A combined phylogenetic strategy illuminates the evolution of Goniodorididae nudibranchs (Mollusca, Gastropoda, Heterobranchia)

Sofía Paz-Sedano [a,*], Juan Moles [b,c], Dimitri Smirnoff [d], Terrence M. Gosliner [d], Marta Pola [a,e]

[a] Department of Biology, Faculty of Sciences, Autonomous University of Madrid, Madrid, Spain
[b] Department of Evolutionary Biology, Ecology, and Environmental Sciences, Faculty of Biology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain
[c] Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain
[d] Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, CA, USA
[e] Biodiversity and Global Change Research Center (CIB-UAM), Campus of International Excellence UAM + CSIC, Madrid, Spain

ABSTRACT

Goniodorididae is a family of small dorid nudibranchs distributed worldwide that feed on entoprocts, ascidians, and bryozoans. The evolutionary relationships between its taxa have been uncertain due to the limited taxa available for phylogenetic analyses; some genera being paraphyletic. The family includes a remarkable number of synonymized genera in which the species richness is unequally distributed, while some genera have dozens of species others are monospecific. Some clades are very uniform morphologically while others are considered highly variable. To increase backbone phylogenetic resolution a target enrichment approach of ultra-conserved elements was aimed at representative Goniodorididae species for the first time. Additionally, we increase species representation by including mitochondrial markers cytochrome *c* oxidase subunit I and ribosomal RNA 16S as well as nuclear Histone 3 and ribosomal RNA 18S from 109 Goniodorididae species, out of approximately 160 currently valid species. Maximum likelihood and Bayesian inference analyses were performed to infer the phylogeny of the family. As a result, two subfamilies and eleven genera were elucidated. The synonymized genera *Bermudella, Cargoa,* and *Ceratodoris* are here resurrected and a new genus, *Naisdoris* gen. nov., is described. The clades included taxa with shared prey preference, showing that trophic behavior could have driven species evolution and morphological uniqueness within the family Goniodorididae.

1. Introduction

The exploration of biodiversity from an integrative taxonomy approach increases our understanding of species concepts by considering their evolutionary trajectories (Padial et al., 2010; Pante et al., 2015). Most molecular analyses include partial sequences of mitochondrial and nuclear markers, which have occasionally led to systematic reassessments at the species, genus, or family level with high support (Hallas & Gosliner, 2015; Pola et al., 2019; Martín-Hervás et al., 2021). However, sometimes these analyses have recovered unresolved phylogenies mainly due to a lack of molecular resolution (Pola et al., 2007; Hallas et al., 2017; Korshunova et al., 2020). In recent years, Next-Generation Sequencing (NGS) has proven to be a reliable method of high-throughput sequencing aiming at resolving deep-node relationships (Smith et al., 2011; Goodheart & Wägele, 2020; Layton et al., 2020; Moles & Giribet, 2021). Target enrichment of ultra-conserved

elements (UCEs) is a method based on the sequencing of hybridizing probes that allow for obtaining hundreds of conserved regions within the genome (Zhang et al., 2019; Moles & Giribet, 2021). However, while conserved areas of orthologous loci from diverse taxa help to resolve recalcitrant nodes, the flanking areas provide enough sequence variability for phylogenetics at a species level (Blair et al., 2019). Target enrichment is proven successful in reconstructing phylogenies of birds (Musher & Cracraft, 2018), mammals (Parada et al., 2021), cnidarians (Quattrini et al., 2018), arthropods (Kieran et al., 2019), or mollusks (Abdelkrim et al., 2018), including heterobranchs (Moles & Giribet, 2021).

Nudibranchia includes great diversity and morphological disparity and is composed of Doridina (dorids) and Cladobranchia suborders (Bouchet et al., 2017). Phylogenomic studies on nudibranchs have exponentially increased in the last decade, most of them focused on Cladobranchia. Transcriptomics recovered well-supported phylogenies

and an understanding of the evolution of different ecological aspects within cladobranchs, such as diet or behavior (Goodheart et al., 2017; Goodheart & Wägele, 2020). A few dorid transcriptomes are also available, mainly belonging to the family Chromodorididae (Layton et al., 2020). Also, a target capture approach has been used for resolving the phylogeny of the genus *Chromodoris* (Layton et al., 2020). This study showed that target capture techniques were efficient for recovering relationships among recently radiated species. Yet these studies are still in their infancy in the hyperdiverse group of nudibranchs.

Goniodorididae is a monophyletic dorid family with convulse systematics related to families in Onchidoridoidea (Hallas & Gosliner, 2015). Twenty-one nominal genera were described, but most of them are considered synonyms. To date, only nine of them are valid (MolluscaBase, 2023a). The systematic relationships between and within genera have been extensively reviewed recently (Smirnoff et al., 2022; Paz-Sedano et al., 2021a, 2022a, 2023a, 2023b). As a result, the genera *Murphydoris* Sigurdsson, 1991, *Trapania* Pruvot-Fol, 1931 and *Goniodorisella* Pruvot-Fol, 1933 are monophyletic. The genera *Okenia* Menke, 1830 and *Goniodoris* Forbes & Goodsir, 1839 were systematically found paraphyletic, gathering in the same clade their respective type species. Moreover, the genus *Pelagella* Gray, 1850 has been recently recovered from its synonymy with *Goniodoris* (Paz-Sedano et al., 2023a). Therefore, the validity of synonyms should be re-evaluated in light of the available molecular data, particularly considering that *Okenia* includes most of the synonymized genera (MolluscaBase, 2023c).

To address the systematics of Goniodorididae, we aimed to provide a UCE-based phylogenomic inference aiming at the intergeneric relationships and a Sanger-based phylogenetic analysis targeting a species level. The latter includes new mitochondrial and nuclear molecular markers for 60 species. Preliminary data on Sanger analyses were used before obtaining a UCE-based dataset (Moles & Giribet, 2021) from a representative species from the putative genera. We carried out a combined interpretation of the results obtained by UCE-based and Sanger-based analyses to evaluate the systematics of Goniodorididae, including synonymized subfamilies, genera, and species. An integrative taxonomical review was performed compiling data on the natural history, morphology, and phylogeny to search for correlations between ecological patterns, morphology, and the evolution of lineages.

2. Material and methods

2.1. Specimens

A total of 146 specimens, representing 60 species of the family Goniodorididae, were loaned by the Australian Museum (AM) (Sidney, Australia), the Bergen University Museum – Natural History (ZMBN) (Bergen, Norway), the California Academy of Sciences (CAS) (San Francisco, California, USA), the California State Polytechnic University (CPIC) (Pomona, California, USA), the National Museum of Natural Sciences (MNCN) (Madrid, Spain), the Queensland Museum (QM) (Brisbane, Australia), the Zoological Museum of the University of Costa Rica (MZUCR) (San José, Costa Rica), the National Museum of Philippines (NMP) (Manila, the Philippines), the Western Australian Museum (WAM) (Perth, Australia), and the Bavarian State Collection of Zoology (ZSM) (Munich, Germany). Morphological examinations were performed on all specimens before sequencing to verify correct identification.

2.2. Sanger sequencing

2.2.1. Taxon sampling

All the specimens were used for Sanger sequencing analyses. Mitochondrial and nuclear molecular markers of all available taxa belonging to Goniodorididae were mined from GenBank (Table S1). Molecular markers were also extracted from UCEs (Table S2). To sum up, phylogenetic analyses based on Sanger sequencing data included a taxonomic

sampling of 109 Goniodorididae species, representing 55 % of the described species of the family, plus 17 undescribed Goniodorididae species (Table S1). An additional 12 species of other nudibranchs belonging to different families were included as outgroups (Table S1).

2.2.2. DNA extraction, amplification, and sequencing

Sanger sequencing was carried out at CAS Center for Computational Genetics (CCG; San Francisco, California, USA), as well as at the Autonomous University of Madrid (UAM; Madrid, Spain). A small sample of foot tissue was cut for DNA extraction using the DNeasy Blood and Tissue Kit (Qiagen) and the SpeedTools Tissue DNA extraction Kit (Biotools), following the manufacturer's protocol. Molecular markers of cytochrome oxidase *c* subunit I (COI), 16S ribosomal RNA (16S), Histone H3 (H3), and 18S ribosomal RNA (18S) were amplified by polymerase chain reaction (PCR). The universal primers used were LCO1490 and HCO2198 for COI (Folmer et al., 1994), 16Sar-L and 16Sbr-H for 16S (Palumbi, 1996), H3AD5′3′ and H3BD5′3′ for H3 (Colgan et al., 1998), and B1 and INREV-RC for 18S (Hallas & Gosliner, 2015). PCR, amplification, and sequencing conditions performed at each institution are specified in the Supporting Information (Table S3). New molecular markers were deposited in GenBank (Table S1).

2.2.3. Extraction of molecular markers from UCEs data

Molecular markers of COI, 16S, H3, and 18S were extracted from UCE data using a BLAST database, with the makeblastdb tool (Cock et al., 2015). Query sequences of Goniodorididae taxa fetched from newly sequenced specimens were used for aligning to the UCEs assemblies, using blastn (Cock et al., 2015) with a cutoff of 1e-10, a 50 % of identical matches, a best-hit algorithm overhang of 0.25, and a best-hit algorithm score of 0.05. The top hit with the lowest e-value and the longest sequences were selected from the hits. Molecular markers obtained were deposited in GenBank (Table S1).

2.2.4. Phylogenetic analyses

Molecular markers were assembled and edited using SeqManII software (DNAStar Inc., Madison, WI, USA). All sequences were blasted in GenBank to check for contamination. Molecular markers were aligned with MAFFT v.7 (Katoh & Standley, 2013), with the L-INS-i iterative refinement algorithm for 16S and 18S and G-INS-I for COI and H3. Five different datasets were conducted to perform phylogenetic inference, one for each molecular marker (COI, 16S, H3, 18S) and one concatenated dataset with a minimum of two to all markers (and all possible combinations could include: COI + 16S + H3 + 18S; COI + 16S + H3; COI + 16S + 18S; COI + H3 + 18S; 16S + H3 + 18S; COI + 16S; COI + H3; COI + 18S; 16S + H3; 16S + 18S; H3 + 18S). JModelTest2 v 2.1.6 was used for evolutionary model selection under the Bayesian Information Criteria (BIC) (Schwarz, 1978) and ran in CIPRES Science Gateway (Miller, M.A., Pfeiffer, W., and Schwartz, T. (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA pp 1 - 8.). Evolutionary models for COI and H3 were selected for each codon position: TIM1 + G, TVM + I, and TIM2 + I + G for the 1st, 2nd, and 3rd codon positions of COI, and TIM2 + G, JC, and TPM2uf + G for the 1st, 2nd, and 3rd codon positions of H3. The evolutionary model TrN + I + G was selected for 16S and 18S. Bayesian inference (BI) was performed in MrBayes v. 3.2.7a, for ten million generations, four independent runs, a sampling frequency of 1000, and a burn-in of 25 %. Nodes with posterior probabilities (pp) $\geq$ 0.95 were considered supported (Alfaro et al., 2003). A maximum likelihood (ML) approach in RAxML-NG (Kozlov et al., 2019) was performed using the website https://raxml-ng.vital-it.ch/#/ with a bootstrapping cutoff of 0.03. Nodes were considered supported by bootstraps values (bs) $\geq$ 75 (Hillis & Bull, 1993). Trees obtained were visualized using FigTree v1.4.3 (Rambaut, 2009) and edited in Adobe Photoshop CC 2014. Unsupported nodes according to pp and bs were collapsed. Biogeographic areas indicated in the tree resulting from the

concatenated matrix were delimited following Kocsis et al. (2017).

2.2.5. Species delimitation tests

Species delimitation tests were carried out on COI to verify species identity. The Bayesian Poisson tree process (bPTP) (Zhang et al., 2013) was conducted by the web tool (https://species.h-its.org). The BI tree was used as input, running 200,000 MCMC generations, thinning = 100, and with a burn-in of 10 %. The assemble species by automatic partitioning (ASAP; Puillandre et al., 2021) was also conducted using the web tool (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html), and under the Kimura (K80) model, with a default ts/tv rate of 2.0, and a 0.05 threshold distance.

2.3. Ultra-Conserved elements

2.3.1. Taxon sampling

Target enrichment analyses included 46 taxa; 38 Goniodorididae species were newly sequenced, as well as five species of other nudibranchs (Table S2). UCEs of *Phyllidia elegans* Bergh, 1869, *Glossodoris acosti* S. B. Matsuda & Gosliner, 2018, and *Polycera hedgpethi* Er. Marcus, 1964 from the Sequence Read Archive (SRA) in the National Center of Biotechnology Information (NCBI) were also included (Table S2).

2.3.2. DNA extraction, library preparation, and sequencing

Genomic DNA was extracted at the UAM using SpeedTools Tissue DNA Extraction Kit (Biotools), and at the ZSM using the E.Z.N.A. mollusk extraction kit (Omega Bio-Tek, Doraville, USA). Both followed the manufacturer's protocols. Extractions were sent to Daicel Arbor Bioscience (MI, USA) for target capture sequencing using a myBaits® probe set (Moles & Giribet, 2021). Briefly, DNA was quantified via a spectrofluorimetric assay and sonicated to produce average inserts of 500 nt. Samples were size-selected to tighten the range of inserts and prepared into dual-indexed Illumina-compatible libraries using A-tailed chemistry. The indexed libraries were quantified with a spectrofluorimetric assay. Capture pools were prepared from up to 200 ng 8–10 libraries per reaction, each capture pool was dried down to 7 μL by vacuum centrifugation. Captures were performed following the myBaits v 5.02 protocol using design REF# 190513–91 (Moles & Giribet, 2021) with an overnight hybridization and wash at 65 °C. Post-capture, half of the volume of the reactions was amplified for 10 cycles and was quantified again with a spectrofluorimetric assay. For captures that did not generate enough material, the second half of the reaction volume was amplified for 12 cycles. Captures were visualized via Bioanalyzer, and dimers were removed from captures that contained it via gel excision. The captures were pooled in two pools at approximately equimolar ratios. Samples were sequenced on the Illumina NovaSeq 6000 platform on partial lanes to approximately 0.6 Gbps of data per sample.

2.3.3. Species assembly and matrix construction

Phyluce v. 1.7.1 (Faircloth, 2016) was used for processing the raw data, alignment cleaning, and preparation of data matrices. Raw reads were demultiplexed per individual and adapter contamination and low-quality bases were trimmed using Trimmomatic v.0.39 (Bolger et al., 2014) implemented in Illumiprocessor v.2.0.9 (Faircloth, 2013). Clean reads were assembled using SPAdes v.3.12 (Bankevich et al., 2012) and duplicates were removed for each assembly using CD-HIT using the default sequence identity threshold -c 0.9 (Li & Godzik, 2006). Contigs were matched to the probe set (Moles & Giribet, 2021), and targeted UCEs loci were captured, extracting the individual FASTA files for the UCEs loci in each taxon. Targeted loci were aligned using MAFFT-auto v.7.455 (Katoh & Standley, 2013) and masked with Gblocks v.0.91 (Castresana, 2000), under the arguments –b1 0.5 –b2 0.5 –b3 10 –b4 4. The final matrix contained 50 % of locus completeness.

2.3.4. Phylogenetic analyses

ML analysis was performed using RAxM-NG (Kozlov et al., 2019), the data set was analyzed as a single partition under the GTR + G model, and a default boot-stopping criterion of 0.03. BI was performed using Exa-Bayes v. 1.5 (Aberer et al., 2014) using the GTR + G model. This was run for one million generations, with four separate runs, each run with one cold and one hot chain, 500-generation sampling frequency, and a 25 % burn-in. Runs were considered successful when the default average standard deviation of split frequencies (ASDSF) reached < 5 %. Trees obtained were visualized using FigTree v1.4.3 (Rambaut, 2009) and edited in Adobe Photoshop CC 2014.

3. Results

The final UCE-based matrix of 50 % locus completeness included 1,222 loci in a final alignment with an average length of 411,037 pb, containing 256,204 informative sites. The contig length range covered from a minimum of 166 pb to a maximum of 908 pb, and the mean contig size per UCE was 336 ± 5 pb. Character summary counted 12,253,231 nucleotides within the matrix, which included 13,539,972 total characters. The concatenated Sanger-based dataset contained 2,173 bp, with 753 parsimony informative sites. Both concatenated UCE-based (Fig. 1) and concatenated Sanger-based (Fig. 2) results successfully supported evolutionary relationships among subfamilies, genera, and species of Goniodorididae.

Phylogenetic analyses using both UCE-based and concatenated Sanger-based datasets highly supported the monophyly of the family Goniodorididae (Sanger pp = 1) (Fig. 1-Fig. 2). Trees of the individual molecular markers COI, 16S, and H3 were included in the Supplementary Material (Figs. S1–S3). UCE-based and concatenated Sanger-based datasets analyses recovered two main clades (Fig. 1-Fig. 2). To improve the clarity of the results, we have named the major clades the same way in Figs. 1 and 2, so that each clade includes the same taxa in both figures. The first clade included *Ancula* Lovén, 1846 (Clade A) and *Trapania* (Clade B) as sister genera, while the second clade included nine groups. Within the latter, *Goniodoridella* (Clade C) appeared as the sister group to all the remaining taxa (Fig. 1-Fig. 2). UCE-based grouped Clade D + Clade E (Fig. 1), and another clade including *Pelagella* (Clade F) as sister to Clade G + *Lophodoris* G. O. Sars, 1878 + Clade H (Fig. 1). Sanger-based analyses recovered Clade I grouping species not included in UCE-based analyses (see the Systematic Section below; Fig. 2). The type species *Okenia elegans* (Leuckart, 1828) and the type species *Goniodoris nodosa* (Montagu, 1808) appeared in the same clade using both UCE-based and Sanger-based results.

Clade A – Included the genus *Ancula* as monophyletic (Sanger pp = 0.99, bs = 75) (Fig. 1-Fig. 2). *Ancula lentiginosa* Farmer, 1964 appeared as sister species to *A. gibbosa* + *A. pacifica* MacFarland, 1905 (Fig. 1). In the Sanger-based dataset, *A. kariyana* Baba, 1990 and *Ancula* sp. A were also included in this clade; and *Ancula* sp. A, *A. pacifica*, and *A. gibbosa* clustered with high support, recovering the last two in a clade as sister species (Fig. 2).

Clade B. - The monophyly of the genus *Trapania* was well supported (Sanger pp = 1, bs = 96) (Fig. 1-Fig. 2). Concatenated Sanger-based analyses of *Trapania* recovered four clades. Relationships between species agreed with the results obtained by Smirnoff et al. (2022) with the addition of the newly sequenced *T. toddi* Rudman, 1987 clustering with *T. euryeia* Gosliner & Fahey, 2008, *T. kanaloa* Smirnoff, Donohoo & Gosliner, 2022, *T. undulata* Smirnoff, Donohoo & Gosliner, 2022 and *T. gibbera* Gosliner & Fahey, 2008. In UCE-based analyses, *T. aurata* joined with *T. vitta*. These species were recovered in a clade with *T. scurra* Gosliner & Fahey, 2008 + *T. miltabrancha* Gosliner & Fahey, 2008 + *T. maculata* Haefelfinger, 1960 + *T. orteai* García-Gómez & Cervera, 1989 + *T. lineata* Haefelfinger, 1960 (Fig. 1-Fig. 2). Species *T. goddardi* Hermosillo & Á. Valdés and *T. velox* (Cockerell, 1901) clustered with species from the East-Atlantic and Mediterranean region, within which *T. maculata* were grouped with *T. orteai* + *T. lineata* + *T. sanctipetrensis* Cervera, García-Gómez & Megina, 2000 + *T. cirrita* Gosliner & Fahey, 2008 (Fig. 2). Sanger-based results of each molecular
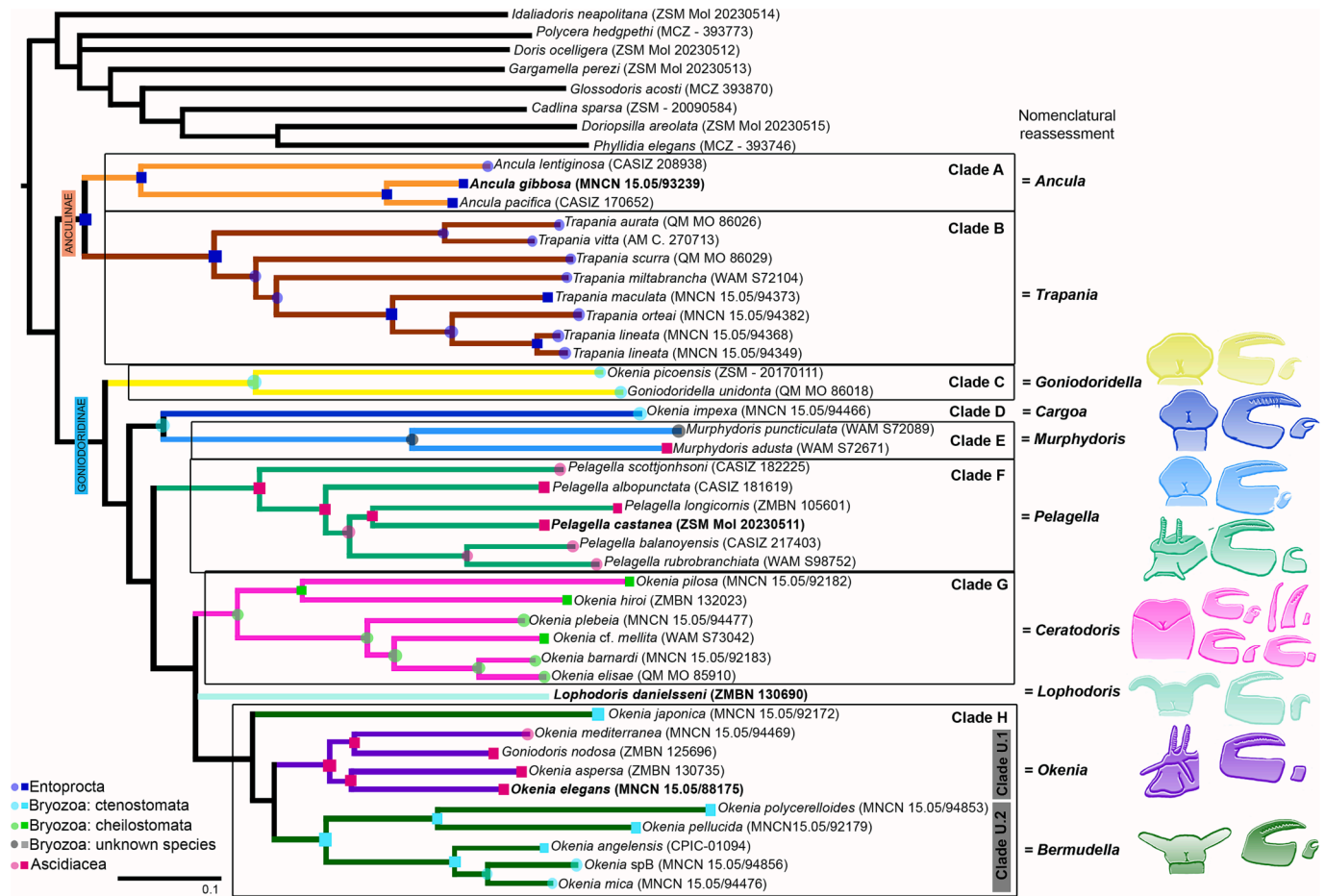
Fig. 1. Tree build based on BI, phylogenetic relationships of the family Goniodorididae based on 2141 UCE loci. Branches are highly supported with bs = 1 and pp = 100. Colored branches represent different genera, including the subfamily Anculinae with *Ancula* (Clade A, orange) and *Trapania* (Clade B, brown); and the subfamily Goniodorinae with *Goniodoridella* (Clade C, yellow); *Cargoa* (Clade D, dark blue); *Murphydoris* (Clade E, light blue); *Pelagella* (Clade F, light green); *Ceratodoris* (Clade G, pink); *Lophodoris* (blue greenish); *Okenia* (Clade U1, purple), and *Bermudella* (Clade U2, dark green). Colored drawings from left to right represent the oral tentacles, the marginal and lateral teeth of the genera. Type species of the genera after nomenclatural reassessment are shown in bold. Prey preference marked with a square refers to a diet; prey preference marked with a circle refers to an expected diet based on genera or where the species has been found. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

marker separately and for the concatenated alignment revealed that *T. darvelli* and *T. reticulata* are the same species (Fig. 2, S1–S3).

Clade C. – Clustered species of *Goniodoridella* + *Okenia picoensis* Paz-Sedano, Ortigosa & Pola, 2017 and *Okenia felis* Gosliner, 2010 (Fig. 1-Fig. 2). *Okenia felis* formed a clade with *O. picoensis*, and *G. borealis* clustered with *Goniodoridella* sp. A, *G. savignyi*, and *G. geminae* Paz-Sedano, Ekimova, Smirnoff, Gosliner, Pola, 2023 (Fig. 2).

Clade D. - Recovered a well-supported clade including *Okenia impexa* Er. Marcus, 1957 and *O. problematica* Pola, Paz-Sedano, Macali, Minchin, Marchini, Vitale, Licchelli & Crocetta, 2019 (Fig. 2).

Clade E. – Included the monophyletic genus *Murphydoris* (Fig. 1-Fig. 2). Results showed three main clades within Clade E: the first clade included undescribed species *Murphydoris* sp. E, sp. F, and sp. G (Sanger pp = 0.98, bs = 94); the second clade related *Murphydoris* sp. B and *Murphydoris* sp. C as sister species; the last clade clustered the sister species *Murphydoris* sp. D and *M. adusta* Paz-Sedano, Smirnoff, Candás, Gosliner & Pola, 2022, with the second group of sister species *M. puncticulata* Paz-Sedano, Smirnoff, Candás, Gosliner & Pola, 2022, and *M. cobbi* Paz-Sedano, Smirnoff, Candás, Gosliner & Pola, 2022 (Sanger pp = 0.97) (Fig. 2).

Clade F. – Results of both analyses clustered all *Pelagella* species in a well-supported clade (Fig. 1-Fig. 2). A first clade showed the species *P. scottjohnsoni* Paz-Sedano, Smirnoff, Gosliner & Pola, 2023 and *P. joubini* (Risbec, 1928) as sister species (Fig. 2). A second clade which

included the remaining *Pelagella* species (Fig. 1), within which *P. albopunctata* Paz-Sedano, Smirnoff, Gosliner & Pola, 2023 clustered with a third clade including *P. longicornis* Paz-Sedano, Smirnoff, Gosliner & Pola, 2023 + *P. castanea* (Alder & Hancock, 1845) and *P. balanoyensis* Paz-Sedano, Smirnoff, Gosliner & Pola, 2023 + *P. rubrobranchiata* Paz-Sedano, Smirnoff, Gosliner & Pola, 2023.

Clade G. – This group included *Okenia* species (Sanger pp = 1, bs = 89) (Fig. 1-Fig. 2). We recovered two main clades: the first one gathered species *Okenia* sp. D, *O. pilosa* (Bouchet & Ortea, 1983), and *O. plana* (Baba, 1960) (Sanger pp = 1, bs = 95) (Fig. 2). Also, the first clade included a second group with the species *O. atkinsonorum* Rudman, 2007 + *O. rosacea* (MacFarland, 1905) + *O. hallucigenia* Rudman, 2004 + *C. hiroi* (Baba, 1938). The second clade recovered *O. plebeia* (Bergh, 1902) as sister to a clade including *O.* cf. *mellita* Rudman, 2004 + *O. tenuifibrata* Paz-Sedano & Pola, 2021 + *O. barnardi* Baba, 1937 + *O. elisae* Paz-Sedano & Pola, 2021 + *O. kendi* Gosliner, 2004 (Fig. 1-Fig. 2).

Clade H. – UCE-based results divided Clade H into two clades (Clade U.1 and Clade U.2) + *O. japonica* Baba, 1949 (Fig. 1), while Sanger-based results divided Clade H into four clades (Clade S.1., Clade S.2, Clade S.3 and Clade S.4) + *O. japonica* + *O. rhinorma* (Fig. 2). UCE-based results showed two clades within Clade U.1, one clustered the species *O. mediterranea* + *Goniodoris nodosa*; the second clustered *O. aspersa* + *O. elegans*. The concatenated Sanger-based dataset included more taxa.
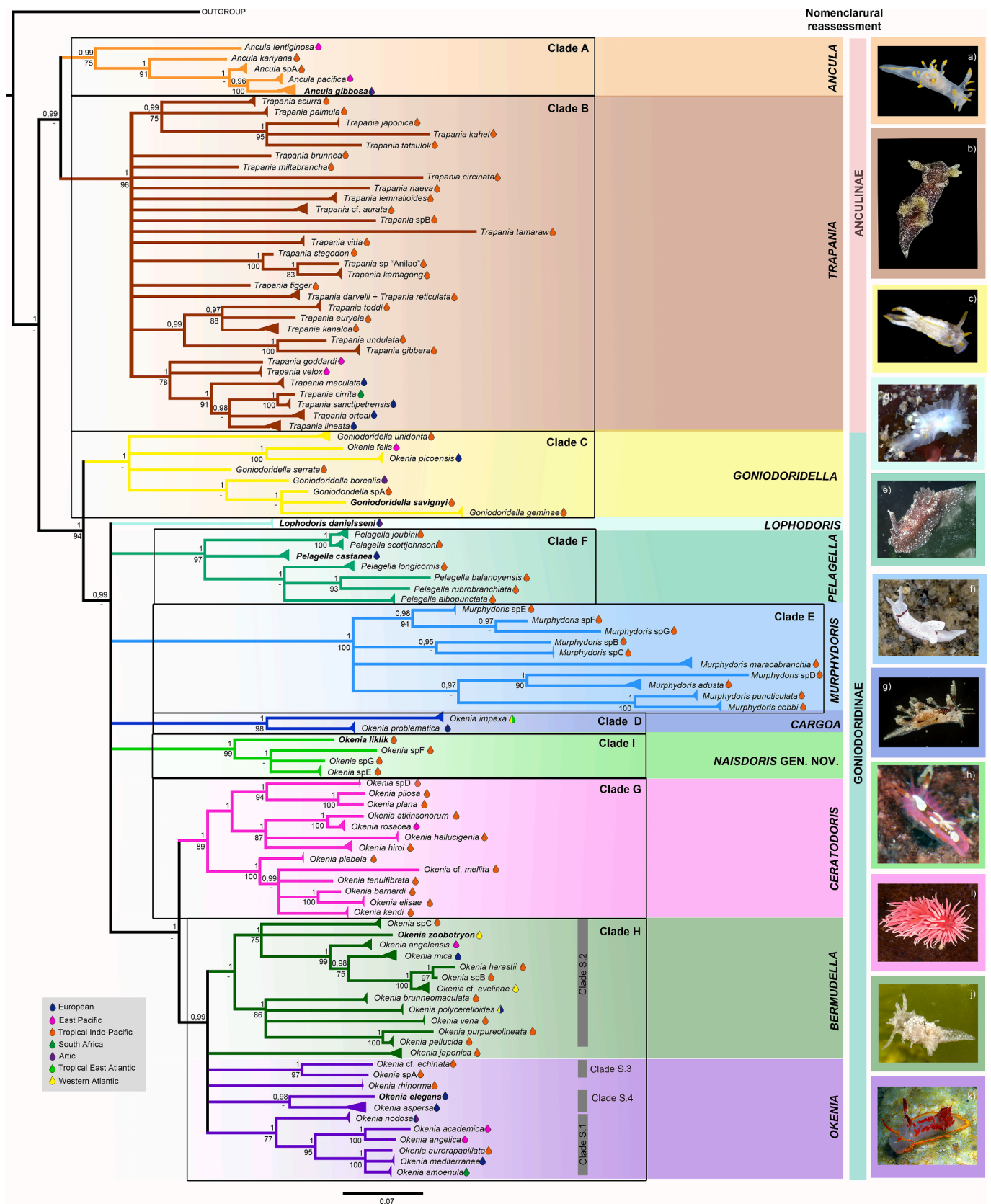
Fig. 2. Phylogenetic relationships (BI/ML) based on the concatenated mitochondrial (COI and 16S) and nuclear (H3 and 18S) molecular markers. Tree build based on BI (bb = above branches; pp = below branches). Colored branches and blocks represent different genera written on the right side, including live pictures of key species. A, *Ancula gibbosa* (photo by Cessa Rauch); B, *Trapania graeffei* (photo by Jose Francisco Martin); C, *Goniodoridella savignyi* (photo by Gary Cobb); D, *Lophodoris danielsseni* (photo by Cessa Rauch); E, *Pelagella castanea* (photo by Patric Van Moer); F, *Murphydoris cobbi* (photo by Gary Cobb); G, *Cargoa impexa* (photo by L. Moro); H, *Naisdoris liklik* (photo by P.J. Aristorenas); I, *Ceratodoris rosacea* (photo by Kristen Roberts); J, *Bermudella zoobotryon* (photo by Marta Pola); K. *Okenia elegans* (photo by Josep Lluis Peralta). Type species of the genera after nomenclatural reassessment in bold.

Clade S1 clustered *Goniodoris nodosa* with the Atlantic and Pacific species *O. academica* Camacho-García & Gosliner, 2004 + *O. angelica* Gosliner & Bertsch, 2004 and *O. aurorapapillata* Paz-Sedano & Pola, 2021 + *O. mediterranea* (Ihering, 1886) + *O. amoenula* (Bergh, 1907). Cluster S.4 recovered a clade with the European *O. elegans* + *O. aspersa* (Alder & Hancock, 1845) as the sister species (Fig. 2).

Clade 2 was recovered in both UCE-based (Clade U.2) and Sanger-based (Clade S.2) analyses (Fig. 1-Fig. 2). Fig. 2 showed a Clade S.2 clustering *Okenia* sp. C + *O. zoobotryon* (Smallwood, 1910) + a clade grouping *B. angelensis* Lance, 1966 + *O. mica* Ortea & Moro, 2014 + *O. harastii* Pola, Roldán & Padilla, 2014 + *Okenia* sp. B, + *O.* cf. *evelinae* Er. Marcus, 1957 (Sanger pp = 1, bs = 99; Fig. 2). The second main clade within Clade S.2 included *O. brunneomaculata* Gosliner, 2004, *O. polycerelloides* (Ortea & Bouchet, 1983), *O. vena* Rudman, 2004, *O. pellucida* Burn, 1967, and *O. purpureolineata* Gosliner, 2004. The latter taxa related as sister species with full support (Fig. 2). In addition, all our phylogenetic analyses, as well as species delimitation tests, showed *O. longiductis* Pola, Paz-Sedano, Macali, Minchin, Marchini, Vitale, Licchelli & Crocetta, 2019 and *O. polycerelloides* as the same species, and thus, *B. longiductis* is synonym of *O. polycerelloides* (Fig. 2, S1–S3).

The species *O. japonica* does not group into any of the clades. However, this species clustered with *Okenia* sp. C in the phylogenetic results for 16S (Fig. S2), which is included in Clade S.2 (Fig. 2). Also, it is recovered in a well-supported clade together with *Okenia* species included in Clade 2 (Clade U.2 and Clade S.2) in the phylogenetic results for H3 (Fig. S3).

Okenia rhinorma Rudman, 2007 did not group into any clade with other *Okenia* species. Concatenated Sanger-based results (Fig. 2) showed a Clade S.3, including the tropical Indo-Pacific *O.* cf. *echinata* Baba, 1949 + *Okenia* sp. A.

Clade I. – Clade I encompassed a well-supported clade that included three undescribed species + *O. liklik* Gosliner, 2004 (Fig. 2) (see systematic details in the Discussion section).

4. Discussion

The Heterobranchia probe set originally targeted Tectipleura heterobranchs (Moles & Giribet, 2021) was successful in inferring phylogenetic relationships within a family of Nudibranchia, one of the most distantly related groups with Tectipleura. UCEs have proven to resolve long-lasting questions about the intergeneric relationships of Goniodorididae, by providing enough resolution at the backbone of the phylogeny. Our results strongly support the monophyly of the family. Moreover, the division of Goniodorididae is backed up by previous studies that proposed the division into two subfamilies based on morphological features (Pruvot-Fol, 1954; Franc, 1968). These are Anculinae Pruvot-Fol, 1954 (*Ancula* and *Trapania*) and Goniodoridinae H. Adams & A. Adams, 1854 (including all the remaining taxa). Although specimens of *Spahria* Risbec, 1928 were not available for the present study, they would be expected to join within Anculinae. Regarding the genera, the obtained results recovered 10 well-supported clades and, integrating them with morphological data, represent relevant changes in the systematics of the family Goniodorididae.

4.1. Intrageneric systematics of Goniodorididae

Subfamily Anculinae Pruvot-Fol, 1954.

Diagnosis: Body slender, without frontal veil or notal edge; appendages at base of rhinophores and gills; gill branches tripinnate. Radular formula N × 1.1.1.1.1, 1.1.0.1.1 or 1.0.1, buccal bulb present (Pruvot-Fol, 1954).

Remarks: Specimens of *Spahria* were not found for the present study. However, if *Spahria* were a member of the Anculinae, the subfamily could have or lack appendages around the gills and the radula formula could also be N × 2.1.0.1.2 (Risbec, 1928).

Ancula Lovén, 1846.

Drepaniella Burn, 1961.

Eucrairia Burn, 1961.

Miranda Alder & Hancock, 1847.

Type species: *Tritonia gibbosa / Ancula gibbosa* (Risso, 1818); 371–372 pp. (by monotypy).

Clade A corresponded to the genus *Ancula*. *Ancula* includes eight species (MolluscaBase, 2023b). *Ancula* species share the characteristics of Anculinae, having a radular formula of N × 1.1.0.1.1 or N × 1.1.1.1.1, masticatory margin of lateral teeth is denticulated and marginal teeth smooth (Burn, 1961; Thompson & Brown, 1984). Although species of *Ancula* have been reported feeding on bryozoa, hydrozoa, and tunicates (McDonald & Nybakken, 1997), other authors have reported *Ancula* feeding on entoprocts (McDonald and Nybakken, 1978; Nybakken and McDonald, 1981; Goddard, 1984; Parera et al., 2020; Behrens et al., 2022). It seems that *Ancula* feeds on the entoprocts that grow in bryozoans, hydrozoans, and tunicate colonies (Parera et al., 2020). This genus is widely distributed from the Indo-Pacific and Atlantic Oceans and the cold waters of the North Sea.

Trapania Pruvot-Fol, 1931.

Drepania Lafont, 1874.

Drepanida MacFarland, 1931.

Type species: *Drepania fusca / Trapania fusca* (Lafont, 1874): 369–370 pp. (by monotypy).

Clade B corresponded to the genus *Trapania*. *Trapania* shares the characteristics of Anculinae, with a pair of curved extra-rhinophoral and extra-branchial appendages, and one lateral tooth. Regarding the trophic specialization of *Trapania* species, many are found on sponges and some on gorgonians, feeding on the associated Entoprocta (Pruvot-Fol, 1931; Sánchez-Tocino & Cervera, 2006; Yonow, 2015; Trainito et al., 2018). Species of *Trapania* have been reported worldwide.

The monophyly of the genus has been well-supported by previous phylogenetic analyses (Gosliner & Fahey, 2008; Smirnoff et al., 2022; Paz-Sedano et al., 2022b) as well as by our results. In the present analyses, the species *T. darvelli* and *T. reticulata* were revealed to be the same species (Figs. S1-S3). Smirnoff et al. (2022) supported *T. darvelli* and *T. reticulata* as different species by ABGD species delimitation analyses of 16S. However, our 16S phylogenetic tree as well as bPTP and ASAP species delimitation analyses of COI appeared to be incongruent with Smirnoff et al. (2022). Moreover, ABGD is an analysis based on pairwise distances (Puillandre et al., 2012) but the distances within the non-coding 16S matrix may change when aligning different datasets, which may contain variable gaps. Further morphological detailed studies are needed to clarify the possible synonymy of *T. darvelli* and *T. reticulata*.

Subfamily Goniodoridinae H. Adams & A. Adams, 1854.

Diagnosis: mantle margin developed, often wide; lateral and dorsal papillae often present with diverse morphology. Radular formula N × 1.1.0.1.1 or 1.0.1. Lateral teeth usually with a robust cusp with a masticatory margin and a wide base. Marginal teeth commonly small. Shape of body and oral tentacles, denticulation of lateral teeth, and shape of marginal teeth are taxonomical characteristics for different genera.

Bermudella Odhner, 1941.

Type species: *Polycerella zoobotryon / Bermudella zoobotryon* (Smallwood, 1910): 143–145 pp. Figure 10. (by monotypy).

Clade H corresponded to the genus *Bermudella,* which was previously synonymized with *Okenia.* The type species is *B. zoobotryon*, included in the well-supported Clade 2. The genus *Bermudella* was erected by Odhner (1941) to separate the species *Polycera zoobotryon* based on the presence of a buccal bulb and the shape of the teeth, which was similar to Goniodorididae. *Bermudella* species have simple, short, and digitiform papillae, homogenously distributed along the sides of the body. Also, few dorsal papillae with similar shape to lateral ones are present, sparse lamellae in rhinophores, and digitiform oral tentacles. Radular formula N × 1.1.0.1.1, lateral teeth with a denticulated masticatory margin. Relatively short, wide, and triangular denticles along the margin.

Marginal teeth with two prominent cusps. A previous morphological assessment also clustered *B. brunneomaculata, B. angelensis, B. pellucida*, and *B. zoobotryon* based on the similarities between the oral tentacles and the sparse rhinophoral lamellae (Gosliner, 2004). Rudman (2004) grouped the *Bermudella* species based on the feeding source: ctenostome bryozoans (i.e., species of *Amathia* Lamouroux, 1812).

Among other species not included in the molecular analyses, *O. mija* Burn, 1967, *O. purpurata* Rudman, 2004, *O. distincta* Baba, 1940, and *O. siderata* Paz-Sedano & Pola, 2021 share the same *Bermudella* features. Thus, we suggest transferring these species to *Bermudella* until new material is sequenced. Considering all species, the genus is distributed from Tropical Indo-Pacific to Western Atlantic and European waters.

Bermudella species clustered together in all results, except for *B. japonica* (Baba, 1949), which appeared related to *Okenia* and *Bermudella* but without a clear phylogenetic position. This separation could be interpreted in several ways: *i)* species of *Okenia* and *Bermudella* belong to the same genus, *Okenia* having priority, or *ii)* *B. japonica* belongs to a different genus that requires a formal description. However, despite the support of the UCE-based analysis, many species of Goniodorididae are still missing from the phylogeny and these results could vary due to an incomplete taxon sampling. Morphologically, *B. japonica* matches with *Bermudella*. In addition, trees resulting from the analyses of the H3 and 16S molecular markers separately clustered *B. japonica* with the rest of the *Bermudella* species with high support (Figs. S2-S3). To keep the most parsimonious option and make the least number of nomenclatural changes possible, we have decided to maintain *B. japonica* as *Bermudella*, in a still unresolved polytomy including *Bermudella* and *Okenia*.

Cargoa Vogel & L. P. Schultz, 1970.

Type species: *Cargoa cupella* Vogel & L. P. Schultz, 1970: 388–392 pp. Fig. 1-5. (by monotypy).

Clade D corresponded to the genus *Cargoa*. The type species is *C. cupella*, not included in the analyses. However, the species *C. impexa* and *C. problematica* share the morphological characteristics of this genus, being representatives of *Cargoa* in our phylogeny. *Cargoa* share the presence of four thin, linear papillae located in front of rhinophores. One or two additional linear papillae may be present, followed by clavated papillae, with swollen tips, which become larger towards the posterior part. One dorsal papilla with the same shape as laterals (Marcus, 1957; Vogel & Schultz, 1970; Pola et al., 2019). *Cargoa* species share a dark brown color and have small radulae with around ten rows of teeth (no more than 20). Lateral teeth with few, thin, and pointed denticles in masticatory margin, increasing in size from inner to outer side. External teeth with two well-developed cusps (Marcus, 1957; Vogel & Schultz, 1970; Pola et al., 2019). Even though there is no clear evidence of the prey preference of the species, these mollusks may feed on ctenostome bryozoans where they have been found wandering (Marcus, 1957; Valdés & Ortea, 1995; Sales et al., 2016; Pola et al., 2019), including species of *Amathia* (Sales et al., 2016), *Margaretta* (Templado, 1982; Pola et al., 2019), and *Anguinella* (Rudman, 2004).

The species *Okenia ghanensis* Edmunds, 2009 shares the morphological characteristics with the three species studied herein, with posterior papillae swollen distally (Edmunds, 2009). Therefore, we suggest transferring this species to *Cargoa*. Species of *Cargoa* are found on both coasts of the Atlantic Ocean and in the Mediterranean Sea.

Ceratodoris Gray, 1850.
Echinodoris Bergh, 1874.
Hopkinsia MacFarland, 1905.
Hopkinsiella Baba, 1938.
Teshia Edmunds, 1966.
Sakishimaia Hamatani, 2001.

Type species: *Ceratodoris eolida* Quoy & Gaimard, 1832: 263–264; plate 18. Figures 11–15. (by monotypy).

Clade G corresponded to the recovered genus *Ceratodoris*, a former synonym of *Okenia*. The type species *C. eolida* was not available for phylogenetic analyses. However, it highly resembles *C. pilosa* and

C. plana, species expected to cluster with. The diagnostic characteristics of *Ceratodoris* are well described by Gray (1850), MacFarland (1905), and Hamatani (2001). The body shape is characteristic, broad, and flattened, with oral tentacles merged with the foot (Rudman, 2004). *Ceratodoris* species often feed on encrusting cheilostome bryozoans (Rudman, 2004).

According to the features of this genus, species not included in the phylogenetic analyses but that may be transferred to *Ceratodoris* are *O. africana* Edmunds, 2009, *O. digitata* (Edmunds, 1966), *O. kondoi* (Hamatani, 2001), *O. lambat* (Gosliner, 2004), *O. nakamotoensis*, *O. nakanoae* Paz-Sedano & Pola, 2021, *O. sapelona* Ev. Marcus & Er. Marcus, 1967, *O. stellata* Rudman, 2004, *O. vancouverensis* (O'Donogue, 1921) and *O. virginiae* Gosliner, 2004. *Ceratodoris* species are more abundant in the Indo-Pacific Ocean, with only a few species distributed in the Atlantic.

Goniodoridella Pruvot-Fol, 1933.

Type species: *Goniodoridella savignyi* Pruvot-Fol, 1933: 117–118; Pl. II. Figures 23–26. (by monotypy).

Clade C corresponded to the genus *Goniodoridella*, grouping different taxonomic taxa into a well-supported clade with the type species *G. savignyi*. The inclusion of *G. picoensis* and *G. felis* within *Goniodoridella* in our results redefines some morphological characteristics of the genus, now with smooth or lamellated rhinophores and serrated or papillate notal edges. Anteriormost papillae conical and posteriormost are commonly the longest and widest (Gosliner, 2010; Paz-Sedano et al., 2017, 2022c, 2023b). Gill branches are thin and simple and grouped in three stalks, one in the middorsal part and one on each side. Each stalk may have one or two-gill branches. Radula may have one lateral tooth or two teeth, one lateral and one marginal. The lateral teeth with denticulated masticatory margins, and denticles are usually small and thin, with the same shape along the margin. When present, a marginal tooth with a single hooked cusp (Gosliner, 2010; Paz-Sedano et al., 2017, 2022c, 2023b). The prey preference of *Goniodoridella* is unknown, although it may be ctenostome bryozoans where the species have been found (Gosliner, 2010).

Regarding other *Okenia* species not included in the molecular analyses, the external and internal characteristics of the species *O. miramarae* Ortea & Espinosa, 2000, *O. cochimi* Gosliner & Bertsch, 2004, and *O. mexicorum* Gosliner & Bertsch, 2004 are closer to *Goniodoridella* than to *Okenia* (Ortea & Espinosa, 2000; Gosliner & Bertsch, 2004). Thus, these species should be tentatively transferred to *Goniodoridella*. *Goniodoridella* species are distributed in the western Pacific and Atlantic Oceans, the Caribbean, and the Mediterranean Seas (Ortea & Espinosa, 2000; Gosliner & Bertsch, 2004; Gosliner, 2010; Paz-Sedano et al., 2017; Trainito et al., 2022).

Murphydoris Sigurdsson, 1991.

Type species: *Murphydoris singaporensis* Sigurdsson, 1991: 260–261 pp. Fig. 1. (by monotypy).

Clade E corresponded to the genus *Murphydoris*, recently reviewed (Paz-Sedano et al., 2022a, 2022c). All the species are known from tropical Indo-Pacific waters. Results obtained agreed with previous studies where the monophyly of the genus was well supported (Paz-Sedano et al., 2022a). *Murphydoris* species have been reported to feed on bryozoans (Sigurdsson, 1991; Swennen & Buatip, 2012) while only *M. adusta* fed on colonial tunicates (Gosliner et al., 2018). Currently, the genus has been only reported with a Tropical Indo-Pacific distribution.

Naisdoris gen. nov.

Zoobank:urn:lsid:zoobank.org:act:A904A4CC-0820-430D-913A-CA06678C485F.

Type species: *Okenia liklik* Gosliner, 2004: 141–143; Fig. 1G, 16, 17 (original designation) (the material is deposited at the California Academy of Sciences; Holotype: CASIZ 168021; Paratypes: CASIZ 168022, CASIZ 168023).

Etymology: name formed by apposition following the etymology of the specific name of the type species, *Nais* derives from Papuan Pidgin meaning 'beauty' and *doris* refers to the common name used for

Doridina.

Diagnosis: The new genus shares intermediate characteristics between *Goniodoridella* and *Lophodoris*. Body elongated with reduced mantle margin, this being serrated and conformed by pointed spicules, and small middorsal, serrated crest. Regarding papillae, two thin elongated ones in front of rhinophores, margins with small ones, and the posterior part with well-developed papillae. Rhinophores lamellated. Gill branches are simple, forming a semicircle around the anus. Oral tentacles are modified as musculature around the mouth. Radular formula N × 1.1.0.1.1, the lateral tooth with small thin denticles at the masticatory margin. The diet is unknown. The species of *Naisdoris* gen nov. are exclusively found in the Indo-Pacific so far (Gosliner, 2004).

Clade I showed a well-supported clade different from any other previously described within *Okenia*, here named *Naisdoris* gen. nov. The genus currently includes the type species *N. liklik* and the undescribed *Naisdoris* sp. E, *Naisdoris* sp. F, and *Naisdoris* sp. G.

Okenia Menke, 1830.

Idalia Leuckart, 1828

Idaliella Bergh, 1881.
Idalina Norman, 1890.
Goniodoris Forbes & Goodsir, 1839.

Type species: *Okenia elegans* Leuckart, 1828: 15 pp. Fig. 2a, b. (by monotypy).

Clade 2 within Clade H included the type species *Okenia elegans* in a well-supported clade. *Okenia* species share the presence of a more developed mantle margin compared to other Goniodoridinae genera, except *Pelagella*. The mantle may have wide, lateral papillae. The most resolved clades share the absence (*O. nodosa* + *O. academica* + *O. angelica* + *O. mediterranea* + *O amoenula*) or presence (*O. elegans* + *O. aspersa*) of a few dorsal papillae (Camacho-García and Gosliner, 2004; Paz-Sedano et al., 2021a). Foot wide and oral tentacles veil-shaped. Gill is formed by multiple tripinnate branches forming a circle around the anus. Rhinophores are long, elongated, and with numerous lamellae. The lateral tooth with small, uniform denticles on the masticatory margin. Marginal teeth are usually flattened, without cusps (Camacho-García & Gosliner, 2004; Gosliner & Bertsch, 2004) or with a small one (Paz-Sedano et al., 2021a). Labial cuticle with jaw elements (Camacho-García & Gosliner, 2004; Gosliner & Bertsch, 2004; Paz-Sedano et al., 2021a). *Okenia* species have previously been grouped due to their dietary habits, feeding on tunicates rather than bryozoans (Gosliner, 2004; Rudman, 2004). Other species not included in the molecular analyses, but sharing morphological characters are *O. hispanica*, Á. Valdés & Ortea, 1995, *O. leachii* (Alder & Hancock, 1854), *O. opuntia* Baba, 1960, *O. ascidicola* M.P. Morse, 1972, *O. luna* Millen, Schrödl, Vargas & Indacochea, 1994, and *O. ameliae* Ortea, Moro & Caballer, 2014. *Okenia* species have a worldwide distribution, from Arctic waters to South Africa, from the Indo-Pacific to the Atlantic Ocean.

Okenia and *Goniodoris* type species were grouped together in our phylogenetic results. These results suggest that *G. nodosa*, and therefore the genus *Goniodoris*, should be synonymized with the older genus, i.e., *Okenia*. However, the morphology of the remaining species of *Goniodoris* not represented in our molecular analyses matches better with *Pelagella*, a genus that already includes species previously assigned to *Goniodoris* (Paz-Sedano et al., 2023a). Thus, we tentatively transferred species of *Goniodoris* to *Pelagella*, except for *Okenia nodosa*, until more species are sequenced.

The genera *Lophodoris* and *Pelagella* were also included in Goniodoridinae, and they were well supported as monophyletic in both Sanger-based and UCE-based analyses. The interspecific relationships agree with previous studies, which describe well the characteristics of the genera (Paz-Sedano et al., 2021b, 2023a). Therefore, we prefer not to repeatedly comment on the results of this genus.

4.2. Prey preference as an evolutionary driver

Diet specialization has been proposed as the driving force in the evolution of sea slugs (Thompson, 1976; Mikkelsen, 2002), particularly in nudibranchs, which are specialists in feeding on one or a few host species (Ekimova et al., 2019). Prey preference can lead to reproductive barriers between populations, and the shift of this preference by specialized taxa could drive their diversification, leading to host-related adaptative radiations (Ekimova et al., 2019). Although this diet specialization is well known, the impact of prey on the evolution of nudibranchs has been scarcely studied due to poorly resolved phylogenies, or a lack of knowledge about the natural history of the species. The influence of the shift towards alternative food sources has been evidenced by phylogenetic analyses in a few lineages within Cladobranchia (Goodheart et al., 2017; Ekimova et al., 2019).

Our phylogenetic results shed light on the radiation of lineages in Goniodorididae correlated to prey preference, and this driver could have led to a particular radular, body shape, and color patterns. For instance, species of Anculinae are reported to feed on entoprocts and share an elongated body shape, with strong jaws and large denticles on the lateral radular teeth. Entoproct feeders graze the calyxes of the prey, and the strong jaws are used to break the exoskeletons (Canning & Carlton, 2000). Entoprocts are usually epibionts of other typically arborescent organisms, such as bryozoans, hydroids, ascidians, gorgonians, or sponges, where *Ancula* and *Trapania* species may be found (Parera et al., 2020; Sánchez-Tocino and Cervera, 2006; Trainito et al., 2018). Nudibranch species with erect arborescent hosts have an elongated shape, with a long narrow foot adapted for clinging to the prey (Thompson, 1976), a common pattern seen in Anculinae species.

Goniodoridinae includes taxa that feed on ascidians and bryozoans. The bryozoans may lack (ctenostome) or possess (cheilostome) mineralized skeleton (Rudman, 2004; Waeschenbach et al., 2012). While *Ceratodoris* species feed on cheilostomes, *Bermudella* and *Cargoa* feed on ctenostomes. Other Goniodoridinae genera found in ctenostome bryozoans, whose predator–prey relationships are unconfirmed are *Goniodoridella, Lophodoris,* and *Murphydoris*, except for *M. adusta*, reported feeding on tunicates (Gosliner et al., 2018). Ascidian feeders include *Okenia* and *Pelagella*. Nudibranch species that feed on ctenostomata bryozoans or ascidians share similar radular morphology, with a common pattern within the superfamily Onchidoridoidea (Nybakken & McDonald, 1981). These taxa have small marginal teeth, and large enlarged lateral teeth, and lack rachidian teeth (Nybakken & McDonald, 1981). The differences between genera can be appreciated in the denticulation of the masticatory margin of the lateral tooth and the absence or presence of cusps in the marginal one (Fig. 1).

Species belonging to the subfamily Goniodoridinae feed on ctenostome bryozoans, commonly arborescent species (Rudman, 2004; Sales et al., 2016). These Goniodoridinae species have elongated and more cylindrical bodies. In addition, the oral tentacles show a reduction in these lineages to a muscular mass around the mouth, which is consistent with the suctorial feeding behavior of animals with non-mineralized preys (Hayward & Ryland, 1985), which graze up and soak polyps (Nybakken & McDonald, 1981).

Regarding ascidian feeders, *Pelagella* and *Okenia* species graze, cut through the epidermis, and suck out the contents by the highly muscular buccal pump, like ctenostome bryozoan feeders (Forrest, 1953). Both *Okenia* and *Pelagella* have been previously considered to be related based on their prey preference and body shape (Rudman, 2004), suggesting that feeding behavior drives their morphological features. Both genera have mantle ridges, a distinct head separated from the foot and mantle, a high body, and a wide foot. These species nestle in cavities which they eat from the ascidians and extend their foot to completely line the walls of the cavity (Thompson & Brown, 1984; Rudman, 2004). Little is known about the specific prey species for *Pelagella* and *Okenia* species; the prey being often referred to as undetermined ascidians. *Pelagella castanea* and *O. nodosa* have been reported to feed on the same ascidian

species, from the genera *Botryllus* and *Dendrodoa* (Forrest, 1953; Thompson & Brown, 1984; Rudman, 2004). *Okenia aspersa* and *O. elegans* have been reported to feed on other genera, such as *Molgula, Ascidiella,* or *Ciona* (Thompson & Brown, 1984). It is possible that the aberrant body shape of *O. nodosa*, and its close resemblance to *Pelagella*, is due to a morphological convergence of this north European species. This convergence could be related to the highly specialized diet of species of *Botryllus* and *Dendrodoa*. Rudman (2004) already suggested that "species of *Goniodoris* have evolved from an *Okenia*-like ancestor, such as *O. aspersa*, which has begun to feed on ascidians, or conversely, bryozoan-feeding in species of *Okenia* may have evolved as a neotenous event from an ascidian-feeding ancestor". The resemblance was already notorious, and our phylogenetic results confirm that *O. nodosa* does not belong to a different genus but is a rather specialized *Okenia* not feeding on bryozoans.

On the contrary, *Ceratodoris* is a cheilostome bryozoan feeder that shows some variability in radula features within the subfamily. Cheilostome bryozoans are divided into ascophoran and anascan, which were defined as having a calcified or non-calcified frontal membrane, respectively (Dick et al., 2009). Most *Ceratodoris* species maintain a pleiomorphic radular shape within Goniodoridinae. These species feed on anascan bryozoans, i.e., *C. plana* on *Membranipora* (Malascostega), *Jellyella* (*Flustrina*), and *Cryptosula* (*Flustrina*); and *C. pilosa* feeds on *Calpensia* (*Flustrina*) (Rudman, 2004). Furthermore, *Ceratodoris* sp. A, *C. pilosa*, *C. plana* feed on encrusting bryozoans, and consequently present flattened bodies, color patterns matching their prey, and a broad radula (Thompson, 1976; Rudman, 2004). The clade *C. hiroi* + *C. hallucigenia* + *C. rosacea* + *C. atkinsonorum* has been reported feeding on ascophora bryozoans with a calcified exoskeleton, belonging to the family Eurystomellidae Levinsen, 1909 (Harmer, 1957; Rudman, 2004; Ostrovsky et al., 2009). These *Ceratodoris* species show a tendency to display a smaller and more elongated radula. *Ceratodoris hiroi* and *C. hallucigenia* have a reduced base of the lateral teeth and stronger, sharper cusps. The related species *C. rosacea* and *C. atkinsonorum* have elongated teeth. It has been hypothesized that the evolution to large and thin radular teeth is an adaptation to break the individual zooecia of the calcified bryozoan membrane (Nybakken & McDonald, 1981). Taxa within this *Ceratodoris* clade share a pinkish-red color pattern, that also matches the color of their prey. These species have been considered aposematic because of their bright color as well as the size of the specimens, being larger than their prey (Rudman, 2004). The diversification of a cryptic and an aposematic clade into related or even sister lineages is no exception within nudibranchs (Gosliner, 2001). However, due to the predator–prey color similarity, we believe that this color pattern may correspond to a cryptic rather than an aposematic coloration, functioning as camouflage on their hosts.

Although the natural history of nudibranch species is poorly known for many species, our results support that their highly specialized predator–prey relationships may have driven the evolution of the Goniodorididae genera. Congruently, morphology and anatomy may be explained by prey specialization. Hence, the evolutionary history and biodiversity of Goniodorididae are better explained from an integrative taxonomic approach. The recent revision of the related family Onchidorididae also showed the importance of including *in situ* observations to better understand species ecology. These data are important when analyzing species through an integrative taxonomic analysis (Furfaro et al., 2022).

CRediT authorship contribution statement

Sofía Paz-Sedano: Conceptualization, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Juan Moles:** Conceptualization, Validation, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision, Funding acquisition. **Dimitri Smirnoff:** Resources. **Terrence M. Gosliner:** Conceptualization, Validation, Resources,

Writing – review & editing, Supervision, Funding acquisition. **Marta Pola:** Conceptualization, Validation, Investigation, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data accessibility statement
Raw reads for newly sequenced samples are deposited in the NCBI Sequence Read Archive (BioProject PRJNA1051643).

Author contribution

Paz-Sedano: Conceptualization, validation, formal analysis, investigation, resources, writing- original draft, writing – review & editing, funding acquisition; **Moles:** Conceptualization, validation, formal analysis, investigation, resources, writing – review & editing, supervision, funding acquisition; **Smirnoff:** resources; **Gosliner:** Conceptualization, validation, resources, writing – review & editing, supervision, funding acquisition; **Pola:** Conceptualization, validation, investigation, resources, writing – review & editing, supervision, funding acquisition.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2023.107990.

References

Abdelkrim, J., Fedosov, A., Kantor, Y., Lozouet, P., Phuong, M., Zaharias, P., Puillandre, N., 2018. Exon-capture based phylogeny and diversification of the venomous gastropods (Neogastropoda, Conoidea). Mol. Biol. Evol. 35, 2355–2374.

Aberer, A.J., Kobert, K., Stamatakis, A., 2014. ExaBayes: massively parallel Bayesian tree inference for the whole-genome era. Mol. Biol. Evol. 31 (10), 2553–2556.

Alfaro, M.E., Zoller, S., Lutzoni, F., 2003. Bayes or bootstraps? A simulation study comparing the performance of Bayesian Markov chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. Mol. Biol. Evol. 20, 255–266.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V. M., Nikolenko, S.I., Pham, S., Prjibelski, A.D., Pyshkin, A.V., Sirotkin, A.V., Vyahhi, N., Tesler, G., Alekseyev, M.A., Pevzner, P.A., 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. J. Comput. Biol. 19 (5), 455–477.

Behrens, D.W., Fletcher, K., Hermosillo, A., Jensen, G.C., 2022. Nudibranchs & sea slugs of the Eastern Pacific. Mola Marine, Bremerton, Washington State.

Blair, C., Bryson Jr, R.W., Linkem, C.W., Lazcano, D., Klicka, J., McCormack, J.E., 2019. Cryptic diversity in the Mexican highlands: thousands of UCE loci help illuminate phylogenetic relationships, species limits and divergence times of montane rattlesnakes (Viperidae: Crotalus). Mol. Ecol. Resour. 19 (2), 349–365.

Bolger, A.M., Lohse, M., Usadel, B., 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics. 30 (15), 2114–2120.

Bouchet, P., Rocroi, J.P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M., Strong, E.E., 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia. 61 (1–2), 1–526.

Burn, R., 1961. *Drepaniella mapae* gen. et spec. nov., a new goniodorid nudibranch from south-eastern Australia. Veliger. 3 (4), 102–104.

Camacho-García, Y., Gosliner, T.M., 2004. A New Species of *Okenia* (Gastropoda: Nudibranchia: Goniodorididae) from the Pacific Coast of Costa Rica. Proc. Calif. Acad. Sci. 4 (55), 431–438.

Canning, M.H., Carlton, J.T., 2000. Predation on kamptozoans (Entoprocta). Invertebr. Biol. 119 (4), 386–387.

Castresana, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol. Biol. Evol. 17 (4), 540–552.

Cock, P. J. A., Chilton, J. M., Grüning, B., Johnson, J. E., Soranzo, N., 2015. NCBI BLAST + integrated into Galaxy. GigaScience. 4(1). Available at https://doi.org/10.1186/s13742-015-0080-7.

Colgan, D.J., Mclauchlan, A., Wilson, G.D.F., Livingston, S., Macaranas, J., Edgecombe, G.D., Cassis, G., Gray, M.R., 1998. Molecular phylogenetics of the Arthropoda: relationships based on histone H and U2 snRNA DNA sequences. Aust. J. Zool. 46, 19–437.

Dick, M.H., Lidgard, S., Gordon, D.P., Mawatari, S.F., 2009. The origin of ascophoran bryozoans was historically contingent but likely. Proc. r. Soc. b: Biol. Sci. 276 (1670), 3141–3148.

Edmunds, M., 2009. Opisthobranchiate Mollusca from Ghana: Goniodorididae. J. Conchol. 40 (1), 37–54.

Ekimova, I., Valdés, Á., Chichvarkhin, A., Antokhina, T., Lindsay, T., Schepetov, D., 2019. Diet-driven ecological radiation and allopatric speciation result in high species diversity in a temperate-cold water marine genus *Dendronotus* (Gastropoda: Nudibranchia). Mol. Phylogenet. Evol. 141, 106609.

Faircloth, B.C., 2016. PHYLUCE is a software package for the analysis of conserved genomic loci. Bioinformatics. 32 (5), 786–788.

Faircloth, B. C., 2013. Illumiprocessor: a trimmomatic wrapper for parallel adapter and quality trimming [WWW Document]. URL https://doi.org/10.6079/J9ILL.

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome C oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. 3, 294–299.

Forrest, J.E., 1953. On the feeding habits and the morphology and mode of functioning of the alimentary canal in some littoral dorid nudibranchiate Mollusca. Proc. Linn. Soc. Lond. 164 (2), 225–235.

Franc, A., 1968. In: Sous-Classe Des Opisthobranches, pp. 608–893.

Furfaro, Trainito, E., Fantin, M., D'Elia, M., Madrenas, E., Mariottini, P., 2022. Mediterranean matters: Revision of the family Onchidorididae (Mollusca, Nudibranchia) with the description of a new genus and a new species. Diversity. 15 (1), 38.

Goddard, J.H.R., 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. Veliger. 27 (2), 143–163.

Goodheart, J.A., Wägele, H., 2020. Phylogenomic analysis and morphological data suggest left-right swimming behavior evolved prior to the origin of the pelagic Phylliroidae (Gastropoda: Nudibranchia). Org. Divers. Evol. 20 (4), 657–667.

Goodheart, J.A., Bazinet, A.L., Valdés, Á., Collins, A.G., Cummings, M.P., 2017. Prey preference follows phylogeny: evolutionary dietary patterns within the marine gastropod group Cladobranchia (Gastropoda: Heterobranchia: Nudibranchia). BMC Evol. Biol. 17 (1), 1–14.

Gosliner, T.M., 2001. Aposematic coloration and mimicry in opisthobranch mollusks: new phylogenetic and experimental data. Bollettino Malacologico 37, 163–170.

Gosliner, T.M., 2004. Phylogenetic systematics of *Okenia, Sakishimaia, Hopkinsiella* and *Hopkinsia* (Nudibranchia: Goniodorididae) with descriptions of new species from the tropical Indo-Pacific. Proc. Calif. Acad. Sci. 55 (1/12), 125–161.

Gosliner, T.M., 2010. Two new species of nudibranch mollusks from the coast of California. Proc. Calif. Acad. Sci. 61 (7), 623–631.

Gosliner, T.M., Bertsch, H.W., 2004. Systematics of *Okenia* from the Pacific coast of North America (Nudibranchia: Goniodorididae) with descriptions of three new species. Proc. Calif. Acad. Sci. 55 (13/25), 414–430.

Gosliner, T.M., Fahey, S.J., 2008. Systematics of *Trapania* (Mollusca: Nudibranchia: Goniodorididae) with descriptions of 16 new species. Syst. Biodivers. 6 (1), 53–98.

Gosliner, T.M., Valdés, A., Behrens, D.W., 2018. Nudibranch & sea slug identification Indo-Pacific, 2nd ed. New World Publications Inc.

Gray, M.E., 1850. Figures of Molluscous Animals, Selected from Various Authors, Etched for the Use of Students, vol. 4. Longman, Brown, Green and Longmans.

Hallas, J.M., Gosliner, T.M., 2015. Family matters: the first molecular phylogeny of the Onchidorididae Gray, 1827 (Mollusca, Gastropoda, Nudibranchia). Mol. Phylogenet. Evol. 88, 16–27.

Hallas, J.M., Chichvarkhin, A., Gosliner, T.M., 2017. Aligning evidence: concerns regarding multiple sequence alignments in estimating the phylogeny of the Nudibranchia suborder Doridina. R. Soc. Open Sci. 4 (10), 171095.

Hamatani, I., 2001. Two new species of Goniodorididae (Opisthobranchia; Nudibranchia) with a new genus from Kuroshima Island, Okinawa. Japan. Venus. 60 (3), 151–156.

Harmer, S.F., 1957. The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora. II. Ascophora, except Reteporidae, with additions to Part 2. Anasca. R. Siboga Expeditie 28. 145 (15), 641–1147.

Hayward, P.J., Ryland, J.S., 1985. Cyclostome Bryozoans: Keys and Notes for the Identification of the Species, Vol. 34. Brill Archive.

Hillis, D.M., Bull, J.J., 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol. 42, 182–192.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30 (4), 772–780.

Kieran, T.J., Gordon, E.R., Forthman, M., Hoey-Chamberlain, R., Kimball, R.T., Faircloth, B.C., Weirauch, C., Glenn, T.C., 2019. Insight from an ultraconserved element bait set designed for hemipteran phylogenetics integrated with genomic resources. Mol. Phylogenet Evol. 130, 297–303.

Kocsis, Á.T., Reddin, C.J., Kiessling, W., 2018. The stability of coastal benthic biogeography over the last 10 million years. Glob. Ecol. Biogeogr. 27 (9), 1106–1120.

Korshunova, T., Fletcher, K., Picton, B., Lundin, K., Kashio, S., Sanamyan, N., Padula, V., Schrödl, M., Martynov, A., 2020. The Emperor's Cadlina, hidden diversity and gill cavity evolution: new insights for the taxonomy and phylogeny of dorid nudibranchs (Mollusca: Gastropoda). Zool. J. Linn. Soc. 189 (3), 762–827.

Kozlov, A.M., Darriba, D., Flouri, T., Morel, B., Stamatakis, A., 2019. RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics. 35 (21), 4453–4455.

Layton, K.K., Carvajal, J.I., Wilson, N.G., 2020. Mimicry and mitonuclear discordance in nudibranchs: New insights from exon capture phylogenomics. Ecol. Evol. 10 (21), 11966–11982.

Li, W., Godzik, A., 2006. Cd-hit: a fast program for clustering and comparing large sets of protein or nucleotide sequences. Bioinformatics. 22 (13), 1658–1659.

MacFarland, F.M., 1905. A preliminary account of the Dorididae of Monterey Bay. California. Proc. Biol. Soc. Wash. 18, 35–54.

Marcus, E.r., 1957. On Opisthobranchia from Brazil 2. J. Linn. Soc. Lond. 43 (292), 390–486.

Martín-Hervás, M.D.R., Carmona, L., Malaquias, M.A.E., Krug, P.J., Gosliner, T.M., Cervera, J.L., 2021. A molecular phylogeny of *Thuridilla* Bergh, 1872 sea slugs (Gastropoda, Sacoglossa) reveals a case of flamboyant and cryptic radiation in the marine realm. Cladistics. 37 (6), 647–676.

McDonald, G.R., Nybakken, J.W., 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. Veliger. 21 (1), 110–118.

Mikkelsen, P.M., 2002. Shelled opisthobranchs. Adv. Mar. Biol. 42, 67–136.

Moles, J., Giribet, G., 2021. A polyvalent and universal tool for genomic studies in gastropod molluscs (Heterobranchia). Mol. Phylogenet. Evol. 155, 106996.

M.A. Miller W. Pfeiffer T. Schwartz Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), (LA 2010 New Orleans) 1 8.

MolluscaBase, eds., 2023a. MolluscaBase. Goniodorididae H. Adams & A. Adams, Accessed through: World Register of Marine Species at 1854 on 2023-04-13.

MolluscaBase, eds., 2023b. MolluscaBase. *Ancula* Lovén, 1846. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=138038 on 2023-04-13.

MolluscaBase, eds., 2023c. MolluscaBase. *Okenia* Menke, 1830. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=138042 on 2023-04-17.

Musher, L.J., Cracraft, J., 2018. Phylogenomics and species delimitation of a complex radiation of Neotropical suboscine birds (Pachyramphus). Mol. Phylogenet. Evol. 118, 204–221.

Nybakken, J.W., McDonald, G.R., 1981. Feeding mechanisms of west American nudibranchs feeding on Bryozoa, Cnidaria and Ascidiacea, with special respect to the radula. Malacologia. 20 (2), 439–449.

Odhner, N.J., 1941. New polycerid nudibranchiate mollusca and remarks on this family. Handlingar: Matematiska Och Naturvetenskapliga Skrifter. 1 (11), 1–20.

Ortea, J., Espinosa, J., 2000. Nueva especie del género *Okenia* Menke, 1830 (Mollusca: Nudibranchia) de Cuba. Avicennia. 12 (13), 84–86.

Ostrovsky, A.N., O'Dea, A., Rodríguez, F., 2009. Comparative anatomy of internal incubational sacs in cupuladriid bryozoans and the evolution of brooding in free-living cheilostomes. J. Morphol. 270 (12), 1413–1430.

Padial, J.M., Miralles, A., De la Riva, I., Vences, M., 2010. The integrative future of taxonomy. Front. Zool. 7 (1), 1–14.

Palumbi, S.R., 1996. Nucleic acids II: the polymerase chain reaction. Mol. Syst. 205–247.

Pante, E., Schoelinck, C., Puillandre, N., 2015. From integrative taxonomy to species description: one step beyond. Syst. Biol. 64 (1), 152–160.

Parada, A., Hanson, J., D'Eiía, G., 2021. Ultraconserved elements improve the resolution of difficult nodes within the rapid radiation of Neotropical sigmodontine rodents (Cricetidae: Sigmodontinae). Syst. Biol. 70 (6), 1090–1100.

Parera, A., Pontes, M., Salvador, X., Ballesteros, M., 2020. Sea-slugs (Mollusca, Gastropoda, Heterobranchia): The other inhabitants of the city of Barcelona (Spain). Butll. Inst. Catalana D'hist. Nat. 84, 75–100.

Paz-Sedano, S., Ortigosa, D., Pola, M., 2017. A new *Okenia* Menke, 1830 from the Azores Island. Portugal. Spixiana. 40 (1), 13–22.

Paz-Sedano, S., Wilson, N.G., Carmona, L., Gosliner, T.M., Pola, M., 2021a. An ocean yet to be discovered: increasing systematic knowledge of Indo-Pacific *Okenia* Menke, 1830 (Nudibranchia: Goniodorididae). Invertebr. Syst. 35 (7), 797–825.

Paz-Sedano, S., Candás, M., Gosliner, T.M., Pola, M., 2021b. Undressing *Lophodoris danielsseni* (Friele & Hansen, 1878) (Nudibranchia: Goniodorididae). Org. Divers. Evol. 21, 107–117.

Paz-Sedano, S., Smirnoff, D., Candás, M., Gosliner, T.M., Pola, M., 2022a. Rediscovering the overlooked genus *Murphydoris* (Nudibranchia: Goniodorididae): the first phylogeny and addition of four new species. Zool. J. Linn. Soc. 196 (1), 250–269.

Paz-Sedano, S., Martín Álvarez, J.F., Gosliner, T.M., Pola, M., 2022b. Reassessing North Eastern Atlantic-Mediterranean species of *Trapania* (Mollusca, Nudibranchia). Zool. Scr. 51 (4), 447–459.

Paz-Sedano, S., Díaz-Agras, G., Gosliner, T.M., Pola, M., 2022c. Revealing morphological characteristics of Goniodorididae genera (Mollusca: Nudibranchia). Org. Divers. Evol. 22, 93–116.

Paz-Sedano, S., Smirnoff, D., Gosliner, T.M., Pola, M., 2023a. When a genus must become two: resurrection of *Pelagella* Gray, 1850 with the description of six new species. J. Molluscan Stud. 89 (2), eyad008.

Paz-Sedano, S., Ekimova, I., Smirnoff, D., Gosliner, T.M., Pola, M., 2023b. Shedding light on a species complex within the genus *Goniodoridella* Pruvot-Fol, 1933 (Nudibranchia, Goniodorididae), with description of three new species. J. Molluscan Stud 89 (4), eyad020.

Platt, A.R., Woodhall, R.W., George, A.L., 2007. Improved DNA sequencing quality and efficiency using an optimized fast cycle 1240 sequencing protocol. Biotechniques. 43, 58–62.

Pola, M., Cervera, J.L., Gosliner, T.M., 2007. Phylogenetic relationships of Nembrothinae (Mollusca: Doridacea: Polyceridae) inferred from morphology and mitochondrial DNA. Mol. Phylogenet. Evol. 43 (3), 726–742.

Pola, M., Hallas, J.M., Gosliner, T.M., 2019. Welcome back Janolidae and *Antiopella*: Improving the understanding of Janolidae and Madrellidae (Cladobranchia, Heterobranchia) with description of four new species. J. Zool. Syst. Evol. Res 57 (2), 345–368.

Pruvot-Fol, A., 1931. Notes de systématique sur les opisthobranches. Bull. Mus. Nat. Hist. Na*T*. 3, 308–316.

A. Pruvot-Fol Mollusques Opisthobranches. Faune de France vol 58 1954 Paris.

Puillandre, N., Lambert, A., Brouillet, S., Achaz, G.J.M.E., 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Mol. Ecol. 21 (8), 1864–1877.

Puillandre, N., Brouillet, S., Achaz, G., 2021. ASAP: assemble species by automatic partitioning. Mol. Ecol. Resour. 21, 609–620.

Quattrini, A.M., Faircloth, B.C., Dueñas, L.F., Bridge, T.C.L., Brugler, M.R., Calixto-Botía, I.F., DeLeo, D.M., Forêt, S., Herrera, S., Lee, S.M.Y., Miller, D.J., Prada, D., Rádis-Baptista, G., Ramírez-Portilla, C., Sánchez, J.A., Rodríguez, E., McFadden, C.S., 2018. Universal target-enrichment baits for anthozoan (Cnidaria) phylogenomics: New approaches to long-standing problems. Mol. Ecol. Resour. 18 (2), 281–295.

Rambaut, A., 2009. FigTree v1.3.1: Tree Figure Drawing Tool. Available at: http://tree.bio.ed.ac.uk/software/figtree/.

J. Risbec Contribution a l'etude des nudibranches Néo-Calédoniens. Thèse présentée à la faculté des sciences de l'Université de Paris pour obtenir le grade de docteur ès-sciences naturelles 1928 Faune des Colonies Française.

Rudman, W.B., 1987. The genus *Trapania* (Nudibranchia: Goniodorididae) in the Indo-West Pacific. J. Molluscan. Stud. 53 (2), 189–212.

Rudman, W.B., 2004. Further species of the opisthobranch genus *Okenia* (Nudibranchia: Goniodorididae) from the Indo-West Pacific. Zootaxa 695 (1), 1–70.

Sales, L., Queiroz, V., Migotto, A.E., 2016. Rediscovery of *Okenia impexa* Marcus 1957 on the Brazilian coast: the first image of a living specimen from Brazil. Spixiana. 39 (2), 203–204.

Sánchez-Tocino, L., Cervera, J.L., 2006. Preliminary data on the diet of *Trapania maculata* Haefelfinger, 1960 and *Trapania hispalensis* Cervera and García-Gómez, 1989 (Mollusca: Nudibranchia). Zool. Baetica. 17, 85–89.

Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6 (2), 461–464.

Sigurdsson, J.B., 1991. A nudibranch, *Murphydoris singaporensis,* new genus and species, from Singapore mangroves (Mollusca: Opisthobranchia: Goniodorididae). Raffles. Bull. Zool. 39, 259–263.

Smirnoff, D.S., Donohoo, S.A., Gosliner, T.M., 2022. Revision to the nomenclatural status of *Trapania* (Nudibranchia: Goniodorididae). Zool. J. Linn. Soc. 196 (1), 314–315.

Smith, S.A., Wilson, N.G., Goetz, F.E., Feehery, C., Andrade, S.C., Rouse, G.W., Giribet, G., Dunn, C.W., 2011. Resolving the evolutionary relationships of molluscs with phylogenomic tools. Nature. 480 (7377), 364–367.

Swennen, C., Buatip, S., 2012. *Murphydoris singaporensis* (Gastropoda: Nudibranchia: Goniodorididae) found in Thailand; with external and first internal description of the specimens. Strombus. 19 (1/2), 9–14.

Templado, J., 1982. Datos sobre los opistobranquios del Cabo de Palos (Murcia). Boll. Malacol. 18 (9–12), 247–254.

T.E. Thompson G.H. Brown Biology of opisthobranch molluscs vol. 2 1984 Ray Society.

Thompson, T. E., 1976. *Biology of Opisthobranch Molluscs*, vol. 1. Ray Society.

Trainito, E., Fantin, M., Furfaro, G., 2018. *Trapania pallida* Kress, 1968 (Gastropoda, Nudibranchia): first record for Italian waters and new additional notes on its diet and on Mediterranean records. Stud. Mar. 31 (2), 32–37.

Trainito, E., Migliore, V., Doneddu, M., 2022. How many seas must a nudibranch sail? *Okenia picoensis* (Mollusca: Nudibranchia: Goniodorididae) conquering the Mediterranean. Stud. Mar. 35 (1), 15–25.

Valdés, A., Ortea, J., 1995. Revised taxonomy of some species of the genus *Okenia* Menke, 1830 (Mollusca: Nudibranchia) from the Atlantic Ocean, with the description of a new species. Veliger. 38 (3), 223–234.

Vogel, R., Schultz, L., 1970. *Cargoa-Cupella* new genus and new species of nudibranch from Chesapeake Bay and the generic status of *Okenia, Idalia* and *Idalla*. Veliger. 12, 388–393.

Waeschenbach, A., Taylor, P.D., Littlewood, D.T.J., 2012. A molecular phylogeny of bryozoans. Mol. Phylogenet. Evol. 62 (2), 718–735.

Yonow, N., 2015. Sea slugs: Unexpected biodiversity and distribution. In: In: Rasul, N., Stewart, I., . (Ed.), The Red Sea. Springer Earth System Sciences. Springer, Berlin, Heidelberg.

J. Zhang P. Kapli P. Pavlidis A. Stamatakis A general species delimitation method with applications to phylogenetic placements Bioinformatics. 29 2013 2869 2862.

Zhang, Y.M., Williams, J.L., Lucky, A., 2019. Understanding UCEs: a comprehensive primer on using ultraconserved elements for arthropod phylogenomics. Insect Syst. Divers. 3 (5), 3.