



Key to sessile gnesiotrochan rotifers: Families, monospecific species in Flosculariidae, species of Atrochidae, Conochilidae, and *Limnias*

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Abstract

Accurate identification of species is key to understanding their ecological roles and evolutionary history. It is also essential in cataloging biodiversity for comparisons among habitat types, responses to climate change, effective management practices, and more. The paucity of taxonomic expertise is increasing and with it the ability to competently identify species, this is particularly true for small taxa including rotifers. In an effort to improve this situation, we collated information on morphological characters from the literature on all valid species of sessile Gnesiotrocha (phylum Rotifera) currently assigned to two orders and four families. We review Order Collotheceae, which comprises families Atrochidae (3 spp.) and Collotheceidae (50 spp.) and Order Flosculariaceae, which includes families Conochilidae (7 spp.) and Flosculariidae (71 species). Based on that information, we provide dichotomous keys to the Families, monospecific species in Flosculariidae, and species of Atrochidae, Conochilidae, and *Limnias*. These keys will aid researchers to identify species in these families and lead to a better understanding of freshwater biodiversity and eco-evolutionary processes.

Key words: Coloniality, dichotomous key, morphology, planktonic, sessile, solitary, Rotatoria

Introduction

Phylum Rotifera (*sensu stricto*) comprises ca. 2000 described species of minute (~ 50 to 3500 µm), aquatic metazoans that exhibit curious life cycles, live in diverse environments, feed in various ways (herbivores, detritivores, carnivores, omnivores, parasites), and possess a wide range of morphologies (Fontaneto & De Smet 2015; Wallace *et al.* 2006; Wallace *et al.* 2015). Yet within this diversity, rotifers hold four characteristics in common: (1) all possess specialized jaws called trophi; (2) all are eutelic; (3) all have an intracytoplasmic lamina (ICL) within their epidermis that is composed of two proteins; and (4) at some point during their life all possess a ciliated anterior end, which is used in locomotion and usually, in the adult, feeding (Wallace *et al.* 2006; Wallace *et al.* 2015). Rotifers are found anywhere water is available for a sufficient time for them to complete their life cycle, sometimes this occurs within a few days (Schröder *et al.* 2007). The environments that they inhabit include lakes and ponds (Obertegger & Flaim 2015; Wang *et al.* 2022), rivers and streams (da Silva *et al.* 2021; Örstan 2021), moist terrestrial (Devetter & Frouz 2011; Pourriot 1979) and boggy soils (Bielańska-Grajner *et al.* 2011; Bielańska-Grajner *et al.* 2017), phytotelmata of various plants (Błędzki & Ellison 1998), birdbaths (Birky *et al.* 2011; Örstan 2020, 2022), and ephemeral desert playas (Brown *et al.* 2020) and rockpools (Brown *et al.* 2022), as well as inland saline (Walsh *et al.* 2008), brackish (Karpowicz *et al.* 2023) and marine waters (Fontaneto *et al.* 2006, 2008).

Rotifers are important for several reasons. In aquatic ecosystems they are the food for protists, other small

zooplankton (including other rotifers and microcrustaceans), insects, and fishes; thus, they are fundamental components in both the classical food web and the microbial loop (Neury-Ormanni *et al.* 2019; Prowe *et al.* 2022; Wallace *et al.* 2015). They are used in aquaculture as food for commercially important target species, including crabs, shrimps, and fishes (Lubzens *et al.* 1989; Turgay *et al.* 2020). Certain rotifers are employed as models in aging studies (Gribble & Mark Welch 2017; Gribble & Snell 2018) and toxicology assessments of various chemicals (Park *et al.* 2022; Shin *et al.* 2022; Snell *et al.* 2019). Regardless of the type of research, it is critical that workers correctly identify the species that they are studying.

A serious problem in identifying rotifers, especially from field samples, is that when fixed in standard preserving fluids, those in which the ICL is poorly developed (illoricate species) usually contract into unidentifiable masses (Wallace *et al.* 2015). Thus, illoricate species are best examined alive. A second challenge is finding appropriate taxonomic keys. Over the past several decades various keys have been published, but many stop at the level of genus (Edmondson 1959; Fontaneto *et al.* 2008; José de Paggi *et al.* 2020; Wallace *et al.* 2016, 2019), are regional in scope (Braioni & Gelmini 1983; Pontin 1978), are written in languages that make them challenging for some to use (Bartoš 1959; Collin *et al.* 1912; Koste 1978; Kutikova 1970; Rudescu 1960), or have limited taxonomic coverage (Bartoš 1951; Meksuwan *et al.* 2018; Ruttner-Kolisko 1974; Vidrine *et al.* 1985; Wallace *et al.* 2018). Also several of these keys use outdated taxonomies. In the mid 1990s an all-encompassing series of taxonomic keys was proposed to address this problem for zooplankton living in inland waters. Each key was to cover a specific group and was to be published under the title of *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. But while the series on Rotifera was to be an exhaustive taxonomic treatise, it was never completed (De Smet 1996; De Smet & Pourriot 1997; Nogrady *et al.* 1995; Nogrady & Segers 2002; Nogrady *et al.* 1993; Segers 1995; Wallace *et al.* 2006).

Most adult rotifers are free moving, either swimming or crawling over surfaces or between small particles in interstitial terrestrial and aquatic sediments (Błędzki & Ellison 2003; Devetter 2010; Ejsmont-Karabin & Karpowicz 2021). However, within superorder Gnesiotrocha (G., *Gnesi*, genuine, G., *trocho*, wheel) approximate 100 species are referred to as sessile rotifers, even though the adults of several species are free-swimming. The young (larvae) of all are free-swimming as well. Currently, these taxa are placed in two orders, Collothecacea (Atrochidae, Collothecidae) and Flosculariaceae (Conochilidae, Flosculariidae) (Koste 1978). As a group the sessile species have received comparatively less attention than their motile counterparts. Nevertheless, sessile rotifers have a wide ecological distribution across habitats (lakes, ponds, and bogs) and an extensive geographic distribution including all continents (Antarctica (Dartnall 1983; Dartnall & Hollowday 1985)), high arctic waters (De Smet 1993; De Smet & Bafort 1990), and islands (Dartnall 1995; Edmondson 1948; Koste & Shiel 1986; Segers & Dumont 1993).

Study of sessile rotifers is challenging for three reasons. (1) All species are illoricate, thus, as noted above, fixation in the field is futile. (2) Most, but not all, are permanently attached to a substratum as adults. Therefore, a complete inventory of the sessile community must examine a wide array of surfaces to which the animals may be bound (Bērziņš 1951; Edmondson 1940; Edmondson 1944; Franch 2021; Tiefenbacher 1972; Wallace 1977). (3) Like all rotifers, their trophi are difficult to isolate, but they also have been insufficiently described and illustrated. Moreover, despite the promise that molecular techniques offer to identify organisms to the level of species, we have not yet reached that state for a sufficient number of taxa (Meksuwan *et al.* 2015).

Although much is known about the biology of the sessile taxa, our knowledge is still inadequate. Some examples include the following. (1) Insufficient work has been done to elucidate their phylogeny (Meksuwan 2015; Meksuwan *et al.* 2015). (2) In the same genus both sessile and planktonic species and both solitary and colonial forms are known (Wallace 1980; Wallace 1987); the evo-ecological drivers of those conditions remain unstudied. (3) Some species appear to have a specific preference for a substratum (Wallace 1980); we do not understand the adaptive significance of these preferences. (4) All species possess juvenile stages (larvae) that undergo a significant rearrangement of organ structure, reminiscent of metamorphosis undergone by the larval stages of numerous aquatic invertebrates (Hochberg *et al.* 2019; Wallace 1980). Indeed neonates of sessile species are so different from adults that they appear to be different species (Wallace 1980); however, we have no knowledge on how metamorphosis is initiated. (5) While the larval corona in Flosculariaceae is retained and grows during ontogeny, the corona in larval Collothecaceae is lost at metamorphosis and is replaced by a bowl- or funnel-shaped structure called the infundibulum (L., funnel) (Hochberg *et al.* 2019). The infundibulum is not an elaboration of the corona; it is a derivative of the larval foregut, replacing the corona during larval metamorphosis (Hochberg *et al.* 2019); the ontogeny of this process and the evolution of these divergent Bauplans remains a mystery. (6) Species in the

Conochilidae and Flosculariidae form intraspecific colonies (e.g., *Floscularia*, *Limnias*, *Sinantherina*) and at least one species of *Ptygura* is known to form interspecific colonies (Wallace 1987); understanding the significance of coloniality has not been adequately addressed. (NB: Used in this context the term colony refers to assemblies of individuals into an integrated cluster, in which colony mates do not share nutritive resources, but which commonly interact (Wallace 1987; Wallace *et al.* 2015).)

In this contribution we provide morphologically based keys to adult sessile gnesiotrochan rotifers: families, monospecific species in Flosculariidae, species of Atrochidae, Conochilidae, and *Limnias*. Examples of these species are shown in Fig. 1. In future contributions we will address the remaining sessile taxa. We anticipate that others will expand these keys with information on the morphology of their trophi. That research is important as it will permit species identification from preserved samples. Finally, usable keys to the sessile taxa are a necessary step in the study of the entire phylum, which, in general, appears to be replete with cryptic species (Kordbacheh *et al.* 2018, 2023; Marrone *et al.* 2023; Michaloudi *et al.* 2018; Mills *et al.* 2017). If we are to refine our understanding of rotifer evolution, especially of the sessile condition, information on the morphology of their trophi and molecular data on several genes is needed.

Methods

To develop the database from which we constructed keys to the sessile taxa, we reviewed previously published works noted above, papers that covered selected taxa (Bērziņš 1951; Edmondson 1939; Edmondson 1940; Dioni 1966; Koste 1978; Wright 1949), and, when possible, the original published descriptions. Only species recognized as valid by the List of Available Names (Jersabek *et al.* 2018) and/or the Rotifer World Catalog (Jersabek & Leitner 2013) were considered. The keys here are based on adult females only.

Superorder Gnesiotrocha de Beauchamp, 1965

Within the diversity exhibited by rotifers, superorder Gnesiotrocha are distinct from superorder Pseudotrocha (order Ploima) in that all gnesiotrochans (1) possess a foot that lack toes, (2) their anterior end is either a funnel-shaped structure or possesses ciliated lobes, and (3) their trophi are either malleoramate or uncinata (Edmondson 1959; Koste 1978; Ruttner-Kolisko 1974; Wallace & Snell 2010; Wallace *et al.* 2006). Ploimids may lack a foot, and, if present, may possess toes; their anterior end and trophi do not resemble that of the sessile taxa. Uncinate trophi possess few teeth: usually one or more large, pincer-like teeth and a few smaller teeth (Fig. 2A); malleoramate trophi possess crescent-shaped manubria and unci with numerous club-shaped teeth (Fig. 2B). Teeth close to the fulcrum are usually larger than those more distant. Trophi in the Flosculariaceae characteristically exhibit a grinding or pounding-like action, which is not seen in the Collotheceae.

Dichotomous key to Collotheceidae

- 1 Anterior end of adults a small to large, cup- or funnel-shaped structure (infundibulum), corona absent; infundibulum with 0–7 extensions (apices, knobs, lobes, tentacles), elongate setae usually present (sometimes with cilia) around the margin; trophi uncinata. **Order Collotheceae** Harring, 1913
[All species are solitary; both sessile and planktonic species are known; juveniles (larvae) possess a ciliated corona used in locomotion, but this is lost at metamorphosis and replaced by the infundibulum.]
- 1' Anterior end of adults with a corona with typical ciliated lobes or fields, or ciliated bands; trophi malleoramate. **Order Flosculariaceae** Harring, 1913
[Species may be solitary or colonial; both sessile and planktonic species are known; juveniles (larvae) possess a corona that is retained (and grows) during ontogeny.]

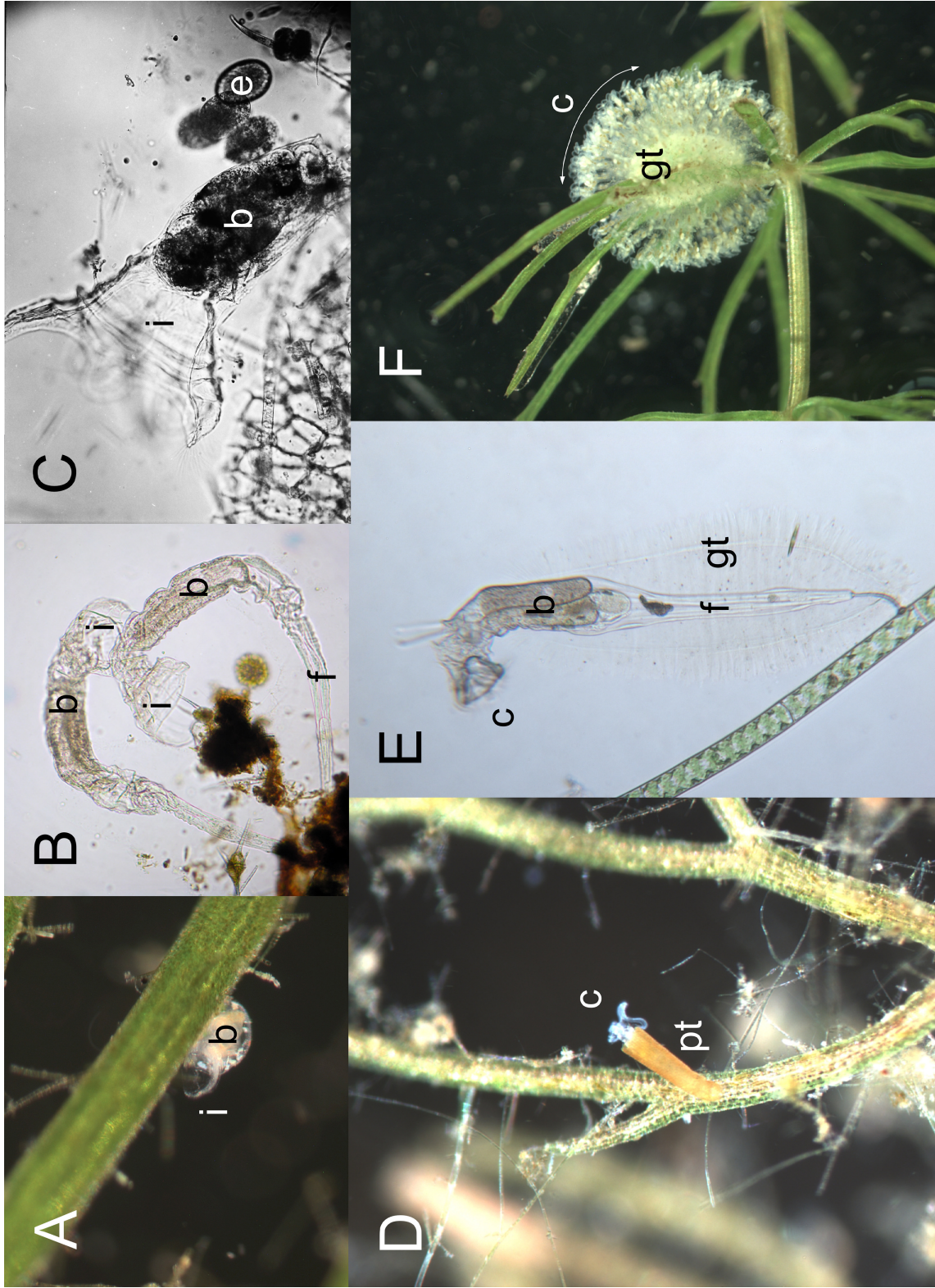


FIGURE 1. Examples of sessile gnesiotrochans *in situ*. A–C. Collotheceae (funnel-shaped anterior end): A. *Cupelopagis*, B. *Acyclus*, C. *Collotheca*. D–F. Flosculariaceae (ciliated anterior end). D. *Floscularia*, E. *Ptygura*, F. *Lacimularia* (colony). Symbols: b = body; c = corona; e = embryo; f = foot; gt = gelatinous tube; i = infundibulum; pt = pellet tube. Arrow in F denotes the coronae of ~25% of the colony. See text for details on animal sizes.

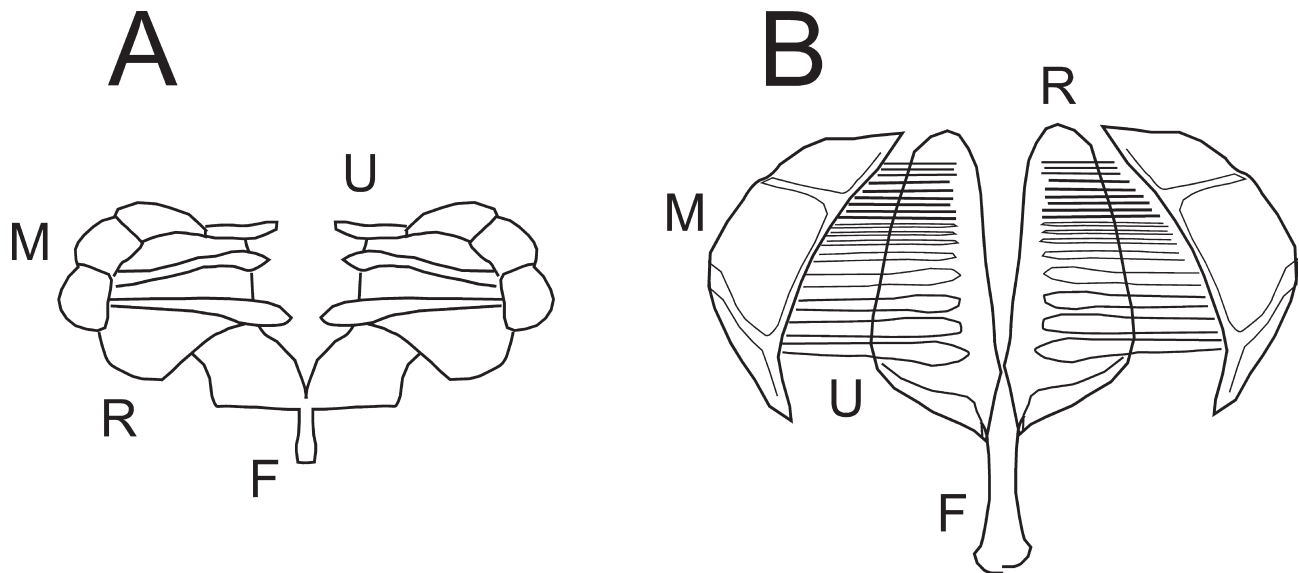


FIGURE 2. Schematic view comparing uncinata (A) and malleoramate trophi (B). Trophi are not drawn to the same scale. Symbols = F = fulcrum; M = manubrium; R – ramus; U = unci. Compare these schematics to the variation of trophi form shown in figures 13.10 and 13.11 in Wallace *et al.* (2015).

Order Collothecacea Remane, 1933 (= Paedotrocha de Beauchamp, 1965)

Collothecacea is a cosmopolitan order of two families (Atrochidae, Collothecidae) comprising a total of five genera dominated by the genus *Collothecha*, which possesses ~50 species (Jersabek & Leitner 2013). Several characteristics separate this order from other taxa. All species possess uncinata trophi and a contoured anterior end that is elaborated into the infundibulum (L., funnel) (Hochberg *et al.* 2019). Prey captured in the infundibulum are moved into a temporary holding chamber called the vestibulum (L., entrance); from there the trophi eventually pull prey into the stomach for digestion. [NB: Edmondson (1959) reverses identification of these the infundibulum and vestibulum (figure 18.102b) and Remane (1929–1933) alternates use of the names in two places (compare figures 159A and 162C).] The margin of the head end may or may not possess lobes or tentacles with cilia and/or setae. All collothecans are raptorial, ambush predators. Predation has been described in *Collothecha* by Meksuwan *et al.* (2013), in *Cupelopagis* by Bevington *et al.* (1995) and Preza (2017).

Generally, these rotifers possess elongate bodies, including a long slender foot. In adults of *Collothecha* and *Stephanoceros* (Collothecidae) the infundibulum is usually edged with cilia or setae; in adults of *Acyclus*, *Atrochus*, and *Cupelopagis* (Atrochidae) these are absent. External gelatinous tubes that surround adult females are present in three genera: *Acyclus*, *Collothecha*, and *Stephanoceros*. Unlike the species of Flosculariidae, no collothecaceans form colonies. However, aggregations of densities above 6 individuals mm² have been reported (Wallace & Edmondson 1986). These clusters probably do not represent contagious settlement by the larvae as is seen in barnacles. Rather, they may indicate recruitment due to a factor(s) associated with the surface of the preferred plant (Wallace 1980). As in the sessile Flosculariidae, *Collothecha* possesses several planktonic species. The monospecific genus *Atrochus* does not affix permanently to surfaces and is capable of some crawling movement (Wierzejski 1893).

The etymon for both the order and one family (Collothecaceae; Collothecidae) refers to the gelatinous tube (G., *collo*, glue + G., *theca*, case). However, into the early part of this century, collothecids were known as *Floscularia* (L., *flosculus*, little flower), which to many observers is a better allusion to their form: a flower-shaped animal situated on a long foot stalk with a funnel-shaped head possessing numerous radiating setae. Nevertheless, for reasons of priority both names were changed by Haring (1913).

Larval collothecids are small (~100–500 µm), often spindle shaped, and with a pair of red eyespots just below a ciliated corona; these are lost in the adults of species that are permanently attached. Organ systems are not well developed and there is often a ciliated cavity at the base of their foot. Only after settlement do they begin metamorphosis to the adult body form and secrete an extracorporeal tube around their body.

Diagnosis. Corona bowl- to funnel-shaped, narrowing at its base, the margin is edged with long setae or short cilia (both often motionless), or cilia and setae lacking. The corona may be elaborated into lobes or tentacles (arms) or lobes absent. Mastax enlarged into a storage chamber (proventriculus). Trophi unciniate. Foot elongate, retractile, but not within the body. Foot ends with attachment disk or peduncle; toes absent. Most species secrete clear gelatinous tubes. Mainly sessile species, but several planktonic and ≥ 1 benthic species. All collothecans are solitary.

Dichotomous key to order Collothecacea

- 1 Infundibulum bearing setae and/or cilia; with or without lobes (tentacles, knobs, or apices); gelatinous tubes; sessile or planktonic **Collothecidae** Bartoš, 1959
- 1' Infundibulum lacking cilia or setae; unlobed or with one long, very flexible lobe, or with short, horny processes; with or without gelatinous tube; sessile or benthic (crawling) **Atrochidae** Bartoš, 1959

Dichotomous key to Collothecidae

- 1 Infundibulum with five very long lobes resembling arms, \sim trunk length or longer; arms either stout with setae in whorls or slender with long slim setae not in whorls; setae always at right angles to arms; clear gelatinous tube; body length $\leq 1500 \mu\text{m}$; sessile; oviparous. (Fig. 3A,B) *Stephanoceros* Ehrenberg, 1832
[In light of the fact that some members of the genus *Collotheca* also possess long lobes (e.g., *Collotheca judayi* Edmondson, 1940; *Collotheca tenuilobata* (Anderson, 1889)), Meksuwan *et al.* (2013) have recommended that the status of both genera be re-evaluated.]
- 1' Infundibulum with lobes absent or short to long, sometime knobbed at the terminus; long setae usually present extending from infundibular margin of the lobes; setae never in whorls and never held at right angles to arms; cilia often present; clear tube may be embedded with algae or with debris; body length $\sim 100\text{--}2,500 \mu\text{m}$; sessile or planktonic; oviparous. (Fig. 3C,D) *Collotheca* Haring, 1913
[In some species (e.g., *C. judayi*) setae are absent and the entire inside surface of the infundibulum is ciliated (Edmondson 1940). While most are sessile, *Collotheca libera* (Zacharias, 1894), *Collotheca mutabilis* (Hudson, 1885), *Collotheca pelagica* (Rousset, 1893), and *Collotheca polyphemus* Haring, 1914 are planktonic, *Collotheca ornata* (Ehrenberg, 1830) occurs in planktonic, benthic, and sessile forms, including on the carapaces of cladocerans (Sebestyén 1957), and *Collotheca crateriformis* (Offord, 1934) is benthic. Nearly all produce a clear gelatinous tube; none are colonial, but may colonize substrata forming dense groupings (Wallace & Edmondson 1986).

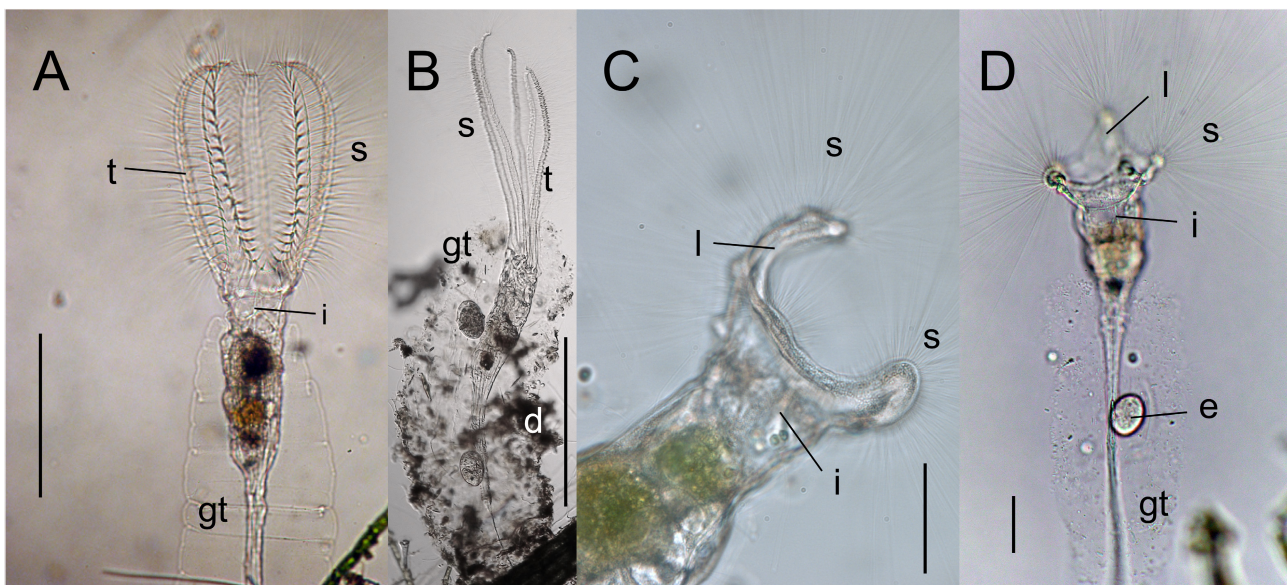


FIGURE 3. Representative Bauplans of the anterior ends of *Stephanoceros* (A, B) and *Collotheca* (C, D). A. *Stephanoceros fimbriatus*. B. *Stephanoceros millsii*. C. *Collotheca campanulata*. D. *Collotheca ornata*. Symbols: e = embryo; d= debris; gt = gelatinous tube; i = infundibulum; l = lobes; s = setae; t = tentacles. Bars: A, B = 500 μm , C, D = 100 μm .

Family Collothecidae Bartoš, 1959

Of the two genera comprising this family, *Collotheca* is numerically dominant; *Stephanoceros* has only two recognized species. Yet this family is commonly ignored in ecological studies and relatively few studies have been done on the general anatomy of these forms to come to meaningful conclusions regarding evolutionary trends and thereby their phylogenetic relationships (Edmondson 1944; Hochberg 2014; Hochberg *et al.* 2019; Meksuwan 2015; Meksuwan *et al.* 2013; Segers *et al.* 2010; Yang *et al.* 2019, 2021).

Unfortunately descriptions of the Collothecidae, especially in the morphology of lobes on the infundibulum and arrangement of cilia and/or setae on its margin, are inconsistent. Lobe morphology varies to such an extent that a definitive description covering all variations is nearly impossible. The issue of what constitutes a lobe presents a serious problem, at least in some species of *Collotheca*. For example, in the species *Collotheca edmondsoni* Bērziņš, 1951 there are three regions on the infundibular margin that possess setae, but these regions may not be recognized as lobes. Also definition and usage of the terms cilia and setae are inconsistent in the literature. In general we have retained the term(s) used by the original author; however, when the original descriptions are unclear, we use the terms cilia and setae to indicate short and long structures, respectively. Additionally, there has been no systematic study of the movements of the setae (Wright 1958).

Collothecaceans are raptorial and feed on a wide variety of prey, including diatoms, photosynthetic and colorless flagellates, dinoflagellates, ciliates, and rotifers (Bērziņš 1951; Bērziņš 1952; de Beauchamp 1912; Koste 1970; Valerio 1975; Wright 1958).

Diagnosis. Infundibulum bearing long setae and/or short cilia lining part or all of infundibular edge; infundibulum without lobes (the entire head lying within a single plane) or elaborated into lobes, bulbs, and/or tentacles (arms); these vary in number (0–7); mouth central; vestibulum present. Most sessile, but several planktonic species. Foot of sessile forms ending with an adhesive disk or peduncle. Tube, when present, a clear gelatinous matrix.

Stephanoceros Ehrenberg, 1832

The etymon of genus (*G.*, *stephanos*, a crown) is an obvious reference to the shape of the anterior end. We follow Meksuwan *et al.* (2013) in recognizing two species in this genus, which may be distinguished based mainly on the shape of long lobes that project from their anterior end and the organization of their setae (cf. Koste 1978).

Diagnosis. Infundibulum of five, long, erect tentacles (lobes or arms) forming a basket, with short and long setae throughout the lobes, very long and radiating or set in numerous parallel rows along the length of each appendage. Adults sessile in tube of clear jelly with periodic ring-like constrictions; number of rings increasing with age. Lateral antennae minute. Foot = body length in young, but 2x body length in adult; peduncle short. Oviparous.

Dichotomous key to species of genus *Stephanoceros*

- 1 Setae on lobes in spiral fans; body length 1500–2500 µm; oviparous. (Fig. 3A) *fimbriatus* (Goldfuss, 1820)
[Information on the myo-anatomy and events during metamorphosis of *Stephanoceros* were presented by Hochberg and Hochberg (2017). Remane (1933) illustrated the growth of the gelatinous tube. Yang *et al.* (2021) provided information on the ultrastructure of the gelatinous secretions of this species and its congener. Gilbert (1993) reviewed literature that described regeneration in this species.]
- 1' Setae on lobes not in spiral fans; setae in two long rows, distally finer and longer; body length 800–1350 µm; oviparous. (Fig. 3B) *millsii* (Kelicott, 1885)
[Ciliation of *S. fimbriatus* is described and figured by Wright (1952) and Koste (1978) and that of *S. millsii* by Koste (1978).]

Atrochidae Bartoš, 1959

This small, enigmatic family comprises three monospecific genera (*Acyclus*, *Atrochus*, *Cupelopagis*). Only *Acyclus* possesses a gelatinous tube. Except for *Cupelopagis*, relatively little is known about the biology of these forms. All possess an infundibulum that is often relatively large and gaping. All possess interesting modes of feeding. *Acyclus* lives within colonies of *Sinantherina socialis* (Linnaeus, 1758) and occasionally *Lacimularia flosculosa*

(Flosculariidae), on whose ova and larvae it feeds. Lacking an attaching foot, *Atrochus* crawls slowly over the bottom and feeds on algae. Although sessile *Cupelopagis* is capable of tracking and orientating toward its animal and protistan prey by detecting vibrations in the water (Bevington *et al.* 1995). Atrochidae was separated from the family Collothecidae because of the atypical anterior end (Koste 1978). However, Koste suggests that the Atrochidae is an artificial grouping; its assignment is retained here as a matter of convenience and to emphasize the uncertain relationship of the three genera to the remaining Collothecacea.

The etymon of the family (G., a, *without* + G., *trochus*, wheel) emphasizes the lack of a ciliated corona, which is present in most Rotifera.

Diagnosis. Infundibulum variously shaped: large asymmetric bowl, or small with a dorsal hood-like lobe, or fringed with short, hollow, finger-like projections, but always lacking setae and cilia as adults. Vestibulum absent. Larvae resemble other Collothecacea: ciliated anterior end providing locomotion. Foot elongate and tapering, or a short thick stalk, or absent. Oviparous or ovoviviparous. Adults sessile with or without gelatinous tube or capable of limited locomotion (crawling).

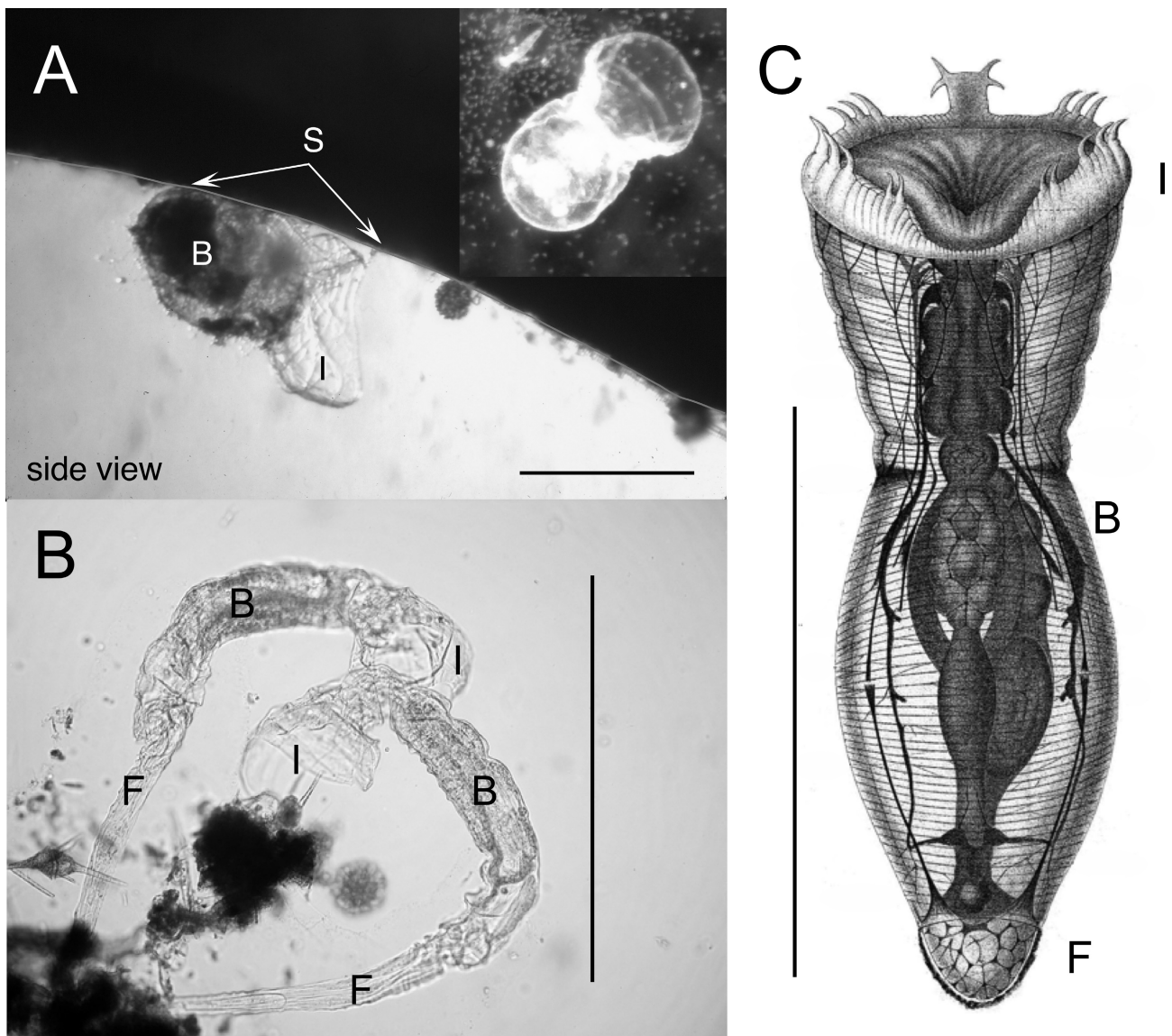


FIGURE 4. Three species in family Atrochidae. A. *Cupelopagis vorax* (Leidy, 1857), side view; insert dorsal view. B. Two individuals of *Acyclus inquietus* Leidy, 1882 removed from a colony of *S. socialis*. C. *Atrochus tentaculatus* Wierzejski, 1893. (C. After Wierzejski, 1893). Symbols: B = body; F = foot; I = infundibulum; G = gelatinous matrix; S = substratum. Bars ~1000 μm .

Dichotomous key to species of family Atrochidae

- 1 Infundibulum large, bowl-shaped, as wide as body width; body a slightly flattened spheroid; mouth (infundibulum) positioned parallel to substratum; sessile by a short, flexible centrally positioned, ventral foot; gelatinous tube absent; body size $\leq 1000 \mu\text{m}$; ovoviviparous. (Fig. 4A) *Cupelopagis vorax* (Leidy, 1857)
[The morphology of this species is reviewed by several workers including Cori (1925), Hünerhoff (1931), Koste (1973), and Vasisht & Dawar (1968, 1969). Bevington *et al.* (1995) and Preze (2017) report studies on feeding.]
- 1' Infundibulum and body not as above; gelatinous tube present or absent; sessile or mobile; foot not a short stalk. 2
- 2(1) Infundibulum with long, prehensile dorsal lobe; transparent gelatinous tube; foot relatively short; sessile, often in colonies of *Sinantherina* and occasionally *Lacinularia* (Flosculariidae). Adult $\leq 1500 \mu\text{m}$; oviparous. (Fig. 4B)
..... *Acyclus inquietus* Leidy, 1882
[*Acyclus* feeds on the ova and young of the colonial rotifers it inhabits. Hochberg *et al.* (2010) reported on the behavior, metamorphosis, and muscular anatomy of this species. An undescribed congener, reported from Thailand (Meksuwan *et al.* 2013), should be explored further.]
- 2' Infundibulum lacking long dorsal lobe, possessing finger-like projections (horny processes) on dorsal side; body elongate oval; tube absent; foot short and hemispherical in shape; 1200–1500 μm ; mobile (crawling), lying on surfaces; ovoviviparous. (Fig. 4C) *Atrochus tentaculatus* Wierzejski, 1893
[Additional work needs to be done on this enigmatic species; consult Koste *et al.* (1984) and Wierzejski (1893).]

Order Flosculariaceae Remane, 1933

Introduction

Flosculariaceae is a cosmopolitan group of five families (Conochilidae, Flosculariidae, Hexarthridae, Testudinellidae, and Trochosphaeridae); the later three are entirely planktonic and are not considered here. Adults of all Conochilidae and Flosculariidae possess four features. (1) They are illoricate, with elongate bodies, usually including a long slender foot and, in many, an elaborately contoured, ciliated corona. (2) While all Conochilidae secrete an indistinct, gelatinous matrix, the tubes of Flosculariidae are generally well-defined. They vary from gelatinous to elaborate structures comprising tubes (pipes) or pellet constructions. (3) Planktonic species are present in both, indeed all Conochilidae are planktonic. (4) Several genera exhibit some of inter- or intraspecific colony formation (Wallace 1987; Wallace *et al.* 2015).

As noted above the name for this order is in reference to the allusion to the flower-like form of the animals.

Dichotomous key to families of the Flosculariaceae

- 1 Adults planktonic, within a loose gelatinous matrix; colonies vary from 1 adult with ≥ 1 juveniles to > 300 individuals; trophi unique: asymmetrical unci, teeth of left unci much longer than on the right **Conochilidae** Haring, 1913
- 1' Adults sessile, facultative sessile, or planktonic animals, usually within a tube of varied construction (gelatinous, pipes, or pellets); solitary or in intra- or inter-species colonies; trophi not as above, either symmetrical or asymmetrical, with teeth of right unci much longer than on the left **Flosculariidae** Remane, 1933

Family Conochilidae Haring, 1913

Family Conochilidae was separated into two genera (*Conochilus* and *Conochiloides*) by Hlava (1904). However, Ruttner-Kolisko (1974) argued that the separation was not warranted and subsumed *Conochiloides* back into genus *Conochilus*. While this practice has continued (Fontaneto & De Smet 2015; Koste 1978), some workers have not followed this change (Bielańska-Grajner *et al.* 2015; Pontin 1978; Stemberger 1979). Segers & Wallace (2001) added *Conochilopsis* to the family; it comprises a single species, originally described as a member of the genus *Lacinularia* (Vidrine *et al.* 1985). Species secrete a gelatinous matrix that affords protection from the predatory rotifer *Asplanchna girodi* Guerne, 1888 (Gilbert 1980). In *Conochilus hippocrepis* (Schrank, 1803), colony size increases in diameter (number of individuals) in relation to the size of a sympatric predatory copepod (Diéguez and Balseiro 1998). The gelatinous matrix is often colonized by bacteria (including cyanobacteria), algae, and protozoans (Fig. 5) (Balvay & Druart 1995). Occasionally population crashes occur due to parasites invading the perivisceral cavity (blastocoel) (Ruttner-Kolisko 1977). Colonies tumble (rotate) while swimming.

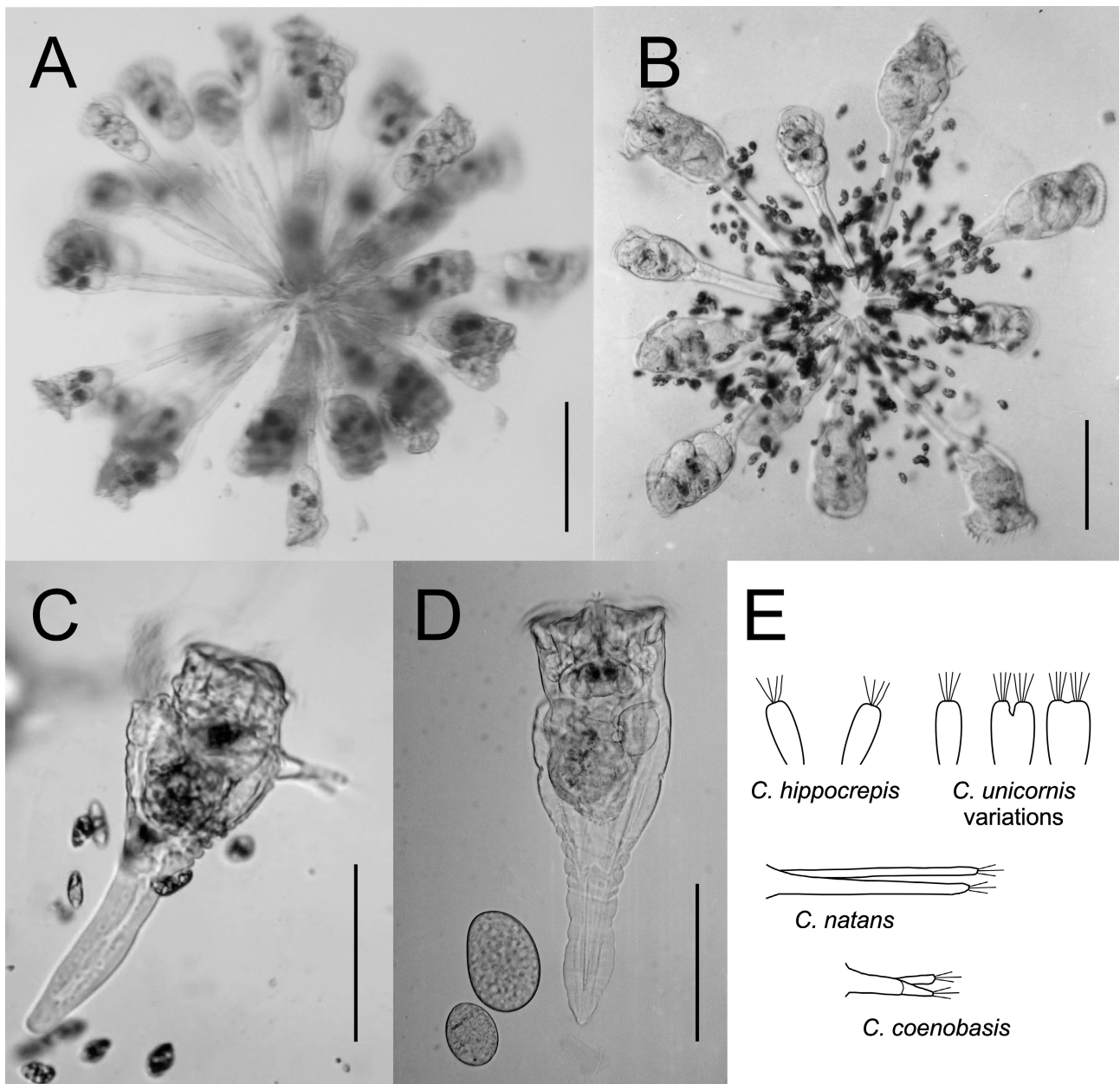


FIGURE 5. Species of Conochilidae. A. *Conochilus hippocrepis* (Schränk, 1803); B. *Conochilus unicornis* Rousselet, 1892; C. *Conochilus coenobasis* (Skorikov, 1914); D. *Conochilus exiguus* (Ahlstrom, 1938). This amphoteric female is evidenced by presence of a subitaneous embryo and a smaller male embryo. (The cone-lip is evident in C and D.) The foot in the variation of *C. unicornis* (*C. norvegicus*) is much longer (~4x) (see below). E. Examples of reported variation in the fusion of antennae in the *Conochilus*: consult Edmondson (1959) and Pejler (1956). Bars: 500 μ m (A,B); 100 μ m (C,D). (E. Redrawn from original art provided by W.T. Edmondson.)

The etymon for this genus (G., *cono*, a cone + G., *chilus*, a lip) was given by Ehrenberg (1834) because the apical field—the fleshy region surrounded by the corona—is inflated by two cone-shaped, lip-like structures located on either side of the mouth (Fig. 6). This structure appears to be depicted in individuals (2 of 7) in figure 3 of *Conochiloides* (*Lacinularia*) *causeyae* by Vidrine *et al.* (1985).

Diagnosis. Apical field with two inflated, cone-shaped, lip-like structures located centrally or dorsally. Corona circular to horseshoe-shaped, as a double ciliated band (trochus and cingulum) with a prominent ventral gap in the cilia present or not. Body shape conical; illoricate integument with unsegmented foot lacking toes. Paired ventral (lateral) antennae separate or fused to various degrees, within or below coronal field; dorsal antenna absent or

minute. Two dorsal eyes beneath corona. U-shaped intestine, anus exiting just above the margin of the gelatinous matrix. Trophi malleoramate: rami symmetrical or slightly to strongly asymmetrical; unci with 3–6 club-shaped (clavate) teeth near fulcrum, (number and form of clavate teeth may be different on each side); numerous, thin accessory teeth beyond clavate ones (distal to fulcrum). Planktonic, either solitary or small to large colonies (5 to >400 or more individuals per colony). Animals clustered within a gelatinous mass produced by glands in foot. Oviparous.

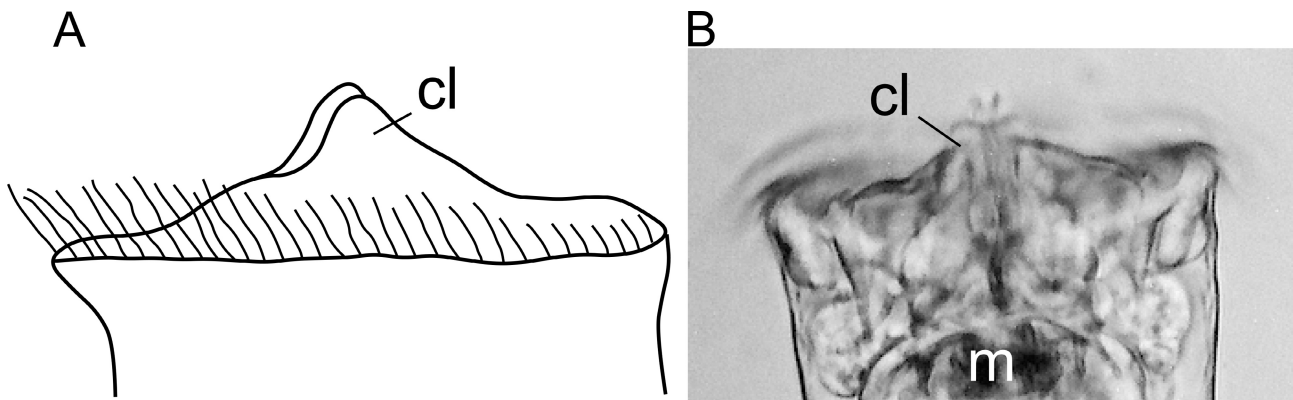


FIGURE 6. Cone-like lips that flank the mouth in Conochilidae. (A) Schematic lateral view. (B) Specimen *in vivo*. Symbols: cl = cone-lip; m = mastax.

Dichotomous key to species in family Conochilidae

- 1 Corona circular (not horseshoe-shaped) with prominent ventral gap absent; ventral (= lateral) antennae not within the corona; resting eggs with spiral furrow, but no hatching furrow evident; body length ~500 μm ; monospecific genus *Conochilopsis causeyae* (Vidrine, McLaughlin, & Willis, 1985)
[Segers and Wallace (2001) described its trophi and reallocated it to a new genus in Conochilidae.]
- 1' Corona horseshoe-shaped with a prominent ventral gap 2
- 2(1') Ventral (= lateral) antennae within corona; colonies of several to many individuals; resting eggs not ornamented, but possess a hatching furrow; genus *Conochilus* (Fig. 5). 3
[Tropi for the two species in genus *Conochilus* were (SEM) are found in Segers & Wallace (2001).]
- 2' Ventral (= lateral) antennae not within corona; resting egg with spiral surface texture, but no hatching furrow evident; genus (*Conochiloides*) *Conochilus* 4
[Tropi for the four species in the former genus *Conochiloides* were drawn by Ahlstrom (1938); SEMs of the trophi for *C. dossuarius* and *C. natans* are shown in Segers and Wallace (2001).]
- 3(2) Antennae not fused; colonies of 30–100 individuals; total body length 400–850 μm (foot:body ratio, 2.2–2.4) *hippocrepis* (Schrank, 1803)
- 3' Antennae fused (except perhaps at distal end) into a single structure; small colonies (5–30 individuals) with total body length 200–450 μm and foot:body ratio, 1.2–1.7 or larger colonies (50–400 or more individuals) with total body length < 1300 μm (foot:body ratio 2.2–2.7). *unicornis* Rousselet, 1892
[Includes a form previously known as *Conochilus norvegicus* Burckhardt, 1943 that produces colonies often with large numbers of individuals possessing elongate bodies that may be the result of allometric growth (Edmondson 1959; Ruttner-Kolisko 1974). De Graaf (1953) provided information on the commensal protists that inhabit the gelatinous matrix and Yang *et al.* (2021) provided information on the ultrastructure of the secretions.]
- 4(2') Antennae not fused; rami symmetrical, with 5–6 large clavate teeth on each uncus; total body length 280–510 μm *natans* (Seligo, 1900)
- 4' Antennae at least partially fused; rami symmetrical or not; variable number of large clavate teeth on each uncus 5
- 5(4') Rami strikingly asymmetrical, one side almost triangular in shape, the other sub-rectangular; 5 clavate teeth on each uncus; total body length 280–500 μm *dossuarius* (Hudson, 1885)
- 5' Rami symmetrical or at least asymmetry scant 6
- 6(5') Unci with 3/3 teeth; total body length 200–250 μm *coenobasis* (Skorikov, 1914)
[Amphoteris females are known in this species (Ruttner-Kolisko 1974).]
- 6' Unci with 4/5 teeth; total body length 170–190 μm *exiguus* (Ahlstrom, 1938)
[An amphoteris female is shown in Fig. 5D.]

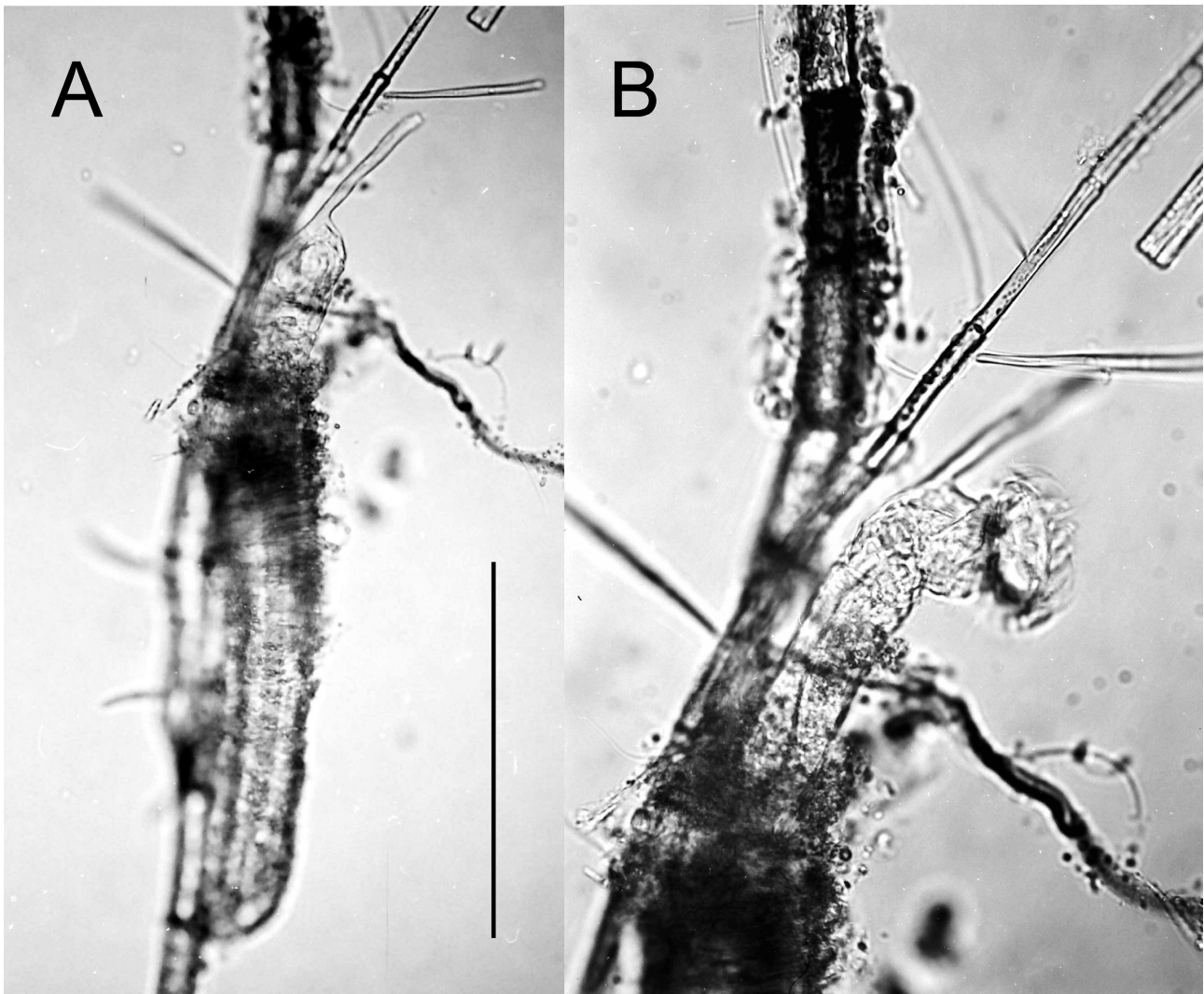


FIGURE 7. *Beauchampia crucigera* attached to filamentous algae. A. Corona retracted; B. corona expanded. Bar = 500 μ m.

Family Flosculariidae Remane, 1933

Flosculariidae is a cosmopolitan family comprising nine genera (*Beauchampia*, *Floscularia*, *Lacinularia*, *Lacinularoides*, *Limnias*, *Octotrocha*, *Pentatrocha*, *Ptygura*, *Sinantherina*) with approximately 60 named species and subspecies. The etymon of the family is as for the order.

Diagnosis. Symmetrical or asymmetrical, malleoramate trophi; typically with elongate bodies and large, circular (slightly elliptical) to lobate, heart-shaped, or ear-like corona. Animals live in a tube formed in various ways or in a secreted gelatinous matrix. They may be solitary or colonial: colonies may be intra- or interspecific. Mostly species are sessile, some are planktonic, two are facultatively sessile.

- 1 Single dorsal antenna, visible when animal contracts, conspicuously long (> body width); gelatinous matrix embedded with debris; sessile; solitary; body length ≤ 1000 μ m; oviparous; monospecific (Fig. 7) *Beauchampia crucigera* (Dutrochet, 1812)
- 1' Two dorsal antennae, not visible when animal contracts, not conspicuously long; gelatinous matrix present or absent 2
- 2(1) Adults with oviferon below anus 3
[The oviferon, a specialized egg-bearing structure where eggs attach (Fig. 8) (Segers & Shiel 2008).]
- 2' Adults without oviferon; gelatinous matrix or constructed tube present 4
- 3(2) Corona with five large lobes; transparent, amorphic, gelatinous matrix; sessile; typically solitary, occasionally small colonies (<3 animals); body length 3000–3500 μ m; oviparous; monospecific *Pentatrocha gigantea* Segers & Shiel, 2008
[Specimens of this monospecific genus were hatched from dry sediments of a temporary waterbody in Australia (Segers

and Shiel 2008). The original description provides illustrations of the adult and SEM photomicrographs of the trophi. Being extremely large and with a corona of five lobes *Pentatrocha* cannot be mistaken for *Sinantherina* or any other sessile rotifer (Meksuwan *et al.* 2011).]

- 3' Corona not as above (heart-shaped); gelatinous matrix is absent; sessile or planktonic; solitary or colonial; body length 750–2500 µm; oviparous. (Fig. 8) *Sinantherina* Bory de St. Vincent, 1826
 [Three species possess bulbous structures called warts (Wallace *et al.* 2023) on their antero-ventral; one species has spines. Five species.]

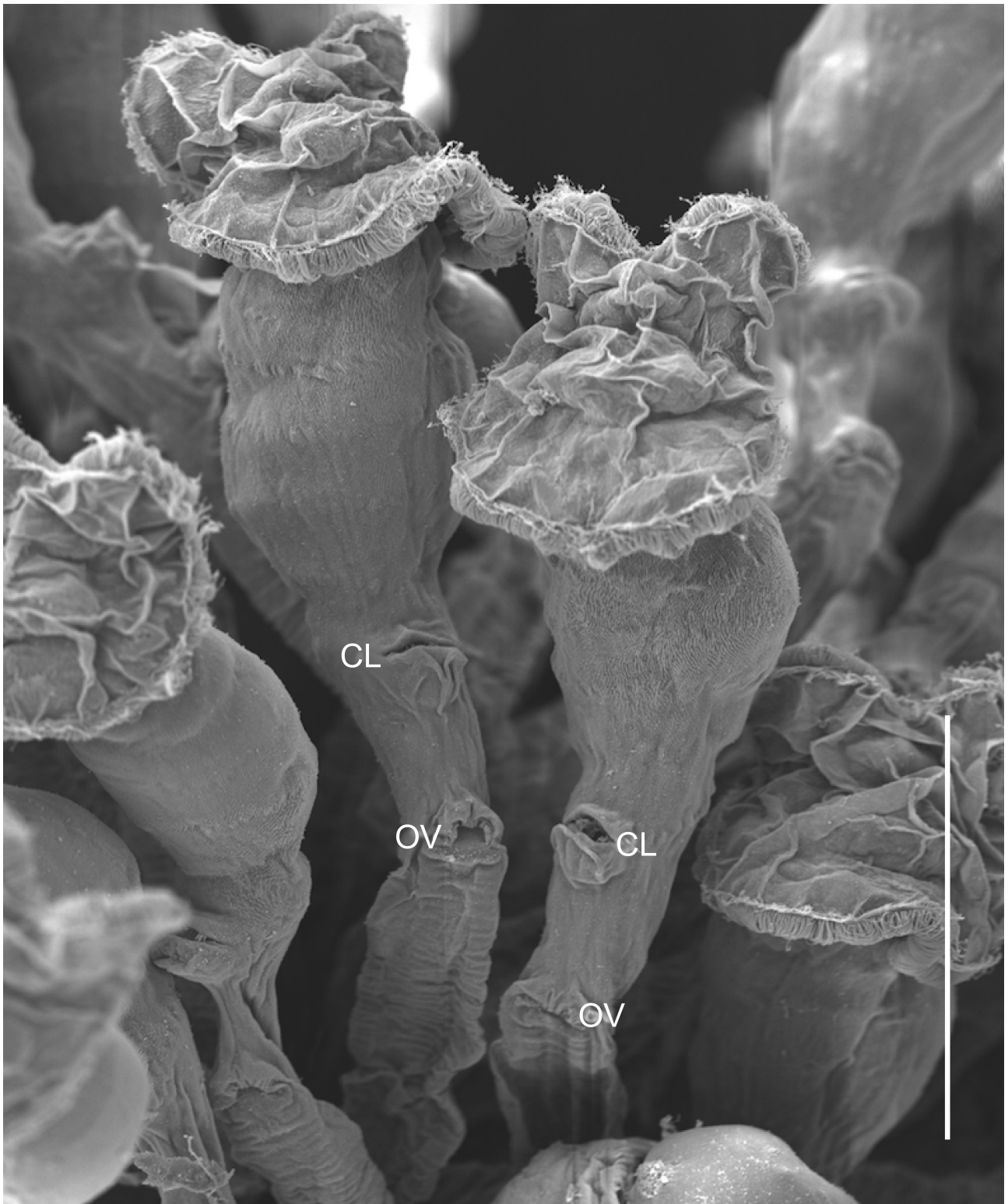


FIGURE 8. Scanning electron photomicrograph (SEM) of part of a colony of *Sinantherina socialis*. The two individuals in the center show the oviferon (OV) below the cloaca (CL). A gelatinous matrix is absent in this genus. (Bar ~ 250 µm.)

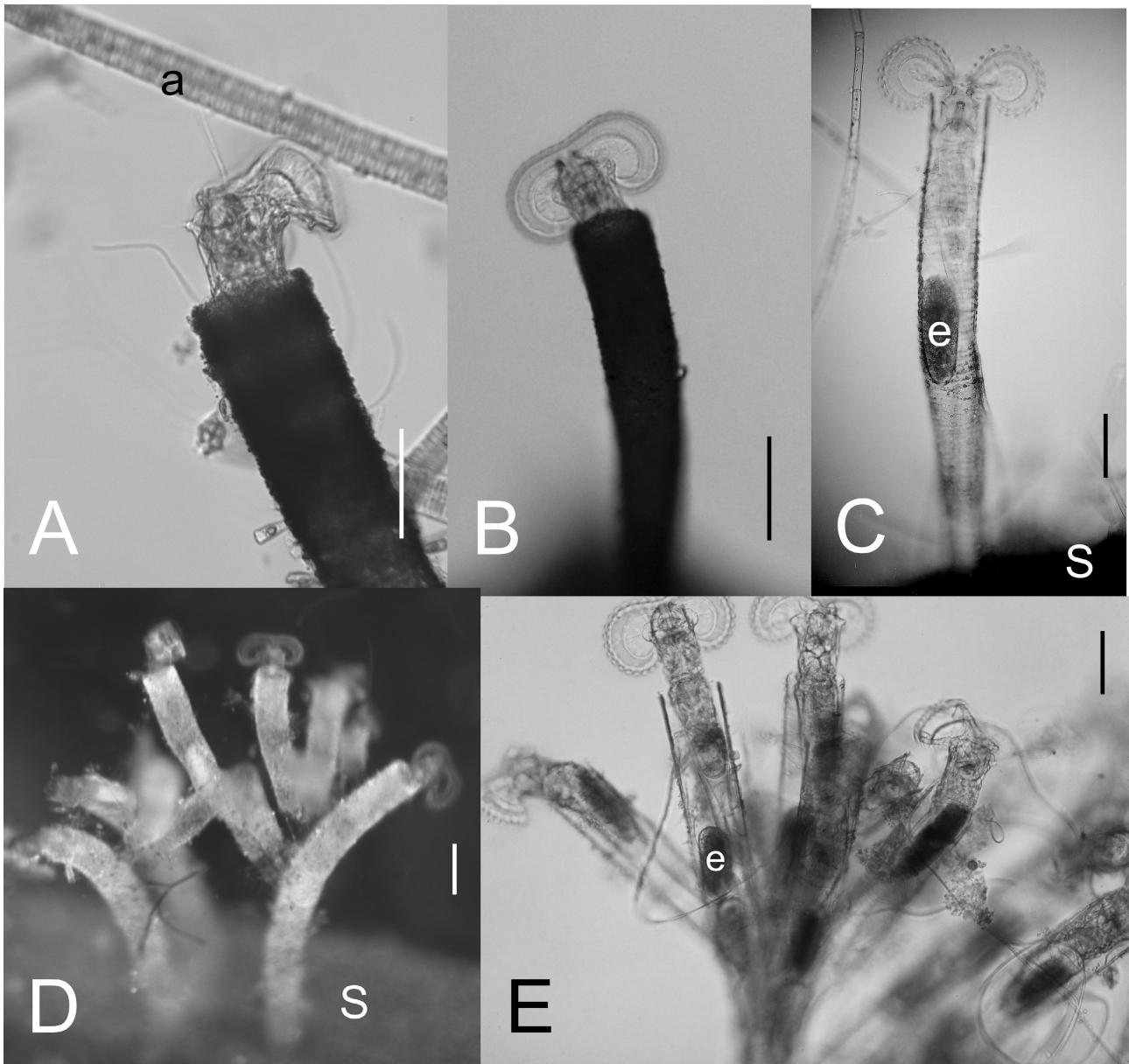


FIGURE 9. Examples of species in the genus *Limnias*: A-B. solitary *Limnias ceratophylli*-group; C. solitary *Limnias melicerta*-group; D. colonial *L. ceratophylli*-group; E. colonial *L. melicerta*-group. Symbols: a = algae; e = embryo; S = substratum. Bars ~ 100 μ m.

- 4(2') Adults in a flexible straight or slightly curved pipe of hardened secretions (either as a stack of semitransparent rings or granular, stucco-like and opaque); sessile; usually solitary (occasional small, branching, colonies, typically ≤ 15); body length ≤ 1000 μ m; oviparous. (Fig. 9)..... *Limnias* Schrank, 1803 [Corona width greater than height, with one pair of lobes; corona with wide dorsal gap and ventral depression. Two groups of *Limnias* are easily recognized by their tubes. (1) The *melicerta*-group (3 species) possess a tube with a ringed structure (Wright 1954; Yang & Hochberg 2018). (2) The *ceratophylli*-group (5 species) lacks rings, its tube resembles a stucco surface. Identification of species requires observations of the shape of the corona and the number and shape of outgrowths (horny processes or projections) on a dorsal plate just beneath the corona (Meksuwan *et al.* 2018). One species, *Limnias ceratophylli* Shrank, 1803 has been reported as epizoic on the Amazonian crocodile, *Melanosuchus niger* (Magnusson 1985). The etymon of this genus (*L.*, *limnos*, lake) apparently refers to the general habitat of these animals. Keys to species of *Limnias* are given by Meksuwan *et al.* (2018) and Wallace *et al.* (2018).]
- 4' Not as above..... 5
- 5(4) Corona with distinct lateral lobes..... 6
- 5' Corona without distinct lateral lobes..... 8

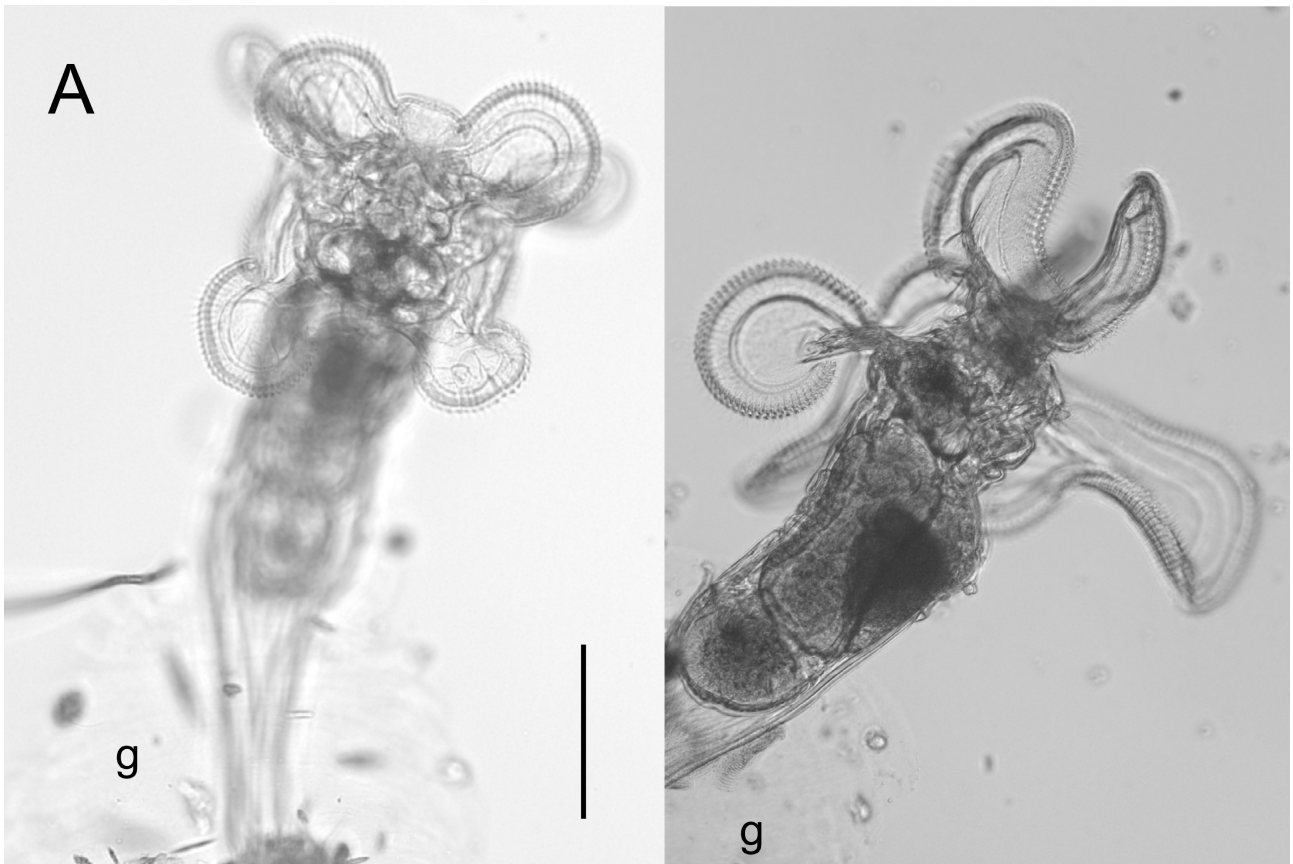


FIGURE 10. *Octotrocha speciosa*. A. dorsal view; B. partial side view which illustrates the elaborate coronal lobes. Symbol: g = gelatinous matrix (tube). Bar = 250 μ m.

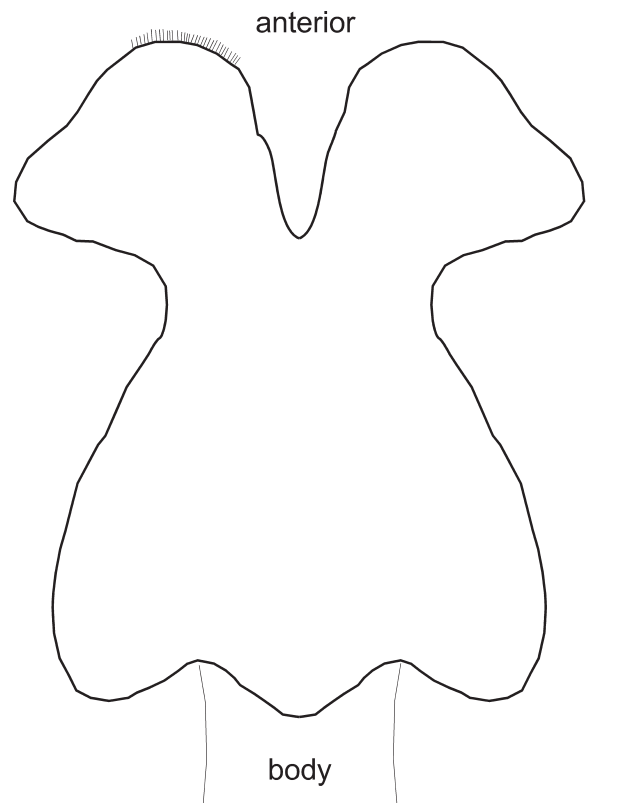


FIGURE 11. *Lacinularoides coloniensis*: schematic dorsal view of the corona. Ciliation is indicated for only a small portion of the coronal margin. Bar = 250 μ m. (Modified after Colledge, 1918).

- 6(5) Corona with four pairs of lateral lobes (= 8 lobes) one pair smaller; gelatinous tube; solitary; body length 1500–2000 μm ; oviparous; monospecific. (Fig. 10). *Octotrocha speciosa* Thorpe, 1893
 [Information on this monospecific genus is provided by Koste & Böttger (1989) and Segers & Shiel (2008).]
- 6' Corona otherwise 7
- 7(6) Corona with 7 lobes (2 small and 5 prominent lateral lobes); sessile in a tough gelatinous tube; solitary (stem female?) or colonial; foot long; body length $\leq 1300 \mu\text{m}$; oviparous; monospecific. (Fig. 11)
 *Lacinaroides coloniensis* (Colledge, 1918)
 [The corona resembles that of *Pentatrocha*, but this species lacks an oviferon; the corona is not as elaborate as in *Octotrocha*. The genus name was derived from the genus *Lacimularia*; a review of this monospecific genus was done by Mekusuwan *et al.* (2011).]

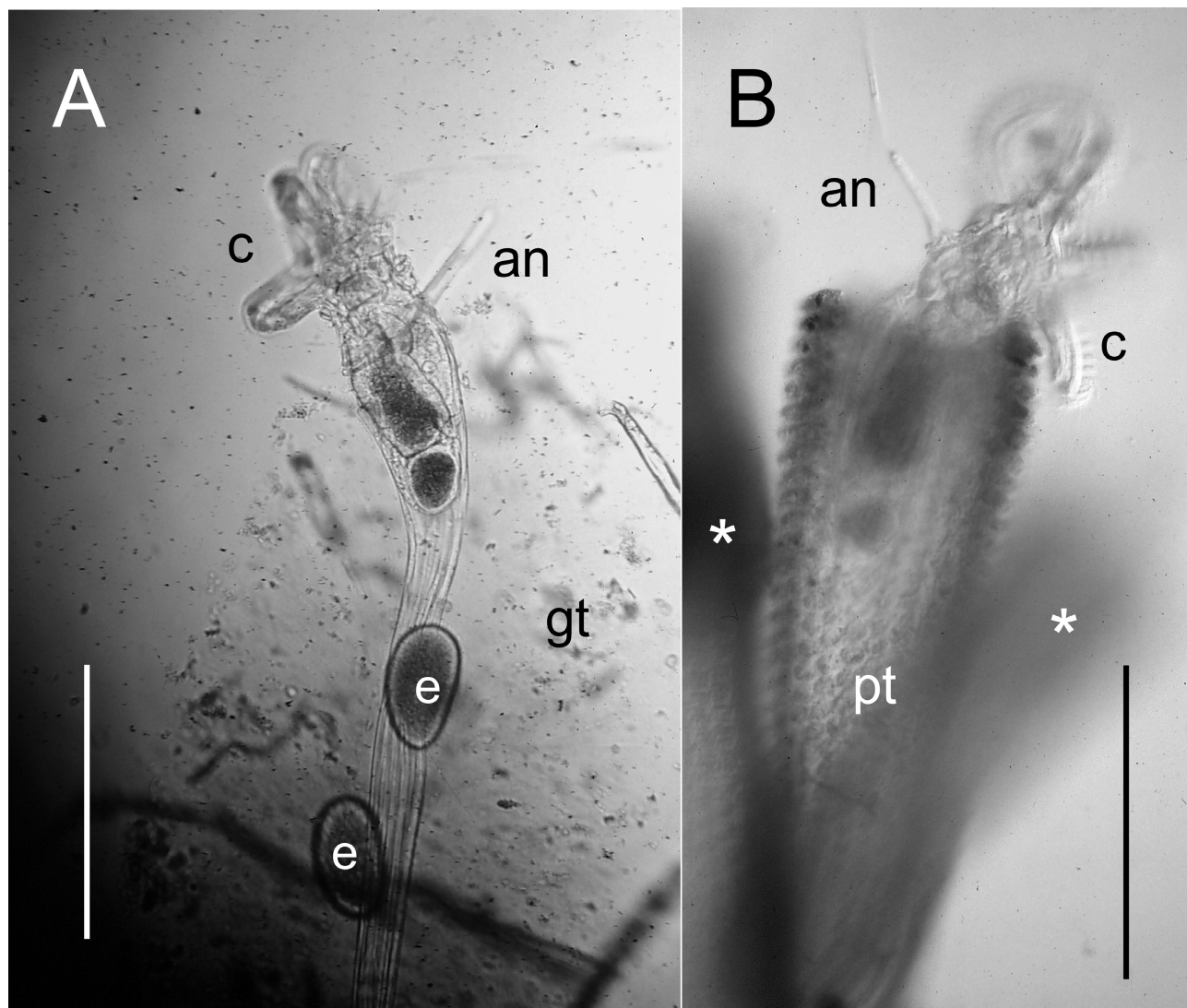


FIGURE 12. Examples of *Floscularia* species. A. *Floscularia melicerta* B. *F. Floscularia conifera* (lateral view). Symbols an = antennae; c = corona; e = embryo; gt = gelatinous tube; pt = pellet tube; * = colony mates (out of focus). Bars = 500 μm .

- 7' Corona with 4 lobes (2 pairs of distinct lateral lobes); sessile; solitary or colonial; tube composed of formed pellets, or gelatinous matrix; body length 500–2000 μm ; oviparous. (Fig. 12) *Floscularia* Cuvier, 1798
 [Two species (*Floscularia conifera* (Hudson, 1886) and *Floscularia ringens* (Linnaeus, 1758) are known to form allorecruitive colonies. Nine species.]
- 8(5') Corona round to slightly elliptical; animals in gelatinous matrix, often with debris (one species with fecal pellets in the matrix); usually solitary, occasionally in intra- or interspecific colonies; body length 200–1400 μm ; oviparous. (Fig. 13)
 *Ptygura* Ehrenberg, 1832
 The taxonomic history of *Ptygura* is complicated; the genus is in need of a comprehensive review (Mekusuwan 2015). [30 species.]
- 8' Corona heart-shaped; animals embedded in common, flocculent gelatinous matrix; sessile or planktonic; usually colonial (usually < 200); body length 900–2000 μm ; oviparous. (Fig. 14) *Lacimularia* Schweigger, 1820
 [In field samples, colonies of 1000s of individuals have been seen (EJW, pers. obs. Seven species.)]

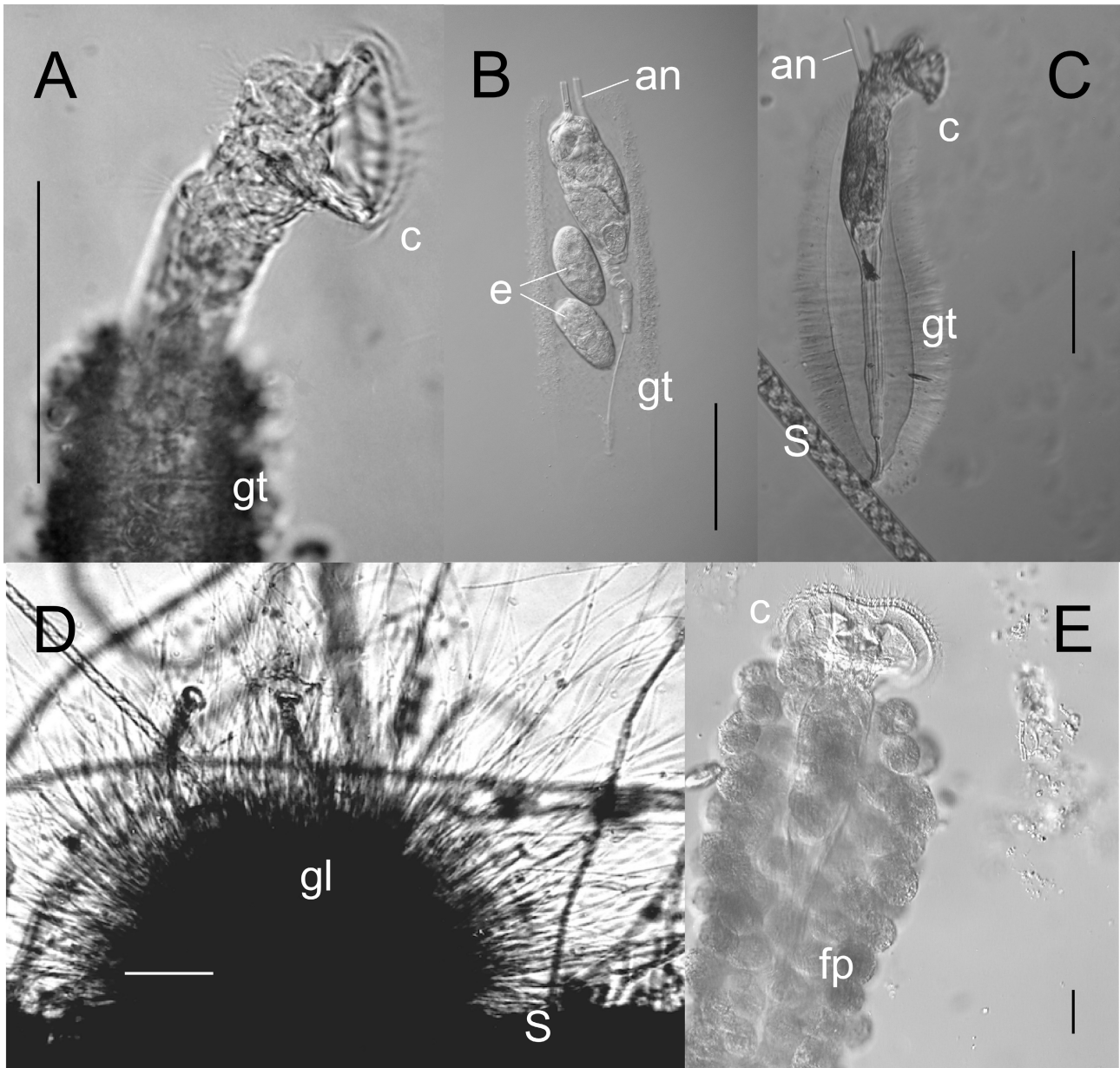


FIGURE 13. Examples of *Ptygura* species. A. *Ptygura beauchampi* Edmondson, 1940; B. *Ptygura libera* Myers, 1934; C. *Ptygura brachiata* (Hudson, 1886); D. *Ptygura mucicola* (Kellicott, 1889); E. *Ptygura pilula* (Cubitt, 1872). Symbols: an = antennae; c = corona; e = embryo; gt = gelatinous tube; fp = fecal pellets (embedded in gt); gl = *Gloeotrichia* sp. (cyanobacteria) attached to a vascular hydrophyte; S = substratum. Bars = 100 μ m.

Declarations

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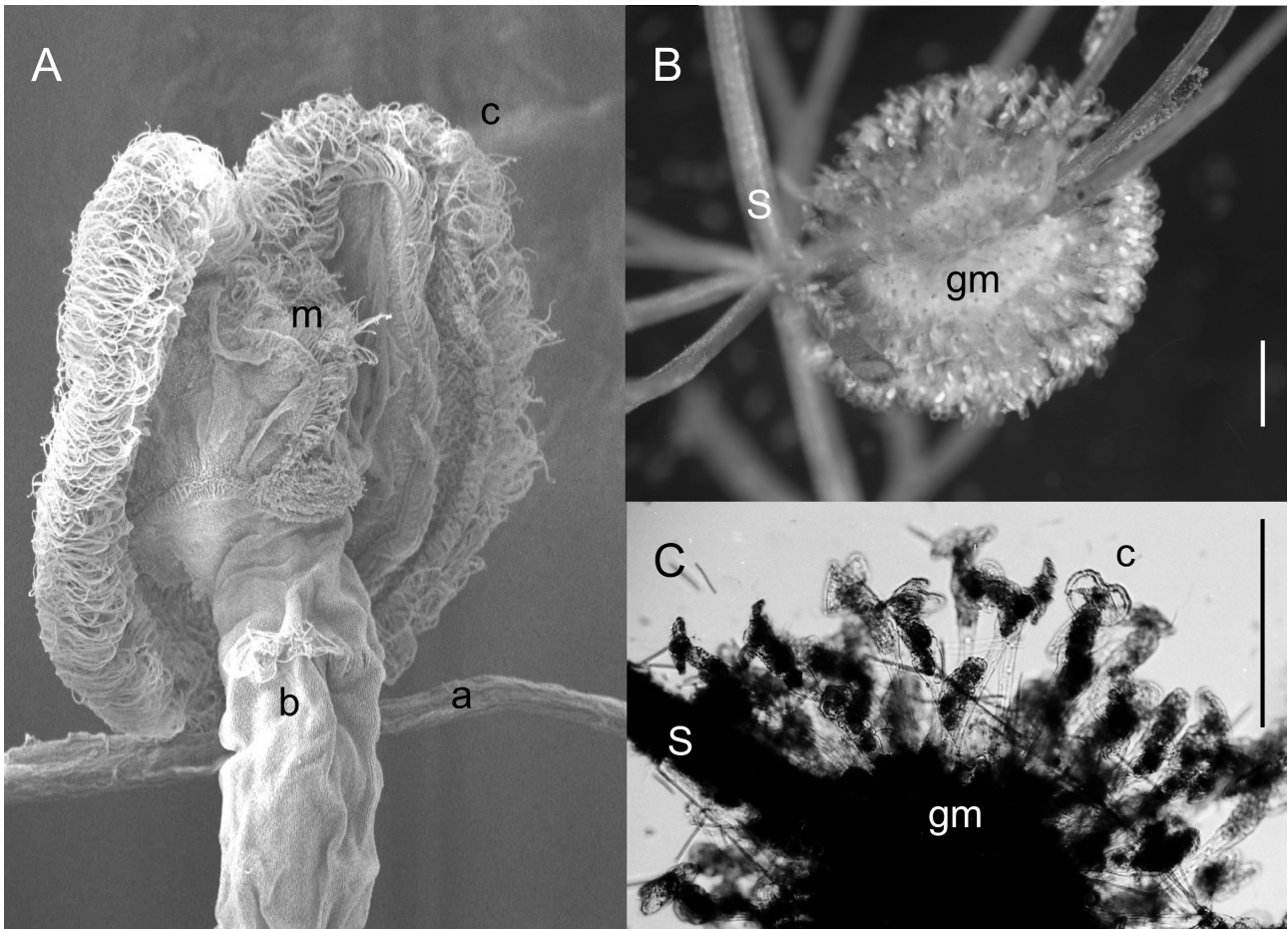


FIGURE 14. Examples of *Lacinularia*. A. SEM dorsal view; B. Complete colony attached to *Ceratophyllum demersum* Linnaeus, 1753; C. Closeup of a colony. Symbols: a = algal filament; b = body; c = corona; gm = gelatinous matrix (embryos are embedded within); m = mouth; S = substratum. Bars = 1,000 μ m.

Conflicts of interest/Competing interests

The authors have no conflicts of interest/competing interests. The sponsors had no role in the design, execution, interpretation, or writing of the study.

Availability of data and material

Not applicable

Code availability

Not applicable

Ethics Approval

No collecting permits were required for this study. None of the specimens that we collected are endangered or threatened. Sampling and processing protocols followed appropriate guidelines established by the local municipalities.

Authors' contributions

Conceptualization, R.L.W.; validation, N.D., A.L., R.L.W.; formal analysis, N.D., A.L., R.H., R.L.W., E.J.W.; investigation, N.D., A.L., R.L.W.; resources, R.L.W.; data curation, R.L.W.; preparation of the original draft, R.L.W.; writing, reviewing, and editing, N.D., A.L., R.H., R.L.W.; E.J.W.; project administration, R.L.W.; funding acquisition, R.H., R.L.W., E.J.W. All authors have read and agreed to the published version of the manuscript.

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