Zootaxa 5471 (4): 401–421
https://www.mapress.com/zt/
Copyright © 2024 Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5471.4.1
http://zoobank.org/urn:lsid:zoobank.org:pub:EC24443B-9EDC-4FF0-8247-083CBC9DDE75

Key to sessile gnesiotrochan rotifers: *Floscularia* (Monogononta; Flosculariidae)

ALEXANDRE LAFLEUR[1,4#], NATALIE DAVIES[1,5#], RICK HOCHBERG[2], ELIZABETH J. WALSH[3] & ROBERT L. WALLACE[1,6*]

[1]*Department of Biology, Ripon College, Ripon, WI, 54971, USA*
[2]*University of Massachusetts Lowell, Lowell, MA, 01854, USA*
Rick_Hochberg@uml.edu; https://orcid.org/0000-0002-5567-5393
[3]*Department of Biological Sciences, University of Texas at El Paso, El Paso, TX, 79968, USA*
ewalsh@utep.edu; https://orcid.org/0000-0002-6719-6883
[4] *lafleura@ripon.edu; https://orcid.org/0000-0002-7312-8457*
[5] *daviesn@ripon.edu; https://orcid.org/0000-0002-9118-3679*
[6] *wallacer@ripon.edu; https://orcid.org/0000-0001-6305-4776*
[#]*The first two authors contributed equally to this paper*
**Corresponding author*

Abstract

Correct identification of species is necessary if we are to understand their biology, ecology, and evolutionary history, as well as to catalog their global biodiversity. This is acutely critical for many micrometazoans like rotifers, which are often difficult to identify because of their small size and complicated morphologies. Rotifers are ubiquitous micrometazoans that are found worldwide in fresh, brackish, and some marine waters. However, their study is hindered by a lack of both taxonomic expertise and concomitantly adequate guides to the identification of some taxa. These deficiencies are particularly true for the sessile species. To help alleviate these impediments, we assembled information from the literature on easily recognizable characters of all nine valid species in one notable genus: *Floscularia* (Monogononta; Gnesiotrocha; Flosculariidae). Using that information we developed a simple, dichotomous key to enable workers to identify species in this genus. Our key emphasizes easily observable characters of adult female morphology, including features of their tubes, anterior ends, trophi, and colony formation abilities, thereby allowing for relatively quick identification.

Key words: Coloniality, dichotomous key, Gnesiotrocha, larvae, morphology, Rotifera, sessile, solitary

Introduction

A fundamental process in biological study is the search for patterns. Indeed the discipline began in antiquity with the grouping of organisms into categories based on similarities in form, function, and process. The physicist Rutherford described that approach as 'stamp collecting' (Johnson 2007). To a certain extent we are still involved in that practice. Nevertheless, knowledge of the range of biological complexity is still wanting at all levels, and the most fundamental of these is our ability to identify organisms. That knowledge gap hinders our ability to map their distributions and understand their evolutionary patterns; these encompass the Linnean, Wallacean, and Darwinian shortfalls. But it also impedes advancing knowledge in other kinds of biodiversity knowledge: i.e., understanding ecological function, abiotic tolerances, and species interactions: the Raunkiaeran, Hutchinsonian, Eltonian shortfalls, respectively (Diniz-Filho *et al.* 2023; Hortal *et al.* 2015). While these knowledge gaps are replete throughout all biology, they are critical for micrometazoans because of the fundamental roles they play in food web dynamics including the microbial loop (Glibert & Mitra 2022) and their importance in other avenues of research including aquaculture, aging, and toxicology (Wallace *et al.* 2023). It is also important that these gaps be filled to develop complete phylogenies (Sørensen & Giribet 2006). Here we continue our focus on the sessile species in phylum Rotifera (*sensu stricto*) begun by Davies *et al.* (2024), a group whose study is hindered by the lack of new taxonomists armed with up to date keys (Ejsmont-Karabin 2019; Fontaneto *et al.* 2012).

Accepted by W. De Smet: 23 May 2024 published: 20 Jun. 2024

Licensed under Creative Commons Attribution-N.C. 4.0 International https://creativecommons.org/licenses/by-nc/4.0/

Although usually less than 1000 µm in size and numbering only about 2000 described species, rotifers have piqued the curiosity of researchers for >200 years. (Davies *et al.* 2024; Edmondson 1959; Fontaneto & De Smet 2015; Wallace *et al.* 2006). This interest stems from the fact that these short-lived, aquatic metazoans possess diverse morphologies and varied life cycles (Wallace *et al.* 2015), as well as reproductive modalities encompassing both obligatorily sexual, obligatorily asexual, and cyclically parthenogenetic (Serra *et al.* 2018). While most rotifers are mobile, either swimming (Obertegger *et al.* 2018), crawling over surfaces (Hochberg & Litvaitis 2000), or navigating among particles in sediments (Ejsmont-Karabin & Karpowicz 2021), the adults of nearly 100 species in superorder Gnesiotrocha live permanently attached to surfaces. These species are referred to as the sessile rotifers (Edmondson 1944). As a group these taxa offer a variety of interesting research subjects including their evolution and understanding the function of diverse morphology, genetics, life history, development, substratum selection, and habitat-dependent adult reproduction and survival. Even though most of these taxa are sessile, some species are obligatorily planktonic, a condition that probably evolved secondarily (Edmondson 1944). Adult sessile rotifers are common on submerged hydrophytes in inland lakes and ponds (Wallace 1980). Many are solitary, but others form colonies (Edmondson 1945; Wallace 1987). The ways in which colonies form have been described by Wallace *et al.* (2015). However, young hatchlings (larvae) from diapausing embryos (resting eggs) are solitary, thus, regardless of the ways colonies are formed a future colony always begins with a single stem female.

Identification of sessile rotifers is based on relatively simple characters, including shape of the corona, presence of sensory and other morphological structures in the apical field, body size, propensity to form colonies, and the fact that many species form extracorporeal coverings that surround their bodies (Yang & Hochberg 2018a, 2018b; Yang *et al.* 2021). Indeed, because these coverings vary in their construction to include gelatinous matrices, flexible, hardened tubes, and pipe-like tubes composed of pellets, their composition is a convenient characteristic on which keys to the genera and even species may be based (Davies *et al.* 2024; Edmondson 1959; Koste 1978). Unfortunately, of all potential features, morphology of their trophi has been nearly neglected. Regardless, use of trophi in identification of rotifers can be difficult for workers inexperienced in their extraction or those engaged in large scale ecological studies where trophi removal can be prohibitively time consuming. Moreover, trophi also may have limited value in the case of some cryptic species (Kordbacheh *et al.* 2018). In such instances, other characters may provide more value and lead to more rapid identification.

Habitats containing sufficient hydrophyte diversity provide adequate niche diversity to allow the development of a rich sessile rotifer community including those in the orders Collothecaceae and Flosculariaceae (Edmondson 1944; Sarma *et al.* 2020; Tiefenbacher 1972; Wallace 1977). Their wide distribution notwithstanding the extant keys to the sessile taxa are not inclusive. For example the key by Meksuwan *et al.* (2013) is regional and that of Koste (1978) is incomplete: i.e., it does not include taxa currently recognized in the List of Available Names of Rotifera (Jersabek *et al.* 2018). Moreover, general information of the sessile taxa are scattered across the literature (Koste 1975; Leutbecher & Koste 1998; Tiefenbacher 1972; Wallace 1977, 1980) and visual documentation of species is limited. And, if DNA barcodes are assigned to misidentified taxa, their study will become undeniably worse (Collins & Cruickshank 2013). Here we provide a key to identification of adult females of the nine species in *Floscularia* (Flosculariidae; Flosculariaceae) an important sessile genus with species commonly found attached to hydrophytes lentic waters in both tropical and temperate systems across the globe.

Identify of sessile rotifers to the level of genus and then species can be difficult. The monospecific species in Flosculariidae (*Beauchampia*, *Lacinularoides*, *Octotrocha*, and *Pentatrocha*), species of Conochilidae, and *Limnias* have been recently considered by Davies *et al.* (2024). A few straightforward features allow differentiation of the remaining genera of Flosculariidae: *Floscularia, Lacinularia, Ptygura,* and *Sinantherina*. *Floscularia* species possess a corona with four lobes and a glandular, ciliated cup called the modulus that secretes a mucilaginous material, which they use in constructing their tube (see below). All adult *Floscularia* lack an oviferon (see below) and are exclusively sessile, either as individuals or forming small to large allorecruitive colonies (Wallace *et al.* 2015) (pseudo-colonies) (Meksuwan 2015). All adult *Lacinularia* possess an oval to heart-shaped corona; they are embedded in a conspicuous, common, gelatinous matrix. All adult *Lacinularia* species lack an oviferon, are usually colonial, and are either sessile or planktonic. Depending on the species, their colony formation is autorecruitive or geminative. *Ptygura* species possess a round to oval-shaped corona, produce a gelatinous tube, and lack an oviferon. Most are sessile and are usually solitary, but they may attached to other sessile rotifers forming allorecruitive colonies (Wallace 1987). *Sinantherina* species possess a heart-shaped or quadrangular corona, lack an obvious gelatinous matrix, and possess an oviferon—a feature that they shares with *Pentatrocha* (Segers & Shiel 2008);

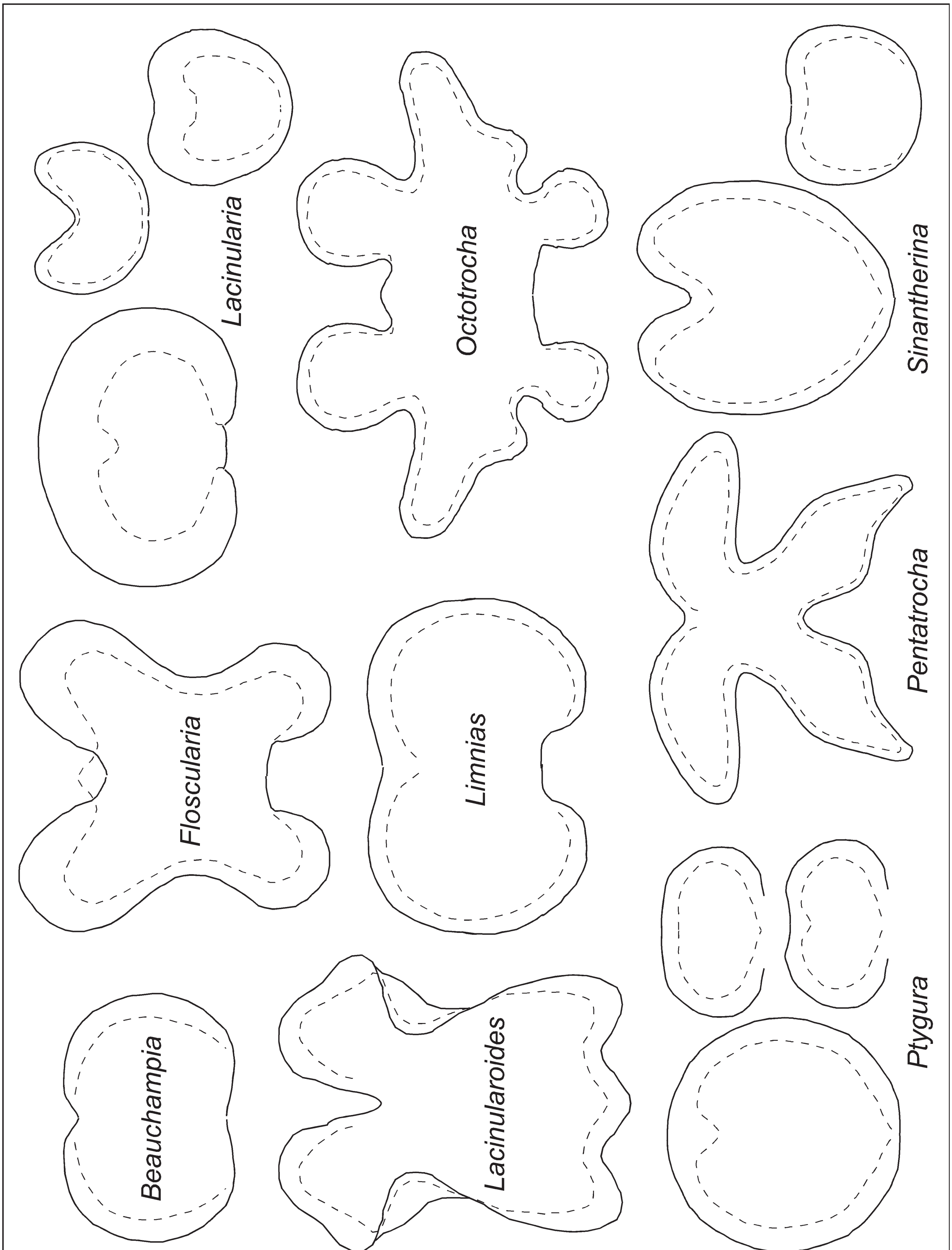

FIGURE 1. Schematic representations of the coronal margins of the nine genera of Flosculariidae. Images are not to scale. The corona is developed into two concentric rings that beat in a metachronous pattern thereby producing feeding currents: trochus (——); cingulum (– – –) (Wallace 2002). Adapted after Bielańska-Grajner *et al.* (2015), Colledge (1918), Koste (1978, 1989), and Remane (1929–1933); *Pentatrocha* (©Magnolia Press, reproduced with permission from the copyright holder [Zootaxa 1750: 19–31] and the authors (Segers & Shiel 2008)).

both sessile or planktonic species are known. Depending on the species, their colony formation is autorecruitive or geminative. However, in identifying genera of Flosculariidae one should avoid relying only on a cursory observation of the corona alone (Fig. 1). First, the coronal margins flex considerably, twisting and stretching. Therefore, they may temporarily present a different contour. Second, there is some overlap in the general outline that may lead to misidentification, particularly in *Lacinularia, Ptygura,* and *Sinantherina*, and perhaps *Limnias*. A neglected field of research is the musculature and surface characteristics of these genera (Hochberg & Hochberg 2017; Hochberg *et al.* 2015; Hochberg & Lilley 2010; Santo *et al.* 2005).

Methods

We constructed keys by reviewing the literature germane to species of *Floscularia*, including Edmondson (1940), Fontaneto *et al.* (2003), Hudson (1875), Koste (1978), and Wright (1950). In all cases we reviewed the original published descriptions, but only species recognized as valid by the List of Available Names (LAN) (Jersabek *et al.* 2018) and/or the Rotifer World Catalog (Jersabek & Leitner 2013) were considered.

Genus *Floscularia* Cuvier, 1798

Before the turn of the century, the genus *Floscularia* was known as *Melicerta* (family Melicertadae) (sic) (Hudson & Gosse 1886) (Latin, *meliceris*, honeycomb). At that time genus *Collotheca* (Greek, *collo*, glue + Greek, *theca*, cup) was referred to as *Floscularia* in family Flosculariadae (sic) (Hudson & Gosse 1886). However, for reasons of priority, Harring (1913) rectified these errors. The etymon of *Floscularia* is an allusion of a fully expanded adult which has the appearance of a flower. The genus comprises nine morphospecies, but based on the LAN we separate the five taxa that Koste (1978) subsumed into a group comprising taxa resembling *Floscularia ringens* (Linnaeus, 1758) (Segers & Shiel 2008).

While the larvae of all *Floscularia* are free swimming, the adults are sessile and either solitary or colonial. At the base of the foot the animal secretes a material is that permanently glues the animal to the substratum. In some cases, this material continues to be released; this results in a slim, extracorporeal shaft called the peduncle. Adult animals may become dislodged from their substratum if they are subjected to rough treatment during sampling or transport. Prolonged storage in fixatives has the same result.

Floscularia species may be differentiated based on several characters some of which offer taxonomical challenges; these are outlined in Table 1 and examples illustrated in Figure 2. Unfortunately, not all of these features are well documented in the literature. All species produce an extracorporeal tube of some form, but its construction varies markedly (i.e., solely gelatinous, gelatinous with large pellets, or composed of small pellets). However, tubes may partially obscured by algae and/or debris and the color of pellets are affected by the colors of particles in the water. Also the color of the gelatinous tube in *Floscularia melicerta* (Ehrenberg, 1832) may vary depending on the edaphic conditions of the habitat. With respect to female morphology, the corona has four lobes, two ventral and two dorsal, but they vary slightly in shape. The coronae of two species remain undescribed (see below). As previously noted, careful observations of the flexible lobes is essential, as they may temporarily adopt unusual conformations. Production of gelatinous tubes in *F. melicerta* and *Floscularia janus* (Hudson, 1881) and the incorporation of individually formed pellets in the tubes of other species is accomplished by a curious structure composed of three units: labium (tongue-like), modulus (cup-shaped), and sublabium (smaller mound) located the anterolateral side (Fig. 2A,B). Mucrons (neck hooks or processes) are located in the dorsal region of the neck just posterior to the corona (Fig. 2C). These small, firm, finger-like processes are best seen at apex of the anterior end in contracted animals. Because their morphology varies, they are useful in species identification (Edmondson 1940; Segers 1997; Segers & Shiel 2008). A peduncle may be present, but its length may vary within a species depending on the age of the animal (Segers & Shiel 2008; Wright 1959) (Fig. 2D). The length of the ventrolateral antennae may be short or long (Edmondson 1940). Morphology of their unci teeth of the trophi varies: they may be weakly or strongly differentiated (Fontaneto *et al.* 2003; Segers 1997; Segers & Shiel 2008) (Fig. 2E). The propensity to form colonies varies among species (Fig. 2F). To identify species of *Floscularia* the best practice is to use a as many of the characteristics noted above as possible.

All *Floscularia* construct tubes, but that process differs from that of other sessile taxa (Yang & Hochberg 2018b; Yang *et al.* 2021) and it even differs within the genus. Yet all employ a gelatinous material to some degree in tube construction. In *F. melicerta*, tube construction is simple: a thick jelly is secreted by the modulus that is then smeared in layers one on top of the other (Wright 1957). As these layers are deposited, they may incorporate dissolved organic matter thereby producing a slightly colored jelly mass rather than a clear one. Algae and debris may become embedded within the jelly, the result being a nearly an opaque tube (see below). In *F. janus* fecal masses are incorporated into the jelly tube (Hudson 1881). [This is also seen in *Ptygura* (*Floscularia*) *noodti* (Koste, 1972) and *Ptygura pilula* (Cubitt, 1872): see figure 156 a,b in Remane (1929–1933) and Abb. 3 in Koste (1972)]. Tube formation reaches its most complex form in those *Floscularia* that mix suspended particles that have been caught by the animal's feeding currents, but not consumed, with gelatinous secretions of the modulus to form spherical or bullet-shaped pellets. These are then laid one upon another—like a brick layer might do—to form a tubular wall resembling the turret of a medieval castle (Remane 1929–1933; Wright 1950). The inside of these tubes is apparently lined with a membranous coat (Fontaneto *et al.* 2003; Yang & Hochberg 2018a). Differences in suspended particles may alter the color of the pellets (see below) (Edmondson 1945; Hudson & Gosse 1886). Consult Bedwell (1877), Cubitt (1870), Wright (1950), Tiefenbacher (1972), and Fontaneto *et al.* (2003) for accounts of the pellet tube and its formation.

Because the tube is conspicuous it is convenient to focus on it to identify species of *Floscularia* (Koste 1978): e.g., using the presence or absence and morphology of pellets, rather than other morphological features of the animal. Nevertheless, as Edmondson (1940) warns "… the character of the tube depends on the nature of the material in the environment … ." Thus, materials suspended in the water may not be integrated into the pellets in the same way in all habitats and at all times. For example, in species forming pellet tubes the pellets produced on one day may be a different color than on another (Edmondson 1945). However, the tube may not be evident in populations of *F. janus* growing in water with low levels of particulates. Additionally, *Floscularia decora* Edmondson, 1940 commonly uses little material in construction of pellets, so its tube may be difficult to discern. And, as noted above, the gelatinous tube of *F. melicerta* may be mistaken for possessing pellets if the jelly has become concealed by debris.

A further complication may arise when relying on tube morphology alone to distinguish two species coexisting in the same habitat. In certain circumstances the pellets produced by *F. ringens* may be somewhat elongate thereby resembling that of *Ptygura noodti* (Koste, 1972). Therefore, to determine whether a species of pellet-forming tube is a species *Floscularia* or *Ptygura* species: e.g., *P. noodti* or *P. pilula*, the shape of the corona should be examined while it is expanded (Meksuwan *et al.* 2011). In preserved samples it will be necessary to remove the animal from its tube to examine it for the presence and form of mucrons (neck hooks), which vary in *Floscularia* (Segers 1997; Segers & Shiel 2008). Mucrons also are present in certain members of *Ptygura,* which offers an additional complexity (Franch *et al.* 2024; Meksuwan *et al.* 2011).

Conclusions

Additional study of species in this genus should include morphology of the trophi, mucrons, and tripartite pellet-forming organ, as well as the extent to which colony formation takes places. No doubt other species of *Floscularia* await discovery. Unpublished notes of Frank Myers outlined a putative species he called *F. glandulata*. According to Myers' notes, the tube of this putative species resembled *F. janus*, but the corona had four, nearly equal lobes and the mucrons were very large and moved like pincers (W.T. Edmondson, pers. commun.). Segers and Shiel (2008) discuss specimens that resemble *F. melicerta*, except for two characteristics: short, ventrolateral antennae and a gelatinous tube that resembles *Ptygura barbata* Edmondson, 1939 and *Ptygura tacita* Edmondson, 1940.

TABLE 1. Important characteristics in differentiating *Floscularia* species.

Species	Tube	Coronal morphology (all are 4-lobed)	Labium (chin)	Mucrons	Peduncle *	Ventrolateral antennae	Unci teeth differentiation	Colony formation	Selected references
armata	Pellets, round, loosely packed	Undescribed (contracted specimen)	†	§	Short	Elongate	Moderate to strong	†	Segers (1997); Segers and Shiel (2008)
bifida	Pellets, round, loosely packed	Relatively large (contracted specimen)	†	Bifid	Long	Elongate	Strong	†	Meksuwan (2015); Segers (1997); Segers and Shiel (2008); Wu *et al.* (2014)
conifera	Pellets, bullet-shaped, densely packed	~2X wide as body; ventral lobes large; dorsal lobes small, round, with deep narrow gap	Long, pointed	‡	Long	Elongate	Weak	Solitary to ~35	Edmondson (1940); (Edmondson 1945); Segers (1997)
decora	Pellets, hexagonal, bullet-shaped, densely packed	>2X wide as body; ventral lobes large, wide V-shaped; dorsal lobes round	†	Smoothly curved	Short	Elongate	Weak	†	Edmondson (1940); Segers and Shiel (2008)
janus	Gelatinous with large ovoid fecal pellets	~2.5X wide as body; ventral lobes large; dorsal lobes very small, almost confluent	Long, stout; with medial notch	None	Short	Short	Weak	Solitary	Hudson (1881); Kutikova (2007); WT Edmondson, pers. commun.
melicerta	Gelatinous only	~2.5X wide as body; ventral lobes large, round; dorsal lobes small, may be held horizontally	Small, reduced	Smoothly curved	Short	Elongate	Strong	Solitary	Hudson (1875); Koste and Böttger (1989, 1992); WT Edmondson, pers. commun.
pedunculata	Pellets, round, densely packed	~2X wide as body; ventral lobes large; dorsal lobes small round, with wide dorsal gap	Short	Smoothly curved	Long	Elongate	Moderate	†	Edmondson (1940); Segers and Shiel (2008); WT Edmondson, pers. commun.

......*Continued on the next page*

TABLE 1. (Continued)

Species	Tube	Coronal morphology (all are 4-lobed)	Labium (chin)	Mucrons	Peduncle *	Ventrolateral antennae	Unci teeth differentiation	Colony formation	Selected references
ringens	Pellets, round, densely packed	>2X wide as body; ventral lobes large; dorsal lobes small	Short, blunt	Smoothly curved	Short	Elongate	Weak	Solitary to ~10	(Fontaneto *et al.* 2003); Segers (1997); Segers and Shiel (2008); (Tiefenbacher 1972; Wright 1950)
wallacei	Pellets, round, densely packed	~3X wide as body; ventral lobes large; dorsal lobes small, with deep, narrow gap	Long	Smoothly curved	Long	Elongate	Very strong	Solitary to small colonies	Segers and Shiel (2008)

Symbols: *—In some species the length of the peduncle has been reported to vary with the age of the animal. †—Not noted in the original description. §—Variable: Sharp, pointing upward; incurved or straight; may have accessory projections near tips. ‡—Curved, pointed, flexed ventrally at nearly right angles.

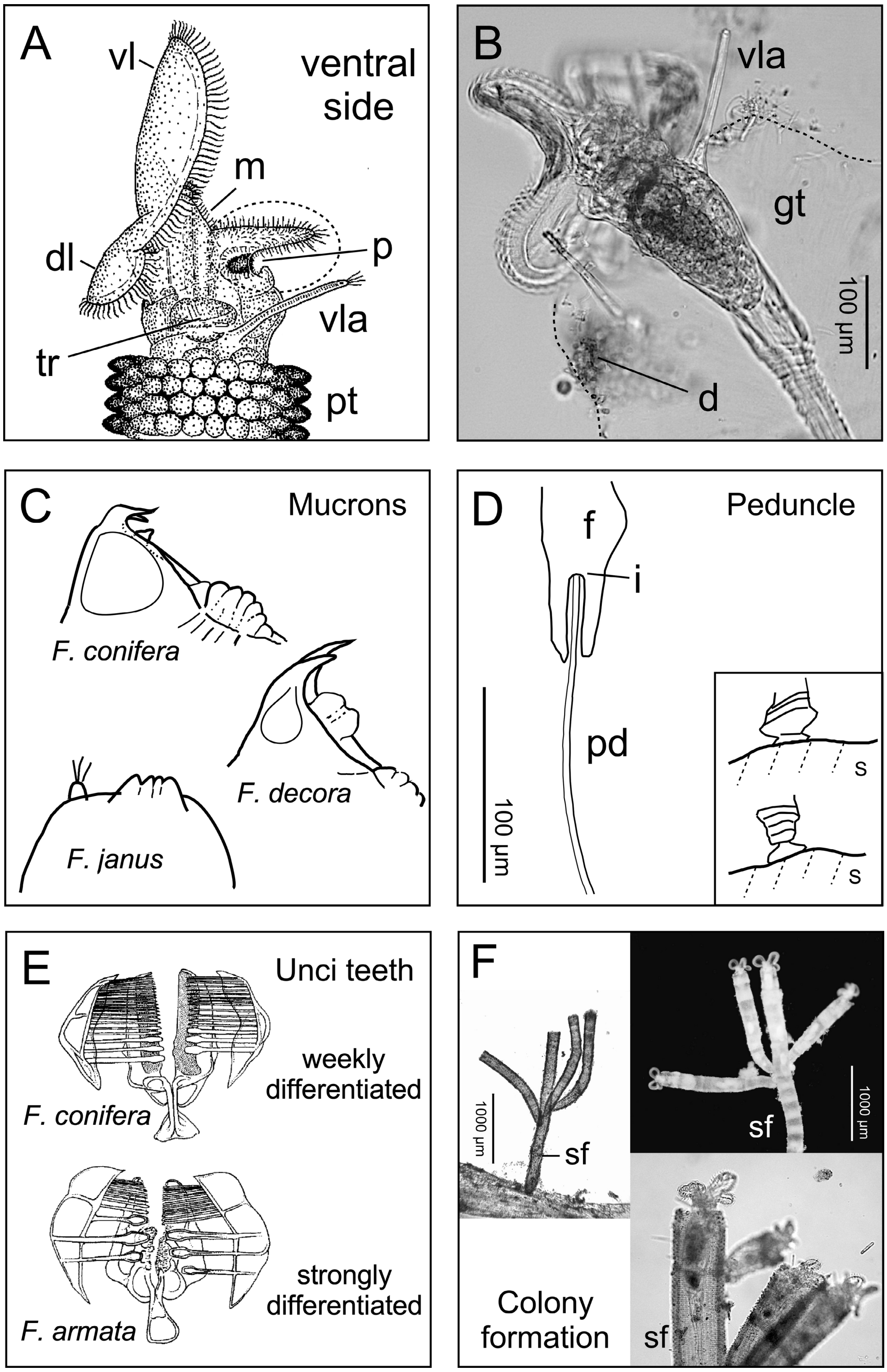

FIGURE 2. Examples of critical characteristics used in differentiating *Floscularia* species. (See Table 1 for additional information.) A, B. Anterior ends showing features of the corona. A. Corona lateral view of *F. conifera*: tripartite pellet-forming organ (encircled with dotted line) with a pellet (p) in th*e modulus;* B. Co*rona vent*rolateral view of *F. melicerta.* C. Presence (*F. conifera and F. decora*) or absence (*F. janus*) of mucrons. D. Long peduncle of *F. pedunculata*; Insert: illustrations of two *Floscularia* spp. lacking peduncles. E. Examples of trophi showing weekly and strongly differentiated unci teeth. F. Examples of allorecruitive colony formation (three small colonies). Tubes in the upper left colony with rings (Edmondson 1945) for details. Symbols: d = debris; dl = dorsal lobe; f = foot; gt = gelatinous tube: dotted line indicates tube; i = insertion point of peduncle to foot; m = mouth; pd = peduncle; pt = pellet tube; s = substratum; sf = stem female of colony; tr = trophi in mastax; vl = ventral lobe; vla = ventrolateral antenna. A, C = Reproduced from original art courtesy of W.T. Edmondson; D. After. Joliet 1883; E. (Reproduced with permission from the copyright holder [Hydrobiologia 354: 165–175; (Segers 1997)).

Diagnosis. Adult females obligatorily sessile, either solitary or colonial. Corona a continuous curve of four flexible lobes (ear-like) with a wide dorsal gap. Dorsal antennae minute; paired ventrolateral antennae conspicuous. A distinctive, glandular, ciliated cup (modulus) with its attending labium located anteroventrally. Tube construction varies among species. Oviparous.

Dichotomous key to species of genus *Floscularia*

1 Animals possessing mucrons; ventrolateral antenna elongate; ventral lobes larger than dorsal lobes; tube with small pellets or with large, ovoid fecal pellets embedded in gelatinous material or with only gelatinous material without pellets (Fig. 2C) 2
[Mucrons, if present, are best seen at apex of the anterior end in contracted animals.]

1' Animals lacking mucrons (Fig. 2C); ventrolateral antenna short; ventral lobes much larger than dorsal lobes, dorsal lobes very small and almost confluent along their dorsal margin; tube comprising gelatinous material embedded with large, egg-shaped masses; total body length ≤1600 µm; solitary (Fig. 3) . . . .*janus* (Hudson, 1881)
[The trophi have been documented by Koste (1978) and Kutikova (2007). Kutikova (2007) reports the masses to be "fecal lumps," but also discusses their production in a modulus structure as follows. "Under the crown, below the oral funnel, an angular lower lip (length 30 µm) protrudes with a pit where fecal lumps (size 83–98 x 45–56 µm) are created for building a house. The pit is lined with cilia." Koste (1978) also refers to the mass as large pellets loosely associated with detritus and feces.] Regardless, if little particulate matter is available, *F. janus* may produce "fairly transparent, irregular tubes" (Edmondson 1940). The larvae of *F. janus* may settle on filamentous algae in a series: i.e., the individuals are assembled in order of size (age) even when adequate space is available for arbitrary settling (Edmondson 1940). Apparently very rare in the plankton, W.T. Edmondson, pers. commun. Cosmopolitan.]

2(1) Mucrons smoothly curved (arched) without accessory projections 5

2' Mucrons other 3

3(2') Mucrons bifid (tips with one tooth point forward and one inwardly) or mucrons complex and variable; pellet tube comprising densely or loosely packed, round pellets 4

3' Mucrons not bifid (tips flexed ventrally at near right angles pointed) (Fig. 2C); pellet tube comprising densely packed, bullet-shaped pellets; labium elongate, pointed; unci teeth weakly differentiated (Fig. 2E) total body length 500–2000 µm; solitary or colonies 2–c.35 individuals. (Fig. 4) . . . . *conifera* (Hudson, 1886)
[The trophi have been documented by Segers (1997). The ultrastructure and tube of this species has been studied by Yang and Hochberg (2018a). Edmondson (1945) studied the dynamics of population growth and the social structure of solitary and colonial animals. The propensity to form colonies in this species has been reported by (Wallace 1987). Cosmopolitan.]

4(3) Mucron tips bifid, (noted above); tube with loosely packed, round pellets; peduncle long (Fig. 5) . . . .*bifida* Segers, 1997
[Tube resembles that of *F. bifida* and *F. ringens* (Segers 1997). The adult (contracted) and trophi (asymmetric) have been documented by Segers (1997). The bifid dorsal hooks are apparently variable (Segers *et al.* 2010). Thailand. South America.]

4' Mucrons variable: large with two, strong, lateral spines, slightly incurved or almost straight pointing ventrally or with accessory projections near ends; pellet tube comprising loosely packed, round pellets; peduncle short (Fig. 6) . . . . *armata* Segers, 1997
[Tube resembles that of *F. ringens* and *F. bifida* (Segers 1997). The adult (contracted) and trophi (asymmetric) have been documented by Segers (1997). Thailand. South America.]

5(2) Tube composed of densely packed pellets; peduncle short or long 6

5' Tube composed solely of firm gelatinous material (clear or colored), embedded and/or covered by algae, bacteria, or debris partly obscuring the animal; labium and modulus broad; total body length ≤1600 µm; solitary (Fig. 7) . . . . *melicerta* (Ehrenberg, 1832)
[The trophi are illustrated by (Koste & Böttger 1989). Drawings showing the layers in the gelatinous tubes were published by (Hudson 1875). The layers of jelly are laid down by the animals as described above. Cosmopolitan.]

6(5) Tube composed of densely packed, clear, hexagonal, bullet-shaped pellets; dorsal hooks large, slightly curved; peduncle short; total body length ~500 µm; solitary or colonies of a few individuals (Fig. 8) . . . . *decora* Edmondson, 1940
[This species uses little particulate material in forming its clear pellets; these are large and hexagonal in shape at the anterior, but are flattened at the base. To our knowledge, the trophi have not been figured. Thailand. North America.]

6' Tube composed of densely packed round pellets; labium long or short; peduncle long or short 7

7(6') Quadridigitate, cuticular processes located on sides of neck; below the labium two conical processes, with a smaller knob in between, below another median knob; labium short, round; peduncle long; total body length ~750 µm; solitary, perhaps colonial (Fig. 9) . . . . *pedunculata* (Joliet, 1883)
[See Koste (1978) Tafel 199, figure 4a–d for additional figures. Figure 116 in Remane (1929–1933) illustrates the long peduncle. W.T. Edmondson (pers. commun.) notes that this species "… has a great resemblance to *F. ringens*." Indeed Joliet (1883) states much the same: "Cette différence dans la forme du tube des deux espèces correspond à un détail anatomique qui constitue à lui seul à peu près toute la différence qui existe entre elles." Nevertheless, these species may be separated based on the presence of the quadridigitate processes and the conical processes, as well as the relative length of their peduncles. To our knowledge, the trophi have not been figured. India. Thailand. North and South America.]

7' Quadridigitate processes absent; conical processes absent; peduncle long; labium long or short 8

8(7') Labium short, blunt; unci teeth weekly differentiated; total body length 500–1900 µm; solitary or colonies of a few individuals (Fig. 10) . . . . *ringens* (Linnaeus, 1758)

[The mucrons resemble that of *F. decora* (Figs. 2C, 8B,C). The trophi have been documented by Fontaneto *et al.* (2003), Koste and Poltz (1987), and Segers (1997). Several workers have reviewed the life history of this species, including tube building (Bedwell 1877; Fontaneto *et al.* 2003; Gosse 1852; Santo *et al.* 2005; Tiefenbacher 1972; Wright 1950). Tiefenbacher (1972) studied animal growth, pellet and colony formation and regeneration of the dorsal lobe. Charles Krebs submitted a winning photomicrograph of *F. ringens* in the 2011 Olympus BioScapes Digital Imaging Competition (https://www.washingtonpost.com/national/health-science/olympus-bioscapes-2011-winners-gallery/2011/11/28/gIQAGqys8N_gallery.html). Cosmopolitan.]

8’ Labium elongate; unci teeth weekly differentiated; solitary or small, allorecruitive colonies; total body length ~1800 µm; (Fig. 11) . . . . *wallacei* Segers & Shiel, 2008

[Specimens of *Floscularia wallacei* were hatched and cultured from rehydrated dry sediments isolated from a billabong in Victoria (Australia) by Segers and Shiel (2008) who also documented its trophi. This species was also reported in Thailand by (Meksuwan *et al.* 2011). Australia. Thailand.]

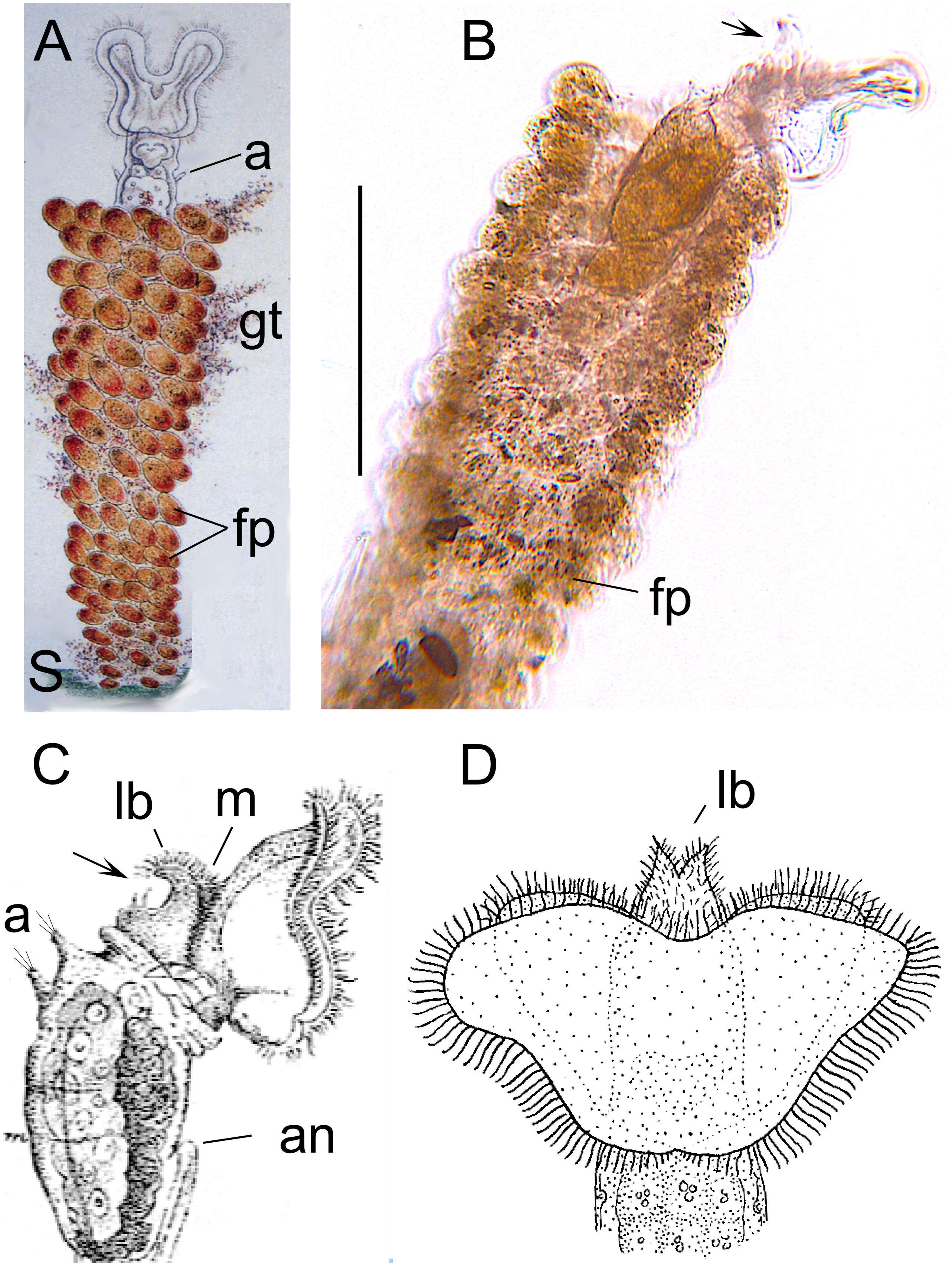

FIGURE 3. *Floscularia janus*. A. Dorsal view of an animal in its tube. B. Lateral view of an animal in its tube. C. Lateral view of an animal removed from its tube. D. Dorsal view of the corona showing medial notch in the labium. Symbols: arrows = modulus; a = antenna; an = anus; fp = fecal pellet; gt = elements of the gelatinous tube; lb = labium; m = mouth; S = substratum. Bar = 500 µm. (B = From Hudson, 1881; C = Reproduced from original art courtesy of W.T. Edmondson.)

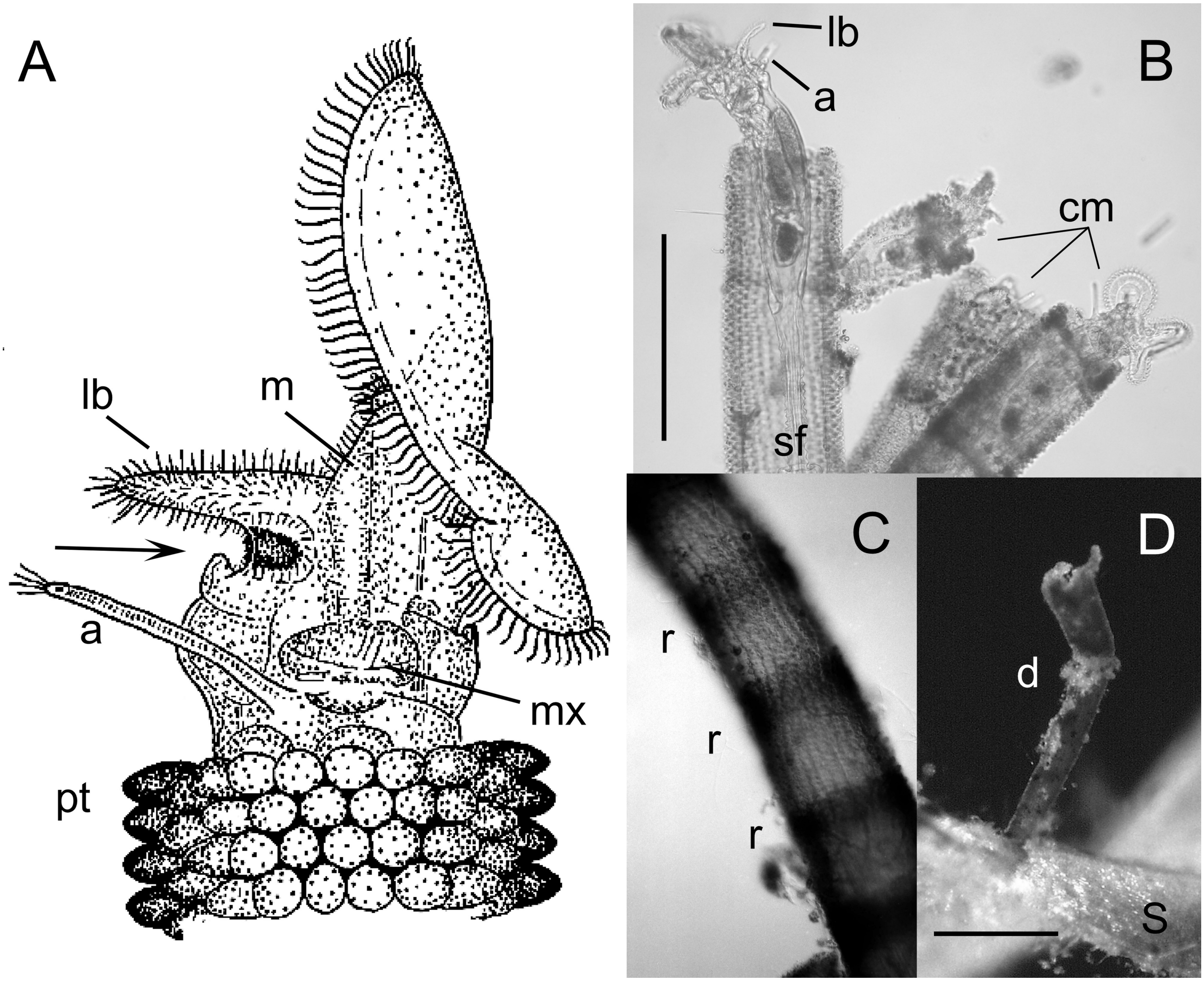

FIGURE 4. *Floscularia conifera*. A. Lateral view of the anterior end. B. Small colony with three individuals attached to a stem female (sf). C. Rings of dark pellets formed after three successive rain storms that took place over approximately three days: consult Edmondson (1945). D. Damaged tube of a solitary individual. Symbols: arrow = modulus with a dark pellet being formed; a = antenna; cm = colony mates; d = damaged region; lb = labium; m = mouth; mx = mastax; pt = pellet tube; r = rings of dark pellets; S = substratum; sf = stem female (previously solitary). Bars = 500 µm. (A. Reproduced from original art courtesy of W.T. Edmondson.)

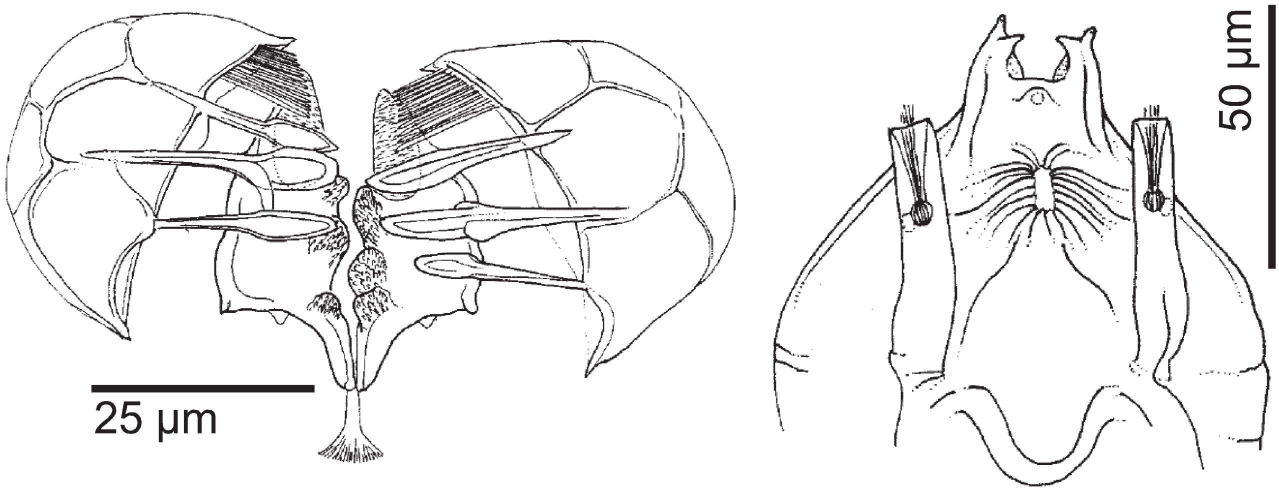

FIGURE 5. *Floscularia bifida*. A. Trophi, caudal view. B. Apical region, ventral view showing mucrons and ventrolateral antennae. Scale bars: as indicated. (Reproduced with permission from the copyright holder [Hydrobiologia 354: 165–175] and the author (Segers 1997)).

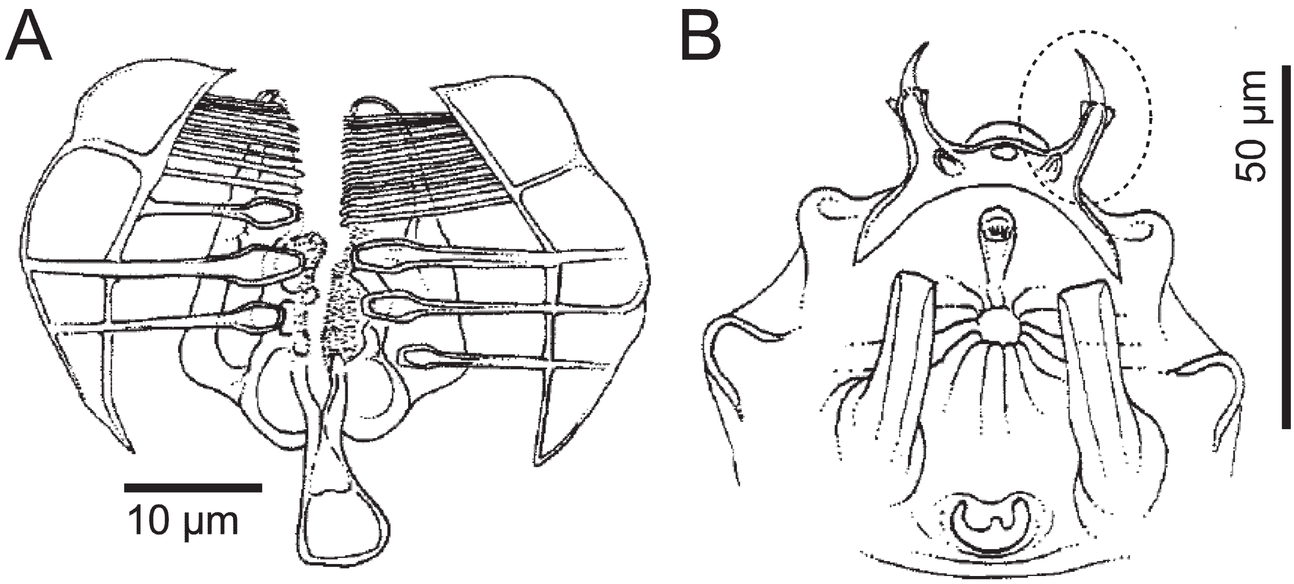

FIGURE 6. *Floscularia armata*. A. Trophi (caudal view). B. Apical region, ventral view showing mucrons and ventrolateral antennae. Dotted oval: variations of the mucrons and accessory projections may occur in different specimens: consult the original descriptions in Segers (1997). Scale bars: as indicated. (Reproduced with permission from the copyright holder [Hydrobiologia 354: 165–175] and the author (Segers 1997)).

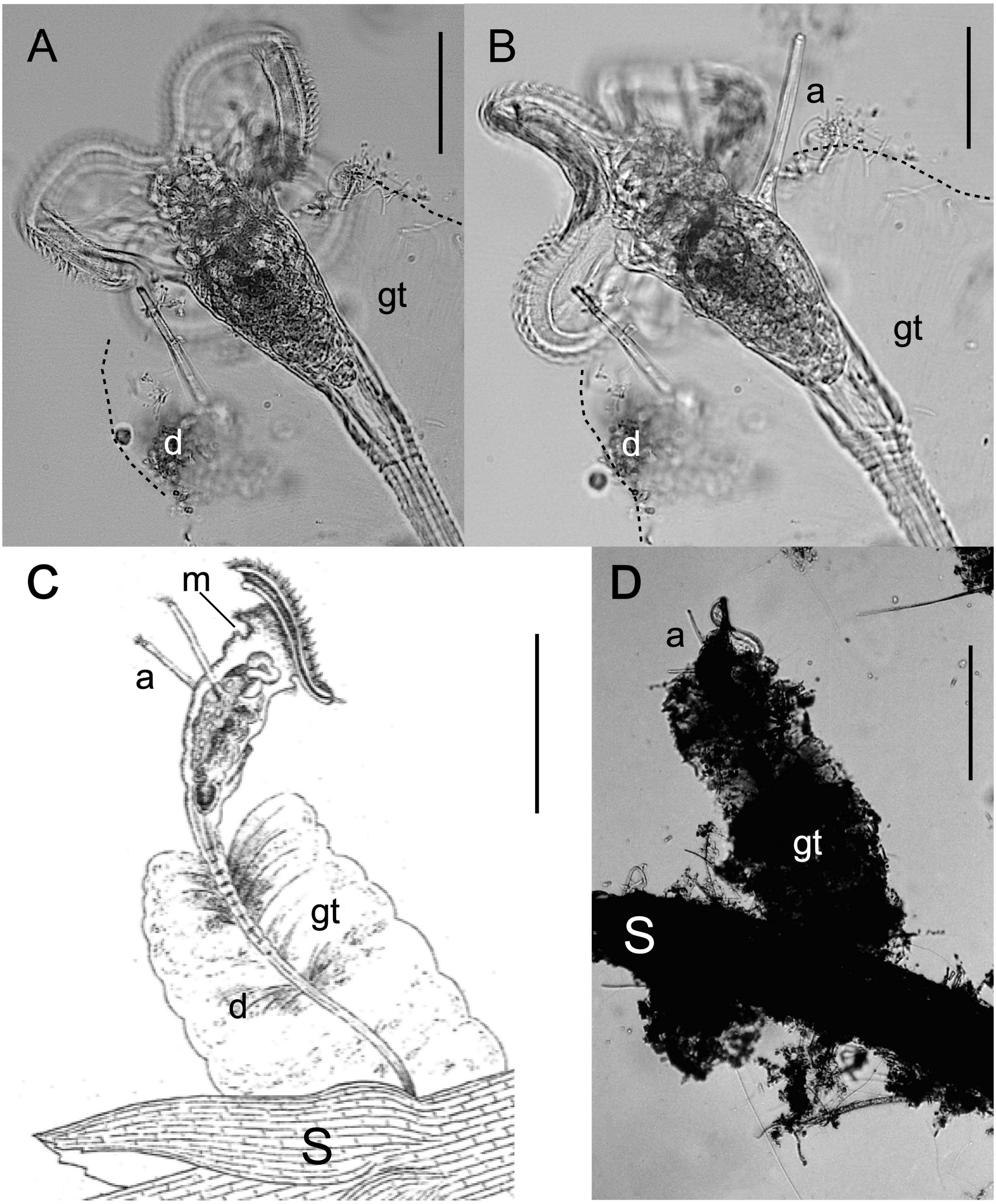

FIGURE 7. *Floscularia melicerta*. A. Anterio-ventral view. B. 3/4th Anterio-ventral view. C. Lateral view with little debris incorporated into its gelatinous tube; D. lateral view—tube with copious amounts of debris obscuring the gelatinous tube. A and B: Dashes outline the periphery of the gelatinous tube. Symbols: a = antenna; d = small bit of debris in the tube; gt = gelatinous tube; m = modulus; S = substratum. Bars: A, B = 100 µm; C, D = 500 µm. (C = From Hudson 1875.)

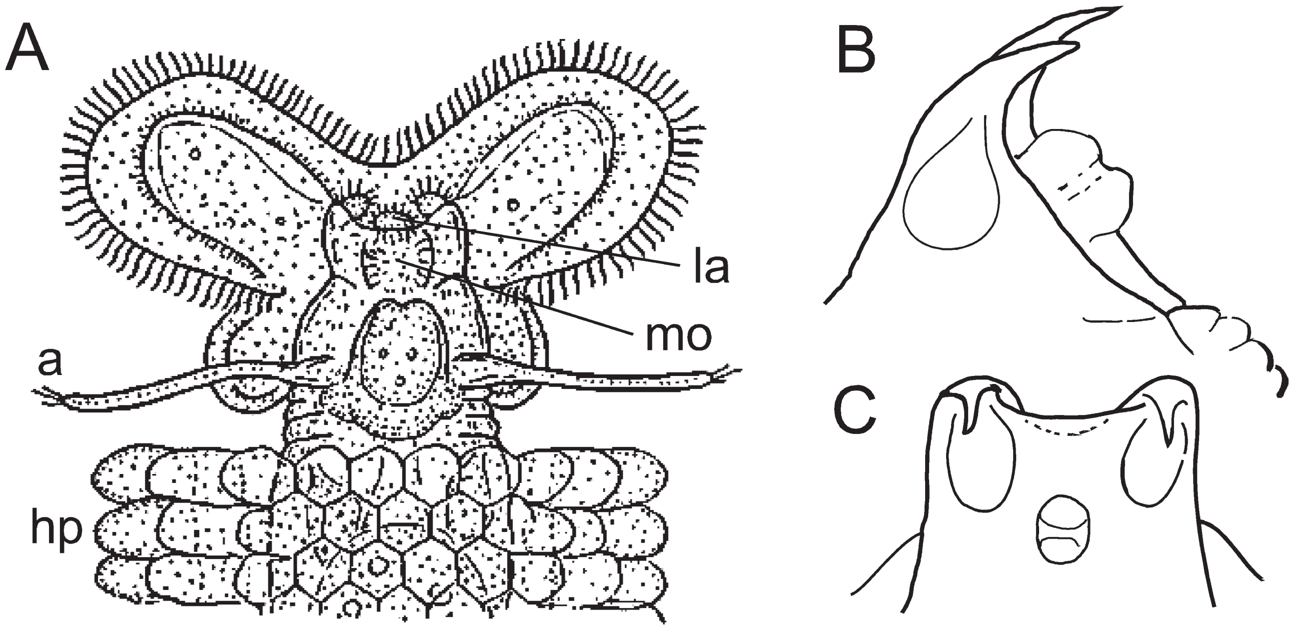

FIGURE 8. *Floscularia decora*. A. Ventral anterior view. B and C. Mucrons. B. Lateral view. C. Ventral view. Symbols: a = antenna (right side); hp = hexagonal, bullet-shaped pellets; la = labium ; mo = modulus. (Reproduced from original art courtesy of W.T. Edmondson).

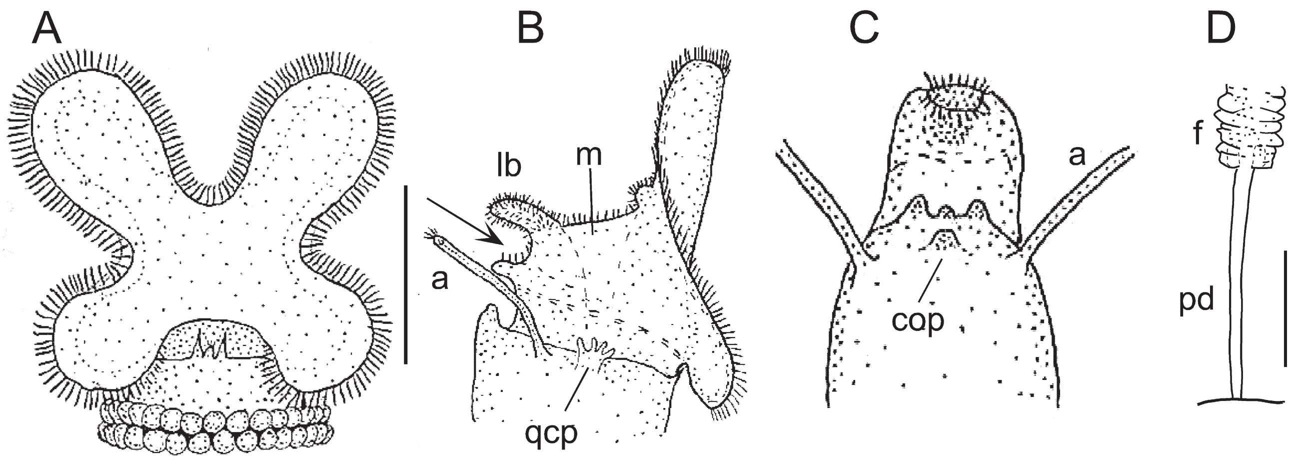

FIGURE 9. *Floscularia pedunculata*. A. Corona, dorsal view. B. Corona, lateral view. C. Corona closed, ventral view. D. Long peduncle. Symbols: arrow = modulus; a = antennae; cop = conical processes; f = foot; m = mouth; pd = peduncle; qcp = quadridigitate, cuticular processes. Bars = 100 µm. (Reproduced from original art courtesy of W.T. Edmondson.)

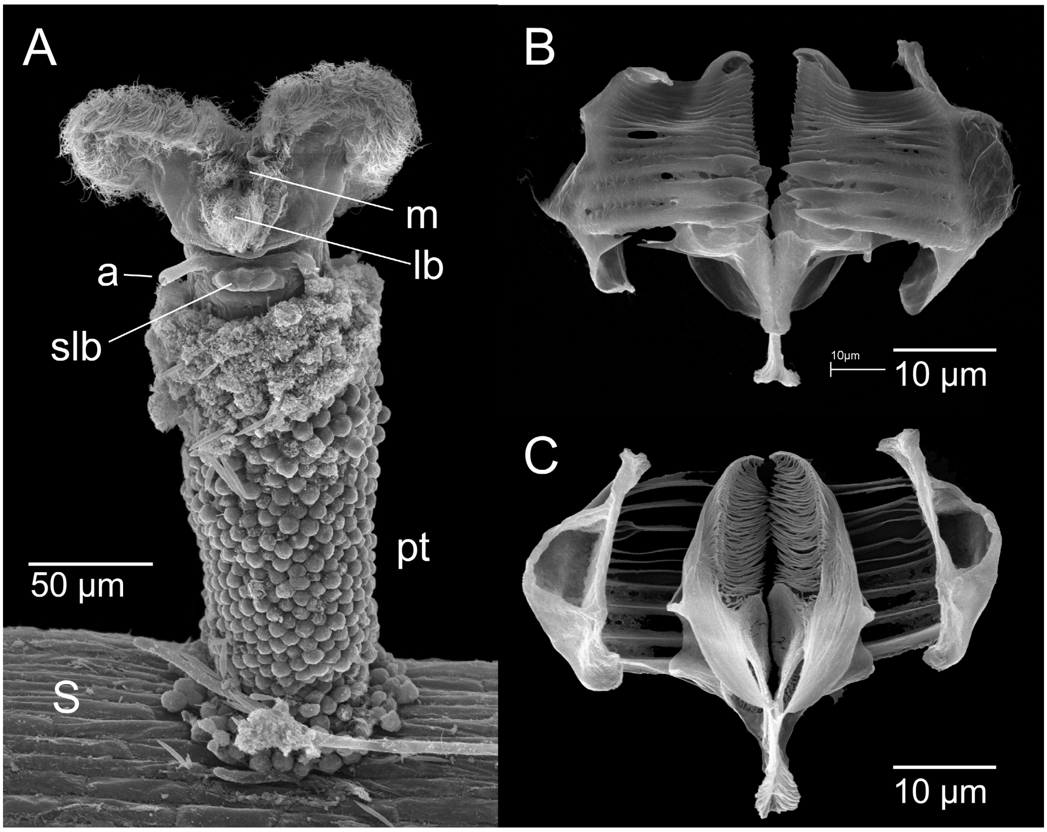

FIG. 10. *Floscularia ringens*. A. Ventral view of an adult. B. Frontal view of trophi. C. Caudal view of trophi. Symbols: a = antenna; lb = labium; m = mouth pt = pellet tube; pt = pellet tube; slb = sublabium; Bars: as indicated. (Reproduced with permission from the copyright holder [Invertebrate Biology 122:231–240] and the authors (Fontaneto *et al.* 2003).)

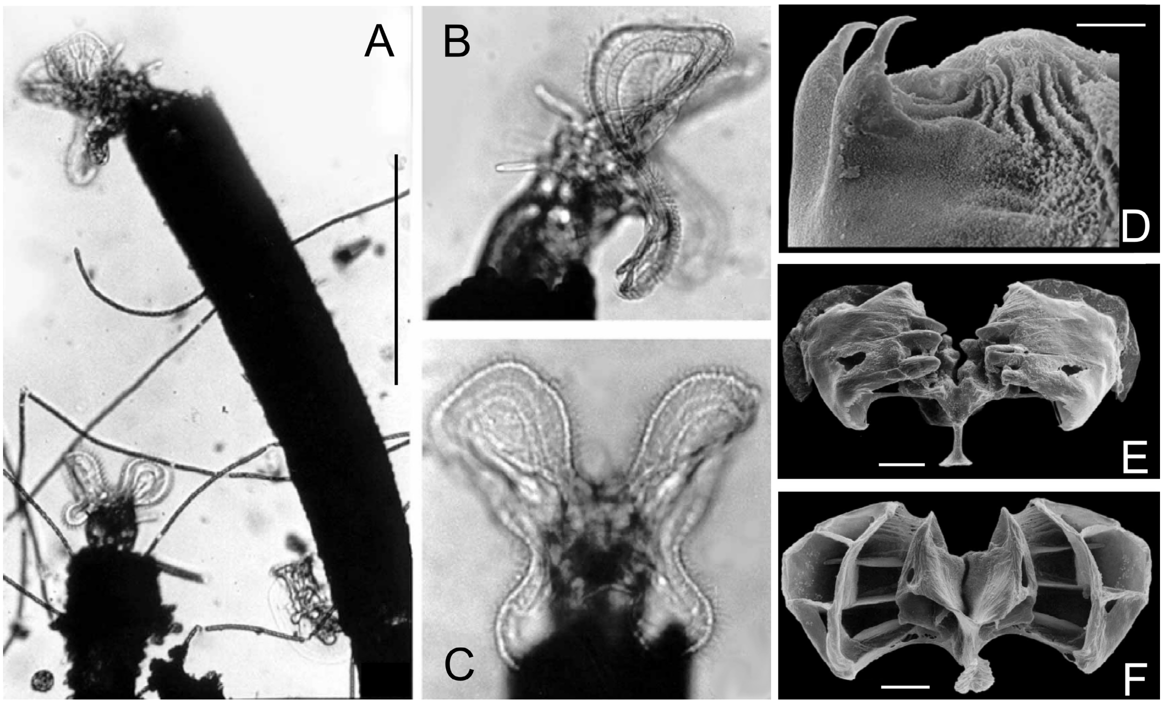

FIGURE 11. *Floscularia wallacei*. A. From culture, young (left) and adult (right). B. Corona, lateral view. C. Corona, dorsal view. D. Mucrons, lateral view. E. Trophi, frontal view. F. Trophi, caudal view. Scale bars: A ~500 µm; D, E, F = 10 µm. (©Magnolia Press, reproduced with permission from the copyright holder [Zootaxa 1750: 19–31] and the authors (Segers & Shiel 2008).)

Declarations

Funding

This work was funded in part by the National Science Foundation (RH: DEB 2051684; EJW: DEB 2051704; RLW: DEB 2051710) and Ripon College (funds for faculty development and the S.O.A.R. program).

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.

Acknowledgments

The authors thank the Ripon College librarians for their help in securing some of the more obscure works cited in this paper; we especially thank the reviewers of an earlier version of this manuscript for their thorough review. RLW thanks Dr. John J. Gilbert for suggesting sessile rotifers as a topic for research and the late Dr. Thomas (Tommy) Edmondson for his encouragement to develop comprehensive keys to the sessile species and donation of his original artwork and documents on sessile rotifers. We also thank Dr. Diego Fontaneto who provided several SEM images. This work was funded in part by the National Science Foundation (RH: DEB 2051684; EJW: DEB 2051704; RLW: DEB 2051710) and Ripon College (funds for faculty development and the S.O.A.R. program).

References

Bedwell, F.A. (1877) The building apparatus of *Melicerta ringens*. *The Monthly Microscopical Journal*, 18, 214–223. https://doi.org/10.1111/j.1365-2818.1877.tb00131.x

Bielańska-Grajner, I., Ejsmont-Karabin, J. & Radwan, S. (2015) *Rotifers (Rotifera): Freshwater Fauna of Poland*. *Vol. 32*. Jagiellonian University Press, Kraków, 580 pp. https://doi.org/10.4467/K9722.1/17.16.6981

Colledge, W. R. (1918) Notes on a new rotifer. *Melicerta coloniensis*. *Proceedings of the Royal Society of Queensland*, 30, 171–174. https://doi.org/10.5962/p.168253

Collins, R.A. & Cruickshank, R.H. (2013) The seven deadly sins of DNA barcoding. *Molecular Ecology Resources*, 13, 969–975. https://doi.org/10.1111/1755-0998.12046

Cubitt, C. (1870) Observations on some points in the economy of *Stephanoceros*. *The Monthly Microscopical Journal*, 3, 240–249. https://doi.org/10.1111/j.1365-2818.1870.tb01943.x

Davies, N., LaFleur, A., Hochberg, R., Walsh, E.J. & Wallace, R.L. (2024) Key to sessile gnesiotrochan rotifers: Families, monospecific species in Flosculariidae, species of Atrochidae, Conochilidae, and *Limnias*. *Zootaxa*, 5397 (4), 497–520. https://doi.org/10.11646/zootaxa.5397.4.3

Diniz-Filho, J.A.F., Jardim, L., Guedes, J.J.M., Meyer, L., Stropp, J., Frateles, L.E.F., Pinto, R.B., Lohmann, L.G., Tessarolo, G., De Carvalho, C.J.B., Ladle, R.J. & Hortal, J. (2023) Macroecological links between the Linnean, Wallacean, and Darwinian shortfalls. *Frontiers of Biogeography*, 15, e59566. https://doi.org/10.21425/f5fbg59566

Edmondson, W.T. (1940) The sessile Rotatoria of Wisconsin. *Transactions of the American Microscopical Society*, 59, 433–459. https://doi.org/10.2307/3222991

Edmondson, W.T. (1944) Ecological studies of sessile Rotatoria, Part I. Factors affecting distribution. *Ecological Monographs*, 14, 32–66. https://doi.org/10.2307/1961631

Edmondson, W.T. (1945) Ecological studies of sessile Rotatoria, Part II. Dynamics of populations and social structure. *Ecological Monographs*, 15, 141–172. https://doi.org/10.2307/1948601

Edmondson, W.T. (1959) Rotifera. *In*: Edmondson, W.T. (Ed.), *Freshwater Biology. 2nd Edition*. John Wiley & Sons, Inc., New York, New York, pp. 420–494.

Ejsmont-Karabin, J. (2019) Does the world need faunists? Based on rotifer (Rotifera) occurrence reflections on the role of faunistic research in ecology. *Hydrobiology*, 104, 49–56. https://doi.org/10.1002/iroh.201901991

Ejsmont-Karabin, J. & Karpowicz, M. (2021) Rotifera in lake subhabitats. *Aquatic Ecology*, 55, 1285–1296. https://doi.org/10.1007/s10452-020-09818-1

Fontaneto, D., Barbosa, A.M., Segers, H. & Pautasso, M. (2012) The 'rotiferologist' effect and other global correlates of species richness in monogonont rotifers. *Ecography*, 35, 174–182. https://doi.org/10.1111/j.1600-0587.2011.06850.x

Fontaneto, D. & De Smet, W.H. (2015) Rotifera. *In*: Schmidt-Rhaesa, A. (Ed.), *Handbook of Zoology: Gastrotricha, Cycloneuralia and Gnathifera. Vol. 3. Gastrotricha and Gnathifera*. De Gruyter, Berlin, pp. 217–300. [http://www.degruyter.com/view/product/180465?format=G] https://doi.org/10.1515/9783110274271.217

Fontaneto, D., Melone, G. & Wallace, R.L. (2003) Morphology of *Floscularia ringens* (Rotifera, Monogononta) from egg to adult. *Invertebrate Biology*, 122, 231–240. https://doi.org/10.1111/j.1744-7410.2003.tb00087.x

Franch, V., Meksuwan, P. & Wallace, R.L. (2024) The dorsal plate is a critical feature in the reassessment of the rotiferan genus *Ptygura* (Monogononta; Gnesiotrocha; Flosculariidae). *Zootaxa*, 5425 (1), 107–123. https://doi.org/10.11646/zootaxa.5428.1.5

Glibert, P.M. & Mitra, A. (2022) From webs, loops, shunts, and pumps to microbial multitasking: Evolving concepts of marine microbial ecology, the mixoplankton paradigm, and implications for a future ocean. *Limnology and Oceanography*, 67, 585–597. https://doi.org/10.1002/lno.12018

Gosse, P.H. (1852) On the architectural instincts of *Melicerta ringens*, an animal of class Rotifera. *Transactions of the Microscopical Society of London*, 3, 58–64. https://doi.org/10.1111/j.1365-2818.1852.tb06030.x

Harring, H.K. (1913) A list of the Rotatoria of Washington and vicinity, with descriptions of a new genus and ten new species. *Proceedings of the United States National Museum*, 46, 387–405.

https://doi.org/10.5479/si.00963801.46-2032.387
Hochberg, A. & Hochberg, R. (2017) Musculature of the sessile rotifer *Stephanoceros fimbriatus* (Rotifera: Gnesiotrocha: Collothecaceae) with details on larval metamorphosis and development of the infundibulum. *Zoologischer Anzeiger*, 268, 84–95.
https://doi.org/10.1016/j.jcz.2016.09.002
Hochberg, R., Hochberg, A. & Chan, C. (2015) Ultrastructure of the rotifer integument: peculiarities of *Sinantherina socialis* (Monogononta: Gnesiotrocha). *Invertebrate Biology*, 134, 181–188.
https://doi.org/10.1111/ivb.12085
Hochberg, R. & Lilley, G.W. (2010) Neuromuscular organization of the freshwater colonial rotifer, *Sinantherina socialis*, and its implications for understanding the evolution of coloniality in Rotifera. *Zoomorphology*, 129, 153–162.
https://doi.org/10.1007/s00435-010-0108-6
Hochberg, R. & Litvaitis, M.K. (2000) Functional morphology of the muscles in *Philodina* sp. (Rotifera: Bdelloidea). *Hydrobiologia*, 432, 57–64.
https://doi.org/10.1023/A:1004003509017
Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 46, 523–549.
https://doi.org/10.1146/annurev-ecolsys-112414-054400
Hudson, C.T. (1875) On a new *Melicerta*. *The Monthly Microscopical Journal*, 14, 225–231.
https://doi.org/10.1111/j.1365-2818.1875.tb00072.x
Hudson, C.T. (1881) On *Oecistes janus* and *Floscularia trifolium*, two new species of rotifers. *Journal of the Royal Microscopical Society*, 1881, 1–6.
https://doi.org/10.1111/j.1365-2818.1881.tb05964.x
Hudson, C.T. & Gosse, P.H. (1886) *The Rotifera; or wheel-animalcules, both British and foreign. Vols. I & II.* Longmans, Green, and Co., London, 128 pp. & 144 pp.
https://doi.org/10.5962/bhl.title.10136
Jersabek, C.D., De Smet, W.H., Hinz, C., Fontaneto, D., Hussey, C.G., Michaloudi, E., Wallace, R.L. & Segers, H. (2018) List of Available Names in Zoology, Candidate Part Phylum Rotifera, species-group names established before 1 January 2000. Available from: https://archive.org/details/LANCandidatePartSpeciesRotifera (accessed 5 May 2024)
Jersabek, C.D. & Leitner, M.F. (2013) The Rotifer World Catalog. World Wide Web electronic publication. Available from: http://www.rotifera.hausdernatur.at/Species/Index/222 (accessed 5 May 2024)
Johnson, K. (2007) Natural history as stamp collecting: a brief history. *Archives of Natural History*, 34, 244–258.
https://doi.org/10.3366/anh.2007.34.2.244
Joliet, L. (1883) Monographie des Mélicertes. *Archives de Zoologie Expérimentale et Générale*, 2 (131–122), 11–13.
Kordbacheh, A., Wallace, R.L. & Walsh, E.J. (2018) Evidence supporting cryptic species within two sessile microinvertebrates, *Limnias melicerta* and *L. ceratophylli* (Rotifera, Gnesiotrocha). *PLoS ONE*, 13, e0205203.
https://doi.org/10.1371/journal.pone.0205203
Koste, W. (1972) Über ein sessile Rädertier aus Amazonien, *Floscularia noodti* sp. n. *Archive für Hydrobiologie*, 70, 534–540.
https://doi.org/10.1127/archiv-hydrobiol/70/1972/534
Koste, W. (1975) Über den Rotatorienbestand einer Mikrobiozönose in einem tropischen aquatischen Saumbiotop, der *Eichhornica-crassipes*-zone im Littoral des Bung-Borapet, einem Strasee in Zentralthailand. *Gewässer u. Abwässer*, 57/58, 43–58.
Koste, W. (1978) *Rotatoria. Die Rädertiere Mitteleuropas. 2 Vols*. Gebrüder Borntraeger, Stuttgart, 673 pp. (text), tafel 234 pp. [in German]
Koste, W. (1989) Das Rädertierporträt. Die sessile Art *Octotrocha speciosa*. *Mikrokosmos*, 78, 115–121.
Koste, W. & Böttger, K. (1989) Rotatorien aus Gewässern Ecudadors. *Amazoniana*, 10, 407–438.
Koste, W. & Böttger, K. (1992) Rotatorien aus Gewässern Ecuadors II. *Amazoniana*, 12, 263–303.
Koste, W. & Poltz, J. (1987) Über die Rädertiere (Rotatoria, Phylum Aschelminthes) des Alfsees, eines Hochwasser-Rückhaltebeckens der Hase, NW-Deutschland, FRG. *Osnabrücker Naturwissenschaftliche Mitteilungen*, 13, 185–220.
Kutikova, L.A. (2007) Пять видов коловраток семейства Flosculariidae (Rotifera), их личинки и метаморфоз [Five species of rotifers of the family Flosculariidae (Rotifera), their larvae and metamorphosis]. *Зоология беспозвоночных*, 4, 161–172. [in Russian]
https://doi.org/10.15298/invertzool.04.2.05
Leutbecher, C. & Koste, W. (1998) Die Rotatorienfauna des Dümmers unter besonderer Berücksichtigung der sessilen Arten Teil I. *Osnabrücker Naturwissenschaftliche Mitteilungen*, 24, 223–255.
Meksuwan, P. (2015) *Systematics and phylogeny of sessile rotifers (Rotifera, Monogononta, Gnesiotrocha)*. Prince of Songkla University, Hat Yai, 140 pp.
Meksuwan, P., Pholpunthin, P. & Segers, H. (2011) Diversity of sessile rotifers (Gnesiotrocha, Monogononta, Rotifera) in Thale Noi Lake, Thailand. *Zootaxa*, 2997 (1), 1–18.
https://doi.org/10.11646/zootaxa.2997.1.1
Meksuwan, P., Pholpunthin, P. & Segers, H. (2013) The Collothecidae (Rotifera, Collothecacea) of Thailand, with the description of a new species and an illustrated key to the Southeast Asian fauna. *ZooKeys*, 315, 1–16.

https://doi.org/10.3897/zookeys.315.5330
Obertegger, U., Cieplinski, A., Raatz, M. & Colangeli, P. (2018) Switching between swimming states in rotifers – case study *Keratella cochlearis*. *Marine and Freshwater Behaviour and Physiology*, 51, 159–173.
https://doi.org/10.1080/10236244.2018.1503541
Remane, A. (1929–1933) Rotatorien. *In*: Grimpe, G. (Ed.), *Bronn's Klassen und Ordnungen des Tierreiches IV. (Vermes). 2 (Aschelminthes). I (Rotatorien, Gastrotrichen und Kinorhychen)*. Akademische Verlagsgesellschaft, Leipzig, pp. 1–448. [in German]
Santo, N., Fontaneto, D., Fascio, U., Melone, G. & Caprioli, M. (2005) External morphology and muscle arrangement of *Brachionus urceolaris, Floscularia ringens, Hexarthra mira* and *Notommata glyphura* (Rotifera, Monogononta). *Hydrobiologia*, 546, 223–229.
https://doi.org/10.1007/s10750-005-4200-8
Sarma, S.S.S., Jiménez-Santos, M.A., Nandini, S. & Wallace, R.L. (2020) Review on the ecology and taxonomy of sessile rotifers (Rotifera) with special reference to Mexico. *Journal of Environmental Biology*, 41, 3–12.
https://doi.org/10.22438/jeb/41/1/MRN-1344
Segers, H. (1997) Contribution to a revision of *Floscularia* Cuvier, 1798 (Rotifera: Monogononta): notes on some Neotropical taxa. *Hydrobiologia*, 354, 165–175.
https://doi.org/10.1023/A:1003166911731
Segers, H., Meksuwan, P. & Sanoamuang, L. (2010) New records of sessile rotifers (Phylum Rotifera: Flosculariacea, Collothecacea) from Southeast Asia. *Belgian Journal of Zoology*, 140, 235–240.
https://doi.org/10.26496/bjz.2010.174
Segers, H. & Shiel, R.J. (2008) Diversity of cryptic Metazoa in Australian freshwaters: a new genus and two new species of sessile rotifer (Rotifera, Monogononta, Gnesiotrocha, Flosculariidae). *Zootaxa*, 1750 (1), 19–31.
https://doi.org/10.11646/zootaxa.1750.1.2
Serra, M., Snell, T. & Wallace, R.L. (2018) Reproduction, overview by phylogeny: Rotifera. *In: Encyclopedia of Reproduction*. Academic Press, Elsevier, Amsterdam, pp. 513–521.
https://doi.org/10.1016/B978-0-12-809633-8.20646-8
Sørensen, M.V. & Giribet, G. (2006) A modern approach to rotiferan phylogeny: combining morphological and molecular data. *Molecular Phylogenetics and Evolution*, 40, 585–608.
https://doi.org/10.1016/j.ympev.2006.04.001
Tiefenbacher, L. (1972) Beiträge zur Biologie und Ökologie sessiler Rotatorien unter besonder Berücksichtigung des Gehäusebaues und der Regenerationsfähigkeit. *Archiv für Hydrobiologie, Beiheft*, 71, 31–78.
Wallace, R.L. (1977) Distribution of sessile rotifers in an acid bog pond. *Archiv für Hydrobiologie*, 79, 478–505.
Wallace, R.L. (1980) Ecology of sessile rotifers. *Hydrobiologia*, 73, 181–193.
https://doi.org/10.1007/BF00019445
Wallace, R.L. (1987) Coloniality in the phylum Rotifera. *Hydrobiologia*, 147, 141–155.
https://doi.org/10.1007/BF00025737
Wallace, R.L. (2002) Rotifers: exquisite metazoans. *Integrative and Comparative Biology*, 42, 660–667.
https://doi.org/10.1093/icb/42.3.660
Wallace, R.L., Hochberg, R. & Walsh, E.J. (2023) The undiscovered country: ten grand challenges in rotifer biology. *Hydrobiology*, 851, 3225–3248.
https://doi.org/10.1007/s10750-023-05247-x
Wallace, R.L., Snell, T.W., Ricci, C. & Nogrady, T. (2006) *Rotifera. Vol. 1. Biology, Ecology and Systematics. 2nd Edition*. Backhuys Publishers, Leiden, 299 pp.
Wallace, R.L., Snell, T.W. & Smith, H.A. (2015) Phylum Rotifera. *In:* Thorp, J.H. & Rogers, D.C. (Eds.), *Thorp and Covich's Freshwater Invertebrates*. Elsevier, Waltham, Massachusetts, pp. 225–271.
https://doi.org/10.1016/B978-0-12-385026-3.00013-9
Wright, H.G.S. (1950) A contribution to the study of *Floscularia ringens*. *Journal of the Quekett Microscopical Club*, Series 4, 3, 103–116.
Wright, H.G.S. (1957) The rotifer fauna of East Norfork: notes of new species and some rarities among sessile forms. *Transactions of the Norfork and Norwich Naturalists' Society*, 18, 1–23.
Wright, H.G.S. (1959) Development of the peduncle in a sessile rotifer. *Journal of the Quekett Microscopical Club*, Series 4, 5, 231–234.
Wu, D., Luo, Y., Wu, B. & Wang, Q. (2014) New record of *Floscularia bifida* (Rotifera) from China. *Journal of Shanghai Normal University(Natural Sciences)*, 43, 266–268.
https://doi.org/10.3969/J.1SSN.100
Yang, H. & Hochberg, R. (2018a) Ultrastructural and elemental characterization of the extracorporeal tube of the sessile rotifer *Floscularia conifera* (Rotifera: Gnesiotrocha). *Invertebrate Biology*, 137, 319–328.
https://doi.org/10.1111/ivb.12230
Yang, H. & Hochberg, R. (2018b) Ultrastructure of the extracorporeal tube and "cement glands" in the sessile rotifer *Limnias melicerta* (Rotifera: Gnesiotrocha). *Zoomorphology*, 137, 1–12.
https://doi.org/10.1007/s00435-017-0371-x

Yang, H., Hochberg, R., Walsh, E.J. & Wallace, R.L. (2021) Ultrastructure of the extracorporeal secretions of four sessile species of Rotifera (Gnesiotrocha) with observations on the chemistry of the gelatinous tube. *Invertebrate Biology*, 140, e12318. https://doi.org/10.1111/ivb.12318