



The molecular phylogenetic position of *Mariplanella piscadera* sp. nov. reveals a new major group of rhabdocoel flatworms: Mariplanellida *status novus* (Platyhelminthes: Rhabdocoela)

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Received: 16 June 2021 / Accepted: 22 December 2021 / Published online: 31 January 2022
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Abstract

Rhabdocoels comprise a large group of flatworms that currently consists of two major subgroups: (1) Kalyptorhynchia with an anterior proboscis and (2) Dalytyphloplanida without a proboscis. Most genera of rhabdocoels can easily be classified into one of these two subgroups, except for the three monotypic representatives of the Mariplanellinae. Comparative morphological data and previous molecular phylogenetic analyses have so far been unable to determine the positions of these rarely encountered microturbellarians within the context of rhabdocoels. Here we describe a new species of Mariplanellinae, *Mariplanella piscadera* sp. nov. from Curaçao (Dutch Caribbean), and present an updated phylogeny inferred from 18S and 28S rDNA sequences, including data from *M. piscadera* sp. nov., *M. frisia*, and a selection of rhabdocoels, proseriates and other trepaxonematan flatworms. Our molecular phylogenetic trees reveal that *Mariplanella* belongs to a distinct higher-level group of rhabdocoels that forms the sister lineage to a clade uniting Kalyptorhynchia and Dalytyphloplanida. Therefore, we update the status of Mariplanellinae to Mariplanellida *status novus*, containing the family Mariplanellidae *status novus*, in order to better reflect our current understanding of rhabdocoel phylogeny and the establishment of now three major subgroups.

Keyword Microturbellaria · Mariplanellinae · Meiofauna · Phylogeny · Curaçao · Caribbean

Introduction

The Rhabdocoela is a major group of flatworms that includes free-living and symbiotic representatives in a wide variety of marine, freshwater and limnoterrestrial habitats around the world. Based on molecular phylogenetic analyses, rhabdocoels are currently classified into one of two higher-level subgroups: Kalyptorhynchia with an anterior proboscis and Dalytyphloplanida without a proboscis (Tessens et al., 2014; Van Steenkiste et al., 2013; Willems et al., 2006). While most genera of rhabdocoels can easily be classified into one of these two groups, the marine interstitial representatives of the trigonostomid subfamily Mariplanellinae Ax & Heller, 1970 have remained enigmatic. This subfamily was provisionally erected to accommodate *Mariplanella frisia* Ax &

Heller, 1970, and placed within the family Trigonostomidae von Graff, 1905, based on a double connection in the female reproductive system (Ax & Heller, 1970). However, the presence of a single ovary casted doubt on a close relationship with other trigonostomids, which always possess paired ovaries. Two other monotypic genera, *Lonchoplanella* Ehlers, 1974, and *Poseidoplanella* Willems et al. 2005, were later added to Mariplanellinae based on this unusual combination of a single ovary and the double connection (Ehlers, 1974; Willems et al., 2005). In addition, *Lonchoplanella axi* Ehlers, 1974, also shares a number of other conspicuous characters with *Mariplanella frisia*, including two types of adenal rhabdites (needle-shaped and elongate viscous) and a muscular copulatory bursa with a sclerotized basal membrane.

The first comprehensive molecular phylogenetic analyses focussing on rhabdocoel interrelationships included 18S rDNA data of *Mariplanella frisia* (Willems et al., 2006). However, support for its phylogenetic position within Dalytyphloplanida was weak and its overall position within Rhabdocoela remained inconclusive. Here, we provide an updated molecular phylogeny inferred from both 18S and

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28S rDNA sequences of rhabdocoels and other flatworm taxa, including new DNA sequences from a novel representative of Mariplanellinae collected from Curaçao (Dutch Caribbean). These data demonstrated a well-resolved phylogenetic position of the Mariplanellinae that supports an updated classification of the Rhabdocoela consisting of three major subgroups: Kalyptorhynchia, Dalytyphloplanida and Mariplanellida *status novus*.

Materials and methods

A live individual of *Mariplanella piscadera* sp. nov. was collected on April 26, 2018 from subtidal sand in Piscaderebaai, Curaçao (12°07'17.5"N 68°58'09.4"W). Coarse sand enriched with organic material at about 2.5 m deep was sampled by hand while snorkeling. Meiofauna were separated from the sediment using the MgCl₂ decantation method (Schockaert, 1996). The individual worm was isolated and observed under a Zeiss Stemi 508 stereoscope and subsequently whole mounted alive to be studied and photographed at the Caribbean Research and Management of Biodiversity Institute (CARMABI) under a portable Leica DMIL inverted microscope using a Sony a6000 digital camera.

Genomic DNA was extracted from the entire individual using the DNeasy Blood & Tissue kit (Qiagen). Manufacturer's instructions were followed, with the exception that DNA was eluted in 60 µL of preheated AE elution buffer (60 °C). Fragments of the nearly complete 18S (1787 bp) and partial 28S rRNA (1669 bp) genes were PCR amplified using the primers and thermocycling conditions in Table S1. Amplicons were visualized on 1.5% agarose gels stained with GelRed™ (Biotium), enzymatically cleaned with Illustra™ ExoProStar S (GE Healthcare) and subsequently sequenced by Genewiz (Brooks Life Sciences) through standard Sanger DNA sequencing using the amplification primers and internal sequencing primers (Table S1). Resulting trace files were assembled into full sequences in Geneious v10.2.3 (Kearse et al., 2012) and subjected to a BLAST search on the NCBI website (<http://blast.ncbi.nlm.nih.gov>) to verify the specimen's taxonomic identity. Both sequences were deposited in GenBank, and sequence accession numbers are provided in Table S2.

The new 18S and 28S rDNA sequences of *Mariplanella piscadera* sp. nov. were aligned with rDNA sequences of 128 representatives of rhabdocoels and several other flatworm groups (Table S2) using the E-INSI algorithm in MAFFT (Kato & Toh, 2008). These alignments were subsequently trimmed with ClipKIT using default settings (Steenwyk et al., 2020) and concatenated in Geneious v10.2.3 in one alignment.

Best-fit partitions and models of molecular evolution corresponding to the 18S and 28S rDNA datasets and

GTR + GAMMA + I, respectively, were recovered for the concatenated dataset (18S + 28S) in PartitionFinder v2.1.1 using a greedy search and all three model selection criteria (AIC, AICc, BIC) (Lanfear et al., 2017). This partition scheme and model were subsequently used in the phylogenetic analyses of the concatenated dataset. The maximum likelihood (ML) analysis was performed with the RAxML v8.2.11 plugin (Stamatakis, 2014) in Geneious v10.2.3 selecting the algorithm for best-scoring ML tree search and nonparametric bootstrapping (1000 replicates). Six pro-rhynchids and five polyclads were selected as the outgroup based on current knowledge of the phylogenetic relationships within flatworms (Egger et al., 2015; Laumer et al., 2015). A Bayesian analysis was performed on the same dataset in MrBayes v3.2.7a (Ronquist & Huelsenbeck, 2003) through XSEDE in the CIPRES Science Gateway v3.3 (<https://www.phylo.org>), using default prior and mcmc settings, in two independent simultaneous runs for 40 million generations. Trees were sampled every 400th generation after a 25% burnin. Convergence was assessed through the LogL values, ESS values (estimated sample size) and the average deviation of split frequencies. The remaining 75,000 trees were summarized in a 50% majority-rule consensus tree. Branch support was evaluated with the ML bootstrap values (bs) and Bayesian posterior probabilities (pp) for the ML and Bayesian tree, respectively. To investigate our support values regarding the phylogenetic position of the genus *Mariplanella*, ML bootstrap and Bayesian posterior probabilities consensus networks were constructed in SplitsTrees v4.17.0 (Huson & Bryant, 2006) based on the 1000 bootstrap pseudoreplicates from the RAxML analysis and a subset of 1000 trees from the combined runs of the Bayesian analysis. MrBayes.t files were thinned with Burntrees v0.3.3 (available from <https://github.com/nylander/Burntrees>) using a 50% burnin. An approximately unbiased (AU) test was conducted in IQ-TREE v1.6.12 (Nguyen et al., 2015) to test alternative placements of *Mariplanella* within the Rhabdocoela. The AU test compared the log-likelihood scores among a set of trees generated in four different partitioned IQ-TREE ML analyses based on the same dataset, including an unconstrained tree search and three constrained tree searches (Table S3). The number of RELI replicates was specified to 100,000.

Results

α-Taxonomic account

Rhabdocoela Ehrenberg, 1831

Mariplanellida Ax & Heller, 1970, *status novus*.

Mariplanellidae Ax & Heller, 1970, *status novus*.

We change the status of the subfamily Mariplanellinae Ax & Heller, 1970 (Dalytyphloplanida, Trigonostomidae) to the taxon *Mariplanellida status novus* and its only family, *Mariplanellidae status novus*, based on the results of the molecular phylogenetic analyses (see **Discussion**).

Type species: Mariplanella frisia Ax & Heller, 1970.

Amended diagnosis: Rhabdoceola with pharynx rosulatus, compact paired vitellaria, unpaired ovary and paired testes. Female system with efferent (female duct) and afferent (bursa, muscular spermatic duct, seminal receptacle, insemination duct) connection between ovary and common genital atrium. Male system with sclerotized stylet.

Mariplanella Ax & Heller, 1970

Diagnosis: see Ax and Heller (1970)

Mariplanella piscadera Van Steenkiste & Leander, sp. nov.

Type material: The only specimen was used for genomic DNA extraction; therefore, the DNA voucher becomes the holotype (BBM MI4941, extracted DNA in buffer stored at -80 °C).

Other material: Images of the live specimen.

Type locality: Piscaderabaai, Curaçao (12°07'17.5"N 68°58'09.4"W). Coarse sand enriched with organic material at about 2.5 m deep.

Etymology: The species epithet refers to the type locality.

Diagnosis: Species of *Mariplanella* with a curved stylet consisting of a proximal funnel surrounded by a thick collar, a tapering distal spiral and a sclerotized connection supporting the bend of the stylet.

Description: The animal was only about 0.35 mm long, and its pharynx rosulatus (ph, Fig. 1a) was at about ¾ of its body length. Eyes were absent. Two types of adenal rhabdite glands were present in its anterior end: (1) needle-shaped rhabdites 3–4 µm long (rh1, Fig. 1b–c) and densely concentrated in the anterior tip, forming a central dark patch that partly envelops the oval brain and stretches toward the sides of the body, and (2) bundles of long viscous strands (rh2, Fig. 1b) that run obliquely from the anterior dark patch toward the sides of the body.

A few details of the atrial organs were visible in the live individual. Posterior to the pharynx, an interconnected larger and smaller dark mass likely corresponds to the sperm-containing bursa (bu, Fig. 1d) and seminal receptacle (sr, Fig. 1d), respectively. The stylet (st, Fig. 1d; Fig. 1e) consisted of a funnel-shaped proximal tube surrounded by a thick collar and that curved backwards into a spiralling distal tip. The bend was reinforced with a sclerotized connection between the proximal tube and the distal spiral. The axial length of the stylet was about 38 µm.

The molecular phylogenetic position of *Mariplanella*

The final trimmed and concatenated 18S + 28S rDNA sequence alignment has 129 sequences belonging to 128 taxa and contains 3797 bp (18S: 1897 bp; 28S: 1900 bp).

The phylogenetic analyses and consensus networks are summarized in Figs. 2, 3 and S1, respectively. Topologies were congruent for both the ML and Bayesian tree after collapsing branches below the thresholds (pp < 0.95 or bs < 70). The results can be summarized as follows: (a) all major flatworms groups in the Trepaxonemata (except for the Neodermata and Bothrioplanida which are not included in the analyses) and their currently understood phylogenetic interrelationships (Egger et al., 2015; Laumer et al., 2015)—including the uncertainty on the precise branching order of Rhabdoceola and Proseriata within the Neophora—are recovered in our trees; (b) the genus *Mariplanella*, represented by *M. frisia* and *M. piscadera* sp. nov., emerges as the sister lineage to a clade consisting of all other rhabdoceols (pp = 0.99; bs = 82), which includes the Kalyptorhynchia (pp = 1; bs = 100) and Dalytyphloplanida (pp = 1; bs = 100); (c) while the AU test did not reject other topologies (p-values > 0.005, Table S3), a closer inspection of our statistical support values in the consensus networks based on ML bootstrap pseudo-replicates (Fig. 3) and Bayesian-sampled topologies (Fig. S1) shows very low pseudo-replicate and topology counts for the two alternative scenarios: (Dalytyphloplanida + (Mariplanellida + Kalyptorhynchia)), pp = 0.002 and bs = 11.3; (Kalyptorhynchia + (Mariplanellida + Dalytyphloplanida)), pp = 0.006 and bs = 6.9; (d) other interrelationships within Kalyptorhynchia, Dalytyphloplanida and Proseriata largely correspond with previous findings (Curini-Galletti et al., 2010; Tessens et al., 2014; Van Steenkiste et al., 2013), except for the basal position of *Ciliopharyngiella constricta* Martens & Schockaert, 1981 as sister lineage to all other proseriates rather than embedded within a clade consisting of unguiphoran proseriates.

Discussion***Mariplanella piscadera* sp. nov. from Curaçao**

While only a limited number of characters were visible in the live specimen from Curaçao using our portable microscope and camera, it can still be recognized as a representative of *Mariplanella*. Both *Mariplanella frisia* and *Lonchoplanella axi* have the two types of adenal rhabdite glands mentioned above, a pharynx rosulatus in the posterior third of the body and the atrial organs in the posterior end (Ax & Heller, 1970; Ehlers, 1974). However, *L. axi* has eyes and a straight stylet, while both the species from Curaçao and *M. frisia* have a curved stylet and lack eyes. The anatomy of *Poseidoplanella*

halleti Willems et al., 2005, differs considerably from *M. frisia* and *L. axi* in having a complex stylet with plate-like parts, a pharynx in the anterior third of the body and atrial organs in the central part of the body (Willems et al., 2005). Based on the images of the live specimen, the stylet of *M. piscadera* sp. nov. clearly differs from that of *M. frisia*. In the latter species, the proximal funnel does not have a thick collar. The distal part of the stylet also forms a blunt angular end in *M. frisia*, while it tapers into a slender spiral in the Caribbean species.

Apart from its type locality, the ecology of this species is not known. Repeated sampling efforts were undertaken in 2016 and 2018 to collect and study meiofaunal flatworms in Piscaderabaai, Curaçao (Gobert et al., 2021; Van Steenkiste

Fig. 2 Phylogenetic position of *Mariplanella* within Trepaxonemata* inferred from 18S and 28S rDNA sequences. Bayesian majority-rule consensus tree of the MrBayes analysis based on the trimmed concatenated alignment. For major flatworm and rhabdocoel groups, branch support values of the Bayesian (pp, posterior probabilities) and ML (bs, bootstrap) analyses are included (pp/bs). Branches with support values of pp < 0.95 or bs < 70 are collapsed. All other branches without annotations have support values of pp ≥ 0.95 and bs ≥ 70. *Exclusive of Neodermata and Bothrioplanida

& Leander, 2018). Because these efforts yielded only one specimen of *Mariplanella piscadera* sp. nov., it is possible that this species is either rare and/or that its occurrence and abundance is influenced by specific environmental conditions. While additional specimens of *M. piscadera* would

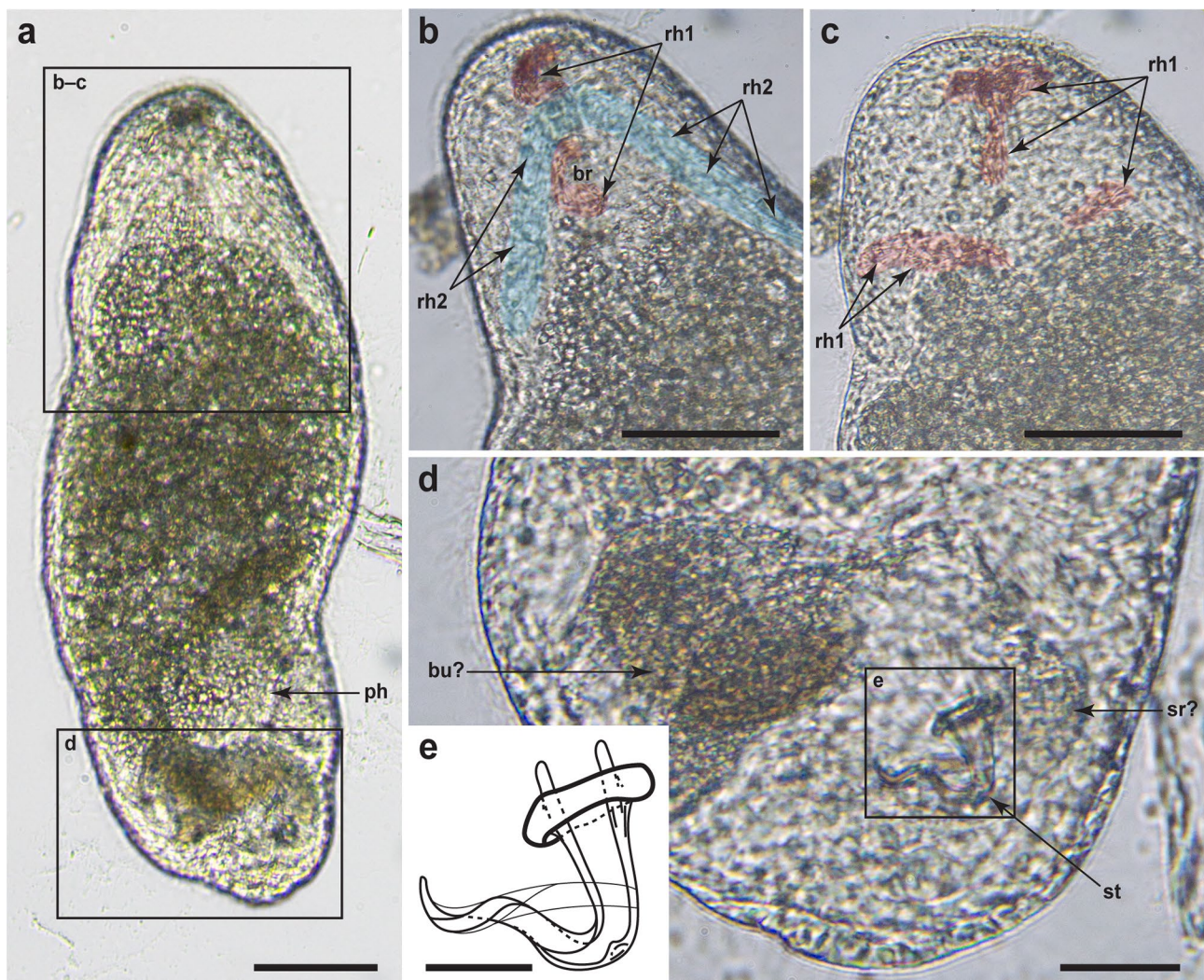


Fig. 1 LM images of the live specimen and stylet drawing of *Mariplanella piscadera* sp. nov. from Curaçao. (a) Full specimen with the pharynx visible as a lighter round outline in the posterior part of the body. (b–c) Detail of the anterior end showing the brain and two types of adenal rhabdite glands (rh1, red overlay; rh2, blue overlay). (d) Detail of the posterior end behind the pharynx show-

ing the stylet and two darker organs corresponding to the bursa and seminal receptacle. (e) Drawing of the stylet based on LM images of the live specimen. Abbreviations: br, brain; bu, bursa; ph, pharynx; rh1, glands with rod- or needle-shaped rhabdites; rh2, strands of viscous rhabdite glands; sr, seminal receptacle; st, stylet. Scale bars: (a–c) = 50 μm; (d) = 20 μm; (e) = 10 μm



have allowed for a more detailed assessment of its anatomy and the preservation of morphological vouchers, the combination of its unique stylet morphology, its type locality, and its 18S and 28S rDNA sequences easily allows for future identification; therefore, the specimen from Curaçao is formally described as a new species.

The discovery of *Mariplanella piscadera* sp. nov. in Curaçao is only the fourth such record of a representative of Mariplanellida *status novus* worldwide. Both *M. frisia* and *L. axi* occur in the Northeastern Atlantic Ocean (North Sea and Baltic Sea), while *P. halleti* was described from the Southern Indian Ocean (Kerguelen). Compared to other groups of rhabdocoels, species of Mariplanellida *status novus* are rarely encountered, even when taking the historical and geographical sampling bias for meiofauna in general and flatworms in particular into account.

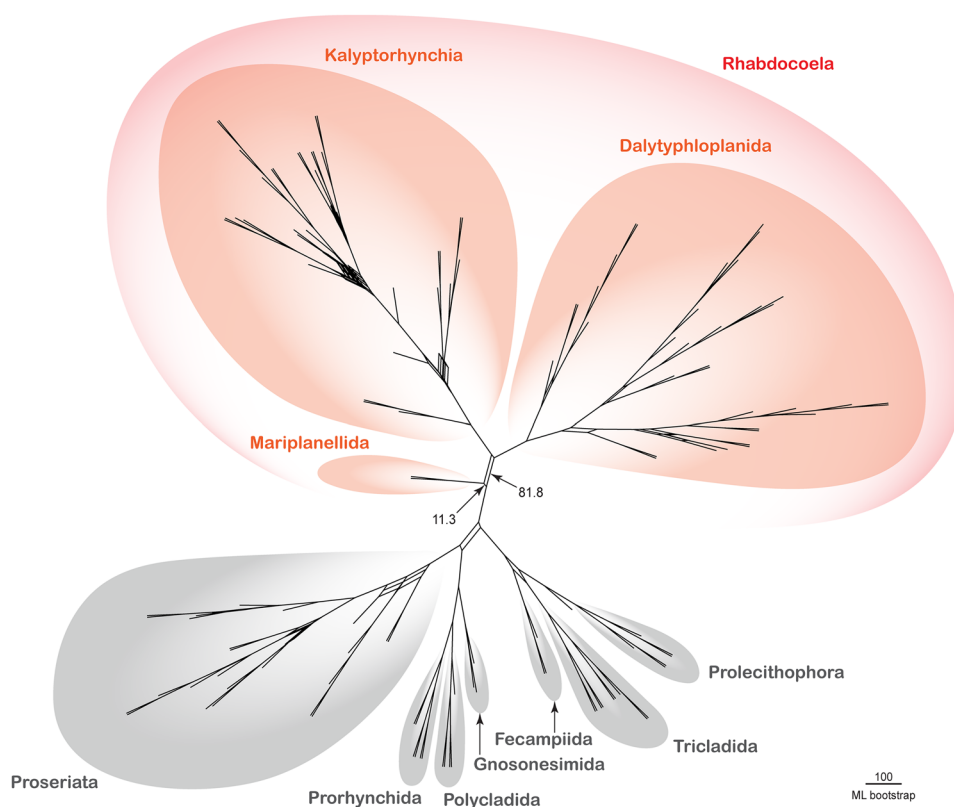
Phylogenetic and taxonomic implications

Over the past two decades, the inclusion of an increasing number of rhabdocoel taxa in molecular phylogenetic analyses has not only helped to confirm the monophyly of the Rhabdocoela as a major group of flatworms, but also established its two large subclades: Kalyptorhynchia and Dalytyphloplanida (Tessens et al., 2014; Van Steenkiste et al., 2013; Willems et al., 2006 and references therein). While kalyptorhynchids have long been considered a monophyletic

group, dalytyphloplanids include a mix of the now paraphyletic “dalyellioids” and “typhloplanoids”, as well as the ectosymbiotic temnocephalids. However, the phylogenetic position of two taxa traditionally considered to be rhabdocoels, *Ciliopharyngiella constricta* and *Mariplanella frisia*, remained unresolved in the analyses of Willems et al. (2006). While representatives of the genus *Ciliopharyngiella* present unique characters as well as characters of both rhabdocoels and proseriates (see Laumer et al., 2015 and references therein for a discussion), the phylogenetic analyses of Curini-Galletti et al. (2010) showed that *C. constricta* is closely related to unguiphoran proseriates. Our analyses also support its position within the Proseriata, but place *C. constricta* as the sister lineage to all other proseriates. More extensive phylogenomic analyses will be needed to verify its exact placement within or vis-à-vis Proseriata.

The uncertain classification of *Mariplanella frisia* in the eponymous rhabdocoel subfamily Mariplanellinae has long been problematic given its aberrant morphology compared to other representatives of the Trigonostomidae to which this subfamily was assigned (Ax & Heller, 1970). In the molecular phylogenetic analyses of 18S rDNA sequences by Willems et al. (2006), *M. frisia* appeared in an unresolved trichotomy with Kalyptorhynchia and Dalytyphloplanida. Consequently, it was clear that *M. frisia* was more closely related to the most basal rhabdocoel lineages than to other trigonostomids, including some support for a clade uniting

Fig. 3 ML bootstrap consensus network of Trepanemata* inferred from 18S and 28S rDNA sequences. Consensus network of the RAxML bootstrap analysis based on the trimmed concatenated alignment. Pseudo-replicate counts (~bs) pertaining to the interrelationships of Mariplanellida *status novus*, Kalyptorhynchia and Dalytyphloplanida are shown with a threshold value of 10. *Exclusive of Neodermata and Bothrioplanida



M. frisia with all dalytyphloplanids. More recent phylogenetic analyses of 18S and 28S rDNA sequences from representatives of the Schizorhynchia and selected taxa of Eukalyptorhynchia (Smith et al., 2015) included *M. frisia* and a number of dalytyphloplanids as an outgroup. Their results show strong support for a clade uniting *M. frisia* with these dalytyphloplanids; however, no other flatworm taxa were included in these analyses to root Rhabdoceola as a clade. With the inclusion of many other trepaxonematan flatworms, our phylogenetic analyses and consensus network analyses show robust support for *Mariplanella* as the sister lineage to a clade consisting of both Dalytyphloplanida and Kalyptorhynchia; the alternative scenarios—*Mariplanella* within Dalytyphloplanida or *Mariplanella* as the sister taxon to the Kalyptorhynchia—are not supported. As such, Mariplanellinae can now be considered a distinct third subgroup of the Rhabdoceola.

While it was already clear that the designation of Mariplanellinae as a subfamily of Trigonostomidae had become untenable based on the molecular phylogenies of Willems et al. (2006), its taxonomic status was never formally updated, most likely because of its uncertain phylogenetic position. Based on our results, we propose a status change for the subfamily Mariplanellinae to better reflect its position as a distinct higher-level rhabdoceol group at the same rank as Kalyptorhynchia and Dalytyphloplanida: Mariplanellida *status novus* contains only one family Mariplanellidae *status novus*, which retains the same representatives as the now former Mariplanellinae, including *Mariplanella frisia*, *Lonchoplanella axi* and *Poseidoplanella halleti*. The inclusion of the latter two genera and species is provisional until molecular data become available to confirm their position within Mariplanellida *status novus*.

The phylogenetic position of Mariplanellida *status novus* as the sister clade to all other rhabdoceols has implications for future research on the evolution of morphological characters in this group of flatworms. Currently, there is limited understanding of ancestral, homologous or homoplasious traits in rhabdoceols. A number of apomorphies for Rhabdoceola have been proposed, including the presence of a pharynx bulbosus (either rosulatus-type or dolliiformis-type) as defined in Artois (2020), and characters related to the protonephridial system and sperm ultrastructure (Willems et al., 2006). The anatomy of the epidermis, rhabdite glands, pharynx, and male and female atrial organs is relatively well studied in *Mariplanella frisia* and *Lonchoplanella axi* (Ax & Heller, 1970; Ehlers, 1974). Based on the phylogenetic position of Mariplanellida *status novus* in our trees, we hypothesize that some of these characters might be plesiomorphic within the Rhabdoceola. For instance, the rhabdoceol pharynx rosulatus is shared by mariplanellids and most likely the common ancestor of Kalyptorhynchia

and Dalytyphloplanida (Raikova et al., 2019). The traditional morphology-based classification of rhabdoceols has predominantly been based on characters of the male and female reproductive organs. A single ovary and the double connection in the female system, either associated with a common genital atrium or with separate male and female gonopores, can be found in several groups of kalyptorhynchids and dalytyphloplanids. However, molecular phylogenies of the Kalyptorhynchia and Dalytyphloplanida have shown that homoplasy is very common (Tessens et al., 2014; Van Steenkiste et al., 2013), and at this point it is impossible to deduct whether the single ovary and double connection are the plesiomorphic states in rhabdoceols or if these conditions originated multiple times independently in the Mariplanellida *status novus*, Kalyptorhynchia and Dalytyphloplanida.

Future comparative morphological studies centered on traits associated with the nervous system, protonephridia and musculature and on ultrastructural diversity (e.g., rhabdite/proboscis glands, sperm) should include mariplanellids and representatives of early branching clades within the Kalyptorhynchia (e.g., Nannorhynchidae) and the Dalytyphloplanida (e.g., Kytorhynchidae for Thalassotyphloplanida, Solenopharyngidae for Neodalyellida). Representatives of the Mariplanellida *status novus* might provide us with important insights into the evolution of key innovations in rhabdoceols, such as the conorhynch proboscis in Kalyptorhynchia and the reduction, loss or incorporation of axonemes in sperm cells.

Sampling Permits for sampling were obtained by the Caribbean Research and Management of Biodiversity Institute (CARMABI).

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s13127-022-00542-2>.

Acknowledgements We are grateful to the Caribbean Research and Management of Biodiversity Institute (CARMABI) and their helpful staff for supporting the sampling campaign in Curaçao. We also like to thank two anonymous reviewers for their valuable suggestions to improve this work.

Author contributions NWLVS and BSL took part in conceptualization; NWLVS involved in methodology; NWLVS took part in formal analysis and investigation; NWLVS and BSL involved in writing—original draft preparation; NWLVS and BSL took part in writing—review and editing; BSL involved in funding acquisition; BSL took part in resources; BSL took part in supervision.

Funding This work was funded by the Canadian Institute for Advanced Research (CIFAR), the Tula Foundation's Hakai Institute and the National Sciences and Engineering Research Council of Canada (NSERC 2019–03986).

Availability of data and material The sequence alignments and molecular phylogenetic trees of this study are available in Mendeley Data, V1, <https://doi.org/10.17632/94w8tfp972.1>. GenBank accession numbers of the sequences generated for this study are included in Table S2.

Declarations

Ethical approval No approval of research ethics committees was required because the work was conducted with unregulated invertebrate species.

Consent for publication All authors consent to the submission and publication of this article upon acceptance.

Conflict of interest The authors have no conflict of interest to declare that are relevant to the content of this article.

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