ABSTRACT

The discovery of bivalved sea slugs in the family Juliidae revolutionized our understanding of shell evolution in molluscs. However, relationships among lineages remain unclear, with generic names shared by extant and fossil taxa. Juliidae provides important fossil calibration points for dating phylogenies and for understanding the convergent evolution of a bivalved shell. Here, we present a revision of the systematics and classification of members of the Juliidae including Recent and fossil taxa by integrating molecular data from five genes, geometric morphometrics, and anatomical data. A list of all Juliidae taxa previously described is provided, along with diagnoses and remarks of genus-level names. Results from a geometric morphometric analysis support a new classification scheme in which the genus *Berthelinia*, previously used for Recent and fossil taxa, is restricted to fossil species, and the genera *Julia* and *Edenttellina* are exclusively used for Recent species. Species of *Edenttellina* supported by molecular analyses are illustrated and anatomical details provided, including examination of protoconchs, radular teeth, and reproductive structures by scanning electron microscopy, along with illustrations of existing type material. Distinct biogeographic patterns in *Julia* and *Edenttellina* are discussed in the context of ecological differences between these two taxa, including host specificity and developmental mode.

Key words: taxonomy, fossil and Recent taxa, molecular phylogenetics, species delineation.

INTRODUCTION

The family Juliidae E. A. Smith, 1885 (Mollusca, Gastropoda, Panpulmonata: Sacoglossa) is morphologically unique among gastropods as the only group with a bivalved shell (Kawaguti & Baba 1959; Keen & A. G. Smith 1961; Kay 1968; Jensen 1996). Juliids were originally described from shell material, and have been historically and consistently classified as members of the Bivalvia (Gould 1862; Deshayes 1863; E. A. Smith 1885; Cossmann 1887; Beets 1944; Habe 1952), except for a few authors who hesitantly assigned single valves from Juliidae to various heterobranch sea slug groups (Carpenter 1857; Crosse 1875; Hedley 1912). However, the discovery of the first living animals by Kawaguti & Baba (1959) made evident their taxonomic placement in the Sacoglossa (Cox & Rees 1960; Burn 1960a), resulting in the re-assignment of previously described taxa (Cox & Rees 1960; Keen 1960b; Kay 1962b; Boettger 1962; Le Renard 1980). Placement of Juliidae within the shelled sacoglossans was confirmed by later phylogenetic studies (Jensen 1996; Händeler & Wägele 2007; Krug et al. 2015).

Depending on the classification scheme (see Keen & A. G. Smith 1961; Boettger 1962; Kay 1968; Le Renard 1980, 1989; Le Renard et al. 1996; Burn 1998, 2006; Schneider et al. 2008), Juliidae includes 3–8 valid genera represented in the fossil record (*Julia* Gould, 1862; *Berthelinia* Crosse, 1875; *Anomalomya* Cossmann, 1887; *Ludovicia* Cossmann, 1887; *Hemiplicatula* Deshayes, 1861; *Saintia* de Raincourt, 1877; *Namnetia* Cossmann 1905; *Gougerotia* Le Renard, 1980; and *Candinia* Le Renard, Sabelli & Taviani, 1996), as well as 2–5 genera containing extant species (*Julia*; *Berthelinia*; *Tamanovalva* Kawaguti & Baba, 1959; *Edenttellina* Gatliff & Gabriel, 1911; and *Midorigai* Burn, 1960). Conflicting classifications resulted primarily from the incongruent use of traits in taxonomic decisions as well as inconsistencies between the neontological and paleontological literature, which underscore the need for taxonomic revision in Juliidae.

Early descriptions of Recent and fossil species relied exclusively on shell morphology (Gould 1862; Cossmann 1887; Crosse 1887; Gatliff & Gabriel 1911; Hedley 1920); characteristics such as the color, thickness, size, and overall shape of the shell and hinge were considered important to characterize and delineate species (Beets 1944, 1949; Howard 1951; Habe 1952; Keen & A.

G. Smith, 1961; Boettger 1962). More recently, after the discovery of living Juliidae, the emphasis has shifted toward the of traits of the reproductive and digestive systems for taxonomic classification, including the radulae (Kawaguti & Baba 1959; Edmunds 1963; Kawaguti 1981; Jensen 1996, 1997a, 1997b, 2015). Descriptions of fossil taxa can only be based on shells because internal anatomical details are rarely preserved, but paleontologists have focused on conchological features such as the shell hinge, the adductor muscle scars, and the protoconch, in addition to overall shell shape (Boettger 1962; Bałuk & Jakubowski 1968; Le Renard 1980, 1989; Le Renard et al. 1996; Schneider et al. 2008).

These different emphases have created two parallel taxonomies within Juliidae, one based exclusively on shell morphology (for fossils and early descriptions of Recent species) and another based on both shell and internal morphology (for contemporary descriptions of Recent species). To make matters worse, the shells in species of Juliidae are difficult to compare as they do not possess many discrete distinguishing characteristics at the species level, apart perhaps from protoconch morphology and the shape and location of the adductor muscle scar (Kawaguti & Baba, 1959; Baba 1961b; Jensen 1997a). At the genus level, shell differences are more apparent; for example, the Recent genera *Julia* and *Berthelinia* are easily distinguishable by the overall shape and thickness of the shell. However, continuous traits are notoriously difficult to quantify, and subjective interpretations of those traits have resulted in authors considering *Berthelinia* as a single genus (Jensen 2011, 2015) or splitting this group into four genera (Burn 1998, 2006).

While molecular approaches can address outstanding taxonomic issues in Recent Juliidae, two of the Recent genera are also represented in the fossil record. An integrative approach to resolve the systematics of this group must therefore evaluate the taxonomy of extinct as well as Recent taxa in a quantitative framework. In this paper, we provide a revised classification of extinct and extant Juliidae at the genus level using a combination of morphological and molecular data. Molecular analyses were conducted using two mitochondrial genes (CO1, 16S) and three nuclear genes (H3, 18S, 28S). Because of the lack of discrete and distinctive traits in the shells of Juliidae, we use geometric morphometrics to quantify differences among shells, along with more traditional characters from radular morphology and other soft body traits. In the course of this study, several species-level Recent taxa were also identified. However, the basis for identifying the recognized species of the genus *Julia*, and descriptions of new species, will be presented in a separate monographic work.

MATERIALS AND METHODS

Source of specimens

Fifty-six specimens of Juliidae covering the geographic range of this group (Fig. 1) were sequenced for the molecular portion of this study (Table 1). Five species were used as outgroups: two species of *Ascobulla* and three of *Volvatella*, based on the results of prior phylogenetic analyses of Sacoglossa (Krug et al. 2015) that recovered *Ascobulla* and *Volvatella* as related members of the Oxynoacea. Specimens were obtained in the field by collecting algal substrate, placing it in trays with seawater, and waiting for animals to crawl out. Specimens were preserved in 95% ethanol and deposited at the California State Polytechnic University Invertebrate Collection (CPIC). Additional specimens and/or photographs of type material were obtained from the following museums: Natural History Museum of Los Angeles County (NHMLA, initialism LACM), California Academy of Sciences, Invertebrate Zoology, San Francisco (CASIZ), Museo de Zoología, Universidad de Costa Rica (MZUC), Muséum National d'Histoire Naturelle, Paris (MHNH), Museums Victoria, Melbourne (MV), Australian Museum, Sydney (AM), Natural History Museum of the United Kingdom, London (NHMUK), Smithsonian Institution, Washington, D.C. (USNM), Zoological Reference Collection, National University of Singapore (ZRC), Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), Paleontological Research Institution, Ithaca (PRI), Florida Museum of Natural History, Gainesville (FMNH), Bernice Pauahi Bishop Museum, Honolulu (BM), and Museum and Art Gallery Northern Territory, Australia (NTM). Sequences for six additional specimens were obtained from GenBank.

DNA extraction, amplification, and sequencing

All tissue samples were obtained from specimens in a sterile environment using flamed forceps and razor blades. Specimens were placed under a dissecting microscope and the shell gently pried open; 0.5 mg of tissue was removed from the mantle or foot, depending on the size of the specimen. DNA extractions were initially performed using a hot Chelex® (Bio-Rad, Hercules, CA, USA) protocol as follows. Tissue samples were macerated and placed in 1 ml of TE buffer (Tris:EDTA). Tubes were capped and placed onto a rotator block for ≥20 min, mixed by vortexing for 15 sec, and centrifuged for 3 min at 21130.2 × g; 975 µL buffer was removed without disturbing the pellet and 175 µL of 10% Chelex® added. Tubes were then heated on a water bath at 56 ºC for ≥20 min. Tube contents were mixed by vortexing for 15 sec, heated dry for 8 min at 100 ºC, mixed by vortexing for 5 sec and centrifuged for 3 min at 21130.2 × g. If DNA yield was low or if specimens were older than 10 years, a Qiagen DNeasy® (Qiagen, Germantown, MD, USA) kit was used for DNA extraction following the manufacturer's protocols.

The Polymerase Chain Reaction (PCR) was performed to amplify the two mitochondrial (CO1, 16S) and three nuclear (H3, 28S, 18S) gene regions using universal primers (Table 2). The PCR master mix volume was 50 µL per reaction, containing: 33.75 µL of H_2O, 0.25 µL of DreamTaq, 5 µL of 10× DreamTaq Buffer, 5 µL of 2 mM dNTPs, 3 µL of 25 nM $MgCl_2$, 1.5 µL of each forward and reverse primers, and 2 µL of DNA template. Reaction conditions for CO1 were: initial 95 ºC denaturation for 3 min, 35 cycles of 94 ºC for 45 sec (denaturation), 45 ºC for 45 sec (annealing), 72 ºC for 45 sec (elongation), followed by a final elongation step at 72 ºC for 10 min. Reaction conditions for 16S and H3 were: initial 94 ºC denaturation for 2 min, 35 cycles of 94 ºC for 30 sec (denaturation), 50 ºC for 30 sec (annealing), 72 ºC for 1 minute (elongation), followed by a final elongation step at 72 ºC for 7 min. Reaction conditions for 28S were: initial 95 ºC denaturation for 2 min, 38 cycles of 94 ºC for 30 sec (denaturation), 52.5 ºC for 30 sec (annealing), 72 ºC for 90 sec (elongation), followed by a final elongation step of 72 ºC for 10 min. Reaction conditions for 18S were: initial 95 ºC denaturation for 2 min, 40 cycles of 94 ºC for 30 sec (denaturation step), 45 ºC for 30 sec (annealing step), 72 ºC for 1 minute (elongation step), followed by a final elongation step at 72 ºC for 7 min. PCR products were purified using Genejet purification kits and sent to Source Bioscience (Santa Fe Springs, CA, USA) for Sanger sequencing. Sequences were assembled and edited in Geneious Pro R8 (Kearse et al. 2012).

Phylogenetic analyses

Alignments for each gene were generated with the MUSCLE (Edgar 2004) option implemented in Geneious. Two concatenated alignments were created, one including all five genes (16S + CO1 + H3 + 18S + 28S) and another including only mitochondrial (mtDNA) genes (16S + CO1). Concatenated alignments were analyzed in JModelTest 2.1.10 (Darriba et al. 2012) using the Akaike Information Criterion (Akaike 1974) to determine the best fit models of sequence evolution. Phylogenetic analyses were conducted using the following taxa as outgroups: *Ascobulla* cf. *ulla* (Marcus & Marcus, 1970), *Ascobulla* sp. 1, *Volvatella* sp. 2*, Volvatella ventricosa* Jensen & Wells, 1990*,* and *Volvatella viridis* Hamatani, 1976. Bayesian analyses were run in MrBayes 3.2.6 (Ronquist et al. 2012) with nst = 6, rates = gamma for all genes, and a separate model for each of the five gene partitions. Markov chain Monte Carlo (MCMC) simulations were performed with two runs of six chains for 10^7 generations, with sampling every 1000 generations. Convergence was assessed with Tracer 1.7 (Rambaut et al. 2018). A 25% burn-in was applied before constructing the majority-rule consensus tree. Maximum likelihood analyses were conducted using raxmlGUI 1.0 (Silvestro & Michalak 2012) using the bootstrap + consensus option (10^4 pseudoreplicates) and the GTR+G model for the entire dataset.

Species delimitation analysis

Automatic Barcoding Gap Discovery (ABGD) species delimitation analysis was performed on CO1 and 16S haplotypes after collapsing identical sequences. Genetic distances among individuals were calculated in MEGA 11 (Tamura et al. 2021) using the Tamura-Nei + G (1.88) model (COI) or K2P + G (0.5) model (16S). Each distance matrix was then analyzed using the ABGD webtool (Puillandre et al. 2012) with default settings except for a reduced relative gap width (X = 1.2). Results from both initial and recursive partitions were compared with support for species hypotheses from morphological data. The 16S analysis was run after changing the default pmax value to 0.5. Analyses performed on each genus separately and on the combined dataset yielded the same outcomes.

A second method of species delimitation analyzed the same distance matrices by Assemble Species by Automatic Partitioning or ASAP (Puillandre et al. 2021), as implemented by the webtool (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html). The number of species supported by the highest ASAP score and the associated barcode gap was compared with the number supported by the barcode gap closest to that recovered by ABGD.

A third method used the Bayesian implementation of the Poisson Tree Processes (bPTP) algorithm (Zhang et al. 2013). An unrooted COI guide tree was generated in RAxML using separate GTR + Γ models for the first two versus third codon positions. The tree was then uploaded to the bPTP webtool (https://species.h-its.org/ptp/) and MCMC simulations run for 10^5 generations, discarding 25% as burn-in. The acceptance rate was 0.13. Outputs of both ML and BI partitions were examined to assess support for all species (see Results). Groups supported by one or more methods of delimitation were considered candidate species and their status further evaluated using morphological data.

Morphological data

At least two preserved specimens of each candidate species of *Edenttellina* recovered in the ABGD analysis were examined morphologically. The two valves were separated exposing the soft parts of the animal, which were photographed using a Leica EZ4D microscope with a built-in digital camera. The anterior portion of the digestive system and the reproductive organs were examined and photographed. The penis of each specimen was dissected and photographed using a Nikon Eclipse E400 microscope with an attached Nikon D70 digital camera. In a few cases, penises were submerged in hexamethyldisilazane for 24 hours until all the liquid evaporated; the resulting hardened structure was mounted for SEM imaging.

To isolate the radula, the buccal mass of 2–3 specimens were placed in 10% sodium hydroxide (NaOH) for ≥48 hr. Radulae were then rinsed in deionized water, placed on an SEM stub, and coated with either an Emitech K550X Sputter Coater (NHMLA) or a Denton Vacuum Desk V HP Sputter Coater (California State Polytechnic University, Pomona). Samples were imaged with a Hitachi S-3000N variable pressure SEM (NHMLA) or a Jeol JSM-6010 variable pressure SEM (California State Polytechnic University, Pomona).

The external surface of the uncoated shell of at least three specimens of each candidate species was photographed using a Leica EZ4D microscope with a built-in digital camera. At least one of the shells was also examined by SEM, including the outer side of the left valve (to illustrate the sculpture), the inner side of the right valve (to illustrate the adductor muscles), the protoconch, and the hinges of both valves.

Geometric morphometrics

Source of images and shell preparation

The list of specimens used in the geometric morphometrics analysis are provided in Table 3. For available species, shells were gently removed from representative specimens with forceps and mounted on stubs for scanning electron microscopy (SEM). Left valves were placed with the lateral portion facing upward to give a view of the larval shell (protoconch). Right valves were placed with the medial portion facing up to give a view of the adductor scar. Shell valves were coated with an Emitech K550X Sputter Coater at the Natural History Museum of Los Angeles (NHMLA) County or a Denton Vacuum Desk V HP Sputter Coater at California State Polytechnic University, Pomona. Specimens were imaged using a Hitachi S-3000N variable pressure SEM at NHMLA or a Jeol JSM-6010 variable pressure SEM either coated or uncoated in low-vacuum at California State Polytechnic University, Pomona. For species that could not be imaged with SEM, photographs with scale bars were obtained from the literature (Table 3).

Image preparation and analysis

SEM images or photographs from the literature were measured using the software FIJI (Schindelin et al. 2012), employing a protocol adapted from Sherratt et al. (2016) and Edie et al. (2022). The segmented line tool was used to measure the scale bar in each image and the scale was set under the analyze tab tool. Each valve image was then outlined using the segmented line tool beginning anterior to the apex and ending posterior to the valve's apex. This line was then transformed into a curved line using the fit spline tool, then converted into XY coordinates, which were processed in the R (R Development Core Team 2008) version of Geomorph (Adams & Otarola-Castillo 2013). Within Geomorph, the XY coordinates were transformed into 100 evenly placed points along the outline of the shell: the first and last points were designated as landmarks anterior and posterior to the apex and the other 98 were designated as sliding semi-landmarks. A Procrustes analysis was performed on each specimen in Geomorph and a Principal

Component Analyses (PCA) was run with a set of specimens (including Recent and fossil taxa) that represented the morphological variation in Juliidae.

RESULTS

Phylogenetic analyses

Both Bayesian and maximum likelihood analyses of the five concatenated genes recovered both *Julia* and *Edenttellina* as monophyletic and well supported, BS=99, PP=0.99 and BS=100, PP=1 respectively (Fig. 2). However, in the mtDNA-only trees (Fig. S1), a specimen of *Julia* sp. 2 is sister to both *Edenttellina* and the rest of *Julia*; *Edenttellina* is also well supported (BS=97, PP=1), as is the other species of *Julia* (BS=81, PP=0.97). The topology of the rest of the concatenated five-gene tree is very similar to the mtDNA analyses. Both trees contain several well-supported clades that correspond to the species recovered in the ABGD analyses (BS/PP support given for the five-gene, mtDNA datasets): *E. singaporensis* (100/1, 96/0.99), *E. babai* (100/1, 97/0.98), *E.* cf. *rottnesti* (100/1, 100/1), *E. caribbea* (100/1, 100/1), *E. chloris* (100/1, 100/1), *Julia* sp. 1 (100/1, 100/1), *Julia* sp. 3 (100/1, 88/0.99), *Julia burni* (1/100, 99/1), *Julia mishimaensis* (100/1, 97/0.99), *J. zebra* (100/1, 100/1). The only species recognized in this study that were either not well supported or had unknown support values are: *E. pseudochloris* (-/-, 77/-), *E. typica* (only one specimen available), *J. exquisita* (68/0.86, 68/0.8), and *Julia* sp. 2 (100/1, only one specimen included in the mtDNA analyses).

Species delimitation

There was no clear barcoding gap in the distribution of pairwise distances for either COI or 16S (Fig. 2). The ABGD analysis for COI distances recovered 10 species entities with a barcoding gap of 13.5% for the initial partition, which corresponded to the morphologically distinctive species described herein (see Systematics) with three exceptions: *E. babai* was lumped with *E. singaporensis*; *E. chloris* was lumped with *E. pseudochloris*; and *J. mishimaensis* was split into two species. The same result was obtained from the recursive partition with a prior maximal distance of 4%, except *E. chloris* and *E. pseudochloris* were recovered as distinct (Table 4, Fig.

2). ABGD results for 16S were the same for the initial partition and recursive partitions using a prior maximal distance of roughly 1%. A barcoding gap of 3.7% was supported, under which described and candidate morphospecies were recovered as separate entities with the following exceptions: *E. caribbea* and *Julia* sp. 1 were both split into two cryptic species; *E. chloris* was lumped with *E. pseudochloris*; and *J. exquisita* was lumped with *Julia* sp. 3 (Table 4).

ASAP analysis of the COI data yielded a significantly favored partition with 16 species under a threshold distance of ~7%. All traditional and candidate species were separated, while *E. caribbea*, *J. mishimaensis* and *J. zebra* were split into two entities, and *Julia* sp. 3 was split into three entities (Table 4). Only a partition with a threshold distance of 12% recovered the 10 species supported by the more conservative ABGD analysis. For 16S, the most favored ASAP partition had a threshold distance of 1.65% and supported 21 species: *E. caribbea*, *J. burni* and *Julia* sp. 1 were each split into two cryptic entities, while *J. mishimaensis*, *J. exquisita*, and *J. zebra* were split into three entities apiece. Results comparable to ABGD were only obtained with a less favored partition that recovered a 4.25% threshold distance.

The bPTP analysis of the COI guide tree supported a mean of 18 species (range: 14 to 21 OTUs). As above, the majority of morphospecies were split into two (*E. caribbea*, *E. pseudochloris, J. mishimaensis*, *J. exquisita*, *J. zebra*) or three (*Julia* sp. 3) cryptic species entities. No species were lumped by bPTP (Table 4).

Morphological data

Morphological examinations of specimens revealed consistent differences between all the species recovered by species delimitation analyses. The species pairs *E. chloris – E. pseudochloris* and *J. exquisita – Julia* sp. 3 were neither recovered as reciprocally monophyletic in the five-gene phylogenetic analyses, nor as distinct species in the ABGD 16S analysis; however, those sister species could be distinguished by morphological differences described herein, and were reciprocally monophyletic in the mtDNA analysis. They are therefore regarded as distinct species. Additionally, specimens assigned to *E. caribbea* were recovered as two species in the 16S ABGD analysis, but no consistent morphological differences were found to support this split, so they are regarded as a single species. The morphology of all species is described, illustrated, and discussed in the Systematics section below.

Geometric morphometrics

In the Principal Component Analysis (PCA) of all examined Juliidae shell material (Table 3), PC1 explained the majority of the variance (85%) while PC2 explained 8% of the variance. On the score plot, five clusters of taxa were broadly separated into distinct quadrats (Fig. 3). All *Julia* spp. had positive scores for PC2, and fell into three clusters separated by PC1 scores. Cluster 1 comprised one fossil, the type specimen of *Prasina borbonica* Deshayes, 1863*,* and one specimen of an extant species identified as *J. japonica* (but no molecular data were available to confirm its phylogenetic placement). Cluster 1 was differentiated from other *Julia* and *Candinia* specimens by large, negative PC1 scores. Cluster 2 included specimens of the fossil genus *Candinia* and two Recent *Julia: J. thecaphora* and one specimen identified as *J. exquisita*. Within cluster 2, more negative PC1 scores separated fossil specimens of *C. krachi* from extant *Julia* spp. Cluster 3 (positive PC1 scores) included the remaining extant *Julia* spp.: *J. mishimaensis, J. zebra*, and specimens provisionally identified as *J. exquisita,*

Two other clusters were separated from *Julia* and *Candinia* by negative PC2 scores, with the exception of one of three specimens of *Berthelinia elegans* with a slightly positive PC2 score but the highest PC1 score (Fig. 3). Cluster 4 included all Recent specimens that were originally classified as *Midorigai, Edenttellina, Tamanovalva,* and *Berthelinia*; all specimens in cluster 4 had negative PC1 scores. Within cluster 4, Recent specimens classified as *Berthelinia* (specimens 19–26) were not separated from those originally classified as *Tamanovalva babai* (specimen 24), *Midorigai australis* (specimen 22)*,* or *E. typica* (specimens 19–20). In contrast, fossil specimens of *B. elegans* (type species for *Berthelinia*) and *Gougerotia* all fell into a distinct cluster 5 distinguished by large and positive PC1 scores. Thus, the morphometric analysis differentiated fossil *Berthelinia* from Recent species assigned to that genus, while supporting all Recent species assigned to *Edenttellina*, *Midorigai, Tamanovalva,* and *Berthelinia* as congeneric.

SYSTEMATICS

SACOGLOSSA VON IHERING, 1876
OXYNOACEA STOLICZKA, 1868 (1847)
FAMILY JULIIDAE E. A. SMITH, 1885

Remarks

Stoliczka (1871) introduced the family name Prasinidae to include the fossil bivalve genera *Modiolopsis* Hall, 1847, *Hippomya* Salter, 1864, *Myoconcha* Sowerby, 1824, *Hippopodium* Sowerby, 1819, the Recent bivalve genus *Phaseolicama* Rousseau *in* Hombron & Jacquinot, 1854 (accepted as *Gaimardia* Gould, 1852), and the bivalved sacoglossans *Prasina* Deshayes, 1863 and *Julia* Gould, 1862. Subsequently, E. A. Smith (1885) proposed the family name Juliidae for *Julia*. Because *Prasina* is a synonym of *Julia* (see remarks on *Julia*), the family names Juliidae and Prasinidae are also synonyms.

Beets (1949) introduced the family name Berthelinidae (for *Berthelinia* Crosse, 1875) for the first time but without a diagnosis, making it invalid (ICZN 1999: Article 13.1). Thus, the first valid introduction of the name Berthelinidae was by Keen & A. G. Smith (1961), who provided a description. Kawaguti & Baba (1959) introduced the family Tamanovalvidae for *Tamanovalva* Kawaguti & Baba, 1959.

Most authors have supported a classification scheme for this group within a single family, Juliidae, and two Recent subfamilies, Juliinae E.A. Smith, 1885 and Berthelininae Keen & A. G. Smith, 1961 (Kay 1968) with the later addition of the fossil subfamily Gougerotiinae Le Renard 1980 (Le Renard et al. 1996). However, as Valdés & Bouchet (2005) pointed out, Prasininae has priority over Juliinae and Tamanovalvinae over Bertheliniinae. However, Valdés & Bouchet (2005) continued using the names Juliinae and Bertheliniinae for taxonomic stability, until a formal proposal is submitted to the International Commission on Zoological Nomenclature. Therefore, Juliinae and Bertheliniinae are used herein.

Members of the family Juliidae were generally classified in the class Bivalvia until the discovery of the first live bivalved sacoglossans by Kawaguti & Baba (1959). Thus, morphological descriptions prior to 1959 often assumed that the narrower end of the shell corresponded to the anterior part of the body as in bivalve convention (see Coan et al. 2000). However, as shown by Kawaguti & Baba (1959) and subsequent papers cited herein, the head of juliids emerges from the wider end of the shell, and therefore the convention in modern Juliidae literature is to refer to that as the anterior end of the shell. This convention is used in the present paper.

The results of the five-gene phylogenetic analyses recovered two Recent clades in Juliidae, one corresponds to the traditional use of the name *Julia* and the other with the traditional use of the name *Berthelinia*. Additionally, geometric morphometrics analyses indicate that these two clades are morphologically distinct. Therefore, the traditional classification with two subfamilies is here maintained. Below we provide systematic descriptions for all genera and species, and for completeness we also list fossil groups not examined in this study. Generic diagnoses are based on Keen & A. G. Smith (1961), Le Renard (1980, 1989), Le Renard et al. (1996) and Jensen (2011).

SUBFAMILY JULIINAE E. A. SMITH, 1885

GENUS *JULIA* GOULD, 1862

Julia Gould 1862: 283. Type species: *Julia exquisita* Gould, 1862, by monotypy.
Prasina Deshayes 1863: 25–29. Type species: *Prasina borbonica* Deshayes, 1863, by monotypy.
Parasina Habe 1951: 122 [error for *Prasina* Deshayes 1863].

Diagnosis

Shell, thick, heavy, opaque, typically colored; oval in lateral view, cordate in anterior/posterior views; anterior margin rounded, narrowing posteriorly, deeply excavated at umbo, with sharp posterior peripheral margin; shell tallest point near mid-length; valves equal in size; hinge with pronounced condyloid (or cardinal) tooth on left valve, right valve with fossette-like hinge socket; protoconch on left valve, towards posterior of shell; adductor muscle scar subcentral; shell typically green with white, brown, or black spots or lines; gill continues across mid-dorsal line to left side; heart on left side near the posterior end of gill; short segment of intestine visible dorsally on surface of digestive gland; mantle cavity extends across mid-dorsal line of shell; radular teeth elongate, blade-shaped, inflated, with row of hair-like denticles along each side; teeth cusps with bifid tips.

Remarks

Carpenter *ex*. Nuttall (1857) introduced the species name *Smaragdinella thecaphora* Carpenter (*ex*. Nuttall), 1857 from Mazatlán, Mexico, and it constitutes the first description of a species now in the genus *Julia*. Carpenter (1857) considered this new species a member of the Gastropoda, primarily because he had access to only one valve. However, when describing the apical morphology of the shell, he noted that it looked remarkably like the ligamental cavity of *Anatinella* Sowerby G. B. II., 1833 (Bivalvia).

Gould (1862) described the genus *Julia* based on the single species *Julia exquisita* Gould, 1862, the type species by monotypy. Although Gould (1862) unequivocally included *Julia* in Bivalvia, he was unsure of the taxonomic placement within this group and discussed its affinities with other bivalve genera including *Vulsella* Röding, 1798 [Family Pteriidae Gray, 1847 (1820)], *Pedum* Bruguière, 1792 (Family Pectinidae Rafinesque, 1815), or even members of the family Veneridae Rafinesque, 1815. However, Gould (1862) also recognized the affinities between *Julia* and heterobranch sea slugs, by indicating, “A beautiful little shell, colored like *Smaragdinella* A. Adams, 1848 from the same islands. The sudden and profound depression in front of the beaks is quite striking, and thus produces a very pointed somewhat upturned anterior end. A single valve looks much like some of the Bullidae, *Chelidonura*, for instance.” Gould’s (1862) short description of *Julia* in Latin summarizes the main diagnostic traits, which are consistent with the modern usage of the name.

Deshayes (1863) introduced the genus name *Prasina* for the species *Prasina borbonica* Deshayes, 1863, the type species by monotypy, collected in Réunion, Indian Ocean. Deshayes (1863) examined a series of single valves collected by Louis Maillard, and because of their green color, brilliant internal surface, and shell projection, initially concluded they belonged to the genus *Smaragdinella*. However, by assembling the shells together, Deshayes (1863) realized they were bivalve shells, regular and symmetrical. Although Deshayes (1863) found the external characteristics of these shells very peculiar, he found other traits in the interior of the valves "of much greater importance," such as the unique shape of the hinge, the insertion of the lunula, and the position of the muscle scars. Thus, Deshayes (1863) introduced the new genus name *Prasina* for these shells, but as in the case of Gould (1862) and *Julia*, Deshayes (1863) was unsure of the taxonomic placement of *Prasina*. Deshayes (1863) proposed that *Prasina* had intermediate characteristics between the monomyarians (bivalves with a single posterior adductor muscle) and the dimyarians (bivalves with two adductor muscles, one anterior one posterior), but proposed it was closer to the family Mytilidae Rafinesque, 1815, of which it could constitute a subfamily. Prophetically, Deshayes (1863) suggested this species could perhaps be, "destined to play a more important role, for it may be that the animal offers in its organization facts of greater zoological value than the shell," and hoped that this small shell would be collected and observed alive. Two additional species of Juliidae were described in the genus *Prasina*, *Prasina cornuta* De Folin *in* De Folin & Périer, 1868 (Recent, Mauritius) and *Prasina lecointreae* Dollfus & Dautzenberg 1901 (Miocene, Touraine, France).

Semper (1865) was the first to note the similarities between *Julia* and *Prasina,* indicating that it was nearly impossible to separate these two genera. E. A. Smith (1885) examined shells of *Julia exquisita* from the Hawaiian Islands and introduced the family name Juliidae for it, although without a taxonomic placement beyond confirming its membership in Bivalvia. One year later, Fischer (1886) formally considered *Julia* as a subgenus of *Prasina* and suggested that *Berthelinia* Crosse, 1875 could also belong to the Prasinidae or Aviculidae Goldfuss, 1820 [=Pteriidae]. Fischer (1886) also discussed the similarities between Prasinidae, which he considered to be bivalves, and Mytilidae.

E. A. Smith (1885) placed *P. borbonica* in the synonymy of *J. exquisita* without further explanation, and Dall (1898) formally synonymized these two genera. Some authors maintained *Prasina* as a synonym of *Julia* but considered *J. borbonica* as a distinct species and pointed out that specimens examined by E. A. Smith (1885) from the Hawaiian Islands belonged to *J. borbonica* (Beets 1944, 1949; Howard 1951; Boettger 1962). Other authors agreed to maintain *Prasina* as a synonym of *Julia* (e.g., Kay 1968; Kawaguti & Yamasu 1982). Kay (1968) went further and indicated that all *Julia* shells she examined from the Indian and Pacific Oceans fell within the range of variation of the Hawaiian specimens and suggested that *J. japonica* and *J. equatorialis* may represent geographic subspecies.

Kawaguti & Baba (1959) described the first live specimens of Juliidae, which they taxonomically placed in the Sacoglossa (Gastropoda) (see remarks on *Edenttellina*). However, these authors did not immediately make a connection between their newly discovered species and the extensive Recent and fossil literature on this group (Cox & Rees 1960; Keen 1960b). Keen (1960b) suggested that when specimens of *Julia* were found alive, they would prove to be gastropods. Just two years later, Kay (1962b) reported the first known live animals within the genus *Julia*, confirming they unequivocally belonged to Sacoglossa.

Additional Recent species of *Julia* have been described from Japan: *Julia japonica* Kuroda & Habe, 1951 [also reported from Pleistocene deposits (Mimoto 1984)], *Julia zebra* Kawaguti, 1981 *Julia mishimaensis* Kawaguti & Yamasu, 1982, and an unnamed species from Okinawa (Mizofuchi & Yamasu 1987); India: *Julia burni* Sarma, 1975; and the Eastern Pacific: *Julia equatorialis* Pilsbry & Olsson, 1944. The genus name *Julia* has also been widely applied to fossil species, including *Julia floridana* Dall, 1898 (Oligocene, Florida), *Julia girondica* Cosssman & Peyrot (*ex*. Benoist), 1914 (Miocene, Nouvelle-Aquitaine, France), *Julia douvillei* Cosssman & Peyrot, 1914 (Oligocene, Nouvelle-Aquitaine, France, tentatively assigned to the Helvetian Stage [=Serravallian] in the original description, but subsequently re-assigned to the Late Oligocene by Schneider et al. 2008), *Julia gardnerae* Woodring, 1925 (Miocene, Jamaica), and *Julia borneensis* Boettger, 1962 (Late Miocene, East Borneo).

Based on the molecular analyses presented here, *Julia* is clearly distinct from other Juliidae genera described to date, and therefore is considered valid. However, the geometric morphometrics analysis recovered substantial morphological diversity that will be examined in more detail in a separate monograph. Several species regarded as *Julia* herein cluster in different groups (Clusters 1–3, Fig. 3) and it is particularly noteworthy that *J. japonica* and *J. borbonica* (Cluster 1, Fig. 3) are substantially distant from the rest of *Julia*. In this study we regard *J. borbonica* as a synonym of *J. exquisita* (see remarks on *J. exquisita*), which is also highly variable morphologically and represented in two different groups of the PCA. Unfortunately, we did not have access to material of *J. japonica* suitable for molecular analysis to determine its phylogenetic placement. Additionally, representatives of the fossil genus *Candinia* are clustered with other members of *Julia* in the PCA, casting doubt on the validity of the former genus. Further work is necessary to resolve these outstanding issues. Currently, *Julia* includes Recent and fossil species, which are listed below in chronological order.

Species list

Smaragdinella thecaphora Carpenter (*ex*. Nuttall) 1857: 533. Type locality: Mazatlán, Mexico.

Julia exquisita Gould 1862: 284. Type locality: Sandwich Islands [= Hawaiian Islands].

Prasina borbonica Deshayes 1863: 29, pl. 4, figs. 4–8. Type locality: Réunion.

Prasina cornuta De Folin *in* De Folin & Périer 1868 [1867–1872]: 83–84, pl. 9, fig. 7. Type locality: Île Maurice [= Mauritius].

† *Julia floridana* Dall 1898: 811, pl. 35, figs. 1–3. Type locality: Chipola River, Florida (Early Miocene).

† *Prasina lecointreae* Dollfus & Dautzenberg 1901: 271. Type locality: Ferrière-Larçon, France (Middle Miocene).

† *Julia girondica* Cosssman & Peyrot (*ex*. Benoist) 1914: 62–63, pl. 12, figs. 19–22. Type locality: Villandraut, France (Early Miocene).

† *Julia douvillei* Cosssman & Peyrot 1914: 63–65, pl. 12, figs. 30–32. Type locality: Peyrehorade, France (Late Oligocene).

Julia equatorialis Pilsbry & Olsson 1944: 86–87, pl. 9, figs. 10–11. Type locality: Caleto Sal, north of Mancora, Peru.

† *Julia gardnerae* Woodring 1925: 87–88, pl. 10, figs. 15–16. Type locality: Bowden, Jamaica (Middle Miocene).

Julia japonica Kuroda & Habe 1951: 86. Type locality: Nada, Wakayama Prefecture, Japan.

† *Julia borneensis* Boettger 1962: 422–423, fig. 3. Type locality: Gunung Mendong, East Borneo (Late Miocene).

† *Julia borbonica erythraea* Selli 1973: 201–203, pl. 30, figs. 8A–C. Type locality: Massawa, Erytraea (Pleistocene).

Julia burni Sarma 1975: 12–15, figs. 1–5. Type locality: Port Blair, Andaman Islands.

Julia zebra Kawaguti 1981: 9–13, figs. 1A, 2–4. Type locality: Mishima, Hagi City and Tsunoshima, Yamaguchi Prefecture, Ishigaki Is., Okinawa Prefecture, Japan.

Julia mishimaensis Kawaguti & Yamasu 1982: 29–31, figs. 1–4. Type locality: Tsunoshima, Yamaguchi Prefecture and Ishigaki Is., Okinawa Prefecture, Japan.

In this study, three additional, probably undescribed species are recognized. As mentioned above the taxonomy of species of *Julia* and the formal description of these new species will be addressed in a separate monograph.

GENUS *CANDINIA* LE RENARD, SABELLI & TAVIANI, 1996

† *Candinia* Le Renard, Sabelli & Taviani 1996: 231–232. Type species: *Candinia pliocaenica* Le Renard, Sabelli & Taviani, 1996, by original designation.

Diagnosis

Shell thick, heavy, oval-trigonal in lateral view, cordate in anterior/posterior views; anterior margin rounded, narrowing abruptly posteriorly into sharp triangular margin; shell tallest point near anterior end; right valve larger than left valve; hinge with anterior, posterior parts interrupted beneath apex, condyloid (or cardinal) tooth on right valve, left valve with fossette-like socket; protoconch on left valve, towards posterior third of shell; adductor muscle scar subcentral.

Remarks

Le Renard et al. (1996) introduced the genus *Candinia* Le Renard, Sabelli & Taviani, 1996 based on the new species *Candinia pliocaenica* Le Renard, Sabelli & Taviani, 1996 from the Pliocene of Italy. Le Renard et al. (1996) included *Candinia* in the subfamily Juliinae, and indicated that *Candinia* is distinguishable from *Julia* by differences in shell hinge morphology. Le Renard et al. (1996) also suggested *Berthelinia krachi* Bałuk & Jakubowski, 1968, a Miocene species from Poland, is also a member of *Candinia*. Subsequently, Schneider et al. (2008) described another species of *Candinia*, *Candinia lakoniae* Schneider, Hochleitner & Janssen, 2008 from the

Pliocene of Greece. In the PCA analysis presented here (Fig. 3), members of *Berthelinia krachi* [= *Candinia krachi*] are morphologically indistinguishable from some species of *Julia* indicating that these two genera could be synonyms.

Species list

† *Berthelinia krachi* Bałuk & Jakubowski 1968: 294–297, pl. 1, figs. 1–5. Type locality: Korytnica, 24 km SSW of Kielce, Holy Cross Mountains, Poland (Middle Miocene).

† *Candinia pliocaenica* Le Renard, Sabelli & Taviani 1996: 232–234, figs. 1–4. Type locality: Pietrafitta, Tuscany, Italy (Early Pliocene).

† *Candinia lakoniae* Schneider, Hochleitner & Janssen 2008: 83–89, figs. 3–4. Type locality: Glykovrysi, Lakonia, Peloponnese, Greece (Late Pliocene).

SUBFAMILY BERTHELINIINAE KEEN & A. G. SMITH, 1961

GENUS *BERTHELINIA* CROSSE, 1875

† *Berthelinia* Crosse 1875: 79. Type species: *Berthelinia elegans* Crosse, 1875, by monotypy.

† *Ludovicia* Cossmann 1887: 45. Type species: *Ludovicia squamula* Cossmann, 1887, by monotypy.

† *Anomalomya* Cossmann 1887: 169–170. Type species: *Anomalomya corrugata* Cossmann, 1887, by monotypy.

† *Cossmannella* Boettger 1962: 414 [non *Cossmannella* Mayer-Eymar, 1896; Bivalvia], unnecessary replacement for *Ludovicia* Cossmann, 1887.

† *Squamulina* Le Renard 1989: 23 [not *Squamulina* Schultze, 1854; Foraminifera], replacement name for *Cossmannella* Boettger, 1962.

Diagnosis

Shell thin, delicate, semi-quadrangular in lateral view; anterior margin rounded, narrowing posteriorly, tapering into round tail end; shell tallest point near anterior end; right valve slightly smaller; hinge with inconspicuous condyloid (or cardinal) tooth on right valve, left valve with fossette-like socket; protoconch on left valve, slightly behind mid-length point; single, adductor muscle scar subcentral.

Remarks

Crosse (1875) introduced the genus name *Berthelinia* Crosse, 1875 based on a single specimen collected in the Miocene of the Paris Basin (Courtagnon), which he described as a new species, *Berthelinia elegans*. Because Crosse (1875) had only one valve, and due to its small size and reduced number of whorls, he speculated with the possibility that it could be an embryonic shell. Crosse (1875) struggled with the taxonomic placement of this species and suggested that it was probably related to the gastropod genera *Pileopsis* Lamarck, 1822 [= *Capulus* Montfort, 1810, family Capulidae Fleming, 1822] or *Hipponyx* [incorrect spelling of *Hipponix* Defrance, 1819, family Hipponicidae Troschel, 1861]. Fischer (1886) suggested for the first time that *Berthelinia* was a bivalve, possibly related to the Prasinidae Stoliczka, 1871 (a synonym of Juliidae) or Aviculidae Goldfuss, 1820 [=Pteriidae].

Cossmann (1887) formally described the genus *Ludovicia* Cossmann, 1887 (Deshayes' manuscript name), for the new species *Ludovicia squamula* Cossmann, 1887, based on the shells from the Eocene of the Paris Basin. Cossmann (1887) placed *Ludovicia* in the bivalve family Galeommidae [sic.] [= Galeommatidae Gray, 1840]. Hedley (1920) indicated that W. J. Wintle pointed out to him that *Ludovicia* Cossmann, 1887 is preoccupied by the genus name *Ludovicius* Rondani, 1843, because according to Marschall (1873) this name was rendered as *Ludovicia* by Rondani (1845). Boettger (1962) agreed with this assessment and proposed the replacement name *Cossmannella* Boettger, 1962 for *Ludovicia* Cossmann, 1887. However, a review of the pertinent literature shows that Rondani (1843) introduced the new genus name *Ludovicius* in the family Dolichopoda [Diptera]. Subsequently, Rondani (1845) reported the name *Ludovicius* again with the same spelling, and Marschall (1873: p. 336) listed the name as 'Ludovicia' with authorship of Rondani, 1845. Because there is no evidence that Marschall's (1873) spelling was an intentional emendation (ICZN 1999: Article 33.2), it is considered here as an incorrect subsequent spelling (ICZN 1999: Article 33.5) and therefore unavailable for the purposes of homonymy. Thus, *Ludovicia* Cossmann, 1887 remains available and *Cossmannella* Boettger, 1962 is an unnecessary replacement. Later, Le Renard (1989) noticed that *Cossmannella* Boettger, 1962 was preoccupied by *Cossmannella* Mayer-Eymar, 1896 [Bivalvia] and proposed the replacement name *Squamulina* Le Renard, 1989, which is also preoccupied by *Squamulina* Schultze, 1854 [Foraminifera].

Cossmann (1887) described additional species of bivalves in the family Prasinidae, including the new genus name *Anomalomya* Cossmann, 1887, based on the new species *Anomalomya corrugata* Cossmann, 1887. Cossmann (1887) also examined additional specimens of *Berthelinia elegans*, which he formally placed in the Prasinidae. Cossmann (1887) noticed that specimens of *Berthelinia* from Le Ruel (Haravilliers, France) differed slightly from those found in coarse limestone, and introduced a variety, *Berthelinia elegans elata,* for those specimens.

Crosse & Fischer (1887) further commented on the taxonomic placement of *Berthelinia* in Pelecypoda (= Bivalvia) based on newly discovered complete specimens of *B. elegans* that included both valves and with visible muscle scars. Crosse & Fischer (1887) had difficulties placing *Berthelinia* among bivalves and speculated that it was probably related to the families Aviculidae and Prasinidae as suggested by Fischer (1886). On a postscript in the same article, Crosse & Fischer (1887) mentioned that after their paper was written, they received the second delivery of Cossmann's (1887) illustrated catalog of the fossil shells of the Eocene of the environs of Paris, where this author placed *Berthelinia* in the family Prasinidae.

The discovery the first live bivalved sacoglossans by Kawaguti & Baba (1959) prompted the reclassification of *Berthelinia* as a gastropod (Burn 1960b; Keen 1960b), see remarks on *Edenttellina*. Based on morphological similarities, some authors considered *Ludovicia* and *Anomalomya* as subgenera of *Berthelinia* (Keen & A. G. Smith 1961; Boettger 1962), whereas others maintained them as separate genera (Le Renard et al. 1996; Schneider et al. 2008).

In this study, morphological evidence indicates that *Berthelinia* cannot be used for Recent species. The PCA analysis recovered Recent and fossil species of Berthelliniinae in two distinct clusters, indicating they are morphologically distinct. Therefore, the genus *Berthelinia* is used herein only for the extinct taxa listed below.

Species list

† *Berthelinia elegans* Crosse 1875: 79–81, pl. 2, fig. 3. Type locality: Courtagnon, France (Eocene).

† *Ludovicia squamula* Cossmann 1887: 45–46, pl. 2, figs. 21–22. Type locality: Parnes, France (Eocene).

† *Anomalomya corrugata* Cossmann 1887: 170, pl. 7, figs. 30–31. Type locality: Le Fayel, France (Late Eocene).

† *Berthelinia elegans elata* Cossmann 1887: 175, pl. 7, figs. 24–27. Type locality: Le Ruel, France (Early-Late Eocene).

† *Berthelinia? elongata* Cossmann 1906: 262–263, pl. 20, figs. 18–19. Type locality: Bois-Gouët, Loire-Atlantique, France (Early Eocene).

† *Berthelinia burni* Ludbrook & Steel 1961: 229, pl. 12. Type locality: Elizabeth Oval bore, Hundred of Munno Para, 15 miles north of Adelaide, Australia (Early Pliocene).

† *Berthelinia oligocaenica* Janssen 1979: 75–78, figs. 1–2 (Middle Oligocene).

GENUS *NAMNETIA* COSSMANN, 1905

† *Namnetia* Cossmann 1905b: 147. Type species: *Namnetia discoides* Cossmann, 1905, by monotypy.

Diagnosis

Shell thin, delicate, ovoid, nearly round in lateral view; anterior, posterior margins rounded, similar in height, or posterior end narrower, sharper; shell tallest point near center; hinge with anterior, posterior parts interrupted beneath apex, condyloid (or cardinal) tooth on right valve, left valve with fossette-like socket; protoconch on left valve, near mid-length point; single, adductor muscle scar nearly central.

Remarks

Cossmann (1905b) introduced the new genus *Namnetia* Cossmann, 1905 for the species *Namnetia discoides* Cossmann, 1905, and provisionally placed it in the family Galeommidae [sic.] [= Galeommatidae Gray, 1840]. Le Renard (1980) described the new Juliidae species

Anomalomya (*Namnetia*?) *sphaerica* Le Renard, 1980. Le Renard (1980), based on this interpretation of the original description of *Namnetia discoides* by Cossmann (1905b), suggested that *Namnetia* could be a subgenus of *Anomalomya* and belong to the family Juliidae. This placement has not been confirmed with the examination of actual specimens. Le Renard (1989) examined additional specimens of this group and using morphometric data confirmed the placement of *Namnetia* in Juliidae. Le Renard (1989) also considered *Anomalomya sphaerica* Le Renard, 1980 as a possible synonym of *Anisodonta sphaericula* Cossmann, 1886, and proposed both as members of *Namnetia*. Finally, Le Renard (1989) pointed out the similarities between *Namnetia* and *Anomalomya* but preferred to maintain them as separate genera.

Species list

† *Anisodonta sphaericula* Cossmann 1886: 141–142, pl. 2, fig. 34–36. Type locality: Valmondois, France (Late Eocene).

† *Namnetia discoides* Cossmann 1905b: 147, pl. 9, figs. 47–49. Type locality: Bois-Gouët, Loire-Atlantique, France (Middle Eocene).

† *Anomalomya sphaerica* Le Renard 1980: 21–23, fig. 11. Type locality: Baron, Oise, France (Middle Eocene).

GENUS *EDENTTELLINA* GATLIFF & GABRIEL, 1911

Edenttellina Gatliff & Gabriel 1911: 190. Type species: *Edenttellina typica* Gatliff & Gabriel, 1911, by original designation.

Tamanovalva Kawaguti & Baba 1959: 178–179. Type species: *Tamanovalva limax* Kawaguti & Baba, 1959, by original designation.

Midorigai Burn 1960b: 45–46. Type species: *Midorigai australis* Burn, 1960, by original designation.

Diagnosis

Shell thin, delicate, translucent, colorless, semi-quadrangular in lateral view; anterior margin rounded, narrowing posteriorly, tapering into sharp tail end; shell tallest point near anterior end;

right valve slightly smaller; hinge with faint corrugations, lacking teeth or with small condyloid (or cardinal) tooth on right valve, left valve often with reduced triangular hinge socket; protoconch on left valve, slightly behind mid-length point; single, adductor muscle scar subcentral; gill occupies height of right valve; heart dorsally in mantle fold; intestine on surface of mantle floor, behind bulge formed by female reproductive system; mantle cavity covering only right side of the body; radular teeth elongate, blade-shaped, with row of hair-like denticles along each side; teeth cusp either with single sharp tip or bifid.

Remarks

Dautzenberg (1895) reported the first Recent shell of the fossil genus *Berthelinia* based on a right valve (with the protoconch) collected by Schlumberg in Madagascar. Dautzenberg (1895) illustrated and described this shell as a new species, *B. schlumbergeri*, and commented on the taxonomic placement of this group in the Bivalvia (as Pelecypoda).

Gatliff & Gabriel (1911) described the genus *Edenttellina* based on Recent specimens collected in Port Phillip, Australia. Gatliff & Gabriel (1911) designated their new species *Edenttellina typica* Gatliff & Gabriel, 1911 as the type, but mentioned that a second species collected by C. Hedley also belonged to the same genus and was going to be described at a later date. Gatliff & Gabriel (1911) placed *Edenttellina* among other bivalve species but did not discuss the taxonomic placement of this group or compare it with other previously described taxa in Bivalvia. Hedley (1912) suggested that *Edenttellina* was not a bivalve (or pelecypod) but the internal shell of a tectibranch gastropod (obsolete term for some shelled sea slugs). Hedley (1912) also pointed out the similarity between *Edenttellina* and the fossil genus *Ludovicia* Cossmann, 1887. Years later, Hedley (1920) described a second Recent species of *Edenttellina, E. corallensis*, and commented that because this animal had a ligament joining the right and left valves, it was clearly a bivalve. Additionally, Hedley (1920) examined the paratypes of *Ludovicia squamula* Cossmann, 1887 (the type species of *Ludovicia* Cossmann, 1887, borrowed from Dautzenberg), and based on the morphological characteristics of these two taxa considered *Edenttellina* and *Ludovicia* to be congeneric, although he did not explicitly propose a formal synonymization of the two names. Additionally, based on similarities between *Edenttellina* and *Julia exquisita* Gould 1862, Hedley (1920) proposed the placement of *Edenttellina* in the family

Juliidae and related to the Chamacea [= Chamoidea Lamarck, 1809, Bivalvia].

Dall (1918) reported a third Recent species of this group based on two left shells collected in Magdalena Bay, Baja California Sur, Mexico that he described as ?*Scintilla chloris*. Because of the limited material available (only two valves with no protoconch), Dall (1918) did not make the connection between his specimens and previous records by Dautzenberg (1895) and Gatliff & Gabriel (1911), thus he suggested his specimens should probably be placed in the bivalve genus *Scintilla* Deshayes, 1856 (Family Galeommatidae Gray, 1840) until more material became available.

Kawaguti & Baba (1959) discovered the first live specimens of Sacoglossa with a bivalved shell, for which they proposed the new genus *Tamanovalva* and the new species *T. limax*. Kawaguti & Baba (1959) were unaware of any other species of sacoglossans with such an unusual morphology and therefore introduced the new family Tamanovalvidae and the new suborder Tamanovalvacea for this group. Kawaguti & Baba (1959) compared the shell of *Tamanovalva* with that of *Edenttellina*, which they considered a member of Bivalvia, and concluded they were different. However, Cox & Rees (1960) stressed the morphological similarities between *Tamanovalva* and *Edenttellina* as well as to the fossil genus *Ludovicia*, and suggested they could be synonyms. Keen (1960a) agreed with Cox & Rees (1960) but proposed that the fossil genus name *Berthelinia* could be a more senior synonym for this group.

Burn (1960a), in a brief note, described for the first time live specimens of *Edenttellina typica* in Torquay, Victoria, Australia. Burn (1960a) also mentioned collecting a second species of the same group belonging to a different genus. In a second paper the same year, Burn (1960b) reemphasized that *Tamanovalva* is a synonym of *Edenttellina*, but also proposed that these two genera are synonyms with the fossil genus *Berthelinia* from the Eocene of the Paris Basin, as suggested by Keen (1960a). Burn (1960b) confirmed that the species he collected from Victoria belonged to *E. typica* (renamed *Berthelinia typica*) and that *E. corallensis* was a synonym, but that the specimens described by Verco (1916) as *E. typica* constituted a second, distinct species. Burn (1960b) suggested that *T. limax* described by Kawaguti & Baba (1959) was also a synonym of *B. typica*, and ?*Scintilla chloris* Dall, 1918 (from Baja California), although larger, was probably another synonym of *B. typica*. Finally Burn (1960b) considered the second species he collected in Victoria to belong to a new genus of that he named *Midorigai*, based on the new species *Midorigai australis* Burn, 1960. According to Burn (1960b), the main differences between *Midorigai* and *Berthelinia* were the more swollen shape of the shell, the size and arrangement of the protoconch (in a horizontal plane across the hinge line), the presence of two adductor muscles, the foot narrower than the neck, and some other anatomical details.

In subsequent years, a number of papers described additional species of bivalved gastropods and provided alternative assessments of the taxonomy of this group. First, Keen (1960b) formally synonymized *Tamanovalva* with *Edenttellina* and *Berthelinia* and suggested a close relationship with *Julia*, which was not yet known from live animals. This opinion was followed by Ludbrook & Steel (1961) in the description of the new species *Berthelinia burni* Ludbrook & Steel, 1961 [not *Julia burni* Sarma, 1975]. Baba (1961a) provided a comprehensive revision of the morphological characteristics of *Tamanovalva* and compared them with those of *Edenttellina* and other shelled sacoglossans. Baba (1961a) also mentioned that *Tamanovalva* was different from *Edenttellina* in shell and radula morphology, and that *Edenttellina* seems more similar to *Ludovicia* than to *Tamanovalva*, which appears closer to *Berthelinia*. Baba (1961a) concluded that it is difficult to compare Recent and fossil taxa and more data are needed to establish a definitive taxonomy for the group, but should all these genera become synonyms, *Berthelinia* would have priority. In a second paper the same year, Baba (1961b) concluded that *Berthelinia*, *Ludovicia*, *Edenttellina*, *Tamanovalva*, *Midorigai*, and possibly *Anomalomya* were synonyms and provided a detailed review of the radular and conchological characteristics of this group. The same year, Keen & A. G. Smith (1961) described the new subspecies *Berthelinia chloris belvederica* and revisited the taxonomy of the bivalved sacoglossans formally proposing that both *Julia* and *Berthelinia* were members of the family Juliidae. Keen & A. G. Smith (1961) also proposed that the genus *Berthelinia* included five subgenera, *Berthelinia* s. s., tentatively represented by three fossil taxa (including the type *B. elegans*) and the Recent *B. schlumbergeri*; *Ludovicia*, including only the type species *L. squamula*; *Anomalomya*, represented by the type species *A. corrugata* and possibly a Recent undescribed species from Australia; *Midorigai*, only represented by the type species *M. australis*; and *Edenttellina*, including all other Recent species. Boettger (1962) followed a similar classification scheme as proposed by Keen & A. G. Smith

(1961), but regarded *Midorigai* as a distinct genus from *Berthelinia*, instead of a subgenus, and proposed the new subgenus name *Cossmannella* to replace *Ludovicia*, which he erroneously thought it was preoccupied (see remarks of *Berthelinia*). Boettger (1962) also described the new fossil species *Julia borneensis*.

Additional records and new species from the Hawaiian Islands (Kay 1962a, 1962b, 1964) – *Berthelinia pseudochloris*, and the Caribbean (Edmunds 1962, 1963) – *Berthelinia caribbea*, largely followed the classification scheme proposed by Keen & A. G. Smith (1961). However, Burn (1965) indicated that he considered *Berthelinia* an exclusively fossil genus and that the Recent genus *Tamanovalva* was distinct and included the species *T. limax*, *E. corallensis* and *S. chloris*. Burn (1965) also recognized that among the paratypes he described as *M. australis* (Burn 1960b), there were some specimens that belonged to the true *E. typica* as described by Gatliff & Gabriel (1911), a point already made by Baba (1961a). Burn (1965) concluded that the specimens he described in Burn (1960b) as *E. typica* were different from those in the original description by Gatliff & Gabriel (1911) and belonged to the genus *Tamanovalva*, thus he introduced the new name *Tamanovalva babai* for them. Finally, although not clearly stated, Burn (1965) appeared to also consider *Edenttellina* as a valid genus and distinct from both *Tamanovalva* and *Berthelinia*. Burn (1966) described a new species of *Tamanovalva* from Fiji, *T. fijiensis*, and clearly stated that he considered *Edenttellina* and *Tamanovalva* as distinct genera but did not provide distinguishing characters. Burn (1966) also distinguished *Berthelinia* and *Tamanovalva* because of the presence of one and a half whorls in the protoconch of *Tamanovalva* instead of two, as in the protoconch of *Berthelinia*.

Kay (1968) proposed a classification, informed by that of Keen & A. G. Smith (1961) and Boettger (1962), in which *Midorigai* was a subgenus of *Berthelinia* (because it possessed a uniquely swollen shell and two adductor muscle scars) and the subgenus *Berthelinia* could only be applied to fossils. This classification scheme was followed by some authors (e.g. Ganapati & Sarma 1972; Sarma 1975), but Jensen (1993, 1997a, 1997b, 2015) synonymized all the subgenera under *Berthelinia*. Burn (1998, 2006) accepted *Berthelinia* and *Tamanovalva* as synonyms, but retained *Edenttellina* and *Midorigai* as separate genera and continued to use *Tamanovalva*. Importantly, conchological traits often used to distinguish these genera are variable. For example, Edmunds (1963) found that the position of the protoconch varies within *B. caribbea* and Jensen (1993) noted that the overall shape of the shell and the angle of the protoconch varies within *B. rottnesti*, with small specimens having a fairly erect protoconch, and larger specimens having an almost horizontal one. Thus, it seems due to ontogenetic and/or intraspecific variability, these characters are not taxonomically informative.

In this study, molecular phylogenetic analyses revealed that the type species of *Edenttellina, Tamanovalva*, and *Midorigai* belong in the same clade. Therefore, we find no compelling reasons to maintain these as different genera and we agree with Jensen's (1993) proposal to synonymize *Edenttellina, Tamanovalva*, and *Midorigai*. However, geometric morphometric analyses revealed that fossil and Recent members of this group clustered in different groups, with significant morphological differences. Thus, we propose to maintain *Berthelinia* as a valid genus for fossil taxa and retain *Edenttellina* (the oldest available name) for Recent species.

Species list

Berthelinia schlumbergeri Dautzenberg 1895: 37–38, figs. A–B. Type locality: Nosibé [= Nosy Be], Madagascar.

Edenttellina typica Gatliff & Gabriel, 1911: 190, pl. 46, figs. 5–6. Type locality: Portsea, Port Phillip, Victoria, Australia.

?Scintilla chloris Dall 1918: 5. Type locality: Magdalena Bay, Baja California Sur, Mexico.

Edenttellina corallensis Hedley 1920: 76, figs. 6–8. Type locality: Hope Island, Queensland, Australia.

Tamanovalva limax Kawaguti & Baba 1959: 179–180, figs. 1–10. Type locality: Vicinity of the former Tamano Marine Laboratory, Okayama University, by the Great Seto Bridge, Japan.

Midorigai australis Burn 1960b: 46, figs. 8–14. Type locality: Torquay, Victoria, Australia.

Berthelinia chloris belvederica Keen & A. G. Smith 1961: 53–61, figs. 18–19, 21–24, 27–32, pl. 5, lower fig. Type locality: Puerto Ballandra, near La Paz, Baja California Sur, Mexico.

Berthelinia caribbea Edmunds 1963: 731–737, figs. 1–5, pl. 1. Type locality: Port Royal, Jamaica.

Berthelinia pseudochloris Kay 1964: 191–193, fig. 1, pl. 9, figs. 1, 4. Type locality: Near Koloa Landing, Koloa, Kauaʻi, Hawaiian Islands.

Tamanovalva babai Burn 1965: 735–736, fig. 3. Type locality: Point Danger, Torquay, Victoria, Australia.

Tamanovalva fijiensis Burn 1966: 54–55, pls. 15–19. Type locality: Nukulau Island, Viti Levu, Fiji.

Berthelinia ganapatii Sarma 1975: 16–20, figs. 6–13, 28–29. Type locality: Visakhapatnam, India.

Berthelinia waltairensis Sarma 1975: 20–21, figs. 23–27, 30. Type locality: Visakhapatnam, India.

Berthelinia rottnesti Jensen 1993: 209–214, figs. 1–4, 5A, 6A. Type locality: Rottnest Island, Western Australia.

Berthelinia darwini Jensen 1997a: 170–175, figs. 6–9. Type locality: Lee Point, Darwin, Australia.

Berthelinia singaporensis Jensen 2015: 233–235, figs. 1F, 5D–E, 6–7. Type locality: Chek Jawa, Singapore.

EDENTTELLINA SCHLUMBERGERI (DAUTZENBERG, 1895)

Berthelinia schlumbergeri Dautzenberg 1895: 37–38, figs. A–B. Type locality: Nosibé [= Nosy Be], Madagascar.

Type material

Untraceable, not found at the Royal Belgian Institute of Natural Sciences or at the MNHN.

Remarks

Dautzenberg (1895) described *Berthelinia schlumbergeri* Dautzenberg, 1895 based on a single right valve dredged from sand in Nosy Be, Madagascar. The very small shell (0.6 mm long) had the protoconch attached and was illustrated (Dautzenberg 1895: figs. A–B). Based on the size of the teleoconch in relation to the protoconch, it appears to be a juvenile (Dautzenberg 1895). Dautzenberg (1895) described the shell as uniformly white, oval, slightly trapezoid, with a rounded anterior end shorter than the posterior end. The holotype is untraceable and the limited description of the animal does not allow for a reliable identification of this species.

Ganapati & Sarma (1972) reported juvenile shell specimens from the Andaman Islands as *B. schlumbergeri*. Ganapati & Sarma (1972) also indicated that these shells were similar to the Madagascar specimen described by Dautzenberg (1895) but recognized that their species could not be determined until more material of fully grown individuals became available. In a later paper, Sarma (1975) reported two new species of *Berthelinia* from mainland India but made no reference to *B. schlumbergeri*. Gosliner (1987) and Ono (1999) reported and illustrated photographs of specimens identified as *B. schlumbergeri* from Sodwana Bay, South Africa and Okinawa, Japan, respectively. Both photographs show green animals with some white spots on the head and neck, white rhinophoral tips, a green mantle, with the edge of the shell surrounded by alternating white and dark bands. Gosliner (1987) confirmed that his specimens from South Africa fed on *Caulerpa racemosa* (Forsskål) J. Agardh, 1873. The morphological characteristics of *B. schlumbergeri* are consistent with those of *E. pseudochloris* here examined, a species that also feeds on *C. racemosa,* and has planktotrophic development. Therefore, we regard the records of *B. schlumbergeri* by Gosliner (1987) and Ono (1999) to be *E. pseudochloris*. Although it is possible that *B. schlumbergeri* is an older name for *E. pseudochloris* this is impossible to determine with certainty based on the original description.

Because the original description of *B. schlumbergeri* is based on juvenile specimens and lacks details of the internal anatomy, we are unable to confirm the validity of this species. Therefore, *B. schlumbergeri* is here regarded as a *nomen dubium* until more information becomes available.

EDENTTELLINA TYPICA GATLIFF & GABRIEL, 1911

(FIGS. 4A–B, 5A–B, 6–7)

Edenttellina typica Gatliff & Gabriel 1911: 190, pl. 46, figs. 5–6. Type locality: Portsea, Port Phillip, Victoria, Australia.

Type material

Edenttellina typica, syntypes, right and left valve (not from same specimen), ~2.5 mm long (MV F515).

Additional material examined

Griffith Point, Central Bass Strait, Victoria, Australia, 26 Jan 2002, 1 specimen 2.2 mm long (shell) (MV F91829). Torquay, Victoria, Australia 21 Feb 1960, 1 specimen 4.5 mm long (shell) (MV F21195). Point Lonsdale, Victoria, Australia, date unknown, 2 specimens 2–2.5 mm long (shell) (MV F21539). Portsea, Victoria, Australia, date unknown, 1 valve 3.1 mm long (MV F215276).

Description

Body elongate, up to 6.1 mm in length, completely retractable inside of shell. Body color pale green, with minute white speckles on dorsal side of head (Figs. 5A–B). Head elongate, with eye spots located on dorsal swelling near center, surrounded by white pigment. Rhinophores enrolled, green, with or without few white speckles. Oral tentacles short, green. Foot lighter than rest of animal. Mantle visible through shell, pale green, with few longitudinal light brown irregular lines, variable in size; edge surrounded by conspicuous, alternating cream patches composed of densely arranged speckles. Foot not extending beyond posterior end of shell.

Shell up to 4.5 × 3.4 mm in size, tallest point slightly anterior to center, widest point near center; shell shape ovoid, dorsal and ventral margins regularly curved; anterior margin convex, regularly curved, posterior margin narrowing gradually, also regularly curved (Figs. 6C–D). Protoconch on left valve of teleoconch, ~110 µm long, with 1.5 whorls (Fig. 6D). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; small, oval condyloid tooth on right valve at posterior end of hinge, and triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 6E–F). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 6A–B).

Adductor muscle located closer to anterior end of shell, slightly below widest point of shell (Fig. 7), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Figs.

6D). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Penis not observed.

Radula with 19 teeth in descending limb and 5 fully formed teeth + 1 ghost tooth in ascending limb, in 2.5 mm long specimen from Victoria, Australia (MV F21539) (Fig. 8A). Active tooth ~70 µm long, with bifid tip; blade elongate, lacking denticles; base short, slightly curved (Fig. 8B). Ascus containing several disorganized elongate pre-radular teeth.

Biology

Jensen (1980) and Burn (1989) confirmed that *E. typica* feeds exclusively on the alga *Caulerpa brownii* (C. Agardh) Endlicher 1843.

Range

Temperate Australia: Victoria (Gatliff & Gabriel 1911; Burn 2006; present paper), Tasmania (Burn 2006), South Australia (Burn 2006).

Remarks

Gatliff & Gabriel (1911) described *Edenttellina typica* Gatliff & Gabriel, 1911 based on a right and left valve of similar size, but not from the same specimen, collected in Victoria, Australia. Gatliff & Gabriel (1911) described the shells as translucent yellow, small, thin and fragile, fattened, broadly ovate, with the posterior side [anterior end] longer and broader, and hinge short, without teeth. Gatliff & Gabriel (1911) also reproduced photographs of the two valves from inner views, with the right valve having a protoconch attached. They also mentioned additional larger valves that were not included in the original description because of their poorer preservation, as well as specimens of a second species from North Queensland, to be described by C. Hedley (Gatliff & Gabriel 1911).

In 1911, Verco (1911) reported *E. typica* from South Australia that he described in more detail in 1916 (Verco 1916). In the interim, Hedley (1912) commented on the original description of *E. typica* suggesting it may represent the internal shell of a sea slug, but if this animal were to be a bivalve, as suggested by Gatliff & Gabriel (1911), *Edenttellina* could be a synonym of

Ludovicia. Verco (1916) described several right and left valves and one complete shell collected in Guichen Bay, South Australia and provided details on its protoconch and teleoconch morphology. Hedley (1920) described the specimens mentioned by Gatliff & Gabriel (1911) from North Queensland as the new species *Edenttellina corallensis* Hedley, 1920 based on shells collected in Hope Island, and for comparison, illustrated the specimens of *E. typica* reported by Verco (1911, 1916). Hedley (1920) also provided an additional record for *E. typica* from King George Sound, Western Australia. Cotton & Godfrey (1938) described the presence of an anterior tooth in the hinge of *E. typica* and suggested the name *Edenttellina* was inappropriate.

Subsequently, Burn (1960a) reported collecting specimens of *E. typica* alive in Torquay, Victoria, Australia, which he confirmed to be sacoglossans, probably congeneric with the recently described species from Japan, *Tamanovalva limax* Kawaguti & Baba, 1959. Additionally, Burn (1960a) reported a second species of bivalved sacoglossan belonging to a different genus from the same area. In a second paper the same year, Burn (1960b) proposed the synonymy between the genera *Tamanovalva* and *Edenttellina* as well as with the fossil genus *Berthelinia*. Burn (1960b) also suggested that *T. limax* and *E. typica* are synonyms of *?Scintilla chloris* Dall, 1918, originally described from Baja California, Mexico, but not with the specimens identified as *E. typica* by Verco (1911, 1916) and illustrated in Hedley (1920). However, Burn (1960b) treated *Berthelinia typica* as a valid name (despite the fact older names should have priority) and did not use the generic names consistently with his proposed synonymy. Moreover, Burn (1960b) listed several differences between *B. typica* and *T. limax*, although he re-emphasized that *T. limax* and *B. typica* are synonyms, and also synonyms of *E. corallensis* and *?S. chloris*, arguing this latter species was larger but remarkably similar. Burn (1960b) provided a re-description of the shell and radula of *B. typica* based on the specimens collected in Torquay, and described the second species reported in Burn (1960a) as *Midorigai australis* Burn, 1960. Baba (1961a) examined additional specimens from Japan as well as a paratype of *M. australis* sent by Burn. Baba (1961a) noted that this paratype belonged to a species different from *M. australis* as it had smooth radular teeth. Baba (1961a) listed some morphological differences between the shell and radula of *Edenttellina* and *Tamanovalva* but indicated these two genera could be synonyms of *Berthelinia* along with *Ludovicia* and *Midorigai*; a synonymy that was later confirmed by Baba (1961b). Burn (1965) recognized that the paratype of *M. australis* sent to Baba for examination was a juvenile mistakenly placed in the paratype series of *M. australis*, and he now identified this specimen as belonging to the true *E. typica*. Burn (1965) also recognized the specimens he previously identified as *E. typica* belonged to an undescribed species that he named *Tamanovalva babai* Burn, 1965. Revising his previous assessment, Burn (1965) recognized *E. corallensis* and *?S. chloris* as distinct species belonging to the genus *Tamanovalva*. According to Burn (1965) all three species of bivalved sacoglossans found in Victoria, Australia were easily distinguishable as follows: 1) *E. typica* has a uniformly green shell with horizontal parallel black lines on the mantle and smooth and bifid radular teeth (lacking denticles); 2) *T. babai* has a completely green shell and denticulate radular teeth; and 3) *M. australis* has a green shell with numerous yellow patches, a mantle with yellow to cream-colored large rounded spots, and denticulate radular teeth. Burn (1989, 2015) depicted all three species alive. Burn (1965) did not provide further clarification on the specimens reported by Verco (1911, 1916) or illustrated in Hedley (1920), but in 1966 (Burn 1966) reported locating and re-examining those specimens. Based on their shell morphology, Burn (1966) suggested they could constitute a third species with intermediate characteristics between *T. babai* and *E. typica*.

In this study, we sequenced one specimen with the characteristic horizontal parallel black lines on the mantle described for this species, which was genetically distinct from all other species of Juliidae here examined. We also examined the syntypes of *Edenttellina typica* (Figs. 4A–B) and several additional specimens from temperate Australia, which were morphologically similar. Therefore, we propose that *E. typica* is a distinct and valid species. Additionally, phylogenetic analyses place *E. typica* in the same clade as all other species previously assigned to *Berthelinia*. Based on geometric morphometrics analyses (see above) *Berthelinia*, which was described based on fossil shells, is distinct from Recent species. Therefore, Recent species, including *E. typica* are here transferred to *Edenttellina*, which is the oldest available name for this clade.

EDENTTELLINA CHLORIS (DALL, 1918)

(FIGS. 4C–F, 5C–D, 9–11)

?Scintilla chloris Dall 1918: 5. Type locality: Magdalena Bay, Baja California Sur, Mexico.

Berthelinia chloris belvederica Keen & A. G. Smith 1961: 53–61, figs. 18–19, 21–24, 27–32, pl. 5, lower fig. Type locality: Puerto Balladry, near La Paz, Baja California Sur, Mexico.

Type material

?Scintilla chloris, syntypes, right and left valve (not from same specimen), 9 mm long (USNM 218179); right valve 9 mm long (CASIZ 064093).

Berthelinia chloris belvederica, Holotype, dry, 8.2 mm long (CASIZ 064091); paratypes, four valves 2.3–4 mm long (CASIZ 064092).

Additional material examined

Pacific Coast of Baja California.- East of Punta Estrada at Sail Rock, north entrance of Bahía Magdalena, Baja California Sur, Mexico, 30–31 Jan 1974, 3 valves 4–11 mm long, leg. J. McLean (NHMLA 1974-14.9).

Gulf of California.- Punta Pelícano, Puerto Peñasco, Sonora, Mexico, 30 Mar 1979, 1 specimen 10 mm long (shell), leg. C. J. O'Kelley (CASIZ 018381). Half a mile south of Rancho Algodones, near Bahía San Carlos, Sonora, Mexico, Dec 1975, 2 specimens 8 mm long (shells), isolates JC3A–B, leg. Forrest and Poorman (NHMLA 186690). Isla San José, Baja California Sur, Mexico, 2 Apr 1974, 10 specimens 4–9 mm long (shells), leg. G. Sphon (NHMLA 1974-33.1). Bahía Partida, between Isla Partida and Isla del Espiritu Santo, Baja California Sur, Mexico, 10 Apr 1966, 1 specimen 7 mm long (shell), leg. J. McLean (NHMLA 1966-28.30); 3 valves 6–6.5 mm long, leg. J. McLean (NHMLA 1966-28.31); 4 valves, 4–4.5 mm long, leg. J. McLean (NHMLA 1966-28.31). Bahía Candelero, Isla del Espiritu Santo, Baja California Sur, Mexico, 31 Aug 1960, 10 specimens (dry) 1.5–4.5 mm long, leg. M. Keen & A. G. Smith (CASIZ 201953); 1959–60, 6 specimens (dry) 4–7 mm long, leg. Belveder Science Expedition (CASIZ 201955); 18 valves 1–3 mm long (CASIZ 201951); 2 specimens + 2 valves 1–4 mm long (CASIZ 201952). Puerto Ballena, Isla del Espiritu Santo, Baja California Sur, Mexico, 19 Dec 1960, 5 specimens (dry) 3–6.5 mm long, leg. M. Keen & M. L. Valdez de Adcock (CASIZ 201954); 1 specimen (dry) 3 mm long, leg. Belveder Science Expedition (CASIZ 201954). Puerto Balandra, Baja California Sur, Mexico, 4 Oct 1960, 28 specimens (dry) 4–8.5 mm long, leg. A. G. Smith & K. K. Bechtel (CASIZ 201967); 5 specimens (dry) (possible paratypes of *B.*

chloris belvederica) 3.9–7.5 mm long, leg. A. G. Smith & K. K. Bechtel (CASIZ 201965); 17 valves (possible paratypes of *B. chloris belvederica*) 1–3 mm long, leg. A. G. Smith & K. K. Bechtel (CASIZ 201963).

Galapagos Islands.- Flamingo Cove, Isla Floreana, Galapagos Islands, Ecuador, 15 Mar 1971, 1 specimen 5 mm long (shell), leg. Ameripagos Expedition (stn. 10) (NHMLA 1971-52.14); 15–16 Mar 1971, 1 specimen (dry), 4.5 mm long (shell), leg Ameripagos Expedition (stn. 11) (NHMLA 1971-53.15). Punta Espinosa, Isla Fernandina, Galapagos Islands, Ecuador, 25 Jan 1972, 1 shell 9 mm long, leg. R. M. Lease (Searcher stn. 333) (NHMLA 1972-197.8); Nov 1992, 1 specimen 4 mm long (shell), leg. T Gosliner (CASIZ 087112). Bahía Urbina, Isla Isabela, Galapagos Islands, Ecuador, 1–3 m depth, 24 Jan 1972, 2 valves 9 mm long, leg. S. Earle (NHMLA 1972-192.1).

Description

Body elongate, up to 10.5 mm in length, completely retractable inside of shell. Body color vibrant dark green, with minute white speckles throughout (Figs. 5C–D). Head elongate, with eye spots located on dorsal swelling near center, surrounded by white pigment. Rhinophores enrolled, green, with small white speckles often forming a ring at the apex, cluster of white speckles on dorsal side. Oral tentacles short, green with white speckles on long edge. Foot lighter than rest of animal, with small spots along edge. Mantle visible through shell, vibrant dark green, covered with few whitish to pale green spots, variable in size; edge surrounded by conspicuous alternating opaque white patches composed of densely arranged speckles. Foot extending to posterior end of shell, forming small triangular projection.

Shell up to 9 × 5.6 mm in size, tallest point near center, widest point near ventral margin; shell shape ovoid, dorsal margin regularly curved, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin narrowing gradually, forming a nearly triangular, elongate shape, with round end (Figs. 9G–H). Protoconch on left valve of teleoconch, ~110 µm long, with 1.5 whorls (Fig. 9K). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; small, oval condyloid tooth on right valve at posterior end of hinge, and triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 9I–J). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 9A–F).

Adductor muscle located closer to anterior end of shell, slightly below widest point of shell (Fig. 10A), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Figs. 9H). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Anterior half of body in preserved specimens with pair of elongate pharyngeal appendages visible between head retractor muscle and gill (Fig 10B), connecting to the pharyngeal bulb dorsally (Fig. 10C). Penis elongate; distal end pointed, with no stylet visible; proximal end wider, with two strong retractor muscles attached and long, tubular deferent duct (Fig. 10D).

Radula with 29 teeth in descending limb and 9 fully formed teeth + 1 ghost tooth in ascending limb, in 9 mm long specimen from Baja California Sur, Mexico (NHMLA 1974-33.1) (Fig. 11A), and 25 teeth in descending limb and 7 fully formed teeth + 2 ghost teeth in ascending limb, in 8 mm long specimen from Sonora, Mexico (NHMLA 186690) (Fig. 11C). Active tooth ~130 µm long, with sharp, pointed tip; blade elongate with central row of numerous long, delicate denticles; base elongate, slightly curved (Fig. 11B, D). Ascus containing a rod-shaped pre-radular tooth plus about 5 intermediate teeth (Fig. 11C).

Biology

Keen & A. G. Smith (1961) reported finding living animals of this species in shallow water (0–2.5 m depth) on *Caulerpa sertularioides* (S. G. Gmelin) M. Howe, 1905 and *Caulerpa racemosa* var. *turbinata* [= *Caulerpa chemnitzia* (Esper) J. V. Lamouroux, 1809], which is a member of the *Caulerpa racemosa-peltata* species complex (see Belton et al. 2014).

Range

Eastern Pacific Ocean: Baja California (Dall 1918; Keen & A. G. Smith 1961; present paper), Costa Rica (Camacho-García et al. 2005), and Galapagos Islands (Sphon & Mulliner 1972; present paper).

Remarks

Dall (1918) introduced the name ?*Scintilla chloris* Dall 1918 based on two shells collected in Magdalena Bay, Baja California Sur, Mexico. He described the shells as pale green, translucent, with paler rays, the posterior end [anterior] wider, longer, and more rounded than the anterior end [posterior], which was shorter with a hinge, a single noduliform denticle, and a faint lateral lamella (Dall 1918). Dall (1918) interpreted the two shells as left valves and suggested they could belong to the bivalve genus *Scintilla* Deshayes, 1856. Keen & A. G. Smith (1961) examined manuscript illustrations of the type material of this species as well as additional specimens from the Pacific coast of the Baja California Peninsula and concluded that the two shells examined by Dall (1918) were in fact opposite valves. This has been corroborated by recent examination of the type material (USNM 218179) (Figs. 4C–D). Keen & A. G. Smith (1961) placed this species in *Berthelinia* and described the subspecies *B. chloris belvederica* based on additional specimens from the Gulf of California coast of Baja California Sur, which were morphologically different from the type material of *B. chloris chloris*. Specifically, Keen & A. G. Smith (1961) noted that the syntype of *B. chloris chloris* they examined was larger, more inflated, and had a more prominent lamellar tooth in the hinge than their specimens of *B. chloris belvederica.* Boettger (1962) considered the differences between *B. chloris belvederica* and *B. chloris chloris* to fall within the normal range of variation of a species and therefore regarded them as synonyms. This opinion is generally accepted, and more recent records refer to *B. chloris belvederica* as *B. chloris* (Sphon & Mulliner 1972; Camacho-García et al. 2005). We obtained the holotype of *B. chloris belvederica* (Figs. 4E–F) and did not find any distinguishing differences between it and *B. chloris chloris* here examined. Therefore we consider both to be *B. chloris*.

Camacho-García et al. (2005) and Behrens et al. (2022) illustrated live animals of *B. chloris*, which were nearly uniformly green with white dots concentrated on the rhinophores (forming a longitudinal line) and around the eyes, as well as faint white patches around the mantle margin, visible through the shell. Photographs of additional specimens (Fig. 5C–D) are similar but have more white pigment on the mantle, occupying almost the entire periphery of the shell, except for areas interrupted by green pigment, forming a dashed pattern.

For this study, we examined specimens from the Eastern Pacific Ocean (Sonora, Baja California and Galapagos Islands) matching the original description of *B. chloris*. Molecular phylogenies and geometric morphometric analyses nest this species within *Edenttellina* and therefore it is here transferred to this genus. *Edenttellina chloris* is similar to *E. pseudochloris*, but both are morphologically and genetically distinct, thus herein are both are regarded as valid.

EDENTTELLINA CORALLENSIS HEDLEY, 1920

Edenttellina corallensis Hedley 1920: 76, figs. 6–8. Type locality: Hope Island, Queensland, Australia.

Type material

Edenttellina corallensis, syntype, 1 right valve, 5 mm long (AM C.27643).

Remarks

Hedley (1920) introduced the name *Edenttellina corallensis* Hedley, 1920 for several shell specimens collected in Queensland, Australia. Hedley (1920) described the species briefly in the context of its differences with *E. typica*, commenting that the shell of *E. corallensis* was more solid, more compressed, and more pointed “anteriorly” [= posteriorly, based on the convention used in the present paper]. Hedley (1920) also described the color of the shell as pale sulfur yellow. Examination of the syntype of *E. corallensis* does not reveal any distinctive features consistent with any of the material here examined. Therefore, we are unable to determine the taxonomic status of *E. corallensis* and regarded it as a *nomen inquirendum*.

EDENTTELLINA LIMAX (KAWAGUTI & BABA 1959)

(FIGS. 12–14)

Tamanovalva limax Kawaguti & Baba 1959: 179–180, figs. 1–10. Type locality: Vicinity of the former Tamano Marine Laboratory, Okayama University, by the Great Seto Bridge, Japan.

Type material

Unknown (not reported in Higo et al. 1999).

Additional material examined

Tamano Bay, Okayama Prefecture, Japan, 22 Aug 1960, 2 specimens (dry) 3.4 mm long, leg. S. Kawaguti (CASIZ 201960); 3 valves 6–6.5 mm long, leg. S. Kawaguti (CASIZ 201959); 2 specimens (dry) 4.5–5 mm long + 33 veliger shells, leg. S. Kawaguti (CASIZ 201957); 75 veliger shells, leg. S. Kawaguti (CASIZ 201958); 10 veliger shells, leg. S. Kawaguti (CASIZ 201956). Mukaishima Is., Hiroshima Prefecture, Japan, 13 Apr 1960, 1 specimen (wet) 2 mm long (shell), leg. K. Baba (MV F23063).

Description

Live animals not examined, illustrated by Abe (1964: pl. 6, fig. 20) and Hamatani (2000: pl. 379; 2017: pl. 405) as having an elongate body, up to 10 mm in length. Body color pale green, lacking white speckles. Head elongate, with eye spots located on dorsal swelling near center. Rhinophores enrolled, green, with few white speckles. Oral tentacles short, green. Foot lighter than rest of animal. Mantle visible through shell, dark green, covered with large, whitish-beige patches, variable in size; edge surrounded by alternating opaque white patches composed of densely arranged speckles; adductor muscle visible through shell as white patch. Foot forming small triangular projection, not extending beyond posterior end of shell.

Shell up to 6.5 × 4.4 mm in size, tallest point near anterior margin, widest point near ventral margin; shell shape ovoid to quadrangular, dorsal margin regularly curved with distinct apex, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin shorter, narrowing gradually (Figs. 12G–H). Protoconch on left valve of teleoconch, ~150 µm long, with 1.5 whorls (Fig. 12K). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; low, oval condyloid tooth on right valve, triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 12I–J). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 12A–F).

Adductor muscle located in line with highest point of shell, slightly below widest point (Fig. 13A), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Figs. 12H). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Penis short, triangular; distal end pointed, with conical stylet (Fig. 13C); proximal end of penis wider, with two strong retractor muscles attached and tubular deferent duct (Fig. 13B). Pharyngeal bulb as wide as tall (Fig 13D).

Radula with 28 teeth in descending limb and 6 fully formed teeth + 1 ghost tooth in ascending limb, in 4.5 mm long specimen from Tamano Bay, Japan (CASIZ 201957) (Fig. 14A). Active tooth ~135 µm long with sharp, pointed tip; blade elongate with central row of numerous long, delicate denticles; base short, curved (Fig. 14B). Ascus containing one long, rod-shaped pre-radular tooth plus 5 intermediate teeth (Fig. 14C).

Biology

According to Kawaguti & Yamasu (1960), *E. limax* feeds on *Caulerpa okamurai* Weber-van Bosse *in* Okamura, 1897, and lays egg masses with a small number of eggs (11–470); each egg within an ovoid capsule of 250 µm × 270–380 µm on average. And according to Yamasu (1969) it has lecithotrophic development, very similar to that of *E. singaporensis* (Jensen & On, 2018; Wong and Sigwart, 2019).

Range

Wakayama Prefecture and Inland Sea, Japan (Kawaguti & Baba 1959; Hamatani 2017).

Remarks

Kawaguti & Baba (1959) described for the first time live animals of Juliidae under the new name *Tamanovalva limax* Kawaguti & Baba, 1959. For the original description, Kawaguti & Baba (1959) had access to more than 200 specimens collected near the former Tamano Marine Laboratory, Okayama University, Japan. Unfortunately, they did not designate a holotype and we have been unable to locate the type series. Kawaguti & Baba's (1959) description included accounts of the characteristics of the live animals as well as features of the internal anatomy and the shell, all illustrated in great detail. Kawaguti & Baba (1959) described the shell as translucent yellowish white, thin, elongate-oval, narrowing posteriorly, with the umbo behind the mid-length, hinge with no teeth. The live animals' color was described as deep green with opaque white dots on the rhinophores and head, mantle margin sparsely spotted with white and dark brown, and the mantle's deep green color showing through the shell. Other characteristics included having stout, grooved rhinophores, small foot corners, a raised area where the eyes are located, and a short posterior end of the foot, not extending beyond the shell. The radula was formed of 35 blade-like teeth finely denticulate on both edges.

Prabhakara Rao (1965) reported four specimens of bivalved gastropods from India found on *Caulerpa racemosa*. The animals were described as leaf green with opaque white spots with a few dark green spots on the digestive gland. The illustration of the specimens (Prabhakara Rao 1965: fig. 1) and the host alga, are more consistent with those of *E. pseudochloris* and therefore are here assigned to this species. Subsequently, Ganapati & Sarma (1972) reported recently metamorphosed juvenile specimens also found on *C. racemosa* in India and assigned them to *T. limax*. Again, based on the host alga, this record is here considered to be of *E. pseudochloris*.

We examined several specimens from Japan that are morphologically consistent with the characteristics of *T. limax*, some of which were collected and identified by S. Kawaguti. These specimens have a conical stylet in the penis, which is absent in other specimens of Juliidae here examined. Unfortunately, we were unable to obtain sequence data from those specimens, thus we cannot confirm that they are genetically distinct. However, these Japanese specimens are morphologically distinct from other species here recognized and therefore we regard *T. limax* as a valid species, probably endemic to Japan. Finally, because *T. limax* is morphologically coherent with other recent species here considered to be members of *Edenttellina*, it is here transferred to this genus.

EDENTTELLINA AUSTRALIS (BURN, 1960)

(Figs. 4J–K, 5E–F, 15–17)

Midorigai australis Burn 1960b: 46, figs. 8–14. Type locality: Torquay, Victoria, Australia.

Type material

Midorigai australis, Holotype, complete specimen, valves separated, damaged, 4 mm long (MV F21193).

Additional material examined

Portsea, Victoria, Australia, date unknown, 1 valve 2.5 mm long (MV F215277). Pickering Point area, Warrnambool, Victoria, Australia, 23 Feb 2011, 1 specimen 2 mm long (shell) (MV F188699). Dutton Way, Portland Bay, Victoria, Australia, 17 Feb 2012, 1 specimen 4.1 mm long (shell), isolate JC18 (MV F194029). Kitty Miller Bay, Phillip Island, Victoria, Australia, 13 Feb 2008, 2 specimens 1.9–3 mm long (shell) (MV F158625).

Description

Body elongate, up to 5.6 mm in length, completely retractable inside of shell. Body color pale to dark green, with numerous minute white speckles throughout (Figs. 5E–F). Head elongate, with eye spots located on dorsal swelling near center, surrounded by white pigment. Rhinophores enrolled, green, with small white speckles forming two rings. Oral tentacles short, green with white speckles at base. Foot lighter than rest of animal, with small spots along edge. Mantle visible through shell, dark green, covered with large, whitish-beige patches, variable in size; edge surrounded by alternating opaque white patches composed of densely arranged speckles. Foot not extending to posterior end of shell, forming small triangular projection.

Shell up to 4 × 2.6 mm in size, tallest point near anterior margin, widest point near ventral margin; shell shape ovoid to quadrangular, dorsal margin regularly curved with distinct apex, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin shorter, narrowing gradually (Figs. 15E–F). Protoconch on left valve of teleoconch, not observed. Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; no distinct condyloid tooth on right valve, but elongate protuberance at posterior end of hinge, triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 15G–H). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 15A–D).

Adductor muscle located in line with highest point of shell, slightly below widest point (Fig. 16A), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Figs. 15F). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Anterior half of body in preserved specimens with penis visible above adductor muscle (Fig. 16B). Penis elongate; distal end pointed, with very elongated, hollow stylet (Fig. 16D); proximal end of penis wider, with two strong retractor muscles attached and long, tubular deferent duct (Fig. 16C). A single, reduced pharyngeal appendage observed, connected to the dorsal side of the pharyngeal bulb (Fig 16E).

Radula with 35 teeth in descending limb and 6 fully formed teeth + 1 ghost tooth in ascending limb, in 4.1 mm long specimen from Victoria, Australia (MV F194029) (Fig. 17A). Active tooth ~260 µm long with sharp, pointed tip; blade elongate with central row of numerous long, delicate denticles; base short, slightly curved; juvenile teeth bicuspid (Fig. 17B). Ascus containing one long, rod-shaped pre-radular tooth and 3 (possibly 4) intermediate teeth (Fig. 17C).

Biology

This species feeds on *Caulerpa simpliciuscula* (R. Brown ex Turner) C. Agardh, 1823 (Burn 1989). According to Wisely (1962), *E. australis* produces egg masses with 50–52 eggs and operculate veligers with shells 116–118 µm in diameter that hatched after 11–13 days.

Range

Victoria, Australia (Burn 1960a, 1960b; present paper), Tasmania and South Australia (Burn 2006).

Remarks

Burn (1960a) reported finding the first living specimens of *Edenttellina typica* Gatliff & Gabriel, 1911, in Torquay, Victoria, Australia. Burn (1960a) also reported collecting a second species of bivalved gastropod that “undoubtedly” belonged to a different genus in the same group. In a second paper the same year, Burn (1960b) redescribed *E. typica* and transferred it to *Berthelinia*. In addition, Burn (1960b) introduced the new name *Midorigai australis* Burn, 1960 for the second species mentioned in the previous paper. Burn (1960b) described the live animals of *M. australis* as dark green, with large yellowish patches on the rhinophores and the rest of the body, including the mantle, which is densely spotted with large, rounded, yellowish-cream patches and has square-shaped yellow patches along the edges. Burn (1960b) described the shell as translucent olive-green with darker rays of green, squarer than in *Berthelinia*, with the left valve more convex and higher than the right valve, hinge with no teeth.

For this paper, we have studied several specimens collected in Philip Island, Victoria, Australian (~75 km east of Torquay), characterized by having a green body color with numerous, large, rounded yellowish green to opaque white spots, larger on the mantle. We obtained nuclear DNA sequence data for two of them. We also examined the holotype of *M. australis* (Figs. 4J–K) but it is too damaged to draw any conclusions. These animals match the original description of *M. australis* and are here regarded as members of this species. Both the five-gene sequence data and the geometric morphometrics analyses confirm these animals belong in the genus *Edenttellina*, but are genetically distinct from all other species. Thus, we regard *M. australis* as a distinct and valid species of *Edenttellina*.

EDENTTELLINA CARIBBEA (EDMUNDS, 1963)
(Figs. 5G–H, 18–20)

Berthelinia caribbea Edmunds 1963: 731–737, figs. 1–5, pl. 1. Type locality: Port Royal, Jamaica.

Type material

Berthelinia caribbea, Holotype, complete specimen, not examined (NHMUK 1962261), six paratypes (NHMUK 1962262, NHMUK 1962263).

Additional material examined

Bermuda.- Sandys Parish, Bermuda, 1 m depth, 18 Jun 2009, 3 specimens 2.5–3 mm long (shell), leg. Pola et al. (CASIZ 181198–181200). St. George Island, Bermuda, 4 m depth, 10 Jun 2009, 1 specimen 2 mm long (live), leg. Pola et al. (CASIZ 181097).

Caribbean.- Canal off Snake Creek, Plantation Creek, Florida, 14 Jul 1978, 1 specimen (dry) 4 mm long, leg. M. Miller (CASIZ 112229). Andros Island, Bahamas, 3 m depth, 28 Aug 1971, 1 valve 0.9 long, leg. D. R. Moore (CASIZ 112231). Sweeting Cay, Bahamas, tissue only, isolate Bcar10Swe01. Abaco, Bahamas, 1 specimen 4 mm long (shell), leg. C. Redfern (NHMLA 011629). Grande Caye, St. Martin, 4–6 m depth, 21 Apr 2012, 1 specimen 3 mm long (shell), leg. G. Paulay & F. Michonneau (FMNH 451025). Petite Terre, Guadeloupe, 26 May 2012, 1 specimen 1 mm long (shell), isolate JC45, Karubenthos 2012 Expedition (stn. GB31) (MNHN IM-2013-53075). Lagon de Saint François, Guadeloupe, 28 May 2012, 1 specimen 3 mm long (shell), isolate JC46, Karubenthos 2012 Expedition (stn. GB35) (MNHN IM-2013-53074); 1 specimen 2.5 mm long (shell), isolate JC44, Karubenthos 2012 Expedition (stn. GB35) (MNHN IM-2013-53076); 1 specimen 2 mm long (shell), isolate JC43, Karubenthos 2012 Expedition (stn. GB35) (MNHN IM-2013-53077). Guayama Bay, Puerto Rico, 24 Nov 1964, 3 specimens 3–3.5 mm long (shells), leg. Warmke & Modovar (CASIZ 074790). La Parguera, Puerto Rico, 10 Apr 1965, 2 specimens (dry) 1.2–1.8 mm long, leg. P. Glynn (CASIZ 201950). Puerto Viejo, Limón, Costa Rica, 1–8 m depth, 30 Oct 1986, 1 valve 2.5 mm long, leg. R. C. Brusca & P. M. Delaney (NHMLA 1986-202.28). 1 km northeast of Punta Manzanillo, Limón, Costa Rica, 23 m depth, 13 Mar 2001, 1 specimen 4.8 mm long (shell), leg. S. Avila (MZUC INB3321518).

Brazil.- Plage de Gaibu, Cabo de Santo Agostinho, Pernambuco, Brazil, 1985–89, 7 valves 1.8–3.5 mm long, leg. P. Maestrati (MHNH). Base of Mushroom Reef, 3 km southeast of Santa Barbara Island, Abrolhos Archipelago, Brazil, 23 m depth, 27 Jul 1977, 7 valves and fragments, 1–3 mm long, leg. E. Petuch (CASIZ 112230).

Description

Body elongate, up to 6.5 mm in length, completely retractable inside of shell. Body color bright green, with numerous minute white speckles throughout, but more densely arranged on the dorsal side of head (Figs. 5G–H). Head elongate, with eye spots located on dorsal swelling near center, surrounded by white pigment; two parallel brown lines run between base of rhinophores and eye spots, then merge into single brown line running backwards to pericardium; brown spots scattered over rest of head in some specimens. Rhinophores enrolled, green, with high concentration of small white and brown speckles. Oral tentacles short, green with white speckles at base. Foot lighter than rest of animal. Mantle visible through shell, dark green, covered with large, irregular whitish-beige patches, variable in size and numerous transverse white and brown lines; edge surrounded by alternating opaque white patches composed of densely arranged speckles and dark brown patches. Foot not extending to posterior end of shell, forming small triangular projection.

Shell up to 4.8 × 3.5 mm in size, tallest point near anterior margin, widest point near ventral margin; shell shape ovoid, dorsal margin regularly curved with distinct apex, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin shorter, narrowing gradually (Figs. 18G–H). Protoconch on left valve of teleoconch, ~110 µm long, with 1.5 whorls (Fig. 18K). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; large, rounded condyloid tooth at posterior end of hinge on right valve, triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 18I–J). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 18A–D).

Adductor muscle in line with highest and widest points of shell (Fig. 19A), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Figs. 18H). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Anterior half of body in preserved specimens with pair of elongate pharyngeal appendages visible above adductor muscle (Fig 19B), connecting to the pharyngeal bulb posteriorly (Fig. 19C). Penis elongate; distal end pointed, with no stylet visible; proximal end wider, with strong retractor muscle and long, tubular deferent duct (Fig. 19D).

Radula with 25 teeth in descending limb and 11 fully formed teeth + 1 ghost tooth in ascending limb, in 3 mm long specimen from Abaco, Bahamas (NHMLA 011629) (Fig. 20A). Active tooth ~110 µm long (Fig. 20B), with sharp, harpoon-tip shaped, pointed tip; blade elongate with central row of numerous short, delicate denticles (Fig. 20D); base short, curved. Ascus containing 3 disorganized elongate pre-radular teeth (Fig. 20C).

Biology

According to Grahame (1969) *B. caribbea* feeds on *Caulerpa verticillata* J. Agardh, 1847. The species has a short life span, with rapid growth rate, and high fecundity (Grahame 1969). The number of eggs per egg mass vary from 14–32 (Davis 1967) to 35–40, occasionally 80–100 (Grahame 1969). Eggs were about 100 µm in diameter (Clark & Jensen 1981), encased in ovoid capsules about 300 µm, developing into lecithotrophic larvae with a shell width of 230 µm (Grahame 1969); newly hatched veligers settle almost immediately on *Caulerpa* and begin to feed.

Range

Western Atlantic Ocean: Bermuda (present paper), Florida Keys (Moore & Miller 1979; Clark 1994; present paper), Bahamas (Valdés et al. 2006; Redfern 2001, 2013; present paper), Cuba (Espinosa et al. 2006), Puerto Rico (Warmke 1966; Grahame 1969; present paper), Jamaica (Edmunds 1962, 1963), St. Martin (present paper), Guadeloupe (Ortea et al. 2012; present paper), Mexico (Ortigosa et al. 2013; Ortigosa et al. 2015), Belize (Clark & DeFreese 1987), Costa Rica (Espinosa & Ortea 2001; Camacho-García et al. 2014; present paper), Panama (Meeder & Moore 1972), and Brazil (Meeder & Moore 1972; Mello & Perrier 1986; present paper).

Remarks

Edmunds (1963) described *Berthelinia caribbea* Edmunds, 1963 based on live animals collected in Jamaica. The most distinctive external characteristics of this species is the presence of irregular horizontal bands of dark reddish-brown or yellowish-brown on the mantle, showing clearly through the transparent shell in both live and preserved specimens.

Redfern (2013: 280, figs. 780A–C) described and illustrated a second species of *Berthellinia* from the Bahamas, based on shells with a slightly different shell morphology and a more coiled protoconch than those of *B. caribbea*, which he also illustrated. These animals may constitute a distinct species, but in the absence of material for anatomical and molecular work, it cannot be described.

For this paper, we examined and sequenced several specimens from the Caribbean region and Brazil matching the original description of *B. caribbea*. Geometric morphometrics analyses confirmed the shells of these specimens are morphologically similar to those of other species of *Edenttellina*. Additionally, molecular data confirm *B. caribbea* is sister to the rest of *Edenttellina*. Based on those two lines of evidence we transfer *B. caribbea* to *Edenttellina* and confirm that *E. caribbea* is a valid species name.

The ABGD species delimitation analyses based on the 16S gene split *E. caribbea* into two different groups, but this split was not recovered in the COI and H3 analyses. Moreover, there are no obvious morphological differences between these two groups, thus they are here maintained in the same species. The two groups recovered have different geographic ranges, one including Bahamian specimens and the other Caribbean-proper specimens, suggesting a certain degree of genetic isolation between the two populations. Further research including a larger sample size may yet support cryptic diversity in *E. caribbea*.

EDENTTELLINA PSEUDOCHLORIS (KAY, 1964)

(Figs. 4G–H, 4L, 5I–L, 21–23)

Berthelinia pseudochloris Kay 1964: 191–193, fig. 1, pl. 9, figs. 1, 4. Type locality: Near Koloa Landing, Koloa, Kaua‘i, Hawaiian Islands.

Tamanovalva fijiensis Burn 1966: 54–55, pls. 15–19. Type locality: Nukulau Island, Viti Levu, Fiji.

Berthelinia ganapatii Sarma 1975: 16–20, figs. 6–13, 28–29. Type locality: Visakhapatnam, India.

Type material

Berthelinia pseudochloris, Holotype, complete specimen, not examined (BM 8903). Paratype, 1 complete specimen, 3.7 mm long (shell) (CASIZ 018374).

Tamanovalva fijiensis, Holotype, complete specimen, shell dissolved, 1.5 mm long (animal)

(MV F25647).

Berthelinia ganapatii, Holotype and paratypes at the Department of Zoology, Andhra University, Waltair, India, not examined.

Additional material examined

Central Pacific and Hawaiian Islands.- Honokowai Beach Park, Maui, Hawaiian Islands, 2–11 m depth, 9 Oct 2010, 1 specimen 4.5 mm long (shell), isolate JC21 (CASIZ 185144). Mama's Fish House Tide Pool, Maui, Hawaiian Islands, tissue only, isolate Bpse16Mau06. Olivine Pools, Maui, Hawaiian Islands, 15 Jun 2011, 1 specimen 3 mm long (shell), isolate JC11B (CPIC 00315).

Western Pacific.- East of Santa Cruz Is., off Zamboanga, Mindanao, Philippines, 9–18 m depth, 19 Jan 1981, 1 valve 4 mm long, leg. J.M. McLean (NHMLA 1981-71.7). Mabini, Luzon, Philippines, 2001, 1 specimen 5 mm long (shell), isolate JC33B (CASIZ 199470). Momo Beach, Panglao Is., Philippines, 28–32 m depth, 10 Jun 2004, 1 valve 4 mm long, leg. Panglao Marine Biodiversity Project, stn. S8 (MNHN). Pamilacan Is., Philippines, 6–8 m depth, 14 Jun 2004, 1 specimen (dry) 2.8 mm long, leg. Panglao Marine Biodiversity Project, stn. S12 (MNHN). Bingag, Panglao Is., Philippines, 20 m depth, 17 Jun 2004, 1 specimen 4 mm long, leg. Panglao Marine Biodiversity Project, stn. B16 (MNHN). South Megas Islet, Madang, Papua New Guinea, 6 m depth, 14 Nov 2012, 1 valve 4.1 mm long, leg. Expédition Papua Niugini, stn. PS12 (MNHM). Between Kranet Is. and Paeowa Is., Madang, Papua New Guinea, 2–10 m depth, 27 Nov 2012, 1 valve 4.5 mm long, leg. Expédition Papua Niugini, stn. PD52 (MNHM). South Urembo Is., Madang, Papua New Guinea, 10 m depth, 5 Dec 2012, 1 valve 4.5 mm long, leg. Expédition Papua Niugini, stn. PS41 (MNHM). North Riwo, Madang, Papua New Guinea, 3 m depth, 13 Dec 2012, 1 valve 2.3 mm long, leg. Expédition Papua Niugini, stn. PB53 (MNHM). Northwest point of Nusa Is., Kavieng Lagoon, Madang, Papua New Guinea, 3 Jun 2014, 1 specimen 5.1 mm long (shell), leg. Expédition Kavieng 2014, stn. KB03 (MNHN IM-2013-47177). Northwest point of Manne Is., Kavieng Lagoon, Madang, Papua New Guinea, 4 Jun 2014, 1 specimen 3.1 mm long (shell), leg. Expédition Kavieng 2014, stn. KB06 (MNHN IM-2013-47623). Malokilikili, Espiritu Santo, Vanuatu, 7 m depth, 5 Oct 2006, 1 specimen (dry) 4.9 mm long, leg. Santo Marine Biodiversity Survey, stn. FB52 (MNHN). Segond Channel, Wambu

River mouth, Espiritu Santo, Vanuatu, 7 m depth, 6 Oct 2006, 1 valve 4 mm long, leg. Santo Marine Biodiversity Survey, stn. DS91 (MNHN). North Tutuba Is., Espiritu Santo, Vanuatu, 17–19 m depth, 11 Oct 2006, 3 valves 3–4.5 mm long, leg. Santo Marine Biodiversity Survey, stn. DS101 (MNHN). West Tutuba Is., Espiritu Santo, Vanuatu, 70–80 m depth, 14 Oct 2006, 1 valve 4 mm long, leg. Santo Marine Biodiversity Survey, stn. DS103 (MNHN). Off north of Urélapa Is., Espiritu Santo, Vanuatu, 100 m depth, 14 Oct 2006, 1 valve 4 mm long, leg. Santo Marine Biodiversity Survey, stn. EP32 (MNHN). Tutuba Is., Vanatovoa Bay, Espiritu Santo, Vanuatu, 2–4 m depth, 14 Oct 2006, 1 specimen (dry) 2.1 mm long, leg. Santo Marine Biodiversity Survey, stn. FB92 (MNHN). Bruat Channel, North coast of Malo Is., Espiritu Santo, Vanuatu, 35 m depth, 19 Oct 2006, 1 valve 4 mm long, leg. Santo Marine Biodiversity Survey, stn. DS110 (MNHN). Grand Récif Mengalia, Secteur Touho, New Caledonia, Sep 1993, 1 specimen (dry) 2.2 mm long, leg. Expédition Montrouzier, stn. 1245 (MNHN). Banc de Touho, Secteur de Touho, New Caledonia, Sep 1993, 1 specimen (dry) + 4 valves 2–4 mm long, leg. Expédition Montrouzier, stn. 1259 (MNHN). Grand Récif Mengalia, Secteur de Touho, New Caledonia, 10–35 m depth, Sep 1993, 3 valves 3.5–5 mm long, leg. Expédition Montrouzier, stn. 1270 (NHMN). Tié shoal, Secteur de Touho, New Caledonia, 5–25 m depth, Oct 1993, 1 specimen (dry) + 3 valves 2–3.5 mm long, leg. Expédition Montrouzier, stn. 1271 (NHMN). Récif Extérieur, Passe de Touho, Secteur de Touho, New Caledonia, 20 m depth, Sep 1993, 2 valves 4 mm long, leg. Expédition Montrouzier, stn. 1273 (NHMN). Baie de Koumac, Secteur Koumac, New Caledonia, 3–7 m depth, Oct 1993, 1 valve 6.5 mm long, leg. Expédition Montrouzier, stn. 1297 (MNHN). Grand Récif de Koumac, Secteur Koumac, New Caledonia, 12 m depth, Oct 1993, 8 valves 2.1–3.9 mm long, leg. Expédition Montrouzier, stn. 1316 (MNHN). Passe Deverd, Secteur de Koumac, New Caledonia, 15–20 m depth, Oct 1993, 1 specimen (dry) 3.5 mm long, leg. Expédition Montrouzier, stn. 1319 (MNHN). Lansdowne, west of New Caledonia, 427–505 m depth, 20 Oct 2005, 1 specimen (dry) 3 mm long, leg. Campagne Ebisco, stn. DW2617 (MNHN). Lizard Island, Australia, 13 Jul 2006, 1 specimen, sequence only (Tl792LIC).

Indian Ocean.- Ponta do Farol, Inhaca Is., Mozambique, 27 Nov 2011, 1 specimen (dry) 4.5 mm long, leg. Expédition Inhaca, stn. MM6 (MNHN).

Description

Body elongate, up to 8.5 mm in length, completely retractable inside of shell. Body color vibrant dark green, with few, scattered white speckles (Figs. 5I–L). Head elongate, with eyespots located on dorsal swelling near center. Rhinophores enrolled, green, with small white speckles often concentrated at the apex. Oral tentacles short, green. Foot lighter than rest of animal. Mantle visible through shell, vibrant dark green, covered with small white dots; edge surrounded by conspicuous alternating opaque white patches composed of densely arranged speckles. Foot extending to posterior end of shell, forming small triangular projection.

Shell up to 6.5 × 4.6 mm in size, tallest point near anterior end, widest point near ventral margin; shell shape ovoid, dorsal margin with flattened extension near anterior end, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin narrowing gradually, forming a nearly triangular, elongate shape, with round end (Figs. 21G–H). Protoconch on left valve of teleoconch, ~215 µm long, with 1.5 whorls (Fig. 21K). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; small, oval condyloid tooth on right valve at posterior end of hinge, and triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 21I–J). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 21A–F).

Adductor muscle located closer to anterior end of shell, in line with widest point (Fig. 22A, C), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Fig. 21H). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Anterior half of body in preserved specimens with pair of elongate pharyngeal appendages visible anterior or dorsal to adductor muscle, connecting to the pharyngeal bulb posteriorly (Fig. 21B). Penis elongate; distal end pointed, with a cuticularized tip; proximal end wider, with two strong retractor muscles attached (Fig. 21D).

Radula with 33 teeth in descending limb and 5 fully formed teeth in ascending limb, in 5.1 mm long specimen from Papua New Guinea (MNHN IM-2013-47177) (Fig. 23A), and 31 teeth in descending limb and 5 fully formed teeth + 1 ghost teeth in ascending limb, in 4.5 mm long specimen from Maui, Hawaiian Is. (CASIZ 185144). Active tooth ~90–130 µm long, with sharp, pointed tip; blade elongate with central row of numerous long, delicate denticles; base short, curved (Fig. 23B, D). Ascus spirally coiled, with one long, rod-shaped pre-radular tooth, plus several (>5) intermediate teeth (Fig. 23C).

Biology

Kay (1964) reported *Berthelinia pseudochloris* occurs on dense masses of *Caulerpa racemosa* var. *turbinata* [= *Caulerpa chemnitzia*] with little intrusion of other algal species, in areas with constant and frequently heavy surf. Burn (1966) reported collecting *B. fijiensis* on *Caulerpa racemosa* var. *turbinata* [= *Caulerpa chemnitzia*]. Sarma (1975) found *Berthelinia ganapatii* fairly commonly on the Visakhapatnam foreshore during the period December to May among *Caulerpa racemosa*. Sarma (1975) described the egg masses and development of *B. ganapatii*; the number of eggs in egg masses fluctuated from 500–3520, with eggs 50 µm in diameter and capsules 90 µm, indicating this species is probably planktotrophic (see Krug et al. 2015). Both *C. racemosa* and *C. chemnitzia* are closely related species and members of the *C. racemosa-peltata* complex (see Belton et al. 2014).

Range

Hawaiian Islands (Kay 1964; present paper), Japan (Ono 1999), Fiji (Burn 1966), Philippines (present paper), Papua New Guinea (present paper), Vanuatu (present paper), New Caledonia (present paper), India (Prabhakara Rao 1965; Ganapati & Sarma 1972; Sarma 1975), Madagascar (Legendre 1965), Mozambique (present paper), Réunion (Joannot & Vendel 2011), South Africa (Gosliner 1987), and possibly Easter Island (Rehder 1980).

Remarks

Kay (1962a) reported a single specimen of a live bivalved sacoglossan collected in the Hawaiian Islands. Kay (1962a) argued that this animal was morphologically different from other species described to date and probably constituted a distinct species. Kay (1964) formally described the species as *Berthelinia pseudochloris* Kay 1964, based on several specimens collected Near Koloa Landing, Kaua‘i, Hawaiian Islands. Kay (1964) described the shell of this species as small, thin, translucent green, ovate-triangular, rounded anteriorly, narrower posteriorly, with the white protoconch on the left valve, and the hinge with a strong tooth, and frequently a secondary weaker tooth posteriorly. The live animals, subsequently illustrated by Kay (1979), were described as leaf-green, with minute opaque milk-white spots on the oral tentacles, rhinophores and foot; rhinophores with one or two larger white blotches, head and neck are microscopically speckled with brown, mantle with red bands alternating with white patches, visible through the shell ventrally (Kay 1964). We examined several specimens from the Hawaiian Islands matching the characteristics enumerated in the original description of *B. pseudochloris* as well as the shell morphology of the paratype (Figs. 4G–H); these animals are anatomically and genetically distinct from other species here examined and constitute a distinct species. Therefore, we here regard *B. pseudochloris* as a valid species. Additionally, geometric morphometrics and molecular analyses of specimens here examined from the Hawaiian Islands confirm this species is distinct and a member of the Recent genus *Edenttellina*.

Burn (1966) introduced *Tamanovalva fijiensis* Burn, 1966 based on a single specimen collected from Viti Levu, Fiji. The live holotype was described as pale green with cream speckling on the slender, auriculate, and abruptly truncate rhinophores (Burn 1966). The characteristics of the pale-yellow shell included a steeply angled and rather straight anterior margin, a broadly rounded posterior margin, and a small, white protoconch, slightly inclined to the left, anterior to the second third of the shell length. According to Burn (1966) the radula had 5 teeth in the ascending and 25–30 in the descending limbs; radular teeth rather stout, strongly rounded above the simple tip and laterally finely denticulate. Burn (1966) placed this species in *Tamanovalva* because of having one and a half whorls, not two, in the protoconch. Burn (1966) recognized that the holotype of *T. fijiensis* had a similar shell outline to that of *E. pseudochloris* (see Kay1964: fig. 4; Burn 1966: figs. 15–16). Also, both feed on *Caulerpa chemnitzia*, have a white protoconch with 1.5 whorls, and short and wide radular teeth with numerous denticles (Fig. 23; Burn 1966: figs. 18). Given these similarities, we propose that *T. fijiensis* is a synonym of *E. pseudochloris*. A photograph of the holotype of *T. fijiensis* included here (Fig. 4L) confirms the morphological similarities with *E. pseudochloris*.

Sarma (1975) described *Berthelinia ganapatii* Sarma, 1975 based on live specimens collected in Visakhapatnam, India. The color of the rhinophores, neck and foot were described as uniformly yellow, with the tips of the rhinophores speckled with white spots (Sarma 1975); the mantle was deep yellowish-green, with two bright shining yellow patches, all visible through the transparent shell. Sarma (1975) described the shell as deep green but transparent [*sic.*] with yellow rays on the surface, fragile, ovate trigonal in outline, with the anterior margin rounded and abrupt, and the posterior margin longer. The small, erect protoconch was situated at the third quarter of the shell length and the hinge had a weak tooth in the left valve and a strong tooth posteriorly on the right valve. Sarma (1975) described the radula as having blade-like teeth bearing fine denticulations on the sides and having simple tips, with 7 teeth in the ascending row and 35 in the descending row. Sarma (1975) recognized that *B. ganapatii* was close to *E. pseudochloris* but distinguishable by having a more abrupt anterior margin, a longer posterior margin and an erect protoconch. Similarities between these two species are remarkable: they both feed exclusively on species of the *C. racemosa-peltata* complex; they have a hinge with teeth, and fairly similar external coloration. The radula of *B. ganapatii* contains short and broad teeth with numerous denticles (Sarma 1975: fig. 13), very similar to the teeth of *E. pseudochloris* here illustrated (Fig. 23). Finally, both species have planktotrophic development. Because of the similarities between the original descriptions of *B. ganapatii* and *B. pseudochloris*, we regard these two names as synonyms.

Records of *Berthelinia* spp. from several localities in the Indo-Pacific region, including Madagascar (Legendre 1965), India (Prabhakara Rao 1965; Ganapati & Sarma 1972), South Africa (Gosliner 1987), and tropical Japan (Ono 1999) were based on animals very similar to the specimens of *E. pseudochloris* here examined and are here regarded as members of this species. A record of *E. pseudochloris* from Easter Island by Rehder (1980) could not be verified with certainty.

EDENTTELLINA BABAI (BURN, 1965)

(FIGS. 4M–N, 24A–C, 25–27)

Tamanovalva babai Burn 1965: 735–736, fig. 3. Type locality: Point Danger, Torquay, Victoria, Australia.

Type material

Tamanovalva babai, Holotype, complete specimen, valves separated, damaged, 4.5 mm long (MV F23064).

Additional material examined

Harmers Haven, south of Wonthaggi, Victoria, Australia, 13 Mar 2008, 1 specimen 2 mm long (shell), on *Caulerpa cactoides* (Turner) C. Agardh, 1817 (MV F159081). Werribee, Port Philip, Victoria, Australia, 5 m depth, 11 Dec 1995, 2 specimens 3 mm long (shells), leg. CSIRO (MV F112386). Kitty Miller Bay, Philip Island, Victoria, Australia, 13 Feb 2008, 2 specimens 3–3.2 mm long (shells) (MV F158624). Kingston, Norfolk Island, Australia, 1 Mar 1962, >10 specimens 1.5–4.5 mm long (shells), leg. L. Marsh (MV F22716). Queensland, Australia, 9 Oct 2014, 8 specimens 2–3 mm long (shells), leg. K. Kocot (lot 94-5E). Lord Howe Island, Australia, 1 specimen (AM C.469652).

Description

Body elongate, up to 6.7 mm in length, completely retractable inside of shell. Body color uniformly green, with few minute white speckles concentrated on dorsal swelling near center (Figs. 24A–C). Head elongate, with eye spots located on dorsal swelling near center. Rhinophores enrolled, green, with small white dots near tips. Oral tentacles short, green. Foot lighter than rest of animal. Mantle visible through shell, green, lacking other pigmentation. Foot forming small triangular projection, not extending beyond posterior end of shell,.

Shell up to 4.5 × 3.3 mm in size, tallest point halfway between anterior margin, protoconch; widest point near ventral margin; shell shape ovoid, dorsal margin regularly curved with a flattened expansion near anterior end, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin shorter, narrowing gradually (Figs. 25G–H). Protoconch on left valve of teleoconch, ~200 µm long, with 1.5 whorls (Fig. 25K). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; large, elongate condyloid tooth at posterior end of hinge on right valve, triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 25I–J). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 25A–F).

Adductor muscle slightly posterior to highest point of shell, in line with widest point (Fig. 26A), connected to narrow and elongate head retractor muscle. Adductor scar visible on shell (Figs. 25H). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Anterior half of body in preserved specimens with pair of elongate pharyngeal appendages visible below adductor muscle (Fig 26B), connecting to the pharyngeal bulb posteriorly (Fig. 26C). Penis elongate; distal end pointed, with a short stylet (Fig. 26E); proximal end wider, with strong retractor muscle and long, tubular deferent duct (Fig. 26D).

Radula with 23 teeth in descending limb and 5 fully formed teeth + 1 ghost tooth in ascending limb, in 3 mm long specimen from Victoria, Australia (MV F112386) (Fig. 27A) and 22 teeth in descending limb and 5 fully formed teeth + 1 ghost tooth in ascending limb, in 4.5 mm long specimen from Queensland, Australia (lot 94-5E) (Fig. 27D). Active tooth ~100–150 µm long (Fig. 27B, E), with sharp, bifid or pointed tip; blade elongate with central row of numerous elongate, delicate denticles; base short, curved. Ascus containing one long, rod-shaped pre-radular tooth, 4–5 intermediate teeth (Fig. 27C, F).

Biology

Burn (1989) indicated that *T. babai* feeds on *Caulerpa scalpelliformis* (R. Brown ex Turner) C. Agardh, 1817, *Caulerpa geminata* Harvey, 1855 and *C. cactoides* (Turner) C. Agardh, 1817.

Range

Southern and Eastern Australia including Tasmania, Lord Howe Island and Norfolk Island (Burn, 1965, 1989, 2015; present paper).

Remarks

Burn (1965) introduced the name *Tamanovalva babai* Burn 1965 for specimens he previously identified as *Edenttellina typica* (see remarks of *E. typica*). According to Burn (1965) this species is characterized by having an ovate-trigonal shell with a large, vertically oriented protoconch, with 1.5 whorls. Burn (1965) described the live animals as green with a green mantle visible through the shell, and the radula as having denticulate teeth with bifid apices. Burn (1989, 2015) illustrated a specimen from Philip Island, Victoria, which is green with white spots all other the body, but more concentrated in the rhinophores; the mantle is green with numerous reddish-brown spots and white strings visible through the shell.

For this study, we examined several specimens from Victoria, Tasmania and Lord Howe Island, Australia (some of them identified by R. Burn), matching the characteristics of the original description of *T. babai*, as well as those of the holotype of this species (Fig. 4M–N). Two specimens were sequenced successfully and are genetically distinct from other species of Juliidae, but nested with other species of *Edenttellina*. Morphologically, *T. babai* is characterized by having an elongate penial stylet, similar to that of *E. australis*. For all these reasons, we consider *T. babai* a valid and distinct species but it is transferred to the genus *Edenttellina*.

EDENTTELLINA WALTAIRENSIS (SARMA, 1975)

Berthelinia waltairensis Sarma 1975: 20–21, figs. 23–27, 30. Type locality: Visakhapatnam, India.

Type material

Holotype and paratypes at the Department of Zoology, Andhra University, Waltair, India, not examined.

Remarks

Sarma (1975) described the new species *Berthelinia waltairensis* Sarma, 1975 based on live specimens collected in Visakhapatnam, India. The body of live animals was described as leaf-green with the oral tentacles, rhinophores and foot speckled with white, and the mantle dark green and visible through the shell (Sarma 1975). Sarma (1975) illustrated the oval shell, with a round anterior end and narrower posterior end, with the highest point near the anterior end, and the protoconch posterior to mid-length. Sarma (1975) described the white protoconch as having 1.5 whorls, and the hinge with a strong anterior tooth and second weaker posterior tooth. The radula had 7 teeth in the ascending limb and 25 in the descending limb, teeth blade-like with simple tips, and fine denticulations on both sides (Sarma 1975).

We have been unable to obtain specimens matching the original description of *B. waltairensis*, which remains as an uncertain species. However, because of its morphological similarities to other species of *Edenttellina*, it is here transferred to this genus.

EDENTTELLINA CF. *ROTTNESTI* (JENSEN, 1993)

(FIGS. 4O–P, 28–30)

Berthelinia rottnesti Jensen 1993: 209–214, figs. 1–4, 5A, 6A. Type locality: Natural Jetty, Rottnest Island, Western Australia.

Type material

Berthelinia rottnesti, Holotype, complete specimen, 3.5 mm long (WAM S14570), paratypes, 6 specimens (ZMUC).

Additional material examined

Sloping Main, Tasmania, Australia, 3 January 2014, 1 specimen 2.6 mm long (shell), isolate JC40, Morrison Australia Expedition (stn. TA21), leg. Bouchet and Strong (MNHN IM-2013-53068); 1 specimen, 2.5 mm long (shell), isolate JC41, Morrison Australia Expedition (stn. TA21), leg. Bouchet and Strong (MNHN IM-2013-53069); 1 specimen, 2 mm long (shell), isolate JC42, Morrison Australia Expedition (stn. TA21), leg. Bouchet and Strong (MNHN IM-2013-53070); 1 specimen, 1.8 mm long (shell), isolate JC39, Morrison Australia Expedition (stn. TA21), leg. Bouchet and Strong (MNHN IM-2013-53071); 1 specimen, 3 mm long (shell), isolate JC37, Morrison Australia Expedition (stn. TA21), leg. Bouchet and Strong (MNHN IM-2013-53072); 4 specimens 3–3.2 mm long, isolates JC38A–D, Morrison Australia Expedition (stn. TA21), leg. Bouchet and Strong (MNHN IM-2013-53073).

Description

No live specimens were examined for this study. Body completely retractable inside of shell.

Shell up to 3 × 1.8 mm in size, tallest point near anterior margin, widest point near ventral margin; shell shape ovoid, dorsal margin regularly curved, ventral margin more flattened; anterior margin convex, regularly curved, slightly more flattened dorsally, posterior margin shorter, narrowing gradually (Figs. 28G–H). Protoconch on left valve of teleoconch, ~190 µm long, with 1.5 whorls (Fig. 28K). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; large, elongate condyloid tooth at posterior end of hinge on right valve, fossette-like depression on left valve, at posterior end of hinge (Figs. 28I–J). Shell translucent, with no visible markings or spots on shell surface, soft parts of body typically visible through it (Figs. 28A–D) but not always (Figs. 28E–F).

Adductor muscle anterior to highest point of shell, in line with widest point (Fig. 29A). Adductor scar visible on shell (Figs. 28H). Gill large, occupying almost height of body, posterior to adductor muscle, covering anterior portion of digestive gland. Anterior half of body in preserved specimens with a visible elongate head retractor muscle (Fig. 29B). Pharyngeal bulb with a small pharyngeal appendage (Fig. 29C). Penis elongate; distal end pointed, lacking a stylet (Fig. 29D).

Radula with 19 teeth in descending limb and 4 fully formed teeth + 1 ghost tooth in ascending limb, in 2 mm long specimen from Tasmania, Australia (MNHN IM-2013-53073) (Fig. 30A). Active tooth ~140 µm long (Fig. 30B), with sharp, bifid tip; blade elongate with short row of elongate, delicate denticles near tip; base short, curved. Ascus containing a few, very small pre-radular teeth (Fig. 30C).

Remarks

Jensen (1993) introduced the name *Berthelinia rottnesti* Jensen, 1993 based on several specimens collected around Rottnest Island, Western Australia. The body was described as pale, transparent green, with some white spots forming an indistinct band about half way up the rhinophores as well as a marginal band; the mantle was described as green with white spots and brownish, with mostly radiating, lines, including a row of alternating white and brown spots along the mantle edge, not quite reaching the umbo (Jensen 1993). Jensen (1993) noted that the shell and the position of the protoconch were variable, and described the radula as formed of blade-shaped teeth with fine lateral denticles on both sides of the blade, including 4–6 teeth (plus 1 incompletely formed ghost tooth) in the ascending limb, and 22–23 teeth in the descending limb. Based on the observation of a newly metamorphosed specimen, Jensen (1993) suggested that *B. rottnesti* appeared to have direct development.

Jensen (1993) indicated that *B. rottnesti* is anatomically similar to *B. babai*; both species have bifid denticulate teeth and a similar penis; but according to Jensen (1993) the denticles of *B. rottnesti* are shorter than those of *B. babai*; additionally, the morphology of the pharynx is different between these two species. Jensen (1993) also compared *B. rottnesti* with *B. limax* and suggested that they could represent ecotypes of one species. According to Jensen (1993), the small differences between *B. rottnesti* and *B. limax* could be explained by reduced gene flow due to the direct development mode in the two species.

According to Burn (2006) *B. rottnesti*, is the western cognate of, if not identical with, *Midorigai australis* as both species have an obligate association with the green alga *Caulerpa simpliciuscula*. However, the external shell coloration of these two species is very different. *Midorigai australis* is completely covered with pale round spots and *B. rottnesti* is nearly uniformly green. Wells & Bryce (1993) illustrated a live animal possibly belonging to *B. rottnesti* from Western Australia that was green with white spots on the head and neck, more densely covering the rhinophores and the mantle edged by a line of white dots.

Based on the description by Jensen (1993) *B. rottnesti* appears to be different from other species here examined. Unfortunately, we had no access to specimens from Western Australia and therefore could not confirm the validity of this species with molecular data. Therefore, we maintain *B. rottnesti* as a valid species until more material becomes available. Although we did not have molecular data for *B. rottnesti,* this species is morphologically similar to other species within *Edenttellina* here examined. Therefore, *B. rottnesti* is provisionally transferred to this genus.

In this study, we examined specimens from Tasmania with an external morphology and anatomy very similar to those in the original description of *B. rottnesti*. For example, the radular teeth and the penis here examined are very similar to the description of those organs by Jensen (1993). Jensen (1993: fig. 5A) described and illustrated the radular teeth of *B. rottnesti* as having bifid radular teeth with a short row of denticles near the apical end, very similar to the teeth here illustrated (Fig. 55C), no other species of *Edenttellina* here examined has similar characteristics. Jensen (1993; fig. 6A) described the penis of *B. rottnesti* as elongate and lacking a stylet, which is also similar to the material here examined; all other species from southern Australia studied to date have a penial stylet. Additionally, the pharyngeal bulb of the material here examined, with a dorsal pharyngeal appendage is very similar to the descriptions and illustrations by Jensen (1993: fig. 4). Because of the morphological similarities between the Tasmania specimens and the original description of *B. rottnesti* we tentatively assign our specimens to this species. However, due to the geographic distance between Tasmania and Rottnest Island (the type locality of *B. rottnesti*) and the lack of genetic data for *B/E. rottnesti*, we cannot dismiss that the Tasmania specimens could represent an undescribed species.

EDENTTELLINA DARWINI (JENSEN, 1997)

Berthelinia darwini Jensen 1997a: 170–175, figs. 6–9. Type locality: Lee Point, Darwin, Australia.

Type material

Berthelinia darwini, Holotype, complete specimen, 2.5 mm long (NTM P6969), not examined; paratype, East Point, Darwin, Australia, 1 specimen 3.5 mm long (ZMUC), not examined.

Remarks

Jensen (1997a) introduced the new species *Berthelinia darwini* Jensen, 1997 based on several specimens collected in Darwin, Australia. Jensen (1997a) described the shell as nearly elliptical, rounded at both ends and not particularly narrow posteriorly; protoconch about 200 µm long, located just anterior to the posterior third of the shell length, with a variable angle of insertion. Live animals were described as different shades of green with white rhinophoral tips, white mottling scattered over the head and mantle, and brown pigment along the mantle margin, alternating with white patches (Jensen 1997a). The radula had 6–7 fully formed teeth (and one ghost tooth) in the ascending limb, 20–30 in the descending limb, and up to 10 teeth, plus the rod-shaped pre-radular tooth in the coiled ascus; the teeth were blade-shaped with fine lateral denticles and pointed tips. Jensen (1997a) compared the anatomy of *B. darwini* with that of *B. typica* and *B. australis* (the other two species whose anatomy was known) and concluded the penial morphology and the radular teeth were all different. According to Jensen (1997a) the relatively large protoconch of *B. darwini* indicates that this species has direct development. Additionally, this species deposited an egg mass with just 15 eggs with "large" capsules (Jensen 1997a), potentially indicating low dispersal ability. Therefore, it is likely that *B. darwini* may constitute a northern Australia endemic species. Unfortunately, we had no access to specimens from this region. Although we did not have molecular data for *B. darwini,* this species is morphologically similar to other species in *Edenttellina* here examined. Therefore, *B. darwini* is provisionally transferred to this genus.

EDENTTELLINA SINGAPORENSIS (JENSEN, 2015)

(FIGS. 4Q–R, 24D–E, 31–33)

Berthelinia singaporensis Jensen 2015: 233–235, figs. 1F, 5D–E, 6–7. Type locality: Chek Jawa, Singapore.

Type material

Berthelinia singaporensis, Holotype, complete specimen 4 mm long (ZRC MOL.5789).

Additional material examined

Port Dickson, Malaysia, 1 specimen 4.2 mm long (shell), leg. L. Wong, isolate JC87B (CPIC 02538). Johor, Malaysia, 1 specimen 4 mm long (shell), leg. L. Wong, isolate JC88A (CPIC 02539); 1 specimen 4 mm long (shell), leg. L. Wong, isolate JC88B (CPIC 02539).

Description

Body elongate, up to 6.5 mm in length, completely retractable inside shell. Body color bright green; with numerous opaque white spots concentrated on the dorsal side of head (Figs. 24D–E). Head elongate, with eye spots located on dorsal swelling near center. Rhinophores enrolled, green, with small white speckles concentrated on dorsal side. Oral tentacles short, green, edged in white. Foot lighter than rest of animal, edged in white. Mantle visible through shell, brownish-green, covered with small white dots more concentrated at the edge. Foot extending to posterior end of shell, forming small triangular projection.

Shell up to 4.2 × 2.7 mm in size, tallest point near anterior end, widest point near ventral margin; shell shape ovoid, elongate, dorsal margin regularly curved, ventral margin more flattened; anterior margin convex, irregularly curved, slightly more flattened dorsally, posterior margin narrowing gradually, forming a nearly triangular, elongate shape, with round end (Figs. 31E–F). Protoconch on left valve of teleoconch, ~150 µm long, with 1.5 whorls (Fig. 31I). Hinge on dorsal margin of shell, formed by flattened, corrugated, nearly straight area, margin on both valves; condyloid tooth not clearly differentiated, on right valve at posterior end of hinge, and triangular, fossette-like hinge socket on left valve, at posterior end of hinge (Figs. 31G–H). Shell translucent, with no visible markings or spots on shell surface, soft parts of body visible through it (Figs. 32A–D).

Adductor muscle located closer to anterior end of shell, in slightly below widest point (Fig. 32A), connected to narrow and elongate head retractor muscle (Fig. 32B). Adductor scar visible on shell (Figs. 31F). Gill large, occupying 2/3 of body, posterior to adductor muscle, covering dorsal portion of digestive gland. Pharyngeal bulb with a short pharyngeal appendage dorsally. Penis elongate; distal end pointed, with a short stylet (Fig. 32E); proximal end wider, with a strong retractor muscle attached (Fig. 32D).

Radula with 42 teeth in descending limb and 8 fully formed teeth + 1 ghost tooth in ascending limb, in 4 mm long specimen from Johor, Malaysia (isolate JC88B, CPIC 02539) (Fig. 33A). Active tooth saber shaped, ~140 µm long, with sharp, pointed tip; blade elongate with central row of numerous long, delicate denticles; base short, slightly curved (Fig. 33B). Ascus ~50 µm long, containing one long, rod-shaped pre-radular tooth and about 10 intermediate teeth (Fig. 33C).

Biology

This species feeds on at least five species including *Caulerpa racemosa, C. lentellifera* J. Agardh, 1837*, C. serrulata* (Forsskål) J. Agardh, 1837*, C. sertularioides,* and *C. cf. lamourouxii* (Turner) C. Agardh, 1817, without a particular preference (Wong and Sigwart 2019). The egg masses are flat and band-shaped, containing a mean of 46.6 eggs per egg mass (*N* = 50 clutches; range = 8 to 108) with an egg diameter of about 83 µm and capsule size approximately 330 × 250 µm. The larvae hatch as pediveligers with a shell width of 244.11 ± 12.29 µm (*N* = 30) (Jensen & Ong 2018; Wong & Sigwart 2019).

Range

Singapore (Jensen 2015), Malaysia (Wong & Sigwart 2019; present paper).

Remarks

Jensen (2015) introduced the name *Berthelinia singaporensis* Jensen, 2015 based on several specimens collected in Singapore. Jensen (2015) described the shell as broadly rounded anteriorly, more narrowly rounded posteriorly, with the highest point in the anterior half, in front of protoconch; protoconch having 1.5 whorls and located in posterior half of left valve, tilted towards right valve; hinge with a fork and a cardinal tooth on each valve. The live animal was described as uniformly bright green, protoconch white, rhinophoral tips doted in white, some specimens having white dots continuing down the rhinophores (Jensen 2015). Jensen (2015) indicated the radula was composed of 10–11 fully formed teeth (and one ghost tooth) in ascending limb and 26–30 teeth in descending limb plus 1 rod-shaped preradular tooth; the radular teeth were blade-shaped with a row of hair-like denticles along each side, tips with a small knob but not bifid. Finally, the penis was described as having a flexible stylet with peculiar lateral flanges.

In this study, we examined specimens from localities in Malaysia adjacent or very close to

Singapore, which match the characteristics of the original description of *B. singaporensis*. These specimens are genetically distinct from other species examined herein. Because of the morphological similarities of the Malaysian specimens to *B. singaporensis* and the proximity to the type locality, they are here assigned to this species. Moreover, the phylogenetic analyses confirm our specimens of *B. singaporensis* group with other species of *Edenttellina* and therefore the species is transferred to *Edenttellina*.

SUBFAMILY GOUGEROTIINAE LE RENARD, 1980

GENUS *GOUGEROTIA* LE RENARD, 1980

† *Gougerotia* Le Renard 1980: 24. Type species: *Gougerotia orthodonta* Le Renard, 1980, by original designation.

Diagnosis

Shell thick, oval to elongate in lateral view; anterior margin rounded, narrowing into sharper posterior margin; shell tallest point near anterior end; right valve larger, taller than left valve; pseudo-hinge with conspicuous condyloid tooth on right valve inserting into deep socket under protoconch in left valve, splitting hinge into two sections; protoconch conspicuous, on left valve, towards posterior third of shell; adductor muscle scar subcentral.

Species list

† *Gougerotia orthodonta* Le Renard 1980: 23–25, fig. 12. Type locality: Chaussy, Val d'Oise, France and Mercin, Aisne, France (Middle-Late Eocene).

GENUS *HEMIPLICATULA* DESHAYES, 1861

† *Hemiplicatula* Deshayes 1861: 128. Type species: *Placuna solida* Melleville, 1843, by monotypy.

Diagnosis

Shell thick, oval to elongate in lateral view; anterior margin rounded, narrowing into sharper posterior margin; shell tallest point near center; valves similar in size; pseudo-hinge with elongate condyloid tooth on right valve inserting into deep socket in left valve, splitting hinge into two sections; adductor muscle scar subcentral.

Species list

† *Placuna solida* Melleville 1843: 89–90, pl. 1, figs. 6–7. Type locality: Laon, France (Early Eocene).

† *Hemiplicatula pissarroi* Cossmann 1905a: 154–155, pl. 8, figs. 10–11. Type locality: Bois-Gouët, Loire-Atlantique, France (Early Eocene).

GENUS *SAINTIA* DE RAINCOURT, 1877

† *Saintia* de Raincourt 1877: 329, pl. 4, fig. 9. Type species: *Saintia munieri* de Raincourt, 1877, by monotypy.

Diagnosis

Shell thick, oval to round view; anterior and posterior margins rounded, similar in height; shell tallest point near center; pseudo-hinge with deep socket in left valve, splitting hinge into two sections; adductor muscle scar subcentral.

Species list

† *Saintia munieri* de Raincourt 1877: 329, pl. 4, figs. 9-9b. Type locality: Hérouval, France (Early Eocene).

DISCUSSION

Morphometrics

Here we revise the systematics of family Juliidae based on shell morphological data, including new names for Recent and fossil genera. Analyzing shell morphology of both fossil and Recent taxa by geometric morphometrics resolved five distinct clusters of taxa within Juliidae, and informed the generic placement of extinct versus extant species. While PCAs did not include exactly the same specimens as molecular analyses (notably, fossil specimens), the results of both analyses support our revisionary framework for the family.

The PCA of Juliidae recovered three clusters corresponding to subfamily Juliinae and two corresponding to subfamily Bertheliniinae. The subfamily Gougerotiinae was not examined due to the absence of material suitable for morphometrics analysis. Within Juliinae, two clusters correspond to Recent taxa and one included both fossil and Recent taxa. One of the clusters of Recent taxa included specimens identified as *Julia japonica* and *J. borbonica,* the type species of the genus *Prasina*. Based on morphometric analyses, *Prasina* may need to be resurrected for this morphologically distinct group. Unfortunately, we were unable to obtain molecular data for *J. japonica* or *J. borbonica*, which is needed to confirm whether *Prasina* is a distinct genus. The mixed fossil/Recent cluster recovered specimens identified as *Candinia krachi*, which clearly supports the placement of *Candinia* in the subfamily Juliinae. The other cluster of Recent *Julia* taxa included specimens identified as *J. exquisita* as well as *J. zebra, J.* sp. 1*, J. mishimaensis,* and *J. burni.* The Bayesian and ML analyses also recovered these species as a monophyletic group that included *Julia exquisita*, the type species of *Julia*; we therefore retain the name *Julia* for this Recent group if *Prasina* is found to be valid.

The PCA analysis divided Berthelininae into two clusters, one cluster including Recent taxa and the other only fossil taxa. The fossil cluster comprised specimens identified as *Berthelinia elegans, B. elegans elata,* and *Gourgerotia orthodontia.* Because of the morphological similarities between these specimens, *Gourgerotia orthodontia* could be a member of the genus *Berthelinia* (type species *Berthelinia elegans*) but further analysis is needed to confirm this hypothesis. The cluster of Recent taxa comprised specimens that were previously identified as *Midorigai australis, Berthelinia caribbea, Berthelinia singaporensis, Berthelinia pseudochloris, Tamanovalva babai, Edenttellina* cf. *rottnesti*, and *Edenttellina typica.* Due to the morphological distinction between Recent and fossil taxa, *Berthelinia* is herein deemed inappropriate for Recent taxa. We propose that *Edenttellina* (type species *Edenttellina typica*), the oldest genus name available for Recent taxa within the *Berthelinia* lineage, should be reinstated for this group. Supporting the shell morphometric analysis, molecular analyses also recovered this Recent genus as monophyletic. Based on the results from the Bayesian and ML analyses, *Edenttellina* includes *E. caribbea, E. pseudochloris, E. limax, E. chloris, E. australis, E. singaporensis, E. typica, E.* cf. *rottnesti,* and *E. babai*.

Biodiversity of Recent taxa

The molecular results of this study recovered undescribed species of *Julia*, some morphologically similar to previously described species, indicating that morphology-based systematics has been overly conservative and that there are cryptic species awaiting integrative taxonomic study. However, lecithotrophic development (common in Juliidae; Edmunds, 1963; Grahame, 1969) may produce highly subdivided populations that are recovered as distinct entities in species delimitation analyses. For example, specimens of *E. caribbea* that were delimited as distinct species using some molecular datasets were considered to be conspecific by morphological analysis. A high degree of population genetic differentiation can confound delimitation analyses based on the multispecies coalescent model, so it is not surprising that taxa with non-dispersive larval development were oversplit in some of our delimitation analyses (Sukumaran & Knowles 2017). However, the barcoding gaps needed to recover traditionally recognized species in Juliidae (>12% for COI, >4% for 16S) are much higher than those that supported morphologically distinct species in other sacoglossan genera (Krug et al. 2018a, 2018b; McCarthy et al. 2019; Medrano et al. 2019; Rodriguez & Krug 2022; Martín-Hervás et al. 2021, 2023; Moreno et al. 2023, 2025). Thus, detailed morphological study of potential cryptic species, as well as the candidate species documented herein, are warranted to fully resolve the extent of unrecognized biodiversity in Juliidae.

Biogeography and evolution of Recent taxa

Species distributions are notably different in *Julia* versus *Edenttellina,* suggesting distinct evolutionary histories of lineage diversification, dispersal and extinction. *Julia* is restricted to the tropical Indo-Pacific but species have wide ranges, frequently spanning the Hawaiian Islands and west Pacific localities; as a result, sister species often co-occur. In contrast, *Edenttellina* also occurs in temperate Australia, the Caribbean and the Eastern Pacific, so is more globally distributed at the genus level. However, individual *Edenttellina* species typically have more restricted distributions than *Julia* species. Sister species were generally restricted to non-overlapping regions in *Edenttellina,* consistent with predictions of allopatric speciation. A number of *Edenttellina* species are lecithotrophic, producing non-feeding larvae with shorter expected planktonic periods, and hence more limited dispersal potential (Table 5). Reduced dispersal ability may contribute to the smaller geographic range sizes recovered for *Edenttellina* species, but the larval development mode of *Julia* remains largely unknown. The larger ranges of *Julia* spp. suggest planktotrophy is the dominant mode of development, but the more limited biogeography of the genus is surprising given greater apparent connectivity among populations.

It remains unclear whether restricted dispersal increases or decreases net diversity for marine invertebrates over evolutionary timescales, a form of species-level selection. There are few radiations of lecithotrophic lineages in Sacoglossa, in which species selection generally favors planktotrophs (Krug et al., 2015). As our understanding of diversity in Juliidae is refined and more data on development mode becomes available, this family will be important for testing current hypotheses of trait-dependent diversification. Notably, if there are clades of lecithotrophs in this group, juliids may represent an exception to the trend of greater diversification for planktotrophic lineages. Further work clarifying species boundaries and development is needed to delineate radiations of endemic species and better understand how larval type affects species richness in marine heterobranchs (Moreno et al., 2023, 2025).

Diversity in Juliidae may also be influenced by ecological factors such as algal host specialization, as in other sacoglossan clades (Rodriguez and Krug, 2022; Moreno et al., 2023; 2025). Niche partitioning is expected when ecologically similar species co-occur, and may reflect ecological speciation when sympatric sister taxa both feed and mate on distinct hosts. Species of *Edenttellina* are usually found living in physical association with algal hosts, and a few are highly specialized: *E. caribbea* on *C. verticillata* J. Agardh, 1847 (Clark 1994), and *E. pseudochloris* on the *C. chemnitzia-racemosa* complex (Kay, 1964; Sarma, 1975). However, many species feed widely on a range of *Caulerpa* spp., including more than one morphotype, e.g. "feather" (*C. serrulata*, *C. mexicana*, *C. sertularioides*, *C. scalpelliformis, C. taxifolia*), "sea grape" (*C. chemnitzia*, *C. lentillifera*, *C. racemosa*, *C. sedoides*) or "pipecleaner" (*C. brownii*, *C. simpliciuscula*) types. Other sacoglossan genera often specialize within morphotypes or on one species of *Caulerpa*, making *Edenttellina* notably diverse in its diet (Berriman et al. 2018). In other sacoglossans, preference for *Caulerpa* species covaries with levels of secondary metabolites (caulerpenyne, oxytoxin) produced by different algae (Baumgartner et al. 2009). Future studies could examine whether *Edenttellina* species have conserved preferences for particular metabolite levels, which may limit host breadth to a subset of available *Caulerpa* species. However, there is less evidence that speciation via host shifting may drive diversification in *Edenttellina* compared with many other sacoglossan groups, given their relatively wide niche breadth among *Caulerpa*-feeders.

Julia appears even less likely to speciate through host associations, as specimens are not typically found feeding on *Caulerpa*. Without physical host association, it is unclear how ecological speciation could operate in this system (Krug 2011). The feeding behavior of most *Julia* species has not been verified experimentally, but two studies reported *Julia* species feeding on *Caulerpa* species that are components of microalgal communities growing in and on 'live rock': *C. ambigua* for *J. japonica* (Kawaguti & Yamasu 1966), and *C. fastigiata* for an unidentified *Julia* species (Mizofuchi & Yamasu 1987). Recent work has highlighted extensive cryptic diversity in green algal communities comprising minute, filamentous taxa, including *Caulerpa* species (Wade & Sherwood 2023). Future work on the specialization of *Julia* on minute *Caulerpa* species is needed to understand their adaptations to this distinctive niche, and the mechanisms allowing sympatric species of *Julia* to form and coexist.

Based on biogeographic theory, we would hypothesize that the more widespread genus (*Edenttellina*) would accumulate greater diversity, as having lineages in many different regions acts as a hedge against extinction risk (Kiessling and Aberhan, 2007). We would also expect higher diversity *Edenttellina* due to the larger proportion of local endemic species, and the potential for host-dependent ecological speciation due to physical association with preferred algal substrates. However, overall species richness between *Julia* and *Edenttellina* was generally comparable despite their differences in distribution, range size and patterns of host use. One possibility is that the relatively high success of *Julia* is due to its exploitation of an underutilized niche, feeding on microalgal species of *Caulerpa* that are largely inaccessible to most herbivores. Other potential mechanisms fueling diversification in this group, including longer-lived planktotrophic lineages or sexual selection promoting speciation, await further comparative study.

Future work

This study integrated morphological traits with molecular data to produce an updated classification for Juliidae. A quantitative morphometrics approach resolved the relationships of some fossil and extant genera that long challenged systematists. Our updated classification should guide further investigations of the fossil record, informing our understanding of how Juliidae has evolved and providing valuable calibration points for molecular phylogenetics. Many features of their biology make species of *Julia* and *Edenttellina* interesting model systems, notably the convergent evolution of a bivalved shell in Gastropoda and Bivalvia; this innovation is unique among gastropods and presents opportunities to study developmental and biomineralization pathways involved in the transition from a single-shelled larva to a bivalved adult. Unusual patterns of host use and the high proportion of lecithotrophic species in Juliidae also differ from the dominant trends in Sacoglossa and also warrant further study to better understand trait-dependent diversification in heterobranchs.

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FIGURES

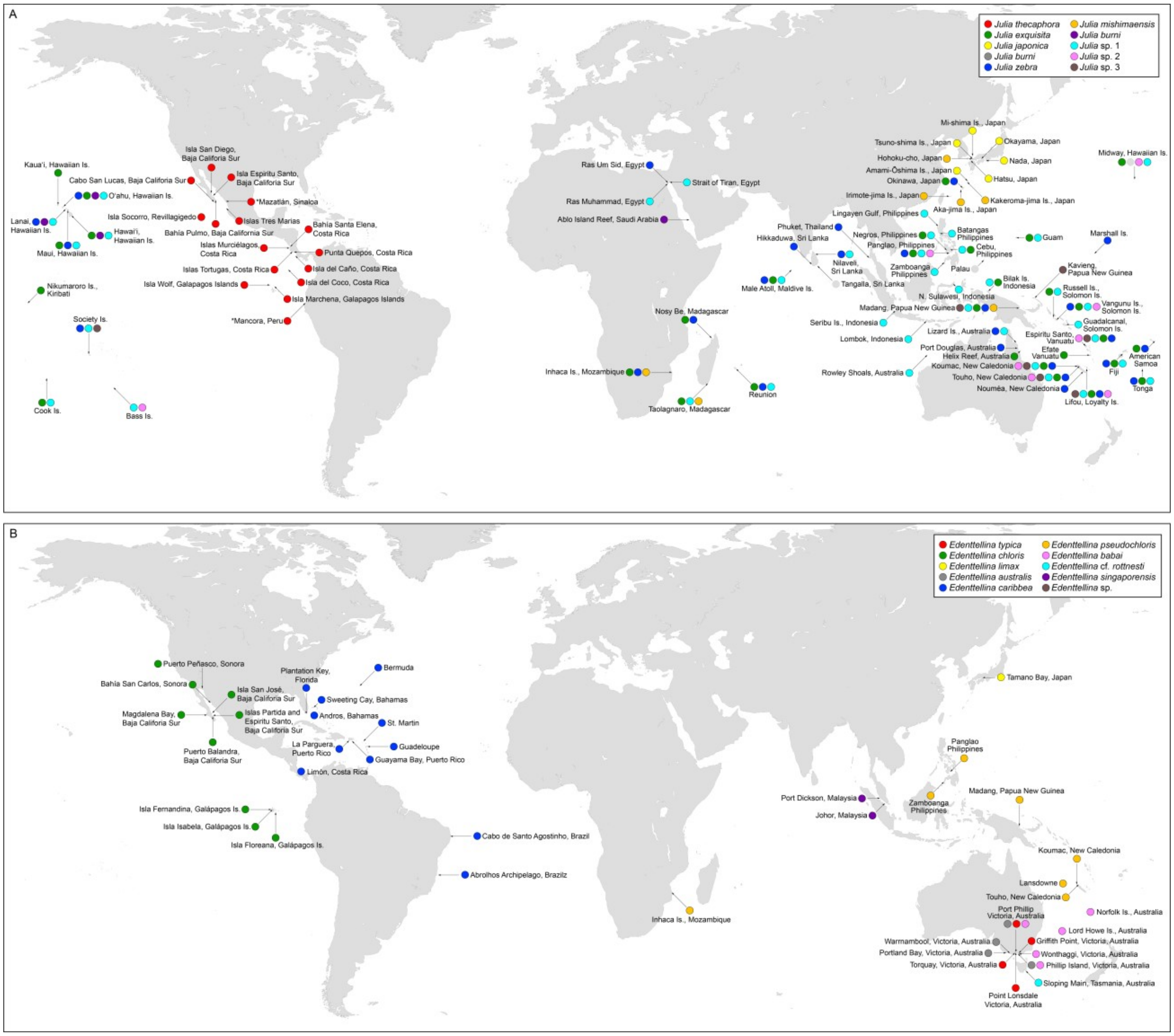

Figure 1. Map of localities where specimens for this study were collected, color-coded by species. A. *Julia*. B. *Edenttellina*.

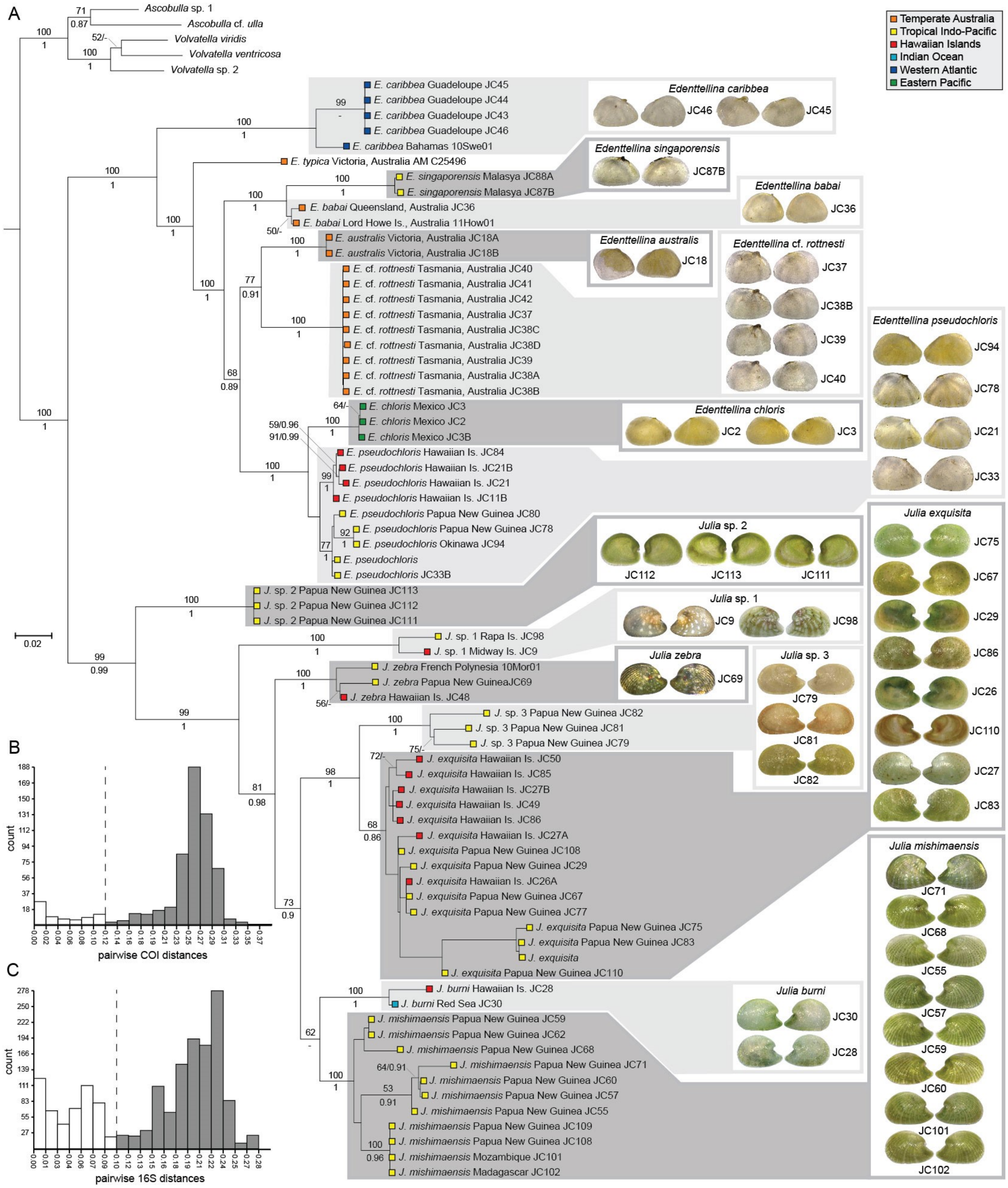

Figure 2. Graphic representation of the phylogeny and species delimitation results in Juliidae, based on sequence data. A. Maximum likelihood consensus phylogram showing relationships among all species examined, based on a concatenated the five-gene concatenated dataset; maximum likelihood (ML) bootstrap support values are above branches, posterior probabilities (PP) are below branches; codes following species names correspond to isolate numbers (see

Table 1). Colored dots on branch tips indicate the geographic origin of the specimen. B–C. Distributions of pairwise distances between sequences and Automatic Barcode Gap Discovery (ABGD) results for COI (B) and 16S (C) alignments. Intraspecific distances are indicated by white bars and interspecific distances by grey bars; the dashed line denotes the threshold for intraspecific divergence estimated by ABGD.

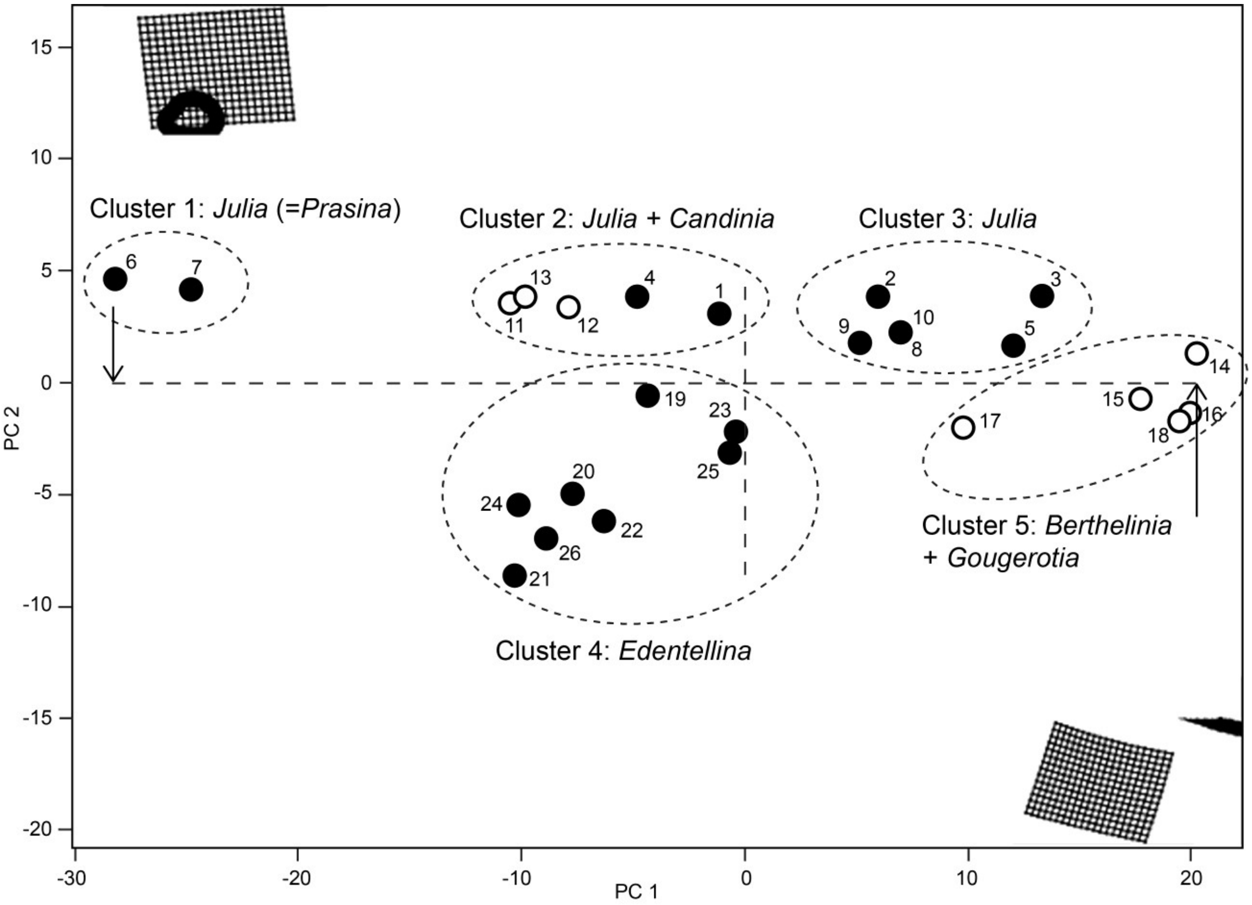

Figure 3. Principal Component Analysis of selected Juliidae species showing five clusters as indicated by points within dashed-line ovals. Patterns on upper left and lower right corners represent shape differences between the average (reference) and target specimens. PC1 explains the majority of the proportion of variance (85%). Specimen data provided in Table 3. Species legend [fossil specimens indicated by white circles, Recent species indicated by solid black circles]: (1) *Julia thecaphora* (Carpenter, 1857), (2) *Julia exquisita* Gould, 1862, (3) *Julia exquisita* Gould, 1862, (4) *Julia exquisita* Gould, 1862, (5) *Julia exquisita* Gould, 1862, (6) *Julia borbonica* (Deshayes, 1863), (7) *Julia japonica* Kuroda & Habe, 1951, (8) *Julia zebra* Kawaguti, 1981, (9) *Julia mishimaensis* Kawaguti & Yamasu, 1982, (10) *Julia mishimaensis* Kawaguti & Yamasu, 1982, (11) *Candinia* (= *Berthelinia*) *krachi* Bałuk & Jakubowski, 1968, (12) *Candinia* (= *Berthelinia*) *krachi* Bałuk & Jakubowski, 1968, (13) *Candinia* (= *Berthelinia*) *krachi* Bałuk & Jakubowski, 1968, (14) *Berthelinia elegans elata* Cossmann, 1887*,* (15) *Berthelinia elegans* Crosse, 1875, (16) *Berthelinia elegans* Crosse, 1875*,* (17) *Berthelinia elegans* Crosse, 1875*,* (18) *Gougerotia orthodonta* Le Renard, 1980, (19) *Edenttellina typica* Gatliff & Gabriel, 1911, (20)

Edenttellina typica Gatliff & Gabriel, 1911, (21) *Edenttellina* (= *Midorigai*) *australis* (Burn 1960), (22) *Edenttellina caribbea* Edmunds, 1963, (23) *Edenttellina pseudochloris* (Kay 1964), (24) *Edenttellina* (= *Tamanovalva*) *babai* (Burn 1965), (25) *Edenttellina* cf. *rottnesti* (Jensen 1993), (26) *Edenttellina singaporensis* (Jensen 2015).

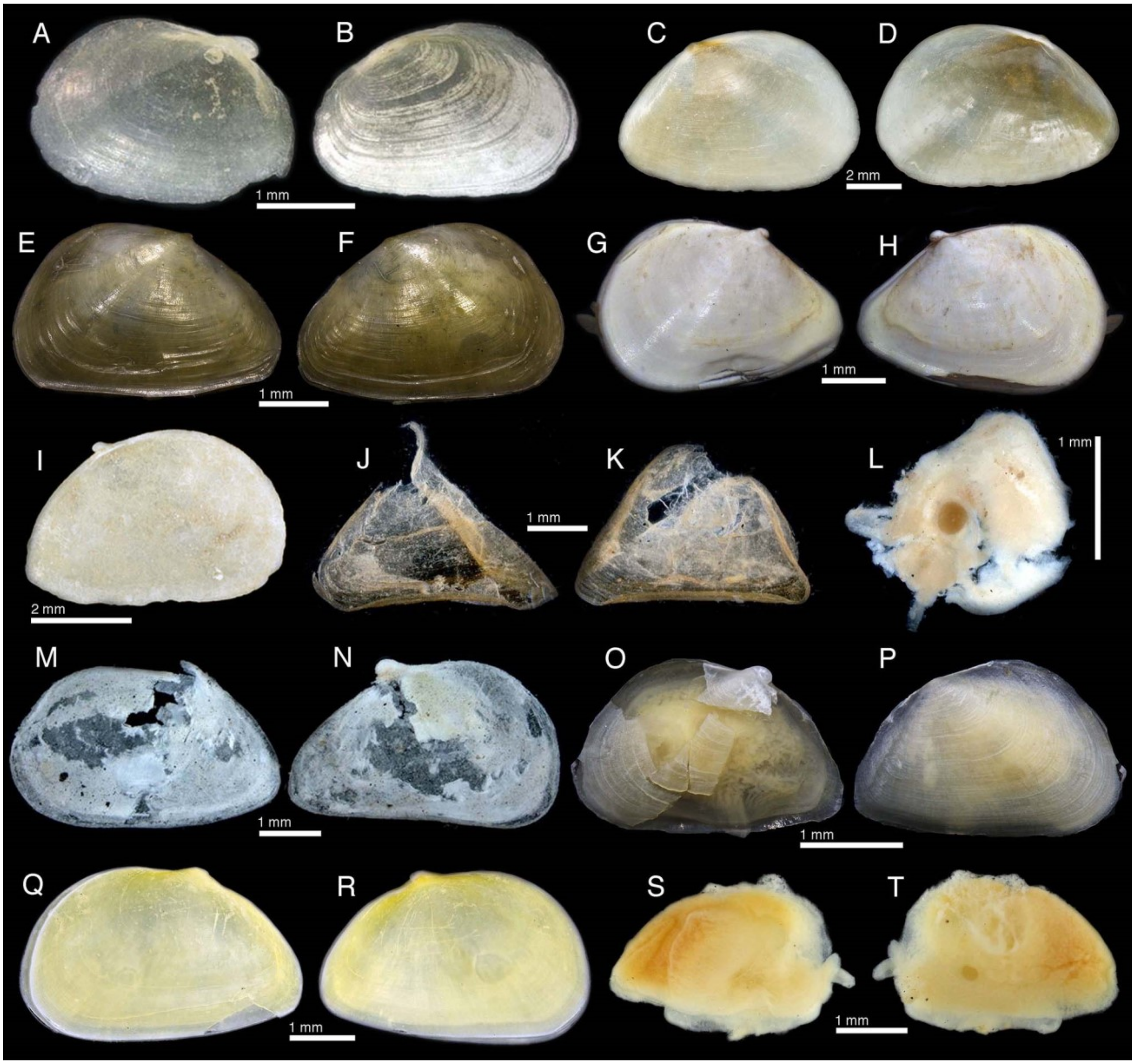

Figure 4. Photographs of type specimens of *Edenttellina* Gatliff & Gabriel, 1911. A–B. *Edenttellina typica* Gatliff & Gabriel, 1911, inner view of right valve (A), outer view of left valve (B) of two syntypes (MV F515), photos: David Staples ©Museums Victoria. C–D. *Scintilla chloris* Dall, 1918, outer view of right valve (C), inner view of left valve (D) of two

syntypes (USNM 218179), photos: Smithsonian Institution. E–F. *Berthelinia chloris belvederica* Keen & A. G. Smith 1961, outer view of left valve (E), outer view of right valve (F) of Holotype (CASIZ 064093). G–H. *Berthelinia pseudochloris* Kay 1964, left view (G) of paratype, right view (H) of same specimen (CASIZ 018374). I. *Edenttellina corallensis* Hedley, 1920 inner view of left valve of syntype (AM C.27643). J–K. *Midorigai australis* Burn, 1960, remains of valves of Holotype (MV F21193), photos: David Staples ©Museums Victoria. L. *Tamanovalva fijiensis* Burn, 1966, left view of preserved Holotype (MV F25647), photo: David Staples ©Museums Victoria. M–N. *Tamanovalva babai* Burn, 1965, outer view of left valve (M), inner view of right valve (N) of preserved Holotype (MV 23064), photos: David Staples ©Museums Victoria. O–P. *Berthelinia rottnesti* Jensen, 1993, outer view of left valve (O), outer view of right valve (P) of Holotype (WAM S14570), photos: Peter Middelfart ©Western Australia Museum. Q–R. *Berthelinia singaporensis* Jensen, 2015, outer view of left valve (Q), outer view of right valve (R), right view of preserved body (S), left view of preserved body (T) of Holotype (ZRC MOL5789), photos: Iffah Iesa ©ZRC.

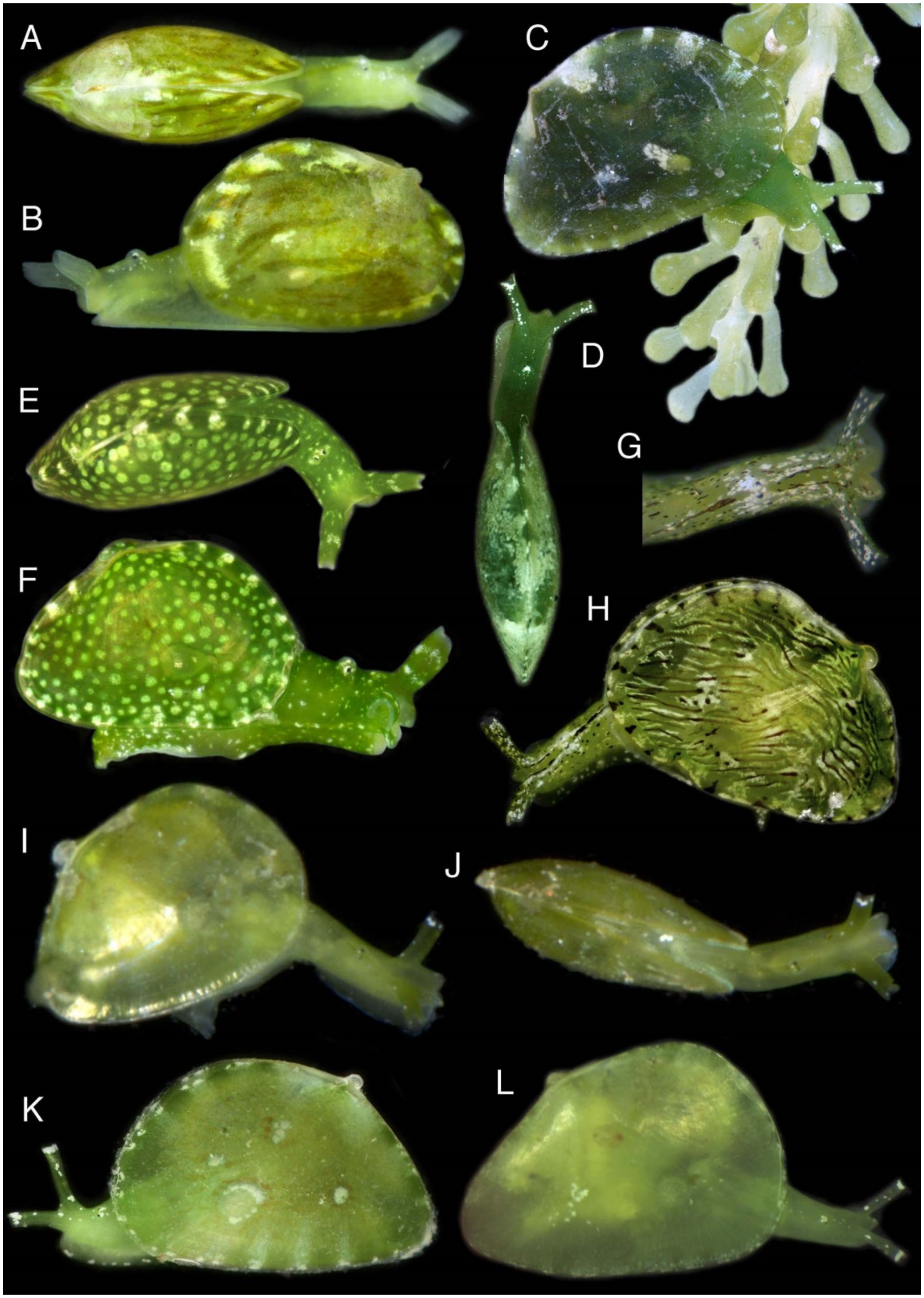

Figure 5. Photographs of live animals of *Edenttellina* Gatliff & Gabriel, 1911. A–B. *Edenttellina typica* Gatliff & Gabriel, 1911, specimen from Southern Australia, photos: L. Altoff, MV Collections. C–D. *Edenttellina chloris* (Dall, 1918), Isla San José, Baja California, Mexico on its

algal host, photo: C. Hogue, NHMLA Archives (C), dorsal view, Floreana Is., Galapagos Is., photo: D. Mulliner, NHMLA Archives (D). E–F. *Edenttellina australis* Burn, 1960, Philip Island, Bass Strait, Victoria, Australia, photos P. Vafiadis, dorsal view (E), lateral view (F). G–H. *Edenttellina caribbea* (Edmunds, 1963), Guadeloupe Is., photos P. Maestrati, detail of the head (G), lateral view (MNHN IM-2013-73231) (H). I–L. *Edenttellina pseudochloris* (Kay 1964), Maui, Hawaiian Is., photos: A. Valdés, lateral view (I), dorsal view (J), Espiritu Santo, Vanuatu (MNHN, stn. FS51), photo: D. Brabant, lateral view (K), Luzon, Philippines (CASIZ 199470), photo: P. Krug, lateral view (L).

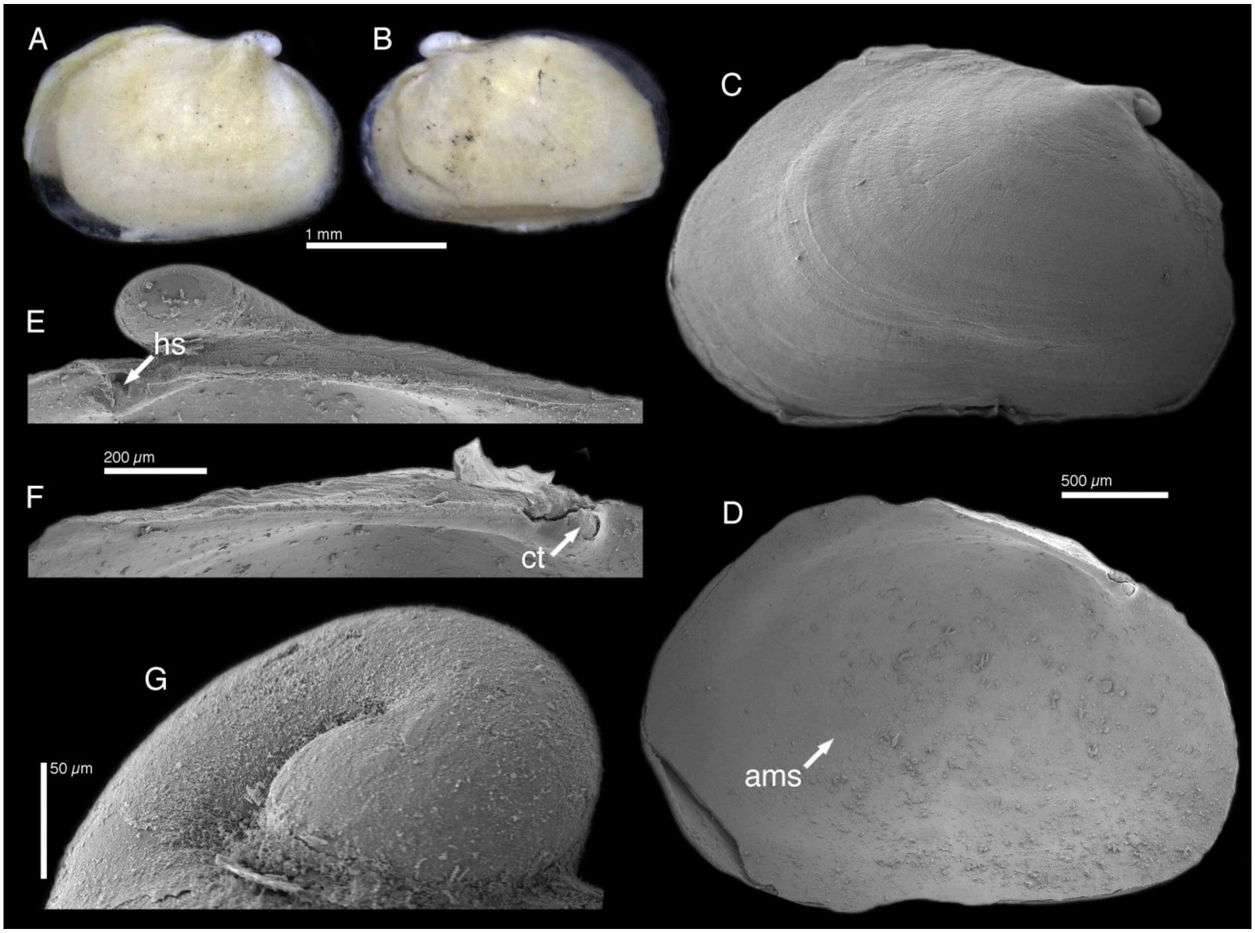

Figure 6. *Edenttellina typica* Gatliff & Gabriel, 1911, shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Victoria, Australia (MV F21539), outer view left valve (A), outer view right valve (B). C–D. SEMs of the right and left valves of the same specimen from Victoria, Australia (MV F21539), outer view left valve (C), inner view right valve (D). E–F. SEMs of the hinge of the right and left valves of two different specimens

from Victoria, Australia (MV F21539), left valve hinge (E), right valve hinge (F). G. Protoconch of a specimen from Victoria, Australia (MV F21539). Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

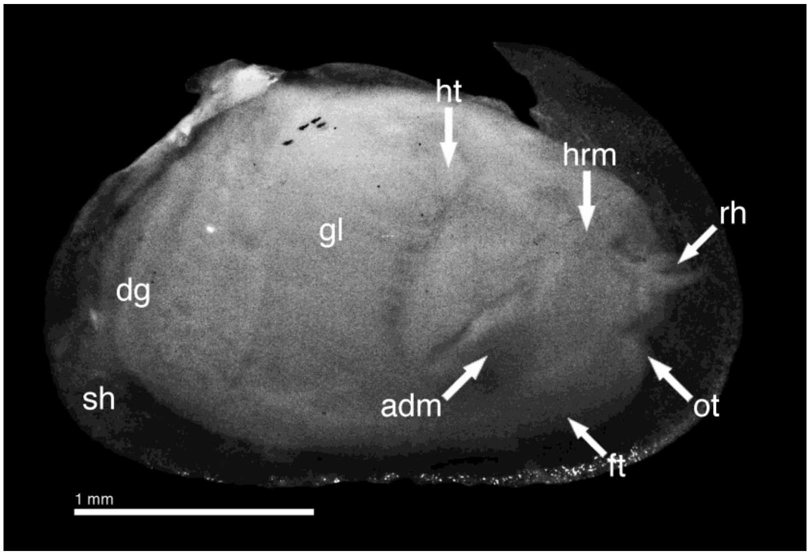

Figure 7. *Edenttellina typica* Gatliff & Gabriel, 1911, internal anatomy. A. General view of the internal anatomy of a specimen from Victoria, Australia (MV F91829). Abbreviations: adm, adductor muscle; dg, digestive gland; ft, foot; gl, gill; hrm, head retractor muscle; ot, oral tentacle; rh, rhinophore; sh, shell.

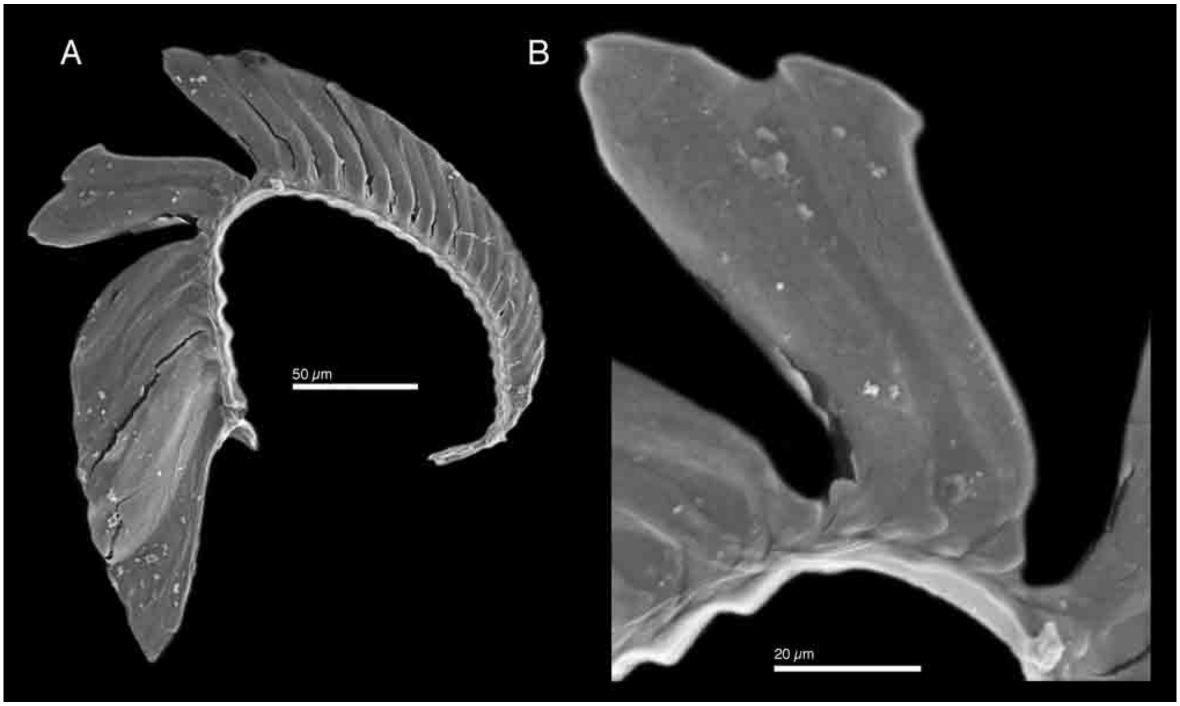

Figure 8. *Edenttellina typica* Gatliff & Gabriel, 1911, SEMs of the radula of a specimen from Victoria, Australia (MV F21539). A. Complete radula. B. Active tooth.

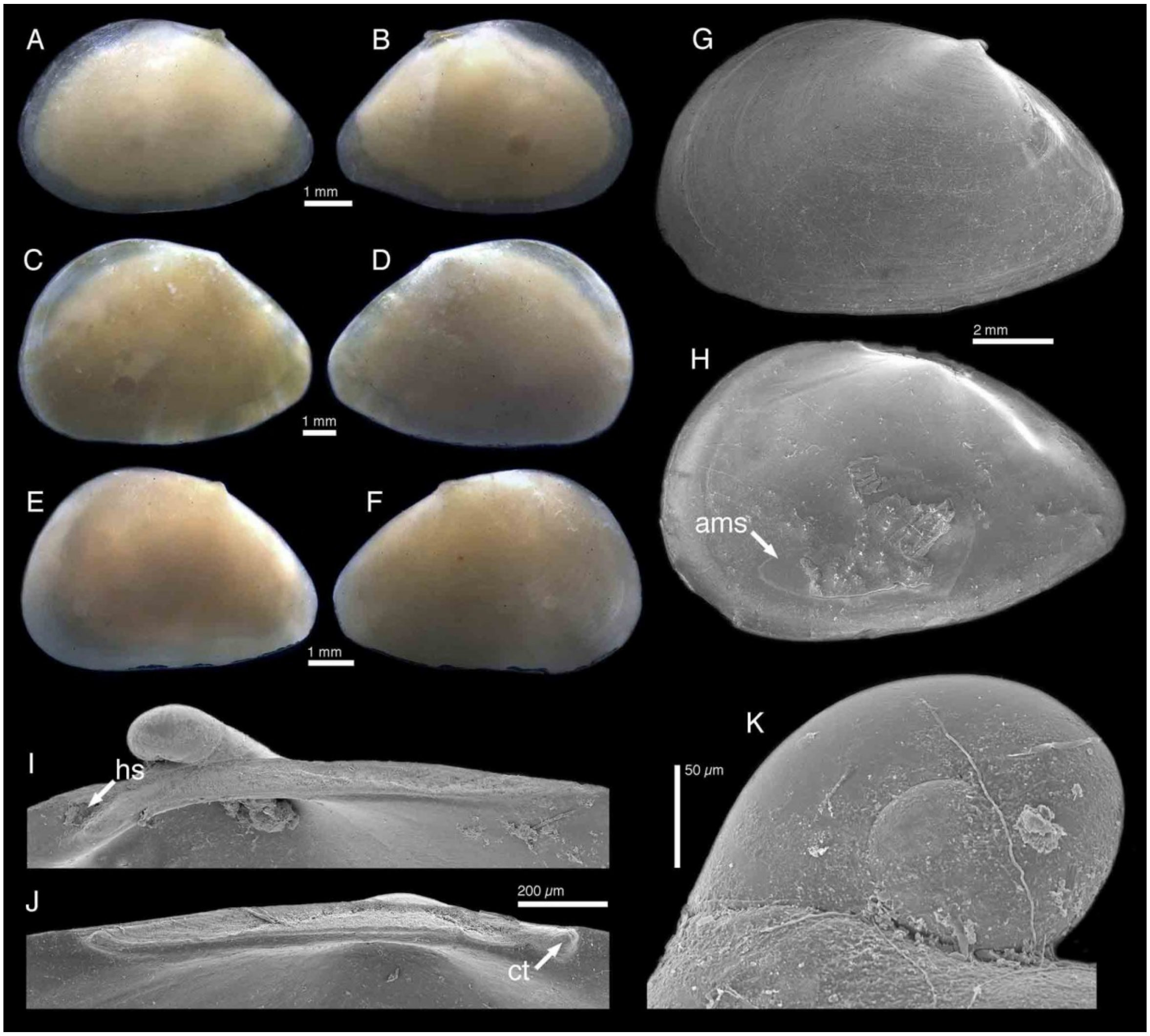

Figure 9. *Edenttellina chloris* (Dall, 1918), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Baja California Sur, Mexico (NHMLA 1974-33.1), outer view left valve (A), outer view right valve (B). C–D. Photographs of t the right and left sides of a preserved specimen from Sonora, Mexico (NHMLA 186690), outer view left valve (C), outer view right valve (D). E–F. Photographs of the right and left sides of a preserved specimen from the Galapagos Is. (NHMLA 1971-52.14), outer view left valve (E), outer view right valve (F). G–H. SEMs of the right and left valves of the same specimen from Baja California Sur, Mexico (NHMLA 1966-28.30), outer view left valve (G), inner view right valve (H). I–J. SEMs of the hinge of the right and left valves of two different specimens from Baja California Sur, Mexico (NHMLA 1966-28.30), left valve hinge (I), right valve hinge (J). K. Protoconch of a specimen

from Baja California Sur, Mexico (NHMLA 1966-28.30). Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

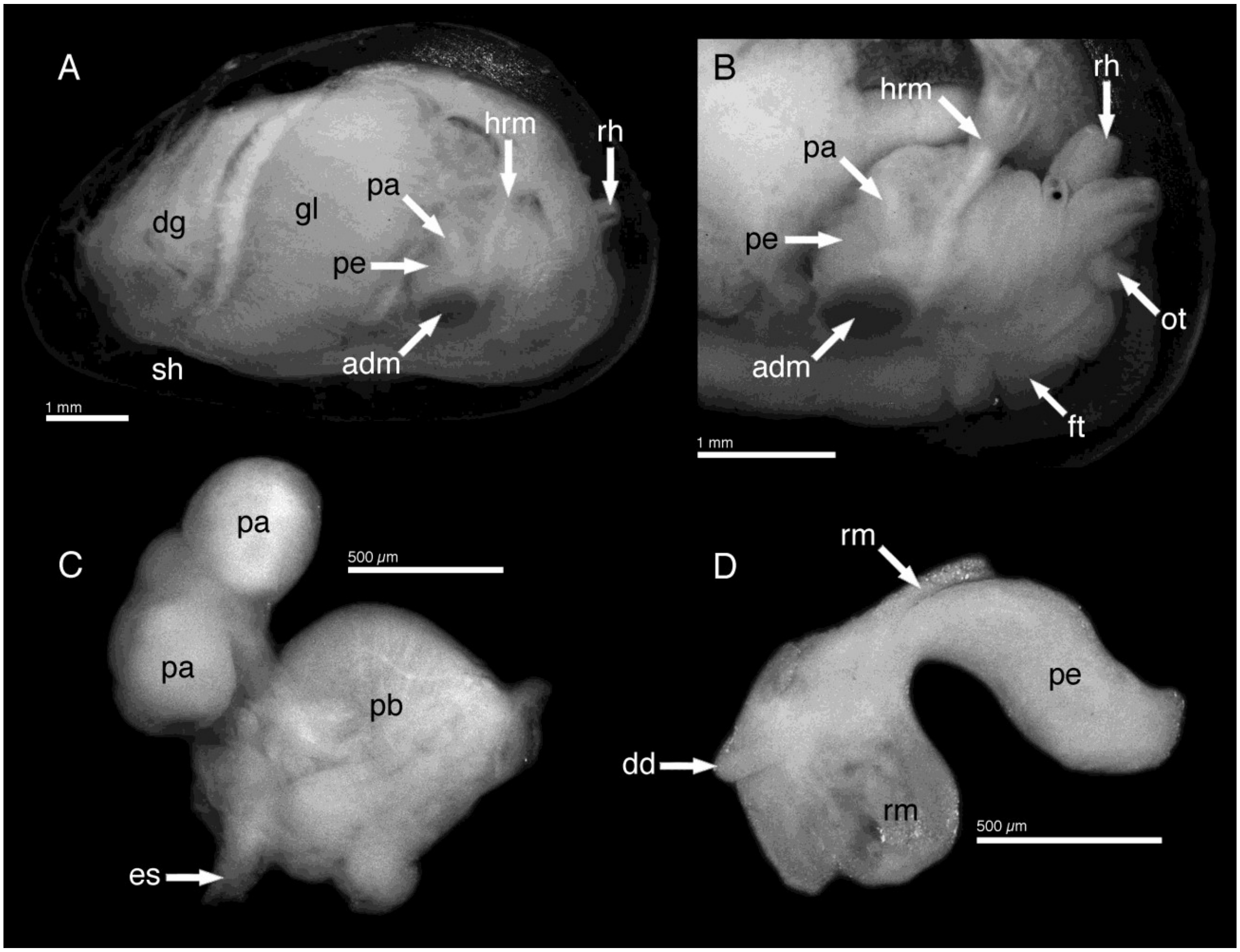

Figure 10. *Edenttellina chloris* (Dall 1918), internal anatomy. A. General view of the internal anatomy of a specimen from Sonora, Mexico (NHMLA 186690). B. Detail of the anterior portion of the body with the mantle removed, same specimen. C. Dissected anterior portion of the digestive system, same specimen. D. Dissected penis, same specimen. Abbreviations: adm, adductor muscle; dd, deferent duct; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ot, oral tentacle; pa, pharyngeal appendage; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sh, shell.

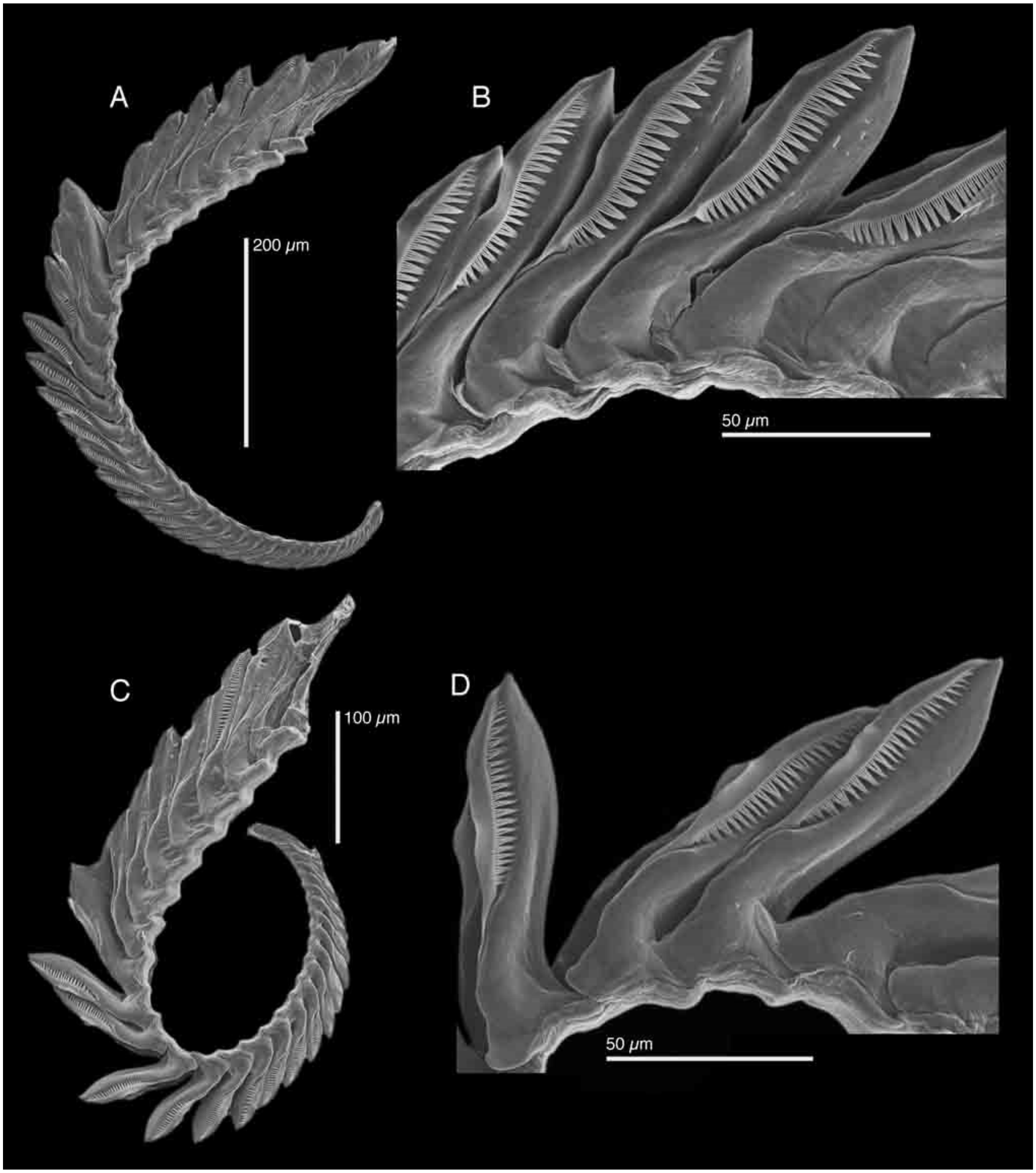

Figure 11. *Edenttellina chloris* (Dall, 1918), SEMs of the radula. A–B. Specimen from Baja California Sur (NHMLA 1974-33.1), complete radula (A). Active tooth (B). C–D. Specimen from Sonora, Mexico (NHMLA 186690), complete radula (C). Active tooth (D).

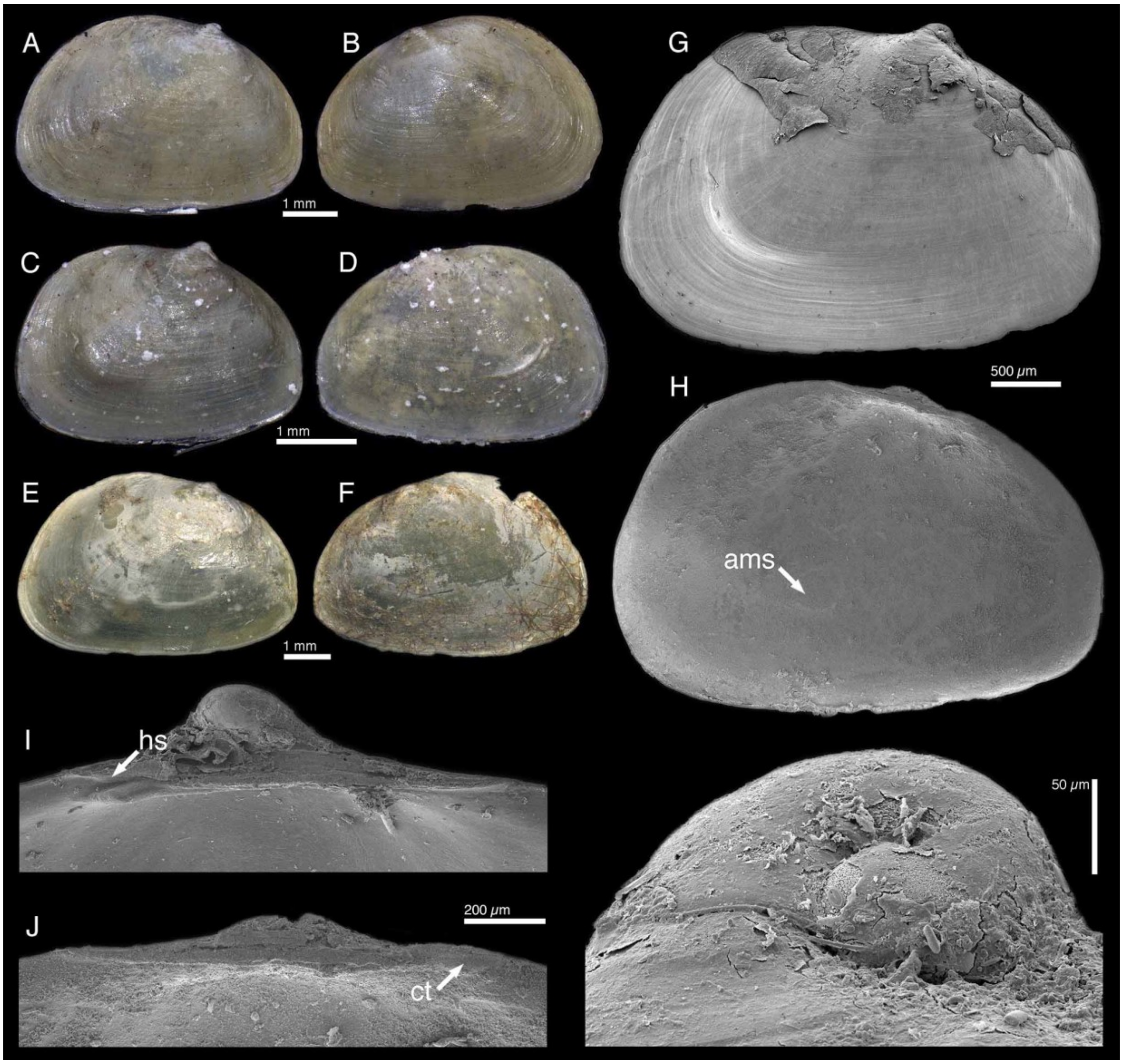

Figure 12. *Edenttellina limax* (Kawaguti & Baba, 1959), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Tamano Bay, Japan (CASIZ 201957), outer view left valve (A), outer view right valve (B). C–D. Photographs of t the right and left sides of a preserved specimen from Tamano Bay, Japan (CASIZ 201957), outer view left valve (C), outer view right valve (D). E–F. Photographs of t the right and left sides of a preserved specimen from Tamano Bay, Japan (CASIZ 201960), outer view left valve (E), outer view right valve (F). G–H. SEMs of the right and left valves of the same specimen from Tamano Bay, Japan (CASIZ 201960), outer view left valve (G), inner view right valve (H). I–J. SEMs of the hinge of the right and left valves of the same specimen, left valve hinge (I), right valve hinge (J). K. K. Protoconch of the same specimen. Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

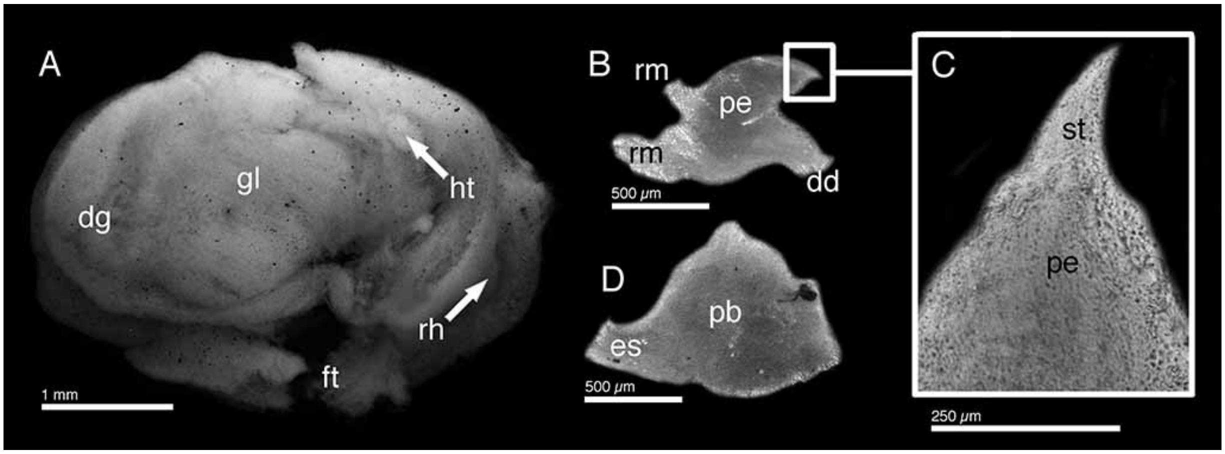

Figure 13. *Edenttellina limax* (Kawaguti & Baba, 1959), internal anatomy. A. General view of the internal anatomy of a specimen from Tamano Bay, Japan (MV F23063). B. Dissected penis, of a rehydrated dry specimen from Tamano Bay, Japan (CASIZ 201957). C. Detail of the hardened penial tip, same specimen. D. Dissected anterior portion of the digestive system, same specimen. Abbreviations: adm, adductor muscle; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ht, heart; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sg, salivary gland; sh, shell; st, penial stylet.

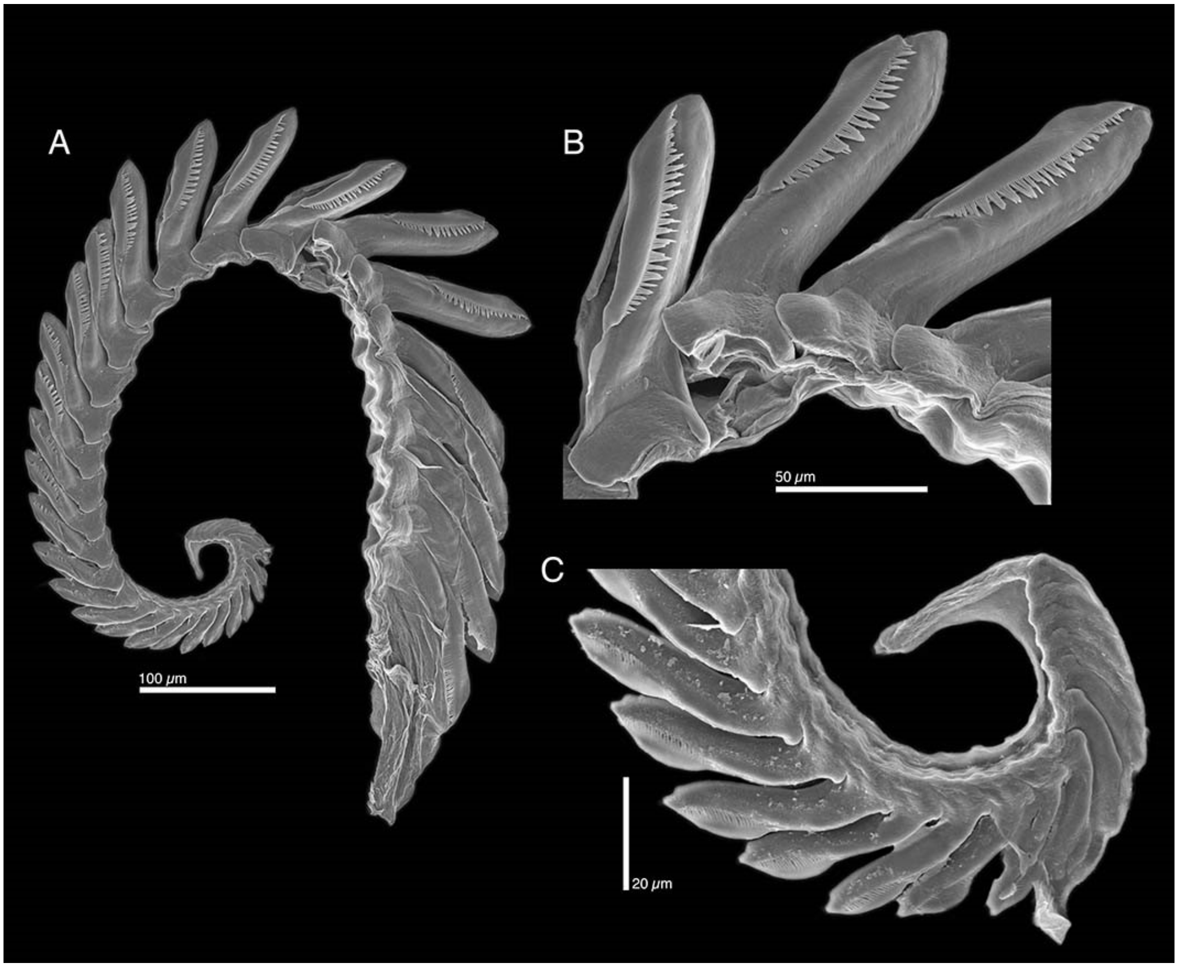

Figure 14. *Edenttellina limax* (Kawaguti & Baba, 1959), SEMs of the radula of a specimen from Tamano Bay, Japan (CASIZ 201957). A. Complete radula. B. Active tooth. C. Ascus.

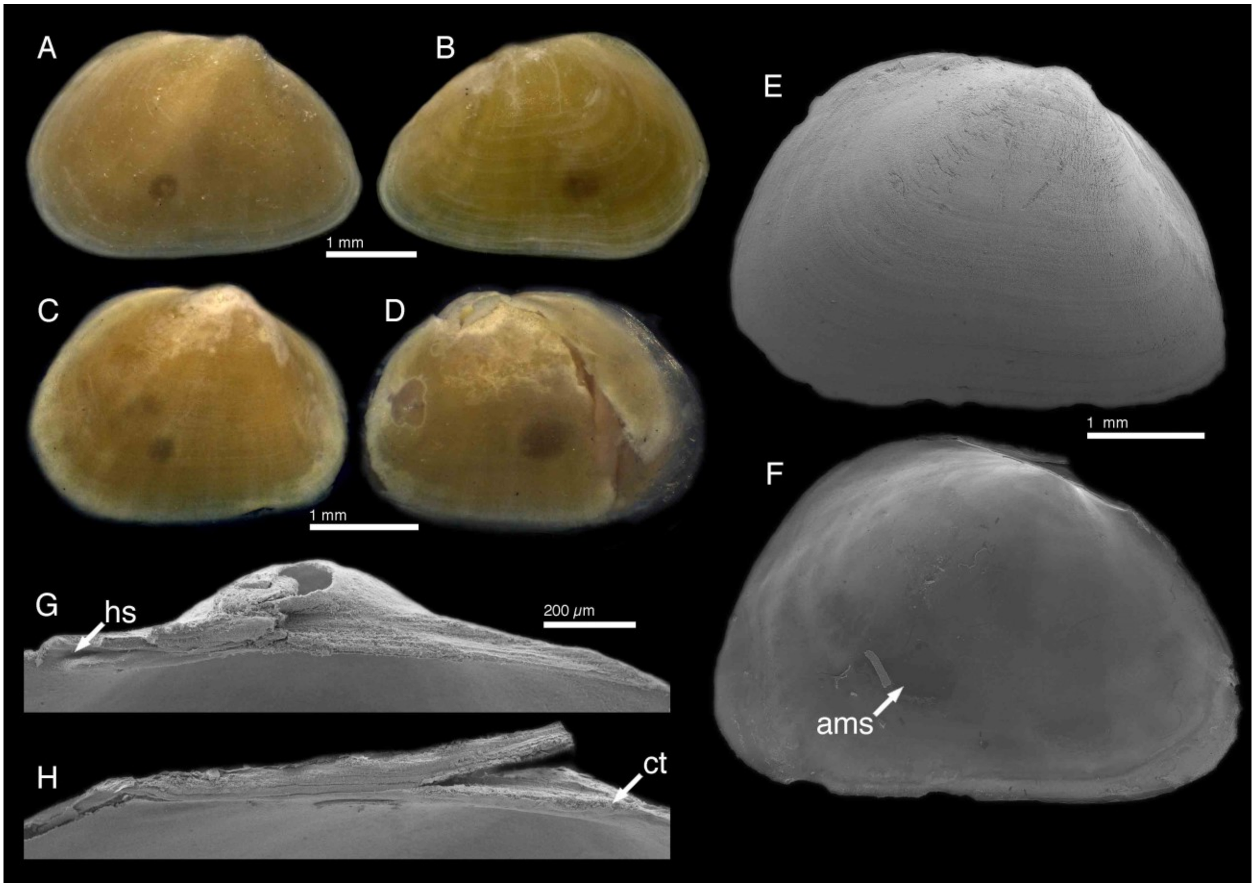

Figure 15. *Edenttellina australis* (Burn, 1960), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Victoria, Australia (MV F188699), outer view left valve (A), outer view right valve (B). C–D. Photographs of t the right and left sides of a preserved specimen from Victoria, Australia (MV F158625), outer view left valve (C), outer view right valve (D). E–F. SEMs of the right and left valves of the same specimen from Victoria, Australia (MV F194029), outer view left valve (E), inner view right valve (F). G–H. SEMs of the hinge of the right and left valves of two different specimens from Victoria, Australia (MV F194029), left valve hinge (G), right valve hinge (H). Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

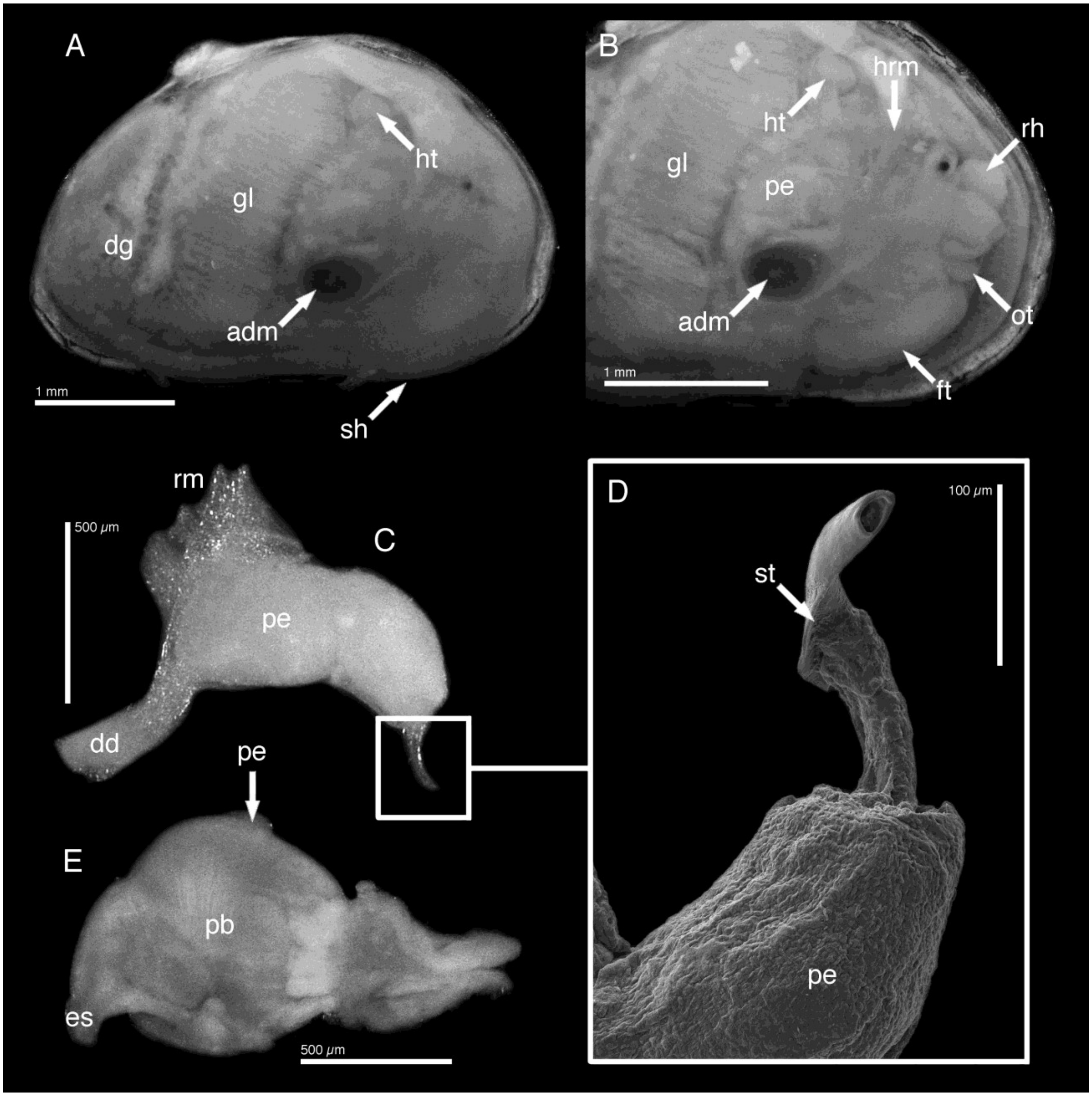

Figure 16. *Edenttellina australis* (Burn, 1960), internal anatomy. A. General view of the internal anatomy of a specimen from Victoria, Australia (MV F158625). B. Detail of the anterior portion of the body with the mantle removed, same specimen. C. Dissected penis, same specimen. D. SEM of the penial stylet, same specimen. E. Dissected anterior portion of the digestive system, same specimen. Abbreviations: adm, adductor muscle; dd, deferent duct; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ht, heart; ot, oral tentacle; pa, pharyngeal appendage; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sh, shell; st, penial stylet.

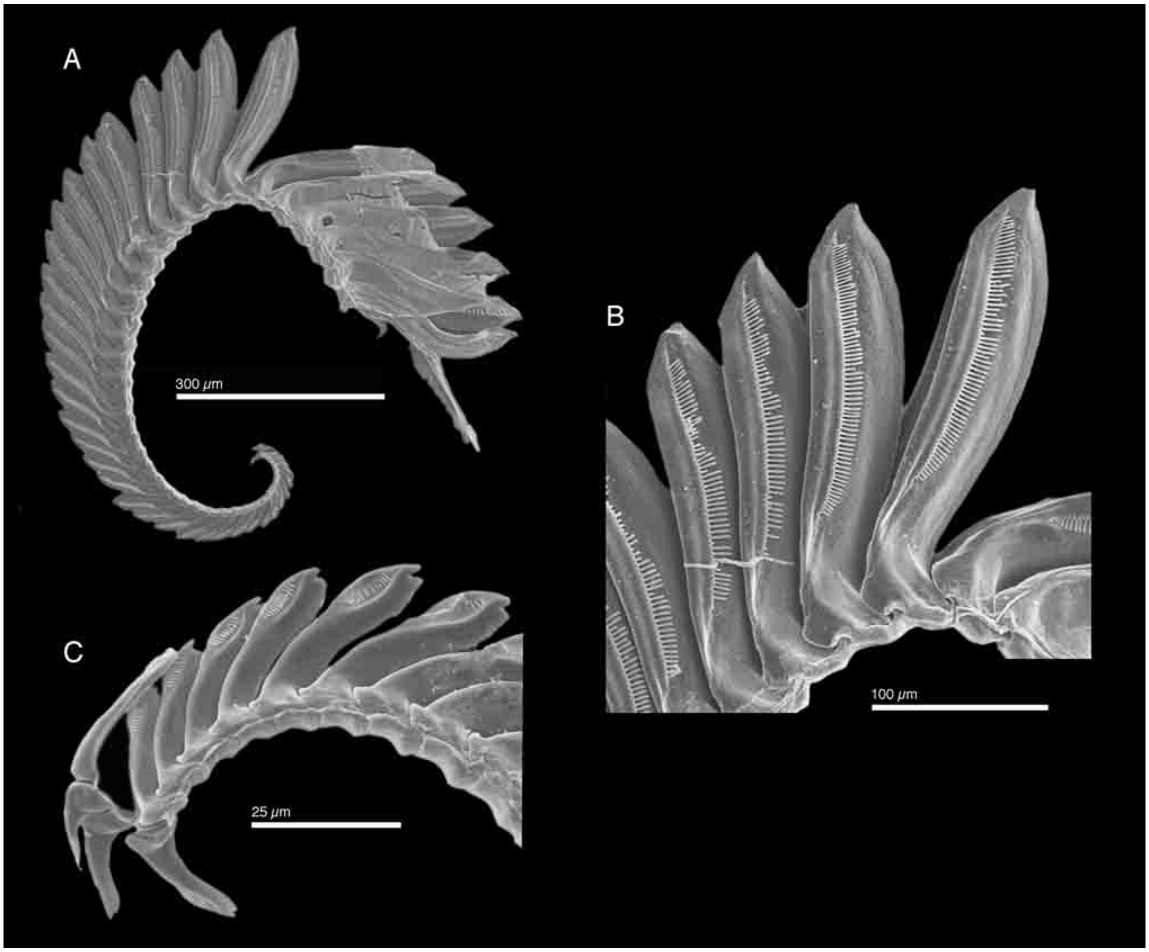

Figure 17. *Edenttellina australis* (Burn, 1960), SEMs of the radula of a specimen from Victoria, Australia (MV F194029). A. Complete radula. B. Active tooth. C. Ascus.

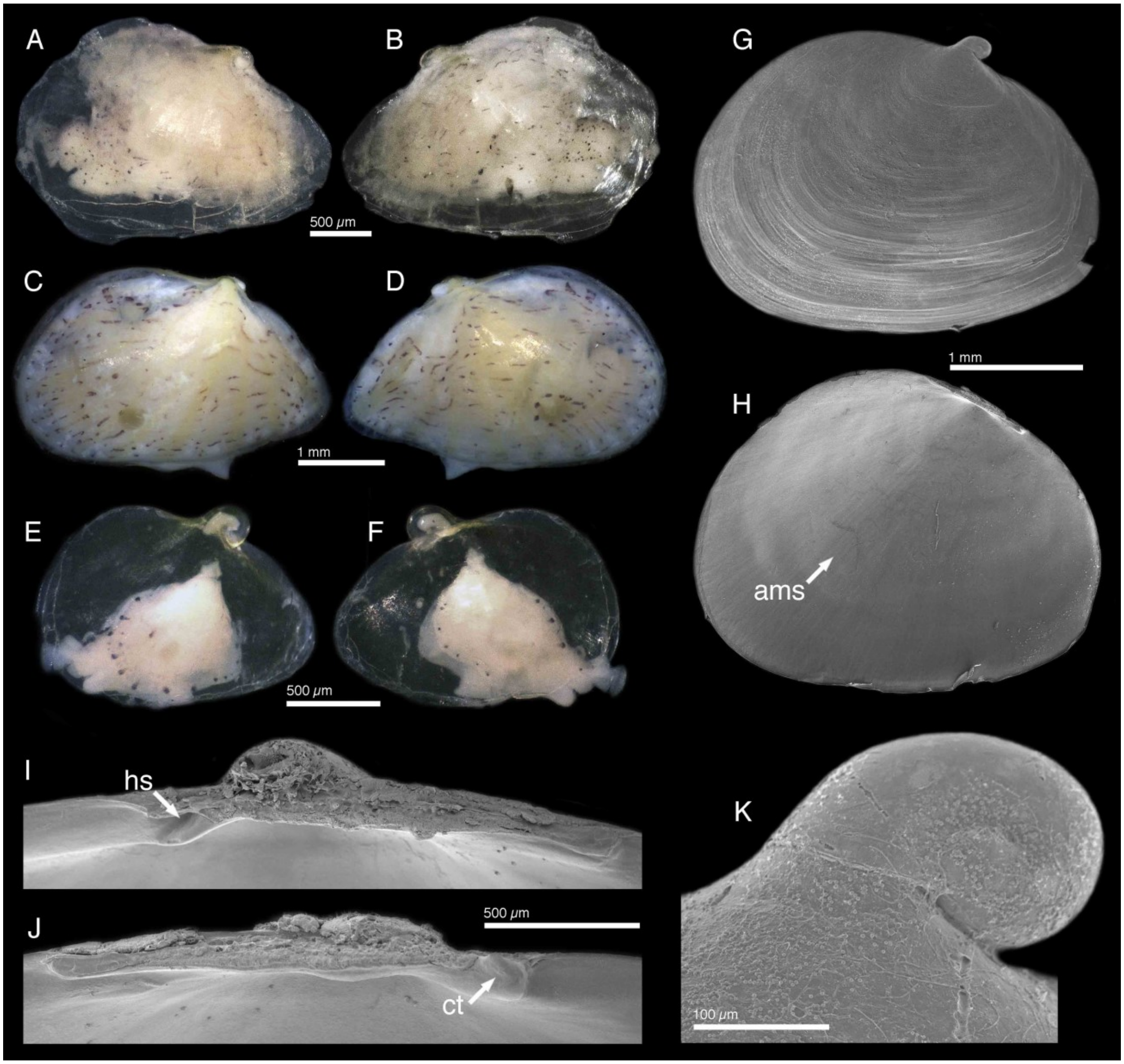

Figure 18. *Edenttellina caribbea* (Edmunds, 1963), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Guadeloupe (MNHN IM-2013-53076), outer view left valve (A), outer view right valve (B). C–D. Photographs of t the right and left sides of a preserved specimen from Bermuda (CASIZ 181198), outer view left valve (C), outer view right valve (D). E–F. Photographs of the right and left sides of a preserved specimen from Guadeloupe (MNHN IM-2013-53075), outer view left valve (E), outer view right valve (F). G–H. SEMs of the right and left valves of the same specimen from Costa Rica (INB0003321518), outer view left valve (G), inner view right valve (H). I–J. SEMs of the hinge of the right and left valves of two different specimens from Costa Rica (INB0003321518), left valve hinge (I), right valve

hinge (J). K. Protoconch of a specimen from Costa Rica (INB0003321518). Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

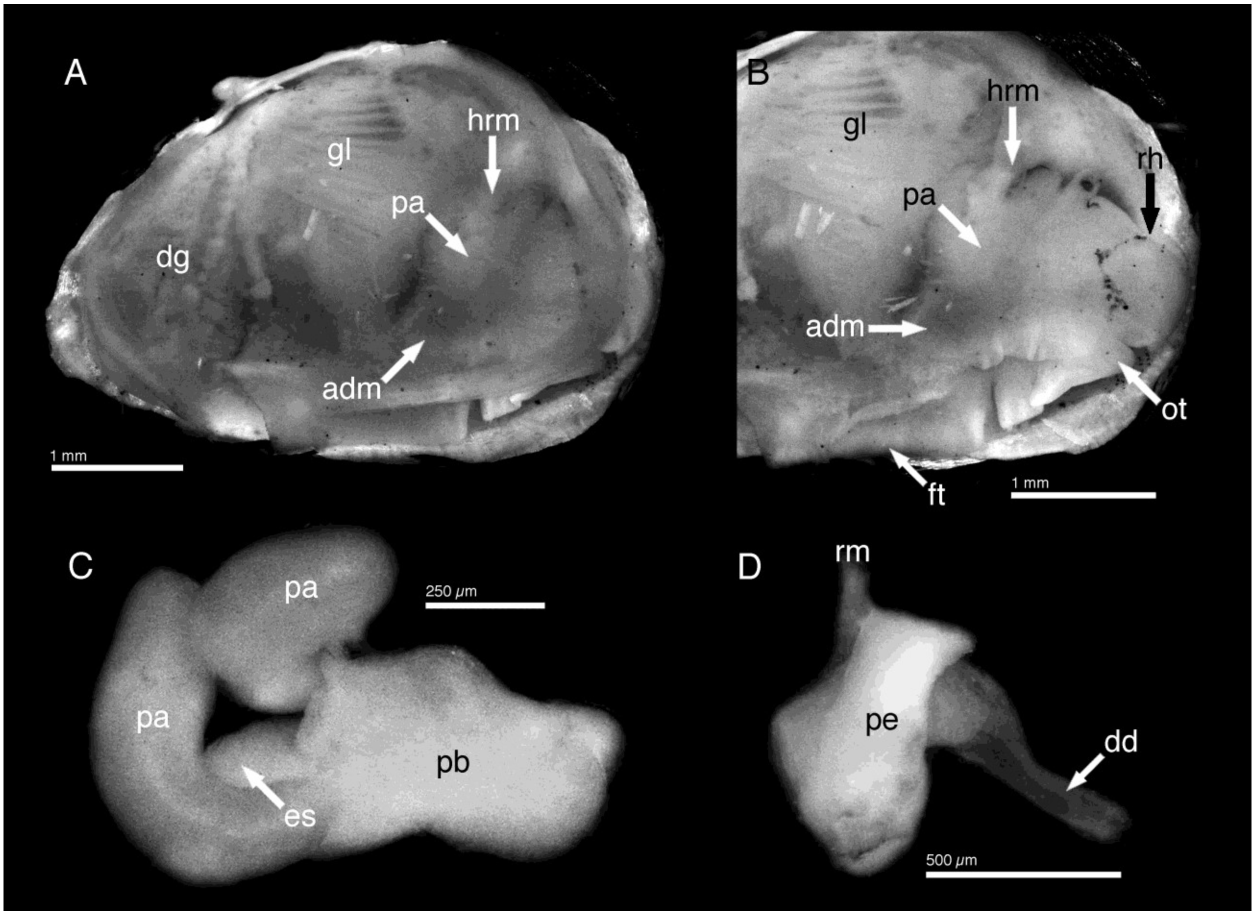

Figure 19. *Edenttellina caribbea* (Edmunds, 1963), internal anatomy. A. General view of the internal anatomy of a specimen from Costa Rica (MZUC INB3321518). B. Dissected anterior portion of the digestive system, same specimen. C. General view of the internal anatomy of a specimen from Maui, Hawaiian Islands (CASIZ 185144). D. Dissected penis, same specimen. Abbreviations: adm, adductor muscle; dd, deferent duct; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ot, oral tentacle; pa, pharyngeal appendage; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sg, salivary gland; sh, shell.

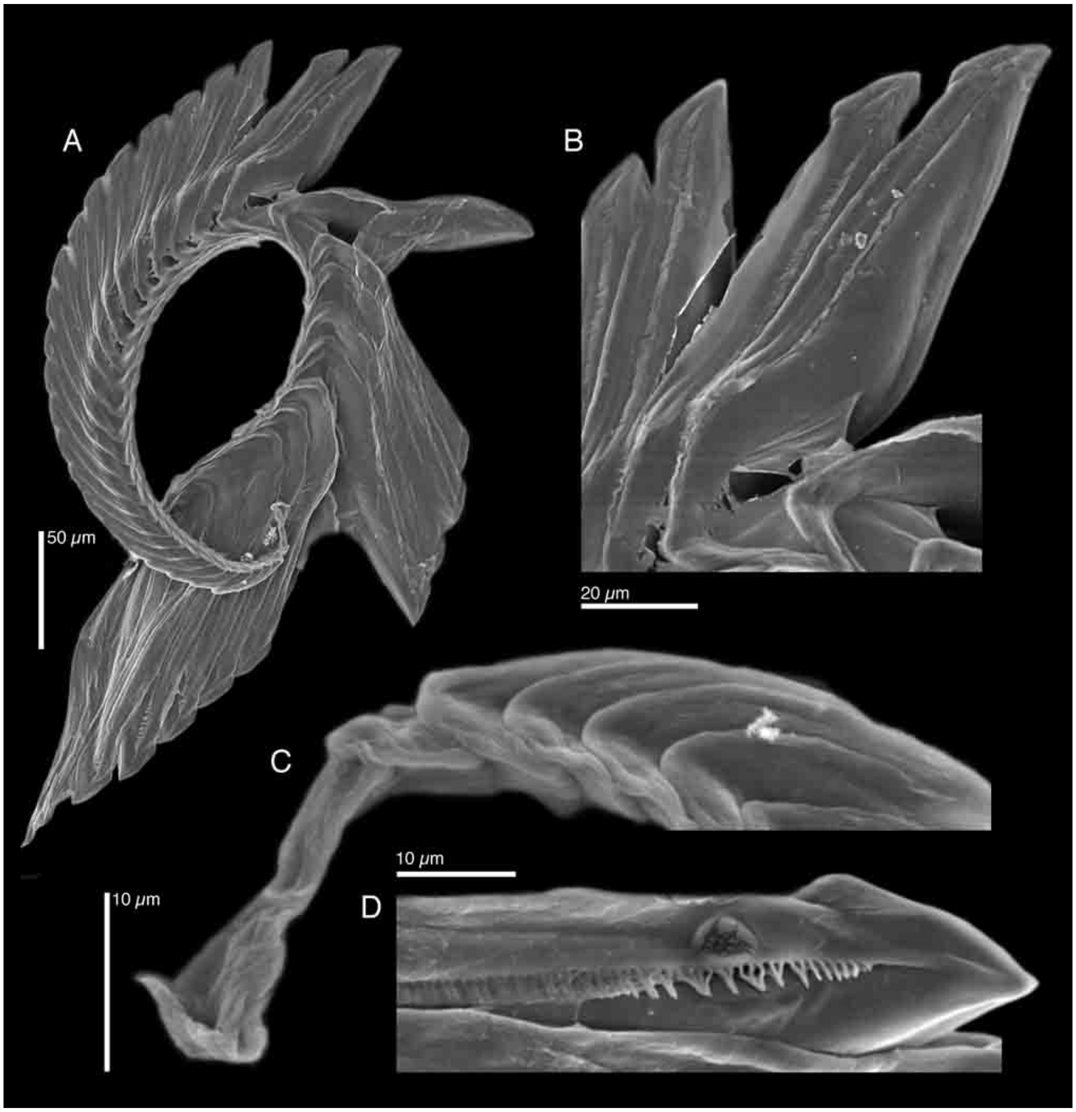

Figure 20. *Edenttellina caribbea* (Edmunds, 1963), SEMs of the radula of specimen from Abaco, Bahamas (NHMLA 011629). A. Complete radula. B. Active tooth. C. Ascus. D. Detail of the denticles.

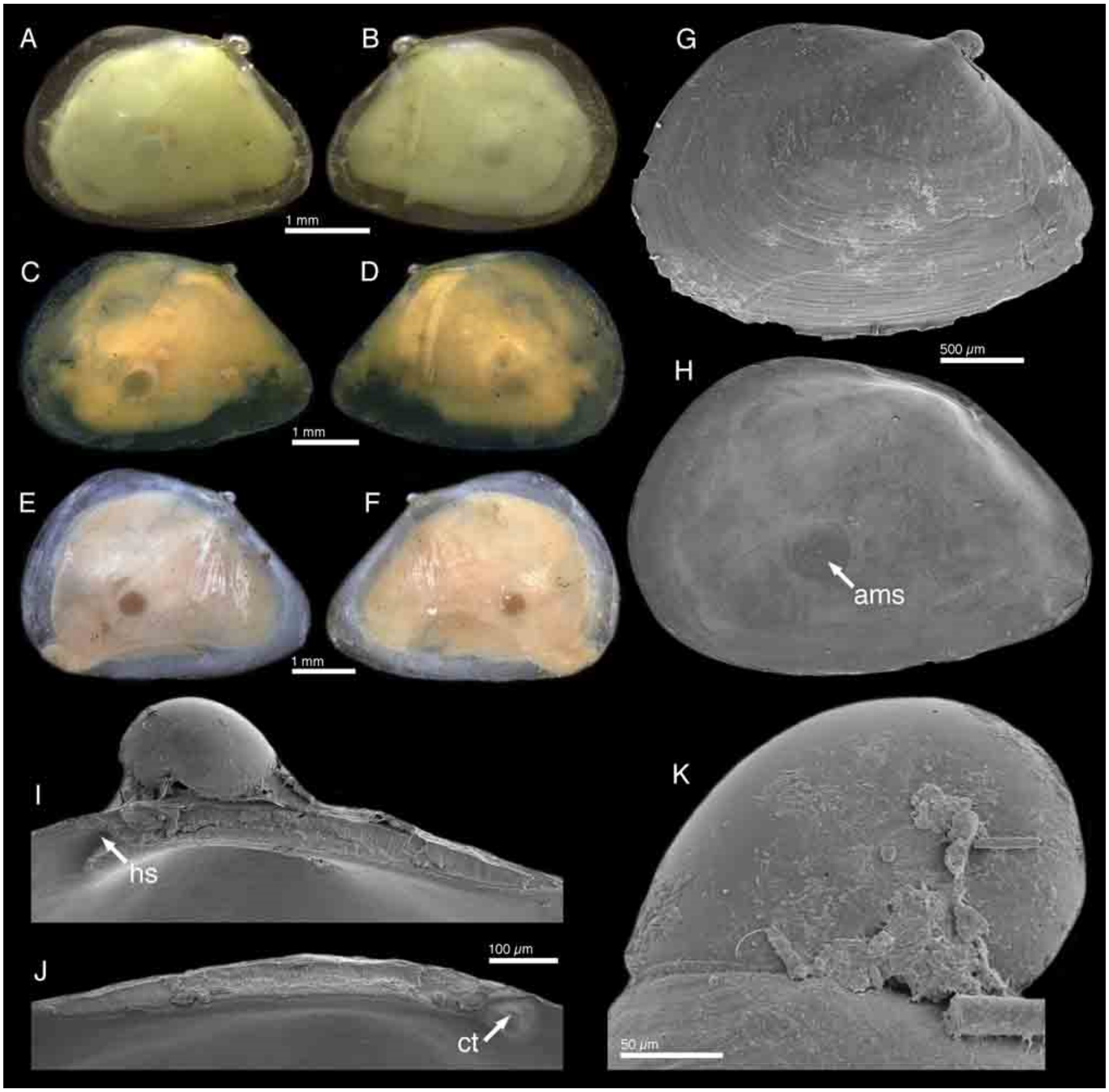

Figure 21. *Edenttellina pseudochloris* (Kay, 1964), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from the Hawaiian Islands (isolate JC84), outer view left valve (A), outer view right valve (B). C–D. Photographs of the right and left sides of a preserved specimen from the Hawaiian Islands (CASIZ 185144), outer view left valve (C), outer view right valve (D). E–F. Photographs of the right and left sides of a preserved specimen from the Philippines (CASIZ 199470), outer view left valve (E), outer view right valve (F). G–H. SEMs of the right and left valves of the same specimen from the Hawaiian Islands (isolate JC84), outer view left valve (G), inner view right valve (H). I–J. SEMs of the hinge of the right and left valves same specimen, left valve hinge (I), right valve hinge (J). K. Protoconch of same specimen. Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

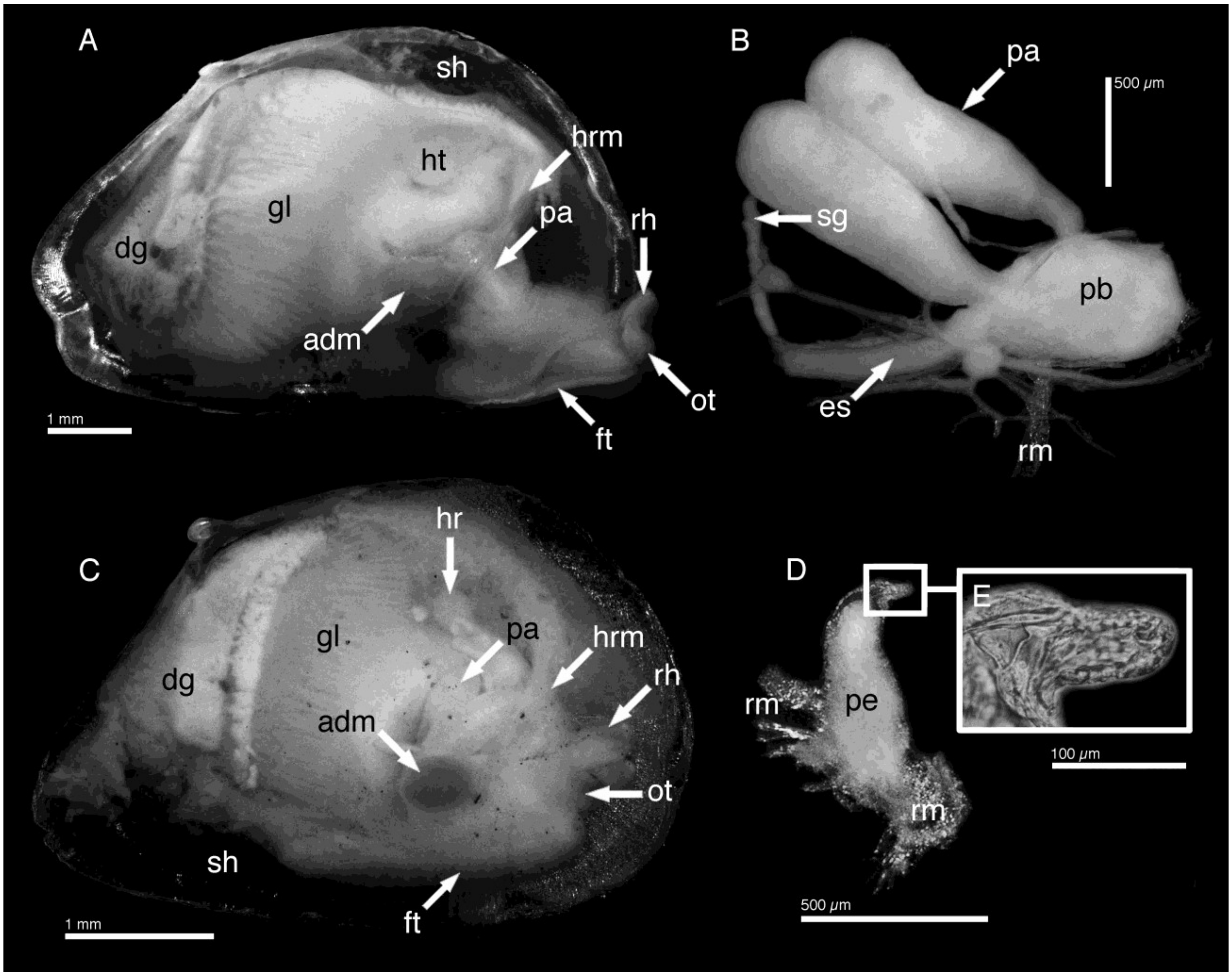

Figure 22. *Edenttellina pseudochloris* (Kay, 1964), internal anatomy. A. General view of the internal anatomy of a specimen from Okinawa, Japan (CASIZ 079359). B. Dissected anterior portion of the digestive system, same specimen. C. General view of the internal anatomy of a specimen from Maui, Hawaiian Islands (CASIZ 185144). D. Dissected penis, same specimen. E. Detail of the hardened penial tip, same specimen. Abbreviations: adm, adductor muscle; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ht, heart; ot, oral tentacle; pa, pharyngeal appendage; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sg, salivary gland; sh, shell.

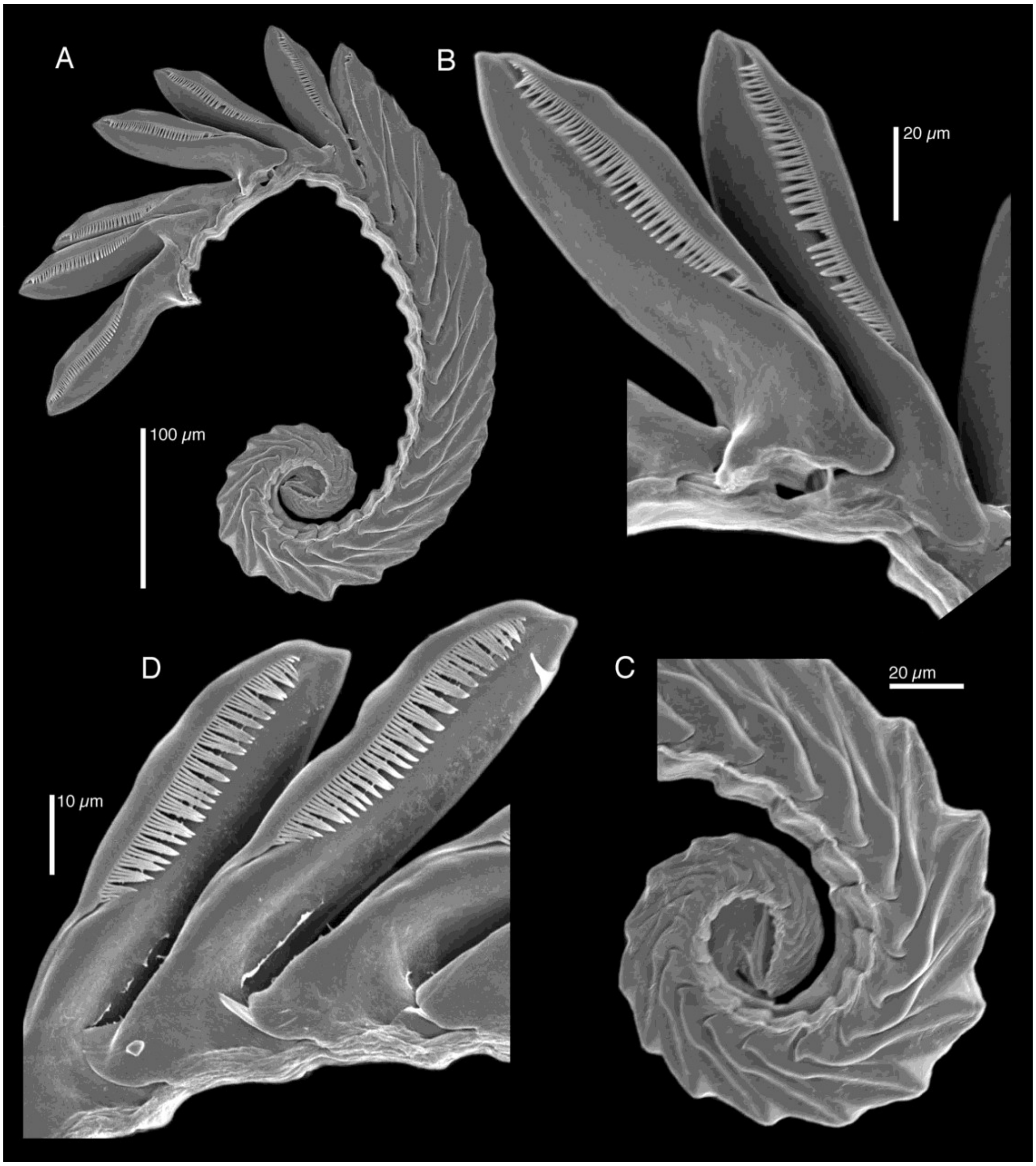

Figure 23. *Edenttellina pseudochloris* (Kay, 1964), SEMs of the radula. A–C. Specimen from Madang, Papua New Guinea (MNHN IM-2013-47177), complete radula (A). Active tooth (B), ascus (C). D. Specimen from Maui, Hawaiian Islands. Active tooth (CASIZ 185144).

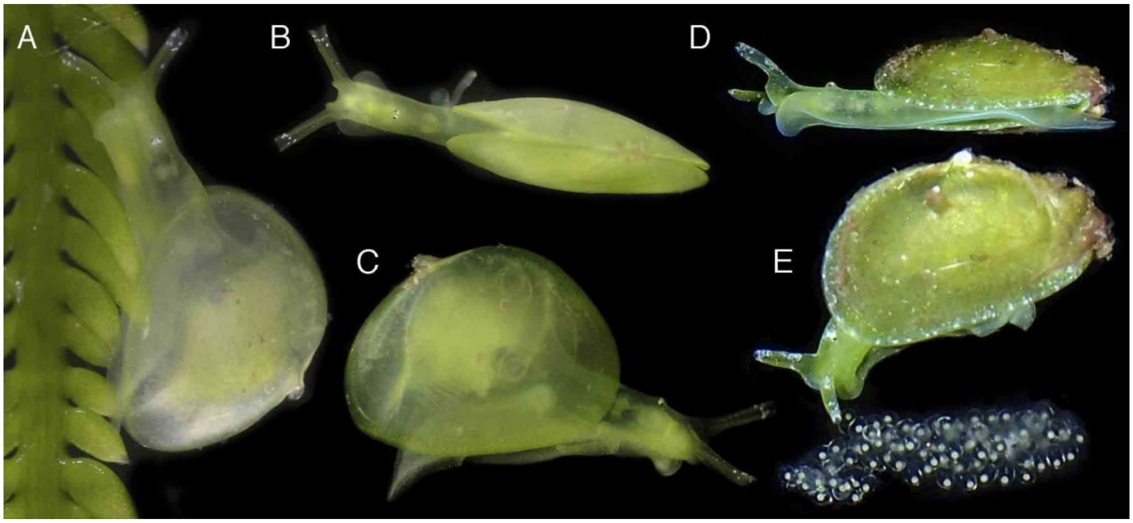

Figure 24. Photographs of live animals of *Edenttellina* spp. A–C. *Edenttellina babai* (Burn 1965), Lord Howe Is. Australia, photos: P. Krug, specimen on its algal host (A), dorsal view (B), lateral view (C). D–E. *Edenttellina singaporensis* (Jensen, 2015), Indonesia, photos: L. Wong, ventral view (D), lateral view and egg mass (E).

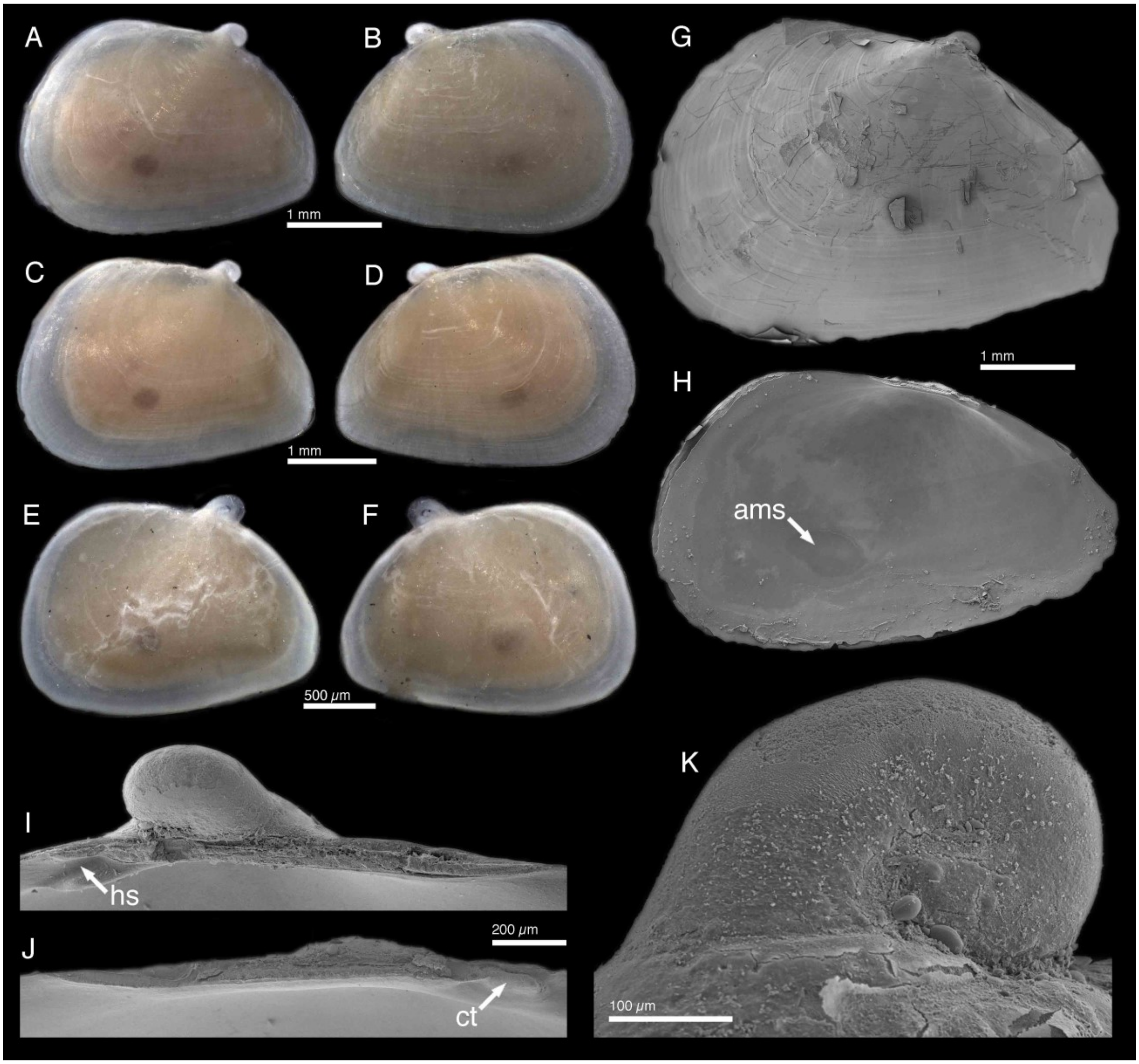

Figure 25. *Edenttellina babai* (Burn, 1965), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Victoria, Australia (MV F158624), outer view left valve (A), outer view right valve (B). C–D. Photographs of the right and left sides of a preserved specimen from Victoria, Australia (MV F158624), outer view left valve (C), outer view right valve (D). E–F. Photographs of the right and left sides of a preserved specimen from Victoria, Australia (MV F159081), outer view left valve (E), outer view right valve (F). G–H. SEMs of the right and left valves of the same specimen from Victoria, Australia (MV F112386), outer view left valve (G), inner view right valve (H). I–J. SEMs of the hinge of the right and left valves same specimen, left valve hinge (I), right valve hinge (J). K. Protoconch of same specimen. Abbreviations: ct, condyloid tooth; hs, hinge socket.

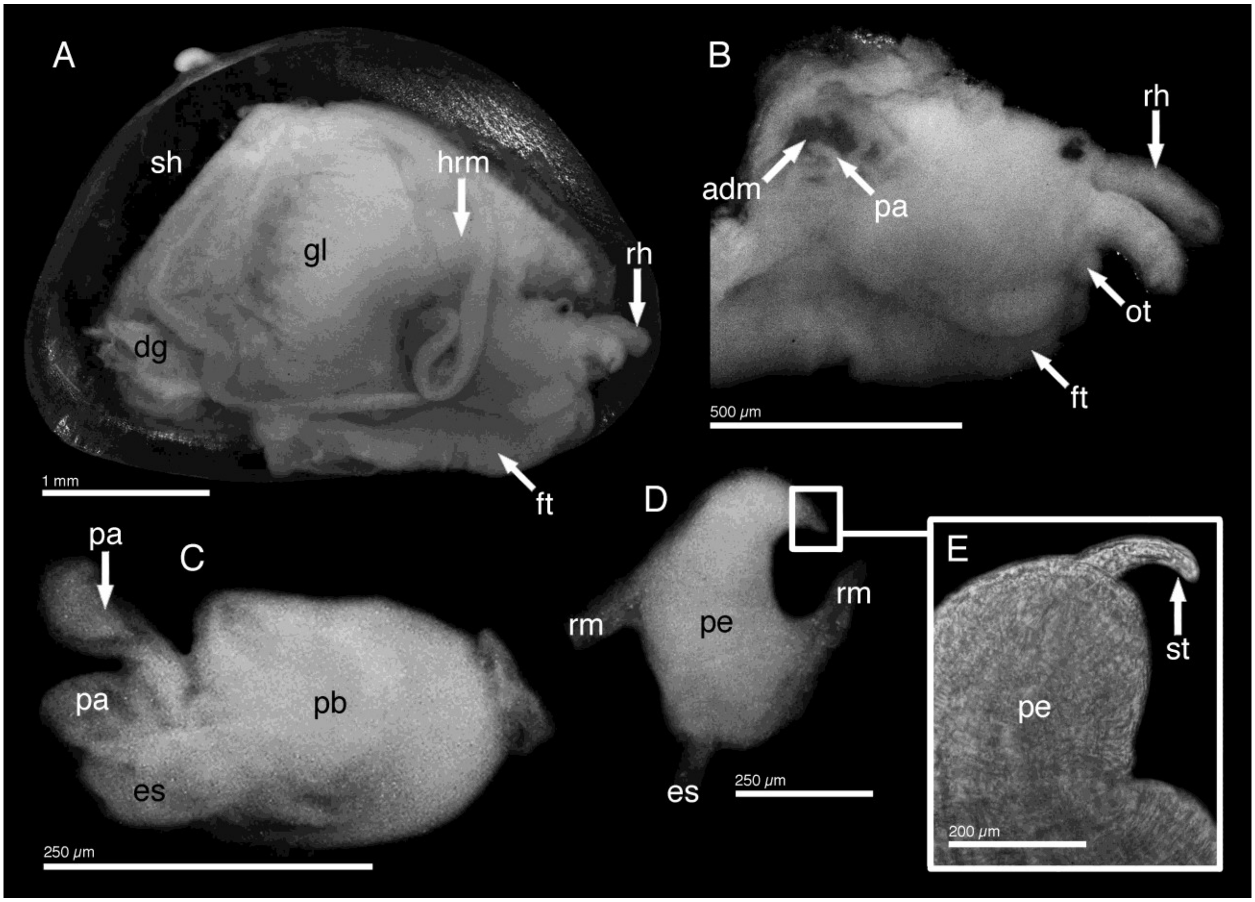

Figure 26. *Edenttellina babai* (Burn, 1965), internal anatomy. A. General view of the internal anatomy of a specimen from Queensland, Australia (lot 94-5E). B. Detail of the anterior portion of the body with the mantle removed, same specimen. C. Dissected anterior portion of the digestive system, same specimen. D. Dissected penis, same specimen. E. Detail of the penial stylet. Abbreviations: adm, adductor muscle; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ot, oral tentacle; pa, pharyngeal appendage; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sh, shell; st, penial stylet.

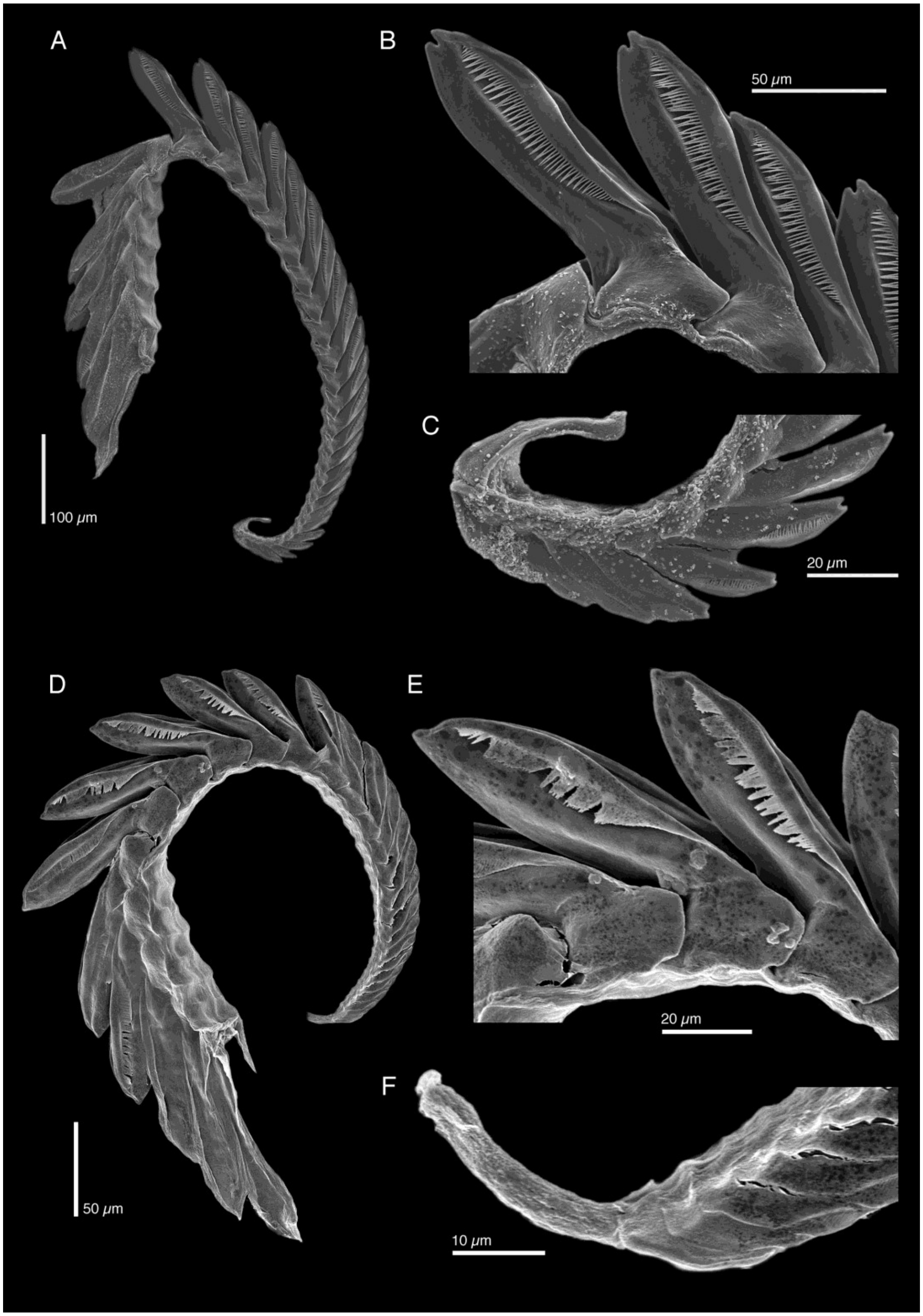

Figure 27. *Edenttellina babai* (Burn, 1965), SEMs of the radula. A–C. Specimen from Victoria, Australia (MV F112386), complete radula (A). Active tooth (B), ascus (C). D–E. Specimen from Queensland, Australia (lot 94-5E), complete radula (D). Active tooth (E), ascus (F).

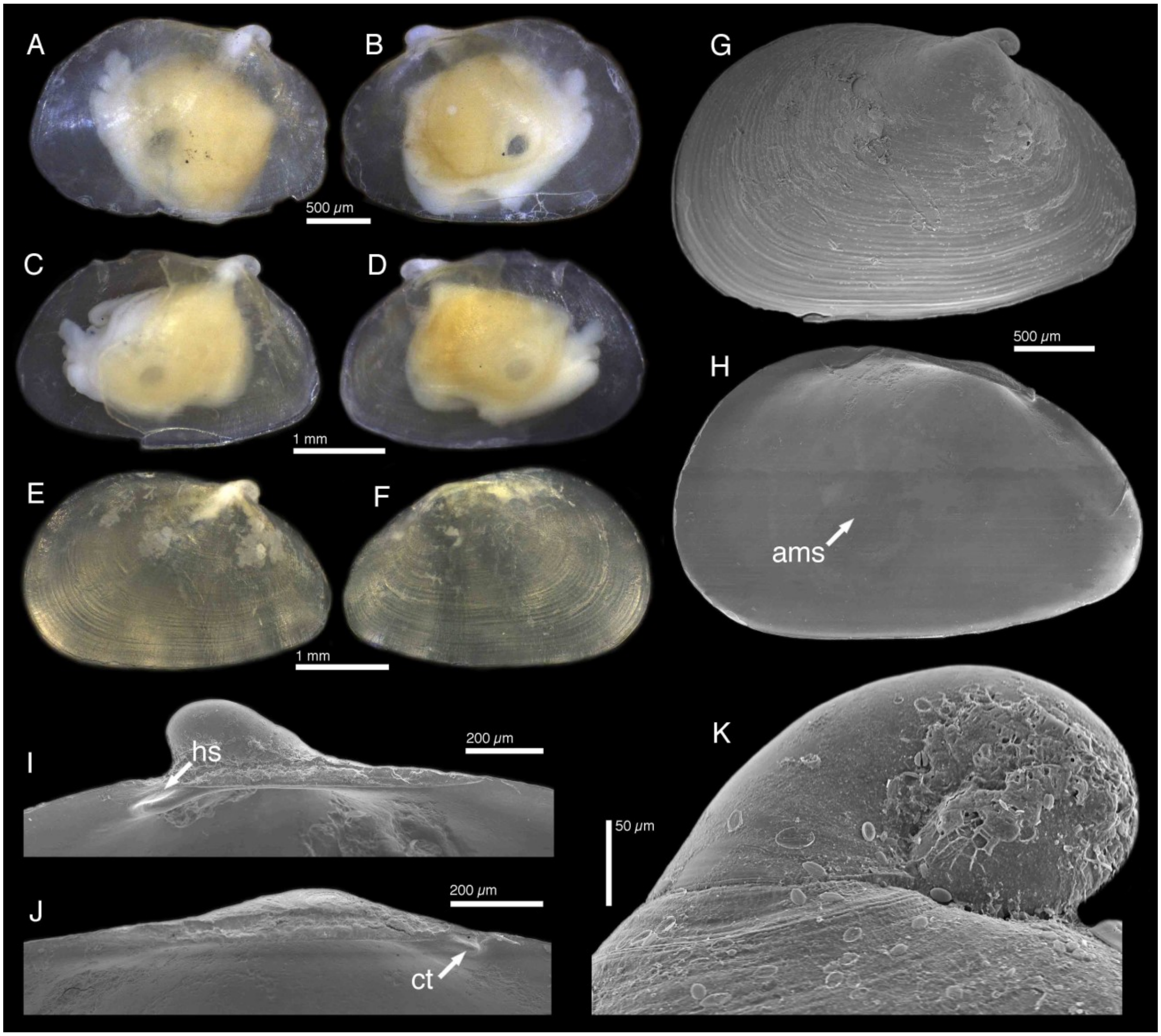

Figure 28. *Edenttellina* cf. *rottnesti* (Jensen, 1993), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Tasmania, Australia (MNHN IM-2013-53071), outer view left valve (A), outer view right valve (B). C–D. Photographs of t the right and left sides of a preserved specimen from Tasmania, Australia (MNHN IM-2013-53070), outer view left valve (C), outer view right valve (D). E–F. Photographs of the right and left sides of a preserved specimen from Tasmania, Australia (MNHN IM-2013-53073), outer view left valve (E), outer view right valve (F). G–H. SEMs of the right and left valves of the same specimen from Tasmania, Australia (MNHN IM-2013-53073), outer view left valve (G), inner view right valve (H). I–J. SEMs of the hinge of the right and left valves of the same specimen from Tasmania, Australia (MNHN IM-2013-53073), left valve hinge (I), right valve hinge (J). K. Protoconch of a specimen from Tasmania, Australia (MNHN IM-2013-53073). Abbreviations:

ct, condyloid tooth.

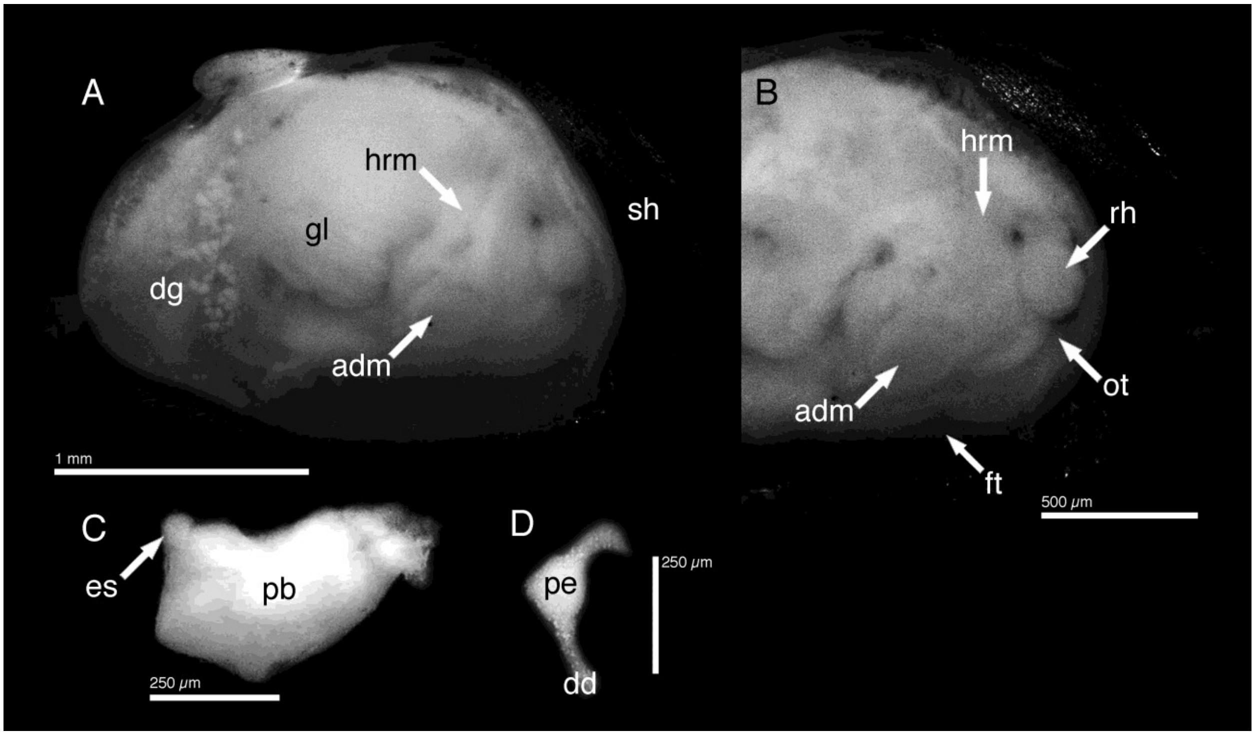

Figure 29. *Edenttellina* cf. *rottnesti* (Jensen, 1993), internal anatomy of a specimen from Tasmania, Australia (MNHN IM-2013-53068). A. General view of the internal anatomy. B. Detail of the anterior portion of the body with the mantle removed. C. Dissected anterior portion of the digestive system. D. Dissected penis. Abbreviations: adm, adductor muscle; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ot, oral tentacle; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sh, shell.

Figure 30. *Edenttellina* cf. *rottnesti* (Jensen, 1993), SEMs of the radula of specimen from Tasmania, Australia (MNHN IM-2013-53073). A. Complete radula. B. Active tooth. C. Ascus.

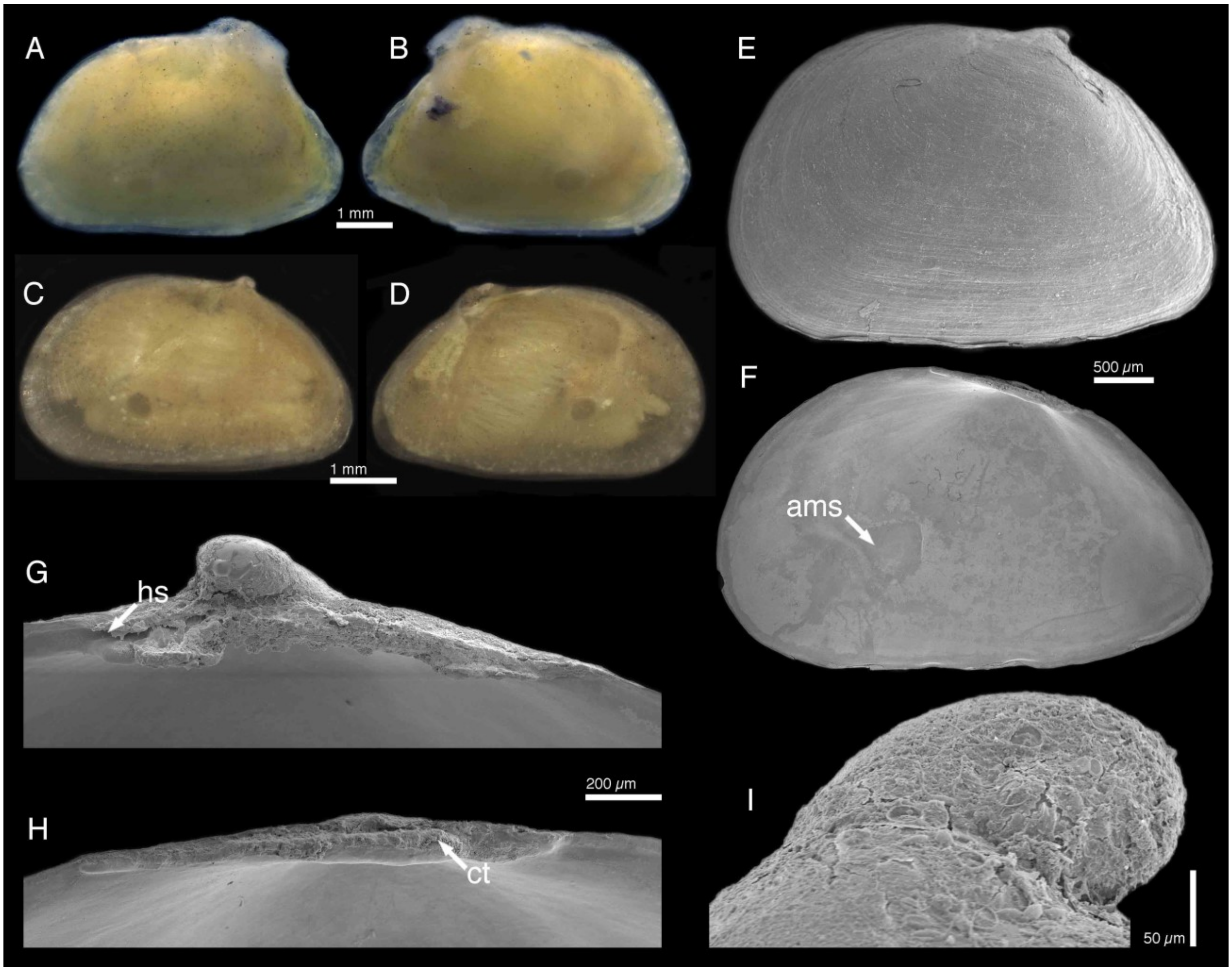

Figure 31. *Edenttellina singaporensis* (Jensen, 2015), shell morphology. A–B. Photographs of the right and left sides of a preserved specimen from Johor, Malaysia (CPIC 02539), outer view left valve (A), outer view right valve (B). C–D. Photographs of t the right and left sides of a preserved specimen from Port Dickson, Malaysia (CPIC 02538), outer view left valve (C), outer view right valve (D). E–F. SEMs of the right and left valves of the same specimen from Port Dickson, Malaysia (CPIC 02538), outer view left valve (E), inner view right valve (F). G–H. SEMs of the hinge of the right and left valves of two different specimens from Port Dickson, Malaysia (CPIC 02538), left valve hinge (G), right valve hinge (H). I. Protoconch of same specimen. Abbreviations: ams, adductor muscle scar; ct, condyloid tooth; hs, hinge socket.

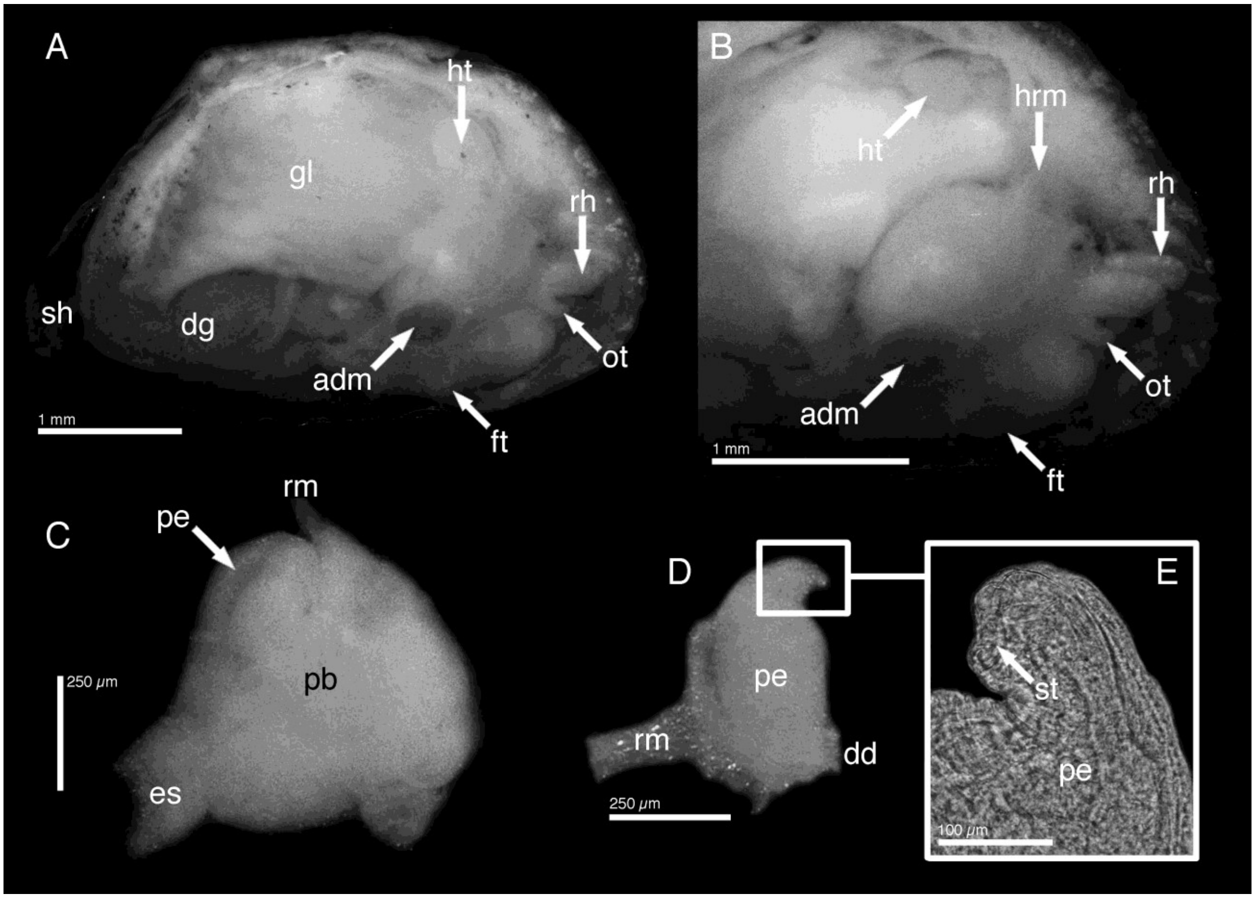

Figure 32. *Edenttellina singaporensis* (Jensen, 2015), internal anatomy. A. General view of the internal anatomy of a specimen from Johor, Malaysia (CPIC 02539). B. Detail of the anterior portion of the body with the mantle removed, same specimen. C. Dissected anterior portion of the digestive system, same specimen. D. Dissected penis, same specimen. E. Detail of the penial stylet. Abbreviations: adm, adductor muscle; dg, digestive gland; es, esophagus; ft, foot; gl, gill; hrm, head retractor muscle; ot, oral tentacle; pa, pharyngeal appendage; pb, pharyngeal bulb; pe, penis; rh, rhinophore; rm, retractor muscle; sh, shell; st, penial stylet.

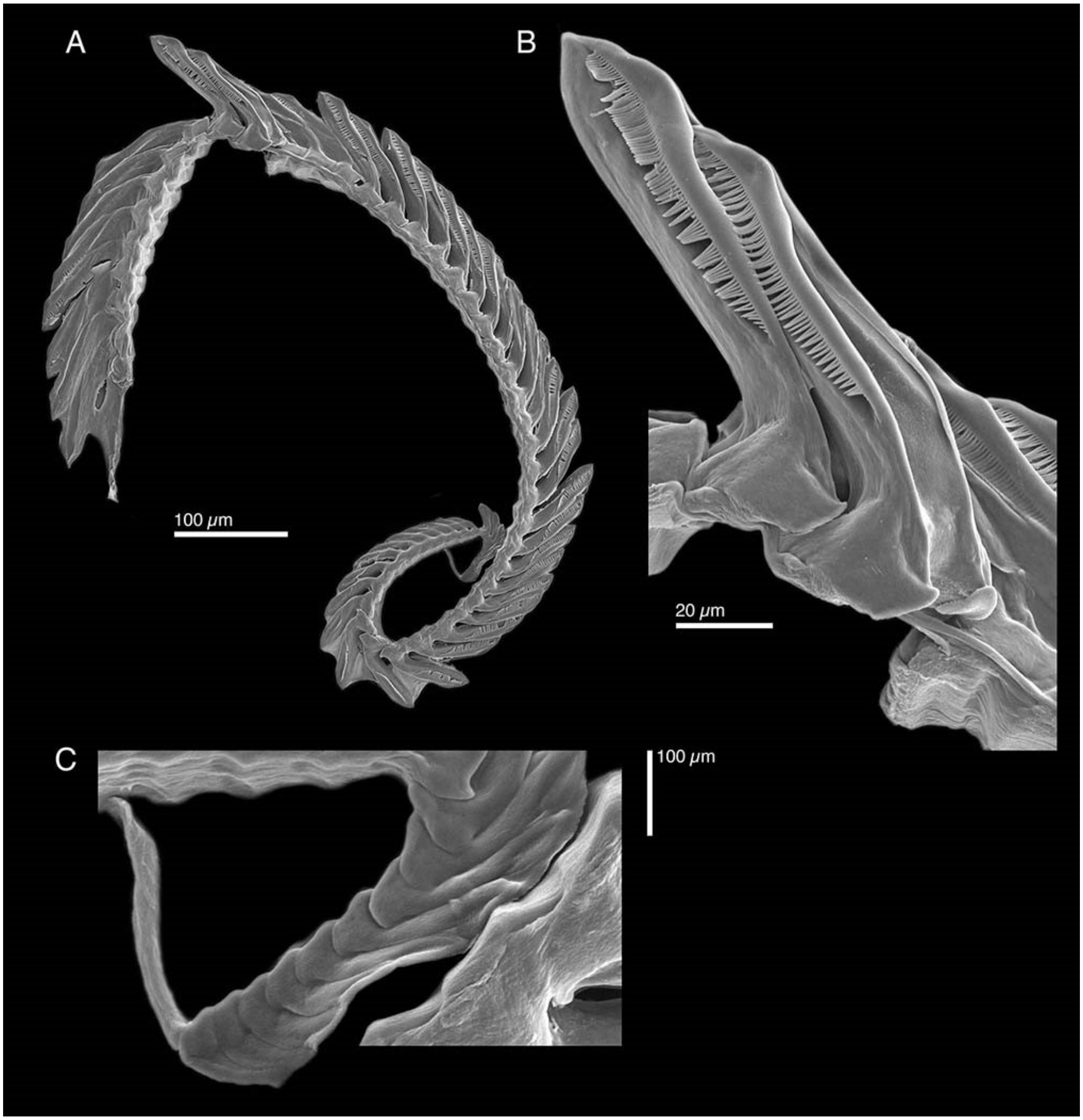

Figure 33. *Edenttellina singaporensis* (Jensen, 2015), SEMs of the radula of specimen from Johor, Malaysia (CPIC 02539). A. Complete radula. B. Active tooth. C. Ascus.

Table 1. List of specimens included in the phylogenetic analyses with species name, locality, isolate number, voucher number and GenBank accession numbers. Species identifications are based on the final results of this study.

				GenBank Accession Numbers				
Species Name	**Locality**	**Isolate**	**Voucher Number**	**CO1**	**16S**	**H3**	**28S**	**18S**
E. australis	Victoria, Australia	JC18A	MV F194029	–	–	PV147786	–	–
E. australis	Victoria, Australia	JC18B	MV F194029	–	–	PV147787	–	–
E. babai	Lord Howe Island, Australia	11How01	AM C.469652	KM086350	KM204189	KM040795	KM230456	PV101952
E. babai	Queensland, Australia	JC36	lot 94-5E	PV077974	PV101963	PV147788	–	–
E. caribbea	Sweeting Cay, Bahamas	–	Bcar10swe01	KM086349	KM204188	KM040794	KM230455	PV101953
E. caribbea	Saint Francois, Guadeloupe	JC43	MNHN IM-2013-53077	PV077975	PV101964	PV147789	–	–
E. caribbea	Saint Francois, Guadeloupe	JC44	MNHN IM-2013-53076	PV077976	PV101965	PV147790	–	–
E. caribbea	Petite Terre, Guadeloupe	JC45	MNHN IM-2013-53075	–	–	PV147791	–	–
E. caribbea	Saint Francois, Guadeloupe	JC46	MNHN IM-2013-53074	–	–	PV147792	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC37	MNHN IM-2013-53072	–	PV101966	PV147793	PV094619	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC38A	MNHN IM-2013-53073	PV077977	PV101967	PV147794	PV094620	PV101954
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC38B	MNHN IM-2013-53073	–	PV101968	PV147795	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC38C	MNHN IM-2013-53073	–	PV101969	PV147796	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC38D	MNHN IM-2013-53073	PV077978	PV101970	PV147797	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC39	MNHN IM-2013-53071	–	PV101971	PV147798	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC40	MNHN IM-2013-53068	PV077979	PV101972	PV147799	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC41	MNHN IM-2013-53069	PV077980	PV101973	PV147800	–	–
E. cf. *rottnesti*	Tasmania, Morrison, Australia	JC42	MNHN IM-2013-53070	PV077981	–	PV147801	–	–
E. chloris	Baja California, Mexico	JC2	NHMLA 1974-33.1	–	PV101974	–	–	–
E. chloris	Baja California, Mexico	JC3A	NHMLA 186690	PV077982	PV101975	PV147802	–	–
E. chloris	Baja California, Mexico	JC3B	NHMLA 186690	PV077983	–	–	–	–
E. pseudochloris	Olivine Pools, Maui, Hawaiian Ids	JC11B	CPIC 00315	–	PV101976	PV147803	–	–
E. pseudochloris	Maui, Hawaiian Is	JC21B	CASIZ 185144	PV077984	PV101977	PV147804	PV094621	PV101955
E. pseudochloris	Mabini, Luzon, Philippines	JC33B	CASIZ 199470	PV077985	PV101978	PV147805	PV094622	–
E. pseudochloris	Kavieng Lagoon, Papua New Guinea	JC78	MNHN IM-2013-47177	PV077986	PV101979	PV147806	–	–
E. pseudochloris	Kavieng Lagoon, Papua New Guinea	JC80	MNHN IM-2013-47623	PV077987	PV101980	PV147807	–	–
E. pseudochloris	Maui, Hawaiian Is	JC84	Bpse-16MAU06	PV077988	PV101981	PV147808	–	–
E. pseudochloris	Okinawa, Japan	JC94	CASIZ 079359	–	PV101982	PV147809	–	–
E. pseudochloris	Lizard Island, Australia	–	Tl792LIC	GQ996666	–	–	GQ996605	–
E. singaporensis	Port Dickson, Malaysia	JC87B	CPIC 02538	PV077989	PV101983	PV147810	PV094623	PV101956
E. singaporensis	Johor, Malaysia	JC88A	CPIC 02539	PV077990	PV101984	PV147811	PV094624	–

E. typica	Victoria, Australia	–	AM C25496	–	–	PV147812	PV094625	PV101957
J. burni	Hoai Bay, Kaua‘i, Hawaiian Is	JC28	CASIZ 189446	–	PV101985	PV147813	–	–
J. burni	Ablo Is, Saudi Arabia	JC30	CASIZ 192355	–	PV101986	PV147814	–	–
J. exquisita	Lizard Island, Australia	–		GQ996661	EU140895	–	GQ996653	–
J. exquisita	Kahului Harbor, Maui, Hawaiian Is	JC26A	NHMLA 181332	PV077991	PV101987	PV147815	–	–
J. exquisita	Mualassa Bay, Maui, Hawaiian Is	JC27A	NHMLA 171215	PV077992	–	PV147816	–	–
J. exquisita	Mualassa Bay, Maui, Hawaiian Is	JC27B	NHMLA 171215	–	–	PV147817	–	–
J. exquisita	Gusom Island, Papua New Guinea	JC29	CASIZ 191494	–	PV101988	PV147818	–	–
J. exquisita	French Frigate Shoals, Hawaiian Is	JC49	FMNH 426995	–	PV101989	PV147819	–	–
J. exquisita	French Frigate Shoals, Hawaiian Is	JC50	FMNH 426999	–	PV101990	PV147820	–	–
J. exquisita	Sinub Island, Papua New Guinea	JC67	MNHN IM-2013-6437	PV077993	PV101991	PV147821	PV094626	–
J. exquisita	Kranket Island, Papua New Guinea	JC75	MNHN IM-2013-1869	PV077994	PV101992	PV147822	PV094627	PV101958
J. exquisita	New Ireland, Papua New Guinea	JC77	MNHN IM-2013-47681	–	PV101993	–	–	–
J. exquisita	Kavieng Lagoon, Papua New Guinea	JC83	MNHN IM-2013-47176	–	PV101994	PV147823	–	–
J. exquisita	Maliko Bay, Maui, Hawaiian Is	JC85	Jexq-16MAU14	–	PV101995	PV147824	–	–
J. exquisita	Maliko Bay, Maui, Hawaiian Is	JC86	Jexq-16MAU62	PV077995	PV101996	PV147825	–	–
J. exquisita	Kavieng Lagoon, Papua New Guinea	JC108	MNHN IM-2013-43570	–	PV101997	PV147826	–	–
J. exquisita	Kavieng Lagoon, Papua New Guinea	JC110	MNHN IM-2013-54735	–	PV101998	PV147827	–	–
J. sp. 1	Midway Atoll, Hawaiian Is	JC9	NHMLA 1985-115	–	PV101999	PV147828	PV094628	PV101959
J. sp. 1	Bohol Island, Philippines	JC98	CASIZ 181558	–	PV102000	PV147829	–	–
J. mishimaensis	Sek Island, Papua New Guinea	JC55	MNHN IM-2013-6760	–	PV102001	PV147830	–	–
J. mishimaensis	Hargun Island, Papua New Guinea	JC57	MNHN IM-2013-3774	PV077996	PV102002	PV147831	PV094629	–
J. mishimaensis	Kranket Island, Papua New Guinea	JC59	MNHN IM-2013-6685	–	–	PV147832	–	–
J. mishimaensis	Kranket Island, Papua New Guinea	JC60	MNHN IM-2013-1871	–	–	PV147833	–	PV101960
J. mishimaensis	Kranket Island, Papua New Guinea	JC62	MNHN IM-2013-95	–	PV102003	PV147834	–	–
J. mishimaensis	Kranket Island, Papua New Guinea	JC68	MNHN IM-2013-1870	PV077997	PV102004	PV147835	PV094630	PV101961
J. mishimaensis	Wonad Island, Papua New Guinea	JC71	MNHN IM-2013-5127	PV077998	PV102005	PV147836	PV094631	–
J. mishimaensis	Banc Cibjane, Mozambique	JC101	MNHN MM18	–	PV102006	PV147837	–	–
J. mishimaensis	Pointe Flacourt, Madagascar	JC102	MNHN TB12	–	PV102007	PV147838	–	–
J. mishimaensis	Kavieng Lagoon, Papua New Guinea	JC109	MNHN IM-2013-43571	–	PV102008	PV147839	–	–
J. sp. 2	Kavieng Lagoon, Papua New Guinea	JC111	MNHN IM-2013-43572	–	PV102009	PV147840	–	–
J. sp. 2	Kavieng Lagoon, Papua New Guinea	JC112	MNHN IM-2013-43574	–	PV102010	PV147841	–	–
J. sp. 2	Kavieng Lagoon, Papua New Guinea	JC113	MNHN IM-2013-43573	–	PV102011	PV147842	–	–
J. sp. 3	New Ireland, Papua New Guinea	JC79	MNHN IM-2013-47683	PV077999	PV102012	PV147843	–	–
J. sp. 3	Kavieng Lagoon, Papua New Guinea	JC81	MNHN IM-2013-47625	PV078000	PV102013	PV147844	–	–
J. sp. 3	Kavieng Lagoon, Papua New Guinea	JC82	MNHN IM-2013-50640	PV078001	–	PV147845	–	–

J. zebra	O‘ahu, Hawaiian Is	JC48	FMNH 426997	–	PV102014	PV147846	–	–
J. zebra	Sek Island, Papua New Guinea	JC69	MNHN IM-2103-6428	PV078002	–	PV147847	–	–
J. zebra	Mo‘orea, French Polynesia	–	Jzeb-10MOR01	KM086410	KM204259	KM040874	KM230546	PV101962

Table 2. Forward and reverse primers used to amplify the genes included in phylogenetic and species delimitation analyses.

Gene	Forward sequence	Reverse sequence	Author
CO1	**LCO1490** 5’-GGTCAACAAATCATAAAGATATTGG-3’	**HCO2198** 5’-TAAACTTCAGGGTGACCAAAAAATCA-3	Folmer et al. (1994)
16S rRNA	**16Sar-L** 5’-CGCCTGTTTATCAAAAACAT-3’	**16Sbr-H** 5’-CCGGTCTGAACTCAGATCACGT-3’	Palumbi (1996)
Histone H3	**Hex AF** 5’-ATGGCTCGTACCAAGCAGACGGC-3’	**Hex AR** 5’-ATATCCTTGGGCATGATGGTGAC-3’	Colgan et al. (1998)
18S rRNA	**28SC1** 5’-ACCCGCTGAATTTAAGCAT-3’	**28SD3** 5’-GACGATCGATTTGCACGTCA-3’	Vonnemann et al. (2005)
28S rRNA	**18S-5’** 5’-CTGGTTGATYCTGCCAGT-3’	**18S1100R** 5’-CTTCGAACCTCTGACTTTCG-3’	Vonnemann et al. (2005), Williams & Reid (2004)

Table 3. Material examined in the PCA analysis including codes represented in Figure 3, specimen voucher number, source of illustrations, and whether it is a fossil or Recent taxon. Species identifications are based on the results of this study, the genera covered are *Julia*, *Candinia*, *Berthelinia*, *Edenttellina*, and *Gougerotia*.

Species	PCA analysis code	Voucher or isolate number	Source of illustration	Fossil (F) or Recent (R)
J. thecaphora	1	NHMLA 1966-19	Present paper	R
J. exquisita	2	NHMLA 1980-193.1	Present paper	R
J. exquisita	3	NHMLA 1980-195.1	Present paper	R
J. exquisita	4	16Mau14	Present paper	R
J. exquisita	5	NHMLA 1985-115	Present paper	R
J. borbonica	6	MNHN-IM-2000-28700	Valdés & Héros (1998)	R
J. japonica	7	CASIZ 067600	Present paper	R
J. zebra	8	MNHN IM-2013-6428	Present paper	R
J. mishimaensis	9	MNHN IM-2013-0095	Present paper	R
J. mishimaensis	10	MNHN IM-2013-5127	Present paper	R
C. krachi	11	–	Bałuk & Jakubowski (1968)	F
C. krachi	12	–	Bałuk & Jakubowski (1968)	F
C. krachi	13	–	Bałuk & Jakubowski (1968)	F
B. elegans elata	14	–	Cossmann (1887)	F
B. elegans	15	–	Crosse (1875)	F
B. elegans	16	–	Crosse & Fischer (1887)	F
B. elegans	17	–	Valdés & Héros (1998)	F
G. orthodonta	18	–	Le Renard (1980)	F
E. typica	19	MV F21539	Present paper	R
E. typica	20	–	Gatliff & Gabriel (1911)	R
E. australis	21	MV F194029	Present paper	R
E. caribbea	22	INB0003321518	Present paper	R
E. pseudochloris	23	16Mau06	Present paper	R
E. babai	24	MV F22716	Present paper	R
E. cf. *rottnesti*	25	MNHN IM-2013-53073	Present paper	R
E. singaporensis	26	JC87B	Present paper	R

Table 4. Comparison of results of the species delimitation analyses and the morphospecies recognized in the study.

<table>
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<tr><th>Morphospecies</th><th colspan="6">COI</th><th colspan="2">16S</th><th colspan="2">COI</th><th colspan="2">16S</th><th colspan="6">COI</th></tr>
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<tr><td><i>E. babai</i></td><td colspan="6"><i>E. babai</i></td><td colspan="2"><i>E. babai</i></td><td colspan="2" rowspan="2"><i>E. babai</i>
<i>E. singaporensis</i></td><td colspan="2"><i>E. babai</i></td><td colspan="6"><i>E. babai</i></td></tr>
<tr><td><i>E. singaporensis</i></td><td colspan="6"><i>E. singaporensis</i></td><td colspan="2"><i>E. singaporensis</i></td><td colspan="2"><i>E. singaporensis</i></td><td colspan="6"><i>E. singaporensis</i></td></tr>
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<tr><td><i>E.</i> cf. <i>rottnesti</i></td><td colspan="6"><i>E.</i> cf. <i>rottnesti</i></td><td colspan="2"><i>E.</i> cf. <i>rottnesti</i></td><td colspan="2"><i>E.</i> cf. <i>rottnesti</i></td><td colspan="2"><i>E.</i> cf. <i>rottnesti</i></td><td colspan="6"><i>E.</i> cf. <i>rottnesti</i></td></tr>
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<i>E. pseudochloris</i></td><td colspan="2" rowspan="2"><i>E. chloris</i>
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<tr><td><i>J. burni</i></td><td colspan="6"><i>J. burni</i></td><td colspan="2"><i>J. burni</i></td><td colspan="2"><i>J. burni</i></td><td><i>J. burni</i></td><td><i>J. burni</i></td><td colspan="6"><i>J. burni</i></td></tr>
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<tr><td><i>J. mishimaensis</i></td><td colspan="3"><i>J. mishimaensis</i></td><td colspan="3"><i>J. mishimaensis</i></td><td colspan="2"><i>J. mishimaensis</i></td><td><i>J. mishimaensis</i></td><td><i>J. mishimaensis</i></td><td><i>J. mishimaensis</i></td><td><i>J. mishimaensis</i></td><td colspan="2"><i>J. mishimaensis</i></td><td colspan="2"><i>J. mishimaensis</i></td><td colspan="2"><i>J. mishimaensis</i></td></tr>
<tr><td><i>J.</i> sp. 2</td><td colspan="6">–</td><td colspan="2"><i>J.</i> sp. 2</td><td colspan="2">–</td><td colspan="2">–</td><td colspan="6">–</td></tr>
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</table>

Table 5. Ecological data on species of Juliidae available in the literature.

Species	Host alga	Number of eggs	Capsule size	Egg size	Protoconch width	Larval shell width	Source
E. australis	*Caulerpa brownii*, *C. simpliciuscula*, *C. scalpelliformis*	50–52			116–118 µm		Burn (1960b, 1989); Wisely (1962)
E. babai	*C. cactoides*, *C. geminata*, *C. scalpelliformis*, *C. sedoides*, *C. simpliciuscula*			90.5 ±2.2 µm		282.1 ± 16.3 µm	Burn (1960b, 1965, 1989); Gascoine & Sartory (1974); present study
E. caribbea	*C. verticillata*	14–100	300 µm	100 µm		~230 µm	Grahame (1969); Davis (1967); Clark & Jensen (1981)
E. chloris	*C. chemnitzia*, *C. sertularioides*						Keen & Smith (1961)
E. corallensis	?						
E. darwini	unidentified *Caulerpa* spp.	45–96	345.6 × 240.2 µm	102.8 ±5.9 µm	~245 µm	~220 µm	Jensen (1997a)
E. limax	*C. okamurae*, *C. racemosa*, *C. serrulata*	11–470	250 × 270–380 µm				Kawaguti & Baba (1959); Kawaguti & Yamasu (1960); Ichikawa 1993
E. pseudochloris	*C. chemnitzia*						Kay (1964)
as *E. fijiensis*	“						
as *E. ganapatii*	*C. racemosa*	500–3520	90 µm	50 µm		90 µm	Sarma (1975)
E. rottnesti	*C. racemosa*, *C. simpliciuscula*		274±17.5 × 203±12.2 µm				Jensen (1993), Williams & Walker (1999)
E. schlumbergeri	*C. racemosa*	–	–	–			Gosliner et al. (2018)
E. singaporensis	*Caulerpa cf. lamourouxii,*	8–108, 200		83 µm		244 ± 12.3 µm	Jensen (2015); Wong & Sigwart (2019); present study

	C. lentillifera, *C. mexicana,* *C. racemosa,* *C. sertularioides,* *C. serrulata,* *C. taxifolia*					
E. typica	*C. brownii,* *C. scalpelliformis*					Burn (1960a, 1965, 1989); Gascoine & Sartory (1974)
E. waltairensis	*C. taxifolia*	–	–	–		Sarma (1975)
J. borbonica	?					
J. burni	?					Sarma (1975)
J. cornuta	?					
J. equatorialis	?					
J. exquisita	?					
J. japonica	*C. ambigua*	>100–2000	100–150 µm	65 µm	200 µm	Kawaguti & Yamasu (1962, 1966)
J. mishimaensis					150 µm	
J. sp.	*C. fastigiata*					Mizofuchi & Yamasu (1987)
J. thecaphora	?					
J. zebra						