ABSTRACT

The genus *Cyerce* Bergh, 1871 has been a model for the study of defensive strategies, including chemical defenses, ceratal autotomy, and crypsis or aposematism. Specialization on different algae and diverse genital armatures also make *Cyerce* a useful system for investigating speciation by host shift versus sexual selection. Here, we review the genus *Cyerce* in the Indo-Pacific using molecular and morphological data. Two mitochondrial genes (CO1, 16S) and one nuclear gene (H3) were sequenced from 154 specimens, including representatives from the Atlantic Ocean. Bayesian and maximum likelihood analyses were used to generate phylogenetic hypotheses. Species delimitation analyses performed on CO1 sequences recovered 17 genetically distinct Pacific and Indian ocean species of *Cyerce*, 10 of which are new to science. Nine new species are named herein (***C. takanoi*** **sp. nov.**, ***C. katiae*** **sp. nov.**, ***C. trowbridgeae*** **sp. nov.**, ***C. blackburnae*** **sp. nov.**, ***C. tutela*** **sp. nov.**, ***C. basi*** **sp. nov.**, ***C. whaapi*** **sp. nov.**, ***C. goodheartae*** **sp. nov.**, and ***C. liliuokalaniae*** **sp. nov.**). The tenth species, from the Red Sea, is not named due to the absence of internal anatomical data. These findings increase the species richness in *Cyerce* by about two-thirds, and demonstrate that even conspicuous taxa harbor considerable cryptic diversity.

Key words: molecular phylogeny; reproductive anatomy; radulae; biodiversity; evolution.

INTRODUCTION

The genus *Cyerce* Bergh, 1871 is considered a monophyletic group of sacoglossan sea slugs in the family Caliphyllidae Tiberi, 1881 (Krug et al., 2022). Species of *Cyerce* are found in the subtropical and tropical regions of the Indo-West Pacific, Eastern Pacific, Caribbean Sea, Mediterranean Sea, and West Africa. *Cyerce* currently includes 8–9 valid species in the Caribbean, Atlantic and Mediterranean (Moreno et al., 2023), and a further 7 valid species from the Indo-Pacific plus several potentially undescribed species (Gosliner et al., 2018). However, the geographic range of individual species varies greatly: *Cyerce elegans* Bergh, 1871 and *Cyerce nigricans* (Pease, 1866) are found throughout large portions of the Indo-West Pacific Ocean, whereas *Cyerce orteai* Valdés & Camacho-García, 2000 and *Cyerce verdensis* Ortea & Templado, 1990 are respectively restricted to portions of the Eastern Pacific and Atlantic (see Valdés & Camacho-García, 2000; Gosliner et al., 2015). Moreover, closely related species of *Cyerce* often occur sympatrically, suggesting factors other than geographic isolation may have played a role in the diversification of this group (Krug et al., 2015; Moreno et al., 2023). Molecular studies of other marine taxa (including sacoglossans) have hypothesized the evolution of sympatric species is influenced by habitat selection and host ecology, and/or sexual selection acting on reproductive systems including armature like penial stylet morphology (Munday et al., 2004; Krug et al., 2016). The diversity of algal hosts and reproductive structures used by *Cyerce* species make this group a useful model system with which to further test hypotheses regarding the drivers of marine biodiversity.

The relationship between host use, chemical defense and behavior remains unclear for species of *Cyerce* but may contribute to the radiation of species complexes. *Cyerce* species biosynthesize polypropionate metabolites that are potent defenses against predation in related sacoglossans (Lin et al., 2023; Li et al. 2023; Scesa et al. 2024), and can autotomize cerata when disturbed (Di Marzo et al., 1991). *Cyerce nigricans* appears to be diurnal (Hay et al., 1989), whereas other species such as *Cyerce elegans* are nocturnal (Rudman, 1999a; Pittman & Fiene, 2003). The aposematic coloration of *C. nigricans* may account for its diurnal behavior, but the polypropionates produced by the slug were not antifeedant to predators in field or lab assays (Cimino & Ghiselin, 1998; Roussis et al., 1989; Gosliner, 2001). *Cyerce cristallina* (Trinchese,

1881) is also aposematic and contains polypropionates (Di Marzo et al., 1991; Marín & Ros, 2004; Moses et al., 2004), but is nocturnal (Rudman, 2003; Ortea et al., 2009). Some species of *Cyerce* are typically found beneath rocks, while others are reported in association with algal hosts from chlorophyte alga genera including *Chlorodesmis* Harvey & Bailey, 1841, *Halimeda* J.V. Lamouroux, 1812, *Udotea* J.V. Lamouroux, 1812, and *Penicillus* Lamarck, 1813 (Thompson, 1977; Kay, 1979; Jensen, 1980; Perrone, 1983; Thompson, 1988; Jensen, 1993b; Händeler & Wägele, 2007; Gosliner et al., 2018). The relationship between coloration, palatability and activity pattern thus requires further study.

Diet specialization has been hypothesized to play a role in endemic radiations of sacoglossans and adaptation to new ecological niches (Krug et al. 2016; Berriman et al. 2018; Krug et al. 2018a,b; Rodriguez & Krug, 2022). Recent work suggested that a radiation of six species of *Cyerce* in the Western Atlantic was driven by ecological drivers such as host specialization acting in concert with sexual selection on penial armature, and reduced dispersal following shifts to short-lived, non-feeding larvae (Moreno et al., 2023). Only one of the six species was recognized before that integrative systematic assessment; if the more species-rich Indo-Pacific harbors a similar proportion of unrecognized species, then the overall diversity of *Cyerce* may be substantially underestimated.

Phylogenetic analyses using molecular and morphological data have been used to reconstruct the evolution of Sacoglossa (Jensen, 1996; Händeler & Wägele, 2007; Christa et al., 2015; Krug et al., 2015; Krug et al., 2022), but a species-level analysis for *Cyerce* is lacking. *Cyerce* have been hypothesized to form a monophyletic group (Christa et al., 2015), but a recent phylogenetic analysis by Krug et al. (2015) placed the monotypic genus *Soghenia* within *Cyerce*, despite differences in external morphology. Moreover, several specimens reported in the literature appear to constitute undescribed species of *Cyerce* (Gosliner et al., 2018), but without a species-level phylogenetic analysis it is not possible to determine whether these constitute new species or color variations of previously named species. A taxonomic revision and phylogenetic reconstruction of *Cyerce* is needed to quantify the species diversity of this group and enable comparative analyses testing alternative models of diversification.

Historically, species of *Cyerce* were classified and described using morphological characters such as features of the cerata, radula, and reproductive system (Jensen, 1996). Based on these traits, some species of *Cyerce* were synonymized despite differing in host ecology. More recently, studies integrating molecular and morphological data recovered nominal species with widespread distributions as complexes of pseudocryptic species that could be differentiated, substantially increasing the biodiversity recognized in many groups (Kienberger et al., 2016; Valdés et al., 2017; Krug et al., 2018b, Medrano et al., 2018). Here, we review the genus *Cyerce* to assess the biodiversity of this group using an integrative approach that incorporates ecological, molecular, and morphological data. A comprehensive literature review was conducted to determine available names and assess the validity of described species of *Cyerce*. Phylogenetic analyses were implemented to determine the evolutionary relationships among species, and four methods of quantitative species delimitation analyses were performed to identify candidate species. The results support the description of nine new species, a significant increase in the global diversity of this genus.

MATERIALS AND METHODS

Source of specimens

Specimens used in this study (*N*=154) were collected and preserved in the field and deposited at the research collections of the Cal State LA; the California State Polytechnic University, Pomona (CPIC); the California Academy of Sciences, San Francisco (CASIZ); the Museum National d'Histoire Naturelle, Paris (MNHN); the Natural History Museum of Los Angeles County (LACM); the Western Australian Museum, Perth (WAM); and the Scripps Institution of Oceanography Benthic Invertebrate Collection, San Diego, California (SIOBIC) (Table 1). Additional information on type specimens was obtained from the Natural History Museum of Denmark, Copenhaguen (NHMD), the Museum of Comparative Zoology, Harvard University (MCZ), the Senckenberg Museum, Frankfurt (SMF), and the Universidad de Costa Rica. Most specimens examined and sequenced were preserved in 70–100% ethanol, but some museum specimens examined were fixed in Bouin's solution or formalin and molecular data could not be obtained for those specimens. Additional sequences of *Cyerce* and other closely related groups were obtained from GenBank (NBCI) and included in phylogenetic analyses (Table 1). Type material of newly described species was deposited at the CASIZ and the MNHN.

DNA extraction, amplification, and sequencing

DNA extractions were conducted using either Chelex 100 Resin (Bio-Rad, Hercules, CA) following the manufacturer's protocol or EZNA Mollusc DNA kits (Omega Bio-Tek, Norcross, GA) also following the manufacturer's protocol, except the tissue lysis step that was extended overnight.

The two mitochondrial genes, cytochrome *c* oxidase I (CO1) and ribosomal RNA (16S), as well as the nuclear gene, Histone H3 (H3) were amplified using universal primers and the polymerase chain reaction (PCR) (Table 2). Each PCR tube contained a total of 50.00 µl, that included: 0.25 µl of 5.00 mg mL^{-1} DreamTaq and 5.00 µl of DreamTaq PCR Buffer (ThermoFischer Scientific, Waltham, MA), 1.00 µl of 40-mM deoxynucleotide triphosphates, 1.00 µl of each primer, 37.25 µl of deionized water, and 2.00 µl of extracted DNA. The reactions were run with the following thermal cycler conditions: 1) CO1 – initial denaturation of 95 °C for 3 min, 35 cycles of 94 °C for 45 sec, 45 °C for 45 sec, 72 °C for 2 min, followed by an elongation step of 10 min at 72 °C; 2) 16S – initial denaturation of 94 °C for 2 min, 30 cycles of 94 °C for 30 sec, 44 °C for 30 sec, 68 °C for 1 min, followed by an elongation step at 68 °C for 7 min; H3 – initial denaturation of 94 °C for 2 min, 30 cycles of 94 °C for 30 sec, 57.2 °C for 30 sec, 68° C for 1 min, followed by an elongation step at 68° C for 7 min. Agarose gel electrophoresis with ethidium bromide was used to verify fragment amplification. PCR products were purified using the ThermoScientific geneJET PCR Purification kit (ThermoFischer Scientific, Waltham, MA) and quantified with a Nanodrop 1000 Spectrophotometer. Purified PCR samples were sent to SourceBioscience (Santa Fe Springs, CA) or Retrogen (San Diego, CA) laboratories for Sanger sequencing. The sequences were assembled and extracted using Geneious 11.1.5 (Kearse et al., 2012). The aligments were conducted using the built in Multiple Sequence Comparison by Log Expectation (MUSCLE) (Edgar, 2004) implemented in Geneious 11.1.5, with default parameters.

Phylogenetic Analyses

Phylogenetic analyses were conducted using Bayesian Inference (BI) and Maximum Likelihood (ML) methods, using a concatenated alignment of all three genes (1,459 bp) for 165 ingroup taxa. *Costasiella ocellifera* (Simroth, 1895) was included as an outgroup based on recent phylogenomic analyses of 1,160 genes in which *Cyerce* was not recovered within its traditional family Caliphyllidae but was the basal lineage in clade Limapontioidea (Krug et al., 2022). GenBank sequences for *Sohgenia palauensis* and *Sohgenia* sp. 1 were also included in our analyses, based on prior work that recovered *Cyerce* paraphyletic with respect to *Sohgenia* despite morphological differences between the two groups (Krug et al., 2015). For ML analysis, RAxML 8.0 (Stamatakis, 2014) was implemented on the CIPRES web platform (Miller et al., 2012), with the optimum number of bootstrap pseudoreplicates determined by the program during the run. A GTR + Γ model was separately parametrized for each gene partition, and for the 3rd codon position versus the 1st + 2nd codon positions of both protein-coding genes (COI, H3). Bootstrap values (BS) ≥70% were considered significant support (Hillis & Bull, 1993).

Bayesian Inference (BI) analyses were conducted with *BayesPhylogenies* (Pagel & Meade, 2004), implementing a mixture model to assign the best-fit of three GTR + Γ models to each nucleotide position in the concatenated alignment. Four replicate runs were performed of one Markov chain apiece; each run was ended after 2×10^7 generations, printing trees every 5×10^3 generations. Stationarity and convergence were assessed from plots visualized with Tracer v1.7 (Rambaut et al., 2018). The last 20% of the tree sample from each run was pooled and a 50% majority-rule consensus tree with mean branch lengths generated using *BayesTrees* (http://www.evolution.reading.ac.uk). Posterior probability (Pp) of nodes was determined from the combined tree sample, taking support values ≥90% as significant (Huelsenbeck & Rannala, 2004).

Species Delimitation Analyses

Four methods of species delimitation were used to analyze a dataset comprising 138 COI haplotypes obtained from *Cyerce* and *Sohgenia* specimens. First, Automated Barcode Gap Discovery (ABGD; Puillandre et al., 2012) was performed on a matrix of pairwise TrN distances uploaded to the ABGD webtool (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html). Analyses used initial values of pmin = 0.001, pmax = 0.1, and a modified minimum relative gap width <1.3 based on results for the *C. antillensis* complex (Moreno et al., 2023). Second, the matrix of TrN distances were analyzed using the web implementation of the ASAP procedure (Puillandre et al., 2021; https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html).

Third, the General Mixed Yule-Coalescent model (GMYC; Pons et al., 2006; Fujisawa & Barraclough, 2013) was used to analyze an ultrametric COI gene tree. Using BEAST2 (Bouckaert et al., 2014), an ultrametric input tree was generated from COI haplotypes under relaxed clock (log normal) and constant-size coalescent model as priors, and a GTR + Γ model with four rate categories. After 10^7 generations, 20% was discarded as burn-in based on Tracer plot inspection, and a consensus tree was then generated in TreeAnnotator. The ultrametric tree was evaluated in the R package SPLITS (Ezard et al., 2009) using a single-threshold model to estimate the transition from among- to within-species branching. The number of candidate species was estimated under a 95% confidence interval, and the ML score for delimited species compared to a null model (all one species) by likelihood ratio test. The experimental multiple-threshold model was also evaluated as an alternative parameterization of the GMYC analysis and returned a highly similar but less significant result compared to the single-threshold model (29 instead of 27 species entities; see Results); we therefore report the results of the single-threshold model, as recommended. Gene trees generated using a Yule model instead of a constant-size coalescent model as the prior also yielded much less significant results and lumped pairs of morphologically distinct species, so the coalescent model was considered appropriate for guide tree inference on this dataset.

Fourth, the Bayesian implementation of the Poisson Tree Processes (bPTP) algorithm was used to analyze a COI guide tree (Zhang et al., 2013). A COI tree rooted on the outgroup taxon 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/), the outgroup removed, and an MCMC analysis run for 5×10^5 generations, discarding 25% as burnin. The acceptance rate was 0.12. Outputs of both ML and BI partitions were examined to assess support for all species (see Results).

Morphology

The external morphology of 1–4 specimens for each species, depending on availability and quality of specimens, was examined (Table 1). Photographs of the live animals were used for species descriptions and were compared to one another to identify morphological traits characteristic of each species. The buccal mass was removed from the anterior portion of the head and placed in 10% sodium hydroxide (NaOH) for 1–3 days to remove any soft tissue surrounding the radula. The radula was then rinsed with distilled water to remove the NaOH. If tissue was not completely dissolved, the buccal mass was incubated in 200 µl of TL buffer with 25 µl of proteinase K at 56 °C overnight, and any remaining tissue removed manually; then the radula was rinsed with distilled water, mounted on a stub and sputter coated with either gold or gold/palladium for examination under a variable pressure scanning electron microscope (SEM), either a Hitachi SU3500 (California Academy of Sciences, San Francisco) or a Jeol JSM-6010 (California Polytechnic State University, Pomona) model.

The male copulatory organ (penis) was dissected from the specimens examined and placed in an acid fuchsin stain solution in 70% ethanol for approximately 15 seconds until the tissue turned pink. Then each penis was subjected a series of dehydration steps in 95% and 100% ethanol. Finally, the penis was placed in xylene for clearing before being mounted with mounting medium on a microscope slide and photographed under a Nikon Eclipse E400 compound microscope.

RESULTS

Species Delimitation Analysis

All four methods of species delimitation generally supported the same 27 species entities (Fig. 1A-C, Table 3). There were only two minor differences among methods. The highest ranking ASAP partition lumped *C. pavonina* with a lineage from Papua New Guinea (*Cyerce goodheartae* sp. nov.) but the other three methods all separated *C. pavonina* as a distinct species (Fig. 1B). bPTP split the two *Cyerce liliuokalaniae* sp. nov. specimens as distinct entities, but the other three methods all lumped them as conspecific. The less favored GMYC multiple thresholds model split geographic isolates of two widely sampled species, *C. antillensis* and *C.*

bourbonica, presumably detecting phylogeographic structure rather than species boundaries compared to the more conservative single-thresholds model. All four methods supported six species in the *C. antillensis* complex as were distinguished in a recent integrative analysis (Fig. 1C).

Notably, all methods also split nominal "*Cyerce nigricans*" into two OTUs: one candidate species was sampled only from New Caledonia, whereas the other was sampled from the Indian Ocean coast of Africa as well as from the Great Barrier Reef, Australia (GenBank accession number DQ237995) (Fig. 1A). All methods also supported four species entities among specimens provisionally identified as "*Cyerce elegans*": one from the Red Sea; one from the Philippines; and two distributed more widely, including the Philippines and New Caledonia (Fig. 1B). Outside of the *C. elegans* and *C. nigricans* complexes, species delimitation supported six additional undescribed species of *Cyerce* that were genetically and morphologically distinct from named taxa, as well as one undescribed species of *Sohgenia* distinct from *S. palauensis*.

Phylogenetic Analyses

Phylogenetic analyses of the concatenated three-gene alignment recovered the 27 lineages of *Cyerce* and *Sohgenia* distinguished by species delimitation, although deeper relationships were not well resolved by the analyses in this study, which focused on species discovery and delimitation (Fig. 1). *Sohgenia* sp. 1 and *S. paluaensis* were recovered as sister taxa (BS=100%) nesting within *Cyerce*. Sister to this lineage but without significant support was a clade supported by BI analysis (Pp=0.98) that included several species with bright orange stripes and spots on different faces of black cerata (Fig. 1A). Within this clade, *C. nigra* was sister to a subclade of three species (Pp=0.99), comprising a lineage sampled once from the Philippines (*Cyerce katiae* sp. nov.) recovered as sister to a nested subclade (Pp=0.99) in which *C. nigricans* and *C.* cf. *nigricans* were sister species.

Both BI and ML analyses supported a second major clade of species (BS=100%) with ornately colored cerata from the Indo-West Pacific, which formed two well supported subclades (Fig. 1A). The first subclade (BS= 100%) comprised two sister species: specimens from Western Australia (*Cyerce tutela* sp. nov.), and a widely distributed lineage of morphologically similar specimens (*Cyerce blackburnae* sp. nov.) from the West Pacific including the Philippines, Guam and New Caledonia. The second subclade (BS= 97%) comprised sister taxa *C. bourbonica*, sampled widely across the West Pacific including the Philippines, Bali, Maui, and Australia, and candidate species *Cyerce trowbridgeae* sp. nov. from the Marshall Islands (Fig. 1A).

All remaining *Cyerce* specimens formed a clade in BI analyses (Pp=0.99), within which one major subclade including all Indo-Pacific taxa (Pp=0.98) was sister to the *C. antillensis* complex of six Caribbean species (BS=96%). Within the larger radiation, one unsupported subclade included many species with inflated, transparent cerata. Four pseudocryptic lineages within the *C. elegans* complex formed a clade (BS= 100%) within which Red Sea specimens were sister to the remaining three candidate species (BS=94%) (Fig. 1B). Candidate species *C. basi* sp. nov., sampled from the Philippines, Vanuatu and New Caledonia, was sister to the remaining two species (BS=98%). Sister to the *C. elegans* complex was a weakly supported clade within which *C. pavonina* was sister to *Cyerce goodheartae* sp. nov. from the Philippines (BS=100%), and candidate species *Cyerce liliuokalaniae* sp. nov. from Hawai'i was sister to *C. orteai* from the East Pacific but with weak support. The remaining complex included species with vibrant, magenta-edged cerata: *C. graeca* from the Mediterranean; *C. kikatarubabai* from the West Pacific; and *C.* cf. *cristallina*, sampled from the Caribbean but known also from the Mediterranean (Fig. 1B); relationships within this group were not well resolved.

Lastly, the *C. antillensis* complex of six species from the Western Atlantic formed a clade (BS= 96%) in which *C. antillensis* was sister to a clade (BS=100%) comprising five recently described species (Supplemental Fig. 1). Within that lineage, *C. piercei* was sister to the remaining species which formed a polytomy of three lineages: a Jamaica endemic (*C. ellingsonorum*); a widely distributed Caribbean species (*C. nicholasi*); and two endemic species supported as sister taxa (BS= 86%, BI=0.90), *C. willetteorum* from the Bahamas and *C. browneveorum* from the Florida Keys (Supplemental Fig. 1).

Morphological Analyses

There were consistent external morphological differences between most clades/candidate species of *Cyerce* recovered by phylogenetic and species delimitation analyses. Internal morphology was also distinct among candidate species with reproductive and radular morphology revealing diagnostic differences. Specimens for which GenBank sequences were used for molecular analyses were not examined morphologically (Table 1).

SYSTEMATICS

In this section the taxonomic status of *Cyerce* and the species recognized in the present paper are discussed. External and internal descriptions are provided for each species. The species are arranged chronologically within the main clades recovered in the phylogenetic analyses and indicated in Figure 1.

Family Caliphyllidae Tiberi, 1881

Genus *Cyerce* Bergh, 1871

Cyerce Bergh, 1871: 98. Type species: *Cyerce elegans* Bergh, 1871, by subsequent designation by Swennen (1961).

Lobiancoia Trinchese, 1881: 116. Type species: *Lobiancoia cristallina* Trinchese, 1881 [=*Cyerce cristallina* (Trinchese, 1881)], by monotypy.

Diagnosis

Foot bifurcated with transverse groove. Body oval, wider anteriorly, tapering posteriorly. Pericardium elevated, oval, papillate or smooth. Anal papillae antero-medially situated between right rhinophore and pericardium. Head with bifurcated rhinophores, and ventral, enrolled oral tentacles shorter than rhinophores. Eyespots at base of rhinophores. Several dorsal leaf-like cerata along both sides of body, lacking tubules of the digestive gland; cerata able to autotomize and regenerate. Cerata morphology variable, from bold to light coloration. Pharyngeal pouch attached to buccal bulb, variable in size. Radula with single row of teeth, constituting a descending and ascending limb, ascus at the base of descending limb. Ascus with several pre-radular teeth of variable sizes. Radular teeth smooth, wide base. Radular teeth morphology variable from elongate and slim to short and moderately wide. Teeth with two rows of denticles along either side. Penis with stylet at opening.

Remarks

Bergh (1871) introduced the genus *Cyerce* for the new species *Cyerce nigra* Bergh, 1871 and *Cyerce elegans* Bergh, 1871, both collected from Palau. Bergh (1871) did not specify the type species, but Swennen (1961) indicated that *C. elegans* is the type, and with this act *C. elegans* became the type by subsequent designation. Bergh (1871) introduced the genus *Cyerce* to describe specimens with a dorsal anus, armed penis, short 'crop' [pharynx], elongated oral teeth, a foot with a transverse groove, and cerata without 'tubules' [branches] of the digestive gland. A few years earlier, Pease (1866) had described the new species *Lobifera nigricans* (Pease, 1866) from the Pacific Islands, which resembles the specimen of *Cyerce nigra* described by Bergh, (1871) but displays some differences. The genus name *Lobifera*, also described by Pease (1866), is an unnecessary replacement name for *Polybranchia* Pease, 1860 (see Swennen, 1961 and Medrano et al., 2019). Although the description of *Lobifera nigricans* by Pease (1866) was short and lacking details of the internal anatomy, external morphological traits such as the presence of a transverse groove across the foot and the presence of fan-like cerata suggests this species belongs to *Cyerce*. Comparisons of the external morphology of *Cyerce nigricans* Pease, 1866 and *Cyerce nigra* Bergh, 1871 are further elaborated under the remarks of *Cyerce nigricans* Pease, 1866 (see below).

Trinchese (1881) introduced the genus *Lobiancoia* for the new species, *Lobiancoia cristallina* collected from the Mediterranean Sea. Trinchese (1881) described *Lobiancoia cristallina* as having bifid rhinophores, head angled with 'auriform tentacles', a transverse groove dividing the foot, compressed dorsal papillae along both sides of the animal without 'lobes of the liver' or 'cnidosacs', and an anal papilla located to the right and front of the pericardial hump. Pelseneer (1892) reported for the first time the genus *Cyerce* from the Mediterranean Sea with the description of the new species *Cyerce jheringi* Pelseneer, 1892. Pruvot-Fol (1954) regarded *Lobiancoia* as a valid genus, different from *Cyerce* which she considered a synonym of *Lobifera*. Portmann (1958) studied a specimen from the Mediterranean Sea he identified as *L. cristallina* and suggested that *C. jheringi* and *L. cristallina* belonged to the same species, effectively synonymizing *Lobiancoia* with *Cyerce*. However, Portmann (1958) maintained this species in the genus *Lobifera*, following the taxonomic revision by Pruvot-Fol (1954). Swennen (1961) clarified the taxonomic position of *Lobifera* as a synonym of *Polybranchia* and corroborated the synonymy of *Lobiancoia* with *Cyerce*, which is widely accepted in modern literature. Moreover, the monophyly of *Cyerce* has been supported by morphological (Jensen, 1996) and some molecular (Christa et al., 2015) studies. Other molecular studies that included the closely related genus *Sohgenia* (which lacks a transverse foot groove) did not resolve whether *Cyerce* was monophyletic (Krug et al., 2015). Here, *Cyerce* Bergh, 1871 is regarded as a valid name for species of Sacoglossa with a transverse groove ventrally along the foot, anal papillae antero-medially between the right rhinophore and pericardium, bifurcated rhinophores, enrolled oral tentacles, cerata without tubules of the digestive gland, and a penis with a penial stylet.

Clade 1

Cyerce nigricans (Pease, 1866)

(Figs. 2A–B, 3, 4A)

Lobifera nigricans Pease, 1866: 206–207. Type locality: Pacific Islands.

Cyerce nigra Bergh, 1871: 113–118 [in part], pl. 16, figs. 23, 26–28. Type locality: Palau.

Cyerce nigra var. ocellata Bergh, 1873: 155–158 [83–86], pl. 9, figs. 8–9, pl. 11, figs. 13–26, pl. 12, figs 2–3. Type locality: Samoa.

Type material

Lobifera nigricans Pease, 1866 – no type material known to exist, not found at MCZ.

Cyerce nigra Bergh, 1871 – holotype at NHMD (GAS-002150), Palau, Jun 1862, not examined.

Cyerce nigra var. *ocellata* Bergh, 1873 – no type material known to exist, it was originally deposited at the Museum Godeffroy, and probably destroyed during WWII (see Bieler & Petit, 2012).

Material examined

Heron Island, Queensland, Australia, 13 Dec 1984, 17 m depth, leg. T. Gosliner, 1 specimen 20 mm preserved length (CASIZ 071449). Pandane Beach, Jangamo, Inhambane Province,

Mozambique, 6 Feb 2008, 0–1.5 m depth, leg. M. Pola & J. Reis, 1 specimen 12 mm preserved length (Isolate MM72, CASIZ 176993); 1 specimen 14 mm preserved length (Isolate MM73, CASIZ 176994); 1 specimen 7 mm preserved length (Isolate MM74, CASIZ 176995).
Pointe Evatra, Toliara, Madagascar, 30 Apr–6 May 2010, 38 m depth, leg. Atimo Vatae, South Madagascar Expedition, 1 specimen (Isolate MM93, CASIZ 194048); 1 specimen 15 mm preserved length (Isolate MM94, CASIZ 194049); 1 specimen (CASIZ 194083).

Range

Widespread in the Indian and Western Pacific oceans (Rudman, 1999c; Nimbs & Smith, 2016; Nakano, 2018; Gosliner et al., 2018; present study).

Description

External morphology. – Body color black, with light banding running along both sides; black line down the middle of the body (Fig. 2A–B). Pericardium oval, elevated, spotted with black. Head black with orange band running down medially between eyes. Rhinophores black, outlined with approximately two orange striations across. Tentacles black with similar pattern to rhinophores. Cerata inflated, fan shaped, black, covered with elevated orange-yellow dots on both sides. Cerata margin outlined by white band. Orange band situated infra-marginally of cerata.

Internal morphology. – Buccal mass about 5 mm in length, buccal bulb and pharyngeal pouch similar in size. Radula with 24 teeth in a 15-mm preserved length specimen (CASIZ 194049). Radular teeth moderately narrow, with wide bases, and sharp tips (Fig. 3A). Tips with small, sharp projections, located medially between first pair of denticles. Approximately two rows of 15 denticles along either side of tooth (Fig. 3B). Denticles recurved, triangle shaped. Denticle size varies along tooth, smaller near base, larger towards middle of tooth, smaller at tip. Ascus with about 25 pre-radular teeth (Fig. 3C). Penis surrounded by thick dark tissue. Penial stylet at opening of penis, about 200 µm (Fig. 4A). Penial stylet cylindrical, straight, hollow with oval opening, pointed triangular tip; wide base.

Ecology

Feeds on the green algae *Chlorodesmis* spp. (Gosliner et al., 2018), typically diurnal.

Remarks

Pease (1866) originally described *Lobifera nigricans* Pease, 1866 based on an undermined number of specimens collected from the "Pacific Islands" (no specific locality was provided). Pease (1866) did not include details of the internal morphology; thus, it is not possible compare the anatomy of the original specimen/s to that of similar specimens subsequently described by Bergh (1871, 1873), or the specimens examined herein and assigned to this species. Pease (1866) described *L. nigricans* as being deep velvet black in color, having cerata with a yellow infra-marginal band and covered with yellow dots, which is consistent with the modern usage of the name (Rudman, 1999c; Gosliner et al., 2018). Bergh (1876) regarded the genus *Lobifera* as "partially identical" to *Cyerce* and for the first time treated *L. nigricans* as a member of *Cyerce*.

Bergh (1871) described the new species *Cyerce nigra* Bergh, 1871 based on a single specimen collected from Palau. Bergh (1871) indicated that the specimen, which was illustrated alive by [Carl Gottfried] Semper [color drawing reproduced by Bergh, 1871: pl. 1, fig. 10 and herein (Fig. 5A–B)] was hardened due to preservation, and the internal organs were accidentally lost while "being softened in aqueous fluid." Bergh (1871) also indicated there was a second specimen belonging to a different "form" also from Palau, which was examined in the field by Semper. Semper made drawings of the radula and the penis of this second specimen [also reproduced by Bergh, 1871: pl. 16, fig. 23, and Bergh, 1871: pl. 16, figs. 26–28, respectively]. Bergh (1871) provided a comprehensive description of the external morphology of the first specimen (holotype), which is currently deposited at the NHMD (GAS-002150) and it is consistent with the current usage of the name *C. nigra* (Rudman, 1999b; Nakano, 2018; Gosliner et al., 2018). For example, Bergh (1871) mentioned that the dorsum of the specimen was back and the cerata were also black above, with a yellow border, yellow spots, and numerous black transverse stripes. Two years later Bergh (1873) re-emphasized the fact that the two specimens collected by Semper in Palau belong to different species, and that the animal that was examined more closely by Semper deviated from the typical *C. nigra* by showing only a few yellow spots on the black cerata, instead of the yellow stripes typical of *C. nigra*. Bergh (1873) examined a third specimen collected from Samoa that according to him was consistent morphologically with the animal examined by Semper in the field and deposited at the Museum Godeffroy. Bergh (1873) described this latter specimen under the new name *Cyerce nigra* var. *ocellata* Bergh, 1873 and reproduced the original drawing of the live animal by Semper (Bergh, 1873: pl. 9, figs. 8–9) and reproduced herein (Fig. 5A–B), which is consistent with the modern usage of the name *C. nigricans* (see Rudman, 1999c; Gosliner et al., 2018). Moreover, the illustrations of the male reproductive system made by Semper, reproduced by Bergh (1871: pl. 16, figs. 26–28), show a short penial stylet with an oval opening and pointed tip; the penial stylet of this specimen closely resembles the specimens of *C. nigricans* here examined. On the contrary, the penial stylet of the specimens of *Cyerce nigra* studied herein is long and curved with a pointed tip (see description of *C. nigra* below). Thus, the specimen examined by Semper in the field clearly belongs to *C. nigricans* as well as the animal from the Museum Godeffroy (Hamburg) that Bergh (1873) described as *Cyerce nigra* var. *ocellata*. This was later confirmed by Bergh (1876), who mentioned that [Andrew] Garrett received one of Pease's specimens of *C. nigricans* for examination and verified it was the same species as *Cyerce nigra* var. *ocellata*. Bergh (1876: pl. 10, figs. 10–11) also illustrated the penis of the specimen of *Cyerce nigra* var. *ocellata*, which is also short and straight, consistent with the drawings by Semper and different from the true *C. nigra*.

Specimens from Lizard and Eagle islands (Australia) identified as *Cyerce nigricans* by Klussman & Dinapoli (2006) and Händeler & Wägele (2007) were recovered as members of this species (Fig. 1). Moreover, images of live specimens identified as *C. nigricans* obtained from the Lizard Island research station of Australia, closely resemble our specimens of *Cyerce nigricans* from the Indian Ocean (see Australian Museum Lizard Island Research Station, 2022) confirming they are cospecific. However, phylogenetic analyses recovered two specimens from New Caledonia originally identified as *C. nigricans* in a distinct clade, named *Cyerce takanoi* sp. nov. herein (Fig. 1A). The species delimitation analyses further supported this clade as a distinct candidate species (Table 3). Morphological examination of specimens of *C. takanoi* sp. nov. and *C. nigricans* reveal these species share several external morphological traits such as the black cerata with orange spots and yellow-orange band along the margin. However, the color pattern of the head of *C. takanoi* sp. nov. differs from the pattern observed in *C. nigricans,* which has a medial orange line along the head of the animal (consistent with the original description), whereas *C.*

takanoi sp. nov. has two orange transverse patches on the head. Also, the presence of scattered orange spots along the margin of the rhinophores of *C. takanoi* sp. nov. rather than a solid orange line in *C. nigricans* seems like a distinction. Moreover, Bergh (1873) mentioned and illustrated yellow longitudinal striations along the body of *Cyerce nigra* var. *ocellata* [= *C. nigricans*] (Figs. 5A–B), which are present in the specimens here examined but are absent in *C. takanoi* sp. nov.

Cyerce nigra Bergh, 1871

(Figs. 2C–D, 4B, 6)

Cyerce nigra Bergh, 1871: 113–118 [in part], pl. 1, fig. 10, pl. 16, figs. 1–22, 24–25. Type locality: Palau.

Type material

Cyerce nigra – holotype at NHMD (GAS-002150), Palau, Jun 1862, not examined.

Material examined

Inner side of Tabat Island, North of Nagada Harbor, near Madang, 11 Aug 1990, 1 specimen, leg. T. Gosliner & D. Mack (CASIZ 75866). Kanaman, Madang Province, Papua New Guinea, 13 Nov 2012, leg. H.H. Tan, 5 specimens 11 mm preserved length (Isolates MM84A–E, CASIZ 191170). Madang Province, Papua New Guinea, 3 Dec 2012, leg. C.-W. Lin, 1 specimen 2 mm preserved length (Isolate MM91, CASIZ 191510). Guam, 2001, 1 specimen (Isolate 09Gua01, LACM pending); Sep 2007, 1 specimen 10 mm preserved length (Isolate 09Gua07, LACM pending); 20 Jun 2009, 1 specimen 2 mm preserved length (Isolate MM110, CPIC 00624).

Range

Western Pacific Ocean (Wells & Bryce, 1993; Rudman, 1999c; Nakano, 2018; Gosliner et al., 2018; present study).

Description

External morphology. – Body color black, with scattered orange spots, outlined with orange-yellow band along margin (Fig. 2C–D). Pericardium oval, black, slightly elevated. Head orange with black line running medially between eyes. Eyes covered by thick dermal tissue. Approximately 2–3 black lines from eyes extending to rhinophores. Rhinophores long, pointed; color semi-translucent with orange patching, speckled with minute white dots; longitudinal black line running length of rhinophores. Forehead outlined with alternating orange and black transverse striations. Tentacles with similar pattern as rhinophores. Cerata inflated, fan shaped, semi-translucent black; one side of each ceras with scattered elevated orange-yellow spots; opposite side with horizontal black striations and minute white to fluorescent green specks forming striations. Both sides of cerata with infra-marginal light orange band, covering several scattered white specks. Ceratal margin outlined by black band. Foot dorsally outlined with orange-yellow band.

Internal morphology. – Buccal mass about 2 mm in length, buccal bulb and pharyngeal pouch similar in size. Radula with 17 teeth in a 2-mm preserved length specimen (CASIZ 191510); 9 teeth on descending limb, 8 teeth on ascending limb (Fig. 6A). Radular teeth moderately narrow, smooth, with wide bases, sharp tips. Leading tooth about 20 µm in length, with approximately two rows of 9 denticles along either side of tooth (Fig. 6B). Denticles rhomboidal shape, some blunt; varying in size along tooth, becoming larger towards tip. Ascus with about 11 pre-radular teeth (Fig. 6C). Penis covered with tissue, with penial stylet at opening, about 200 µm in length (Fig. 4B). Penial stylet cylindrical, thin, curved, hollow with oval opening; pointed triangular tip.

Ecology

Feeds on the green algae *Udotea geppiorum* Yamada, 1930 and potentially other *Udotea* spp. (Gosliner et al., 2018; present study)

Reproduction

Development of specimens in Guam was planktotrophic. Egg masses lacked extra-capsular yolk reserved. One clutch had a mean egg diameter of 57.2 µm ± 1.6 SE (*N*=18). Larval shell size was measured across the aperture to estimate mean size for two clutches at hatching; mean larval shell width was 126.2 µm ± 5.7 SE (*N*=25) for one egg mass, and 132.5 µm ± 3.6 SE (*N*=25) for a second egg mass.

Remarks

Phylogenetic analyses recovered *Cyerce nigra* as a monophyletic group represented in the Western Pacific (Fig. 1), also supported by all methods of species delimitation analyses (Table 3). *Cyerce nigra* was recovered within a clade containing *C. nigricans* and other black and yellow species, but anatomically *C. nigra* shares a long, curved penial stylet with several species from clade 2 such as *Cyerce blackburnae* sp. nov., *Cyerce tutela* sp. nov., and *Cyerce trowbridgeae* sp. nov.

Bergh's (1871) original description of *Cyerce nigra* was based on a single specimen collected in Palau and illustrated alive by Semper; the color drawing was later reproduced by Bergh (1871: pl. 1, fig. 10) and herein (Fig. 5C). Bergh (1871) also illustrated some anatomical traits of a second specimen examined by Semper, which most likely belongs to *C. nigricans* (see above). The current usage of the name *C. nigra* in the literature (Rudman, 1999b; Nakano, 2018; Gosliner et al., 2018) is consistent with the original description and the specimens examined herein. For example, Bergh (1871) mentioned the presence of an infra-marginal yellow band, orange yellow spots on one side and black horizontal stripes on the opposite side of the cerata, both present in the specimens here examined. Bergh (1871) also mentioned the presence of several yellow transverse bands on the forehead of *C. nigra* similarly seen in our specimens. All evidence supports the material studied herein as *C. nigra*.

Specimens of *C. nigra* have been collected from, and observed to feed on, *Udotea* spp. However, DNA barcoding identified several green algal plastids excluding *Udotea* within *C. nigra* (Christa et al. 2014b), including specimens we recovered within *C. nigra* in our analyses (Fig. 1A). This raises the possibility that *C. nigra* has a broader host range but all of our collections and other reports to date confirm an association with *Udotea* (Gosliner et al. 2018). Methodological concerns over how accurately the barcoding approach used by Christa et al. (2014b) can identify ecologically relevant host algae for sacoglossans have been previously noted (Krug et al., 2016; Moreno et al., 2023).

Cyerce takanoi sp. nov.

(Figs. 2E, 7)

Type material

Holotype: Pouebo, New Caledonia, 23 Sep 2018, 1.5 mm preserved length (Isolate AV487, MNHN IM-2013-86235).

Other material examined

Pouebo, New Caledonia, 23 Sep 2018, 1 specimen 2 mm preserved length (Isolate AV484, MNHN IM-2013-86234).

Range

New Caledonia (present study).

Description

External morphology. – Body color olive green to black. Pericardium elevated, oval, light orange with white speckling (Fig. 2E). Head light grey, with black Y-shaped band extending from base of head to rhinophoral tips; two dark orange patches along sides of head, another at forehead. Rhinophores long, dark grey to black with two striations formed by green to fluorescent orange dots. Tentacles with similar pattern as rhinophores. Cerata inflated, fan-shaped, black, scattered with few elevated bright orange spots; few white and fluorescent speckling. Cerata sub-marginally outlined with red-orange to bright orange band on both sides; sub-marginal band covering several small white clusters. Cerata margin outlined with white band and several minute white specks; bordered by two black bands. Foot wider than body. Dorsally, foot black with greyish margin; margin with white speckling. Posterior end of foot extends further than body, pointed.

Internal morphology. – Radula with 10 teeth in a 2-mm preserved length specimen (MNHN IM-2013-86234); 5 teeth on descending limb, 5 teeth on ascending limb (Fig. 7A). Radular teeth moderately elongate with rounded tips. Leading tooth about 120 µm in length, with approximately two rows of 8 denticles visible along either side of tooth (Fig. 7B). Denticles recurved, triangular in shape; all about same size (those visible). Ascus not observed. Penis not observed.

Ecology

Specimens found in association with the green algae *Chlorodesmis* spp.

Etymology

This species is named in honor of Tsuyoshi Takano who collected the algae in which this species was found and in appreciation for his help and friendship to AV during the Koumac expeditions.

Remarks

Specimens of *Cyerce takanoi* sp. nov. from New Caledonia were originally identified as *C. nigricans*. However, these specimens were distinct from *C. nigricans* in all species delimitation methods (Fig. 1A). As noted, *C. takanoi* sp. nov. and *C. nigricans* share similar external morphological characteristics such as having black cerata with elevated orange spots, an infra-marginal yellow-orange band on the cerata, and white band outlining the margin of the cerata. However, the head pattern is different between these two species: *C. nigricans* has a bold medial vertical orange band on the head with two bold orange striations extending across the rhinophores, traits not observed in *C. takanoi* sp. nov. Bergh (1873) also described yellow longitudinal striations along the dorsum of the holotype, observed in our specimens of *C. nigricans* but not in *C. takanoi* sp. nov. The radula of *Cyerce takanoi* sp. nov. is very similar to that of *C. nigricans* but the teeth are considerably smaller. The number of teeth was not considered directly comparable due to the size differences of the specimens examined.

Cyerce katiae sp. nov.

(Figs. 2F, 4C, 8)

Cyerce sp. 4 – Gosliner et al., 2018: 402; Nakano, 2018: 119.

Type material

Holotype: House reef, 3P Resort, Romblon Province, Philippines, 12 mm preserved length, isolate KM28 (CASIZ 222096).

Range

West Pacific Ocean (Gosliner et al., 2018; Nakano, 2018; present paper).

Description

External morphology. – Body color light grey to cream, with dark grey lines creating geometric pattern throughout dorsum (Fig. 2F). Head color light grey with dark grey web-like striations throughout; two gold patches near base; small gold spots at forehead. Rhinophores long, bifurcated with minute white specks scattered along margins, translucent light grey. Oral tentacles with similar color pattern to rhinophores, ventrally located. Pericardium near center of dorsum, with anal papilla located anteriorly. Cerata lobate, inflated, translucent light grey with dark grey web-like striations forming polygons; silvery small white pustules at center of each grey polygon and clustered near the margins of cerata; small gold to dark yellow spots randomly scattered across surface. Cerata increase in size towards posterior end of body; anterior-most cerata lack grey lines. Cerata margin outlined with grey margin and gold spots; conspicuous (probably defensive) glands beneath margin.

Internal morphology. – Buccal mass about 2 mm in length, buccal bulb and pharyngeal pouch similar in size. Radula with 16 teeth in a 12-mm preserved length specimen (CASIZ 222096); 8 on descending limb, 8 on ascending limb (Fig. 8A). Teeth elongate, nearly straight, slightly bent, with approximately two rows of nine denticles along either side of tooth (Fig. 8B). Denticles nearly square, curved inwards, with pointed ends. Ascus with about 18 pre-radular teeth (Fig. 8C). Penial opening directly beneath right rhinophore. Penis with penial stylet at opening (Fig. 4C). Penial stylet hollow, approximately 400 µm long, elongate, slightly curved near the apex, wider at the base.

Ecology

Diet unknown.

Etymology

This species is named in honor of Kati Eschweiler who first found this species in Romblon and brought it to the attention of TG.

Remarks

All methods of species delimitation and phylogenetic analyses supported *Cyerce katiae* sp. nov. as a distinct candidate species (Fig. 1A, Table 3). *Cyerce katiae* sp. nov. was recovered as sister to a clade comprising *C. nigricans* and *C. takanoi* sp. nov. (Fig. 1) and shares with *C. nigricans* and *C. takanoi* sp. nov. yellow gold spots scattered across the cerata. Internally, specimens of *C. takanoi* sp. nov. have different radular teeth from those of *C. katiae* sp. nov. The tip of the teeth cusps in *C. takanoi* sp. nov. are rounded, whereas they are pointed in *C. katiae* sp. nov. Moreover the teeth of *C. takanoi* sp. nov. are much longer and fewer in number than in *C. katiae* sp. nov. Externally, *C. takanoi* sp. nov. and *C. katiae* sp. nov. are also distinct; the cerata of *C. takanoi* sp. nov. are black with an orange inframarginal band and a white marginal band, whereas the cerata of *C. katiae* sp. nov. are translucent grey lacking the orange and white bands but instead having a grey margin and gold spots.

Cyerce katiae sp. nov. is also internally and externally morphologically distinct from *C. nigricans*; the cerata of *C. nigricans* are black with a yellow-orange inframarginal band and a white band along the margin, differing from *C. katiae* sp. nov. The penial stylet in *C. katiae* sp. nov. is wider at the base, slightly curved, with a blunted tip, whereas the penial stylet in *C. nigricans* is straight with a pointed triangular tip. The radular morphology of *C. katiae* sp. nov. also differs from that of *C. nigricans*, as the tooth cusps are flatter with denticles that have a wider edge than the base; the denticles are also more square-shaped in *C. katiae* sp. nov. than in *C. nigricans*, which are more triangular. The cerata of *C. katiae* sp. nov. are more oval than the fan-shaped cerata observed in *C. nigricans* and *C. takanoi* sp. nov. Lastly, the head of *C. katiae* sp. nov. does not have any of the orange-yellow banding across the rhinophores or head as observed in *C. nigricans* or in *C. takanoi* sp. nov. *Cyerce katiae* sp. nov. is morphologically distinct from all other *Cyerce* species, as this is the only species to have web-like grey striations forming polygons throughout the body, and cerata with scattered white pustules and gold spots throughout, as well as two distinct gold patches at the base of the head. Therefore, *Cyerce katiae* sp. nov. is here described as a new species.

Clade 2

Cyerce bourbonica Yonow, 2012

(Figs. 9B, 11A, 10)

Cyerce sp. 1 – Händeler & Wägele, 2007: 249; Christa et al., 2014a: suppl. table 1.

Cyerce sp. 2 – Wägele et al 2006: 49; Händeler & Wägele, 2007: 249; Christa et al., 2014a: suppl. table 1.

Cyerce bourbonica Yonow, 2012: 16–19, pl. 14, pl. 15. Type locality: L'Étang Salé, Réunion, Indian Ocean.

Type material

Cyerce bourbonica – holotype at SMF (337104), L'Étang Salé, Réunion, 14 Dec 2009, 1 m depth, not examined.

Material examined

Hekili Point, Maui, Hawaiian Islands, USA, 1 Apr 2010, 1 m depth, leg. C. Pittman, 1 specimen 3 mm preserved length (Isolate MM77, CASIZ 182729). Village, Ka'anapali, Maui, Hawaiian Islands, USA, 27 Nov 2008, 3-12 m depth, leg. C. Pittman, 1 specimen (Isolate MM75, CASIZ 180338). Ennubuj-Ennylabegan Reef, Ennubuj Is., Kwajalein Atoll, Marshall Islands, 12 Apr 2010, 2 specimens 3–4 mm preserved length (Isolate MM78A, CASIZ 185099). In front of Sheraton Nusa Indah, Bali, Indonesia, 25 Oct 2000, leg. T.M. Gosliner, 2 specimens (Isolate MM71, CASIZ 142130). Barracuda Point, Madang Province, Papua New Guinea, Nov–Dec 2012, 6 m depth, leg. T.M. Gosliner, 1 specimen (Isolate MM83, CASIZ 190808).

Range

Widespread in the Indo-Pacific, from the Hawaiian Islands (present study) to the western Indian Ocean (Yonow, 2012).

Description

External morphology. – Body color light cream to pale green (Fig. 9B). Head light cream to pale green, with white pustules throughout. Tentacles and rhinophores light cream with pale green irregular patching; white pustules with translucent halo at base scattered throughout; few bright yellow spots at tips; small black dots on rhinophores. Cerata lobate, inflated, translucent white to light cream, with pale green irregular patches; white pustules and specks scattered throughout, white specks concentrated below ceratal margin. Ceratal margin outlined with cream band and uniformly distributed bright yellow spots; few black dots sub-marginally on both sides of each ceras. Translucent (probably defensive) gland sacs embedded in tissue beneath cerata margin. Ceratal peduncle greyish, darker than rest of cerata. Foot color light cream dorsally, with white pustules and bright yellow spots scattered throughout.

Internal morphology. – Buccal mass about 1 mm, buccal bulb and pharyngeal pouch similar in size. Radula with more than 7 teeth in a 3-mm preserved length specimen (CASIZ 182729) (Fig. 10A). Teeth somewhat narrow, smooth, with blunt tips slightly curved downward (Fig. 10B). Teeth with two rows of approximately 13 blunt and rhomboidal-shaped denticles along either side; denticles distributed evenly across tooth. Size of denticles differ along tooth, smaller near base, larger distally. Penis with embedded penial stylet (Fig. 11A), penial stylet cylindrical, hollow with oval opening.

Ecology

Associated with the green algae *Halimeda* spp. Typically found beneath rocks.

Remarks

Cyerce bourbonica Yonow, 2012 was described from several specimens collected from La Réunion and illustrated alive. The original description referenced morphological traits including semi-translucent beige to green “angular” cerata, minute papillae on surface of cerata, and ceratal margin pigmented with orange and sub-marginal black spots, all observed in our specimens.

Yonow (2012) also described basal dark globular patches inside the cerata that were observed in our preserved specimens. The radular teeth described by Yonow (2012) are slightly curved, slender, closely resembling those from our specimens. Although not mentioned in the description, images of the radula in Yonow (2012: figs. 3C–D) show teeth possessing square-shaped denticles similar to those observed in our specimens. Yonow (2012) described the penis as lacking a stylet, whereas our specimens had a deeply embedded stylet, potentially explaining why Yonow (2012) was unable to view a stylet in her specimens.

In phylogenetic analyses, *C. bourbonica* formed a clade with three new species: *C. trowbridgeae* sp. nov., *C. blackburnae* sp. nov., and *C. tutela* sp. nov. (Fig. 1A). All these species shared traits including a small pharyngeal pouch approximately the same size as the buccal bulb, and yellow spots along the ceratal margin. However, *C. bourbonica* differs from *C. blackburnae* sp. nov. in having smaller and wider radular teeth with smoother denticle edges. The radular teeth of *C. bourbonica* are much shorter and wider than the teeth of *C. tutela* sp. nov., and the teeth of *C. bourbonica* have blunt denticles whereas sharp triangular denticles are present on the teeth of *C. tutela* sp. nov. Morphological differences between *C. bourbonica* and its sister species *C. trowbridgeae* sp. nov. are described below under the remarks of *C. trowbridgeae* sp. nov.

Cyerce trowbridgeae sp. nov.

(Figs. 9A, 11B, 12)

Cyerce sp. 2 – Gosliner et al. 2018: 402 upper right photo.
Cyerce sp. 6 – Nakano, 2018: 119.

Type material

Holotype: Bigej-Meck Reef, Kwajalen Atoll, Marshall Islands, 6 Aug 2007, 7 mm preserved length, isolate MM76 (CASIZ 181975).

Range

Marshall Islands (present study) and Japan (Nakano, 2018).

Description

External morphology. – Body color greyish-brown (Fig. 9A). Head beige with light brown striations; light grey banding outlining eyes, extending to rhinophores. Rhinophores beige with light brown to burgundy reticulated striations throughout; scattered yellow spots at tips. Cerata flat, slightly inflated, obovate; color greyish-brown with vein-like light brown striations throughout; outer side of cerata scattered with small elevated white minute specks; inner side of cerata scattered with black to dark brown elevated spots. Ceratal margin outlined with several elevated bright yellow spots creating dentate-like structure; two dark grey bands along either side. Foot beige dorsally with light brown vein-like striations; foot margin with light grey and scattered bright yellow spots.

Internal morphology. – Buccal mass about 1 mm in length; buccal bulb similar in size as pharyngeal pouch. Teeth elongated, with short triangular denticles (Figs. 12A–B). Penial stylet elongate, curved, about 200 µm in length, cylindrically shaped, hollow with oval opening (Fig. 11B).

Ecology

Found on the green algae *Halimeda* spp.

Etymology

This species is named in honor of Cynthia Trowbridge in recognition of her long career and outstanding contributions to the biology and ecology of sacoglossans.

Remarks

All species delimitation analyses supported *Cyerce trowbridgeae* sp. nov. as distinct from *C. bourbonica*, which was its sister taxon in phylogenetic analyses (Fig. 1A). External characteristics shared between *Cyerce trowbridgeae* sp. nov. and *C. bourbonica* include yellow spots outlining the margin of the cerata and small white pustules throughout the cerata observed in both species. However, *Cyerce trowbridgeae* sp. nov. was morphologically distinct from all other *Cyerce* spp. examined, possessing greyish cerata with light-brown reticulated striations, white elevated specks on the outer ceratal surface, and black to dark brown elevated spots on the inner ceratal surface. The cerata of *C. bourbonica* are lobate and light cream to greyish (depending on locality) whereas cerata of *C. trowbridgeae* sp. nov. are fan-shaped and a much darker shade of brown. Moreover, *C. trowbridgeae* sp. nov. has dark brown reticulated striations across the cerata, head, and rhinophores that are not present in *C. bourbonica*. A dark grey band outlines the margin of the cerata, foot, and head in *C. trowbridgeae* sp. nov. that is only faintly observed along the ceratal margin of *C. bourbonica*. The radular teeth of *C. bourbonica* are much shorter and wider than those of *C. trowbridgeae* sp. nov. The denticles along the radular teeth of *C. trowbridgeae* sp. nov. are also more numerous and more triangular in shape than of the denticles in *C. bourbonica*. Also, *C. bourbonica* appears to have a short straight penial spine whereas that of *C. trowbridgeae* sp. nov. is elongate and curved.

Cyerce blackburnae sp. nov.

(Figs. 9C, 11C, 13)

Cyerce sp. 2 – Nakano, 2018: 118.
Cyerce sp. 3 – Christa et al., 2014a: suppl. table 1.
Cyerce sp. 2 – Krug et al., 2015: 989, 991

Type material

Holotype: Barracuda Point, Madang, Papua New Guinea, 8 Dec 2012, 6–9 m depth, leg. J. Goodheart (Isolate MM92, CASIZ 191605).

Other material examined

Cement Mixer Reef, WNW of Rasch Pass, in line with Ruo Island, Madang Papua New Guinea, 3-6 m depth, 1 specimen 15 mm preserved length, 11 Jan 1988, leg. T. Gosliner (CASIZ 070412). Anemone Reef, East of Ruo Island, Madang, Papua New Guinea, 15 Feb 1988, 1 specimen 18 mm preserved, leg. T. Gosliner (CASIZ 070408). Guam, Sep 2001, 1 specimen 7 mm preserved length (Isolate 09Gua01, LACM 186691); Sep 2010, 1 specimen 7 mm preserved length (Isolate 09Gua10, LACM 186693). Tirso dive site, north of Three P. Reef, Romblon

Island, Philippines, 3 Apr 2017, leg. F. Imhof, 1 specimen 7 mm preserved length (Isolate KM26, CASIZ 222039). Paliton Wall, Siquijor Island, Viasayas, Philippines, 4 Apr 2016, 1 specimen (Isolate KM29, CASIZ 217329). Rempi, Madang, Papua New Guinea, 19 Nov 2012, 6 m depth, leg. J. Goodheart, 1 specimen 4 mm preserved length (Isolate MM86, CASIZ 191324).

Range

Western Pacific Ocean (Christa et al. 2014a; Nakano, 2018; present study)

Description

External morphology. – Body color cream white to greyish (Fig. 9C). Head cream white with reticulated dark brown striations; dark brown spots outlining head margin. Rhinophores long, translucent white, with two rows of reticulated dark brown striations throughout; few light yellowish-cream patches present, concentrated near rhinophoral tips. Cerata bulbous, oblong; color ranges from beige to translucent white, with reticulated dark brown striations; small white papillose structures scattered throughout cerata. Elevated circular clusters scattered throughout cerata; cluster color varies from whitish to tan to bright yellow; few clusters outlined by circular brown band. Whitish-fuchsia patch and several minute white specks beneath ceratal margin, located on both sides of cerata. Ceratal margin wavy, outlined with pale yellow spots. Foot color cream white dorsally, with few brown dots scattered throughout; margin outlined by pale yellow band.

Living specimens also exhibited a distinctive swimming behavior when disturbed, contracting the cerata on alternating sides of the body to create a rowing effect that propelled the animal through the water.

Internal morphology. – Radula with 10 teeth in a 7-mm preserved length specimen (CASIZ 222039), 12 teeth in a 7 mm long specimen (Isolate 09Gua01, LACM 186691); 7 teeth on descending limb (two broken, including tip of leading tooth), 5 teeth on ascending limb (Fig. 13A). Teeth narrow, elongate, about 200 µm long, with blunt tips. Approximately two rows of twenty-seven denticles along either side of tooth. Denticles rhombus shaped, distributed evenly along teeth (Fig. 13B, D). Ascus with about 11 pre-radular teeth (Fig. 13C). Penis with penial stylet at opening. Penial stylet elongated, curved, cylindrical with slanted oval opening, distinct small hook (Fig. 11C).

Ecology

Specimens were collected on, and fed upon, *Udotea geppii* in Guam.

Etymology

This species is named in honor of Christine Blackburn, friend and colleague of PK, for her lifetime of work on ocean science and climate policy, including the development of marine protected areas during her time as Assistant Secretary for Conservation and Management at the National Oceanic and Atmospheric Administration; and for letting many trips be taken over by the collection of sea slugs.

Reproduction

Development of specimens in Guam was planktotrophic. Egg masses lacked extra-capsular yolk reserved. One clutch had a mean egg diameter of 52.9 µm ± 1.8 SE (*N*=17), and while mean egg diameter for a second clutch was 55.6 µm ± 1.8 SE (*N*=25). Mean larval shell width measured across the aperture was 134.3 µm ± 3.0 SE (*N*=25) for one clutch.

Remarks

All methods of species delimitation analysis distinguished *Cyerce blackburnae* sp. nov. from the superficially similar *Cyerce tutela* sp. nov., which were sister taxa in phylogenetic analyses (Fig. 1A). *Cyerce blackburnae* sp. nov. and *C. tutela* sp. nov. share morphological traits such as bright yellow-white pustules scattered across cerata and outlining the ceratal margin. Both species have long and straight teeth with recurved rhomboidal denticles. The penial stylet is also long and curved in both species, with a distinct small hook at the tip of the stylet. The species are differentiated by rhinophores that are much more elongated in *C. blackburnae* sp. nov., and translucent white to beige cerata with reticulated brown spots in *C. blackburnae* sp. nov. not observed in *C. tutela* sp. nov. The cerata of *C. tutela* sp. nov. have a distinct infra-marginal banding pattern of black, fuchsia, and orange that is not observed in specimens of *C. blackburnae* sp. nov., which have a single fuchsia infra-marginal band on the cerata.

Cyerce blackburnae sp. nov. and *C. trowbridgeae* sp. nov. both have the reticulated brown striations across the cerata and yellow spots outlining the ceratal margin. However, the cerata in *C. trowbridgeae* sp. nov. are much darker and lack the fuchsia infra-marginal band that is present in *C. blackburnae* sp. nov. *Cyerce blackburnae* sp. nov. is morphologically distinct from all other species of *Cyerce*, as the only species that has translucent white cerata with reticulated dark brown striations, elevated white pustules and circular clusters, an infra-marginal band of fuchsia, and white overlaying white specks.

Cyerce tutela sp. nov.

(Figs. 9D–E, 11D, 14)

Cyerce sp. 2 – Nakano, 2018: 118.

Type Material

Holotype: SW end of West Lewis Island, Dampier Archipelago, Western Australia, Australia, 29 Mar 2017, 10m depth, coll. L. Kirkendale, NG. Wilson, M. Condy (WAM S110017).

Other material examined

Port Hedland, Western Australia, Australia, 20 Oct 2017, intertidal, coll. D. Koehler-Teufel (WAM S71546). Port Hedland, Western Australia, Australia, 01 Sep 2021, intertidal, coll. D. Koehler-Teufel (WAM S58153).

Range

Mid to northern Western Australia (present study), from Exmouth to Port Hedland.

Description

External morphology. – Body white with scattered black dots throughout (Fig. 9D–E). Head white, scattered with black spots throughout; base of head with greyish black patch; small greyish patch at forehead. Rhinophores white with black spotting, black patches at tips. Tentacles short, white, with scattered black dots throughout. Cerata inflated, obovate, translucent white, with scattered black spots, few elevated pale yellow, white pustules throughout. Cerata with infra-marginal banding of fuchsia, orange; black spots clustering beneath orange band. Cerata margin slightly undulating, outlined with pale yellow to black to pale yellow band, translucent defensive glands present. Foot white dorsally with scattered black spots throughout.

Internal morphology. – Buccal mass approximately 4 mm in length, buccal bulb similar in size to pharyngeal pouch. Teeth moderately narrow, slightly bent, about 50 µm in length; tips blunt (Fig. 14A–B). Denticles rhomboidal, recurved backward. Ascus with more about 6 pre-radular teeth (Fig. 14C). Penial stylet at opening of penis (Fig. 11D). Penial stylet cylindrical, curved, about 100 µm in length, hollow with oval opening at tip; tip pointed, with small distinct hook.

Ecology

Associated with the green algae *Udotea* spp.

Etymology

This species is named in honor of the traditional owners and first peoples of Australia who continue to work to protect the lands and sea. The latin noun 'tutela' means protection and care, and alludes to the Roman concept of guardianship.

Remarks

All methods of species delimitation analysis distinguished *Cyerce tutela* sp. nov. from *Cyerce blackburnae* sp. nov., which were sister taxa in phylogenetic analyses (Fig. 1A). *Cyerce tutela* sp. nov. is morphologically distinct from all other species of *Cyerce* including *Cyerce blackburnae* sp. nov. as detailed in the remarks for *Cyerce blackburnae* sp. nov. Like *C. blackburnae* sp. nov., living *C. tutela* also exhibited distinctive swimming behavior when disturbed (Alex Hoschke & Glenn Whisson pers. comm.). This species has been found intertidally in Port Hedland, and subtidally off Exmouth and Dampier.

Clade 3

Cyerce elegans Bergh, 1871

(Figs. 15A, 16, 17A)

Cyerce elegans Bergh, 1871: 99–113, pl. 1, fig. 9, pl. 9, figs. 13–17, pls. 13–15, pl. 16, figs. 23–25. Type locality: Palau.

?*Cyerce elegans* var. Bergh, 1888: 769–771, pl. 77, figs. 6–7, pl. 78, figs. 8–9.

Cyerce sp. 3 Gosliner et al., 2018: 402 middle left photo.

Type material

Cyerce elegans – one syntype at NHMD (GAS-002149), Palau, Sep 1859, not examined.

Material examined

Riwo Island, Madang Province, Papua New Guinea, 27 Nov 2012, 1 specimen 6.5 mm preserved length (Isolate MM89, CASIZ 191446). Verde Island Passage, Luzon Island, Batangas Province, Philippines, 12 May 2014, 1 specimen 18 preserved length (Isolate MM20, CASIZ 199264). Maricaban Strait, Mabini (Calumpan Peninsula), Luzon Island, Philippines , 2.5 m depth, 30 Mar 2017, 1 specimen (Isolate KM27, CASIZ 222101). Bohol Island, Philippines, 0-5 m depth, Sept. 2003, 1 specimen, leg., J. Hinterkircher (CASIZ 173751).

Range

Widespread in the Indo-West Pacific, from the Maldives to the Hawaiian Is. (Rudman, 1999a; Gosliner et al., 2018; present paper).

Description

External morphology. – Body color pale green to cream, with white speckling, outlined by reddish brown band with grey base (Fig. 15A). Pericardium elevated, smooth, oval, cream; clear tubules extending from pericardium throughout body; tubules do not enter cerata. Anal papillae anterior to pericardium, cream. Head cream. Rhinophores, tentacles elongated, translucent white. Cerata inflated, obovate, translucent white, with minute white speckling throughout. Cerata peduncle cream to pink. One to two fluorescent blue to green spots on each ceras, one spot nearer to base and second above. Ceratal margin outlined by reddish-brown band; triangular clusters of white specks distributed throughout. Foot color pale yellowish-cream, greyish hue.

Internal morphology. – Radula from an 18 mm (preserved length) specimen (CASIZ 199264) with 11 teeth, 6 on descending limb, 5 on ascending limb (Fig. 16A). Teeth narrow, slightly bent, elongate, about 100 µm in length; tips concave, blunt (Fig. 16B). Tooth with two rows of ~23 triangular denticles along either side; denticles smaller near base and tip. Ascus with about 15 pre-radular teeth (Fig. 16C). Penis with no stylet visible (Fig. 17A) in several specimens examined.

Ecology

Diet unknown.

Remarks

Bergh (1871) described *Cyerce elegans* Bergh, 1871 based on 10 specimens collected in Palau. The animals were described based on an illustration by Semper [reproduced by Bergh, 1871: pl. 1, fig. 9 and herein (Fig. 5D)] as having "water-clear, faintly yellowish-white, translucent" cerata with a "one or more green dots formed by peculiar yellowish bodies" at the base and "reddish-brown" margin with large spots. All these external morphological traits were also observed in specimens from Papua New Guinea and the Philippines assigned to this species, but in the specimens examined herein there was only a single fluorescent green or blue spot at the base of each ceras. Bergh (1871) also described the presence of an "elongated horseshoe-shaped arch" on the dorsum from which branches extend to the base of each ceras. Bergh (1871) was most likely describing the pericardium, with tubules extending across the body as observed in our specimens. Regarding the internal anatomy, Bergh (1871) described the radular teeth as having a blunt tip, wide base, "slightly bent, tapered," and denticles "directed backwards" that became smaller and "crowded" at the tip. These radular traits are also observed in our specimens assigned to this species. Because of the consistencies between the characteristics of the material here examined and the original description, we confidently assigned these specimens to *C. elegans*. Finally, Bergh (1871) described the penis of *C. elegans* as having a "sharply curved hook, which tapers very sharply." Although the penis was dissected from several of our specimens, we were unable to observe any penial stylet and therefore could not verify the presence of a hook-shaped stylet in the male reproductive system as described and illustrated by Bergh (1871: pl. 15, figs. 12–14).

Bergh (1888) reported a single specimen of a variety (or color form) of *C. elegans* from Mauritius, with descriptions of the live animal based on notes and a drawing of a ceras by [Karl August] Moebius [Möbius] reproduced by Bergh (1888: pl. 77, fig. 6) and herein (Fig. 5E). The specimen was described as light brown in color, with white spots on the rhinophores and oral tentacles, and translucent light brown cerata with yellowish-white triangular spots along the margin; from these spots are connecting "white veins" and lines throughout; green to blue "cells" at the base. Our specimens assigned to *C. elegans* also have the triangular spots along the margin of the cerata as described by Bergh (1888) but lack the radiating "veins" and lines from these spots; however, these lines are present in other species of the same clade described below, including *C.* sp., which is also reported from the Indian Ocean. It is therefore likely that the specimen described by Bergh (1888) belongs to a different species of the *C. elegans* species complex. Other specimens assigned to *C. elegans* in the literature (e.g., Rudman, 1999a; Yonow, 2008; Gosliner et al., 2018; Nakano, 2018) probably belong to other species of the *C. elegans* species complex as well.

Species delimitation analyses supported specimens preliminarily identified as *Cyerce elegans* as four separate entities which were also recovered in phylogenetic analyses, collectively termed here as the *C. elegans* complex. In additional to the material identified as *C. elegans* Bergh (1871), our analyses differentiated three pseudocryptic taxa: *Cyerce* sp. from the Red Sea; *Cyerce basi* sp. nov. from PNG, the Philippines and New Caledonia; and *Cyerce whaapi* sp. nov. from the Philippines and New Caledonia (Fig. 1B, Table 3). Members of the *C. elegans* complex share clear, thickened cerata with triangular clusters of small white specks along the margin and a fluorescent spot at the base of each ceras varying from green to blue or light brown. However, the specimens of *C. elegans sensu stricto* all exhibit a reddish-brown ceratal margin as described by Bergh (1871), a trait not observed in *Cyerce* sp., *Cyerce basi* sp. nov., or *Cyerce whaapi* sp. nov. *Cyerce elegans* was sister to *C. whaapi* sp. nov., which had more inflated and translucent cerata with faint vein-like striations extending from larger, deeper triangular clusters along the margin compared to *C. elegans*; additionally, the fluorescent spot at the ceratal base was green to light brown in *Cyerce whaapi* sp. nov. but blue to green in *C. elegans*. Radular morphology was similar between *Cyerce whaapi* sp. nov. and *C. elegans*; teeth were elongate, slightly bent, with concave tips and short, conical denticles.

Cyerce basi sp. nov., which overlapped with *C. elegans* in Papua New Guinea, was recovered as sister to *C. whaapi* sp. nov. and *C. elegans. Cyerce basi* sp. nov. had white vein-like striations throughout the cerata, observed in *Cyerce whaapi* sp. nov. but not in *C. elegans*. The triangular clusters along the cerata margin of *C. basi* sp. nov. have brown specks and are much deeper and larger than in *C. elegans*. The cerata of *C. basi* sp. nov. are also more inflated and translucent than in *C. elegans*. The radular morphology of *C. basi* sp. nov. is similar to that of *C. elegans* but the teeth of *C. basi* sp. nov. have a pointed tip between the first pair of denticles, not observed in *C. elegans*. We could not obtain specimens of *Cyerce* sp. for morphological analysis; therefore, we could not compare the internal morphology to our specimens of *Cyerce elegans*.

Cyerce sp.

(Figs. 15B)

Material examined

Al-Fasar Reef, Makkah Province, Saudi Arabia (Red Sea), 13 Oct 2016, 1 specimen, leg. G. Rouse (SIOBIC M15387).

Description

External morphology. – Body color beige, with dark brown patches dorsally running along both sides of body (Fig. 15B). Head color beige. Rhinophores long, translucent beige, with white speckling at tips. Oral tentacles beige. Cerata inflated, obovate, translucent with white speckling throughout; light fluorescent green spot at base of each ceras. Ceratal margin with evenly distributed large clusters of white specks; row of white (possibly defensive) glands along margin. Foot color translucent white.

Internal morphology. – Material could not be obtained for examination of internal morphology.

Range

Red Sea (present study).

Ecology

Diet unknown.

Remarks

Species delimitation and phylogenetic analyses all supported *Cyerce* sp. as a candidate species distinct from other members of the *C. elegans* species complex (Fig. 1B, Table 3). *Cyerce* sp. was recovered as sister to the rest of the complex. In external morphology, *Cyerce* sp. differed from other complex members by having cerata that are much more inflated and translucent than in *C. elegans*, but lacking white veins or lines across the cerata observed in *C. basi* sp. nov. and *C. whaapi* sp. nov. The penial stylet of *C. elegans* could not be observed and therefore could not make be compared with other complex members. Because of the absence of anatomical data, this species is not formally described herein.

Bergh's (1871) description of *C. elegans* included details of the external morphology such as a yellowish-white body, translucent yellowish-white cerata, a green spot at the base of each ceras, and a reddish-brown band outlining the ceratal margin with large spots. The specimens of *C.* sp. here examined closely resemble this description, but lack the reddish-brown ceratal margin. We were unable to examine the internal anatomy of *Cyerce* sp. but features of the external anatomy distinguish this delimited entity from all other complex members.

Cyerce basi sp. nov.

(Figs. 15C, 17B, 18)

Type material

Holotype: Koumac, New Caledonia, 11 Sep 2018, leg. Koumac 2.1 Expedition (stn. KM202), 14 mm preserved length (Isolate AV251, MNHN IM-2013-86242)

Other material examined

Wongat Island, Madang Province, Papua New Guinea, 29 Nov 2012, 1 specimen 3 mm preserved length (Isolate MM87, CASIZ 191437). Koumac, New Caledonia, 11 Sep 2018, leg. Koumac 2.1 Expedition (stn. KR644), 1 specimen 10 mm preserved length (Isolate AV684, MNHN MNHN IM-2013-86241). Segond Channel, near Maritime College, Espiritu Santo Is., Vanuatu, 4 Oct 2006, 8 m depth, leg. Y. Camacho & M. Pola, 1 specimen (Isolate 06Van01, CASIZ 177095). Near Madang Lighthouse, Madang, Papua New Guinea, 30 m depth, 15 Jan 1988, 1 specimen, leg. R. C. Willan (CASIZ 065775). Cement Mixer Reef, Madang Papua New Guinea, 23 m depth, 24 Nov 1990, 1 specimen, leg. T. Gosliner and G. Williams (CASIZ 075849). "Lago de Oro House Reef," south side of reef/lagoon channel, Verde Island Passage coast, Philippines, 13 May 2014, 1 specimen (CASIZ 199270).

Range

Vanuatu, Papua New Guinea, New Caledonia (present study).

Description

External morphology. – Body translucent, nearly transparent (Fig. 15C). Rhinophores translucent white with white speckling at tips. Cerata leaf-like, inflated, obovate, translucent, with red hue in some specimens, with white vein-like striations throughout; fluorescent green spot at base of each ceras. Several brown structures inside cerata, not part of digestive gland. White vein-like striations connect to infra-marginal white clusters along ceratal margin, white clusters with brown speckles. Cerata margin outlined with minute white specks.

Internal morphology. – Buccal mass about 1 mm in length; pharyngeal pouch larger than buccal bulb. Radula with 10 teeth in a 10 mm preserved length specimen (MNHN IM-2013-86241); 5 teeth on descending limb (leading tooth tip broken off), 5 teeth on ascending limb (Fig. 18A). Teeth narrow, elongate, slightly bent, about 200 µm in length, with pointed tips (Fig. 18B). Approximately two rows of 15 denticles along either side of active tooth. Denticles short, blunt, triangular. Denticle size varies along tooth, smaller at the base, larger distally. Ascus containing about 5 pre-radular teeth (Fig. 18C). Penial stylet embedded in penis, curved inward, extended tip pointed downward, about 100 μm in length (Fig. 17B).

Ecology

Diet unknown.

Etymology

This species is named in honor of Johan Bas, underwater photographer and naturalist from Nouméa, New Caledonia, in appreciation for the numerous specimens he collected for this and other studies.

Remarks

Species delimitation and phylogenetic analyses all supported *Cyerce basi* sp. nov. as a candidate species distinct from other members of the *C. elegans* species complex (Fig. 1B, Table 3). *Cyerce basi* sp. nov. was recovered as sister to the clade of *C. whaapi* sp. nov. and *C. elegans* (Fig. 1B). Both *C. basi* sp. nov. and *C. whaapi* sp. nov. have white vein-like striations throughout the cerata, but *C. elegans* does not. The white clusters along the cerata margin are also very similar in *C. basi* sp. nov. and *C. whaapi* sp. nov., being larger and deeper than in *C. elegans*. In radular morphology, the teeth of *C. basi* sp. nov. have a distinct pointed tip that clearly protrudes beyond the most distal pair of denticles, whereas in *C. whaapi* sp. nov., the tip of the teeth is very inconspicuous, and the distal pair of denticles are located near the end of the teeth.

Bergh's (1871) original description of *C. elegans* did not mention vein-like structures throughout the cerata as observed in our specimens of *C. basi* sp. nov. However, the specimen of *C. elegans* described by Bergh (1888) from the Indian Ocean as *C. elegans* var. did exhibit the white vein-like striations as observed in our specimens. Bergh (1888) also described the penial stylet as being a sharp-angled, tapered hook and refers to the illustration of the penial stylet from his original description of *Cyerce elegans* Bergh, 1871, suggesting these two specimens potentially had similar penial stylets. The penial stylet of our specimens of *C. basi* sp. nov. closely resembles the stylet described by Bergh (1871), as being short, recurved, with an oval opening and pointed tip. Bergh (1888) also described the radular morphology of the specimen from the Indian Ocean as similar to the radula of *C. elegans* from Palau. The radula of our specimens of *C. basi* sp. nov. also closely resembles the radula described by Bergh (1871, 1888).

Cyerce whaapi sp. nov.

(Figs. 15D, 17C, 19)

Type material

Holotype: Koumac, New Caledonia, 8 Sep 2018, leg. Koumac 2.1 Expedition (stn. KM301), 11 mm preserved length (Isolate AV162, MNHN IM-2013-86238).

Other material examined

Koumac, New Caledonia, 4 Sep 2018, leg. Koumac 2.1 Expedition (stn. KM200), 1 specimen 7 mm preserved length (Isolate AV016, MNHN IM-2013-86240); 1 specimen 7 mm preserved length (Isolate AV017, MNHN IM-2013-86239); 8 Sep 2018, leg. Koumac 2.1 Expedition (stn. KM301), 1 specimen 7 mm preserved length (Isolate AV163, MNHN IM-2013-86237); 1 specimen 3 mm preserved length (Isolate AV165, MNHN IM-2013-86236).

Range

Based on available evidence this species could be endemic to New Caledonia.

Description

External morphology. – Body color beige to light cream (Fig. 15D). Pericardium elevated, oval, light brown. Anal papillae light brown. Head color beige with greyish tint. Rhinophores long, translucent white, with white speckling at tips. Cerata inflated, obovate, translucent brown, with faint white vein-like striations throughout; small single white to fluorescent green spot at base of each ceras. Ceratal margin outlined with white specks, faint thin light brown band; submarginally, several large clusters of white specks evenly distributed along margin; margin wavy.

Internal morphology. – Buccal mass about 4 mm in length; pharyngeal pouch much larger than buccal bulb. Radula with 10 teeth in a 7-mm preserved length specimen (MNHN IM-2013-86239); 3 on descending limb, 7 on ascending limb (Fig. 19A). Teeth narrow, elongate, slightly bent, about 100 µm in length (Fig. 19C). Approximately two rows of 17 short, triangular denticles. Denticle size varies along tooth, smaller at the base, larger as they ascend, significantly smaller at tooth tip. Ascus with about 12 pre-radular teeth (Fig. 19B). Penial stylet embedded in penis (Fig. 17C), short, curved inward; tip pointed.

Etymology

This species is named in honor of Rocky Whaap of the Tribu de Wanap, Koumac, New Caledonia who participated in various research expeditions and collected important specimens for this study.

Ecology

Diet unknown.

Remarks

Species delimitation and phylogenetic analyses all supported *Cyerce whaapi* sp. nov. as a candidate species sister to *C. elegans* and distinct from other complex members (Fig. 1B, Table 3). Morphologically, *C. whaapi* sp. nov. could be distinguished from *C. elegans* by having cerata that were slightly more inflated and with faint white vein-like striations extending from the white clusters along the ceratal margin. The color of the spot at the base in *C. whaapi* sp. nov. ranges from fluorescent green to light brown but was fluorescent blue to green in *C. elegans*.

The description of *C. elegans* var. by Bergh (1888) closely resembles *C. whaapi* sp. nov., having translucent light-brown cerata with white vein-like striations and white clusters along the margin. However, the vein-like striations in *C. whaapi* sp. nov. are fainter and do not extend towards the middle of the cerata as observed in the illustration by Bergh (1888: pl. 77, fig. 6) and the specimens of *Cyerce basi* sp. nov. here examined. The penial stylet and radular morphology of our specimens of *C. whaapi* sp. nov. also closely resembles the specimen described by Bergh (1888).

Clade 4

Cyerce pavonina Bergh, 1888

(Figs. 20A, 21, 22A)

Cyerce pavonina Bergh, 1888: 764–769, pl. 77, figs. 3–5, pl. 78, figs. 10–18, pl. 79, figs. 22–25. Type locality: Mauritius.

Type material

Cyerce pavonina – no type material known to exist, not found at NHMD.

Material examined

"The Deep Blue," 13.91763ºN 120.6039ºE, Verde Island Passage, Calatagan, Luzon Island, Philippines, 18 May 2014, 1 specimen 11 mm preserved length, leg. VIP Team (Isolate MM42, CASIZ 202132). Diamond Head, Oahu, Hawaiian Islands, USA, 1 Oct 2000, 1 m depth, leg. C. Pittman, 1 specimen (CASIZ 163778).

Range

Western Pacific and Indian Ocean (Rudman, 2008; Gosliner et al., 2018).

Description

External morphology. –Body color light brown (Fig. 20A). Pericardium elevated, circularly shaped, lighter than rest of body. Rhinophores light brown, covered with white flecks scattered throughout. Cerata inflated, obovate; outer side dark brown with translucent tubercles and white flecks; inner side lighter brown with cream patch, two dark dorso-medial brown spots, one brown spot located below ceratal margin, another spot located beneath first. Cerata margin outlined with dark yellowish to orange band, with white tubercles appearing to give cerata dentate-like structure. Dorsal side of the foot light brown, foot sole greenish grey.

Internal morphology. – Buccal mass about 1 mm in length; pharyngeal pouch much larger than buccal bulb. Radula with 10 teeth in a 11-mm preserved length specimen (CASIZ 202132); 6 on descending limb, 4 on ascending limb (Fig. 21A). Teeth elongate, with wide bases. Leading tooth about 200 µm in length, with approximately two rows of 24 triangular denticles along either side (Fig. 21B). Size of denticles vary along tooth, smaller near base and tip. Ascus not observed. Penis with penial stylet at opening (Fig. 22A). Penial stylet cylindrical, hollow with oval opening, about 200 µm in length.

Ecology

Associated with the green algae *Halimeda* spp.

Remarks

Bergh's (1888) original description of *Cyerce pavonina* Bergh, 1888 was based on a single preserved specimen from Mauritius and field notes provided by [Karl August] Moebius [Möbius]. The main diagnostic characteristics of this species as described by Bergh (1888) included a yellow-brown head color, dorsal yellow-brown cerata covered with whitish warts, and a grey foot sole. Bergh (1888) further described the cerata of *C. pavonina* as being leaf-shaped with both sides covered by tubercles and a brown tip and white base. Bergh (1888) also described the outer side of the cerata as having a brown color darker than the inner side, which was described as white or lighter in color. The color illustration of *C. pavonina* by Möbius, reproduced by Bergh (1888: pl. 77, fig. 3) and herein (Fig. 5F) also shows two dorso-medial brown spots, a trait that along with the brown cerata covered with whitish tubercles closely resembles the characteristics of our specimens. The radular morphology of *C. pavonina* was also described and illustrated by Bergh (1888: pl. 78, figs. 16–17), which closely resembles that of our specimens; both have very narrow and elongate teeth with numerous denticles and wide bases. All these morphological traits described by Bergh (1888) closely resembles the specimens studied herein and therefore we confidently assign our specimens to *C. pavonina*.

Kay (1979) described a specimen from the Hawaiian Islands as *C. nigricans* that closely resembles *C. pavonina*. The description of the cerata color by Kay (1979) is very similar to our specimen of *C. pavonina*, as being translucent brown with an orange yellow band along the margin. Kay (1979) also mentioned the cerata as dark brown with white spots on one side of the cerata and white pustules with blue spots on the other, a trait that we did not observe in our specimens. The identity of Kay's (1979) specimens remains unclear as additional species with similar external morphology are present in the Hawaiian Islands; see description of *C. liliuokalaniae* sp. nov.

Rudman's (2008) morphological description of a specimen of *Cyerce pavonina* from Tanzania closely resembles the specimen studied herein. However, Rudman's (2008) specimen appeared to have a light brown band across the head of the animal, a trait we could not verify in our specimens. Whether the specimen described by Rudman (2008) and our specimens belongs to the same species would require further investigation. Moreover, examination of online images of *C. pavonina* from the Philippines indicated that they have a light brown band across the head. Therefore, multiple pseudocryptic species may be currently identified as *C. pavonina*.

Cyerce pavonina was recovered in the phylogenetic analyses as sister to *C. goodheartae* sp. nov. (Fig. 1B), but differed in color and radular morphology. Compared to *C. pavonina*, the cerata of *C. goodheartae* sp. nov. were more translucent, light brown, and lacked tubercles throughout. The radular teeth of *C. goodheartae* sp. nov. are shorter and wider than those of *C. pavonina*. The radular and penial morphology of *C. pavonina* are also similar to those of *C. liliuokalaniae* sp. nov. in several respects. For example, both species have very elongate, slender radular teeth with triangular denticles, and short, cylindrical penial stylets.

Bergh (1888) mentioned the penial stylet of *Cyerce pavonina* appeared to be similar morphologically to that of *C. nigra*, but shorter in length. The penial stylet of *C. nigra* is cylindrical with an oval opening, but it has a sharp, pointed tip, clearly differing from *Cyerce pavonina*.

Cyerce orteai Valdés & Camacho-García, 2000
(Figs. 20B, 23)

Cyerce orteai Valdés & Camacho, 2000: 445–456, figs. 1–5. Type locality: Playa Cabuya, Cóbano, Puntarenas Prov., Costa Rica,

Type material

Cyerce orteai – holotype at the Universidad de Costa Rica (INBio CRI001500521) [formerly at the Instituto Nacional de Biodiversidad], Playa Cabuya, Cóbano, Puntarenas Prov., Costa Rica, 29 Jan 1999, not examined.

Material examined

Punta Mita, Nayarit, Mexico, Jan 1976, leg. F. & R. Poorman, 5 specimens 12–14 mm preserved length (Isolates MM104A–E, LACM 153499). El Anclote, Nayarit, Mexico, 17 Feb 2008, leg. A. Hermosillo, 1 specimen 13 mm preserved length (Isolate MM107, LACM 175024). Playa Cabuya, Cóbano, Puntarenas, Costa Rica, 29 Jan 1999, 2 specimens 12–14 mm preserved length (Isolates MM43A–B, CASIZ 115230, paratypes).

Range

Tropical Eastern Pacific, from Nayarit, Mexico (present study) to Costa Rica (Valdés & Camacho-García, 2000).

Description

External morphology. – Body color light cream to olive green (Fig. 20B). Pericardium white, with light brown striations forming web-like pattern. Head color light cream, covered by dark reddish-brown, mask-like band around eyes, with few white specks. Rhinophores light cream with dark reddish-brown markings, white specks scattered throughout. Cerata inflated, obovate, translucent white, with dark brown striations forming weblike pattern around translucent tubercles; tubercles scattered throughout cerata, with minute white spots at centers. Cerata color varies by specimen size; bolder dark reddish-brown striations in larger specimens. Ceratal margin outlined with dark yellow thick band and pronounced white spots dorsally. Dense white specks beneath ceratal margin. Ceratal peduncle light cream. Foot color white with white specks.

Internal morphology. – Radula with 10 teeth in a 14-mm preserved length specimen (LACM 153499); 6 teeth on descending limb, 4 teeth on ascending limb (Fig. 23A). Teeth very narrow, elongated, slightly curved with concaved tip. Leading tooth about 300 µm in length, with approximately two rows of 20 conical denticles along either side (Fig. 23B). Denticles blunt, short, varying in size along tooth, smaller near base and tip, slightly enlarged towards middle of tooth. Ascus contains about 12 pre-radular teeth (Fig. 23C). A penial stylet was not observed in any of the specimens dissected but it was described by Valdés & Camacho-García (2000).

Ecology

Diet unknown. Found beneath rocks.

Remarks

Valdés & Camacho-García (2000) described *Cyerce orteai* Valdés & Camacho-García, 2000 based on several live specimens collected from the Pacific coast of Costa Rica and illustrated the external and internal morphology. Subsequent records extended the geographic range of this species as far north as Baja California, Mexico (Angulo-Campillo, 2002). The specimens here examined from Nayarit, Mexico are within the known range of the species and closely resemble the original description as well as several paratypes from Costa Rica also studied herein. Valdés & Camacho-García (2000) described external characteristics such a dark brown mask-like pattern on the head; dark brown cerata with elevated translucent tubercles; and white spots along the cerata margin that are also present in the specimens from Nayarit. The radula described by Valdés & Camacho-García (2000) also closely resembles the radula dissected from the specimens from Nayarit, sharing similar elongated teeth with recurved conical denticles. Although not mentioned by Valdés & Camacho-García (2000), the images of the radular teeth have a distinct tip very similar to what we observed in the specimens from Nayarit. However, Valdés & Camacho-García (2000) describe tubercles along the rhinophores and tentacles, not observed in our specimens. Regardless, phylogenetic analyses recovered our specimens and the specimens described by Valdés & Camacho-García (2000) in a single clade with COI distances <0.5% (Fig. 1B). Therefore, the material here examined belongs to *C. orteai*.

Cyerce orteai shares several internal and external morphological characteristics with *C. pavonina*, despite being found on opposite sides of the Pacific Ocean. For instance, the radular teeth of both *C. pavonina* and *C. orteai* are long and narrow, with concave tips and short triangular denticles. The cerata of *C. orteai* have similar translucent tubercles to those observed in *C. pavonina*, although the tubercles are larger and more pronounced in *C. orteai*. *Cyerce pavonina* also has two dorso-medial brown spots on the inner side of the cerata, while *C. orteai* does not possess brown spots on either side of the cerata. Finally, the orange-yellowish band with white tubercles along the margin of the cerata is present in both species. Because of these similarities, some authors (e.g., Pittman & Fiene, 2000) suggested that *C. orteai* could be a synonym of *C. pavonina*. However, species delimitation analyses all supported *C. orteai* as a distinct taxon, and in phylogenetic analyses, *C. orteai* was not sister to *C. pavonina* despite their superficial similarity in appearance. Thus, *C. orteai* is regarded herein as a valid species restricted to the Eastern-Pacific, while records of *C. orteai* from the tropical Indo-Pacific likely represent *C. pavonina, C. goodheartae* sp. nov. or *C. liliuokalaniae* sp. nov.

Cyerce goodheartae sp. nov.

(Figs. 20C, 22B, 24)

Cyerce sp. 1 Gosliner et al. 2008: 70 uppermost photo; Gosliner et al., 2018, 402: upper left photo.

Type material

Holotype: Wongat Island, Madang Province, Papua New Guinea, 26 Nov 2012, leg. J. Goodheart (Isolate MM88, CASIZ 191438).

Other material examined

Cement Mixer Reef, Madang Province, Papua New Guinea, 11 Dec 2012, 1 specimen 4.5 mm preserved length (Isolate MM82, CASIZ 190784). Madang Province, Papua New Guinea, 17 Nov 2012, 1 specimen (Isolate MM85, CASIZ 191278). Southeast of Tab Island, Madang Province, Papua New Guinea, 30 Nov 2012, leg. V. Knutson, 1 specimen (Isolate MM90, CASIZ 191487). Anemone Reef, Madang, Papua New Guinea, 15 m depth, 10 Jan 1988, 1 specimen, leg. T. Gosliner (CASIZ 070407). Hole in the Wall, near Hussein Village, Madang, Papua New Guinea, 20 m depth, 1 specimen, 3 Feb 1988, leg. T. Gosliner (CASIZ 070411).

Range

Papua New Guinea (present study).

Description

External morphology. – Body color olive green with reddish brown markings (Fig. 20C). Pericardium oval-shaped, white, with small, elevated bumps. Anus anterior to pericardium, white. Head cream with light brown markings outlining eyes, extending into rhinophores. Rhinophores translucent white, with small white clusters concentrated at tips. Oral tentacles translucent white with white specks scattered throughout. Cerata inflated, oblong, translucent white with small white specs scattered throughout; one light dorso-medial brown spot on both sides of each ceras. Ceratal margin outlined with faint reddish band; elevated small opaque white clusters give cerata frosted, dentate-like appearance. Several small white clusters concentrated beneath ceratal margin. Foot longer than body, translucent dorsally with several white specks and light brown striations.

Internal morphology. – Buccal mass about 1 mm in length, pharyngeal pouch larger than buccal bulb. Radula with 16 teeth in a 4.5-mm preserved length specimen (CASIZ 190784); 8 on descending limb, 8 on ascending limb (Fig. 24A) and 16 teeth in a 4.5-mm preserved length specimen (CASIZ 191278); 7 on descending limb, 9 on ascending limb (Fig. 24C). Leading tooth short, about 200 µm in length, slightly curved near tip; approximately two rows of eighteen denticles along either side of tooth (Figs. 24B, E). Ascus containing several pre-radular teeth of various sizes (Fig. 24D). Denticle shape varies along tooth, from triangular to square; denticle size smaller near base. Penis with small stylet at opening (Fig. 22B). Penial stylet short, about 200 µm in length, cylindrically shaped, hollow with oval opening.

Ecology

Diet unknown.

Etymology

This species is named in honor of our friend and colleague Jessica Goodheart, who collected the holotype of this species as well as many other specimens here examined.

Remarks

Three methods of species delimitation supported *C. goodheartae* sp. nov. as a distinct candidate species that was sister to *C. pavonina* in phylogenetic analyses (Fig. 1B). *Cyerce goodheartae* sp. nov. is morphologically distinct from all other species in possessing translucent light brown cerata with white speckling, a dorso-medial brown spot, and elevated white clusters outlining the margin. Both *C. goodheartae* sp. nov. and *C. pavonina* share a similar penial stylet and similar external morphology of their rhinophores and cerata. However, in *Cyerce goodheartae* sp. nov. the cerata are a lighter transluscent brown and lack the translucent tubercles found throughout the darker cerata in *C. pavonina*. Radular morphology also distinguishes the species: teeth in *Cyerce goodheartae* sp. nov. are slightly curved and moderately wide with larger denticles compared to teeth in *C. pavonina* which are long and narrow with reduced denticles. The tooth tip is also bent downward with several reduced denticles in *C. pavonina*, whereas the tooth tip is blunt in *C. goodheartae* sp. nov.

Cyerce liliuokalaniae sp. nov.

(Figs. 20D, 22C, 25)

Type material

Holotype: Waikiki, Honolulu, O‘ahu, Hawaiian Islands, USA, 24 Jun 2018, one specimen 11 mm preserved length (Isolate KG02, LACM 3859).

Other material examined

Specimens identified in the field as *Cyerce nigricans* were recovered as two distinct lineages in the clade also including the morphologically distinct *Cyerce katiae* sp. nov. (Fig. 1). This is further supported by species delimitation analysis (Table 3) that recovered *Cyerce takanoi* sp.

nov. and *Cyerce nigricans* as different species. The material of *Cyerce takanoi* sp. nov. examined herein could not be fully studied due to the difficulty of dissecting the penis from small specimens and further investigation is needed. Regardless, the external morphological traits of *Cyerce takanoi* sp. nov. closely resembles those of *Cyerce nigricans*.
Maliko Bay, Maui, Hawaiian Islands, USA, 28 Jun 2016, one specimen 9 mm preserved length (Isolate 16Mau69 (LACM pending).

Other material examined

Maui, Hawaiian Islands, USA, one specimen preserved, isolate 16Mau69.

Range

Hawaiian Islands (present study).

Description

External morphology. – Body color light cream to pale green, with white specks throughout (Fig. 20D). Pericardium creamy-white, irregularly shaped, located dorso-medially. Head light cream with few white specks scattered throughout; dark burgundy patch covering rhinophores, surrounding eyes. Rhinophores bifurcated, cream with small white specks scattered sparsely throughout. Oral tentacles translucent white with white specks scattered throughout. Cerata bulbous, obovate, translucent white, with web-like burgundy striations forming hexagonal patterns, white specks scattered throughout. Cerata margin covered with white specks, forming elevated clusters. Regenerating cerata are translucent clear with light burgundy striations. Foot wider than body, with elongated posterior end; foot light cream to translucent white dorsally, with burgundy hue along the edges.

Internal morphology. – Buccal mass about 3 mm in length, buccal bulb smaller than pharyngeal pouch. Radula with 10 teeth in a 11-mm preserved length specimen (CPIC 02301); 6 teeth on descending limb (leading tooth broken), 4 teeth on ascending limb (Fig. 25A). Teeth narrow, elongated, with small triangular, denticles spaced broadly along tooth (Fig. 25B). Size of denticles vary along radula, smaller near base, larger towards middle of the tooth, irregularly sized near tooth tip. Ascus contains about 6 pre-radular teeth (Fig. 25C). Penial stylet deeply embedded into penis, short, cylindrical (Fig. 22C).

Ecology

Diet unknown. Found beneath rocks.

Etymology

This species is named in honor of Lydia Liliʻu Loloku Walania Kamakaʻeha, Queen Liliʻuokalani, the last sovereign monarch of Ke Aupuni Hawaiʻi (the Kingdom of Hawaiʻi) until her overthrow by the US government on January 17, 1893.

Remarks

Species delimitation analyses supported *Cyerce liliuokalaniae* sp. nov. as a candidate species, with one method further splitting the two sequenced samples into distinct entities. Phylogenetic analyses recovered *Cyerce liliuokalaniae* sp. nov. sister to *C. orteai* from the Eastern Pacific Ocean (Fig. 1B). *Cyerce liliuokalaniae* sp. nov. was distinct from *C. orteai* by not having tubercles throughout the cerata, rhinophores, or tentacles and by lacking the two brown spots located dorso-medially in the cerata. The thick yellow-orange band outlining the cerata margin in *C. orteai* was also not observed in *Cyerce liliuokalaniae* sp. nov. Denticles were also more densely arranged along the teeth of *C. orteai* compared to *Cyerce liliuokalaniae* sp. nov. The juvenile specimen of *C. orteai* described by Valdés and Camacho (2000) closely resembles *C. liliuokalaniae* sp. nov. However, the juvenile specimen was also described as having several tubercles covering the rhinophores and oral tentacles, whereas there are no tubercles on the rhinophores or oral tentacles of *C. liliuokalaniae* sp. nov. Moreover, the burgundy web-like striations on the cerata of *Cyerce liliuokalaniae* sp. nov. are not present in *C. pavonina* or *C. goodheartae* sp. nov. Overall, *Cyerce liliuokalaniae* sp. nov. is morphologically distinct from all other species of *Cyerce* by having white specks present over the entirety of the animal and translucent cerata with web-like burgundy striations that lack tubercles.

Clade 5

Cyerce kikutarobabai Hamatani, 1976

(Figs. 26, 27, 28)

Cyerce kikutarobabai Hamatani, 1976: 283–286, pl. 1, figs. 1A–C, figs. 2A–C. Type locality: Yoron Island, Amami Islands, Japan.

Type Material

Cyerce kikutarobabai – Holotype untraceable (see remarks), 1 Apr 1975, 9 mm in length.

Material examined

Okinawa, Ryūkyū Islands, Japan, 23 Apr 1992, 3 m depth, leg. B. Bolland, 1 specimen 5 mm preserved length (CASIZ 086574). Tulumben, Bali, Indonesia, 1 Oct 2001, leg. M. Miller, 2 specimens (Isolates MM41A–B, CASIZ 172614). Nouméa, New Caledonia, 16 Sep 2022, 1 specimen 7 mm preserved length, leg. Luc Bourdil (Isolate 22NC304, MNHN IM-2019-26210); 18 Sep 2022, 1 specimen, leg. Luc Bourdil (Isolate 22NC102). Nouméa, New Caledonia, 10 m depth, 14 Oct 2019, 1 specimen 10 mm preserved length, leg. Alain Doulas (Isolate KM71, MNHN IM-201926193).

Range

Western Pacific Ocean (Hamatani, 1976; Rudman, 2001; Nakano, 2018; Gosliner et al., 2018; present study).

Description

External morphology. – Body color ochre, margin transcalent white (Fig. 26). Pericardium inflated, antero-dorsal, opaque white. Anal papilla located between right rhinophore and pericardium. Head color translucent, with burgundy hue; darker burgundy mask-like patch surrounding eyes. Rhinophores long, translucent with burgundy hue, with few white spots concentrated near tips. Tentacles translucent with burgundy hue. Cerata inflated, obovate; pale cream, with dorso-medial reddish-brown patch; circular pale yellow to cream spots, irregularly sized, covering reddish-brown patch. Cerata margin outlined with yellow-orange band.

Internal morphology. – Buccal mass about 1 mm in length, buccal bulb smaller than pharyngeal pouch. Radula with 11 teeth in a 10-mm preserved length specimen (MNHN IM-201926193); 5 teeth on descending limb, 7 teeth on ascending limb (Fig. 27A). Teeth moderately wide, slightly curved, about 40 µm in length, with blunt tips (Fig. 27B). Two rows of approximately twenty rhombus-shaped denticles along either side of tooth. Size of denticles vary along tooth, smaller towards base and tip. Penial stylet short, about 100 µm in length, slightly curved, with oval opening, curved blunt tip (cup-like), located at opening of penis (Fig. 28).

Ecology

Associated with green algae of the genus *Halimeda*.

Remarks

Hamatani's (1976) original description of *Cyerce kikutarobabai* Hamatani, 1976 includes details of the external and internal morphology that closely resemble the specimens examined herein. Hamatani (1976) described the cerata of *C. kikutarobabai* as having a reddish-purple coloration (more intense towards the cerata margin), yellow-orange irregular round patches on each side of the cerata, and a yellow-orange band outlining the ceratal margin, all consistent with the cerata of specimens examined here. Moreover, Hamatani (1976) described the color of the rhinophores and tentacles as reddish-purple, similarly observed in our specimens. However, Hamatani (1976) did not describe white spots on the rhinophores as observed in the material here examined. A reddish-purple pattern surrounding the eyes was also described by Hamatani (1976) and resembles the 'mask-like' pattern on the head of our specimens. Hamatani (1976) did not describe a penial stylet for his specimens. However, our specimens possess a stylet, suggesting this trait could be variable or that the stylet was retracted into the tissue examined by Hamatani (1976). By internal and external morphology, *C. kikutarobabai* is distinct from all other *Cyerce* spp.

The holotype of *C. kikutarobabai* is untraceable and probably lost. It could not be found in the zoological collection of the Seto Marine Biological Laboratory (Tomoyuki Nakano, pers. comm.). According to Kazunori Hasegawa (pers. comm.), most of Hamatani's type specimens were donated by his family to the Osaka Museum of Natural History. Currently the Hamatani collection is in the process of being fully transferred to the Osaka Museum, curated, and re-organized, but the holotype of *Cyerce kikutarobabai*, has yet to be located at the time of the publication of the present paper.

In molecular phylogenetic analyses, *C. kikutarobabai* was recovered in a clade with the Mediterranean species *C. graeca* and *C. cristallina* (known also from the Western Atlantic). Notably, the external morphology of *C. kikutarobabai* and *C. cristallina* are highly similar: both species have maroon to purple rhinophores and heads with large white oval patches around the eyes, and translucent cerata edged in white with a prominent medial stripe or patch the same maroon to purple color as the head. Cerata of both species are also flecked with small light-colored spots.

DISCUSSION

Biodiversity

Prior to the present study and other recent work, 12 species of *Cyerce* were generally considered valid worldwide, although a number of undescribed morphospecies were recognized (Moreno et al., 2023). Using an integrative approach, we here recovered a total of 17 Pacific and Indian Ocean species of *Cyerce*. The total number of species in *Cyerce* is therefore at least 25 taxa, including the six Caribbean species delimited in the *C. antillensis* complex by Moreno et al. (2023), and two to three additional Atlantic species (Ortea and Templado, 1988). Our study substantially increases the recognized biodiversity of *Cyerce*, and highlights the challenges of pseudocryptic species complexes that mask marine biodiversity and often include regional endemics of potential conservation importance.

Prior morphological (Jensen, 1996) and molecular studies (Christa et al. 2015; Krug et al., 2015) suggested *Cyerce* was monophyletic, but both our ML and BI analyses recovered *Cyerce* as paraphyletic. Earlier molecular analyses included representatives of other sacoglossan genera not included in our analyses, which could affect the rooting of phylogenies. Alternatively, our comprehensive sampling of *Cyerce* spp. might reflect more accurately the relationships of

Cyerce and *Sohgenia*; further analyses involving more nuclear loci are needed to fully resolve these generic relationships (Krug et al., 2022).

Nominal specimens of *Cyerce elegans* were recovered in four distinct clades in phylogenetic analyses, and species delimitation analysis further supported these clades as candidate species. *Cyerce basi* sp. nov., *Cyerce whaapi* sp. nov., and *Cyerce elegans* are partially sympatric species with overlapping geographic ranges in Papua New Guinea, the Philippines, and/or New Caledonia. We consider these pseudocryptic species given limited external morphological differences among the taxa that were not apparent until molecular analyses were conducted. A distinct reddish band outlined the cerata margin in *Cyerce elegans*, a trait described by Bergh (1871) that was not observed in the other species. We could not compare the internal morphology among all four species, as the penial stylet from specimens of *Cyerce elegans* was either missing or deeply embedded into the tissue. We were also unable to obtain specimens of *Cyerce* sp. from the Red Sea for anatomical examination. The diet of the newly delimited species was not established as these taxa were not affiliated with a host alga.

Specimens identified in the field as *Cyerce nigricans* were recovered as two distinct lineages in the clade also including the morphologically distinct *Cyerce katiae* sp. nov. (Fig. 1). This is further supported by species delimitation analysis (Table 3) that recovered *Cyerce takanoi* sp. nov. and *Cyerce nigricans* as different species. The material of *Cyerce takanoi* sp. nov. examined herein could not be fully studied due to the difficulty of dissecting the penis from small specimens and further investigation is needed. Regardless, the external morphological traits of *Cyerce takanoi* sp. nov. closely resembles those of *Cyerce nigricans*.

Biogeography

The results of the present study differ from the biogeographic patterns observed in phylogeographic studies of other non-sacoglossan sea slug groups, which often recover the Indo-Pacific species forming a monophyletic group that is sister to Eastern Pacific and Atlantic species perhaps as the result of vicariant events (Gosliner & Johnson, 1999; Ornelas-Gatdula et al., 2012; Valdés, 2004; Ghanimi et al., 2020). In the present study, species from the Indo-West Pacific were sometimes sister to an Eastern Pacific (*C. orteai*) or Atlantic (*C. graeca* and *C.* cf.

cristalina) lineage, a pattern consistent with previous studies of other sacoglossans (Krug et al., 2015; Krug et al., 2016; Berriman et al., 2018; Medrano et al., 2018). For instance in clade 2, the sole Eastern Pacific species, *C. orteai*, was recovered as more closely related to a Central Pacific taxon, *Cyerce liliuokalaniae* sp. nov., than to any Caribbean species. It has been hypothesized the formation of the Isthmus of Panama inhibited gene flow between Caribbean and East Pacific populations, leading to a vicariant event resulting in sister species distributed on either side of the Isthmus (Knowlton, 1993; Leigh et al., 2014). One possibility is that the formation of the Isthmus of Panama led to a vicariant event of a once widespread *Cyerce*, followed by the extinction of *Cyerce* on the Eastern Pacific, and the recolonization of the Eastern Pacific from an Indo-Pacific ancestor (Medrano et al., 2018). Alternatively, the divergence of *C. orteai* from *Cyerce liliuokalaniae* sp. nov. could be attributed to interrupted gene flow caused by the East Pacific Barrier (ECP), an extensive stretch of deep water that limits colonization and reduces larval exchange between the eastern Pacific and the rest of the Indo-West Pacific (Briggs, 1961; Lessios et al., 1999; Valdés, 2004). Although genetically distinct, *C. orteai* and *Cyerce liliuokalaniae* sp. nov. were recovered as a sister clade to the Indo-West Pacific species, *C. pavonina* and *C. goodheartae* sp. nov. The isolation of the Hawaiian Archipelago could also serve as a barrier to gene flow among populations from the Indo-Pacific (Scheltema & Williams, 1983; Bowen et al., 2016; Crandall et al., 2019). Whether this geographic barrier is playing a role in the divergence of these two clades requires further investigation.

Previous studies have hypothesized the formation of geographic barriers could be associated with the speciation of marine taxa in the Indo-West Pacific (Crandall et al., 2019). The deep trench between the Vanuatu archipelago and New Caledonia was hypothesized to promote restricted ranges and divergence of heterobranch sea slug taxa (Valdés, 2001) and could explain the apparent endemic range of *C. whaapi* sp. nov. However, we do not see this pattern occurring in other species of the *Cyerce elegans* species complex, as *Cyerce basi* sp. nov., which was collected from Vanuatu, New Caledonia, and Papua New Guinea. Broader geographic sampling is expected to inform our understanding of the ranges of the newly described *Cyerce* species and shed light on these issues. Molecular data of specimens from the East Atlantic and Mediterranean remains needed to provide further insight into the global biogeography of *Cyerce.*

Diet and radular morphology

Our phylogenetic hypotheses support several radiations of *Cyerce*, possibly driven in part by adaptations to different hosts. Previous studies have suggested host use in sacoglossans is closely associated to the adaptive evolution of the radular morphology and pharyngeal musculature of the buccal mass (Jensen, 1983; Jensen, 1993; Krug et al., 2016; Berriman et al., 2018). Radular traits such as tooth shape and functionality of those traits have also been hypothesized to covary with algal host use, suggesting these characters could be attributed to host ecology (Jensen 1997; Krug et al., 2018a). We therefore considered whether the buccal mass and radular morphology could be related to host specialization within *Cyerce* given our findings.

There were some consistent morphological differences in radular morphology between the clades recovered in the phylogenetic analyses. For example, species in clade 1 have slightly, regularly curved teeth with large denticles on the distal half, whereas species in clade 2 have very elongate, narrow, straight teeth with triangular denticles. Species in clade 3 have curved teeth with very large denticles, similar to the teeth of species in clade 4, but in the latter the denticles are smaller in comparison to the width of the cusp. Tooth shape thus holds some phylogenetic signal and is somewhat conservative, as was external morphology in many cases, although both provided traits that could differentiate pseudocryptic species following molecular species delimitation.

Host use may be less conserved than tooth shape in *Cyerce*, in contrast, with species from different clades often feeding on the same algae. For instance, both *C. nigra* (clade 1) and *Cyerce tutela* sp. nov. (clade 2) consume *Udotea* spp. Despite having distinct radular morphologies, *Cyerce trowbridgeae* sp. nov. and *C. bourbonica* (clade 2), *C. elegans* (clade 3) and *C. pavonina* (clade 4) all feed on *Halimeda* spp. (Gosliner et al., 2015; Pittman and Fiene, 2003). Congeneric lineages can switch among host algae without convergence in radular tooth shape (Krug et al., 2016), suggesting varying tooth morphologies may be effective at piercing the cell wall of a given alga; radular shape is thus unlikely to constrain host shifts in Sacoglossa. The flexible host use in *Cyerce* suggests ecological speciation may be one factor driving reproductive isolation in this group, with multiple shifts likely having occurred from *Halimeda* to *Udotea*, *Chlorodesmis*, *Penicillus* and other hosts (Moreno et al., 2023). Further information on the diet of some poorly known species is needed, however. Moreover, the lack of physical host association for many *Cyerce* species suggests host-mediation reproductive isolation is not as likely to contribute to speciation in this group as in other sacoglossans that are usually found living on the algae they consume.

Sexual Selection

The penial stylet has been hypothesized to be plesiomorphic within Sacoglossa, but also independently re-evolving repeatedly within some sacoglossan lineages (Jensen, 1997b; Smolensky et al., 2009). Anatomical examinations of the male reproductive system in species of *Cyerce* revealed distinct penial stylets. Gascoigne (1974) suggested there are two different types of stylets in sacoglossans: 'penetrant' and 'coupling' that differ functionally in the administration of sperm transfer during copulation. Gascoigne (1974) described 'penetrant' stylets as 'rigid' and 'slightly curved' or 'straight,' as observed in *Cyerce nigricans*. In contrast, 'coupling' stylets can be short, 'tea-pot spout' shaped, or 'long and flexible'. Species of *Cyerce* exhibit both 'coupling' and 'penetrant' stylet types. Some species have long, curved penial stylets, such as *C. nigra* (clade 1) and clade 2 species, whereas short, straight stylets were found in clade 4. Because there are correlations between stylet morphology and phylogeny, sexual selection could have promoted reproductive barriers among lineages during the early radiation of *Cyerce*, a process that has been observed in other sacoglossans and marine taxa more generally (Munday et al., 2014; Krug et al., 2016). Traits such as genital morphology under sexual selection can also be involved in speciation of sympatric taxa, particularly during reinforcement scenarios, so the more subtle variations used here to delimit species could also reflect selective forces involved in the speciation process (Churchill et al., 2013; Krug et al., 2016; Moreno et al. 2023).

Concluding remarks

The integration of molecular and morphological analyses support at least 25 species of *Cyerce*, more than doubling the recognized biodiversity of this genus. Our results support the hypothesis that host specialization and sexual selection contributed to speciation of *Cyerce*, notably resulting in the forming of pseudocryptic species complexes (*C. nigricans*, *C. elegans*) resolved in this study. This systematic revision of Indian and Pacific Ocean *Cyerce* adds to the growing evidence that marine heterobranch diversity remains badly underestimated, and will facilitate subsequent comparative analyses of trait-based diversification in Sacoglossa.

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FIGURES

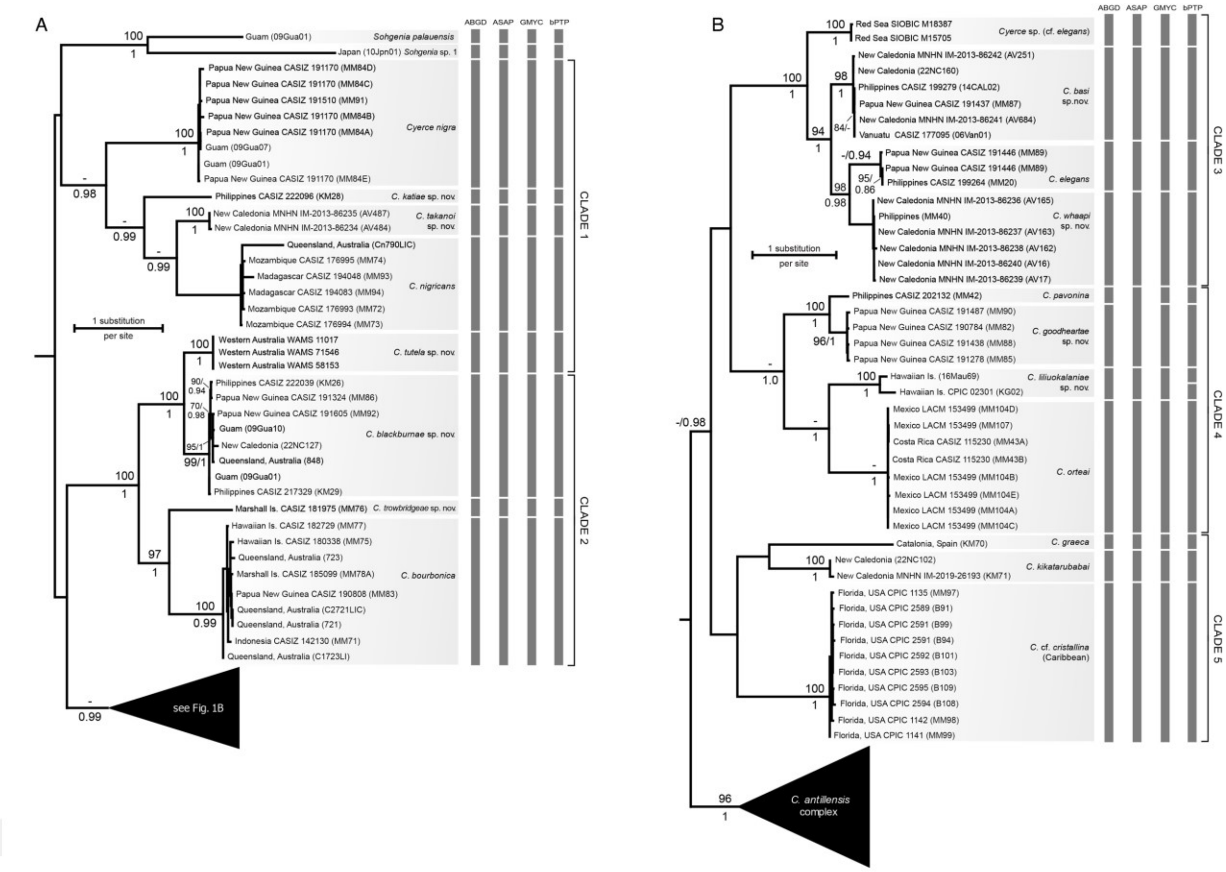

Figure 1. Consensus maximum likelihood concatenated tree of all three genes (16S, CO1, H3) recovered 19 distinct lineages of *Cyerce* arranged into 5 main clades, plus two species *Sohgenia* included as outgroups. Posterior probabilities (below branches) greater than 0.90 and ML bootstrap values (above branches) greater than 70 considered well supported. Results of four species delimitation analyses are indicated by vertical bars; horizontal shaded bars enclose specimens grouped as species recognized herein.

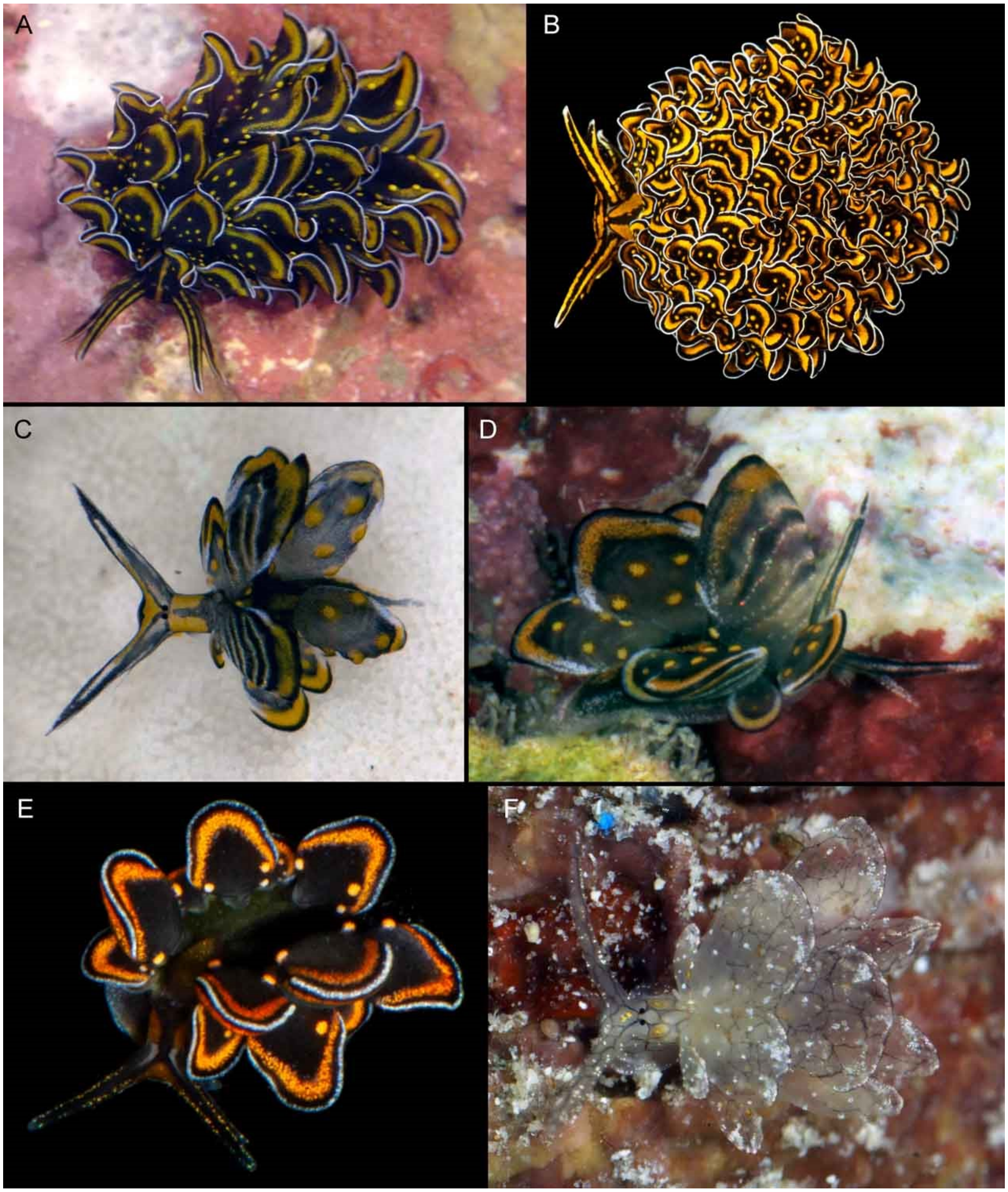

Figure 2. Photographs of live animals of *Cyerce* clade 1. **A–B.** *Cyerce nigricans* (Pease, 1866), specimen from South Madagascar, isolate MM94, CASIZ 194083 (A), specimen from Poum, New Caledonia (B). **C–D.** *Cyerce nigra* Bergh, 1871, specimen from Guam, isolate MM110, CPIC 00624 (C), specimen from Papua New Guinea, isolate MM91, CASIZ 191510 (D). **E.** *Cyerce takanoi* sp. nov., specimen from Puoebo, New Caledonia isolate AV484, MNHN IM-2013-86234. **F.** *Cyerce katiae* sp. nov., specimen from Romblon, Philippines, isolate KM28, CASIZ 222096.

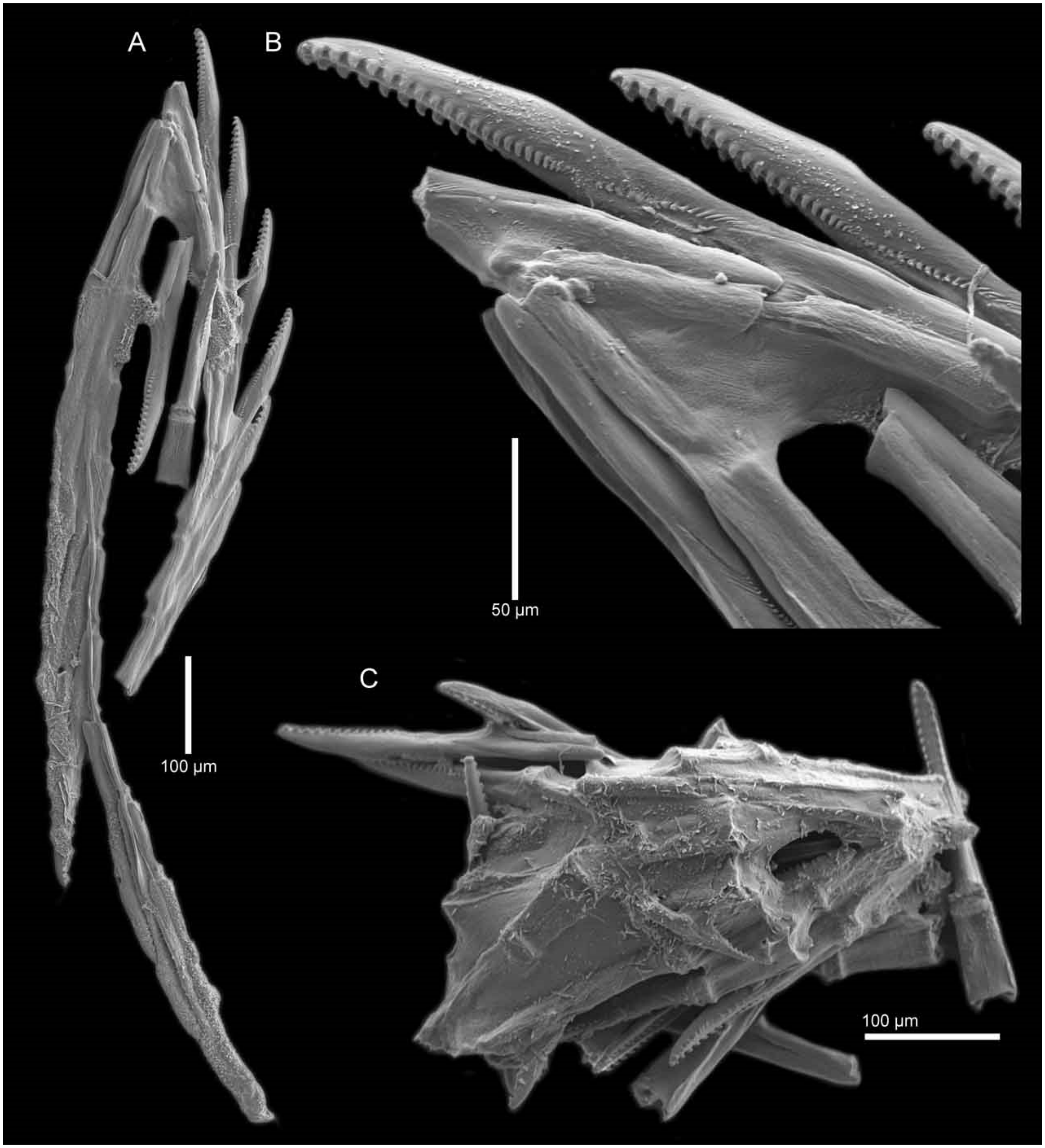

Figure 3. SEM micrographs of the radula of *Cyerce nigricans* (Pease, 1866), specimen from Pandane Beach, Mozambique, isolate MM72, CASIZ 176993. **A.** Complete radula with descending and ascending limb, ascus no longer attached to end of descending limb. **B.** Active teeth. **C.** Complete ascus.

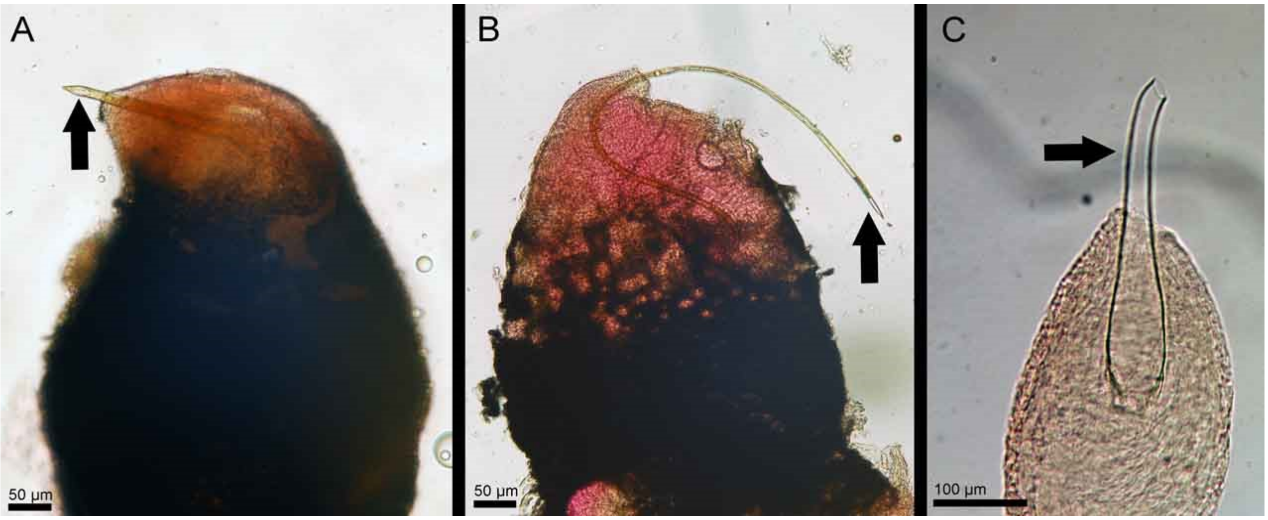

Figure 4. Stained penises of species of *Cyerce* showing the penial stylets (indicated by black arrows). **A.** *Cyerce nigricans* (Pease, 1866), specimen from Pandane Beach, Mozambique, isolate MM72, CASIZ 176993. **B.** *Cyerce nigra* Bergh, 1871, specimen from Guam, isolate 09Gua07, LACM pending. **C.** *Cyerce katiae* sp. nov., specimen from Romblon, Philippines, isolate KM28, CASIZ 222096.

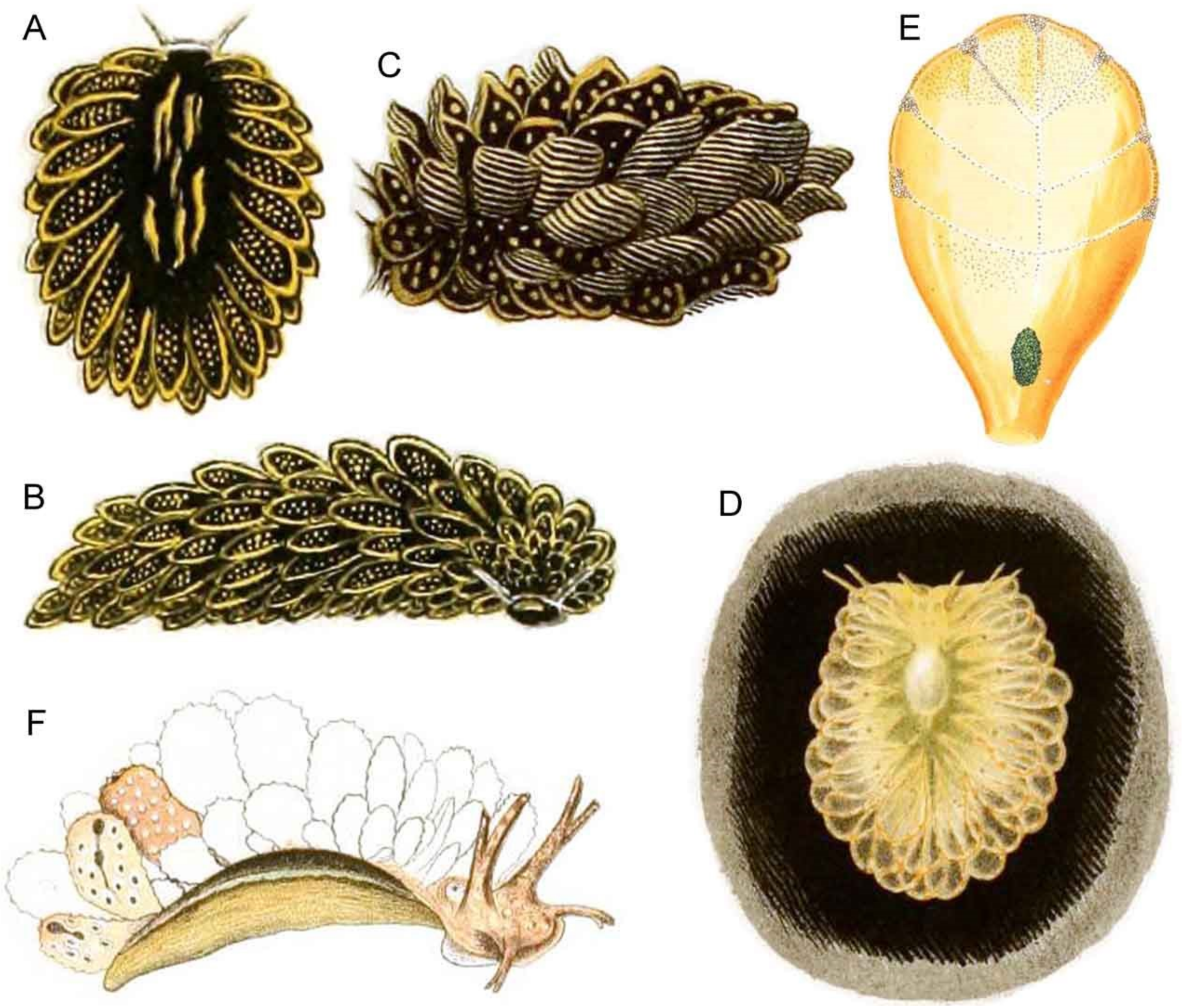

Figure 5. Drawings published with the original descriptions of two species of *Cyerce*. **A–B.** *Cyerce nigra* var. *ocellata* Bergh (1873: pl. 9, figs. 8–9) [= *Cyerce nigricans* (Pease, 1866)], drawing attributed to Eduard Heinrich Graeffe. **C.** *Cyerce nigra* (Bergh, 1871: pl. 1, fig. 10), drawing attributed to Carl Gottfried Semper. **D.** *Cyerce elegans* (Bergh, 1871: pl. 1, fig. 9), drawing attributed to Carl Gottfried Semper. **E.** *Cyerce elegans* var. (Bergh, 1888: pl. 77, fig. 6), drawing attributed to Karl August Möbius. **F.** *Cyerce pavonina* (Bergh, 1888: pl. 77, fig. 3), drawing attributed to Karl August Möbius.

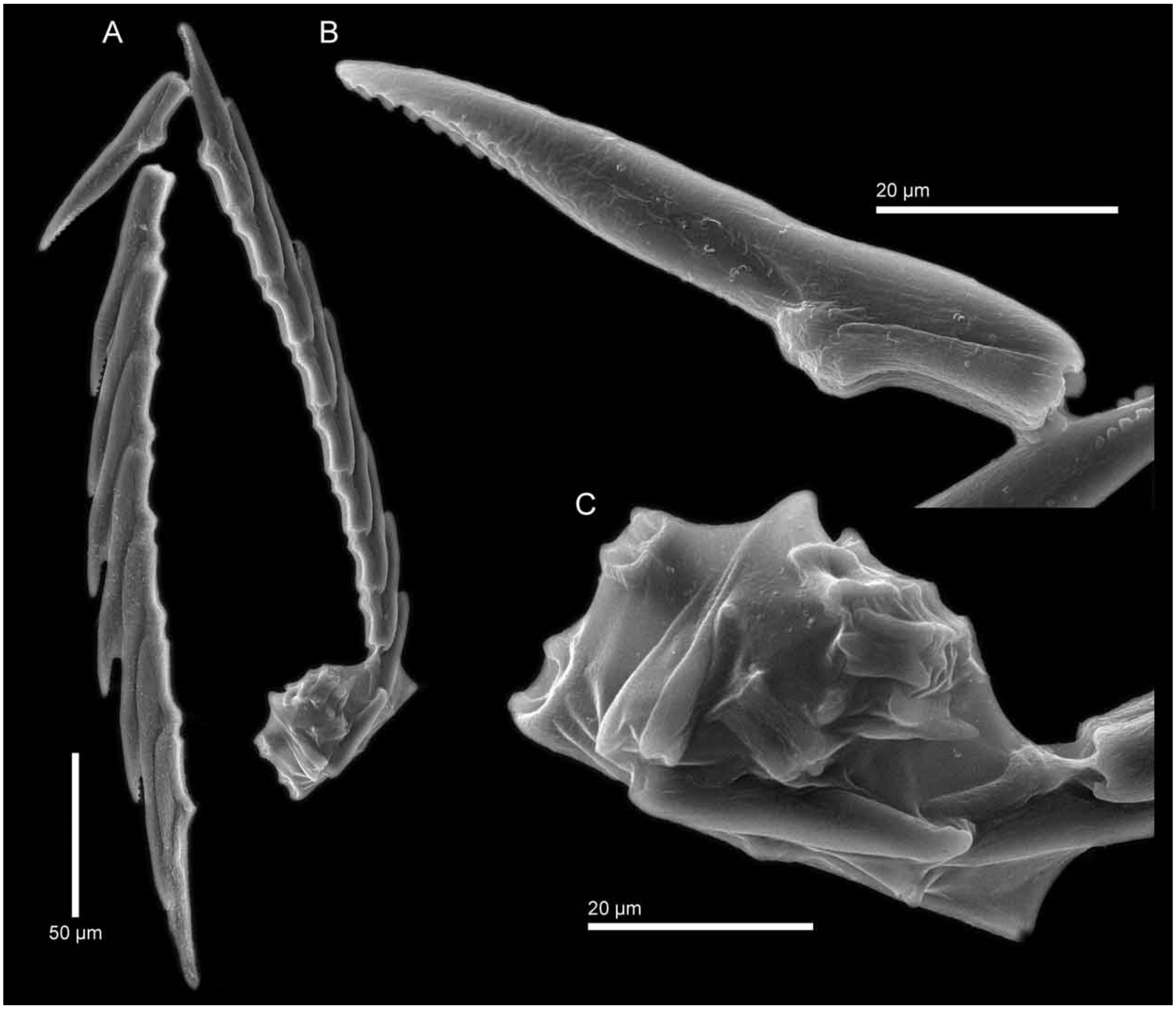

Figure 6. SEM micrographs of the radula of *Cyerce nigra* Bergh, 1871, specimen from Madang, Papua New Guinea, isolate MM91, CASIZ 191510. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Active tooth. **C.** Complete ascus.

Figure 7. SEM micrographs of the radula of *Cyerce takanoi* sp. nov. **A.** Complete radula with descending and ascending limb, ascus missing. **B.** Active tooth.

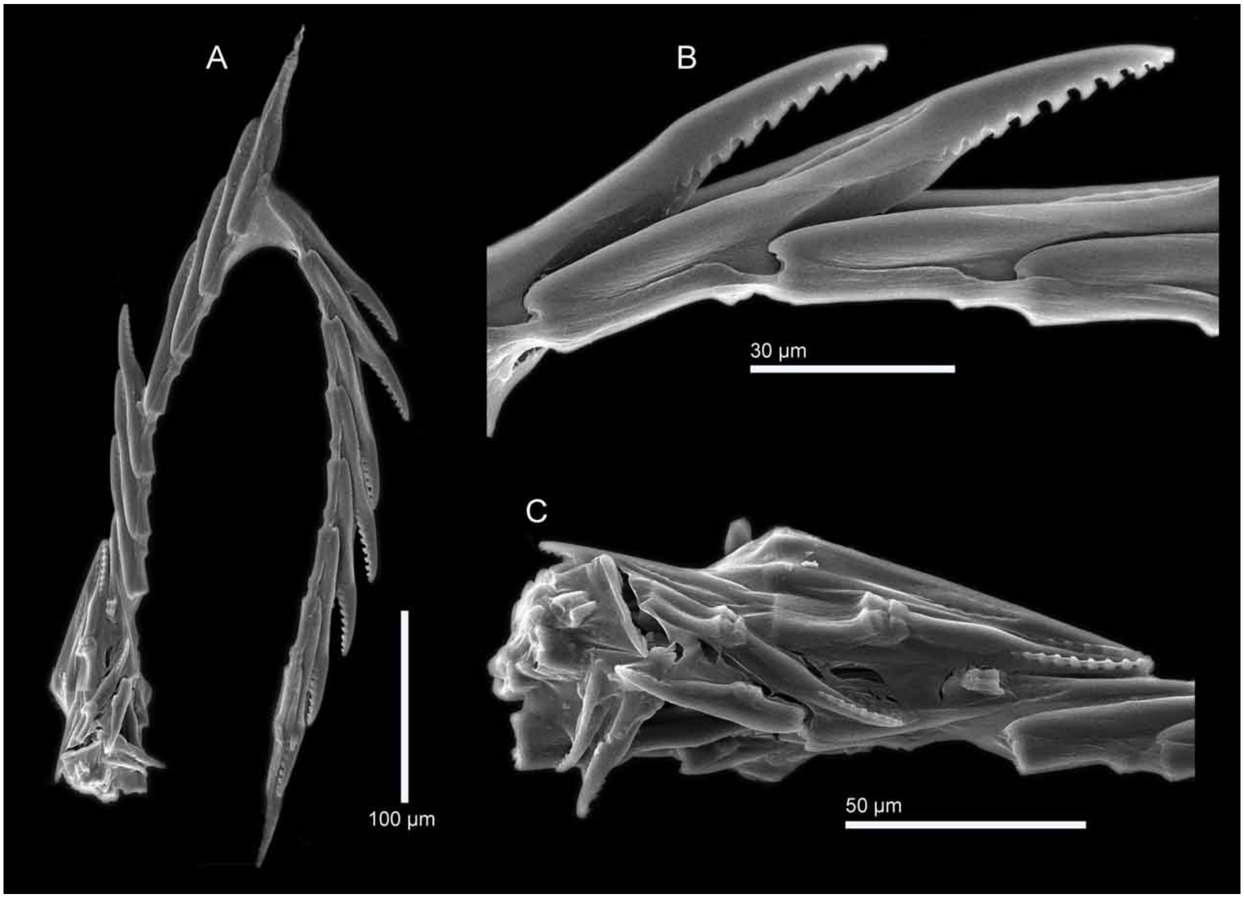

Figure 8. SEM micrographs of the radula of *Cyerce katiae* sp. nov., specimen from Romblon, Philippines, isolate KM28, CASIZ 222096. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Active tooth. **C.** Complete ascus.

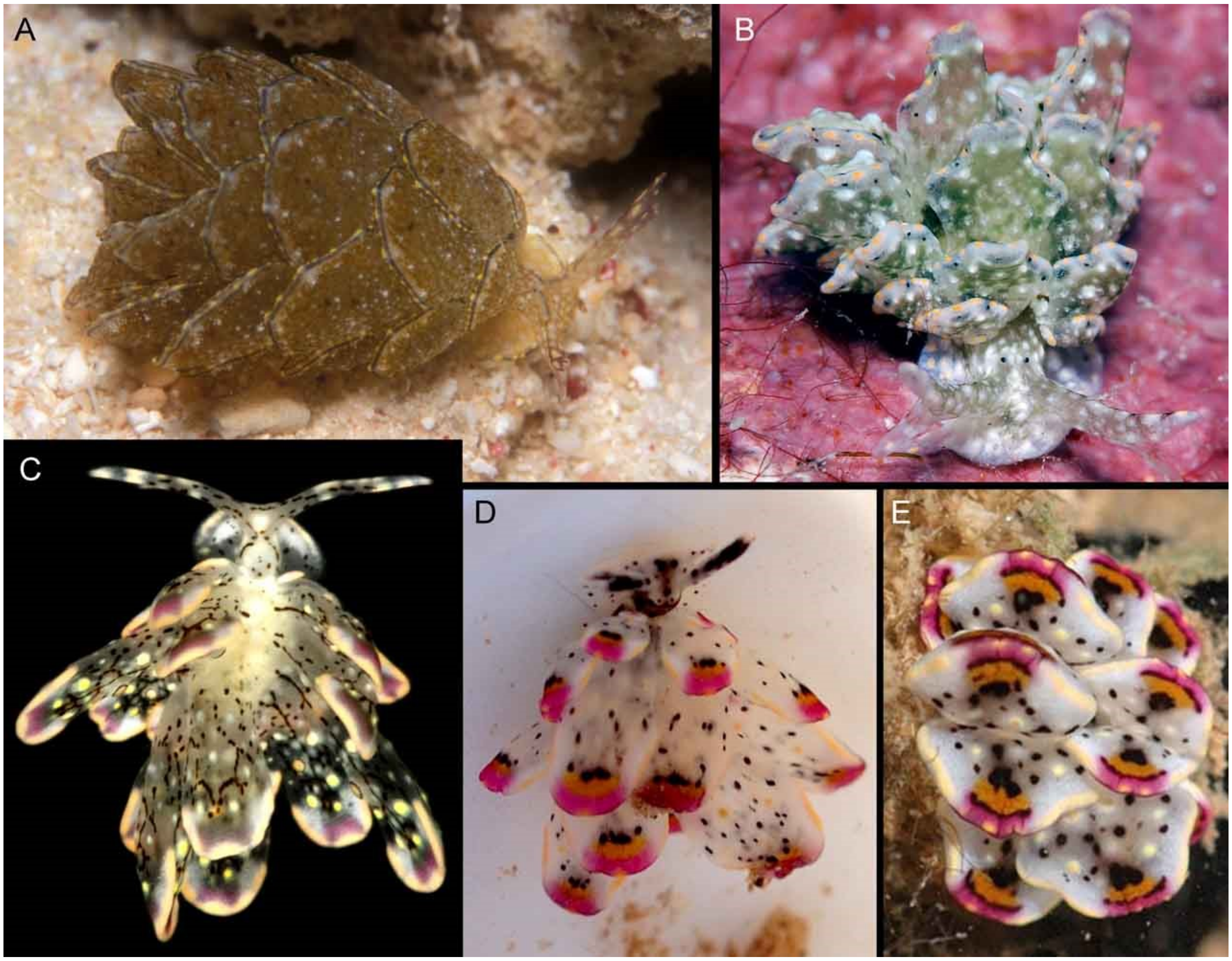

Figure 9. Photographs of live animals of *Cyerce* clade 2. **A.** *Cyerce trowbridgeae* sp. nov., specimen from the Kwajalen Atoll, Marshall Islands, isolate MM76, CASIZ 181975. **B.** *Cyerce bourbonica* Yonow, 2012, specimen from the Kwajalen Atoll, Marshall Is., isolate MM78A, CASIZ 185099. **C.** *Cyerce blackburnae* sp. nov., specimen from Madang, Papua New Guinea, isolate MM86, CASIZ 191324. **D–E.** *Cyerce tutela* sp. nov., specimen from Western Australia, WAM S71546, on white background (G), in situ (H), photos by D. Koehler-Tuefel.

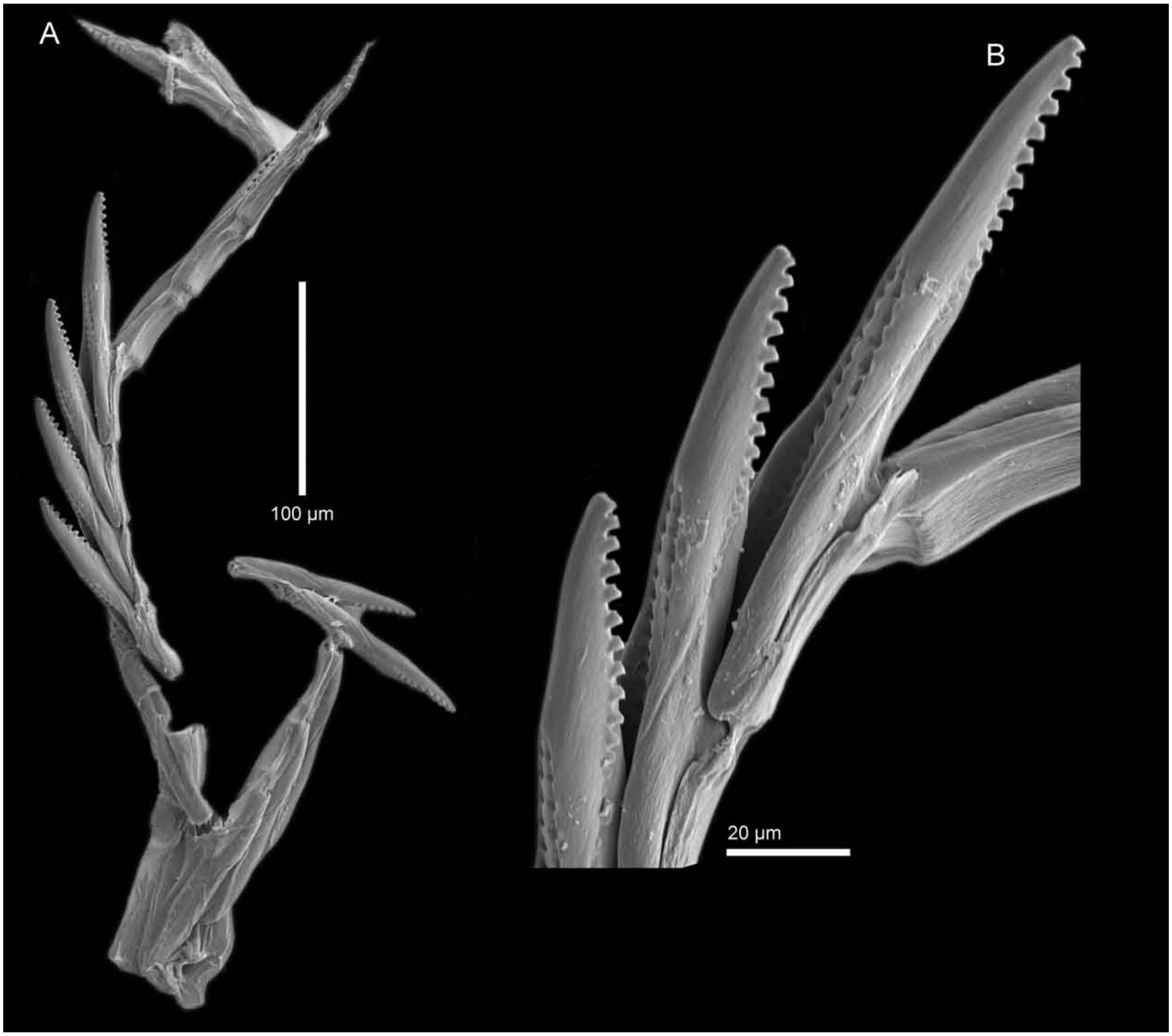

Figure 10. SEM micrographs of the radula of *Cyerce bourbonica* Yonow, 2012, specimen from Maui, Hawaiian Is., USA, isolate MM77, CASIZ 182729. **A.** Fragment of the radula. **B.** Active tooth.

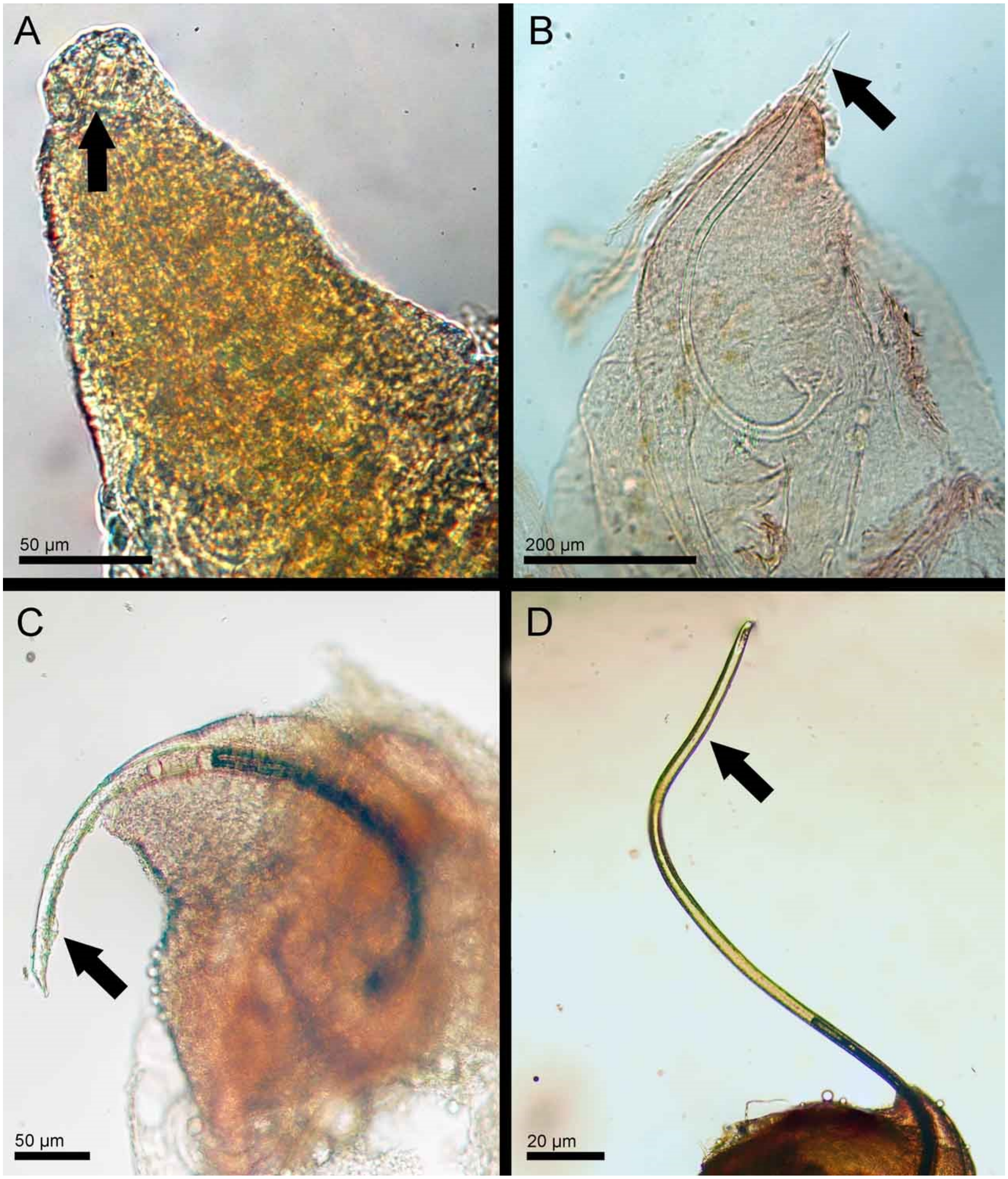

Figure 11. Stained penises of species of *Cyerce* showing the penial stylets (indicated by black arrows). **A.** *Cyerce bourbonica* Yonow, 2012, specimen from Maui, Hawaiian Is., USA, isolate MM77, CASIZ 182729. **B.** *Cyerce trowbridgeae* sp. nov., specimen from the Kwajalen Atoll, Marshall Islands, isolate MM76, CASIZ 181975. **C.** *Cyerce blackburnae* sp. nov., specimen from Romblon, Philippines, isolate KM26, CASIZ 222039. **D.** *Cyerce tutela* sp. nov., specimen from Dampier, Western Australia, isolate WAMS71546.

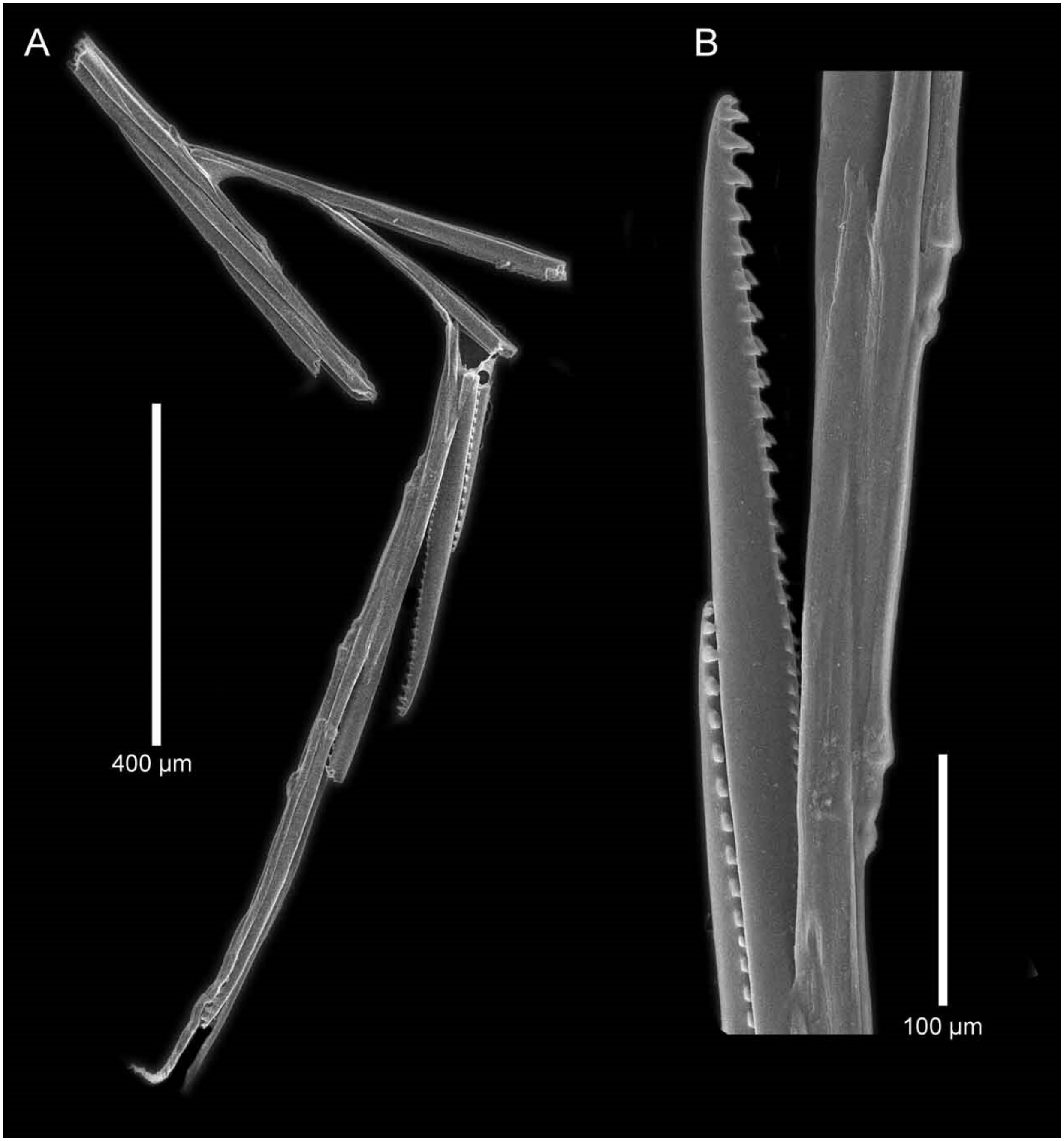

Figure 12. SEM micrographs of the radula of *Cyerce trowbridgeae* sp. nov., specimen from the Kwajalen Atoll, Marshall Islands, isolate MM76, CASIZ 181975. **A.** Fragment of the radula. **B.** Active tooth.

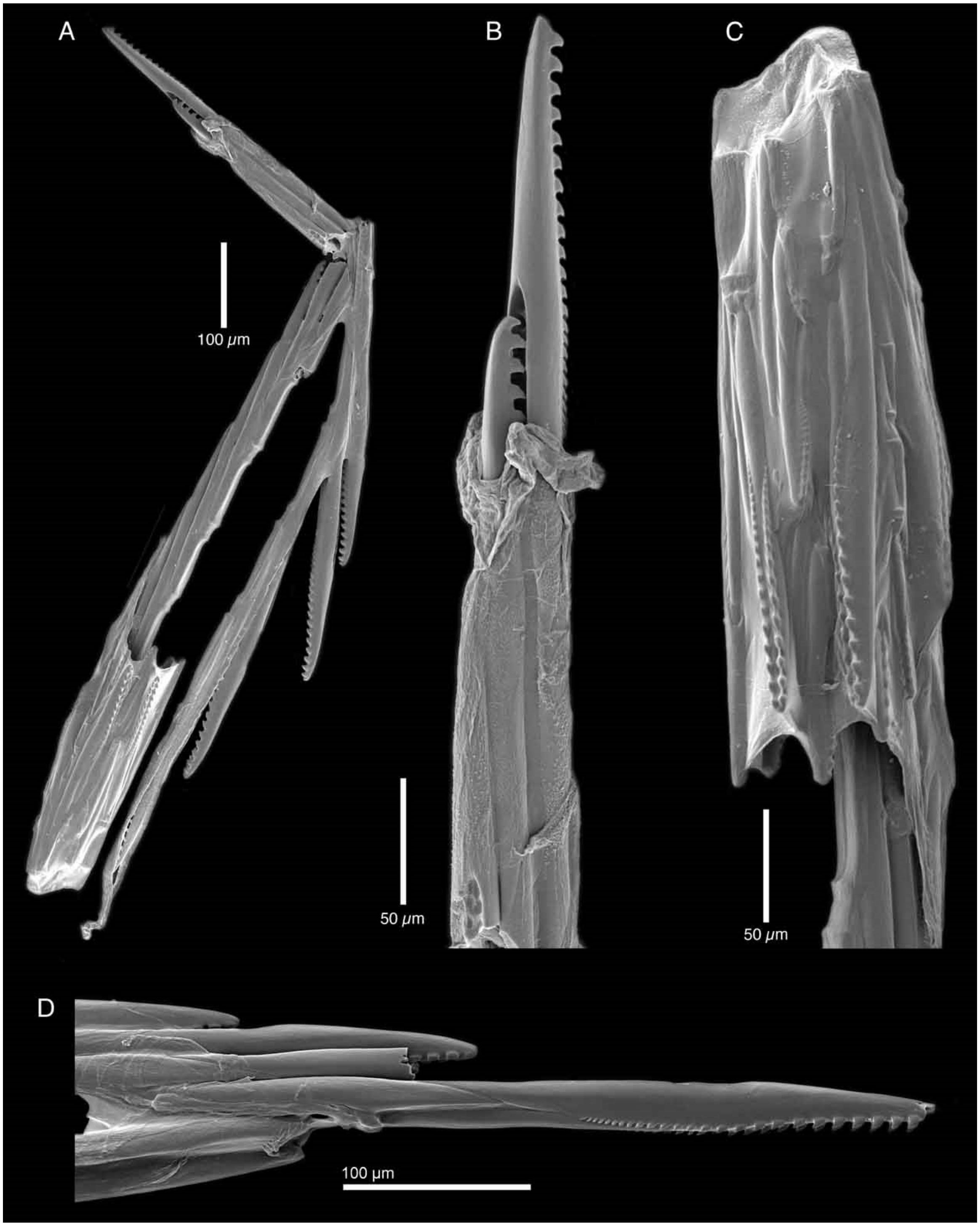

Figure 13. SEM micrographs of the radula of *Cyerce blackburnae* sp. nov. **A–C.** Specimen from Romblon, Philippines, isolate KM26, CASIZ 222039; complete radula with descending and ascending limb, ascus attached to end of descending limb (A); active tooth (B); ascus (C). **D.** Specimen from Guam, isolate 09Gua01, LACM 186691; active tooth.

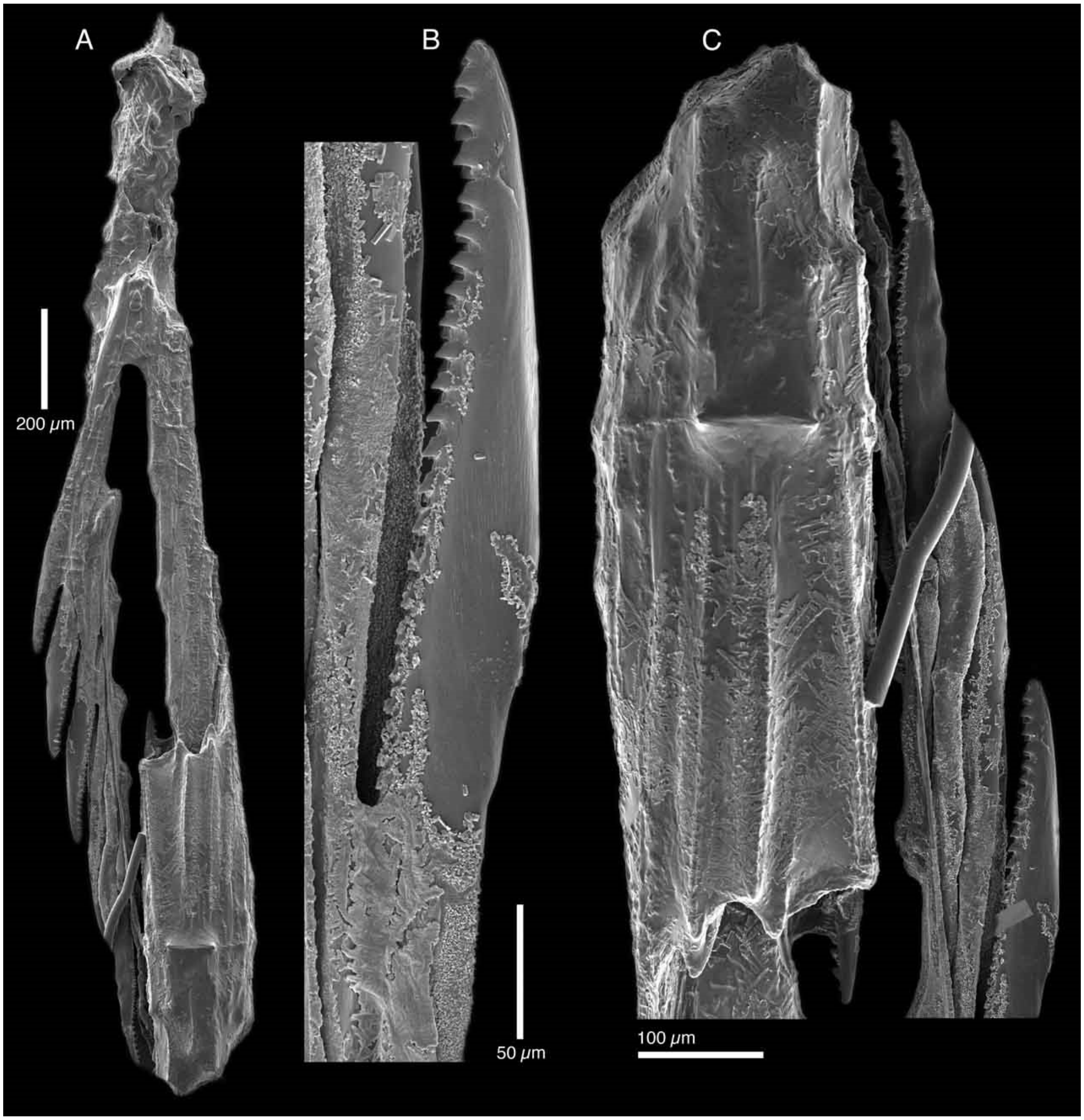

Figure 14. SEM micrographs of the radula of *Cyerce tutela* sp. nov., specimen from Dampier, Western Australia, isolate WAMS71546. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Tooth of ascending limb. **C.** Complete ascus.

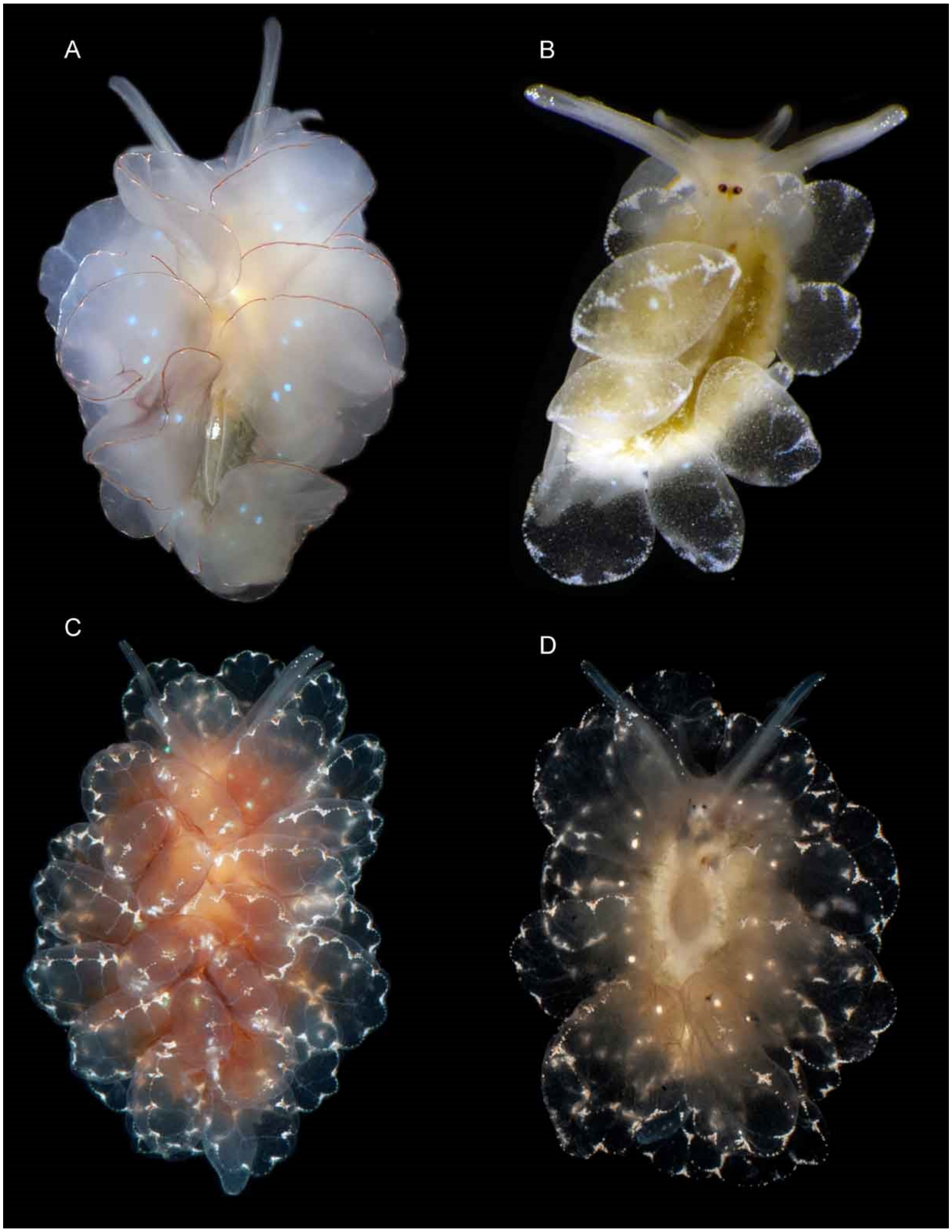

Figure 15. Photographs of live animals of *Cyerce* clade 3. **A.** *Cyerce elegans* Bergh, 1871, specimen from Luzon, Philippines, isolate MM20, CASIZ 199264. **B.** *Cyerce* sp., specimen from Makkah, Saudi Arabia (Red Sea), SIOBIC M15387, photo by G. Rouse. **C.** *Cyerce basi* sp. nov., specimen from Koumac, New Caledonia, isolate AV251, NHMN IM-2013-86242. **D.** *Cyerce whaapi* sp. nov., specimen from Koumac, New Caledonia, isolate AV17, NHMN IM-2013-86239.

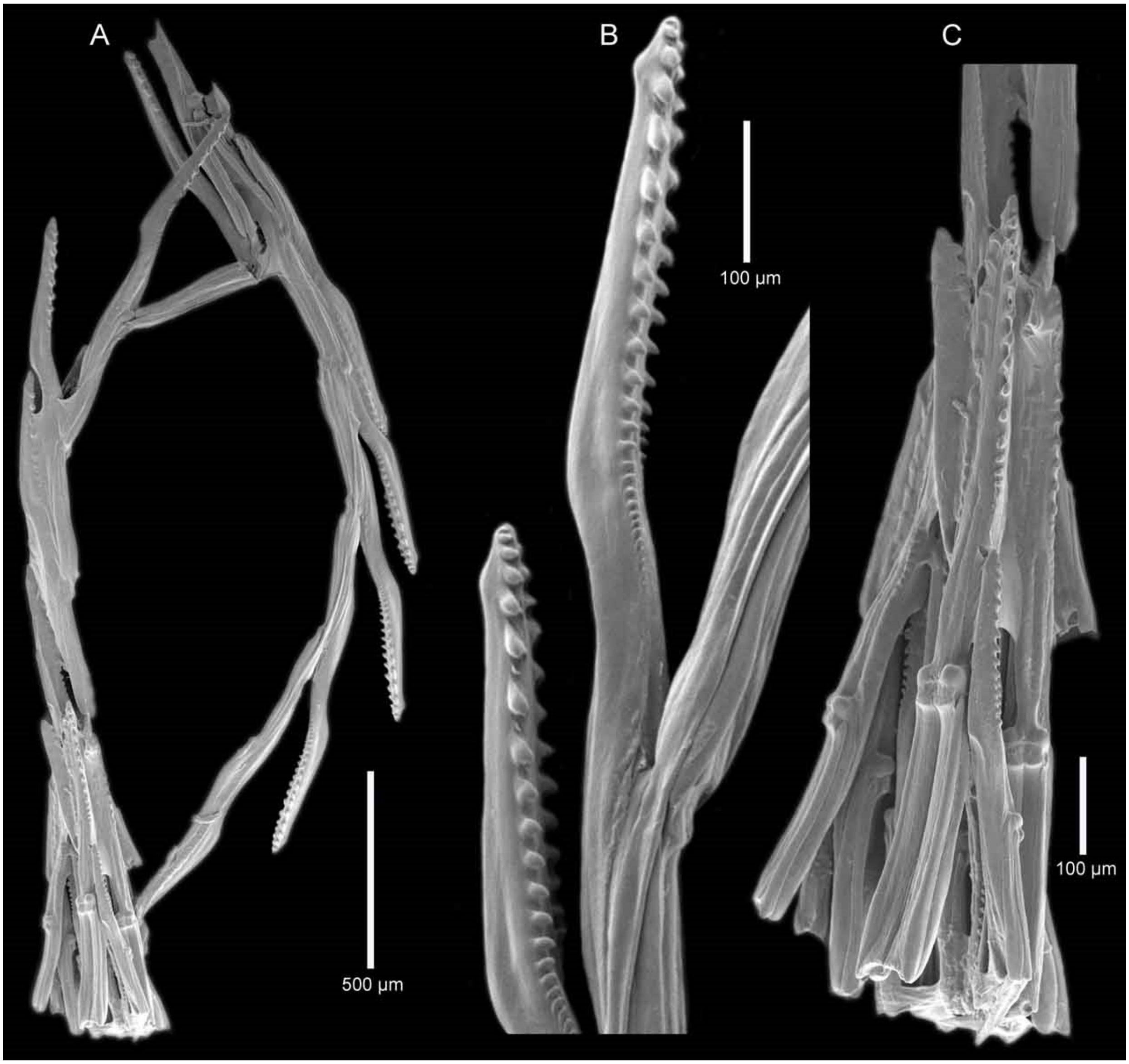

Figure 16 SEM micrographs of the radula of *Cyerce elegans* Bergh, 1871, specimen from Madang, Papua New Guinea, isolate MM20, CASIZ199264. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Active tooth. **C.** Complete ascus.

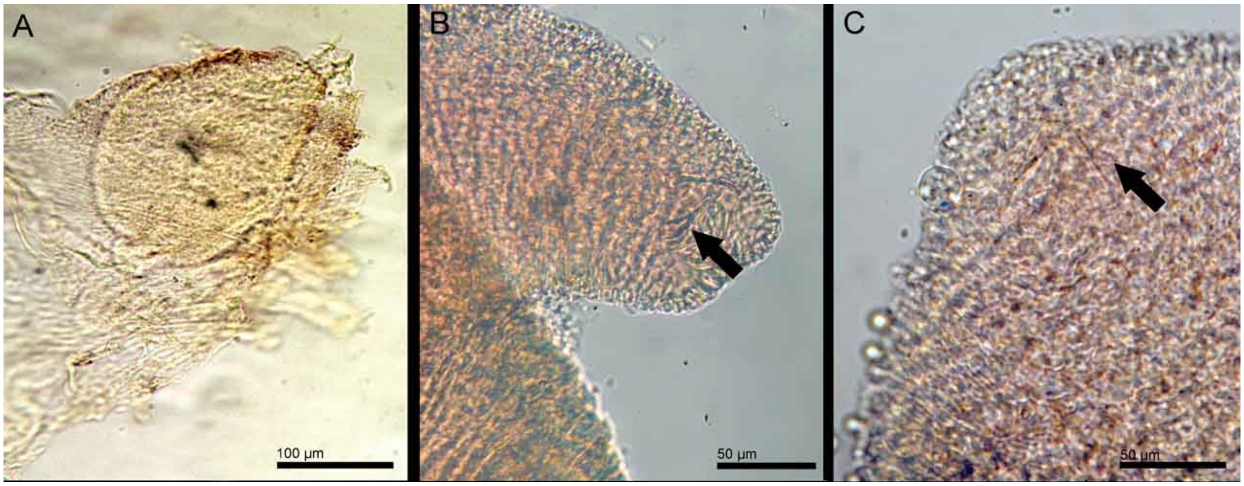

Figure 17. Stained penises of species of *Cyerce* showing the penial stylets (indicated by black arrows). **A.** *Cyerce elegans* Bergh, 1871, specimen from Madang, Papua New Guinea, isolate MM20, CASIZ199264. **B.** *Cyerce basi* sp. nov., specimen from Koumac, New Caledonia, isolate AV684, MNHN IM-2013-86241. **C.** *Cyerce whaapi* sp. nov., specimen from Koumac, New Caledonia, isolate AV017, MNHN IM-2013-86239.

Figure 18. SEM micrographs of the radula of *Cyerce basi* sp. nov., specimen from Koumac, New Caledonia, isolate AV684, MNHN IM-2013-86241. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Active tooth. **C.** Complete ascus.

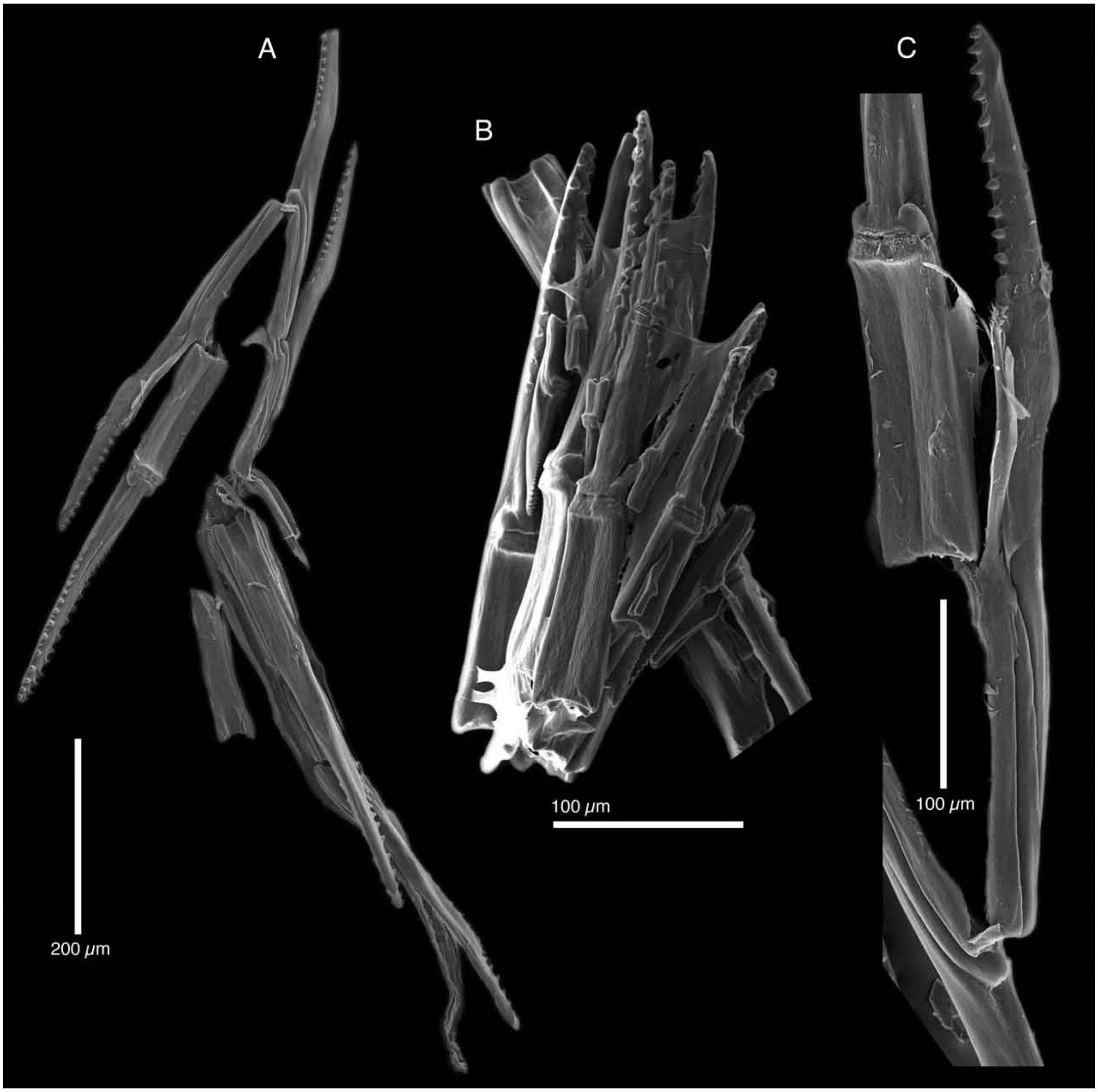

Figure 19. SEM micrographs of the radula of *Cyerce whaapi* sp. nov., specimen from Koumac, New Caledonia, isolate AV017, MNHN IM-2013-86239. **A.** Complete radula with descending and ascending limb. **B.** Complete ascus. **C.** Active tooth.

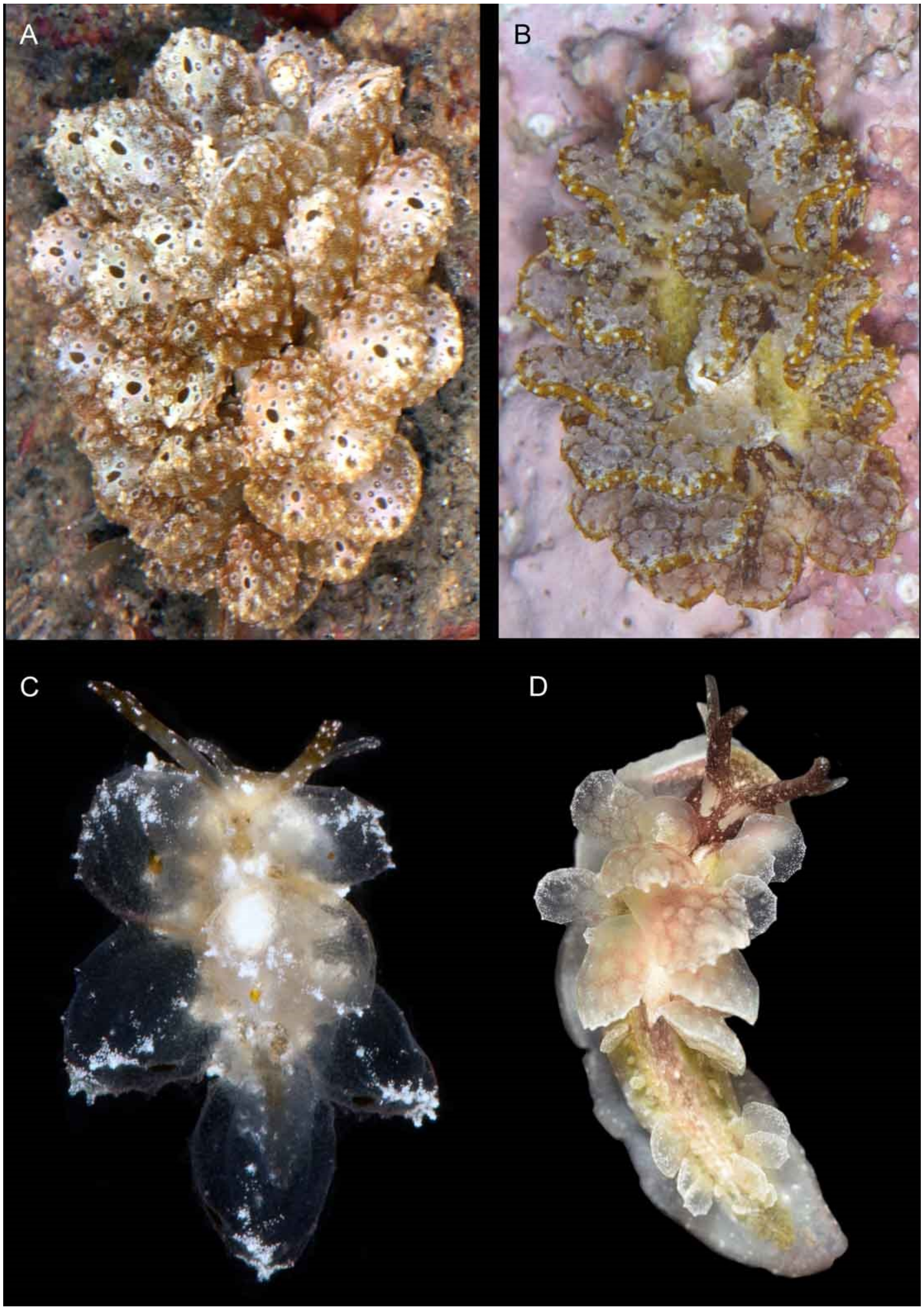

Figure 20. Photographs of live animals of *Cyerce* clade 4. **A.** *Cyerce pavonina* (Bergh, 1888), specimen from Luzon, Philippines, isolate MM42, CASIZ 202132. **B.** *Cyerce orteai* Valdés & Camacho-García, 2000, specimen from Nayarit, Mexico, isolate MM107, LACM 175024. **C.** *Cyerce goodheartae* sp. nov., specimen from Madang, Papua New Guinea, isolate MM90,

CASIZ 191487. **D.** *Cyerce liliuokalaniae* sp. nov., specimen from the Hawaiian Is., USA, isolate KG02, CPIC 02301.

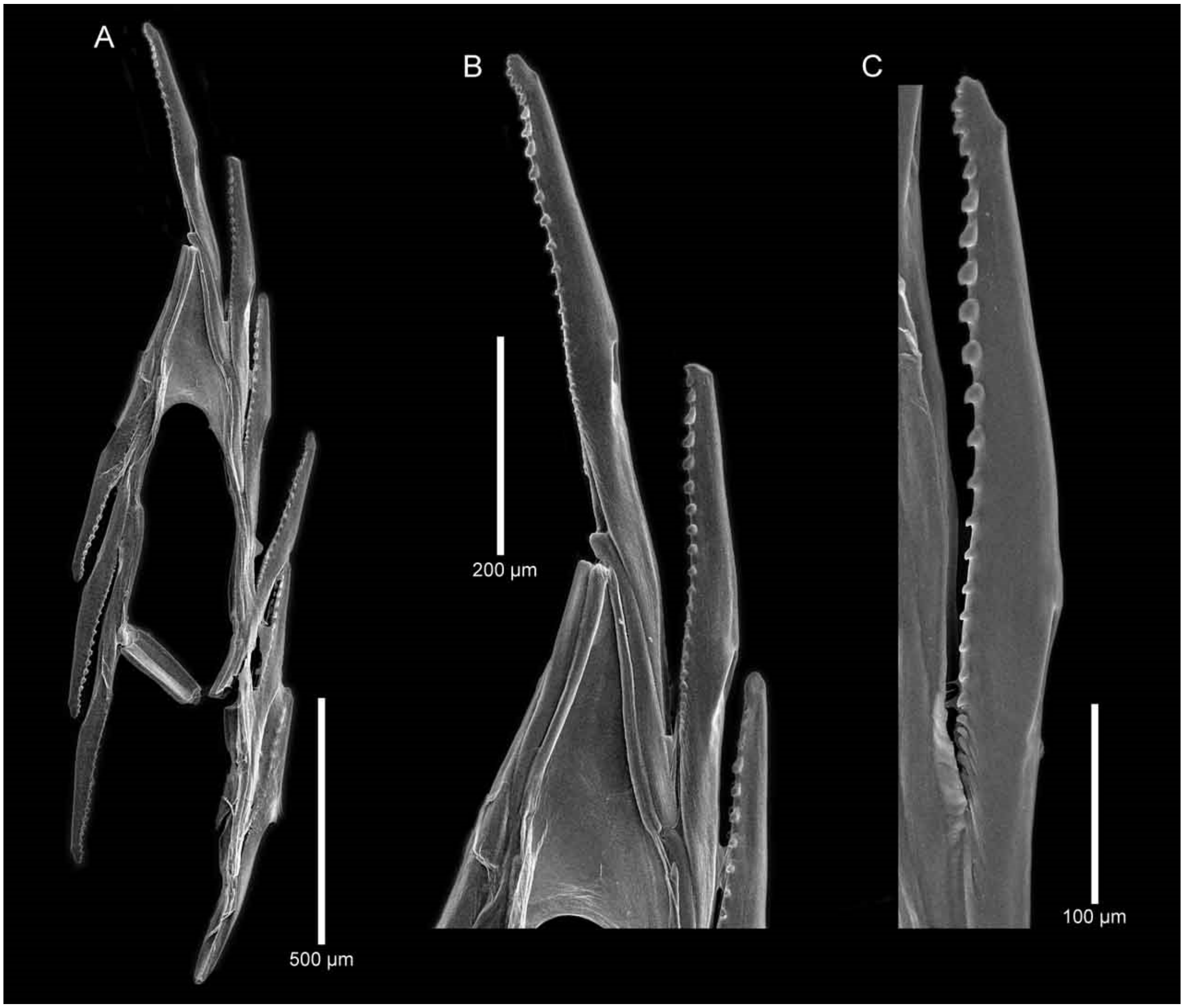

Figure 21. SEM micrographs of the radula of *Cyerce pavonina* Bergh, 1888, specimen from Luzon, Philippines, isolate MM42, CASIZ 202132. **A.** Complete radula with descending and ascending limb. **B.** Active tooth. **C.** Detail of the active tooth denticulation.

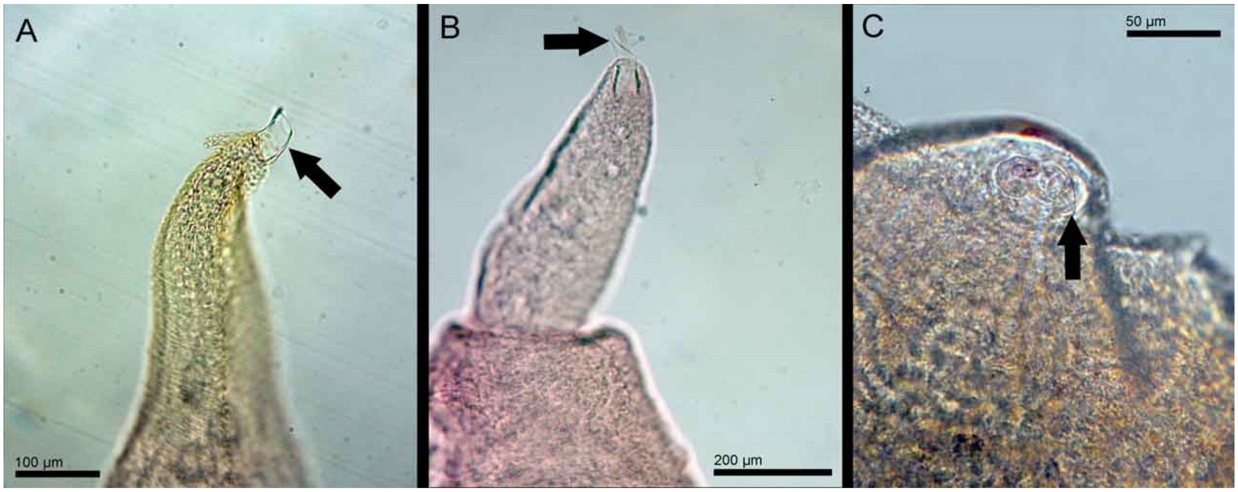

Figure 22. Stained penises of species of *Cyerce* showing the penial stylets (indicated by black arrows). **A.** *Cyerce pavonina* Bergh, 1888, specimen from Luzon, Philippines, isolate MM42, CASIZ 202132. **B.** *Cyerce goodheartae* sp. nov., specimen from Madang, Papua New Guinea, isolate MM82, CASIZ 190784. **C.** *Cyerce liliuokalaniae* sp. nov., specimen from Oahu, Hawaiian Is, USA, isolate KG02, CPIC 02301.

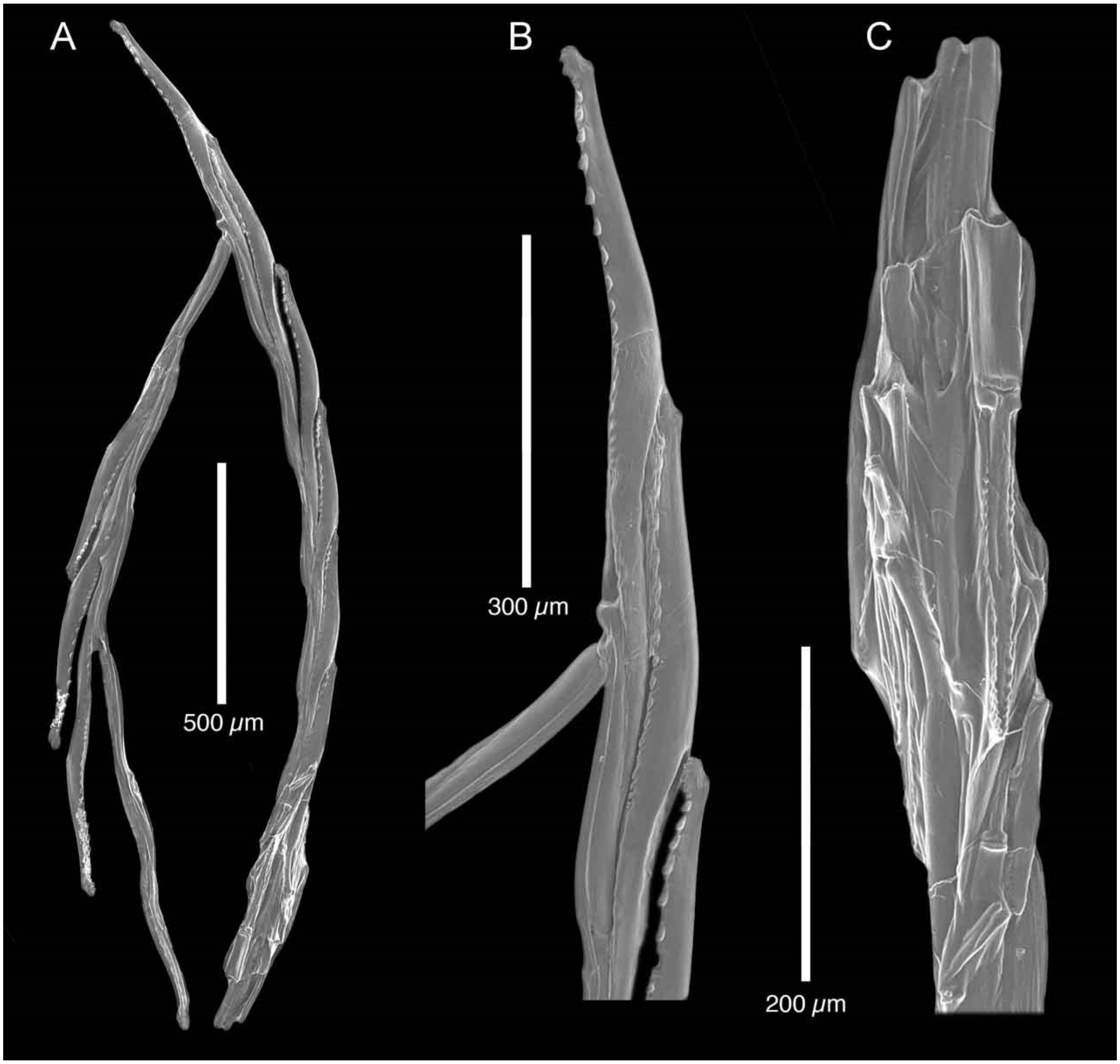

Figure 23. SEM micrographs of the radula of *Cyerce orteai* Valdés & Camacho-García, 2000, specimen from Nayarit, Mexico, LACM 153499. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Active tooth. **C.** Complete ascus.

Figure 24. SEM micrographs of the radula of *Cyerce goodheartae* sp. nov. **A–B.** Specimen from Madang, Papua New Guinea, isolate MM82, CASIZ 190784; complete radula with descending and ascending limb (A); active tooth (B). **C–E.** Specimen from Madang, Papua New Guinea, isolate MM85, CASIZ 191278; complete radula with descending and ascending limb (C); ascus (D); detail of teeth of ascending limb (E).

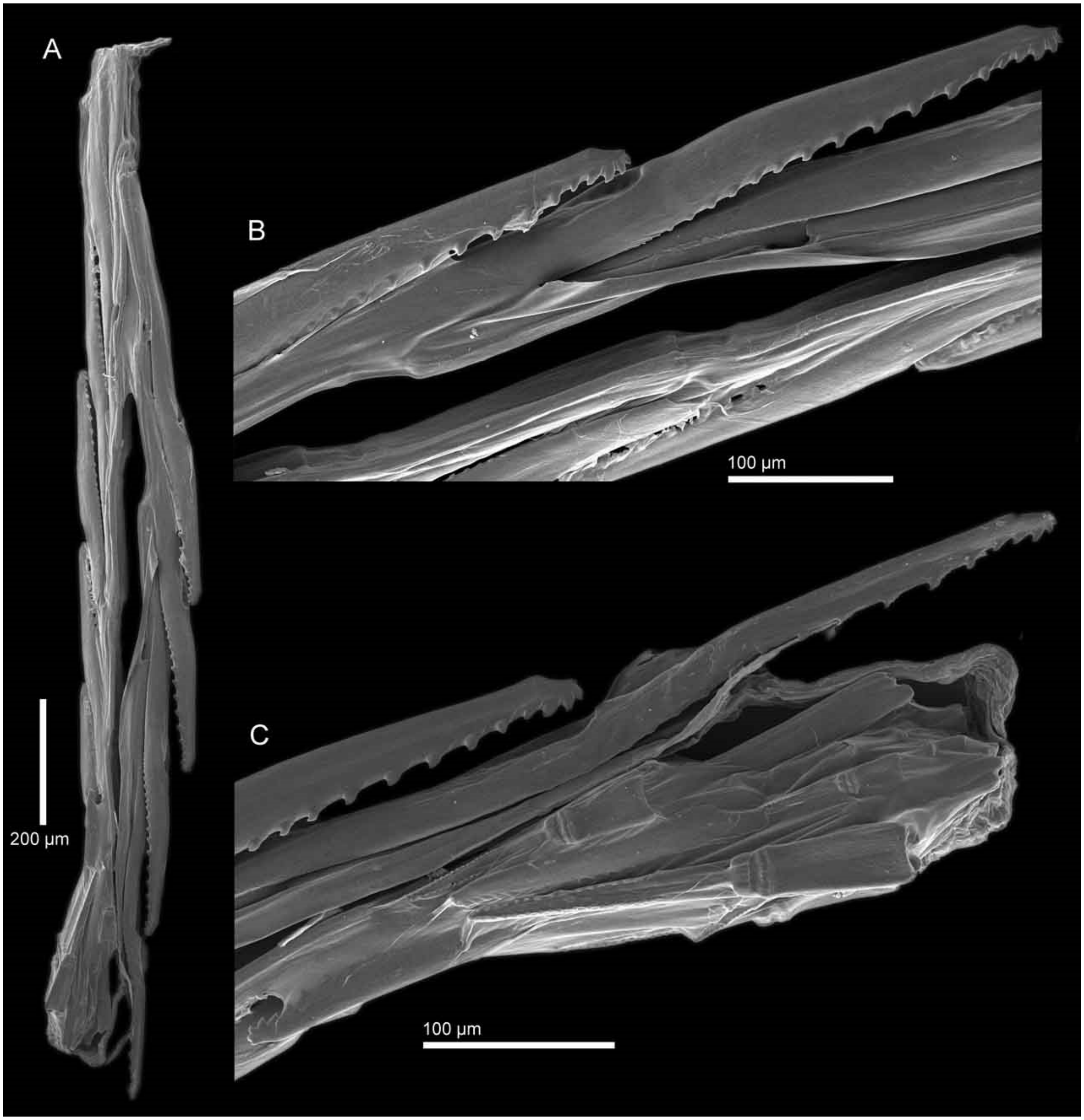

Figure 25. SEM micrographs of the radula of *Cyerce liliuokalaniae* sp. nov., specimen from Oahu, Hawaiian Is, USA, isolate KG02, CPIC 02301. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Tooth of ascending limb. **C.** Complete ascus.

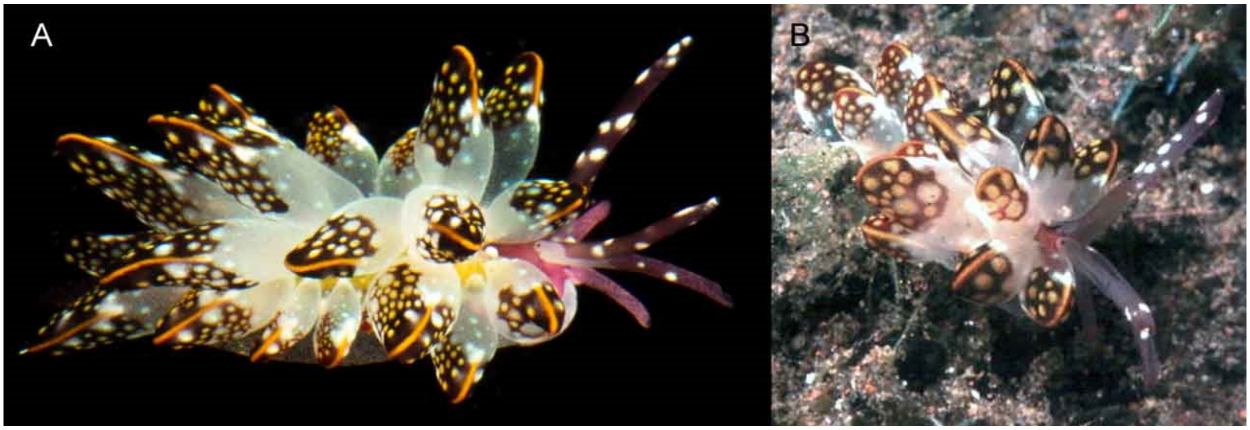

Figure 26. Photographs of live animals of *Cyerce kikutarobabai* Hamatani, 1976. **A.** Specimen from Nouméa, New Caledonia, isolate 22NC304, MNHN IM-2019-26210. **B.** Specimen from Bali, Indonesia, isolate MM41A, CASIZ 172614A.

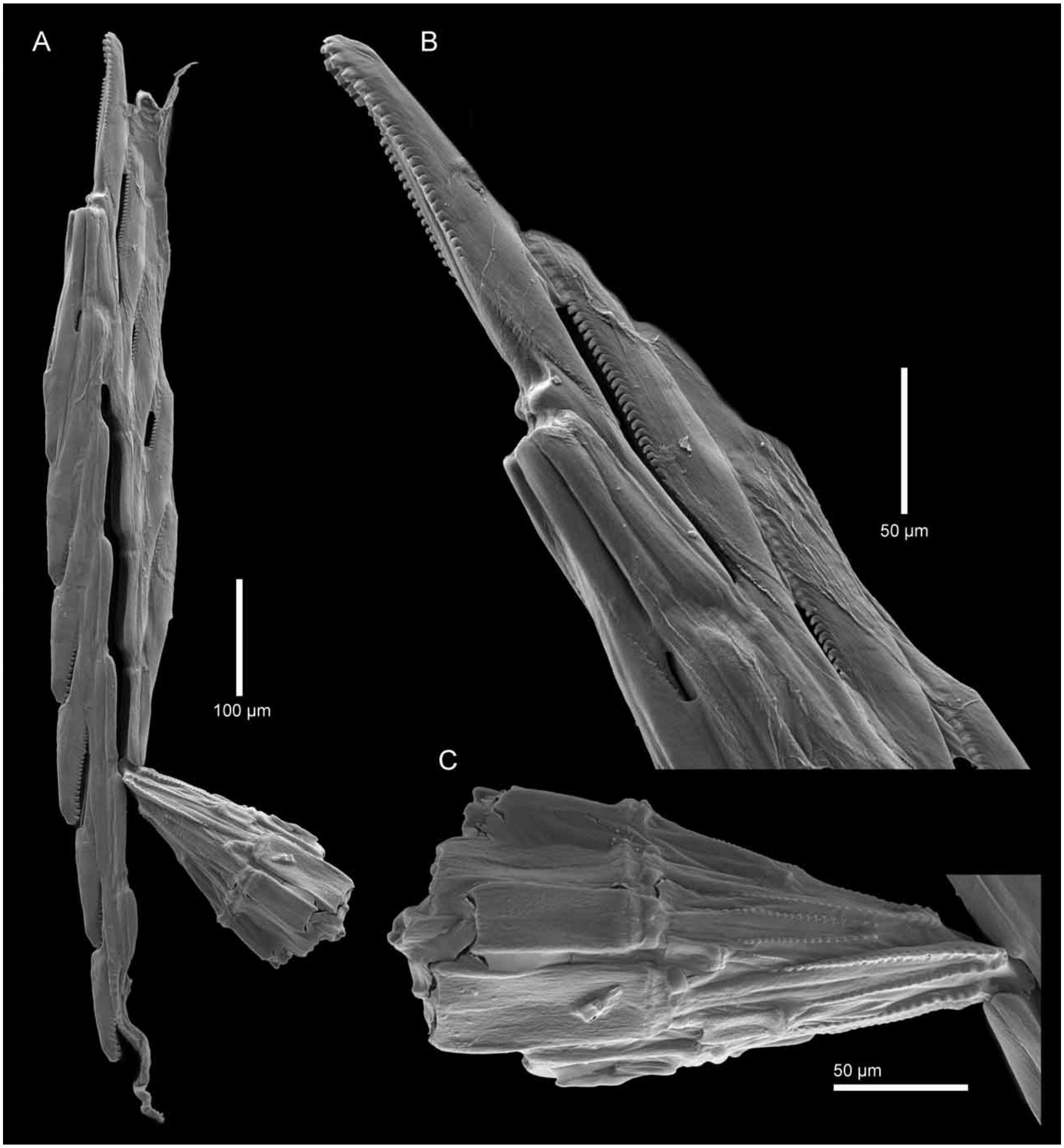

Figure 27. SEM micrographs of the radula of *Cyerce kikutarobabai* Hamatani, 1976, specimen from Nouméa, New Caledonia, isolate KM71, MNHN IM-201926193. **A.** Complete radula with descending and ascending limb, ascus attached to end of descending limb. **B.** Active tooth. **C.** Complete ascus.

Figure 28. Stained penis of *Cyerce kikutarobabai* Hamatani, 1976, isolate 22NC304 (MNHN IM-2019-26210) showing the penial stylet (indicated by a black arrow).