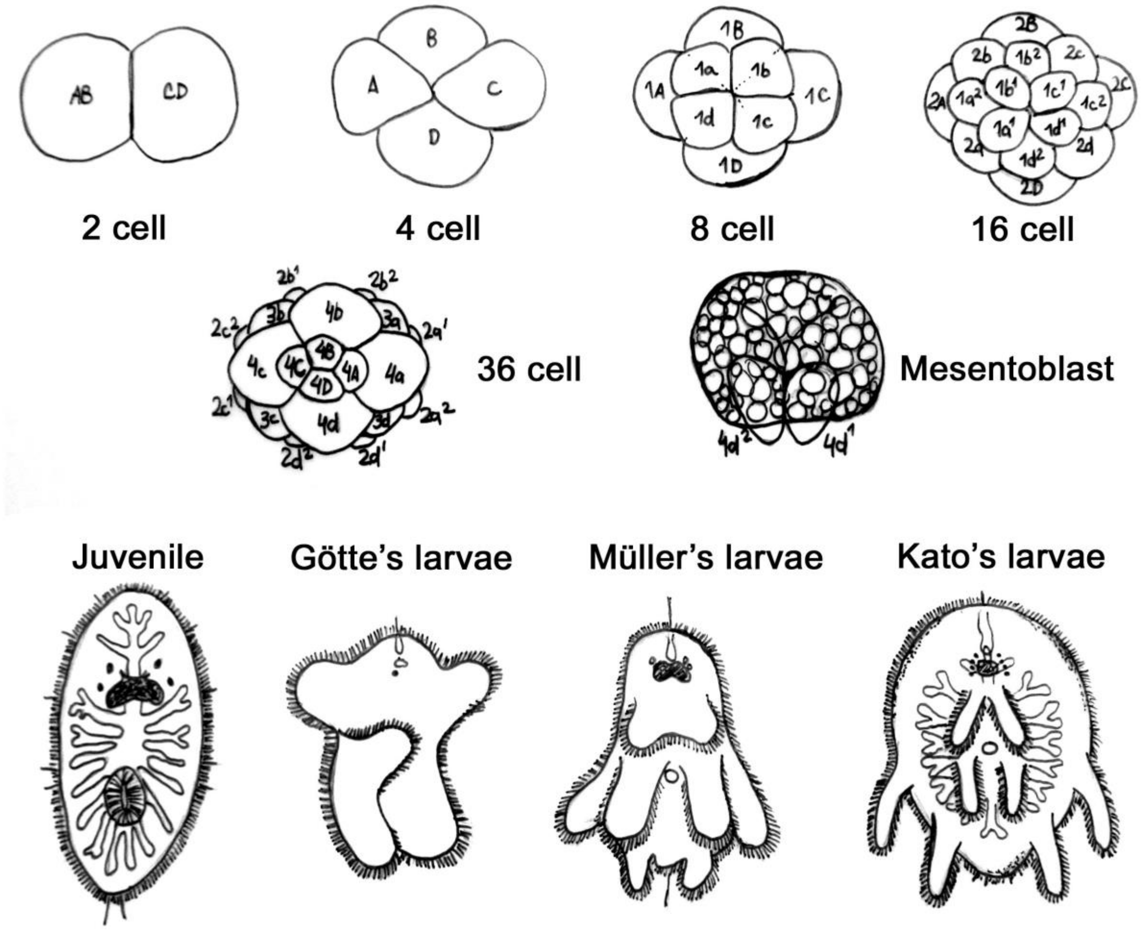


Figure 3: Polycladida cleavage, development and larval types.

Polyclads are the only Platyhelminthes to have spiral determinate cleavage forming quartets of micromeres (like in molluscs and annelids) and lobed larvae (Ballarin & Galleni, 1984). The first quartet gives rise to lateral and anterior ectoderm of larvae, second quartet to dorsal and ventral ectoderm and circular muscles, third quartet to small clones of ectoderm, and forth quartet to larval structure, longitudinal muscles, mesenchyme, and endoderm (Boyer et al., 1998). Macromeres and most micromeres of the forth quartet (4A-4D and 4a-c) degenerate (Lapraz et al., 2013) The whole endoderm and part of the mesoderm are then formed by the 4d and 2d micromeres (Egger et al., 2015) in polyclads and might point to a reason for endodermal lack of structures like the coelom and anus.

Relevance of the group

Polyclads have been used in studies to understand the origin of basal metazoans and the evolution of Platyhelminthes (Laumer & Giribet, 2014; Egger et al., 2015) and the transition from the cnidarian-like diffuse nervous system to the centralized one found in bilaterians (Lapraz et al., 2013). They can be models of Spiralia ancestral form for understanding developmental pathways (Boyer, 1989). These flatworms are also models for understanding brain connections in other animals (Davies et al., 1985), and genes regulating neurogenesis, pluripotency and cell-type specification (Gold et al., 2014). As they present nerve plexus and central ganglion (brain) with different cell types (multi, hetero and bipolar neurons), rare in other invertebrates, polyclads make a good model for higher animals nervous systems (Koopowitz, 1986). They are considered good models for evolutionary development studies as embryos can be obtained without eggshell and develop normally in culture (Egger et al., 2007) and also because they present unique characters, inside Platyhelminthes, as type of cleavage and larval stage (Lapraz et al., 2013).

This group of animals is considered pest in cultures of scleractinian corals (Hume et al., 2014), but it is mostly known by being a pest in clams and oyster aquaculture (Newman et al., 1993). Pest control studies are important in that context and so far pointed to the use of salinity manipulation (O'Connor & Newman, 2001; Lee & Jonhston, 2007) as more effective than poisonous chemicals and low oxygen. The group can also be used for understanding species introduction and its effects on the local biota, in aquaculture (Sluys et al., 2005) and in the natural environment (Marquina et al., 2014; Vella et al., 2016). As well as in studies about transportation via shipping or ballast waters, activities that could justify the broad cosmopolitan distribution of some polyclad species (Merory & Newman, 2005).

The group is also a good model for ecological studies of aposematism, mimicry (Ang & Newman, 1998), hermaphrodite reproduction behavior and sex role (Michiels & Newman, 1998). Studies on toxicity and pharmacological active compounds are especially relevant as cytotoxins were identified in polyclads (Newman et al., 2000) and are in higher concentration in the polyclad than in its prey (Schupp et al., 1999). Some substances were already used in pre-clinical trials as anti-cancer agents (Newman et al., 2000) and tested on leukemia (Schupp et al., 2001). Polyclads were also used in studies to understand mechanisms of biosynthesis of compounds (Yotsu-Yamashida et al., 2013).

Systematics of Polycladida

Polycladida is an order of free-living Platyhelminthes. There is much controversy about the placement of the phylum Platyhelminthes, which was recovered as sister to Sipuncula (Mallatt & Winchell, 2002), or Gastrotricha (Telford et al., 2015). Polycladida belongs to the Spiralia based on its cleavage pattern, quartet fate, dual origin of the mesoderm

(Boyer et al., 1998), Hox genes (Saló et al., 2001), 18S rDNA and larval types evidences (Balavoine, 1998). Based on myogenesis, there is a close evolutionary relation to unsegmented lophotrochozoans (Bolaños & Litvaitis, 2009). Presently the phylum is said to be robustly placed in Spiralia by transcriptomic (Egger et al., 2015) and phylogenomic evidences (Telford et al., 2015) together with Mollusca, Annelida, Nemertea, and other in Lophotrochozoa. The position within Spiralia is especially apparent in polyclads as they retain quartet spiral cleavage pattern and indirect development, considered to be ancestral. Also there was some controversy about the monophyly of Platyhelminthes (Egger et al., 2009) because some characters separated (genes) and others joined (stem cell characters, special mode of epidermal replacement) groups like the Acoela to the phylum. However, recently the acoels were excluded of Platyhelminthes (Phillippe et al., 2007; Cannon et al., 2016). Origin of the flatworm body plan has been attributed to one or two hypotheses: a planuloid, acelomate worm-like ancestor; or an archeocoelomate, primitive coelomate ancestor who secondarily lost the coelom and anus (Balavoine, 1998).

The position of Polycladida inside Platyhelminthes is also controversial (Figure 4). Initially, the order was grouped with other Platyhelminthes based on the presence of lamellate rhabdites, duoglandular adhesive system, multiciliary terminal cells of the protonephridia, and simple pharynx surrounded by nerve ring around the mouth, in the clade Rhabditophora (Ehlers, 1986). Inside that group they were related to other flatworms based on the arrangement 9+“1” of axonemes in biflagellate sperm with a complex central axis and protractile pharynx (Littlewood et al., 1999). Ehlers' (1986) morphological reconstruction placed Polycladida not as the most basal Platyhelminthes (Figure 4) as thought in previous works. The first molecular data sets showed the order to be monophyletic and close to Proseriata (Campos et al. 1998: 18S rDNA), or to be sister group to the Macrostomorpha (Littlewood et al., 1999: 28S rDNA; Littlewood & Olson, 2001: small subunit). Rhabditophora was recovered as monophyletic by most studies, but Trepaxonemata was not (Littlewood et al., 1999). Critics were made to the former synapomorphies, implying there was no evidence for homology and some axoneme characters could have been secondary lost. The same result was also recovered using a different taxa data set and the recommendation was to abandon the use of Trepaxonemata, but keep using Rhabditophora (Litvaitis & Rohde, 1999). More recent results showed Catenulida as most basal and sister of all other Platyhelminthes, followed by Polycladida (Laumer & Giribet, 2014: multilocus) or, alternatively by Macrostomorpha, instead of polyclads (Egger et al., 2015: phylogenomics) as already pointed by Ehlers (1986). Polycladida was recovered as sister to the Prorhynchida-

Lecithoepitheliata (Laumer et al., 2015; forming the taxon Amplimatricata; Egger et al., 2015) and together sister to all other Rhabditophora.

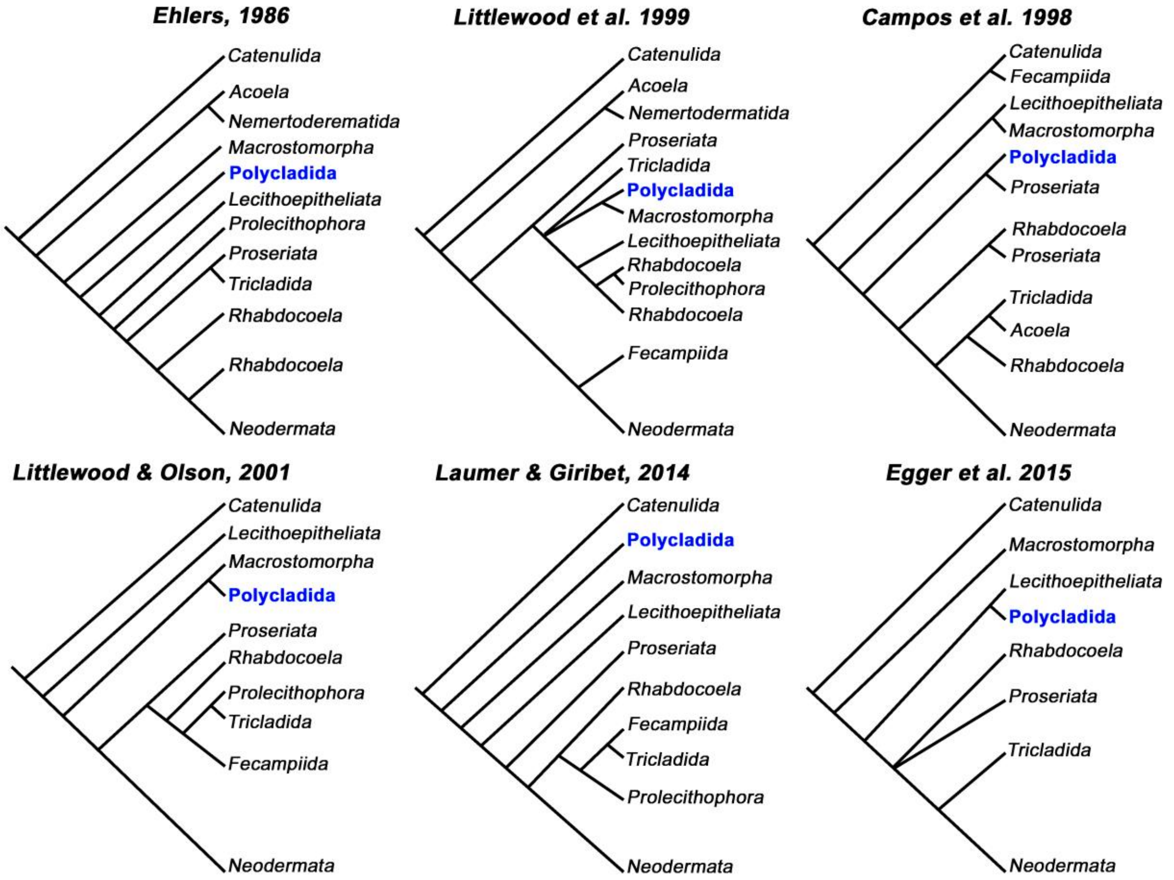


Figure 4: Position of Polycladida inside Platyhelminthes according to different studies.

Lang (1884) was the first author to recognize Polycladida as a monophyletic group based on morphological characters, creating the name of the order, and to organize the known families into a classification system. He based his system on the general organization of morphological characters of polyclads, as to consider only one organ system would create an unnatural system (Lang, 1884). Before Lang (1884), Schmarda (1859) proposed an organization for species of polyclads, but at the time they were in the order Dendrocoela of the taxon Vermes and only five families were known. Later, Laidlaw (1903) proposed a classification based on prostatic vesicle characters and Meixner (1907) also contributed to develop a classification, but he focused on the revision of only one family. Bock (1913) developed the third system for Polycladida classification, with description and standard names for characters. He did not consider natural the groups proposed by Laidlaw (1903), and the prostatic vesicle alone to be a good parameter. Bock (1913) then tried to come up with a more natural classification system, and considered eyespots to be good characters to use in the classification as they seemed homologous. They were considered good because of their position related to where the tentacles are placed in each suborder. The placement of tentacles might be influenced by the position of other organs. In general, acotyleans have the pharynx more centralized in the body, the reproductive system in the second half or last third of the body, the male reproductive system is directed backwards, female system can be elongated and uteri are located anterior to the female structures (Figure 5A). Cotyleans, on the other hand, have the pharynx anterior to the half of the body, reproductive system anterior or central, male reproductive system directed forward, female system short, and uteri posterior to female structures (Figure 5B).

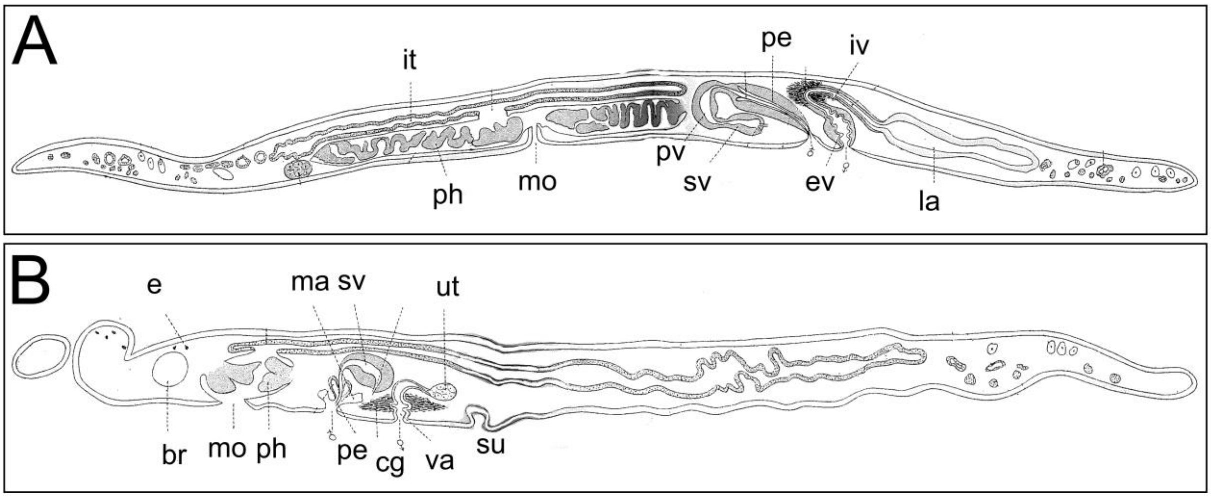


Figure 5: Polycladida general view in sagittal section of entire worm. A- typical Acotylea organization; B- typical Cotylea organization. br: brain; cg: cement glands; e: eyes; ev: external vagina; it: main intestine; iv: internal vagina; la: Lang's vesicle; ma: male atrium; mo: mouth; pe: penis; ph: pharynx; pv: prostatic vesicle; s: stylet; su: sucker; sv: seminal vesicle; ut: uteri; va: vagina. Figures modified from Jacubowa, 1906.

Currently, there are two different classification systems of Polycladida: one is based on internal features of the male reproductive system (Faubel, 1983, 1984b); and the other is based on the arrangement of eyespots on the body (Prudhoe, 1985). Faubel (1983) classified superfamilies in Acotylea based on the absence of true prostatic vesicle (Ilyplanoidea), the presence of true free prostatic vesicle (Stylochoidea), or of a true interpolated prostatic vesicle (Leptoplanoidea). In Cotylea, superfamilies were divided based on the type of pharynx, which can be either ruffled (Pseudocerotoidea) or tubular (Euryleptoidea). Prudhoe (1985) instead divided Acotylea in superfamilies with frontal eyespots (Cestoplanoidea), with frontal, tentacular and cerebral eyespots (Stylochoidea) and with tentacular and cerebral eyespots

(Planoceroidea). They are conflicting with each other and present different families and genera. Intriguingly, both classifications were established almost simultaneously, both are based on selected features from different single organ systems rather than on comprehensive morphocladistic analyses, and both systems are still in use although they are largely non-compatible on family and generic level. This makes current systematics of Polycladida confusing. Most authors choose to use Faubel's classification (Marquina et al., 2015) because they find internal characters more reliable than the external ones. The few molecular studies available pointed to the monophyly of polyclad suborders (Aguado et al., 2015). However, when considering Chromoplanidae and Boniniidae, molecular data pointed to the lack of support for the monophyly of Cotylea and Acotylea (Laumer & Giribet, 2014). This means that the discussion about Polycladida systematics is far from being closed.

Biodiversity of Polycladida

Polyclads have been studied around the world, mainly in the Indo-Pacific (Collingwood, 1876; Plehn, 1896c; Newman & Cannon, 1994), Mediterranean (Lang, 1884), North Sea (Hallez, 1894), Scandinavia (Jensen, 1878), Atlantic and Pacific coasts of the USA (Hyman, 1952; Heath & McGregor, 1912; Freeman, 1933), Japan (Kato, 1935) and Brazil (Marcus, 1947; Du Bois-Reymond Marcus, 1955). Some efforts were made in the Atlantic and south coast of Africa (Palombi, 1939; Prudhoe, 1989), Hawaii (Hyman, 1960; Poulter, 1975), Pacific coast of South America (Marcus, 1954b). In total there are around 850 species considered valid today (115 species are *incerta sedis*) and, for those, few have designated type material or even any material deposited in museums or research institutions. The number of known species around the world (Figure 6) shows collection bias resulted by limited collection effort. Some researchers also invested effort on popularization of science (Newman & Cannon, 2003) which is an important initiative to attract new researchers to the group and to increase awareness to polyclads for the general public. However, the number of researchers working on the group is still small. This is attributed to the delicacy of the body of polyclads, which easily disintegrate by handling or sampling. This delicacy and unknown aspects of polyclad biology also prevented the culture of many species in laboratory. Another difficulty in the study is the histological process of producing serial sections to study the internal anatomy, which is very time consuming.

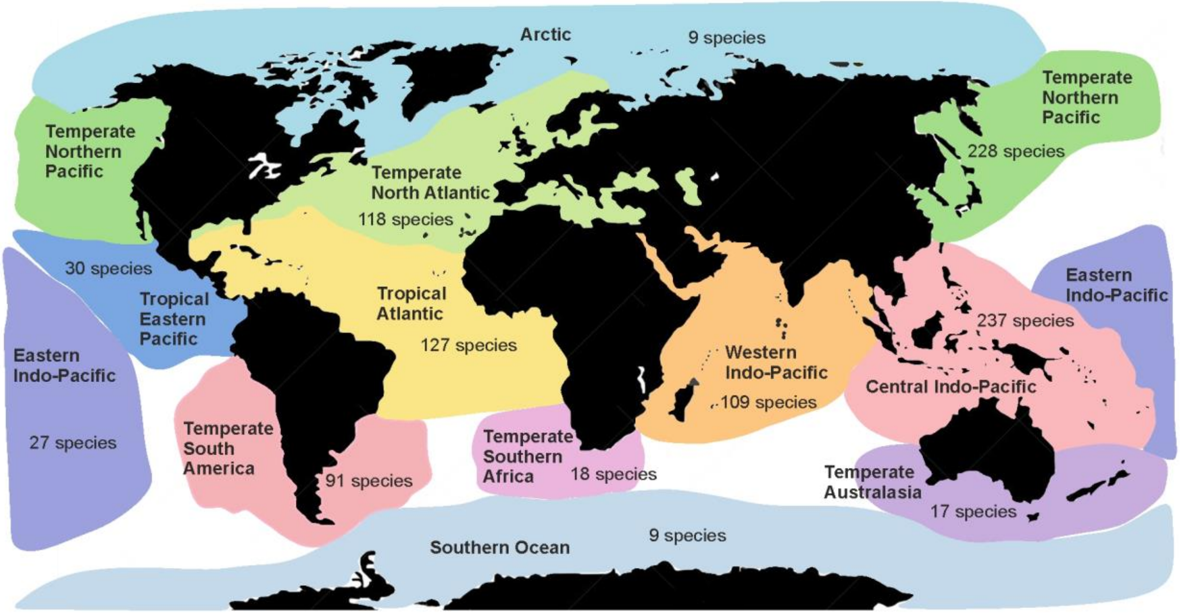


Figure 6: Polycladida species in each marine realm.

The first species to be described from Brazil (Plehn, 1896a; Palombi, 1923) do not have an exact type locality. Later on, a couple of German refugees, Ernst Marcus and Eveline Du Bois-Reymond Marcus settled in São Paulo (Southeastern Brazil) and after war time started investigating marine invertebrate fauna (Côrrea, 1991). They described 55 species of polyclads (Marcus, 1947, 1948, 1949, 1950, 1952, 1954a; Du Bois-Reymond Marcus, 1955, 1957, 1958, 1965; Marcus & Marcus, 1968). After Ernst Marcus passed away, his wife and collaborator worked mostly with nudibranchs (Du Bois-Reymond Marcus, 1970) and the study of Polycladida stagnated. Other researchers also contributed with descriptions of species (Côrrea, 1949, 1957; Hyman, 1955a; Smith, 1960), but Ernst and Eveline Marcus were by far the most productive. In Brazil one of the most sampled types of environment was that of intertidal boulders, which has a great extension and heterogeneity and is considered nursery zones (Aldana et al., 2016). Also, the studies in the country were restricted to a small part of the coast near the southern limit on the Tropical Atlantic waters. As a result of that sample bias scarcely any species was found in common between Caribbean and Brazil (Hyman, 1955b) at the time. But through more samples Marcus & Marcus (1968) reported more species in common and, recently, more species that co-occur in both areas were found (Bahia & Padula, 2009; Bahia et al., 2014). Unfortunately, as it is also the case for polyclads around the world, many descriptions were based on single specimens and some on juveniles, and no type material was designated, labeled with codes in the publication or deposited in a museum

(Marcus, 1947). Only after the ICZN modification, making type material designation obligatory, had Ernst and Eveline Marcus started to do so (Du Bois-Reymond Marcus, 1958, 1965; Marcus & Marcus, 1968). But even so, no specimen labelling or voucher material was mentioned in their publications (Marcus, 1947, 1949, 1950). In those cases designation of types (neotypes or lectotypes) should be done when needed and material should be deposited in museums as identification of life specimens only by photos is very uncertain (Hyman, 1953). Also, types are usually the most reliable way for zoologists to test species hypotheses (Amorim et al., 2016).

Gaps in knowledge

There are many gaps in the knowledge of the group, mostly related to the small number of researchers working on it, and to the discontinuity in time of the studies conducted so far. These "lacunae" were attributed to the difficulty in handling specimens by Marcus & Marcus (1968). There is a sampling bias, with many regions of the world not sufficiently sampled yet, and most species were collected in the intertidal area only, with deeper waters remaining largely unexplored (Rawlinson, 2008). In Brazil the sampled areas represent 1/17 of the coast (Marcus & Marcus, 1968). New species described in new genera or families (Bulnes et al., 2003; Brusa & Damborena, 2013) show that we do not yet grasp the morphological diversity of the group. The effect of Polycladida predation on invertebrate communities and rocky shore food webs is still unknown (Aldana et al., 2016). Ecological importance in general is a gap, and is possibly related to difficulties in experimental measurement of micro-predators like polyclads (Janiak et al., 2017). It is also difficult to study experimentally the mechanisms related to nematocysts (Goodheart & Bely, 2017) and zooxanthellae sequestration. Related to reproduction and larval development experiments, only 31 species, representing 8% of known species, were investigated (Balarin & Galleni, 1984; Rawlinson, 2014). Many details of polyclad reproduction, like cellular mechanisms related to transport through parenchyma in internal fertilization (Gammoudi et al., 2012), and larval settlement are still unknown (Newman et al., 2000), as are aspects of physiology, ultrastructure, hermaphrodite behavior (Michiels & Newman, 1998), biochemistry (Newman & Cannon, 1995), and chemoreceptors.

Apart from new discoveries in the group, the absence or cryptic state of type material represents a most relevant and grave gap in the knowledge of Polycladida. Most species descriptions were made before the reformation of the International Code of Zoological

Nomenclature, and thus lack completely any type designation or material deposited in museums or research institutions. For Brazilian species the types were considered unknown for a long time and recently with databases available online (http://www.gbif.org) it was possible to begin to have an idea where to search. The consequence of that gap is that contemporary researchers are unable to compare fresh collected material to reference specimens and this can bring various taxonomic problems. Another most relevant gap is the application of phylogenetic concepts (Wagner, 1989) on the study of polyclads. These flatworms were often used in phylogenetic studies of Platyhelminthes (Ehlers, 1986; Campos et al., 1998; Littlewood et al., 1999; Litvaitis & Rohde, 1999; Laumer & Giribet, 2014; Egger et al., 2015), but relations inside the order were not explored. A Polycladida phylogeny has never been inferred, either by morphological or molecular methods. Phylogenetic hypotheses for the order were developed (Lang, 1884; Laidlaw, 1903; Bock, 1913; Marcus & Marcus, 1966; Faubel, 1983, 1984b; Prudhoe, 1985), but not yet tested with cladistics or phylogenetic methods. This is particularly important when we consider the two conflicting classification systems, which basically assumed homology of the characters used for defining each system. Phylogenetic studies are still limited to one cotylean family (Litvaitis & Newman, 2001), one acotylean genus (Tajika et al., 1991) and family (Doignon et al., 2003), and part of the suborder Cotylea (Rawlinson & Litvaitis, 2008).

Most works published on Polycladida so far are related to taxonomy and morphological aspects. Molecular approaches reached the group with some delay. Sequences were used in Platyhelminthes phylogeny, to investigate coloration pattern (Litvaitis & Newman, 2001) and a species complex (Litvaitis et al., 2010). In GenBank platform around 50 sequences of partial nuclear 28S rDNA, mostly from one family, and less than 15 mitochondrial DNA (mtDNA) COI sequences were available until recently. Polyclad mitochondrial genes are not yet comprehensibly studied and there is to date great difficulty in sequencing them; few sequences are available from scarce studies (Sato et al., 2001; Laumer & Giribet, 2014). Only recently the first polyclad mitogenomes were published (Aguado et al., 2015). This might be related to the presence of different start codons and a remarkable diversity in gene arrangements, also inside the same family (Aguado et al., 2015). The field of DNA taxonomy, which uses DNA (COI or other markers) to delineate species boundaries, is still not yet fully applied to Polycladida, as it requests a database for comparison with freshly sampled material (Kvist, 2013). As seen in other groups such as molluscs (Padula et al., 2016), integrative taxonomy tools can be efficient to resolve difficult cases and provide more comprehensive insights into evolutionary history.

Aims of the thesis

Based on the gaps of knowledge about polyclads we aim to apply an integrative taxonomic approach, with photos of life specimens, histology, and molecular data to the study of Polycladida (Platyhelminthes: Rhabditophora). Here I address specifically three gaps in knowledge and intended to:

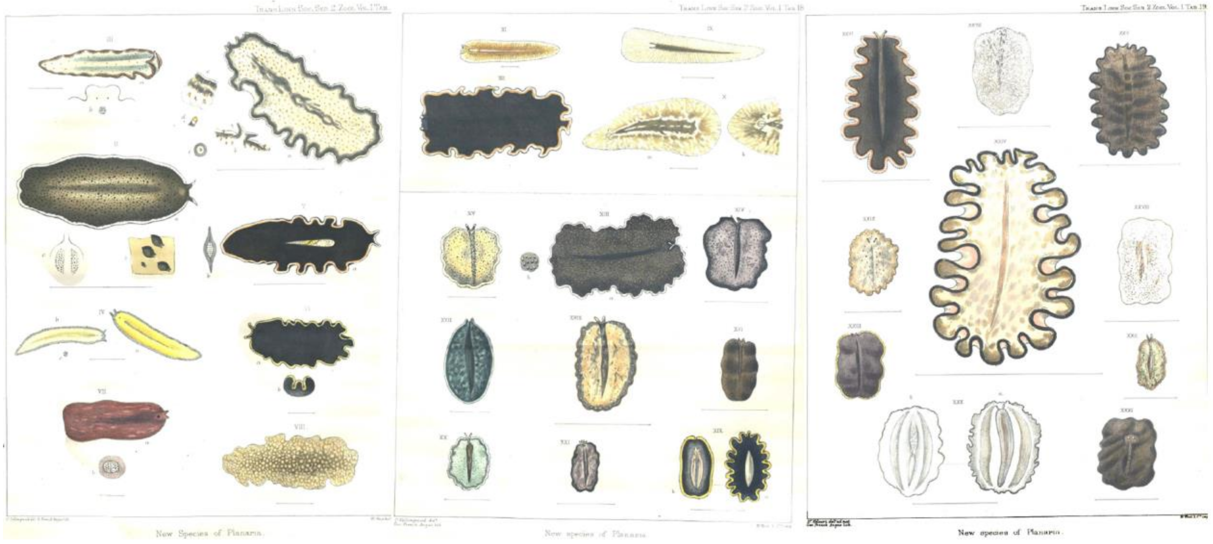
(1) do an inventory of Polycladida biodiversity in areas not sampled previously, particularly in Brazil, describing new species and investigating geographic range of species;

(2) list and revise all species reported from Brazil, determining type material deposited in museums and studied by Ernst and Eveline Marcus, recognizing holotypes and designate lectotypes when necessary;

(3) present the first Polycladida molecular phylogeny, investigate the relationships between superfamilies of Polycladida, comparing traditional conflicting classification systems, based on morphology, with new molecular data; diagnose monophyletic groups and suggest changes to the Polycladida classification when necessary; and establish a new classification system and systematic framework to the evolution of Polycladida.

RESULTS

PART 1: BIODIVERSITY OF POLYCLADIDA



Chapter 1.

First records of the order Polycladida (Platyhelminthes, Rhabditophora) from reef ecosystems of Alagoas State, north-eastern Brazil, with the description of *Thysanozoon alagoensis* sp. nov.

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First records of the order Polycladida (Platyhelminthes, Rhabditophora) from reef ecosystems of Alagoas State, north-eastern Brazil, with the description of *Thysanozoon alagoensis* sp. nov.

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The 230 km long coast of Alagoas State, in north-eastern Brazil, has diverse reef ecosystems, made from corals and of sandstone, that harbour a wide range of marine invertebrate fauna. Little is known about turbellarians of the order Polycladida in most parts of the Brazilian coast, with no record from Alagoas up to date. To fill this gap expeditions were conducted on the reefs from the central coast of Alagoas, where 11 Polycladida species were found: Pericelis cata, Enchiridium evelinae, Pseudoceros bicolor *and a possible new colour variation of this species,* Pseudoceros rawlinsonae, Pseudobiceros pardalis, Thysanozoon brocchii, Thysanozoon alagoensis *sp. nov.*, Armatoplana leptalea, Adenoplana evelinae, Latocestus brasiliensis, Phaenocelis medvedica. *The species are described in detail through photos of live specimens and histological sections. The present work adds six species to the north-eastern Brazilian coast, one of them a new species, and all 11 species are for the first time reported from Alagoas State. Also, it is the first time that* Phaenocelis medvedica, Adenoplana evelinae, Latocestus brasiliensis *and* Armatoplana leptalea *are illustrated by full colour photos of live specimens and histological sections.*

Keywords: marine flatworms, Brazilian biodiversity, taxonomy

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INTRODUCTION

Animals belonging to the order Polycladida are free-living platyhelminthes, with most species known from tropical seas. About 900 species have been described around the world (Newman & Cannon, 2003). Among them, about 125 were reported from the Tropical Western Atlantic, 70 occur in Brazil, 46 being endemic (Quiroga *et al.*, 2004a; Bahia *et al.*, 2014). From the Brazilian coast, the existing knowledge is mostly the result of works conducted between 1950 and 1970, based on specimens collected at São Paulo region (Marcus, 1947, 1948, 1949, 1950, 1952). Recent contributions, including new local and country records were made by Bahia & Padula (2009), Bahia *et al.* (2012, 2014) and Queiroz *et al.* (2013).

On the north-eastern Brazilian coast, such as in the state of Alagoas, reef ecosystems are abundant and have a rich biological diversity (Correia & Sovierzoski, 2009). These reefs include a benthic fauna, which provide various natural substrates for the Polycladida, composed mainly of sponges (Cedro *et al.*, 2007, 2011, 2013; Bispo *et al.*, 2014), corals (Correia, 2011) and bryozoans (Vieira *et al.*, 2007, 2008, 2010). A variety of algae also provides habitats for numerous associated organisms (Santos & Correia, 1994, 1995, 2001), which are important environments for flatworms and other small invertebrates such as opisthobranch molluscs (Padula *et al.*, 2012) and echinoderm brittle stars (Lima *et al.*, 2011, 2013). However, there is a significant lack of information, particularly about marine platyhelminthes in this region, with no record of the order Polycladida from Alagoas reef ecosystems. Herein we aim to present the first records of Polycladida from Alagoas coast, including the description of a new species.

MATERIALS AND METHODS

Alagoas coast is approximately 230 km long, and it is limited by the Persinunga River on the north and by the São Francisco River on the south (8°54′S–35°9′W and 10°30′S–36°23′W), The main ecosystems that can be found are coral and sandstone reefs, lagoons, rivers and mangroves. The coral reefs were formed on calcareous sedimentary rock, composed of an aggregation of dead organisms, including skeletons of corals and hydrocorals combined with crusts of calcareous algae and other invertebrates (Correia & Sovierzoski, 2009). Many of these fringing reefs are located near the beach line, where the top of the reef platform is exposed during low tides. The sandstone reefs were formed by old sandbanks solidified through sedimentation, starting from chemical

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reactions with calcium carbonate from the Quaternary Period, and are generally arranged in rows parallel to the coastline and near the outlets of rivers and estuaries (Correia & Sovierzoski, 2009; Correia, 2011).

All specimens were manually collected under rocks at the intertidal zone or in the sublittoral by snorkelling or scuba diving along the edge of the reef platforms during low tide. Collections were conducted in January 2008 and January 2012, and were carried out in reef ecosystems along the central coast of Alagoas State, Brazil (Figure 1). Seven reef ecosystems were sampled: coral reefs of Ponta Verde (9°39′57″S–35°41′32″W), Jatiúca (9°39′12″S–35°41′46″W), Piscina dos Amores (9°40′39″S–35°42′10″W), Pajuçara (9°41′06″S–35°43′22″W) and Riacho Doce (9°34′55″S–35°39′25″), and sandstone reefs of Francês (9°46′03″S–35°50′13″W) and Saco da Pedra (9°44′26″S–35°48′59″W) (Figure 1).

In the laboratory, specimens were photographed alive with a digital camera. Afterwards, they were fixed in 10% frozen formalin, following a modified methodology (Newman & Cannon, 2003), and transferred to 70% ethanol for histological preparation. Specimens were measured after fixation (length mm × width mm). The identification was based on morphological characteristics, colouration pattern, ocelli position and slides of the reproductive structures stained by haematoxylin-eosin method (Bolaños *et al.*, 2007). Specimens were compared with original descriptions and previous publications (Marcus, 1949, 1950, 1952; Marcus & Marcus, 1968; Bolaños *et al.*, 2007). Collected material was deposited on the Platyhelminthes collection in the Museu Nacional/Universidade Federal do Rio de Janeiro, Brazil (MNRJ-PLAT).

RESULTS

There were 35 specimens found belonging to 11 species of the order Polycladida. *Pericelis cata, Enchiridium evelinae, Pseudoceros bicolor, Pseudoceros rawlinsonae, Pseudobiceros pardalis, Thysanozoon brocchii, Thysanozoon alagoensis* sp. nov., *Armatoplana leptalea, Adenoplana evelinae, Latocestus brasiliensis* and *Phaenocelis medvedica*. The species *Enchiridium evelinae* was the most common, with 15 specimens collected, and found in all sampled reefs. Greater species richness was observed at Saco da Pedra reef. The lowest richness was found at Piscina dos Amores coral reef. All occurrences reported here are the first records of Polycladida from Alagoas ecosystems (Table 1). As some of the species found in this study were treated on previous papers by the authors, just the material examined, with measurements, distribution and remarks are included.

SYSTEMATICS

Order POLYCLADIDA Lang, 1884
Suborder COTYLEA Lang, 1884
Family PERICELIDAE Laidlaw, 1902
Genus *Pericelis* Laidlaw, 1902
Pericelis cata Marcus & Marcus, 1968
(Figure 2B)

Fig. 1. Map of reef environments studied at Alagoas State, north-eastern Brazil.

Table 1. Species and number of specimens found at each reef ecosystem on the Alagoas coast.

SPECIES	Ponta Verde	Francês	Riacho Doce	Saco da Pedra	Piscina dos Amores	Pajuçara	Number of specimens
Enchiridium evelinae	1	2	2	6	2	2	15
Pseudoceros bicolor				2			2
Pseudoceros rawlinsonae				1			1
Pseudoceros cf. *bicolor*		2					2
Pseudobiceros pardalis				1			1
Thysanozoon brocchii		1		2			3
Thysanozoon alagoensis sp. nov.				1			1
Pericelis cata				1			1
Phaenocelis medvedica	1						1
Armatoplana leptalea			3	1			4
Adenoplana evelinae				1		1	2
Latocestus brasiliensis	1					1	2
No. of species	3	3	2	9	1	3	Total:11/35

EXAMINED MATERIAL

One mature specimen (18 × 16 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 96, 13 slides). Collected 26 January 2012 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

This species was recorded from Curaçao (type locality; Marcus & Marcus, 1968), Colombian Caribbean (Quiroga *et al.*, 2004b), Cabo Frio, south-eastern Brazil (Bahia & Padula, 2009) and Salvador, north-eastern Brazil (Queiroz *et al.*, 2013). This is the first record of this species from Alagoas State.

REMARKS

The specimen herein studied was smaller than those found at Cabo Frio, south-eastern Brazil (Bahia & Padula, 2009) and those from Bahia State, north-eastern Brazil (Queiroz *et al.*, 2013). During the collections two specimens of *P. cata* were placed in the same container as some specimens of the opisthobranch mollusc *Micromelo undatus*. When freed to be photographed the *Pericelis* were much damaged and one was not useful for study. This could have happened because of some fighting with the molluscs or some toxic chemical compound they might present.

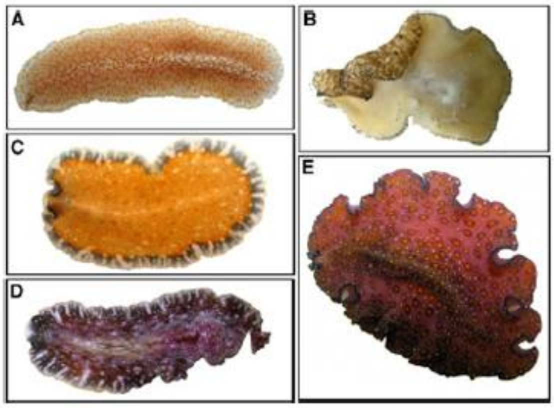

Fig. 2. (A) *Enchiridium evelinae* (MNRJ-PLAT 80); (B) *Pericelis cata* (MNRJ-PLAT 96); (C) *Pseudoceros bicolor* (MNRJ-PLAT 85); (D) *Pseudoceros rawlinsonae* (MNRJ-PLAT 87); (E) *Pseudobiceros pardalis* (MNRJ-PLAT 92).

Family PROSTHIOSTOMIDAE Lang, 1884
Genus *Enchiridium* Bock, 1913
Enchiridium evelinae Marcus, 1949
(Figure 2A)

EXAMINED MATERIAL AND LOCALITY

One mature specimen (MNRJ-PLAT 77, 32 × 9 mm) collected 6 January 2008 at Brazil, Alagoas, Maceió, Ponta Verde coral reef. One mature specimen (MNRJ-PLAT 78, 29 × 8 mm) collected 7 January 2008 at Pajuçara coral reef, Maceió, Alagoas, Brazil. Two specimens (MNRJ-PLAT 79, 26 × 6 mm and 30 × 8 mm) collected 9 January 2008 at Francês sandstone reef, Maceió, Alagoas, Brazil. Two specimens (MNRJ-PLAT 80, 21 × 7 mm and 32 × 10 mm). One as sagittal sections of reproductive structures (21 slides). Collected 10 January 2008 at Riacho Doce coral reef, Maceió, Alagoas, Brazil. Five specimens (MNRJ-PLAT 81, 6 × 3 mm, 12 × 5 mm, 16 × 6 mm, 21 × 7 mm and 23 × 8 mm) collected 11 January 2008 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil. Two specimens (MNRJ-PLAT 82, 21 × 7 mm and 22 × 7 mm) collected 13 January 2008 at Piscina dos Amores coral reef, Maceió, Alagoas, Brazil. One specimen (MNRJ-PLAT 83, 18 × 7 mm) collected 7 February 2008 at Pajuçara coral reef, Maceió, Alagoas, Brazil. One specimen (MNRJ-PLAT 84, 26 × 11 mm) collected 27 January 2012 at Saco da Pedra sandstone reef, Maceió, Alagoas, Brazil. All specimens preserved in 70% ethanol.

GEOGRAPHIC DISTRIBUTION

Originally described from São Paulo State, south-eastern Brazil (Marcus, 1949) reported to Rio Grande do Norte State (Bahia *et al.*, 2012), Rio de Janeiro State (Bahia *et al.*, 2014) and now Alagoas State, north-eastern Brazil. It is also known from Curaçao (Marcus & Marcus, 1968). This species is considered by Rawlinson (2008) as representative of seagrass habitat. We found our specimens both in sandstone and coral reefs and *E. evelinae* was the most common species in our samplings. This is the first record of this species from Alagoas State.

REMARKS

This species was observed copulating (video in Supplementary material). It presented reciprocal insemination and a somewhat violent penis-fencing behaviour. Unfortunately the following eggmass laying could not be observed. Also one specimen of *Enchiridium evelinae* ate a specimen of *Adenoplana evelinae* during a fortnight in the same Petri dish. We noticed differences in colouration between the specimens found in Alagoas and those from Rio de Janeiro, the latter sometimes has a different distribution of the dorsal brown spots, with them more densely disposed in the median line (personal observation).

Family PSEUDOCEROTIDAE Lang, 1884
Genus *Pseudoceros* Lang, 1884
Pseudoceros bicolor Verrill, 1901
(Figures 2C & 3)

EXAMINED MATERIAL

One mature specimen (12 × 8 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 85, 9 slides). One mature specimen (MNRJ-PLAT 86, 10 × 8 mm) collected 26 January 2012. Both collected at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil and preserved in 70% ethanol. One mature specimen (11 × 10 mm) as sagittal section of reproductive structures (MNRJ-PLAT 90, 16 slides). One mature specimen (15 × 10 mm) as sagittal section of reproductive structures (MNRJ-PLAT 91, 15 slides). Both collected 25 January 2012 at Francês sandstone reef, Marechal Deodoro, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

Described from Bermudas (type locality; Verrill, 1901), reported from Curacao (Marcus & Marcus, 1968), Caribbean coast of Colombia (Quiroga *et al.*, 2004b), Florida, Virgin Islands, Jamaica, Belize, Honduras, Caribbean coast of Panama (Rawlinson, 2008) and south-eastern Brazil (Bahia & Padula, 2009). This is the first record of this species from north-eastern Brazil.

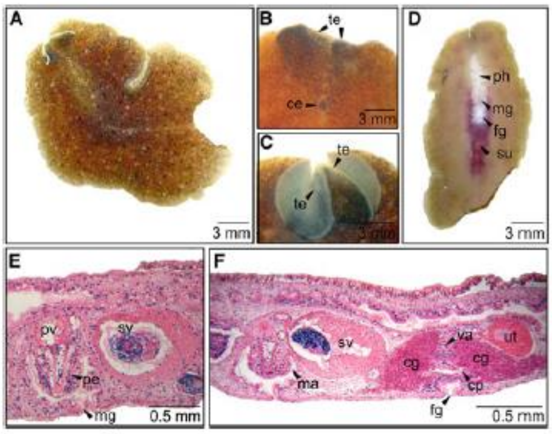

Fig. 3. *Pseudoceros* cf. *bicolor* (A) *in vivo*; (B) and (C) detail of the anterior region; (D) ventral view; (E) sagittal section of male reproductive structures; (F) sagittal section of male and female reproductive structures. ce, cerebral eyespots; cg, cement glands; cp, cement pouch; fg, female gonopore; ma, male atrium; mg, male gonopore; pe, penis; ph, pharynx; pv, prostatic vesicle; su, sucker; sv, seminal vesicle; te, tentacular eyespots; ut, uteri; va, vagina.

REMARKS

The specimens MNRJ-PLAT 85 and 86 are in accordance with the description and posterior amendment. Specimens MNRJ-PLAT 90 and MNRJ-PLAT 91 (at Table 1 counted separately as *Pseudoceros* cf. *bicolor*) were somewhat different from the former specimens. Their background colour was yellowish orange with scattered white and dark spots (Figure 3A); whitish translucent marginal band with a thin light yellow outermost line, only seen in live specimens. Seminal vesicle muscularized and elongated. Prostatic vesicle rounded and small, located above the penial papillae (Figure 3E). They resemble *Pseudoceros bicolor* in its background coloration pattern, but it lacks the white marginal band with black languettes characteristic of this species. Also the colour has hints of orange that are absent in specimens from the same locality and from other regions of the Brazilian coast (Bahia & Padula, 2009), and the seminal vesicle of these specimens is more elongated than rounded as usually found in *P. bicolor*. The material differs from the recently described *P. juani* in body proportion length × width, this species has a more elongated body (Bahia *et al.*, 2014) than the *Pseudoceros* specimens found in Alagoas. Also, the seminal vesicle of *P. juani* is proportionally much larger than in *P. bicolor* and in the two specimens studied. However both *P. juani* and the two studied specimens have both scattered white and dark spots and there is a hint of orange in Alagoas' specimens, which is the background colour of *P. juani*, therefore we cannot rule out that those specimens can be some morphotype between *P. bicolor* and *P. juani*, despite the latter having no record in Alagoas so far. These two specimens are here, for now, identified as *P. bicolor*; this should be confirmed through a future molecular analysis.

Pseudoceros rawlinsonae Bolaños, Quiroga & Litvaitsi, 2007
(Figure 2D)

EXAMINED MATERIAL

One mature specimen (10 × 6 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 87, 18 slides). Collected 11 January 2008 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

Originally described from the American Virgin Islands and Bonaire (Bolaños *et al.*, 2007). After the revision of *Pseudoceros bicolor* complex, *P. rawlinsonae* was also reported from Florida, Honduras, Jamaica, Bahamas, Curaçao (Litvaitis *et al.*, 2010) and south-eastern Brazil (Bahia & Padula, 2009, as *P. bicolor*; Bahia *et al.*, 2014). This is the first record of this species from north-eastern Brazil.

Genus *Pseudobiceros* Faubel, 1984
Pseudobiceros pardalis (Verrill, 1900)
(Figure 2E)

EXAMINED MATERIAL

One specimen (45 × 37 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 92, 35 slides). Collected 27 January 2012 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

Pseudobiceros pardalis was described from Bermudas (Verrill, 1900) and reported from Bahamas, south Florida and Panama (Bolaños *et al.*, 2007). It was recently reported for the first time from Brazil, but south from Alagoas (Bahia *et al.*, 2014). This is the first record of this species from north-eastern Brazil.

REMARKS

Our specimens have lighter colouration than the ones in the original description (Verrill, 1900) and re-description (Bolaños *et al.*, 2007), but darker than reported from south-eastern Brazil (Bahia *et al.*, 2014), probably due to differences in size and the nutritional conditions of the animals. The specimens found in the Caribbean (Bolaños *et al.*, 2007) have a concentration of white dots near the margin that is not so clear in Brazilian specimens (Figure 2E), both from Alagoas and from Rio de Janeiro (Bahia *et al.*, 2014).

Genus *Thysanozoon* Grube, 1840
Thysanozoon brocchii (Risso, 1818)
(Figure 4)

EXAMINED MATERIAL

Two specimens (22 × 18 mm and 6 × 4 mm), the mature as sagittal sections of reproductive structures (MNRJ-PLAT 93, 29 slides). Collected 11 January 2008 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil. One specimen (17 × 20 mm) (MNRJ-PLAT 94) collected 25 January 2012 at Francês sandstone reef, Marechal Deodoro, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

Cosmopolitan species described from Naples, Italy (type locality; Risso, 1818) and other parts of the Mediterranean Sea, UK, south and west from Africa, Florida, Colombian Caribbean, Brazil, Japan and New Zealand (Prudhoe, 1985; Quiroga *et al.*, 2004b). It was also reported from Canary Islands (Vera *et al.*, 2008), Argentina (Brusa *et al.*, 2009), from north-eastern (Bahia *et al.*, 2012) and south-eastern Brazil (Bahia *et al.*, 2014). This is the first record from Alagoas State.

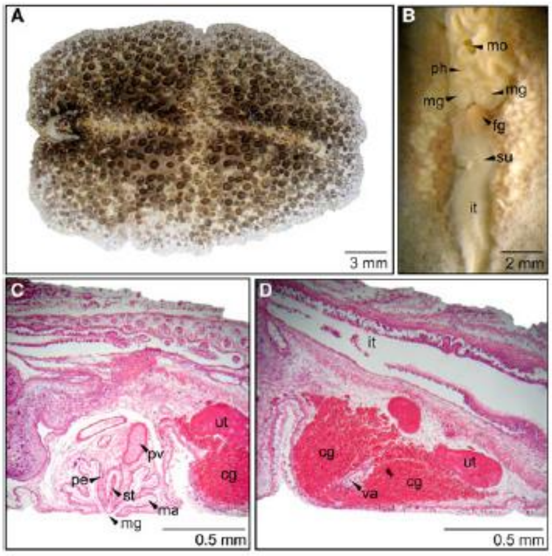

Fig. 4. *Thysanozoon brocchii* (A) *in vivo*; (B) detail of the ventral surface; (C) sagittal section of the male reproductive structures; (D) sagittal section of the female reproductive structures. cg, cement glands; fg, female gonopore; it, intestine; ma, male atrium; mg, male gonopore; mo, mouth; pe, penis; ph, pharynx; pv, prostatic vesicle; st, stylet; su, sucker; ut, uteri; va, vagina.

REMARKS

The specimens found at Alagoas all have rounded papillae and brownish colouration (Figure 4A). This is not the case in some south-eastern Brazil and in the Mediterranean Sea specimens (Bahia *et al.*, 2014). Specimens from those areas can have slender papillae and black to greyish colouration, and European specimens present a red marginal band (Bahia pers. obs.).

Thysanozoon alagoensis sp. nov.
(Figures 5 & 6)

TYPE MATERIAL

Holotype: one specimen (19 × 16 mm), as sagittal sections of reproductive structures (MNRJ-PLAT 95, 26 slides). Collected 27 January 2012 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil, 4 m deep.

GEOGRAPHIC DISTRIBUTION

The species is only known from the type locality.

ETYMOLOGY

The specific name *alagoensis* makes reference to the geopolitical division of Brazil, Alagoas State, where the holotype specimen was found.

DIAGNOSIS

Greyish background colour with reddish brown papillae, reddish brown margin and dark almost black tentacles with a hint of yellowish pigmentation on the border. Unpigmented line present at the median line of the body. Tentacular eyespots arranged in a line at the border and a group of eyespots at each tentacular tip. Pharynx ruffled with seven simple folds. Seminal vesicle elongated and huge. Its extension reaches the front of the penial papillae and the seminal duct come in a curve to join the penis. Prostatic vesicle small and comma shaped. Male atrium simple. Greatly developed spermiducal vesicles.

DESCRIPTION

Colour: Greyish background colour with reddish brown papillae, reddish brown margin and dark almost black tentacles (Figure 5A). Some papillae are more lightly coloured, more like the background colour. Unpigmented line present at the median line of the body from the tentacles until the last 1/6 of the body length (Figure 5A).

Form: Elongated with papillated dorsal surface (Figure 5B) with slender whitish tipped papillae.

Tentacles: Dark almost black tentacles with a hint of yellowish pigmentation on the border. More rounded than pointed, reaches 1 mm.

Eyes: Cerebral eyes numerous and arranged in a horseshoe shaped group (Figure 6B). Tentacular eyespots arranged in a line at the border (Figure 6A) and a group of eyespots at each tentacular tip (about 20). Frontally, in between psedotentacles, there are also clusters of eyespots, it is not clear if as an extension of the border eyespots groups or distinctive cluster

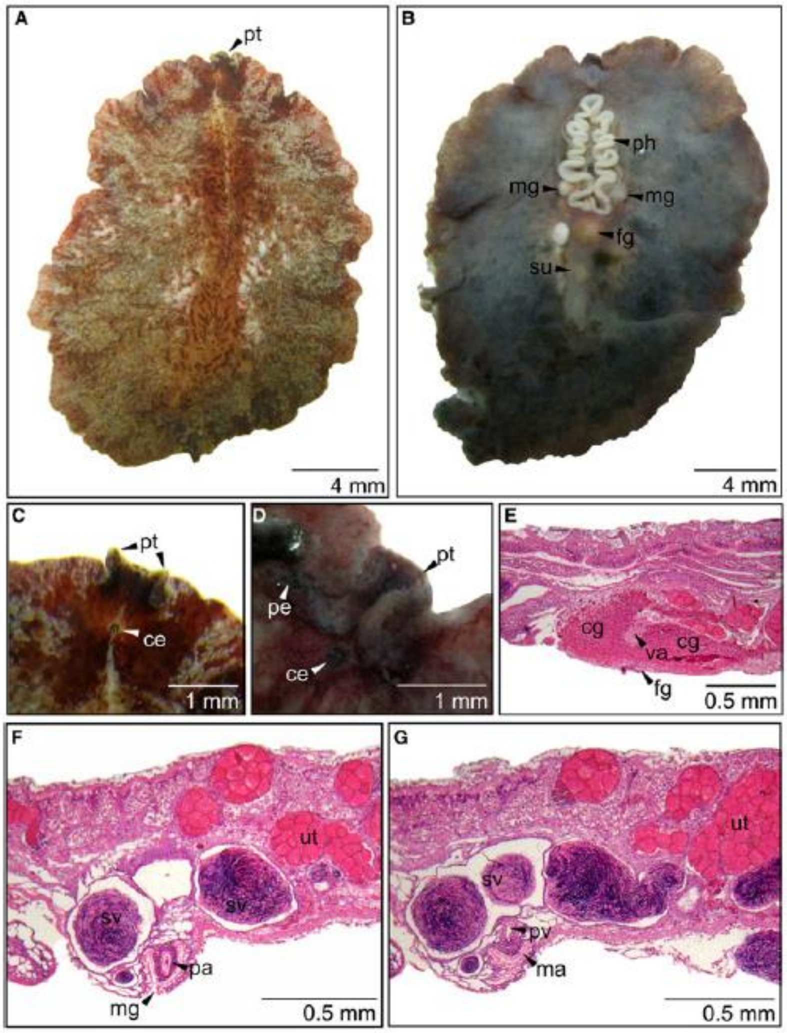

Fig. 5. *Thysanozoon alagoensis* sp. nov. (A) *in vivo*; (B) ventral view; (C) detail of the anterior margin, showing pseudotentacles; (D) detail of cerebral and tentacular eyespots; (E) sagittal section of female reproductive structures; (F) and (G) sagittal sections of male reproductive structures. ce, cerebral eyespots; cg, cement glands; fg, female gonopore; ma, male atrium; mg, male gonopore; pa, penis papilla; pe, pseudotentacular eyespots; ph, pharynx; pt, pseudotentacles; pv, prostatic vesicle; su, sucker; sv, seminal vesicle; ut, uteri; va, vagina.

(Figure 6A). Ventral eyespots groups (Figure 6C) with about 25 eyespots.

Digestive system: Pharynx ruffled with seven simple folds (Figure 5B). Reaches 6 mm. Mouth opens at 6 mm from the anterior margin.

Epidermis and body wall: Thin epidermis (Figure 5D) and body wall (0.04 mm), even thinner ventrally (0.01). Sucker with 0.7 mm diameter is 2 mm behind the female pore.

Gonopores: Two male and one female gonopores present, 1.5 mm apart (Figure 5B). Male pores at 7 mm from the anterior margin, both measure 0.5 mm and the female pore 1 mm.

Male reproductive system: Seminal vesicle elongated and huge (Figure 5E). Its extension reaches the front of the penial papillae and the seminal duct comes in a curve to join the penis. Penis papillae (Figure 5D) 0.18 mm. Prostatic vesicle small (0.09 mm) and comma shaped (Figure 5E). Its duct joins the ejaculatory duct and enters the penis papillae (Figure 6D). Seminal vesicle elongated and spermiducal vesicles greatly developed and reaching the region right above the male gonopore (Figure 5E), maybe dislodging the seminal vesicle. Male atrium simple and 0.2 mm deep (Figure 5E).

Female reproductive system: Uteri well developed and full of eggs (0.089 mm diameter). Cement glands also well developed (Figure 5C).

TAXONOMIC REMARKS

Our specimen has a simple male atrium, different from the folded atrium found in *Thysanozoon brocchii*. Also the *T. alagoensis* has a different colouration pattern, and the dorsal papillae of this species are slender and *Thysanozoon brocchii* have rounder ones (Table 2). Other similar species such as *Thysanozoon californicum* (Hyman, 1953a) also has slender papillae and elongated pharynx with seven simple folds, but the colouration pattern differs from the Brazilian species

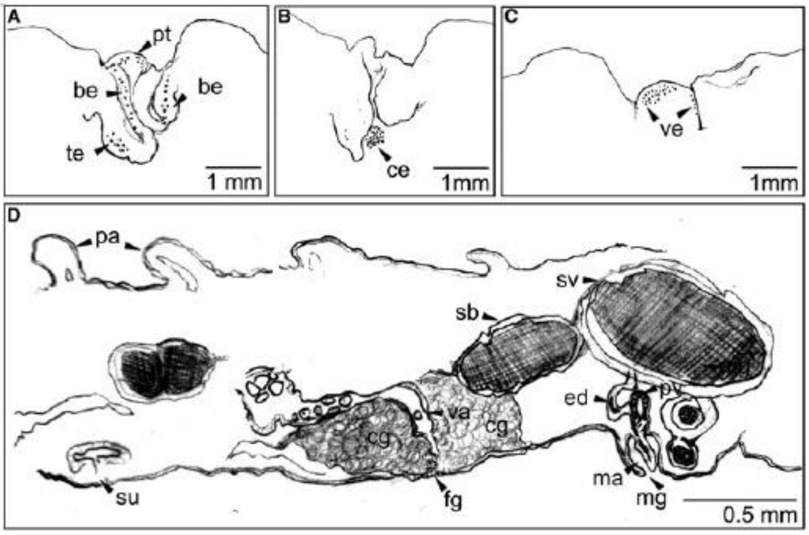

Fig. 6. *Thysanozoon alagoensis* sp. nov. (A) detail of pseudotentacular eyespots; (B) cerebral eyespots; (C) ventral eyespots; (D) tentative reconstruction of serial sections. be, pseudotentacle border eyespots; ce, cerebral eyespots; cg, cement glands; ed, ejaculatory duct; fg, female gonopore; ma, male atrium; mg, male gonopore; pa, papilla; pt, eyespots between pseudotentacles; pv, prostatic vesicle; sb, spermiducal bulbs; su, sucker; sv, seminal vesicle; te, pseudotentacles tips eyespots; va, vagina; ve, ventral eyespots.

(Table 2). The most similar species found in the literature is *Thysanozoon mirtae*, recently described from Argentina (Bulnes *et al.*, 2011). However, there are marked differences between them, *T. mirtae* has a smaller pharynx (5.5 mm) and with fewer folds. This is especially distinctive as the specimen from Argentina is much larger, almost double the size of ours, and it would be expected that a larger specimen would have a larger pharynx. Also, the pseudotentacles of the Argentinian species are colourless and the ones in *T. alagoensis* are dark with yellowish tips. The Argentinian species also present rounded black spots in the dorsal surface that are absent in our specimen (Bulnes *et al.*, 2011). Both *T. alagoensis* and *T. mirtae* have slender, elongated papillae, which are also found in *Thysanozoon skottsbergi* (Bock, 1913) and *T. distinctum* (Stummer-Traunfels, 1895), but the former has darker pigmentation on the papillae and the latter has a golden yellow margin which is markedly different from the reddish brown margin of *T. alagoensis* sp. nov. and *T. mirtae*. Both also have apparent spermiducal vesicles, but in *T. alagoensis* sp. nov. they are greatly developed. Yet another difference between these two South American species is the parenchymatic musculature, developed in *T. alagoensis* sp. nov. and not in *T. mirtae*. Other valid species of the genus are compared in Table 2. It is repeatedly stated in the literature that the female system is very uniform throughout the genus, therefore it was not included in the comparative table.

Suborder ACOTYLEA Lang, 1884
Family CRYPTOCELIDAE Laidlaw, 1902
Genus *Phaenocelis* von Stummer-Traunfels, 1933
Phaenocelis medvedica Marcus, 1952
(Figure 7)

EXAMINED MATERIAL

One specimen (19 × 5 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 97, 9 slides). Collected 6 January 2008 at Ponta Verde coral reef, Maceió, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

This species was described from São Paulo State, Brazil (Marcus, 1952), and is also known from the Caribbean coast of Colombia (Quiroga *et al.*, 2004b). Here it is reported for the first time from north-eastern Brazil.

DIAGNOSIS

Rosaceous colour with brown pigment spots in two rows longitudinal to the body, parallel to the body axis (Figure 7A). Marginal eyespots small and present all over the body margin, disposed in a line (Figure 7D). Cerebral eyespots scarce and disposed right in front of the brain; tentacular eyespots scarce in two small groups (Figure 7C, D). Pharynx 1/3 of the body size and centrally disposed. Muscular layers disposed in the following order: longitudinal, circular, diagonal and longitudinal (Figure 7B).

REMARKS

Our specimen was immature and wounded at the level of reproductive structures, therefore on sagittal section it is possible only to identify the Lang's vesicle (Figure 6C, D).

Family STYLOCHOPLANIDAE Faubel, 1983
Genus *Armatoplana* Faubel, 1983
Armatoplana leptalea (Marcus, 1947)
(Figure 8)

EXAMINED MATERIAL

Three specimens (16 × 5 mm, 10 × 3 mm and 10 × 3 mm), one as sagittal sections of reproductive structures (MNRJ-PLAT 98). Collected 10 January 2008 at Riacho Doce coral reef, Maceió, Alagoas, Brazil. One specimen (11 × 4 mm) (MNRJ-PLAT 99, 5 slides). Collected 11 January 2008 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil.

Table 2. *Thysanozoon* species characteristics comparison.

Thysanozoon species	Colour pattern	Papillae	Pharynx	Male system	Distribution
T. brocchii (Risso, 1818)	Dark brown to yellowish brown, cream cross sometimes present at the dorsal surface	Slightly slender to rounded	Five simple folds	Seminal vesicle elongated and located diagonally to the body. Folded male atrium. Spermiducal vesicles absent	Naples, Italy, Mediterranean Sea, UK, south and west of Africa, Florida, Caribbean coast of Colombia, Brazil, Japan, New Zealand and Canary Islands
T. californicum Hyman, 1953a	Reddish grey with mauve margin, papillae yellowish cream in the median line, reddish grey in the rest of the body and mauve in the margins	Slender and elongated	Seven simple folds	Not sectioned	California
T. cruciatum Schmmarda, 1859a	Light brown with reddish touch, cream cross can be present at the dorsal surface. Greyish brown papillae	Conic	Three simple folds	Not sectioned	New Zealand, Australia
T. discoideum Schmmarda, 1859a	Yellowish orange to blood red, with dark reddish brown median line. Papillae brownish black to black. Dark brown tentacles	Slender, almost cylindrical	Five simple folds	Not sectioned	Sri Lanka and Eastern Africa
T. distinctum Stummer-Traunfels, 1895	Light yellow, whitish median line and golden yellow margin. Blackish and whitish (more numerous) papillae. Tentacles blackish at base and yellow at tips	Slender, small and elongated	Five simple folds	Oval seminal vesicle. Spermiducal vesicles absent	Edam and Java, Indonesia
T. flavotuberculatum Hyman, 1939d	Greyish with irregular small black flecks. Scarce yellow papillae	Few oval papillae	?	Immature sectioned	Bermudas
T. hawaiiensis Hyman, 1960	Light ochre with dull green papillae	Cylindrical	Five simple folds	Not sectioned	Hawaii
T. langi Stummer-Traunfels, 1895	Bright dirty violet, with darker violet mottling over papillae	Short and rounded	Five simple folds	Not sectioned	Ambon, Indonesia
T. minutum Stummer-Traunfels, 1895	Yellowish grey with live red median line, whitish margin and tentacle margin. Yellowish brown papillae with reddish brownish yellow and bright round spots	Short and conic	Five simple folds	Not sectioned. Vas deferens well developed	Java, Indonesia
T. mirtae Bulnes *et al.* 2011	Greenish yellow covered with rounded black spots, reddish brown papillae, tentacles unpigmented	Slender and elongated	Three simple folds	Vas deferens form spermiducal vesicles. Seminal vesicle with well-developed muscular wall and is arranged dorsally to the male prostatic vesicle and stylet. Rounded prostatic vesicle	Argentina
T. nigropapillosum (Hyman, 1959a)	Black with pale yellowish margin. Black papillae with white tips	Short and rounded	Five simple folds	Not sectioned	Ifaluk, Micronesia
T. nigrum Girard, 1851	Black with grey patches and fine specks of white. Blackish papillae tinged with greenish yellow	Slender and pointed	?	Oval prostatic vesicle. Wide, long and coiled seminal duct	Florida and Bermudas

Continued

Table 2. Continued

***Thysanozoon* species**	**Colour pattern**	**Papillae**	**Pharynx**	**Male system**	**Distribution**
T. raphaeli Bolaños *et al.*, 2007	Brown-blackish with yellowish orange papillae. Small white slash-like marks, hardly visible, in the margin. Black tentacles sometimes outlined by white marks	Short and rounded	?	Seminal vesicle elongated and prostatic vesicle rounded. Spermiducal vesicles absent	Belize and Panama
T. skottsbergi Bock, 1923c	Yellowish with touch of greenish grey, blackish median line, lighter papillae tipped with black. Black tentacles	Slender	Five simple folds	Not sectioned	Juan Fernandez Islands
T. alagoensis sp. nov.	Greyish background colour with reddish brown papillae, reddish brown margin and dark almost black tentacles with a hint of yellowish pigmentation on the border. Unpigmented line present at the median line of the body	Slender and elongated	Pharynx ruffled with seven simple folds	Seminal vesicle elongated and huge, reaches the front of penial papillae. Ejaculatory duct comes in a curve to join the penis. Prostatic vesicle small and comma shaped. Male atrium simple. Greatly developed spermiducal vesicles	Brazil

GEOGRAPHIC DISTRIBUTION

This species was described from São Paulo State, Brazil (Marcus, 1947), and also known from Bahia State and localities in the Caribbean, such as Antigua, Barbuda, Curaçao and Florida (Marcus & Marcus, 1968). This is the first record of this species from Alagoas State.

DIAGNOSIS

Light brown colouration, mostly transparent (Figure 8A). Few eyespots posteriorly to tentacular region; tentacular eyespots in a densely disposed group. Cerebral and pre-cerebral eyespots disposed in long parallel groups. Pharynx in the anterior half of the body. Vagina wall ciliated and muscular (Figure 8C, D). Long penis with stylet, seminal vesicle highly muscularized (Figure 8B), Lang's vesicle present, granular vesicle elongated and directed backwards.

REMARKS

Our specimens slightly differ in the fact that the seminal vesicle is located under the granular vesicle and not behind it as illustrated in Marcus (1947: Figure 32), which can be due to the size of the specimens or fixation contraction. It is the first time that this species is illustrated with coloured photos of internal structures and live specimens.

Family LATOCESTIDAE Laidlaw, 1902
Genus *Latocestus* Plehn, 1896
Latocestus brasiliensis Hyman, 1955
(Figure 9)

EXAMINED MATERIAL

One specimen (7 × 1.5 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 101, 6 slides). Collected 7 February 2008 at Pajuçara coral reef, Maceió, Alagoas,

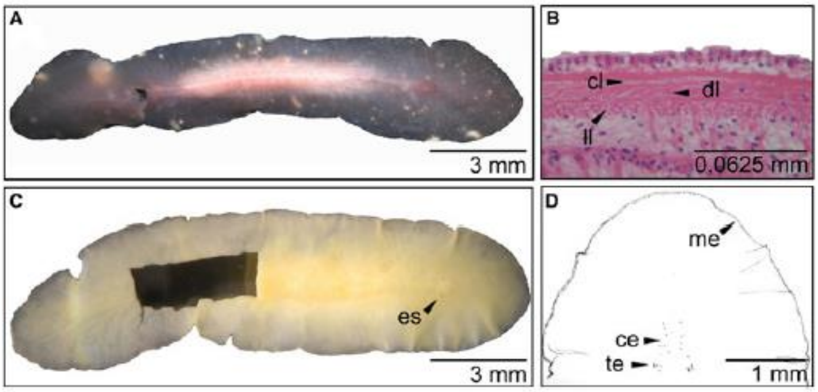

Fig. 7. *Phaenocelis medvedica* (A) *in vivo*; (B) sagittal section showing muscular layers; (C) fixed worm; (D) anterior region detail showing eyespots. ce, cerebral eyespots; cl, circular layer; dl, diagonal layer; es, eyespots; ll, longitudinal layer; lv, Lang's vesicle; me, marginal eyespots; te, tentacular eyespots.

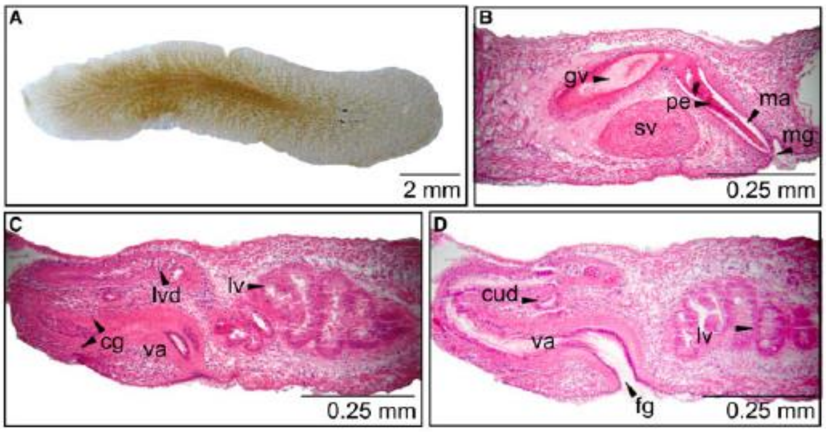

Fig. 8. *Armatoplana leptalea* (A) *in vivo*; (B) sagittal section of the male reproductive structures; (C) and (D) sagittal sections of the female reproductive structures. cud, common uterine duct; fg, female gonopore; gv, granular vesicle; lv, Lang's vesicle; lvd, Lang's vesicle duct; mg, male gonopore; pe, penis; sv, seminal vesicle; va, vagina.

Brazil. One specimen (10 × 2 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 107, 8 slides). Collected 28 January 2012 in algae at Ponta Verde coral reef, Maceió, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION

In the original description Hyman (1955) did not mention the exact type locality and only writes the unspecific term 'off São Francisco'. However, in a later paper (Schmitt, 1926, p. 89), she states that the collector (Waldo L. Schmitt) travelled in southern Brazil in 1925, including Santa Catarina State. Off the coast of this region there is an island called São Francisco do Sul, and, most probably, Hyman referred to it in the original description. It is the first time it is reported after almost 60 years after the original description. This is the first record of this species in north-eastern Brazil.

DIAGNOSIS

Colour greyish beige (Figure 9A). Body form elongated, anterior part pointed, tentacles absent, marginal eyespots around

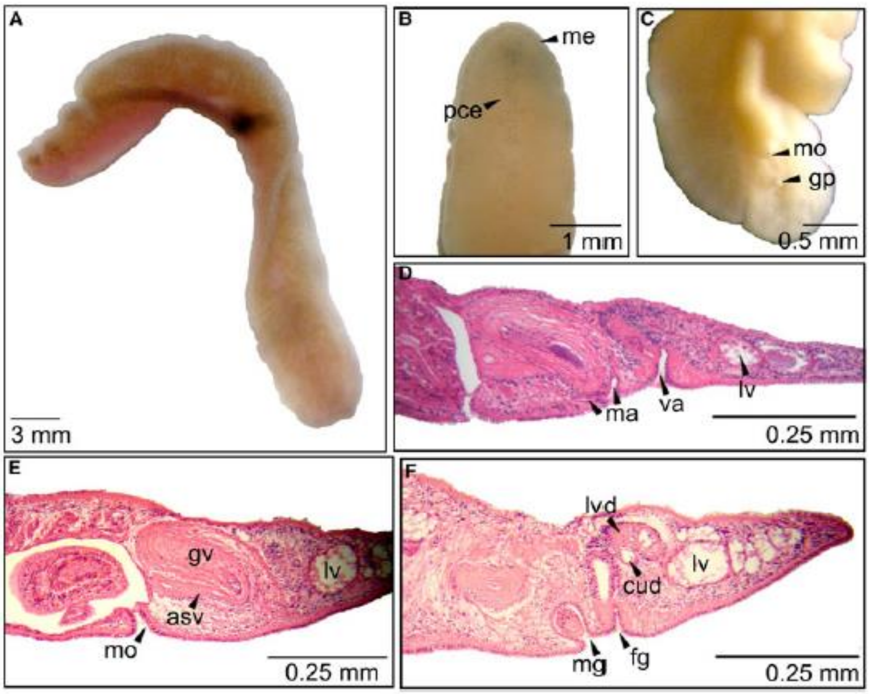

Fig. 9. *Latocestus brasiliensis* (A) *in vivo*; (B) detail of anterior region showing eyespots; (C) detail of the ventral posterior region showing mouth and gonopores; (D), (E) and (F) sagittal sections of reproductive structures. asv, accessory seminal vesicle; cud, common uterine duct; fg, female gonopore; gp, gonopores; gv, granular vesicle; lv, Lang's vesicle; lvd, Lang's vesicle duct; ma, male atrium; me, marginal eyespots; mg, male gonopore; mo, mouth; pce, precerebral eyespots; va, vagina.

all body, precerebral eyespots in a fan-like arrangement (Figure 9B). Pharynx at the last third of the body. Mouth opens at posterior part of the body right in front of reproductive structures. Male aparat directed forward (Figure 9D). Male and female gonopores separated (Figure 9D, F). Female atrium and vagina ciliated, vagina turned backwards and connects to Lang's vesicle by a repeatedly expanded and constricted duct (Figure 9F). Granular vesicle and accessory seminal vesicle very muscularized (Figure 9E), elongated and directed forward.

REMARKS

Our specimens fit the original description and the redefinition of the genus by Faubel (1983). Other species of the genus, like *Latocestos callizona* Marcus, 1947 have different body form, eyespots arrangement and differences in reproductive structures both masculine and feminine. The species *Latocestus atlanticus* Plehn, 1896 also has a different eyespots arrangement. The species *Prolatocestus ocellatus* (Marcus, 1947) is mostly similar, but it has a common genital aperture and therefore is located in another genus. The material here studied fits the original description both internally and in eyespots arrangement.

Family DISCOCELIDAE Laidlaw, 1902
Genus *Adenoplana* Stummer-Traunfels, 1933
Adenoplana evelinae Marcus, 1950
(Figure 10)

EXAMINED MATERIAL

One specimen (14 × 10 mm) as sagittal sections of reproductive structures (MNRJ-PLAT 102, 8 slides). Collected 18 January 2007 at Pajuçara, Maceió, Alagoas, Brazil. One specimen (12 × 6 mm), collected 9 January 2008 at Brazil, Alagoas, Maceió, Recife do Francês (eaten by a *Enchiridium evelinae*). One specimen (21 × 12 mm) (MNRJ-PLAT 103, 6 slides) collected 26 January 2012 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil, under rocks.

GEOGRAPHIC DISTRIBUTION

This species was described from São Paulo State, Brazil (Marcus, 1950) and is endemic from Brazil. This is the first record of this species from north-eastern Brazil and it is the second and northernmost record in the Brazilian coast.

DIAGNOSIS

Transparent body makes it possible to see gut contents (Figure 10A, B). Marginal eyespots (Figure 10C) surround all body, are arranged in a scattered broad line and become scarcer after the first third of the body. Tentacular eyespots located before the brain level (Figure 10C). Cerebral eyespots groups extend towards the margin and begin before the brain level (Figure 10C). Male and female gonopores separated. Prostatoid organs present in the penis tissue (Figure 10F) and granular vesicle; male atrium spacious, vagina, common uterine duct and Lang's vesicle duct ciliated (Figure 10E).

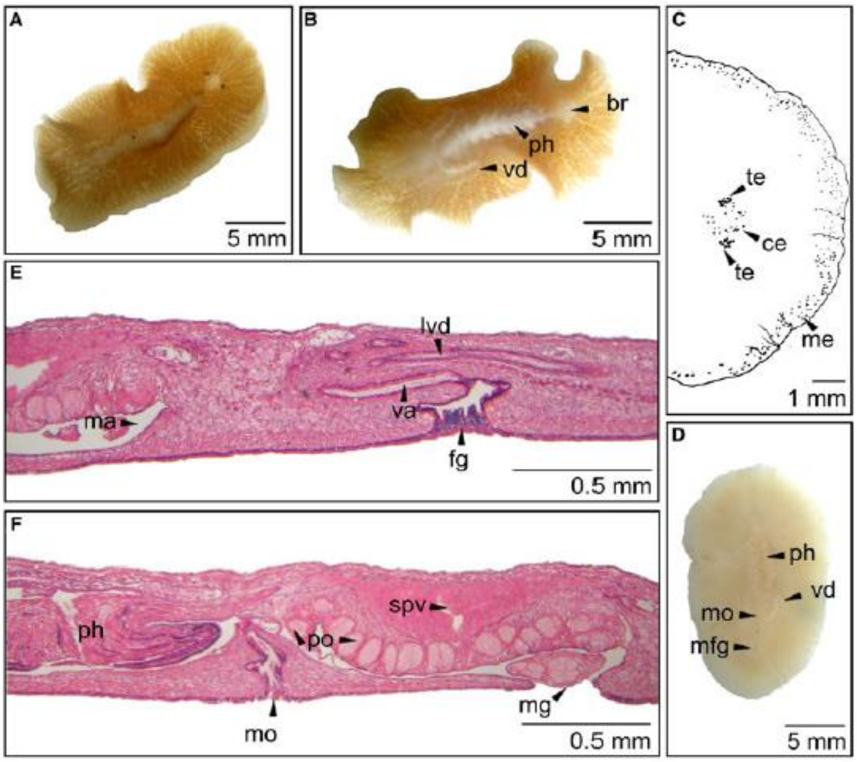

Fig. 10. *Adenoplana evelinae* (A) *in vivo*; (B) *in vivo*, ventral view; (C) detail of the anterior margin; (D) ventral view; (E) and (F) sagittal sections of reproductive structures. br, brain; ce, cerebral eyespots; fg, female gonopore; lvd, Lang's vesicle duct; me, marginal eyespots; mfg, male and female gonopores; mg, male gonopore; mo, mouth; ph, pharynx; po, prostatoids; spv, spermiductal vesicle; te, tentacular eyespots; va, vagina; vd, vas deferens.

External vagina directed forward and female ducts directed backwards, towards the Lang's vesicle.

REMARKS

The other Tropical Western Atlantic *Adenoplana* species, *A. obovata* (Schmmarda, 1859a), does not have marginal eyespots surrounding the entire body margin (Hyman, 1955), as *Adenoplana evelinae* has. The South American species *A. platae* also has marginal eyespots all over the body, however it presents a rather elongated cerebral eyespots group and it begins at the brain level (Hyman, 1955).

DISCUSSION

The north-eastern Brazilian coast is mostly unexplored concerning polyclad biodiversity and most works about Brazilian Polycladida have been made on the south-eastern coast (Marcus, 1949, 1950, 1952). Until recently, only two species were reported from this region: *Stylochoplana walsergia* and *Armatoplana leptalea*, both from Bahia State, south of Alagoas State (Marcus & Marcus, 1968). Bahia *et al.* (2012), based on material from Rio Grande do Norte State, reported six other species: *Enchiridium evelinae, Phrikoceros mopsus, Pseudobiceros evelinae, Thysanozoon brocchii, Hoploplana divae*. And recently, Queiroz *et al.* (2013) recorded *Pericelis cata* from Bahia State.

The present work adds six species to the north-eastern Brazilian coast: *Pseudoceros bicolor, Pseudoceros rawlinsonae, Thysanozoon alagoensis* sp. nov., *Phaenocelis medvedica, Latocestus brasiliensis* and *Adenoplana evelinae*. One of them is a new species and all 11 species are for the first time reported from Alagoas State. It is also the first time that *Phaenocelis medvedica, Adenoplana evelinae, Latocestus brasiliensis* and *Armatoplana leptalea* are illustrated by full colour photos of live specimens and histological sections. Our results emphasize that the Order Polycladida is not well known on the Brazilian coast and that the biodiversity of reef areas in Alagoas State is underestimated. More studies focused on polyclads are necessary to access their biodiversity throughout the Brazilian coast.

The different areas sampled in this study are subject to different levels of human impact (Correia & Sovierzoski, 2010). The area with highest species richness, Saco da Pedra reef, has a good conservation status as it is within a Biological Reserve (Correia & Sovierzoski, 2009). In contrast areas such as Piscina dos Amores coral reef, Pajuçara and Jatiúca reefs are more impacted reef areas, inside the urban perimeter of the city of Maceió and the city harbour. Apparently, polyclads can be used as bioindicators of environmental quality as they are more abundant and diverse in more pristine areas (personal observation). Since the 1980s the urban occupation in Maceió, and in the Brazilian coast in general, is growing without much planning and care, which threatens the biodiversity of reef areas. It is alarming that we are losing biodiversity before we even know its identity, and studies such as this one are relevant efforts to prevent or call attention to it.

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Supplementary material and methods

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0025315415000922.

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Chapter 2.

First records of polyclads (Platyhelminthes, Polycladida) associated with *Nodipecten nodosus* (Linnaeus, 1758)

Mar Biodiv
DOI 10.1007/s12526-015-0425-6

SENCKENBERG

SHORT COMMUNICATION

First records of polyclads (Platyhelminthes, Polycladida) associated with *Nodipecten nodosus* (Linnaeus 1758) aquaculture

Juliana Bahia[1,2]

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Abstract Free-living marine Platyhelminthes of the order Polycladida are known to interact with molluscs, especially bivalves. The impact and damage of polyclads that feed on farmed oysters can be so significant that they are known as oyster leeches. The present contribution identifies three species of polyclads associated with scallop aquaculture at Ilha Grande, southeastern Brazil: one cotylean, *Lurymare matarazzoi*, and two acotyleans, *Imogine tica* and *Imogine refertus*. This is the first time these species are illustrated with photographs of live specimens and histological sections after their original description. This is also the first record of an association of polyclads with a pectinid mollusc. The ecological role of polyclads is still little known, and experiments are lacking. However, it shows that native flatworm species are interacting with *Nodipecten nodosus* in experimental aquaculture, feeding either on the molluscs or on the associated fauna.

Keywords Brazilian marine flatworms · Associated fauna · Molluscs · Pectinidae · *Lurymare* · *Imogine*

Introduction

Among the free-living marine Platyhelminthes of the order Polycladida are known cases of ecological interactions with molluscs (Perrone 1987; Newman and Cannon 2003). Some species are commensals of gastropods, such as *Hoploplana usaguia* Smith 1960 (Smith 1960), or symbionts, such as the polyclad *Zygantroplana ups* González & Salar-Vallejo 1995 (González and Salazar-Vallejo1996). Some mimic nudibranchs of the genus *Phyllidiella* Bergh 1869, such as *Pseudoceros imitatus* Newman & Cannon 1994 (Newman et al. 1994). Others feed on various bivalve species, such as *Bankia martensi* (Stempell 1899) (Brusa and Damborenea 2014), mussels, *Teredo* sp., and, most commonly, species of oyster (Galleni et al. 1980; Sluys et al. 2005). The records of polyclad predation on molluscs are for acotyleans, mostly from the families Stylochidae and Notoplanidae. There is, so far, only one record of a member of Prosthiostomidae associated with molluscs, *Prosthiostomum ostreae* Kato 1937, found on oyster shells (Kato 1937). The present study identifies, for the first time, some polyclad species associated with a commercial mollusc aquaculture site in Brazil.

Materials and methods

All specimens were collected at an aquaculture site of the bivalve *Nodipecten nodosus* (Linnaeus 1758), situated at Praia dos Meros, Ilha Grande, southeastern Brazil (23°13′6.66″S; 44°20′26.41″W). Polyclad specimens were photographed live with a digital camera; fixed on frozen 10 % formalin, following the methodology modified from Newman and Cannon (2003); transferred to 70 % ethanol; and then sent to the author for identification. The portions containing the reproductive structures were dissected for histological preparation. Specimens were measured after fixation (length × width, in mm). The identification was based on morphological characteristics, coloration pattern, ocelli position, and reconstruction of the reproductive structures from histological sections stained with

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the hematoxylin–eosin method. Data were compared to original descriptions and other literature. The collected material was deposited in the Platyhelminthes Collection of the Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ-PLAT).

Results (Figs. 1 and 2)

SYSTEMATICS

Order POLYCLADIDA Lang 1884
Suborder Cotylea Lang 1884
Family Prosthiostomidae Lang 1884
Genus *Lurymare* Marcus and Marcus 1968
Lurymare matarazzoi (Marcus 1950)

Synonyms: *Prosthiostomum matarazzoi* Marcus 1950; *Euprosthiostomum matarazzoi* Faubel 1984

Material examined: One specimen (MNRJ-PLAT 111, 11×4.5 mm) as sagittal sections of reproductive structures (nine slides), remainder of animal in 70 % ethanol. Collected 19.08.2009.

Distribution: This species was described from São Sebastião, São Paulo State, Brazil (Marcus 1950) and afterwards recorded from Bonaire (Marcus and Marcus 1968) and Colombia (Quiroga et al. 2004). In all these locations, it was collected in natural environments.

Diagnosis: Body elongated, translucent beige or light brown; tentacles absent, marginal eyespots in broad band reaching level of cerebral eyespots. Pharynx short, tubular, large sucker. Prostatic vesicles involved by the same muscular sheath, one positioned ventrally and the other dorsally to the ejaculatory duct, seminal vesicle oval and large, also included in same muscular sheath. Cement glands few.

Taxonomic remarks:

Marcus and Marcus (1968) transferred this species from the genus *Prosthiostomum* (Marcus 1950) to *Lurymare* Marcus and Marcus 1968, based on the presence of a muscle sheath containing prostatic vesicles. This transfer was supported by Prudhoe (1985), but Faubel (1984) placed it in the genus *Euprosthiostomum* Bock 1925. However, this assignment is questionable, as Faubel (1984) stated that *Euprosthiostomum* has separate free prostatic vesicles, which is not the case in this species. The description and drawings of Marcus (1950) show the prostatic vesicles together in an 8-shaped muscular sheath, and *Lurymare* is defined as having "prostatic vesicles in a common muscle sheath which may include the seminal vesicle", thus being the only prosthiostomid genus that presents this character, in both reviews (Faubel 1984; Prudhoe 1985). Also, Marcus and Marcus (1968), who both described the species and created the genus, used this character to include "*Prosthiostomum matarazzoi*" in the new genus *Lurymare*. The specimen studied here accords with the original description of *L. matarazzoi* by Marcus (1950) and the later citation by Marcus and Marcus (1968), and, therefore, this species should be included in *Lurymare*, as previously stated by Marcus and Marcus (1968) and Prudhoe (1985). However, in our specimen, it was possible to see a hint of a muscular sheath that may also unite the seminal vesicle to the prostatic vesicles, which was not noted in the original description.

Comparing with other species of *Lurymare*, *L. katoi* Poulter 1975 has the eyespots differently arranged, with the cerebral group shorter and closer together than the elongated group of cerebral eyespots in *L. matarazzoi*. It also has gold to

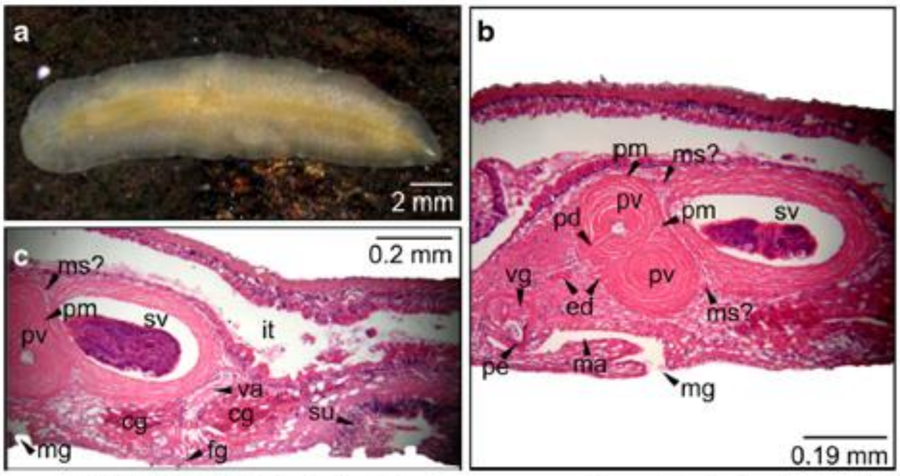

Fig. 1 *Lurymare matarazzoi* (MNRJ-PLAT 111). **a** In vivo dorsal view; **b** sagittal section of male reproductive structures; **c** sagittal section of female reproductive structures. *cg* cement glands, *ed* ejaculatory duct, *fg* female gonopore, *it* main intestine, *ma* male atrium, *mg* male gonopore, *ms?* muscular sheath, *pd* prostatic duct, *pe* penis, *pm* prostatic vesicles muscular sheath, *pv* prostatic vesicle, *su* sucker, *sv* seminal vesicle, *va* vagina, *vg* vesicula granulorum

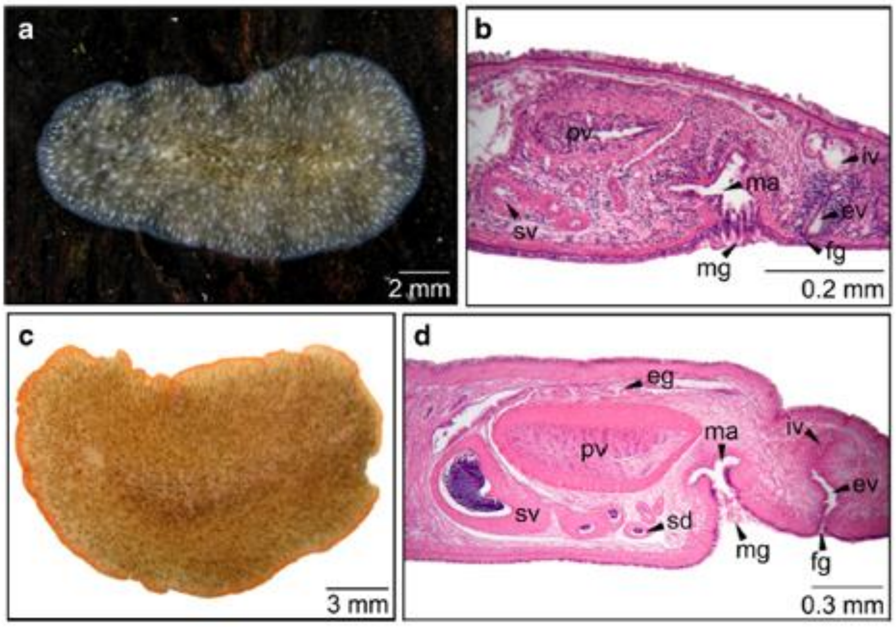

Fig. 2 *Imogine* species. **a** *Imogine tica* (MNRJ-PLAT 110) in vivo dorsal view; **b** sagittal section of male and female reproductive structures; **c** *Imogine refertus* (MNRJ-PLAT 109) in vivo dorsal view; **d** sagittal section of male and female reproductive structures. *eg* extra-vesicle glands, *ev* external vagina, *fg* female gonopore, *iv* internal vagina, *ma* male atrium, *mg* male gonopore, *pv* prostatic vesicle, *sd* seminal duct, *sv* seminal vesicle

orange-red pigment granules (Poulter 1975), which are absent from the material studied here. *Lurymare monosorum* (Schmarda 1859) has a much longer pharynx, its marginal eyespots reach past the level of the brain, and, also, has reddish-brown dorsal coloration with a dark-brown median line (Schmarda 1859; Stummer-Traunfels 1933). *Lurymare singulare* (Laidlaw 1904) lacks cerebral eyespots (Marcus 1950); *L. purum* (Kato 1937) has white coloration, and its pharynx is much smaller and distant from the copulatory structures (Kato 1937; Marcus 1952); and *L. delicatum* (Palombi 1939) has two dorsal longitudinal lines on each side of the median line. *Lurymare drygalskii* (Bock 1913) has fewer cerebral eyespots (Prudhoe 1989), and *L. russoi* (Palombi 1939) has accessory vesicles smaller than the stylet, a different arrangement of cerebral eyespots, and a larger pharynx (Prudhoe 1989).

The Brazilian *L. gabriellae* (Marcus 1949) has only eight eyespots (Marcus 1952) and *L. utarum* (Marcus 1952) also has a different coloration pattern with a brown median line (Marcus 1952), absent in *L. matarazzoi*. These species also differ in the orientation of the efferent duct (Marcus 1952). The identity of the specimen found in Colombia, and named *Prosthiostomum matarazzoi*, cannot be confirmed through comparison with our specimen, as Quiroga et al. (2004) provided neither a description of a living specimen nor histological photographs.

Suborder Acotylea Lang 1884
Family Stylochidae Stimpson 1857
Genus *Imogine* Girard 1853
Imogine tica Marcus 1952

Material examined: One specimen (MNRJ-PLAT 110, 9.5×5.8 mm) as sagittal sections of reproductive structures (eight slides), remainder of specimen in 70 % ethanol. Collected 18.08.2009.

Distribution: The species was described from São Paulo State, southeastern Brazil (Marcus 1952). This is the first record from Rio de Janeiro State.

Diagnosis: Dorsal surface yellowish-gray with scattered dark-green and white spots; nuchal tentacles small and elongated, anterior to brain level. Marginal eyespots extending past brain level, few frontal eyespots; cerebral eyespots extending from slightly anterior to tentacles to brain level, tentacular eyespots on most of the tentacle. Tripartite seminal vesicle, separate male and female openings. Penis pouch present; prostatic vesicle oval and elongated.

Taxonomic remarks: Our specimen fits the original description (Marcus 1952) of *Imogine tica*. It is smaller than the specimens described by Marcus, but it is mature. Two other species were described from the Brazilian coast, assigned to *Stylochus* Ehrenberg 1831, but then relocated to *Distylochus* Faubel 1983 because of their bipartite seminal vesicle (du Bois-Reymond Marcus 1955). The remaining Brazilian species of *Imogine*, *I. cata* (Du Bois-Reymond Marcus 1958), also has a penis pouch, but differs in having a common genital pore (Du Bois-Reymond Marcus 1958). *Imogine megalops* (Schmarda 1859) has a similarly arranged band of marginal eyespots. However, it has the nuchal tentacles set more closely, fewer cerebral eyespots, and differences in the internal anatomy (Stummer-Traunfels 1933; Hyman 1955b). *Imogine oculifera* (Girard 1853) has a different coloration pattern, with rose-red spots on the dorsal surface (Hyman 1955b); and *I. zebra* (Verrill 1882) also has a different, striped coloration pattern and an erect prostatic vesicle (Hyman 1939). The Japanese species *I. rutilus* Yeri and Kaburaki 1918 and *I. ijimai* Yeri and Kaburaki 1918 differ from *I. tica* in both the coloration pattern (darker coloration over the pharynx area) and the arrangement of the eyespots (Yeri and Kaburaki 1918). *Imogine mediterranea* Galleni 1976 has more cerebral eyespots than the specimen studied here, and lacks a penis pouch (Galleni 1976). *Imogine minimus* Palombi 1940 has a different arrangement of the eyespots and is much smaller in overall size (Palombi 1940), and both *I. refertus* Du Bois-Reymond Marcus 1965 and *I. orientalis* Bock 1913 have a larger seminal vesicle than *I. tica* (Du Bois-Reymond Marcus 1965; Galleni 1976). Compared to *I. ellipticus* Girard 1850, our specimen lacks the short stylet and has more numerous cerebral eyespots (Hyman 1939), and *I. meridianus* Prudhoe 1989 lacks a penis pouch and has a different eyespot arrangement (Prudhoe 1989).

Imogine refertus Du Bois-Reymond Marcus 1965

Material examined: One specimen (MNRJ-PLAT 109, 27 × 19 mm) as sagittal sections of reproductive structures (15 slides), remainder of specimen and another, whole in 70 % ethanol. Collected 19.08.2009 at 10 m depth.

Distribution: São Paulo State, southeastern Brazil (Du Bois-Reymond Marcus 1965).

Diagnosis: Background color beige with greenish-brown freckles, orange marginal band, orange elongated nuchal tentacles; marginal eyespots in broad band, no frontal eyespots, few cerebral eyespots, nuchal eyespots on tentacular structure. Pharynx highly ruffled. Gonopores open separately; penis pouch present; tripartite seminal vesicle as large as prostatic vesicle; prostatic vesicle oval and horizontally elongated, of polyglandular type, with thick muscular wall. Extra-vesicular glands scattered in parenchyma surrounding prostatic vesicle. Prostatic duct and penis papilla both short.

Taxonomic remarks: Our specimen fits the definition of *Imogine*, based on the presence of the tripartite seminal vesicle. *Imogine oculifera* has a reddish marginal band as well, but its tentacles are unpigmented and it has darker dorsal flecks or spots. It also lacks a penis pouch, having only a male atrium. Our specimens cannot be assigned to *I. cata* because this species has a single aperture for both the male and female gonopores, while our specimen has separate gonopores. It also differs from *I. tica* in the relative size of the prostatic vesicle, which is much larger in the specimen that we studied, proportionally to the penis papilla and other male structures, than in *I. tica* (Marcus 1952).

Imogine meridianus has similar internal features but different coloration and eyespot arrangement (Prudhoe 1989). *Imogine mediterranea* has similar internal features except for the male atrium, but it has a different coloration pattern (Galleni 1976). The Japanese species *I. ijimai* also has colored tentacles (dark brown), but they are conical rather than pointed, and this species has a different cerebral eyespot arrangement and purplish-gray spots (Yeri and Kaburaki 1918). *Imogine megalops* also has a huge prostatic vesicle and curved vagina, as does our specimen (Stummer-Traufels 1933), but ours has a penis pouch, as observed in *I. tica*.

Most species of *Imogine* have transparent tentacles (Jennings and Newman 1996a, b; Bulnes et al. 2005; Bulnes 2010). The Australian *I. meganae* has pigmented tentacles and marginal band, but these are yellow rather than orange (Jennings and Newman 1996b). It also has widely separated tentacles, and the prostatic vesicle of the same size as the tripartite seminal vesicle, and separate gonopores. However, it has a different eyespot arrangement to our specimen (Jennings and Newman 1996b). The only two species of *Imogine* that also have orange tentacles are *I. arenosa* (Willey 1897) and *I. refertus* (Du Bois-Reymond Marcus 1965). *Imogine arenosa* has a colorless margin and more widely separated eyespots (Willey 1897), which differ from the material studied here, but, unfortunately, there are no details of the internal anatomy to compare. In *I. refertus*, the entire dorsal surface, not only the margins, is orange (Du Bois-Reymond Marcus 1965).

Despite this difference in coloration, the present material fits the original description of *I. refertus* in relative size, morphology and position of reproductive structures, presence of a penis pouch, distance between tentacles, eyespot arrangement, and, also, the reticular design of the orange pigmentation layer (Du Bois-Reymond Marcus 1965). Therefore, the specimen is identified as *I. refertus*. The specimen described by Du Bois-Reymond Marcus (1965) is twice as large as the present material, and the coloration in polyclads can vary depending on the feeding status, diet, or age of the specimen.

Discussion

The impact and damage caused by polyclads that feed on farmed oysters are so well known and significant that these animals are known as oyster leeches (Pearse and Wharton 1938). Hyman (1955a) described an acotylean, introduced from Japan through oyster farming, which had a destructive effect on local cultures and direct economic impact.

The lion's paw scallop *N. nodosus* ranges from the Caribbean Sea to Brazil, occurs in low densities in the natural environment, and is harvested by diving and from experimental cultures (Minchin 2003). This bivalve was relatively recently considered of aquacultural interest (Lodeiros et al. 1998) and, if transported to new culture areas, could bring polyclads among its associated fauna, with possible impacts on the local mollusc community. The presence of two species of acotylean flatworms, belonging to a genus whose representatives are well known for their predation on bivalves (Galleni et al.

1980), at an aquaculture site of *N. nodosus* indicates that they may be preying on the pectinid, although there are no records of predation by polyclads on pectinid bivalves.

A few cases of cotylean polyclad–mollusc interactions are known, and members of this suborder are also known to prey on ascidians (Marcus 1950). According to Galleni et al. (1980), only two species, both belonging to the family Pseudocerotidae, prey on oysters. Among the Prosthiostomidae, *P. montiporae* preys on coral, and *E. viscosum* was found inside an uninhabited hermit crab shell (Palombi 1936). *Prosthiostomum ostreae* was found by Kato (1937) inside empty oyster shells. The species was not reported as a predator of molluscs by Galleni et al. (1980), possibly because Kato (1937) provided no clear evidence of its predation on the oyster. The present finding adds a further prosthiostomid species to the list of potential predators of bivalves. However, whether this flatworm actually feeds on *N. nodosus* or on its associated fauna has yet to be tested by experiments.

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Chapter 3.

Pseudobiceros wirtzi sp. nov. (Polycladida: Cotylea) from Senegal with revision of valid species of the genus

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Pseudobiceros wirtzi sp. nov. (Polycladida: Cotylea) from Senegal with revision of valid species of the genus

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Abstract

The genus *Pseudobiceros* was established based on the presence of two male gonopores, duplicated male reproductive structures, smooth dorsal surface, complex folded pseudotentacles, and simple ruffled pharynx. We describe here a new species of *Pseudobiceros* from the African continent that has been repeatedly reported and photographed over the years, but lacked a formal description. *Pseudobiceros wirtzi* **sp. nov.** is described based on morphological and histological characters. Our bibliographical revision of the genus considers 39 species to be valid. We applied the diagnostic characters of *Pseudobiceros* to *Pseudoceros* species listed before the split between these genera, and to species listed as *incertae sedis*. *Pseudobiceros punctatus* (Laidlaw 1902) **nov. comb.** shows typical features of *Pseudobiceros*. We also discuss other species with historically conflictive generic placements or problematic synonymy and summarize distributions and species characteristics in a comparative table. Most *Pseudobiceros* species still need re-descriptions to fill gaps regarding internal and pharynx details. Further sampling on the Eastern Africa coast and on mid-Atlantic Islands should prove useful in getting a general view of polyclad biodiversity and biogeography in the Tropical and South Atlantic.

Key words: Pseudocerotidae, taxonomy, marine biodiversity, tropical Atlantic

Introduction

Polyclads belonging to the suborder Cotylea are abundant and conspicuous in tropical seas, especially members of the family Pseudocerotidae, which accounts for most species (Tyler *et al.* 2006–2015). The genus *Pseudobiceros* was described by Faubel (1984) based on the presence of two male gonopores, duplicated male reproductive structures and smooth dorsal surface. Newman and Cannon (1994) include additional diagnostic characters such as shape of pseudotentacles, cerebral eyespots, arrangement of pseudotentacular eyes, and pharynx. The genus *Pseudoceros* was described as having simple folded pseudotentacles and a deeply ruffled pharynx, while *Pseudobiceros* has complex folded pseudotentacles with either ear-like, or square form, and a ruffled simple pharynx. Many species that currently belong to *Pseudobiceros* were originally described and placed within *Pseudoceros*. Thus, with the establishment of *Pseudobiceros*, many new combinations were suggested by Faubel (1984), Newman & Cannon (1994, 1997), and Bolaños *et al.* (2007). Faubel (1984) also wrote a list of *incertae sedis* species of *Pseudoceros* that most likely contain *Pseudobiceros* species that were poorly described at first.

There are few works on Polycladida from the African continent. Most are from South Africa (Palombi 1936, 1939), and the Indian Ocean side, Zanzibar (Laidlaw 1903b), Somalia (Meixner 1907), and Mozambique (Prudhoe 1989). Atlantic Africa remained mostly unexplored except for an article describing material collected in Cape Verde (Laidlaw 1906) and another from different areas of occidental Africa (Palombi 1940). Most of the contributions regard acotyleans polyclads, with few records of cotyleans (Prudhoe 1989; Laidlaw 1903a; Palombi 1939). A checklist from the Canary Islands was also published (Vera *et al.* 2008) but it does not describe or assign names to the Pseudocerotidae species found. One of those species is an undescribed species of *Pseudobiceros* which has been photographed for many years and is present in different field guides and books (Newman & Cannon 2003; Pérez Sanchéz & Batet 1991; Wirtz & Debelius 2003). Here we formally describe this new species based on morphological and histological features. As during the species description a revision of other species

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belonging to the same genus was made, this short revision is also presented together with our results. We hope the results of the bibliographical revision can be used as a more complete record for further studies and a guide for the revision of deposited material as well as the re-description of many species included in the genus, which was beyond the scope of the present paper.

Material and methods

The studied specimens were either collected by hand or photographed in the infralitoral zone. Specimens were collected in Senegal (14°45'N, 17°30'W) and Cape Verde (16°59'52.17"N, 24°57'44.36"W), additional records were photographed at Madeira (32°44'39.88"N, 16°41'31.84"W). Specimens were photographed alive in the field and then fixed in 10% frozen formalin, following modified methodology (Newman & Cannon 1995b). Measurements were taken after fixation (length mm x width mm). The specimens found at Senegal were fixed entirely and directly in 96% ethanol, too damaged and thus could not be used for histological sections. The identification was based on morphological characteristics, coloration pattern, ocelli position and slides of the reproductive structures stained by hematoxilin-eosin method (Bolaños *et al.* 2007). Specimens were compared with original descriptions and posterior publications of all *Pseudobiceros* species (Marcus 1950; Faubel 1984; Newman & Cannon 1994, 1997 and references therein). Collected material was deposited on the Platyhelminthes collection of Zoologische Staatsammlung München Invertebrata varia.

Results

After a broad bibliographic revision, we list 38 species valid in *Pseudobiceros* and describe a new species (Table 1). We summarize results from different lists in which some species were present in some revisions, but absent in others. Also, we put together information that was previously separated in different articles and in languages as different as Latin, German, Portuguese, and English. Some of the species listed by Faubel (1984) are not present in later articles (Newman & Cannon 1994, 1997). One is *Pseudobiceros ferrugineus* (Faubel 1984), described and illustrated by Hyman (1959) with two gonopores, but, only one male gonopore was found in its holotype (Newman & Cannon 1994). The species *Pseudobiceros flavomarginatus* was also missing in Newman & Cannon (1994, 1997), but herein found to be misplaced in *Pseudobiceros* (Table 1). The species *Pseudobiceros miniatus*, *P. rubrocinctus*, *P. schmardae*, *P. undulatus* and *P. viridis* were also missing from Newman & Cannon's (1994, 1997) revisions and are discussed here. Another case is the species *Pseudobiceros punctatus*, which is absent from both Faubel (1984) and Newman & Cannon (1994, 1997). Additionally, two unidentified species were described by Newman & Cannon (1997), but due to lack of material they have not name the animals, only using the codes sp. 1 and sp. 2. As they have not included these animals in their list of valid species and as to be valid a species has to have a name, we do not include these species in our list. We consider that *Pseudobiceros* sp. 1 and *Pseudobiceros* sp. 2 (Newman & Cannon 1997) need more morphological and histological information to be described and think they can be cited in synonym lists in future articles that actually name and describe those species.

Systematics

Phylum Platyhelmithes

Order Polycladida Lang, 1884

Suborder Cotylea Lang, 1884

Family Pseudocerotidae Lang, 1884

Genus *Pseudobiceros* Faubel, 1984

Type species: *Pseudobiceros strigosus* (Marcus, 1950) junior synonym of *Pseudobiceros gratus* (Kato, 1937)

Taxonomic remarks. The confusion about the genus *Pseudobiceros* begins with its type species. *Pseudoceros strigosus* was a name created by Marcus (1950) to solve confusion resulted from the misuse of the specific name *striata* (in the originally *Eurylepta* description (Schmarda 1859)) or *striatus* (after it was relocated in *Pseudoceros* (Stummer-Traunfels 1933, p. 3487 and fig. 95) He stated a distinction between *P. striatus sensu* Schmarda (1859, p. 27 and fig. 62) and *sensu* Keelart (1858, p. 137; Keelart *in* Collingwood 1876, p. 97 and fig. 25), since one is described as white with dark stripes and the other as dark with bright stripes. Hyman (1959a) solved the confusion stating *P. gratus* (Kato 1937) is synonymous to the original Schmarda species and thus there was no need for the new name given by Marcus. Faubel (1984) followed Marcus' opinion, while Newman & Cannon (1994) followed Hyman. We find that Hyman (1959) is right and *Pseudobiceros gratus* has priority over *P. strigosus*. However, *Pseudobiceros strigosus* is still the name of the genus type. There is only observation that must be done to Newman & Cannon (1994), *Pseudoceros habroptilus* (Hyman 1959) should not be included in *Pseudobiceros gratus* synonym list, as it was described without information about reproductive structures, and it was draw with two median lines instead of one, as present in *Pseudobiceros gratus*.

Pseudobiceros bedfordi (Laidlaw, 1903a)

Taxonimic remarks. *Pseudobiceros bedfordi* has under its synonym list (Table 1) the species *Pseudoceros micronesianus*, described by Hyman (1955). However, Faubel (1984) makes a new combination of this species adding it to *Pseudobiceros*, but citing Hyman 1953 as the author, and considering *P. bedfordi* and *P. micronesianus* as separate species. There is no species with that name in Hyman (1953), so that might have been a misspelling. Later, Newman & Cannon (1994), despite not commenting Faubel's list (1984), already clarified that the species described by Hyman (1955) is synonym of *Pseudobiceros bedfordi*, after examining its holotype. Here we support that decision and do not consider *Pseudobiceros micronesianus* as a valid species.

Pseudobiceros hancockanus (Collingwood, 1876)

Taxonomic remarks. This species was subject to much confusion concerning its synonym list. It was originally described as *Proceros hancockanus* (Collingwood 1876) and assigned to *Prosthecereus* by Lang (1884) and to *Pseudoceros* by Laidlaw (1903). Marcus (1950) also recognized *Prosthecereus*-like pseudotentacles in the drawings. Kaburaki (1923), however, synonymized it to another Collingwood (1876) species: *Pseudoceros malayaensis* (originally described as *Stylochopsis* and assigned to *Pseudoceros* by Bock (1913)) which has the same color pattern and color but was represented with different pseudotentacles. Bock (1913) also listed both species as synonyms, but argued that a final decision about their identity should be let open. Faubel (1984) did not include both species in *Pseudoceros*, *Pseudobiceros*, *Prosthecereus* or in the *incertae sedis* species list. Newman & Cannon (1994) treated both as synonyms; adding information from fresh material, they transferred the species to *Pseudobiceros*. Here we follow Newman & Cannon's (1994) position. It is, however, necessary to revise all the species showing black background color and orange or yellow margin, using museum and fresh material.

Pseudobiceros luteomarginatus (Yeri & Kaburaki, 1918)

Taxonomic remarks. This species is listed as synonymous to *Pseudobiceros flavomarginatus* by Faubel (1984). However, the original description (Laidlaw 1902) divides *Pseudoceros* species in forms with a pair of penes or single penis, and *P. flavomarginatus* is under the species with single penis. This fact was already pointed out by Marcus (1950), who considered *Pseudoceros flavomarginatus* and *luteomarginatus* as separate species based on the number of gonopores and color information. The original *Pseudoceros luteomarginatus* description (Yeri & Kaburaki 1918) stated clearly (p. 38; plate I, fig. 5) that this Pseudocerotidae has two male gonopores and smooth dorsal surface. So we think that the synonym and new combination presented by Faubel (1984) was result of some confusion about the literature consulted. Thus we argue that *Pseudobiceros flavomarginatus* should be left in *Pseudoceros*, as it has only one male gonopore, and that *Pseudoceros luteomarginatus* should be transferred to

Pseudobiceros, as it has two male gonopores. Since the transference of *P. luteomarginatus* was indirectly done by Faubel (1984), we consider that he had established this new combination. It is, however, unclear why the species mentioned above were ignored from Newman & Cannon's (1994, 1997) *Pseudobiceros* species list. *Pseudoceros flavomarginatus* was mentioned in the discussion of *Pseudobiceros periculosus* (Newman & Cannon 1994) where it was wrongly stated that Laidlaw did not give any additional details about gonopores.

Pseudobiceros miniatus (Schmarda, 1859)

Taxonomic remarks. This species was originally described as *Eurylepta miniata* (Schmarda 1859). Then its genus was discussed by Diesing (1862), who transferred it to *Proceros*, and Lang (1884), who transferred it to *Yungia*. Later, Stummer-Traunfels (1933) placed it into *Pseudoceros*. The drawings about Schmarda material inside Stummer-Traunfels' paper (p. 3539, fig. 90), depict the species with two male gonopores, thus Faubel (1984) transferred it to *Pseudobiceros*. The presence of two male pores was also noted by Marcus (1950). We support that decision, as the species cannot belong to *Yungia* or *Pseudoceros* because of its two male gonopores. It is not clear why the species was not included into Newman & Cannon's (1994, 1997) list of *Pseudobiceros* valid species.

Pseudobiceros periculosus Newman & Cannon, 1994

Taxonomic remarks. The species belongs to a color group showing a dark background and orange to yellow margin that should be thoroughly revised. Prudhoe (1977) reported from Queensland a species with two male gonopores which he misidentified as *Pseudoceros flavomarginatus*. This species was listed under single male gonopore *Pseudoceros* species (Laidlaw 1902, p. 297 and 298), but Prudhoe's specimen belongs to a dark-background *Pseudobiceros*. The description by Prudhoe fits the species *Pseudobiceros periculosus* (Newman & Cannon 1994) in marginal and background color, elongated cerebral eyespots group, and geographical proximity.

Pseudobiceros punctatus (Laidlaw, 1902) nov. comb.

Taxonomic remarks. The species "*Pseudoceros*" *punctatus* is also absent from any species lists but Marcus' (1950). The original description (Laidlaw, 1902) let no doubt of the specimen having two male gonopores, because it was listed under the *Pseudoceros* species with a pair of penes. It is, thus transferred here to *Pseudobiceros* as a new combination. The species still lacks a re-description that would contain internal and pharynx details.

Pseudobiceros rubrocinctus (Schmarda, 1859)

Taxonomic remarks. This species was originally described as *Eurylepta rubrocincta* (Schmarda 1859) and its genus placement became subject of further discussion (Diesing 1962, Lang 1884). The original description stated that the pharynx is cylindrical, but later drawing (Stummer-Traunfels 1933) of the material showed it was lacking from the pharynx pouch. The species was placed in *Pseudoceros* by Stummer-Traunfels (1933), who also showed it presents two male gonopores. This information was listed by Marcus (1950) and later Faubel (1984) transferred the species to *Pseudobiceros*. However, it is not present in Newman & Cannon's (1994, 1997) revisions. Here we support Faubel's decision and list it as a valid species.

Pseudobiceros schmardae Faubel, 1984

Taxonomic remarks. The name was created to resolve confusion that resulted from the original description of *Prosthecereus latissimus* (Schmarda 1859). Drawings of the type material show that two different animals were described under the same name; one clearly refers to *Prosthecereus* (Stummer-Traunfels 1933, fig. 103a) as it was illustrated by Schmarda (1859, p. 32); and the other animal with two male gonopores (fig. 103b) shows characteristics typical for *Pseudobiceros*. The species was entirely put under *Pseudoceros* and the variation of number of gonopores was considered a plastic character (Stummer-Traunfels 1933, Marcus 1950). With the creation of the genus *Pseudobiceros*, Faubel (1984) created the new name to encompass the flatworm described by Schmarda and illustrated with two male gonopores. The species was not considered in Newman & Cannon's (1994, 1997) revisions. However, we support it is a valid species (Table 1).

Pseudobiceros splendidus (Stummer-Traunfels, 1933)

Taxonomic remarks. The name *Pseudoceros splendidus* was created by Stummer-Traunfels (1933) to substitute *Pseudoceros suberbus* (Lang 1884), because the specific name *suberbus* was already occupied when he transferred the yellow-background species *Eurylepta suberba* (Schmarda 1859) to *Pseudoceros*. The name *Pseudobiceros splendidus* corresponds to a dark-background yellow-orange margin species with a broad geographic distribution, therefore we recommend its revision with all other dark-background species.

Pseudobiceros undulatus (Kelaart, 1858)

Taxonomic remarks. The species was originally described as *Planaria undulata* (Kelaart 1858) and synonymized with Schmarda's (1859) *Eurylepta suberba* and later mentions in different genera (Diesing 1962, Stummer-Traunfels 1933), by Marcus (1950). Stummer-Traunfels (1933) illustrated the species having two male gonopores, thus it was transferred to *Pseudobiceros* by Faubel (1984). There is, however, a disparity in the drawings presented by Schmarda (1859), without a clear purplish median line, and Collingwood (1876), with the median line. This species should be further studied with the examination of fresh specimens as to solve if there is such color plasticity. It is unclear why this species was left out by Newman & Cannon (1994, 1997).

Pseudobiceros viridis (Kelaart 1858)

Taxonomic remarks. The species *Pseudoceros viridis* was included in *Pseudobiceros* in Faubel's (1984) revision based evidences that it has two instead of one male gonopore and pointed ear like tentacles (Stummer-Traunfels 1933, p. 3543; Marcus 1950). However, this species is not present in Newman & Cannon's (1994) revision. Later described mottled green species such as *Pseudobiceros brogani* and *Pseudobiceros kryptos* (Newman & Cannon, 1997) are externally similar to *P. viridis* and are also from the Indo-Pacific. They should be compared with *P. viridis* material from the type locality and corresponding histological slides so as to confirm these three species are indeed different.

Pseudobiceros wirtzi sp. nov.

Figures 1 and 2

Type material. Holotype: One specimen 21 x 16 mm collected October 2009 at Senegal, near Ngor Island (Voucher ZSM20160015HT).

Paratypes: Two specimens in 96% ethanol collected 14.10.2009 at Santo Antão, Cape Verde (Voucher ZSM20160016PT)

Geographic distribution. Senegal and Cape Verde. Additional photographic records from Madeira (17.03.2009, photo cortesy prof. Dr. Peter Wirtz) and Canarias Islands (Vera *et al.* 2008).

Etymology. The species is named after Prof. Dr. Peter Wirtz, who provided the material and has contributed with numerous marine invertebrate field guides over the years.

Diagnosis. Black to very dark brown background color with narrow yellow lines, some of them partly white, mostly on their tips. Thin lines scattered on dorsal surface, without distinctive orientation; most transverse but not straight, curving and some even splitting.

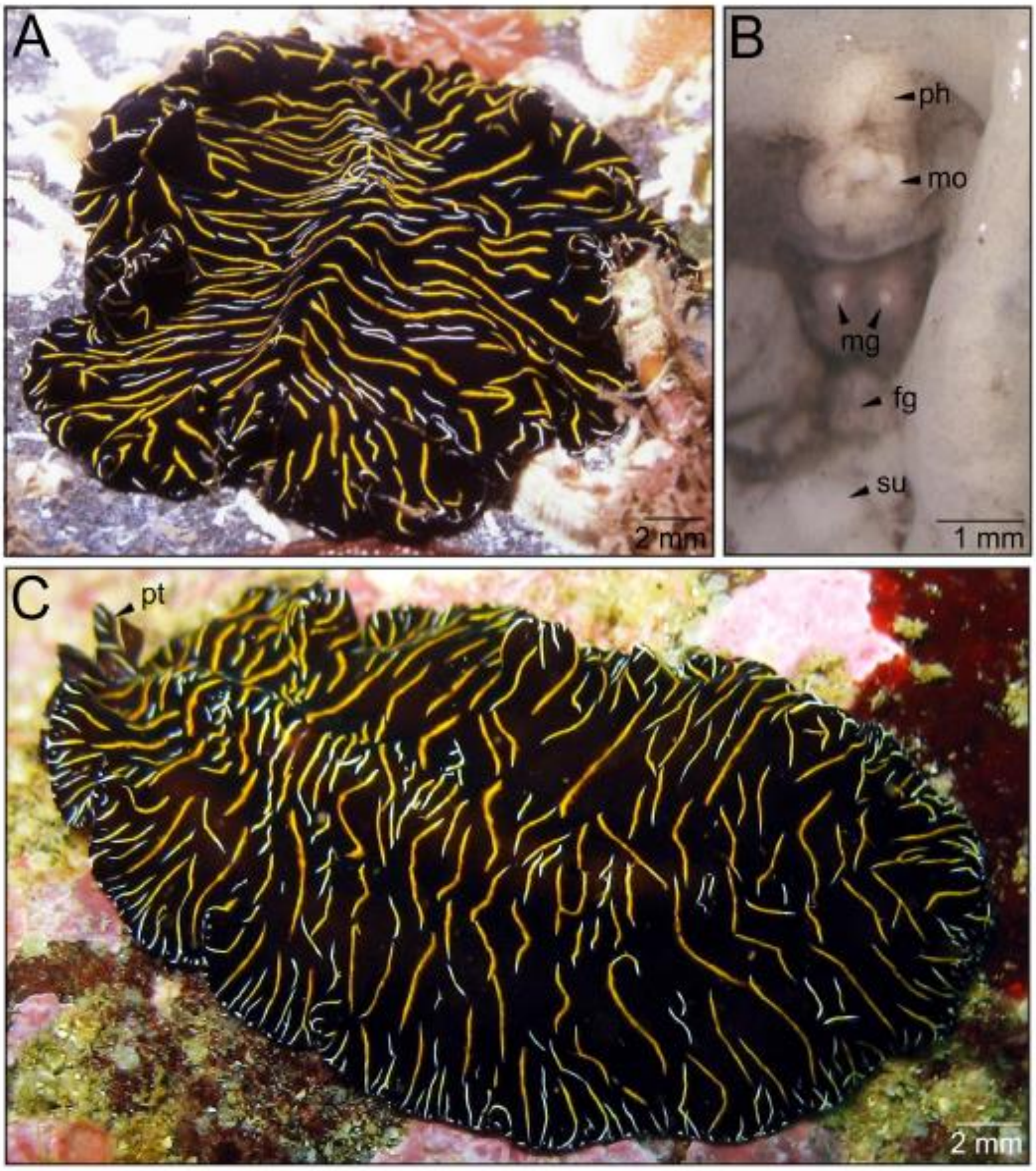

FIGURE 1. A—*Pseudobiceros wirtzi* **sp. nov.** *in situ* from Madeira; B—detail of the ventral surface; C—*P. wirtzi* **sp. nov.** *in situ* from Senegal. fg: female gonopore; mg: male gonopore; mo: mouth; ph: pharynx; pt: pseudotentacles; su: sucker.

Description. Color: Black to very dark brown background color. Narrow yellow lines, some of them partly white, mostly on their tips. Thin lines scattered on dorsal surface, without distinctive orientation; most transverse but not straight, curving and some even splitting. In Senegal specimen lines white when nearer to margin; in Madeira worms, yellow lines and all white lines in middle of body (Fig. 1A, C).

Form: body rounded, delicate constitution, ruffled margin.

Pseudotentacles: pointed ear-like, about 2 mm long (Fig. 1C, Fig. 2A).

Eyes: cerebral eyespots arranged in horseshoe shape cluster of approximately 18 eyespots. Deep dark coloration and contracted pseudotentacular area making eyespots counting difficult. Ventral pseudotentacular eyespots in four groups, two in sinus between folds, and other two on each broad flap of marginal tentacles (Fig. 1A). Dorsally, two groups with evenly spaced eyespots in broader part of pointed ear-like tentacle, and two groups, one in each pseudotentacular tips (Fig. 1A). These more densely arranged as in main pseudotentacle structure.

Digestive system: mouth opens at 4 mm from anterior margin, pharynx short with 4 to 5 shallow folds, 1.7 mm long (Fig. 1B).

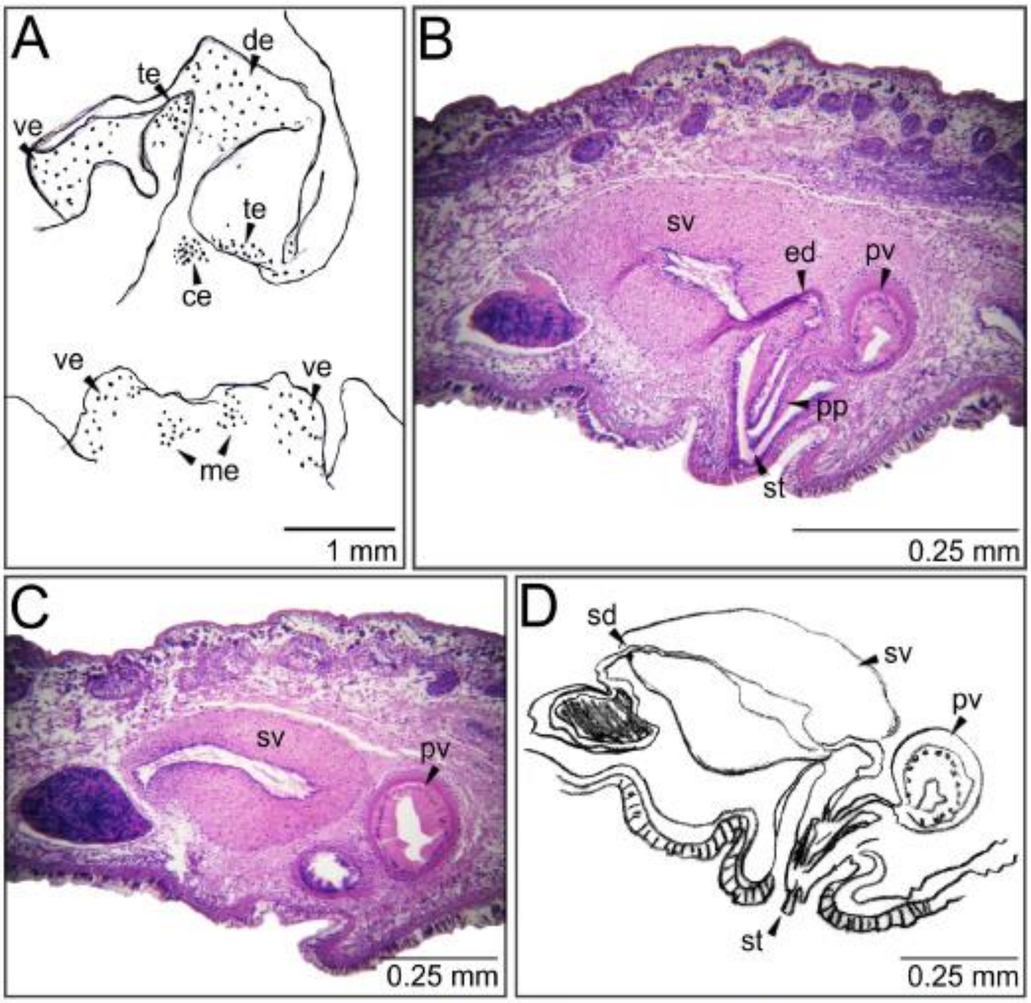

FIGURE 2. A—*Pseudobiceros wirtz* **sp. nov.** dorsal and ventral diagrams of the pseudotentacular area; B and D—sagittal sections of male reproductive structures; C—diagram of reconstruction of slides. ce: cerebral eyespots; de: dorsal eyespots; ed: ejaculatory duct; me: middle ventral eyespots; pp: penis papilla; pv: prostatic vesicle; te: pseudotentacular tip eyespots; sd: seminal duct; st: stylet; sv: seminal vesicle; ve: ventral eyespots.

Body wall: sucker 1 mm in diameter, located at 1.2 mm from female gonopore. Ventrally, epidermis almost twice as thick as basement membrane, densely ciliated. Muscular layers thin, outer longitudinal, followed inward by circular and inner diagonal.

Gonopores: two male and one female gonopores. Male pores 0.5 mm in diameter at 5.5 mm from anterior margin; female pore 1 mm behind male gonopore, 6 mm in diameter (Fig. 1B).

Male reproductive system: seminal vesicle large and elongated, 0.5 mm long and 0.3 mm broad. Prostatic vesicle rounded and 0.19 mm in diameter (Fig. 2B, C, D). Ejaculatory duct straight, 0.2 mm long. Male atrium shallow, penis papillae 0.25 long and stylet short.

Female reproductive system: specimen seems to be immature, since we have not found in our slides female structures, like cement glands, vagina and uteri.

Taxonomic remarks. The presence of two male gonopores, smooth dorsal surface, simple and shallow folded pharynx and complex folded pseudotentacles place the new species in the genus *Pseudobiceros*. Pseudocerotidae species with black background and yellow and white lines color pattern are not common. *Pseudoceros zebra* generally resembles the studied species in its color pattern (Rüppell & Leuckart 1828), but, they belong to different genera. *Pseudoceros zebra* present the complex ruffled pharynx typical for *Pseudoceros*, while *Pseudobiceros wirtzi* **sp. nov.** has few simple folds in its pharynx. In addition, the newly described species lacks a marginal band

and exhibits a dorsal surface with thin yellow and white transverse and multiple lines in multiple directions, mostly transverse, instead of the lack of pigmentation between black areas showed by *Pseudoceros zebra*.

In Marcus' (1950), Faubel's (1984), and Newman & Cannon's (1994) revisions of accepted *Pseudoceros* and *Pseudobiceros* species, no other *Pseudobiceros* species match the color pattern presented by *P. wirtzi*. Newman & Cannon pointed out species with transverse lines pattern such as *Pseudobiceros bedfordi, P. dendricticus, P. flavolineatus, P. fulgor,* but all present a distinctive margin, which is lacking in our specimens. *Pseudobiceros bedfordi*, (Laidlaw 1903a) has a much more complex color pattern with wider stripes instead of lines, and with blotches, mottling, and different colored dots that are absent from *P. wirtzi*. *Pseudobiceros dendricticus*, has yellow background color and brown longitudinal lines and a yellow median line (Prudhoe 1989), instead of black background color and yellow and white lines as the studied specimens. *Pseudobiceros flavolineatus* (Prudhoe 1989) is the one that most resembles *P. wirtzi*, but it presents a double row of dark spots on its margin, has a reddish brown background color and the narrow yellow lines are disposed from the median line to the margin without touching each other, in a concentric design, which is not the case in *P. wirtzi*. The Australian species *P. fulgor* (Newman & Cannon 1994) has white stripes instead of yellow and a lighter background color of brownish orange or deep pink, and presents yellow or cream blotches and black margin that are absent in *P. wirtzi*, in addition to a rounded seminal vesicle instead of elongated. The studied specimens belong to the same species as the ones illustrated in Pérez Sanchéz & Moreno Batet (1990, p: 101), Wirtz & Debelius (2003, p: 84) and Newman & Cannon (2003, p: 84). It was also recently reported, but not described, as Pseudocerotidae sp4 from Canary Islands by Vera *et al.* (2008).

Discussion and conclusions

According to Faubel (1984) and Newman & Cannon (1994), the pseudocerotid genera *Pseudoceros* and *Pseudobiceros* can be unambiguously separated by several features. We applied such diagnostics to *Pseudoceros* species listed by Marcus (1950), Faubel (1984), Prudhoe (1985) and Newman & Cannon (1994, 1997) and to species listed as *incertae sedis*. We thus transferred one further species to *Pseudobiceros* that resulted from a new combination. Most confusion was because older descriptions (eg.: Stimpson 1857; Kelaart 1858) lacked figures and details of the described species, listing a limited number of external morphological features. Later descriptions based only on drawings (Prudhoe 1989), when the revision of type material was not possible, also mislead the assignment of a species to its correct genus. The species newly transferred to *Pseudobiceros* still lack a through description, especially of internal characters. As an example for a modern descriptive standard we here describe a new species showing distinctive internal and external features. Complex external color patterns are usually suitable to differentiate polyclad species (Newman & Cannon 1995a) but may fail in case of cryptic species (Litvaitis *et al.* 2010). Also, relying only in color patterns is risky since there might be polychromatism and selection pressure for mimicry at play (Padula in proof stage). This can confuse taxonomists and result in wrong or confusing identification. But, at the same time it can open a whole new field for the study of marine invertebrate ethology.

Biogeographical data on polyclads is virtually absent. Nevertheless, large or beautiful species like the herein described one and others, like *Prostheceraeus giesbrechtii*, *Prostheceraeus roseus*, *Yungia aurantiaca*, *Pseudoceros velutinus*, *Pseudoceros* cf. *maximus*, *Thysanozoon brocchii*, are usually reported in invertebrate identification guides or species lists (Pérez Sanchéz & Moreno Batet 1990; Wirtz & Debelius 2003, Newman & Cannon 2003, Vera *et al.* 2008). There is accumulating evidence suggesting that the biogeographical province West African Transition may share more species with the Lusitanian province than with other Tropical Atlantic provinces (Spalding *et al.* 2007). This is a very preliminary conclusion, since there is a lack of studies in that area. However, after almost one decade of sampling in different parts of the Southwestern Atlantic (Bahia *et al.* 2012, 2014 and 2015) we have not found any amphi-Atlantic polyclad species. This is not the case for ecologically similar groups like nudibranchs (Goodheart *et al.* 2015) and it is already well corroborated for reef fishes (Floeter *et al.* 2008). Further sampling on Eastern Africa coast and on mid-Atlantic Islands will provide valuable evidence for understanding the polyclad's biogeography in the Tropical and South Atlantic.

TABLE 1. Valid *Pseudobiceros* species.

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros apricus Newman & Cannon, 1994	Transparent orange with raised white microdots and irregular scattered large white dots, darker pigment in the median line. Marginal band black with white dots, pseudotentacles grey-black with white tips. Gut content occasionally orange.	South Great Barrier Reef	Square pseudotentacles. Pharynx large and elongated with about 8 folds at each side. Oval seminal vesicle (4 to 5 times larger than the prostatic vesicle), short ejaculatory duct. Shallow female atrium.	Newman & Cannon 1994, 1997	-
Pseudobiceros bajae (Hyman, 1953)	Black with whitish speckles.	Gulf of California	Pointed ear-like pseudotentacles. Pharynx elongated with 5 folds. Spermiducal vesicles present, oblong prostatic vesicle. Long and coiled ejaculatory duct.	Hyman 1953 Newman & Cannon 1994, 1997	*Pseudoceros bajae* Hyman, 1953 *Pseudobiceros bajae* Newman & Cannon, 1994
Pseudobiceros bedfordi (Laidlaw, 1903a)	Purplish brown background color with numerous transverse arcs, stripes, spots and dashes of yellowish white, pink or buff color, distributed irregularly but bilateral symmetric. Margin dark sometimes spotted with green	Singapore, Philippines, Palau Is., Micronesia, North Great Barrier Reef, West Australia, Sulawesi, Indonesia, Mozambique and Vietnam	Pointed ear-like pseudotentacles. Small pharynx with 6 folds at each side. Short seminal vesicle, long ejaculatory duct, prostatic vesicle elongated. Shallow female atrium.	Laidlaw 1903a Bock 1913 Kato 1943 Marcus 1950 Hyman 1954, 1955, 1959a Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros bedfordi* Laidlaw, 1903a *Pseudoceros micronesianus* Hyman, 1955 *Pseudobiceros micronesianus* Faubel, 1984
Pseudobiceros brogani Newman & Cannon, 1997	Background variable, olive green or light brown, mottled with white; brown and white dots present; darker medially. Margin wide olive green with narrow dark green and white interrupted rim or wide orange brown with narrow dark grey and white interrupted rim. Tentacles tips white without marginal bands.	West Australia	Square pseudotentacles. Pharynx small with 5-6 folds at each side. Rounded prostatic vesicle, disform seminal vesicle, short ejaculatory duct and long stylet.	Newman & Cannon 1997	
Pseudobiceros caribbensis Bolaños, Quiroga & Litvaitis, 2007	Transparent brown, darker medially; irregular patches of numerous and densely concentrated white dots at the median line. Dorsal surface covered with dark brown and white dots.	Curaçao, Jamaica, Florida and Honduras. French Mediterranean?	Pointed ear-like pseudotentacles. Pharynx small with about 5 folds. Large and oval seminal vesicle, rounded prostatic vesicle. Long stylet and straight ejaculatory duct.	Bolaños, Quiroga & Litvaitis 2007	-

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TABLE 1. (Continued)

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros cinereus (Palombi, 1931)	Greyish with black margin and one grey line at each side of the median line.	New Guinea	Square-shaped pseudotentacles	Palombi 1931 Marcus 1950 Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros cinereus* *Pseudobiceros cinereus* Faubel, 1984 *Pseudobiceros cincereus* Newman & Cannon, 1994
Pseudobiceros damawan Newman & Cannon, 1994	Background mottled grey and white with black spots medially light orange, marginal band orange interrupted by white spots	Papua New Guinea, South Great Barrier Reef and West Australia	Square pseudotentacles. Large pharynx with about 9 folds at each side. Rounded seminal vesicle short ejaculatory duct and short stylet.	Newman & Cannon 1994, 1997	-
Pseudobiceros dendriticus (Prudhoe, 1989)	Yellow background dappled with dark brown, median line yellow with branches that extend to the margin. Black narrow margin, are between margin and brown dapple is reddish brown	Mozambique	Pharynx with shallow folds. Two male gonopores. Folded tentacles.	Prudhoe 1989 Newman & Cannon 1994, 1997	*Pseudoceros dendriticus* Prudhoe, 1989 *Pseudobiceros dendricticus* Newman & Cannon, 1994
Pseudobiceros evelinae (Marcus, 1950)	Wine red with three marginal bands; inner black, middle orange and thinner outer black band	Southeastern and Northeastern Brazil	Pointed ear-like pseudotentacles. Pharynx elongated with 7 folds. Rounded seminal vesicle, oblong prostatic vesicle.	Marcus 1950 Faubel 1984 Newman & Cannon 1994, 1997 Bahia et al. 2012, 2014	*Pseudoceros evelinae* Marcus, 1950 *Pseudobiceros evelinae* Faubel, 1984
Pseudobiceros flavocanthus Newman & Cannon, 1994	Black background with inner white and outer yellow marginal band	Papua New Guinea	Pointed ear-like pseudotentacles. Pharynx long but with few folds (5) Elongated seminal vesicle, rounded prostatic vesicle and short ejaculatory duct. Shallow male and female atrium.	Newman & Cannon 1994, 1997	-
Pseudobiceros flavolineatus (Prudhoe, 1989)	Reddish brown background with yellow distributed from median line to margin rarely touching each other. In the margin irregular double row of black spots.	Mozambique	Pointed ear-like pseudotentacles. Pharynx with about 5 folds at each side.	Prudhoe 1989 Newman & Cannon 1994, 1997	*Pseudoceros flavolineatus* Prudhoe, 1989 *Pseudobiceros flavolineatus* Newman & Cannon,1994
Pseudobiceros flowersi Newman & Cannon, 1997	Background from bright olive to dark brown, chocolate brown or black near the margin. Small specimens with speckles of white. Narrow white median line bordered by darker pigment. Three marginal bands inner black and wide, middle olive green or brown and outer white rim. Tentacles tips white and white triangle in between.	North Great Barrier Reef and Philippines	Square pseudotentacles. Pharynx short and with few folds. Oblong seminal vesicle and oval prostatic vesicle, Short stylet and ejaculatory duct.	Newman & Cannon 1997	-

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TABLE 1. (Continued)

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros fulgor Newman & Cannon, 1994	Broken streaks Background orange brown or deep pink with numerous broken irregular, longitudinal and transverse white stripes. Yellowish or cream blotches over the dorsal surface. Black margin	Philippines, South great barrier Reef, Indonesia, Marshall Islands, Micronesia	Pointed ear-like pseudotentacles. Pharynx short with 4 folds at each side. Rounded seminal and prostatic vesicles. Shallow male and female atrium.	Newman & Cannon 1994, 1997	-
Pseudobiceros fulvogriseus (Hyman, 1959)	Light grey background with flushed with yellowish brown. Light median line and light rim at the margin. Brown tentacles with light margin.	Palau Is.	Pointed ear-like pseudotentacles. Pharynx short with 5 folds.	Hyman 1959 Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros fulvogriseus* Hyman, 1959 *Pseudobiceros fusvogriseus* Faubel, 1984
Pseudobiceros gardineri (Laidlaw, 1902)	Grey background scattered with irregular black marks of varying size	Hulule Atoll	Pointed ear-like pseudotentacles. Small pharynx with 5 folds. Two male gonopores.	Laidlaw 1902 Marcus 1950 Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros gardineri* Laidlaw, 1902 *Pseudobiceros gardineri* Faubel, 1984
Pseudobiceros gloriosus Newman & Cannon, 1994	Black background with orange inner marginal band, middle pink and purple external narrow band (trim)	Papua New Guinea, Fiji, south and north Great Barrier Reef, West Australia and Vanuatu	Square pseudotentacles. Large pharynx with 8 folds at each side. Oval seminal and prostatic vesicles. Long ejaculatory duct, long stylet and shallow male and female antra.	Newman & Cannon 1994, 1997	-
Pseudobiceros gratus (Kato, 1937)	Background cream to yellow, with three black to brown lines, one broader median and two marginal that join at the ends of the median line. Dark brown margin.	South and North Great Barrier Reef, Papua New Guinea, Ceylon, Japan, Micronesia and Hawaii	Pointed ear-like pseudotentacles. Short pharynx with about 6 folds.	Schmarda 1859 Stummer-Traunfels 1933 Kato 1937, 1944 Marcus 1950 Hyman 1959 Faubel 1984 Newman & Cannon 1994, 1997	*Eurylepta striata* Schmarda, 1859 *Proceros striatus* Diesing, 1862 *Pseudoceros striatus* Stummer-Traunfels, 1933 *Pseudoceros gratus* Kato, 1937 *Pseudoceros strigosus* Marcus, 1950 pro *Pseudoceros striatus* (Schmarda) *Pseudobiceros strigosus* Faubel, 1984
Pseudobiceros hancockanus (Collingwood, 1876)	Black with inner orange and outer white marginal bands. Pseudotentacles with marginal band.	South Great Barrier Reef, Laccadives, Japan, Singapore, Philipines	Square pseudotentacles. Small pharynx with 5 folds. Elongated seminal vesicle, more like spermiducal bulbs. Oval prostatic vesicle.	Collingwood 1876 Laidlaw 1903 Bock 1913 Kaburaki 1923 Marcus 1950 Newman & Cannon 1994	*Proceros hancockanus* Collingwood, 1876 *Stylochopsis malayensis* Collingwood, 1876 *Prosthecereus hancockanus* Lang, 1884 *Pseudoceros hancockanus* Laidlaw 1903, Kaburaki 1923, Marcus, 1950 *Pseudoceros malayensis* Bock, 1913

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TABLE 1. (Continued)

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros hymanae Newman & Cannon, 1997	Purple or dark purple background with bright orange or yellow margin and black narrow rim. Tentacles black, with bands only laterally.	Hawaii, Papua New Guinea, South Great Barrier Reef	Square pseudotentacles. Rounded prostatic vesicle. Oblong seminal vesicle	Hyman 1960 Newman & Cannon 1997	*Pseudoceros affinis* Hyman, 1960
Pseudobiceros izuensis (Kato, 1944)	Pale green mottled with white and dotted with black. Olive green margin with radial streaks and sepia brown median line laced with white. Sepia brown pseudotentacles with white tips and dots.	Palau Is.	Pointed ear-like pseudotentacles. Pharynx large with about 7 folds. Two male gonopores.	Kato 1944 Hyman 1959 Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros izuensis* Kato, 1944 *Pseudobiceros izuensis* Faubel, 1984
Pseudobiceros kyptos Newman & Cannon, 1997	Mottled olive green to lime green and white, large irregular brown and olive green spots on the margin	Papua New Guinea, North and South Great Barrier Reef, West Australia, Bali, Indonesia, Lord Howe Islands	Square pseudotentacles. Small pharynx. Elongated seminal vesicle and rounded prostatic vesicle. Short ejaculatory duct.	Newman & Cannon 1997	-
Pseudobiceros luteomarginatus (Yeri & Kaburaki, 1918)	Velvety black background with yellow inner and brick brown outer marginal band.	India Misaki, Japan	Oval prostatic vesicle and long stylet. Spermiducal bulbs present.	Yeri & Kaburaki 1918 Kato 1937 Marcus 1950 Faubel 1984	*Pseudoceros luteomarginatus* Yeri & Kaburaki, 1918 *Pseudobiceros luteomarginatus* Faubel, 1984
Pseudobiceros mikros Newman & Cannon, 1997	Transparent mottled brown and grey with white dots in round clusters. White margin with yellow rim. White triangle between pseudotentacles.	Papua New Guinea	Pointed ear-like pseudotentacles. Small pharynx. Rounded seminal and prostatic vesicle. Spermiducal bulbs present. Coiled ejaculatory duct. Short stylet.	Newman & Cannon, 1997	-
Pseudobiceros miniatus (Schmarda, 1859)	Rusty-orange background with darker median line, whitish freckles, and bluish-white inner and dark-blue outter margin	Sri Lanka	Pointed ear-like pseudotentacles. Two male gonopores.	Schmarda 1959 Diesing 1862 Lang 1884 Stummer-Tranufels 1933 Marcus 1950 Faubel 1984	*Eurylepta miniata* Schmarda, 1859 *Proceros miniatus* Diesing, 1862 *Yungia miniata* Lang, 1884 *Pseudoceros miniatus* Stummer-Traunfels, 1933 *Pseudobiceros miniatus* Faubel, 1984
Pseudobiceros murinus Newman & Cannon, 1997	Transparent mottled green-grey with white and black dots, darker medially with red or brown. Margin with yellow-orange band and narrow clear rim.	Papua New Guinea	Pointed ear-like pseudotentacles. Rounded prostatic vesicle and rounded oblong seminal vesicle. Long ejaculatory duct.	Newman & Cannon, 1997	-

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TABLE 1. (Continued)

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros nigromarginatus (Yeri & Kaburaki, 1918)	Blackish brown with narrow black margin and two light colored longitudinal bands one at each side of the median line	Japan	Pointed ear-like pseudotentacles. More or less parallel prostatic and seminal vesicles. Both oblong.	Yeri & Kaburaki 1918 Marcus 1950 Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros nigromarginatus* Yeri & Kaburaki, 1918 *Pseudobiceros nigromarginatus* Faubel, 1984
Pseudobiceros pardalis (Verrill, 1900)	Purple-brownish background blending into black towards the margin, with large orange and smaller yellow dots outlined by a black shadow. Numerous, small white spots along the margin.	Bermudas, Bahamas, South Florida, Panama, Brazil	Square pseudotentacles. Long pharynx with about 8 folds. Rounded prostatic vesicle and oval seminal vesicle. Long stylet and short ejaculatory duct.	Verrill 1900 Marcus 1950 Bolaños et al. 2007 Bahia et al. 2012, 2014, 2015	*Pseudoceros pardalis* Verrill, 1900 *Pseudobiceros pardalis* Bolaños et al. 2007
Pseudobiceros periculosus Newman & Cannon, 1994	Black background with wide orange marginal band and pseudotentacles black.	South Great Barrier Reef and Hawaii	Square pseudotentacles. Pharynx large with about 8 folds. Seminal vesicle large, oval and right above and mostly anterior to the rounded prostatic vesicle. Ejaculatory duct loops over the prostatic vesicle and join the prostatic duct posteriorly. Small stylet. Deep male and female antra.	Newman & Cannon 1994, 1997	*Pseudoceros flavomarginatus* (*sensu* Prudhoe 1977; p. 592)
Pseudobiceros phillippinensis (Kaburaki, 1923)	Black purplish, bright purple median line bordered at each side by ash-grey band. Outer orange marginal band and inner white band that gets greyish toward the background color.	Philippines	Pointed ear-like pseudotentacles. Two male gonopores.	Kaburaki 1923 Marcus 1950 Faubel 1984 Newman & Cannon 1994, 1997	*Pseudoceros phillippinensis* Kaburaki, 1923 *Pseudobiceros phillippinensis* Faubel, 1984
Pseudobiceros punctatus (Laidlaw, 1902) **nov. comb.**	Greyish pale yellow with small black dots.	Maldives	Pointed ear-like pseudotentacles. Two male gonopores.	Laidlaw 1902 Marcus 1950	*Pseudoceros punctatus*
Pseudobiceros rubrocinctus (Schmarda, 1859)	Greenish-black or velvety-black with scares with points. Scarlet-red margin.	Sri Lanka	Possibly square pseudotentacles. Cylindrical pharynx? Two male gonopores.	Schmarda 1859 Diesing 1962 Lang 1884 Stummer-Tranufels 1933 Marcus 1950 Faubel 1984	*Eurylepta rubrocincta* Schmarda, 1859 *Schmardea rubrocincta* Diesing, 1862 *Yungia rubrocincta* Lang, 1884 *Pseudoceros rubrocinctus* Stummer-Traunfels, 1933 *Pseudobiceros rubrocinctus* Faubel, 1984
Pseudobiceros schmardae Faubel, 1984	Reddish-yellow with brownish median line and rounded freckles of the same color.	Sri Lanka	Pointed ear-like. Two male gonopores. Small pharynx with 4 to 5 folds.	Schmarda 1859 Stummer-Tranfels 1933 Marcus 1950 Faubel 1984	*Prosthecereus latissimus* (type B) Schmarda, 1859 *Pseudoceros latissimus* Stummer-Traunfels, 1933 *Pseudobiceros schmardae* Faubel, 1984

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TABLE 1. (Continued)

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros sharroni Newman & Cannon, 1997	Opaque green-grey, lighter medially and marginally and extremely narrow orange rim. Pseudotentacle with orange rim.	Palau Is.	Pointed ear-like pseudotentacles. Rounded seminal vesicle, long and coiled ejaculatory duct and oblong prostatic vesicle.	Newman & Cannon 1997	-
Pseudobiceros splendidus (Lang, 1884)	Deep bluish or purplish black, marginal bands inner white or orange yellow, outer black	Mediterranean Vietnam, Galapagos Puerto Rico Bermuda, Mozambique	Two male gonopores.	Lang 1884 Stummer-Traunfels, 1933 Marcus 1950 Prudhoe 1989 Newman & Cannon 1994, 1997	*Pseudoceros suberbus* Lang, 1884 *Pseudoceros splendidus* Stummer-Traunfels, 1933
Pseudobiceros stellae Newman & Cannon, 1994	Black or chocolate brown background with raised white microdots, larger dots forming flower like arrangement. Pseudotentacle tips white.	Western Australia, South and north Great Barrier Reef, Papua New Guinea and Hawaii	Square pseudotentacles. Pharynx short with 5 folds. Seminal vesicle narrow, prostatic vesicle oblong and long ejaculatory duct. Long stylet. And deep male and female antra.	Newman & Cannon 1994	*Pseudobiceros* sp. Poulter, 1987 pl. 2.1.2 e.
Pseudobiceros undulatus (Keelart, 1858)	Pale yellow with purplish median line. Undulating and spots purplish-brown. Margin purplish.	Sri Lanka	Pointed ear-like pseudotentacles. Long pharynx with about 10 folds. Two male gonopores.	Keelart 1858 Collingwood 1976 Schmarda 1859 Diesing 1862 Stummer-Tranfels 1933	*Planaria undulata* Keelart, 1858 *Eurylepta suberba* Schmarda, 1859 *Proceros suberbus* Diesing, 1862 *Eurylepta undulata* Collingwood, 1876 *Pseudoceros suberbus* Stummer-Traunfels, 1933 *Pseudoceros undulatus* Marcus, 1950 *Pseudobiceros undulatus* Faubel, 1984
Pseudobiceros uniaborensis Newman & Cannon, 1994	Black or dark brown background with three narrow marginal bands: inner orange, middle transparent grey and outer white rim. White spots might be present dorsally. Pseudotentacles black with white tips.	Western Australia, South and north Great barrier Reef, Papua New Guinea, Philippines and Iran	Pointed ear-like pseudotentacles. Pharynx long with about 11 small folds at each side. Large oval seminal vesicle spermiducal bulb like. Oblong prostatic vesicle, short ejaculatory duct and deep male and female antra.	Newman & Cannon 1994, 1997 Maghsoudlou & Rahimian 2014	-

… …continued on the next page

TABLE 1. (Continued)

***Pseudobiceros* species**	**Color pattern**	**Distribution**	**Available information**	**Literature**	**Synonyms**
Pseudobiceros viridis (Kelaart, 1858)	Green mottled brown, dark grizzly brown.	Sri Lanka	Pointed ear-like pseudotentacles. Short pharynx with five folds.	Kelaart 1858 Collingwood 1876, Hyman 1959, 1960 Faubel 1984	*Planaria viridis* Keelart, 1858 *Prosthecereus viridis* Schmarda, 1859 *Eurylepta viridis* Keelart *in* Collingwood, 1876 *Pseudoceros viridis* Stummer-Traunfels, 1933 *Pseudoceros virescens* Hyman, 1959
Pseudobiceros wirtzi **sp. nov.**	Black background color. Thin yellow lines, some partly white, scattered on dorsal surface, without distinctive orientation, also most not straight, curving and some even splitting.	Cape Verde, Senegal, Madeira and Canary Is.	Pointed ear-like pseudotentacles. Pharynx short with 4 to 5 shallow folds	Wirtz & Debelius 2003 Vera *et al.* 2008 Wirtz 2009 Wirtz 2011 Present paper	*Pseudoceros* sp. Pérez Sanchéz & Moreno Batet, 1990 *Pseudoceros* sp. nov. Wirtz & Debelius, 2003 *Pseudobiceros* sp. 9 Newman & Cannon 2003 *Pseudobiceros* sp4 Vera *et al.* 2008 *Pseudobiceros new species* Wirtz, 2009 *Pseudobiceros* n. sp. Wirtz, 2011

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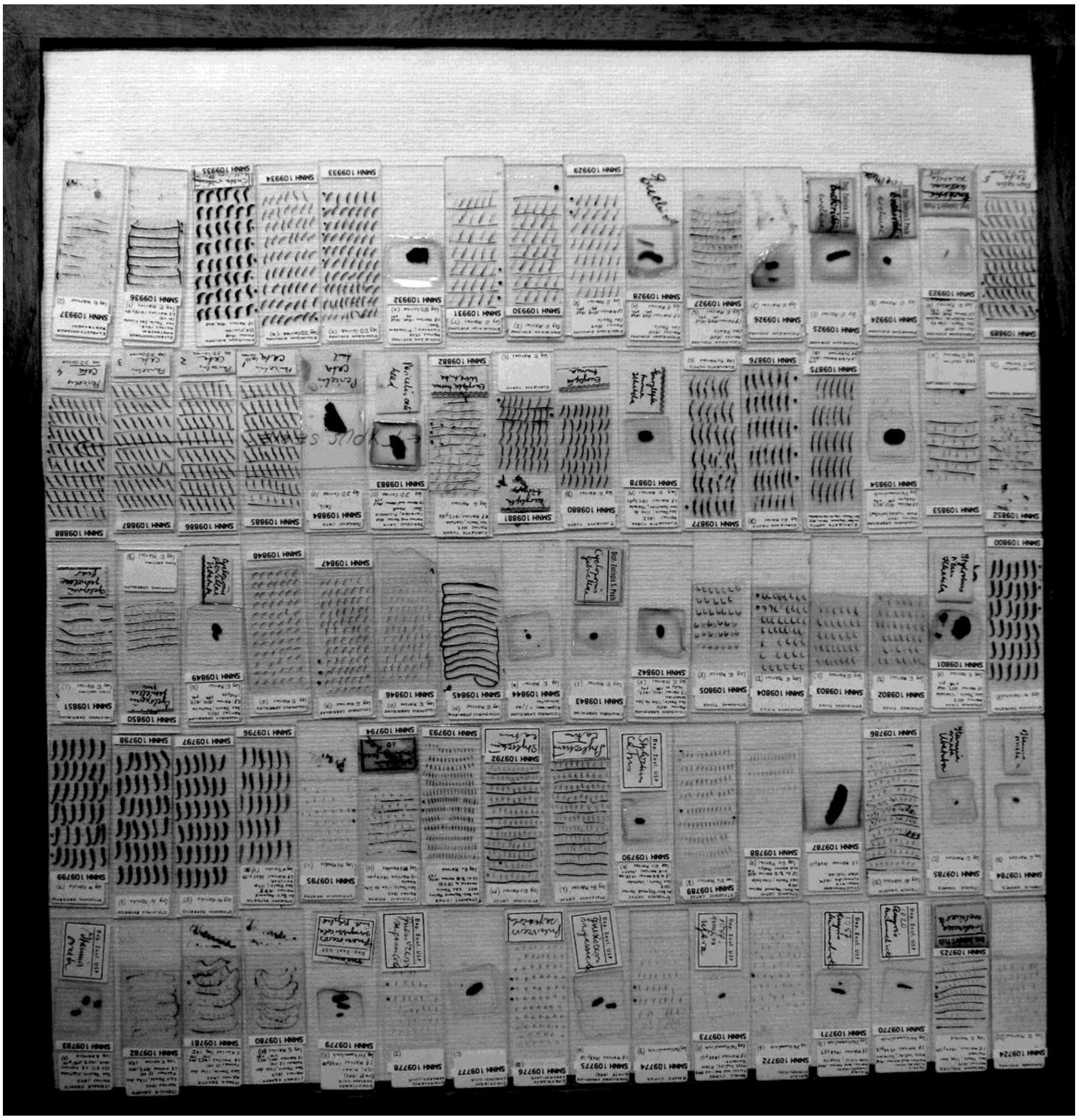
PART 2: POLYCLADIDA TAXONOMY



Chapter 4.

Brazilian Polycladida (Rhabditophora: Platyhelminthes): Re-discovery of Marcus type material and general revision

Brazilian Polycladida (Rhabditophora: Platyhelminthes): Re-discover of Marcus type material and general revision

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Abstract

Polyclads are a conspicuous group of marine invertebrates, the most charismatic members of the phylum Platyhelminthes. From Brazil, a total of 71 polyclad species were reported or described. Only three of them were recently described, five are recent records for the Brazilian coast, and 55 were described by Ernest and Eveline Marcus, who were by far the most productive workers. However, they quite often published in Portuguese or German, rather than English, and have not designated type material or specified material deposited in museum collections. Most of the polylcad material studied by the Marcus was found to be in the Stockholm Natural History Museum. Here we summarize the knowledge about Brazilian polyclad biodiversity, give information about deposited material in different museums for future reference, and designate type material for the species that did not have any. We examined 58 polyclad species reported from Brazil and designated type material and information available on type series of 52 species. Lectotypes (89 vouchers) were designated for 30 species and paralectotypes (73 specimens / 70 vouchers) were designated for 22 Brazilian species. Among the 261 type vouchers examined in this work, 22 species (77 vouchers) had material recognized as holotypes and 2 vouchers were recognized as paratypes. Of the total number of species reported from Brazil, 10 species remain without information about type material. In the present paper we also create a new family (Triadommidae **nov. fam.**) based on characters presented by the type genus and we make a new combination (*Lurymare cynarium* **nov. comb.**). Eleven species have their geographical distribution range broadened and 42 were photographed for the first time, five of those were photographed live as well. The numbers of Brazilian polyclad species is expected to rise when different regions and environments are surveyed.

Keywords

type material, polyclads, Brazil, taxonomy, holotypes and lectotypes

INTRODUCTION

Polyclads are a conspicuous group of marine invertebrates, the most charismatic members of the phylum Platyhelminthes. Polycladida are free-living Platyhelminthes inhabiting all kind of marine environments, like coral reefs, rocky shores, soft bottoms and deep-water (Newman & Cannon 2003; Quiroga et al. 2006). Polyclads have a simple and dorsoventrally flattened body, with a much ramified intestine, and their hermaphrodite reproductive anatomy and external morphology (eyespots arrangements, tentacles, and pharynx) are used in taxonomy (Hyman 1951). In general, polyclads live associated with invertebrates on which they feed (Marcus & Marcus 1951), and are used as models in studies about mimetism (Newman et al. 1994) and aposematism (Ang & Newman 1998), regeneration (Egger et al. 2007), toxicology and predation (Ritson-Williams et al. 2006), pharmacologically compounds (Schupp et al. 2001). These animals can also damage oyster aquaculture (Sluys et al. 2005).

About 1000 species of Polycladida are described in the world (Faubel 1983, 1984; Prudhoe 1985). The first polyclad material recorded from Brazil was by Plehn (1896), *Latocestus atlanticus* collected somewhere on Rio de Janeiro. Among the researchers that worked on the Brazilian coast are Palombi (1923), Smith (1960), Corrêa (1949, 1957) and Hyman (1955b). However no other researchers were more productive than Ernst Marcus and Eveline Du Bois-Reymond Marcus (Marcus, 1947, 1949, 1950, 1952, Marcus & Marcus 1966, 1968). The continued research on polyclads almost stopped in 1968, when Ernst Marcus passed away and then Eveline Marcus turned her attention to other invertebrates (Du Bois-Reymond Marcus, 1970). The study of this group of animals was resumed recently (Bahia & Padula, 2009, Bahia et al. 2014, Bulnes & Torres, 2014). The new inputs on the study of this group were based on samples of previously unexplored areas in Northeastern Brazil (Bahia et al. 2012, 2015; Queiroz et al. 2013; Bulnes & Torres, 2014) and in the Southeastern Brazil Cabo Frio (Bahia & Padula, 2009; Bahia et al. 2014) region which is a transition zone between the Tropical Southwestern Atlantic and Warm Temperate Southwestern Atlantic biogeographic provinces (Spalding et al. 2007). This point is also transition between the Tropical Atlantic and the Temperate South America biogeographic realm.

Most descriptions of Brazilian material were made in Portuguese, by germans with the help of native speakers (Marcus 1947), others were made in Italian (Palombi 1923) or German (Du Bois-Reymond 1965). Despite the good intention of making information available to local researchers publishing in not wide spread languages can result in limited understanding and consequently taxonomic errors. Authors from other areas of the world might not acknowledge those papers or treat their information poorly, unable to interpret the data. Another problem related to the study of polyclads in Brazil is that most of the descriptions did not designate type material and did not mention material deposited in museum collections. (Marcus 1949, 1950, 1952). From 1956 on the International Code of Zoological Nomenclature (ICZN) stated that is mandatory to designate type material in the description of a new species (http://iczn.org/iczn/index.jsp) and then the studies about polyclads started to follow that rule (Du Bois Reymond Marcus 1958, 1965). The importance of type material is until today being debated (Amorim et al. 2016) and we see it as a relevant way for contemporary and future researchers to check a taxon hypothesis. Type series are analogous to replicable methods of an experiment, and museum material can be subject of research for many years, serving also as repository of biodiversity (Kemp 2015).

In total 71 polyclad species were reported or described from Brazil. Only three of them were recently described (Bahia et al. 2014, 2015; Bulnes & Torres 2014), five are recent records for the Brazilian coast (Bahia & Padula 2009, Bahia et al. 2014), and 55 were described by Ernest and Eveline Marcus in the years between 1947 and 1968. The material collected and worked by the Marcus was found to be in the Stockholm Natural History Museum, by donation of Eveline Du Bois-Reymond Marcus and the first author had the opportunity to examine it. In addition, polyclads were collected along the Brazilian coast, photographed alive and studied comparatively. The aims of this paper are to (1) summarize the knowledge about Brazilian polyclad biodiversity, (2) give information about deposited material in different museums for future reference, and to (3) designate type material for the species that did not have formally designated type series.

MATERIAL AND METHODS

Collections of fresh material were made in different areas of the Brazilian coast (Figure 1), all specified at the material examined of each species. Animals were photographed alive and fixed in frozen in 4% formalin, and then preserved in ethanol 70%. We made a revision of literature to find all records from the Brazilian coast (table 1). Additionally, material studied by Ernst and Eveline Marcus, and later donated by Eveline Marcus to the Swedish Natural History Museum, was also examined and vouchers are described here. Vouchers deposited in other museums were searched for in http://collections.peabody.yale.edu/ and similar databases (http://www.gbif.org). Dates given throughout the paper are in the day / month / year format. As established by the International

Code of Zoological Nomenclature the information contained in the voucher labels are listed (table 2). For the species without designation of type material we considered, as stablished by the ICZN, all available specimens from an original series as syntypes; in the cases it was possible to distinguish the specimens, we differentiated into designating lectotypes and paralectotypes. This decision was made based on the syntypes that were illustrated by Ernst and Eveline Marcus and that were in best conditions. For the species that had a holotype originally designated (without museum voucher number at the time), we listed the holotype material and considered other material of the original type series as paratypes. The systematic classification followed here is the result of the confrontation of Faubel's (1983, 1984) and Prudhoe's (1985) systems with molecular data, which resulted in a new system (Bahia et al. *in press*). This new concept for Polycladida phylogenetic relationships tried to combine as much characters as possible, instead of putting weight on only characters related to few organs. Thus, *Cestoplana* and *Theama* were placed in Cotylea and some families were accepted despite their status in one or other system.

The legend of museums cited in Table 1: AM – Australian Museum; AMNH – American Museum of Natural History; AK – Auckland War Memorial Museum; CYMX – Centro de Investigación y de Estudios Avanzados, Unidad Mérida, Instituto Politécnico Nacional; CNHE-IBUNAM – Colección Nacional de Helmintos del Institudo de Biologia de la Universidad Autónoma de México; DZUSP – Coleção do Departamento de Zoologia da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo; H - Rijksmuseum van Natuurlijke Historie in Leiden; INV-PLA – Instituto de Investigaciones Marinas y Costeras (INVEMAR); MACN – Museo Argentino de Ciencias Naturales; MCZ – Museum of Comparative Zoology, Harvard University; MNRJ-PLAT – Museu Nacional do Rio de Janeiro; NHMUK – Natural History Museum, London; NMV – Museum Victoria; QM – Queensland Museum; SMF – Senckenberg; SMNH – Swedish Natural History Museum; UF – Florida Museum of Natural History; UNH – University of New Hampshire; USNM – United States Natural History Museum; YPBM – Yale Peabody Museum; ZMA – Zoological Museum of Amsterdam, University of Amsterdam; ZMB – Senckenberg, Collection Vermes; ZMUH – Zoologisches Institut und Zoologisches Museum der Universität von Hamburg.

The label of structures pointed in figures are: ce- cerebral eyespots; ced- common ejaculatory duct; cg- cement glands; cgd- cement gland duct; cp- cement pouch; cud- common uterine duct; ed- ejaculatory duct; edp- ejaculatory duct pouch; es- sphincter between external and internal vagina; ev- external vagina; fa- female atrium; fe- frontal eyespots; fp- female pore; gp- gonopore(s); iv- internal vagina; la- Lang's vesicle; lad- Lang's vesicle duct; ma-

male atrium; me- marginal eyespots; mo- mouth; mp- male pore; ms ms- muscular sheath; mv- marginal vesicles; p- penis; pa- papillae; pe- pseudotentaculat eyespots; pg- prostatic glands; ph- pharynx; po- prostatoid organs; pp- penis papilla; ps- penis sheath; pt- pseudotentacles; pv- prostatic vesicle; s- stylet; su- sucker; sv- seminal vesicle; te- tentacular eyespots; tn- tentacles; ut- uteri; va- vagina; vb- vagina bulbosa; vs- vas deferens.

RESULTS

Of the 71 polyclad species reported or described from Brazil, here we examined 58. No type material is known from: *Zygantroides henriettae*, *Zygantroides plesia*, *Stylochoplana walsergia*, *Hoploplana usaguia*, *Latocestus atlanticus*, *Chromyella saga*, *Cycloporus variegatus*, *Eurylepta aurantiaca*, *Euryleptides brasiliensis* and *Pseudobiceros pardalis*. The authors have recently contributed with collection of fresh material of species described by Ernst and Eveline Marcus, color photos of live specimens and histological sections, descriptions in English and description of two new species (Table 1; see results in Bahia et al 2012, 2014, 2015, Bahia 2016). In this study photos of live material from five species and from all type material examined was illustrated (Figure 2-49). Among the material deposited in the Stockholm Natural History Museum 261 vouchers were of types. From those 77 vouchers are of 22 holotypes and 2 are paratypes (19 holotypes were recognized in this paper). An amount of 89 vouchers, belonging to 30 species, are designated here lectotypes and 73 specimens (70 vouchers) designated as paralectotypes of 22 Brazilian species (Table 2). Another 10 specimens (23 vouchers) from 2 species are recognized as syntypes in this work. This material is listed below together with new material collected by the author and deposited in scientific collections. All species examined were illustrated with color photos of the type material and freshly collected material, when available.

Systematics

Suborder: Acotylea Lang 1884
Family: Euplanidae Marcus & Marcus, 1966
Genus: *Euplana* Girard, 1893
Euplana hymanae Marcus, 1947
Figure 2

Type species of the genus.

Euplana gracilis (Girard, 1850), type by subsequent designation.

Material examined.

Syntypes. One specimen as whole mount of the anterior part (SMNH 109690, 3 x 2.8 mm) and serial sections of the posterior part (SMNH 109054 and SMNH 109055). One specimen as whole mount (SMNH 109691, 7.5 x 2.5 mm). One specimen as whole mount of anterior part (SMNH 109052, 2.5 x 1.9mm) and serial sections of the posterior part (SMNH 109056 and SMNH 109057). One specimen as whole mount of the anterior part (SMNH 109053, 2.2 x 1.5 mm) and serial sections of the posterior part (SMNH 109058). One specimen as whole mount (SMNH 109692, 8 x 3 mm). Four specimens in a whole mount (SMNH 109693, 5.5 x 3 mm, 4.2 x 3 mm, 4.2 x 3 mm and 2.5 x 2 mm). One specimen as serial sections of posterior part (SMNH 109694, SMNH 109695, SMNH 109696). One specimen as serial sections of entire worm (SMNH 109697, SMNH 109698, SMNH 109699, SMNH 109700, SMNH 109701, SMNH 109702, SMNH 109703, SMNH 109704). All collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when they were collected.

Additional material. One specimen divided in four slides. SMNH 109048, SMNH 109049, SMNH 109050 and SMNH 109051 with the whole worm as serial sections. No data on when and where it was collected. One specimen as whole mount (SMNH 109059). Collected at Guarujá (23°59'45"S; 46°14'59"W). No data on when it was collected.

Distribution. The species is known (Marcus 1947) from the type locality (Ilha de Palmas, Southeastern Brazil) and some nearby localities (Guarujá).

Remarks. In the original description, Marcus (1947, pg. 129 and 130) did not mention the number of specimens collected and on which the description was based. Ernst Marcus had labelled the slides with consecutive letters from A to I and they correspond to animals from the type locality. We assume that the letters and corresponding animals are also in consecutive order (eg. whole mounts of partial worms correspond to the following serial sections in a consecutive manner), following that logic we order the syntypes. Another series of slides labelled with number from 78 to 90, also from the type locality, is to be considered syntypes as well, and the same consecutive logic is used to correspond to anterior parts and serial sections. Thus, we designate here the material deposited at the SMNH as syntypes (Figure 2B). It includes eleven worms: four specimens (labelled from A to I) and seven specimens (labelled from 78 to 90). Reproductive structures in both type series and additional material are marked with blue dots. Prudhoe (1985) considered *Euplana hymanae* valid, but stated its generic identification might be questionable due to presence of elongated prostatic organ, vasa deferentia laterally to uterine canals and ejaculatory duct with papilla, that he considered as diagnostic to *Notoplana*. In Prudhoe's system the species is in the family Leptoplanidae. However, Faubel (1983) creates the family Euplanidae, since species with different diagnostic characters where assigned to the genus. He restringes the diagnostic features to animal with true seminal vesicle, elongated ejaculatory duct and considered *E. hymanae* as valid. We follow Faubel's arrangement. As the genus was not sampled regarding molecular data it is unclear its position in a new system (Bahia et al. *in press*).

Family: Ilyplanidae Faubel, 1983

Genus: *Zygantroides* Faubel, 1983

Zygantroides henriettae (Corrêa, 1949)

Figure 3

Type species of the genus.

Zygantroides henriettae (Corrêa, 1949), type by posterior designation.

Synonims.

Zygantroplana henriettae Corrêa, 1949

Stylochoplana angusta Marcus, 1947 p.110, not *Leptoplana angusta* Verrill 1892, p.485, not *Zygantroplana angusta* Hyman 1952, p.196

Material examined.

Additional material. One specimen as whole mount of entire worm (SMNH 109141; 4 x 1.8 mm). Three specimens in a whole mount of entire worms (SMNH 109142; 3.1 x 1.2 mm, 5 x 2 mm and 4 x 2.1 mm). One specimen as whole mount of entire worm (SMNH 109143; 3.1 x 1.5 mm). One specimen as whole mount of anterior part (SMNH 109144; 3 x 2.8 mm) and as sagittal sections of posterior part (SMNH 109149 and SMNH 109150). One specimen as whole mount of entire worm (SMNH 109145; 4.5 x 1.5 mm). Three specimens in a whole mount of anterior parts (SMNH 109146; 3 x 2 mm, 2 x 2 mm and 1.9 x 1.2 mm), the corresponding sections in (SMNH 109148, SMNH 109151, SMNH 109152 and SMNH 109153). Three specimens as whole mount of entire worms (SMNH 109147; 4.2 x 2 mm, 4.1 x 1.8 mm and 4.2 x 1.8 mm). One specimen as sagittal sections of entire worm (SMNH 109154). All collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Distribution. Southeastern Brazil (Marcus 1947; Corrêa 1949).

Remarks. The material examined here was initially identified as *Stylochoplana angusta* by Marcus (1947). That species was originally described as *Leptoplana angusta* (Verrill 1892) and transferred to the genus *Stylochoplana* by Hyman (1939b), because of similarities to that genus. But Hyman (1939b) also admitted that it did not fit entirely that genus. The material studied in 1947 by Marcus corresponds to what is deposited at the SMNH. Corrêa (1949), based on freshly collected material and that of Marcus (1947) then argued that the differences between the Brazilian and North American material are enough to separate them in different species. Thus she described it as *Zygantroplana henriettae*. The material directly described by her was from Espírito Santo State, thus the material found at the SMNH from São Paulo State is here considered additional material. Later, Hyman (1952) transferred Verrill's type material also to *Zygantroplana,* a genus previously overlooked by her and said to fit perfectly the species. Hyman (1952) also commented that the *Zygantroplana* from Brazil is very similar to *Zygantroplana angusta* and could be considered a geographic variation of it but is not clear if she meant *Zygantroplana henriettae* or *Z. plesia* (Corrêa 1949) as she did not mention the species name. Faubel (1983) place both Corrêa's species in *Zygantroides*, a new Ilyplanidae genus, which points against the synonimization of the Brazilian species to Verrill's species. The North American species (Verrill 1892), Faubel placed as new combination, *Comoplana angusta*, in a new genus *Comoplana*. Prudhoe (1985, p.199) also states Marcus' (1947) species was renamed *Zygantroplana henriettae* and left both species in *Zygantroplana*. Here we follow Faubel's arrangements.

Family: Leptoplanidae Stimpson, 1857

Genus: *Parviplana* Hyman, 1953

Parviplana lynca (Du Bois-Reymond Marcus, 1958)

Figure 4

Type species of the genus.

Parviplana hymanae Faubel, 1983, new name for *Parviplana californica* (Hyman 1953), type species by original designation.

Material examined.

Holotype. One specimen as serial sections of entire worm (SMNH 109197 and SMNH 109198). Collected at Cananéia, São Paulo State, Brazil (25°01'26"S; 47°55'20"W). No data on when it was collected.

Paratype. One specimen as whole mount of entire worm (SMNH 109196; 6 x 3.5 mm). Collected at Cananéia, São Paulo State, Brazil (25°01'26"S; 47°55'20"W). No data on when it was collected.

Additional material. Three specimens (MNRJ-PLAT 158, 6x3 mm; 6.3x4 mm; 5.3x3 mm), one as sagittal sections of reproductive structures (09 slides), rest of the animal in ethanol 70%. Collected at Ilha do Bonfim, Angra dos Reis, Rio de Janeiro State, Brazil (23°01'24,47"S; 44°19'53,93"W).

Distribution. Southeastern Brazil (Du Bois-Reymond Marcus 1958). This is the first record from Rio de Janeiro State.

Remarks. In the original description Eveline Marcus designated as holotype a “slide containing the sagittal sections of the copulatory organs of a 6.3 mm long worm”. The corresponding material is deposited in the SMNH together with a specimen in a whole mount. This flatworm is to be considered a paratype, since it was part of the 48 specimens collected in the original description. The species was originally described (Du Bois-Reymond Marcus 1958) as *Stylochoplana lynca*. Hyman (1953) created the genus *Parviplana* to fit leptoplanids with massive bulbous female antrum and interpolated prostatic vesicle without chambers. Faubel (1983) rearranged the species in a new combination, since it fitted Hyman genus diagnosis and present the male complex enclosed in a muscular bulb. Prudhoe (1985) ignored those similarities and left the genus in *Stylochoplana* group A (without stylet). Here we follow Faubel's arrangement. The material studied by Marcus looks exactly like the fresh material collected by us. Quiroga et al. (2004b) did not mention the species as distributed in the Tropical Western Atlantic.

Family: Notoplanidae Marcus & Marcus, 1966

Genus: *Notocomplana* Faubel, 1983

Notocomplana evelinae (Marcus, 1947)

Figure 5

Type species of the genus.

Notocomplana humilis (Stimpson, 1857), type by posterior designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109139; 3.3x2.8 mm) and as serial sections of posterior part (SMNH 109135, SMNH 109136). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on about when it was collected.

Paralectotypes. One specimen as whole mount of entire worm (SMNH 109133; 4.8 x 1.6 mm). One specimen as whole of entire worm (SMNH 109134; 10 x 2.1 mm). One specimen as whole mount of entire worm (SMNH 109137; 5 x 1.2 mm) together with a *Stylochoplana* sp. as labelled by Ernst Marcus. One specimen as whole mount of entire worm (SMNH 109138; 6 x 1.8 mm). One specimen as whole mount of entire worm (SMNH 109140; 5 x 1.9 mm). All collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data about when they were collected.

Distribution. The species is known from Southeastern Brazil (Marcus 1947).

Remarks. The original description is based on six specimens and in the SMNH there are in total exactly six animals. The slides deposited at the SMNH were numbered by Ernst Marcus from 71 to 77. We designate as lectotype the only specimen that has serial sections. The vouchers SMNH 109133 and SMNH 109134 possibly corresponds to figure 50 and 49, respectively. The species was originally described as *Pucelis evelinae* and it was the type of the genus *Pucelis* (Marcus 1947). This was proposed as a new combination to *Notocomplana* by Faubel (1983), due to its *Notoplana*-like organization but lack of stylet and presence of true prostatic vesicle. Prudhoe (1985), despite of pointing that there were not enough differences between *Pucelis* and *Notoplana*, considered it a valid genus. Here we follow Faubel's arrangement.

Notocomplana martae (Marcus, 1948)

Figure 6

Material examined.

Lectotype. One specimen as sagittal sections of entire worm (SMNH 109090 and SMNH 109091). Collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109088; 3 x 0.9 mm). One specimen as sagittal sections of entire worm (SMNH 109089). One specimen in a whole mount of entire worm (SMNH 109163) with other flatworms from other species, one being a *Alloioplana aulica*. All collected at Ilha de Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Distribution. Southeastern Brazil (Marcus 1948).

Remarks. The original description is based on three specimens. All of them are in the SMNH collection. The voucher SMNH 109088 corresponds to the drawing of figure 105 of Marcus (1948). As one of the specimens in serial sections is much destroyed we designate it as paralectotype and the better preserved material is designated the lectotype of *Notocomplana martae*. Faubel (1983) placed it in *Notocomplana* because of its lack of stylet, different from other Notoplana species. Prudhoe (1985) left it in *Notoplana*, group D (without stylet and penis pocket). The genus kept valid and uniting species with distinct diagnostic features. Thus, here we follow Faubel's organization. The genus together with *Notoplana* and *Leptoplana* need revision and more molecular data to be arranged with more accuracy in a system (Bahia et al. *in press*).

Notocomplana syntoma (Marcus, 1947)

Figure 7

Material examined.

Holotype. One specimen as whole mount of anterior part of worm (SMNH 109120) and serial sections of the posterior part (SMNH 109121, SMNH 109122, SMNH 109123, SMNH 109124). Collected at São Vicente, Baía de Santos, São Paulo State, Brazil (23°58'55"S; 46°22'35"W). No data on collection date.

Additional material. One specimen as whole mount of anterior part of the worm (SMNH 109118; 4x4 mm) and as serial sections of posterior part (SMNH 109125, SMNH 109126, SMNH 109127, SMNH 109128). One specimen as whole mount of entire worm (SMNH

109119; 8x4 mm). Both collected at São Vicente, Baía de Santos, São Paulo State (23°58'55"S; 46°22'35"W). No data on when they were collected. One specimen as whole mount of entire worm (SMNH 109129; 14x6 mm). One specimen as whole mount of entire worm (SMNH 109130; 9x3 mm). Both collected at Ilha das Palmas, São Paulo State (24°00'31.5"S; 46°19'28.5"W). No data on when they were collected.

Distribution. This species is known from São Paulo State (Marcus 1947, 1948).

Remarks. Among the material deposited in the SMNH the ones labelled with consecutive numbers from 57 to 61 are to be considered as one specimen. This animal's sections fit the original description drawings (Marcus 1947, figure 39 and 42). The slides numbered by Ernst Marcus from 1 to 7 (2 and 3 are missing) are also to be considered as one worm, as in Marcus (1948) there is only one worm from São Vicente (p.182). Other slides, as the vouchers SMNH 109118 and SMNH 109119 fit drawings of Marcus (1948; figure 110) about further material collected on the type locality. Also from Marcus (1948) specimens are the vouchers SMNH 109129 and SMNH 109130. The original description (Marcus 1947) is based on only one specimen and based on drawings evidences we recognize here the slides numbered by Ernst Marcus from 57 to 61 as the holotype of *Notocomplana syntoma*, as he have not designated type material. About the material collected in South Brazil, *Notoplana sawayai* has similar eyespots arrangement, but internally they differ in the orientation of the vesicles (Marcus, 1947), in *N. sawayai* the prostatic vesicle is almost above the seminal vesicle and in the studied material it is in front of the seminal vesicle. In *Notocomplana syntoma* the case is the same and also the Lang's vesicle is more elongated that what we observed (Marcus, 1947). *Notoplana plecta* differs from the studied material in the arrangement of eyespots but it is rather similar internally (Marcus, 1947). Prudhoe (1985), as with the previous species, also place it in *Notoplana* group D, because its lack of stylet. We follow Faubel's placement of the species in *Notocomplana*.

Genus: *Notoplana* Laidlaw, 1903b

Notoplana divae Marcus, 1948

Figure 8

Type species of the genus.

Notoplana dubia (Schmarda, 1859), type by posterior designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109073, 2 x 2.2 mm) and serial sections of posterior part (SMNH 109071, SMNH 109072). Collected at Caiobá, Paraná State, Brazil (25°51'S; 48°32'W). No data on when it was collected.

Paralectotypes. Two specimens in a whole mount of entire worms (SMNH 109070, 6.1 x 3 mm-brown and 4.1 x 2.1 mm-red). Red collected at São Vicente, São Paulo State, Brazil (23°58'55"S; 46°22'35"W) and brown collected at Caiobá, Paraná State, Brazil (25°51'S; 48°32'W). No data on when they were collected.

Additional material. One specimen as whole mount of entire worm (SMNH 109074, 7.2 x 3.1 mm). One specimen as whole mount of entire worm (SMNH 109075, 3.1 x 2 mm). Both collected at Forte de Itaipú, São Paulo State, Brazil (24°01'06.6"S; 46°23'54.2"W).

Distribution. The species is so far known from Paraná State, South Brazil and São Paulo State, Southeastern Brazil (Marcus 1948).

Remarks. The original description is based on an immature specimen from Baía de Santos, São Paulo State and two mature specimens from Caiobá, Paraná State (Marcus 1948). Here we designate one of the specimens from Paraná as the lectotype. The remaining specimens deposited in the SMNH are either the paralectotype or additional material (not mentioned in Marcus papers). As evidences for that decision the lectotype slides were labelled by Ernst Marcus with number from 1 to 3, and the additional material is labelled with A and B. The voucher SMNH 109070 has worms from different localities and they are labelled differently by Ernst Marcus (different colours corresponding to different regions). The species was found between algae and bryozoans. Animals collected in Itaipú (according to labels) are considered to have been collected at Forte de Itaipú, São Paulo State, as other species with similar labels. The species is considered valid by Faubel (1983) and included in *Notoplana* group A (with stylet and penis pocket) by Prudhoe (1985).

Notoplana micheli Marcus, 1949

Figure 9

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109099; 3x2 mm), together with another smaller anterior part, and as sagittal sections of posterior part (SMNH 109100). Collected at Ilha do Francês, Espírito Santo State, Brazil (20°54'40"S; 40°45'00"W).

Paralectotype. One specimen as whole mount of anterior part (SMNH 109099; 2.9 x 1.5 mm), together with a larger anterior part, and as sagittal sections of posterior part (SMNH 109101). Collected at Ilha do Francês, Espírito Santo State, Brazil (20°54'40"S; 40°45'00"W).

Distribution. Southeastern Brazil (Marcus 1949).

Remarks. Here we designate the larger worm divided in whole mount and serial sections as the lectotype of *Notoplana micheli*, because it fits the drawings of the original description (Marcus 1949). The designation is made with the purpose of clarifying the application of the name of the taxon. Both lectotype and paralectotype anterior parts are in one whole mount. Faubel (1983) considered the species valid and Prudhoe (1985) too, placing it in *Notoplana* group A (with stylet and penis pocket).

Notoplana plecta Marcus, 1947

Figure 10

Material examined.

Holotype. One specimen as sagittal sections of posterior part (SMNH 109102 and SMNH 109103). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Distribution. Southeastern Brazil (Marcus 1947).

Remarks. Here we recognize the sectioned specimens deposited at the SMNH as the species holotype, since Marcus (1947) did not designate holotype in the description. The voucher SMNH 109103 corresponds to the drawing of figure 48 of the original description (Marcus 1947) and the description is based on one flatworm. The species is considered valid by Faubel (1983) and Prudhoe (1985) who placed it in *Notoplana* group A. There is also, possibly, a material of this species together with specimens of *Armatoplana leptalea* in the voucher SMNH 109104 (a whole mount with three anterior parts). However, as the identification is with question marks we did not consider it here. For now that voucher should be considered as containing a *Notoplana* cf. *plecta*.

Notoplana sawayai Marcus, 1947

Figure 11

Material examined.

Lectotype. One specimen as whole mount of the anterior part (SMNH 109111; 3 x 2 mm) and as sagittal sections of posterior part (SMNH 109112, SMNH 109113). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Paralectotype. One specimen as whole mount of anterior part (SMNH 109110; 5.5 x 4 mm) and as sagittal sections of posterior part (SMNH 109114, SMNH 109115, SMNH 109116). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Additional material. One specimen as whole mount of entire worm (SMNH 109117; 9 x 3 mm). Collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. Southeastern Brazil (Marcus 1947).

Remarks. The original description is based on two specimens that are deposited at the SMNH collection. One of the worms presents wrinkled sections. We designate the better visible specimen as the lectotype and the other specimen as paralectotype of *Notoplana sawayai*. Additional to the type series there is another specimen deposited in the collection, it is from another locality, but it was not mentioned in any paper by Ernst or Eveline Marcus. The species is placed on *Notoplana* group A by Prudhoe (1985), but there is a mistake as the species is from Marcus and not Kato. Faubel (1983) also considered it valid.

Family Pleioplanidae Faubel, 1983

Genus: *Pleioplana* Faubel, 1983

Pleioplana megala (Marcus, 1952)

Figure 12

Type species of the genus.

Pleioplana atomata (O.F. Müller, 1776), type by posterior designation.

Material examined.

Lectotype. One specimen as whole mount of most of the worm (SMNH 109094; 13 x 9 mm) and as serial sections of reproductive part (SMNH 109095 and SMNH 109096). Collected at

São Paulo, Brazil (either Ilha de São Sebastião 23º49'S; 45º24'W) in June 1951 or Ubatuba 23°27'S; 45°06'W on September 1951).

Additional material. One specimen as whole mount of anterior part (SMNH 109097; 9.2 x 6 mm) and serial sections of posterior part (SMNH 109098). Collected 12.01.1966 at Piscadera Baai, Curaçao (12°07'51"N 68°58'09"W).

Distribution. The species is found at Southeastern Brazil (Marcus 1952) and Curaçao (Marcus & Marcus 1968; Quiroga et al. 2004).

Remarks. The original description (Marcus 1952) is based on three animals from Ilha de São Sebastião and two from Ubatuba, in São Paulo State. Deposited in the SMNH we only found one worm from Brazil and another from Curaçao. As the slides corresponding to the Brazilian material has written on them only São Paulo, as locality, it is unclear if the type locality is Ilhabela or Ubatuba. Thus we add general coordinates that include both these areas. Despite the lack of details we designate the slides labelled from A to C as the lectotype of the species. The additional material from Curaçao is labelled with the letters M and N. The species was originally described as *Notoplana megala* (Marcus 1952), and later combined in a new genus. Faubel created the family Pleioplanidae and the genus *Pleioplana* to place former *Notoplana* species with chambered prostatic vesicles. However, Prudhoe (1985) does not recognize chambered vesicle as a diagnostic character, simply grouping it in *Notoplana* group A, to point a difference between other *Notoplana* species. Here we follow Faubel's position.

Family: Stylochoplanidae Faubel, 1983

Genus: *Alloioplana* Plehn, 1896

Alloioplana aulica (Marcus, 1947)

Figure 13

Type species of the genus.

Alloioplana delicata Plehn, 1896, type by original designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109156; 4 x 3.2 mm) and as serial sections of posterior part (SMNH 109159, SMNH 109160, SMNH 109161, SMNH 109162). Collected at Ilha de Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Paralectotype. Three specimens in a whole mount (SMNH 109155; 6 x 2.5 mm, 6 x 2.2 mm, 4 x 1.9 mm). Two specimens in a whole mount of entire worms (SMNH 109157; 6 x 2.8 mm, 5.8 x 3 mm). Three specimens in a whole mount (SMNH 109158; 6 x 2 mm, 5 x 2.1 mm, 4.9 x 1.9 mm). One specimen in a whole mount of entire worm (SMNH 109163; 4 x 2.1 mm) with other flatworms from other species, one being a *Notocomplana martae* (*N.martae* in the label). All collected at Ilha de Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Additional material. One specimen as whole mount of entire worm (SMNH 109164; 5 x 2 mm). Collected at Guarujá, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). One specimen (MNRJ-PLAT 156, 9x4 mm) as sagittal sections of reproductive structures (06 slides), rest of the animal in ethanol 70%. Collected 17.01.2012 at Praia do Segredo, São Sebastião, Brazil (23º 49,65'S; 45º 25,36' W).

Distribution. São Paulo State, Brazil.

Remarks. Among the material deposited at the SMNH there are 10 specimens from the 20 on which the original description was based. As the slides are numbered consecutively by Ernst Marcus (from 40 to 48) we assume they are from the same location. There is also one flatworm, from another location, that is then listed with the additional material. We designate here the only specimen from the type locality that has serial sections as the lectotype. The other specimens are designted as paralectotypes. The voucher SMNH 109163 has appart from *Alloiplana aulica*, also specimens of *Notocomplana martae*, 3 juvenile polyclads, 1 triclad, 1 *Leucolesma* sp., as labelled by Ernst Marcus. The species was originally described as *Stylochoplana aulica* (Marcus 1947). Faubel (1983) considered it as new combination in the genus *Alloioplana*, as it fits the diagnostic features of that genus (Plehn 1896). Prudhoe (1985), however, left it in *Stylochoplana* group D (with stylet) and considered *Alloioplana* a synonym of it. Historically, there were discussions about the familiar position of this genus, either in Leptoplanidae (Marcus 1947; Prudhoe 1985) or in Planoceridae (Hyman 1953). Alternatively, Faubel (1983) created the family Stylochoplanidae to include species with smooth lined prostatic vesicles. Here we follow Faubel's placement as the species fits the diagnostic features of both family and genus. Molecular samples from this genus would be very important for investigating where it would fit in a monophyletic group.

Genus: *Armatoplana* Faubel, 1983

Armatoplana divae (Marcus, 1947)

Figure 14

Type species of the genus.

Armatoplana panamensis (Plehn, 1896), type by posterior designation.

Material examined.

Holotype. One specimen as whole mount of most of the worm (SMNH 109167; 9 x 7 mm) and as serial sections of reproductive part (SMNH 109168, SMNH 109169, SMNH 109170, SMNH 109171). Collected at Ilha das Palmas, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Additional material. One specimen as serial sections of posterior part (SMNH 109172). Collected at Ilha das Palmas, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected. One specimen (MNRJ-PLAT 159) as sagittal sections of reproductive structures (10 slides), rest of the animal in ethanol 70%. Collected 08.11.2007 at Ponta da Fortaleza, Arraial do Cabo, Brazil (22°58'12.6"S; 42°00'42.8"W).

Distribution. The species is known from São Paulo (Marcus 1947) Brazil, Caribbean Colombia (Quiroga et al. 2004a, b) and this is the first record from Rio de Janeiro State.

Remarks. The original description is based on a single specimen and this corresponds to the one found at the SMNH. Marcus (1947) did not designate a holotype in the original description, thus this is the holotype by monotypy. An additional slide with sections from another worm, also from the type locality is then listed under additional material. The species was originally described as *Stylochoplana divae* (Marcus 1947). Faubel (1983) while creating Stylochoplanidae, created the genus *Armatoplana* for species with very long stylet and voluminous prostatic vesicle. The species fits those diagnostic characteres and was put into a new combination by Faubel (1983). Prudhoe (1985), on the other hand, left the species in *Stylochoplana* group D (with variable developed tentacles, stylet and well separated cerebral and tentacular eye clusters). Here we follow Faubel's arrangement. The color pattern and general external morphology of Quiroga et al. (2004a) specimen fit that of our material.

Armatoplana leptalea (Marcus, 1947)

Figure 15

Material examined.

Holotype. One specimen as whole mount of the anterior part (SMNH 109180; 6x4.8 mm) and serial sections of posterior part (SMNH 109181, SMNH 109182, SMNH 109183). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on collection date.

Additional material. One specimen as serial sections of posterior part (SMNH 109184, SMNH 109185). Collected at Ilhabela, São Paulo State, Brazil (23°49'S 45°22'W). One specimen as serial sections of reproductive structures (SMNH 109186, SMNH 109187, SMNH 109188). Collected at Ilha das Palmas, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). One specimen as whole mount of anterior part (SMNH 109189; 4x3.9 mm) and serial sections (SMNH 109191). One specimen as whole mount of entire worm (SMNH 109190; 12x4 mm). One specimen as whole mount of anterior part (SMNH 109192; 4x4.2 mm) and as serial sections of posterior part (SMNH 109193). One specimen as whole mount of anterior part (SMNH 109194. 5 x 4 mm) and as serial sections of posterior part (SMNH 109195). All collected 20.11.1948 at Curaçao (12°07'N; 68°58'W). Two specimens (MNRJ-PLAT 122, 23x8; 13.5x5 mm), one as sagittal sections of reproductive structures (15 slides), rest of the animal in ethanol 70%. Collected 28.10.2007. One specimen (MNRJ-PLAT 123, 13x5.5 mm). Collected 20.04.2008. Both collected at Praia das Conchas, Cabo Frio, Brasil (22^{o}52'15,40"S; 41^{o}58'5186"W). One specimen (MNRJ-PLAT 124, 11x4 mm) collected 16.05.2008 at Praia do Forno, Arraial do Cabo, Brazil (22°58'06,41"S; 42°00'50,78"W). Three specimens (MNRJ-PLAT 125, 16x5; 14x5; 11.5x4 mm) collected 18.05.2008. Four specimens (MNRJ-PLAT 126), one as sagittal sections of reproductive structures (11 slides), rest of the animal in ethanol 70%. Collected 14.12.2008. Both samples collected at Canal de Itajuru, Cabo Frio, RJ, Brasil (22º53'11"S; 42º00'08"W). One specimen (MNRJ-PLAT 150, 8x4 mm) collected 21.01.2012 at Praia do Segredo, São Sebastião, Brazil (23º 49,65'S; 45º 25,36' W).

Distribution. Southeastern and Northeastern Brazil (Marcus 1947, 1948; Bahia et al. 2015), also from Abrolhos Archipelago (Marcus & Marcus 1968), Antigua, Barbuda, Curaçao, and Florida (Marcus & Marcus 1968; Quiroga et al. 2004b). The species is also reported from the Caribbean Mexico (Pineda-López, 1981). This is the first record from Rio de Janeiro State.

Remarks. The original description (Marcus 1947) is based on only one immature specimen and later Marcus (1948) studied a mature worm. The voucher SMNH 109180 fits the original description, and its sections are in the three following vouchers, which has slides numbered from 36 to 39. Marcus (1947) did not designate holotype in the description, thus this is recognized as the holotype of *Armatoplana leptalea* by monotypy. Other material from this species deposited on the SMNH are the flatworms studied both by Marcus (1948, two worms) and Marcus & Marcus (1968, four worms). The species was originally described as *Stylochoplana leptalea.* Faubel (1983) placed the species as new combination in *Armatoplana* (stylochoplanid with long stylet and voluminous prostatic vesicle). Prudhoe (1985) placed it in *Stylochoplana* group C (without tentacles, eyes in elongated clusters and penis with stylet). We follow Faubel's system position. In our search for Brazilian polyclad species in the GBIF database we found also material deposited in Mexico (Table 1). The record for this country was not published in a scientific journal, only in a thesis (Pineda-López, 1981).

Genus: *Interplana* Faubel, 1983

Interplana evelinae (Marcus, 1952)

Figure 16

Type species of the genus.

Interplana evelinae (Marcus, 1952), type by posterior designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109173; 13 x 9 mm) and as serial sections of posterior part (SMNH 109176, SMNH 109177, SMNH 109178, SMNH 109179). Collected at São Paulo State, Brazil (see remarks).

Paralectotype. One specimen as serial sections of posterior part (SMNH 109174, SMNH 109175). Collected at São Paulo State, Brazil (see remarks).

Distribution. This species is known from São Paulo State, Southeastern Brazil (Marcus 1952)

Remarks. Among the slides deposited in the SMNH there are two specimens and these correspond to the two flatworms on which the original description is based. Three of the slides were labelled by Ernst Marcus from A to C and the remaining slides are labelled from 1 to 4. According to size the whole mount A has its serial sections on the slides 1-4. As this is the only worm with both whole mount and sections we designate it the lectotype of *Interplana* *evelinae*. Unfortunately the slide labels only indicate São Paulo State as locality and it is not possible to know which one was collected where. The two possible locations cited in the description are Ilha das Palmas (24°00'31.5"S; 46°19'28.5"W) and Itanhém (24°11'25.9"S; 46°47'33.8"W). This species was originally described as *Stylochoplana evelinae* (Marcus 1952) and was transferred by Faubel (1983), in a new combination, to the newly create genus *Interplana*. The species is also the type of the genus, which highlights the importance of specifying the type material. Prudhoe (1985), on the other hand, left it in the original genus. Here we follow Faubel's arrangement.

Genus: *Stylochoplana* Stimpson, 1857

Stylochoplana divae (Marcus, 1949)

Figure 17

Type species of the genus.
Stylochoplana maculata (Quatrefages, 1845), type by posterior designation.

Material examined.
Lectotype. One specimen as serial sections of entire worm (SMNH 109672 and SMNH 109674). Collected at Ilha das Palmas, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).
Paralectotype. One specimen as whole mount of entire worm (SMNH 109669; 4 x 1 mm). One specimen as whole mount of entire worm (SMNH 109670; 7.1 x 1.5 mm). One specimen as whole mount of entire worm (SMNH 109671; 6.5 x 1.3 mm). One specimen as serial sections of entire worm (SMNH 109673). All collected at Ilha das Palmas, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Distribution. The species is known only from the type locality in Southeastern Brazil (Marcus 1949).

Remarks. We designate as lectotype the slides of the worm that corresponds to the drawings of the original description (Marcus 1949, figure 116). The species was described as *Candimba divae*. Faubel (1983) extinguished the genus, synonymized it to *Stylochoplana* (with papillate penis) due to incongruence in the penis morphology among *Candimba* species. Prudhoe (1985) considered *Candimba* valid and left *C. divae* as the only species of that genus, tranfering *C. rabita* to *Candimboides*. Here we follow Faubel's system (1983). Molecular samples added to the morphological information available could help to understand the position of the genus (Bahia et al. *in press*).

Stylochoplana selenopsis Marcus, 1947

Figure 18

Material examined.

Holotype. One specimen as whole mount of anterior part (SMNH 109199; 1.5 x 1.8 mm) and serial sections of posterior part (SMNH 109200, SMNH 109201, SMNH 109202). Collected at São Vicente, São Paulo State, Brazil (23°58'55"S; 46°22'35"W).

Additional material. Two specimens in a whole mount (SMNH 109203; 4 x 1.8 mm and 4 1.9 mm). One specimen as serial sections of whole worm (SMNH 109204). Collected at Ubatuba, São Paulo State, Brazil (23°27'S; 45°06'W). One specimen as whole mount of entire worm (SMNH 109205; 9 x 4 mm). One specimen as whole mount of entire worm (SMNH 109206; 7 x 3.2 mm). One specimen as whole mount of entire worm (SMNH 109207; 9 x 3.5 mm). One specimen as whole mount of entire worm (SMNH 109208; 8 x 3 mm). One specimen as serial sections of entire worm (SMNH 109209). All collected 22.09.1948 at Baía de Santos, São Paulo State, Brazil (23°59'S; 46°21'W). One specimen as whole mount of anterior part (SMNH 109658, 5x3.1 mm), together with part of a *Pentaplana divae.*

Distribution. The species is known from São Paulo State (Marcus 1947, 1949) so far.

Remarks. The original description (Marcus 1947) is based on one immature specimen that fits the vouchers SMNH 109199 to SMNH 109202. The first slide is labelled with the type locality and the animal is small and immature. Therefore it is recognized as the holotype of *Stylochoplana selenopsis* by monotypy. Additional material studied by Marcus (1949) is also deposited in the SMNH collection and is listed here. In total there are nine specimens. Both Faubel (1983) and Prudhoe (1985) left the species in *Stylochoplana*. Prudhoe placed it in *Stylochoplana* group A (without stylet, with variable tentacle development and tentacular and cerebral eyespot clusters well separated).

Family: Cryptocelidae Laidlaw, 1903a

Genus: *Cryptocelis* Lang, 1884

Cryptocelis lilianae Marcus & Marcus, 1968

Figure 19

Type species of the genus.

Cryptocelis alba (Schmidtlein, 1880), type by posterior designation.

Material examined.

Holotype. One specimen as whole mount of anterior part (SMNH 109687; 2.2 x 2.7 mm), together with paratype, and as sagittal sections of posterior part (SMNH 109688 and SMNH 109689). Collected off Ubatuba, São Paulo State, Brazil (23°27'S; 45°06'W).

Paratype. One specimen in whole mount (SMNH 109687; 7 x 3 mm) together with the holotype. Collected off Ubatuba, São Paulo State, Brazil (23°27'S; 45°06'W).

Distribution. The species is only known from the type locality so far.

Remarks. The type series included six specimens, but only two are deposited at the SMNH. In the original description is said the holotype is "one whole mount and 2 slides with sagittal sections of the copulatory organs". Thus it fits the material found in the SMNH, and the slides are here recognized as holotype and paratype of *Cryptocelis lilianae*. Both Faubel (1983) and Prudhoe (1985) accepted *Cryptocelis* as valid genus and left *C. lilianae* in that genus.

Genus: *Phaenocelis* Stummer-Traunfels, 1933

Phaenocelis medvedica Marcus, 1952

Figure 20

Type species of the genus.

Phaenocelis purpurea (Schmarda, 1859), type by posterior designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109708; 6 x 4 mm) together with a *Lurymare utarum*, and as sagittal sections of posterior part (SMNH 109709). Collected 11.1949? at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109707; 19.9 x 6 mm).Collected 11.1949? at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen (MNRJ-PLAT 19, 22x5 mm) as sagittal sections of reproductive structures (13 slides), rest of the animal in ethanol 70%. Collected 13.03.2009 at Praia de Búzios, Nísia Floresta, Brazil (06^{o}00'41"S; 35^{o}06'24"W). One specimen (MNRJ-PLAT 118, 40x11 mm) as sagittal sections of reproductive structures (16 slides), rest of the animal in ethanol 70%.Collected 09.12.2007 at Enseada 3, Ilha do Papagaio, Cabo Frio, Brazil (22°53'53,21"S; 41°58'59,40"W). Five specimens (MNRJ-PLAT 119, 21.5 x 7; 23 x 7.5; 19 x 5; 24 x 7; 12 x 4.5 mm) collected 20.04.2008 at Praia das Conchas, Cabo Frio, Brazil (22^{o}52'15,40''S; 41^{o}58'5186''W). Three specimens (MNRJ-PLAT 120, 26 x 10; 12 x 6; 8 x 7 mm) collected 18.04.2010 at Canal de Itajuru, Cabo Frio, Brazil (22º53'11''S; 42º00'08''W). Three specimens (MNRJ-PLAT 121, 21 x 6.5; 23 x 8; 23 x 7.8 mm) collected 19.04.2010 at Praia da Tartaruga, Búzios, Brazil (22°45'20,83''S; 41°54'12,32''W). One specimen (MNRJ-PLAT 138, 20 x 10 mm) collected 18.01.2012 at Praia do Segredo, São Sebastião, Brazil (23º 49,65'S; 45º 25,36' W).

Distribution. Southeastern and Northeastern Brazil (Marcus 1952; Bahia et al. 2015), Caribbean coast of Colombia (Quiroga et al. 2004a and b). This is the first record from Rio de Janeiro State and from Rio Grande do Norte State.

Remarks. The type series contained 27 worms (Marcus 1952), but in the SMNH there are only two specimens. Thus we designate the one divided in both whole mount and sections as the lectotype of *Phaenocelis medvedica*, and the whole mount of an entire worm as the paralectotype. Both Faubel (1983) and Prudhoe (1985) considered the species valid in *Phaenocelis.* It is not totally clear, only by the general morphology photo, if the species found in the Caribbean Sea (Quiroga et al. 2004a), really belongs to *Phaenocelis medvedica*. Here we add two new localities to the species distribution, corroborating it as commonly distributed throughout the Brazilian coast.

Family: Triadommidae **nov. fam.**

Diagnosis.

Polyclad with tentacular and cerebro-frontal eyespots arrangement; marginal eyespots; tentacles lacking. Male reproductive system with seminal vesicle or spermiducal bulbs; armed penis with elongated pointed stylet. Female reproductive system with bursa copulatrix and Lang's vesicle lacking.

Remarks.

On the Turbellaria database (Tyler et al. 2016) the species of Triadomma appears placed in the family Notocirridae, which might be a mistake, since no mention to that is found on the literature (Faubel 1983). Due to a confusing combination of characters, such as internal features that look like *Notoplana* or even *Armatoplana* and external characters that look like Cryptocelidae we advise the genus should be revised and deserves its own separate family. Molecular data on the genus can be very helpful to point a solution for the placement of the taxa. A Polycladida phylogeny (Bahia et al. *in press*) showed that combination of characters previously used by one or other systematic systems (Faubel 1983, 1984; Prudhoe 1985) is more efficient in separating polyclads in monophyletic groups. For now, since the genus present mixed characteristics of Notoplanidae (internal male system characteristics) and Cryptocelidae (eyespots arrangement) we create its own family.

Genus: *Triadomma* Marcus, 1947

Triadomma curvum Marcus, 1949

Figure 21

Type species of the genus.

Triadomma evelinae Marcus, 1949, type by original designation.

Material examined.

Lectotype. One specimen as sagittal sections of entire worm (SMNH 109717). Collected 09.1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109714; 2.8 x 1.2 mm). One specimen as whole mount of entire worm (SMNH 109715; 3 x 1.5 mm). One specimen as whole mount of entire worm (SMNH 109716; 3.6 x 1.1 mm). All collected 09.1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is known from Southeastern Brazil (Marcus 1949).

Remarks. All the four specimens from the type series described by Marcus (1949) are deposited in the SMNH. We designate here as lectotype of *Triadomma curvum* the one that was sectioned. The other three specimens are then designated paralectotypes. In Faubel (1983) the species is placed in the family Notoplanidae due to features of the male apparatuses. Prudhoe (1985), on the other hand, placed it in Cryptocelidae as also did Marcus

(1949), based on the presence of marginal eyespots, which are absent from notoplanids. No *Triadomma* species is mentioned by Quiroga et al. (2004b) as present in the Tropical Western Atlantic.

Triadomma evelinae Marcus, 1947

Figure 22

Material examined.

Lectotype. One specimen as sagittal sections of entire worm (SMNH 109720, SMNH 109721, SMNH 109722). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected.

Paralectotype. One specimen as whole mount of entire worm (SMNH 109718; 6 x 2.8 mm). One specimen as whole mount of entire worm (SMNH 109719; 6.3 x 2.8 mm). One specimen as sagittal sections of entire worm (SMNH 109723). One specimen as sagittal sections of entire worm (SMNH 109724). One specimen as sagittal sections of entire worm (SMNH 109725). All collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected.

Distribution. The species is only known from Southeastern Brazil (Marcus 1947).

Remarks. The species is the type species of the genus, which makes even more important the localization of the type material. In the original description is written the type series has several specimens, without any further specification. In the SMNH there are six of them, the bigger one that has sagittal sections is here designated as the lectotype of *Triadomma evelinae,* and the remaining specimens are designated paralectotypes. As discussed above the species was originally placed in the family Cryptocelidae and posteriorly in Notoplanidae. (Faubel 1983). However, we highlight the need for revision as the genus presents characters combined that can place it in very different families, depending which traits you take into consideration. It is very likely that the genus will need its own family when more information is obtained. So here we place the genus in its own newly created family. The species is not mentioned by Quiroga et al. (2004b) species list and in the Turbellaria database (Tyler et al. 2016) the species is placed in a wrong family (see discussion above).

Family: Discocelidae Laidlaw 1902

Genus: *Adenoplana* Stummer-Traunfels, 1933

Adenoplana evelinae Marcus, 1950

Figure 23

Type species of the genus.

Adenoplana obovata (Schmarda, 1859), type by posterior designation.

Material examined.

Lectotype. One specimen divided in five slides. SMNH 109605 with the anterior part in a whole mount (6 x 7.5 mm). SMNH 109607, SMNH 109608, SMNH 109609, and SMNH 109610 with serial sections of the posterior part. Collected 11.1949 at Ilha de São Sebastião, São Paulo State, Brasil (23º49'S; 45º24'W).

Paralectotype. One specimen (SMNH 109606, 16 x 8 mm) as whole mount. Collected 11.1949 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen (MNRJ-PLAT 18, 13.5 x 8 mm) as sagittal sections of reproductive structures (22 slides), rest of the animal in ethanol 70%. Collected 09.03.2009 at Praia de Santa Rita, Extremoz, Rio Grande do Norte State, Brazil, (05°41'44" S; 35°11'39"W). One specimen (MNRJ-PLAT 127, 16 x 8 mm) in ethanol 70%. Collected 27.09.2008 at Ilha do Bonfim, Angra dos Reis, Rio de Janeiro State, Brazil (23°01'24,47"S; 44°19'53,93"W). One specimen (MNRJ-PLAT 128, 17 x 10.5 mm) as sagittal sections of reproductive structures (12 slides), rest of the animal in ethanol 70%. Collected 16.10.2009. One specimen (MNRJ-PLAT 129, 14 x 7 mm) in ethanol 70%. Collected 04.02.2012. Both collected at Praia das Conchas, Cabo Frio, RJ, Brasil (22°52'15,40"S; 41°58'51,86"W).

Distribution. Southeastern and Northeastern Brazil (Marcus 1950; Bahia et al. 2015). Here for the first time reported from Rio Grande do Norte and Rio de Janeiro States.

Remarks. The type material is deposited in Stockholm in five vouchers containing five slides. Marcus (1950) said the larger of two worms is the one from which the diagnostic measurements were taken. He mentioned that one was in a whole mount and the other in serial sections (the posterior part, the anterior part also as whole mount). The SMNH 109606 animal in whole mount fits the drawing in figure 142 (p. 171 in Marcus, 1950). The voucher SMNH 109605 contains just the anterior part of a worm in whole mount. The remaining body is in the slides from SMNH 109607 to SMNH 109610. Since most measurements were taken from the latter worm we designated it as the lectotype and the other worm is then the paralectotype. Gonopores are indicated by black marks on the slides, as also the mouth. This species was recently illustrated (Bahia et al. 2015). It was noted that this species might present a transparent or opaque body, depending on the environment it was found. No clear relation of this observation to any specific characteristic of the sampled localities was found, but the transparent colormorph, was only found in Northeastern Brazil, so far. Both Faubel (1983) and Prudhoe (1985) considered the species valid. Here we present, for the first time, color photos of internal characters and external morphology details for this species.

Family: Callioplanidae Hyman, 1953

Genus: *Callioplana* Stimpson, 1857

Callioplana evelinae Marcus, 1954

Figure 24

Type species of the genus.

Callioplana marginata Stimpson, 1857, type species by original designation.

Material examined.

Lectotype. One specimen in a whole mount of anterior part (SMNH 109663; 5.1 x 4.2 mm) together with one paralectotype, and serial sections of posterior part (SMNH 109664, SMNH 109665, SMNH 109666). Collected 11.1952 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109663; 9 x 4.5 mm) together with the lectotype. One specimen as serial sections of entire worm (SMNH 109667 and SMNH 109668). Both collected at 06.1953 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is known from Southeastern Brazil (Marcus 1954) and Yucatán Peninsula, Mexico (Ardisson, 2005).

Remarks. Here we designate the only worm that is in both whole mount and serial sections as the lectotype of *Callioplana evelinae*. Both Faubel (1983) and Prudhoe (1985) considered the species valid as originally described. The species was not mentioned by Quiroga et al. (2004b) as a Tropical Western Atlantic species, but it is recorded from Mexico in a technical report (Ardisson, 2005). The deposited material, corresponding to that record, is listed in

GBIF (http://www.gbif.org) database, and this extends the range of the species to the Caribbean.

Family: Hoploplanidae Stummer-Traunfels, 1933

Genus: *Hoploplana* Laidlaw, 1902

Hoploplana divae Marcus, 1950

Figure 25

Type species of the genus.

Hoploplana villosa (Lang, 1884), type species by posterior designation.

Material examined.

Holotype. One specimen as serial sections of entire worm (SMNH 109060, SMNH 109061). Collected November 1949 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen as whole mount of anterior part (SMNH 109062, 2x2.5 mm) and serial sections of the posterior part (SMNH 109063, SMNH 109064). Collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W), no data on when it was collected. One specimen as whole mount of entire worm (SMNH 109065, 2.1x2 mm). Collected at Piscadera Baai, Curaçao (12°07'51"N 68°58'09"W). Collected between 1930 and 1964. One specimen (MNRJ-PLAT 157, 6.5x5 mm) as sagittal sections of reproductive structures (08 slides), rest of the animal in ethanol 70%. Collected 20.01.2012 at Itaçucê, South from São Sebastião, Brazil (23°49'54.2"S; 45°26'35.8"W).

Distribution: Southeastern and Northeastern Brazil (Marcus, 1950; Bahia et al. 2012), Curaçao (Marcus & Marcus 1968), this is the first record for Rio de Janeiro State.

Remarks. The original description did not designate type material, but was based on one specimen (Marcus 1950), which is part of the material deposited at the SMNH. Therefore, we recognize it here as the holotype by monotypy. There is more material also from the type locality deposited in the same collection, but since it was not mentioned in the description we considered as additional material together with material collected by us. Also, material studied by Ernst and Eveline Marcus (1968) is here listed. Both Faubel (1983) and Prudhoe (1985) considered it as valid species, but Prudhoe considered in its separate family, because of tentacles, eyespots distribution and general morphology, instead as in Leptoplanidae

(Faubel 1983). Here we follow Prudhoe's (1985) arrangement. Which was corroborate by molecular data (Bahia et al. *in press*). As previously reported from Northeastern Brazil (Bahia et al. 2012), the specimens collected in Rio de Janeiro State were also found over bryozoans.

Genus: *Itannia* Marcus, 1947

Itannia ornata Marcus, 1947

Figure 26

Type species of the genus.

Itannia ornata Marcus, 1947, type by original designation.

Material examined.

Holotype. One specimen as sagittal section of entire worm (SMNH 109780, SMNH 109781 and SMNH 109782). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Additional material. Three specimens in a whole mount of entire worms (SMNH 109783; 4 x 1.9 mm, 3.7 x 2.1 mm and 3 x 2 mm). One specimen as whole mount of entire worm (SMNH 109784; 3 x 1.8 mm). One specimen as whole mount of entire worm (SMNH 109785; 2 x 1 mm). One specimen as sagittal sections of entire worm (SMNH 109786). All collected at Ubatuba, São Paulo State, Brazil (23°27'S; 45°06'W).

Distribution. The species is only known from Southeastern Brazil (Marcus 1947, 1952).

Remarks. The original description was based on one worm (Marcus 1947). The material in the vouchers SMNH 109780, SMNH 109781 and SMNH 109782 corresponds to that specimen. This, because they are labelled with the type locality, or consecutive letters that indicate it was collected in the same place and it corresponds to the drawings of the original description. Thus it is here recognized as the holotype by monotypy. Other six specimens from another location are also deposited in the SMNH and are listed under additional material. This species is the type species of the genus and the only valid species of it, which highlight the importance of finding and designating type material. Firstly, the species was put in the family Planoceridae (Marcus 1947) due to presence of tentacles and internal features of male and female reproductive structures. Faubel (1983) place the genus in Leptoplanidae based on internal features of the prostatic vesicle. However, Prudhoe (1985) put the genus in the family Hoploplanidae, as it has nuchal tentacles, and internal organization much more similar to *Hoploplana* than to other typical leptoplanids (eg. *Notoplana*, *Leptoplana*). Here we follow Prudhoe's (1985) arrangement. We consider *Itannia ornata* var. *murna* as a synonym, as there are not enough differences to justify the separation of the material studied by Eveline Marcus (DuBois-Reymond Marcus, 1957) as a different species.

Family: Stylochidae Stimpson, 1857

Genus: *Distylochus* Faubel, 1983

Distylochus isifer Du Bois-Reymond Marcus, 1955a

Figure 27A, B and C

Type species of the genus.

Distylochus pusillus (Bock, 1913), type by posterior designation.

Material examined.

Lectotype. One specimen as sagittal sections of posterior part (SMNH 109793). Collected 05.1953 at Cananéia, São Paulo State, Brazil (25°01'26"S; 47°55'20"W).

Distribution. The species is only known from Southeastern Brazil (Du Bois-Reymond Marcus, 1955a).

Remarks. The type series contains seven specimens but only one slide is present on the SMNH collection. We then designate the serial sections as the lectotype of *Distylochus isifer*. The species was firstly described as *Stylochus isifer* (Du Bois-Reymond Marcus, 1955a) and then transferred to the subgenus *Stylochus* (Marcus & Marcus 1968). Faubel (1983) then transferred it to the new genus *Distylochus* due to its bipartite seminal vesicle. Prudhoe (1985), however, considered the species still as in the subgenus *Stylochus*. Here we follow Faubel's arrangement.

Distylochus martae (Marcus, 1947)

Figure 27D, E and F

Material examined.

Holotype. One specimen as sagittal sections of entire worm (SMNH 109794 and SMNH 109795). Collected at Praia da Enseada, Ilha de Santo Amaro, São Paulo State, Brazil (23°59'S; 46°13'W). No data on when it was collected.

Distribution. The species is only known from the type locality at Southeastern Brazil.

Remarks. The original description is based on one worm and it fits the material deposited at the SMNH. Marcus (1947) did not designate holotype in the description, thus it is here recognized as the holotype of *Distylochus martae* by monotypy. The species was originally described as *Stylochus martae* (Marcus 1947) and later placed on the subgenus *Stylochus* (Marcus & Marcus 1968). Prudhoe (1985) followed that resolution, but Faubel (1983) transferred the species to *Distylochus*, based on the form of the seminal vesicle. Here we follow Faubel's arrangement.

Genus: *Imogine* Girard, 1853

Imogine cata Du Bois-Reymond Marcus, 1958

Figure 28

Type species of the genus.
Imogine oculifera Girard, 1853, type species by original designation.

Material examided.
Holotype. One specimen as serial sections of entire worm (SMNH 109788 and SMNH 109789). Collected 11.1957 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).
Additional material. One specimen as whole mount of entire worm (SMNH 109790; 4 x 2.3 mm). One specimen as serial sections of posterior part (SMNH 109791 and SMNH 109792). One specimen (MNRJ-PLAT 130, 19x14 mm) as sagittal sections of reproductive structures (20 slides), rest of the animal in ethanol 70%. Collected 09.12.2007 at Enseada 2, Ilha do Papagaio, Cabo Frio, Brazil (22°53'45,43"S; 41°59'5,54"W). One specimen (MNRJ-PLAT 131, 17.5x13 mm) as sagittal sections of reproductive structures (09 slides), rest of the animal in ethanol 70%. Collected 30.03.2008 at Saco do Mimi, Ilha do Papagaio, Cabo Frio Brazil (22°53'30,85"S; 41°59'9,52"W).

Distribution. The species was described from São Paulo, Southeastern Brazil (Du Bois-Reymond Marcus 1958). This is the first record from Rio de Janeiro State.

Remarks. The original description (Du Bois-Reymond Marcus 1958) is based on one worm and it corresponds to the material deposited in the SMNH. Du Bois-Reymond Marcus (1958) did not designate holotype in the description, thus we recognize it here as the holotype of *Imogine cata* by monotypy. Part of the 16 specimens studied by Marcus & Marcus (1968) is also in the same collection. The anterior part of the specimen present in the vouchers SMNH 109791 and SMNH 109792 is missing. Here we provide for the first time color photos of fresh material and of material from the type series. Both Faubel (1983) and Prudhoe (1985) considered *Imogine* as subgenus, and list the present species as *Stylochus (Imogine) cata*, as also determined by Marcus & Marcus (1968). Bulnes et al. (2005) and Marquina et al. (2014), however, considered that there are enough differences between those forms to designate them as genera. Thus, here we follow that arrangement.

Imogine refertus Du Bois-Reymond Marcus, 1965

Figure 29

Material examined.

Holotype. One specimen as serial sections of the posterior part (SMNH 109796, SMNH 109797, SMNH 109798, SMNH 109799, SMNH 109800). Collected 18.11.1964 at Ilha Porchat, Baía de Santos, São Paulo State, Brazil (23°58'50.5"S; 46°22'12.8"W).

Additional material. One specimen (MNRJ-PLAT 153) collected 18.01.2012 at Parcel da Pedra Lisa, Ilhabela, Brazil (23°47'27.42"S; 45°08'43.86"W). One specimen (MNRJ-PLAT 154) in 70% ethanol. Collected 20.01.2012 at Theresina, Sul de Ilhabela, Brazil (23°55'06.6"S; 45°27'30.2"W).

Distribution. The species is known from Southeastern Brazil (Du Bois-Reymond Marcus 1965; Bahia 2016).

Remarks. As described by Eveline Marcus, the holotype was the anterior part in ethanol and the posterior part in sagittal sections, in 11 slides. From this material five slides are deposited on the SMNH and correspond to the holotype of *Imogine refertus*. The species was originally described as *Stylochus* (Du Bois-Reymond Marcus 1965), and rearranged in sub-genera by Marcus & Marcus (1968). This was also followed by Faubel (1983) and Prudhoe (1985), but later the sub-genus *Imogine* was brought to genus level by Bulnes et al. (2005). Here we follow that resolution. As the species was recently illustrated with color photos of fresh material (Bahia 2016), here we only add photos of the holotype.

Imogine tica Marcus, 1952

Figure 30

Material examined.

Lectotype. One specimen as whole mount of most of the worm (SMNH 109801; 9.8 x 7 mm) and sagittal sections of the reproductive part (SMNH 109802, SMNH 109803, SMNH 109804, SMNH 109805). Collected 06.1951? at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen (MNRJ-PLAT 132, 13x9 mm) as sagittal sections of reproductive structures (09 slides), rest of the animal in ethanol 70%. Collected 31.12.2008 at Saco da Hípica, Ilha do Papagaio, Cabo Frio, RJ, Brasil (22°53'53,95"S; 41°58'42,11"W). One specimen (MNRJ-PLAT 133, 33x20 mm) as sagittal sections of reproductive structures (17 slides), rest of the animal in ethanol 70%. Collected 08.01.2010 at Enseada do Pinguim, Ilha dos Pargos, Cabo Frio, RJ, Brasil (22°51'31.03"5S; 41°54'22.38"0W).

Distribution. Southeastern Brazil (Marcus 1952; Bahia 2016).

Remarks. The original description is based on three worms and the slides of one of these worms are deposited in the SMNH. We thus designate these slides the lectotype of *Imogine tica*. The species was recently illustrated with photos of fresh material (Bahia 2016), and here we only add photos of the lectotype. The studied species was originally described as *Stylochus ticus* (Marcus 1952), and then placed in the subgenus *Imogine* (Marcus & Marcus, 1968) due to its tripartite seminal vesicle. Both Faubel (1983) and Prudhoe (1985) also follow that resolution. Bulnes et al. (2005) erected the subgenus to genus level and here we follow that arrangement.

Family: Stylochocestidae Bock, 1913

Genus: *Pentaplana* Marcus, 1949

Pentaplana divae Marcus, 1949

Figure 31

Material examined.

Lectotype. One specimen divided in two slides. SMNH 109654 with serial sections of posterior part and SMNH 109655 with whole mount of anterior part (4.5 x 3 mm). Collected 07.07.1948 at Ilha Porchat, Baía de Santos, São Paulo State, Brazil (23°58'50.5"S; 46°22'12.8"W).

Paralectotypes. Two specimens in a whole mount (SMNH 109656, 6 x 2.9 mm, 4 x 2.9 mm). One specimen as whole mount of entire worm (SMNH 109657, 8.5 x 5 mm). One specimen as whole mount of anterior part (SMNH 109658, 3.2 x 3 mm), together with part of a *Stylochoplana selenopsis*. One specimen as whole mount of the entire worm (SMNH 109659, 6 x 2.2 mm). Two specimens in a whole mount (SMNH 109660, 5 x 2.8 mm, 4.2 x 2.7 mm). One specimen as serial sections of posterior part (SMNH 109661). One specimen as serial sections of posterior part (SMNH 109662). Collected 22.09.1948 at Forte de Itaipú, Baía de Santos, São Paulo State, Brazil (24°01'06.6"S; 46°23'54.2"W).

Distribution. Species so far known only from type locality in Southeastern Brazil.

Remarks. The original description is based on one worm from Ilha Porchat and eight worms from Forte de Itaipú, both located in the Santos Bay. Ernst Marcus numbered the slides of his collection and assigned consecutive letters to the slides. The material here studied is missing the slides C and D. The voucher SMNH 109658 contains two different species as whole mounts, one being *Pentaplana divae* and the other *Stylochoplana selenopsis*. It is not possible to determine to which from the serial sections slides (SMNH 109661 or SMNH 109662) of paralectotypes correspond the anterior part as whole mount (SMNH 109658). Here we designate as lectotype of *Pentaplana divae* the specimen labelled from the type locality which is divided in whole mount and sagittal sections. The remaining specimens deposited at the SMNH are the designated paralectotypes. The species is the type of the genus and therefore the type series is an especially important finding. Faubel (1983) considered the species valid and placed the genus in the family Stylochocestidae, according to characters related to the prostatic vesicle. Prudhoe (1985), however, placed the species in Latocestidae, as also did Marcus (1949) in the original description, due to eyespots organization and general morphology traits. Here we follow Marcus' and Prudhoe's arrangement.

Family: Latocestidae Laidlaw, 1903b

Genus: *Latocestus* Plehn, 1896

Latocestus callizona (Marcus, 1947)

Figure 32

Type species of the genus.

Latocestus atlanticus Plehn, 1896, type by original designation.

Material examined.

Holotype. One specimen as whole mount of anterior part (SMNH 109614; 3.1 x 2.8 mm) and serial sections of posterior part (SMNH 109611, SMNH 109612, SMNH 109613). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected.

Distribution. The species is known from Southeastern Brazil (Marcus 1947).

Remarks. The material deposited at the SMNH is from the type locality of the species and fits the drawings from the original description (Marcus 1947). The specimen is immature in the female copulatory organs. This fits the description, based on one flatworm. Marcus (1947) did not designate holotype in the description, thus here we recognize it as holotype of *Latocestus callizona* by monotypy. The species was originally described as *Alleena callizona* (Marcus 1947). Faubel (1983) then transferred the species in a new combination to the genus *Latocestus*. Prudhoe (1985) also considered the genus *Alleena* synonym of *Latocestus*, but he did not list this species under that genus. Here we follow that arrangement.

Genus: *Nonatona* Marcus, 1952

Nonatona euscopa Marcus, 1952

Figure 33

Type species of the genus.

Nonatona euscopa Marcus, 1952, type species by original designation.

Material examined.

Holotype. One specimen as serial sections of the posterior part (SMNH 109650, SMNH 109651, SMNH 109652, SMNH 109653). Collected 02.1951 at Caiobá, Paraná State, Brazil (25°51'S; 48°32'W).

Distribution. The species is only known from South Brazil (Marcus 1952).

Remarks. The original description is based on one specimen and it corresponds to the material deposited at the SMNH. Marcus (1952) did not designate holotype in the description, thus, we recognize the examined material as holotype of *Nonatona euscopa* by monotypy. This is the type species of the genus and the only species of it so far, which highlights the importance of designating type material. Both Faubel (1983) and Prudhoe (1985) considered it a valid species, placed in Latocestidae.

Genus: *Prolatocestus* Faubel, 1983

Prolatocestus ocellatus (Marcus, 1947)

Figure 34

Type species of the genus.

Prolatocestus ocellatus (Marcus, 1947), type species by monotypy.

Material examined.

Lectotype. One specimen as whole mount of most of the worm (SMNH 109647; 12 x 4 mm) and serial sections of posterior part (SMNH 109641, SMNH 109642 and SMNH 109643). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected.

Paralectotype. One specimen as whole mount of most of the worm (SMNH 109645; 7 x 1.8 mm) and serial sections of posterior part (SMNH 109640). One specimen as whole mount of entire worm (SMNH 109644; 10 x 3.2 mm). One specimen as whole mount of entire worm (SMNH 109646; 10 x 3.5 mm). One specimen as whole mount of entire worm (SMNH 109648; 10 x 1.5 mm). All collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when they were collected.

Additional material. Three specimens in a whole mount (SMNH 109649; 6.2 x 1.2 mm, 6.1 x 1.2 mm and 12 x 2.2 mm). Collected at Ilhabela, São Paulo State, Brazil (23°49'S; 45°22'W).

Distribution. The species is known from Southeastern Brazil (Marcus 1947, 1949).

Remarks. The original description is based on 10 specimens from Ilha das Palmas (Marcus 1947) and in 1949 another five specimens were described from São Sebastião. According to the sections and size of whole mounts of partial worms we here designate the larger of both worms the lectotype of *Prolatocestus ocellatus*. The remaining specimens from Ilha das Palmas are designated paralectotypes and the material studied in 1949 is listed under additional material. The species was originally described as *Latocestus ocellatus* (Marcus 1947) and then placed in the new genus *Prolatocestus* by Faubel (1983) due to its prostatic vesicle lining and common genital aperture for both male and female pores. Prudhoe (1985), however, considered it in *Latocestus*. Here we follow Faubel's arrangement and also present for the first time color photos of fresh material. The specimen collected near the type locality fits the original description.

Suborder: Cotylea Lang, 1884

Family: Cestoplanidae Lang, 1884

Genus: *Cestoplana* Lang, 1884

Cestoplana salar Marcus, 1949

Figure 35

Type species of the genus.

Cestoplana rubrocincta (Grube, 1840), type by posterior designation.

Material examined.

Holotype. One specimen as whole mount of almost entire worm (SMNH 109682; 6.8 x 1.1 mm) and serial sections of posterior part (SMNH 109683). Collected 11.1948 at Ilha das Palmas, Baía de Santos, Sao Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Additional material. One specimen (MNRJ-PLAT 155, 6.2x1.5 mm) as sagittal sections of reproductive structures (06 slides), rest of the animal in ethanol 70%. Collected 18.01.2012 at Praia do Segredo, São Sebastião, Brazil (23º 49,65'S; 45º 25,36' W).

Distribution. The species was described from São Paulo State, Brazil

Remarks. The original description was based on one specimen (Marcus 1949) and it corresponds to the material deposited at the SMNH. The slides fit the drawings and description, but Marcus (1949) did not designate holotype, thus we recognize it the holotype of *Cestoplana salar* by monotypy. Also the specimen recently collected fits the description of the species and the key of polyclads (Du Bois-Reymond Marcus 1955b). Both Faubel (1983) and Prudhoe (1985) considered the species valid and in the family Cestoplanidae. They differed in their placement in the superfamily level, which is discussed by Bahia et al. (in press). After consideration of morphological and molecular characters the family is placed in Cotylea (Bahia et al. in press). Here we follow that systematic placement.

Cestoplana techa Du Bois-Reymond Marcus, 1957

Figure 36

Material examined.

Lectotype. One specimen as whole mount of anterior part of worm (SMNH 109684; 8 x 4 mm) and sagittal sections of posterior part (SMNH 109685 and SMNH 109686). Collected 11.1955 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen (MNRJ-PLAT 114, 23x4.5 mm) in 70% ethanol. Collected 10.12.2007. Two specimens (MNRJ-PLAT 115, 32x7; 32x9 mm), one as sagittal sections of reproductive structures (18 slides), rest of the animal in ethanol 70%. Collected 14.12.2008. Six specimens (MNRJ-PLAT 116, 28x10; 23x9; 21x8; 27x9; 21x8; 20x7 mm), one as sagittal sections of reproductive structures (10 slides), rest of the animal in ethanol 70%. Collected 18.04.2010. All above specimens collected at Canal de Itajuru, Cabo Frio, Brazil (22º 53' 11" S; 42º 00' 08" W). Two specimens (MNRJ-PLAT 117, 12x2; 12x2.3 mm) in 70% ethanol. Collected 19.04.2012 at Praia da Tartaruga, Búzios, Brazil (22°45'20,83"S; 41°54'12,32"W).

Distribution. The species is known from Southeastern Brazil (Du Bois-Reymond Marcus 1957) and possibly Colombia (Quiroga et al. 2004a, b). This is the first record for Rio de Janeiro State.

Remarks. The type series as described by Du Bois-Reymond Marcus (1957) contain three specimens, but in the SMNH there is only one worm. This is then here designated as the lectotype of *Cestoplana techa*, We here identify our specimens as *C. techa* as it lacks eyespots in the median line, differently from *C. rubrocincta*, the most similar species (Du Bois-Reymond Marcus, 1957). Both species has the same color pattern and more or less coloration, between orange and red. Both Faubel (1983) and Prudhoe (1985) recognized the species as valid in Cestoplanidae. Recent integrative taxonomy results point that Cestoplanidae and its genus should be included in Cotylea (Bahia et al. in press). Here we follow that systematic placement. In Colombia (Quiroga et al. 2004a) *C. rubrocincta* was reported, however, further examination of the specimens should be done. It is not clear from the results presented (photo record) if the worms have or have not the median line with eyes, which is the only diagnostic feature between *C. techa* and *C. rubrocincta*.

Family: Theamatidae Marcus, 1949

Genus: *Theama* Marcus, 1949

Theama evelinae Marcus, 1949

Figure 37

Type species of the genus.

Theama evelinae Marcus, 1949, type by original designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH type 5076a; 2 x 0.2 mm) and sagittal sections of posterior part (SMNH type 5076b). Collected 1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotypes. One specimen as whole mount of entire worm (SMNH type 5076c; 2.8 x 0.2 mm). One specimen as whole mount of entire worm (SMNH type 5076d; 5 x 0.1 mm). One specimen as whole mount of entire worm (SMNH type 5076e; 4 x 0.2 mm). All collected 1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is known from Southeastern Brazil (Marcus 1949).

Remarks. The original description is based on four worms and they correspond to the ones deposited at the SMNH and already stored at the type safe. However, it is unknown in the literature a formal designation of type material. The material deposited at the SMNH was examined by Curini-Galletti et al. (2008) and mentioned as original material, but no formal designation was made. Here we designate the specimen divided in whole mount and serial sections as the lectotype of *Theama evelinae* and the other specimens as paralectotypes. The species is type of the genus and the genus of its family, which highlights the importance of designation of type material. Both Faubel (1983) and Prudhoe (1985) recognized the species as valid. As is the case for *Cestoplana* morphological and molecular data pointed that the family should be included in Cotylea (Bahia et al. in press). Here we follow the systematic placement.

Family: Pericelidae Laidlaw, 1902

Genus: *Pericelis* Laidlaw, 1902

Pericelis cata Marcus & Marcus, 1968

Figure 38

Type species of the genus.

Pericelis beyerleyana (Collingwood, 1876), type by subsequent designation.

Material examined.

Holotype. One specimen as whole mount of head (SMNH 109883), whole mount of posterior margin (SMNH 109884) and as sagittal sections of middle part (SMNH 109885, SMNH 109886, SMNH 109887, SMNH 109888, SMNH 109889). Collected 31.12.1965 at Piscadera Baai, Curaçao (12°07'51"N 68°58'09"W).

Distribution. The species is known from Curaçao (Marcus & Marcus 1968), Colombia (Quiroga et al. 2004a) and Northeastern and Southeastern Brazil (Bahia et al. 2014, 2015).

Remarks. The material deposited at the SMNH fits exactly the description of the holotype as "fore end and the hind end in whole mounts and a series of sagittal sections of the copulatory organs". The original description states that in total the type series had five specimens, from which four (paratypes) are missing.

Family: Prosthiostomidae Lang, 1884

Genus: *Enchiridium* Bock, 1913

Enchiridium evelinae Marcus, 1949

Figure 39A, B, C and D

Type species of the genus.

Enchiridium periommatum Bock, 1913, type by original designation.

Material examined.

Lectotype. One specimen as whole mount of anterior part (SMNH 109924; 3.4 x 2.9 mm) and sagittal sections of posterior part (SMNH 109929, SMNH 109930, SMNH 109931). Collected 11.1948 at Ilha de Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W).

Paralectotypes. One specimen as whole mount of entire worm (SMNH 109923; 3.5 x 0.8 mm). One specimen as whole mount of entire worm (SMNH 109925; 10.7 x 2.6 mm). Two specimens in a whole mount (SMNH 109926; 5.8 x 2.7 mm and 4.8 x 1 mm). One specimen as sagittal sections of entire worm (SMNH 109927). One specimens in a whole mount (SMNH 109928; 11 x 3 mm) together with another Prosthiostomidae (8 x 1.5 mm). All collected 09.1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen as whole mount of anterior part (SMNH 109932; 9.3 x 6 mm) and sagittal sections of median part (SMNH 109933, SMNH 109934). Collected 1966 at Piscadera Baai, Curaçao (12°07'51"N; 68°58'09"W). One specimen as sagittal sections of posterior part (SMNH 109935). Collected at Florida, USA (27°S; 81°N). One specimen (MNRJ-PLAT 140, 28x12 mm) collected 18.01.2012 at Coroa da Ilha de Búzios, Ilhabela, Brazil (23°47'20.10"S; 45°08'44.58"W). One specimen (MNRJ-PLAT 141, 27x8 mm) collected at Naufrágio Theresina, Sul de Ilhabela, SP, Brazil (23°55'06.6"S; 45°27'30.2"W).

Distribution. Southeastern and Northeastern Brazil (Marcus 1949, Bahia et al. 2012, 2014, 2015), Curaçao (Marcus & Marcus 1968), Colombia (Quiroga et al 2004a) and Florida.

Remarks. The original description says six specimens collected at Ilha de São Sebastião were immature and one worm collected at Ilha das Palmas was mature. Despite not having the locality information on the slide label, the only worm from São Paulo that is mature is the one in the vouchers SMNH 109924, SMNH 109929, SMNH 109930 and SMNH 109931. Thus, we designate here the one that is both in whole mount and serial sections as the lectotype of *Enchiridium evelinae*. The other six worms are designated paralectotypes and material studied by Marcus & Marcus (1968) is listed under additional material. However, the description uses all of them without distinction to describe the species. Material deposited in the SMNH is similar to that studied by Bahia et al. (2012, 2015).

Enchiridium gabriellae (Marcus, 1949)

Figure 39E and F

Material examined.

Holotype. One specimen as sagittal sections (SMNH 109949). Collected 01.1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is only known from the type locality.

Remarks. The species was firstly described as *Prosthiostomum evelinae* (Marcus 1949) due to its exceptionally little number of eyespots, but in the description is mentioned that the prostatic vesicles are joined in a muscular envoltory, a diagnostic character of the genus *Enchiridium*. This can also be clearly seen in the drawings, as well as the typical orientation of the close together prostatic vesicles found in *Enchiridium*. Marcus & Marcus (1968) transferred the species to *Lurymare*, but as also shown in the description drawing the prostatic vesicles are not enclosed together with the seminal vesicle (Figure 39F). Thus, later, Faubel (1984) transferred the species to *Enchiridium*. The original description is based on one worm and it fits the material deposited at the SMNH, but Marcus (1949) did not designate holotype in the description, thus we recognize it as holotype of *Enchiridium gabriellae* by monotypy.

Genus: *Euprosthiostomum* Bock, 1925

Euprosthiostomum mortenseni Marcus, 1948

Figure 40

Type species of the genus.

Euprosthiostomum adhaerens Bock, 1925, type by original designation.

Material examined.

Holotype. One specimen as whole mount of anterior part (SMNH 109939; 2mm long) and sagittal sections of posterior part (SMNH 109936, SMNH 109937, SMNH 109938). Collected 12.11.1947 at São Vicente, São Paulo State, Brazil (23°58'55"S; 46°22'35"W).

Distribution. The species is known only from type locality.

Remarks. The material deposited at the SMNH fits the original description of one immature worm. However, Marcus (1948) did not designate holotype in the description, thus, here we recognize it the holotype of *Euprosthiostomum mortenseni* by monotypy. However, by the material available it is not possible to see reproductive structures that can be used for diagnosis, as the worm is immature. Therefore, when more material is available it will be possible to confront the original description to the updated definitions of the prosthiostomid genera and then place the species in the corresponding genus.

Genus: *Lurymare* Marcus & Marcus, 1968

Lurymare cynarium Marcus, 1950 **nov. comb.**

Figure 41

Type species of the genus.

Lurymare drygalskii (Bock, 1931), type by posterior designation.

Material examined.

Lectotype. One specimen as sagittal sections of entire worm (SMNH 109945, SMNH 109946, SMNH 109947). Collected 11.1949 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotypes. One specimen as sagittal sections (SMNH 109942 and SMNH 109943). Two specimens in a whole mount (SMNH 109944; 4 x 0.6 mm and 2 x 1 mm). One specimen as sagittal sections of entire worm (SMNH 109948). All collected 11.1949 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is only known from the type locality in Southeastern Brazil (Marcus 1950).

Remarks. The original description of the species is based on eight specimens, one mature, 2 almost mature, 3 in male phase and 2 immature (Marcus 1950). In the description Marcus (1950) wrote that the prostatic vesicles are well separated and the drawing of sagittal section also showed that (Marcus 1950, p.189). However, the drawing of the general view of the worm and the reproductive structures in whole mount show that the prostatic vesicles are close together (Marcus 1950, p.191). The vesicles were drawn the same way as in the drawing of *Lurymare matarazzoi* (Marcus 1950, p.187). Additionally to that, and most importantly, the slides made by Ernst Marcus and deposited at the SMNH also show the prostatic close together and envolved by a muscular sheath (Figure 41E). It is unclear why Marcus (1950) stated that the vesicles were separated and why he drew them differently in his figures. When we compare the whole mount drawing of *Prosthiostomum gilvum* (Marcus 1950, p.187) to the present species it is possible to see the vesicles separated, different from the description of *Prosthiostomum cynarium*. Only two genera of Prosthiostomidae present prostatic vesicle close together: *Enchiridium* and *Lurymare*. However, only the later has the closely placed vesicles also together with the seminal vesicle, as can be seen in this species (Figure 41D, E).

The slides and whole mounts studied here fit the diagnosis of the genus *Lurymare* (Marcus & Marcus 1968; Faubel 1984). Thus here we put the species as new combination in the genus *Lurymare*. We also designate the largest worm, and the most mature, as the lectotype of *Lurymare cynarium*, the remaining specimens are designated paralectotypes.

Lurymare matarazzoi (Marcus, 1950)

Figure 42E, F and G

Material examined.

Lectotype. One specimen as whole mount of entire worm (SMNH 109956; 12x2.8 mm). collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109957; 12x2.5 mm). Collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Additional material. One specimen as whole mount of entire worm (SMNH 109958; 4.9x1.5 mm). Collected at Curaçao (12°10'10.4520"N; 68°59'24.0756"W). One specimen in a whole mount of anterior part (SMNH 109960; 3x1.2 mm) together with an anterior part of *Prosthiostomum pulchrum*) and as sagittal sections of posterior part (SMNH 109959). Collected 09.1930 at Kralendijka, Bonaire, West Indies (12°9'2.52"N; 68°16'36.12"W).

Distribution. The species is known from Southeastern Brazil (Marcus 1950; Bahia 2016), Curaçao and Bonaire (Marcus & Marcus 1968) and Colombia (Quiroga et al. 2004a).

Remarks. The original description is based on "numerous" specimens. In the SMNH there are two worms from the type locality, but none present serial sections of reproductive parts. Thus, we designate the most mature worm as the lectotype and leave the other one as paralectotype of *Lurymare matarazzoi*. The voucher SMNH 109958 is not cited in any work by Ernst and Eveline Marcus. The species was originally described as *Prosthiostomum matarazzoi* (Marcus 1950), then transferred by Marcus & Marcus (1968) to the genus *Lurymare* because of the prostatic vesicles united by a muscular capsule are also enclosed with the seminal vesicle in a muscular sheath. However, Faubel (1984), despite the diagnostic features, placed the species in *Euprosthiostomum*. As this genus present separated prostatic vesicles, it can not host the present species. In the material deposited in the SMNH is possible to observe in the slides the muscular capsule around both the prostatic vesicles and the seminal vesicle (Figure 41F). As already discussed by Bahia (2016), based on fresh material, and now examining the type material, we reinforce the placement of the species in *Lurymare*.

Lurymare utarum (Marcus, 1952)

Figure 42A, B, C and D

Material examined.

Lectotype. One specimen as sagittal sections of the middle part (SMNH 109967 and SMNH 109968). Anterior part as whole mount (SMNH 109708; 6x4.5 mm) together with an anterior part of *Phaenocelis medvedica*. Collected 11.1951? at Ilha de São Sebastião, São Paulo State (23º49'S; 45º24'W).

Additional material. One specimen as whole mount of anterior and posterior part (SMNH 109969; 5x4 mm and 9x5 mm) and sagittal sections of middle part (SMNH 109970). Collected 01.1959 at Virginia Beach, Virginia Key, Florida, U.S.A. (25°43'59.1"N; 80°09'58.5"W).

Distribution. The species is known from southeastern Brazil (Marcus 1952; Bahia et al. 2014), Florida (Marcus & Marcus 1968) and Colombia (Quiroga et al. 2004a).

Remarks. This species was originally described as *Prosthiostomum utarum* (Marcus 1952). Marcus & Marcus (1968) then transferred it to *Lurymare* based on a muscular sheath containing the both prostatic vesicles (already enclosed in a muscular sheath) and the seminal vesicle. The original description drawings and the type material here examined both show that the vesicles are together in a muscular sheath, thus we reinforce the arguments discussed in Bahia et al. (2014) and place the species in *Lurymare*. The original description is based on six worms, but at the SMNH there is only one worm from the type locality. Thus we designate it the lectotype of *Lurymare utarum*. Unfortunatelly, the anterior part of the lectotype is in a whole mount together with the anterior part of the lectotype of *Phaenocelis medvedica* (Figure 20). The additional material deposited at the SMNH corresponds to that studied in Marcus & Marcus, 1968.

Genus: *Prosthiostomum* Quatrefages, 1845

Prosthiostomum gilvum Marcus, 1950

Figure 43

Type species of the genus.

Prosthiostomum siphunculus (Delle Chiaje, 1822), type by posterior designation.

Material examined.

Lectotype. One specimen as whole mount of the anterior part (SMNH 109954; 4 x 3 mm) and sagittal sections of posterior part (SMNH 109950, SMNH 109951, SMNH 109952, SMNH 109953). Collected 11.1949 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109955; 9 x 2.8 mm). Collected 11.1949 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is known from the type locality in Southeastern Brazil (Marcus 1950) and Colombia (Quiroga et al. 2004a).

Remarks. The original description is based on two specimens and both are deposited at the SMNH. We here designate the one divided in both whole mount and serial sections as the lectotype of *Prosthiostomum gilvum,* and the remaining voucher is designated paralectotype. The designation is made with the purpose of clarifying the application of the name of the taxon. The species present separate prostatic vesicles, each with its own muscular sheath (Figure 43D and E), in opposition to the genera *Lurymare* and *Enchiridium*. Therefore, both Faubel (1984) and Prudhoe (1985) maintained the species in the genus *Prosthiostomum*. The specimen reported from Colombia (Quiroga et al. 2004a), lack illustration of internal features as to proper identify the specimen.

Family Euryleptidae Lang, 1884

Genus: *Acerotisa* Strand, 1928

Acerotisa bituna Marcus, 1947

Figure 44A, B and C

Type species of the genus.

Acerotisa inconspicua (Lang, 1884), type by posterior designation.

Material examined.

Holotype. One specimen as serial sections of entire worm (SMNH 109589 and SMNH 109590). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected.

Additional material. One specimen as serial sections of entire worm (SMNH 109591). Four specimens in a whole mount (SMNH 109592) together with a juvenile *Pseudoceros* sp.. All collected at Piscadera Baai, Curaçao (12°07'51"N 68°58'09"W). No data on when they were collected.

Distribution. The species is known from Southeastern Brazil (Marcus 1947) and from Curaçao (Marcus & Marcus 1968).

Remarks. The original description is based on one specimen that fits with the one deposited at the SMNH. Marcus (1947) did not designate a holotype in the description, thus, we recognize this material as the holotype of *Acerotisa bituna* by monotypy. Unfortunately the corresponding slides are with fungus or are dry and it is not possible to observe all the details of the cuts (Figure 44B). The species was placed in *Acerotisa* by both Faubel (1984) and Prudhoe (1985).

Acerotisa leuca Marcus, 1947

Figure 44D and E

Material examined.

Syntypes. Two specimens in a whole mount (SMNH 109593, 2.1 x 1.8mm and 1.6 x 1.1 mm) collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data about when the material was collected.

Additional material. One specimen as whole mount of entire worm (SMNH 94662, 0.6 x 0.25 mm) together with *Convoluta* sp. specimens. One specimen as whole mount of entire worm (SMNH 94676, 1.5 x 1 mm) together with a *Cycloporus gabriellae* and another *Acerotisa* species. One specimen as whole mount of entire worm (SMNH 109594, 1.5 x 1 mm). One specimen as serial sections of entire worm (SMNH 109595, SMNH 109596, SMNH 109597). No data about where and when the material was collected.

Distribution. The species is so far only known from the type locality.

Remarks. The original description (Marcus, 1947) describes and gives few measurements of one worm, and it is unclear the origin of most of the material deposited at SMNH. In other publications no mention is made to that material, however, it is clear that it was studied by Ernst Marcus. Only one slide has locality written on it and it corresponds to the type locality (Ilha das Palmas). This slide is numbered with a 1 and following slides are numbered from 1 to 4. We believe they were also collected at Ilha das Palmas. In total there are six worms in slides. And unfortunately two of three slides with serial sections are dry or with fungus. Thus, among the present material we are not able to designate lectotype and paralectotypes, and thus leave them all as syntypes. Material mixed with other species is considered as additional material. One syntype slide that contains both *Acerotisa leuca* and *Cycloporus gabriellae* have two collection numbers, we understand that those numbers are written consecutivelly, respectively representing each of the specimens. Another slide with confusing numbers is the one labelled SMNH 94662 which also contains the code SMNH 9476 written on it.

Genus: *Cycloporus* Lang, 1884

Cycloporus gabriellae Marcus, 1950

Figure 45

Type species of the genus.

Cycloporus papillosus (Sars in Jensen, 1878), type by posterior designation.

Material examined.

Lectotype. One specimen as serial sections of entire worm (SMNH 109846, SMNH 109847, SMNH 109848). Collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W). No data about when it was collected.

Paralectotypes. One specimen as whole mount of entire worm (SMNH 109842, 5.1x3 mm). One specimen as whole mount of entire worm (SMNH 109843, 3.1x2.3 mm). Two specimens in a whole mount (SMNH 109844, 3x2.8 mm and 1.2x0.9 mm) together with two juveniles of *Cycloporus* and one juvenile from *Latocestus*. One specimen as serial sections of entire worm (SMNH 109845, juvenile or “larvae”). All collected at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W). No data about when it was collected.

Additional material. One specimen as whole mount of entire worm (SMNH 94675, 1.3x1.05 mm) together with an *Acerotisa leuca* and possibly an *Acerotisa bituna*. No data about locality or collection date. One specimen as whole mount of anterior part of worm (SMNH 109849, 6.5x3 mm) and as serial sections of posterior part (SMNH 109850, SMNH 109851, SMNH 109852, SMNH 109853). Collected September 1951 at Ubatuba, São Paulo State, Brazil (23°27'S; 45°06'W). One specimen as whole mount of entire worm (SMNH 109854) and its food, an ascidian. Collected at West Indies (no further specification).

Distribution. The species is known from the Brazilian coast, from the type locality (Marcus 1950), Ubatuba (Marcus 1952) and from Rio de Janeiro State (Bahia et al. 2014) and also from the West Indies (Marcus & Marcus 1968).

Remarks. In the original description (Marcus 1950), the author states the collection of five specimens, but the material deposited in the SMNH contain more animals, all additional worms being juveniles. The slides that correspond to specimens of the type locality are labelled with consective letters from K to Q, thus we consider them as to be from the type series and designate the worm as serial sections of the whole specimen as the lectotype and the remaining material as paralectotypes. The voucher SMNH 109845 corresponds to the drawings of figure 168 (Marcus 1950) of a juvenile or larvae. It was not possible to find the mouth as depicted by Marcus (1950). Another group of slides are labelled with consecutive letters from A to E and correspond to material collected in Ubatuba (Southeasthern Brazil) and studied by Ernst Marcus in 1952. The voucher SMNH 109854 is labelled as being from West Indies and in the studied material from Marcus & Marcus (1968) there are two specimens that could fit that: one from Bird Island (West of Dominica) and the other from Antigua. It is unclear from which locality the animal was collected. Both Faubel (1984) and Prudhoe (1985) placed the species in *Cycloporus*.

Genus: *Eurylepta* Ehrenberg, 1831

Eurylepta neptis Du Bois-Reymond Marcus, 1955a

Figure 46D and E

Type species of the genus.

Eurylepta cornuta (O.F. Müller, 1776), type by posterior designation.

Material examined.

Lectotype. One specimen as sagittal sections of posterior part (SMNH 109875, SMNH 109876, SMNH 109877). Collected 11.1953 at Taquanduva, Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is known only from the type locality in Southeastern (Du Bois-Reymond Marcus 1955a).

Remarks. The species is placed in Eurylepta by both Faubel (1984) and Prudhoe (1985). The original description is based on four worms; one of them is deposited at the SMNH. Thus, we designate it the lectotype of *Eurylepta neptis*. The anterior part of it is missing, but the sections fit the drawings of the description.

Eurylepta piscatoria (Marcus, 1947)

Figure 46A, B and C

Material examined.

Holotype. One specimen as serial sections of entire worm (SMNH 109601, SMNH 109602, SMNH 109603). Collected at Ilha das Palmas, Baía de Santos, São Paulo State, Brazil (24°00'31.5"S; 46°19'28.5"W). No data on when it was collected.

Additional material. One specimen as whole mount of entire worm (SMNH 109604; 1x0.5 mm). Collected 09.1930 at Kralendijk, Bonaire (12°08'41.3"N; 68°16'36.0"W).

Distribution. The species is known from southeastern Brazil (Marcus 1947) and Bonaire (Marcus & Marcus 1968) and possibly Florida (Hyman 1952, p. 199).

Remarks. The species was originally described as *Acerotisa piscatoria* (Marcus 1947), as according to Marcus (1947, p. 136) it did not have marginal tentacles but only slight projections of the margin. The placement in this genus was maintained by Prudhoe (1985). However, Faubel (1984) placed the species in new combination in the genus *Eurylepta*, due to the absence of a frontal branch of the main intestine. The weight of this character was not tested yet, and the placement of an atentaculated species in the genus should be addressed in future studies with more material available. For now we follow Faubel's (1984) position, but consider it should be revised using more data. The original description is based on one worm and in the SMNH collection only one of the worms is from the type locality. However, Marcus (1947) did not designate holotype in the description, therefore we recognize it the holotype of *Eurylepta piscatoria* by monotypy, the remaining material is listed under additional material.

Eurylepta turma Marcus, 1952

Figure 46F, G, H, I and J

Material examined.

Lectotype. One specimen as sagittal sections of anterior part of worm (SMNH 109882). Collected 09.1951? at Ubatuba, São Paulo State, Brazil (23°27'S; 45°06'W).

Paralectotype. One specimen as whole mount of entire worm (SMNH 109878; 6.1 x 4.2 mm). One specimen as sagittal sections of anterior/middle part (SMNH 109880 and SMNH 109881). Both collected 11.1951? at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is known from Southeastern Brazil (Marcus 1952).

Remarks. The labelling of the slides point to the consecutive letters meaning slides from a same locality. The species has two different type localities. Here we designate the worm from the first locality mentioned in the description, and that is a whole in serial sections as the lectotype of *Eurylepta turma*, the remaining specimens are designated paralectotypes. Both Faubel (1984) and Prudhoe (1985) placed the species in *Eurylepta.*

Family: Pseudocerotidae Lang, 1884

Genus: *Acanthozoon* Collingwood, 1876

Acanthozoon hispidum (Du Bois-Reymond Marcus, 1955a)

Figure 47A, B and C

Type species of the genus.

Acanthozoon auropunctatum (Kelaart, 1858), type by posterior designation.

Material examined.

Lectotype. One specimen as sagittal sections of middle part of the worm (SMNH 109991, SMNH 109992 and SMNH 109993). Collected 06.12.1953 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is only known from the type locality in Southeastern Brazil (Du Bois-Reymond Marcus 1955a).

Remarks. The species was originally described as *Pseudoceros (Acanthozoon) hispidus* (Du Bois-Reymond Marcus 1955a). As the species is papillated, and could not be included in *Pseudoceros*, it was transferred by Hyman (1959, p. 583) to *Acanthozoon*, which was from them on considered as a genus and not a subgenus. Both Faubel (1984) and Prudhoe (1985) follow that decision. The original description is based on two worms, but in the SMNH there is only part of a worm as serial sections of reproductive part. Here we designate this material as the lectotype of *Acanthozoon hispidum*.

Genus: *Phrikoceros* Newman & Cannon, 1996

Phrikoceros mopsus (Marcus, 1952)

Figure 47D and E

Type species of the genus.
Phrikoceros baibaiye Newman & Cannon, 1996, type by original designation.

Material examined.
Lectotype. One specimen as sagittal sections of anterior part of worm (SMNH 109994, SMNH 109995 and SMNH 109996). Collected 11.1951 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).
Additional material. One specimen (MNRJ-PLAT 148, 12x8 mm) collected 01.12.2008 at Parcel da Pedra Lisa, Ilhabela, Brasil (23°47'27.42"S; 45°08'43.86"W). One specimen (MNRJ-PLAT 149, 23x24 mm) collected 18.01.2012 at Coroa da Ilha de Búzios, Ilhabela, São Paulo State, Brazil (23°47'20.10"S; 45°08'44.58"W).

Distribution. Rio Grande do Norte State, Southeastern Brazil (Marcus 1952; Bahia et al. 2012, 2014), Antigua, Curaçao, Barbuda (Marcus & Marcus 1968), Colombia (Quiroga et al. 2004a) and Argentina (Brusa et al. 2009; Bulnes et al. 2011).

Remarks. The species was described as *Pseudoceros mopsus* (Marcus 1952), Faubel (1984) and Prudhoe (1985) maintained that placement, and it was later transferred to *Phrikoceros* by Quiroga et al. (2004a) in a new combination. Here we follow that position. The original description (Marcus 1952) is based on two worms, but only one is deposited at the SMNH. Thus, we designated the corresponding slides as the lectotype of *Phrikoceros mopsus*.

Genus: *Pseudoceros* Lang, 1884

Pseudoceros bicolor Verrill, 1901

Type species of the genus.
Pseudoceros velutinus (Blanchard, 1847), type by posterior designation.

Material examined. Two specimens (MNRJ-PLAT 112, 15x9; 27x14 mm) collected 25.09.2009 at Saco do Cardeiro, Arraial do Cabo, Rio de Janeiro State, Brazil (22° 57' 55,71" S; 42° 00' 07,32" W).

Distribution. The species is known from Bermudas (Verrill 1901), Curaçao (Marcus & Marcus 1968), Colombia (Quiroga et al. 2004a), Florida, Virgin Islands, Jamaica, Belize, Honduras, Caribbean coast of Panama (Rawlinson 2008), southeastern and northeastern Brazil (Bahia & Padula 2009, Bahia et al. 2012, 2014).

Remarks. The material collected in Southeastern Brazil has a different coloration pattern than previously observed for the species (Bolaños et al. 2007; Bahia et al. 2014) and it was illustrated in Litvaitis et al. (2010, p.840, Figure 4N).

Pseudoceros chloreus Marcus, 1949

Figure 48

Material examined.
Holotype. One specimen as whole mount of the entire worm (SMNH 109975; 6 x 3 mm). Collected 09.1948 at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W).

Distribution. The species is only known from the type locality in Southeastern Brazil.

Remarks. Marcus (1949) based the description of this species on one immature worm. The material deposited at the SMNH fits the original description, except for the destroyed pseudotentacular area, which Marcus (1949) did not mention. Marcus (1949, p.86) mentioned that the tentacles protrude from the margin in a half moon shape. The drawings also show a half moon form that is not usually found in *Pseudoceros.* Addtionally, the cerebral eyespots are separated in two groups, which is also not common in *Pseudoceros*, that usually present horse-shoe shaped arrangement (Newman & Cannon 1994). The species presents an arrangement very similar to that found in Euryleptidae. Marcus (1949) did not mention details about the pharynx form, but in the drawings is possible to see it is also not fitting the diagnostic ruffled pharynx from *Pseudoceros*, and being more like the tubular typical Euryleptidae pharynx. Unfortunately there are no sections of the species. Faubel (1984, p. 238) listed the species under *Incertae Sedis*, but Prudhoe (1985) considered it valid. The tentacles resemble those illustrated by Hyman (1953, p. 365, 366) in *Pseudoceros mexicanus*, another species listed as *Incertae Sedis*, but considered as member of Pseudocerotidae. In face of those evidences and the lack of internal morphology details, we leave the species as *Incertae Sedis* until additional material can be collected and studied. As Marcus (1949) did not designate holotype in the description, here we recognize the material donated by Eveline Marcus as the holotype of *Pseudoceros chloreus* by monotypy, but we emphasize that this species should be collected again and revised at the generic level.

Pseudoceros rawlinsonae Bolaños, Quiroga & Litvaitis, 2007

Material examined.

Additional material. One specimen (MNRJ-PLAT 139, 39x30 mm) collected 20.01.2012 at Naufrágio Theresina, Sul de Ilhabela, São Paulo State, Brazil (23°55'06.6"S; 45°27'30.2"W).

Distribution. Southernmost record of this species so far, reaching subtropical waters of São Paulo State (Spalding et al. 2007).

Genus: *Pseudobiceros* Faubel, 1984

Pseudobiceros evelinae (Marcus, 1950)

Figure 49

Type species of the genus.

Pseudobiceros strigosus (Marcus, 1950) junior synonym of *Pseudobiceros gratus* (Kato, 1937), type by posterior designation.

Material examined.

Holotype. One specimen as whole mount of the anterior part (SMNH 109990; 6 x8 8 mm) and sagittal sections of posterior part (SMNH 109981, SMNH 109982, SMNH 109083, SMNH 109984, SMNH 109985, SMNH 109986, SMNH 109987, SMNH 109988, SMNH 109989). Collected 27.07.1949 at Forte de Itaípu, Baía de Santos, São Paulo State, Brazil (24°01'06.6"S; 46°23'54.2"W).

Additional material. One specimen (MNRJ-PLAT 142, 15x7 mm) collected 30.11.2008 at Naufrágio Velásquez, Ilhabela, Brazil (23°53,882'S; 45°27,724'W)

Distribution. Southeastern Brazil (Marcus 1950; Bahia et al. 2014) and Rio Grande do Norte State (Bahia et al. 2012).

Remarks. The original description is based on one specimen and the material deposited at the SMNH fits the original description (Marcus 1950). The author did not designate holotype in the description, thus here we recognize it as the holotype of *Pseudobiceros evelinae* by monotypy. Additional material studied by Marcus (1952) is not deposited at the SMNH.

Genus: *Thysanozoon* Grube, 1840

Thysanozoon brocchii (Risso, 1818)

Type species of the genus.

Thysanozoon brocchii (Risso, 1818), type by posterior designation.

Material examined.

Additional material. One specimen as whole mount of entire worm (SMNH 109999; 6 x 4 mm). One specimen as whole mount of entire worm (SMNH 110004; 2.2 x 2 mm) labelled as juvenile. Collected 1949? at Ilha de São Sebastião, São Paulo State, Brazil (23º49'S; 45º24'W). One specimen as whole mount of anterior and posterior part of worm (SMNH 110000) and as sagittal sections (SMNH 110001 and SMNH 110002). One specimen as sagittal sections of middle part of worm (SMNH 110003). One specimen as sagittal sections of middle part of worm (SMNH 1100005, SMNH 110006 and SMNH 110007). Collected at Ilha das Palmas (24°00'31.5"S; 46°19'28.5"W) or Ilha de São Sebastião (23º49'S; 45º24'W), São Paulo State, Brazil. One specimen as sagittal sections of middle part (SMNH 109998). Collected 1966 at Piscadera Baai, Curaçao (12°07'51"N; 68°58'09"W). Two specimens (MNRJ-PLAT 113, 33x22; 35x22 mm) collected 18.05.2009 at Enseada da Vale, Ilha Guaíba, Mangaratiba, Brazil. Two specimens MNRJ-PLAT 143 (9x10 mm) and MNRJ-PLAT 145 (18x14 mm). Both collected 18.01.2012 at Coroa da Ilha de Búzios, Ilhabela, Brazil (23°47'20.10"S; 45°08'44.58"W). Two specimens MNRJ-PLAT 144 (10x11 mm) and MNRJ-PLAT 146 (15x17 mm) collected 18.01.2012 at Parcel da Pedra Lisa, Ilhabela, Brazil (23°47'27.42"S; 45°08'43.86"W). One specimen (MNRJ-PLAT 147, 5x5 mm) collected

19.01.2012 at Saco do Eustáquio, Ilhabela, São Paulo State, Brazil (23°50'11.5"S 45°14'33.9"W).

Distribution. Cosmopolitan species (Bahia et al. 2015).

Remarks. The material deposited at the SMNH is to be considered additional material of the species, however in the case the many variations of *Thysanozoon brocchii* are revised and further separated these can the type material of *T. lagidium*. Among the slides there are material studied in 1949, 1952 and 1968 by Ernst and Eveline Marcus. Most of the slides do not have locality specification, or have only a broad version of it, but Marcus (1949) specified it the description. However, material studied by Marcus (1952) can be from either two localities, and it is not specified which specimens were collected where.

DISCUSSION

In this study we have re-examined a large museum collection, found and recognized holotypes, designated lectotypes and organized information available on type series of 52 species. Lectotypes were designated for 30 species. This effort is unprecedent in Polycladida and is a much needed one, as many species still remain without designated type material. We followed in this paper the recommendation 73F of the ICZN (http://iczn.org/iczn/index.jsp) that states the avoidance of assumption of holotype, assumption was only made when the description was based on only one flatworms and the locality written on the slides corresponded to the type locality. For the other situations we, as recommended, designated a lectotype rather than assuming a holotype. Designation of lectotypes was also recently done for material described by Newman & Cannon (1998) from Australia (Hall & Adlard 2012). Lack of type material, damaged or lost holotypes, and poor descriptions are also common in sea slugs (Schrödl & Haszprunar 2016) and this is a huge problem for the nomenclatural stability.

In Polycladida, because of that kind of problem many species are unsolvably put in *Incertae sedis* lists (Faubel 1984). This is especially grave when the species lacking a holotype is the type of a genus, as *Euryleptides brasiliensis*, among others. The importance of type material is stated clearly by the International Code of Zoological Nomenclature (http://iczn.org/iczn/index.jsp) and recently has been subject of strong debate since some species had photographs designated as holotype (Marshall & Evenhuis 2015). The critics to that procedure are multiple and justifiable (Amorim et al. 2016) and advocate to improve species delimitation procedures with the addition of as much information as possible. Holotypes are to be considered ways to test a hypothesis, which is what a species represents. They should be available to other researchers to allow verification and test of the validity of that hypothesis against their own interpretations and against new technologies that could provide more information about the species type material. For example, recently procedures have been described for extraction of DNA from animals fixed in formalin (Ruane & Austin 2017) and for scanning of museum material (Carbayo & Lenihan 2016).

As otherwise stated by Quiroga et al. (2004b) *Alloioplana wyona* (Marcus & Marcus, 1968) was never recorded from Brazil. This species is described from Curaçao, its description was written in English and mentioned material to be deposited (H1132) at the Rijksmuseum van Natuurlijke Historie in Leiden. Also *Notoplana insularis* Hyman, 1939c was never reported from Brazil. It was described from the West Indies, Trinidad and Florida (Hyman, 1939c; Hyman, 1955c) in English, and there is material deposited (USNM 20423). This species was also later found in Colombia (Quiroga et al. 2004b). One example of problems that can be caused by descriptions in languages not widely used in the academic zoological environment is the case of *Comoplana angusta* and *Zygantroides henriettae*, species that were mistaken or confused by each other, due to possible misinterpretation of a description in Portuguese. Marcus (1947) first thought it was *Comoplana*, but later after discussing with him, Corrêa (1949), in a paper also in Portuguese, solved the confusion. However, Hyman (1952) misinterpreted taxonomical remarks and added more confusion to the situation. As result the material from Brazil (Marcus 1947), deposited in the SMNH and labelled as *Comoplana angusta*, is really *Zygantroides henriettae*, but unfortunately not the type material.

Most of Brazilian polyclad species were described before digital photography development and widespread use (Marcus 1947, Marcus & Marcus 1968) and new information can be now added with this tool, mainly about color and color pattern. These characters are considered by Hyman (1951), Newman & Cannon (2003) and Litvaitis et al. (2010) as valid and informative, especially at the species level. Also with digital photography, and its combination with improvements on microscopy in the 70 years, it is possible to have more information on internal anatomy characters and to provide that information to future researchers. Marine flatworms are relatively poorly studied (Braccini et al. 2016) and a general assessment of “macroturbellaria” in Brazil (Carbayo & Froehlich 2008) has pointed towards 66 species in Brazilian waters. This number increased after the the study of Brazilian Polycladida was resumed, now the number of species are 71 in total, included in 40 genera, and 21 families. From those 39 are from the suborder Acotylea and 32 from Cotylea, according to a recent redefinition by Bahia et al. (in press). These numbers and the numbers of Cotylea are expected to rise when more reef ecosystems are surveyed, as they have higher polyclad diversity (Prudhoe 1985; Rawlinson 2008). From the 3000 km of reefs of North and Northeastern Brazilian coast only few areas were sampled (Bahia et al. 2012; Queiroz et al. 2013; Bahia et al 2014). Most species described so far were collected on bolders and small stones environment (Marcus, 1950; Bahia et al. 2015).

Relationship between Brazilian and Caribbean fauna is recognized in different vertebrate and invertebrate groups (Spalding et al. 2007 and references therein). The species *Eurylepta piscatoria* (Marcus, 1947), *Acerotisa bituna* Marcus, 1947, *Cycloporus gabriellae* Marcus, 1950 and *Enchiridium evelinae* Marcus, 1949 were described from Brazil and were posteriorly found in the Caribbean (Marcus & Marcus, 1968). And the species *Pericelis cata*, *Pseudoceros bicolor, Pseudoceros rawlinsonae* and *Pseudobiceros pardalis* were described from the Caribbean and later found in the Brazilian coast (Bahia & Padula 2009; Bahia et al. 2014). The presence of deep reefs in the mouth of the Amazon River (Moura et al. 1999; Moura et al. 2016), shows that it connects biogeographic provinces more importantly than previously thought. It is not a barrier for benthic organisms or their larvae with intracapsular metamorphosis, as some polyclads (Rawlinson 2014), but can be for larval dispersion as many other polyclads (Rawlinson 2014). Because of the relative high level of endemism is unlikely that the Brazilian polyclads are a subset of Caribbean fauna. However, the collecting bias is also high, with few localities sampled in the South Atlantic, and few places were surveyed in the Caribbean as well. Thus, it is not possible to draw a more conclusive picture of biogeography of the group. This is also the case for species diversity comparisons, since much of the eastern Atlantic and Pacific remains unsampled.

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FIGURE LEGENDS

Figure 1: Geopolitic map of Brazil, with names of coastal States. Brazilian States marked with circles were sampled in studies about Polycladida.

Figure 2: *Euplana hymanae*. A: general view; B: Syntypes slides; C and D: sagittal section of male structures.

Figure 3: *Zygantroides henriettae*. A: general view; B: anterior part; C, D, E and F: sagittal sections of reproductive structures.

Figure 4: *Parviplana lynca*. A: *P. lynca in vivo*; B and C: dorsal and ventral view; D, E and F: sagittal sections of reproductive strucutures; G: general view of paratypes; H: sagittal section of the holotype; I: holotype slide.

Figure 5: *Notocomplana evelinae*. A: lectotype slides; B, C and D: sagittal sections of male reproductive structures; E: sagittal section of female reproductive structure.

Figure 6: *Notocomplana martae*. A: paralectotype general view; B: lectotype slides; C and D: sagittal sections of reproductive structures.

Figure 7: *Notocomplana syntoma*. A: holotype anterior part; B: holotype slides; C: sagittal section of reproductive structures.

Figure 8: *Notoplana divae*. A: general view; B: lectotype anterior part; C: lectotype slides; D, E and F: sagittal sections of reproductive structures.

Figure 9: *Notoplana micheli*. A: lectotype anterior part; B: lectotype slides; C and D: sagittal sections of the reproductive structures.

Figure 10: *Notoplana plecta*. A: holotype slides; B, C and D: sagittal sections of reproductive strucutres.

Figure 11: *Notoplana sawayai*. A: lectotype anterior part; B: lectotype slides; C, D and E: sagittal sections of reproductive structures.

Figure 12: *Pleioplana megala*. A: anterior part of lectotype; B: lectotype slides; C and D: sagittal sections of reproductive structures.

Figure 13: *Alloioplana aulica*. A and B: dorsal and ventral view of MNRJ-PLAT 156; C: detail of anterior part; D: sagittal section of reproductive structure of MNRJ-PLAT 156; E: lectotype slides; F, G and H: sagittal section of lectotype; I: anterior part of lectotype.

Figure 14: *Armatoplana divae*. A and B: dorsal and ventral general view of MNRJ-PLAT 159; C and D: sagittal sections of MNRJ-PLAT 159; E: general view of holotype; F: holotype slides; G and H: sagittal sections of reproductive structures.

Figure 15: *Armatoplana leptalea*. A: *A. leptalea in vivo*; B: detail of the anterior part; C: general dorsal view; D, E, F, and G: sagittal sections of reproductive sections; H: anterior part of holotype; I: holotype slides; J, K and L: sagittal sections of reproductive structures.

Figure 16: *Interplana evelinae*. A: anterior part of holotype; B: holotype slides; C and D: sagittal sections of reproductive strucutures.

Figure 17: *Stylochoplana divae*. A: general view of paralectotype; B: lectotype slides; C and D: sagittal sections of reproductive structures.

Figure 18: *Stylochoplana selenopsis*. A: anterior part of holotype; B and C: sagittal sections of reproductive structures of holotype; D: holotype slides.

Figure 19: *Cryptocelis lilianae*. A: general view of paratype; B: anterior part of holotype; C: holotype slides; D, E and F: sagittal sections of reproductive structures.

Figure 20: *Phaenocelis medvedica*. A: *P. medvedica in vivo*; B: detail of anterior part; C: detail of ventral view; D, E and F: sagittal sections of reproductive structures; G: detail of the anterior part of paralectotype; H: paralectotype general view; I: lectotype slides; J and K: sagittal sections of reproductive structures.

Figure 21: *Triadomma curvum*. A: *T. curvum* general view of paralectotype; B: lectotype slide; C and D: sagittal sections of reproductive structures.

Figure 22: *Triadomma evelinae*. A: *T. evelinae* general view; B: lectotype slides; C: detail of posterior part; D, E and F: sagittal sections of reproductive structures.

Figure 23: *Adenoplana evelinae*. A: *A. evelinae in vivo*; B: ventral view; C: detail of anterior part; D: ventral view *in vivo*; E: sagittal section of reproductive structures; F: lectotype slides; G: lectotype anterior part.

Figure 24: *Callioplana evelinae*. A: general view of paralectotype; B: lectotype slides; C, D, E and F: sagittal sections of reproductive structures.

Figure 25: *Hoploplana divae*. A: *H. divae in vivo* MNRJ-PLAT 157; B: holotype slides; C: sagittal section of reproductive structures of holotype; D: detail of anterior part of MNRJ-PLAT 157; E and F: details of dorsal and ventral epidermis; G and H: sagittal sections of reproductive structures.

Figure 26: *Itannia ornata*. A: general view of paratype; B and C: details of tentacular and cerebral eyespots; D: holotype slides; E: sagittal section of reproduction structures.

Figure 27: *Distylochus isifer* and *Distylochus martae*. A: *D. isifer* lectotype slide; B and C: *D. isifer* sagittal sections of reproductive structures; D: *D. martae* slides of holotype; E and F: *D. martae* sagittal sections of reproductive structures.

Figure 28: *Imogine cata*. A: *I. cata in vivo*; B: ventral view; C and D: sagittal sections of fresh material; E: holotype slides; F: detail of anterior part; G, H and I: sagittal sections of holotype.

Figure 29: *Imogine refertus*. A: holotype slides; B-E: sagittal sections of reproductive structures of holotype.

Figure 30: *Imogine tica*. A: *I. tica in situ*; B: ventral view; C: sagittal section of fresh material; D: detail of anterior part; E: detail of anterior part of lectotype; F: slides of lectotype; G and H: sagittal sections of lectotype.

Figure 31: *Pentaplana divae*. A: general view; B: detail of anterior part of lectotype; C: slides of lectotype; D: sagittal section of reproductive structures.

Figure 32: *Latocestus callizona*. A: detail of anterior part; B: slides of holotype; C-E: sagittal sections of reproductive structures.

Figure 33: *Nonatona euscopa*. A: slides of holotype; B-D: sagittal sections of reproductive structures.

Figure 34: *Prolatocestus ocellatus*. A: general view; B: lectotype slides; C: detail of anterior part; D-F: sagittal sections of reproductive structures.

Figure 35: *Cestoplana salar*. A: *C. salar in vivo*; B: detail of anterior part of MNRJ-PLAT 155; C-D: sagittal sections of MNRJ-PLAT 155; E: detail of anterior part of holotype; F: holotype slides; G-I: sagittal sections of holotype.

Figure 36: *Cestoplana techa*. A: *C. techa in vivo*; B: lectotype slides; C: detail of anterior part; D-E: sagittal sections of fresh material; F-H: sagittal sections of lectotype.

Figure 37: *Theama evelinae*. A: general view; B: anterior part of lectotype; C: type series slides; D-F: sagittal sections of lectotype.

Figure 38: *Pericelis cata*. A: holotype slides.

Figure 39: *Enchiridium evelinae* and *Enchiridium gabriellae*. A: *E. evelinae* lectotype slides; B-D: *E. evelinae* sagittal sections of reproductive structures. E: *E. gabriellae* holotype slide; F: *E. gabriellae* sagittal section.

Figure 40: *Euprosthiostomum mortenseni*. A: detail of the anterior part; B: holotype slides.

Figure 41: *Lurymare cynarium* nov. comb. A: *L. cynarium* general view; B: lectotype slides; C-E: sagittal sections of reproductive sections.

Figure 42: *Lurymare matarazzoi* and *Lurymare utarum*. A: *L. utarum* anterior part; B: *L. utarum* lectotype slides; C and D: *L. utarum* sagittal sections of reproductive structures. E: *L. matarazzoi* lectotype slides; F: *L. matarazzoi* detail of male structures in whole mount; G: *L. matarazzoi* sagittal section.

Figure 43: *Prosthiostomum gilvum*. A: general view; B: lectotype slides; C: detail of anterior part; D-E: sagittal sections of reproductive structures.

Figure 44: *Acerotisa bituna* and *Acerotisa leuca*. A: *A. bituna* holotype slides; B: *A. bituna* sagittal section of entire worm; C: *A. bituna* general view; D: *A. leuca* general view; E: *A. leuca* syntype slides.

Figure 45: *Cycloporus gabriellae*. A: general view; B, D and E: sagittal sections of reproductive structures; C: lectotype slides.

Figure 46: *Eurylepta neptis*, *Eurylepta piscatoria* and *Eurylepta turma*. A: *E. piscatoria* holotype slides; B and C: *E. piscatoria* sagittal sections; D: *E. neptis* sagittal sections of reproductive structures; E: *E. neptis* lectotype slides; F: *E. turma* detail of anterior part; G: *E. turma* lectotype slide; H, I and J: *E. turma* lectotype sagittal sections of reproductive structures.

Figure 47: *Acanthozoon hispidum* and *Phrikoceros mopsus*. A: *A. hispidum* lectotype slides; B and C: *A. hispidum* sagittal sections of male reproductive structures; D: *P. mopsus* lectotype slides; E: *P. mopsus* sagittal section of reproductive structures.

Figure 48: *Pseudoceros chloreus*. A: holotype slide; B: detail of cerebral eyespots; C: detail of marginal eyespots; D: detail of anterior part of holotype.

Figure 49: *Pseudobiceros evelinae*. A: detail of the anterior part of holotype; B: holotype slides.

Table 1. Species found in Brazil and their status regarding type material, material deposited in museums, color illustrations, geographic distribution and new contribution to knowledge about them. Holotypes in **bold** and newly designated lectotypes in **bold***.

Species recorded from Brazil	Type material	Deposited Material	Color photos	Language of description	Literature	Geographical distribution	Recent contribution
ACOTYLEA							
Family Euplanidae							
Euplana hymanae Marcus, 1947	SMNH 109052 SMNH 109053 SMNH 109054 SMNH 109055 SMNH 109056 SMNH 109057 SMNH 109058 SMNH 109690 SMNH 109691 SMNH 109692 SMNH 109693 SMNH 109694 SMNH 109695 SMNH 109696 SMNH 109697 SMNH 109698 SMNH 109699 SMNH 109700 SMNH 109701 SMNH 109702 SMNH 109703 SMNH 109704	SMNH 109048 SMNH 109049 SMNH 109050 SMNH 109051 SMNH 109059	Yes (present study)	Portuguese	Marcus, 1947 Hyman, 1953 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Type material information and color photos
Family Ilyplanidae							
Zygantroides plesia (Correa, 1949)	No?	-	No	Portuguese	Correa, 1949 Du Bois-Reymond Marcus, 1955b	Paraná State, Brazil	-
Zygantroides henriettae (Correa, 1949)	No?	SMNH 109141 SMNH 109142 SMNH 109143 SMNH 109144	Yes (present paper)	Portuguese	Marcus, 1947 Correa, 1949 Hyman, 1952 Du Bois-Reymond	Espírito Santo, São Paulo, and Paraná States, Brazil	Color photos

		SMNH 109145 SMNH 109146 SMNH 109147 SMNH 109148 SMNH 109149 SMNH 109150 SMNH 109151 SMNH 109152 SMNH 109153 SMNH 109154			Marcus, 1955b Faubel, 1983 Prudhoe, 1985		
Family Leptoplanidae							
Parviplana lynca (Du Bois-Reymond Marcus, 1958)	SMNH 109196 **SMNH 109197** **SMNH 109198**	MNRJ-PLAT 158	Yes (present paper)	English	Du Bois-Reymond Marcus, 1958	Southeasthern, Brazil	Type material information, color photos, deposited material, additional geographic range
Family Notoplanidae							
Notocomplana evelinae (Marcus, 1947)	SMNH 109133 SMNH 109134 **SMNH 109135*** **SMNH 109136*** SMNH 109137 SMNH 109138 **SMNH 109139*** SMNH 109140	-	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Notocomplana martae (Marcus, 1948)	SMNH 109163 SMNH 109088 SMNH 109089 **SMNH 109090*** **SMNH 109091***	-	Yes (present paper)	Portuguese	Marcus, 1948 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Notocomplana syntoma (Marcus, 1947)	**SMNH 109120*** **SMNH 109121*** **SMNH 109122*** **SMNH 109123*** **SMNH 109124***	SMNH 109118 SMNH 109119 SMNH 109125 SMNH 109126 SMNH 109127 SMNH 109128 SMNH 109129 SMNH 109130	Yes (present paper)	Portuguese	Marcus, 1947 Marcus, 1948 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation, color photos
Notoplana divae Marcus, 1948	**SMNH 109071*** **SMNH 109072***	SMNH 109070 SMNH 109074	Yes (present	Portuguese	Marcus, 1948 Du Bois-Reymond	São Paulo State and Paraná State, Brazil	Lectotype designation, color photos

	SMNH 109073*	SMNH 109075	paper)		Marcus, 1955b		
Notoplana micheli Marcus, 1949	**SMNH 109099*** **SMNH 109100*** SMNH 109101	-	Yes (present paper)	Portuguese	Marcus, 1949 Du Bois-Reymond Marcus, 1955b	Espírito Santo State, Brazil	Lectotypes and paralectotype designation, color photos
Notoplana plecta Marcus, 1947	**SMNH 109102*** **SMNH 109103***	-	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation, color photos
Notoplana sawayai Marcus, 1947	SMNH 109110 **SMNH 109111*** **SMNH 109112*** **SMNH 109113*** SMNH 109114 SMNH 109115 SMNH 109116	SMNH 109117	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Family Pleioplanidae							
Pleioplana megala (Marcus, 1952)	**SMNH 109094*** **SMNH 109095*** **SMNH 109096***	SMNH 109097 SMNH 109098	Yes (present paper)	Portuguese	Marcus, 1952 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil Curaçao	Lectotype designation, color photos
Family Stylochoplanidae							
Allioioplana aulica (Marcus, 1947)	SMNH 109155 **SMNH 109156*** SMNH 109157 SMNH 109158 **SMNH 109159*** **SMNH 109160*** **SMNH 109161*** **SMNH 109162***	SMNH 109163 SMNH 109164 MNRJ-PLAT 156	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos, deposited material, English description, additional geographic range
Armatoplana divae (Marcus, 1947)	**SMNH 109167*** **SMNH 109168*** **SMNH 109169*** **SMNH 109170*** **SMNH 109171***	SMNH 109172 INV-PLA 0004 INV-PLA 0005 INV-PLA 0006 MNRJ-PLAT 159	Yes (this paper)	Portuguese and English	Marcus, 1947 Du Bois-Reymond Marcus, 1955b Quiroga et al. 2004a	São Paulo and Rio de Janeiro State, Brazil Caribbean Colombia	Lectotype designation, color photos, deposited material, English description, additional geographic range
Armatoplana leptalea (Marcus, 1947)	**SMNH 109180*** **SMNH 109181*** **SMNH 109182*** **SMNH 109183***	SMNH 109184 SMNH 109185 SMNH 109186 SMNH 109187 SMNH 109188 SMNH 109189 SMNH 109190	Yes	Portuguese and English	Marcus, 1947 Marcus, 1948 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Pineda-López, 1981 Bahia et al. 2015	Southeastern and Northeastern Brazil Antigua, Barbuda, Curaçao, Mexico and Florida	Lectotype designation, color photos, deposited material, English description, additional geographic range

		SMNH 109191 SMNH 109192 SMNH 109193 SMNH 109194 SMNH 109195 YPM IZ 084191 YPM IZ 084192 IBUNAM-CNHE II.138 MNRJ-PLAT 98 MNRJ-PLAT 99 MNRJ-PLAT 122 MNRJ-PLAT 123 MNRJ-PLAT 124 MNRJ-PLAT 125 MNRJ-PLAT 126					
Interplana evelinae (Marcus, 1952)	**SMNH 109173*** SMNH 109174 SMNH 109175 **SMNH 109176*** **SMNH 109177*** **SMNH 109178*** **SMNH 109179***	-	Yes (present paper)	Portuguese	Marcus, 1952 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Stylochoplana divae (Marcus, 1949)	SMNH 109669 SMNH 109670 SMNH 109671 **SMNH 109672*** SMNH 109673 **SMNH 109674***	-	Yes (present paper)	Portuguese	Marcus, 1949 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Stylochoplana selenopsis Marcus, 1947	**SMNH 109199*** **SMNH 109200*** **SMNH 109201*** **SMNH 109202***	SMNH 109203 SMNH 109204 SMNH 109205 SMNH 109206 SMNH 109207 SMNH 109208 SMNH 109209	Yes (this paper)	Portuguese	Marcus, 1947 Marcus, 1949 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation and color photos.
Stylochoplana walsergia Marcus & Marcus, 1968	No?	-	No	English	Marcus & Marcus, 1968	Bahia State, Brazil	-

Family Cryptocelidae							
Cryptocelis lilianae Marcus & Marcus, 1968	**SMNH 109687** **SMNH 109688** **SMNH 109689**	-	Yes (present paper)	English	Marcus & Marcus, 1968	São Paulo State, Brazil	Type material information
Phaenocelis medvedica Marcus, 1952	SMNH 109707 **SMNH 109708*** **SMNH 109709***	YPM IZ 084189 INV-PLA 0008 INV-PLA 0009 MNRJ-PLAT 19 MNRJ-PLAT 97 MNRJ-PLAT 118 MNRJ-PLAT 119 MNRJ-PLAT 120 MNRJ-PLAT 121 MNRJ-PLAT 138	Yes	Portuguese and English	Marcus, 1952 Du Bois-Reymond Marcus, 1955b Quiroga et al. 2004a Quiroga et al. 2004b Bahia et al. 2015	Southeastern and Northeastern Brazil, Curaçao and Caribbean coast of Colombia	Lectotype and paralectotype designation, color photos, english description, additional geographic range, deposited material
Family Triadommidae							
Triadomma curvum Marcus, 1949	SMNH 109714 SMNH 109715 SMNH 109716 **SMNH 109717***	-	Yes (present paper)	Portuguese	Marcus, 1949 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos. Inclusion in own genus.
Triadomma evelinae Marcus, 1947	**SMNH 109720*** **SMNH 109721*** **SMNH 109722*** SMNH 109718 SMNH 109719 SMNH 109723 SMNH 109724 SMNH 109725	-	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos. Inclusion in own genus.
Family Discocelidae							
Adenoplana evelinae Marcus, 1950	**SMNH 109605*** SMNH 109606 **SMNH 109607*** **SMNH 109608*** **SMNH 109609*** **SMNH 109610***	MNRJ-PLAT 18 MNRJ-PLAT 102 MNRJ-PLAT 103 MNRJ-PLAT 127 MNRJ-PLAT 128 MNRJ-PLAT 129	Yes	Portuguese and English	Marcus, 1950 Du Bois-Reymond Marcus, 1955b Quiroga et al. 2004a Bahia et al. 2015	Southeatern and Northeastern Brazil	Lectotype and paralectotype designation, color photos, english description, deposited material, additional geographic range
Family Callioplanidae							
Callioplana evelinae Marcus, 1954	**SMNH 109663*** **SMNH 109664*** **SMNH 109665*** **SMNH 109666***	CYMX 3067 CYMX 3546 CYMX 4002 CYMX 4003	Yes (present paper)	Portuguese	Marcus, 1954b Du Bois-Reymond Marcus, 1955b Ardisson, 2005	São Paulo State, Brazil and Mexico	Lectotype and paralectotype designation, color photos

	SMNH 109667 SMNH 109668	CYMX 4114 CYMX 4233 CYMX 5297 CYMX 13316 CYMX 13338 CYMX 13365 CYMX 13417 CYMX 13449 CYMX 13481 CYMX 13852 CYMX 13886 CYMX 13920 CYMX 14524 CYMX 14546 CYMX 14566 CYMX 14582 CYMX 14602 CYMX 14622					
Family Hoploplanidae							
Hoploplana divae Marcus, 1950	**SMNH 109060* SMNH 109061***	SMNH 109062 SMNH 109063 SMNH 109064 SMNH 109065 H1464? MNRJ-PLAT 17 MNRJ-PLAT 157	Yes (cuts, present paper)	Portuguese and English	Marcus, 1950 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Bahia et al. 2012	Southeastern and Northeastern Brazil Curaçao	Lectotype designation, color photos, additional geographic range, deposited material
Hoploplana usaguia Smith, 1960	**USNM 30249**	-	No	English	Smith, 1960	São Paulo State, Brazil	-
Itannia ornata Marcus, 1947	**SMNH 109780* SMNH 109781* SMNH 109782***	SMNH 109783 SMNH 109784 SMNH 109785 SMNH 109786	Yes (present paper)	Portuguese	Marcus, 1947 Marcus, 1952 Du Bois-Reymond Marcus, 1955b Du Bois-Reymond Marcus, 1958	São Paulo State, Brazil	Lectotype designation
Family Stylochidae							
Distylochus isifer (Du Bois-Reymond Marcus, 1955)	**SMNH 109793***	-	Yes (present paper)	English	Du Bois-Reymond Marcus, 1955a Marcus & Marcus, 1968	São Paulo State, Brazil	Lectotype designation, color photos
Distylochus martae	**SMNH 109794***	-	Yes	Portuguese	Marcus, 1947	São Paulo State, Brazil	Lectotype designation,

(Marcus, 1947)	**SMNH 109795***		(present paper)		Marcus & Marcus, 1968 Du Bois-Reymond Marcus, 1955b		color photos
Imogine cata (Du Bois-Reymond Marcus, 1958)	**SMNH 109788*** **SMNH 109789***	SMNH 109790 SMNH 109791 SMNH 109792 MNRJ-PLAT 130 MNRJ-PLAT 131	Yes (present paper)	English	Du Bois-Reymond Marcus, 1958 Marcus & Marcus, 1968	Southeastern Brazil	Lectotype and paralectotype designation, color photos, deposited material, additional geographic range
Imogine refertus Du Bois-Reymond Marcus, 1965	**SMNH 109796** **SMNH 109797** **SMNH 109798** **SMNH 109799** **SMNH 109800**	MNRJ-PLAT 109 MNRJ-PLAT 153 MNRJ-PLAT 154	Yes (present paper)	German and English	Du Bois-Reymond Marcus, 1965 Bahia, 2016	Southeastern Brazil	Type material information, color photos, deposited material, additional geographic range
Imogine tica (Marcus, 1952)	**SMNH 109801*** **SMNH 109802*** **SMNH 109803*** **SMNH 109804*** **SMNH 109805***	MNRJ-PLAT 110 MNRJ-PLAT 132 MNRJ-PLAT 133	Yes	Portuguese and English	Marcus, 1952 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Bahia, 2016	Southeastern Brazil	Lectotype designation, color photos, deposited material, english description, additional geographic range
Family Stylochocestidae							
Pentaplana divae Marcus, 1949	**SMNH 109654*** **SMNH 109655*** SMNH 109656 SMNH 109657 SMNH 109658 SMNH 109659 SMNH 109660 SMNH 109661 SMNH 109662	-	No Yes (present paper)	Portuguese	Marcus, 1949 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Family Latocestidae							
Latocestus atlanticus Plehn, 1896	No?	-	No	German	Plehn, 1896a Bock, 1913 Marcus & Marcus, 1968	Cape Verde Rio de Janeiro State	-
Latocestus callizona (Marcus, 1947)	**SMNH 109611*** **SMNH 109612*** **SMNH 109613*** **SMNH 109614***	-	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation and color photos
Latocestus brasiliensis Hyman, 1955b	**USNM 26929**	MNRJ-PLAT 101 MNRJ-PLAT 107	Yes	English	Hyman, 1955b Marcus & Marcus, 1968 Bahia et al. 2015	South and Northeastern Brazil	Color photos, deposited material, additional geographic range

Nonatona euscopa Marcus, 1952	**SMNH 109650*** **SMNH 109651*** **SMNH 109652*** **SMNH 109653***	-	Yes (present paper)	Portuguese	Marcus, 1952 Du Bois-Reymond Marcus, 1955b	Paraná State, Brazil	Lectotype designation and color photos
Prolatocestus ocellatus (Marcus, 1947)	SMNH 109640 **SMNH 109641*** **SMNH 109642*** **SMNH 109643*** SMNH 109644 SMNH 109645 SMNH 109646 **SMNH 109647*** SMNH 109648	SMNH 109649	Yes (present paper)	Portuguese and English	Marcus, 1947 Marcus, 1949 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968	São Paulo State Brazil	Lectotype and paralectotype designation, color photos
COTYLEA							
Family Cestoplanidae							
Cestoplana salar Marcus, 1949	**SMNH 109682*** **SMNH 109683***	MNRJ-PLAT 155	Yes (present paper)	Portuguese	Marcus, 1949 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation, color photos, deposited material, english description, additional geographic range
Cestoplana techa Marcus Du Bois-Reymond Marcus, 1957	**SMNH 109684*** **SMNH 109685*** **SMNH 109686***	MNRJ-PLAT 114 MNRJ-PLAT 115 MNRJ-PLAT 116 MNRJ-PLAT 117 INV-PLA 0003?	Yes (present paper)	English	Du Bois-Reymond Marcus, 1957	São Paulo State, Brazil	Lectotype designation, color photos, additional geographic range
Family Theamatidae							
Theama evelinae Marcus, 1949	**Type 5076a** **Type 5076b** Type 5076c Type 5076d Type 5076e	-	Yes (present paper)	Portuguese	Marcus, 1949 Du Bois-Reymond Marcus, 1955b Curini-Galletti et al. 2007	São Paulo State, Brazil	Type material information and coloful photos
Family Pericelidae							
Pericelis cata Marcus & Marcus, 1968	**SMNH 109883** **SMNH 109884** **SMNH 109885** **SMNH 109886** **SMNH 109887** **SMNH 109888** **SMNH 109889**	INV-PLA 0030 INV-PLA 0031 UF IZ 000489 MNRJ-PLAT 02 MNRJ-PLAT 03 MNRJ-PLAT 24 MNRJ-PLAT 96	Yes	English	Marcus & Marcus 1968 Quiroga et al. 2004b Bahia & Padula 2009 Queiroz et al. 2013 Bahia et al. 2014 Bahia et al. 2015	Curaçao (type locality), Colombian Caribbean Rio de Janeiro State and Northeastern Brazil	Type material information, color photos Deposited material First record from Brazil Deposited material

	H1020b?						
Family Amyellidae							
Chromyella saga Correa, 1958	No	-	No	English	Corrêa, 1957	Rio de Janeiro State, Brazil	-
Family Prosthiostomidae							
Enchiridium evelinae Marcus, 1949	SMNH 109923 **SMNH 109924*** SMNH 109925 SMNH 109926 SMNH 109927 SMNH 109928 **SMNH 109929*** **SMNH 109930*** **SMNH 109931***	SMNH 109932 SMNH 109933 SMNH 109934 SMNH 109935 MNRJ-PLAT 05 MNRJ-PLAT 06 MNRJ-PLAT 07 MNRJ-PLAT 48 MNRJ-PLAT 49 MNRJ-PLAT 50 MNRJ-PLAT 51 MNRJ-PLAT 52 MNRJ-PLAT 53 MNRJ-PLAT 54 MNRJ-PLAT 55 MNRJ-PLAT 56 MNRJ-PLAT 57 MNRJ-PLAT 58 MNRJ-PLAT 59 MNRJ-PLAT 60 MNRJ-PLAT 61 MNRJ-PLAT 77 MNRJ-PLAT 78 MNRJ-PLAT 79 MNRJ-PLAT 80 MNRJ-PLAT 81 MNRJ-PLAT 82 MNRJ-PLAT 83 MNRJ-PLAT 84 MNRJ-PLAT 140 MNRJ-PLAT 141	Yes	Portuguese and English	Marcus, 1949 Marcus, 1952 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Bahia et al. 2012 Bahia et al. 2014 Bahia et al. 2015	Southeastern and Northeastern Brazil and Curaçao	Lectotype and paralectotype designation Color photos Deposited material Additional geographic range English description
Enchiridium gabriellae (Marcus, 1949)	**SMNH 109949***	-	Yes (present paper)	Portuguese	Marcus, 1949 Marcus, 1950 Du Bois-Reymond	São Paulo State, Brazil	Lectotype designation and color photos

					Marcus, 1955b Marcus & Marcus, 1968 Poulter, 1975		
Euprosthiostomum mortenseni Marcus, 1948	**SMNH 109936*** **SMNH 109937*** **SMNH 109938*** **SMNH 109939***	-	Yes (present paper)	Portuguese	Marcus, 1948 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation and color photos
Lurymare cynarium (Marcus, 1950)	SMNH 109942 SMNH 109943 SMNH 109944 **SMNH 109945*** **SMNH 109946*** **SMNH 109947*** SMNH 109948	-	Yes (present paper)	Portuguese	Marcus, 1950 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Type material information, new combination to *Lurymare*
Lurymare matarazzoi (Marcus, 1950)	**SMNH 109956*** SMNH 109957	SMNH 109958 SMNH 109959 SMNH 109960 H1057? INV-PLA 0046 INV-PLA 0047 MNRJ-PLAT 111	Yes	Portuguese and English	Marcus, 1950 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Poulter, 1975 Bahia, 2016	Southeastern Brazil Bonaire Colombia	Type designation, color photos English description Additional geographic range Deposited material
Lurymare utarum Marcus, 1952	**SMNH 109967*** **SMNH 109968***	SMNH 109969 SMNH 109970 YPM IZ 084327 INV-PLA 0048 MNRJ-PLAT 62	Yes	Portuguese and English	Marcus, 1952 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Poulter, 1975 Quiroga et al. 2004b Bahia et al. 2014	Southeastern Brazil Colombia, Virgin Islands and Florida	Lectotype designation Color photos Additional geographic range Deposited material
Prosthiostomum gilvum Marcus, 1950	**SMNH 109950*** **SMNH 109951*** **SMNH 109952*** **SMNH 109953*** **SMNH 109954*** SMNH 109955	INV-PLA 0039 INV-PLA 0040 INV-PLA 0041 INV-PLA 0042	Yes	Portuguese	Marcus, 1950 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1951 Quiroga et al 2004a, b	São Paulo State, Brazil Colombia	Lectotype and paralectotype designation, color photos
Family Euryleptidae							
Acerotisa bituna Marcus, 1947	**SMNH 109589*** **SMNH 109590***	SMNH 109591 SMNH 109592 H1460	Yes (present paper)	Portuguese and English	Marcus, 1947 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968	São Paulo State, Brazil Curaçao	Lectotype designation and color photos

Acerotisa leuca Marcus, 1947	SMNH 109593	SMNH 9476 (SMNH 94662) SMNH 109594 SMNH 109595 SMNH 109596 SMNH 109597	No	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Type material information and color photos
Cycloporus gabriellae Marcus, 1950	SMNH 109842 SMNH 109843 SMNH 109844 SMNH 109845 **SMNH 109846*** **SMNH 109847*** **SMNH 109848***	SMNH 94675 SMNH 109849 SMNH 109850 SMNH 109851 SMNH 109852 SMNH 109853 SMNH 109854 H1393? MNRJ-PLAT 63 MNRJ-PLAT 64 MNRJ-PLAT 65 MNRJ-PLAT 66 MNRJ-PLAT 67	Yes	Portuguese and English	Marcus, 1950 Marcus, 1952 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968 Bahia et al. 2014	São Paulo State and Rio de Janeiro State, Brazil Curaçao and Antigua	Lectotype and paralectotype designation, color photos, additional geographic range, deposited material
Cycloporus variegatus Kato, 1934	No?	NMV F 172738 NMV F 172739 NMV F 172746 NMV F 172812 NMV F 202549 QM G 211063 QM G 211209 MNRJ-PLAT 68 MNRJ-PLAT 69 MNRJ-PLAT 70 MNRJ-PLAT 71 MNRJ-PLAT 72 MNRJ-PLAT 73 MNRJ-PLAT 74 MNRJ-PLAT 75	Yes	English	Kato, 1934b, 1937a, 1944 Dawydoff, 1952 Bahia et al. 2014	Japan and Vietnam	Color photos, deposited material, First record from Brazil
Eurylepta aurantiaca Heath & McGregor, 1912	**CAS IZ 21870**	USNM 23781 INV-PLA 0038 MNRJ-PLAT 76	Yes	English	Heath & Mc Gregor, 1913 Hyman, 1953 Hyman 1955a Stasek, 1966 Morris et al. 1981	San Diego, USA to Vancouver, Canada Colombia	Color photos First record from Brazil Deposited material

					Quiroga et al. 2004a Bahia et al. 2014		
Eurylepta neptis DuBois Reymond Marcus, 1955	**SMNH 109875*** **SMNH 109876*** **SMNH 109877***	-	Yes (present paper)	English	Du Bois-Reymond Marcus, 1955a and b	São Paulo State, Brazil	Lectotype designation and color photos
Eurylepta piscatoria (Marcus, 1947)	**SMNH 109601*** **SMNH 109602*** **SMNH 109603***	SMNH 109604 H1057?	Yes (present paper)	Portuguese	Marcus, 1947 Du Bois-Reymond Marcus, 1955b Marcus & Marcus, 1968	São Paulo State, Brazil Bonaire, Florida	Lectotype designation and color photos
Eurylepta turma Marcus, 1952	SMNH 109878 SMNH 109880 SMNH 109881 **SMNH 109882***	-	Yes (present paper)	Portuguese	Marcus, 1952 Du Bois-Reymond Marcus, 1955a and b	São Paulo State, Brazil	Lectotype and paralectotype designation, color photos
Euryleptides brasiliensis Palombi, 1923	No?	-	No	Italian	Palombi, 1923	Brazilian coast (?)	-
Family Pseudocerotidae							
Acanthozoon hispidum (Du Bois-Reymond Marcus, 1955)	**SMNH 109991*** **SMNH 109992*** **SMNH 109993***	-	Yes (present paper)	English	Du Bois-Reymond Marcus, 1955a and b Hyman, 1959	São Paulo State, Brazil	Lectotype designation and color photos
Phrikoceros mopsus (Marcus,1952)	**SMNH 109994*** **SMNH 109995*** **SMNH 109996***	YPM IZ 084324 INV-PLA 0034 INV-PLA 0035 UF IZ 000490 UF IZ 000491 UF IZ 000492 MNRJ-PLAT 08 MNRJ-PLAT 09 MNRJ-PLAT 10 MNRJ-PLAT 25 MNRJ-PLAT 26 MNRJ-PLAT 27 MNRJ-PLAT 28 MNRJ-PLAT 29 MNRJ-PLAT 30 MNRJ-PLAT 31 MNRJ-PLAT 32 MNRJ-PLAT 148	Yes	Portuguese and English	Marcus, 1952 Du Bois-Reymond Marcus, 1955b Marcus & Marcus 1968 Quiroga et al. 2004a Brusa et al. 2009 Bulnes et al. 2011 Bahia et al. 2012 Bahia et al. 2014	Rio Grande do Norte State, Southeastern Brazil Antigua, Curaçao, Barbuda, Jamaica, Colombia and Argentina	Lectotype designation Color photos, English description, Deposited material, Additional geographic range

		MNRJ-PLAT 149					
Pseudoceros astrorum Bulnes & Torres, 2014	**MZUSP PL 1558** **MZUSP PL 1559**	MNRJ-PLAT 88 MNRJ-PLAT 89	Yes	English	Torres & Bulnes, 2014	Ceará State Northeastern Brazil	New described species, deposited material
Pseudoceros bicolor Verrill, 1901	**YPM IZ 020104**	YPM IZ 047939 YPM IZ 047938 INV-PLA 0032 INV-PLA 0033 UF IZ 000561 UF IZ 000562 UF IZ 000730 MNRJ-PLAT 35 MNRJ-PLAT 36 MNRJ-PLAT 85 MNRJ-PLAT 86 MNRJ-PLAT 112	Yes	English	Verrill 1901 Hyman, 1939a Marcus, 1950 Marcus & Marcus 1968 Quiroga et al. 2004b Rawlinson 2008 Bahia & Padula 2009 Litvaitis et al. 2010 Bahia et al. 2014 Bahia et al. 2015	Birds Islands, Bahamas, Curacao, Caribbean coast of Colombia, Florida, Virgin Islands, Saint Martin, Jamaica, Belize, Honduras e Caribbean coast of Panama and Southeastern and Northeastern Brazil	First record from Brazil
Pseudoceros chloreus Marcus, 1949	**SMNH 109975***	-	Yes (present paper)	Portuguese	Marcus, 1949 Marcus, 1950 Du Bois-Reymond Marcus, 1955b	São Paulo State, Brazil	Lectotype designation
Pseudoceros juani Bahia, Padula, Quiroga & Lavrado, 2014	**MNRJ-PLAT 40**	-	Yes	English	Bahia *et al.* 2014	Rio de Janeiro State	New described species
Pseudoceros rawlinsonae Bolanos, Quiroga & Litvaitis, 2007	**UNH-USVI 029**	YPM IZ 047940 MNRJ-PLAT 01 MNRJ-PLAT 37 MNRJ-PLAT 38 MNRJ-PLAT 39 MNRJ-PLAT 04 MNRJ-PLAT 87 MNRJ-PLAT 139	Yes	English	Bolaños et al. 2007 Bahia and Padula, 2009 Litvaitis et al. 2010 Bahia et al. 2014 Bahia et al. 2015	American Virgin Islands and Bonaire. Florida, Honduras, Jamaica, Bahamas and Curaçao and Southeastern and Northeastern Brazil	First record from Brazil
Pseudobiceros evelinae (Marcus, 1950)	**SMNH 109981*** **SMNH 109982*** **SMNH 109983*** **SMNH 109984*** **SMNH 109985*** **SMNH 109986*** **SMNH 109987***	MNRJ-PLAT 11 MNRJ-PLAT 12 MNRJ-PLAT 13 MNRJ-PLAT 20 MNRJ-PLAT 21 MNRJ-PLAT 22 MNRJ-PLAT 23	Yes	Portuguese and English	Marcus, 1950 Marcus, 1952 Du Bois-Reymond Marcus, 1955b Bahia et al. 2012 Bahia et al. 2014	Southeastern Brazil and Rio Grande do Norte State	Lectotype designation Color photos, Deposited material, English description, Additional geographic range

	SMNH 109988* **SMNH 109989*** **SMNH 109990***	MNRJ-PLAT 142					
Pseudobiceros pardalis (Verrill, 1900)	No?	ZMUH V13187 ZMUH V13186 UNH-PAN 028 USNM 1104638 UNH-PAN 029 USNM 1104639 UNH-PAN 056 USNM 1104685 MNRJ-PLAT 33 MNRJ-PLAT 34 MNRJ-PLAT 92	Yes	English	Verrill, 1900 Marcus, 1950 Bolaños et al. 2007 Bahia et al. 2014	Bermudas, Bahamas, south Florida and Panama and Rio de Janeiro State and Northeastern Brazil	First record from Brazil Deposited material
Thysanozoon alagoensis Bahia, Padula, Dorigo & Soviersosky, 2015	**MNRJ-PLAT 95**	-	Yes	English	Bahia et al. 2015	Alagoas State	New described species
Thysanozoon brocchii (Risso, 1818)	**ZMB-Collection Vermes 3205**	YPM IZ 037574 SMNH 101763 SMNH 101825 SMNH 101826 SMNH 101827 SMNH 101828 SMNH 101829 SMNH 101830 SMNH 101831 SMNH 101832 SMNH 101833 SMNH 101834 SMNH 101835 SMNH 101836 SMNH 101837 SMNH 101838 SMNH 101839 SMNH 101840 SMNH 101841 SMNH 101842	Yes	Italian? English, portuguese	Risso, 1818 Prudhoe 1985 Quiroga et al. 2004b Vera et al. 2008 Brusa et al. 2009 Bahia et al. 2012 Bahia et al. 2014	Naples, Italy (type locality). Mediterranean Sea, United Kingdon, south and west from Africa, Florida, Caribbean coast of Colombia, Brazil, Japan and New Zealand. Canary Islands, Argentina and from Northeastern Brazil and southeastern Brazil	Color photos, deposited material, additional geographic range. * vouchers of former *T. lagidium* from Brazil

	SMNH 101843 SMNH 101846 SMNH 101847 SMNH 101848 SMNH 101849 SMNH 101850 SMNH 101851 SMNH 101852 SMNH 101853 SMNH 101854 SMNH 101855 SMNH 101856 SMNH 101857 SMNH 101858 SMNH 101859 SMNH 101860 SMNH 101861 SMNH 101862 SMNH 101863 SMNH 101865 SMNH 101866 SMNH 101880 SMNH 101883 SMNH 101882 SMNH 101884 SMNH 101885 SMNH 101886 SMNH 101887 SMNH 101888 SMNH 101889 SMNH 101890 SMNH 101891 SMNH 101892 SMNH 101893 SMNH 101894 SMNH 101895 SMNH 101896 SMNH 101898 SMNH 101899

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	SMNH 110006*	
	SMNH 110007*	
	MCZ IZ 135378	
	MCZ ANNb-594	
	MCZ ANNb-1532	
	MCZ ANNb-1814	
	AK MA 79220	
	AK MA 135165	
	AK MA 138152	
	SMF 1460-11235	
	SMF 1589-11236	
	MACN-IN 4349	
	AM 6.11362	
	UF IZ 000674	
	ZMA V.Pl. 215	
	ZMA V.Pl. 216	

	ZMA V.Pl. 217 ZMA V.Pl. 551 NHMUK 1897.5.9.1-2 NHMUK 1897.1.10.2-8 NHMUK 1900.5.1.43-45 ZMB 308 ZMB 1716 ZMB 1967 ZMB 2726-Q ZMB 3203 ZMB 3204 ZMB 3205 MNRJ-PLAT 14 MNRJ-PLAT 15 MNRJ-PLAT 16 MNRJ-PLAT 41 MNRJ-PLAT 42 MNRJ-PLAT 43 MNRJ-PLAT 44 MNRJ-PLAT 45 MNRJ-PLAT 46 MNRJ-PLAT 47 MNRJ-PLAT 93 MNRJ-PLAT 94 MNRJ-PLAT 113 MNRJ-PLAT 143 MNRJ-PLAT 144 MNRJ-PLAT 145 MNRJ-PLAT 146 MNRJ-PLAT 147	

Table 2. Holotype, paratypes, lectotypes, paralectotypes and syntypes vouchers and labels of respective slides deposited in the SMNH. Holotypes in **bold** and newly designated lectotypes in **bold***.

Species	Voucher	Description	Status	Label
Euplana hymanae Marcus, 1947	SMNH 109690	Whole mount of anterior part of worm. From type locality.	Syntype	*Euplana hymanae*. Marcus 1947. Sao Paulo; Baía de Santos; Ilha das Palmas. Cf Marcus 1947 p129. leg E Marcus (A). Polyclade. 4/5.
	SMNH 109054	Serial sections of posterior part of SMNH109690.	Syntype	*Euplana hymanae*. SMNH 109054. leg E Marcus (E).
	SMNH 109055	Serial sections of SMNH 109690. Reproductive structures on rows 5-8 (marked with blue dot).	Syntype	*Euplana hymanae*. SMNH 109055. leg E Marcus (F). Dept. Zoologia S. Paulo. *Euplana hymanae*.
	SMNH 109691	Whole mount of entire worm.	Syntype	*Euplana hymanae*. SMNH 109691. leg E Marcus (B). *Euplana hymanae*.
	SMNH 109052	Whole mount of anterior part.	Syntype	*Euplana hymanae*. SMNH 109052. leg E Marcus (C).
	SMNH 109056	Serial sections of posterior part of SMNH 109052.	Syntype	*Euplana hymanae*. SMNH 109056. leg E Marcus (G).
	SMNH 109057	Serial sections of SMNH 109052. Reproductive structures on rows 6 and 7 (marked with blue dot).	Syntype	*Euplana hymanae*. SMNH 109057. leg E Marcus (H).
	SMNH 109053	Whole mount of anterior part.	Syntype	*Euplana hymanae*. SMNH 109053. leg E Marcus (D).
	SMNH 109058	Serial sections of posterior part of SMNH 109053. Reproductive structures on rows 7, 8 and 9 (marked with blue dot).	Syntype	*Euplana hymanae*. SMNH 109058. leg E Marcus (I).

	SMNH 109692	Whole mount of entire worm from type locality	Syntype	*Euplana hymanae*. Marcus 1947. Sao Paulo; Baía de Santos; Ilha das Palmas. Cf Marcus 1947 p129. leg E Marcus (78).
	SMNH 109693	4 worms in whole mount. From type locality.	Syntype	*Euplana hymanae*. SMNH 109693. leg E Marcus. (79). *Euplana hymanae* Marc. 79.
	SMNH 109694	Serial sections of posterior part.	Syntype	*Euplana hymanae*. SMNH 109694. leg E Marcus (80).
	SMNH 109695	Serial sections of posterior part of SMNH 109694. Reproductive structures on rows 4-6 (marked with blue dot). Dirty slide.	Syntype	*Euplana hymanae*. SMNH 109695. leg E Marcus (81).
	SMNH 109696	Serial sections of posterior part of SMNH 109694.	Syntype	*Euplana hymanae*. SMNH 109696. leg E Marcus (82).
	SMNH 109697	Serial sections of entire worm.	Syntype	*Euplana hymanae*. SMNH 109697. leg E Marcus (83).
	SMNH 109698	Serial sections of SMNH 109697	Syntype	*Euplana hymanae*. SMNH 109698. leg E Marcus (84). *Euplana hymanae* Marc. 84.
	SMNH 109699	Serial sections of SMNH 109697	Syntype	*Euplana hymanae*. SMNH 109699. leg E Marcus (85). *Euplana hymanae* Marc. 85.
	SMNH 109700	Serial sections of SMNH 109697	Syntype	*Euplana hymanae*. SMNH 109700. leg E Marcus (86). *Euplana hymanae* Marc. 86.
	SMNH 109701	Serial sections of SMNH 109697	Syntype	*Euplana hymanae*. SMNH 109701. leg E Marcus (87). *Euplana hymanae* Marc. 87.
	SMNH 109702	Serial sections of SMNH 109697 Reproductive structures on rows 1-4 (marked with blue dot).	Syntype	*Euplana hymanae*. SMNH 109702. leg E Marcus (88).
	SMNH 109703	Serial sections of SMNH 109697	Syntype	*Euplana hymanae*. SMNH 109703. leg E Marcus

				(89).
	SMNH 109704	Serial sections of SMNH 109697	Syntype	*Euplana hymanae*. SMNH 109704. leg E Marcus (90). *Euplana hymanae* Marc. 90.
Parviplana lynca (Du Bois-Reymond Marcus, 1958)	**SMNH 109197**	Serial sections of entire worm sections continue on next slide.	Holotype	*Stylochoplana lynca*. Leg Ev Marcus. (B). SMNH 109197.
	SMNH 109198	Serial sections of SMNH 109197 reproductive structures on rows 5-7 (marked with blue dot).	Holotype	SMHH 109198. *Stylochoplana lynca*. Leg Ev Marcus (C).
	SMNH 109196	Whole mount of entire worm. The designated holotype is the slide containing the sections, therefore this is a paratype.	Paratype	*Stylochoplana lynca*. du Bois-Reymond Marcus 1958. Sao Paulo; Cananeia. cf du B-R Marcus. Leg du B-R Marcus (A). SMNH 109196.
Notocomplana evelinae (Marcus, 1947)	**SMNH 109139***	Whole mount of anterior part of worm. The only one that is not entire in whole mount.	Lectotype	*Pucelis evelinae*. SMNH 109139. leg E Marcus (76). Dept. Zoologia S. Paulo. *Pucelis evelinae* Marc. 76.
	SMNH 109135*	Serial sections of SMNH 109139. Since the only whole mount with an anterior part is the SMNH 109139, these sections are from this worm, which should be then the lectotype.	Lectotype	*Pucelis evelinae*. SMNH 109135. leg E Marcus (72). *Pucelis evelinae* Marc. 72.
	SMNH 109136*	Serial sections of SMNH 109139. As the slides are numbered in sequence, they are all from the type locality.	Lectotype	*Pucelis evelinae*. SMNH 109136. leg E Marcus (73). *Pucelis evelinae* Marc. 73.
	SMNH 109133	Whole mount of entire worm. Fits figure 50 of Marcus (1947).	Paralectotype	*Pucelis evelinae*. Marcus 1947. Sao Paulo, Ilha das Palmas. Cf Marcus 1947 p128. leg E Marcus (70). SMNH 109133

	SMNH 109134	Whole mount of entire worm. Fits figure 49 of Marcus (1947)	Paralectotype	*Pucelis evelinae*. SMNH 109134. leg E Marcus (71).
	SMNH 109137	2 worms in whole mount. Together with *Notocomplana* there is a *Stylochoplana* sp?	Paralectotype	*Pucelis evelinae*. *Stylochoplana* sp. SMNH 109137. leg E Marcus (74). Dept. Zoologia S. Paulo. *Pucelis evelinae*. *Stylochoplana* sp. 74.
	SMNH 109138	whole mount of entire worm	Paralectotype	*Pucelis evelinae*. SMNH 109138. leg E Marcus (75). Dept. Zoologia S. Paulo. *Pucelis evelinae* Marc. 75.
	SMNH 109140	whole mount of entire worm	Paralectotype	*Pucelis evelinae*. Marcus 1947. Nymont. 1976. leg E. Marcus 77. SMNH 109140.
Notocomplana martae (Marcus, 1948)	**SMNH 109090***	Serial sections of entire worm. Sections continue on following slide. Reproductive structures on row 8 (marked with blue dot).	Lectotype	*Notoplana martae*. Marcus 1948. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1948 p180. leg E Marcus (C). SMNH 109090.
	SMNH 109091*	Serial sections of entire worm. Continuation of previous slide. Reproductive structures on rows 1 and 2 (marked with blue dot).	Lectotype	*Notoplana martae*. SMNH 109091. leg E Marcus (D).
	SMNH 109089	Serial sections of entire worm. Other worm from Ilha das Palmas (according to the description drawings). Very destroyed sections in some important parts. Therefore left as paralectotype. Hint of reproductive structures circled and marked with blue dot. In rows 6 and 7.	Paralectotype	*Notoplana martae*. SMNH 109089. leg E Marcus (B).

	SMNH 109088	Whole mount of entire worm. Fits the drawing of figure 105.	Paralectotype	*Notoplana martae*. Marcus 1948. Sao Paulo; Ilha das Palmas; Ilhabela. Cf Marcus 1948 p180. leg E Marcus (A). SMNH 109088.
	SMNH 109163	Whole mount with different species. Juvenile worm of *Allioioplana aulica* together with other animals, including a Maricola.	Paralectotype	*Stylochoplana aulica*. *N. martae*. 3 juv polyclads. 1 triclad. *Leucolesma*? Leg E Marcus. 48. SMNH 109163. *St. Aulica*. Dept. Zoologia S. Paulo. 3 junge Polycladen. 1 Trclade. *Leucolesma*?
Notocomplana syntoma (Marcus, 1947)	**SMNH 109120***	Whole mount of anterior part of worm. According to the original description drawings, this animal corresponds to the lectotype. It fits Marcus 1947 figure 39.	Holotype	*Notoplana syntoma*. Marcus 1947. Sao Paulo; Sao Vicente. Cf Marcus 1947 p123, 1948 p183. SMNH 109120. Dept. Zoologia S. Paulo. *Notoplana syntoma*. M. 57.
	SMNH 109121*	Serial sections of SMNH 109120 These consecutive sections fit the drawing of the original description, figure 42 of Marcus 1947.	Holotype	*Notoplana syntoma*. SMNH 109121. leg E Marcus (58).
	SMNH 109122*	Serial sections of SMNH 109120	Holotype	*Notoplana syntoma.* SMNH 109122. leg E Marcus (59).
	SMNH 109123*	Serial sections of SMNH 109120. Reproductive structures on rows 1 and 2 (marked with blue dot). Dirty slide.	Holotype	*Notoplana syntoma*. SMNH 109123. leg E Marcus (60).
	SMNH 109124*	Serial sections of SMNH 109120. Reproductive structures on rows 1 and 2 (marked with blue dot).	Holotype	*Notoplana syntoma*. SMNH 109124. leg E Marcus (61).
Notoplana divae Marcus, 1948	**SMNH 109071***	Serial sections of posterior part. Serial sections of the other worm collected in Caiobá, as it is mature and sectioned will	Lectotype	*Notoplana divae*. Marcus 1948. Paraná; Caioba. Cf Marcus 1948 p178. leg E Marcus. (1). SMNH 109071.

		be considered the lectotype.		
	SMNH 109072*	Serial sections of SMNH 109071. Reproductive structures in rows 2, 3 and 4 (marked with blue dot).	Lectotype	*Notoplana divae*. SMNH 109072. leg E Marcus (2). Dept. Zoologia S. Paulo. *Notoplana divae*. 2. 1947.
	SMNH 109073*	Whole mount of anterior part of 109071.	Lectotype	*Notoplana divae*. SMNH 109073. leg E Marcus (3).
	SMNH 109070	2 worms in whole mount. The original description is based on 1 imature and 2 mature specimens. One of the mature is to be designated the lectotype. Then the type locality is to be primary Caiobá, Paraná. And the paralectotypes will be then one from Caiobá and the other from São Vicente. This corresponds to the two worms in this slide.	Paralectotypes	Notoplana divae. Marcus 1948. Sao Paulo; Vicente (red). Paraná; Caioba (brown). Cf Marcus 1948 p178. leg E Marcus. SMNH 109070. Dept. Zoologia S. Paulo. Notoplana divae. S. Vicente red. Caiobá brown.
Notoplana micheli Marcus, 1949	**SMNH 109099*/** SMNH109099	Whole mount of anterior parts of 2 worms. The drawings fits better the larger worm. It is to be the lectotype and the smaller the paralectotype.	Lectotype / Paralectotype	*Notoplana micheli*. Marcus 1949. Espirito Santo; Ilha do Frances. Cf Marcus 1949 p78. leg P Sawaya (A). SMNH 109099. Dept. Zoologia S. Paulo. *Notoplana micheli*. M. Ilha do Francês.
	SMNH 109100*	Serial sections of larger SMNH 109099. Fits the drawing of figure 112. Reproductive structures on rows 2 and 3 (marked with blue dot).	Lectotype	*Notoplana micheli*. SMNH 109100. leg P Sawaya (B).
	SMNH 109101	Serial sections of smaller SMNH 109099. Dirty slide. Difficult to see. Reproductive structures on rows 5-7 (marked with blue dot).	Paralectotype	*Notoplana micheli*. SMNH 109101. leg P Sawaya (C).

Notoplana plecta Marcus, 1947	**SMNH 109102***	Serial sections of posterior part of worm. Animal from type locality, thus to be designated lectotype.	Holotype	*Notoplana plecta*. Marcus 1947. Sao Paulo; Baia de Santos. Cf Marcus 1947 p124. leg E Marcus (62). SMNH 109102.
	SMNH 109103*	Serial sections of SMNH 109102. Dirty slide. Reproductive structures on rows 1 and 2 (marked with blue dot). Fits drawing of figure 48.	Holotype	*Notoplana plecta*. SMNH 109103. leg E Marcus (63). *Notoplana plecta*. Marc. 63.
Notoplana sawayai Marcus, 1947	**SMNH 109111***	Whole mount of anterior part of worm. The worm sections corresponds to following slides, according to size	Lectotype	*Notoplana sawayai*. SMNH 109111. leg E Marcus (64). Dept. Zoologia S. Paulo. *Notoplana sawayai* Marc. 64.
	SMNH 109112*	Serial sections of SMNH 109111, sections continue on following slide.	Lectotype	*Notoplana sawayai*. SMNH 109112. leg E Marcus (65). *Notoplana sawayai* Marc. 65.
	SMNH 109113*	Serial sections of SMNH 109111. Reproductive structures on rows 1, 2 and 3 (marked with blue dot)	Lectotype	*Notoplana sawayai*. SMNH 109113. leg E Marcus (66). *Notoplana sawayai* Marc. 66.
	SMNH 109110	Whole mount of anterior part of worm. The worm sections correspond to SMNH 109114-116, according to size.	Paralectotype	*Notoplana sawayai*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p121. leg E Marcus (64). Dept. Zoologia S. Paulo. *Notoplana sawayai* Marc. 64.
	SMNH 109114	Serial sections of SMNH 109110. Reproductive structures on row 6 (marked with blue dot). Since the sections are from a wrinkled worm and it is difficult to see the structures this should be the paralectotype.	Paralectotype	*Notoplana sawayai*. SMNH 109114. leg E Marcus (67).
	SMNH 109115	Serial sections of SMNH 109110.	Paralectotype	*Notoplana sawayai*. SMNH 109115. leg E Marcus

		Reproductive structures on rows 1, 2 and 3 (marked with blue dot).		(68). *Notoplana sawayai* Marc. 68.
	SMNH 109116	Serial sections of SMNH 109110. Continuation of of previous sections.	Paralectotype	*Notoplana sawayai*. SMNH 109116. leg E Marcus (69). *Notoplana sawayai* Marc. 69.
Pleioplana megala (Marcus, 1952)	**SMNH 109094***	Whole mount of worm. There is no specification of locality. But since both Ubatuba and Ilha de Sao Sebastiao are in São Paulo, this to be the closest to a type.	Lectotype	*Notoplana megala*. Marcus, 1952. Sao Paulo. Cf Marcus 1952 p85, 1968 p42. leg.: E. Marcus (A). SMNH 109094
	SMNH 109095*	Serial sections of middle part of SMNH 109094. Sections continue on following slide.	Lectotype	*Notoplana megala*. SMNH 109095. leg.: E. Marcus (B).
	SMNH 109096*	Serial sections of middle part of SMNH 109094. Reproductive structures on rows 4-7 (marked with blue dot).	Lectotype	*Notoplana megala*. SMNH 109096. leg.: E. Marcus (C).
Alloioplana aulica (Marcus, 1947)	**SMNH 109156***	Whole mount of the anterior part. The only animal that was sectioned is to be considered the lectotype.	Lectotype	*Stylochoplana aulica*. SMNH 109156. leg E Marcus (41). *Stylochoplana aulica*.
	SMNH 109159*	Serial sections of posterior part of SMNH 109156. Sections continue on the following 3 slides.	Lectotype	*Stylochoplana aulica*. SMNH 109159. leg E Marcus (44). *Stylochoplana aulica* Marc. 44.
	SMNH 109160*	Serial sections of posterior part of SMNH 109156. Reproductive structures on rows 4 and 5 (marked with blue dot). Dirty slide.	Lectotype	*Stylochoplana aulica*. SMNH 109160. leg E Marcus (45). *Stylochoplana aulica* Marc. 45.
	SMNH 109161*	Serial sections of posterior part of SMNH 109156. Reproductive structures on rows	Lectotype	*Stylochoplana aulica*. SMNH 109161. leg E Marcus (46).

		1-3 (marked with blue dot). Dirty slide.		
	SMNH 109162*	Serial sections of posterior part of SMNH 109156. Continuation of previous sections.	Lectotype	*Stylochoplana aulica*. SMNH 109162. leg E Marcus (47).
	SMNH 109155	3 worms in whole mount. The original description is based on ca. 20 specimens. Here there are at least 13. One of them is in both whole mount and serial sections, and then designated as lectotype. The others (including this one) are then paralectotypes.	Paralectotype	*Stylochoplana aulica*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p114. leg E Marcus (40). SMNH 109155. Dept. Zoologia S. Paulo. *Stylochoplana aulica*. Marc. 40.
	SMNH 109157	2 worms in whole mount.	Paralectotype	*Stylochoplana aulica*. SMNH 109157. leg E Marcus (42). *Stylochoplana aulica*.
	SMNH 109158	3 worms in whole mount.	Paralectotype	*Stylochoplana aulica*. SMNH 109158. leg E Marcus (43). *Stylochoplana aulica*.
Armatoplana divae (Marcus, 1947)	**SMNH 109167***	Whole mount of entire worm, except for the sectioned part. The original description is based on 1 worm.	Holotype	*Stylochoplana divae*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p112. leg DD Correa (51). SMNH 109167. Dept. Zoologia S.Paulo. *Stylochoplana divae* Marc. 51.
	SMNH 109168*	Serial sections of posterior/middle part of SMNH 109167. Sections continue on the following 3 slides.	Holotype	*Stylochoplana divae*. SMNH 109168. leg DD Correa. (52).
	SMNH 109169*	Serial sections of posterior/middle part of SMNH 109167.	Holotype	*Stylochoplana divae*. SMNH 109169. leg DD Correa. (53).
	SMNH 109170*	Serial sections of posterior/middle part of SMNH 109167. Reproductive structures	Holotype	*Stylochoplana divae*. SMNH 109170. leg DD Correa. (54). *Stylochoplana divae* Marc. 54.

		on rows 1-3 (marked with blue dot). Dirty slide.		
	SMNH 109171*	Serial sections of posterior/middle part of SMNH 109167. Reproductive structures on rows 1-3 (marked with blue dot). Dirty slide.	Holotype	*Stylochoplana divae*. SMNH 109171. leg DD Correa. (55).
Armatoplana leptalea (Marcus, 1947)	**SMNH 109180***	Whole mount of anterior part. The original description is based on 1 specimen (imature). This worm fits the description. Its posterior part is on the following 3 slides (according to consecutive labelling.	Holotype	*Stylochoplana leptalea*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p.118, 1948 p.177, 1968 p.24. Leg.: E. Marcus ( ). SMNH 109180.
	SMNH 109181*	Serial sections of posterior part of SMNH 109180. Sections continue on next slide.	Holotype	*Stylochoplana leptalea*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p.118, 1948 p.177, 1968 p.24. Leg.: E. Marcus (37). SMNH 109181.
	SMNH 109182*	Serial sections of posterior part of SMNH 109180. Reproductive structures on rows 3 and 4 (marked ith blue dot). Dirty slide.	Holotype	*Stylochoplana leptalea*. SMNH 109182. leg E Marcus. (38).
	SMNH 109183*	Serial sections of posterior part of SMNH 109180.	Holotype	*Stylochoplana leptalea*. SMNH 109183. leg E Marcus. (39). *Stylochoplana leptalea* Marc. 39
Interplana evelinae (Marcus, 1952)	**SMNH 109173***	Whole mount of the anterior part. The original description is based on 2 worms. This is the largest and its sections are deposited also together (correspondence by size).	Lectotype	*Stylochoplana evelinae*. Marcus 1952. Sao Paulo. Cf Marcus 1952 p83. leg E Marcus (A). SMNH 109173.

	SMNH 109176*	serial sections of SMNH 109073 sections continue on following 3 slides	Lectotype	*Stylochoplana evelinae*. Marcus 1952. Sao Paulo. Cf Marcus 1952 p83. leg E Marcus (1). SMNH 109176. 1.
	SMNH 109177*	Serial sections of SMNH 109073. Reproductive structures on rows 1 and 2 (marked with blue dot).	Lectotype	*Stylochoplana evelinae*. SMNH 109177. leg E Marcus (2). 2.
	SMNH 109178*	Serial sections of SMNH 109073. Reproductive structures on rows 2-4 (marked with blue dot).	Lectotype	*Stylochoplana evelinae*. SMNH 109178. leg E Marcus (3). 3.
	SMNH 109179*	Serial sections of SMNH 109073. Continuation of previous sections.	Lectotype	*Stylochoplana evelinae*. SMNH 109179. leg E Marcus (4). 4.
	SMNH 109174	Serial sections of posterior part of worm. The rest of the worm is unknown.	Paralectotype	*Stylochoplana evelinae*. SMNH 109174. leg E Marcus (B).
	SMNH 109175	Serial sections of SMNH 109174 Reproductive structures on rows 3-5 (marked with blue dot).	Paralectotype	*Stylochoplana evelinae*. SMNH 109175. leg E Marcus (C).
Stylochoplana divae (Marcus, 1949)	**SMNH 109672***	Serial sections of entire worm. These sections continue not in the next slide but in SMNH 109674, by the form of the sections.	Lectotype	*Candimba divae*. Marcus 1949. Sao Paulo; Ilha das Palmas (XI 48). Cf Marcus 1949 p76. leg E Marcus. SMNH 109672.
	SMNH 109674*	Serial sections of SMNH 109672 Reproductive structures on rows 6-9 (marked with blue dot). The sections fit the illustration of figure 116 of the original description.	Lectotype	*Candimba divae*. Marcus 1949. see other glasses. *Candimba*. SMNH 109674.
	SMNH 109669	Whole mount of entire worm.	Paralectotype	*Candimba divae*. Marcus 1949. Sao Paulo, Ilha das

				Palmas (XI 48). Cf Marcus 1949 p76. leg E Marcus. SMNH 109669.
	SMNH 109670	Whole mount of entire worm.	Paralectotype	*Candimba divae*. Marcus 1949. Sao Paulo, Ilha das Palmas (XI 48). Cf Marcus 1949 p76. leg E Marcus. SMNH 109670.
	SMNH 109671	Whole mount of entire worm.	Paralectotype	*Candimba divae*. Marcus 1949. Sao Paulo, Ilha das Palmas (XI 48). Cf Marcus 1949 p76. leg E Marcus. SMNH 109671.
	SMNH 109673	Serial sections of entire worm. Reproductive structures on rows 6 and 7 (marked with blue dot). The specimen is more imature than the other one sectioned.	Paralectotype	*Candimba divae.* Marcus 1949. see other glasses. SMNH 109673. *Candimba*.
Stylochoplana selenopsis Marcus, 1947	**SMNH 109199***	Whole mount of anterior part of worm. The original description is based on one imature worm. This is the only slide with the type locality and the worm is small, imature.	Holotype	*Stylochoplana selenopsis*. Sao Paulo; Sao Vicente. Cf Marcus 1947 p116, 1949 p74. leg E Marcus (48). SMNH 109199.
	SMNH 109200*	Serial sections of posterior part of SMNH 109199. According to consecutive labels this should correspond to the sections of SMNH 109199. Reproductive structures on rows 4 and 5 (marked with blue dot).	Holotype	*Stylochoplana selenopsis*. SMNH 109200. leg E Marcus (48).
	SMNH 109201*	Serial sections of posterior part of SMNH 109199. Continuation of previous sections	Holotype	*Stylochoplana selenopsis*. SMNH 109201. leg E Marcus (49).

	SMNH 109202*	Serial sections of posterior part of SMNH 109199. Continuation of previous sections.	Holotype	*Stylochoplana selenopsis*. SMNH 109202. leg E Marcus (50).
Cryptocelis lilianae Marcus & Marcus, 1968	**SMNH 109687**	Whole mount of entire worm and anterior part of worm. Together with the holotype head there is a paratype.	Holotype/ Paratype	*Cryptocelis lilianae*. Marcus and Marcus 1968. Sao Paulo; Ubatuba. Cf Marcus 1968 p13. leg L Forneris (A). SMNH 109687. Dep. Zool. USP. *Cryptocelis lilianae*. Type head.
	SMNH 109688	Serial sections of posterior part of SMNH 109687 Reproductive structures on row 1 (marked with blue dot).	Holotype	*Cryptocelis lilianae*. Leg L. Forneris (B). SMNH 109688. Dep. Zool. USP. *Cryptocelis lilianae*. Typ.
	SMNH 109689	Serial sections of posterior part of SMNH 109687. Reproductive structures on rows 10 and 11 (marked with blue dot).	Holotype	*Cryptocelis lilianae*. Leg L. Forneris (C). SMNH 109689. *Cryptocelis lilianae*. Typ.
Phaenocelis medvedica Marcus, 1952	**SMNH 109708***	Whole mount of 2 anterior parts. One anterior part is from *Phaenocelis* and the other from *Lurymare utarum*.	Lectotype	*Phaenocelis medvedica*. SMNH 109708. leg E Marcus (B). *Phaenocelis medvedica*. *Prosthiostomum utarum*.
	SMNH 109709*	Serial sections of posterior part of SMNH 109708. Reproductive structures on rows 3-6 (marked with blue dots).	Lectotype	*Phaenocelis medvedica*. SMNH 109709. leg E Marcus (C).
	SMNH 109707	Whole mount of entire worm. It fits the drawing of the description.	Paralectotype	*Phaenocelis medvedica*. Marcus 1952. Sao Paulo; Ilha de Sao Sebastiao (Ilhabela). Cf Marcus 1952. p81. leg E Marcus (A). SMNH 109707. *Phaenocelis medvedica*. Ilhabela.
Triadomma curvum Marcus, 1949	**SMNH 109717***	Serial sections of entire worm. Reproductive structures on rows 4-6 (marked with blue dot).	Lectotype	*Triadomma curvum*. SMNH 109717. leg E Marcus (D). *Triadomma*.

	SMNH 109714	Whole mount of entire worm. The description is based on 4 worms collected on Ilha de Sao Sebastiao. The one sectioned is to be considered the lectotype.	Paralectotype	*Triadomma curvum*. Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1949 p70. leg E Marcus (A). SMNH 109714. Dept. Zoologia S. Paulo. *Triadomma curvum* M.
	SMNH 109715	Whole mount of entire worm.	Paralectotype	*Triadomma curvum*. SMNH 109715. leg E Marcus (B). Dept. Zoologia S. Paulo. *Triadomma curvum*.
	SMNH 109716	Whole mount of entire worm.	Paralectotype	*Triadomma curvum*. SMNH 109716. leg E Marcus (C).
Triadomma evelinae Marcus, 1947	**SMNH 109720***	Serial sections of entire worm.	Lectotype	*Triadomma evelinae*. SMNH 109720. leg E Marcus (18).
	SMNH 109721*	Serial sections of SMNH 109720. Reproductive structure on row 1 (marked with blue dot).	Lectotype	*Triadomma evelinae*. SMNH 109721. leg E Marcus (19).
	SMNH 109722*	Serial sections of SMNH 109720. Reproductive structures on rows 2-5 (marked with blue dot).	Lectotype	*Triadomma evelinae*. SMNH 109722. leg E Marcus (20).
	SMNH 109718	Whole mount of entire worm.	Paralectotype	*Triadomma evelinae*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p107. leg E Marcus (16). SMNH 109718. *Triadomma evelinae*. Marc. 16.
	SMNH 109719	Whole mount of entire worm.	Paralectotype	*Triadomma evelinae*. SMNH 109719. leg E Marcus (17). *Triadomma evelinae*. Marc. 17.
	SMNH 109723	Serial sections of entire worm.	Paralectotype	*Triadomma evelinae*. SMNH 109723. leg E Marcus (21).
	SMNH 109724	Serial sections of entire worm. Without	Paralectotype	*Triadomma evelinae*. SMNH 109724. leg E Marcus

		reproductive structures, but it also is just part of a worm, continuation of slices in other slide.		(22).
	SMNH 109725	Serial sections of entire worm. With male structures in rows 6 and 7 of the slide. Material from Ilha de Palmas. Type species of the genus.	Paralectotype	*Triadomma evelinae*. Marcus 1947. Sao Paulo; Ilha das Palmas. cf Marcus 1947 p107. leg E Marcus. SMNH 109725. Dept. Zoologia S. Paulo. *Triadomma evelinae*
Adenoplana evelinae Marcus, 1950	**SMNH 109605***	Whole mount of anterior part. Since this if the worm that was sectioned, it is designated lectotype. Most of measurements were taken from this worm	Lectotype	*Adenoplana evelinae*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p76. leg E Marcus (A). SMNH 109605.
	SMNH 109607*	Serial sections of 109605. Sections of lectotype	Lectotype	*Adenoplana evelinae*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p76. leg E Marcus (1). SMNH 109607.
	SMNH 109608*	Serial sections of 109605. Two last sections are what Marcus drew in figure 144. Reproductive structures visible on rows 4-7 (marked with blue dot).	Lectotype	*Adenoplana evelinae*. SMNH 109608. leg E Marcus (2).
	SMNH 109609*	Serial sections of 109605. Two upper rows of sections show the male gonopore. All rows contain reproductive structures.	Lectotype	*Adenoplana evelinae*. SMNH 109609. leg E Marcus (3).
	SMNH 109610*	Serial sections of 109605. Three lower rows of sections show the female gonopore. All rows contain reproductive	Lectoype	*Adenoplana evelinae*. SMNH 109610. leg E Marcus (4).

		structures. (blue dots). Black marks show the female gonopore.		
	SMNH 109606	Whole mount of entire worm also part ot the original description.	Paralectotype	*Adenoplana evelinae*. SMNH 109606. leg E Marcus (B). Dept. Zoologia S. Paulo. *Adenoplana evelinae*.
Callioplana evelinae Marcus, 1954	**SMNH 109663***	Whole mount of entire worm and anterior part of worm. Sectioned worm is the lectotype.	Lectotype / Paralectotype	*Callioplana evelinae*. Marcus 1954. Sao Paulo; Ilhabela (Ilha de Sao Sebastiao). Cf Marcus 1954 p476. leg E Marcus (A). SMNH 109663. *Callioplana evelinae*. Ilhabela.
	SMNH 109664*	Serial sections of posterior part of worm (SMNH 109663).	Lectotype	*Callioplana evelinae*. SMNH 109664. leg E Marcus (B).
	SMNH 109665*	Serial sections of SMNH 109663. Reproductive structures on rows 1 and 2 (marked with blue dot).	Lectotype	*Callioplana evelinae*. SMNH 109665. leg E Marcus (C).
	SMNH 109666*	Serial sections of SMNH 109663.	Lectotype	*Callioplana evelinae*. SMNH 109666. leg E Marcus (D).
	SMNH 109667	Serial sections of entire worm. Reproductive structures on rows 5-7 (marked with blue dot).	Paralectotype	*Callioplana evelinae*. Marcus 1954. Sao Paulo; Ilhabela (Ilha de Sao Sebastiao). Cf Marcus 1954 p476. leg E Marcus (M). SMNH 109667.
	SMNH 109668	Serial sections of SMNH 109667. Continuation of previous sections	Paralectotype	*Callioplana evelinae*. SMNH 109668. leg E Marcus (N).
Hoploplana divae Marcus, 1950	**SMNH 109060***	Serial sections of entire worm. Reproductive structures on rows 9 and 10 (marked with blue dot). The slide lacks the voucher number from SMNH. Probably because there is no space.	Holotype	*Hoploplana divae*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950, 1968. leg E Marcus (A).
	SMNH 109061*	Serial sections of entire worm.	Holotype	*Hoploplana divae*. Leg E Marcus (B). SMNH

		Reproductive structures on rows 1-3 (marked with blue dot).		109061
Itannia ornata Marcus, 1947	**SMNH 109780***	Serial sections of entire worm. Type species of the genus. Reproductive structures absent. According to drawing it corresponds to the type specimen, thus to be designated lectotype.	Holotype	*Itannia ornata*. Marcus 1947. Sao Paulo, Ilha das Palmas (I47). Cf Marcus 1947 p135, 1952 p88. leg E Marcus (91). SMNH 109780.
	SMNH 109781*	Serial sections of entire worm (SMNH 109780). Reproductive structures in rows 4 and 5 (marked with blue dots). Slide with dirt or something that make it hard to focus.	Holotype	*Itannia ornata*. Marcus 1947. Sao Paulo, Ilha das Palmas (I47). Cf Marcus 1952 p135, 1947 p88. leg E Marcus (92). SMNH 109781.
	SMNH 109782*	Serial sections of entire worm (SMNH 109780). Reproductive structures absent. Continuaton of the two previous slides.	Holotype	*Itannia ornata*. Marcus 1947. Sao Paulo, Ilha das Palmas. (I47). Cf Marcus 1952, 1947. leg E Marcus (93). SMNH 109782.
Distylochus isifer (Du Bois-Reymond Marcus, 1955)	**SMNH 109793***	Serial sections of posterior part. Reproductive structures on rows 6 and 7 (marked with blue dot).	Lectotype	*Stylochus isifer*. du Bois-Reymond Marcus 1955. Sao Paulo Cananeia (V53). Cf du B-R Marcus 1955 p37. leg Ev Marcus. SMNH 109793.
Distylochus martae (Marcus, 1947)	**SMNH 109794***	Serial sections of entire worm. Slide with dirty medium. The sections continue in the following slide. The slides fit the drawing made by Marcus.	Holotype	*Stylochus martae* Marcus 1947. Sao Paulo; Ilha de Sto Ambro. Cf Marcus 1947 p104. leg MV Mendes (10). *Stylochus martae* Marc. 10. SMNH 109794
	SMNH 109795*	Serial sections of SMNH 109794. Reproductive structures on rows 4 and 5 (marked with blue dot). The sections are continuation of previous slide.	Holotype	*Stylochus martae*. SMNH 109795. leg MV Mendes (11).

Imogine cata Du Bois-Reymond Marcus, 1958	**SMNH 109788***	Serial sections of entire worm. The sections continue on the next slide. Material from Ilhabela (type locality)	Holotype	*Stylochus catus*. du Bois-Reymond Marcus 1958. Sao Paulo; Ilhabela. Cf du B-R Marcus 1958 p401 and Marcus 1968 p11. leg E Marcus (A). SMNH 109788.
	SMNH 109789*	Serial sections of SMNH 109788. The sections are continuation of previous slide and contain retracted tentacle (marked with blue dot, in row 9). Sections with reproductive structures slightly folded (marked with black dots, are in row 4 and 5)	Holotype	*Stylochus catus*. SMNH 109789. leg E Marcus (B).
Imogine refertus Du Bois-Reymond Marcus, 1965	**SMNH 109796**	Serial sections of posterior part. The sections continue on the following 4 slides.	Holotype	*Stylochus refertus*. du Bois-Reymond Marcus 1965. Sao Paulo; Ilha Porchat. Cf Marcus 1965 p129. leg W Narcho (4). SMNH 109796.
	SMNH 109797	Serial sections of 109796. Some reproductive structures (vas deferens) are visible.	Holotype	*Stylochus refertus*. leg W Narcho (5). SMNH 109797.
	SMNH 109798	Serial sections of 109796. No gonopores or vesicles visible.	Holotype	*Stylochus refertus*. Leg W Narcho (6). SMNH 109798.
	SMNH 109799	Serial sections of 109796. Slides dirty. Reproductive structures on rows 1 and 2 (marked with blue dot).	Holotype	*Stylochus refertus*. Leg W Narcho (7). SMNH 109799.
	SMNH 109800	Serial sections of 109796. Slides dirty. Reproductive structures on rows 4, 5 and 6 (marked with blue dot).	Holotype	*Stylochus refertus*. Leg W Narcho (8). SMNH 109800
Imogine tica	**SMNH 109801***	Whole mount of most of worm, rest of	Lectotype	*Stylochus ticus*. Marcus 1952. Sao Paulo; Ilhabela.

Marcus, 1952		the body of the animal in sections of reproductive parts (in following slides). Therefore is to be designated lectotype.		Cf Marcus 1952 p79, 1968 p11. leg E Marcus (A). *Stylochus ticus*. Ilhabela.
	SMNH 109802*	Serial sections of SMNH 109801. Cover slides with fungus.	Lectotype	*Stylochus ticus*. SMNH 109802. leg E Marcus (B).
	SMNH 109803*	Serial sections of SMNH 109801. Cover slides with fungus.	Lectotype	*Stylochus ticus*. SMNH 109803. leg E Marcus (C).
	SMNH 109804*	Serial sections of SMNH 109801. Reproductive structures in row 6 and 7 (marked with blue dot).	Lectotype	*Stylochus ticus*. SMNH 109804. leg E Marcus (D).
	SMNH 109805*	Serial sections of SMNH 109801.	Lectotype	*Stylochus ticus*. SMNH 109805. leg E Marcus (E).
Pentaplana divae Marcus, 1949	**SMNH 109654***	Serial sections of posterior part of SMNH 109655. Type species of the genus. The original description is based on 1 worm from Ilha Porchat and 8 worms from Forte Itaipú.	Lectotype	*Pentaplana divae*. Marcus 1949. Sao Paulo; Baia de Santos; Ilha Porchat. Cf Marcus 1949 p68. leg E Marcus (A).
	SMNH 109655*	Whole mount of anterior part of worm.	Lectotype	*Pentaplana divae*. SMNH 109655. leg E Marcus (B).
	SMNH 109656	2 worms in whole mount.	Paralectotypes	*Pentaplana divae*. Marcus 1949. Sao Paulo; Baia de Santos; Forte de Itaipú. Cf Marcus 1949 p68. leg DD Correa (E).
	SMNH 109657	Whole mount of entire worm.	Paralectotype	*Pentaplana divae*. SMNH 109657. leg DD Correa (F). Dept. Zoologia S. Paulo. *Pentaplana divae* M.
	SMNH 109658	Whole mount of 2 anterior parts. One anterior part is from a *Stylochoplana selenopsis*.	Paralectotype	*Pentaplana divae*. SMNH 109658. leg DD Correa (G). *Stylochoplana selenopsis*.

	SMNH 109659	Whole mount of entire worm. type species of the genus.	Paralectotype	*Pentaplana divae*. SMNH 109659. leg DD Correa (H). *Pentaplana*.
	SMNH 109660	2 worms in whole mount	Paralectotypes	*Pentaplana divae*. SMNH 109660. leg DD Correa (I). Dept. Zoologia S. Paulo. *Pentaplana divae*.
	SMNH 109661	Serial sections of posterior part of worm. This and the next slides are from two different worms, from the second location.	Paralectotype	*Pentaplana divae*. SMNH 109661. leg DD Correa (J).
	SMNH 109662	Serial sections of posterior part of worm.	Paralectotype	*Pentaplana divae*. SMNH 109662. leg DD Correa (K). Dept. Zoologia S. Paulo. *Pentaplana divae*. M.
Latocestus callizona (Marcus, 1947)	**SMNH 109611***	Serial sections of posterior part of 109614. Slides with fungus.	Holotype	*Allena callizona*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p103. leg E Marcus (12). SMNH 109611.
	SMNH 109612*	Serial sections of posterior part of 109614. Slides with fungus. Reproductive structures in rows 3, 4 and 5 (marked with blue dot).	Holotype	*Allena callizona*. SMNH 109612. leg E Marcus (13). *Allena callizona* Marc. 13.
	SMNH 109613*	Serial sections of posterior part of 109614. Slides with fungus.	Holotype	*Allena callizona*. SMNH 109613. leg E Marcus (14).
	SMNH 109614*	Whole mount of anterior part. Material from type locality. Fits drawings.	Holotype	*Allena callizona*. SMNH 109614. leg E Marcus (15).
Nonatona euscopa Marcus, 1952	**SMNH 109650***	Serial sections of posterior part of worm. Type species of the genus.	Holotype	*Nonatona euscopa*. Marcus 1952. Paraná; Caioba. Cf Marcus 1952 p78. leg E Marcus (A). SMNH 109650.
	SMNH 109651*	Serial sections of SMNH 109650. Reproductive structures on rows 1 and 2	Holotype	*Nonatona euscopa*. SMNH 109651. leg E Marcus (B).

		(marked with blue dot).		
	SMNH 109652*	Serial sections of SMNH 109650. Reproductive structures on rows 1-5 (marked with blue dot).	Holotype	Nonatona euscopa. SMNH 109652. leg E Marcus (C).
	SMNH 109653*	Serial sections of SMNH 109650.	Holotype	Nonatona euscopa. SMNH 109653. leg E Marcus (D).
Prolatocestus ocellatus (Marcus, 1947)	**SMNH 109647***	Whole mount of almost entire worm.	Lectotype	*Latocestus ocellatus*. SMNH 109647. leg E Marcus (8).
	SMNH 109641*	Serial section of posterior part of worm. These are sections from SMNH 109647.	Lectotype	*Latocestus ocellatus*. SMNH 109641. leg E Marcus (2).
	SMNH 109642*	Serial sections of SMNH 109647.	Lectotype	*Latocestus ocellatus*. SMNH 109642. leg E Marcus (3).
	SMNH 109643*	Serial sections of SMNH 109647. Reproductive structures on rows 2-6 (mared with blue dot).	Lectotype	*Latocestus ocellatus*. SMNH 109643. leg E Marcus (4).
	SMNH 109640	Serial sections of posterior part of worm. The original descriptions is based on 10 specimens. And in 1949 another 5 specimens were collected in São Sebastião. These are sections from SMNH 109645.	Paralectotype	*Latocestus ocellatus*. Marcus 1946. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p100, 1949 p67. leg E Marcus (1). SMNH 109640.
	SMNH 109644	Whole mount of entire worm.	Paralectotype	*Latocestus ocellatus*. SMNH 109644. leg E Marcus (5).
	SMNH 109645	Whole mount of almost entire worm.	Paralectotype	*Latocestus ocellatus*. SMNH 109645. leg E Marcus (6). *Latocestus ocellatus* Marc. 6.
	SMNH 109646	Whole mount of entire worm.	Paralectotype	*Latocestus ocellatus*. SMNH 109646. leg E Marcus

				(7). Dept. Zoologia S. Paulo. *Latocestus ocellatus* Marc. 7.
	SMNH 109648	Whole mount of entire worm.	Paralectotype	*Latocestus ocellatus*. SMNH 109648. leg E Marcus (9). Dept. Zoologia S. Paulo. Latocestus ocellatus Marc. 9.
Cestoplana salar Marcus, 1949	**SMNH 109682***	Whole mount of almost entire worm.	Holotype	SMNH 109682. *Cestoplana salar*. Marcus 1949. Sao Paulo; Ilha das Palmas. Cf Marcus 1949 p79. leg E Marcus. Cestopl.
	SMNH 109683*	Serial sections of posterior part of SMNH 109683. Reproductive structures on row 7 and 8 (marked with blue dot).	Holotype	*Cestoplana salar*. Marcus 1949. Sao Paulo; Ilha das Palmas. Cf Marcus 1949 p79. leg E Marcus. SMNH 109683
Cestoplana techa Marcus Du Bois-Reymond Marcus, 1957	**SMNH 109684***	Whole mount of anterior part of worm. The original description is based on 3 worms. Here is the lectotype.	Lectotype	*Cestoplana techa*. du Bois-Reymond Marcus 1957. Sao Paulo; Ilhabela. Cf d B-R Marcus 1957 p174. leg Ev Marcus (A). SMNH 109684. *Cestoplana techa.*
	SMNH 109685*	Serial sections of posterior part of SMNH 109684. Reproductive structures on rows 8-10 (marked with blue dot).	Lectotype	SMNH 109685. *Cestoplana techa*. Leg Ev Marcus (B).
	SMNH 109686*	Serial sections of SMNH 109684. Continuation of previous slides.	Lectotype	*Cestoplana techa*. Leg Ev Marcus (C). SMNH 109686.
Theama evelinae Marcus, 1949	**Type 5076a**	Whole mount of anterior part of worm. In total type series has 4 specimens: 1 whole mount (5076a); 1 as serial sections (5076b) and 3 whole mounts (5076c-e).	Lectotype	*Theama evelinae*. Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao; Ilhabela. Cf Marcus 1949 p72. leg E Marcus (A). Dept. Zoologia S. Paulo. *Theama evelinae* vorderteil. Ilhabela 1948. 5076a.
	Type 5076b	Serial sections of posterior part of SMNH 5076a. The first 2 slides are lectotypes	Lectotype	*Theama evelinae*. Leg E Marcus (B). 5076b.

		and the rest paralectotypes. Reproductive structures ow rows 5 and 6 (marked with blue dot).		
	Type 5076c	Whole mount of entire worm. Worm is divided in two.	Paralectotype	*Theama evelinae*. Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao; Ilhabela. Cf Marcus 1949 p72. leg E Marcus (K). Dept. Zoologia S. P. *Theama evelinae*. 5076c.
	Type 5076d	Whole mount of entire worm.	Paralectotype	*Theama evelinae*. Marcus 1949. leg E Marcus (L). Dept. Zoologia S. P. *Theama evelinae*. 5076d.
	Type 5076e	Whole mount of entire worm.	Paralectotype	*Theama evelinae*. Leg E Marcus (M). 5076e.
Pericelis cata Marcus & Marcus, 1968	**SMNH 109883**	Whole mount of head of the worm. There is a paper under the slides that state typus series. It should also include all until 109889. From Curaçao Piscadera Baai.	Holotype	*Pericelis cata*. Marcus & Marcus 1968. Curaçao; Piscadera Baai. Head. Cf Marcus & Marcus 1968 p59. leg DD Correa (O). SMNH 109883. *Pericelis cata*. head.
	SMNH 109884	Whole mount of posterior margin of SMNH 109883. Final part of the holotype worm.	Holotype	*Pericelis cata*. SMNH 109884. tail. leg DD Correa (O). SMNH 109883. *Pericelis cata*. 3. tail.
	SMNH 109885	Serial sections of middle of SMNH 109883. Serial sections of holotype, it continues until SMNH 109889.	Holotype	SMNH 109885. *Pericelis cata*. Leg DD Correa 1
	SMNH 109886	Serial sections of middle of SMNH 109883. Serial sections continue on following slides.	Holotype	SMNH 109886. *Pericelis cata*. Leg DD Correa 2.
	SMNH 109887	Serial sections of middle of SMNH 109883. Ventral sucker is visible. Serial sections continue on following slides.	Holotype	SMNH 109887. *Pericelis cata*. Leg DD Correa 3.

	SMNH 109888	Serial sections of middle of SMNH 109883. Reproductive structures on rows 2, 3, 4, 5, 6, 7 and 8 (marked with blue dot).	Holotype	SMNH 109888. *Pericelis cata*. Leg DD Correa 4.
	SMNH 109889	Serial sections of middle of SMNH 109883. Reproductive structures on rows 1, 2 and 3 (marked with blue dot).	Holotype	SMNH 109889. *Pericelis cata*. Leg DD Correa 5.
Enchiridium evelinae Marcus, 1949	**SMNH 109924***	Whole mount of anterior part. The rest of the worm is in serial sections that begin in SMNH 109929. No locality.	Lectotype	*Enchiridium evelinae*. SMNH 109924. leg E Marcus (B). Dept. Zoologia S. Paulo. *Enchiridium evelinae*.
	SMNH 109929*	Serial sections of posterior part. Sections (from SMNH 109924) continue in following slides. Reproductive structures in rows 6 and 7 (marked with blue dot).	Lectotype	*Enchiridium evelinae*. Marcus 1949. Sao Paulo. Cf Marcus 1949 p91, 1968 p92. leg E Marcus (R). SMNH 109929
	SMNH 109930*	Serial sections of posterior part. There are reproductive structures marked with blue dots. The slides fit the drawing in figure 131 of Marcus 1949.	Lectotype	*Enchiridium evelinae*. Leg E Marcus (S). SMNH 109930
	SMNH 109931*	Serial sections of posterior part. Reproductive structures (female pore) in rows 1, 2 and 3 (marked with blue dot).	Lectotype	*Enchiridium evelinae*. Leg E Marcus (T). SMNH 109931
	SMNH 109923	Whole mount of entire worm. Juvenile worm? Animal from type locality.	Paralectotype	*Enchiridium evelinae*. Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao; Ilhabela. Cf Marcus 1949 p91, 1968 p92. leg E Marcus (A). SMNH 109923. Dept. Zoologia S. Paulo. *Enchiridium evelinae*. Ilhabela. 1948.

	SMNH 109925	Whole mount of entire worm. No locality.	Paralectotype	*Enchiridium evelinae*. SMNH 109925. leg E Marcus (C). Dept. Zoologia S. Paulo. *Enchiridium evelinae*.
	SMNH 109926	2 worms in whole mount. No locality. One worm is juvenile without pigmentation and marginal eyespots only in the anterior part. The larger one has dots on dorsal surface. The animals are almost the same size fixed, but have different body proportions and pigmentation. Could be different species (maybe different genera?).	Paralectotypes	*Enchiridium evelinae*. SMNH 109926. leg E Marcus (D).
	SMNH 109927	Serial sections of entire worm. The label says only Sao Paulo. There are some markings on the slide (black dots) that indicate the ventral sucker. The worm seems imature.	Paralectotype	*Enchiridium evelinae*. Marcus 1949. Sao Paulo. Cf Marcus 1949 p91, 1968 p92. leg E Marcus (G). SMNH 109927.
	SMNH 109928	2 worms in whole mount Again apparently two different species. In this the unpigmented worm is bigger than both worms in the SMNH 109926 slide.	Paralectotypes	*Enchiridium evelinae*. Marcus 1949. Sao Paulo. Cf Marcus 1949 p91, 1968 p92. leg E Marcus (K). SMNH 109928.
Enchiridium gabriellae (Marcus, 1949)	**SMNH 109949***	Serial sections of entire worm. Reproductive structures on row 7 and 8 (marked with blue dot). Worm seems to be not fully developed.	Holotype	*Prosthiostomum gabriellae*. Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1949 p88. leg E Marcus. SMNH 109849. Dept. Zoologia S. Paulo. *Prosthiostomum gabriellae*. Ilhabela. 1948.
Euprosthiostomum	**SMNH 109936***	Serial sections of posterior part. Sections	Holotype	*Euprosthiostomum mortenseni*. Marcus 1948. Sao

mortenseni Marcus, 1948		continue in following slide. Imature worm. Just hint of male reproductive structures on row 1 and 2 (marked with blue dot).		Paulo, Sao Vicente (XI 47). Cf Marcus 1948 p184. leg E Marcus (1). SMNH 109936.
	SMNH 109937*	Serial sections of posterior part of 109936. Fits the description.	Holotype	*Euprosthiostomum mortenseni*. SMNH 109937. leg E Marcus (2).
	SMNH 109938*	Serial sections of posterior part of 109936. Continuation of previous slides. On them there are black marks that point in which sections is the ventral sucker	Holotype	*Euprosthiostomum mortenseni*. SMNH 109938. leg E Marcus (3).
	SMNH 109939*	Whole mount of anterior part of 109936. The anterior part correspond to the rest of the worm sectioned in previous slides, the lectotype.	Holotype	*Euprosthiostomum mortenseni*. SMNH 109939. Leg E Marcus (4).
Lurymare cynarium (Marcus, 1950)	**SMNH 109945***	Serial sections of entire worm. The sections continue on the next slides.	Lectotype	*Prosthiostomum cynarium*. Leg E Marcus (D). SMNH 109945.
	SMNH 109946*	Serial sections of SMNH 109945. Continuation of previous sections, go on to the following slide. Reproductive structures on rows 6 to 10.	Lectotype	*Prosthiostomum cynarium*. Leg E Marcus (E). SMNH 109946.
	SMNH 109947*	Serial sections of SMNH 109945. Continuation of previous slides.	Lectotype	*Prosthiostomum cynarium*. leg E Marcus (F). SMNH 109947.
	SMNH 109942	Serial sections of entire worm. Sections continue in the following slide. Reproductive structures and ventral sucker on rows 10 and 11 (marked with	Paralectotype	*Prosthiostomum cynarium*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p99. leg E Marcus (A). SMNH 109942.

		blue dot). Worm is not fully developed.		
	SMNH 109943	Serial sections of SMNH 109942 continuation of previous slide. Reproductive structures on row 1 (marked with blue dot). Worm is not fully developed.	Paralectotype	*Prosthiostomum cynarium*. Leg E Marcus (B). SMNH 109943.
	SMNH 109944	2 worms in whole mount. The whole mount includes the anterior part of a worm and an entire worm.	Paralectotypes	*Prosthiostomum cynarium*. Leg E Marcus (C). SMNH 109944.
	SMNH 109948	Serial sections of entire worm. Imature worm. Hint of reproductive structures and ventral sucker on row 12 (marked with blue dot).	Paralectotype	*Prosthiostomum cynarium*. Leg E Marcus (G). SMNH 109948. *Prosthiostomum cynarum*.
Lurymare matarazzoi (Marcus, 1950)	**SMNH 109956***	Whole mount of entire worm. Worm collected on the type locality. There are no sections of any worm of that area. This is the more mature of the two.	Lectotype	*Prosthiostomum matarazzoi*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p94, 1968 p89. leg E Marcus (A). SMNH 109956. Dept. Zoologia S. Paulo. *Prosthiostomum matarazzoi*.
	SMNH 109957	Whole mount of entire worm. Worm looks a little imature when compared to the previous one.	Paralectotype	*Prosthiostomum matarazzoi*. SMNH 109957. leg E Marcus (B).
Lurymare utarum Marcus, 1952	**SMNH 109967***	Serial sections of middle part. Material from type locality, therefore, lectotype. The rest of the worm or the rest of the type series is unknown. Serial sections continue on next slide. Reproductive structures on row 1 (marked with blue	Lectotype	*Prosthiostomum (Lurymare) utarum* Marcus 1952. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1952 p98, 1968 p90. leg E Marcus (A). *Prosthiostomum utarum*. SMNH 109967.

		dot and black line).		
	SMNH 109968*	Serial sections of middle part of SMNH 109968. Continuation of previous slide. Reproductive structures on rows 1-6 (marked with blue dot).	Lectotype	*Prosthiostomum (Lurymare) utarum* SMNH 109968. leg E Marcus (B). *Prosthiostomum utarum*.
Prosthiostomum gilvum Marcus, 1950	**SMNH 109950***	Serial sections of posterior part. Slide with fungus or dryed mounting medium. The sections continue in the following 3 slides.	Lectotype	Dept. Zoologia S.Paulo. *Prosthiostomum gilvum*. SMNH 109950. *Prosthiostomum gilvum*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p98. leg E Marcus (1).
	SMNH 109951*	Serial sections of SMNH109950. Slide with fungus/dryed mounting medium. Reproductive structures on rows 2-6 (marked with blue dot).	Lectotype	*Prosthiostomum gilvum*. SMNH 109951. leg E Marcus (2).
	SMNH 109952*	Serial sections of SMNH 109950. Slide with fungus/dryed mounting medium.	Lectotype	*Prosthiostomum gilvum*. SMNH 109952. leg E Marcus (3).
	SMNH 109953*	Serial sections of SMNH109950. Slide with fungus/dryed mounting medium. Continuation of previous slide.	Lectotype	*Prosthiostomum gilvum*. SMNH 109953. leg E Marcus (4).
	SMNH 109954*	Whole mount of anterior part of SMNH109950. Rest of the body of the animal in previous slides. Therefore is the worm to be designated lectotype.	Lectotype	*Prosthiostomum gilvum*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p98. leg E Marcus (5) SMNH 109954.
	SMNH 109955	Whole mount of entire worm. It is possible to see the separate prostatic vesicles.	Paralectotype	*Prosthiostomum gilvum*. SMNH 109955. leg E Marcus (6). Dept. Zoologia S. Paulo. *Prosthiostomum gilvum*.
Acerotisa bituna	**SMNH 109589***	Serial sections of entire worm. Slide with	Holotype	*Acerotisa bituna*. Marcus 1947. Sao Paulo; Ilha das

Marcus, 1947		fungus or something on the cover glass. From Ilha das Palmas, thus the type. Folded sections. Reproductive structures on row 1 (marked with blue dot).		Palmas. Cf Marcus 1947 p138, 1968 p80. leg E Marcus (97). SMNH 109589.
	SMNH 109590*	Serial sections of entire worm. Slide with fungus or something on the cover glass.	Holotype	*Acerotisa bituna*. SMNH 109590. leg E Marcus (98).
Acerotisa leuca Marcus, 1947	SMNH 109593	2 worms in whole mount. Material from type locality. The description is based on one animal. So one these two are possible from other collection.	Syntypes	*Acerotisa leuca*. Marcus 1947. Sao Paulo; Ilha das Palmas, Ilhabela. Cf Marcus 1947 p 139. leg E Marcus (1). SMNH 109593. Dept. Zoologia S. Paulo. *Acerotisa leuca*. Ilhabela. 1
Cycloporus gabriellae Marcus, 1950	**SMNH 109846***	Serial sections of entire worm. Sections continue in following 2 slides.	Lectotype	*Cycloporus gabriellae*. Leg E Marcus (O). SMNH 109846.
	SMNH 109847*	Serial sections of 109846. Continuation of previous sections and it goes on to the following.	Lectotype	*Cycloporus gabriellae*. Leg E Marcus (P). SMNH 109847.
	SMNH 109848*	Serial sections of 109846. Reproductive structures on row 2, 3 and 4 (marked with blue dot).	Lectotype	*Cycloporus gabriellae*. Leg. E Marcus (Q). SMNH 109848.
	SMNH 109842	Whole mount of entire worm. The locality stated in the label is the type locality.	Paralectotype	*Cycloporus gabriellae*. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p89, 1952 p96. leg E Marcus. (K). SMNH 109842.
	SMNH 109843	Whole mount of entire worm. Fungus on cover slide or mounting medium.	Paralectotype	*Cycloporus gabriellae*. SMNH 109843. leg E Marcus (L). Dept. Zoologia S. Paulo. *Cycloporus gabriellae*.
	SMNH 109844	5 worms in whole mount. 2 are *Cycloporus*. 3 worms are juveniles and it	Paralectotypes	*Cycloporus gabriellae*. 4 specimens + 1 juv *Latocestus*. SMNH 109844. leg E Marcus (M).

		is not possible to identify with security. No locality.		
	SMNH 109845	Serial sections of entire juvenile or "larvae". Correspond to the serial sections of larvae (figure 168 of Marcus 1950). Very small animal. It is possible to see a sucker. Most likely a juvenile. Not possible to find the mouth as depicted by Marcus.	Paralectotype	*Cycloporus gabriellae*. Leg E Marcus (N). SMNH 109845.
Eurylepta neptis DuBois Reymond Marcus, 1955	**SMNH 109875***	Serial sections of posterior part. No reproductive structures detectable.	Lectotype	*Eurylepta neptis*. du Bois-Reymond Marcus 1955. Sao Paulo; Ilha de Sao Sebastiao. SMNH 109875. cf du Bois-Reymond Marcus 1955 p42. leg Ev Marcus (A).
	SMNH 109876*	Serial sections of SMNH 109875. Reproductive structure on rows 2, 3, 4 and 5 (marked with blue dot). Sections fit the drawings of du Bois-Reymond 1955 (figure 17 and 16).	Lectotype	*Eurylepta neptis*. leg Ev Marcus (B). SMNH 109876.
	SMNH 109877*	Serial sections of SMNH 109875. Many sections very destroyed. Reproductive structures on row 1 (marked with blue dot). Sucker also visible.	Lectotype	SMNH 109877. *Eurylepta neptis*. Leg Ev Marcus (C).
Eurylepta piscatoria (Marcus, 1947)	**SMNH 109601***	Serial sections of entire worm. Slide with fungus or something on the cover glass. From Ilha de Palmas, thus probably the type. Sections continue in the next 2	Holotype	*Acerotisa piscatoria*. Marcus 1947. Sao Paulo; Ilha das Palmas. Cf Marcus 1947 p136, 1968 p82. leg E Marcus (94).SMNH 109601.*Acerotisa piscatoria*. 94.

		slides.		
	SMNH 109602*	Serial sections of SMNH 109601. Slide with fungus or something on the cover glass. Reproductive structure in rows 4 and 5 (marked with blue dot). The reproductive cuts are not very clear.	Holotype	*Acerotisa piscatoria*. SMNH 109602. leg E Marcus (95). *Acerotisa piscatoria*. 95.
	SMNH 109603*	serial sections of SMNH 109601 slide with fungus or something on the cover glass.	Holotype	*Acerotisa piscatoria*. SMNH 109603. leg E Marcus (96).
Eurylepta turma Marcus, 1952	**SMNH 109882***	Serial sections of anterior part of worm. Slide label matches the first mentioned type locality. Anterior part of the worm goes until the ventral sucker. Reproductive structures are on rows 7, 8 and 9 (marked with black dots (original) and blue dots).	Lectotype	*Eurylepta turma*. Marcus 1952. Sao Paulo; Ubatuba. Cf Marcus 1952 p94. leg E Marcus. *Eurylepta turma*. Ubatuba. SMNH 109882
	SMNH 109878	Whole mount of entire worm. Material from Ilha de Sao Sebastiao, Ilhabela. Worms missing some pieces of the posterior part, but reproductive structures are intact. As the first locality cited in the description is Ubatuba, from there should be the lectotype, and then this worm is to be considered paralectotype. There is no SMNH 109879 in the same tray or in sequence of *Eurylepta turma*.	Paralectotype	*Eurylepta turma*. Marcus 1952. Sao Paulo; Ilha de Sao Sebastiao; Ilhabela. Cf Marcus 1952 p94. leg E Marcus (A). SMNH 109878. *Eurylepta turma*. Ilhabela.

	SMNH 109880	Serial sections of anterior/middle part of the worm. Most of the worm body is on the slide, just anterior and posterior tip seems to be missing. Sections contnue in the following slide.	Paralectotype	*Eurylepta turma*. SMNH 109880. leg E Marcus (B). *Eurylepta turma*.
	SMNH 109881	Serial sections of SMNH 109880. Continuation of previous sections. Reproductive structures on rows 5 and 6 (marked with blue dots and black lines).	Paralectotype	SMNH 109881. *Eurylepta turma*. *Eurylepta turma*. Leg E Marcus (C). Ilhabela. (written directly on the slide)
Acanthozoon hispidum (Du Bois-Reymond Marcus, 1955)	**SMNH 109991***	Serial sections of middle part. Original description was based in two worms. This is one of them. Drawings fit this slides. Sections continue through the next 2 slides. Label with collection number is missing.	Lectotype	*Pseudoceros (Acanthozoon) hispidus* du Bois-Reymond Marcus 1955. Sao Paulo; Ilha de Sao Sebastiao. Cf du B-R Marcus 1955 p39. leg Ev Marcus (A).
	SMNH 109992*	Serial sections of middle part of SMNH 109991. Reproductive structures in row 5-9 (marked with blue dot).	Lectotype	*Pseudoceros hispidus*. Leg Ev Marcus (B). SMNH 109992. *Pseudoceros (Acanthozoon) hispidus*.
	SMNH 109993*	Serial sections of middle part of SMNH 109991. Continuation of sections.	Lectotype	*Pseudoceros hispidus*. Leg Ev Marcus (C). SMNH 109993.
Phrikoceros mopsus (Marcus,1952)	**SMNH 109994***	Serial sections of anterior part of worm. Sections continue through the next 2 slides. Labelled with the type locality and therfore the lectotype.	Lectotype	*Pseudoceros mopsus*. Marcus 1952. Sao Paulo; Ilha de Sao Sebastiao; Ilhabela. Cf Marcus 1952 p91, 1968 p75. leg E Marcus (A). *Pseudoceros mopsus*. Ilhabela. SMNH 109994.
	SMNH 109995*	Serial sections of SMNH 109994. Continuation of sections. Reproductive	Lectotype	*Pseudoceros mopsus.* SMNH 109995. leg E Marcus (B). *Pseudoceros mopsus*. Ilhabela.

		structures on row 6 (marked with blue dot).		
	SMNH 109996*	Serial section of SMNH 109994. Reproductive structures on rows 1 and 2 (marked with blue dot).	Lectotype	*Pseudoceros mopsus*. SMNH 109996. leg E Marcus (C). *Pseudoceros mopsus*. Ilhabela.
Pseudoceros chloreus Marcus, 1949	**SMNH 109975***	Whole mount of entire worm. Animal fits the original description, except for the destroyed pseudotentacular area. Which Marcus did not mentioned.	Holotype	*Pseudoceros chloreus*.Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1949 p86. leg E Marcus. SMNH 109975. Dept. Zoologia S. Paulo. *Pseudoceros chloreus*.
Pseudobiceros evelinae (Marcus, 1950)	**SMNH 109981***	Serial sections of middle part of worm. Slide label has type locality and the sections fit the orginal description, which was based on one worm. Serial sections continue on the next 8 slides.	Holotype	*Pseudoceros evelinae* Marcus 1950. Sao Paulo; Forte Itaipu. Cf Marcus 1950 p81. leg E Marcus (1). SMNH 109981.
	SMNH 109982*	Serial sections of SMNH 109981.	Holotype	*Pseudoceros evelinae* SMNH 109982. leg E Marcus (2).
	SMNH 109983*	Serial sections of SMNH 109981.	Holotype	*Pseudoceros evelinae*. leg E Marcus (3). SMNH 109983.
	SMNH 109984*	Serial sections of SMNH 109981 Reproductive structures on rows 1-3 (marked with blue dot)	Holotype	*Pseudoceros evelinae*. leg E Marcus (4). SMNH 109984.
	SMNH 109985*	Serial sections of SMNH 109981. Reproductive structures in all rows.	Holotype	*Pseudoceros evelinae*. leg E Marcus (5). SMNH 109985. Pseudoceros evelinae. 5. mitte.
	SMNH 109986*	Serial sections of SMNH 109981 reproductive structures in all rows. Therefore blue dot on the slide	Holotype	*Pseudoceros evelinae*. leg E Marcus (6). SMNH 109986.

	SMNH 109987*	Serial sections of SMNH 109981.	Holotype	*Pseudoceros evelinae*. leg E Marcus (7). SMNH 109987. *Pseudoceros evelinae*. 7.
	SMNH 109988*	Serial sections of SMNH 109981.	Holotype	*Pseudoceros evelinae*. SMNH 109988. leg E Marcus (8).
	SMNH 109989*	Serial sections of SMNH 109981. Continuation of serial sections	Holotype	*Pseudoceros evelinae*. SMNH 109889. leg E Marcus (9).
	SMNH 109990*	Whole mount of anterior part. Whole mount fits the illustration by Marcus of the pseudotentacular area.	Holotype	*Pseudoceros evelinae* Marcus 1950. Sao Paulo; Forte Itaipu. Cf Marcus 1950 p81. leg E Marcus. SMNH 109990. Dep. Zoologia S. Paulo. *Pseudoceros evelinae*.

FIGURES

Figure 1

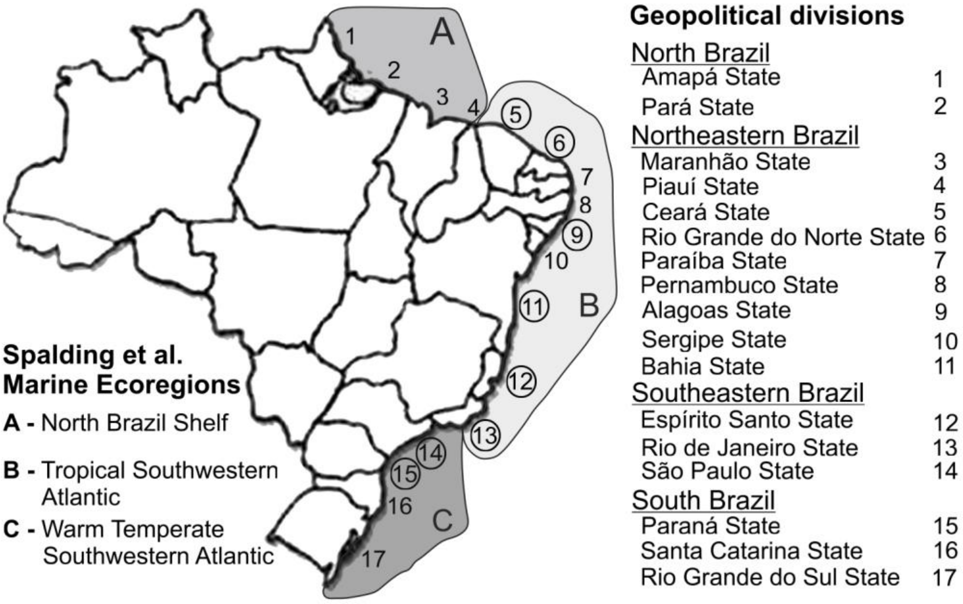


Figure 2

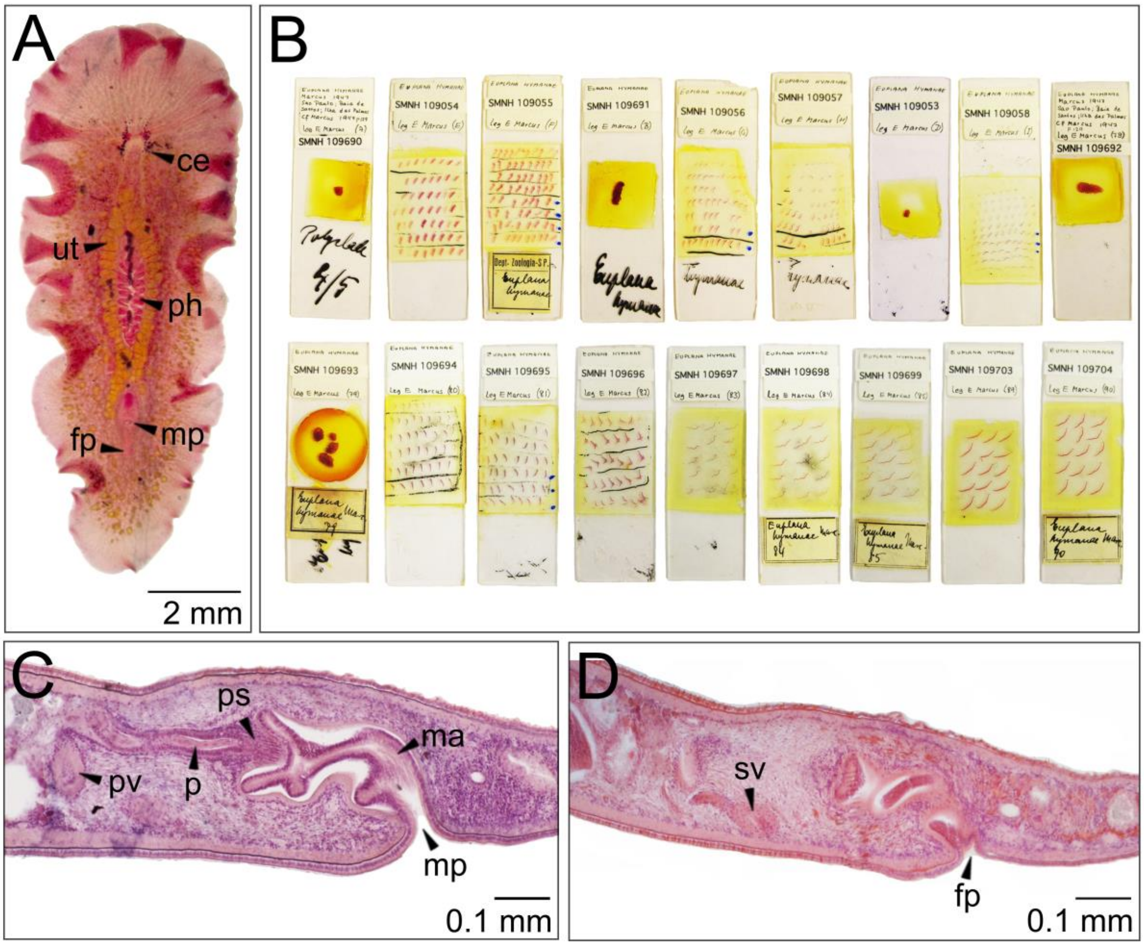
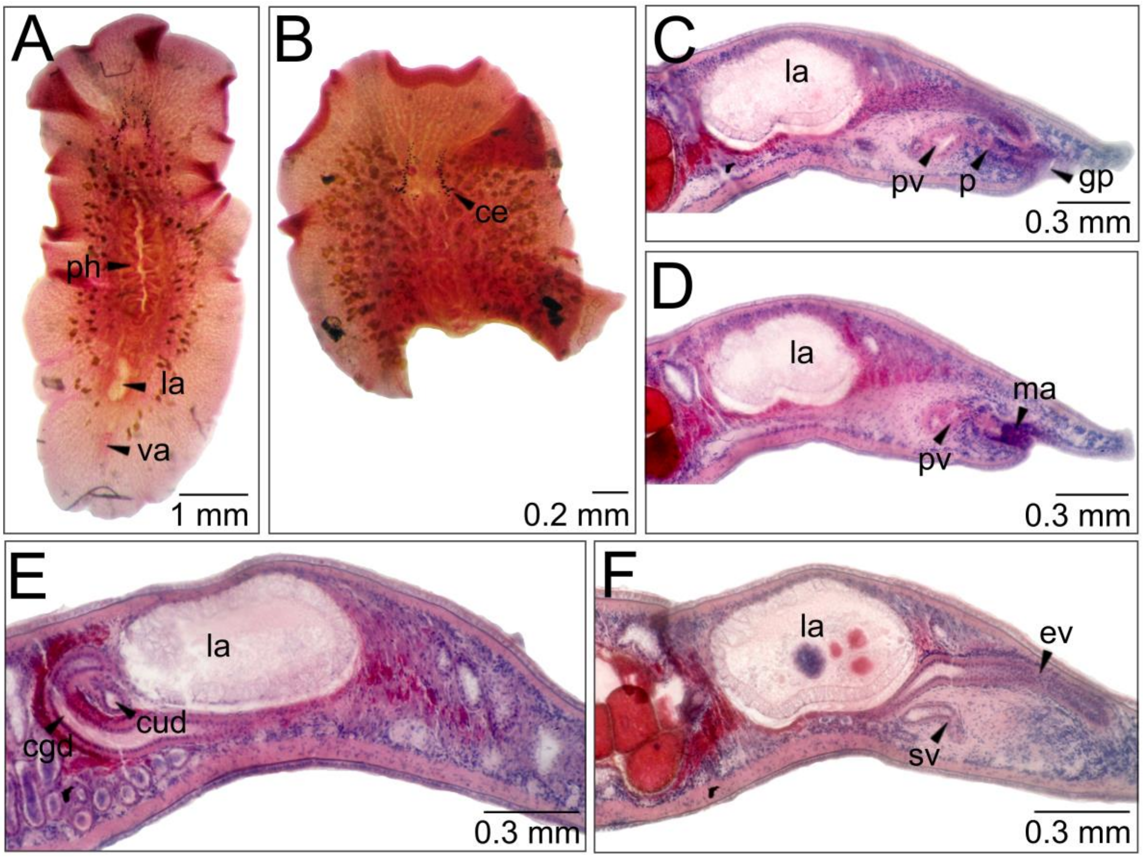


Figure 3


A
ph
la
va
1 mm
B
ce
0.2 mm
C
la
pv
p
gp
0.3 mm
D
la
ma
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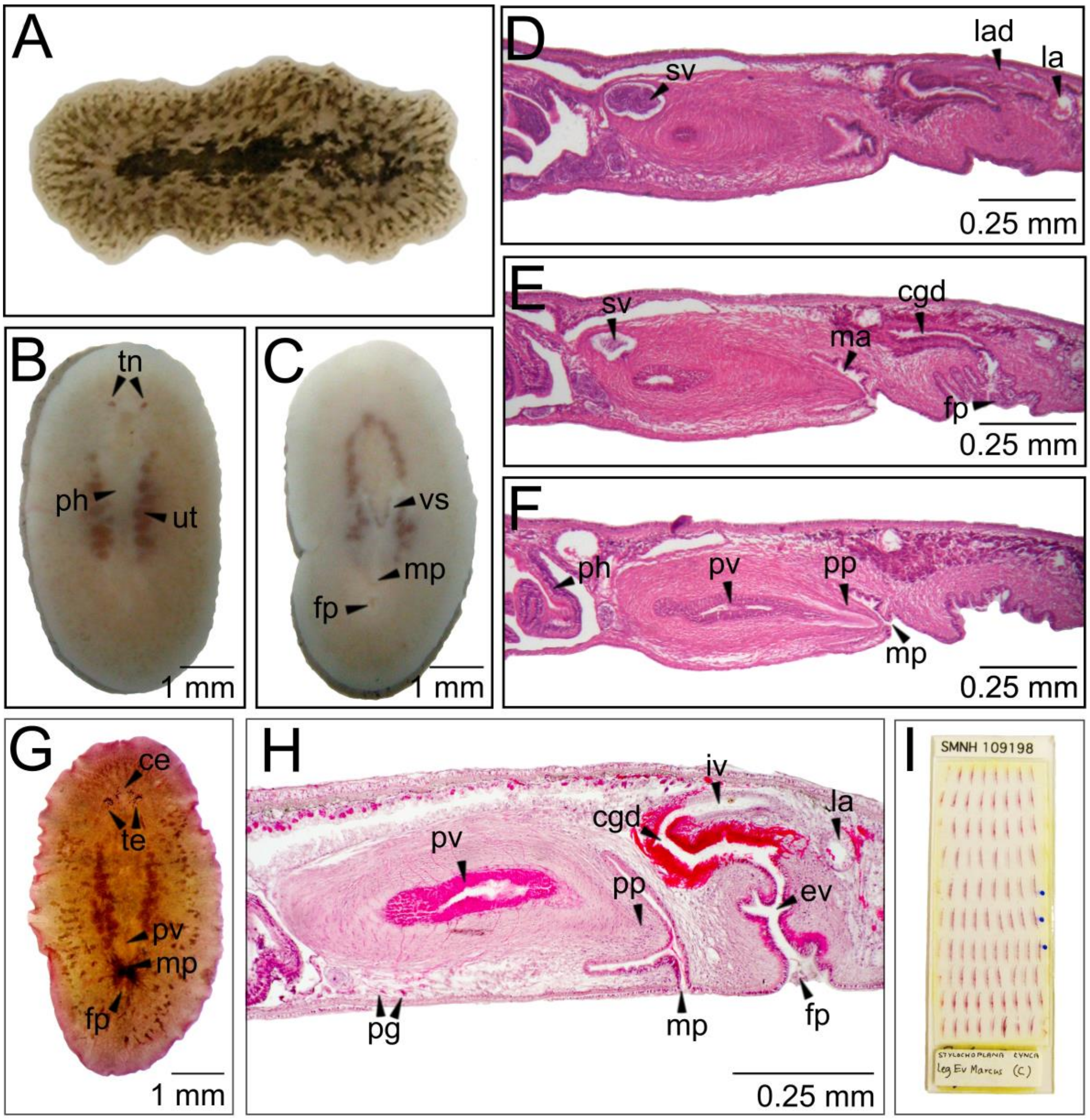
0.3 mm
E
la
cud
cgd
0.3 mm
F
la
ev
sv
0.3 mm

Figure 4


A
D
sv
lad
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E
sv
cgd
ma
fp
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tn
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H
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0.25 mm
I
SMNH 109198
STYLOCHOPLANA EVNCA
leg Ev Marcus (C)

Figure 5

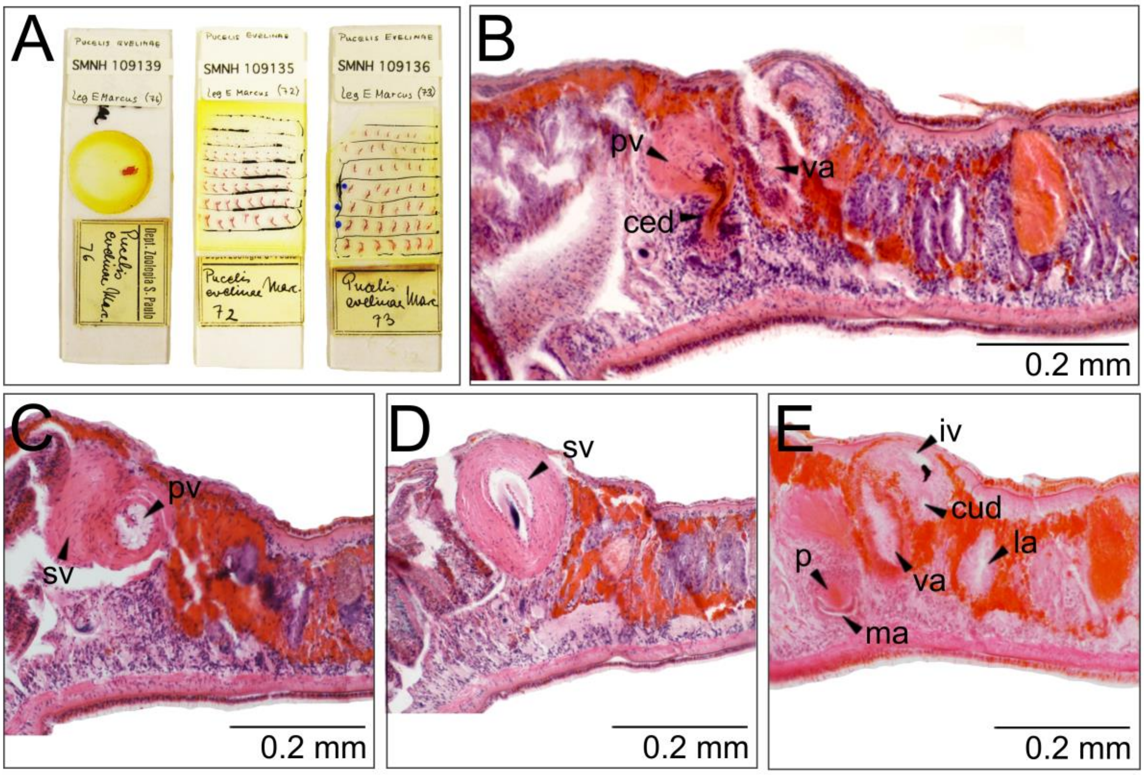


Figure 6

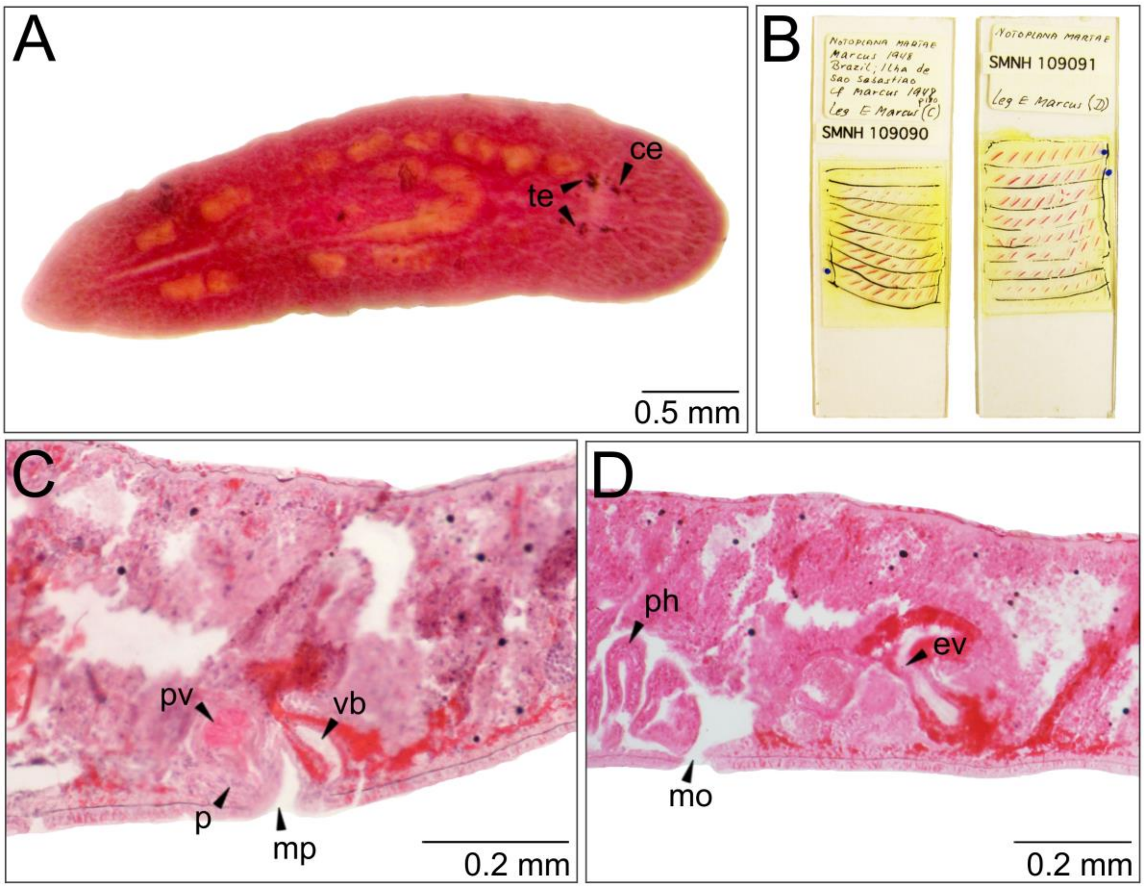


Figure 7

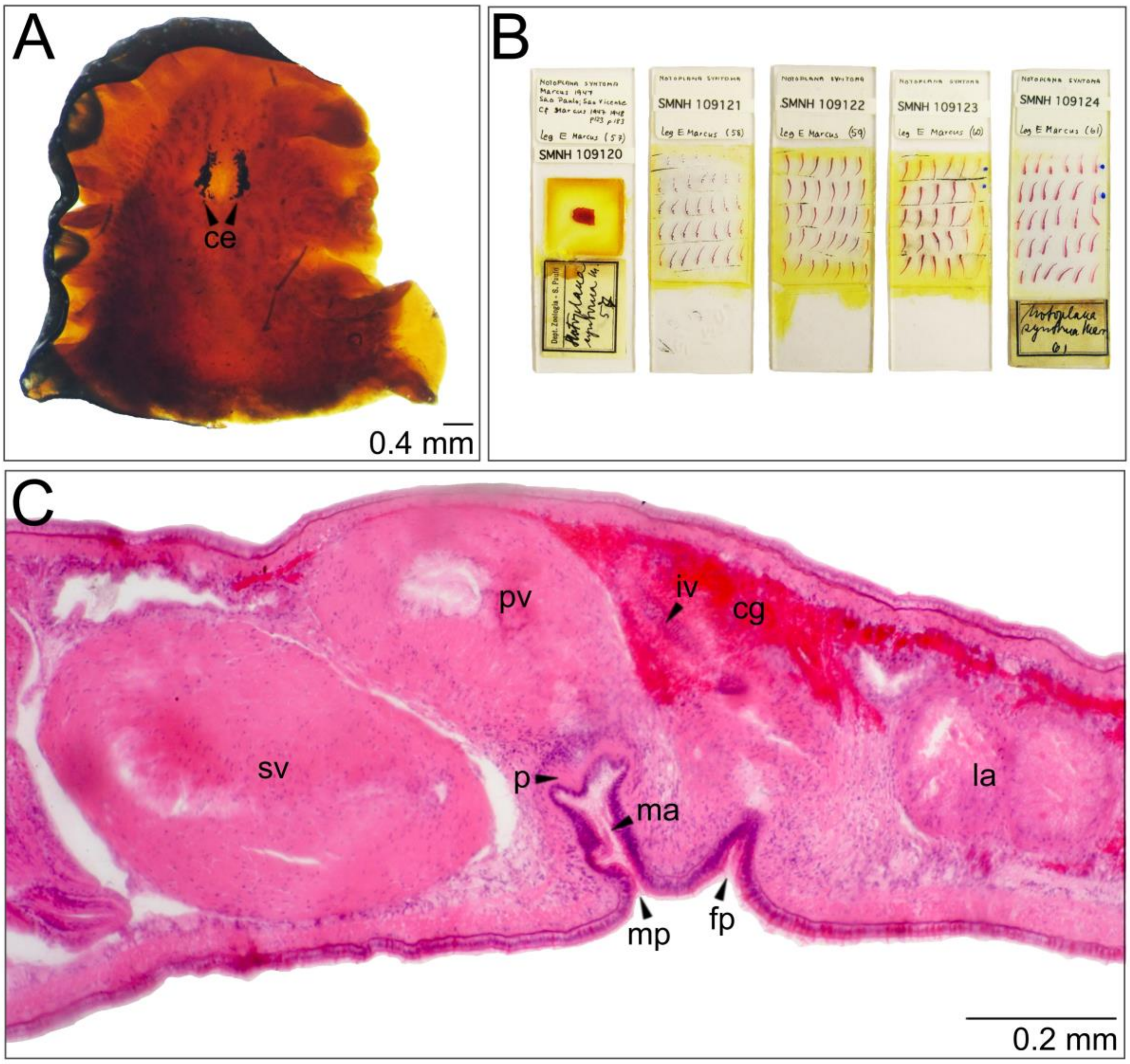

A
ce
0.4 mm
B
NOTOPLANA SYNTOMA
Marcus 1947
São Paulo; São Vicente
Cf Marcus 1947 1948
p123 p183
leg E Marcus (57)
SMNH 109120
Dept. Zoologia - S. Paulo
Notoplana syntoma 4.
57
NOTOPLANA SYNTOMA
SMNH 109121
leg E Marcus (58)
NOTOPLANA SYNTOMA
SMNH 109122
leg E Marcus (59)
NOTOPLANA SYNTOMA
SMNH 109123
leg E Marcus (60)
NOTOPLANA SYNTOMA
SMNH 109124
leg E Marcus (61)
Notoplana syntoma Mer
61
C
pv
iv
cg
sv
p
ma
la
mp
fp
0.2 mm

Figure 8

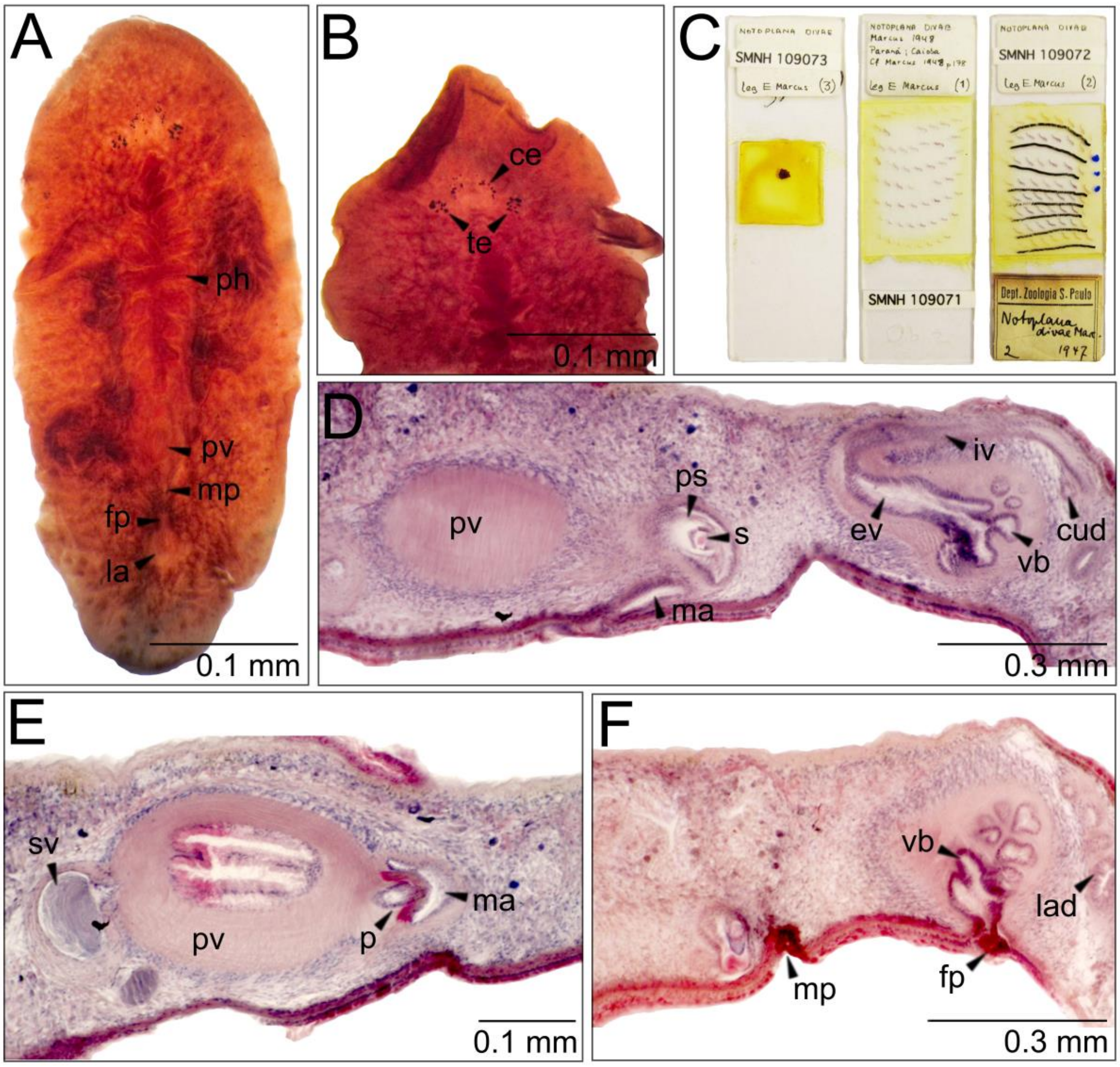


Figure 9

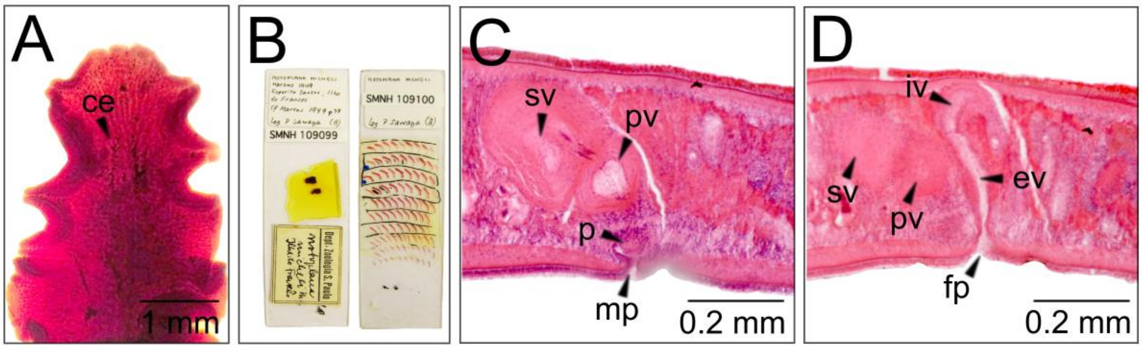


Figure 10

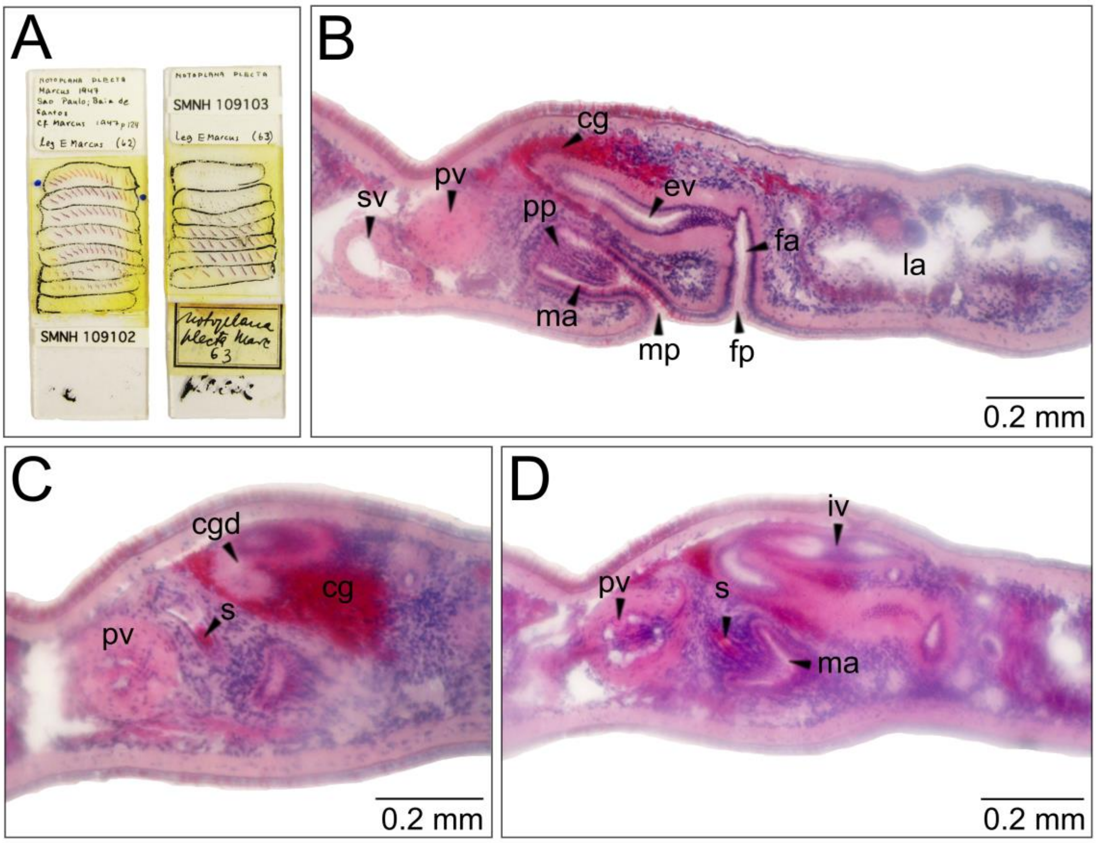


Figure 11

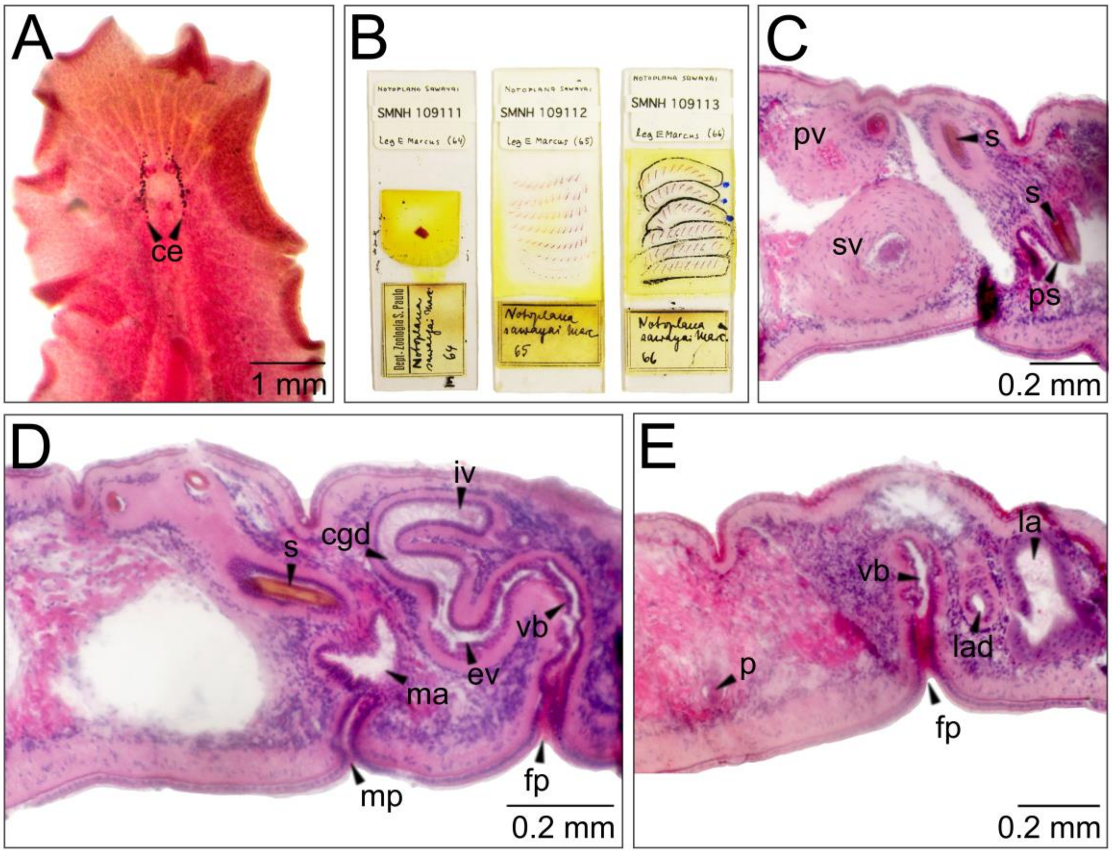


Figure 12

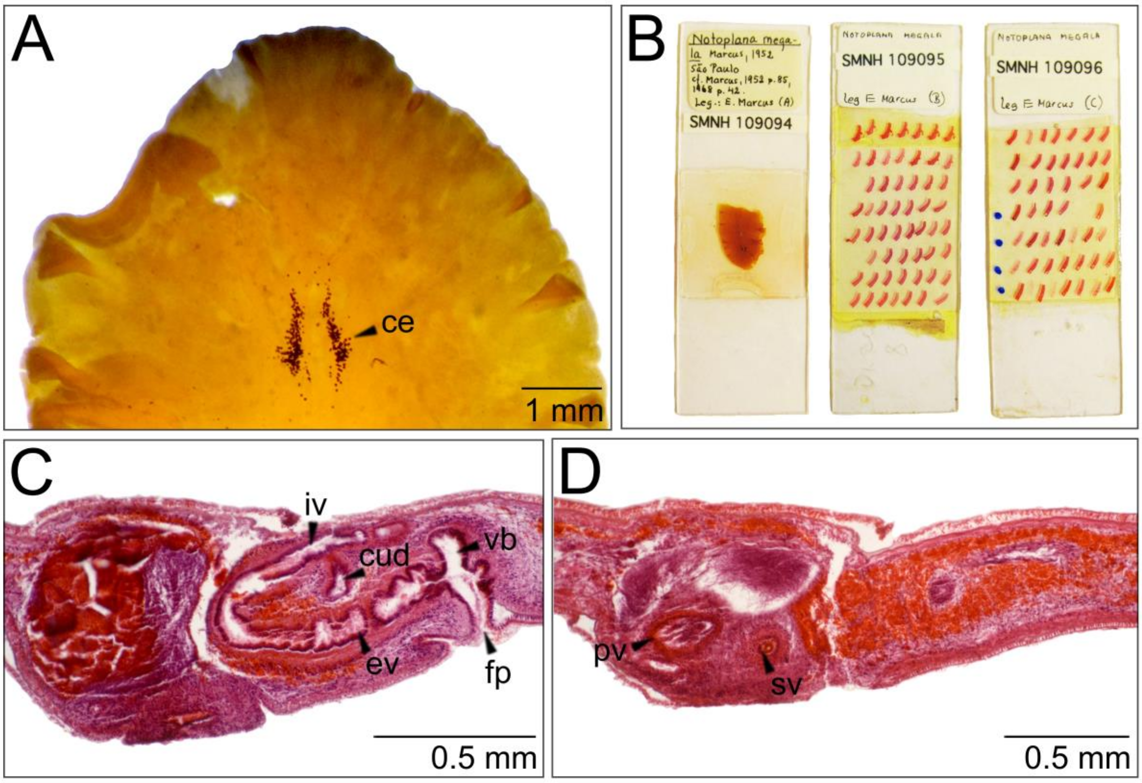

A
ce
1 mm
B
Notoplana megala Marcus, 1952
São Paulo
cf. Marcus, 1952 p. 85, 1968 p. 42.
Leg.: E. Marcus (A)
SMNH 109094
NOTOPLANA MEGALA
SMNH 109095
leg E Marcus (B)
NOTOPLANA MEGALA
SMNH 109096
leg E Marcus (C)
C
iv
cud
vb
ev
fp
0.5 mm
D
pv
sv
0.5 mm

Figure 13

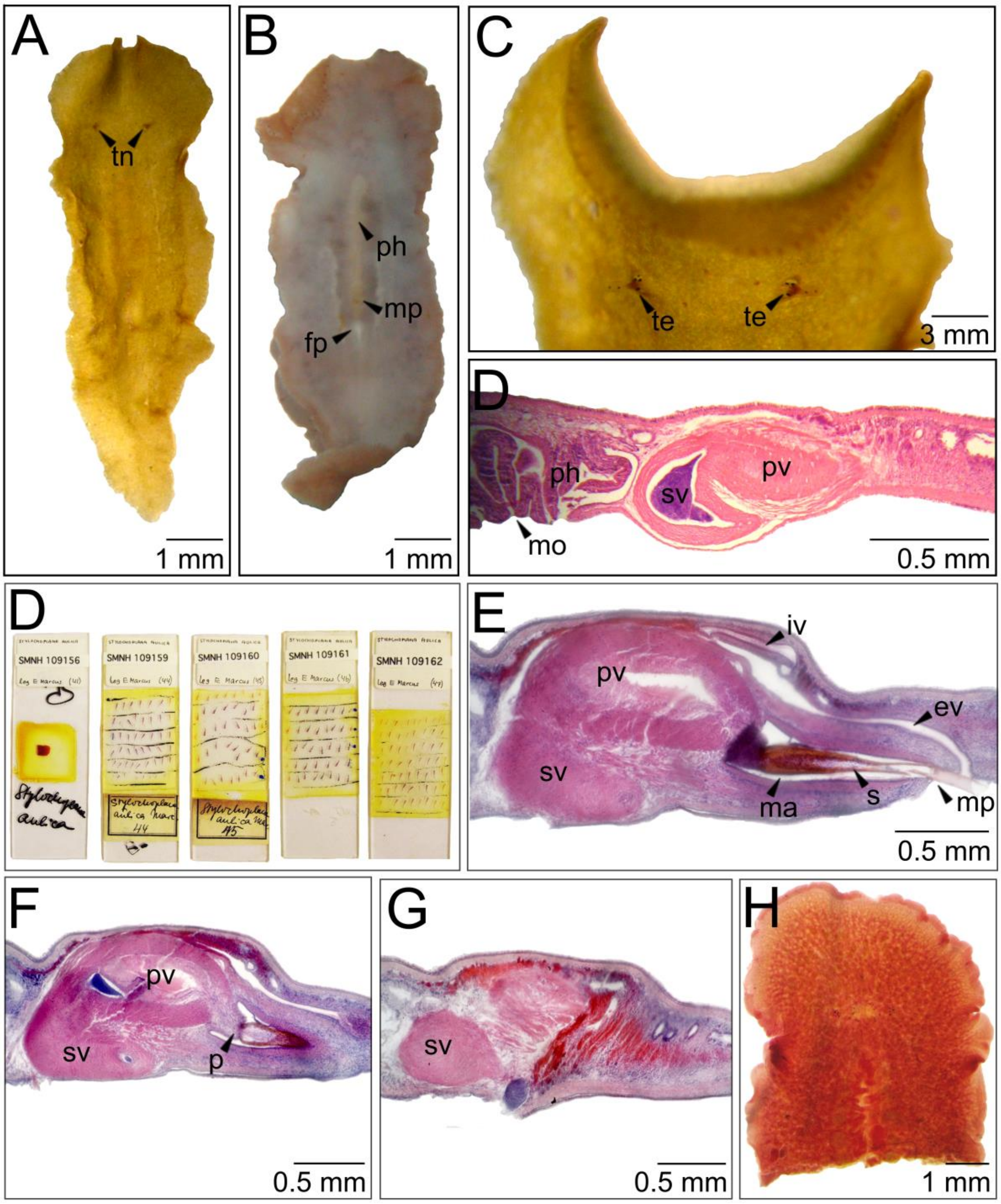

A
tn
1 mm
B
ph
mp
fp
1 mm
C
te
te
3 mm
D
ph
sv
pv
mo
0.5 mm
D
SMNH 109156
SMNH 109159
SMNH 109160
SMNH 109161
SMNH 109162
E
iv
pv
ev
sv
ma
s
mp
0.5 mm
F
pv
sv
p
0.5 mm
G
sv
0.5 mm
H
1 mm

Figure 14

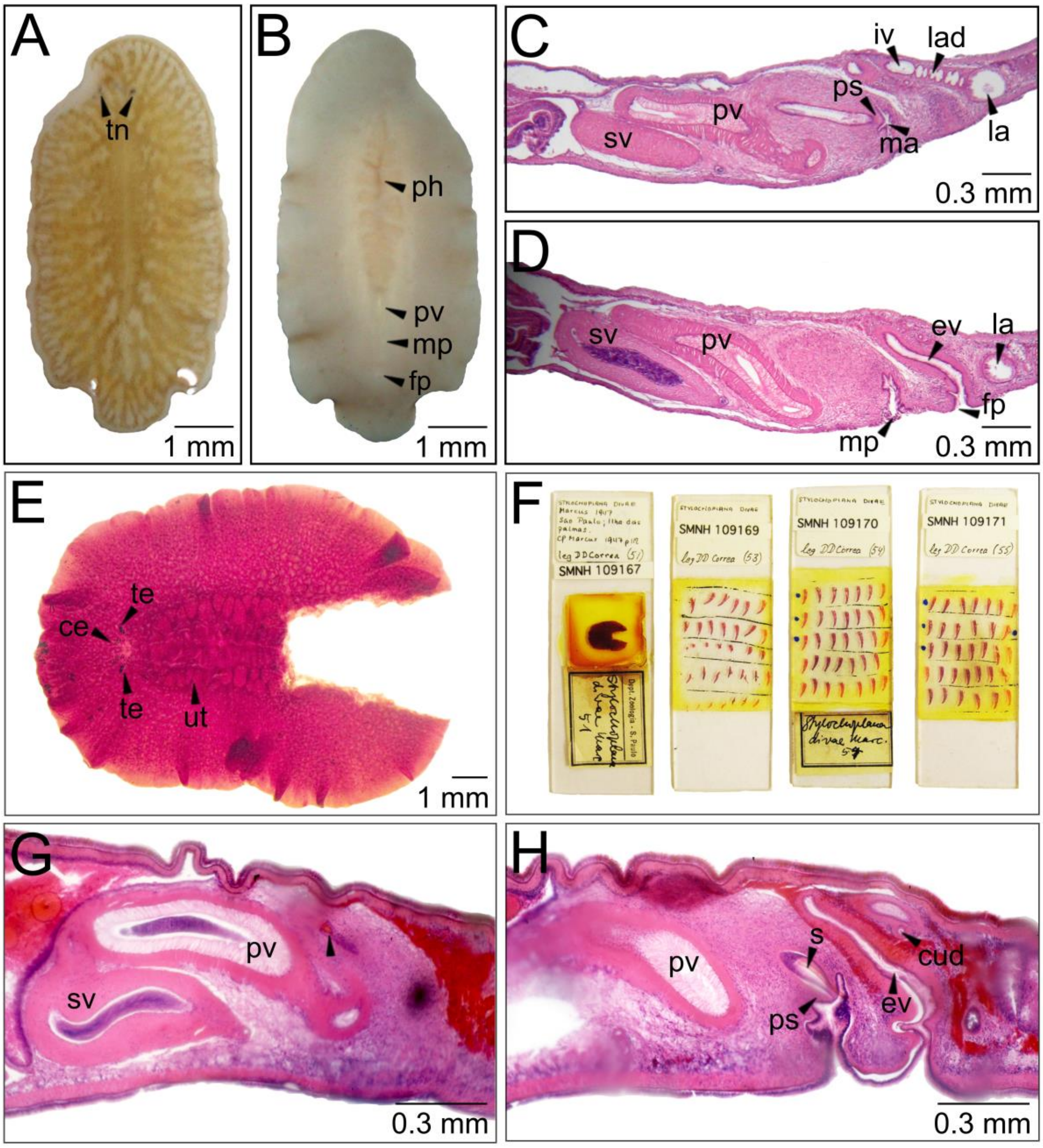

A
tn
1 mm
B
ph
pv
mp
fp
1 mm
C
iv
lad
ps
pv
sv
ma
la
0.3 mm
D
sv
pv
ev
la
fp
mp
0.3 mm
E
te
ce
te
ut
1 mm
F
STYLOCHOPLANA DIVAE
Marcus 1947
Sao Paulo; Ilha das palmas.
CP Marcus 1947 p 12
leg DD Correa (51)
SMNH 109167
Dept. Zoologia - S. Paulo
Stylochoplana divae Marc
51
STYLOCHOPLANA DIVAE
SMNH 109169
leg DD Correa (53)
STYLOCHOPLANA DIVAE
SMNH 109170
leg DD Correa (54)
Stylochoplana divae Marc.
54
STYLOCHOPLANA DIVAE
SMNH 109171
leg DD Correa (55)
G
pv
sv
0.3 mm
H
pv
s
cud
ps
ev
0.3 mm

Figure 15

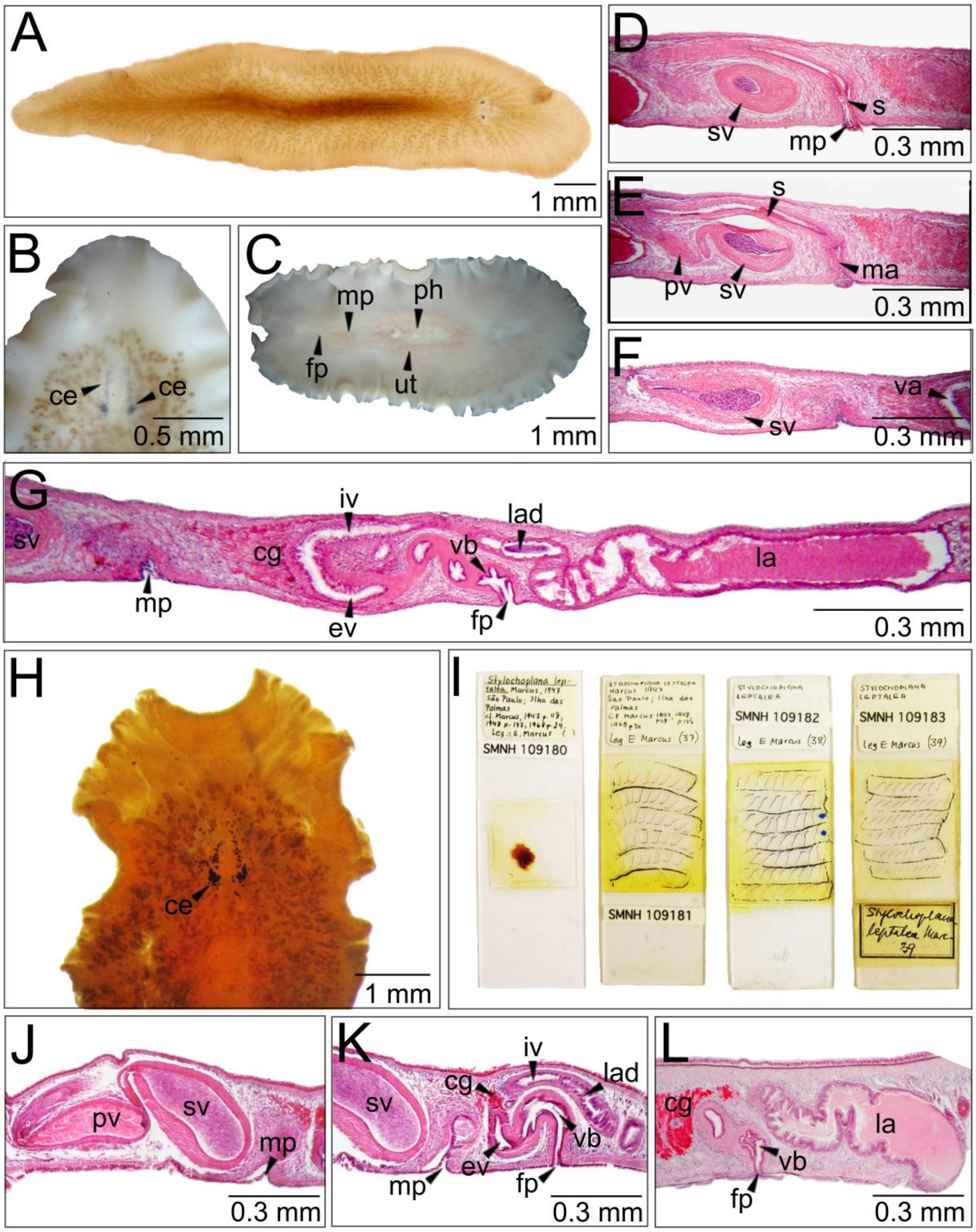

A
1 mm
D
s
sv
mp
0.3 mm
E
s
pv
sv
ma
0.3 mm
B
ce
ce
0.5 mm
C
mp
ph
fp
ut
1 mm
F
va
sv
0.3 mm
G
sv
iv
lad
cg
vb
la
mp
fp
ev
0.3 mm
H
ce
1 mm
I
Stylochoplana leptalea Marcus, 1947
São Paulo; Ilha das Palmas
cf. Marcus, 1947 p. 118, 1948 p. 177, 1968 p. 24.
Leg.: E. Marcus ( )
SMNH 109180
STYLOCHOPLANA LEPTALEA Marcus 1947
Sao Paulo; Ilha das Palmas
Cf Marcus 1947, 1948, 1968 p24
Leg E Marcus (37)
SMNH 109181
STYLOCHOPLANA LEPTALEA
SMNH 109182
Leg E Marcus (38)
STYLOCHOPLANA LEPTALEA
SMNH 109183
Leg E Marcus (39)
Stylochoplana leptalea Mar. 39
J
pv
sv
mp
0.3 mm
K
iv
lad
sv
cg
vb
ev
mp
fp
0.3 mm
L
cg
la
vb
fp
0.3 mm

Figure 16

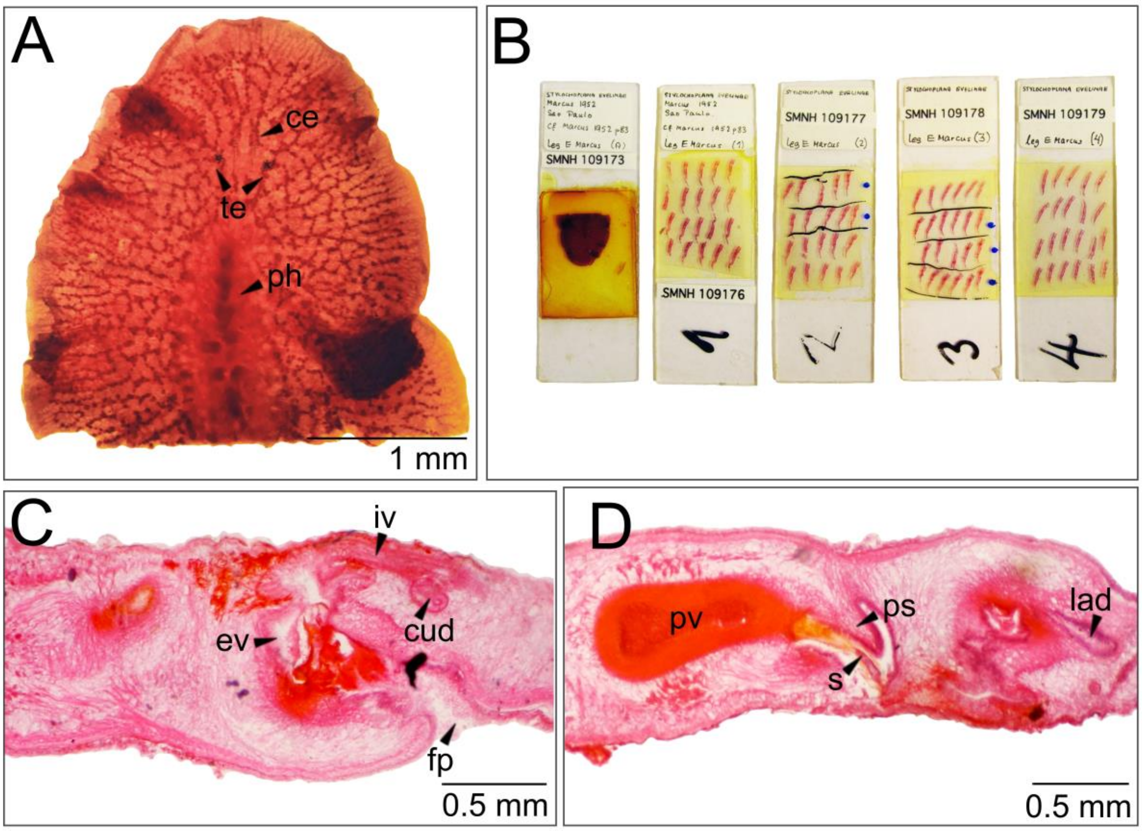


Figure 17

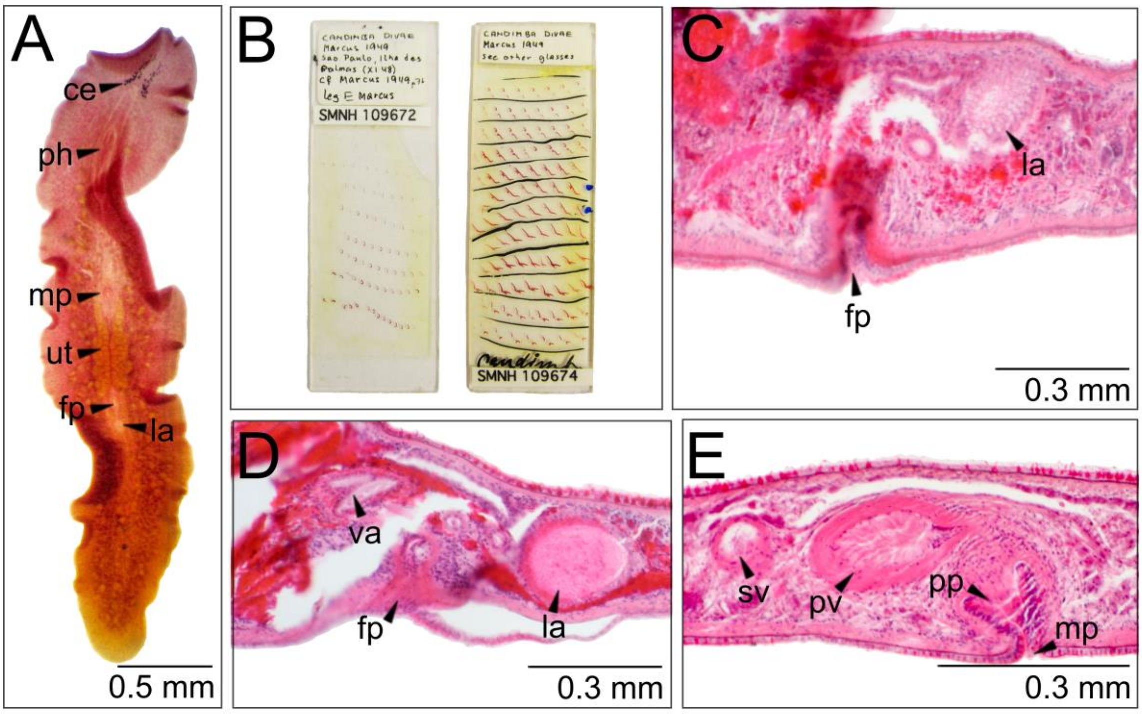


Figure 18

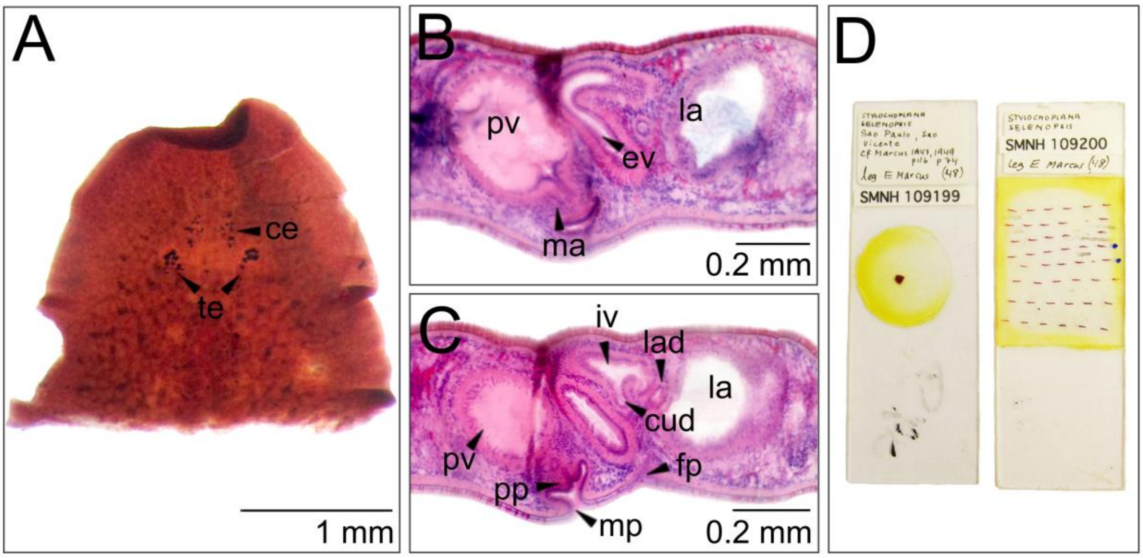


Figure 19

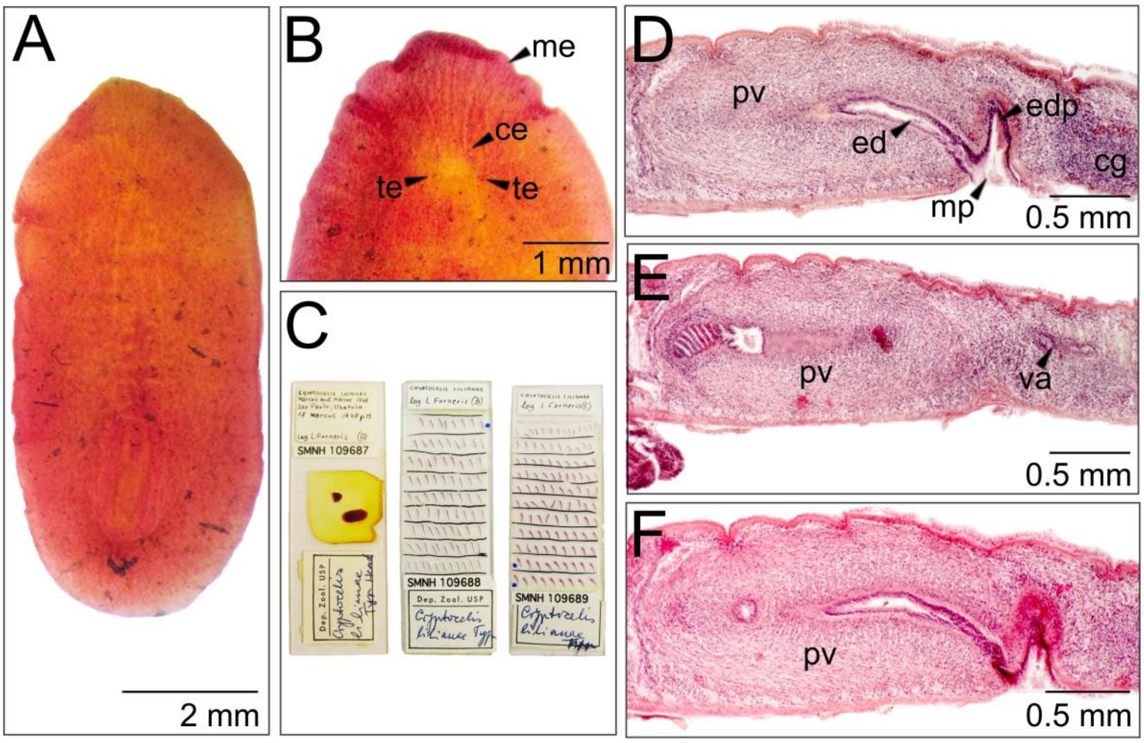


Figure 20

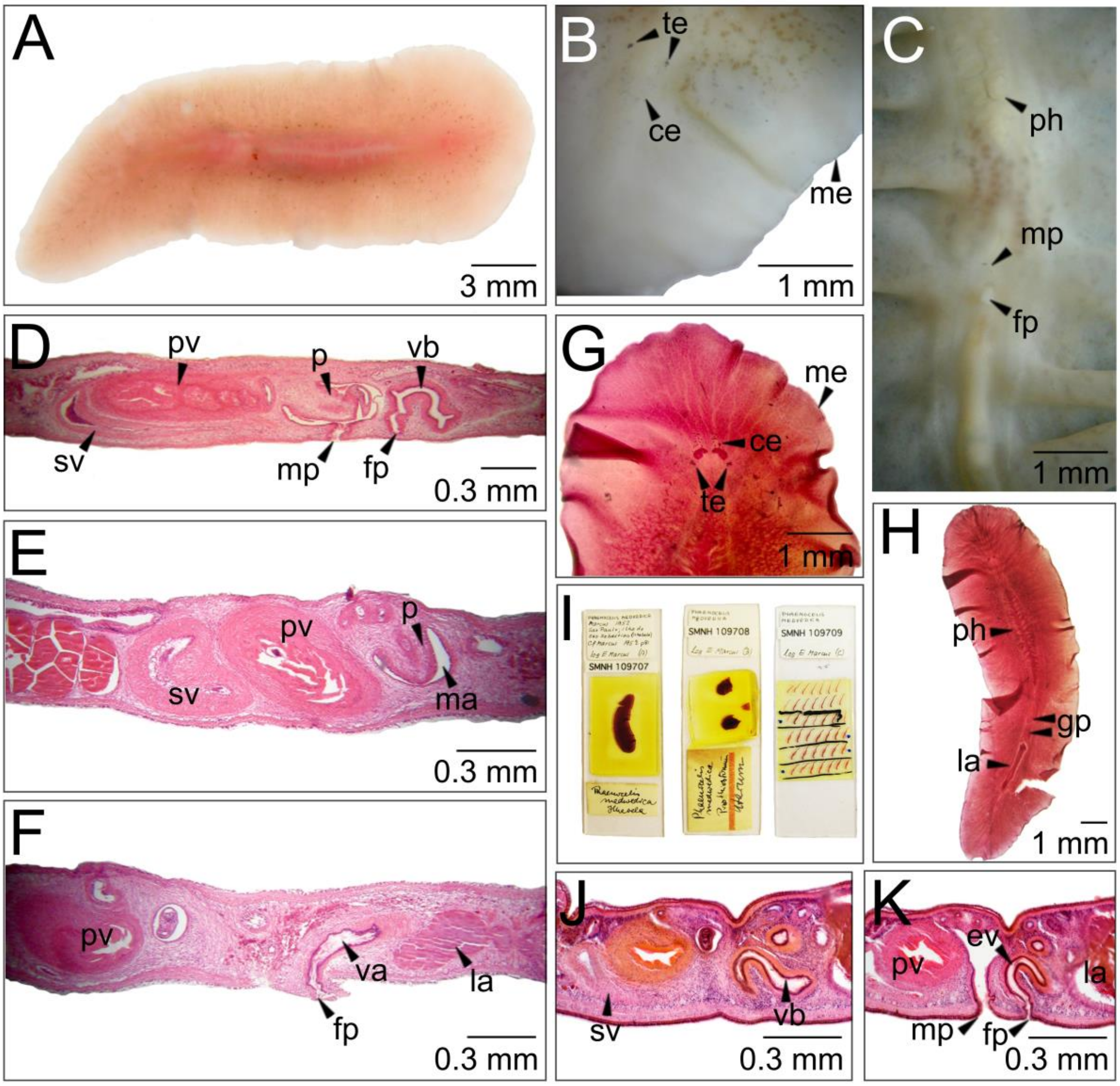


Figure 21

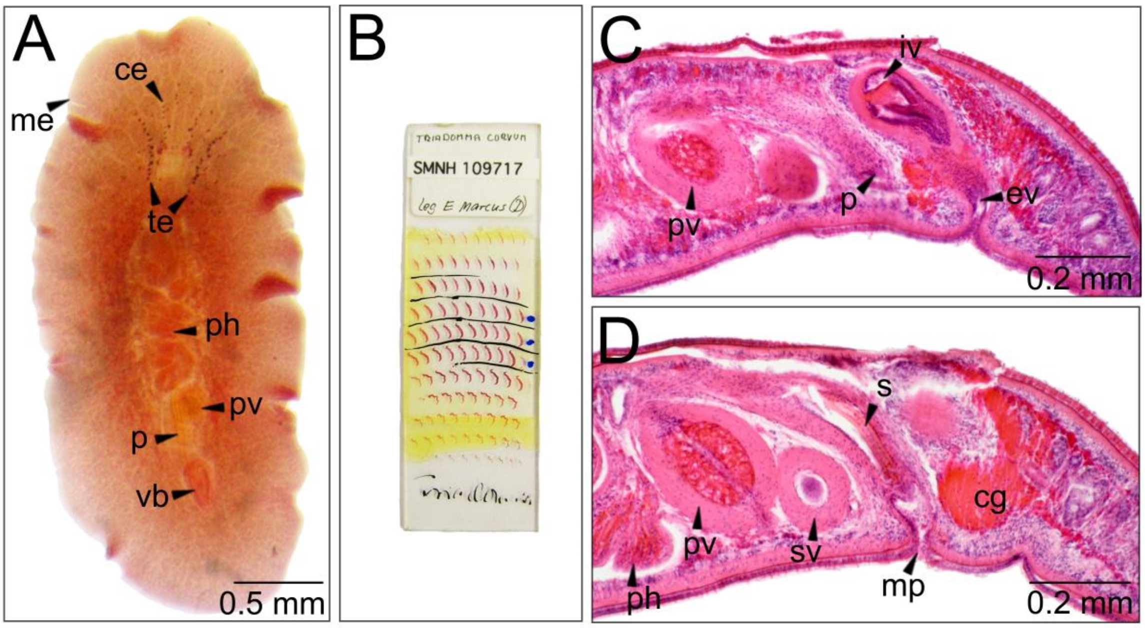


Figure 22

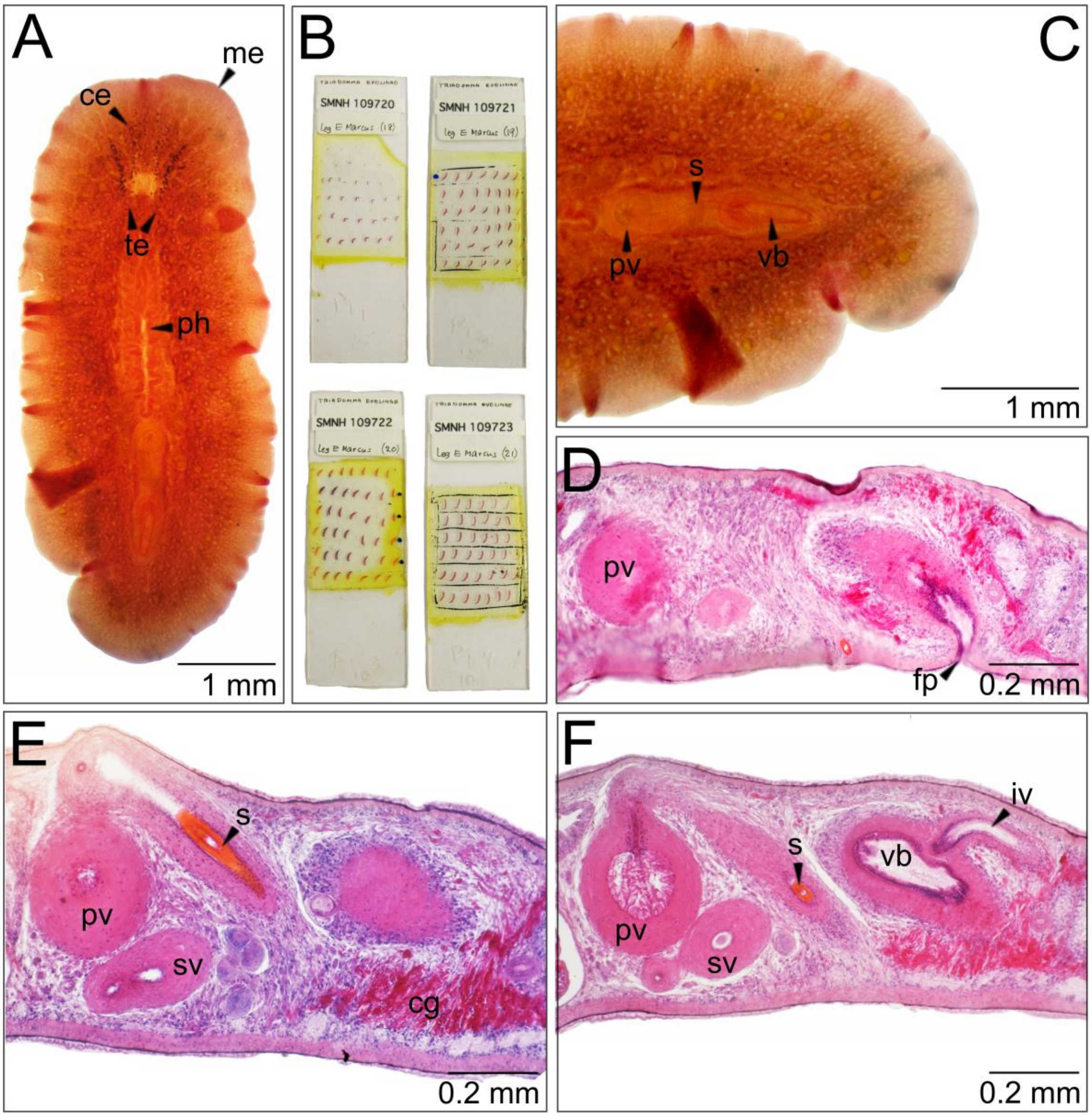

A
me
ce
te
ph
1 mm
B
TRIADOMMA EVELINAE
SMNH 109720
leg E Marcus (18)
TRIADOMMA EVELINAE
SMNH 109721
leg E Marcus (19)
TRIADOMMA EVELINAE
SMNH 109722
leg E Marcus (20)
TRIADOMMA EVELINAE
SMNH 109723
Leg E Marcus (21)
C
s
pv
vb
1 mm
D
pv
fp
0.2 mm
E
s
pv
sv
cg
0.2 mm
F
iv
s
vb
pv
sv
0.2 mm

Figure 23

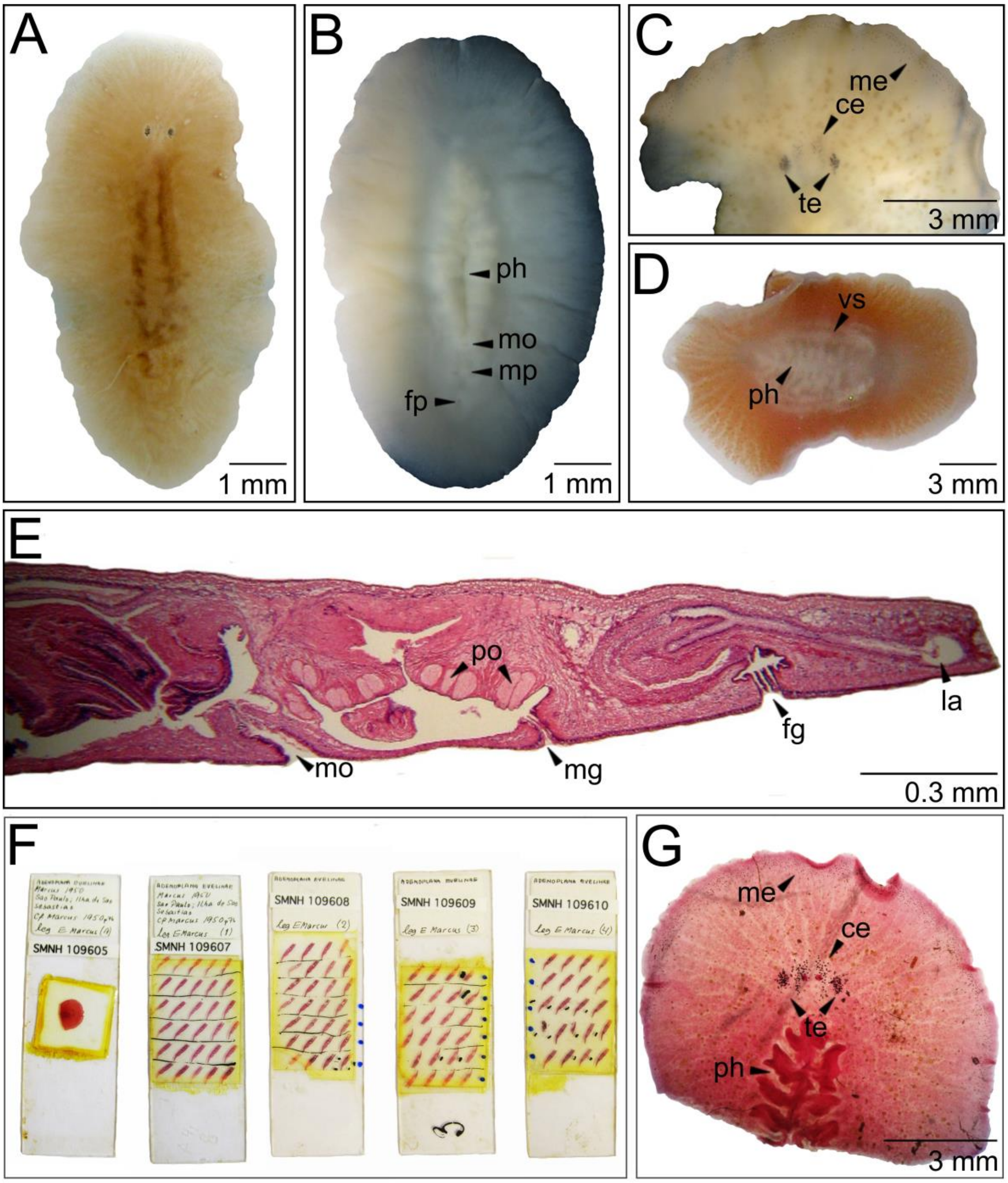

A
1 mm
B
ph
mo
mp
fp
1 mm
C
me
ce
te
3 mm
D
vs
ph
3 mm
E
po
la
fg
mo
mg
0.3 mm
F
ADENOPLANA EVELINAE
Marcus 1950
São Paulo; Ilha de São Sebastião
Cf. Marcus 1950 p.76
leg E. Marcus (1)
SMNH 109605
ADENOPLANA EVELINAE
Marcus 1950
São Paulo; Ilha de São Sebastião
Cf. Marcus 1950 p.76
leg E. Marcus (1)
SMNH 109607
ADENOPLANA EVELINAE
SMNH 109608
leg E. Marcus (2)
ADENOPLANA EVELINAE
SMNH 109609
leg E. Marcus (3)
ADENOPLANA EVELINAE
SMNH 109610
leg E. Marcus (4)
G
me
ce
te
ph
3 mm

Figure 24

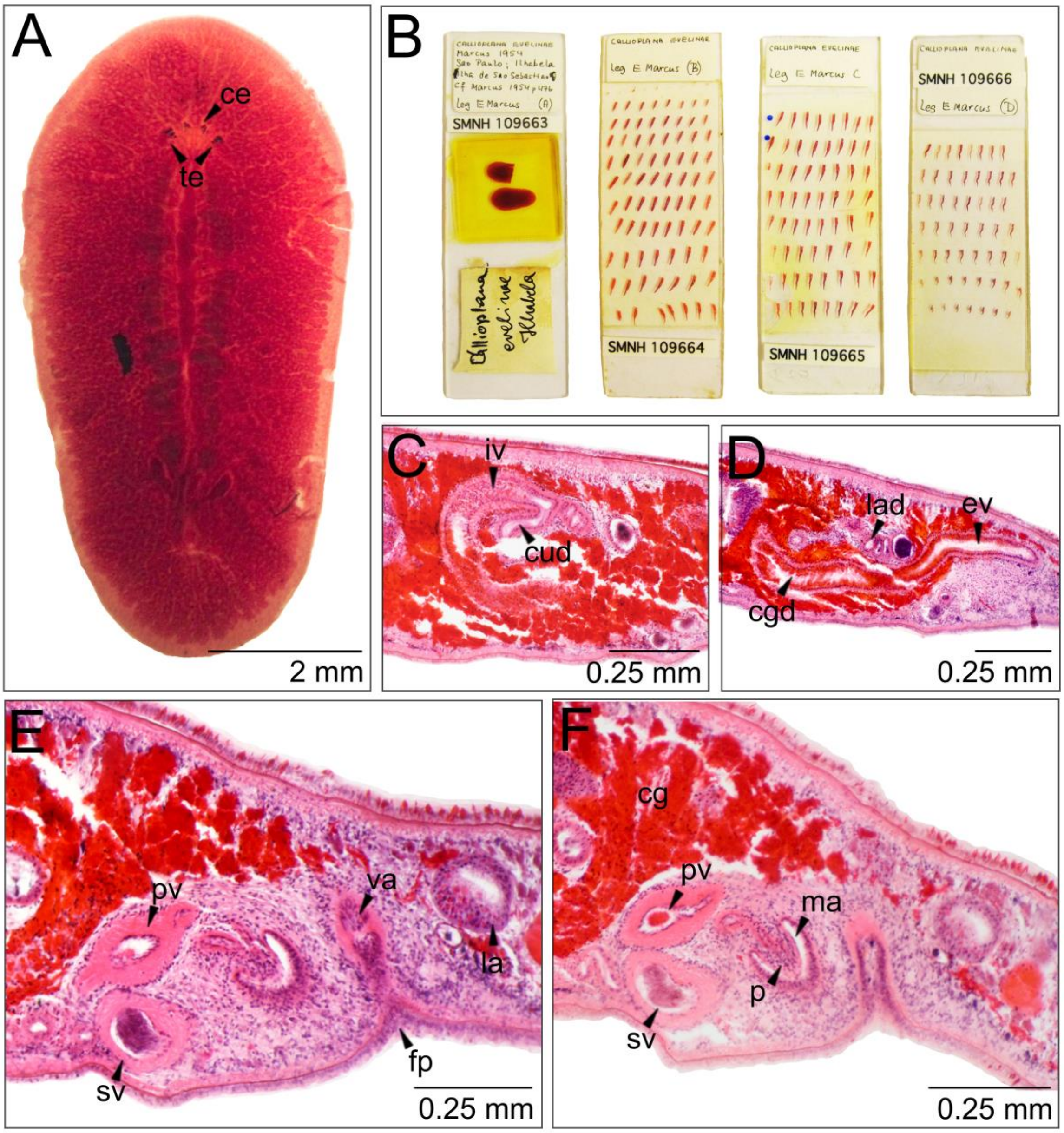

A
ce
te
2 mm
B
CALLIOPLANA EVELINAE
Marcus 1954
Sao Paulo; Ilhebela
Ilha de Sao Sebastiao
cf Marcus 1954 p476
leg E Marcus (A)
SMNH 109663
Callioplana evelinae Ilhabela
CALLIOPLANA EVELINAE
leg E Marcus (B)
SMNH 109664
CALLIOPLANA EVELINAE
leg E Marcus C
SMNH 109665
CALLIOPLANA EVELINAE
SMNH 109666
leg E Marcus (D)
C
iv
cud
0.25 mm
D
lad
ev
cgd
0.25 mm
E
pv
va
la
sv
fp
0.25 mm
F
cg
pv
ma
p
sv
0.25 mm

Figure 25

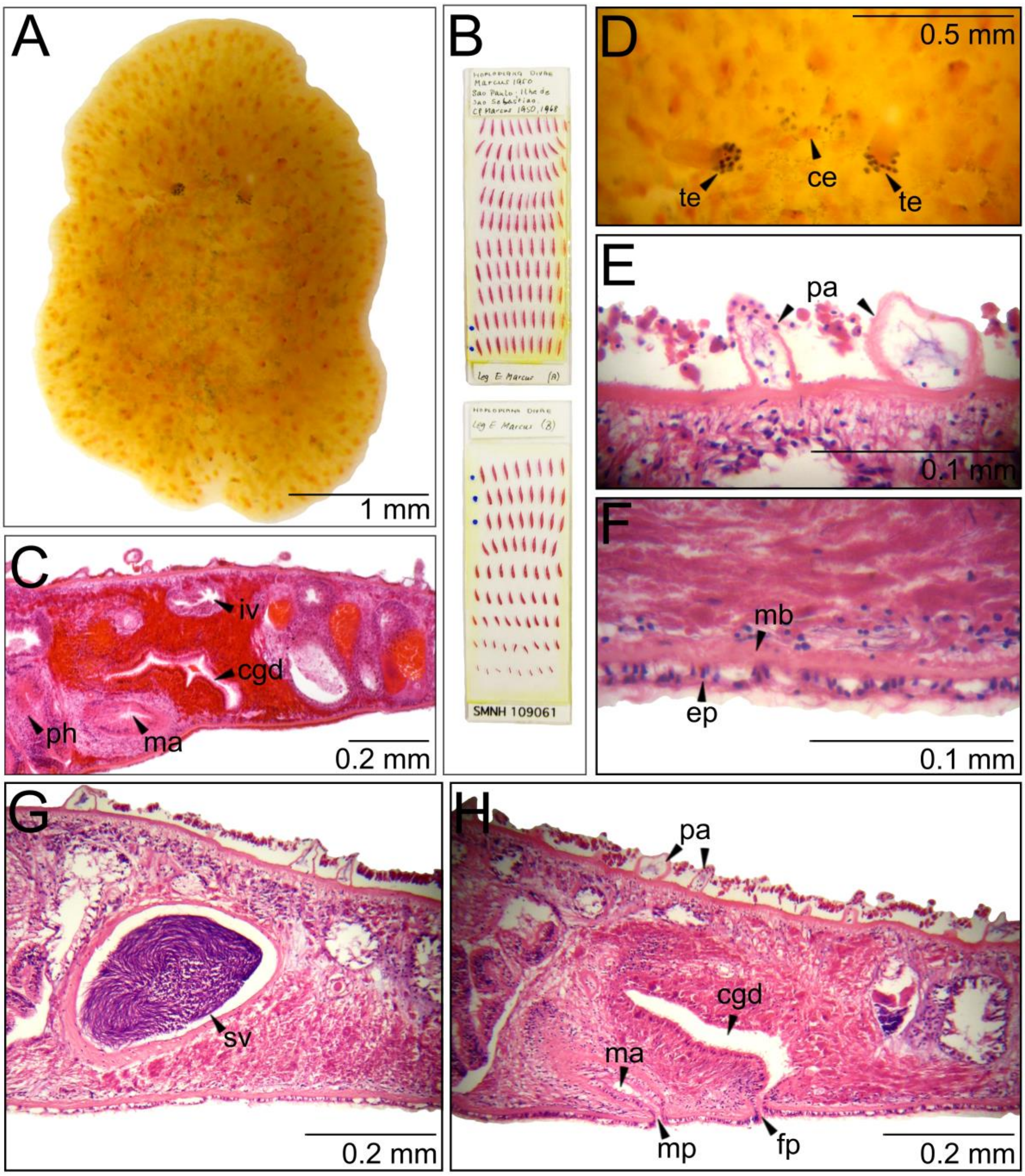

A
1 mm
B
HOPLOPLANA DIVAE
Marcus 1950
Sao Paulo: Ilha de
Sao Sebastiao
Cf Marcus 1950, 1968
Leg E Marcus (A)
HOPLOPLANA DIVAE
Leg E Marcus (B)
SMNH 109061
C
iv
cgd
ph
ma
0.2 mm
D
0.5 mm
te
ce
te
E
pa
0.1 mm
F
mb
ep
0.1 mm
G
sv
0.2 mm
H
pa
cgd
ma
mp
fp
0.2 mm

Figure 26

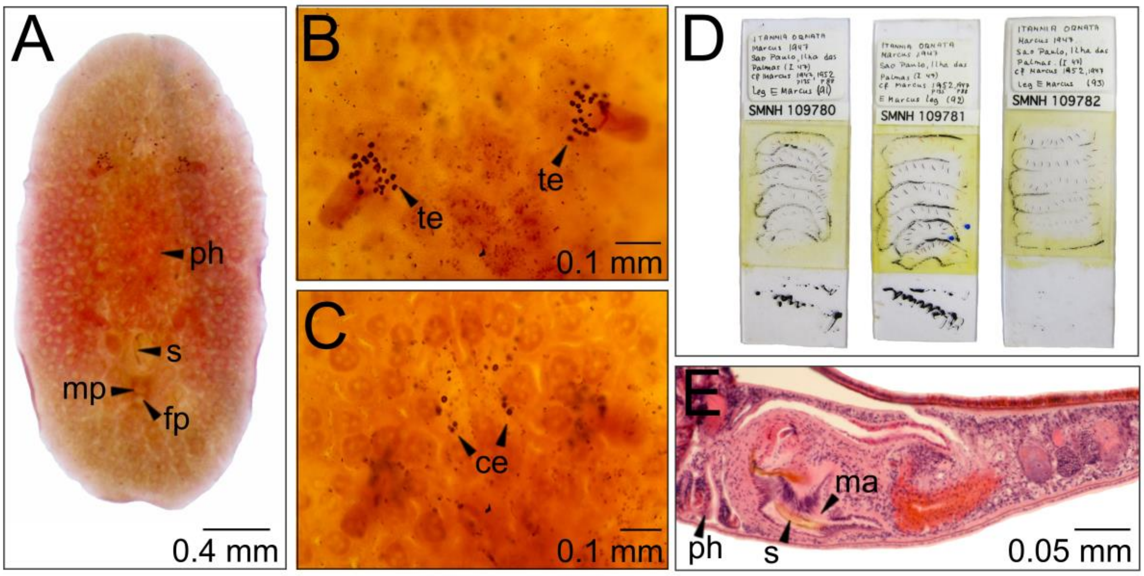


Figure 27

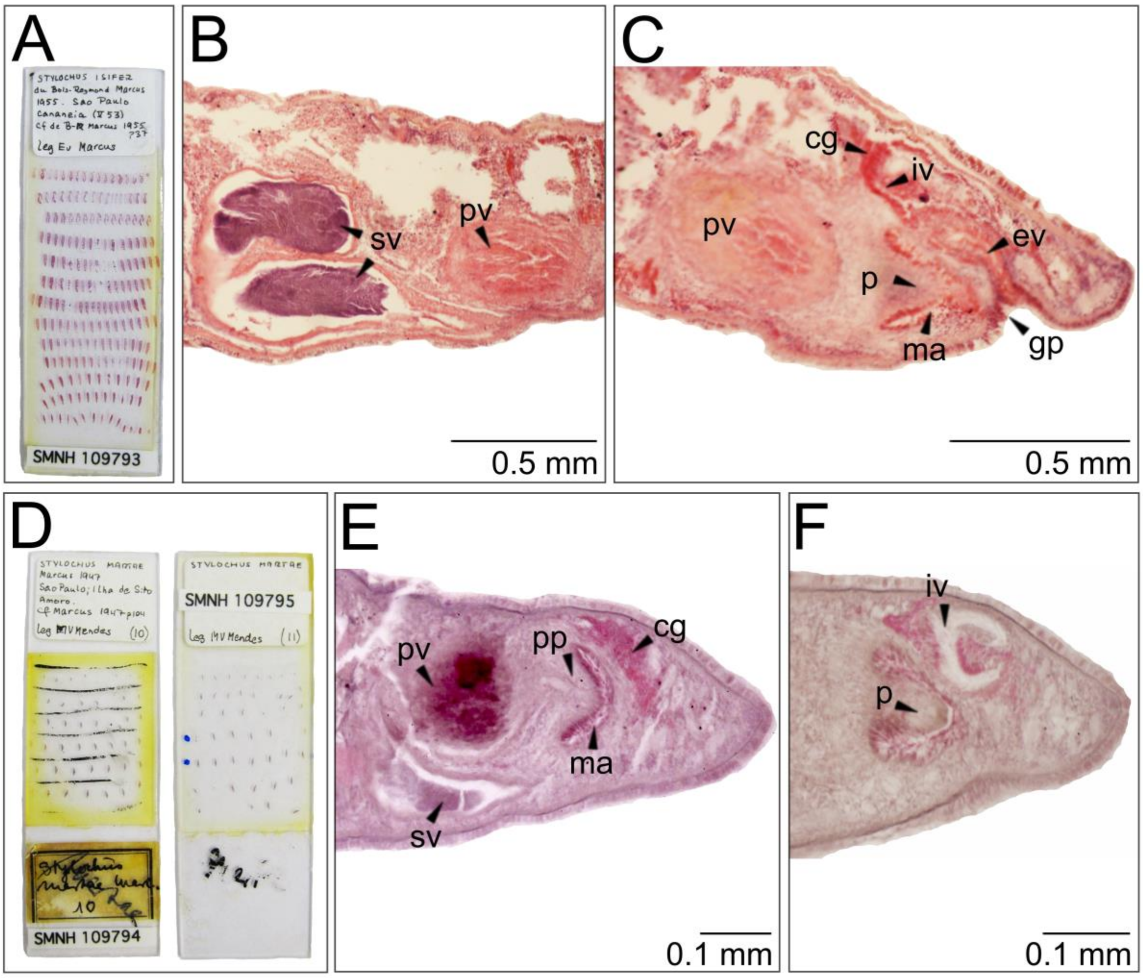


Figure 28

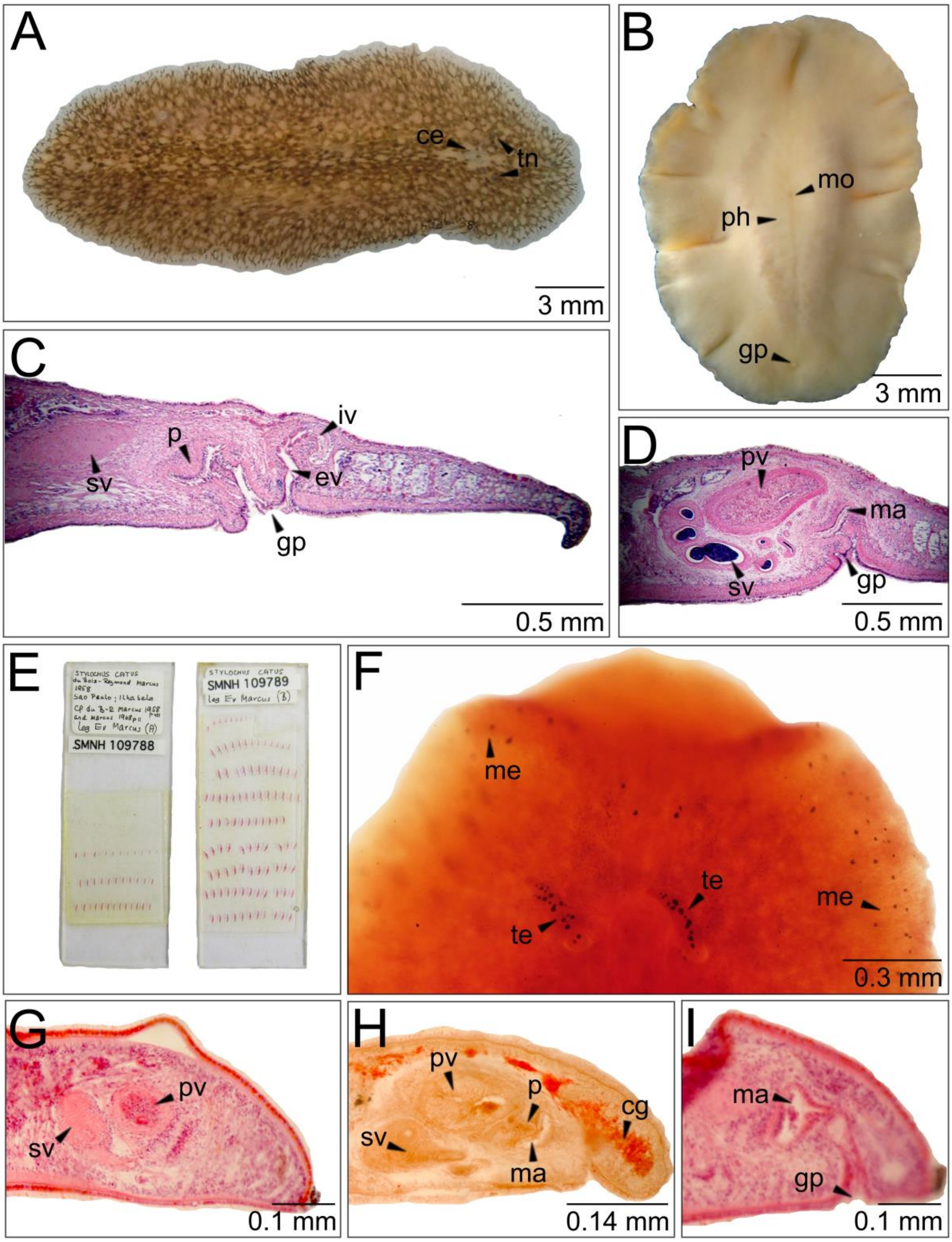

A
ce
tn
3 mm
B
mo
ph
gp
3 mm
C
iv
p
sv
ev
gp
0.5 mm
D
pv
ma
sv
gp
0.5 mm
E
STYLOCHUS CATUS
du Bois-Reymond Marcus
1958
Sao Paulo; Ilhabela
Cf du B-R Marcus 1958 p 401
and Marcus 1968 p 11
leg Ev Marcus (A)
SMNH 109788
STYLOCHUS CATUS
SMNH 109789
leg Ev Marcus (B)
F
me
te
te
me
0.3 mm
G
pv
sv
0.1 mm
H
pv
p
cg
sv
ma
0.14 mm
I
ma
gp
0.1 mm

Figure 29

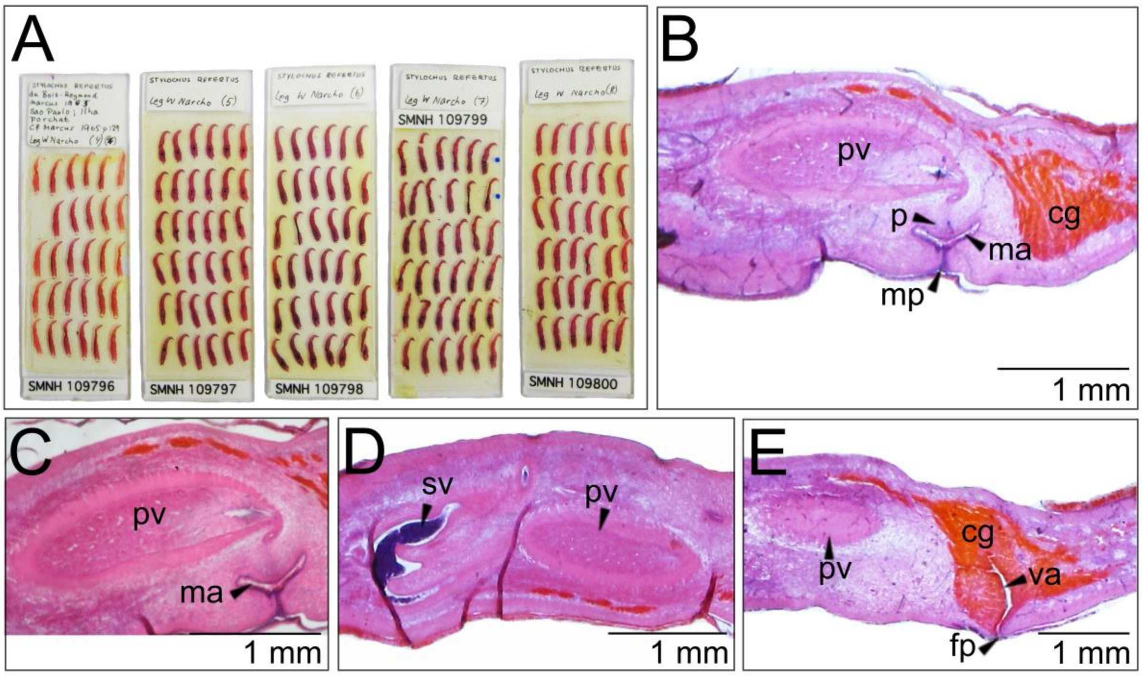

A
STYLOCHUS REFERTUS
du Bois-Reymond
Marcus 1965
Sao Paulo; Ilha
Porchat
Cf Marcus 1965 p.129
Leg W Narcho (4)
STYLOCHUS REFERTUS
Leg W Narcho (5)
STYLOCHUS REFERTUS
Leg W Narcho (6)
STYLOCHUS REFERTUS
Leg W Narcho (7)
SMNH 109799
STYLOCHUS REFERTUS
Leg W Narcho (8)
SMNH 109796
SMNH 109797
SMNH 109798
SMNH 109800
B
pv
p
ma
cg
mp
1 mm
C
pv
ma
1 mm
D
sv
pv
1 mm
E
pv
cg
va
fp
1 mm

Figure 30

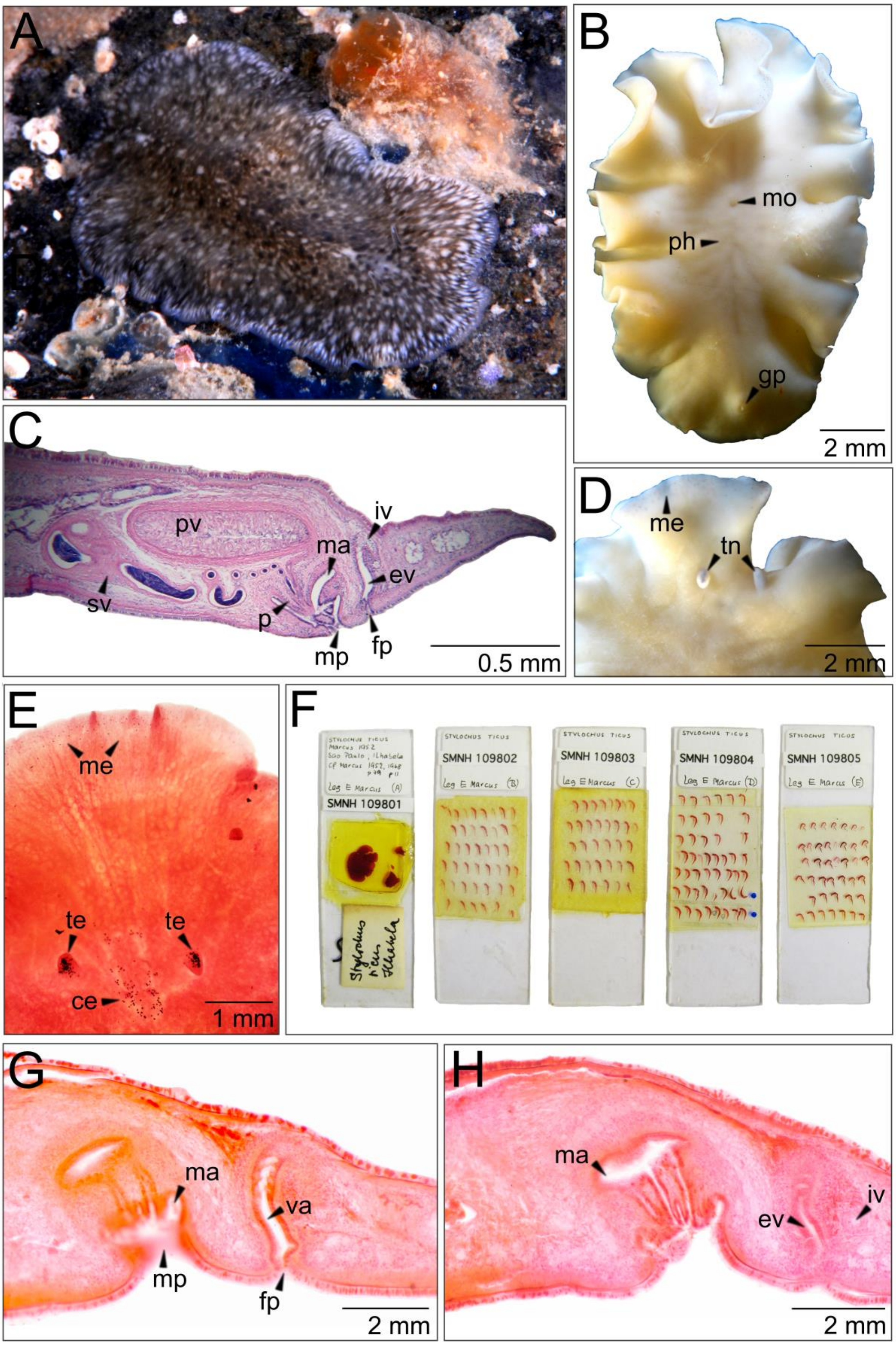

A
B
mo
ph
gp
2 mm
C
pv
iv
ma
ev
sv
p
mp
fp
0.5 mm
D
me
tn
2 mm
E
me
te
te
ce
1 mm
F
STYLOCHUS TICUS
Marcus 1952
São Paulo, Ilhabela
Cf Marcus 1952, 1968
p 79 p 11
Leg E Marcus (A)
SMNH 109801
Stylochus ticus Ilhabela
STYLOCHUS TICUS
SMNH 109802
Leg E Marcus (B)
STYLOCHUS TICUS
SMNH 109803
Leg E Marcus (C)
STYLOCHUS TICUS
SMNH 109804
Leg E Marcus (D)
STYLOCHUS TICUS
SMNH 109805
Leg E Marcus (E)
G
ma
va
mp
fp
2 mm
H
ma
iv
ev
2 mm

Figure 31

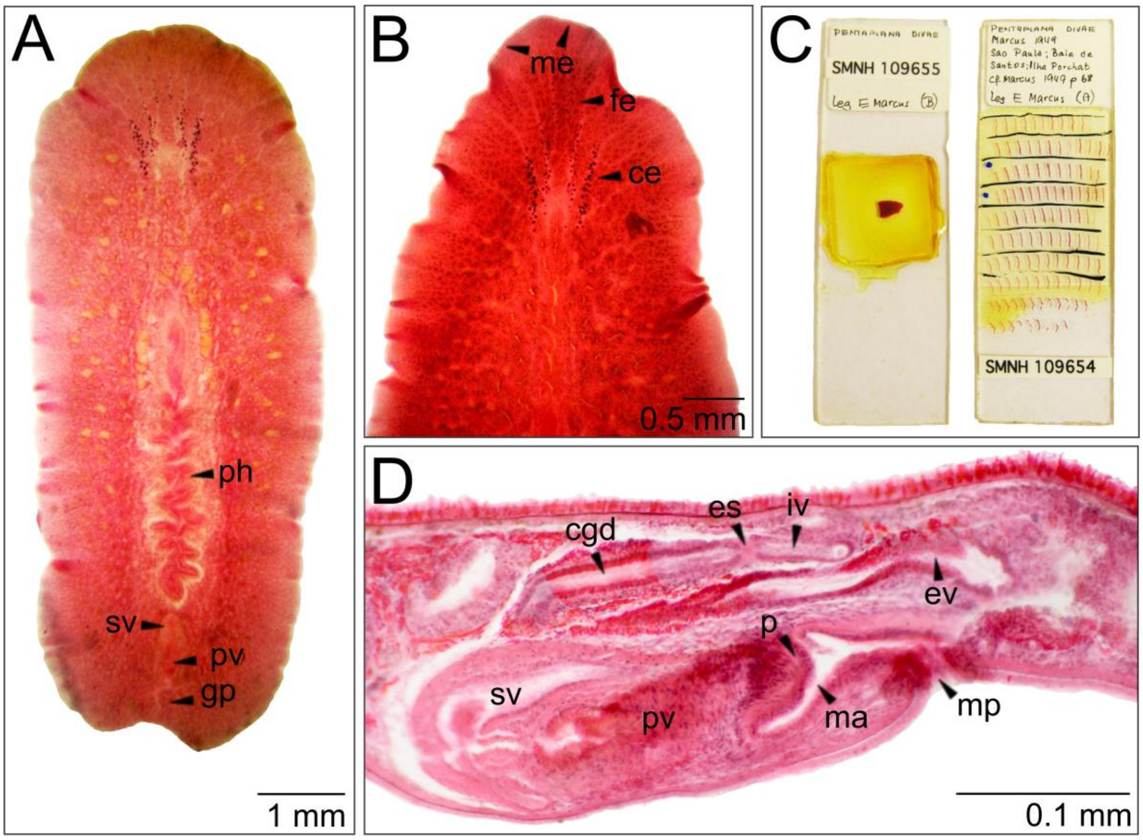


Figure 32

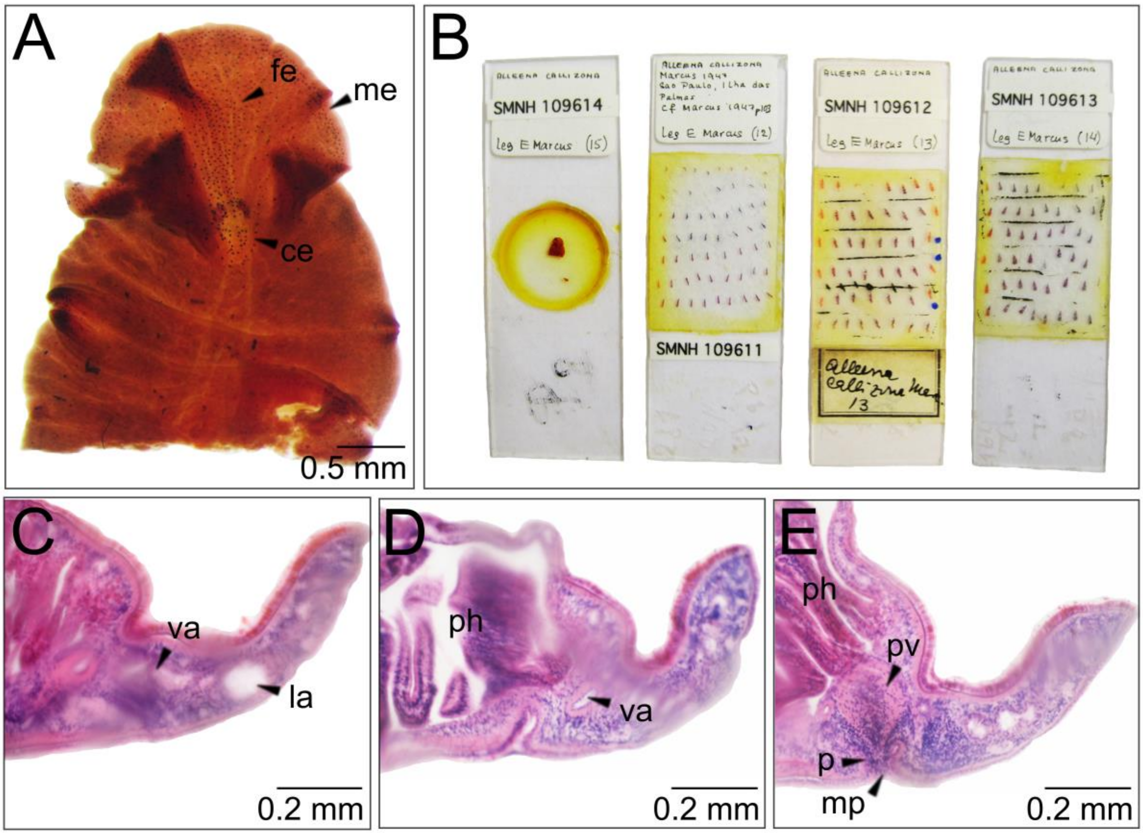


Figure 33

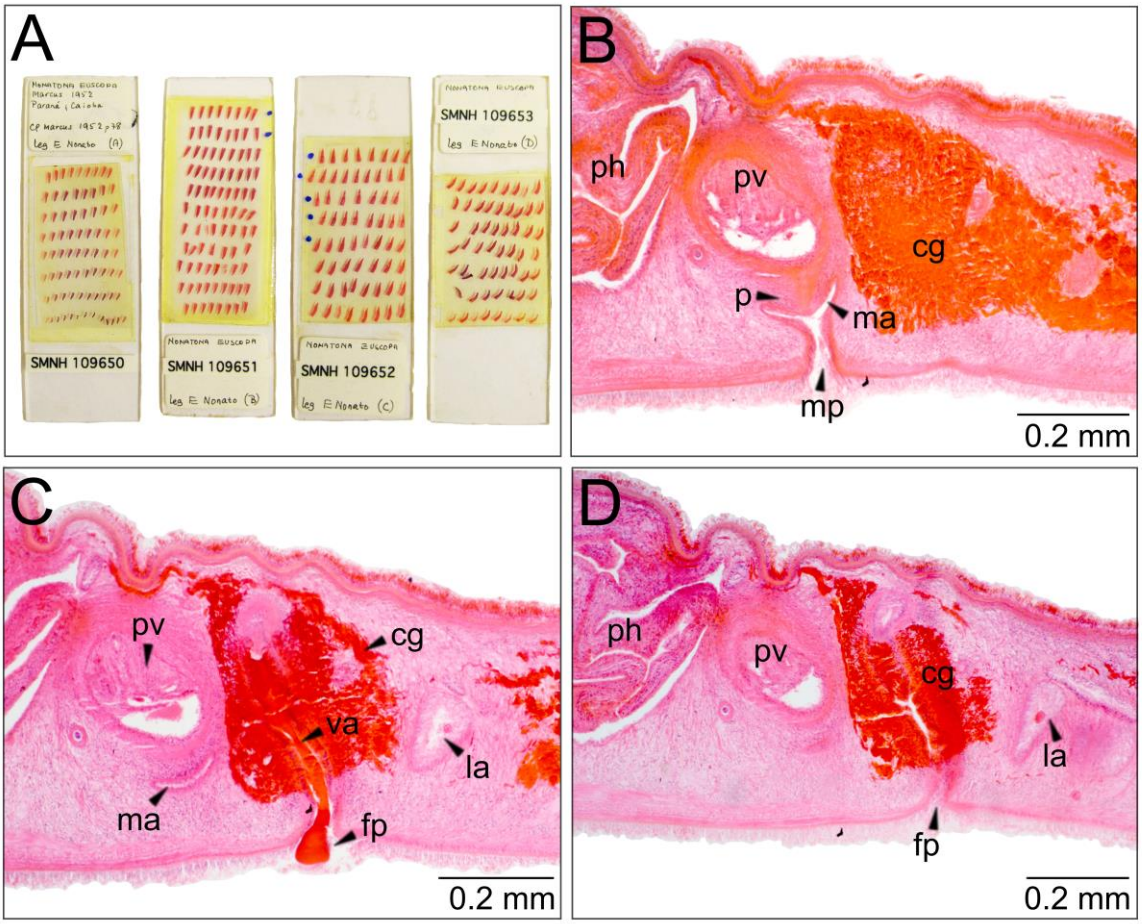

A
NONATONA EUSCOPA
Marcus 1952
Paraná ; Caioba
CP Marcus 1952 p78
leg E Nonato (A)
SMNH 109650
NONATONA EUSCOPA
SMNH 109651
leg E Nonato (B)
NONATONA EUSCOPA
SMNH 109652
leg E Nonato (C)
NONATONA EUSCOPA
SMNH 109653
leg E Nonato (D)
B
ph
pv
cg
p
ma
mp
0.2 mm
C
pv
cg
va
la
ma
fp
0.2 mm
D
ph
pv
cg
la
fp
0.2 mm

Figure 34

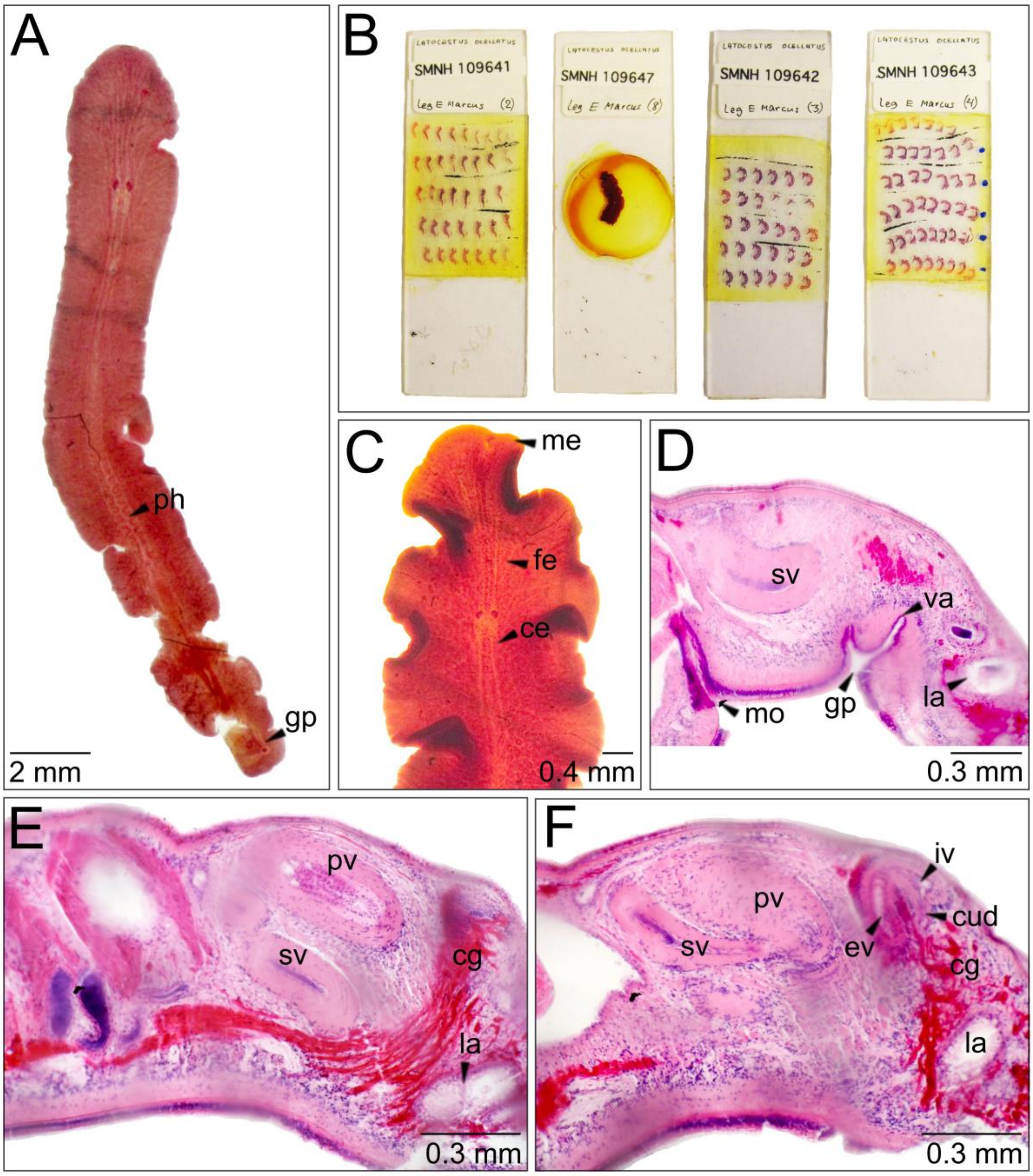

A
ph
gp
2 mm
B
LATOCESTUS OCELLATUS
SMNH 109641
Leg E Marcus (2)
LATOCESTUS OCELLATUS
SMNH 109647
Leg E Marcus (8)
LATOCESTUS OCELLATUS
SMNH 109642
Leg E Marcus (3)
LATOCESTUS OCELLATUS
SMNH 109643
Leg E Marcus (4)
C
me
fe
ce
0.4 mm
D
sv
va
la
mo
gp
0.3 mm
E
pv
sv
cg
la
0.3 mm
F
iv
pv
cud
sv
ev
cg
la
0.3 mm

Figure 35

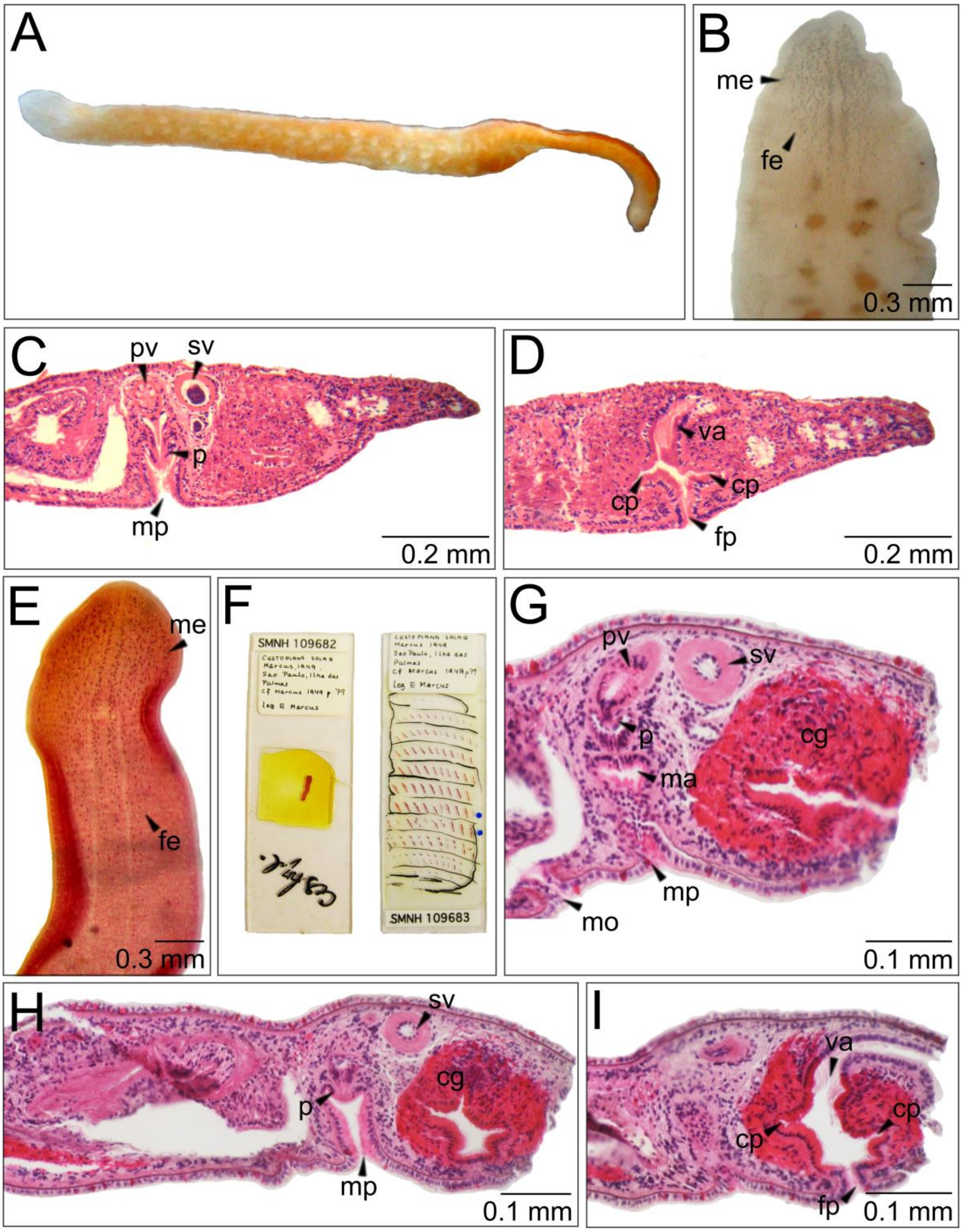

A
B
me
fe
0.3 mm
C
pv
sv
p
mp
0.2 mm
D
va
cp
cp
fp
0.2 mm
E
me
fe
0.3 mm
F
SMNH 109682
Cestoplana salar Marcus, 1949, Sao Paulo, Ilha das Palmas cf Marcus 1949 p 79 leg E Marcus
Cestopl.
Cestoplana salar Marcus 1949 Sao Paulo, Ilha das Palmas cf Marcus 1949 p 79 leg E Marcus
SMNH 109683
G
pv
sv
p
cg
ma
mp
mo
0.1 mm
H
sv
cg
p
mp
0.1 mm
I
va
cp
cp
fp
0.1 mm

Figure 36

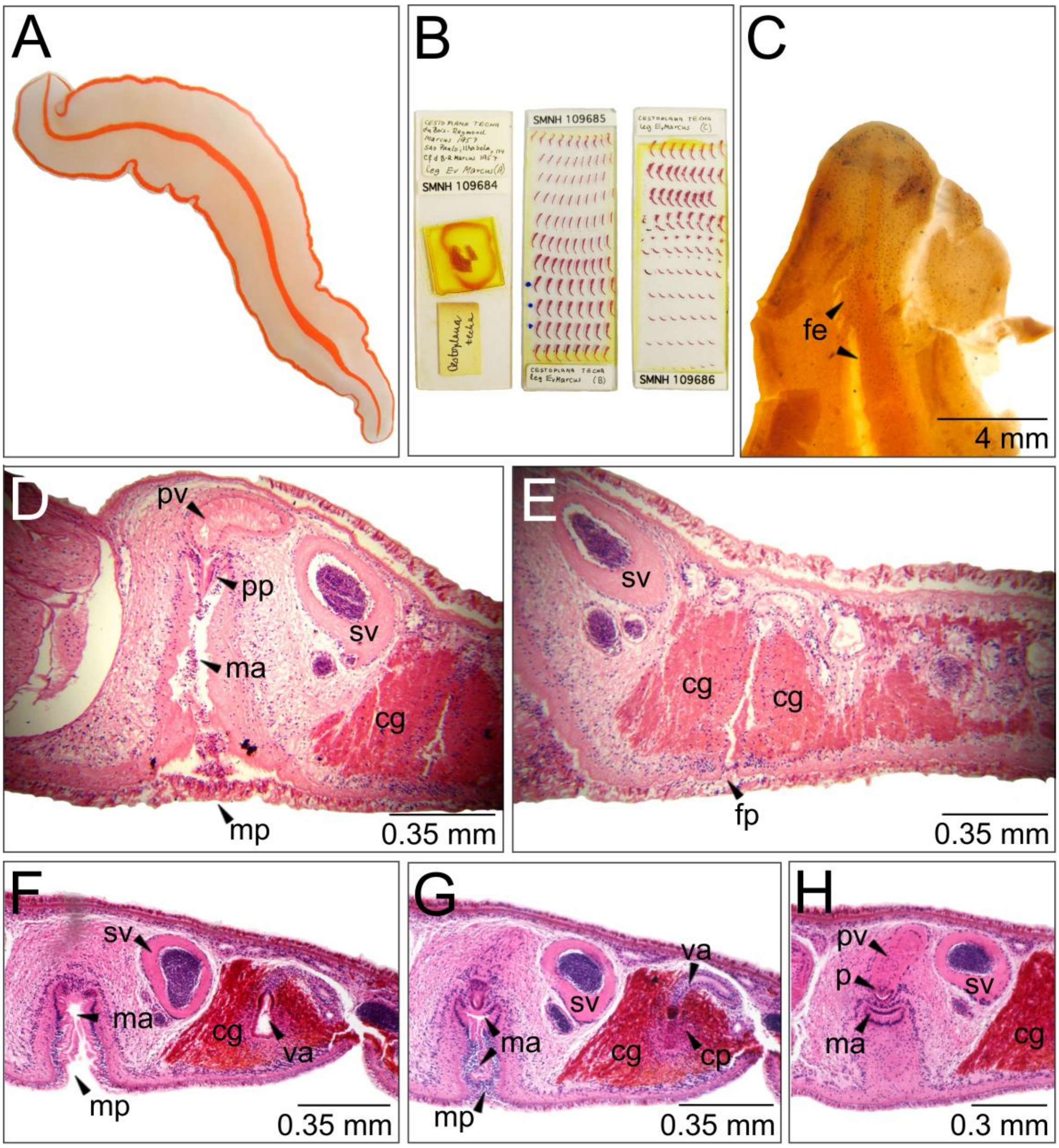

A
B
CESTOPLANA TECHA
du Bois-Reymond
Marcus 1957
Sao Paulo, Ilhabela, 1.IV
Cf d B-R Marcus 1957
leg Ev Marcus (A)
SMNH 109684
Cestoplana techa
SMNH 109685
CESTOPLANA TECHA
leg EvMarcus (B)
CESTOPLANA TECHA
leg EvMarcus (C)
SMNH 109686
C
fe
4 mm
D
pv
pp
sv
ma
cg
mp
0.35 mm
E
sv
cg
cg
fp
0.35 mm
F
sv
ma
cg
va
mp
0.35 mm
G
va
sv
ma
cg
cp
mp
0.35 mm
H
pv
p
sv
ma
cg
0.3 mm

Figure 37

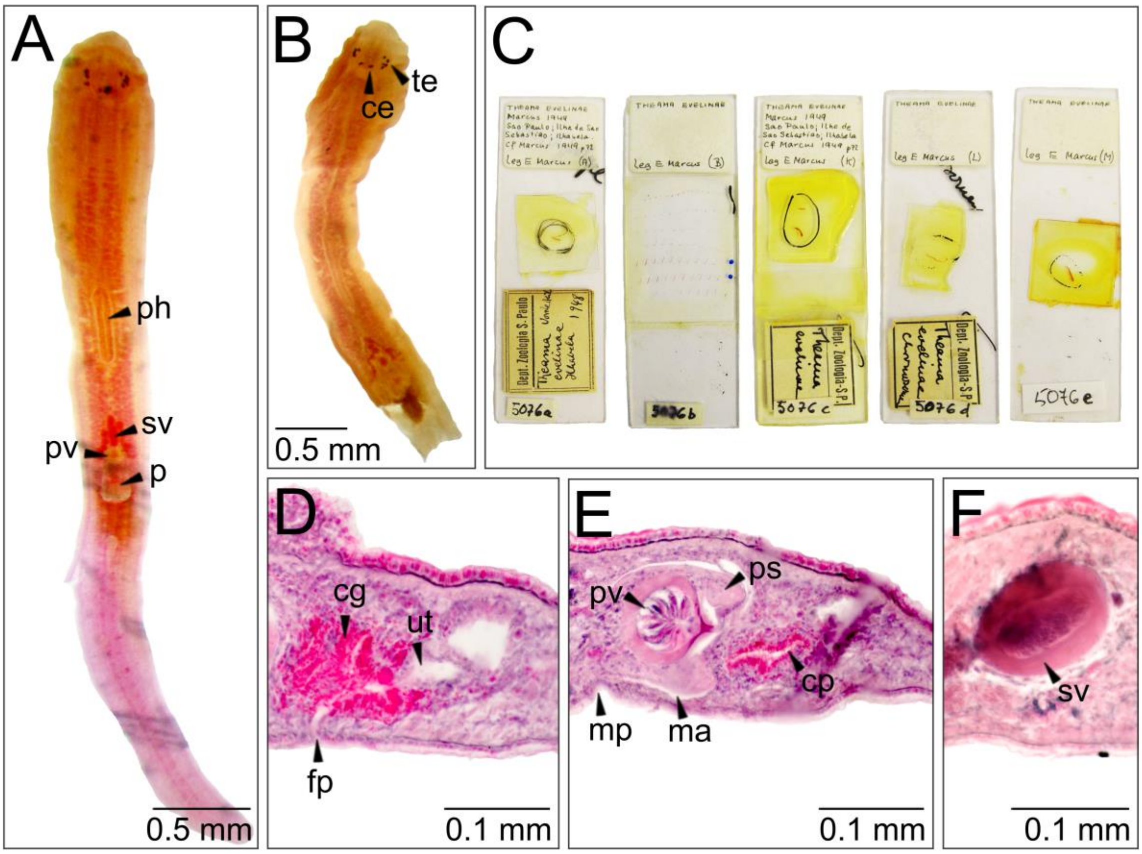


Figure 38

Figure 39

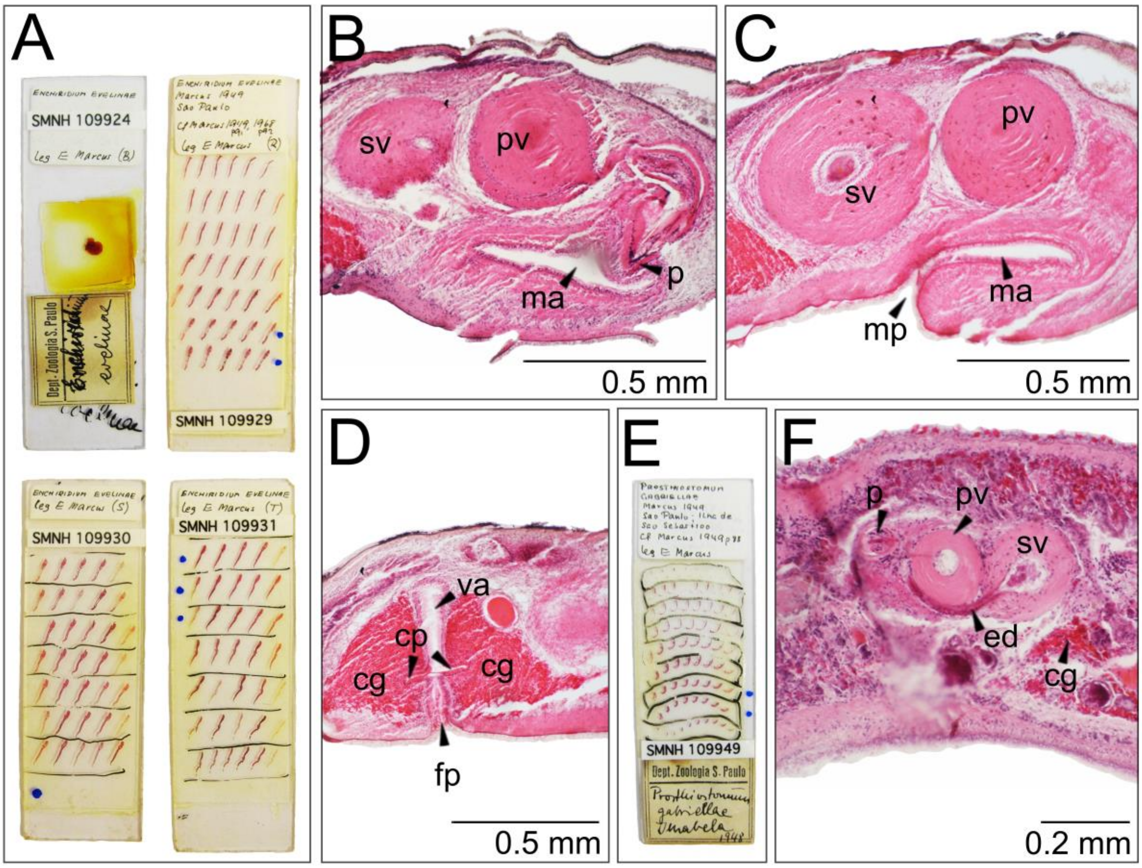


Figure 40

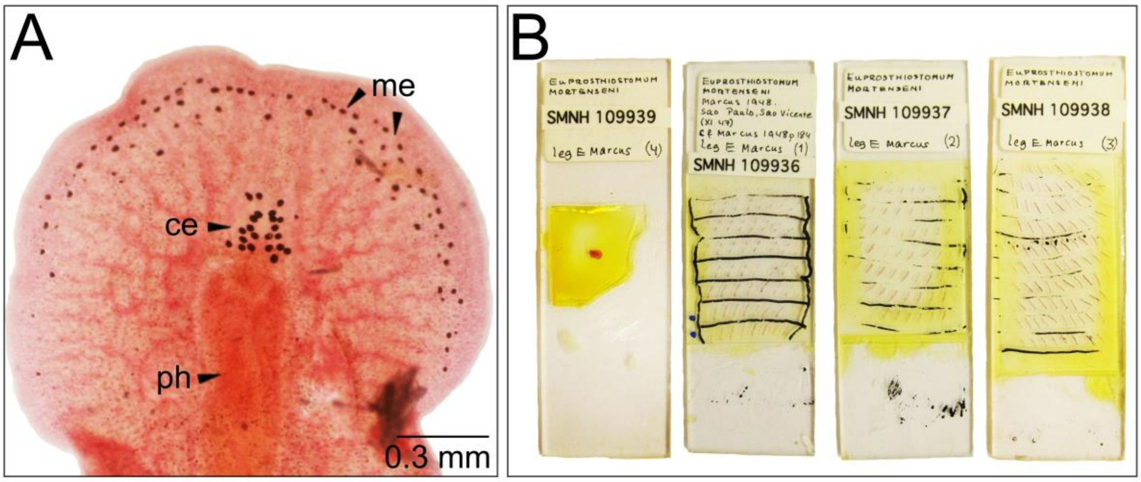


Figure 41

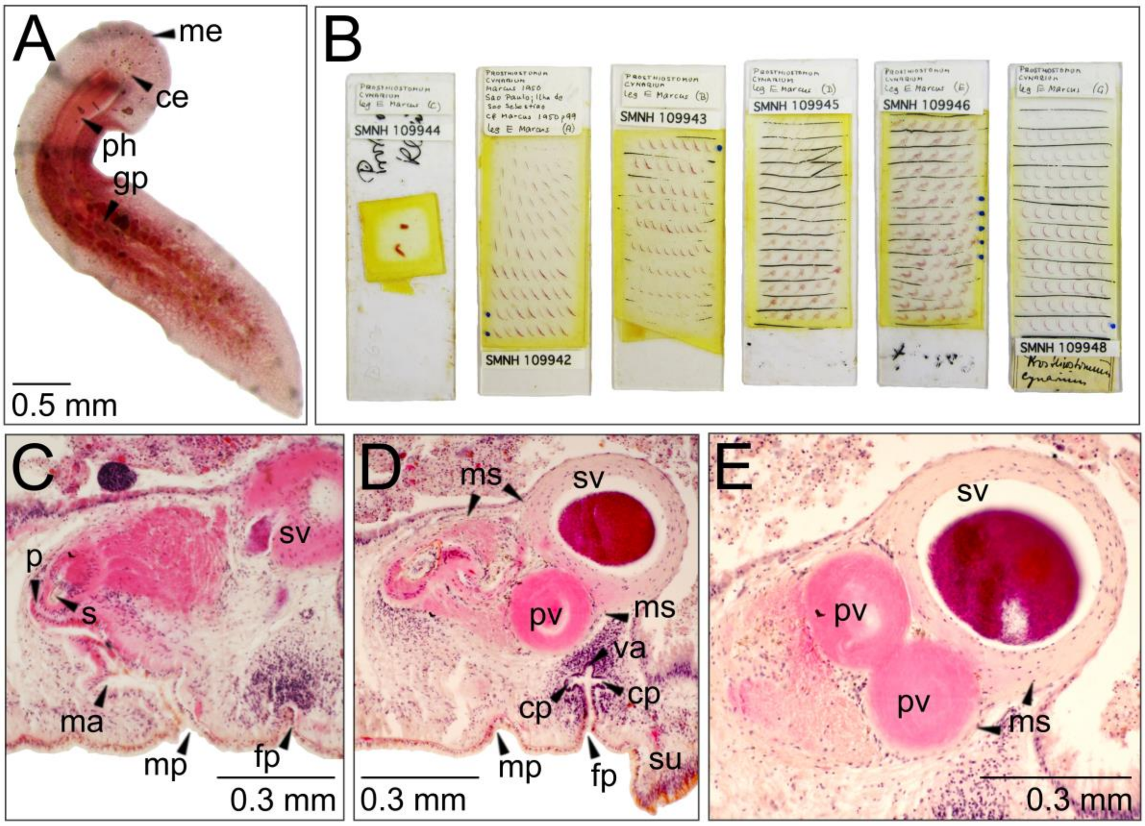

A
me
ce
ph
gp
0.5 mm
B
PROSTHIOSTOMUM CYNARIUM leg E Marcus (C)
SMNH 109944
PROSTHIOSTOMUM CYNARIUM Marcus 1950 São Paulo; Ilha de São Sebastião cf Marcus 1950 p99 leg E Marcus (A)
SMNH 109942
PROSTHIOSTOMUM CYNARIUM leg E Marcus (B)
SMNH 109943
PROSTHIOSTOMUM CYNARIUM leg E Marcus (D)
SMNH 109945
PROSTHIOSTOMUM CYNARIUM leg E Marcus (E)
SMNH 109946
PROSTHIOSTOMUM CYNARIUM leg E Marcus (G)
SMNH 109948
Prosthiostomum cynarium
C
p
s
sv
ma
mp
fp
0.3 mm
D
ms
sv
pv
ms
va
cp
cp
mp
fp
su
0.3 mm
E
sv
pv
pv
ms
0.3 mm

Figure 42

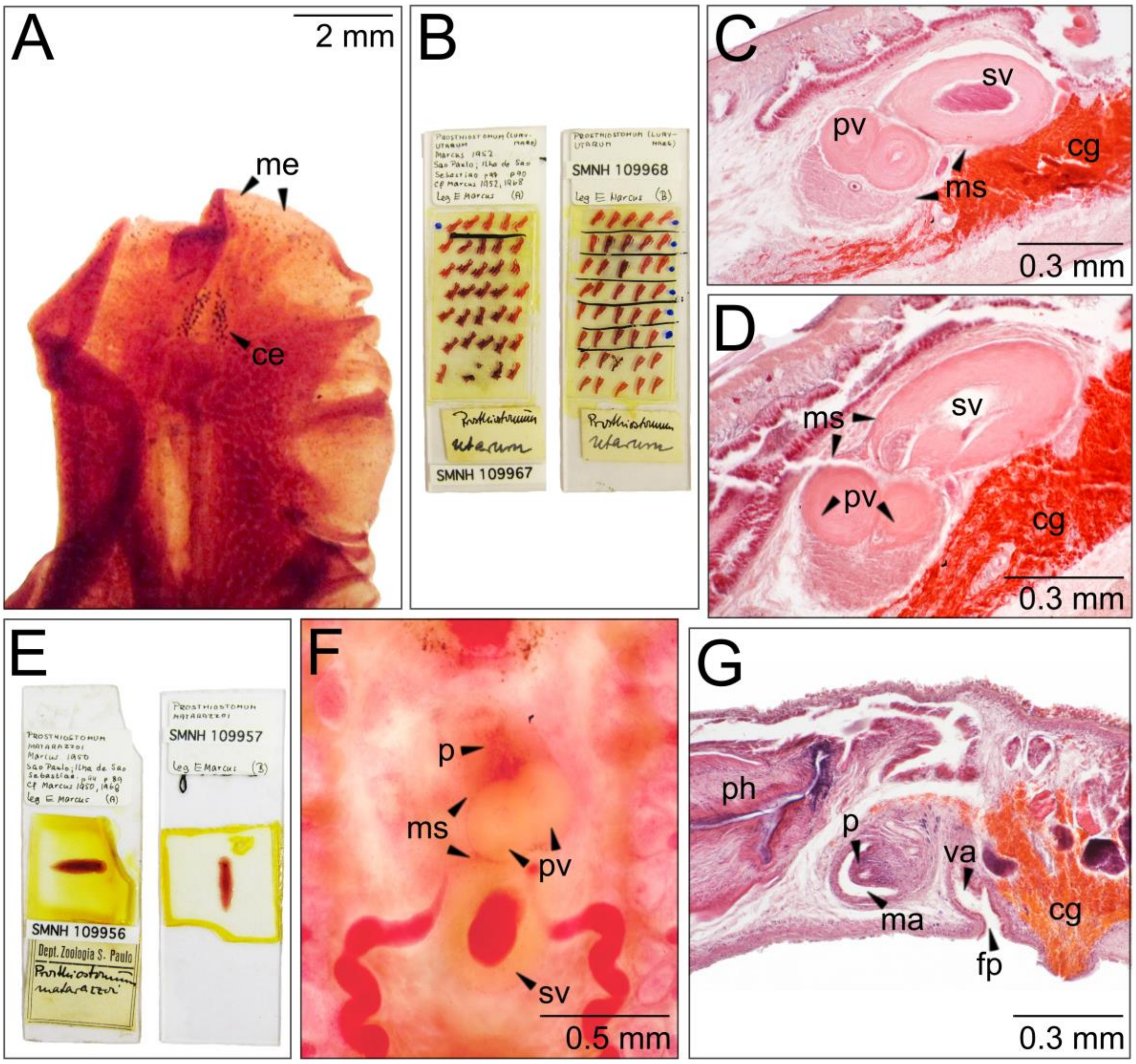

A
2 mm
me
ce
B
PROSTHIOSTOMUM (LURYMARE) UTARUM
Marcus 1952
Sao Paulo; Ilha de Sao Sebastiao p97 p90
Cf Marcus 1952, 1968
Leg E Marcus (A)
PROSTHIOSTOMUM (LURYMARE) UTARUM
SMNH 109968
Leg E Marcus (B)
Prosthiostomum utarum
Prosthiostomum utarum
SMNH 109967
C
sv
pv
cg
ms
0.3 mm
D
ms
sv
pv
cg
0.3 mm
E
PROSTHIOSTOMUM MATARAZZOI
Marcus 1950
Sao Paulo; Ilha de Sao Sebastiao. p94 p89
Cf Marcus 1950, 1968
leg E Marcus (A)
PROSTHIOSTOMUM MATARAZZOI
SMNH 109957
leg E Marcus (3)
SMNH 109956
Dept. Zoologia S. Paulo
Prosthiostomum matarazzoi
F
p
ms
pv
sv
0.5 mm
G
ph
p
va
ma
cg
fp
0.3 mm

Figure 43

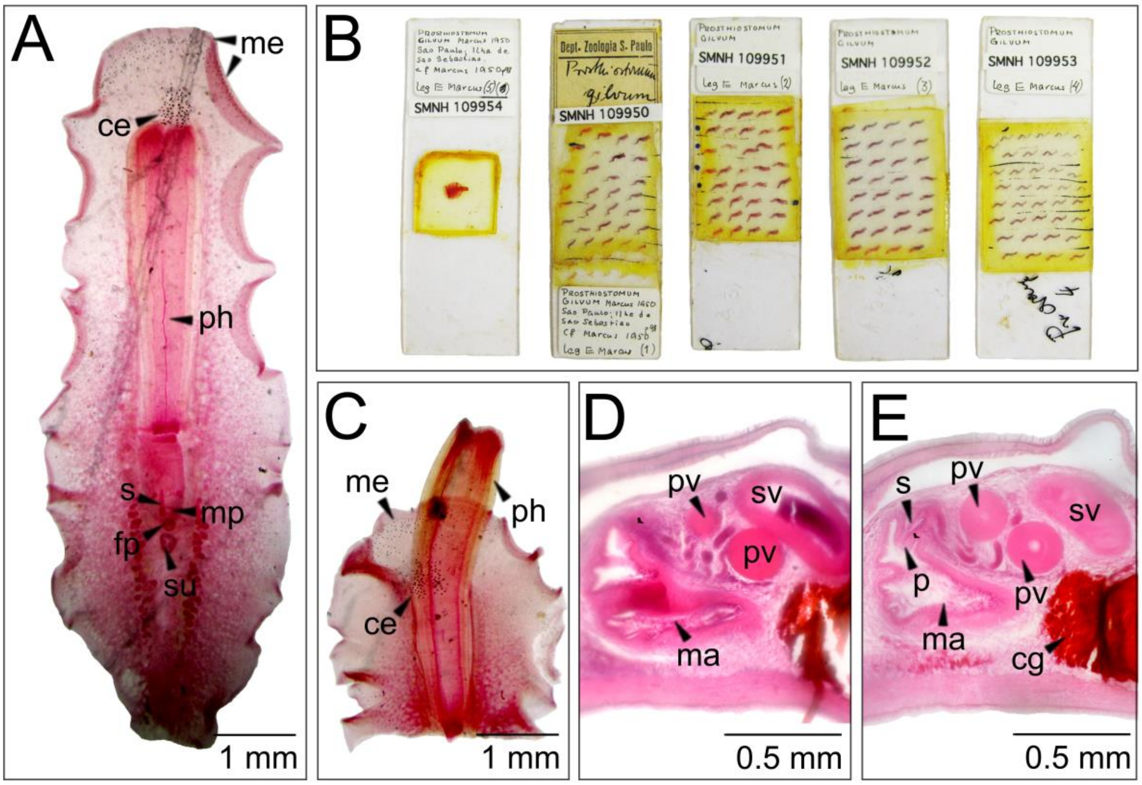


Figure 44

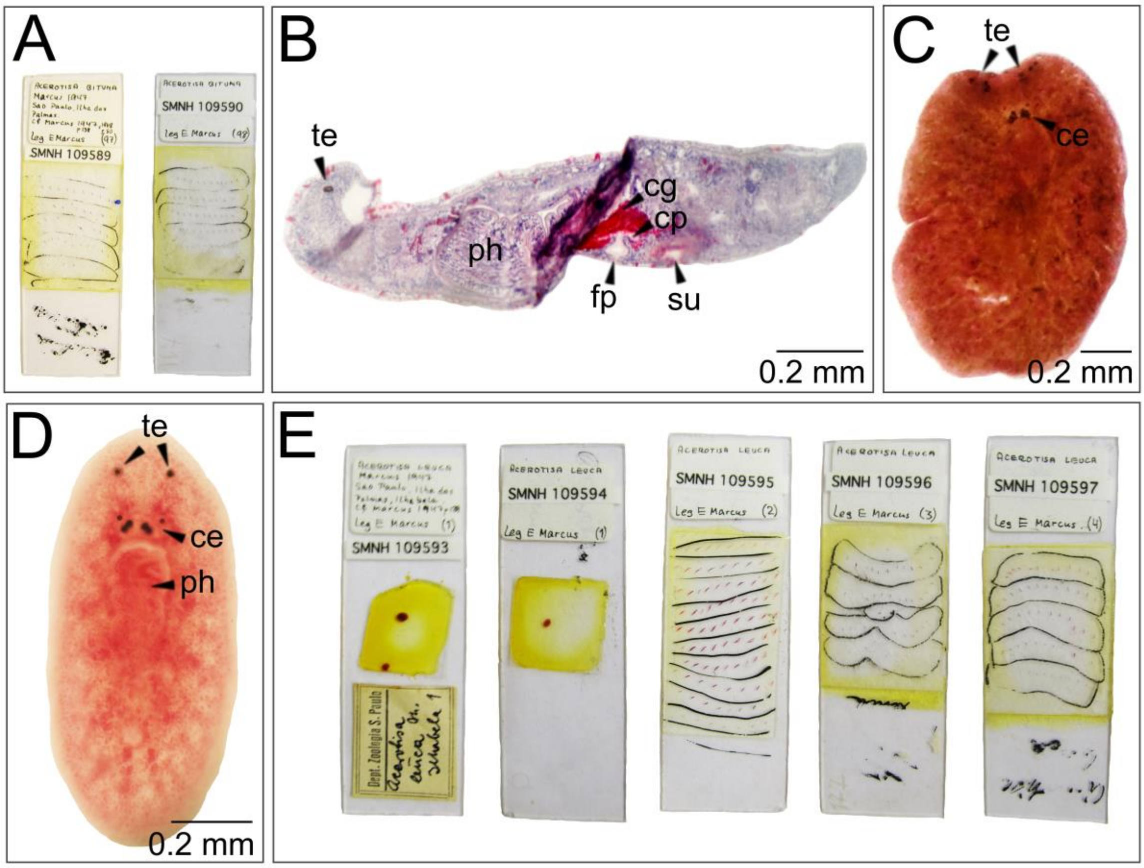


Figure 45

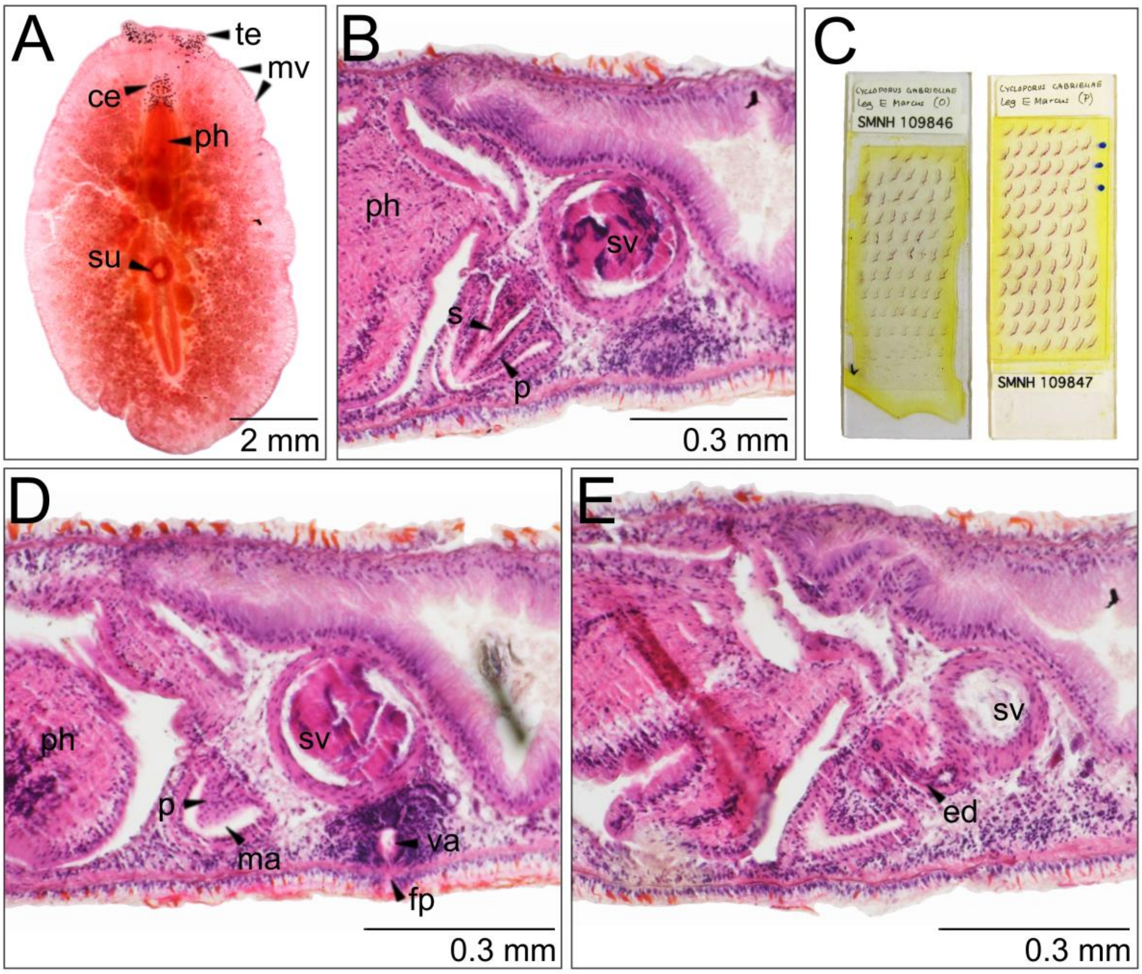

A
te
mv
ce
ph
su
2 mm
B
ph
sv
s
p
0.3 mm
C
CYCLOPORUS GABRIELLAE
Leg E Marcus (O)
SMNH 109846
CYCLOPORUS GABRIELLAE
Leg E Marcus (P)
SMNH 109847
D
ph
sv
p
ma
va
fp
0.3 mm
E
sv
ed
0.3 mm

Figure 46

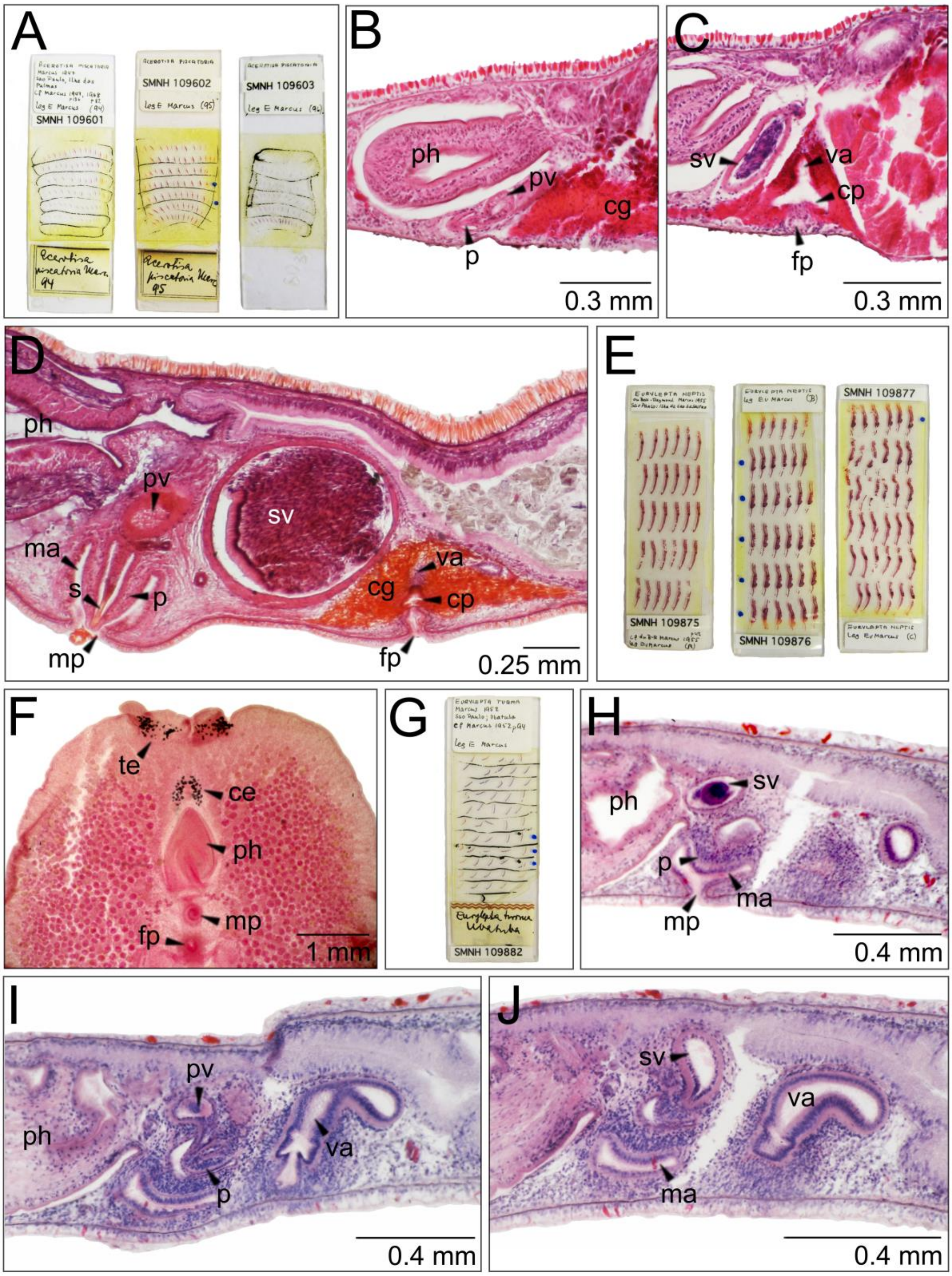

A
ACEROTISA PISCATORIA
Marcus 1947
Sao Paulo, Ilha das Palmas
cf Marcus 1947, 1968
leg E Marcus (94)
SMNH 109601
Acerotisa piscatoria Marc. 94
ACEROTISA PISCATORIA
SMNH 109602
leg E Marcus (95)
Acerotisa piscatoria Marc. 95
ACEROTISA PISCATORIA
SMNH 109603
leg E Marcus (96)
B
ph
pv
cg
p
0.3 mm
C
sv
va
cp
fp
0.3 mm
D
ph
pv
sv
ma
s
p
va
cg
cp
mp
fp
0.25 mm
E
EURYLEPTA NEPTIS
SMNH 109875
EURYLEPTA NEPTIS
leg Ev Marcus (B)
SMNH 109876
SMNH 109877
EURYLEPTA NEPTIS
leg Ev Marcus (C)
F
te
ce
ph
mp
fp
1 mm
G
EURYLEPTA TURMA
Marcus 1952
Sao Paulo; Ubatuba
cf Marcus 1952 p94
leg E Marcus
SMNH 109882
H
sv
ph
p
ma
mp
0.4 mm
I
pv
ph
va
p
0.4 mm
J
sv
va
ma
0.4 mm

Figure 47

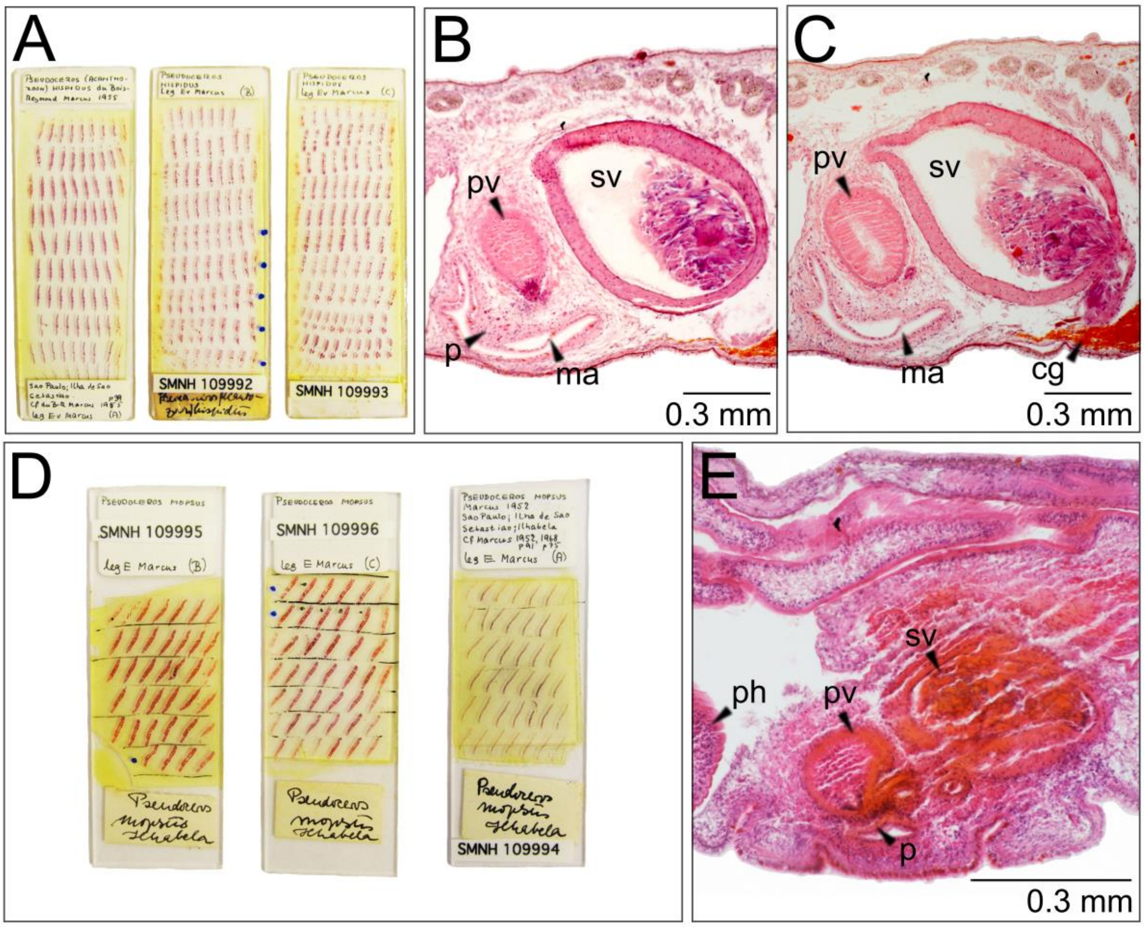


Figure 48

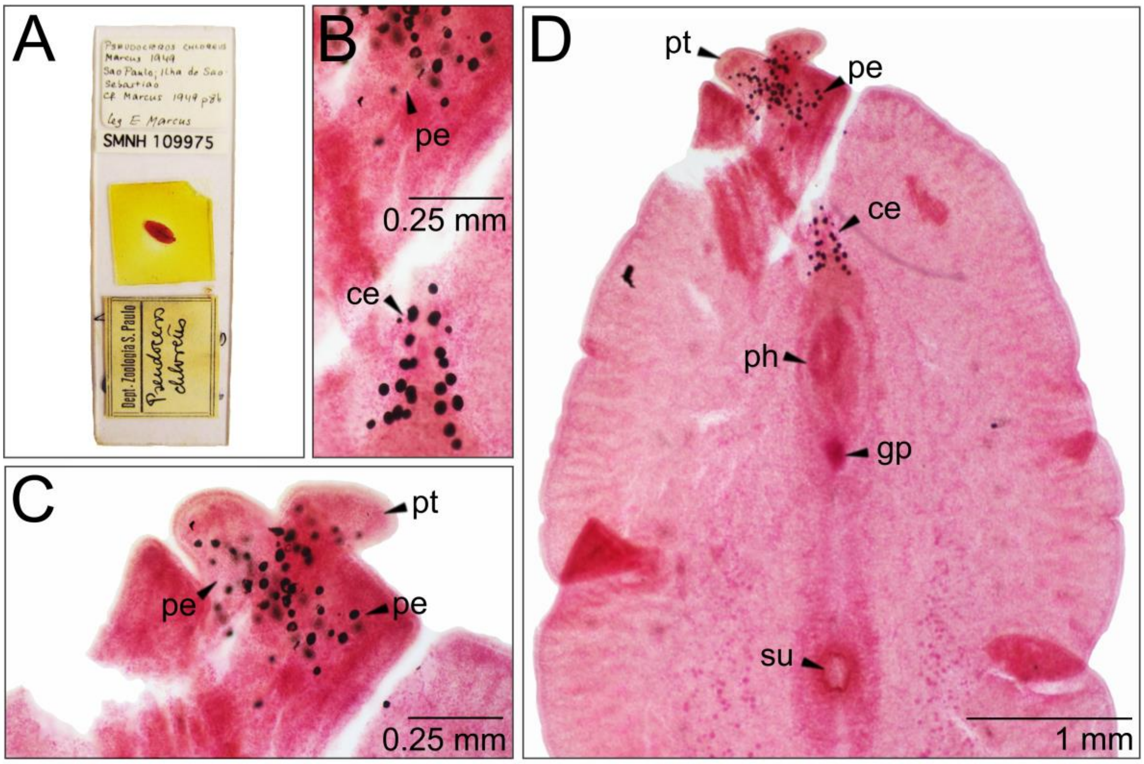
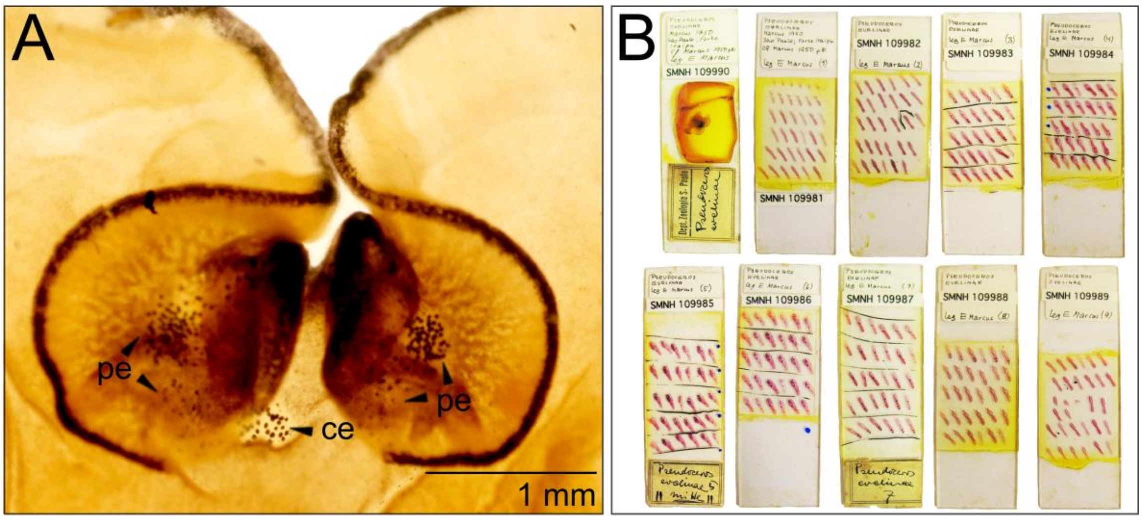
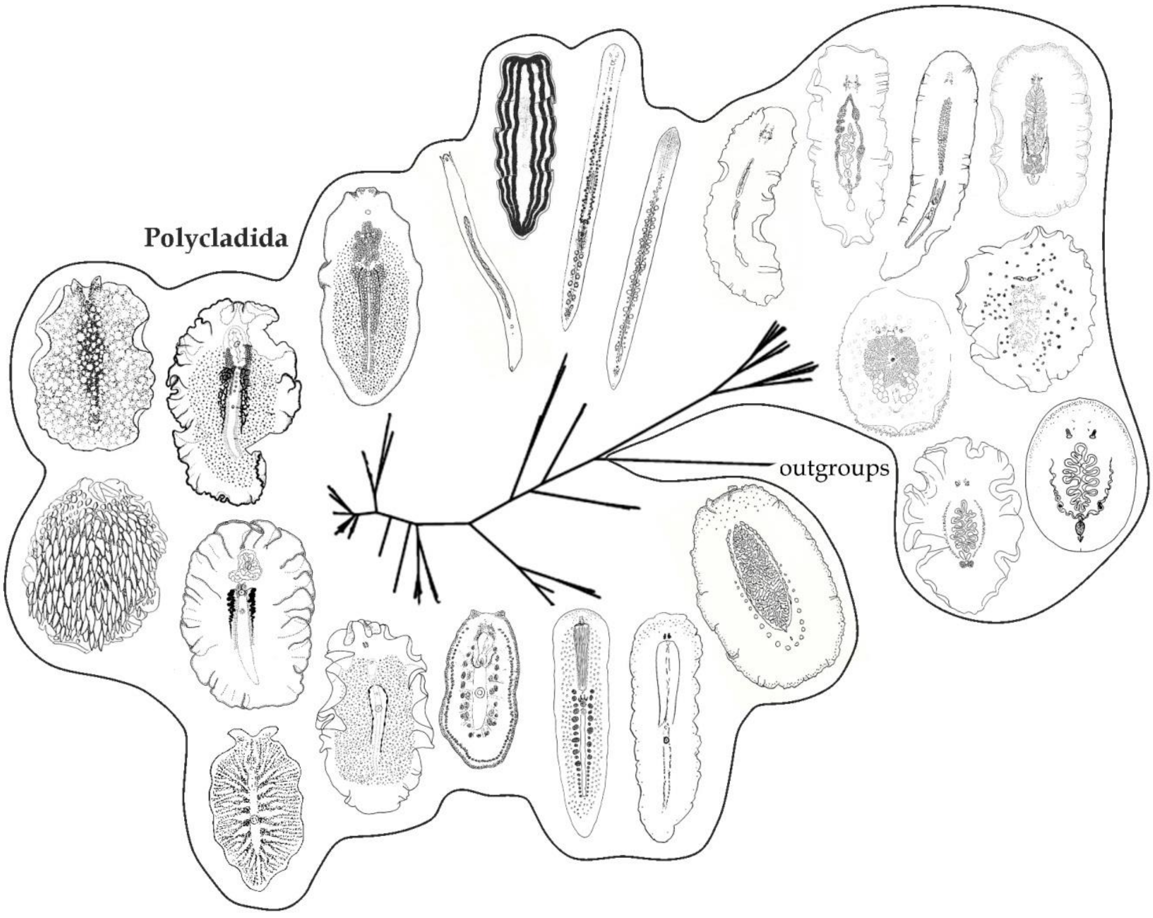


Figure 49


A
pe
pe
ce
1 mm
B
SMNH 109990
leg E Marcus
Dept. Zoologia S. Paulo
Pseudoceros evelinae
SMNH 109981
leg E Marcus (1)
SMNH 109982
leg E Marcus (2)
leg E Marcus (3)
SMNH 109983
leg E Marcus (4)
SMNH 109984
leg E Marcus (5)
SMNH 109985
Pseudoceros evelinae 5
leg E Marcus (6)
SMNH 109986
leg E Marcus (7)
SMNH 109987
Pseudoceros evelinae 7
SMNH 109988
leg E Marcus (8)
SMNH 109989
leg E Marcus (9)

PART 3: POLYCLADIDA PHYLOGENY



Chapter 5.

Polycladida phylogeny and evolution: Integrating evidence from 28S rDNA and morphology

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ORIGINAL ARTICLE

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Polycladida phylogeny and evolution: integrating evidence from 28S rDNA and morphology

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Abstract Polyclad flatworms have a troubled classification history, with two contradicting systems in use. They both rely on a ventral adhesive structure to define the suborders Acotylea and Cotylea, but superfamilies were defined according to eyespot arrangement (Prudhoe's system) or prostatic vesicle characters (Faubel's system). Molecular data available cover a very limited part of the known polyclad family diversity and have not allowed testing morphology-based classification systems on Polycladida yet. We thus sampled a suitable marker, partial 28S ribosomal DNA (rDNA), from Polycladida (19 families and 32 genera), generating 136 new sequences and the first comprehensive genetic dataset on polyclads. Our maximum likelihood (ML) analyses recovered Polycladida, but the traditional suborders were not monophyletic, as the supposedly acotyleans *Cestoplana* and *Theama* were nested within Cotylea; we suggest that these genera should be included in Cotylea. The partial 28S rDNA trees were generally well supported and robust but in conflict with both Faubel's and Prudhoe's superfamilies. Therefore, we compiled morphological and anatomical characters for all taxa used and examined their distribution on our molecular tree. Combining morphological and molecular evidence, we redefined polyclad superfamilies. Acotylea contain tentaculated and atentaculated groups and is now divided in three superfamilies. The suborder Cotylea can be divided in five superfamilies. In general, there is a trait of anteriorization of sensory structures, from the plesiomorphic acotylean body plan to the cotylean gross morphology. Traditionally used characters, such as prostatic vesicle, eyespot distribution, and type of pharynx, are all homoplastic and likely have misled polyclad systematics so far.

Keywords Platyhelminthes · Marine flatworms · Cotylea · Acotylea · Molecular phylogenetics · Morphology

Introduction

Polycladida are free-living Platyhelminthes that inhabit marine environments, as different as coral reefs, rocky shores, soft bottoms, and deepwater (Newman and Cannon 2003; Quiroga et al. 2006) as also artificial aquaculture structures (Bahia 2015). Around 1000 species of Polycladida are known in the world (Rawlinson 2008; Tyler et al. 2016). The main characteristic of this group of Platyhelminthes is the simple and dorsoventrally flattened body, with a much ramified intestine (Hyman 1951). Characters used in taxonomy of the order Polycladida are the hermaphrodite reproductive anatomy and external morphology (eyespot arrangements, tentacles, and pharynx) (Hyman 1951; Faubel 1984; Prudhoe 1985). Coloration pattern is also used to distinguish closely related species (Newman and Cannon 1995; Litvaitis et al. 2010). In general, polyclads have cryptic behavior, living under rocks, often associated with invertebrates on which they feed (Marcus and Marcus 1951; Newman and Cannon 2003). They are important predators in hard bottom environments

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(Rawlinson et al. 2011) and are models in studies involving regeneration (Egger et al. 2007), toxicology and predation (Ritson-Williams et al. 2006), pharmacologically active compounds (Schupp et al. 2001), mimetism (Newman and Cannon 1995), and aposematism (Ang and Newman 1998). These animals can also damage mollusk aquaculture (Pearse and Wharton 1938; Sluys et al. 2005).

Polyclads are a conspicuous group of marine invertebrates, possibly the most charismatic members of the phylum Platyhelminthes, and even so are still poorly studied (Littlewood et al. 1999). Their position within Platyhelminthes is controversial, as historically polyclads were considered basal in the phylum, in Trepaxonemata as sister group to the Neoophora (Ehlers 1985, 1986) or together with Macrostomorpha (Litvaitis and Rhode 1999; Janssen et al. 2015). However, recently, they were proposed as sister group to Lecithoepitheliata as a whole (Egger et al. 2015; Sòla et al. 2015) or to Prorhynchida (Laumer et al. 2015). Polycladida systematics has had a troubled history as well. One of the first phylogenetic hypotheses suggested that the genera *Cestoplana* and *Prosthiostomum* (Fig. 1b) were the most derived ones in Acotylea and Cotylea, respectively (Lang 1884). Laidlaw (1903c) illustrated another hypothesis of relationship between cotyleans (Fig. 1a). Later, Marcus and Marcus (1966) developed the first comprehensive Polycladida systematic key, which was based on the scattered taxonomic polyclad bibliography (Schmmarda 1859; Lang 1884; Laidlaw 1903a, 1903b, 1903c; Bock 1923; Marcus 1950; Hyman 1955). This system was further improved in independent approaches by Faubel (1983, 1984) and Prudhoe (1985). Faubel (1984) also proposed a phylogenetic arrangement (Fig. 1c) for the order. Both Faubel and Prudhoe and previous authors divided polyclads in the suborders Acotylea and Cotylea, differentiated by a ventral adhesive structure. However, Faubel's and Prudhoe's concepts resulted in massive conflict on superfamily level.

Faubel (1983) divided Acotylea in superfamilies based on the absence of true prostatic vesicle (Ilyplanoidea = Emprosthommatidae), presence of true free prostatic vesicle (Stylochoidea = Craspedommatidea), or true interpolated prostatic vesicle (Leptoplanoidea). Prudhoe (1985) used instead the distribution of eyespots dividing Acotylea in superfamilies with frontal eyespots (Cestoplanoidea), with frontal, tentacular, and cerebral eyespots (Stylochoidea = Craspedommatidea) and with tentacular and cerebral eyespots (Planoceroidea = Schemmathomatidea). The suborder Cotylea was divided by Faubel (1984) based on different characters, two monospecific superfamilies were created, one with male apparatus behind female structures (Opisthogenoidea) and the other with triclad-like digestive system

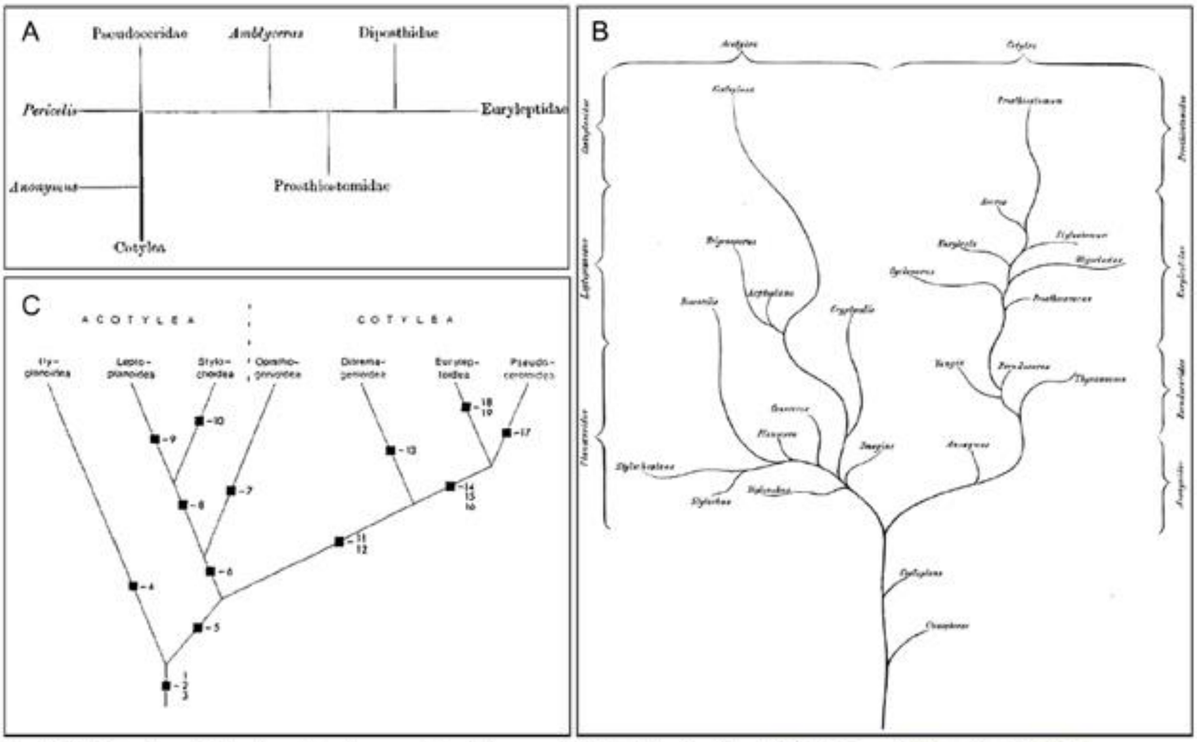


Fig. 1 Traditional morphology-based hypotheses on the phylogeny of Polycladida. **a** Laidlaw (1903c). **b** Lang (1884). **c** Faubel (1984)

(Ditremagenidea). The other cotyleans were divided in a group with ruffled pharynx (Pseudocerotoidea) and other with tubular pharynx (Euryleptoidea). Prudhoe did not divide the cotyleans in superfamily groupings, since there was not an important difference between eyespot arrangements within Cotylea.

A recent morphology-based cladistic study by Rawlinson and Litvaitis (2008) focused on Cotylea, with interesting results about genus relationships, many of them not being monophyletic. But so far, no molecular study has ever tested the homology of the characters used in traditional systematic taxonomy. There is no molecular phylogenetic hypothesis on Polycladida or its major subclades either. Some molecular data, mainly 28S ribosomal DNA (rDNA) and some 18S rDNA sequences, are available from a couple (not more than seven) of polyclad species that were included into Platyhelminthes phylogenies (Campos et al. 1998; Littlewood et al. 1999; Litvaitis and Rhode 1999; Litvaitis and Newman 2001). Within Polycladida, a phylogeny of the family Pseudocerotidae included 18 species (Litvaitis and Newman 2001) and focused on relations between genera, but the information is not on an online database. There are also molecular data available from a study focused on a species complex (Litvaitis et al. 2010). Egger et al. (2015) changed the prevailing hypothesis on the origin of polyclads and, recently, some polyclad COI and 16S sequences were included in other Platyhelminthes phylogeny papers (Laumer and Giribet 2014; Laumer et al. 2015). The first mitogenomic information supported the monophyly of Polycladida and its suborders (Aguado et al. 2015). However, this latter study included just three species and one of them unidentified. Molecular phylogeny of polyclads is thus in an initial stage mainly because of low taxon coverage.

Considering this relevant gap of knowledge and the conflicting morphology-based classifications, the aim of this paper is to present the first integrative phylogeny of Polycladida. We thus (1) collected representatives of as many polyclad families as possible in a global approach; (2) obtained morphological information from the literature and our material; (3) generated novel molecular data, specifically of a nuclear marker (28S rDNA) useful both in deep and shallow phylogenetics (Littlewood et al. 1999; Litvaitis et al. 2010); (4) correlated molecular phylogenetic results with morphological evidence; (5) proposed a new classification system based on phylogenetic principles; and (6) evaluated the evolution of the main features within Polycladida and its major subgroups.

Material and methods

Taxon sampling and morphological characters

Material used for DNA extraction was collected by the authors or sent by contributors from different regions (Table 1).

Table 1 Species list, localities, and number of samples included in the phylogeny and respective GenBank accession numbers

Species	Localities	GenBank accession number
Adenoplana evelinae Marcus, 1950	Brazil	*KY263647*
Phaenocelis medvedica Marcus, 1952	Brazil	*KY263701* *KY263702* *KY263703* *KY263704* *KY263705* *KY263706*
Idioplana australiensis Woodworth, 1898	Australia	HQ659008
Imogine refertus Du Bois-Reymond Marcus, 1965	Brazil	*KY263694*
Stylochus sp.	Australia	AF131707
Stylochus sp.	Peru	*KY263743*
Imogine zebra (Verrill, 1882)	US Atlantic coast	AF342800
Imogine oculifera Girard, 1853	Florida	HQ659007
Hoploplana californica Hyman, 1953	California	KC869850
Hoploplana divae Marcus, 1950	Brazil	*KY263692* *KY263693*
Armatoplana leptalea (Marcus, 1947)	Brazil	*KY263648* *KY263649*
Leptoplana sp. *or Notoplana* sp.	Spain, Brazil	*KY263695* *KY263650* *KY262696* *KY263698* *KY263651*
Notoplana australis (Schmarda, 1859)	Australia	AY157153 HQ659015
Melloplana ferruginea (Schmarda, 1859)	Florida	HQ659014
Echinoplana celerrima Haswell, 1907	Australia	HQ659020
Paraplanocera oligoglena (Schmarda, 1859)	Hawaii	KC869849
Planocera sp.	Greece	*KY263699*
Theama sp.	Panama	KC869845
Cestoplana rubrocincta (Grube, 1840)	Australia	HQ659009
Cestoplana techa Du Bois-Reymond Marcus, 1957	Brazil	*KY263652* *KY263654* *KY263655*
Cestoplana salar Marcus, 1949	Brazil	*KY263653*
Boninia divae Marcus and Marcus, 1968	Panama	KC869846
Chromoplana sp.	Panama	KC869847
Chromyella sp.	Panama	KC869848
Pericelis cata Marcus and Marcus, 1968	Caribbean, Brazil	EU679115 EU679114 *KY263700*
Pericelis orbicularis (Schmarda, 1859)	Panama	EU679116
Phrikoceros mopsus (Marcus, 1952)	Brazil	*KY263707* *KY263709*

Table 1 (continued)

Species	Localities	GenBank accession number
		KY263711 *KY263712* *KY263714*
Monobiceros langi Faubel, 1984	Tenerife, Spain, Greece	*KY263710* *KY263713* *KY263738* *KY263777* *KY263778*
Pseudoceros astrorum Bulnes and Torres, 2014	Brazil	*KY263737*
Pseudoceros bicolor Verrill, 1901	Belize, Panama, Curaçao, Jamaica, Florida, Brazil	GQ398096 GQ398095 GQ398097 GQ398100 GQ398099 GQ398098 *KY263729* *KY263730* *KY263732* *KY263735*
Pseudoceros harrisi Bolaños, Quiroga and Litvaitis, 2007	Panama	EF514802
Pseudoceros bimarginatus Meixner, 1907	Papua New Guinea	*KY263728*
Pseudoceros cf. *maximus* Lang, 1884	Spain	*KY263708*
Pseudoceros rawlinsonae Bolaños, Quiroga and Litvaitis, 2007	US Virgin Islands, Bahamas, Florida, Brazil	GQ398102 GQ398101 EF514803 *KY263731* *KY263733* *KY263734* *KY263736*
Pseudoceros velutinus (Blanchard, 1847)	Spain and Greece	*KY263726* *KY263727* *KY263739* *KY263740* *KY263741* *KY263742*
Pseudobiceros caribbensis Bolaños, Quiroga and Litvaitis, 2007	Florida and Jamaica	EF514806 EF514805 EF514804
Pseudobiceros evelinae Marcus, 1950	Brazil	*KY263716* *KY263717* *KY263718* *KY263719* *KY263720* *KY263721* *KY263722*
Pseudobiceros pardalis (Verrill, 1900)	Panama and Brazil	EF514808 EF514807 *KY263723*
Pseudobiceros splendidus (Lang, 1884)	Florida	HQ659016
Pseudobiceros bedfordi (Laidlaw, 1903b)	Papua New Guinea	*KY263715*
Pseudobiceros wirtzi Bahia and Schrödl, 2016	Senegal	*KY263725*

Table 1 (continued)

Species	Localities	GenBank accession number
Pseudobiceros sp.	Santa Helena Island	*KY263724*
Maiazoon orsakii Newman and Cannon, 1996	Papua New Guinea	*KY263697*
Thysanozoon alagoensis Bahia, Padula, Correa and Sovierzoski, 2015	Brazil	*KY263747*
Thysanozoon brocchii Risso, 1818	Australia, Sicily, Spain, Brazil	HQ659017 *KY263744* *KY263745* *KY263746* *KY263748* *KY263749* *KY263750* *KY263751* *KY263752* *KY263753* *KY263754* *KY263755* *KY263756* *KY263757* *KY263758* *KY263759* *KY263760* *KY263761* *KY263762* *KY263763* *KY263764* *KY263765* *KY263766* *KY263767* *KY263768* *KY263769* *KY263770* *KY263771* *KY263772* *KY263773* *KY263774* *KY263775* *KY263776* *KY263779* *KY263780* *KY263781*
Thysanozoon raphaeli Bolaños, Quiroga and Litvaitis, 2007	Panama and Belize	EF514810 EF514809
Yungia sp.	Florida	HQ659018
Cycloporus gabriellae Marcus, 1950	Brazil	*KY263656* *KY263658*
Cycloporus variegatus Kato, 1934	Brazil, Spain	*KY263657* *KY263659* *KY263660* *KY263661*
Prostheceraeus vittatus (Montagu, 1815)	Sweden	AJ315647
Prostheceraeus roseus Lang, 1884	Tenerife	*KY263688* *KY263689* *KY263690* *KY263691*
	Florida	HQ659013

Table 1 (continued)

Species	Localities	GenBank accession number
Maritigrella crozieri (Hyman, 1939a)		*KY263686* *KY263687*
Maritigrella newmanae Bolaños, Quiroga & Litvaitis, 2007	Belize and US Virgin Islands	EF514801 EF514800 EF514798 EF514799
Amakusaplana acroporae Rawlinson, Gillis, Billings & Borneman, 2011	Aquariums US East Coast	JQ791553 JN711500 HQ659011 HQ659010
Enchiridium evelinae Marcus, 1949	Brazil	*KY263662* *KY263663* *KY263664* *KY263666* *KY263667* *KY263668* *KY263669* *KY263670* *KY263671* *KY263672* *KY263674* *KY263675* *KY263676* *KY263677* *KY263678* *KY263681* *KY263682* *KY263683* *KY263684* *KY263685*
Enchiridium sp.	Santa Helena Island	*KY263665* *KY263673* *KY263680*
Enchiridium sp.	Peru	*KY263679*
Prosthiostomum siphunculus (Delle Chiaje, 1822)	Spain	HQ659012
Macrostomum lignano[a] Ladurner, Schärer, Salvenmoser and Rieger, 2005	Laboratory culture in Innsbruck	HQ659019
Hofstenioplesia haswelli[a] Steinböck and Reisinger, 1924	Belize	KC869862
Prorhynchus stagnalis[a] Schultze, 1851	Michigan	KC869866
Microstomum lineare[a] (Müller OF, 1773)	Connecticut	KC869844

Italic values indicate the new sequences

[a] Outgroups

Specimens were, in most cases, fixed for morphological study too, and in total were from 55 species. We sampled as many different polyclad families as possible, covering 32 genera and 19 families in total (Table 2). General analyses included all those samples (136 sequences) and polyclad (45) and outgroup (4) sequences available on GenBank. Authors of species or genera included in the study are also cited in the references. As outgroups, we selected the Rhabditophora *Macrostomum lignano* Ladurner, Schärer, Salvenmoser & Rieger, 2005; *Hofstenioplesia haswelli* Steinböck & Reisinger, 1924; *Prorhynchus stagnalis* Schultze, 1851; and *Microstomum lineare* (Müller OF 1773), based on recent studies on Platyhelminthes phylogeny (Laumer and Giribet 2014; Laumer et al. 2015; Egger et al. 2015). In the RAxML analysis' batch only, *Macrostomum* was listed as outgroup. Initial trees with and without outgroups were obtained, and after the initial analysis, some discrepant sequences (for example, *Chromoplana*—KC869847.1, *Thysanozoon brocchii*—HQ659017.1, and *Stylochus* sp.—AF131707.1) were excluded from further analyses. Morphological characters used in Table 2 were obtained from the literature herein cited and from material collected and analyzed by the authors. Some of the specimens studied here are illustrated in Figs. 2, 3, 4, and 5, and some morphological or anatomical characters are depicted in Fig. 6. Histological sections were prepared and stained with hematoxilin-eosin as described in Bolaños et al. (2007). Figure 1 was produced using photographs of parts of drawings of Lang (1884), Laidlaw (1903c), and Faubel (1984). Figures 7 and 8 were produced using photographs of parts of drawings of Marcus (1947, 1949, 1950, 1952), Hyman (1939b, 1939c, 1953), Marcus and Marcus (1968), Prudhoe (1978), and Newman and Cannon (1994, 1996, 2000)—Taylor & Francis Ltd. (http://www.tandfonline.com). Respective permit was asked and granted from the journals that are still active. Since the type of development can also be variable inside the same genus (Rawlinson et al. 2008), and this information is mostly available for acotyleans, we have not included that feature in our table (Table 2). We did include the recent results of Quiroga et al. (2015) about nervous system in polyclads. We use the expression "gross morphology," as used by Rawlinson and Litvaitis (2008), descriptively as the general structural body plan (set of features) that characterizes a group of organisms studied (i.e., neither as a construction typical for phyla nor in a phylogenetic sense).

DNA extraction, amplification, and sequencing

Genomic DNA of each specimen was extracted using the NucleoSpin Tissue Kit (Macherey-Nagel GmbH & Co). Partial 28S rDNA marker was amplified through polymerase chain reaction (PCR) using 28S universal primers (LSU fw1 and LSU rev2) and the protocol of Sonnenberg et al. (2007). PCR was performed in 25 ml of reaction volume containing 22 ml of water, 0.5 ml of a forward and reverse PCR primer (10 pm/μl), 2 ml of template DNA solution, and one puReTaq Ready-To-Go PCR Bead (GE Healthcare). The cycling parameters for amplification of 28S were performed with an initial denaturation for 4 min at 94 °C; followed by 45 cycles of denaturation for 20 s at 94 °C, annealing for 20 s at 52.5 °C, and extension for 90 s at 72 °C; and ended with a 8-min

Table 2 Genera and families sampled in this study and their general morphological characters

Family	Genus	Tentacles	Eyespot location	Brain and nerve cords	Dorsal surface and shape	Pharynx form and location	Sucker or adhesive structure	Orientation of the male apparatus	Type of prostatic vesicle	Stylet and armed structures	Type of vagina	Lang's vesicle
Acotylea												
Discocelidae Laidlaw, 1903c	*Adenoplana* Stummer-Traunfels, 1933	Absent	Marginal, nuchal, and cerebral	Large, bilobed, with capsule?	Smooth and oval	Ruffled central	Absent	Backwards. Gonopores open in the posterior part	Without true prostatic vesicle, prostatoid organs instead	Absent	Simple and long	Present, sac, or horse-shoe shaped
Cryptocelidae Laidlaw, 1903b	*Phaenocelis* Stummer-Traunfels, 1933	Absent	Marginal, frontal, nuchal, and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth and elongated (other shapes in the family)	Ruffled anterior	Absent	Backwards. Gonopores open in the posterior part	True interpolated	Absent	Vagina bulbosa, long, looping	Present, rod--like, elongated
Pseudostylochidae Faubel, 1983	*Idioplana* Woodworth, 1898	Present and nuchal	Marginal, nuchal, and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth	Ruffled oblong in different parts of the body	Absent	Backwards	True free and oblong	Absent	Simple and long. Female dorsal to male apparatus	Present, bulbous
Stylochidae Stimpson, 1857	*Stylochus* Ehrenberg, 1851	Present and nuchal	Marginal, frontal, nuchal, and cerebral	?	Smooth and oval	Ruffled central	Absent	Backwards. Gonopores open in the posterior part. Simple seminal vesicle	True free	Absent	Simple and short	Absent
	Imogine Girard, 1853	Present and nuchal	Marginal, nuchal, and cerebral	?	Smooth and oval	Ruffled central	Absent	Backwards. Tripartite seminal vesicle	True free	Absent	Simple	Absent
Leptoplanidae Stimpson, 1857	*Leptoplana* Ehrenberg, 1831	Absent	Nuchal and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth	Ruffled central or anterior	Absent, present between gonopores in *Leptoplana tremellaris*	Backwards. Enclosed in a muscular structure	True interpolated	Absent or present cirrus	Simple, long, looping	Reduced
Notoplanidae Faubel, 1983	*Notoplana* Laidlaw, 1903b	Absent	Nuchal and cerebral	?	Smooth	Ruffled central	Absent	Backwards	True interpolated	Present cirrus	Vagina simple or bulbosa	Present

Table 2 (continued)

Family	Genus	Tentacles	Eyespot location	Brain and nerve cords	Dorsal surface and shape	Pharynx form and location	Sucker or adhesive structure	Orientation of the male apparatus	Type of prostatic vesicle	Stylet and armed structures	Type of vagina	Lang's vesicle
Hoploplanidae Stummer-Traunfels, 1933	*Hoploplana* Laidlaw, 1902	Present and nuchal	Nuchal (ring-like) and cerebral	?	Papillated or smooth and oval or rounded	Deeply ruffled and central	Absent	Backwards. Seminal vesicle absent, spermiducal bulbs instead	True interpolated very small	Present stylet	Simple and short	Absent
Planoceridae Lang, 1884	*Planocera* Blainville, 1828	Present and nuchal	Nuchal (ring-like) and cerebral	Large, slightly bilobed, with capsule. Thick, well developed	Smooth	Deeply ruffled and central	Absent	Backwards	True free, normal	Cirrus with spines or hooks	Vagina bulbosa	Reduced or present
	Paraplanocera Laidlaw, 1903a	Present and nuchal	Nuchal (ring-like) and cerebral	Large, slightly bilobed, with capsule. Thick, well developed	Smooth	Deeply ruffled and central	Absent	Backwards	True free, bipartite	Cirrus with spines or hooks	Vagina bulbosa	Reduced or present
Stylochoplanidae Faubel, 1983	*Armatoplana* Faubel, 1983	Absent	Nuchal and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth	Ruffled anterior	Absent	Backwards	True interpolated	Tubular stylet	Vagina bulbosa	Present
Pleioplanidae Faubel, 1983	*Melloplana* Faubel, 1983	Absent	Nuchal and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth	Ruffled central or anterior	Absent	Backwards	True interpolate with tubular chambers	Absent	Vagina bulbosa	Present
Gnesiocerotidae Marcus and Marcus, 1966	*Echinoplana* Haswell, 1907	Absent	Nuchal and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth and elongated	Ruffled central, anterior or posterior	Absent	Backwards	True interpolate	Cirrus with spines and hooks	Vagina bulbosa	Present

Table 2 (continued)

Family	Genus	Tentacles	Eyespot location	Brain and nerve cords	Dorsal surface and shape	Pharynx form and location	Sucker or adhesive structure	Orientation of the male apparatus	Type of prostatic vesicle	Stylet and armed structures	Type of vagina	Lang's vesicle
Theamatidae Marcus, 1949	*Theama* Marcus, 1949	Absent	Cerebral and frontal	?	Smooth and narrow and elongated	Ruffled and central to posterior	Absent	Backwards. Gonopores open in the posterior part	True interpolated	Stylet or sclerotized ejaculatory duct lining	Simple and short cement pouch present	Absent
Cestoplanidae Lang, 1884	*Cestoplana* Lang, 1884	Absent	Frontal	Large, bilobed, with capsule. Thick and well developed	Smooth and narrow and elongated	Ruffled and posterior	Present and posterior	Perpendicular or forwards. May present duplicated structures	True interpolated	Absent	Short. Cilliated cement pouch present	Absent or present
Cotylea												
Boniniidae Bock, 1923	*Boninia* Bock, 1923	Marginal and lobed	Cerebral and frontal	Anteriorly located, with capsule. Thin, round, well developed	Smooth and narrow and elongated, oblong	Ruffled and anterior or central	Present and posterior	Perpendicular or backwards	Absent prostatoid organs	Armed prostatoid organs	Cement pouch present	Present
Chromoplanidae Bock, 1922	*Chromoplana* Bock, 1922	Absent	Few marginal and cerebral	?	Smooth and elongated or oval	Ruffled and anterior	Present and posterior	Forwards	True interpolated	Absent	Simple, and short cement pouch present	Absent
Amyellidae Faubel, 1984	*Chromyella* Corrêa, 1958	Absent	Cerebral and tentacular	?	Smooth and elongated	Ruffled and anterior	Absent?	Forwards	Absent	Absent	Cement pouch lacking	Absent
Pericelidae Laidlaw, 1902	*Pericelis* Laidlaw, 1902	Marginal, well separated, and infolded	Tentacular, marginal, frontal, and cerebral	Large, bilobed, with capsule. Thick and well developed	Smooth and elongated oval	Deeply ruffled and central	Present and posterior	Backwards, enclosed in a muscular bulb	True interpolated	?	Simple cement pouch present	Absent
Pseudocerotidae Lang, 1884	*Pseudoceros* Lang, 1884	Marginal and simple folds	Tentacular and cerebral	Small, round, not bilobed. Thin.	Smooth and oval	Deeply ruffled and anterior	Present anterior	Forwards and single	Free and anterior--dorsal to ejaculatory duct	Stylet present	Cement pouches present	Absent

Table 2 (continued)

Family	Genus	Tentacles	Eyespot location	Brain and nerve cords	Dorsal surface and shape	Pharynx form and location	Sucker or adhesive structure	Orientation of the male apparatus	Type of prostatic vesicle	Stylet and armed structures	Type of vagina	Lang's vesicle
	Pseudobiceros Faubel, 1984	Marginal and square or ear-like folds	Tentacular and cerebral	Small, round, not bilobed. Thin.	Smooth and elongated oval	Ruffled anterior	Present anterior	Forwards and double	Free and antero-dorsal to ejaculatory duct	Stylet present	Cement pouches present	Absent
	Thysanozoon Grube, 1840	Marginal and ear-like folds	Tentacular and cerebral	Small, round, not bilobed. Thin.	Papillated and oval	Ruffled anterior	Present anterior	Forwards and double	Free and anterior or medio-dorsal to ejaculatory duct	Stylet present	Cement pouches present	Absent
	Yungia Lang, 1884	Marginal and ear-like folds	Tentacular and cerebral	?	Smooth	Ruffled and anterior intestine branches ending in the body surface	Present anterior	Forwards and single	Free and antero-dorsal to coiled ejaculatory duct	Stylet present	Cement pouches present	Absent
	Maiazoon Newman and Cannon, 1996	Marginal and square folds	Tentacular and cerebral	?	Smooth and elongated oval	Ruffled and anterior	Present and central	Forwards and double	Free and antero-dorsal to ejaculatory	Stylet present	Cement pouches present, three to five female gonopores	Absent
	Monobiceros Faubel, 1984	Marginal and ear-like folds	Tentacular and cerebral	?	Smooth and elongated oval	Ruffled and anterior	Present and anterior	Forward and double but with only one gonopore	Free	Stylet present	Cement pouches present	Absent
	Phrikoceros Newman and Cannon, 1996	Marginal and ear-like or square folds	Tentacular and cerebral	?	Smooth and elongated oval	Ruffled anterior	Present anterior	Forward and single	Free and anterior to ejaculatory duct	Stylet present	Cement pouches present	Absent
Euryleptidae Lang, 1884	*Cycloporus* Lang, 1884	Marginal and bumps	Tentacular and cerebral	Large, bilobed, with capsule?	Smooth or papillated and oval	Tubular and anterior, marginal digestive vesicles present	Present middle	Forwards and single	Free and antero-dorsal to the ejaculatory duct	Stylet present	Simple and short cement pouches and multiple uterine vesicles present	Absent

Table 2 (continued)

Family	Genus	Tentacles	Eyespot location	Brain and nerve cords	Dorsal surface and shape	Pharynx form and location	Sucker or adhesive structure	Orientation of the male apparatus	Type of prostatic vesicle	Stylet and armed structures	Type of vagina	Lang's vesicle
	Eurylepta Ehrenberg, 1831	Marginal and extensions	Cerebral and tentacular	Large, bilobed, with capsule?	Smooth and oval	Tubular and anterior	Present middle	Forward and single	Free and antero-dorsal to the ejaculatory duct	Stylet present	Simple and short cement pouches and pair of uterine vesicles present	Absent
	Prosthecereus Schmarda, 1859	Marginal and pointed extensions	Cerebral	?	Smooth and oval	Tubular and anterior	Present middle	Forward and single	Free and antero-dorsal to the ejaculatory duct	Stylet present	Cement pouches present and multiple uterine vesicles	Absent
	Maritigrella Newman and Cannon, 2000	Marginal and long extensions	Cerebral and tentacular	Small, slightly bilobed. Thin	Smooth and elongate oval	Tubular, small and anterior	Present anterior	Forward and single	Free and antero-dorsal to the ejaculatory duct	Stylet present	Cement pouches present	Absent
Prosthiostomidae Lang, 1884	*Enchiridium* Bock, 1913	Absent	Cerebral and marginal encircling all body	Small, slightly bilobed, no capsule. Thin	Smooth and elongate	Tubular anterior	Present middle	Forwards and two prostatic vesicles, stylet bent backwards	Free and bond in a muscular bulb antero-dorsal to ejaculatory duct	Stylet present	True mucous chamber present	Absent
	Prosthiostomum Quatrefages, 1845	Absent	Cerebral and marginal only anterior	Large, bilobed, with capsule?	Smooth and elongate	Tubular anterior	Present middle	Forwards and two prostatic vesicles	Free and lateral or ventral to ejaculatory duct	Stylet present	True mucous chamber present	Absent
	Lurymare Marcus and Marcus, 1968	Absent	Cerebral and marginal only anterior	?	Smooth and elongate	Tubular anterior	Present middle	Forwards and two prostatic vesicles	Free and bond in a muscular bulb that usually involve the seminal vesicle	Stylet present	True mucous chamber present	Absent
	Amakusaplana Kato, 1938	Absent	Cerebral and marginal very close to each other	?	Smooth and elongate oval	Tubular anterior	Absent?	Forwards and two prostatic vesicles	Free and at each side of the ejaculatory duct	Stylet present	Cement pouches present	Absent

extension at 72 °C. Successful PCR products were purified using the NucleoSpin Extract II (Macherey-Nagel GmbH & Co). Cycle sequencing using Big Dye 3.1 and the PCR primers (2 pm/μl) were conducted in the Genomic Service Unit of the Department of Biology, Ludwig-Maximilians-University Munich, Germany.

Sequence alignment and phylogenetic analyses

Novel sequences, 136 in total, were edited using MEGA5 and 6 (Tamura et al. 2011, 2013), and consensus sequences were generated in BioEdit (Hall 1999). Some sequences were edited and consensus generated in Geneious R6 (version 6.1.5) (http://www.geneious.com; Kearse et al. 2012). All of them are now available in GenBank (Table 1). Alignment included 185 sequences in total and were generated with Muscle (Edgar 2004) using the default settings. Hypervariable areas of the alignment were recognized through GBlocks (http://molevol.cmima.csic.es/castresana/Gblocks_server.html), using the less stringent options, and pruned. The general Polycladida alignment has 185 sequences and was 803 base pair (bp) long; the separate Cotylea alignment had 154 sequences and was 888 bp long. The separate Acotylea alignment had 32 sequences with 874 bp. Maximum likelihood (ML) single-gene trees were generated using RAxML v. 7.2.6 (Stamatakis 2006), under GTR model, and node support was assessed with non-parametric bootstrapping with 2000 replicates. In addition to the complete dataset, we ran separated analyses of Cotylea (*Hoploplana* as outgroup) and Acotylea (*Pericelis* and *Cestoplana* as outgroups) to test phylogenetic hypotheses obtained from the general analysis and to improve resolution within superfamily and family level. ML trees were visualized in FigTree v. 1.2 (http://tree.bio.ed.ac.uk/software/figtree/) and edited for publication in Adobe Photoshop CS3 and Corel Photo-Paint X6. Traditional and potentially relevant morphological characters were selected and coded into states (absence/presence of sucker, of single or multiple gonopores, of an accessory vesicle, of pseudotentacles, and of eyes and tentacles and their position). The character states were plotted on the molecular tree as recommended by Halanych (2016), and apomorphies were estimated using parsimony. We evaluated the major competing historic and the herein recovered phylogenetic hypotheses, using the Shimodaira-Hasegawa test (Shimodaira and Hasegawa 2001) and the approximately unbiased test (Shimodaira 2002) in RAxML v. 7.2.6 (Stamatakis 2006) and Consel (Shimodaira and Hasegawa 2001). The main dataset and the PROTGAMMAGTR model were used for these analyses. We tested topological constraints of the whole systems of Faubel, Prudhoe, and the one proposed herein, as well as constraining each of the superfamilies individually. Additionally, we also evaluated the suborders Acotylea and Cotylea in traditional and newly proposed arrangement.

Results

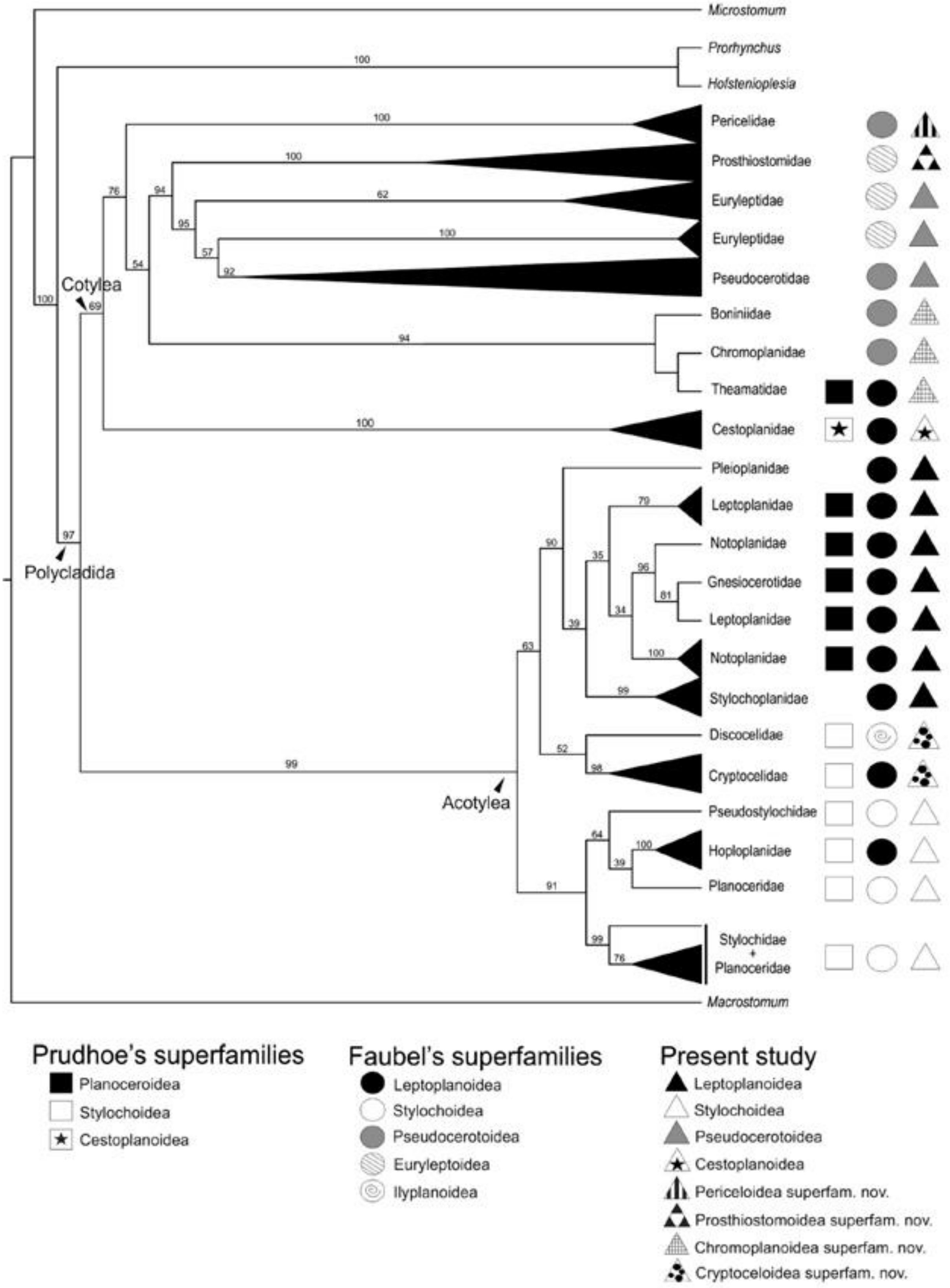
General tree topology

In our general polyclad tree (Figs. 2 and 3), Polycladida was recovered as monophyletic (97% bootstrap support (BS)). Acotylea in a traditional sense was not monophyletic, because *Cestoplana* was recovered sister to Cotylea (Fig. 3) with high support (BS 69). *Theama*, another genus traditionally included in Acotylea, clustered quite deeply within Cotylea, as sister clade to *Boninia* and *Chromyella*, two basal cotylean genera (Fig. 3). All other acotyleans clustered together with high support (BS 99). *Cestoplana* appeared in the tree as sister of all other Cotylea (Fig. 3). *Pericelis* branches off as sister of all further cotyleans, followed by a clade, consisting of *Boninia*, *Chromyella*, and *Theama*, as sister group to the remaining Cotylea (Figs. 3 and 8). The same topology was recovered in analyses focusing only on Acotylea or Cotylea, with just slightly different bootstrap values (Supplementary Figs.2 and 3).

Prosthiostomidae, Euryleptidae, and Pseudocerotidae were recovered as a clade (BS 94). Prosthiostomids (BS 100) as sister to a combined clade (BS 95) of the genera included in Pseudocerotidae (BS 92) and Euryleptidae, the latter family paraphyletic (Fig. 2). *Prostheceraeus*, *Maritigrella*, and *Cycloporus* resulted sisters of Pseudocerotidae, but the two species of *Cycloporus* did not clustered in the same clade, as *Cycloporus gabriellae* branched independently (Fig. 3). Within Pseudocerotidae, *Pseudobiceros*, despite divided in two clades, formed a monophyletic group with the genera *Maiazoon* and one *Thysanozoon*, and *Yungia* grouped with *Phrikoceros* and *Monobiceros*. And these clades together with other *Thyzanozoon* formed a monophyletic group of genera with multiplication of reproductive structures (BS 95). The acotylean clade (BS 99) of the tree shows a clade formed by Stylochidae, Planoceridae, and Hoploplanidae (BS 91) as the sister group of the clade with remaining Acotylea (BS 63) (Fig. 2). A clade with Discocelidae and Cryptocelidae (BS 52) is sister group to a clade grouping paraphyletic Leptoplanidae and Notoplanidae with Gnesioceridae, Stylochoplanidae, and Pleioplanidae (BS 90) (Fig. 2).

Classification systems

On suborder and superfamily level, our molecular phylogenetic hypothesis is not compatible with either Faubel's or Prudhoe's systems. The suborders Acotylea and Cotylea, as traditionally considered, were rejected in the approximately unbiased (AU) hypothesis test, but not in the Shimodaira-Hasegawa (SH) test (Table 3). A new arrangement (Fig. 2) was tested and not rejected, with high p values (Table 3). Compared to our trees, just one of Prudhoe's superfamilies was monophyletic, Cestoplanoidea (Fig. 2). Stylochoidea appears mixed with


Microstomum
Prorhynchus
Hofstenioplesia
Pericelidae
Prosthiostomidae
Euryleptidae
Euryleptidae
Pseudocerotidae
Boniniidae
Chromoplanidae
Theamatidae
Cestoplanidae
Pleioplanidae
Leptoplanidae
Notoplanidae
Gnesiocerotidae
Leptoplanidae
Notoplanidae
Stylochoplanidae
Discocelidae
Cryptocelidae
Pseudostylochidae
Hoploplanidae
Planoceridae
Stylochidae + Planoceridae
Macrostomum
Cotylea
Polycladida
Acotylea
100
100
100
76
94
62
95
100
57
92
54
100
69
94
100
97
79
90
35
96
81
39
34
100
63
99
52
98
99
64
100
39
91
99
76
Prudhoe's superfamilies
Planoceroidea
Stylochoidea
Cestoplanoidea
Faubel's superfamilies
Leptoplanoidea
Stylochoidea
Pseudocerotoidea
Euryleptoidea
Ilyplanoidea
Present study
Leptoplanoidea
Stylochoidea
Pseudocerotoidea
Cestoplanoidea
Periceloidea superfam. nov.
Prosthiostomoidea superfam. nov.
Chromoplanoidea superfam. nov.
Cryptoceloidea superfam. nov.

◀ **Fig. 2** Polycladida family-level 28S rDNA phylogeny (RAxML; *numbers* refer to the bootstrap support values). Cladogram with superfamilies according to Faubel's (represented by *circles*) and Prudhoe's (represented by *squares*) classification systems and the classification proposed in this study (represented by *triangles*)

Planoceroidea in two clades (BS 91 and 63, respectively). In the Acotylea, genera with nuchal, cerebral, and marginal eyespots, like *Adenoplana* and *Imogine*, grouped with genera with only nuchal and cerebral eyespots (for example, *Leptoplana* and *Hoploplana*) (Fig. 3). Similarly, our molecular trees do not support Faubel's classification (Fig. 2) and only Illyplanoidea appeared as monophyletic. Groups with interpolated prostatic vesicle (superfamily Leptoplanoidea) clustered with genera that present free prostatic vesicle (superfamily Stylochoidea) in both the Acotylea and the Cotylea branches. In Cotylea, the type of pharynx was not an autapomorphy of monophyletic groups either; genera with tubular pharynx (Faubel's Euryleptoidea) clustered with genera with ruffled pharynx (Faubel's Pseudocerotoidea) (Fig. 2). Therefore, superfamilies in this suborder were also not monophyletic.

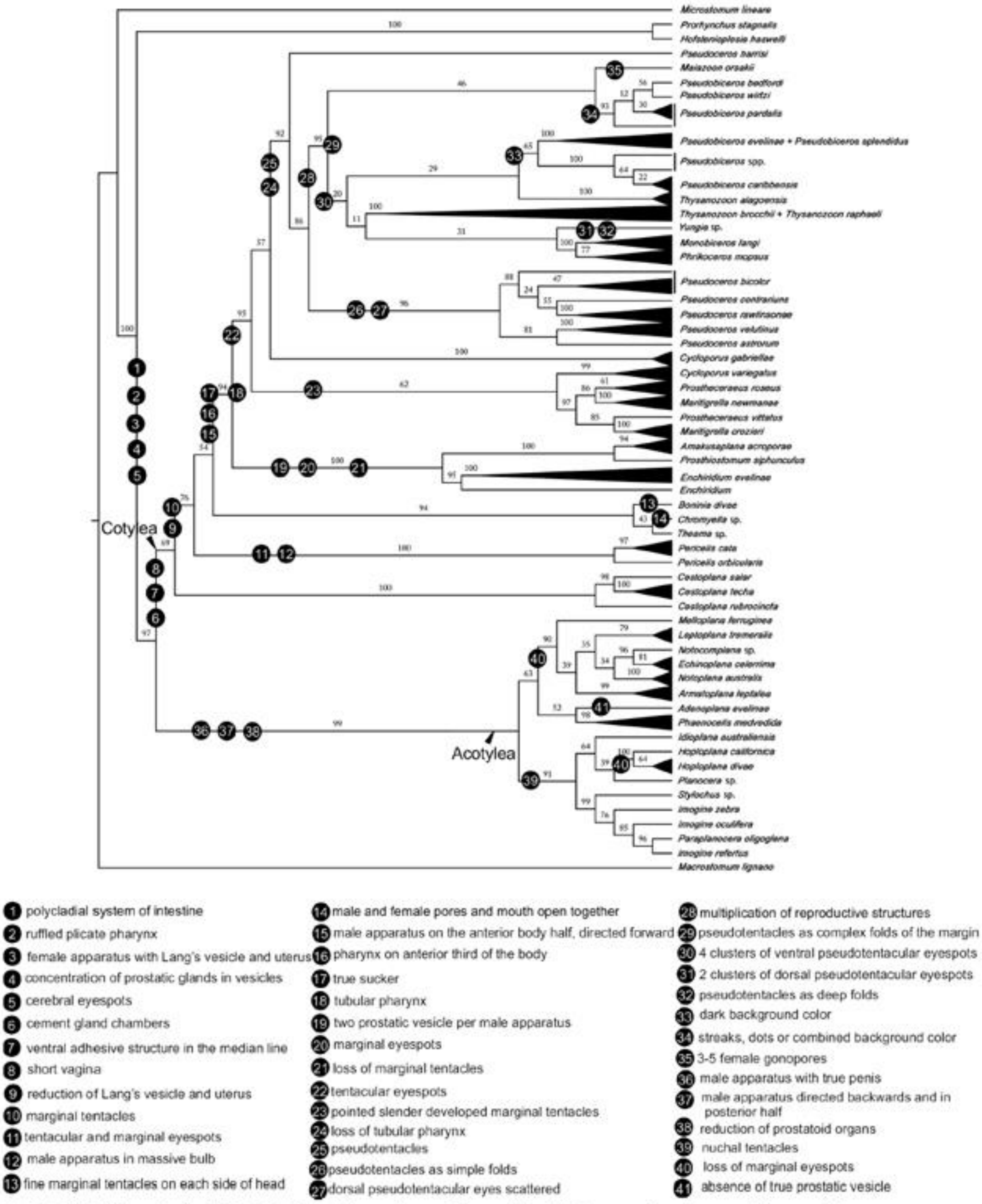
These results were corroborated by the hypothesis tests, which showed that both Faubel's and Prudhoe's systems were significantly rejected by the molecular data (Table 3). Individually, Faubel's Ilyplanoidea, Leptoplanoidea, and Pseudocerotoidea were rejected in both AU and SH tests, as were also Prudhoe's Planoceroidea and Stylochoidea. However, Euryleptoidea sensu Faubel was rejected only in the AU test, but not in the SH test, and Stylochoidea sensu Faubel and Cestoplanoidea sensu Prudhoe were not rejected significantly (Table 3). Despite the non-monophyletic status of the traditional superfamilies, conventional family groups were in general recovered in our trees, and, in Cotylea, most resulted in monophyletic with high bootstrap support values. One exception was the paraphyletic Euryleptidae, with *C. gabriellae* sister to the Pseudocerotidae. In addition to Cycloporus, the genera *Maritigrella*, *Prostheceraeus*, and *Thysanozoon* were also not monophyletic in our tree. The genus *Pseudobiceros* was also non-monophyletic, but divided in two groups, and the one including *Pseudobiceros pardalis*, *P. bedfordi*, and *P. wirtzi*, grouped with *Maiazoon*. The other *Pseudobiceros* group was composed of *Pseudobiceros evelinae*, *P. splendidus*, and *P. caribbensis*.

Morphological characters

Our direct observation of specimens (Figs. 4, 5 and 6) and the analysis of literature on genera we were not able to collect were summarized in a table with main morphological characters (Table 2). We describe the distribution of the taxonomically important characters on our 28S gene tree and infer potential apomorphies using parsimony. According to our study, the ancestral polyclad probably had cerebral eyespots; lacked marginal, tentacular, or nuchal eyespots; also lacked ventral adhesive structure and tentacles; was oval shaped with smooth dorsal surface; had a simply ruffled pharynx in middle body; was hermaphrodite with one male and one female gonopore; had male pore in posterior half of the body; lacked stylet; and had free prostatic vesicle and long vagina. In general, there is relatively little homoplasy regarding traditional characters. Assuming that cerebral eyespots were ancestrally present in Polycladida, but tentacles were not, a true sucker, tubular pharynx (lost in Pseudocerotidae), an accessory vesicle, multiplied reproductive structures, marginal and nuchal tentacles, and tentacular and nuchal eyespots have only evolved once (Fig. 2). Marginal tentacles were lost only once in Polycladida subclades. All these apparently unique incidents can be interpreted as apomorphies supporting the molecular-based topology. On our tree, only the distribution of the tentacular and marginal eyespots is more complex implying multiple potential gains or losses; while our tree shows one of several possible scenarios, the evolution of these features remains ambiguous. Similarly, there is no clear pattern in the distribution of taxa with interpolated or free prostatic vesicle (Table 2); we therefore do not show this feature in Fig. 2.

The Acotylea sensu stricto were divided in a tentaculated (with nuchal tentacles) and atentaculated group (Figs. 3 and 7). The tentaculated group presented members with both interpolated and free prostatic vesicle and genera with only nuchal and cerebral eyespots as well as with marginal, nuchal, and cerebral eyespots (Table 2 and Figs. 3 and 7). It included *Hoploplana*, *Paraplanocera*, *Planocera*, *Idioplana*, *Stylochus*, and *Imogine* (Fig. 3) However, in the atentaculated group, there is a clear division between a group with marginal, cerebral, and nuchal eyespots and another with only cerebral and nuchal eyespots (Fig. 7). *Adenoplana* and *Phaenocelis* were grouped together, and these genera share the atentaculated condition with marginal, cerebral, and nuchal eyespots (Table 2 and Figs. 3 and 7).

The Cotylea, apart from the basal *Cestoplana*, *Pericelis*, and the *Chromyella*, *Boninia*, and *Theama* clade, presented a large clade that included all Pseudocerotidae, Euryleptidae, and Prosthiostomidae. The *Chromyella-Boninia-Theama* clade (BS 94) consists of animals with elongated bodies and mixed cotylean-acotylean features (Table 2 and Fig. 8). The Pseudocerotidae (BS 92) is the only group with pseudotentacles (Table 2 and Figs. 3 and 8). Two groups are formed inside this cluster. One (BS 95) shows possible multiplication of reproductive structures (either male or female) and complex folded pseudotentacles and is composed of *Thysanozoon*, *Pseudobiceros*, *Yungia*, *Monobiceros*, *Phrikoceros*, and *Maiazoon* (Fig. 3). The other group (BS 96) has single reproductive structures and simple folded pseudotentacles (Table 2), composed basically by



① polycladial system of intestine
② ruffled plicate pharynx
③ female apparatus with Lang's vesicle and uterus
④ concentration of prostatic glands in vesicles
⑤ cerebral eyespots
⑥ cement gland chambers
⑦ ventral adhesive structure in the median line
⑧ short vagina
⑨ reduction of Lang's vesicle and uterus
⑩ marginal tentacles
⑪ tentacular and marginal eyespots
⑫ male apparatus in massive bulb
⑬ fine marginal tentacles on each side of head
⑭ male and female pores and mouth open together
⑮ male apparatus on the anterior body half, directed forward
⑯ pharynx on anterior third of the body
⑰ true sucker
⑱ tubular pharynx
⑲ two prostatic vesicle per male apparatus
⑳ marginal eyespots
㉑ loss of marginal tentacles
㉒ tentacular eyespots
㉓ pointed slender developed marginal tentacles
㉔ loss of tubular pharynx
㉕ pseudotentacles
㉖ pseudotentacles as simple folds
㉗ dorsal pseudotentacular eyes scattered
㉘ multiplication of reproductive structures
㉙ pseudotentacles as complex folds of the margin
㉚ 4 clusters of ventral pseudotentacular eyespots
㉛ 2 clusters of dorsal pseudotentacular eyespots
㉜ pseudotentacles as deep folds
㉝ dark background color
㉞ streaks, dots or combined background color
㉟ 3-5 female gonopores
㊱ male apparatus with true penis
㊲ male apparatus directed backwards and in posterior half
㊳ reduction of prostatoid organs
㊴ nuchal tentacles
㊵ loss of marginal eyespots
㊶ absence of true prostatic vesicle

Fig. 3 Polycladida species-level 28S rDNA ML phylogenetic tree with morphological characters plotted as potential apomorphies

Pseudoceros. The Prosthiostomidae (BS 100) is the only cotylean family with accessory vesicles (more than one prostatic vesicle per male system) and with only cerebral and marginal eyespots.

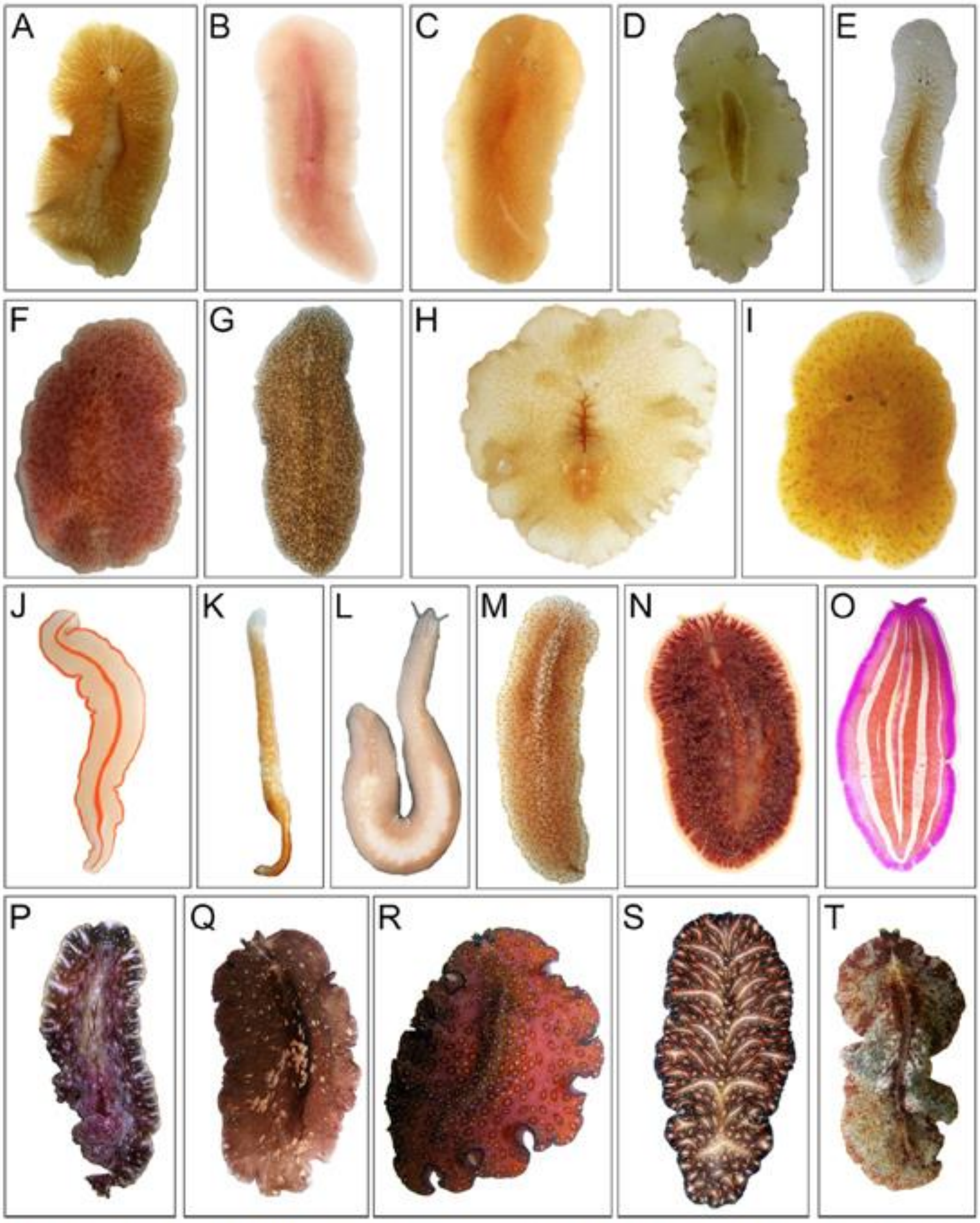


Fig. 4 Selected polyclad species used in this study. **a** *Adenoplana evelinae*. **b** *Phaenocelis medvedica*. **c** *Notoplana* sp. **d** *Notocomplana* sp. **e** *Armatoplana leptalea*. **f** *Melloplana ferruginea*. **g** *Imogine* sp. **h** *Planocera* sp. **i** *Hoploplana divae*. **j** *Cestoplana techa*. **k** *Cestoplana salar*. **l** *Boninia divae*. **m** *Enchiridium evelinae*. **n** *Cycloporus variegatus*. **o** *Prostheceraeus roseus*. **p** *Pseudoceros rawlinsonae*. **q** *Pseudobiceros* sp. **r** *Pseudobiceros pardalis*. **s** *Pseudobiceros bedfordi*. **t** *Thysanozoon alagoensis*

Discussion

Gene tree compared to morphology

Our molecular data is limited to a single, but informative gene, covering a large portion of polyclad biodiversity. As expected, the partial 28S rDNA appears quite powerful to reconstruct a backbone topology of Polycladida. All our 28S rDNA trees on different taxon sets were fully resolved, congruent, and received quite strong bootstrap support throughout. The monophyly of Polycladida and of most of the traditionally accepted polyclad families was recovered. Remarkably, the distribution

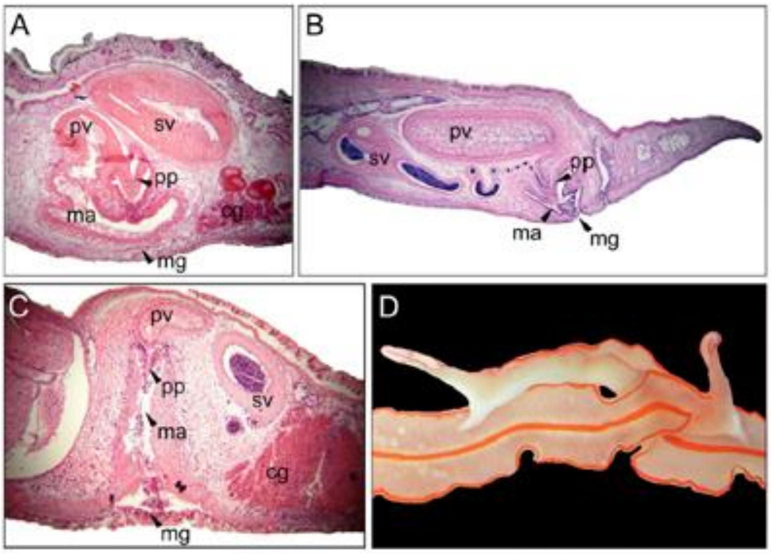


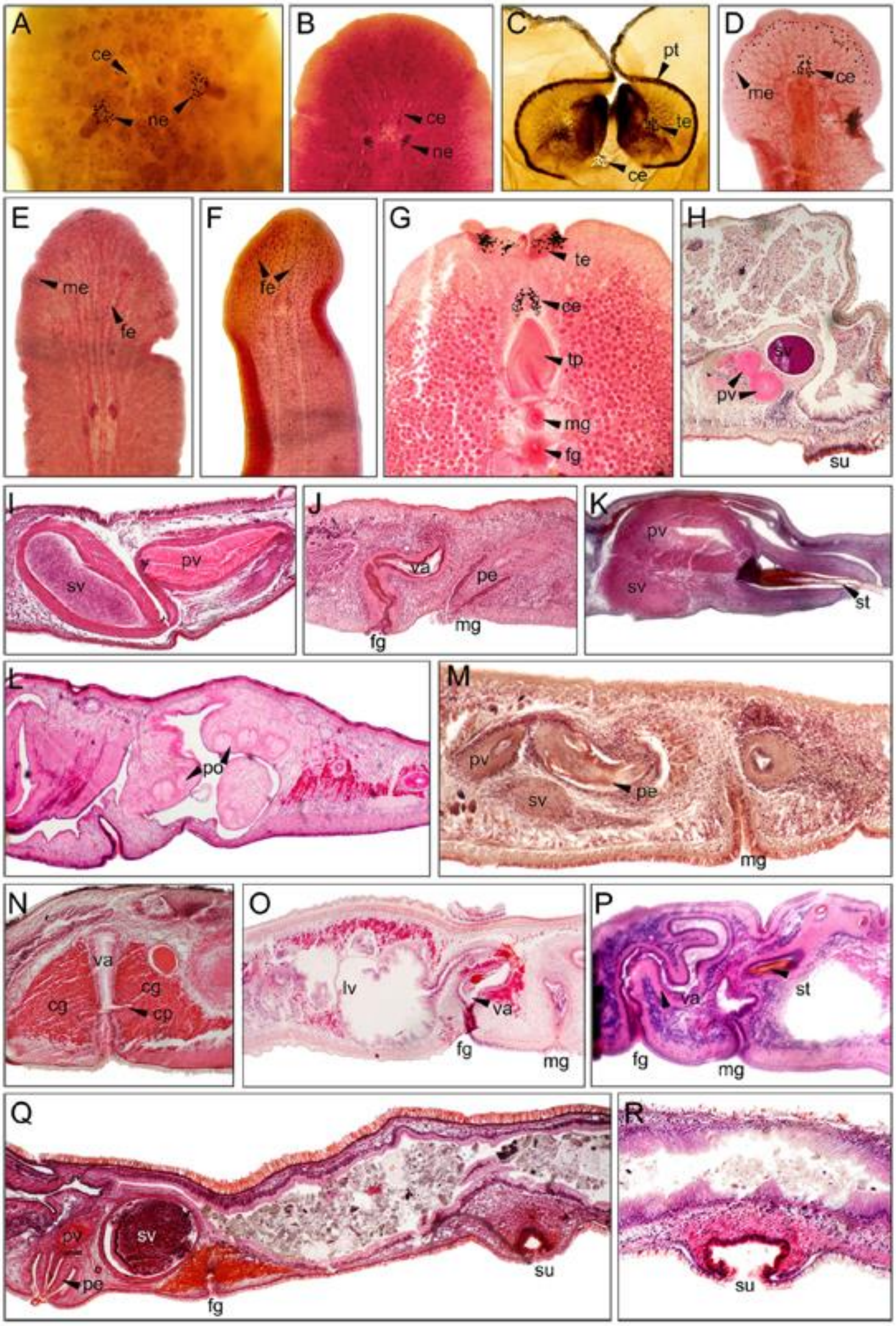
Fig. 5 Cotylea and Acotylea general male system organization. **a** *Pseudobiceros* with forward directed male structures and mucous glands. **b** *Imogine* with backward directed male structures. **c** *Cestoplana* with perpendicular to forward directed male structures and mucous glands. **d** *Cestoplana* specimens during simultaneous hypodermic impregnation

of most of the traditionally important morphological features, on our molecular tree, is reasonable; several of the herein recovered, novel molecular clades are supported by potential synapomorphies (Fig. 3). It is also important to note that the few characters showing a complex distribution on our molecular tree (characters 21 and 22 and type of prostatic vesicle) do not follow any apparent common pattern; rather than suggesting alternative topologies, these characters may have been independently subject to multiple losses or, less likely, convergent gain. We thus conclude that our single-gene tree is supported rather than rejected by available morphological evidence. Major discrepancies to traditional hypotheses refer to suborder and superfamily level only. We thus hypothesize that our 28S rDNA trees more correctly reflect Polycladida evolution than any of Faubel's and Prudhoe's contradicting systems which were based on single morphological characters considered to be important, i.e., having more weight than others. This was corroborated by our hypothesis test, which rejected both Faubel's and Prudhoe's systems and most of their superfamilies.

Differences to earlier morphology-based hypotheses

The most obvious difference of our tree to conventional Polycladida taxonomy is the paraphyly of both classical Cotylea and Acotylea. Lang (1884) and Faubel (1984) also pointed to non-monophyletic suborders, due to distribution of an adhesive structure and female system characters in different families, and a lack of synapomorphies of characters that each considered phylogenetically robust. Cladistic analyses (Rawlinson and Litvaitis 2008) recovered Cotylea as monophyletic, but they used as outgroup typical acotyleans and not *Cestoplana* or *Theama*, "acotyleans" with mixed characters. In our tree, this paraphyly resulted from some supposedly acotylean taxa clustered within Cotylea. Rather than causing confusion or implying higher levels of morphological homoplasy, such results may even relieve some of the traditional problems. As the type of prostatic vesicle was shown to be an inadequate character to divide acotylean families, it is not a reliable character to separate acotyleans from cotyleans either. *Theama* and *Cestoplana* were said to present characters that are dominantly represented in cotylean families (Laidlaw 1903c; Faubel 1983). Theamatidae as well as Cestoplanidae present cement-mucous gland chambers (cement pouch) and lack nuchal eyespots, true uteri, and Lang's vesicle (Lang 1884; Marcus 1949; Faubel 1983); both families also have a similar gross morphology with extremely elongated body and rounded anterior end (Fig. 8). In *Cestoplana*, the orientation of the male apparatus is posterior to the male gonopore (Fig. 5c), and the walls of the male antrum are folded to form a penis sheath, just as found in Cotylea (Laidlaw 1903c). The genus also presents an adhesive pad which resembles the ventral sucker, a diagnostic character of cotyleans. We also observed

Fig. 6 Morphological and anatomical characters used in Polycladida ▶ taxonomy. **a** Nuchal tentacles in *Hoploplana and eyespots related to it*. **b** Nuchal and cerebral eyespots. **c** Pseudotentacles in *Pseudobiceros*. **d** Marginal eyespots in *Prosthiostomum*. **e** Eyespots in *Latocestus*. **f** Eyespots in *Cestoplana*. **g** Tubular pharynx and marginal tentacles in *Cycloporus*. **h** Pair of prostatic vesicles in *Lurymare*. **i** Interpolated prostatic vesicle. **j** Long vagina. **k** Stylet. **l** Prostatoids in *Adenoplana*. **m** Penis structure. **n** Short vagina, cement glands, and cement pouch. **o** Lang's vesicle. **p** Looping vagina. **q** Free prostatic vesicle. **r** Sucker. *ce* cerebral eyespots, *cg* cement glands, *cp* cement pouch, *fe* frontal eyespots, *fg* female gonopore, *lv* Lang's vesicle, *me* marginal eyespots, *mg* male gonopore, *ne* nuchal eyespots, *pe* penis, *po* prostatoids, *pt* pseudotentacles, *pv* prostatic vesicle, *te* tentacular eyespots, *tp* tubular pharynx, *st* stylet, *su* sucker, *sv* seminal vesicle, *va* vagina



(Fig. 5d) that a *Cestoplana* species showed hypodermic impregnation as part of reproduction behavior, which is not common in Acotylea but often found in Cotylea (Rawlinson et al. 2008). *Theama* also presents the male structures before

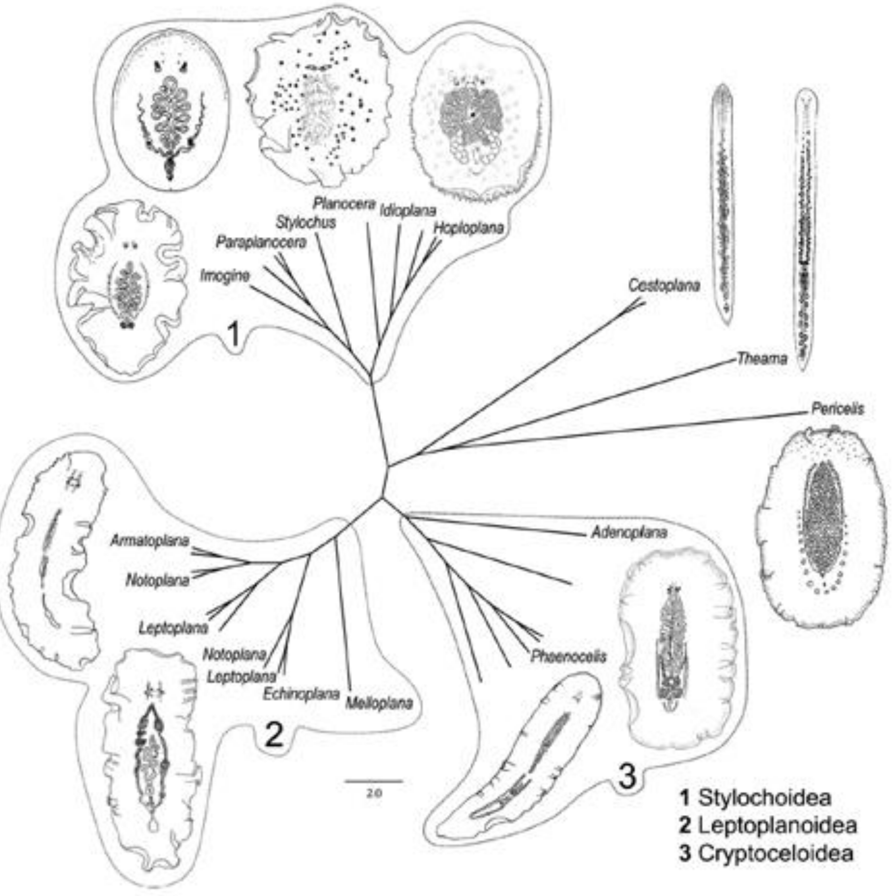


Fig. 7 Acotylea 28S rDNA phylogeny showing genus gross morphology and the new systematic division of the monophyletic superfamilies. Figures from Hyman (1939b, 1939c), Hyman (1953), Marcus (1949, 1950, 1952), Marcus and Marcus (1968), and Prudhoe (-1978) (under permission of University of Chigago Press, Australian Museum Scientific Publications and Bulletin of the American Museum of Natural History)

the male gonopore but lack ventral adhesive structures (Curini-Galletti et al. 2008). However, both families present interpolated prostatic vesicle, which was considered an acotylean feature (Faubel 1983). Also, characters as position of gonopores at the last part of the body and the absence of clear cerebral eyespots have historically placed both genera in Acotylea (Faubel 1983; Prudhoe 1985). Bock (1922) and Laidlaw (1903c) stated that *Cestoplana* was an exception in Acotylea and that it is closely related to cotyleans, but the group remained in its position because of prostatic vesicle features, which we showed are not robust characters. Additionally, our hypothesis tests (Table 3) showed that both traditional Acotylea and Cotylea were rejected in the AU test, while the new arrangement with *Cestoplana* and *Theama* in Cotylea was not rejected in any test (Table 3). We suggest that these genera should then be included in an emendation of the Cotylea, as molecular and morphological evidences point to that hypothesis. This will be further discussed in the "Polycladida reclassification" section.

In Polycladida, according to our results (Table 2, Fig. 2), groups with interpolated prostatic vesicle clustered with genera that present a free prostatic vesicle, both in the Acotylea and the Cotylea branches. This represents a groundbreaking change in polyclad classification, as characters related to the prostatic vesicle were used to build entire classification systems, in particular by Faubel (1983) and Laidlaw (1903c). In Cotylea, *Cestoplana* and *Pericelis* seem to be basal genera within Cotylea and *Boninia* possibly evolved from a common ancestor to *Theama* and *Chromyella*, being also basal in the cotylean branch of the tree. Morphology-based cladistic analyses made by Rawlinson and Litvaitis (2008), covering 34 genera, differ from our molecular tree in the base of the Cotylea branch. In their trees, *Boninia* is shown as most basal, followed by a clade that includes *Pericelis*. Our results put *Cestoplana* as most basal and then *Pericelis* as sister of all further cotyleans. *Boninia* groups with *Chromyella* and *Theama* as also shown by Laumer and Giribet (2014). Perhaps not so surprisingly, early divergent Cotylea taxa still share characters with Acotylea (Table 2), such as the orientation of male reproductive structures, type of prostatic vesicle, Lang's vesicle (Bock 1922; Curini-Galletti et al. 2008), and type of nervous system (Quiroga et al. 2015). *Pericelis* is grouped with acotyleans in this recent study, and *Boninia* in a separate category between suborders, which corroborates the hypothesis of a more basal position within Cotylea.

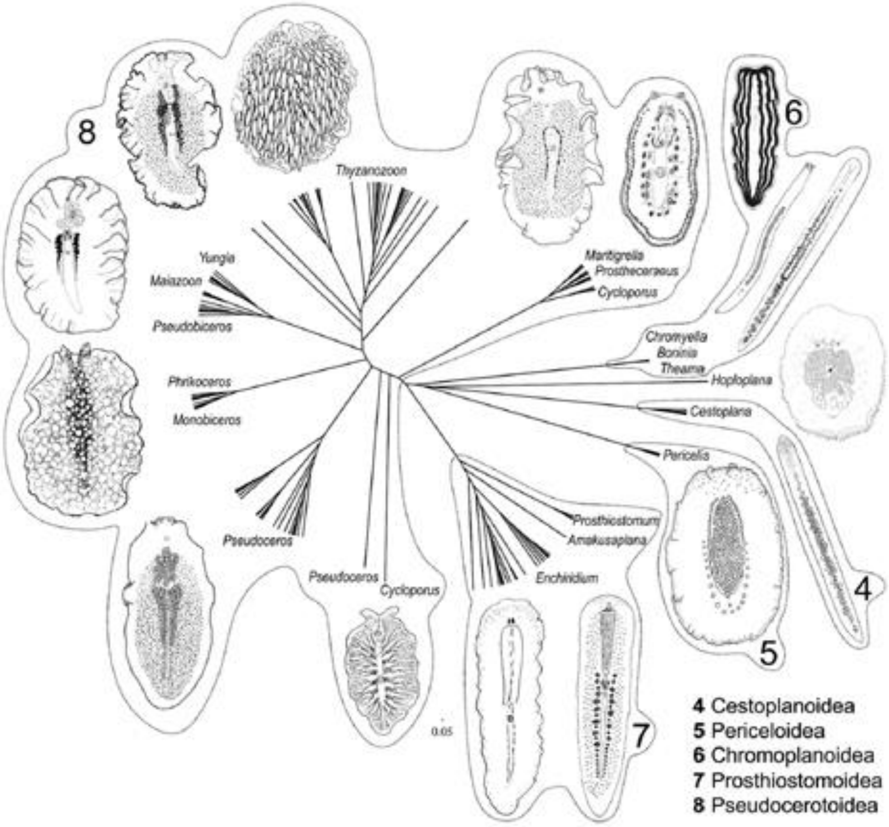


Fig. 8 Cotylea 28S rDNA phylogeny showing genus gross morphology and the new systematic division of monophyletic superfamilies. Figures from Marcus (1947, 1949, 1950, 1952), Marcus and Marcus (1968), and Newman and Cannon (1994, 1996, 2000) (under permission of Taylor & Francis Ltd.; http://www.tandfonline.com)

One species of *Cycloporus* with more evident marginal tentacles (*C. gabriellae*; Figs. 3, 6g and 8) grouped sister to Pseudocerotidae and another species (*Cycloporus variegatus*; Fig. 3) grouped with other samples of Euryleptidae. This points to the need of revision of *Cycloporus*. The genera *Maritigrella* and *Prosthecereus* were mixed up and should be revised and probably merged, because beside molecular evidence, they share morphological characters (Table 2). *Maritigrella newmanae* grouped with *Prostheceraeus roseus* and *Maritigrella crozieri* grouped with *Prostheceraeus vittatus* in our trees, and the difference between those genera is not clear. Newman and Cannon (2000) while gathering evidence to create the new euryleptid genus *Maritigrella* do not compare it with *Prostheceraeus*, only with other less similar genera of that family. According to Rawlinson and Litvaitis (2008), the difference between genera is that *Maritigrella* lacks tentacular eyes, uterus, and uterine vesicles, and it has transverse streaks as a common color pattern, and in their morphology-based cladistic results, these genera group separately, in contrast with our results. The drawings and photos included in the diagnosis of *Maritigrella* fit illustrations of *Prosthecereus* well. Therefore, we recommend the revision of both genera in order to create more natural systematic units. No Euryleptidae grouped with Prosthiostomidae. A phylogenetic tree presented by Rawlinson and Stella (2012) also showed *M. crozieri* clustered with pseudocerotids instead of with the prosthiostomid clade. Euryleptids with tubular pharynx clustered with pseudocerotids with ruffled pharynx, which means that the pharynx type is also a non-reliable character for phylogeny.

The sample of *Pseudoceros harrissi* (Bolaños et al. 2007) was recovered as sister group of a clade with all other Pseudocerotidae genera, rendering the genus *Pseudoceros* paraphyletic; this unusual species thus should be further studied, and potentially, a new genus needs to be established. The genus *Monobiceros* grouped with *Phrikoceros*, and externally, species of both genera are very similar (Table 2); the reproductive system of *Phrikoceros* species should be checked whether or not they differ from *Monobiceros* having two male systems that open in one common gonopore. The pseudocerotid genera with multiplication of reproductive structures, *Thysanozoon*, *Monobiceros*, *Pseudobiceros*, *Yungia*, and *Maiazoon*, grouped together in our tree. This was not observed in the Pseudocerotidae molecular framework of Litvaitis and Newman (2001), except for the *Thysanozoon-Pseudobiceros* grouping. This means that multiplication of reproductive structures has more phylogenetic significance than previously thought (Prudhoe 1985).

Table 3 Hypotheses test results of Faubel's, Prudhoe's, and the new system, their superfamilies, and of suborders Acotylea and Cotylea in traditional and new arrangement, using approximately unbiased (AU) and Shimodaira-Hasegawa (SH) tests

Constraint	Log-likelihood	AU-test p value	SH-test p value
Unconstrained	−0.0	0.571	0.989
Faubel's superfamilies monophyletic	292.9	*2E−004*	*0*
Faubel's Euryleptoidea monophyletic	24.5	*0.018*	0.542
Faubel's Ilyplanoidea monophyletic	188.8	*4E−006*	*0*
Faubel's Leptoplanoidea monophyletic	241.5	*1E−041*	*0*
Faubel's Pseudocerotoidea monophyletic	113.8	*6E−055*	*0.002*
Faubel's Stylochoidea monophyletic	5.9	0.212	0.912
Prudhoe's superfamilies monophyletic	303.6	*6E−102*	*0*
Prudhoe's Cestoplanoidea monophyletic	0.0	0.574	0.994
Prudhoe's Planoceroidea monophyletic	279.1	*9E−013*	*0*
Prudhoe's Stylochoidea monophyletic	139.8	*8E−042*	*0*
Bahia's superfamilies monophyletic	0.0	0.574	0.991
Bahia's Cestoplanoidea monophyletic	0.4	0.591	0.948
Bahia's Periceloidea monophyletic	0.0	0.574	0.994
Bahia's Chromoplanoidea monophyletic	0.1	0.558	0.980
Bahia's Pseudocerotoidea monophyletic	0.0	0.571	0.994
Bahia's Prosthiostomoidea monophyletic	0.0	0.573	0.992
Bahia's Cryptoceloidea monophyletic	0.1	0.499	0.980
Bahia's Stylochoidea monophyletic	0.0	0.574	0.992
Bahia's Leptoplanoidea monophyletic	0.1	0.560	0.980
Acotylea traditional monophyletic	30.5	*0.017*	0.426
Cotylea traditional monophyletic	26.0	*0.034*	0.514
Acotylea new arrangement monophyletic	0.0	0.573	0.993
Cotylea new arrangement monophyletic	0.1	0.562	0.980

Significant rejection indicated by italic

In Acotylea, Bulnes et al. (2005) stated that Stylochidae and Pseudostylochidae are closely related, since they share the plesiomorphic ruffled pharynx, have penis papilla, and lack cirrus. However, representatives of these families grouped far from each other, pointing that these characters are also evolving independently. Those two families differ in the presence or absence of extra-vesicular glands of the prostatic vesicle (Bulnes et al. 2005); the potential phylogenetic signal of this character should be investigated further. Arrangement of eyespots, absence or presence of tentacles, and position of pharynx or reproductive structures were believed to vary with environmental and physiological conditions (Faubel 1983; Bulnes et al. 2003). However, our results indicate otherwise, especially regarding tentacles (Figs. 2 and 3), showing little homoplasy and thus good potential for characterizing clades on our tree.

Polycladida character evolution

The origin of Polycladida is not much debated in the literature, but Ax (1995) stated that these worms are the first "real" platyhelminths, as they are remarkably flat. An early, persistent hypothesis was that Polycladida may have originated from a Ctenophore-like ancestor (Lang 1884; Laidlaw 1902), which is corroborated by ontological and anatomical features. One possible reason for the lack of debate is that most of the potentially closely related groups have very distinct lifestyles, being meiofaunal Platyhelminthes, while polyclads can be classified as "macroturbellarians" of benthic habit. This means that morphological convergence related to habitat is very common and makes it hard the diagnosis of homologous characters between groups. The closer outgroups, from the order Prorhynchida (Fig. 3), also present a seminal vesicle closely associated to the prostatic vesicle, in an almost interpolated arrangement (Palombi 1928). The same group can also present stylet (like the order Macrostomida) and gonopore insemination (Marcus and Marcus 1951; Janssen et al. 2015), suggesting that these are the plesiomorphic states of such characters in Polycladida. The Prorhynchida, as Polycladida, lacks the regenerative ability, common in other groups of Rhabditophora (Marcus and Marcus 1951), like *Macrostomum* (Fig. 3). Concluding from the distribution of characters within Polycladida, the ancestral flatworm may have possessed cerebral and marginal eyespots but lacked tentacles (Table 2 and Fig. 3). The character that is traditionally used to divide Polycladida basally in two suborders, a sucker, can have different muscular arrangements, and in polyclads might have different positions (Faubel 1984; Rawlinson and Litvaitis 2008). Some acotyleans present an adhesive structure but it is either lateral to the median line or anterior to the female gonopore (Faubel 1984). An adhesive structure behind the female gonopore might have evolved once, thus being an autapomorphy of Cotylea. Then, the adhesive structure might also have evolved to a true sucker once in the tree (Fig. 3), in the ancestor of pseudocerotids, prosthiostomids, and euryleptids.

Quiroga et al. (2015), based on 12 polyclad species from 11 families, showed that Cotylea presents a less developed nervous system (thinner nerve chords, lacking globuli cell masses, and not bilobed brain capsule) than Acotylea. However, cotyleans evolved special external sensory structures, like pseudotentacles and a more concentrated eyespot arrangement, also leading to cephalization. These different morphological traits might be related to different strategies or behaviors, as Acotylea tend to be cryptic and Cotylea less so. Marginal eyespots could have (a) originated three or four times in the tree and be lost two times or (b) evolved once, early in the tree, and have been lost three times (Fig. 3), which seems more parsimonious. The family Prosthiostomidae is one of the three cotylean groups that have marginal eyespots (Table 2). In this suborder, eyespot arrangement apparently evolved from an ancestral cotylean condition showing cerebral, marginal, and tentacular eyespots (like in *Pericelis*; Table 2) to the division in the following two groups: one with cerebral and marginal eyespots (loss of tentacular clusters) and the other with cerebral and tentacular (loss of marginal clusters) eyespots (Figs. 3 and 8). In Acotylea, *Adenoplana* and *Phaenocelis* group share cerebral, nuchal, and marginal eyespot character with the tentaculated group (Table 2 and Fig. 3), which points to a plesiomorphic trait. Eyespot groupings thus appear less reliable than previously thought (Lang 1884; Prudhoe 1985), possibly having evolved independently throughout acotylean genera.

Lang (1884) hypothesized that nuchal and marginal tentacles have different origins, while Laidlaw (1903c) believed them to have a common origin and therefore be homologous. Our results support Lang's hypothesis as more parsimonious, since for tentacles to have originated once, they would have been lost at least four times in the tree (Fig. 3). The alternative being marginal tentacles evolving in the ancestor of *Pericelis* and all other cotyleans, and being lost once, in Prosthiostomidae. And in Acotylea, nuchal tentacles appear to have evolved one time (Fig. 3), in the ancestor of Stylochidae, Planoceridae, and Hoploplanidae clade (Table 2 and Fig. 7). Some hypotheses about the origin of this kind of tentacles are (a) nuchal tentacles are homologous to dorsal tentacles of some ctenophores (Lang 1884) and (b) are peculiar for Polycladida and originated from marginal tentacles that shifted to lie dorsally (Laidlaw 1903c). The results presented here clearly support the latter hypothesis. According to Laidlaw (1903c), the movement of tentacles to the dorsal surface also carried the eyespots related to that structure; thus, nuchal eyespots would be homologous to tentacular or pseudotentacular eyespots. The tree presented here shows that acotyleans without tentacles also have nuchal eyespots, a trait that does not occur in Cotylea and may point that the character is not homologous. Also, there is no intermediary condition of tentacles and corresponding eyes at an intermediary position between margin and post-cerebral area; thus, both types of tentacles appeared independently. However, there is a need for more evidences (i.e., evolutionary developmental biology) to make further assumptions about tentacles and nuchal and tentacular eyespots. Marginal tentacles either (a) have originated once and have been lost two times (Figs. 3 and 8), once in Prosthiostomidae and once in *Theama* and *Chromyella* clade; or (b) have originated three times, and in one of them evolving into highly complex structures (in the Pseudocerotidae + "Euryleptidae" group), or suffering reduction (in *Cycloporus*); or even (c) have originated six times, once in *Pericelis*, then in *Boninia*, then in *Cycloporus* + *Prosthecereus* + *Maritigrella* clade, and finally in Pseudocerotidae. In general, our molecular tree and preliminary reconstruction of character evolution suggest a trait of anteriorization of sensory structures, from the plesiomorphic acotylean body plan, over the somewhat intermediate condition in "acotylean" taxa here assigned to Cotylea, to the traditional cotylean gross morphology.

Among cotyleans, *Thysanozoon* appeared as a sister group of both the *Monobiceros-Phrikoceros* and *Pseudobiceros*, *Yungia*, and *Maiazoon* clusters; this points to a single origin of multiplication of reproductive structures (Fig. 3 and Table 2). Lang (1884) considered the type of pharynx a character with "more weight" than others, and Faubel (1984) designated a superfamily based on that character. However, no Euryleptidae grouped with Prosthiostomidae in the trees presented in this study. Thus, the tubular pharynx might have originated (a) once and then have been lost in Pseudocerotidae (b) or evolved at least three times independently (Fig. 8). We consider (a) more parsimonious. A much more severe conflict concerns the type of prostatic vesicle, as it presents a high variability and is clearly subject of parallel evolution; thus, this character should not be used as a defining trait between groups. Traditionally used morphological characters related to reproductive structures also showed convergence in other Platyhelminthes groups such as Macrostomorpha (Janssen et al. 2015). The penis and the cirrus structures that evolved in some groups seem to be homologous, as was found in Macrostomorpha (Janssen et al. 2015), and transitions from one structure to the other might have happened multiple times in different platyhelminths, but this still needs to be tested in polyclads. The type of vagina differs in general terms between the two suborders, being more often looping in Acotylea and short in Cotylea. This is most likely related to the presence of hypodermic impregnation in cotylean polyclads and other close-related Platyhelminthes (Rawlinson et al. 2008; Janssen et al. 2015); in this case, the vagina is mainly for egg deposition and spermatophores are injected anywhere in the skin (Bock 1922).

Polycladida reclassification

The position of traditionally acotylean *Theama* and *Cestoplana* in our trees, grouping with or within Cotylea, is an important finding of our work and calls for a revision of the classification of polyclad suborders. Since Lang (1884) proposed both suborders, many authors disputed the character "exceptions" in *Cestoplana* (Laidlaw 1903c; Marcus & Marcus 1966; Faubel 1984, Curini-Galletti et al. 2008), but all conservatively let the genus in Acotylea. Some authors emphasized that suborders were non-monophyletic because of the lack of synapomorphies (Faubel 1984). However, the synapomorphies are there (Fig. 3). The main problem was that the whole superfamily systematics (Faubel 1983, 1984; Prudhoe 1985) was based on one or few characters. Lang (1884) already criticized such a procedure as inadequate to get to a natural system of classification; in his opinion, systematists should look to the whole set of characters present in a polyclad. For nomenclatural stability, we do not create new names here but rather emend the traditional concept and maintain both suborders as monophyletic groups. We thus transfer both families, Cestoplanidae and Theamatidae, to Cotylea based on the morphological and anatomical characters (Table 2) shared with this suborder and based on new molecular data presented here. We also use as evidence that both genera grouped in our trees with morphologically similar taxa, such as *Boninia* (Fig. 8), which do not show clear clusters of eyespots either (Marcus and Marcus 1968). Additionally, our results are corroborated both by Rawlinson and Stella (2012) who showed a *Cestoplana* clustered with cotyleans (28S rDNA) instead of in the Acotylea branch and by Laumer and Giribet (2014), who showed *Theama* grouped with cotyleans instead of acotyleans in a Bayesian tree (28S and 18S rDNA and cytochrome B data). The hypothesis tests (Table 3) are compatible with our hypothesis of a monophyletic Cotylea with *Cestoplana* and *Theama* as part of it.

As Acotylea diagnosis, we consider the presence of Lang's vesicle, male reproductive system directed backwards, tentacles, when present, nuchal. Eyespot groups can be nuchal, cerebral, and marginal (Table 2). Cotylea are diagnosed by the presence of an adhesive structure behind the female gonopore, cement gland pouch, male reproductive structures directed forward or perpendicular, and cerebral, marginal/frontal, or pseudotentacular eyespot groups (Table 2). Cases of species that presented adhesive structures inside Acotylea showed that structure beside or before the female gonopore. Thus, we did not consider them to be homologous to more posterior adhesive structures.

Our results indicate that some characters traditionally used for polyclad classification have more potential, in the sense of phylogenetic signal, than others. For example, the type of prostatic vesicle and eyespot distribution vary in closely related groups and the same states may appear independently in non-related groups, having a patchy distribution (Telford et al. 2015). Rawlinson and Litvaitis (2008) had pointed out that the two competing systems were not totally supported by their cladistic analyses, but no further details were given. However, some characters (e.g., tentacular or nuchal eyespot groups) considered by Prudhoe (1985) and Lang (1884) had more weight in systematics than the ones used by Faubel (1983, 1984). This can be possible because they are related to the nervous system, which has been proved a more robust character in evolutionary studies (Quiroga et al. 2015). Gross morphology, followed by sensory organs, was regarded by Rawlinson and Litvaitis (2008) as the most informative character, in comparison with features of the digestive and reproductive systems. This was corroborated by our results (Figs. 7 and 8) and contradicts Laidlaw (1903c), who thought that the prostatic vesicle was the most informative character, followed by nuchal tentacles and eyes. Marcus and Marcus (1966) and Bock (1913) proposed eyespots as most informative in Acotylea, followed by orientation of male structures and male vesicular structures, and in Cotylea, pharynx would be most informative and then eyespots. Both ideas were also contradicted by our results. As suggested by Laidlaw (1903c) and Rawlinson and Litvaitis (2008), and other authors as well, reproductive characters are useful in the genus level, and color pattern can also be informative at species level (Litvaitis et al. 2010). Since cladistic and molecular results pointed to the gross morphology (diagnosis or general morphology) as an important combination of characters, we suggest that it should be also considered in defining superfamilies, an idea already proposed by Lang (1884) on the earlier phylogenetic hypothesis. Therefore, some more parsimonious arrangements (focused on monophyletic groups) than previous systems, according to combined molecular and morphological data, are indicated here, as a new system.

In general, Acotylea can be divided in three groups that correspond to a new superfamily-level classification (Fig. 7). One has rounded body, nuchal tentacles, and cerebral, nuchal, and sometimes marginal eyespots, which includes *Hoploplana*, *Imogine*, *Stylochus*, *Idioplana*, *Planocera*, and *Paraplanocera* (Fig. 7) and their corresponding families Hoploplanidae, Stylochidae, Pseudostylochidae, and Planoceridae. This group is to be called superfamily Stylochoidea Poche, 1926, as this is the oldest family name included in the group. Another group has oval to elongated body, without tentacles, and with cerebral, nuchal, and marginal eyespots. It includes *Adenoplana* and *Phaenocelis* (Fig. 7) and their families, Discocelidae and

Cryptocelidae. This is to be called Cryptoceloidea superfam. nov., by Cryptocelidae and Discocelidae being equally old families, but the latter gets priority by alphabetical order. And finally, one group has elongated body, without tentacles, with only cerebral and nuchal eyespots, and with true interpolated prostatic vesicle and Lang's vesicle, which includes *Armatoplana*, *Notoplana*, *Leptoplana*, *Echinoplana*, and *Melloplana* (Fig. 7). The last group is to be called superfamily Leptoplanoidea Faubel, 1984, as also used in other systems, due to nomenclatural priority; it includes families Stylochoplanidae, Notoplanidae, Leptoplanidae, Gnesioceridae, and Pleioplanidae.

On the other hand, Cotylea can be divided into five superfamilies (Fig. 8). One group with extremely elongated body, frontal eyespots, and true interpolated prostatic vesicle contains *Cestoplana*; this is to be called superfamily Cestoplanoidea Poche, 1926 (Fig. 8). Another group, with rounded body, frontal cerebral, and marginal eyespots, includes *Pericelis* (Fig. 8), to be called Periceloidea superfam. nov.. A clade with extremely to mildly elongated body and frontal and cerebral eyespots includes *Theama*, *Chromyella*, and *Boninia* (Fig. 8) and the corresponding families Theamatidae, Amyellidae, and Chromoplanidae. This group is to be called Chromoplanoidea superfam. nov., as the oldest family included is Chromoplanidae. Another group with elongated body, tubular pharynx, and cerebral and marginal eyespots includes *Prosthiostomum*, *Enchiridium*, and *Amakusaplana* (Fig. 8). This includes the family Prosthiostomidae and is to be called Prosthiostomoidea superfam. nov.. One last group with oval body, and cerebral and tentacular eyespots, and developed marginal tentacles includes all Pseudocerotidae and Euryleptidae (Fig. 8). This group is to be called superfamily Pseudocerotoidea Faubel, 1984. None of the proposed superfamilies were rejected in the hypothesis tests and are thus considered likely (Table 3).

Among the families that were not sampled in this or other studies are the acotyleans Enantidae, Stylochocestidae, Limnostylochidae, and Apidioplanidae, which present mixed sets of morphological characters (Faubel 1983, 1984; Prudhoe 1985). The families Euplanidae, Latocestidae, and Didangiidae may contain basal cotylean genera. Ilyplanidae, Mucroplanidae, Palauidae, Notocirridae, and Camdimboididae possibly belong to Leptoplanoidea. Discoprosthidae and Callioplanidae may once be included in Stylochoidea. Polyposthiidae and Plehniidae possibly belong to Cryptoceloidea. The family Gnesiocerotidae, despite being sampled in this study, also needs more sampling as it presents mixed morphological characters among its genera. The families Leptoplanidae, Pleioplanidae, Notoplanidae, and Stylochoplanidae deserve a separate study and should be more extensively sampled in order to be better understood and possibly divided into monophyletic groups. For the moment, we stay with the separate family approach by Faubel (1983) but cannot conclude much about the relationships between these historically confused groups. Among the cotyleans, the families Opisthogeniidae, Ditremageniidae, Dicteroidae, Diposthidae, and Stylochoididae still need to be tested, with molecular and more morphological information. Anonymidae, Laidlawiidae, and Euryleptididae possibly belong to Pseudocerotoidea.

In general, most of the early morpho-anatomical studies (Lang 1884; Laidlaw 1903c; Bock 1913; Hyman 1955; Marcus and Marcus 1966) were successful in classifying systematic units on genus level. There are some exceptions (e.g., *Pseudoceros*, *Leptoplana*) that were later solved by improved working methods that allowed better observation of living and fixed specimens (Newman and Cannon 2003). As indicated by Prudhoe (1985, p. 101), our results suggest that the genus *Hoploplana* should have its own family, Hoploplanidae, since it was recovered far away in the tree from the Leptoplanidae (Figs. 2 and 3). Prudhoe also pointed out that this family might be related to *Planocera*, which was corroborated by molecular data (Figs. 2 and 3). The genus *Idioplana* should also be included in a separate family from the Stylochidae, as proposed by Faubel (1983; Pseudostylochidae), and not be treated as a subfamily (Prudhoe 1985), since in our trees, it appears as a reciprocally monophyletic group. The position of the *Pseudoceros* clade as a sister group of the *Pseudobiceros* and *Thysanozoon* clade is in accordance with results of Litvaitis and Newman (2001). The relation between those two genera, however, is different, according to our molecular results; *Thysanozoon* appears as a sister group to the *Pseudobiceros*, *Yungia*, and *Maiazoon* clade, instead of originating from a *Pseudobiceros* clade (Litvaitis and Newman 2001). Morphology-based cladistic results by Rawlinson and Litvaitis (2008) also pointed to a non-monophyletic *Pseudobiceros*.

Conclusions

Our first comprehensive molecular approach on Polycladida provided strong evidence that traditional views on the phylogeny and evolution of major subgroups were misled. Both external morphological and anatomical characters, which were widely used in Polycladida systematics, are prone to convergent evolution. Characters related both to the prostatic vesicle and to eyespot distribution have evolved independently in different groups of polyclads as also happened with the pharynx type in the Cotylea. Thus, we established a new system based on an integrative dataset with morphological and molecular characters. Based on phylogenetic principles, we reclassified Polycladida into monophyletic suborders and superfamilies, which may better reflect the interrelationships between polyclads. Characters such as tentacles/pseudotentacles, orientation of male reproductive structures, and cement pouch were considered to have more phylogenetic signal than has been historically attributed to them.

Characters related to developmental biology and ultrastructure should be investigated to better understand the relationship between polyclads and to provide a framework for developmental studies. Other taxa representing additional polyclad families should be explored considering a broad variety of morphological, anatomical, and molecular characters. There is much yet to be understood about genetic variation in polyclads (Telford et al. 2000) and a need to map and recognize truly homologous characters (Telford et al. 2015) in order to improve our initial reconstruction of character evolution. Here we present novel, integrative molecular, and morphological datasets that opened a new field of interpretations and hypotheses about Polycladida phylogeny and character evolution to be tested against new information from future studies exploring Polycladida systematics and biology.

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Figure captions

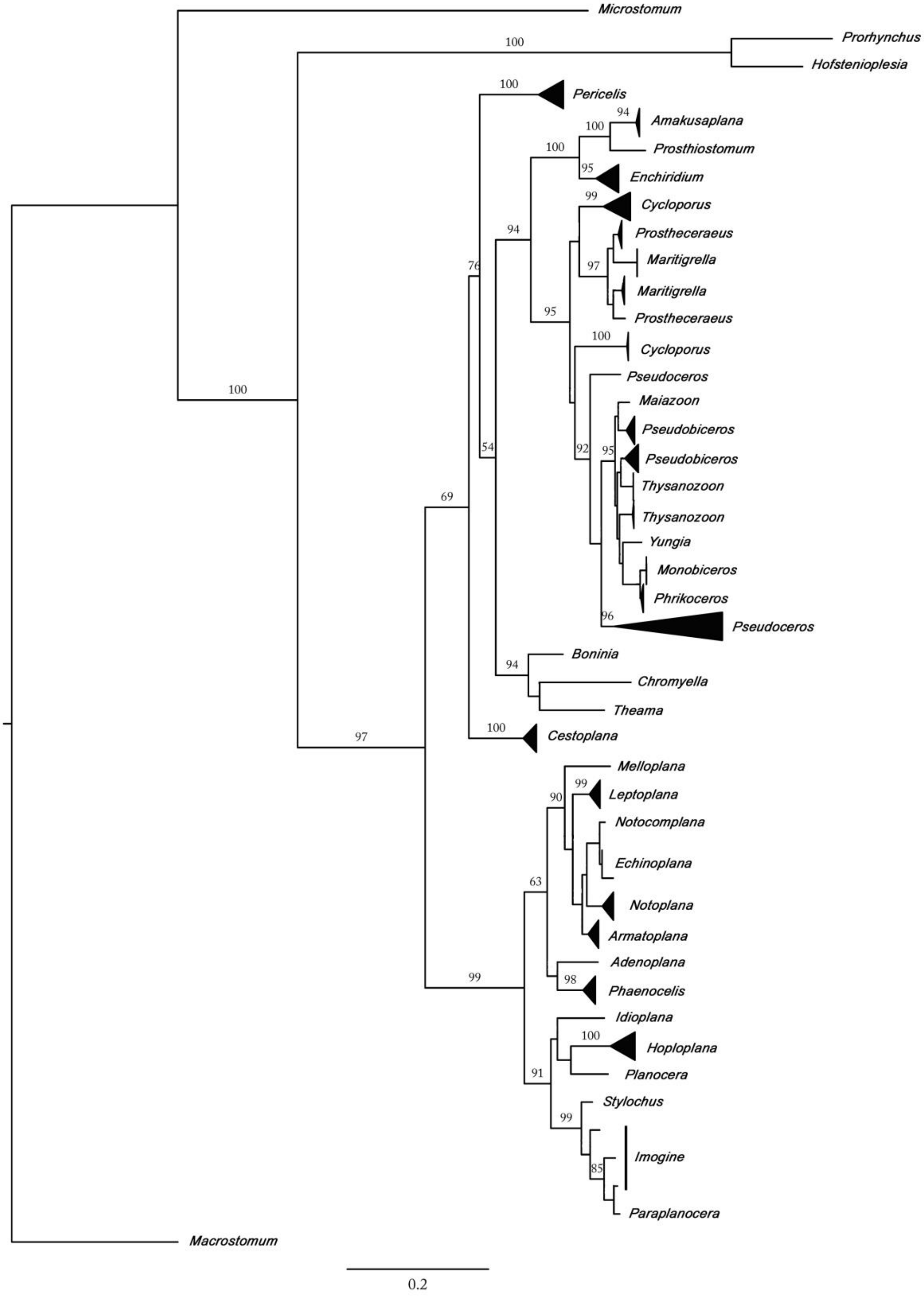
Supplementary Figure 1: Polycladida 28S rDNA phylogram (RAxML, numbers refer to bootstrap support values).

Supplementary Figure 2: Acotylea 28S rDNA phylogram (RAxML, numbers refer to bootstrap support values).

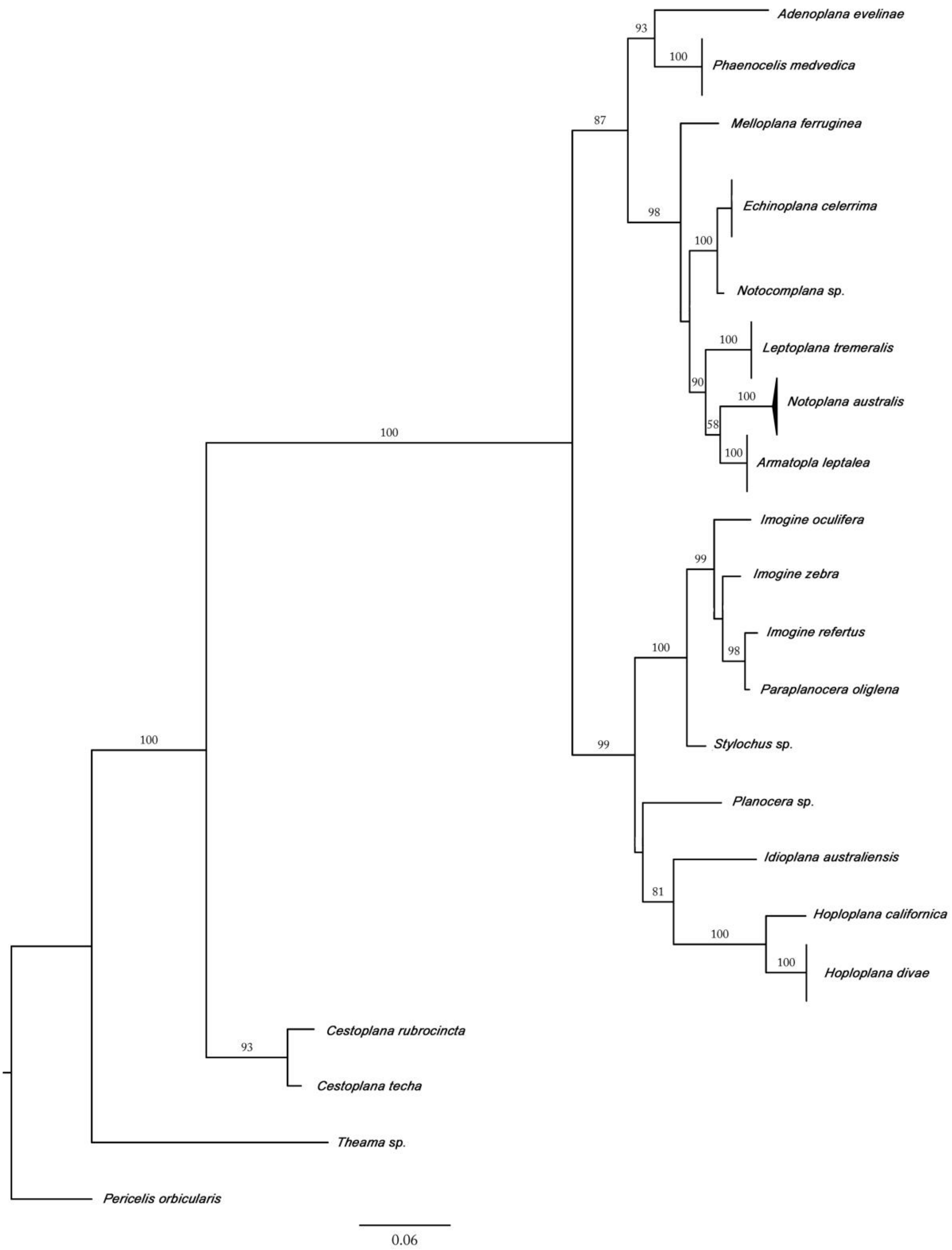
Supplementary Figure 3: Cotylea 28S rDNA phylogram (RAxML, numbers refer to bootstrap support values);

Figures

Supplementary figure 1



Supplementary figure 2



Supplementary figure 3

DISCUSSION

Integrative Polycladida taxonomy and implications to biodiversity and biogeography

Recente samples from areas not previously studied resulted in new records for Brazil and three newly described species (Bahia & Padula, 2009; Bahia et al., 2014, 2015, Bulnes & Torres, 2014); more results like those are to be expected for most of the Brazilian coast as predicted by Marcus & Marcus (1968). Out of the 71 species known from Brazil three are cosmopolitan, 48 are considered endemic, one is shared with Cape Verde and 18 are shared with the Caribbean area. Despite being a preliminary result due to the sampling bias, this result is consistent with other groups such as reef fishes (Floeter et al., 2008). Middle Atlantic preliminary polyclad samples (Azores, Ascension, and Santa Helena) provided by collaborators showed more affinity with Mediterranean than Southwestern Atlantic faunas, as was also shown for the Canary Islands (Vera et al., 2009). Biogeographical connections to the West coast of Africa are still largely unexplored. Preliminary results of integrative species delimitation from samples of *Phaenocelis medvedica* from the Caribbean and Brazil showed separation between populations of those two areas that could justify species separation (Bahia et al., unpublished data). However, 28S rDNA results from the cosmopolitan species *Thysanozoon brocchii* showed no differences between Brazil, Middle Atlantic, and Mediterranean (Bahia et al. unpublished data). This means that, despite being a good marker to support color pattern in species complexes inside some Pseudocerotidae genera (Litvaitis & Newman, 2001; Litvaitis et al., 2010), analyses based on 28S marker have not confirmed differences in color between *Thysanozoon* specimens. The possible inferences are that: *Thysanozzon brocchii* is truly cosmopolitan; or its 28S rDNA rate of evolution is too slow to indicate potential recent diversification. The relation of cosmopolitan geographic distributions and species introduction must be considered in polyclad research as it can be an effective way of dispersion for biofouling (Chapman et al., 2013) and can have an impact on native biotas (Vella et al., 2016). Some *Pseudobiceros* species discussed by Bahia & Schrödl (2016) were re-described (Marquina et al., 2015; Bolaños et al., 2016) and valid species were also corroborated as new combinations of the genus *Lurymare* (Marquina et al., 2015).

Mitochondrial DNA and multilocus approaches are very welcome in polyclads and the few studies available so far (Laumer & Giribet, 2014; Aguado et al., 2015) showed promising results. We tried universal and modified COI primers (Geller et al., 2013), but they did not work for most of our samples, only for five species, limiting their use for the phylogeny presented here. Further studies are required in order to improve methodology in this area. Problems of getting mtDNA from polyclads are widespread due to the variable mitochondrial gene order (Telford et al., 2000) that prevents adhesion of general primer in the DNA strand and calls for the design of specific primers. However, as the gene order can also change in the same family (Aguado et al., 2015), primers for single mitochondrial markers have to be developed on an almost species-specific basis. Furthermore, successfully getting mtDNA is possibly prevented as polysaccharides in tissue and mucus presumably co-precipitate with the DNA, and inhibit the activity of DNA polymerase (Jaksch et al., 2016). As a consequence of this problem, barcoding is not yet applied in polyclads as it is in other groups (Morinière et al., 2016). Just recently, one study (Vella et al., 2016) reported barcoding in Polycladida, but it is based on 28S and 18S rDNA markers. Next-Generation Sequencing (NGS) is a promising technique in systematics and population genetics (Jex et al., 2009) as it can survey the whole genetic variation in a large number of individuals (Gilad et al., 2009), which is also the case for phylogenomics (Egger et al., 2015). However, standard procedures to work and interpret large data sets are still under discussion (Shade & Teal, 2015) and general rules to delineate species boundaries are still being created (Fontaneto et al., 2015) analogous to what happened with morphological characters in the last century. In the case of polyclads, variation is not yet understood or properly defined (Bahia, unpublished data) and there is a need for more information on molecular diversity. In some aspects molecular data can behave like morphological data and there are processes that mask how we see characters (Gilad et al., 2009). Most likely, a code like the ICZN should be created for regulating DNA taxonomy. For now, some guidelines were proposed (Jörger & Schrödl, 2013; Padial et al., 2010), but they should be formalized in an obligatory minimum set of practices to be required from researchers. The "promise" of such techniques being quick and easy, allowing both taxonomists and non-taxonomists to obtain working hypotheses about species boundaries (Fontaneto et al., 2015) must be considered carefully, since the interpretation of results without taxonomic knowledge of a group can do more harm than good. As already stated by Bahia et al. (2014) and other researchers (Bolaños et al., 2016), integrative methods, combining morphological, color, biological and molecular data will generate more reliable identifications. Adding ecological information on species already known (Bahia, 2016) could also help in species delimitation. However, combining different datasets in one bigger analysis is still challenging (Padial et al., 2010; Jörger et al., 2012), and such integration of data should be conducted carefully. Once such pieces of information are combined, it will be possible to develop a stable biogeographic and a phylogenetic framework of relations between polyclads.

Polycladida type material and museum collections

The re-discovery of Ernst and Eveline Marcus' type material is very important for the contemporary and future study of Polycladida as the lack of type material, holotypes that are damaged or lost, and poor descriptions are a huge problem for the nomenclatural stability (Schrödl & Haszprunar, 2016). Here (Chapter 4) we were able to designate lectotypes of 30 species and recognized holotypes of 22 Brazilian species. This is a relevant input for Polycladida study in the Tropical Atlantic, since currently, only 10 out the 71 species reported from Brazil remain without information about type material. Holotypes are to be considered as ways to test a hypothesis, which is what a species represents, and they should be available to other researchers to allow verification and test of the validity of that hypothesis against their own interpretations and in the light of new technologies that could provide more information about the species type material. It is expected that type material designations (Hall & Adlard, 2012) and re-descriptions of old species (Marquina et al., 2015; Bolaños et al., 2016) will expand the knowledge on Polycladida biodiversity, or at least improve its quality. This is so because the use of color photographs and the evolution of microscopes and histological techniques in the last 50 years made possible to document details that were lost in previous descriptions or simply not possible to observe (Newman & Cannon, 2003). In addition, techniques such as tomographic scan are being developed in order to enable obtaining additional morphological (Carbayo & Lenihan, 2016) and new molecular protocols are being applied in order to get information (Jaksch et al., 2016) from old material. Museomics can prove useful in exploring marine flatworm material deposited in museums, especially because samples fixed in formalin previously considered lost cases, as most polyclads samples, are being successfully sequenced (Ruane & Austin, 2017). However, material included in slides was not yet targeted for molecular data, and represent most of the type material known to be deposited in scientific institutions (Bahia & Schrödl, submitted).

Museum material is very important as it provides evidence for testing species hypotheses and it has gained importance in the eyes of molecular biologists due to DNA barcoding projects (Jaksch et al., 2016), but it is also a repository of biodiversity (Kemp, 2015). Nowadays, marine biodiversity is under threat, human activities like fishing by trawling may have consequences comparable to habitat loss due to deforestation and spread of agriculture (Costello, 2015). Another human-related problem, namely climate-driven oceanographic changes, may affect different oceanic dispersal pathways and change the potential for dispersal and connectivity in various marine taxa (Wilson et al., 2016) in addition to posing a great risk of species loss before they are known. In that context, invertebrates can also be used to draw attention to biodiversity conservation, and programs for all marine taxa as a whole, rather than only for charismatic marine taxa, can be effective (Ressureição et al., 2011). Databases are valuable as a reference for taxonomic and biodiversity research, and as a tool for communication with the society (Ruggiero et al., 2015); this requires specialists on taxonomy to give the most up to date classification and biodiversity information as possible. Efforts to protect marine biodiversity require specialists in taxonomy, biogeography and ecology of species (Wägele et al., 2011; Costello, 2015) and a joint effort could accelerate both the discovery and the assessment of the conservation status of species. However, the number of Polycladida taxonomists is dangerously low. Historically, researchers working on polyclads were scattered in Germany, Austria, Italy, France, Sweden, Russia, Japan, US, Brazil and England (Rieger, 1998); currently there are specialists in Colombia (Quiroga et al., 2004), Argentina (Brusa et al., 2009; Bulnes et al., 2011), Spain (Marquina et al., 2014), Brazil / Germany (Bahia et al., 2017), Singapore (Bolaños et al., 2016), Taiwan (Wei-ban et al., 2013), Iran (Khalili et al., 2009; Maghsoudlou & Rahimian, 2013), Tunisia (Gammoudi et al., 2009), India (Apte & Pitale, 2011), Canada, and the United States (Litvaitis et al., 2010). Unfortunately, none of them is leading a laboratory specialized on the study of the group as it happens in other Platyhelminthes groups and other marine invertebrates. This means the study of the group is under constant threat, especially in the current scientific crisis.

Polycladida phylogeny in the new integrative era

Towards a molecular tree hypothesis

Our molecular results and their combination to morphological evidence are a unique progress in Polycladida phylogeny (Chapter 5, Bahia et al., 2017). We sampled 19 families and 32 genera, all representing novel 28S rDNA data, and in total we contributed with 136 new sequences. The resulting single gene tree is largely robust and consistent with morphology (Bahia et al., 2017, Figure 2). However, a single gene tree is not ideal for inferring phylogenetic relationships, due to changes in the gene sequence, such as duplication, horizontal transfer, incomplete lineage sorting, conversion, that can make a gene tree different from a species tree (Telford et al., 2015); thus there is an urgent need for more markers, or preferably mitogenomic or phylogenomic information. Nevertheless, especially in the context of difficulties of getting different molecular markers (Laumer & Giribet, 2014), our 28S rDNA-based hypothesis is a good starting point for reinvestigating relationships between Polycladida. We used the largest data set of polyclads used in molecular studies so far, which resulted in a broad sampling of the diversity in 28S rDNA, and adding more data always produced more robust trees in our analysis. It is expected that even larger samples, including strategic taxa and larger gene data sets will improve the quality of the trees as they reduce most effects of stochastic error (Telford et al., 2015).

Multi-locus results available for Polycladida were obtained from one study (Laumer & Giribet, 2014) to date, which included nine species. The results presented in that paper, with *Chromyella* grouping with Cotylea instead of Acotylea, were corroborated by our 28S rDNA results. This adds more evidence for the robustness of our findings (Chapter 5, Bahia et al. 2017). Next-generation sequencing is a promising way of having more information to delimit species, genera, and higher groups. The main difficulty of dealing with the amount of data one can get with the new breakthrough technologies is that we do not understand its variation yet (Schrödl & Stöger, 2014). For mitogenomics, it was found that this trait is less conserved than previously thought and the order presents a remarkable diversity in gene arrangements even in the same genus (Aguado et al., 2015). Mitogenomic data showed that Platyhelminthes do not have the conserved mt-gene blocks proposed for bilaterians nor the putative ground pattern of Spiralia (Aguado et al., 2015). This apparently contradicts the assumed position of the phylum nested in Spiralia (Egger et al., 2015), but it can be due to the limitations of sampling only the mitochondrial genome, which in Platyhelminthes is shown to have exceptional high substitution rates (Bernt et al., 2013) and can undermine its value in phylogenetic analyses.

Phylogenomics are also a promising advance to study genetic diversity as it provides many sequences including loci that are conservative enough for interpreting order level relationships. However, so far only one study (Egger et al., 2015) provided data on polyclads and it included only four species. The issues concerning this method include obtaining RNA samples and adequate funding for basic research on the topic. Other techniques that provide big data on genetic diversity are still in their infancy or are too expensive and will probably be more affordable in the future. Combining these new advances in accessing genetic data with morphological and developmental data will be, possibly, a more comprehensive and reliable way to understand phylogenetic relationships. Mapping morphological characters on molecular or phylogenomic trees can help to build more natural classification systems, as it improves the diagnosis of monophyletic groups, and rule out non-homologous characters. In the future, character evolution should be inferred by software (see e.g. Jörger et al., 2014); but for now mapping selected characters on the polyclad 28S gene tree also serves for an initial estimation of character states and their changes in certain nodes.

Character evolution

Our results (Bahia et al., 2017, Figure 2 and 3) point out that the closer outgroup also presents a seminal vesicle closely associated to the prostatic vesicle, in an almost interpolated arrangement, a stylet and gonopore insemination, and it lacks strong regenerative ability suggesting that these are the plesiomorphic states of such characters in Polycladida. In addition, the ancestral flatworm may have possessed cerebral and marginal eyespots, but lacked tentacles. The character that is traditionally used to divide Polycladida in two suborders, i.e. the ventral sucker or adhesive structure behind the female gonopore, might have evolved once. Marginal eyespots could have (a) originated three or four times in the tree and be lost two times or (b) evolved once, early in the tree, and have been lost three times, which seems more parsimonious. In Cotylea, eyespot arrangement apparently evolved from an ancestral condition showing cerebral, marginal, and tentacular eyespots to the division in the following two groups: one with cerebral and marginal eyespots (loss of tentacular clusters) and the other with cerebral and tentacular (loss of marginal clusters) eyespots (See Bahia et al., 2017, Figure 3). In Acotylea, eyespot groupings appear less reliable than previously thought, possibly having evolved independently throughout acotylean genera. Our results support that nuchal and marginal tentacles have different origins (Lang, 1884), as tentacles would have been lost at least four times in the tree in order to have originated once. The alternative being marginal tentacles evolving in the ancestor of *Pericelis* and all other cotyleans, and being lost once, which seems more parsimonious. In Acotylea, nuchal tentacles appear to have evolved one time. The hypothesis (Laidlaw, 1903) that nuchal tentacles originated from marginal tentacles that shifted to lie dorsally was not supported by our results (Chapter 5, Bahia et al., 2017). That hypothesis also stated that nuchal eyespots would be homologous to tentacular or pseudotentacular eyespots; however, our results show that acotyleans without tentacles also have nuchal eyespots, a trait that does not occur in Cotylea. Furthermore, there is no intermediary condition of tentacles and corresponding eyes at an intermediary position between margin and post-cerebral area; thus, both types of tentacles might have appeared independently, and are not homologous. Marginal tentacles either (a) have originated once and have been lost two times; or (b) have originated three times, and in one of them evolved into highly complex structures, or were reduced; or even (c) have originated six times. In general, our molecular tree and preliminary reconstruction of character evolution suggest a trait of anteriorization of sensory structures, from the plesiomorphic acotylean body plan, over the somewhat intermediate condition in "acotylean" taxa here assigned to Cotylea (Chapter 5, Bahia et al., 2017), to the traditional cotylean gross morphology. Our results also point to a single origin of multiplication of reproductive structures. The tubular pharynx might have originated (a) once and then have been lost once (b) or evolved at least three times independently. We consider (a) more parsimonious. A much more severe conflict between our data and one of the traditionally used classification systems (Faubel, 1983, 1984b) concerns the type of prostatic vesicle, as it presents a high variability and is clearly subject to parallel evolution; thus, this character should not be used as a defining trait between superfamily groups.

Why did previous classifications fail?

Our molecular trees and combined phylogenetic hypotheses imply a quite low overall level of homoplasy in the characters we assessed, and several of them may be synapomorphies that characterize a certain clade (Bahia et al., 2017, Figures 3, 7 and 8). According to our results, the characters used by Faubel and Prudhoe, in their classification systems, showed high evolutionary plasticity, which is quite remarkable. Homology of morphological features has actually never been carefully assessed in Polycladida. In previous phylogenetic hypotheses (Lang, 1884; Bock, 1913) homology was assumed or supposed basically without discussions. Faubel (1983, 1984b) and Prudhoe (1985) discussed its character states and evolution, but the homology probability of the characters used to define their systems was not evaluated according to homology criteria, nor was the polarity of character states adequately assessed. Most importantly, single characters are hardly able to solve complex phylogenetic relationships; to consider only one organ system in reconstructing polyclad phylogenies or establishing classifications would risk creating an unnatural system, as stated by Lang (1884) and Marcus & Marcus (1966). However, using single characters or organs was exactly what Bock (1913), Faubel (1983, 1984b) and Prudhoe (1985) did. In the case of considering only the sexual organs, it would combine very heterogeneous forms such as *Cestoplana*, *Leptoplana* and *Hoploplana* or Stylochidae with Euryleptidae and

Pseudocerotidae (Lang, 1884). Homologies are features that are likely to be similar due to common ancestry (Nixon & Carpenter, 2012) and due to their conservation in position despite changes in form and function (Wagner, 1989). This could be thought of prostatic vesicle, eyespots distribution, and tentacles characters. However, homology is also related to the uniqueness and rare character that can be used to define monophyletic groups (Wagner, 1989), and in that point the distribution of those characters, except for tentacles, is too patchy to be able to define monophyletic groups. In Polycladida no further study was performed in order to access homology of characters used in systematics, while here (Chapter 5, Bahia et al., 2017) we tried at least to rule out those that clearly are not homologous. It is unclear why polyclads are so plastic in certain characters and not in others, but it is possible that by being an old animal group, time passed long enough for parallel adaptations, secondarily loss and extinction of intermediary forms to occur (Fitch et al., 2002). In addition, Polycladida systematics or taxonomic studies (Rawlinson & Litvaitis, 2008) have so far only stated that classification systems (Faubel, 1983, 1984b; Prudhoe, 1985) are conflicting, but they did not try to solve or argue in favor of one or the other. Our efforts are the first ones in that direction, and we further emphasize that forms with intermediary or mosaic-like character states may be crucial for understanding Polycladida. Taxa with "mixed" characters should thus be considered and interpreted together with other polyclads, regardless of any difficulties in drawing conclusions. Only then can the systematics of the groups go further instead of relying upon generalizations.

Towards a new classification

Current researchers keep choosing between two systems of classification and sometimes find out that some families are not monophyletic (Rawlinson & Litvaitis, 2008; Brusa & Damborena, 2013), which is unsatisfactory. Within the framework of this thesis, the first steps towards a new system were accomplished (Bahia et al., 2017) and are presented in Chapter 5. As the groups created by Faubel (1983, 1984b) were recovered polyphyletic (Leptoplanoidea and Pseudocerotoidea) or paraphyletic (Stylochoidea and Eryleptoidea) and some of the superfamilies created by Prudhoe (1985) were also polyphyletic (Planoceroidea and Stylochoidea), we traced congruent patterns of features in our molecular tree, to find points that could be explained by common ancestry (Brower & de Pinna, 2012). Accordingly and in order to establish a classification system based on monophyly, we emended both traditional suborders, transferring two "acotylean" genera and their corresponding families to Cotylea. (Bahia et al., 2017) separated acotyleans from cotyleans based on: position of ventral sucker (when present) in relation to the gonopores, position of reproductive organs, location of uteri in relation to female genital pore, presence or absence of marginal tentacles, grouping of eyes on the front margin, type of tentacles and position of the eyes. From those, the only internal characters so far are the position of reproductive organs and the location of uteri. Further investigations of e.g. the ultrastructure and other details of the nervous and reproductive systems may reveal more potential synapomorphies. We also divided Acotylea in three superfamilies and Cotylea in five superfamilies (Bahia et al., 2017). These new interpretations may prompt future research activity and will be tested and supplemented by data to come.

For example, differences in sperm (Liana & Litvaitis, 2007) and nervous system (Quiroga et al., 2015) were found between Acotylea (attached axonemal, flagella middle or different levels, elongated nucleous only in posterior part; large encapsulated brain; thick main nervous chords, well defined globuli cell masses, dorsoventrally flattened and submerged in the parenchyma) and Cotylea (free axonemal, anterior location, nucleous along the entire sperm body; slightly or not bilobed small brains, thin main nerve chords, poorly defined globuli cell masses or completely absent). However, it is yet unclear if the characters are not subject to excessive variation, as argued for the extinction of Trepaxonemata (Litvaitis & Rohde, 1999) or as general feature of hermaphrodites (Michiels & Newman, 1998). More effort should be made to investigate intrageneric and intrafamiliar variations to conclude if the characters would fit phylogenetic purposes. Additionally, those characters should be analyzed in more basal Cotylea (*Pericelis*, *Cestoplana*), since in many cases they present apparently plesiomorphic combinations of characters from both suborders.For example, *Pericelis* has many “acotylean” characters (ruffled and centrally located pharynx) (Bock, 1913) and *Boninia* (Bock, 1923) has “cotylean” characters (marginal tentacles, arrangement of eyes, sucker, uteri behind the female pore, uterine vesicle, vagina with cement pouch) and acotylean characters (Lang’s vesicle, interpolated prostatic vesicle). The genus *Cestoplana* also has mixed characters between Cotylea (cement glands and cement pouch, male system directed backwards) and Acotylea (interpolated prostatic vesicle) (Laidlaw, 1903). This is also the case for *Chromoplana*. That genus is said to have the male system as in *Cestoplana*, which points to a close relationship (Bock, 1922) that was found in the molecular results (Bahia et al., 2017). Lang’s vesicle and interpolated prostatic vesicle have clearly not evolved once, but several times independently (Bahia et al., 2017) and apparently, this is also the case for sperm characters (Liana & Litvaitis, 2010), thus it cannot be used as a diagnostic character for a monophyletic group as used by Faubel (1983, 1984b). The nervous system organization might be influenced by the size and position of the pharynx and behavior (Quiroga et al., 2015). As in Acotylea, the pharynx is located centrally, and then the brain is more posterior, larger, with developed globuli, possibly adapted to more complex neural integration and cryptic benthic behavior. On the other hand, Cotylea shows an anteriorization of the nervous system (pre-cephalization). However, the genera *Pericelis*, *Cestoplana* and *Boninia* present mixed nervous system characters. Thus, the nervous system is apparently more related to the type of body than to a certain suborder, but further investigation on *Cestoplana*, *Latocestos*, *Theama,* and *Chromoplana* is needed. The genus *Stylostomum* can also be an intermediary basal Cotylea (Holleman, 2001) and it would be important to add its samples to get a more complete phylogeny, as well as samples from the genus *Latocestus* and *Semonia*. Based on the information of those key genera it would be possible to make decisions on the boundaries of Polycladida suborders, as there are still place for doubt in the placement of certain genera. For example, based on the evidence from 28S rDNA of 14 species (Rawlinson et al., 2011) and nervous system (Quiroga et al., 2015) evidences, *Pericelis* was shown together with *Cestoplana* as sister to Acotylea, which was not corroborated by our results (Bahia et al., 2017) that recovered those genera as sister to Cotylea.

We have not yet fully resolved polyclad phylogeny nor have we provided a stable classification, but we most likely established a better initial baseline for those future developments. Classifications may be considered reliable once they are based on congruent topologies from analyses of different data sets, such as molecular and morphological ones.

Pieces missing from the phylogenetic puzzle

From a morphological perspective, the main challenge now is to explore characters in rare and little studied groups, to sort features (morphological, molecular, developmental and from other fronts) that are not prone to high rates of mutation or to high levels of convergence, to establish a matrix and to run morphocladistic analyses, which have never been done in Polycladida yet. Future morphological studies may also concentrate on exploring some characters that promise some signal in deeper polyclad phylogeny, such as eyespots (Marcus & Marcus, 1966) and their relation to the nervous system. The duplication of the reproductive system, the tentacles, the pharynx, and the eyes (Litvaitis & Newman, 2001) might be good characters, as well as the number of lateral intestinal branches (Newman & Cannon, 2002), the stylet and the distance between female gonopore and sucker (Marquina et al., 2015). Characters that showed phylogenetic signal in our results (Bahia et al., 2017) such as tentacles/pseudotentacles, orientation of male reproductive structures, and cement pouch should also be further investigated. Other characters related to reproduction and development should be investigated and considered with care in phylogenies as they do not seem to be totally dictated by phylogeny (Monro & Marshall, 2015), with the same genus presenting different types of larvae and type of development (Bock, 1913; Ballerin & Galleni, 1984; Lapraz et al., 2013). Moreover, a few reproduction-related features, such as the mode of insemination, are not related to systematic position, as the armed penis is not always related to hypodermical impregnation, and Lang's vesicle is not always related to true copula. This seems to be also the case for sequestration of nematocysts (Goodheart & Bely, 2017). However, organ formation and Hox genes (Saló et al., 2001) should be investigated in Polycladida in order to diagnose those that could provide homologous characters and therefore could be used in phylogeny. New species described in newly created genera or families (Brusa & Damborena, 2013, Bulnes et al., 2003) are also important to understand the polyclad character diversity and to develop a more natural system of classification.

Conclusions

In this study, I contribute with new and original data concerning biodiversity, type material and phylogeny of Polycladida. Together with collaborators, I was able to describe two new species, present type material from 52 species and add 136 new sequences of polyclad taxa to molecular databases. These results fill the gaps about type material of most of Brazilian species and about a first Polycladida phylogeny. A new classification system is set, but in order to improve hypotheses of Polycladida evolution, more complete molecular data and samples of key taxa are required. A phylogeny based on multi-markers and phylogenomics should be done for Polycladida, and possible correlations to morphological data can help to choose characters that can be homologous and then rule out those diagnosed as homoplasious. Additional studies about ecological, physiological, and developmental aspects of polyclads should also contribute to the knowledge on the group. For now, this thesis adds important and novel information about Polycladida, opens a new pathway and raises new questions for future research.

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Curriculum vitae

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PERSONAL INFORMATION

Date of Birth: 27 November 1986 (Rio de Janeiro, Brazil)
Address: Münchhausenstraße 21, 81247, Munich, Germany
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EDUCATION

2013 – present: **Ph. D.** In Biology at Ludwig Maximilian University, Munich

Thesis: Polycladida Biodiversity: an integrative approach

Supervisors: PD Dr. Michael Schrödl (ZSM) and Prof. Dr. Gerhard Haszprunar (LMU and ZSM).

2010 – 2012: **M. Sc.** in Zoology at Museu Nacional / Universidade Federal do Rio de Janeiro, Brazil

Dissertation: “Morphological characterization and biological and ecological observations on suborder Cotylea Lang, 1884 species (Platyhelminthes: Polycladida) from Cabo Frio, RJ, Brazil”

Supervisors: Profa. Dr. Helena Passeri Lavrado (UFRJ) and Prof. Dr. Sigmer Quiroga (Universidad Magdalena, Colombia)

2005 – 2009: **B. Sc.** in Biological Sciences, Marine Biology at Universidade Federal do Rio de Janeiro, Brazil

Monography: “Identification and quantification of an introduced octocoral in Sepetiba Bay, RJ”.

Supervisor: Profa. Dr. Andrea de Oliveira Ribeiro Junqueira.

2004: ABITUR (Vestibular) Colégio Palas, Rio de Janeiro, Brazil.
1998 – 2004: Colégio Palas, Rio de Janeiro, Brazil.
1994 – 1997: Colégio Martins, Rio de Janeiro, Brazil.

PUBLICATIONS IN PEER-REVIEWED JOURNALS

(10) **Bahia, J**., Padula, V. & Schrödl, M. (in press). Polycladida phylogeny and evolution: Integrating evidence from 28S rDNA and morphology. **Organism Diversity and Evolution**, 1-26.

(9) Padula, V., **Bahia, J.**, Stöger, I., Camacho-García, Y., Malaquias, M.A.E., Cervera, J.L., Schrödl, M. (2016) A test of color-based taxonomy in nudibranchs: Molecular phylogeny and species delimitation of the Felimida clenchi (Mollusca: Chromodorididae) species complex. **Molecular Phylogenetics and Evolution**, 103: 215-229.

(8) **Bahia, J.** & Schrödl, M. (2016) *Pseudobiceros wirtzi* sp. nov. (Polycladida: Cotylea) new species from Senegal with revision of valid species of the genus. **Zootaxa**, 4097(1), 101-117.

(7) **Bahia, J.** (2015) First records of polyclads (Platyhelminthes, Polycladida) associated with *Nodipecten nodosus* (Linnaeus 1758) aquaculture. **Marine Biodiversity**, 1-5. DOI: 10.1007/s12526-015-0425-6

(6) **Bahia, J.**, Padula, V., Correia, M.D. & Sovierzoski, H.H. (2015) First records of the order Polycladida (Platyhelminthes, Rhabditophora) from reef ecosystems of Alagoas State, north-eastern Brazil, with the description of

Thysanozoon alagoensis sp. nov.. **Journal of the Marine Biological Association of the United Kingdom**, 95(8): 1-14.

(5) **Bahia, J.**; Padula, V.; Quiroga, S.; Passeri-Lavrado, H. (2014) Taxonomy of Cotylea (Platyhelminthes: Polycladida) from Cabo Frio, with the description of a new species. **Zootaxa**, 3873(5): 495-525.

(4) Padula, V.; **Bahia, J.**; Correia, M.; Sovierzoski, H. (2012) New records of Opisthobranchia (Mollusca: Gastropoda) from Alagoas, Northeastern Brazil. **Marine Biodiversity Records**, 5: 1-11.

(3) **Bahia, J**.; Padula, V. & Delgado, M. (2012) Five new records and morphological data of five polyclad species (Platyhelminthes: Turbellaria) from Rio Grande do Norte, Northeastern Brazil. **Zootaxa**, 3170: 31-44.

(2) Padula, V.; **Bahia, J.**; Vargas, C. & Lindner, A. 2011. Mollusca, Nudibranchia: new records and southward range extensions in Santa Catarina, Southern Brazil. **Checklist,** 7(6): 806-808.

(1) **Bahia, J.** & Padula, V., 2009. First Record of *Pseudoceros bicolor* and *Pericelis cata* (Platyhelminthes: Polycladida) from Brazil. **Marine Biodiversity Records**, 2: 1-5. Doi: 10.1017/S1755267209000918.

SUBMITED MANUSCRIPTS

(S) **Bahia, J.**, Leão Braccini, J.A., Leal-Zanchet, A.M. Synopsis of the knowledge on the Brazilian marine biota: flatworms of the phyla Platyhelminthes and Acoelomorpha. **Biota Neotropica.**

(S) Bulnes, V.N., **Bahia, J.**, Goulart Araujo, A.P., Carbayo, F. The benthic hyperdiversity of a subtropical coastal bay under an integrative approach. **Zootaxa**.

(S) Bahia, J. & Schrödl, M. Brazilian Polycladida (Rhabditophora: Platyhelminthes): re-discovery of Marcus type material and general revision.

MANUSCRIPT IN PREPARATION

Bahia, J., Brown, J., Wirtz, P. & Schrödl, M. Polyclad species from Santa Helena and Middle Atlantic Islands.

INTERNSHIPS

2006 – 2012: Benthos Laboratory, Marine Biology Department, Universidade Federal do Rio de Janeiro, Brazil.

WORK EXPERIENCE

2005 – 2012: Secretary at DxPele Consultoria Diagnóstica, Rio de Janeiro, Brazil. Organizing patients files, corresponding paraffin blocks and slides, receiving material and attending patients.

AWARDS RECEIVED

2011: Honorable mention, Post-graduation Program of Zoology. Museu Nacional do Rio de Janeiro / UFRJ.

2009: 2nd place in the "Brazilian Association of Marine Biology Award for students (Student Science Competition)", Undergraduate Category, in the II Brazilian Marine Biology Congress, with the work "Quantification of the introduced octocoral *Erythropodium caribaeorum* in four sampling locations in Sepetiba Bay, RJ".

GRANTS RECEIVED

2016: Research grant (SE-TAF-5521) for SYNTHESYS Project, Sweden.

2012 – 2017: PhD Fellowship. CNPq / DAAD (National Council of Technological and Scientific Development), Germany.

2010 – 2012: Master Fellowship. CAPES (Coordination for the Improvement of Higher Education Personal), Brazil.

2007 – 2009: Scientific initiation grant (IC-PIBIC). CNPq (National Council of Technological and Scientific Development), Brazil.

PARTICIPATION ON SCIENTIFIC MEETINGS

---

15 participations: 23 works presented
4 oral presentations

PARTICIPATION ON POPULARIZATION OF SCIENCE EVENTS

---

7 participations: 4 courses given
1 Works presented
3 Courses taken

ACADEMIC REPRESENTATION

---

04 – 12.2007: Representation of undergratuate students of the Biological Sciences - Marine Biology graduation course. Marine Biology Department, Biology Institute, Universidade Federal do Rio de Janeiro.

LECTURES GIVEN

2016: “Designating new type material for Brazilian species described by Ernst and Eveline Marcus”. Zoology Department, Swedish Museum of Natural History Museum, Sweden.

2012: “Morphological characterization and biological aspects of species from the suborder Cotylea (Platyhelminthes: Polycladida) from Cabo Frio, RJ, Brazil.” During the XXIX Congresso Brasileiro de Zoologia, Salvador, Brazil.

2008: “Reproduction in Polycladida”. During the Discipline Biology of Marine Benthos, from the Marine Biology Department, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

EXTENSION COURSES GIVEN

2010: “Adaptations to marine life”. Biology Week Universidade Estadual do Rio de Janeiro, Rio de Janeiro, Brazil. Duration: 4h 30min.

“Reproductive strategies of marine invertebrates”. XIV Biology Week Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. Duration: 8 hours.

2009: “Marine Biology”. XIII Biology Week Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. Duration: 8 hours.

2008: “Nudibranchs and marine flatworms diversity”. XII Biology Week Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. Duration: 8 hours.

THESIS SUPERVISION

2016 – 2017 : External supervisor of B.Sc. thesis of Mariela Ramos Sanchéz
Thesis: Platelmintos policládidos (Platyhelminthes: Rhabditophora) del litoral de Oaxaca
Supervisor: Dr. José Rolando Bastida Zavala

TECHNICAL ACTIVITIES AND COLABORATIONS WITH MEDIA

2011: Article “Marine flatworms from Cabo Frio”. InforMar Magazine, p. 8 - 13, Brazil.

2009: Column “Animals from the Reefs” with the note “Marine flatworm”. Projeto Coral Vivo Notícias Magazine, October, p. 7, Brazil.

2008: Teaching material (handout) for the discipline Basic Marine Biology, Marine Biology Department, Biology Institute, UFRJ.

PEER-REVIEW IN SCIENTIFIC PUBLICATIONS

2016: Ecologica Montenegrina (ISSN 2336-9744)
Cahiers de Biologie Marine (ISSN 0007-9723)
Zootaxa (ISSN Online 1175-5334 and Print 1175-5326)
European Journal of Taxonomy (ISSN 2118-9773)

2015: Marine Biodiversity Records (1755-2672)
Zootaxa (ISSN Online 1175-5334 and Print 1175-5326)

2014: Bulletin of Marine Science (0007-4977)

2013: The Raffles Bulletin of Zoology (0217-2445)

TUTORSHIP OF UNDERGRADUATE COURSES

2008: Discipline Biology of the Marine Benthos, Marine Biology Department, Biology Institute, Universidade Federal do Rio de Janeiro. Including field trips.

Discipline Zoology I, Zoology Department, Biology Institute, Universidade Federal do Rio de Janeiro.

Discipline Marine Ecosystems, Marine Biology Department, Biology Institute, Universidade Federal do Rio de Janeiro.

Tutorship in fieldtrip of the discipline Basic Marine Biology. Marine Biology Department, Biology Institute, Universidade Federal do Rio de Janeiro.

PARTICIPATION ON RESEARCH PROJECTS

2009: Part of the team of the project “Ecology of introduced benthonic species from Sepetiba Bay and Ilha Grande Bay, RJ, Brazil”.

2007 – 2009: Scientific Initiation Project “Distribution, frequency and abundance of an introduced octocoral in Sepetiba Bay, RJ, Brazil”.

2006 – 2008: Participation in the Project Macrobentic comunities of natural and artificial substrates from Sepetiba Bay, RJ, Brazil, with emphasis on the dynamics of introduced species. Activities: sorting of biological material, manufacture of slides for Porifera identification; coordination of sample sorting (part conducted in the Benthos laboratory / Universidade Federal do Rio de Janeiro).

COMPLEMENTARY EDUCATION

2014: Taxonomy and Systematics of Tropical Polyclads. Smithsonian Tropical Research Institute, Bocas del Toro, Panama. Duration: 10 days.

2008: Evolutive Biogeography. XXVII Brazilian Zoology Congress, Curitiba, Brazil. Duration: 12 hours.

2007: Crustaceans biology and development. XI Biology Week UFRJ, Rio de Janeiro, Brazil. Duration: 12 hours.

Marine Biodiversity: concepts and definitions. XII COLACMAR, Florianópolis, Brazil. Duration: 7 hours.

2006: Unraveling life in oceanic depths. X Biology Week UFRJ, Rio de Janeiro, Brazil. Duration: 10 hours.

Zoological Ilustration. XXVI Brazilian Zoology Congress, Londrina, Brazil. Duration: 8 hours.

LANGUAGE

Portuguese	●●●●●
English	●●●●○
Spanish	●●●●○
German	●●●○○

OTHER HABILITIES

Field work	●●●●●
Scientific photography	●●●●○
Curation of scientific collection	●●●○○

LABORATORY WORK

Sample handling	●●●●●
DNA extraction	●●●●○
PCR protocols	●●●●○
Gel electrophoresis	●●●●○
DNA clean-up	●●●●○

SOFTWARES

Microsoft Office	●●●●●
Adobe Photoshop	●●●●○
Corel Photo-Paint	●●●○○
Geneious	●●●●○
MEGA	●●●●○
RaxML	●●●●○

PARTICIPATION ON SCIENTIFIC MEETINGS

15 participations: 23 works presented
4 oral presentations

PARTICIPATION ON POPULARIZATION OF SCIENCE EVENTS

7 participations: 4 courses given
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