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Tellinoidea, one of the most diverse superfamilies of Bivalvia, includes 954 extant species classified into five families. While the monophyly of Tellinoidea is well corroborated by morphological and molecular data, the monophyly of the individual families and their relationships remain contentious, hampering further macroevolutionary studies. By using an ultraconserved elements probe set recently developed for the class Bivalvia, we captured 825 UCEs from 33 fresh and historical museum specimens and produced a phylogeny for Tellinoidea with strong support for its internal relationships. Our analyses recovered Donacidae as monophyletic, whereas Solecurtidae was inferred as paraphyletic, and Psammobiidae, Semelidae, and Tellinidae were resolved as polyphyletic lineages. The results reinforce the need for reassessment of these families, as phylogenetic evidence suggests, for example, that semelids and the genus *Sanguinolaria* are nested within Tellinidae. Leveraging this phylogenetic framework, we estimated ancestral states of four key traits: burrowing depth, feeding habit, tentacle form, and number of siphonal tentacles in the incurrent aperture. Our results show lineage-specific variations of the siphon anatomy and specialization for deposit-feeding behavior. Overall, we also highlight evolutionary convergences and discuss potential scenarios for the diversification of tellinoids in shallow water environments.

1 | Introduction

The superfamily Tellinoidea is one of the most diverse groups of bivalves, with 954 extant species classified into five families: Donacidae, Psammobiidae, Semelidae, Solecurtidae, and Tellinidae (Table 1) (MolluscaBase, 2025). The taxon emerged in near-shore or inner shelf environments during the Middle Triassic (Jablonski & Bottjer, 1990), and lineages such as Icanotiidae, Quenstedtiidae, Sowerbyidae, Tancrediidae, and Unicardiopsidae went extinct during the evolution of the group (MolluscaBase, 2025). Currently, Tellinoidea is widespread in shallow waters of tropical and temperate regions, with some species also distributed in freshwater and brackish water environments, as well as the deep sea (e.g., Purchon, 1963; Allen & Sanders, 1966; Narchi, 1972). All tellinoidean species are infaunal, living in soft sediment with a variety of behaviors, including shallow and deep burrowing (e.g., Stanley, 1970; Arruda *et al.*, 2003). The group is economically important for many human coastal populations as a fisheries resource, for example, the "tarioba" [*Iphigenia brasiliensis* (Lamarck, 1818)] in Brazil, the "pipi" [*Latona deltoides* (Lamarck, 1818)] in Australia, and *Donax trunculus* (Linnaeus, 1758) in the Mediterranean region, which receives many common names (e.g., Narchi, 1972; O'Connor & O'Connor, 2011; Marie *et al*., 2016).

Phylogenetically, Tellinoidea has been recovered as monophyletic in several analyses, based on both molecular and morphological data (e.g., Taylor *et al*., 2007; Yuan, *et al*., 2012; Bieler *et al*., 2014; Combosch *et al*., 2017; Lemer *et al*., 2019; Sun *et al*., 2020; Tang *et al*., 2025). A conspicuous synapomorphy of tellinoids is the complex of the cruciform muscle and its associated sensory organ, located at the base of the incurrent siphon. Nevertheless, the monophyly of its families and their relationships remain contentious, with most studies using limited taxonomic sampling or focusing on large-scale resolution of the bivalve tree. The only exception is Donacidae, which had its monophyly corroborated and the relationships among genera well explored recently (Moncada *et al*., 2022; González-Delgado *et al*., 2024). Unfortunately, the knowledge of many aspects of the evolutionary and functional biology of Tellinoidea is hampered by the lack of a robust phylogenetic background. In addition, the diversity of the superfamily is reflected in the feeding habits, which include suspension-feeding, common for most autobranch bivalves (i.e., bivalves with hypertrophied gills used for feeding in addition to respiration), nonselective suspension-feeding, characterized by suspension feeders that ingest passively deposited food particles, and deposit-feeding, when the ingestion of deposited particles happens actively (Pohlo, 1982). Deposit-feeders use the long incurrent siphon as a vacuum cleaner to indiscriminately suck up detritus, an unusual feeding behavior among siphonate bivalves (Ponder *et al*., 2019). Nonetheless, the phylogenetic distribution and how many times this feeding behavior evolved are still open questions. Furthermore, there is consensus that the siphons have key roles in the evolution of infaunal bivalves (Stanley, 1968; Nigro *et al*., 2025), but how these organs impacted the evolution and diversity of Tellinoidea remains a mystery.

As resolving the internal relationships of Tellinoidea has proven difficult, an integrative approach combining molecular markers with anatomic data was a promising avenue (Giribet & Wheeler, 2002; Bieler *et al*., 2014). In this context, museomics, i.e., the large-scale analysis of the DNA content of museum collections (Fong *et al*., 2023), has proven an effective tool to increase taxonomic sampling. Sequence capture approaches, as opposed to methods that require non-selective PCR amplification, have been highly successful for phylogenomics, providing the ability to include data from museum specimens, where DNA is typically highly degraded, and avoiding the need to sequence whole genomes or transcriptomes, which are expensive and complex to analyze (Derkarabetian *et al*., 2019). Ultraconserved elements (UCEs) fit into these approaches and have been used to resolve the evolutionary relationships of many animal groups, including heterobranch gastropods (Moles & Giribet, 2021), malacostracan crustaceans (Geburzi *et al*., 2024), and mite harvesters (Derkarabetian *et al*., 2024). Furthermore, two UCE probe sets were recently designed for Bivalvia, both successfully captured UCEs to investigate relationships at multiple taxonomic levels (González-Delgado *et al*., 2024; Li *et al*., 2024).

Here, we leverage the UCE probe set of González-Delgado *et al*. (2024) to provide a phylogenomic treatment of Tellinoidea, effectively capturing 825 ultraconserved elements (UCEs) from 33 species. As this approach has been successfully applied to both high-quality and extremely degraded DNA (e.g., Derkarabetian *et al*., 2019; González-Delgado *et al*., 2024), we used fresh (i.e., collected up to 20 years ago and preserved in ca. 95% ethanol at -20 ºC) and historical (i.e., collected more than 10 years ago and preserved in 70–80% ethanol at room temperature) specimens to optimize taxonomic sampling. In addition, we applied the phylogenetic framework obtained to investigate the evolution of lifestyles and siphonal tentacles by using comparative methods, providing insights into the diversification of siphons in shallow-water tellinoids.

2 | Material and Methods

2.1 | Taxonomic sampling

The taxonomic classification adopted herein is in accordance with MolluscaBase (2025). We obtained specimens from MCZ (Museum of Comparative Zoology), MDBio (Museum of Biological Diversity of State University of Campinas), and NMNH (Smithsonian National Museum of Natural History). In total, we collected molecular and morphological data from 33 tellinoidean species in 19 genera (Table 2). Most species were recently collected in Brazil, but we also included species from Australia, Ghana, Japan, Nigeria, Portugal, Puerto Rico, Scotland, Spain, Sweden, Tokelau (New Zealand), and the USA. We emphasize that although these institutions house a large number of tellinoidean specimens in their collections, alcohol-preserved specimens do not represent a substantial portion of their holdings. Furthermore, the DNA quality of some historical samples also precluded their inclusion in the final dataset, as many samples from the 20th century were fixed in formalin (see González-Delgado *et al.*, 2024).

Recent phylogenomic investigations have pointed to Cardioidea as the sister group of Neoheterodontei, i.e., Myida, Sphaeriida, and Venerida (González *et al.*, 2015; González-Delgado *et al.*, 2024) and Tellinoidea close to Adapedonta and Galeommatida (González-Delgado *et al.*, 2024; Li *et al.*, 2024). However, we chose five species from the family Cardiidae as the outgroup, adopting a more traditional standpoint (e.g., Bieler *et al.*, 2014; Combosch *et al.*, 2017; Lemer *et al.*, 2019; Tang *et al.*, 2025).

2.2 | DNA extraction, library preparation, and UCE sequence capture

Genomic DNA was extracted from the adductor muscle or foot of larger specimens while the whole animal was used in the case of small individuals. Qiagen's DNeasy Blood and Tissue kit was used following the manufacturer's protocol, with a final elution of 200 µL of ddH_2O for fresh samples. For historical samples, a protocol for degraded DNA extraction using silica-based magnetic beads was used (Tin *et al.*, 2014), with some in-lab modifications (Derkarabetian *et al.*, 2019). In this case, the final elution volume was 50 µL of ddH_2O. All extractions were quantified on a Qubit 2.0 fluorometer using a dsDNA High Sensitivity kit (Life Technologies, Inc.).

After DNA extraction, libraries were prepared following the manufacturer's protocol for the KAPA HyperPlus kit, with some in-lab modifications for historical samples. The DNA input to start the library preparation was 200 ng in 17.5 µL. For fresh samples, enzymatic fragmentation to a target length of 500–700 bp was achieved with the 17.5 µL DNA sample plus 5 µL KAPA Fragmentation Enzyme and 2.5 µL KAPA Fragmentation Buffer (10X). The total volume (25 µL) was incubated for 3 min at 37 °C. For historical samples, DNA fragmentation was not necessary as DNA is naturally shredded. End-repair and A-tailing were conducted using the KAPA HyperPlus enzyme mix for fresh, enzymatically fragmented samples, and KAPA HyperPrep enzyme mix for historical, naturally fragmented samples, with 30 min incubation at 65 °C. The adapter ligation was done using 30 µL End repair and A-tailing reaction product, a mix of 15 µL Ligation Buffer with 5 µL DNA Ligase, and 5 µL individual i5/i7 dual indexing adapters (Glenn *et al.*, 2019), incubating at 20 °C for 30 min on a thermocycler. A post-ligation cleanup was carried out using freshly prepared Serapure SpeedBeads (Rohland & Reich, 2012) with 0.8X beads for fresh samples and 2.5X beads for historical samples. Library amplification used 15 µL of ligated libraries, with 25 µL 2X KAPA HiFi HotStart

ReadyMix, and 5 µL KAPA Library Amplification mix (primers). The amplification of fresh samples followed the thermal protocol: 45 s at 98 °C, 18 cycles of 15 s at 98 °C, 30 s at 60 °C, 60 s at 72 °C, and 5 min at 72 °C for the final extension. In the case of the historical samples, the only modification was 20 cycles because the amount of DNA was in general smaller. Amplified libraries were purified with SpeedBeads (1X for fresh, 2.5X for historical), quantified, and pooled into 1000 ng batches of eight samples, each pool containing 125 ng of each library.

Hybridization was done using the Bivalvia probe set designed by González-Delgado *et al.* (2024) and following the myBaits® Hybridization Capture for Targeted NGS manual version 5.02. Hybridization time for all samples was 24 h at 60 °C. Hybridized pools with 15 µL were amplified for 14-18 cycles using the same thermal protocol as described above, purified with AMPure beads (1.8X for all pools), quantified on a Qubit 2.0, and size estimated on an Agilent TapeStation 2200. A final 1X bead cleanup was performed on pools where adapter-dimers were present. Finally, 12 pools were obtained, each one with > 500 ng/mL. Amplified, hybridized pools were pooled in equimolar amounts and sequenced on an Illumina NovaSeq platform (paired-end, 150 bp) at the Bauer Core Facility, Faculty of Arts and Sciences, Harvard University.

2.3 | Bioinformatics and phylogenetic analyses

Following the workflow by Faircloth (2016), raw Illumina reads were demultiplexed and processed using PHYLUCE v1.7.2. Adapters and low-quality bases were removed with illumiprocessor (Faircloth, 2013), which implements trimmomatic (Bolger *et al*., 2014), and the contigs were assembled with SPAdes v3.15.5 (Prjibelski *et al*., 2020). Probes were matched to the assembled contigs with the PHYLUCE script phyluce_assembly_match_contigs_to_probes, with a 65% threshold value for minimum locus coverage and identity.

The selected UCE loci were aligned with MAFFT (Katoh & Standley, 2013), with the following default parameters: gap open penalty = 1.7, offset value = 0.14. Alignments were trimmed with GBlocks (Castresana, 2000; Talavera & Castresana, 2007), using conservative settings suitable for phylogenetic analysis at higher taxonomic levels, i.e., -b1 0.5, -b2 0.85, -b3 4, -b4 8. We built a 50% gene occupancy matrix (meaning that a locus was selected if present in 50% or more taxa). A final cleaning step was performed using CIAlign (Tumescheit *et al*., 2022) to crop long gaps near the leading and trailing ends and to remove paralogous and outlier sequences.

Phylogenetic trees of the concatenated matrices were reconstructed under maximum likelihood (ML) with IQ-Tree v. 2.2.6 (Minh *et al.*, 2020), using ModelFinder (Kalyaanamoorthy *et al.*, 2017) for model selection (the best-fit model was GTR+F+I+G4), and 1500 replicates of ultrafast bootstrapping (Hoang *et al.*, 2018). The ML trees were visualized with FigTree v. 1.4.4 (Rambaut, 2006–2019) and edited in Adobe Photoshop CS6 (Adobe Corporation).

2.4 | Evolution of siphonal and ecological traits

To explore the evolution of siphons within Tellinoidea, we estimated the ancestral state of four key traits: burrowing depth, feeding habit, tentacle form, and number of tentacles in the incurrent aperture. All traits were coded, and states were assigned to species based on direct observation under a stereomicroscope complemented with literature information (Supplementary Table 1). General terms and definitions used here for bivalve anatomy are in accordance with Carter *et al.* (2012). In addition, we consider simple tentacles as a single digitiform or lobed projection in opposition to branched tentacles; while digitiform tentacles are long, finger-like structures, lobed tentacles are shorter and more compact.

Species were classified as shallow or deep burrowers according to the criterion proposed by Stanley (1970), i.e., species with a burial depth of the posterior shell margin less than 30 mm were considered shallow burrowers, whereas those exceeding this depth were considered deep burrowers. Burrowing depth was verified in the field for several species. Specimens of *Donax* were actively collected by hand in the intertidal zone, while other species were sampled in the infralittoral during low tide using a digging spade inserted into the sediment to depths of up to 26 cm, with the species being collected from the middle to the lower part of the blade. For species previously collected and deposited in museum collections, burial depth was obtained from the literature (Supplementary Table 2). To refine species assignments, our classification of shallow and deep burrowers was further compared with the observational studies of Stanley (1970) and Kondo (1987).

Regarding the feeding habit, the species were classified as suspension- or deposit-feeders based on data compiled from the literature (Supplementary Table 2). For species with the feeding habit unknown, states were assigned based on congeneric relatives, i.e., *Gari* sp. and *G. modesta* based on *G. fervensis* (see Yonge, 1949), *Solecurtus sanctaemarthae* based on *S. strigilatus* (Linnaeus, 1758) (see Bromley & Asgaard, 1990), *Ameritella janeiroensis* based on *A. texana* (Dall, 1900) (see Aller & Yingst, 1985), *Eurytellina angulosa* and *E. punicea* based on *E. lineata* (see Arruda *et al*., 2003), *Macoma* sp. based on *Macoma* species (see Reid & Reid, 1969), and *Strigilla pisiformis* based on *S. carnaria* (see Arruda *et al*. 2003). It is important to highlight that some species classified as deposit feeders may exhibit facultative suspension feeding behavior and consume suspended particles under certain environmental conditions, as observed in *Austromacoma biota* (see Piffer et al., 2011). However, since this is considered a facultative behavior, with counterarguments (see Riisgård & Kamermans, 2001), a conservative approach with a binary classification was adopted for our analyses. We also chose not to divide suspension feeders into selective and non-selective categories. This distinction was originally proposed by Pohlo (1982), who based it on the morphology of the siphonal tentacles of the incurrent aperture, that is, selective suspension feeders would actively reject larger particles using digitiform tentacles, whereas non-selective suspension feeders would passively ingest food particles because lobate tentacles (short tentacles in Pohlo's conception) do not completely occlude the siphonal aperture. However, bivalves possess additional mechanisms of particle selection, e.g., rejection currents, therefore the passage of food particles through the siphonal aperture does not necessarily imply their ingestion.

Ancestral state estimations were inferred in the R environment. For discrete traits, three evolutionary models (equal rates, ER; symmetrical rates, SYM; and all rates different, ARD) were compared based on their Akaike Information Criteria (AIC) scores to determine the optimal model of transition rates under a maximum likelihood framework, using the *geiger* package, version 2.0.7 (Pennell *et al*. 2014). Subsequently, the evolution of these traits was estimated across the phylogeny, performing Bayesian stochastic character mapping (Bollback, 2006) in the *phytools* package version 0.7-80 (Revell, 2012). Finally, 1000 simmap trees were summarized to indicate the estimates of ancestral states for each node according to their posterior probabilities.

3 | Results

3.1 | Phylogenetic relationships

The phylogenetic hypothesis of Tellinoidea, obtained from UCE data, is presented in Figure 1. The phylogeny provides maximal support (100% bootstrap support, BS) for the monophyly of Tellinoidea. All the remaining nodes had maximal branch support except for three nodes highlighted in the tree (with values of 72%, 80%, and 89% BS).

Donacidae is the sister group of the remaining tellinoids, being the only family recovered as monophyletic, with all nodes receiving maximal support, except for the node comprising *Donax denticulatus*, *D. gemmula* and *D. variabilis*, which received a BS of 72%. Donacidae comprises two main clades, one composed of the brackish and freshwater species *Iphigenia brasiliensis* and *Galatea paradoxa*, respectively, and another including species from sandy beaches, i.e., *Latona deltoides* + *Donax* spp. Species of *Donax* from the Western Atlantic, i.e., *D. denticulatus*, *D. gemmula*, *D. hanleyanus*, and *D. variabilis*, form one clade, while species from Europe, i.e., *D. trunculus* and *D. vittatus*, group together in a different clade.

Psammobiidae was recovered as polyphyletic. *Sanguinolaria sanguinolenta* is nested with typical tellinids from the subfamilies Strigillinae and Tellininae. Although the exact position of *S. sanguinolenta* received low support (89% BS), its membership to this tellinid subclade receives maximal support. The remaining psammobiids, i.e., *Asaphis violascens* and three species of *Gari*, appear nested within Solecurtidae, with all nodes in this subclade receiving maximal support. The genus *Tagelus*, represented by *T. divisus* and *T. plebeius*, forms a monophyletic group, sister group to a clade composed of *A. violascens*, *Solecurtus sanctaemarthae,* and three species of *Gari*. The genus *Gari* is paraphyletic, with *Gari* sp. and *G. fervensis* more closely related to *S. sanctaemarthae* than to *G. modesta*.

Semelidae, Tellinidae, and *S. sanguinolenta* form a clade. Within this group, the semelids *Abra nitida* and *Cumingia sinuosa* constitute the sister group to a clade with the psammobiid *S. sanguinolenta* and tellinids from the subfamilies Strigillinae and Tellininae. Tellinids from the subfamily Macominae and *Macomangulus tenuis* (a Tellininae) are sister group to a clade composed of *Semele proficua* and *S. purpurascens*. Therefore, Semelidae and Tellinidae also appear as polyphyletic lineages. The internal phylogenetic relationships within this clade are also in conflict with existing taxonomy. The subfamily Tellininae *sensu stricto* is polyphyletic, and the genera *Ameritella* and *Eurytellina* are not monophyletic, with *A. versicolor* appearing nested within *Eurytellina*, rendering the latter paraphyletic, with *A. janeiroensis* appearing stemward of *S. sanguinolenta*.

3.2 | Trait evolution

Equal rates (ER) model represented the optimal evolutionary model for the burrowing depth, feeding habit, and number of siphonal tentacles, while symmetrical rates (SYM) was the best-fit model for the morphology of siphonal tentacles.

The analysis indicates the ancestor of all Tellinoidea as a shallow burrower and suspension feeder (Fig. 2A, B). Transitions to the deep burrowing habit occurred twice, once in *Iphigenia* and another one in the ancestor of Psammobiidae + Solecurtidae and species from the clade *S. sanguinolenta* + Semelidae + Tellinidae (Fig. 2A). The transition to a deposit feeding habit evolved only once (in the ancestor of *S. sanguinolenta* + Semelidae + Tellinidae) (Fig. 2B), with a secondary loss in *Semele*, a genus of suspension feeders (Fig. 2B).

According to the ancestral state estimation analyses, the most recent common ancestor of Tellinoidea probably had an incurrent aperture with six digitiform tentacles (Fig. 3A, B, 4A), contrasting with Cardioidea, in which the incurrent aperture has digitiform tentacles of a greater number (Fig. 3A, 4B). Transitions to lobed tentacles (Fig. 4C) also occurred thrice: in *Solecurtus*, in the most common ancestor of *S. sanguinolenta* + Semelidae + Tellinidae, and in *A. biota*. Digitiform tentacles were gained independently twice, once in *Strigilla pisiformis* and once in *Semele proficua* + *S. purpurascens* (Fig. 3A). Furthermore, *S. purpurascens* shows 12 tentacles (Fig. 4D), a condition also acquired independently in *Asaphis violascens* (Fig. 3B). Based on our sampling, the total loss of siphonal tentacles (Fig. 4E) occurred independently six times within the clade *S. sanguinolenta* + Semelidae + Tellinidae, i.e., in *Abra nitida* + *Cumingia sinuosa*; *Ameritella janeiroensis*; *A. versicolor*; *Macoma* sp. + *Psammotreta brevifrons*; *Macomangulus tenuis*; and *Scissula similis* (Fig. 3A, B). Finally, branched tentacles (Fig. 4F) have a single origin in the clade *Donax* + *Latona* (Fig. 3A), and a siphonal aperture with 24 tentacles was acquired by the ancestor of all Donacidae (Fig. 3B).

4 | Discussion

4.1 | Phylogenetic relationships

The phylogeny of Tellinoidea has been previously investigated using a multitude of approaches. However, the dataset presented here is the first to provide a phylogenetic hypothesis for the taxon using UCEs. The largest taxonomic sampling for Tellinoidea prior to this study included 34 species (Tang *et al.*, 2025). Here, we used a similar sampling size of 33 species, recognizing that this is only a fragment of the group's diversity, with only ca. 3.5% of the tellinoids represented. The study, however, clearly highlights the need for broad taxonomic revision at the family and genus levels, and shows a path towards incorporating large numbers of samples in genomic analyses of bivalves.

Summarizing the evolutionary relationships among Tellinoidea families is far from straightforward. Their uncertain status has led to multiple, often conflicting, hypotheses, with some patterns gradually emerging over time. The first molecular assessment by Taylor *et al*. (2007), based on two Sanger-sequenced markers (18S rRNA and 28S rRNA), inferred nearly all families that included two terminals or more as non-monophyletic. Their topology placed a paraphyletic Psammobiidae, due to the nesting of a Donacidae species, as sister group to the remaining families, and Solecurtidae (with a single representative) as sister group to Semelidae + Tellinidae. Relationships within that clade were particularly ambiguous, with some semelids clustering with Macominae and others with Tellininae and Strigillinae. Subsequent analyses incorporating additional molecular markers (16S rRNA, COI, and histone H3 in addition to 18S rRNA and 28S rRNA) and morphological traits (Bieler *et al*., 2014) also failed to recover Tellinidae as monophyletic. Instead, Tellininae emerged as sister group to the four remaining families, but Macominae was sister group to Semelidae, and Solecurtidae was sister group to Donacidae + Psammobiidae. However, this analysis was limited by sparse sampling, with only two tellinid species included. A similar topology was later recovered by Combosch *et al*. (2017) using the same five markers, who supported Tellininae as sister group to the other families, but recovered Macominae nested within Semelidae and Psammobiidae again rendered paraphyletic by a donacid lineage. More recent mitogenomic approaches consistently indicated Psammobiidae as polyphyletic, with multiple basal lineages, and positioned Donacidae as sister group to all remaining families (Sun *et al*., 2020; Tang *et al*., 2025). In these studies, Semelidae was either inferred as sister group to (Tellinidae + (Psammobiidae + Solecurtidae)) (Sun *et al*., 2020) or found nested within Tellinidae (Tang *et al*., 2025). Our results broadly agree with these mitogenomic studies, but with Semelidae resolved as polyphyletic, with some lineages clustering with Macominae and others with Tellininae (as in Taylor *et al*., 2007; Bieler *et al*., 2014; Combosch *et al*., 2017), the latter also appearing polyphyletic in our tree.

The results for Donacidae are congruent with recent investigations that recovered the family as a well-supported monophyletic group based on comprehensive taxonomic sampling (Moncada *et al*., 2022; González-Delgado *et al*., 2024). The family has distinctive morphological characters, such as a duplicated middle mantle fold (Narchi, 1972, 1978; Passos & Domaneschi, 2004) and the incurrent siphon shorter than the excurrent one (Mikkelsen & Bieler, 2007; Batistão *et al*., 2024). Here, we highlight the incurrent aperture with 24 tentacles as a synapomorphy of the family. In contrast to the consistent monophyly of the family, the relationships among genera are divergent. Based on four Sanger-sequenced markers, two mitochondrial (16S rRNA and cytochrome *c* oxidase subunit I [COI]) and two nuclear (18S rRNA and 28S rRNA) markers, *Latona* appeared as the sister group to other donacids, i.e., *Donax* + *Galatea* + *Iphigenia* (Moncada *et al*., 2022). However, our analysis recovered *Donax* + *Latona* as the sister group to *Galatea* + *Iphigenia*, as in the previous UCE-based phylogenomic tree of González-Delgado *et al*. (2024). In addition, anatomical and behavioral data support the phylogenomic results. For example, *Donax* and *Latona* live in the intertidal and surf zones of sandy beaches, with some species showing a tidal migration behavior (Ansell, 1983). Furthermore, *Donax* and *Latona* share branched tentacles in the incurrent siphon, a trait that evolved once in Tellinoidea (Fig. 2A). Conversely, *Galatea* and *Iphigenia* live in freshwater and brackish waters, respectively, which suggests a common ancestor that invaded environments with less salinity, early in the evolution of the family.

Psammobiidae has been pointed out as non-monophyletic polyphyletic in previous molecular approaches. Based on two Sanger-sequenced markers (18S rRNA and 28S rRNA) of three species, i.e., *Asaphis violascens*, *Gari virgata* (Lamarck, 1818), and *G. elongata* (Lamarck, 1818), the family was recovered as paraphyletic (Taylor *et al*., 2007). A more recent analysis of five Sanger-sequenced markers (16S rRNA, 18S rRNA, 28S rRNA, COI, and histone H3) of *A. deflorata* (Linnaeus, 1758) and *G. maculosa* (Lamarck, 1818), also recovered the group as paraphyletic, with *G. maculosa* nested with the donacid *Latona deltoides* (see Combosch *et al*., 2017). Based on mitochondrial protein-coding genes and rRNA genes of two species, *Hiatula diphos* (Linnaeus, 1771) and *Nuttallia obscurata* (Reeve, 1857), the group was revealed as polyphyletic (Ozawa *et al*., 2017). Additionally, a mitogenomic analysis containing five species, i.e., *G. elongata*, *H. acuta* (Y.-Y. Cai & Q.-Q. Zhuang, 1985), *H. chinensis* (Mörch, 1853), *H. ovalis* Bertin, 1880, and *Nuttallia obscurata*, also corroborated the family as polyphyletic (Sun *et al*., 2020). Additionally, a recent mitogenomic analysis containing 11 psammobiids, the most extensive sampling for the family to date, also recovered Psammobiidae as polyphyletic, with two solecurtids nested within a clade of Psammobiidae, and *Gari togata* (Deshayes, 1855) and *Nuttallia obscurata* (Reeve, 1857) constituting the first two offshoots within Tellinoidea (Tang *et al*., 2025).

We also recovered Psammobiidae as polyphyletic, with *Asaphis* and *Gari* clustered with solecurtids, and *Sanguinolaria* as the sister group of a subclade of tellinids. These results are also in line with a recent anatomical investigation that pointed out that, unlike in other families of Tellinoidea, Psammobiidae does not have a uniform pattern of siphonal architecture (Batistão *et al.*, 2024). For example, *A. violascens* and *G. solida* (Gray, 1828) have siphons more similar to those observed in Solecurtidae (see Narchi, 1980; Domaneschi, 1992) than to those of other psammobiids, while the siphons of *S. sanguinolenta* resemble those of the Semelidae and Tellinidae (Batistão *et al.*, 2024). The diagnosis of the family Psammobiidae has always been questionable, based on characters that appear homoplastic in Tellinoidea, e.g., lateral teeth and a missing posterior flexure (Willan, 1993). Consequently, our data reinforce the notion that Psammobiidae, as currently delimited, is not a valid family. Lastly, the nominal genus *Psammobia* Lamarck, 1818 was considered a subgenus of *Gari* by Willan (1993), which separated *Gari sensu stricto* of *Gari* (*Psammobia*) by morphological traits. As the genus *Gari* was inferred as paraphyletic in our analyses, with *G.* (*Psammobia*) *fervensis* closer to *Solecurtus* and *Asaphis* than to *G. modesta* (placed in *Gari sensu stricto*), we emphasize the need for a taxonomic revision of the genus, with a possible revival of *Psammobia*. Future studies with increased taxonomic sampling and morphological characters will be needed to establish a new definition for Psammobiidae and its genera.

Regarding Semelidae and Tellinidae, an analysis with two Sanger-sequenced markers (18S rRNA and 28S rRNA), recovered them as polyphyletic, with the tellinids *Macomangulus tenuis* and *Strigilla euronia* Hedley, 1908 forming a clade with the semelid *Abra alba* (W. Wood, 1802), while the tellinids *Macoma balthica* (Linnaeus, 1758) and *M. nasuta* (Conrad, 1837) grouped with the semelids *Semele carnicolor* (Hanley, 1845) and *S. zebuensis* (Hanley, 1843) in a separate clade (see Taylor *et al.*, 2007). In another investigation using five Sanger-sequenced markers (16S rRNA, 18S rRNA, 28S rRNA, COI, and histone H3) (Bieler *et al.*, 2014), the tellinid *M. balthica* clustered with *A. alba*, and not with the tellinid *S. similis*. Not surprisingly, phylogenetic investigations using Sanger-sequenced markers of new species and mitochondrial genomes have already pointed out Semelidae and Tellinidae as non-monophyletic groups, supporting a close relationship of Macominae *sensu stricto* with some semelids and of Tellininae *sensu stricto* with other semelids (see Combosch *et al.*, 2017; Wang *et al.*, 2023). However, recent phylogenetic investigations based on the genera *Scrobicularia* and *Semele* recovered Semelidae as a monophyletic group nested within Tellinidae (Tang *et al.*, 2025).

Phylogenetic analysis of the sequenced UCEs confirms the non-monophyly of Semelidae and Tellinidae, a result not entirely surprising, considering that the shell and siphonal morphology of semelids and tellinids are very similar (see Willan, 1998; Batistão *et al.*, 2024). The main difference between Semelidae and Tellinidae is the ligament with an internal portion, i.e., a resilium, a characteristic that probably evolved several times within Tellinoidea (Willan, 1998; Coan, 2003), as it has been shown to be more labile than originally thought in other bivalve clades, such as arcids (e.g., Ubukata, 2003). The resilium is probably a trait retained by paedomorphosis several times in some lineages of Tellinidae, which is likely explained by juveniles of Tellinoidea having a small internal ligament (e.g., Webb, 1986; Kamenev & Nadtochy, 1999). Consequently, the resilium cannot be interpreted as a synapomorphy of Semelidae. Therefore, our data strongly suggest that Semelidae, as currently delimited, is not a valid group. Thus, this study reinforces previously proposed hypotheses by introducing new elements, i.e., additional species and a sequence capture approach. Likewise, the genera *Eurytellina* and *Ameritella* were found to be nonmonophyletic, with *A. versicolor* clustering within *Eurytellina*, and *A. janeiroensis* appearing stemward of *S. sanguinolenta*. As *Tellina versicolor* is the type species of *Ameritella*, our results indicate that the genus is invalid. However, the redefinition of the genus must be carried out with accuracy, based on morphological and molecular characters from a broader ranger of species.

4.2 | Evolution of siphonal and ecological traits

We recovered the ancestor of all Tellinoidea as a shallow burrower and suspension feeder (Fig. 2A, B), in line with paleontological evidence based on the pallial sinus of extinct lineages of Tellinoidea. For example, the pallial line is absent in *Unicardiopsis* (Unicardiopsidae) and *Tancredia* (Tancrediidae) and small in *Quenstedtia* (Quenstedtiidae) (Pohlo, 1982). A similar condition is observed in Donacidae, recovered as the sister group of the remaining tellinoids, where all species are suspension feeders with short siphons, except *Iphigenia*, which acquired a deep burrowing habit (Fig. 2A). According to our analyses, the deep-burrowing habit originated in the common ancestor of Psammobiidae, Semelidae, Solecurtidae, and Tellinidae (Fig. 2A), representing a trait that evolved prior to the emergence of deposit-feeding behavior (Fig. 2B).

The results also suggest that the form and number of siphonal tentacles are influenced by the ecological niche of the species, for example, the acquisition of branched tentacles in Tellinoidea occurred only in a clade of suspension feeders that live in the surf zone of sandy beaches, i.e., *Donax* + *Latona* (Fig. 3A). Most species of these genera exhibit tidal migrations (see Ansell, 1983), an unusual behavior compared to most tellinoids that remain permanently burrowed. Compared to other siphonate bivalves, branched tentacles also occur in other lineages that live in turbulent environments, for example, the venerids *Meretrix meretrix* (Linnaeus, 1758), *Periglypta puerpera* (Linnaeus, 1771), and *Venerupis aspera* (Quoy & Gaimard, 1835) (see Sartori *et al*., 2008). Therefore, we interpret the branched tentacles as a possible adaptation to turbulent environments, representing an example of evolutionary convergence across the Bivalvia tree of life.

In contrast, species of the clade *S. sanguinolenta* + Semelidae + Tellinidae show an apparent reduction of the siphonal tentacles, i.e., from digitiform to lobed, including an evolutionary trend of complete loss of tentacles, which convergently occurred at least six times (Fig. 3A, B). The main function of siphonal tentacles is to act as strainers, serving as an initial barrier for particle selection; however, performing a sieving action is less important when detritus is the primary source of food (see Yonge, 1949). Not surprisingly, Pohlo (1982) delineated three feeding categories for tellinoids based on siphonal tentacle morphology. According to his framework, digitiform tentacles (termed *straining tentacles* by Pohlo) were associated with selective suspension feeding, whereas lobed tentacles (referred to as *short tentacles* by Pohlo) were linked to non-selective suspension feeding. Furthermore, lobed tentacles and siphonal apertures lacking tentacles were also related to deposit feeding. Consistent with this, we also interpret the reduction and loss of siphonal tentacles as a trait associated with deposit feeding. One curious exception is *Strigilla pisiformis*, a deposit feeder with six digitiform tentacles. Other exceptions within the clade *S. sanguinolenta* + Semelidae + Tellinidae are *Semele proficua* and *S. purpurascens*, exclusive suspension feeders with six and twelve digitiform tentacles, respectively (Domaneschi, 1982, 1995; Batistão *et al*. 2024). Based on our analyses, the deposit-feeding habit was likely lost in the *Semele* lineage, and digitiform tentacles were acquired independently, representing an example of convergent evolution in lineages that have reverted to exclusive suspension feeding. Curiously, a transition to the lobed form is also convergent in *Solecurtus*, a group of suspension feeders (Bromley & Asgaard, 1990) not included in the clade *S. sanguinolenta* + Semelidae +

Tellinidae. Since we do not distinguish between selective and non-selective suspension feeders, our results support Pohlo's (1982) proposed associations, indicating that lobed tentacles are a common feature in both suspension and deposit feeders. Moreover, lobed tentacles are also convergent in other lineages of suspension-feeding bivalves, such as in the venerid *Dosinia kaspiewi* Fischer-Piette & Delmas, 1967 (see Sartori *et al*., 2008), indicating that lobed tentacles are not restricted to deposit feeders. Finally, some venerids such as *Paratapes undulatus* (Born, 1778), have also lost the siphonal tentacles of the incurrent aperture (Sartori *et al*., 2008), demonstrating that factors other than feeding influence the morphology of the siphonal aperture.

Another lineage of bivalves that typically employs deposit feeding is Protobranchia. By using extensile palp proboscides, protobranchs collect and sort detritus below the sediment surface. Most protobranchs thrive in the deep sea, with few species found on beaches, where tellinoids are abundant, especially in the subtidal habitat (Zardus, 2002; Huber, 2010). Furthermore, Tellinoidea is one of the few groups of Autobranchia with a lineage able to exploit deposited organic matter as the main food resource, which also occurs in a few species of Mactridae (e.g., Defeo & Scarabino, 1990; Barnes & Morton, 1997). Therefore, it is tempting to associate the species diversity of Tellinoidea with a deposit-feeding habit, since the group thrived in an environment not properly colonized by Protobranchia. Not surprisingly, the clade *S. sanguinolenta* + Semelidae + Tellinidae corresponds to 77.6% of the living species in Tellinoidea (see Table 1). The use of the incurrent siphon as a vacuum for surface detritus is probably a key innovation, i.e., a innovation that allowed the group to exploit a novel mode of life (Jablonski, 2022).

Finally, an investigation revealed that transitions of the incurrent and excurrent apertures of the mantle of Mytilidae (treated as siphons by some authors, e.g., Soot-Ryen, 1955) are associated with differential presence on the substrate, indicating possible adaptations and convergences in different lineages (Audino *et al*., 2020). Our results also point to possible adaptations and convergences, exemplifying the importance of exploring macroevolutionary questions in truly siphonate bivalves (Anomalodesmata + Imparidentia) and inferring evolutionary trends for a megadiverse group in tropical shallow waters. The same approach with other diverse lineages of siphonate bivalves, e.g., Veneroidea, may bring new insights into the evolution of these organs, given that siphons have already been indicated as playing a key role in the taxonomic diversity of Veneridae, the most speciose family of Bivalvia (Nigro *et al*., 2025). The siphons emerged likely as an evolutionary response to the diversification of predatory pressures during the Mesozoic Marine Revolution (see Vermeji, 1977), but opened the vault of new ecological scenarios to distinct infaunal lineages of soft and hard substrates.

5 | Conclusion

In conclusion, we provide a well-supported evolutionary tree of Tellinoidea using UCEs. The analysis recovered Donacidae as monophyletic, while Psammobiidae, Semelidae, Solecurtidae, and Tellinidae were non-monophyletic. Other lineages recovered as non-monophyletic are the subfamily Tellininae and the genera *Ameritella*, *Eurytellina*, and *Gari*. Accordingly, the resulting topology facilitated incremental advancements within a large superfamily and provided a meaningful benchmark for evaluating a sequence-capture approach. Furthermore, an investigation of siphonal and ecological traits revealed possible adaptations and convergences of forms and habits at different taxonomic levels, with the deposit-feeding habit as a possible key innovation for the group. In general, our results demonstrate that siphons are a valuable data source for macroevolutionary questions and that UCEs are a feasible way forward to explore phylogenetic relationships of tellinoids as well as for other bivalves.

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Figure 1. Maximum likelihood phylogenetic hypothesis of Tellinoidea, based on 50% occupancy matrix containing 33 taxa, including both historical and recently collected samples. Donacidae is the only family recovered as monophyletic, while Psammobiidae, Semelidae, Solecurtidae, and Tellinidae are non-monophyletic taxa.

Figure 2. Evolution of the mode of life and feeding habit in Tellinoidea. Ancestral state estimation of burrowing depth (A) and feeding habit (B) in all five extant families of Tellinoidea, under an evolutionary model of equal transition rates estimated by Bayesian stochastic character mapping. The deep burrowing behavior evolved twice and the deposit feeder habit once in Tellinoidea.

Figure 3. Evolution of the form and number of siphonal tentacles in the incurrent aperture of Tellinoidea. Ancestral state estimation of form (A) and number (B) of siphonal tentacles of the incurrent aperture in all five extant families of Tellinoidea, under an evolutionary model of symmetrical transition rates (A) and equal transition rates (B) estimated by Bayesian stochastic character mapping. Branched tentacles evolved in *Donax* + *Latona* while the loss of tentacles happened at least six times within the clade *Sanguinolaria sanguinolenta* + Semelidae + Tellinidae.

Figure 4. Siphonal tentacle morphology. (A) Digitiform tentacles of *Dallocardia muricata* (Cardiidae), (B) *Semele proficua*, and (C) *S. purpurascens*. (D) Lobed tentacles of *Solecurtus sanctaemarthae* (Photo courtesy of Alvaro E. Migotto). (E) Siphonal aperture devoid of tentacles of *Ameritella versicolor*. (F) Branched tentacles of *Latona deltoides* (Photo courtesy of Denis Riek).

Table 1. Families of Tellinoidea with the number of extant based on MolluscaBase and taxonomic sampling used in the study. Apart from these, Tellinoidea has five extinct families, i.e., Icanotiidae, Quenstedtiidae, Sowerbyidae, Tancrediidae, and Unicardiopsidade.

Family	Number of extant species	Number of species used in the study	Percentage representation of our sample
Donacidae J. Fleming, 1828	111	9	8,1%
Psammobiidae J. Fleming, 1828	102	5	4,9%
Semelidae Stoliczka, 1870 (1825)	161	4	2,5%
Solecurtidae A. d'Orbigny, 1846	40	3	7,5%
Tellinidae Blainville, 1814	540	12	2,2%

Table 2. Taxa of Tellinoidea and outgroup included in the UCE-based phylogenomic analysis. The specimens are from different scientific collections: MCZ (Museum of Comparative Zoology), NMNH (National Museum of Natural History), and ZUEC BIV (Bivalvia collection of Museum of Biological Diversity of State University of Campinas). The species *Scissula similis* is originates from the BivAToL project (Bivalve Assembling the Tree-of-Life), therefore the code does link to other publications but not to the specimen. Finaly, the specimens were classified as 'fresh' when collected up to 20 years ago and preserved in ca. 95% ethanol at -20 ºC and as 'historical' when collected more than 10 years ago and preserved in 70–80% ethanol at room temperature.

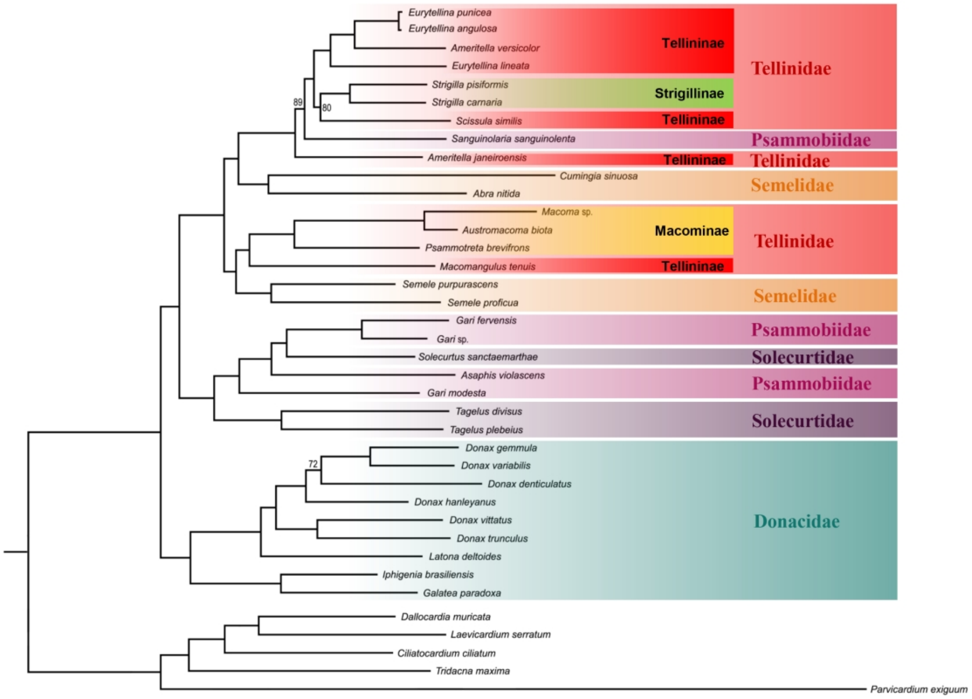
Family	**Species**	**Country**	**Voucher**	**Sample condition**	**Year**	**Age (years)**
Donacidae	*Donax denticulatus* Linnaeus, 1758	Puerto Rico	NMNH 660273	Historical	1964	61
Donacidae	*Donax gemmula* J. P. E. Morrison, 1971	Brazil	ZUEC BIV 3837	Fresh	2012	13
Donacidae	*Donax hanleyanus* R. A. Philippi, 1847	Brazil	ZUEC BIV 8423	Fresh	2022	3
Donacidae	*Donax trunculus* Linnaeus, 1758	Portugal	ZUEC BIV 4394	Fresh	2013	12
Donacidae	*Donax variabilis* Say, 1822	USA	MCZ 393936	Fresh	2019	6
Donacidae	*Donax vittatus*	Scotland	MCZ 393679	Fresh	2019	6

	(da Costa, 1778)					
Donacidae	*Iphigenia brasiliensis* (Lamarck, 1818)	Brazil	ZUEC BIV 8416	Fresh	2021	4
Donacidae	*Galatea paradoxa* (Born, 1778)	Ghana	MCZ 396035A	Fresh	2020	5
Donacidae	*Latona deltoides* (Lamarck, 1818)	Australia	MCZ 378960	Fresh	2008	17
Psammobiidae	*Asaphis violascens* (Forsskål, 1775)	Tokelau (New Zealand)	NMNH 768341	Historical	1976	49
Psammobiidae	*Gari* sp.	Japan	MCZ 378911	Fresh	2004	21
Psammobiidae	*Gari fervensis* (Gmelin, 1791)	Spain	MCZ 371762	Historical	2002	23
Psammobiidae	*Gari modesta* (Deshayes, 1855)	Australia	MCZ 378976	Fresh	2002	23
Psammobiidae	*Sanguinolaria sanguinolenta* (Gmelin, 1791)	Brazil	ZUEC BIV 8426	Fresh	2022	3
Semelidae	*Abra nitida* (O.	Sweden	MCZ 378812	Fresh	2004	21

	F. Müller, 1776)					
Semelidae	*Cumingia sinuosa* A. Adams, 1850	USA	MCZ 359000	Historical	1972	53
Semelidae	*Semele proficua* (Pulteney, 1799)	Brazil	ZUEC BIV 2477	Fresh	2010	15
Semelidae	*Semele purpurascens* (Gmelin, 1791)	Brazil	ZUEC BIV 8442	Fresh	2023	2
Solecurtidae	*Solecurtus sanctaemarthae* d'Orbigny, 1853	Brazil	ZUEC BIV 8405	Fresh	2022	3
Solecurtidae	*Tagelus divisus* (Spengler, 1794)	Brazil	ZUEC BIV 2461	Fresh	2010	15
Solecurtidae	*Tagelus plebeius* ([Lightfoot], 1786)	Brazil	ZUEC BIV 8428	Fresh	2022	3
Tellinidae	*Ameritella janeiroensis* (Jaeckel, 1927)	Brazil	ZUEC BIV 2444	Fresh	2010	15
Tellinidae	*Ameritella versicolor* (De Kay, 1843)	Brazil	ZUEC BIV 8441	Fresh	2023	2

Tellinidae	*Austromacoma biota* (Arruda & Domaneschi, 2005)	Brazil	ZUEC BIV 1856	Fresh	2010	15
Tellinidae	*Eurytellina angulosa* (Gmelin, 1791)	Brazil	ZUEC BIV 3434	Fresh	2010	15
Tellinidae	*Eurytellina lineata* (W. Turton, 1819)	Brazil	ZUEC BIV 8437	Fresh	2023	2
Tellinidae	*Eurytellina punicea* (Born, 1778)	Brazil	ZUEC BIV 1967	Fresh	2010	15
Tellinidae	*Macomangulus tenuis* (da Costa, 1778)	Scotland	MCZ 393670	Fresh	2019	6
Tellinidae	*Macoma* sp.	Nigeria	NMNH 796535a	Historical	1979	46
Tellinidae	*Psammotreta brevifrons* (Say, 1834)	Brazil	ZUEC BIV 8440	Fresh	2023	2
Tellinidae	*Scissula similis* (J. Sowerby, 1806)	USA	BivAToL-7	Fresh	2005	20
Tellinidae	*Strigilla carnaria*	Brazil	ZUEC BIV 8461	Fresh	2023	2

	(Linnaeus, 1758)					
Tellinidae	*Strigilla pisiformis* (Linnaeus, 1758)	Brazil	ZUEC BIV 3786	Fresh	2012	13
OUTGROUP						
Cardiidae	*Ciliatocardium ciliatum* (O. Fabricius, 1780)	Denmark	MCZ 378920	Fresh	2010	15
Cardiidae	*Dallocardia muricata* (Linnaeus, 1758)	Brazil	ZUEC BIV 3437	Fresh	2011	14
Cardiidae	*Laevicardium serratum* (Linnaeus, 1758)	Curaçao (Netherlands)	MCZ 383045	Fresh	2015	10
Cardiidae	*Parvicardium exiguum* (Gmelin, 1791)	Spain	MCZ 379119	Fresh	2004	21
Cardiidae	*Tridacna maxima* (Röding, 1798)	Cultured	MCZ 381362	Fresh	2014	11



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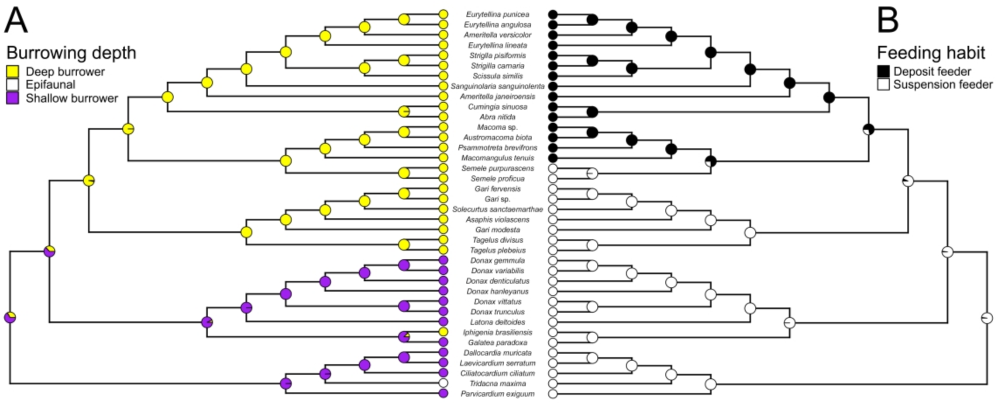

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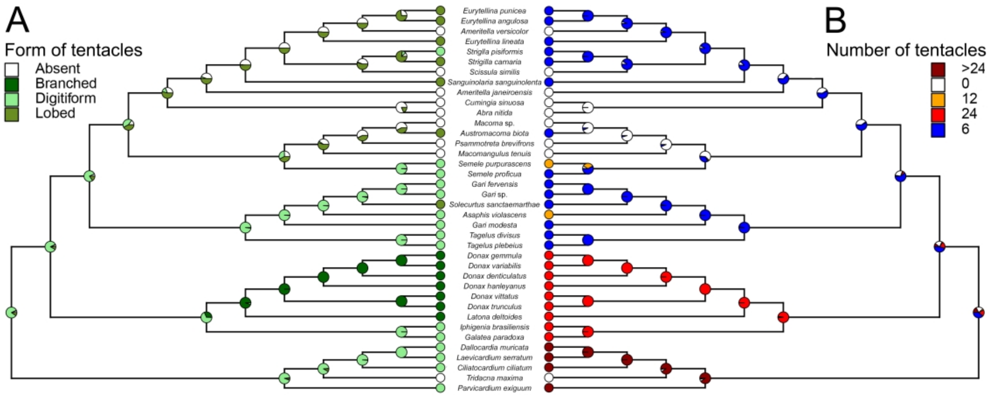

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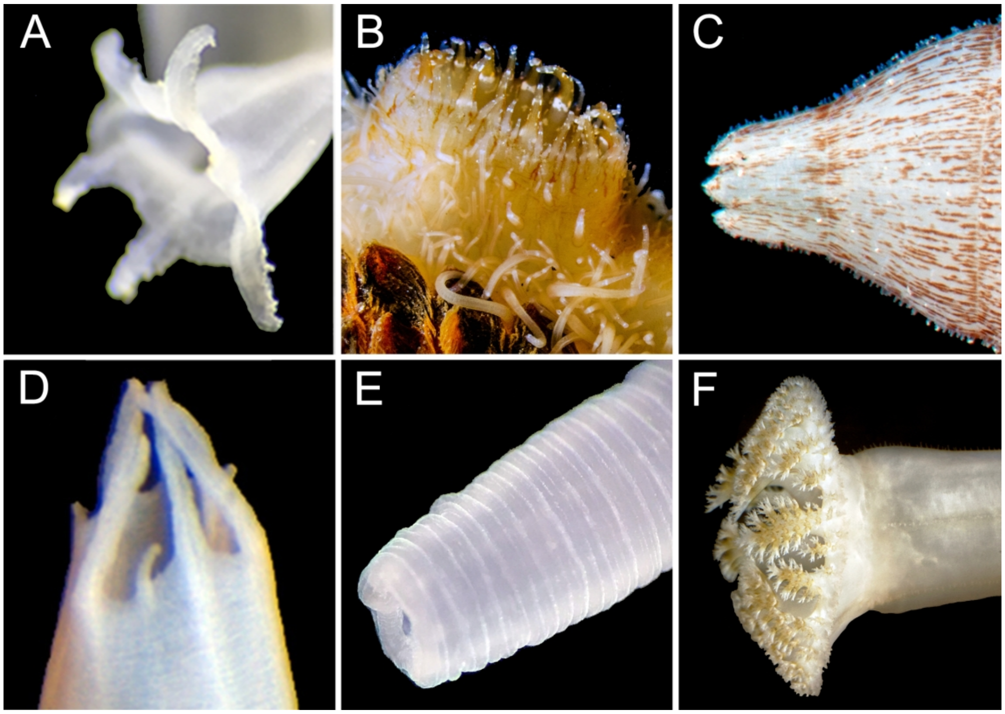

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183x129mm (300 x 300 DPI)