POLYCLADIDA BIODIVERSITY AND SYSTEMATICS: AN INTEGRATIVE APPROACH

DISSERTATION PRESENTED TO OBTAIN THE DEGREE OF DOCTOR AT THE FACULTY OF BIOLOGY OF THE LUDWIG-MAXIMILIAN UNIVERSITY OF MUNICH

DISSERTATION ZUR ERLANGUNG DES DOKTORGRADES DER FAKULTÄT FÜR BIOLOGIE DER LUDWIG-MAXIMILIANS-UNIVERSITÄT MÜNCHEN

VORGELEGT VON / PRESENTED BY

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24.05.2017
This study was funded by a PhD scholarship provided by the *Brazilian National Council for Scientific and Technological Development* (CNPq-Brazil) and the *German Academic Exchange Service* (DAAD)
Declaration of Originality

I, Juliana Bahia Maceira, declare that this thesis is my own work and has not been submitted in any other form for another degree or diploma at any university or other institute of tertiary education. To the best of my knowledge and belief, this Ph.D. dissertation contains no material previously published or written by another person except where due references are made.

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Eidesstattliche Erklärung / Erklärung


München, den

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Juliana Bahia Maceira
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München,

Prof. Dr. Michael Schrödl

Juliana Bahia Maceira
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. Polyclads 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 Polycladida, 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+2 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 apparatus. 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;
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 (Gallen 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 (Gallen 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 Polycladida 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.,
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.
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.
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, which harbor a wide range of marine invertebrates. Little is known about the distribution of this family 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 of the central coast of Alagoas, where 12 Polycladida species were found: *Pericelis cata*, *Enchiridium evelinae*, *Pseudoceros bicolor* and a possible new color variation of this species, *Pseudoceros rawlinsiae*, *Pseudoceros parvallis*, *Thysanozoon brevifrons*, *Thysanozoon alagoensis* sp. nov., *Arimatophana leptakea*, *Aedonoplana 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 12 species are the first time reported from Alagoas State. Also, it is the first time that *Phaenocelis medvedica*, *Aedonoplana evelinae*, *Latocestus brasiliensis* and *Arimatophana leptakea* are illustrated by full color photos of live specimens and histological sections.

Keywords: marine flatworms, Brazilian biodiversity, taxonomy

Submitted 2 June 2014; accepted 29 May 2015; first published online 8 June 2015

**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 in Brazil, 46 being endemic (Quiroga et al., 2004; 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 Persimunga River on the north and by the São Francisco River on the south (8°34′5″–35′39″S and 10°30′5″–36′25″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
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 & Sovierzonski, 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), Jacuia (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°44'54"S - 35° 39'25"W), 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% formalin, following a modified methodology (Newman & Cannon, 2003), and transferred to 70% ethanol for histological preparation. Specimens were measured after fixation (length mm x 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 Platynematinae 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 ewelinae, Pseudoceros bicolor, Pseudoceros rawlinsonae, Pseudoceros parvulus, Thyasira coen bromchi, Thyasira alagoensis sp. nov., Armatorhina leptalea, Adenophora ewelinae, Latococcus brasiliensis and Phacocelis medvedica. The species Enchiridium ewelinae 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 POLYCLADIDAE Lang, 1884
Suborder COTYLEA Lang, 1884
Family PERICELIIDAE 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.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>Ponta Verde</th>
<th>Francês</th>
<th>Riacho Doce</th>
<th>Saco da Pedra</th>
<th>Piscina dos Amores</th>
<th>Pajuçara</th>
<th>Number of specimens</th>
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<td>No. of species</td>
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<td>9</td>
<td>1</td>
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<td>Total: 15/55</td>
</tr>
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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., 2006b), Cabo Frio, south-eastern Brazil (Bahiia & 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 (Bahiia & 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 undulatus. 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.

Family PROSTHISTOSTOMIDAE Lang, 1884
Genus Enchiridium Bock, 1943
Enchiridium eviniae 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 (Bahiia et al., 2012), Rio de Janeiro State (Bahiia 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. eviniae 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 Enchoriopsis evlinea ate a specimen of Adenocephala evlinea 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 (13 x 8 mm) as sagittal sections of reproductive structures (MNRI-PLAT 85, 9 slides). One mature specimen (MNRI-PLAT 86, 10 x 8 mm) collected 24 January 2013. Both collected at Saco da Pedra sandstone reef, Maréchal Deodoro, Alagoas, Brazil and preserved in 70% ethanol. One mature specimen (15 x 10 mm) as sagittal section of reproductive structures (MNRI-PLAT 90, 16 slides). One mature specimen (15 x 10 mm) as sagittal section of reproductive structures (MNRI-PLAT 91, 15 slides). Both collected 25 January 2013 at Frades sandstone reef, Maréchal Deodoro, Alagoas, Brazil.

GEOGRAPHIC DISTRIBUTION
Described from Bermuda (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 & Pauda, 2009). This is the first record of this species from north-eastern Brazil.

REMARKS
The specimens MNRI-PLAT 85 and 86 are in accordance with the description and posterior amendment. Specimens MNRI-PLAT 90 and MNRI-PLAT 91 (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. Prostate 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 lenticules 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 & Pauda, 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 x 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 these 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 Rolános, Quiroga & Litvaitis, 2007
(Figure 2D)

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

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

Genus Pseudobiscuteros Faubel, 1984
Pseudobiscuteros pardalis (Verrill, 1900)
(Figure 2F)

EXAMINED MATERIAL
One specimen (45 x 37 mm) as sagittal sections of reproductive structures (MNRI-PLAT 92, 35 slides). Collected 27 January 2012 at Saco da Pedra sandstone reef, Maréchal Deodoro, Alagoas, 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; cp, cement glands; cs, cement sacs; eg, cement gland; fsf, female gonopore; ma, male atrium; mg, male gonopore; pd, penis; ph, pharynx; pv, prostate vesicle; ss, sucker; st, seminal vesicle; te, testicular epiplasm; ut, ureter; va, vagina.
Geographic Distribution

*Pseudolimnias paralina* was described from Bermuda (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 *Thysanozone* Grube, 1840

*Thysanozone brocchi* (Riso, 1818)

(Figure 4)

Examined Material

Two specimens (22 x 18 mm and 6 x 4 mm), the mature as sagittal sections of reproductive structures (MNRF-PLAT 93, 29 slides). Collected 21 January 2012 at São da Pedra sandstone reef, Maráchel Deodoro, Alagoas, Brazil. One specimen (17 x 20 mm) (MNRF-PLAT 94) collected 25 January 2012 at Francês sandstone reef, Maráchel Deodoro, Alagoas, Brazil.

Geographic Distribution

Cosmopolitan species described from Naples, Italy (type locality; Riso, 1818) and other parts of the Mediterranean Sea, UK, south and west from Africa, Florida, Colombian Caribbean, Brazil, Japan and New Zealand (Prudden, 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.

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.).

*Thysanozone alagoensis* sp. nov.

(Figures 5 & 6)

Type Material

Holotype: one specimen (19 x 16 mm), as sagittal sections of reproductive structures (MNRF-PLAT 95, 26 slides). Collected 27 January 2012 at São da Pedra sandstone reef, Maráchel 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 eyespot 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. Gland developed spermidinal 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 eyespot arranged in a line at the border (Figure 6A) and a group of eyespots at each tentacular tip (about 20). Frontally, in between pseudotentacles, there are also clusters of eyespots, it is not clear if as an extension of the border eyespots groups or distinctive cluster
(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. Penial 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 spermatidic 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 brochii*. Also the *T. alogensis* has a different colouration pattern, and the dorsal papillae of this species are slender and *Thysanozoon brochii* have rounder ones (Table 2). Other similar species such as *Thysanozoon californianum* (Hyman, 1951a) 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 section. be: pseudotentacle border eyespot; co: cerebral eyespot; cg: cement glands; ed: excretory duct; fg: female gonopore; ma: male atrium; mg: male gonopore; pa: papilla; pt: eyespot between pseudotentacles; pb: prostatic vesicle; sb: spermatidal bulb; su: sucker; sv: seminal vesicle; te: pseudotentacles tips; vs: vagina; ve: ventral eyespot.

(Table 3). The most similar species found in the literature is Thysanozoon miriae, recently described from Argentina (Bulnes et al., 2011). However, there are marked differences between them, *T. miriae* has a smaller pharynx (3.5 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 Argentinean species are colourless and the ones in *T. alagoensis* are dark with yellowish tips. The Argentinean 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. miriae* have slender, elongated papillae, which are also found in Thysanozoon stummi (Brock, 1913) and *T. districatum* (Stummi-Trumel, 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. miriae*. Both also have apparent spermatidal 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. miriae*. 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 Lackow, 1902
Genus Phaeocelis von Stummi-Trumel, 1933
Phaeocelis medvedica Marcus, 1952
(Figure 7)

**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.

**DIAGNOSTIC**

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 STYLOCHIDAE Faubel, 1983
Genus Armatoptana Faubel, 1983
Armatoptana leptacea (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 (MNRI-PLAT 98). Collected 10 January 2008 at Râdo Doce coral reef, Maceió, Alagoas, Brazil. One specimen (12 × 4 mm) (MNRI-PLAT 99, 5 slides). Collected 11 January 2008 at Saco da Pedra sandstone reef, Marechal Deodoro, Alagoas, Brazil.
| T. brocchi (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, Spermidivulc 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, 1932 | 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. crassatum Schonmuara, 1899 | 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. discoidatum Schonmuara, 1899 | 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 Stammer-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, Spermidivulc vesicles absent | Eilam and Java, Indonesia |
| T. flavotuberculatum Hyman, 1930 | Greyish with irregular small black flecks. Scarce yellow papillae | Few oval papillae | ? | Immature sectioned | Bermuda |
| T. hawaiiensis Hyman, 1930 | Light ochre with dull green papillae | Cylindrical | Five simple folds | Not sectioned | Hawaii |
| T. laege Stammer-Traunfels, 1895 | Bright dirty violet, with darker violet motting over papillae | Short and rounded | Five simple folds | Not sectioned | Ambon, Indonesia |
| T. minutum Stammer-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. miriu Baillou et al. 2011 | Greenish yellow covered with rounded black spots, reddish brown papillae, tentacles unpigmented | Slender and elongated | Three simple folds | Vas deferens form spermidivulc vesicles. Seminal vesicle with well-developed muscular wall and is arranged dorsally to the male prostatic vesicle and stylet. Rounded prostatic vesicle | Argentina |
| T. nigropapillatum (Hyman, 1930) | Black with pale yellowish margin. Black papillae with white tips | Short and rounded | Five simple folds | Not sectioned | Palau, Micronesia |
| T. nigrosum 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 Bermuda |

Continued
Table 2. Continued

<table>
<thead>
<tr>
<th>Thysanozoon species</th>
<th>Colour pattern</th>
<th>Papillae</th>
<th>Pharynx</th>
<th>Male system</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. sphallii</em> Bolatto et al., 2007</td>
<td>Brown-blackish with yellowish orange papillae. Small white slash-like marks hardly visible in the margin. Black tentacles sometimes outlined by white marks</td>
<td>Short and rounded</td>
<td>?</td>
<td>Seminal vesicle elongated and prostactic vesicle rounded. Spermidinal vesicles absent</td>
<td>Belize and Panama</td>
</tr>
<tr>
<td><em>T. skottsbergi</em> Bock, 1927</td>
<td>Yellowish with touch of greenish grey. Blackish median line, lighter papillae tipped with black. Black tentacles</td>
<td>Slender</td>
<td>Five simple folds</td>
<td>Not sectioned</td>
<td>Juan Fernandez Islands</td>
</tr>
<tr>
<td><em>T. alagoaesii</em> sp. nov.</td>
<td>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</td>
<td>Slender and elongated</td>
<td>Pharynx ruffled with seven simple folds</td>
<td>Seminal vesicle elongated and huge, reaches the front of penial papillae. Ejaculatory duct comes in a curve to join the penis. Prostasic vesicle small and comma shaped. Male atrium simple. Greatest developed spermidinal vesicles</td>
<td>Brazil</td>
</tr>
</tbody>
</table>

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, Curacao 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 LATOCERITIDAE Laidlaw, 1902
Genus Latoceras Pfeil, 1896
*Latoceras brasiliensis* Hyman, 1955 (Figure 9)

EXAMINED MATERIAL

One specimen (7 × 1.5 mm) as sagittal sections of reproductive structures (MNRI-PLAT 101, 6 slides). Collected 7 February 2008 at Pajuçara coral reef, Maceió, Alagoas,
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. 83), she states that the collector (Waldo L. Schmitt) traveled 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 eyesteps around...
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 apert 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 contractile duct (Figure 9F). Granular vesicle and accessory seminal vesicle very muscularized (Figure 9F), 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 *Latococetus pallipes* Marcus, 1947 have different body form, eyespots arrangement and differences in reproductive structures both masculine and feminine. The species *Latococetus atlanticus* Pielm, 1896 also has a different eyespots arrangement. The species *Prolatococetus 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 x 10 mm) as sagittal sections of reproductive structures (MNRI-PLAT 102, 8 slides). Collected 28 January 2007 at Pajuçara, Maceió, Alagoas, Brazil. One specimen (12 x 6 mm), collected 9 January 2008 at Brazil, Alagoas, Maceió, Recife do Frades (eaten by a *Enchirodon elongatus*). One specimen (21 x 12 mm) (MNRI-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. Prostatoïd organs present in the penis tissue (Figure 10F) and granular vesicle; male atrial spacious, vagina, common uterine duct and Lang’s vesicle duct ciliated (Figure 10E).

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**Fig. 10.** *Adenoplana evelinae* (A) in vitro (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 gonopores; h, Lang's vesicle duct; me, marginal eyespots; mg, male and female gonopores; mo, male gonopore; mo, mouth; ph, pharynx; po, prostatoïd spv, spermoidal 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 Aedonoplana species, A. oborata (Schmarda, 1859), does not have marginal eyespots surrounding the entire body margin (Hyman, 1955), as Aedonoplana eveleinæ has. The South American species A. platoe 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: Stylodicha wulfferg and Aedonoplana leptolia, 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: Enchidium evelinae, Phikoceros mopsas, Pseudococeros evelinae, Thysanozoon brocchi, Hoploplana divae. And recently, Queiroz et al. (2013) recorded Pericellidae while collecting from Bahia State.

The present work adds six species to the north-eastern Brazilian coast: Pseudococeros bicolor, Pseudococeros flavinervis, Thysanozoon alagoensis sp. nov., Phikoceros medvedevi, Latococcus brasiliensis and Aedonoplana eveleinæ. One of them is a new species and 11 species are for the first time reported from Alagoas State. It is also the first time that Phikoceros medvedevi, Aedonoplana eveleinæ, Latococcus brasiliensis and Aedonoplana leptolia 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 polycladids 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 & Soverijzers, 2010). The area with highest species richness, São da Pedra reef, has a good conservation status as it is within a Biological Reserve (Correia & Soverijzers, 2009). In contrast areas such as Piscina dos Amores coral reef, Pajucara and Jatuba reefs are more impacted reef areas, inside the urban perimeter of the city of Maceió and the city harbour. Apparently, polycladids 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.

ACKNOWLEDGEMENTS

We thank Arnaldo Campos Rez on for histological slides and EcoScuba for the logistic support. We also thank Juan Lucas Cervera, Juan Carlos Garcia-Gomez, Luis Sanchez, Manuel Malaquias, Anderson Miranda, Elizabeth Torres, Victor Pedro, Lilian Freitas, Alvaro Borba and Leandro Vieira for help in collections and sorting material.

FINANCIAL SUPPORT

We are grateful to CAPES (Coordenação de Aperfeiçoamento de Pessoal do Ensino Superior) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for Juliana Bahia's scholarship during the collections. Both Juliana Bahia and Vinicius Padula have PhD grants from CNPq-Brazil and DAAD-Germany.

Supplementary material and methods

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

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Chapter 2.
First records of polyclads (Platyhelminthes, Polycladida) associated with *Nodipecten nodosus* (Linnaeus, 1758)
First records of polyclads (Platyhelminthes, Polycladida) associated with Nodipten nodosus (Linnaeus 1758) aquaculture

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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 considered as oyster leeches. The present contribution identifies three species of polyclads associated with scallop aquaculture at Ilha Grande, southeastern Brazil: one corylcean, Lurymare matorazzoi, and two acotyleans, Imaginiae tica and Imaginiae reftora. 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 Nodipten nodosus in experimental aquaculture, feeding either on the molluscs or on the associated fauna.

Keywords Brazilian marine flatworms · Associated fauna · Molluscs · Pectinidae · Lurymare · Imaginiae

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 Hoplura usagia, Smith 1960 (Smith 1960), or symbiotic: such as the polyclad Zygocrypta ugo, González & Salazar-Vallejo 1995 (González and Salazar-Vallejo 1996). Some mimic nudibranchs of the genus Physidella Bergh 1869, such as Pseudoceros initiatus, Newman & Cannon 1994 (Newman et al. 1994). Others feed on various bivalve species, such as Bankia martensi, Stempell (1899) (Brusa and Darboeassn 2014), mussels, Terebrosp., and, most commonly, species of oyster (Gallieni et al. 1980; Shu et al. 2005). The records of polyclad predation on molluscs are for acotyleans, mostly from the families Stylochidae and Notopolinidae. There is, so far, only one record of a member of Prosthistiomiidae associated with molluscs, Prosthistiomiostromae, 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 Nodipten nodosus (Linnaeus 1758), situated at Paim dos Menos, Ilha Grande, southeastern Brazil (23°7'56"S; 44°19'26"4,1"W). Polyclad specimens were photographed alive 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, genital position, and reconstruction of the reproductive structures from histological sections stained with

Published online: 23 December 2015
the hematoxylin–eosin method. Data were compared to original descriptions and other literature. The collected material was deposited in the Platymastixthes 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 Prosthodistomidae Lang 1884

Genus Lurynaire Marcus and Marcus 1968
Lurynaire maturazzoi (Marcus 1950)
Euprosthodistomum maturazzoi 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 Bouaire (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 Prosthodistomum (Marcus 1950) to Lurynaire Marcus and Marcus 1968, based on the presence of a muscle sheath containing prostatic vesicles. This transfer was supported by Pradhowe (1985), but Faubel (1984) placed it in the genus Euprosthodistomum Bock 1925. However, this assignment is questionable, as Faubel (1984) stated that Euprosthodistomum 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 S-shaped muscular sheath, and Lurynaire is defined as having "prostatic vesicles in a common muscle sheath which may include the seminal vesicle", thus being the only prosthodistomid genus that presents this character, in both reviews (Faubel 1984; Pradhowe 1985). Also, Marcus and Marcus (1968), who both described the species and created the genus, used this character to include "Prosthodistomum maturazzoi" in the new genus Lurynaire. The specimens studied here accord with the original description of L. maturazzoi by Marcus (1950) and the later citation by Marcus and Marcus (1968), and, therefore, this species should be included in Lurynaire, as previously stated by Marcus and Marcus (1968) and Pradhowe (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 noted in the original description.

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

![Fig. 1 Lurynaire maturazzoi (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, vg vagina, ig vesicular granuloma]
Fig. 2. *Imagote species a Imagote tica* (MNRI-PLAT 110) in vivo dorsal view; b sagittal section of male and female reproductive structures; c *Imagote referens* (MNRI-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, hv internal vagina, ma male atrium, mg male gonopore, pv prostatic vesicle, sd seminal duct, sv seminal vesicle

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**Material examined:** One specimen (MNRI-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 Sào 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; nasal tentacles small and elongated, anterior to brain level. Marginal eyestrips extending past brain level, few frontal eyestrips; cerebral eyestrips extending from slightly anterior to tentacles to brain level, tentacular eyestrips 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 *Imagote 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 *Dispylochus Faubel 1983* because of their bipartite seminal vesicle (*Du Bois-Reymond Marcus 1955*). The remaining Brazilian species of *Imagote* (*I. catt* (*Du Bois-Reymond Marcus 1958*), also has a penis pouch, but differs in having a common genital pore (*Du Bois-Reymond Marcus 1958*). *Imagote megaloeps* (Schmarda 1859) has a similarly arranged band of marginal eyestrips. However, it has the nuchal tentacles set more closely, fewer cerebral eyestrips, and differences in the internal anatomy (*Stummer-Traunfels 1933; Hyman 1955b*). *Imagote oculifera* (Girard 1853) has a different coloration pattern, with
rose-red spots on the dorsal surface (Hyman 1935b); and
*H. zebra* (Verrell 1882) also has a different, striped coloration pattern and an erect prostatic vesicle (Hyman 1939). The Japanese species *I. rufulus* Yeri and Kaburaki 1918 and *I. jiunai* Yeri and Kaburaki 1918 differ from *I. tica* in both the coloration pattern (darker coloration over the pharynx area) and the arrangement of the eye spots (Yeri and Kaburaki 1918). *Imagene mediterranea* Galleni 1976 has more cerebral eye spots than the specimen studied here, and lacks a penis pouch (Galleni 1976). *Imagene minimus* Polombi 1940 has a different arrangement of the eye spots and is much smaller in overall size (Polombi 1940), and both *I. referlus* Du Bois-Reymund Marcus 1965 and *I. orientalis* Boie 1913 have a larger semin al vesicle than *I. tica* (Du Bois-Reymund Marcus 1965; Galleni 1976). Compared to *I. ellipticus* Girard 1850, our specimen lacks the smooth style and has more numerous cerebral eye spots (Hyman 1939), and *I. meridianus* Prudhoe 1989 lacks a penis pouch and has a different eye spot arrangement (Prudhoe 1989).

*Imagene referlus* Du Bois-Reymund Marcus 1965

**Material examined:** One specimen (MNRI-PAT 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-Reymund Marcus 1965).

**Diagnosis:** Background color beige with greenish-brown flecks, orange marginal band, orange elongated nuchal tentacles; marginal eye spots in broad band, no frontal eye spots, a few cerebral eye spots, nuchal eye spots 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 polynuclear type, with thick muscular wall. Extern-vesicular glands scattered in parenchyma surrounding prostatic vesicle. Prostatic duct and penis papilla both short.

**Taxonomic remarks:** Our specimen fits the definition of *Imagene*, based on the presence of the tripartite seminal vesicle. *Imagene referlus* 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 specimen cannot be assigned to *I. tica* because this species has a single aperture for both the male and the 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).

*Imagene meridianus* has similar internal features but different coloration and eye spot arrangement (Prudhoe 1989).

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

Most species of *Imagene* have transparent tentacles (Jennings and Newman 1996b, b), Bulnes et al. 2005; Bulnes 2010). The Australian *I. megaleos* 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 eye spot arrangement to our specimen (Jennings and Newman 1996b). The only two species of *Imagene* that also have orange tentacles are *I. arenosus* (Willey 1897) and *I. referlus* (Du Bois-Reymund Marcus 1965). *Imagene arenosus* has a colorless margin and more widely separated eye spots (Willey 1897), which differ from the material studied here, but, unfortunately, there are no details of the internal anatomy to compare. In *I. referlus*, the entire dorsal surface, not only the margins, is orange (Du Bois-Reymund Marcus 1965).

Despite this difference in coloration, the present material fits the original description of *I. referlus* in relative size, morphology and position of reproductive structures, presence of a penis pouch, distance between tentacles, eye spot arrangement, and, also, the reticular design of the orange pigmentation layer (Du Bois-Reymund Marcus 1965). Therefore, the specimen is identified as *I. referlus*. The specimen described by Du Bois-Reymund 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 well known and significant that these animals are known as oyster leeches (Pearse and Wharton 1938). Hyman (1953a) described an acolyte, introduced from Japan through oyster farming, which had a destructive effect on local cultures and direct economic impact.

The lion's paw scallop *N. nodosa* 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 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 acolyte flatworms, belonging to a genus whose representatives are well known for their predation on bivalves (Galleni et al.
at an aquaculture site of *N. nodosa* 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-mollusk interactions are known, and members of this suborder are also known to prey on ascidians (Marcus 1950). According to Gallenl et al. (1980), only two species, both belonging to the family Pseudocentridae, prey on oysters. Among the Prostheciosmidae, *P. montipora* preys on coral, and *E. vieira* was found inside an uninhabited hermit crab shell (Palombi 1936). *Prostheciosma oostae* was found by Kato (1937) inside empty oyster shells. The species was not reported as a predator of molluscs by Gallenl et al. (1980), possibly because Kato (1937) provided no evidence of its predation on the oyster. The present finding adds a further prostheciosmid species to the list of potential predators of bivalves. However, whether this flatworm actually feeds on *N. nodosa* or on its associated fauna has yet to be tested by experiments.

Acknowledgments I thank Dr. Vinicius Padula for the collection and donation of material herein studied, Adailo de Campos Perez for the helpful histological work, Prof. Dr. Michael Schrödl for helpul advisng me, and CNPq, Brazil (National Council for Scientific and Technological Development) for funding.

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Chapter 3.

*Pseudobiceros wirtzi* sp. nov. (Polycladida: Cotylea) from Senegal with revision of valid species of the genus
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. 2009–2015). 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 Pseudobiceros 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 Sánchez & Batet 1991; Witz & 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...
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 hematoxylin-eosin method (Belaños 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 Zoologisehe 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 ferruginus (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 miniatius, P. rubrocinclus, P. schmaradei, 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 Platyhelminthes

Order Polycladida Lang, 1884

Suborder Cotylea Lang, 1884

Family Pseudocerotidae Lang, 1884

Genus Pseudobiceros Faubel, 1984

Type species: Pseudobiceros strangulus (Marcus, 1950) junior synonym of Pseudobiceros gratus (Kato, 1937)
Taxonomic remarks. The confusion about the genus *Pseudobiceps* begins with its type species. *Pseudoceros striigus* was a name created by Marcus (1950) to solve confusion resulted from the misuse of the specific name *sirius* (in the originally *Eunectes* description (Schmarda 1859)) or *sirius* (after it was relocated in *Pseudoceros* (Stummer-Traunfels 1933, pp. 3487 and fig. 9). He stated a distinction between *P. sirius sensu* Schmarda (1859, p. 27 and fig. 62) and sensu Keelert (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 name given by Marcus. Fauber (1984) followed Marcus’ opinion, while Newman & Cannon (1994) followed Hyman. We find that Hyman (1959) is right and *Pseudobiceps gratus* has priority over *P. striigus*. However, *Pseudobiceps striigus* 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 *Pseudobiceps gratus* synonym list, as it was described with information about reproductive structures, and it was draw with two median lines instead of one, as present in *Pseudobiceps gratus*.

*Pseudobiceps bedfordi* (Laidlaw, 1903a)

Taxonomic remarks. *Pseudobiceps bedfordi* has under its synonym list (Table 1) the species *Pseudoceros microstimans*, described by Hyman (1955). However, Fauber (1984) makes a new combination of this species adding it to *Pseudobiceps*, but citing Hyman 1953 as the author, and considering *P. bedfordi* and *P. microstimans* 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 Fauber’s list (1984), already clarified that the species described by Hyman (1955) is synonym of *Pseudobiceps bedfordi*, after examining its holotype. Here we support that decision and do not consider *Pseudobiceps microstimans* as a valid species.

*Pseudobiceps hancocki* (Collingwood, 1876)

Taxonomic remarks. This species was subject to much confusion concerning its synonym list. It was originally described as *Proceros hancocki* (Collingwood 1876) and assigned to *Prosthecoerus* by Lang (1884) and to *Pseudoceros* by Laidlaw (1903). Marcus (1950) also recognized *Prosthecoerus*-like pseudotentacles in the drawings. cabinski (1923), however, synonymized it to another *Collingwood* (1876) species: *Pseudoceros malayensis* (originally described as *Stylochus* 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 left open. Fauber (1984) did not include both species in *Pseudoceros, Pseudobiceps, Prosthecoerus* or in the *incertae sedis* species list. Newman & Cannon (1994) treated both as synonyms; adding information from fresh material, they transferred the species to *Pseudobiceps*. 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.

*Pseudobiceps luteomarginatus* (Yeri & Kaburaki, 1918)

Taxonomic remarks. This species is listed as synonymous to *Pseudoceros flavomarginatus* by Fauber (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 Fauber (1984) was result of some confusion about the literature consulted. Thus we argue that *Pseudoceros 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. Pseudobiceros 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 minimatus** (Schmarda, 1859)

**Taxonomic remarks.** This species was originally described as *Eurypleta minimata* (Schmarda 1859). Then its genus was discussed by Diesing (1862), who transferred it to Proceres, and Lang (1884), who transferred it to *Yungia*. Later, Stummer-Traunfels (1913) 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 rubrocinets** (Schmarda, 1859)

**Taxonomic remarks.** This species was originally described as *Eurypleta rubrocinets* (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 *Prosthecerus latissimus* (Schmarda 1859). Drawings of the type material show that two different animals were described under the same name; one clearly refers to *Prosthecerus* (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 borgani and Pseudobiceros kryptos (Newman & Cannon, 1997) are extremely 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 courtesy 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.

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**FIGURE 1.** A—*Pseudobicerca 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 sinuses 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).
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 papilae 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 uterus.

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*. Pseudocerorididae 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’s (1950), Faubel’s (1984), and Newman & Cannon’s (1994) revisions of accepted *Pseudoceros* and *Pseudobicer* species, no other *Pseudobicer* species match the color pattern presented by *P. wirtzi*. Newman & Cannon pointed out species with transverse lines pattern such as *Pseudoceros bedfordii*, *P. dendriticus*, *P. flavolineatus*, *P. fulgor*, but all present a distinctive margin, which is lacking in our specimens. *Pseudoceros bedfordii* (Laidlaw 1903b) has a much more complex color pattern with wider stripes instead of lines, and with blotches, motting, and different colored dots that are absent from *P. wirtzi*. *Pseudoceros dendriticus*, 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. *Pseudoceros 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 Sánchez & 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 *Pseudocerotaiidae sp* from Canary Islands by Vera et al. (2008).

**Discussion and conclusions**

According to Faubel (1984) and Newman & Cannon (1994), the pseudocerotid genera *Pseudoceros* and *Pseudobicer* 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 *Pseudobicer* that resulted from a new combination. Most confusion was because older descriptions (eg: Simpson 1857; Kelart 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 *Pseudobicer* still lack a thorough 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 (Pudifinus 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 *Prosthecercus gierbrechti*, *Prosthecercus roseus*, *Yangia aurantiaca*, *Pseudoceros velhinius*, *Pseudoceros cf. maximus*, *Thysanozoon brocchii*, are usually reported in invertebrate identification guides or species lists (Pérez Sánchez & 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 ampul–Atlantic polyclad species. This is not the case for ecologically similar groups like nudibranchs (Goodnight 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>
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<tr>
<th><strong>Pseudobiceros species</strong></th>
<th><strong>Color pattern</strong></th>
<th><strong>Distribution</strong></th>
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<th><strong>Literature</strong></th>
<th><strong>Synonyms</strong></th>
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<tr>
<td><em>Pseudobiceros apricus</em></td>
<td>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.</td>
<td>South Great Barrier Reef</td>
<td>Square pseudotentacles. Pharynx large and elongated with about 5 folds at each side. Oval seminal vesicle (4 to 5 times larger than the prostatic vesicle), short ejaculatory duct. Shallow female atrium.</td>
<td>Newman &amp; Cannon 1994, 1997</td>
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<td>(Newman &amp; Cannon, 1994)</td>
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<tr>
<td><em>Pseudobiceros baiac</em></td>
<td>Black with whitish speckles.</td>
<td>Gulf of California</td>
<td>Pointed ear-like pseudotentacles. Pharynx elongated with 5 folds. Sporomidal vesicles present, oblong prostatic vesicle. Long and coiled ejaculatory duct.</td>
<td>Hyman 1953</td>
<td><em>Pseudobiceros baiac</em> <em>Hyman, 1953</em></td>
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<td>(Laidlaw, 1903a)</td>
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<td><em>Pseudobiceros micronesium</em> <em>Hyman, 1955</em></td>
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<tr>
<td><em>Pseudobiceros breganti</em></td>
<td>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. Tentacle tips white without marginal bands.</td>
<td>West Australia</td>
<td>Square pseudotentacles. Pharynx small with 5-6 folds at each side. Rounded prostatic vesicle, disform seminal vesicle, short ejaculatory duct and long styllet.</td>
<td>Newman &amp; Cannon 1997</td>
<td><em>Pseudobiceros micronesium</em> <em>Faibel, 1984</em></td>
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<td>(Newman &amp; Cannon, 1997)</td>
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<td><em>Pseudobiceros caribbeanus</em></td>
<td>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.</td>
<td>Curacao, Jamaica, Florida and Honduras, French Mediterranean</td>
<td>Pointed ear-like pseudotentacles. Pharynx small with about 5 folds. Large and oval seminal vesicle, rounded prostatic vesicle. Long styllet and straight ejaculatory duct.</td>
<td>Bolaños, Quiroga &amp; Litvaitis 2007</td>
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<td>(Bolaños, Quiroga &amp; Litvaitis, 2007)</td>
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<tr>
<td><em>P. cinereus</em> (Palombi, 1931)</td>
<td>Greyish with black margin and one grey line at each side of the median line.</td>
<td>New Guinea</td>
<td>Square-shaped pseudotentacles</td>
<td>Palombi 1931</td>
<td><em>P. cinereus</em></td>
</tr>
<tr>
<td><em>P. dendriticus</em> Prudhoe, 1989</td>
<td>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</td>
<td>Mozambique</td>
<td>Pharynx with shallow folds. Two male gonopores. Folded tentacles.</td>
<td>Prudhoe 1989</td>
<td><em>P. dendriticus</em> Prudhoe, 1989</td>
</tr>
<tr>
<td><em>P. flavolineatus</em> Prudhoe, 1989</td>
<td>Reddish brown background with yellow distributed from median line to margin rarely touching each other. In the margin irregular double row of black spots.</td>
<td>Mozambique</td>
<td>Pointed ear-like pseudotentacles. Pharynx with about 5 folds at each side.</td>
<td>Prudhoe 1989</td>
<td><em>P. flavolineatus</em> Prudhoe, 1989</td>
</tr>
<tr>
<td><em>P. flowersi</em> Newman &amp; Cannon, 1997</td>
<td>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.</td>
<td>North Great Barrier Reef and Philippines</td>
<td>Square pseudotentacles. Pharynx short and with few folds. Oblong seminal vesicle and oval prostatic vesicle. Short style and ejaculatory duct.</td>
<td>Newman &amp; Cannon 1997</td>
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### TABLE 1. (Continued)

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<th>Pseudobiceros species</th>
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</thead>
</table>
| *Pseudobiceros fujor* 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 5 folds. | Hyman 1959
Faulb 1984
*Pseudobiceros fujor* Newman, 1994
*Pseudobiceros fujor* Faulb, 1984 |
| *Pseudobiceros gardineri* (Laidlaw, 1902) | Grey background scattered with irregular black marks of varying size. | Hulde Atoll                                      | Pointed ear-like pseudotentacles.
Small pharynx with 5 folds. Two male gonopores. | Laidlaw 1902
Marcus 1950
Faulb 1984
*Pseudobiceros gardineri* Faulb, 1984 |
| *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. | Schmida 1859
Stummer-Teunfels 1933
Kato 1937, 1944
Marcus 1950
Hyman 1959
Faulb 1984
*Pseudobiceros striatus* Stummer-Teunfels, 1933
*Pseudobiceros gratus* Kato, 1937
*Pseudobiceros gratos* Marcus, 1950
*Pseudobiceros striatus* (Schmida)   |
Laidlaw 1903
Bock 1913
Kabunki 1923
Marcus 1950
Newman & Cannon 1994 | *Procerostrica hancockiana* Collingswood, 1876
*Stylochipsis malaysiensis* Collingswood, 1876
*Pseudobiceros hancockianus* Lang, 1884
*Pseudobiceros hancockiana* Laidlaw 1903, Kabunki 1923, Marcus 1950
*Pseudobiceros malaysiensis* Bock, 1913 |

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<th><strong>Pseudobiceps species</strong></th>
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<th><strong>Distribution</strong></th>
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<th><strong>Literature</strong></th>
<th><strong>Synonym</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pseudobiceps kypos</em> Newman &amp; Cannon, 1997</td>
<td>Mottled olive green to lime green and white, large irregular brown and olive green spots on the margin</td>
<td>Papua New Guinea, North and South Great Barrier Reef, West Australia, Bali, Indonesia, Lord Howe Islands</td>
<td>Square pseudotentacles. Small pharynx. Elongated seminal vesicle and rounded prostatic vesicle. Short ejaculatory duct.</td>
<td>Newman &amp; Cannon 1997</td>
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<th><strong>TABLE 1. (Continued)</strong></th>
<th><strong>Pseudobicersopisces</strong></th>
<th><strong>Color pattern</strong></th>
<th><strong>Distribution</strong></th>
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<th><strong>Synonyms</strong></th>
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<tbody>
<tr>
<td><em>Pseudobicers nigromarginatus</em> (Yer &amp; Kaburaki, 1918)</td>
<td>Blackish brown with narrow black margin and two light colored longitudinal bands on each side of the median line</td>
<td>Japan</td>
<td>Detailed study on the distribution and color patterns.</td>
<td>Year &amp; Kaburaki 1918</td>
<td>Marcus 1950, Faust 1984</td>
<td><em>Pseudobicers nigromarginatus</em> *Yer &amp; Kaburaki, 1918 *Pseudobicers nigromarginatus *Faust, 1984</td>
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<td><strong>TABLE 1.</strong> (Continued)</td>
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<tr>
<td><em>Pseudobiceros splendens</em> (Lang, 1884)</td>
<td>Deep bluish or purplish black, marginal bands inner white or orange yellow, outer black</td>
<td>Mediterranean, Vietnam, Galapagos, Puerto Rico, Bermuda, Mozambique</td>
<td>Two male gonopores.</td>
<td>Lang 1884 Stummer-Transfelds, 1933 Marcus 1950 Puchoe 1989 Newman &amp; Cannon 1994, 1997</td>
<td><em>Pseudobiceros suberbus</em> Lang, 1884 <em>Pseudobiceros splendens</em> Stummer-Transfelds, 1933</td>
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<th>Pseudobicerus species</th>
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Acknowledgments

We thank Prof. Dr. Peter Wirtz for the collection, donation, and photographs of the material. We also thank Arnaldo Campos Perez for the histological sections and CNPq-DAAD for the PhD fellowship to the first author. We are grateful for the helpful comments of two anonymous reviewers.

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http://dx.doi.org/10.11646/zootaxa.3873.5.3

http://dx.doi.org/10.1017/S0025315415000922


http://dx.doi.org/10.1111/zco.12237


http://dx.doi.org/10.5479/si:00963801.105-3352.65

http://dx.doi.org/10.5479/si:00963801.108-3410.543


Lang, A. (1884) Die Polycladen (Steeplanarian) des Golfs von Neapel und der angrenzenden Meeresabschnitte. Eine
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 polyclad 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 established 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 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 1.9 mm) 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 were 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.

**Synonyms.**

*Zygantroplana henriettae* Corrêa, 1949


**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 synonymization 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.
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 (23°49'S; 45°24'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 parallectotype 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

**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.*
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).

Paralecotype. 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 (23°49′S; 45°24′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 meegala* (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 23°49'S; 45°24'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 designated as paralectotypes. The voucher SMNH 109163 has apart 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 Stylochoplanae 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°52'15.40"S; 41°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 (22°53'11"S; 42°00'08"W). One specimen (MNRJ-PLAT 150, 8x4 mm) collected 21.01.2012 at Praia do Segredo, São Sebastião, Brazil (23° 49.65'S; 45° 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*).

*Stylochoplan 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 *Pentaplan 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 *Stylochoplan 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 *Stylochoplan*. Prudhoe placed it in *Stylochoplan* 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 (23°49'S; 45°24'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 (23°49'S; 45°24'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°00'41"S; 35°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°52’15,40”S; 41°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 (22°53’11”S; 42°00’08’’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 (23° 49,65’S; 45° 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 Notoplanidae 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 eveilinae 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 (23°49'S; 45°24'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 (23°49'S; 45°24'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 (23°49’S; 45°24’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 (23°49’S; 45°24’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 color morph, 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 (23°49'S; 45°24'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 (23°49'S; 45°24'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 (23°49'S; 45°24'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 (23°49'S; 45°24'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 examined.

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 (22º53’45,43”S; 41º59’5,54”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 (22º53’30,85”S; 41º59’9,52”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

**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 (23°49'S; 45°24'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''S; 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 Pentaplanida 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 Pentaplanida 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

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

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 (23° 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.
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 (23°49' S; 45°24' 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 (22° 53' 11" S; 42° 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 (23°49’S; 45°24’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 (23°49’S; 45°24’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.
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

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 (23°49'S; 45°24'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 (23°49'S; 45°24'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: \textit{Lurymare} Marcus & Marcus, 1968

\textit{Lurymare cynarium} Marcus, 1950 \textbf{nov. comb.}

Figure 41

\textbf{Type species of the genus.}
\textit{Lurymare drygalskii} (Bock, 1931), type by posterior designation.

\textbf{Material examined.}

\textit{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 (23°49'S; 45°24'W).

\textit{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 (23°49'S; 45°24'W).

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

\textbf{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 \textit{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 \textit{Prosthiostomum gilvum} (Marcus 1950, p.187) to the present species it is possible to see the vesicles separated, different from the description of \textit{Prosthiostomum cynarium}. Only two genera of Prosthiostomidae present prostatic vesicle close together: \textit{Enchiridium} and \textit{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 (23°49' S; 45°24' 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 (23°49' S; 45°24' 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*.  

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*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 (23°49’S; 45°24’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 (23°49'S; 45°24'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 (23°49'S; 45°24'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 consecutively, 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 (23°49’S; 45°24’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 (23°49’S; 45°24’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 consecutive 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 (Southeastern 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 (23°49'S; 45°24'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*.


*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 (23º47'27.42''S; 45º08'43.86''W). One specimen (MNRJ-PLAT 149, 23x24 mm) collected 18.01.2012 at Coroa da Ilha de Búzios, Ilhabela, São Paulo State, Brazil (23º47'20.10''S; 45º08'44.58''W).


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*. 

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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

**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*. Additionally, 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 it 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 x 8 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 (23°49'S; 45°24'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 110005, 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 (23°49'S; 45°24'W), São Paulo State, Brazil. One specimen as sagittal sections of middle part (SMNH 109998). Collected 1966 at Piscadera Baai, Curacao (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.

ACKNOLEDGEMENTS
We thank the SYNTHEYS program for the fellowship (SE-TAF-5521) granted to the first author; and Prof. Dr. Ulf Jondelius, the SYNTHEYS staff and SMNH staff for hosting and work aid. We also thank Prof. Dr. Veronica Bulnes for information about type material location and Dr. Marcela Bolaños for a very helpful recommendation letter for getting the fellowship. The first author is a fellowship-holder from CNPq (Brazil) and DAAD (Germany).
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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 structures; 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 structures.

**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 structures.

**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 reproductive 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: *Pentaplaninae 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: *Pericellis 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: *Euprocthiostomum 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: *Prothiostomum 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***.

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<th>Language of description</th>
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<p>| Euprosthiostomum mortensi 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 |
| 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 &amp; Marcus, 1951 Quiroga et al 2004a, b | São Paulo State, Brazil Colombia | Lectotype and paralectotype designation, color photos |
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* Vouchers of former *Thysanozoon lagidium* from Brazil.
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NHMUK 1900.5.1.43-45
ZMB 308
ZMB 1716
ZMB 1967
ZMB 2726-Q
ZMB 3203
ZMB 3204
ZMB 3205
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MNRJ-PLAT 41
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MNRJ-PLAT 94
MNRJ-PLAT 113
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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**.

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<tr>
<td>SMNH 109139*</td>
<td>Whole mount of anterior part of worm. The only one that is not entire in whole mount.</td>
<td>Lectotype</td>
<td>Pucelis evelinae. SMNH 109139. leg E Marcus (76). Dept. Zoologia S. Paulo. Pucelis evelinae Marc. 76.</td>
<td></td>
</tr>
<tr>
<td>SMNH 109135*</td>
<td>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.</td>
<td>Lectotype</td>
<td>Pucelis evelinae. SMNH 109135. leg E Marcus (72). Pucelis evelinae Marc. 72.</td>
<td></td>
</tr>
<tr>
<td>SMNH 109136*</td>
<td>Serial sections of SMNH 109139. As the slides are numbered in sequence, they are all from the type locality.</td>
<td>Lectotype</td>
<td>Pucelis evelinae. SMNH 109136. leg E Marcus (73). Pucelis evelinae Marc. 73.</td>
<td></td>
</tr>
<tr>
<td>Sample Number</td>
<td>Description</td>
<td>Type</td>
<td>Remarks</td>
<td></td>
</tr>
<tr>
<td>---------------</td>
<td>-------------</td>
<td>------</td>
<td>---------</td>
<td></td>
</tr>
<tr>
<td>SMNH 109134</td>
<td>Whole mount of entire worm. Fits figure 49 of Marcus (1947)</td>
<td>Paralectotype</td>
<td>Pucelis evelinae. SMNH 109134. leg E Marcus (71).</td>
<td></td>
</tr>
<tr>
<td>SMNH 109091*</td>
<td>Serial sections of entire worm. Continuation of previous slide. Reproductive structures on rows 1 and 2 (marked with blue dot).</td>
<td>Lectotype</td>
<td>Notoplana martae. SMNH 109091. leg E Marcus (D).</td>
<td></td>
</tr>
<tr>
<td>SMNH 109089</td>
<td>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.</td>
<td>Paralectotype</td>
<td>Notoplana martae. SMNH 109089. leg E Marcus (B).</td>
<td></td>
</tr>
<tr>
<td>SMNH 109163</td>
<td>Whole mount with different species. Juvenile worm of Alloioplana auilca together with other animals, including a Maricola.</td>
<td>Paralectotype</td>
<td>Stylochoplana auilca. N. martae. 3 juv polyclads. 1 triclad. Leucolesma? Leg E Marcus. 48. SMNH 109163. St. Auilca. Dept. Zoologia S. Paulo. 3 junge Polycladen. 1 Trclade. Leucolesma?</td>
<td></td>
</tr>
</tbody>
</table>

| 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). |
| 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 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 immature 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. |

<p>| <strong>SMNH 109100</strong>* | Serial sections of larger SMNH 109099. Fits the drawing of figure 112. Reproductive structures on rows 2 and 3 (marked with blue dot). | Lectotype | <em>Notoplana micheli</em>. SMNH 109100. leg P Sawaya (B). |
| <strong>SMNH 109101</strong> | Serial sections of smaller SMNH 109099. Dirty slide. Difficult to see. Reproductive structures on rows 5-7 (marked with blue dot). | Paralectotype | <em>Notoplana micheli</em>. SMNH 109101. leg P Sawaya (C). |</p>
<table>
<thead>
<tr>
<th>Specimen ID</th>
<th>Description</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109111*</td>
<td>Whole mount of anterior part of worm. The worm sections corresponds to following slides, according to size.</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109112*</td>
<td>Serial sections of SMNH 109111, sections continue on following slide.</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109113*</td>
<td>Serial sections of SMNH 109111. Reproductive structures on rows 1, 2 and 3 (marked with blue dot).</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109114</td>
<td>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.</td>
<td>Paralectotype</td>
</tr>
<tr>
<td>SMNH 109115</td>
<td>Serial sections of SMNH 109110.</td>
<td>Paralectotype</td>
</tr>
</tbody>
</table>
### Notoplana sawayai

- **SMNH 109116**: Reproductive structures on rows 1, 2 and 3 (marked with blue dot).
- **Paralectotype**: Notoplana sawayai. SMNH 109116. leg E Marcus.

### Notoplana megala

- **SMNH 109094**: Whole mount of worm. There is no specification of locality. But since both Ubatuba and Ilha de Sao Sebastiao are in Sao Paulo, this to be the closest to a type.

### Alloioplana aulica

- **SMNH 109160**: Reproductive structures on rows 4 and 5 (marked with blue dot). Dirty slide.
- **Lectotype**: Stylochoplana aulica. SMNH 109160. leg E Marcus (45).
| **SMNH 109162*** | 1-3 (marked with blue dot). Dirty slide. | Lectotype | *Stylochoplana aulica*. SMNH 109162. leg E Marcus (47). |
| **SMNH 109157** | 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*. SMNH 109157. leg E Marcus (42). *Stylochoplana aulica*. |
| **SMNH 109158** | 2 worms in whole mount. | Paralectotype | *Stylochoplana aulica*. SMNH 109158. leg E Marcus (43). *Stylochoplana aulica*. |
| **SMNH 109168*** | Serial sections of posterior/middle part of SMNH 109167. Sections continue on the following 3 slides. | Holotype | *Armatoplana divae*. SMNH 109168. leg DD Correa. (52). |
| **SMNH 109169*** | Serial sections of posterior/middle part of SMNH 109167. | Holotype | *Armatoplana divae*. SMNH 109169. leg DD Correa. (53). |
| **SMNH 109170*** | Serial sections of posterior/middle part of SMNH 109167. Reproductive structures | Holotype | *Armatoplana divae*. SMNH 109170. leg DD Correa. (54). *Armatoplana divae* Marc. 54. |
| **SMNH 109171*** | on rows 1-3 (marked with blue dot). Dirty slide. | **Holotype** | *Stylochoplana divae*. SMNH 109171. leg DD Correa. (55). |
| SMNH 109181* | Serial sections of posterior part of SMNH 109180. Sections continue on next slide. | **Holotype** | *Stylochoplana leptalea*. SMNH 109182. leg E Marcus. (38). |
| 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 109183. leg E Marcus. (39). *Stylochoplana leptalea* Marc. 39 |
| SMNH 109183* | Serial sections of posterior part of SMNH 109180. | **Holotype** | |
| **Interplana evelinae** (Marcus, 1952) | 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 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 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). |

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<p>| <strong>Stylochoplana divae</strong> (Marcus, 1949) | | |
| <strong>SMNH 109672</strong> | Serial sections of entire worm. These sections continue not in the next slide but in SMNH 109674, by the form of the sections. | Lectotype | <em>Candimba divae</em>. Marcus 1949. Sao Paulo; Ilha das Palmas (XI 48). Cf Marcus 1949 p76. leg E Marcus. SMNH 109672. |
| <strong>SMNH 109674</strong> | 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 | <em>Candimba divae</em>. Marcus 1949. see other glasses. <em>Candimba</em>. SMNH 109674. |
| <strong>SMNH 109669</strong> | Whole mount of entire worm. | Paralectotype | <em>Candimba divae</em>. Marcus 1949. Sao Paulo, Ilha das |</p>
<table>
<thead>
<tr>
<th>Specimen ID</th>
<th>Description</th>
<th>Type</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109673</td>
<td>Serial sections of entire worm. Reproductive structures on rows 6 and 7</td>
<td>Paralectotype</td>
<td>Candimba divae. Marcus 1949. see other glasses. SMNH 109673. Candimba.</td>
</tr>
<tr>
<td>SMNH 109199*</td>
<td>Whole mount of anterior part of worm. The original description is based on</td>
<td>Holotype</td>
<td>Stylochoplana selenopsis. Sao Paulo; Sao Vicente.</td>
</tr>
<tr>
<td></td>
<td>one immature worm. This is the only slide with the type locality and the</td>
<td></td>
<td>Cf Marcus 1947 p116, 1949 p74. leg E Marcus (48). SMNH 109199.</td>
</tr>
<tr>
<td>SMNH 109200*</td>
<td>Serial sections of posterior part of SMNH 109199. According to consecutive</td>
<td>Holotype</td>
<td>Stylochoplana selenopsis. SMNH 109200. leg E Marcus (48).</td>
</tr>
<tr>
<td></td>
<td>labels this should correspond to the sections of SMNH 109199. Reproductive</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>structures on rows 4 and 5 (marked with blue dot).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SMNH 109201*</td>
<td>Serial sections of posterior part of SMNH 109199. Continuation of previous</td>
<td>Holotype</td>
<td>Stylochoplana selenopsis. SMNH 109201. leg E Marcus (49).</td>
</tr>
<tr>
<td></td>
<td>sections</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SMNH 109202</strong>*</td>
<td>Serial sections of posterior part of SMNH 109199. Continuation of previous sections.</td>
<td>Holotype</td>
<td><strong>Stylochoplana selenopsis</strong>. SMNH 109202. leg E Marcus (50).</td>
</tr>
<tr>
<td><strong>SMNH 109687</strong></td>
<td>Whole mount of entire worm and anterior part of worm. Together with the holotype head there is a paratype.</td>
<td>Holotype/Paratype</td>
<td><strong>Cryptocelis lilianae</strong>. Marcus and Marcus 1968. Sao Paulo; Ubatuba. Cf Marcus 1968 p13. leg L. Forneris (A). SMNH 109687. Dep. Zool. USP. <strong>Cryptocelis lilianae</strong>. Type head.</td>
</tr>
<tr>
<td><strong>SMNH 109688</strong></td>
<td>Serial sections of posterior part of SMNH 109687 Reproductive structures on row 1 (marked with blue dot).</td>
<td>Holotype</td>
<td><strong>Cryptocelis lilianae</strong>. Leg L. Forneris (B). SMNH 109688. Dep. Zool. USP. <strong>Cryptocelis lilianae</strong>. Typ.</td>
</tr>
<tr>
<td><strong>SMNH 109689</strong></td>
<td>Serial sections of posterior part of SMNH 109687 Reproductive structures on rows 10 and 11 (marked with blue dot).</td>
<td>Holotype</td>
<td><strong>Cryptocelis lilianae</strong>. Leg L. Forneris (C). SMNH 109689. <strong>Cryptocelis lilianae</strong>. Typ.</td>
</tr>
<tr>
<td><strong>SMNH 109708</strong>*</td>
<td>Whole mount of 2 anterior parts. One anterior part is from <strong>Phaenocelis</strong> and the other from <strong>Lurymare utarum</strong>.</td>
<td>Lectotype</td>
<td><strong>Phaenocelis medvedica</strong>. SMNH 109708. leg E Marcus (B). <strong>Phaenocelis medvedica</strong>. <strong>Prothiostomum utarum</strong>.</td>
</tr>
<tr>
<td><strong>SMNH 109709</strong>*</td>
<td>Serial sections of posterior part of SMNH 109708. Reproductive structures on rows 3-6 (marked with blue dots).</td>
<td>Lectotype</td>
<td><strong>Phaenocelis medvedica</strong>. SMNH 109709. leg E Marcus (C).</td>
</tr>
<tr>
<td><strong>SMNH 109717</strong>*</td>
<td>Serial sections of entire worm. Reproductive structures on rows 4-6 (marked with blue dot).</td>
<td>Lectotype</td>
<td><strong>Triadomma curvum</strong>. SMNH 109717. leg E Marcus (D). <strong>Triadomma</strong>.</td>
</tr>
<tr>
<td><strong>SMNH 109714</strong></td>
<td>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.</td>
<td>Paralectotype</td>
<td><em>Triadomma curvum</em>. Marcus 1949. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1949 p70. leg E Marcus (A). SMNH 109714. Dept. Zoologia S. Paulo. <em>Triadomma curvum</em> M.</td>
</tr>
<tr>
<td><strong>SMNH 109716</strong></td>
<td>Whole mount of entire worm.</td>
<td>Paralectotype</td>
<td><em>Triadomma curvum</em>. SMNH 109716. leg E Marcus (C).</td>
</tr>
<tr>
<td><strong>SMNH 109720</strong></td>
<td>Serial sections of entire worm.</td>
<td>Lectotype</td>
<td><em>Triadomma evelinae</em>. SMNH 109720. leg E Marcus (18).</td>
</tr>
<tr>
<td><strong>SMNH 109721</strong></td>
<td>Serial sections of SMNH 109720. Reproductive structure on row 1 (marked with blue dot).</td>
<td>Lectotype</td>
<td><em>Triadomma evelinae</em>. SMNH 109721. leg E Marcus (19).</td>
</tr>
<tr>
<td><strong>SMNH 109722</strong></td>
<td>Serial sections of SMNH 109720. Reproductive structures on rows 2-5 (marked with blue dot).</td>
<td>Lectotype</td>
<td><em>Triadomma evelinae</em>. SMNH 109722. leg E Marcus (20).</td>
</tr>
<tr>
<td><strong>SMNH 109723</strong></td>
<td>Serial sections of entire worm.</td>
<td>Paralectotype</td>
<td><em>Triadomma evelinae</em>. SMNH 109723. leg E Marcus (21).</td>
</tr>
<tr>
<td><strong>SMNH 109724</strong></td>
<td>Serial sections of entire worm. Without</td>
<td>Paralectotype</td>
<td><em>Triadomma evelinae</em>. SMNH 109724. leg E Marcus</td>
</tr>
</tbody>
</table>
reproductive structures, but it also is just part of a worm, continuation of slices in other slide.

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109605*</td>
<td>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</td>
<td>Lectotype</td>
<td>Adenoplana evelinae. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p76. leg E Marcus (A). SMNH 109605.</td>
</tr>
<tr>
<td>SMNH 109608*</td>
<td>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).</td>
<td>Lectotype</td>
<td>Adenoplana evelinae. SMNH 109608. leg E Marcus (2).</td>
</tr>
<tr>
<td>SMNH 109609*</td>
<td>Serial sections of 109605. Two upper rows of sections show the male gonopore. All rows contain reproductive structures.</td>
<td>Lectotype</td>
<td>Adenoplana evelinae. SMNH 109609. leg E Marcus (3).</td>
</tr>
<tr>
<td>SMNH 109610*</td>
<td>Serial sections of 109605. Three lower rows of sections show the female gonopore. All rows contain reproductive</td>
<td>Lectotype</td>
<td>Adenoplana evelinae. SMNH 109610. leg E Marcus (4).</td>
</tr>
<tr>
<td>SMNH 109606</td>
<td>Whole mount of entire worm also part of the original description.</td>
<td>Paralectotype</td>
<td><em>Adenoplana evelinae</em>. SMNH 109606. leg E Marcus (B). Dept. Zoologia S. Paulo. <em>Adenoplana evelinae</em>.</td>
</tr>
<tr>
<td>SMNH 109664*</td>
<td>Serial sections of posterior part of worm (SMNH 109663).</td>
<td>Lectotype</td>
<td><em>Callioplana evelinae</em>. SMNH 109664. leg E Marcus (B).</td>
</tr>
<tr>
<td>SMNH 109665*</td>
<td>Reproductive structures on rows 1 and 2 (marked with blue dot).</td>
<td>Lectotype</td>
<td><em>Callioplana evelinae</em>. SMNH 109665. leg E Marcus (C).</td>
</tr>
<tr>
<td>SMNH 109666*</td>
<td>Serial sections of SMNH 109663.</td>
<td>Lectotype</td>
<td><em>Callioplana evelinae</em>. SMNH 109666. leg E Marcus (D).</td>
</tr>
<tr>
<td>SMNH 109668</td>
<td>Serial sections of SMNH 109667. Continuation of previous sections</td>
<td>Paralectotype</td>
<td><em>Callioplana evelinae</em>. SMNH 109668. leg E Marcus (N).</td>
</tr>
</tbody>
</table>

### Callioplana evelinae Marcus, 1954

**SMNH 109606**
- Whole mount of entire worm also part of the original description.

**SMNH 109663**
- Whole mount of entire worm and anterior part of worm. Sectioned worm is the lectotype.

**SMNH 109664**
- Serial sections of posterior part of worm (SMNH 109663).
- Lectotype *Callioplana evelinae*. SMNH 109664. leg E Marcus (B).

**SMNH 109665**
- 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).

**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.

**SMNH 109061**
- Serial sections of entire worm.
- Holotype *Hoploplana divae*. Leg E Marcus (B). SMNH
<table>
<thead>
<tr>
<th>Reproductive structures on rows 1-3 (marked with blue dot).</th>
<th>109061</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SMNH 109794</strong>*</td>
<td>Serial sections of entire worm. Slide with dirty medium. The sections continue in the following slide. The slides fit the drawing made by Marcus.</td>
</tr>
<tr>
<td><strong>SMNH 109795</strong>*</td>
<td>Serial sections of SMNH 109794. Reproductive structures on rows 4 and 5 (marked with blue dot). The sections are continuation of previous slide.</td>
</tr>
</tbody>
</table>
### Imogine cata Du Bois-Reymond Marcus, 1958

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Description</th>
<th>Taxonomy</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109789*</td>
<td>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)</td>
<td>Holotype</td>
</tr>
</tbody>
</table>

### Imogine refertus Du Bois-Reymond Marcus, 1965

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Description</th>
<th>Taxonomy</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109797</td>
<td>Serial sections of 109796. Some reproductive structures (vas deferens) are visible.</td>
<td>Holotype</td>
</tr>
<tr>
<td>SMNH 109800</td>
<td>Serial sections of 109796. Slides dirty. Reproductive structures on rows 4, 5 and 6 (marked with blue dot).</td>
<td>Holotype</td>
</tr>
</tbody>
</table>

### Imogine tica

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Description</th>
<th>Taxonomy</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109801*</td>
<td>Whole mount of most of worm, rest of</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109802*</td>
<td>Serial sections of SMNH 109801. Cover slides with fungus.</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109803*</td>
<td>Serial sections of SMNH 109801. Cover slides with fungus.</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109804*</td>
<td>Serial sections of SMNH 109801. Reproductive structures in row 6 and 7 (marked with blue dot).</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109805*</td>
<td>Serial sections of SMNH 109801.</td>
<td>Lectotype</td>
</tr>
</tbody>
</table>

**Pentaplana divae**
Marcus, 1949

<p>| 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 | Pentaplanidae. 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 | Pentaplanidae. SMNH 109655. leg E Marcus (B). |
| SMNH 109657 | Whole mount of entire worm. | Paraelectotype | Pentaplanidae. SMNH 109657. leg DD Correa (F). Dept. Zoologia S. Paulo. Pentaplanidae M. |
| SMNH 109658 | Whole mount of 2 anterior parts. One anterior part is from a <em>Stylochoplana selenopsis</em>. | Paraelectotype | Pentaplanidae. SMNH 109658. leg DD Correa (G). Stylochoplana selenopsis. |</p>
<table>
<thead>
<tr>
<th>Specimen Code</th>
<th>Description</th>
<th>Type</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109659</td>
<td>Whole mount of entire worm. Type species of the genus.</td>
<td>Paralectotype</td>
<td>\textit{Pentaplana divae}. SMNH 109659. leg DD Correa (H). \textit{Pentaplana}.</td>
</tr>
<tr>
<td>SMNH 109661</td>
<td>Serial sections of posterior part of worm. This and the next slides are from two different worms, from the second location.</td>
<td>Paralectotype</td>
<td>\textit{Pentaplana divae}. SMNH 109661. leg DD Correa (J).</td>
</tr>
<tr>
<td>SMNH 109651</td>
<td>Serial sections of SMNH 109650. Reproductive structures on rows 1 and 2</td>
<td>Holotype</td>
<td>\textit{Nonatona euscopa}. SMNH 109651. leg E Marcus (B).</td>
</tr>
</tbody>
</table>

**Latocestus callizona** (Marcus, 1947)

<table>
<thead>
<tr>
<th>Specimen Code</th>
<th>Description</th>
<th>Type</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109612*</td>
<td>Serial sections of posterior part of 109614. Slides with fungus. Reproductive structures in rows 3, 4 and 5 (marked with blue dot).</td>
<td>Holotype</td>
<td>\textit{Allena callizona}. SMNH 109612. leg E Marcus (13). \textit{Allena callizona} Marc. 13.</td>
</tr>
<tr>
<td>SMNH 109613*</td>
<td>Serial sections of posterior part of 109614. Slides with fungus.</td>
<td>Holotype</td>
<td>\textit{Allena callizona}. SMNH 109613. leg E Marcus (14).</td>
</tr>
<tr>
<td>SMNH 109614*</td>
<td>Whole mount of anterior part. Material from type locality. Fits drawings.</td>
<td>Holotype</td>
<td>\textit{Allena callizona}. SMNH 109614. leg E Marcus (15).</td>
</tr>
</tbody>
</table>

**Nonatona euscopa**

Marcus, 1952
| SMNH 109652* | Serial sections of SMNH 109650. | 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 (marked 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 109646 | Whole mount of entire worm. | Paralectotype | *Latocestus ocellatus*. SMNH 109646. leg E Marcus |
| **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. |
| **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 on rows 5 and 6 (marked with blue dot).

**Type 5076c**
Whole mount of entire worm. Worm is divided in two.  
Paralectotype


**Type 5076d**
Whole mount of entire worm.  
Paralectotype

**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

**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.**
<table>
<thead>
<tr>
<th>Specimen Number</th>
<th>Description</th>
<th>Taxonomic Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109888</td>
<td>Serial sections of middle of SMNH 109883. Reproductive structures on rows 2, 3, 4, 5, 6, 7 and 8 (marked with blue dot).</td>
<td>Holotype</td>
</tr>
<tr>
<td>SMNH 109889</td>
<td>Serial sections of middle of SMNH 109883. Reproductive structures on rows 1, 2 and 3 (marked with blue dot).</td>
<td>Holotype</td>
</tr>
<tr>
<td>SMNH 109924*</td>
<td>Whole mount of anterior part. The rest of the worm is in serial sections that begin in SMNH 109929. No locality.</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109929*</td>
<td>Serial sections of posterior part. Sections (from SMNH 109924) continue in following slides. Reproductive structures in rows 6 and 7 (marked with blue dot).</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109930*</td>
<td>Serial sections of posterior part. There are reproductive structures marked with blue dots. The slides fit the drawing in figure 131 of Marcus 1949.</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109931*</td>
<td>Serial sections of posterior part. Reproductive structures (female pore) in rows 1, 2 and 3 (marked with blue dot).</td>
<td>Lectotype</td>
</tr>
<tr>
<td>SMNH 109923</td>
<td>Whole mount of entire worm. Juvenile worm? Animal from type locality.</td>
<td>Paralectotype</td>
</tr>
</tbody>
</table>

*Enchiridium evelinae* Marcus, 1949
| 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). |
| **mortenseni**  
| **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) | 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** |  
| 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. |
| **Lurymare matarazzoi**  
| | **SMNH 109957** | Whole mount of entire worm. Worm looks a little immature when compared to the previous one. | Paralectype | Prosthiostomum matarazzoi. SMNH 109957. leg E Marcus (B). |
| **Lurymare utarum**  
<table>
<thead>
<tr>
<th>Specimen</th>
<th>Description</th>
<th>Class</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMNH 109968*</td>
<td>Serial sections of middle part of SMNH 109968. Continuation of previous slide. Reproductive structures on rows 1-6 (marked with blue dot).</td>
<td>Lectotype</td>
<td>Prosthiostomum (Lurymare) utarum SMNH 109968. leg E Marcus (B). Prosthiostomum utarum.</td>
</tr>
<tr>
<td>SMNH 109951*</td>
<td>Serial sections of SMNH109950. Slide with fungus/dried mounting medium. Reproductive structures on rows 2-6 (marked with blue dot).</td>
<td>Lectotype</td>
<td>Prosthiostomum gilvum. SMNH 109951. leg E Marcus (2).</td>
</tr>
<tr>
<td>SMNH 109952*</td>
<td>Serial sections of SMNH 109950. Slide with fungus/dried mounting medium.</td>
<td>Lectotype</td>
<td>Prosthiostomum gilvum. SMNH 109952. leg E Marcus (3).</td>
</tr>
<tr>
<td>SMNH 109954*</td>
<td>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.</td>
<td>Lectotype</td>
<td>Prosthiostomum gilvum. Marcus 1950. Sao Paulo; Ilha de Sao Sebastiao. Cf Marcus 1950 p98. leg E Marcus (5) SMNH 109954.</td>
</tr>
<tr>
<td>SMNH 109955</td>
<td>Whole mount of entire worm. It is possible to see the separate prostatic vesicles.</td>
<td>Paralectotype</td>
<td>Prosthiostomum gilvum. SMNH 109955. leg E Marcus (6). Dept. Zoologia S. Paulo. Prosthiostomum gilvum.</td>
</tr>
<tr>
<td>Acerotisa bituna</td>
<td>SMNH 109589*</td>
<td>Serial sections of entire worm. Slide with</td>
<td>Holotype</td>
</tr>
<tr>
<td><strong>SMNH 109590</strong></td>
<td>Serial sections of entire worm. Slide with fungus or something on the cover glass.</td>
<td>Holotype Acerotisa bituna. SMNH 109590. leg E Marcus (98).</td>
<td></td>
</tr>
<tr>
<td><strong>Cycloporus gabriellae Marcus, 1950</strong></td>
<td>Serial sections of entire worm. Sections continue in following 2 slides.</td>
<td>Lectotype Cycloporus gabriellae. Leg E Marcus (O). SMNH 109846.</td>
<td></td>
</tr>
<tr>
<td><strong>SMNH 109846</strong></td>
<td>Serial sections of 109846. Continuation of previous sections and it goes on to the following.</td>
<td>Lectotype Cycloporus gabriellae. Leg E Marcus (P). SMNH 109847.</td>
<td></td>
</tr>
<tr>
<td><strong>SMNH 109847</strong></td>
<td>Serial sections of 109846. Reproductive structures on row 2, 3 and 4 (marked with blue dot).</td>
<td>Lectotype Cycloporus gabriellae. Leg E Marcus (Q). SMNH 109848.</td>
<td></td>
</tr>
<tr>
<td><strong>SMNH 109843</strong></td>
<td>5 worms in whole mount. 2 are Cycloporus. 3 worms are juveniles and it</td>
<td>Paralectotypes Cycloporus gabriellae. 4 specimens + 1 juv Latocestus. SMNH 109844. leg E Marcus (M).</td>
<td></td>
</tr>
<tr>
<td>Specimen</td>
<td>Description</td>
<td>Location</td>
<td>Remarks</td>
</tr>
<tr>
<td>----------</td>
<td>-------------</td>
<td>----------</td>
<td>---------</td>
</tr>
<tr>
<td>SMNH 109845</td>
<td>Serial sections of entire juvenile or &quot;larvae&quot;. 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.</td>
<td>No locality.</td>
<td>Paralectotype Cycloporus gabriellae. Leg E Marcus (N). SMNH 109845.</td>
</tr>
<tr>
<td><strong>SMNH 109602</strong>&lt;sup&gt;*&lt;/sup&gt;</td>
<td>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.</td>
<td>Holotype</td>
<td>Acerotisa piscatoria. SMNH 109602. leg E Marcus (95). Acerotisa piscatoria. 95.</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td><strong>SMNH 109603</strong>&lt;sup&gt;*&lt;/sup&gt;</td>
<td>Serial sections of SMNH 109601 slide with fungus or something on the cover glass.</td>
<td>Holotype</td>
<td>Acerotisa piscatoria. SMNH 109603. leg E Marcus (96).</td>
</tr>
<tr>
<td><strong>SMNH 10982</strong>&lt;sup&gt;*&lt;/sup&gt;</td>
<td>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).</td>
<td>Lectotype</td>
<td>Eurylepta turma. Marcus 1952. Sao Paulo; Ubatuba. Cf Marcus 1952 p94. leg E Marcus. Eurylepta turma. Ubatuba. SMNH 109882</td>
</tr>
<tr>
<td><strong>SMNH 109878</strong></td>
<td>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.</td>
<td>Paralectotype</td>
<td>Eurylepta turma. Marcus 1952. Sao Paulo; Ilha de Sao Sebastiao; Ilhabela. Cf Marcus 1952 p94. leg E Marcus (A). SMNH 109878. Eurylepta turma. Ilhabela.</td>
</tr>
<tr>
<td>SMNH 109991*</td>
<td>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.</td>
<td>Lectotype</td>
<td><em>Pseudoceros (Acanthozoon) hispidus</em> du Bois-Reymond Marcus 1955. Sao Paulo; Ilha de Sao Sebastiao. Cf du B-R Marcus 1955 p39. leg Ev Marcus (A).</td>
</tr>
<tr>
<td>SMNH 109993*</td>
<td>Serial sections of middle part of SMNH 109991. Continuation of sections.</td>
<td>Lectotype</td>
<td><em>Pseudoceros hispidus</em>. Leg Ev Marcus (C). SMNH 109993.</td>
</tr>
<tr>
<td><strong>SMNH 109981</strong>*</td>
<td>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.</td>
<td><strong>Holotype</strong></td>
<td><em>Pseudoceros evelinae</em> Marcus 1950. Sao Paulo; Forte Itaipu. Cf Marcus 1950 p81. leg E Marcus (1). SMNH 109981.</td>
</tr>
<tr>
<td><strong>SMNH 109982</strong>*</td>
<td>Serial sections of SMNH 109981.</td>
<td><strong>Holotype</strong></td>
<td><em>Pseudoceros evelinae</em> SMNH 109982. leg E Marcus (2).</td>
</tr>
<tr>
<td><strong>SMNH 109983</strong>*</td>
<td>Serial sections of SMNH 109981.</td>
<td><strong>Holotype</strong></td>
<td><em>Pseudoceros evelinae</em> leg E Marcus (3). SMNH 109983.</td>
</tr>
<tr>
<td><strong>SMNH 109984</strong>*</td>
<td>Serial sections of SMNH 109981 Reproductive structures on rows 1-3 (marked with blue dot)</td>
<td><strong>Holotype</strong></td>
<td><em>Pseudoceros evelinae</em>. leg E Marcus (4). SMNH 109984.</td>
</tr>
<tr>
<td><strong>SMNH 109985</strong>*</td>
<td>Serial sections of SMNH 109981. Reproductive structures in all rows.</td>
<td><strong>Holotype</strong></td>
<td><em>Pseudoceros evelinae</em>. leg E Marcus (5). SMNH 109985. Pseudoceros evelinae. 5. mitte.</td>
</tr>
<tr>
<td><strong>SMNH 109986</strong>*</td>
<td>Serial sections of SMNH 109981 reproductive structures in all rows. Therefore blue dot on the slide</td>
<td><strong>Holotype</strong></td>
<td><em>Pseudoceros evelinae</em>. leg E Marcus (6). SMNH 109986.</td>
</tr>
<tr>
<td>Sample Code</td>
<td>Description</td>
<td>Holotype</td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>-------------</td>
<td>----------</td>
<td></td>
</tr>
<tr>
<td>SMNH 109988*</td>
<td>Serial sections of SMNH 109981.</td>
<td>Pseudoceros evelinae. SMNH 109988. leg E Marcus (8).</td>
<td></td>
</tr>
<tr>
<td>SMNH 109989*</td>
<td>Serial sections of SMNH 109981.</td>
<td>Pseudoceros evelinae. SMNH 109889. leg E Marcus (9).</td>
<td></td>
</tr>
</tbody>
</table>
FIGURES

Figure 1

Geopolitical divisions

North Brazil
- Amapá State 1
- Pará State 2

Northeastern Brazil
- Maranhão State 3
- Piauí State 4
- Ceará State 5
- Rio Grande do Norte State 6
- Paraíba State 7
- Pernambuco State 8
- Alagoas State 9
- Sergipe State 10
- Bahia State 11

Southeastern Brazil
- Espírito Santo State 12
- Rio de Janeiro State 13
- São Paulo State 14

South Brazil
- Paraná State 15
- Santa Catarina State 16
- Rio Grande do Sul State 17

Spalding et al. Marine Ecoregions

A - North Brazil Shelf
B - Tropical Southwestern Atlantic
C - Warm Temperate Southwestern Atlantic

Figure 2

A: [Image of tissue section]

B: [Image of various specimens]

C: [Image of tissue section]

D: [Image of tissue section]
Figure 3
Figure 13
Figure 14
Figure 18

Figure 19
Figure 20

Figure 21
Figure 22
Figure 25
Figure 43

Figure 44

218
Figure 45

A

B

C

D

E

2 mm

0.3 mm

0.3 mm

219
PART 3: POLYCLADIDA PHYLOGENY
Chapter 5.

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

Juliana Bahia 1,2 • Vinicius Padula 3 • Michael Schrödl 1,2

Received: 29 August 2016 / Accepted: 12 December 2016
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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 acotylean Cestopiana and Theana 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 hermaphroditic reproductive anatomy and external morphology (eyespots arrangement, 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.

Electronic supplementary material The online version of this article (doi:10.1007/s13127-017-0327-y) contains supplementary material, which is available to authorized users.

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2 Springer

Published online: 11 May 2017

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(Rawlinson et al. 2011) and are models in studies involving regeneration (Egger et al. 2007), toxicology and prediction (Risson-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 Neocophora (Ehlers 1985, 1986) or together with Macrostomomorpha (Litvaitis and Rhode 1999; Janssen et al. 2015). However, recently, they were proposed as sister group to Lechioplathelinta as a whole (Egger et al. 2015; Sola et al. 2015) or to Prothyrnchida (Lammer et al. 2015). Polycladida systematics has had a troubled history as well. One of the first phylogenetic hypotheses suggested that the genera Cestoplana and Prosthococcom (Fig. 1b) were the most derived ones in Acotylea and Cotylea, respectively (Lang 1884). Laidlaw (1906c) 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 (Schmarda 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 (Hyplanoidae = Eumastomatidae), presence of true free prostatic vesicle (Stylochoideae = Craspedommatidae), or true interpolated prostatic vesicle (Leptobolinoidae). Prudhoe (1985) used instead the distribution of eyespots dividing Acotylea in superfamilies with frontal eyespots (Cestoplanoidea), with frontal, tentacular, and cerebral eyespots (Stylochoidea = Craspedommatidae) and with tentacular and cerebral eyespots (Planoceroidae = Schemmatommatidae). The suborder Cotylea was divided by Faubel (1984) based on different characters, two monospecific superfamilies were created, one with male apparatus behind female structures (Opisthogeneoida) and the other with triclaid-like digestive system.

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

(Ditremenaginidae). The other coryeleans were divided into a group with ruffled pharynx (Pseudocerotidae) and other with tubular pharynx (Eurylepididae). Prudhoe did not divide the coryeleans in superfamilies groupings, since there was not an important difference between eyespot arrangements within Cobytea.

A recent morphometric-cladistic study by Rawlinson and Litvaitis (2008) focused on Cobytea, 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 subclasses 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 Platycladinae 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). Eger et al. (2015) changed the prevailing hypothesis on the origin of polyclads and, recently, some polyclad CO1 and 16S sequences were included in other Platycladinae phylogeny papers (Launer and Giribet 2014; Launer 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).

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<thead>
<tr>
<th>Species</th>
<th>Localities</th>
<th>GenBank accession number</th>
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<tbody>
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<tr>
<td>Phaeocelis media Marcus, 1952</td>
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</tr>
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<tr>
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<td>AF131797</td>
</tr>
<tr>
<td>Stylochus sp.</td>
<td>Peru</td>
<td>KY263713</td>
</tr>
<tr>
<td>Imagine australis Du Bois-Reymond Marcus, 1965</td>
<td>Brazil</td>
<td>KY263694</td>
</tr>
<tr>
<td>Imagine australis</td>
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<tr>
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<tr>
<td>Imagine australis Du Bois-Reymond Marcus, 1965</td>
<td>Brazil</td>
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*Footer: Springer*
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<tbody>
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<td><em>Pseudobiscus bicolor</em> Verlil, 1901</td>
<td>Belice, Panama, Curacao, Jamaica, Florida, Brazil</td>
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<td>Panama</td>
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<tr>
<td><em>Pseudobiscus bisnargatus</em> Mainsor, 1957</td>
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<td><em>Pseudobiscus cf. maximus</em> Lang, 1884</td>
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<tr>
<td><em>Pseudobiscus rubriventer</em> Belizos, Quiroga and Litvaitis, 2007</td>
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<td><em>Pseudobiscus badfordi</em> (Laidlaw, 1933b)</td>
<td>Papua New Guinea</td>
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<tr>
<td><em>Pseudobiscus wirzi</em> Bahia and Schrödl, 2016</td>
<td>Senegal</td>
<td>KY263725</td>
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</table>
Polycladida phylogeny and evolution

Table 1 (continued)

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<td><em>Maritigrella crozieri</em> (Hyman, 1930a)</td>
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<td><em>Maritigrella newmani</em> Bolanos, Quiroga &amp; Litvaitis, 2007</td>
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<td><em>Amakusaglana acutiporae</em> Rawlinson, Gillis, Billings &amp; Berman, 2011</td>
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<td>KY261652, KY261655</td>
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<td><em>Enchiridium sp.</em> Santa Helena Island</td>
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<td>KY261665, KY261667</td>
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<td><em>Enchiridium sp.</em> Peru</td>
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<td>KY261672, KY261667</td>
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<tr>
<td><em>Macrostomum lineare</em> Schärer, Schärer, Salvermoser and Rieger, 2005</td>
<td>Laboratory culture in Limmattal</td>
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<td><em>Hepserpiaeplopsis haswellii</em> Steinböck &amp; Reisinger, 1924</td>
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<tr>
<td><em>Proshliaxtonomum spinulaceum</em> Schärer, 1851</td>
<td>Michigan</td>
<td>KC698966</td>
</tr>
<tr>
<td><em>Macrostomum lineare</em> Müller &amp; Fowle, 1773</td>
<td>Connecticut</td>
<td>KC698844</td>
</tr>
</tbody>
</table>

Italic values indicate the new sequences.

*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 lineare* Lauder, Schärer, Salvermoser & Rieger, 2005; *Hepserpiaeplopsis haswell* Steinböck & Reisinger, 1924; *Proshliaxtonomum spinulaceum* Schärer, 1851; and *Macrostomum lineare* (Müller & Fowle, 1773), based on recent studies on Polycladida phylogeny (Launder & Giribet 2014; Launder 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 decayed sequences (for example, *Chromoplaena*—KC869847.1, *Thysanozoon brochii*—HQ659017.1, and *Styloceras 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 hematoxylin-eosin as described in Bolanos et al. (2007). Figure 1 was produced using photographs of parts of drawings of Lang (1884), Laidlaw (1903), 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, 2006)–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 acolyceans, 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 f1 and LSU rev2) and the protocol of Sonnenberg et al. (2007). PCR was performed in 25 μl of reaction volume containing 22 μl of water, 0.5 μl of a forward and reverse PCR primer (10 pm/μl), 2 μl 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>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Eyespot Location</th>
<th>Tentacles</th>
<th>Dorsal Surface and Shape</th>
<th>Pharynx Form and Location</th>
<th>Sucker or Adhesive Structure</th>
<th>Orientation of the Male Apparatus</th>
<th>Type of Prostatic Vessel</th>
<th>Stylet and Armed Structures</th>
<th>Type of Vagina</th>
<th>Lang’s Vesicle</th>
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</thead>
<tbody>
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<td>Actinosoma</td>
<td>A. spinosa</td>
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<td>Smooth and oval</td>
<td>Ruffled central</td>
<td>Absent</td>
<td>Backwards, Gonopores open in the posterior part</td>
<td>Without true prostatic vesicle, prostate gland organs instead of true seminal vesicle</td>
<td>True interpolated</td>
<td>Absent</td>
<td>Present, sac-like, elongated</td>
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<td>C. parva</td>
<td>Marginal, nuchal, and cerebral</td>
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<td>Smooth and oval</td>
<td>Ruffled anterior</td>
<td>Absent</td>
<td>Backwards, Gonopores open in the posterior part</td>
<td>True interpolated</td>
<td>Absent</td>
<td>Vagina bulbosa, long, looping</td>
<td></td>
</tr>
<tr>
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<td>P. phalanx</td>
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<td>Present</td>
<td>Smooth and oval</td>
<td>Ruffled anterior</td>
<td>Absent</td>
<td>True free and elongated</td>
<td>Absent</td>
<td>Present</td>
<td>Present, bulbous</td>
<td></td>
</tr>
<tr>
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<td>S. elongata</td>
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<td>Present</td>
<td>Smooth and oval</td>
<td>Ruffled anterior</td>
<td>Absent</td>
<td>Backwards, Gonopores open in the posterior part</td>
<td>True free</td>
<td>Absent</td>
<td>Simple and short</td>
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<tr>
<td>Imagona Giraud, 1853</td>
<td>Present and nuchal</td>
<td>Marginal, nuchal, and cerebral</td>
<td>Present</td>
<td>Smooth and oval</td>
<td>Ruffled anterior</td>
<td>Absent</td>
<td>Backwards, Tripartite seminal vesicle</td>
<td>True free</td>
<td>Absent</td>
<td>Simple</td>
<td></td>
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<tr>
<td>Leptoplanae</td>
<td>L. arenaceae</td>
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<td>Absent</td>
<td>Smooth and oval</td>
<td>Ruffled central or anterior</td>
<td>Absent</td>
<td>Backwards, Enclosed in a muscular structure</td>
<td>True interpolated</td>
<td>Absent or present</td>
<td>Simple, long, looping</td>
<td></td>
</tr>
<tr>
<td>Notoplanae</td>
<td>N. phalanx</td>
<td>Nuchal and cerebral</td>
<td>Absent</td>
<td>Smooth and oval</td>
<td>Ruffled central</td>
<td>Absent</td>
<td>Backwards, Present or present cirrus</td>
<td>True interpolated</td>
<td>Absent</td>
<td>Vagina simple or bulbosa</td>
<td></td>
</tr>
<tr>
<td>Family</td>
<td>Genus</td>
<td>Tentacles</td>
<td>Eyespots</td>
<td>Brain and nerve cords</td>
<td>Dorsal surface and shape</td>
<td>Pharynx form and location</td>
<td>Sucker or adhesive structure</td>
<td>Orientation of the male apparatus</td>
<td>Type of prostatic vesicle</td>
<td>Stylet and armed structures</td>
<td>Type of vagina</td>
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<td><strong>Hoploplana</strong>&lt;br&gt;Laidlaw, 1902</td>
<td>Present and rucal</td>
<td>Nuchal (ring-like) and cerebral</td>
<td>Absent</td>
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<td>Deeply ruffled and central</td>
<td>Backwards</td>
<td>True inepitelated, very small</td>
<td>Present</td>
<td>Simple and short</td>
<td>Absent</td>
</tr>
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<td><strong>Planoceridae</strong>&lt;br&gt;Lang, 1884</td>
<td><strong>Planocera</strong>&lt;br&gt;Bainville, 1828</td>
<td>Present and rucal</td>
<td>Nuchal (ring-like) and cerebral</td>
<td>Large, slightly bilobed, with capsule, Thick, well developed</td>
<td>Smooth</td>
<td>Deeply ruffled and central</td>
<td>Backwards</td>
<td>True free, normal</td>
<td>Cirrus with spines or hooks</td>
<td>Vagina bulbosa Reduced or present</td>
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<td>Absent</td>
<td>Smooth</td>
<td>Ruffled</td>
<td>Backwards</td>
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<td>Tubular</td>
<td>Vagina bulbosa Present</td>
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<td><strong>Armatopiana</strong>&lt;br&gt;Faubel, 1983</td>
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<td>Smooth</td>
<td>Ruffled or elongated</td>
<td>Backwards</td>
<td>True interpolated</td>
<td>Absent</td>
<td>Vagina bulbosa Present</td>
<td></td>
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<tr>
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<td><strong>Melaspelana</strong> Faubel, 1983</td>
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<td>Nuchal and cerebral</td>
<td>Large, bilobed, with capsule, Thick and well developed</td>
<td>Smooth</td>
<td>Ruffled</td>
<td>Backwards</td>
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<td><strong>Cynioctotidae</strong> Marcus and Marcus, 1966</td>
<td><strong>Echinoplana</strong> Haswell, 1907</td>
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<td>Smooth and elongated</td>
<td>Ruffled, central, anterior or posterior</td>
<td>Backwards</td>
<td>True interpolated</td>
<td>Cirrus with spines and hooks</td>
<td>Vagina bulbosa Present</td>
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<tr>
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<td>Genus</td>
<td>Tentacles</td>
<td>Eyespot Location</td>
<td>Brain and nerve cords</td>
<td>Dorsal surface and shape</td>
<td>Pharynx form and location</td>
<td>Sucker or adhesive structure</td>
<td>Orientation of the male apparatus</td>
<td>Type of prostatic vesicle</td>
<td>Stylet and armament structures</td>
<td>Type of vagina vesicle</td>
</tr>
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<tr>
<td>Thermaidae</td>
<td>Therman Marcus, 1949</td>
<td>Absent</td>
<td>Cerebral and frontal</td>
<td>?</td>
<td>Smooth and narrow and elongated</td>
<td>Ruffled and central to posterior</td>
<td>Absent</td>
<td>Backwards, Genopores open in the posterior part</td>
<td>True interpolated</td>
<td>Stylet or sclerotized ejaculatory duct lining</td>
<td>Absent</td>
</tr>
<tr>
<td>Cestoplanaidae</td>
<td>Cestoplana Lang, 1884</td>
<td>Absent</td>
<td>Frontal</td>
<td>Large, biolied, with capsule, Thick and well developed</td>
<td>Smooth and narrow and elongated</td>
<td>Ruffled and posterior</td>
<td>Present and posterior</td>
<td>Perpendicular or forwards, May present duplicated structures</td>
<td>True interpolated</td>
<td>Absent</td>
<td>Short, Ciliated</td>
</tr>
<tr>
<td>Cotylea</td>
<td>Beninia Bock, 1923</td>
<td>Marginal and lobed</td>
<td>Cerebral and frontal</td>
<td>Anteriorly located, with capsule, Thin, round, well developed</td>
<td>Smooth and narrow and elongated, oblong</td>
<td>Ruffled and anterior or central</td>
<td>Present and posterior</td>
<td>Perpendicular or backwards</td>
<td>Absent prostatoïd organs</td>
<td>Armed prostatoïd organs</td>
<td>Cement pouch present</td>
</tr>
<tr>
<td>Chromoplanaidae</td>
<td>Chromoplana Bock, 1922</td>
<td>Absent</td>
<td>Few marginal and cerebral</td>
<td>?</td>
<td>Smooth and elongated or oval</td>
<td>Ruffled and anterior</td>
<td>Present and posterior</td>
<td>Forwards</td>
<td>True interpolated</td>
<td>Absent</td>
<td>Simple, and short cement pouch present</td>
</tr>
<tr>
<td>Amyelidae</td>
<td>Amyelia Corrêa, 1958</td>
<td>Absent</td>
<td>Cerebral and tentacular</td>
<td>Tentacular, marginal, frontal, and cerebral</td>
<td>Large, biolied, with capsule, Thick and well developed</td>
<td>Smooth and elongated oval</td>
<td>Deeply ruffled and central</td>
<td>Present and posterior</td>
<td>Backwards, enclosed in a muscular bulb</td>
<td>True interpolated</td>
<td>Absent</td>
</tr>
<tr>
<td>Pericellidae</td>
<td>Pericell Laidlaw, 1902</td>
<td>Marginal, well separated, and infolded</td>
<td>Tentacular and cerebral</td>
<td>Small, round, not biolied, Thin.</td>
<td>Smooth and oval</td>
<td>Deeply ruffled and anterior</td>
<td>Present anterior</td>
<td>Forwards and single</td>
<td>Free and anterior-dorsal to ejaculatory duct</td>
<td>Stylet present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td>Pseudocentrotidae</td>
<td>Pseudocentrot Lang, 1884</td>
<td>Marginal and simple folds</td>
<td>Tentacular and cerebral</td>
<td>Tentacular and cerebral</td>
<td>Small, round, not biolied, Thin.</td>
<td>Smooth and oval</td>
<td>Deeply ruffled and anterior</td>
<td>Present anterior</td>
<td>Forwards and single</td>
<td>Free and anterior-dorsal to ejaculatory duct</td>
<td>Stylet present</td>
</tr>
<tr>
<td>Family</td>
<td>Occurs</td>
<td>Tentacles</td>
<td>Eyespot location</td>
<td>Brain and nerve cords</td>
<td>Dorsal surface and shape</td>
<td>Pharynx form and location</td>
<td>Sucker or adhesive structure</td>
<td>Orientation of the male apparatus</td>
<td>Type of prostatic vesicle</td>
<td>Styel and armed structures</td>
<td>Type of vagina</td>
</tr>
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<tr>
<td><em>Pseudobacetus</em></td>
<td>Faubel, 1984</td>
<td>Marginal and square or ear-like folds</td>
<td>Tentacular and cerebral</td>
<td>Small, round, not bilobed. Thin.</td>
<td>Smooth and elongated oval</td>
<td>Ruffled anterior</td>
<td>Present anterior</td>
<td>Forwards and double</td>
<td>Free and antero-dorsal to ejaculatory duct</td>
<td>Styel present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td><em>Thysanocerus</em></td>
<td>Grube, 1840</td>
<td>Marginal and ear-like folds</td>
<td>Tentacular and cerebral</td>
<td>Small, round, not bilobed. Thin.</td>
<td>Smooth and elongated oval</td>
<td>Ruffled anterior</td>
<td>Present anterior</td>
<td>Forwards and double</td>
<td>Free and antero-dorsal to ejaculatory duct</td>
<td>Styel present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td><em>Yungia Lang, 1884</em></td>
<td></td>
<td>Marginal and ear-like folds</td>
<td>Tentacular and cerebral</td>
<td>?</td>
<td>Smooth</td>
<td>Ruffled and anterior intestine branches ending in the body surface</td>
<td>Present and central</td>
<td>Forwards and double</td>
<td>Free and antero-dorsal to coiled ejaculatory duct</td>
<td>Styel present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td><em>Malacocerus</em></td>
<td>Newman and Canon, 1996</td>
<td>Marginal and square folds</td>
<td>Tentacular and cerebral</td>
<td>?</td>
<td>Smooth</td>
<td>Ruffled and anterior</td>
<td>Present and anterior</td>
<td>Forwards and double</td>
<td>Free and antero-dorsal to ejaculatory duct</td>
<td>Styel present</td>
<td>Cement pouches present, three to five female gonopores</td>
</tr>
<tr>
<td><em>Monobacetus</em></td>
<td>Faubel, 1984</td>
<td>Marginal and ear-like folds</td>
<td>Tentacular and cerebral</td>
<td>?</td>
<td>Smooth</td>
<td>Ruffled and anterior</td>
<td>Present and anterior</td>
<td>Forwards and double but with only one gonopore</td>
<td>Free</td>
<td>Styel present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td><em>Phrikaceras</em></td>
<td>Newman and Canon, 1996</td>
<td>Marginal and ear-like or square folds</td>
<td>Tentacular and cerebral</td>
<td>?</td>
<td>Smooth</td>
<td>Ruffled and anterior</td>
<td>Present and anterior</td>
<td>Forwards and single</td>
<td>Free and antero-dorsal to ejaculatory duct</td>
<td>Styel present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td><em>Euryleptidae Lang, 1884</em></td>
<td></td>
<td>Marginal and bumps</td>
<td>Tentacular and cerebral</td>
<td>Large, bilobed, with capsule?</td>
<td>Smooth or papillated and oval</td>
<td>Tubular and anterior, marginal digestive vessels present</td>
<td>Present middle</td>
<td>Forwards and single</td>
<td>Free and antero-dorsal to the ejaculatory duct</td>
<td>Styel present</td>
<td>Simple and short cement pouches and multiple uterine vesicles present</td>
</tr>
<tr>
<td>Family</td>
<td>Genus</td>
<td>Tentacles</td>
<td>Eyestalk location</td>
<td>Brain and nerve cords</td>
<td>Dorsal surface and shape</td>
<td>Pharynx form and location</td>
<td>Pharynx or adhesive structure</td>
<td>Orientation of the male apparatus</td>
<td>Type of prostatic vesicle</td>
<td>Stylet and armed structures</td>
<td>Type of vagina</td>
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</tr>
<tr>
<td>Euryclita</td>
<td>Ehrenberg, 1831</td>
<td>Marginal and extensions</td>
<td>Cerebral and tentacular</td>
<td>Large, bilobed, with capsule?</td>
<td>Smooth and oval</td>
<td>Tubular and anterior</td>
<td>Present middle</td>
<td>Forward and single</td>
<td>Free and antero-dorsal to the ejaculatory duct</td>
<td>Stylet present</td>
<td>Simple and short cement pouches and pair of urine vesicles present</td>
</tr>
<tr>
<td>Proscocera</td>
<td>Schmarda, 1859</td>
<td>Marginal and pointed extensions</td>
<td>Cerebral</td>
<td>?</td>
<td>Smooth and oval</td>
<td>Tubular and anterior</td>
<td>Present middle</td>
<td>Forward and single</td>
<td>Free and antero-dorsal to the ejaculatory duct</td>
<td>Stylet present</td>
<td>Cement pouches present and multiple urinome vesicles present</td>
</tr>
<tr>
<td>Martitigrella</td>
<td>Newman and Caron, 2000</td>
<td>Marginal and long extensions</td>
<td>Cerebral and tentacular</td>
<td>Small, slightly bilobed, Thinn</td>
<td>Smooth and elongate oval</td>
<td>Tubular, small and anterior</td>
<td>Present anterior</td>
<td>Forward and single</td>
<td>Free and antero-dorsal to the ejaculatory duct</td>
<td>Stylet present</td>
<td>Cement pouches present</td>
</tr>
<tr>
<td>Prostheostomidae</td>
<td>Hock, 1913</td>
<td>Absent</td>
<td>Cerebral and marginal enucleating all body</td>
<td>Small, slightly bilobed, no capsule, Thinn</td>
<td>Smooth and elongate oval</td>
<td>Tubular and anterior</td>
<td>Present middle</td>
<td>Forwards and two prostatic vesicles, stylet never backwards</td>
<td>Free and bond in a muscular bulb antero-dorsal to ejaculatory duct</td>
<td>Stylet present</td>
<td>True mucous chamber present</td>
</tr>
<tr>
<td>Prostheostomum</td>
<td>Quatrefages, 1845</td>
<td>Absent</td>
<td>Cerebral and marginal only anterior</td>
<td>Large, bilobed, with capsule?</td>
<td>Smooth and elongate oval</td>
<td>Tubular anterior</td>
<td>Present middle</td>
<td>Forwards and two prostatic vesicles</td>
<td>Free and lateral or ventral to ejaculatory duct</td>
<td>Stylet present</td>
<td>True mucous chamber present</td>
</tr>
<tr>
<td>Lucymare Marcus and Marcus, 1968</td>
<td>Absent</td>
<td>Cerebral and marginal only anterior</td>
<td>?</td>
<td>Smooth and elongate oval</td>
<td>Tubular anterior</td>
<td>Present middle</td>
<td>Forwards and two prostatic vesicles</td>
<td>Free and bond in a muscular bulb usually involve the seminal vesicle</td>
<td>Stylet present</td>
<td>True mucous chamber present</td>
<td>Absent</td>
</tr>
<tr>
<td>Amaralophasma</td>
<td>Kato, 1938</td>
<td>Absent</td>
<td>Cerebral and marginal very close to each other</td>
<td>?</td>
<td>Smooth and elongate oval</td>
<td>Tubular anterior</td>
<td>Present middle</td>
<td>Forwards and two prostatic vesicles</td>
<td>Free and bond at each side of the ejaculatory duct</td>
<td>Stylet present</td>
<td>Cement pouches present</td>
</tr>
</tbody>
</table>
Polychaeta phylogeny and evolution

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 MEGAS5 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/astrosenew/CGBlocks_server.html), using the less stringent
options, and pruned. The general Polychaeta alignment has
185 sequences and was 802 base pair (bp) long; the separate
Cotylea alignment had 154 sequences and was 888 bp long.
The separate Acetylena 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
data set, we ran separate analyses of Cotylea (Hoploplana as
outgroup) and Acetylena (Pericelis and Cestoplane as
outgroups) to test phylogenetic hypotheses obtained from the
general analysis and to improve resolution within superfamilies
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 re-
commended by Halkynych (2016), and apomorphies were
estimated using parsimony. We evaluated the major competing
hypotheses 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 PROTGAMMA/GTR model were used for these
analyses. We tested topological constraints of the whole systems
of Faebel, Pudhoe, and the one proposed herein, as well as
constraining each of the superfamilies individually. Additionally,
we also evaluated the suborders Acetylena and Cotylea in traditional
and newly proposed arrangement.

Results

General tree topology
In our general polyclad tree (Figs. 2 and 3), Polychaeta was
recovered as monophyletic (97% bootstrap support (BS)).
Acetylena in a traditional sense was not monophyletic, because
Cestoplane was recovered sister to Cotylea (Fig. 3) with high
support (BS 69). Thea, another genus traditionally included
in Acetylena, clustered quite deeply within Cotylea, as sister
clad to Bonnia and Chromyella, two basal cotylean genera
(Fig. 3). All other acetyleans clustered together with high
support (BS 93). Cestoplane 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 Bonnia,
Chromyella, and Thea, as sister group to the remaining
Cotylea (Figs. 3 and 8). The same topology was recovered in
analyses focusing only on Acetylena or Cotylea, with just
slightly different bootstrap values (Supplementary Figs. 2
and 3).

Prostomiotomidae, Euryleptidae, and Pseudoceroidea were
recovered as a clade (BS 94). Prostomiotomids (BS 100) as
sister to a combined clade (BS 95) of the genera included in
Pseudoceroidea (BS 92) and Euryleptidae, the latter family
paraphyletic (Fig. 2). Prostheceraeus, Marigrella, and
Cycloporus resulted sisters of Pseudoceroidea, but the two
species of Cycloporus did not cluster in the same clade, as
Cycloporus gabrielaei branched independently (Fig. 3).
Within Pseudoceroidea, Pseudobocerus, despite divided in
two clades, formed a monophyletic group with the genera
Manocon and one Tsyscanzoon, and Tanga grouped with
Phylacocera and Monobocerus. And these clades together with
other Tsyscanzoon formed a monophyletic group of genera
with multiplication of reproductive structures (BS 95). The
acetylent clade (BS 99) of the tree shows a clade formed by
Stylochidae, Planoceridae, and Hoploplanaidae (BS 91) as the
sister group of the clade with remaining Acetylena (BS 63)
(Fig. 2). A clade with Diococeridae and Cryptoceridae (BS 52)
is sister group to a clade grouping paraphyletic
Leptopanicidae and Notoplanaidae with Gnoseoceridae, Styllochidae,
and Pleoplandidae (BS 90) (Fig. 2).

Classification systems
On suborder and superfamilial level, our molecular phylogenetic
hypothesis is not compatible with either Faebel's or Pudhoe's
systems. The suborders Acetylena 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 Pudhoe's superfamilies was monophyletic, 
Cesioplanidae (Fig. 2). Stylochoidae appears mixed with
Fig. 2 Polycladida family-level 28S rDNA phylogeny (RAxML: numbers refer to bootstrap support values). Cladograms 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).

Planococenidae in two clades (BS 91 and 63, respectively). In the Acothyla, genera with nuchal, cerebral, and marginal eyespots, like Adenoplana and Imagine, grouped with genera with only nuchal and cerebral eyespots (for example, Leptoplana and Hopleoplaana) (Fig. 3). Similarly, our molecular trees do not support Faubel's classification (Fig. 2) and only Illyplanoidea appeared as monophyletic. Groups with intercalated prostatic vesicle (superfamily Leptoplanoidea) clustered with genera that present free prostatic vesicle (superfamily Stylochoida) in both the Acothyla and the Cystyla branches. In Cystyla, the type of pharynx was not an autapomorphy of monophyletic groups either, genera with tubular pharynx (Faubel's Euryplanoidea) clustered with genera with ruffled pharynx (Faubel's Pseudocerotidae) (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 Illyplanoidea, Leptoplanoidea, and Pseudocerotidae were rejected in both AU and SH tests, as were also Prudhoe's Planococenidae and Stylochoida. However, Euryplanoidea sensu Faubel was rejected only in the AU test, but not in the SH test, and Stylochoida sensu Faubel and Cystylanoidea 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 Cystyla, most resulted in monophyletic with high bootstrap support values. One exception was the paraphyletic Euryplanoidea, with C. gabrielleae sister to the Pseudodertidae. In addition to Cyclopans, the genera Maritigrella, Prostheceraeus, and Thyssanozoon were also not monophyletic in our tree. The genus Pseudobicer was also non-monophyletic, but divided in two groups, and the one including Pseudobicerus pandalii, P. bedfordi, and P. wirtzi, grouped with Pseudobicerus. The other Pseudobicerus group was composed of Pseudobicerus evelinae, P. splendida, 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 in posterior half of the body; lacked style; 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 intercalated or free prostatic vesicle (Table 2); we therefore do not show this feature in Fig. 2.

The Acothyla sensu stricto were divided in a tentaculata (with nuchal tentacles) and atentaculata group (Figs. 3 and 7). The tentaculata group presented members with both intercalated 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, Paraipapillaela, Planocera, Idioplaana, Stylochus, and Imagine (Fig. 3). However, in the atentaculata 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 Phaonocelis were grouped together, and these genera share the atentaculata condition with marginal, cerebral, and nuchal eyespots (Table 2 and Figs. 3 and 7).

The Cystyla, apart from the basal Cystylana, Pericetis, and the Chromyella, Boninia, and Theama clade, presented a large clade that included all Pseudodertidae. Euryplanoidea, and Prostheceraeus. The Chromyella-Boninia-Theama clade (BS 94) consists of animals with elongated bodies and mixed cystylan-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 clade. One (BS 95) shows possible multiplication of reproductive structures (either male or female) and complex folded pseudotentacles and is composed of Thyssanozoon, Pseudobicerus, Yangia, Monobicerus, Phrikocera, and Malacozoon (Fig. 3). The other group (BS 96) has single reproductive structures and simple folded pseudotentacles (Table 2), composed basically by...
**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.
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
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 superfamly 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 Thea, “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. Thea and Cestoplana were said to present characters that are dominantly represented in cotylean families (Laidlaw 1903c; Faubel 1983). Theamatidae as well as a Cestoplanaeidae present cement-nucus gland chambers (cement pouch) and lack nuchal eyespots, true uteri, and Lang's vesicles (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. 5e), and the walk of the male antenna 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. 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). *Thecoma* also presents the male structures before
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 eyestalks have historically placed both genera in Acotylea (Faubel 1983; Predhowe 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 Theuma 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 "Polyelida 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 Theuma and Chromyella, being also basal in the cotylean branch of the tree. Morphology-based cladistic analyses made by Rawlinson and Livaitis (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 Theuma as also shown by Launey and Girbet (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.
One species of *Cycloporus* with more evident marginal tentacles (*C. gabriellae*; Figs. 3, 6g and 8) grouped sister to *Pseudocerotidae* and another species (*Cycloporus variagatus*; Fig. 3) grouped with other samples of *Euryplectidae*. This points to the need of revision of *Cycloporus*. The genera *Mariagrella* and *Prothestecerus* were mixed up and should be revised and probably merged, because beside molecular evidence, they share morphological characters (Table 2). *Mariagrella newmanae* grouped with *Prothestecerus roseus* and *Mariagrella crozieri* grouped with *Prothestecerus vitatus* in our trees, and the difference between those genera is not clear. Newman and Cannon (2000) while gathering evidence to create the new eurypletid genus *Mariagrella* do not compare it with *Prothestecerus*, only with other less similar genera of that family. According to Rawlinson and Litvaitis (2008), the difference between genera is that *Mariagrella* 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 *Mariagrella* fit illustrations of *Prothestecerus* well. Therefore, we recommend the revision of both genera in order to create more natural systematic units. No *Euryplectidae* grouped with *Prothesteceriidae*. A phylogenetic tree presented by Rawlinson and Stella (2012) also showed *M. crozieri* clustered with pseudocerotids instead of with the prothestecrid clade. *Euryplectids* 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 *Pseudocer us horiisi* (Belaños et al. 2007) was recovered as sister group of a clade with all other *Pseudoceridae* genera, rendering the genus *Pseudocer us* paraphyletic; this unusual species thus should be further studied, and potentially, a new genus needs to be established. The genus *Monobiceps* grouped with *Phirikoceros*, and externally, species of both genera are very similar (Table 2); the reproductive system of *Phirikoceros* species should be checked whether or not they differ from *Monobiceps* having two male systems that open in one common gonopore. The pseudocerotid genera with multiplication of reproductive structures, *Thysanozoon, Monobiceps, Pseudobiceps, Xiangia*, and *Mainzoon*, grouped together in our tree. This was not observed in the Pseudocerotidae molecular framework of Litvaitis and Newman (2001), except for the *Thysanozoon-Pseudobiceps* grouping. This means that multiplication of reproductive structures has more phylogenetic significance than previously thought (Prudhoe 1985).
In Acotylea, Bulnes et al. (2005) stated that Stylochiidae and Pseudostylochiidae 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-vascular glands of the prosthetic 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 Platylminthes, 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 Prothrylchida (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 stylies (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 Prothrylchida, 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 acolyteans 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, prosthioicotids, and eurylepidids.

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 eyespots 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 Prosthioicotidae is one of the three cotylean groups that have marginal eyespots (Table 2). In this suborder, eyespots 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 Phaeocelis group share cerebral, nuchal, and marginal eyepatch character with the tentacular group (Table 2 and Fig. 3), which points to a pleiosomorphic trait. Eye spot groupings thus appear less reliable than previously thought (Lang 1884; Prudhoe 1985), possibly having evolved independently throughout acolytean 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 Prosthioicotidae. And in Acotylea, nuchal tentacles appear to have evolved one time (Fig. 3), in the ancestor of Stylochidae, Plancoceridae, and Hoploplanae 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 echiurans (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 acolyteans 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 intermediate condition of tentacles and corresponding eyes at an intermediate position between margin and post-cerebral area; thus, both types of tentacles appeared independently. However, there is a need for more evidence (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 Prosthioicotidae and once in Theana and Chromyolla clade; or (b) have originated three times, and in one of them evolving into highly complex structures (in the Pseudocerotidae + “Eurylepididae” group), or suffering reduction (in Cycloporus); or even (c) have originated six times, once in Pericelis, then in Boninia, then in Cycloporus + Prosthocerus + Martigrella 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 pleisiomorphic acolytean body plan, over the somewhat intermediate condition in “acolytean” taxa here assigned to Cotylea, to the traditional cotylean gross morphology.

Among cotyleans, Thysonozoon appeared as a sister group of both the Monobicer-Phithiocerida and Pseudobiceros, Yangia, and Maiazoza clades; 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 Eurylepididae grouped with Prosthioicotidae in the trees presented in this study. Thus, the tubular pharynx might have originated (a) once and then 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 1993c; Marcus & Marcus 1986; Faubel 1984, Curtin-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 superfamly 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 non-monophyletic stability, we do not create new names here but rather extend the traditional concept and maintain both suborders as monophyletic groups. We thus transfer both famlies, Cestoplanae and Theamae, 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 Bonamb (Fig. 8), which do not show clear clusters of eyespots either (Marcus and Marcus 1986). Additionally, our results are corroborated both by Rawlinson and Stella (2012) who showed a Cestoplana clustered with cotyleans (28S tDNA) instead of in the Acotylea branch and by Langer and Giribet (2014), who showed Theama grouped with cotyleans instead of acotyleans in a Bayesian tree (28S and 18S tDNA 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 prostastic 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 Livaitis 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 (Quirroga et al. 2015). Gross morphology, followed by sensory organs, was regarded by Rawlinson and Livaitis (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 (1993c), who thought that the prostastic vesicle was the most informative character, followed by nuchal tentacles and eyes. Marcus and Marcus (1996) and Bock (1913) proposed eyespots of 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 (1993c) and Rawlinson and Livaitis (2008), and other characters as well, reproductive characters are useful in the genus level, and color pattern can also be informative at species level (Livaitis 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, as 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 superfamly-level classification (Fig. 7). One has rounded body, nuchal tentacles, and cerebral, nuchal, and sometimes marginal eyespots, which includes Hoploplana, Imogene, Stylochas, Xiphoplana, Planocera, and Panplanocera (Fig. 7) and their corresponding families Hoploplanae, Stylochidae, Pseudostylochidae, and Planoceridae. This group is to be called superfamly Stylochoidae 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 Pheanocellus (Fig. 7) and their families, Discocelididae and
Cryptocelidae. This is to be called Cryptoceloidea superfamily, 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 tenacles, with only cerebral and masticatory eyes, and with true intercalated prostatic vesicle and Lang’s vesicle, which includes Armatoplana, Notoplana, Leptoplana, Echinothela, and Melloplana (Fig. 7). The last group is to be called superfamily Leptoplanoidea Faubel, 1984, as also used in other systems, due to its monoprotandry; it includes families Stylochopladinidae, Notoplanae, Leptoplanae, Nesoicidae, and Pseudoceridae.

On the other hand, Cystoidea can be divided into five superfamilies (Fig. 8). One group with extremely elongated body, frontal eyes, and true intercalated prostatic vesicle contains Cestoplana; this is to be called superfamily Cestoplanoidea Poche, 1926 (Fig. 3). Another group, with rounded body, frontal cerebral, and marginal eyes, includes Pericelis (Fig. 8), to be called Pericelioidea superfamily, nov. A clade with extremely to mildly elongated body and frontal and cerebral eyes, including Theca, Chromoidea, and Bonitida (Fig. 8) and the corresponding families Zeatoidae, Amyelidae, and Chromopladinidae. This group is to be called Chromopladinoida superfamily, nov., as the oldest family included is Chromopladinidae. Another group with elongated body, tubular pharynx, and cerebral and marginal eyes includes Parabia, Echinothela, and Ancylospalana (Fig. 8). This includes the family Prosthiodontidae and is to be called Prosthiodontoida superfamily, nov. One last group with oval body, and cerebral and tentacular eyes, and developed marginal tentacles includes all Pseudoceridae and Euryplanae (Fig. 8). This group is to be called superfamily Pseudoceroida Faubel, 1984. None of the proposed superfamilies were rejected in the hypothesis test and are thus considered likely (Table 3).

Among the families that were not sampled in this or other studies are the acornans Enantiidae, Stylolochocidae, Limnostylochidae, and Acoelopladinidae, which present mixed sets of morphological characters (Faubel 1983, 1984; Pindho 1985). The families Euplanidae, Laticestidae, and Discocelidae may contain basal cryptobian genera, Hyplana, Microplanae, Palaunidae, Notociridae, and Camptiphoridae possibly belong to Leptoplanoidea. Discoprostrophiidae and Callioplidae may once be included in Stylolochocidae. Polyplacophora and Pleuroplanae possibly belong to Cryptocelidae. The family Gresiocrinitidae, despite being sampled in this study, also needs more sampling as it presents mixed morphological characters among its genera. The families Leptoplanae, Pleoplatinae, Notopladae, and Stylochopladinae 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 cyrtaceans, the families Opisthognathidae, Ditremagnidae, Ditcrooididae, Diphostoidae, and Stylochoididae still need to be tested, with molecular and more morphological information. Anomunidae, Laidlawiidae, and Eurypodiidae possibly belong to Pseudoceroida.

In general, most of the early morpho-anatomical studies (Lang 1884; Laidlaw 1903; Bock 1913; Hyman 1955; Marcus and Marcus 1966) were successful in classifying systematic units on genus level. However, some discrepancies (e.g., Pseudoceroida, Leptoplanoidea) that were later solved by improved working methods that allowed better observation of living and fixed specimens (Newman and Cunnin 2003). As indicated by Pindho (1985, p. 101), our results suggest that the genus Hoploplana should have its own family, Hoploplanae, since it was recovered far away from the tree of the Leptoplanoidea (Figs. 2 and 3). Pindho also pointed out that this family might be related to Planocera, which was corroborated by molecular data (Figs. 2 and 3). The genus Idiopla should also be included in a separate family from the Stylochidae, as proposed by Faubel (1983; Pseudolophoida), and not be treated as a subfamily (Pindho 1985), since in our tree, it appears as a reciprocally monophyletic group. The position of the Pseudoceridae clade as a sister group of the Pseudobiceros and Thysanocera clade is in accordance with results of Littearsis and Newman (2001). The relation between these two genera, however, is different, according to our molecular results: Thysanocera appears as a sister group to the Pseudobiceros, Yungia, and Mauzaco clade, instead of originating from the Pseudobiceros clade (Littearsis and Newman 2001). Morphology-based clades are described by Rawlinson and Littearsis (2008) and 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 misted. Both external morphological and anatomical characters, which were widely used in Polycladida systematics, are prone to convergent evolution. Characters related both to the prostomate vesicle and to eyespot distribution have evolved independently in different polyclads as also happened with the pharynx type in the Cystoidea. 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 superfamilies and superfamilies, which may better reflect the interrelationships between polyclads. Characters such as tentacles, orientation of male reproductive structures,
Acknowledgements We are thankful to colleagues that helped in the collection and providing material studied here: Prof. Dr. Juan Lucas Cervera and Msc. Patricia Pérez (Universidad de Cádiz, Spain), Artane Dimitri (USA), Prof. Dr. Peter Wirth, Dr. Judith Brown, Dr. Yuri Deard, Dr. Bastian Brüning, Prof. Dr. Fernanda Cavalcanti, and Prof. Dr. Emilio Lanna (Universidade Federal da Bahia, Brazil). Our thanks extend to Arnaldo Campos Pêrez (Hospital Universitário Clementino Fraga Filho, Universidade Federal do Rio de Janeiro, Brazil) and Dr. Isabel Birning (ZSM, Germany) for the help in the laboratory work and MSc. Isabella Stöger for both the laboratory and analysis help. We thank Prof. Dr. Ulf Jonellus (Swedish Natural History Museum) and the SYNTHESIS program for the access to the Polycladida collection of the SNHM. We also thank an anonymous referee and the Editor Prof. Dr. Andreas Warnering for their helpful critique and comments. The first and second authors are CNPq (Brazil) and DAAD (Germany) fellowship holders. Lab work was supported by the Deutsche Forschungsgemeinschaft (DFG; to MS).

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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
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: Thysanozoon 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 (Leptoplanoida 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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ACKNOWLEDGEMENTS

I would like to thank the sea, especially the Atlantic. And I am grateful for support from panaquildos, verrückitas, philosophers, translators and historians, and a pre-apocalyptic frog. I also wish to thank the helpful teachings or discussion with Vinicius Padula, Isabella Stöger, Maria Isabel Berning, Basti, Daniel Marquina, Rene Ong, Marcela Bolaños, Sigmer Quiroga, Veronica Bulnes, Tom Littlewood, Ulf Jondelius, and Michael Schrödl.
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**SUBMITTED MANUSCRIPTS**


(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*.

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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.

EXTENSION COURSES GIVEN


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


THESIS SUPERVISION

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.

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”.


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.


Zoological Ilustration. XXVI Brazilian Zoology Congress, Londrina, Brazil. Duration: 8 hours.
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<tr>
<th>LANGUAGE</th>
<th>SOFTWARES</th>
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<td>Portuguese</td>
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<td>Field work</td>
<td>Sample handling</td>
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<td>DNA extraction</td>
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<td>Scientific photography</td>
<td>PCR protocols</td>
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<td>Curation of scientific collection</td>
<td>Gel electrophoresis</td>
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<td>DNA clean-up</td>
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<th>LABORATORY WORK</th>
<th>PARTICIPATION ON SCIENTIFIC MEETINGS</th>
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<td>Sample handling</td>
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<td>DNA extraction</td>
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<td>PCR protocols</td>
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<th>SOFTWARES</th>
<th>PARTICIPATION ON POPULARIZATION OF SCIENCE EVENTS</th>
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<tr>
<td>Microsoft Office</td>
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