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Key to sessile gnesiotrochan rotifers: *Lacinularia* and *Sinantherina* (Monogononta; Flosculariidae)

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Abstract

Understanding the general biology, biodiversity, ecology, and evolutionary history of organisms necessitates correct identification. Found worldwide in fresh, brackish, and some marine waters, rotifers can be difficult to identify due to their small size, complex characteristics, and dearth of keys to their identification. Moreover, many species lack a hard body wall (i.e., illoricate species), thus they are nearly impossible to identify when preserved. As a result detailed study of many illoricate rotifers is wanting. This is especially acute for the sessile rotifers where quality illustrations, either as line art or light or scanning electron photomicrographs, of adults and trophi is deficient. This leads to a serious impediment in providing a comprehensive accounting for some species. *Lacinularia* and *Sinantherina* (Monogononta; Gnesiotrocha; Flosculariidae) are two sessile genera in which the literature provides inadequate treatment. In this contribution we (1) provide simple, dichotomous keys for the identification of all valid species of both genera and (2) present collated information on their morphology thereby detailing where additional research is needed. Both keys focus on easily observable characters of adult female morphology, including features of their coronae, antennae, colony formation behaviors, and presence/absence of eyespots in the adults. We hope that our effort promotes additional research on these two genera, including better documentation of their trophi and general body morphology.

Key words: Coloniality, larval behavior, identification, oviferon, planktonic, solitary, warts

Introduction

Lack of modern, easily accessible keys is an impediment to identification of species. As a result, researchers are unable to provide accurate information on the spatial and temporal distribution of species, ecological interactions, and evolutionary relationships. Depending on the taxa in question, this deficiency may have far-reaching effects, including recognition at only higher taxonomic levels or worse, misidentification of species. Moreover, lack of sufficient accurate data hampers our ability to clarify the seven shortfalls of biodiversity knowledge (Hortal *et al.* 2015). This problem is critical in microscopic taxa, such as rotifers where both the lack of up-to-date keys and lack of the education of new taxonomists is a serious hinderance to a thorough understanding of these micrometazoans (Ejsmont-Karabin 2019; Fontaneto *et al.* 2012; Wallace *et al.* 2024).

Despite their small size (~50–2000 µm) and numbers (ca. 2000 species), rotifers have attracted the attention of researchers for over 200 years (Davies *et al.* 2024; Edmondson 1959; Fontaneto & De Smet 2015; Wallace *et al.* 2006). Curiosity about this taxon comes from the fact that these short-lived, aquatic metazoans have diverse morphologies, occupy wide-ranging habitats, and possess varied reproductive modalities: i.e., depending on the group they reproduce either asexually, sexually, or by cyclical parthenogenesis (Serra *et al.* 2018). Rotifers (*sensu stricto*) are closely related to the Acanthocephala (Vasilikopoulos *et al.* 2024; Wallace *et al.* 2015).

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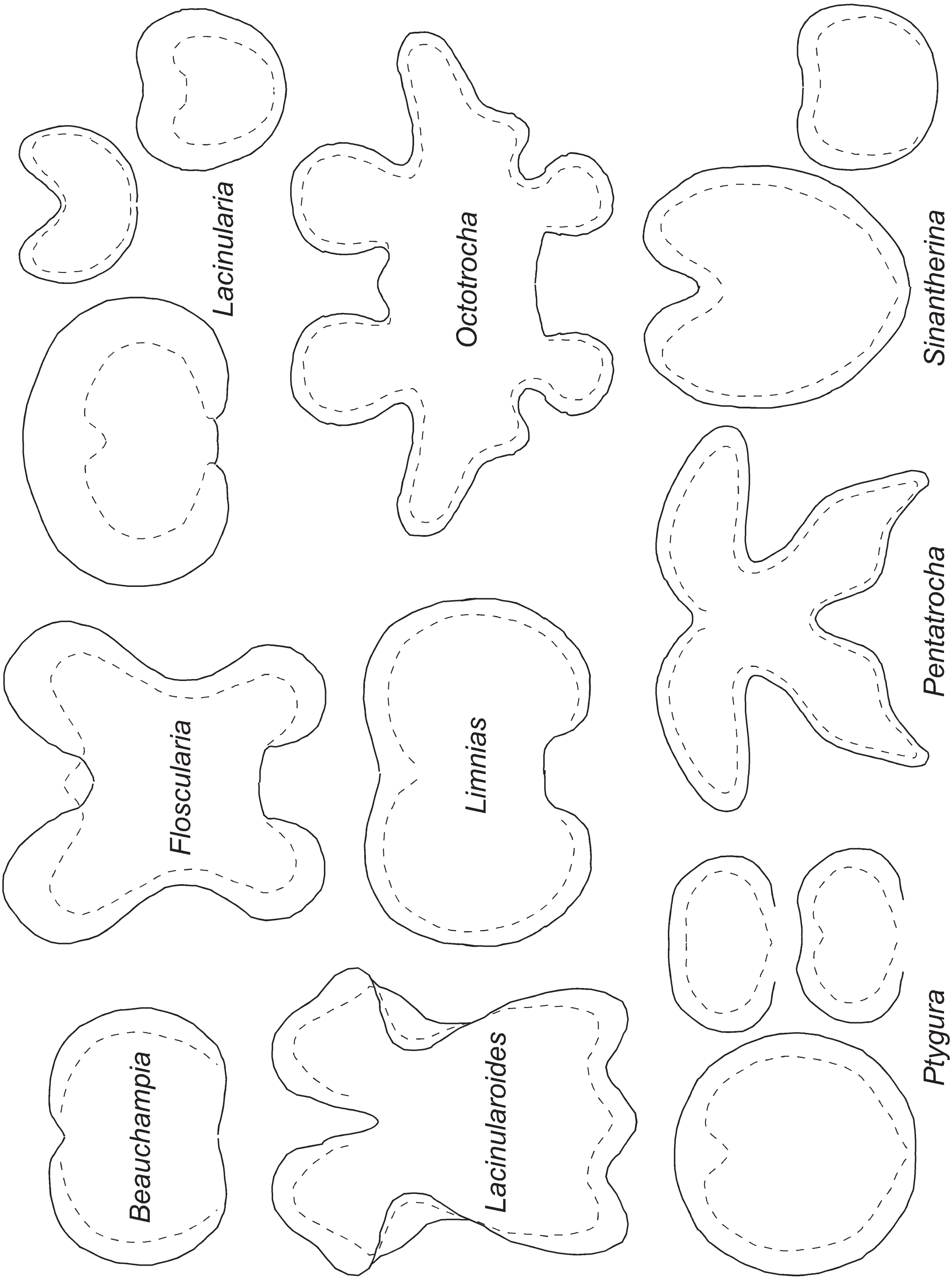

FIGURE 1. Schematic representations of the coronal margins of the nine genera of Flosculariidae. Images are not to scale. The corona is composed of two concentric rings that that beat in a metachronous pattern thereby producing feeding currents: trochus (——); cingulum (– – –) (Wallace 2002; Wallace *et al.* 2006). From ©Magnolia Press, reproduced with permission from the copyright holder [Zootaxa 5471: 401–421] and the authors (Lafleur *et al.* 2024).

All rotifers are mobile at some point in their life (Lafleur *et al.* 2024). Many swim (Obertegger *et al.* 2018), but others crawl over surfaces (Hochberg & Litvaitis 2000) or among the particles in aquatic sediments (Ejsmont-Karabin & Karpowicz 2021) or terrestrial soils (Pourriot 1979). However, the adults of ~100 species of gnesiotrochans are known as the sessile rotifers (Edmondson 1944), even though several species are actually planktonic. Regardless, the young (larvae) of species with truly sessile adults are mobile for a brief period of time before they settle. Settlement occurs when a larva, having encountered a suitable surface, makes an irrevocable choice and attaches itself permanently to the substratum (Wallace 1975, 1980). After attachment the larva metamorphoses with its tissues reorganizing into the adult form (Fontaneto *et al.* 2003; Hochberg & Hochberg 2017; Kutikova 1995; Wright 1959). The sessile taxa are worthy of study due to these qualities and a variety of research topics that they offer (Lafleur *et al.* 2024).

Identification of sessile rotifers requires knowledge of several simple characters; these include morphology of the antenna and corona, colony formation, and the presence or absence of extracorporeal coverings (tubes and gelatinous matrices) (Davies *et al.* 2024; Lafleur *et al.* 2024; Yang & Hochberg 2018a, 2018b; Yang *et al.* 2021). Regrettably, morphology of the trophi of sessile species remains mostly neglected, but as Lafleur *et al.* (2024) notes, use of trophi in identification of rotifers can be difficult and time consuming; trophi also may have little value in the case of some cryptic species (Kordbacheh *et al.* 2018).

Larvae of sessile rotifers usually settle on hydrophytes (Tiefenbacher 1972; Wallace 1980), but other surfaces are sometimes used. For example, *Limnias ceratophylli* Shrank, 1803 has been reported on the ventral surface of *Melanosuchus niger* (Spix, 1825) (Magnusson 1985) and *Ptygura beauchampi* Edmondson, 1940 is known to attach to the concave surfaces of planorbid snails (Edmondson 1944). Thus, habitat preference among the sessile species is a curious phenomenon. Some appear to be nearly indifferent to the surface to which they attach. For example, when held in glass or plastic dishes, and denied a plant surface, larvae of *Collotheca campanulata* (Dobie, 1849), *Cupelopagis vorax* (Leidy, 1857), and *Sinantherina socialis* (Linnaeus, 1758) will settle on any surface (authors, pers. obs.). On the other hand, in these circumstances the larvae of some populations of *Ptygura beauchampi* Edmondson, 1940 will never settle (RLW, pers. obs.). Nevertheless, localities with high hydrophyte diversity offer sufficient habitat for development of a rich sessile rotifer community (Lafleur *et al.* 2024). Yet despite their wide distribution and curious habitat preferences up-to-date keys to the sessile taxa are generally lacking and those that are present are scattered across the literature (Lafleur *et al.* 2024). This knowledge gap is especially problematic should taxa be misidentified and assigned to DNA barcodes (Collins & Cruickshank 2013).

TABLE 1. Important characteristics the nine genera of Flosculariidae, summarized from (Davies *et al.* 2024; Lafleur *et al.* 2024).

Genus	Corona	Tube	Antennae	Oviferon	Warts or spines	Selected references*
Beauchampia	Oval	Present	Single dorsal	Absent	Absent	1
Floscularia	Four lobes	Gelatinous or pellets	Paired	Absent	Absent	2
Lacinularia	Oval to heart-shaped	Present	Paired	Absent	Absent	3
Lacinularoides	Five-Seven lobes	Gelatinous matrix	Paired	Absent	Absent	4
Limnias	One pair	Firm pipe	Paired	Absent	Absent	5
Pentatrocha	Five, large lobes	Gelatinous matrix	Paired	Present	Absent	6
Ptygura	Round—slightly elliptical	Present	Paired	Absent	Absent	7
Octotrocha	Eight lobes	Gelatinous matrix	Paired	Absent	Absent	8
Sinantherina	Heart-shaped to quadrangular	Absent	Paired	Present	Present	9

*—Koste (1978). 1—Meksuwan (2015); 2—Edmondson (1945); Fontaneto *et al.* (2003); Wright (1950); 3—Kutikova (1995); Pourriot *et al.* (1972); Sa-Ardrit *et al.* (2013); Shephard (1896, 1899); Thorpe (1893); Vasisht and Dawar (1970); (Vidrine *et al.* 1985); Wallace (1987); 4—Meksuwan *et al.* (2011); 5—Kordbacheh *et al.* (2018); Meksuwan *et al.* (2018); 6—Segers and Shiel (2008); 7—Edmondson (1940, 1948, 1949); Franch (2021); Franch *et al.* (2024); 8—Segers *et al.* (2010); Segers and Shiel (2008); 9—Brown and Walsh (2019); Canella (1952); Champ and Pourriot (1977a); Champ and Pourriot (1977b); Edmondson (1940); Felix *et al.* (1995); Garcia (2004); Hochberg *et al.* (2015); Hochberg and Lilley (2010); Hochberg *et al.* (2010); Rico-Martínez and Walsh (2013); Sa-Ardrit *et al.* (2013); Sanoamuang and Savatenalinton (2001); Segers and Shiel (2008); Smith and Knight Jr. (1971); Surface (1906); Thorpe (1889, 1893); (Vidrine *et al.* 1985); Wallace (1987, 1993); Wallace *et al.* (2023); Walsh *et al.* (2006).

Previously we have reviewed the important differences among the nine genera of Flosculariidae (Davies *et al.* 2024; Lafleur *et al.* 2024) (Table 1 and Fig. 1). Here we continue our contribution to the systematics of the sessile rotifers by providing keys to identification of the adult females in two other important genera of Flosculariidae: *Lacinularia* (7 species) and *Sinantherina* (5 species). While some species in these genera have received considerable attention, most have received little. Our aim is to stimulate research on all species with the expectation that other researchers will publish additional information on their morphology. Future work should include images of adult morphology using light and SEM, but it is especially critical that a formal analysis of their trophi be undertaken.

Methods

We reviewed the original published descriptions of the species when possible, but also reviewed other literature noted in Table 1. Only those species recognized as valid by the List of Available Names (LAN) (Jersabek *et al.* 2018) and reviewed in the Rotifer World Catalog (Jersabek & Leitner 2013) are considered here.

Results

Adults of *Lacinularia* and *Sinantherina* possess an intriguing combination of life styles; some are sessile, others planktonic; some solitary, others colonial (Dioni 1966; Wallace 1987). However, in all species at the base of the foot is a material that is secreted and permanently glues the animals to either their substratum or to a dense gelatinous rod. Thus, in some cases, this material continues to be released, resulting in a slim extracorporeal shaft called the peduncle. And in some colonial species, the peduncles of all colony members coalesce into a common dowel (central rod) to which the feet of all members attach (e.g., *Lacinularia racemovata* Thorpe, 1893). The peduncle may be lengthened into an elongate stalk as in *Lacinularia striolata* Shephard, 1899. The shapes of their coronae appear different, but as noted by Lafleur *et al.* (2024) relying on a cursory observation of the corona alone is insufficient for two reasons. (1) Margins of the coronae may temporarily deform (twisting and stretching); thus, their contours may appear different from published descriptions. (2) The general contours of the coronae of *Lacinularia* and *Sinantherina* are similar. As noted by Lafleur *et al.* (2024) additional research on the musculature and surface characteristics of the sessile genera is warranted.

The most critical issue in the study of *Lacinularia* and *Sinantherina* is a basic lack of images of the species, including line art and light and scanning electron photomicrographs of adults and trophi.

Genus *Lacinularia* Schweigger, 1820

Lacinularia is composed of seven morphospecies, which can be misidentified as members of the genus *Sinantherina*. This means that at least two errors were made. (1) The gelatinous matrix present in *Lacinularia* was overlooked. (To avoid confusion presence of the matrix may be demonstrated by using methylene blue, which stains the boundary of the jelly.) (2) A region of the foot was mistaken for an oviferon. Additionally, in certain *Sinantherina* species, the presence of warts or spines were overlooked (see below).

Etymon of genus name (L., *Lacin*, a flap) is obscure, but may refer to the corona.

Diagnosis. Corona round or heart-shaped (kidney-shaped). Ventrolateral antennae short. Animals forming spherical to elliptical colonies (usually 20 to >100 individuals per colony, but occasionally many more) with a flocculent gelatinous matrix, often embedded with algae and other debris. Sessile species may form continuous mats over the substratum. Oviferon absent, eggs held within a gelatinous matrix. Oviparous. Planktonic or sessile.

Bhardwaj and Dattagupta (1984) provide information on colony formation in *Lacinularia racemovata* Thorpe, 1893 and *Lacinularia flosculosa* (O.F. Müller, 1773). The species named *Lacinularia causeyae* (Vidrine *et al.* 1985) was relocated to a new genus in the Conochilidae: *Conochilopsis causeyae* (Segers & Wallace 2001). All species inhabit a gelatinous matrix (tube), which becomes a confluent matrix in the six species forming colonies; *Lacinularia megalotrocha* Thorpe, 1893 is solitary. When compared to other sessile species (e.g., *Floscularia*), all species of *Lacinularia* possess small ventral antennae. Table 2 provides a compilation of the important characteristics of this genus.

TABLE 2. Important characteristics of *Lacinularia* species.

Taxa*	Planktonic or Sessile	Dorsal gap	Corona	Eyespots	Ventral sinus	Foot	Peduncle	Coloniality
racemovata	Planktonic	Small to wide	Circular, slightly wider than body	Present	Shallow	Long	Central rod	Colonial as a prolate spheroid
ismailoviensis	Planktonic	Small	Circular to oval, 2x body	Present	Slightly flattened	Long	Central rod	Colonial, spherical to elliptical
megalotrocha	Sessile	Small	Kidney-shaped, wide	Absent	Deep	Moderate	Absent	Solitary
elongata	Sessile	Distinct	Heart to oval, slightly wider than body	Absent	Absent	Long	Absent	Colonial
flosculosa	Sessile	Small	Kidney, much wider than body	Absent	Deep	Long	Absent	Colonial
striolata	Sessile	Absent	Heart to slightly oval, as wide as body	Present	Shallow	Long	Elongated stalk	Colonial
pedunculata	Sessile	Absent	Heart to oval, wider than body	Present	Shallow	Long	Peduncle	Colonial

*—*Lacinularia reticulata* Anderson & Shephard, 1892 is considered to be species inquirenda.

Dichotomous key to species of genus *Lacinularia*

1 Planktonic (colonies infrequently attached to substratum) 2

1’ Sessile 3

2(1) Corona circular, with shallow ventral sinus, slightly wider than body, dorsal gap present; body constricted at base; two eyespots present; colonial (prolate spheroid); total body length 450–750 µm. (Fig. 2A–C) . . . . *racemovata* Thorpe, 1893
[Colonies of ~150 individuals attached to central rod of firm gelatinous material. Colony length is 2x width and rotates about its long axis. An adult and trophi are illustrated by Banik (1996), but reported as *L. elliptica*, a junior subjective synonym.]

2’ Corona nearly circular to oval-shaped, slightly flattened ventrally; dorsal gap tiny; two eyespots present; colonial (spherical); total body length 700–900 µm. (Fig. 2D–G) . . . . *ismailoviensis* (Poggenpol, 1872)
[The trophi are sketched by Poggenpol (1872), Dioni (1966), and Kutikova (2007). Kutikova (2007) illustrated the male and resting eggs and notes that colonies may attach to a substratum. The corona depicted in Figure 4 by Poggenpol (1872) is more elliptical than circular as is illustrated in Figure 5 of Kutikova (2007) and Figure 2 of Vidrine *et al.* (1985).]

3(1’) Dorsal gap in corona present (small or distinct) 4

3’ Dorsal gap absent; corona with shallow ventral sinus; colonies attached to the substratum by a long stalk (peduncle) 6

4(3) Corona heart to kidney shaped with deep ventral sinus 5

4’ Corona oval- to spherical shape, slightly wider than the body, with short axis held at right angles to trunk; ciliated between trochus and cingulum; dorsal gap distinct; body narrow, elongate; long foot ($\frac{2}{3}$ whole length); eyespots absent; colonial; total body length 800–1000 µm. (Fig. 3A–C) . . . . *elongata* Shephard, 1896
[Shephard (1896) reports that this species may form spherical colonies or assemble into a continuous cluster resembling a “thick felt” (i.e., a mat). Shephard attributes that the “dirty brown colour” of the colonies may be characteristics of the species, but this may be a matter of the water conditions. Shephard’s rudimentary illustration of the trophi shows them to be asymmetrical.]

5(4) Corona, deep ventral sinus; dorsal gap small; eyespots absent; solitary; total body length ~1000 µm. (Fig. 3D) . . . . *megalotrocha* Thorpe, 1893

5’ Corona broad, deep ventral sinus; dorsal gap small; eyespots absent; colonial; total body length ≤ 2000 µm. (Fig. 4) . . . . *flosculosa* (Müller, 1773)
[Depending on the substratum to which it attaches, colonies of *L. flosculosa* are more-or-less spherical, but as in *L. elongata* this species may colonize substrata forming a massive continuous mat: see Figure 1 in Pourriot *et al.* (1972). Koste *et al.* (1995) illustrates the adult, trophi, and colony form, as well the males, apparently with eyespots.]

6(5) Corona as wide as body, with very shallow ventral sinus; no dorsal gap; body ovoid; foot long, ca. $\frac{4}{5}$ of body length; eyespots placed close to coronal edge; total body length ≤ 2600 µm; colonial. (Fig. 5A–C) . . . . *striolata* Shephard, 1899
[A detailed anatomy is illustrated by (Shephard 1899), who also notes the following features. (1) The integument is striated. (2) Corona moderately inclined to body forming a 45° ancle with the axis of the body. (3) The peduncle (stalk), which increases

in length (≤12 mm) as the animals age, anchors the colony to its substratum. It is formed from the combined secretions of all members of the colony. (4) Shephard estimates that the spherical colonies of 5 mm in diameter may have >3600 individuals.] (5) Gut is absent in the male, but possesses two eyespots, dorsal antenna, and a ciliated cup near the posterior. (6) The larvae aggregate into groups, thereby forming colonies of the same age; this behavior is termed geminative colony formation (Wallace *et al.* 2015). However, colony formation by the stem female was not described. (7) While feeding individuals in *L. striolata* colonies apparently arrange themselves into arrays, as has been described by Wallace (1987) in *S. socialis*. (8) Shepard hints at amphoteric reproduction.]

6’ Corona ~2–3x body width, with very shallow ventral sinus; trochus and cingulum widely separated; two eyespots, ½ way down the corona, close to trochus; foot <⅘ of body length; peduncle long; total body length 750–1000 µm; colonial. (Fig. 5D–E) . . . . *pedunculata* Hudson, 1889

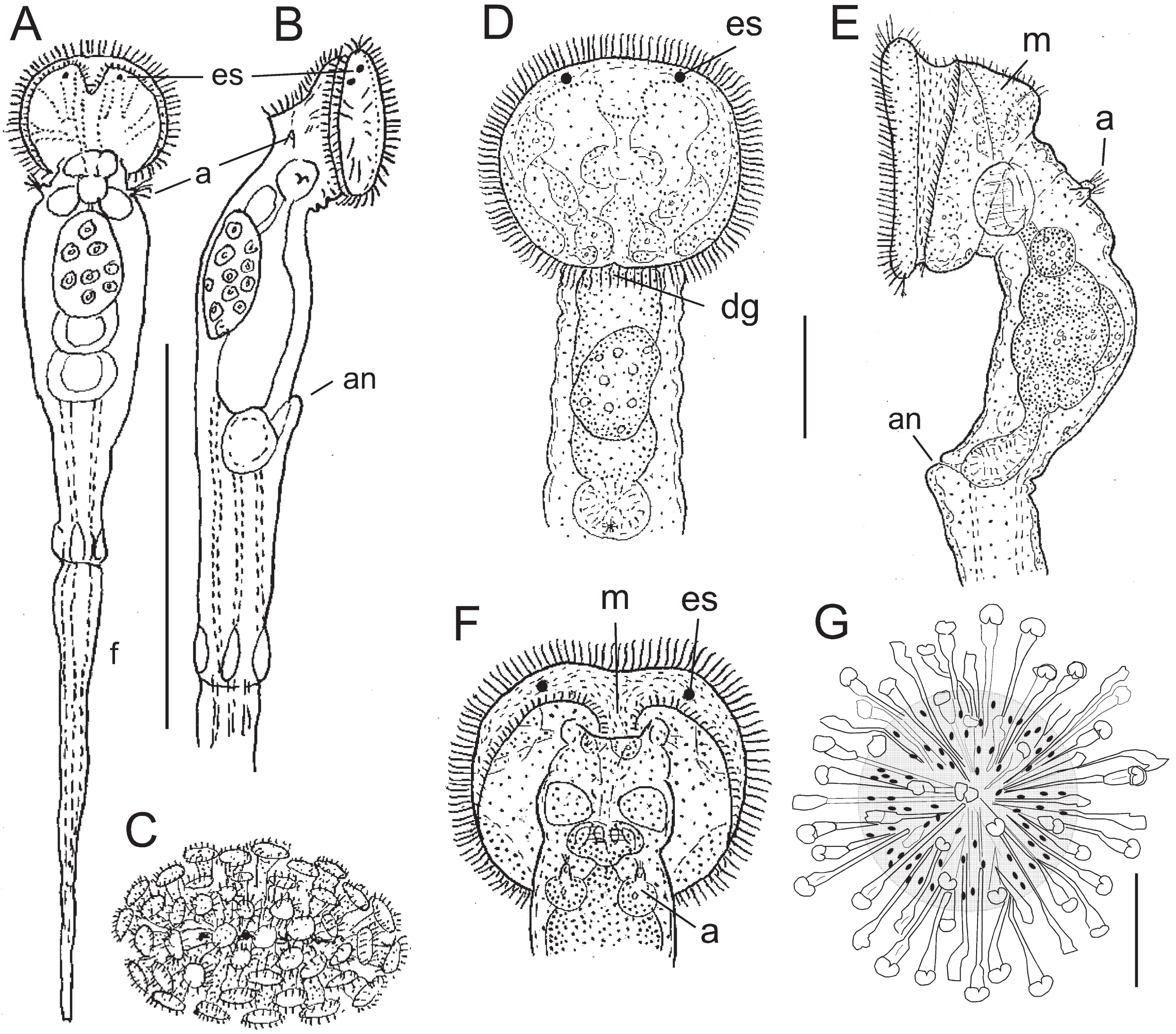

FIGURE 2. Two planktonic *Lacinularia* species. A–C. *Lacinularia racemovata*. A. Ventral view. B. Lateral view. C. Free swimming elliptical colony. D–G. *Lacinularia ismailoviensis*. D. Dorsal view. E. Lateral view. F. Ventral view. G. Colony: dark spots are embryos; shading illustrates the gelatinous matrix. Symbols: a = antenna; an = anus; dg = dorsal gap; es = eyespot; f = foot; m = mouth. Bars: A–B. ~ 250 µm; D–E = 50 µm; G. = 500 µm. (A–C. Reproduced from art provided by W.T. Edmondson; D–F. Reproduced from art provided by W.T. Edmondson; G. After Poggenpol (1892)).

Conclusions

We recommend that additional studies of all species of *Lacinularia* be done on the morphology of the corona and trophi, presence of pigmented eyespots in young, adults and males, development of the peduncle, and on colony formation (Wallace 1987; Wallace & Snell 2010; Wallace *et al.* 2006). Indeed, adequate illustrations as line art and/or light and SEM photomicrographs are needed, particularly of the trophi. Comparative study of *L. ismailoviensis* and *L. racemovata* are especially warranted. Additional inquiry of *Lacinularia reticulata* also is justified.

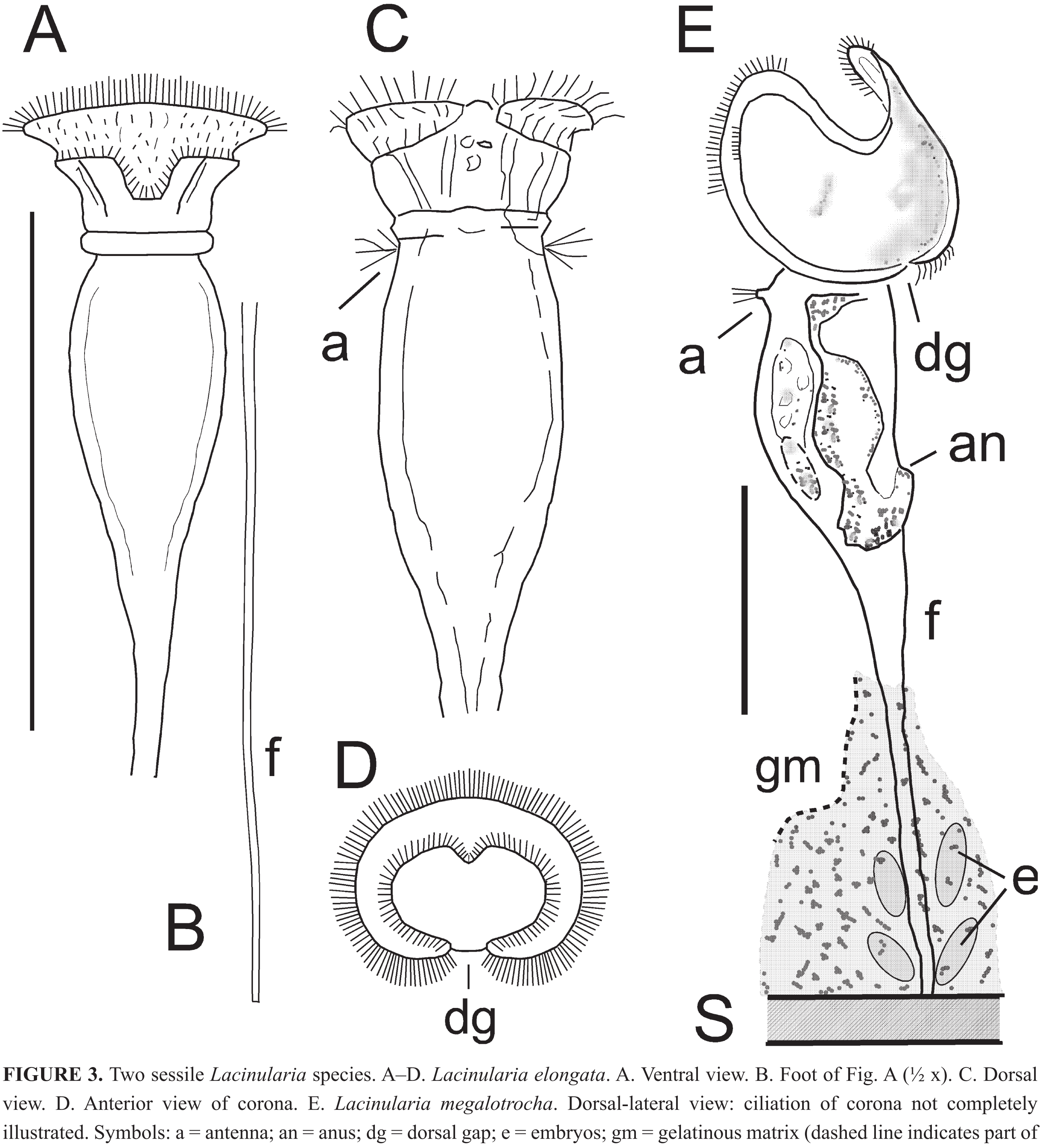

FIGURE 3. Two sessile *Lacinularia* species. A–D. *Lacinularia elongata*. A. Ventral view. B. Foot of Fig. A (½ x). C. Dorsal view. D. Anterior view of corona. E. *Lacinularia megalotrocha*. Dorsal-lateral view: ciliation of corona not completely illustrated. Symbols: a = antenna; an = anus; dg = dorsal gap; e = embryos; gm = gelatinous matrix (dashed line indicates part of the margin); f = foot; S = substratum. Bars = 250 µm. (A. After Thorpe, 1893; B–E. After Shephard, 1896).

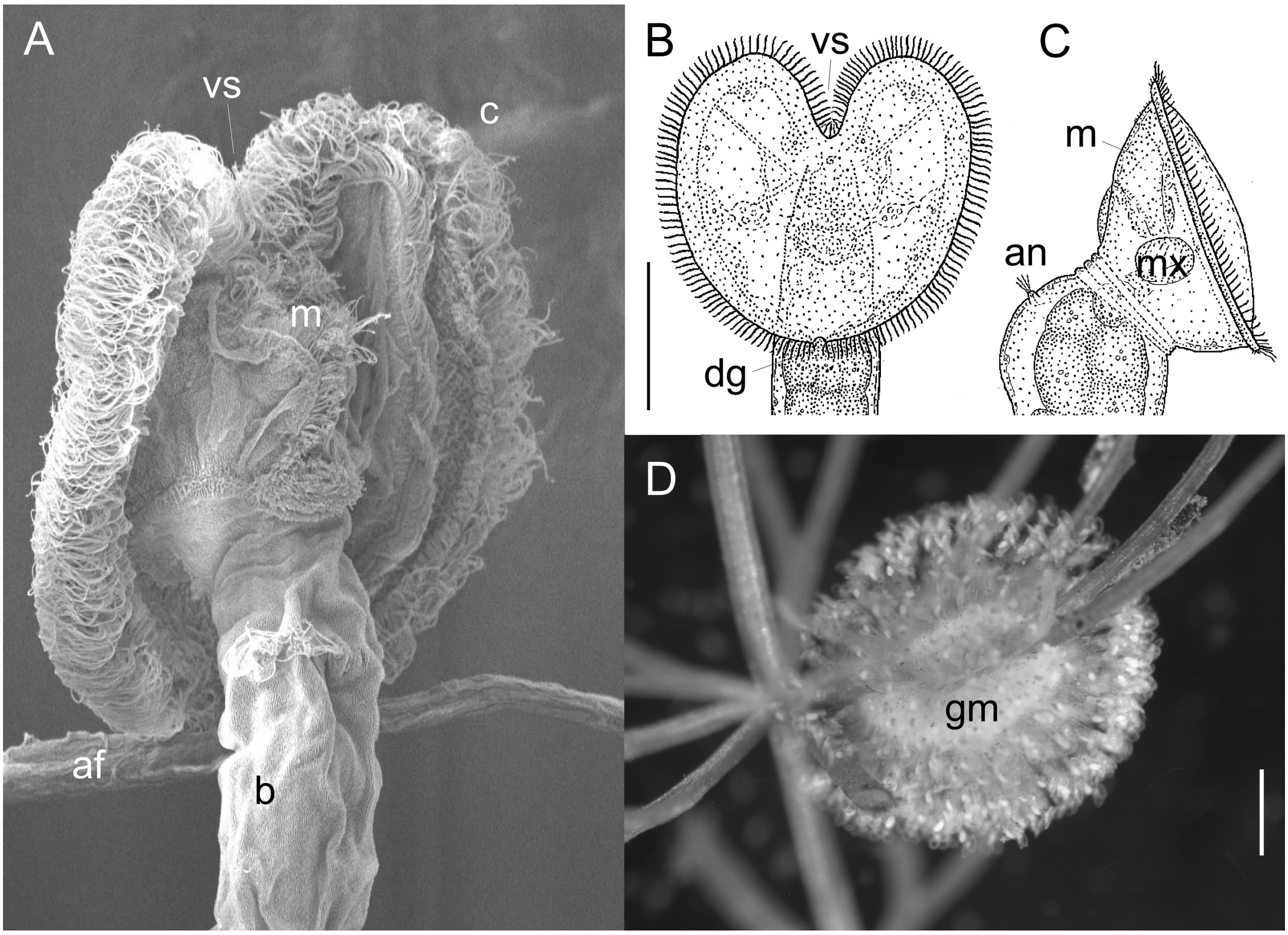

FIGURE 4. *Lacinularia flosculosa*. A. SEM 3/4th ventral view. B. Dorsal view C. Lateral view. D. Colony attached to *Ceratophyllum demersum* Linnaeus, 1753. Symbols: af = algal filament; an = antenna; b = body; c = corona; gm = gelatinous matrix (embryos are embedded within); m = mouth; mx = mastax; Bars: B = 100 µm; D = 1,000 µm. (B, C. Reproduced from art provided by W.T. Edmondson).

Genus *Sinantherina* Bory de St. Vincent, 1826

Sinantherina is composed of five morphospecies, but unlike *Lacinularia*, *Sinantherina* possess an oviferon and they lack a gelatinous matrix.

Diagnosis. Corona either heart-shaped or quadrangular; dorsal gap in coronal ciliation limited or absent. Dorsal and ventral antennae small. Some species with distinctive elliptical bodies (warts) located just below the corona on the ventral and/or dorsal sides. One species with ventral spines, but lacks warts. Foot of various lengths depending on species. Pigmented eyespots in juveniles (larvae) and planktonic adults, but lacking in adults of sessile species. Embryos brooded by adult females, fastened to specialized egg-bearing structure (oviferon) located on foot always below anus. No extensive gelatinous matrix (perhaps very limited amounts at base of foot). Adult females usually colonial with small (5–12 individuals) to large colonies (>200 individuals), but occasionally solitary. Sessile with newborn females free-swimming until attachment or remaining within parent colony or planktonic. (NB: The oviferon is shared with *Pentatrocha gigantea*, but the morphology of the coronae are distinctly different (Segers & Shiel 2008).) Oviparous.

Of the five valid species, three possess glandular structures called warts for which there is evidence that they possess unpalatability factors (Felix *et al.* 1995; Hochberg *et al.* 2015; Wallace *et al.* 2023; Walsh *et al.* 2006) and one species has spines that may provide defense against fishes with a small mouth gape (Wallace 1987). Information on colony formation in a few species of *Sinantherina* is provided by Bhardwaj and Dattagupta (1984) and (Garcia 2004). A review of this genus that includes a key to the species is provided by Dioni (1966). Table 3 provided a compilation of the important characteristics of this genus.

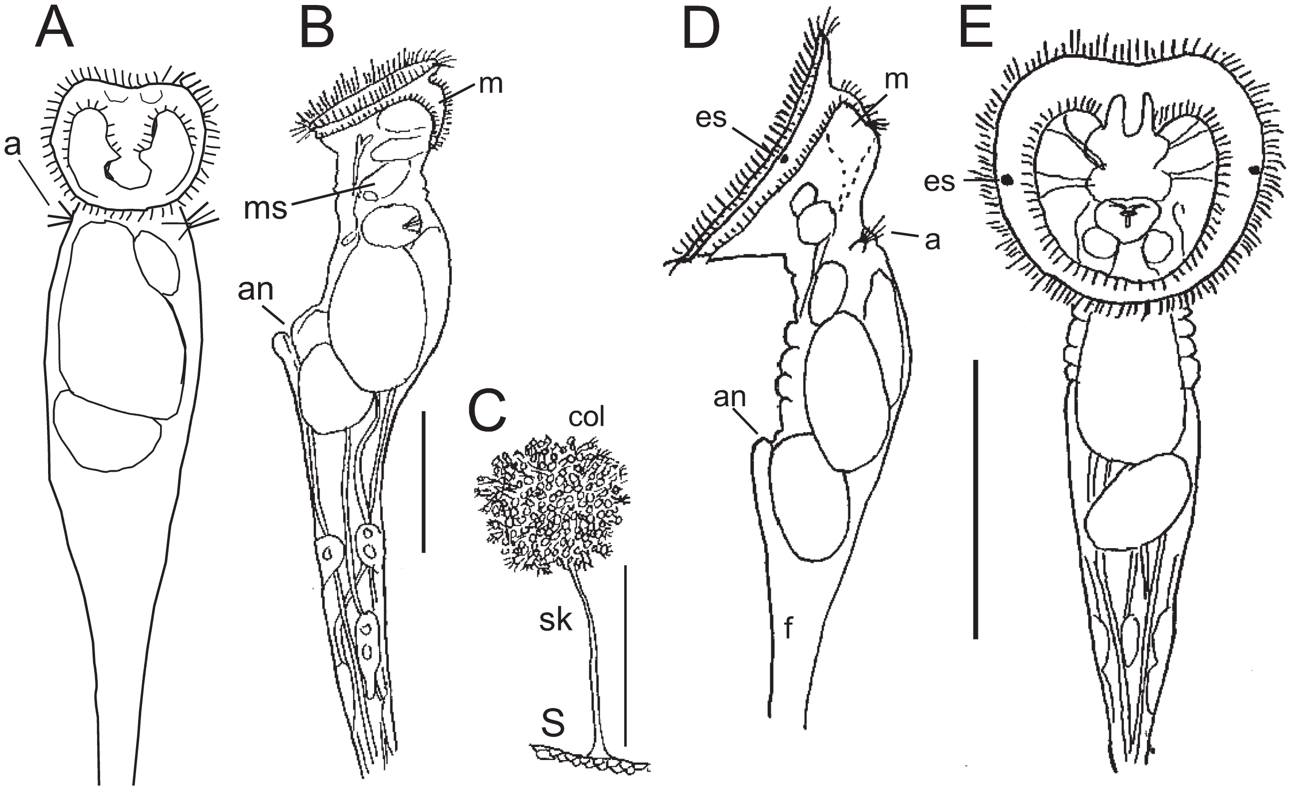

FIGURE 5. Two sessile *Lacinularia* species. A–C. *Lacinularia striolata*. A. Corona dorsal view. B. Lateral view. C. Colony on stalk attached to substratum. Eyespots not illustrated. D–E. *Lacinularia pedunculata*. D. Lateral. E. Dorsal. Symbols: a = antenna; an = anus; col = colony attached to peduncle stalk (sk); es = eyespot; m = mouth.; ms = mastax; S = substratum; sk = stalk. Bars: B = 100 µm; C ≤ 12 mm; D–E = 250 µm. (A–C. After Shephard 1899; D–E. Reproduced from art provided by W.T. Edmondson).

TABLE 3. Important characteristics of *Sinantherina* species.

Taxa	Planktonic or Sessile	Warts	Spines	Eyespots	Ventral sinus	Dorsal gap	Coloniality
semibullata	Planktonic	1 pair	Absent	Present	Shallow	Distinct, but narrow	Colony comprised of individuals of different ages
procera	Sessile	2 pair	Absent	Absent	Deep	Tiny	Colonial
socialis	Sessile	2 pair	Absent	Absent	Deep and narrow	Tiny	Colony comprised of individuals of the same age
ariprepes	Sessile	Absent	Absent	Absent	Moderate	Tiny	Colony comprised of individuals of different ages
spinosa	Planktonic	Absent	Present	Present	Shallow	Small	Colony comprised of individuals of different ages

Dichotomous key to species of genus *Sinantherina*

1 Warts (1 or 2 pairs) present on the anterio-ventral surface 2
[Depending on the lighting conditions, these glands may appear to be white (epi- illumination) or dark (transmitted light).]

1’ Warts absent 4

2(1) One pair of warts; corona quadrilateral, flexed dorsally; shallow ventral sinus; ventral antennae small; adults with 2 eyespots; planktonic, but may secrete a thread and adhere to a hydrophyte; colonial (~25–100 individuals); total body length ~1250 µm. (Fig. 6A–C) . . . . *semibullata* (Thorpe, 1889)
[Adult females with 2 eyespots in the upper edge of the corona between the trochus and cingulum; males possess two eyespots.

The trophi may be slightly asymmetrical (Fig. 6C). Trophi also are presented by Banik (1996) and Dioni (1966). Temporary attachment by a common thread has been observed (Gunter & Knight Jr. 1978). Unlike the illustration of Koste (1978) and Vidrine *et al.* (1985), the coronae of all individuals in a free swimming colony point in the direction of the colony movement. Colony size in a population in Wisconsin (43.9086417; -89.0952805) was recorded to be as follows: n=24, $\bar{x}$ =57.2, SD=17.6 (RLW, pers. obs.). A detailed analysis of this species was provided by Canella (1952).]

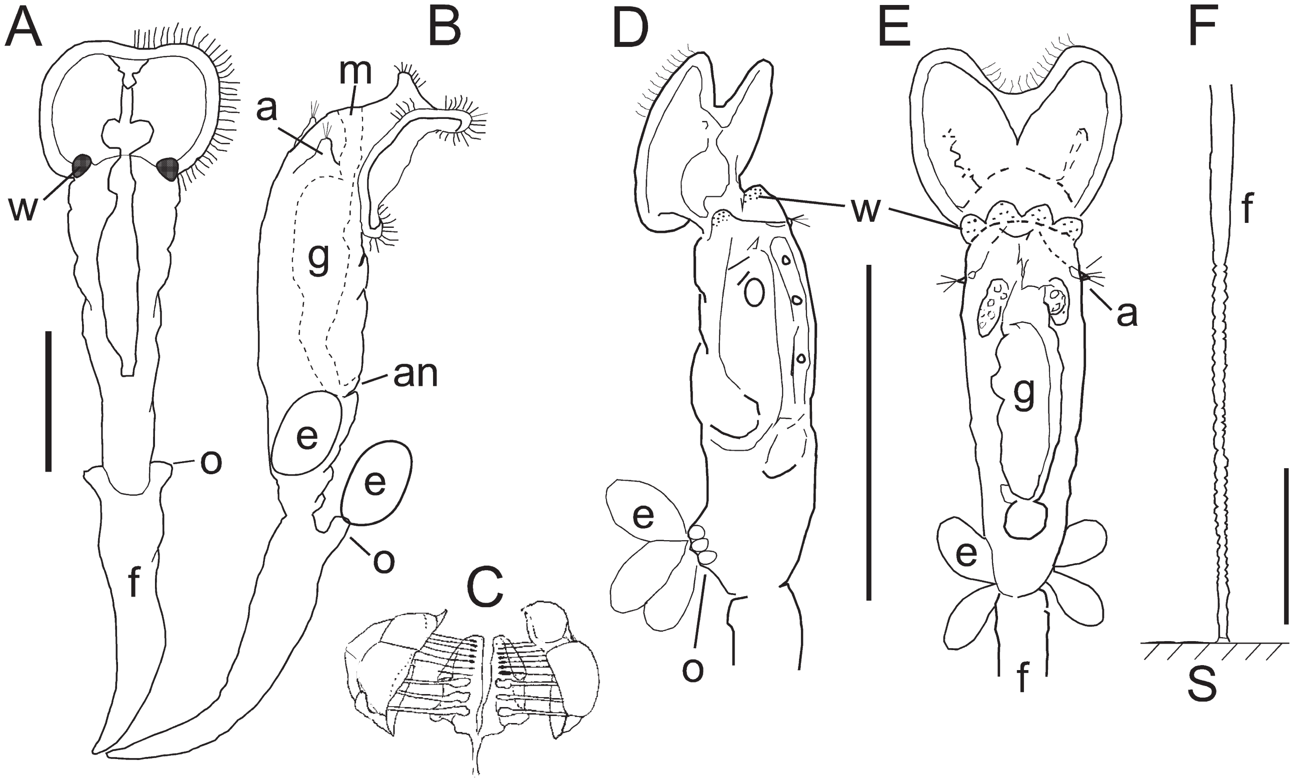

FIGURE 6. Two *Sinantherina* species possessing warts. A–C. *Sinantherina semibullata*. A. Ventral view. B. Lateral view. C. Trophi. *Sinantherina procera*. D. Lateral view. E. Ventral view. F. Elongate foot. Complete coronal ciliation not depicted in the adults of either species. Symbols: an = anus; a = antenna; e = embryos; f = foot; g = gut; m = mouth; o = oviferon; w = warts; S = substratum. Bars = 250 µm. (A, B. After Thorpe 1889; C–F. Reproduced from art provided by W.T. Edmondson. No scale was provided for C).

2’ Two pairs of warts; corona with deep ventral sinus; two ventral antennae 3

3 Foot long (¾ the length of the whole animal); colonial (~40–50 individuals); oviferon small, rudimentary (mere protuberance topped with 3 knobs); total body length <1000–2500 µm; colonial (large). (Fig. 6D–F) . . . . *procera* (Thorpe, 1893)
[Eyespots present in larvae and male; absent in the adult. An adult and trophi are documented by Banik (1996), who reports that colonies comprise individuals of the same age (size), with numbers varying between 12 and 65 individuals.]

3’ Foot not long; total body length ≤ 2000 µm; colonial (15 to ≥200 individuals), all adults about same size (age). (Fig. 7) . . . . *socialis* (Linnaeus, 1758)
[Trophi are documented by Melone *et al.* (1998). The biology and ecology of this species has been explored by many researchers (Champ 1978; Champ & Pourriot 1977a; Champ & Pourriot 1977b; Dioni 1966; Felix *et al.* 1995; Garcia 2004; Hochberg *et al.* 2015; Hochberg & Lilley 2010; Rico-Martínez & Walsh 2013; Wallace 1993; Wallace *et al.* 2023; Walsh *et al.* 2006). NB: We have noticed that young larval colonies may join (fuse) with an established colony thereby forming an integrated unit of mixed ages. Resting eggs (diapausing embryos) may be too large to pass through the cloaca and may be seen in the foot and even on the corona (Edmondson 1940).]

4(1’) Foot wide and short; adults lacking eyespots; solitary or small to large colonies (≤200 individuals); total body length ~ 650 µm; sessile; colonial. (Fig. 8) . . . . *ariprepes* Edmondson, 1939
[The trophi are documented by Dioni (1966) and Koste (1978). Dioni (1966) also comments on the behavior of both the larvae and adults, and on the morphology of this species. Edmondson (1939) described *S. ariprepes* as “… a very restless species, throwing itself about from side to side, rapidly contracting and expanding; its activity is broken by short periods of repose.” As seen in S. *socialis*, diapausing embryos may be present in the foot.]

4’ Foot long; numerous, tiny spines present on anterio-ventral surface numerous just below the corona (small, irregularly placed, thorn-like shapes); ventral sinus shallow; dorsal gap small; eyespots present on upper edge of corona; planktonic, but may secrete a thread and adhere to a hydrophyte; spherical colonies (20–100 individuals); total body length 800–1000 µm; colonial. (Fig. 9) . . . . *spinosa* (Thorpe, 1893)

[The trophi are documented by (Banik 1996) and Koste (1978). Bhardwaj (1985) reports colonies comprise individuals of the same age (size), but Weber (1898) [Plate 12, Figure 1] illustrates a multigenerational colony (see also Figure 18). When disturbed this species partly contracts, curving itself into the form of a question mark (some authors describe it as an S-shape); this behavior exposes the spines, which appear to be arrayed randomly. The spines are thought to act as a deterrent to predation, perhaps by fishes that have small gape sizes (Felix *et al.* 1995; Thorpe 1893), but they also may deter some predatory invertebrates. This species may occasionally attach to hydrophytes by a fragile mucus thread (Thorpe 1893; Weber 1898).]

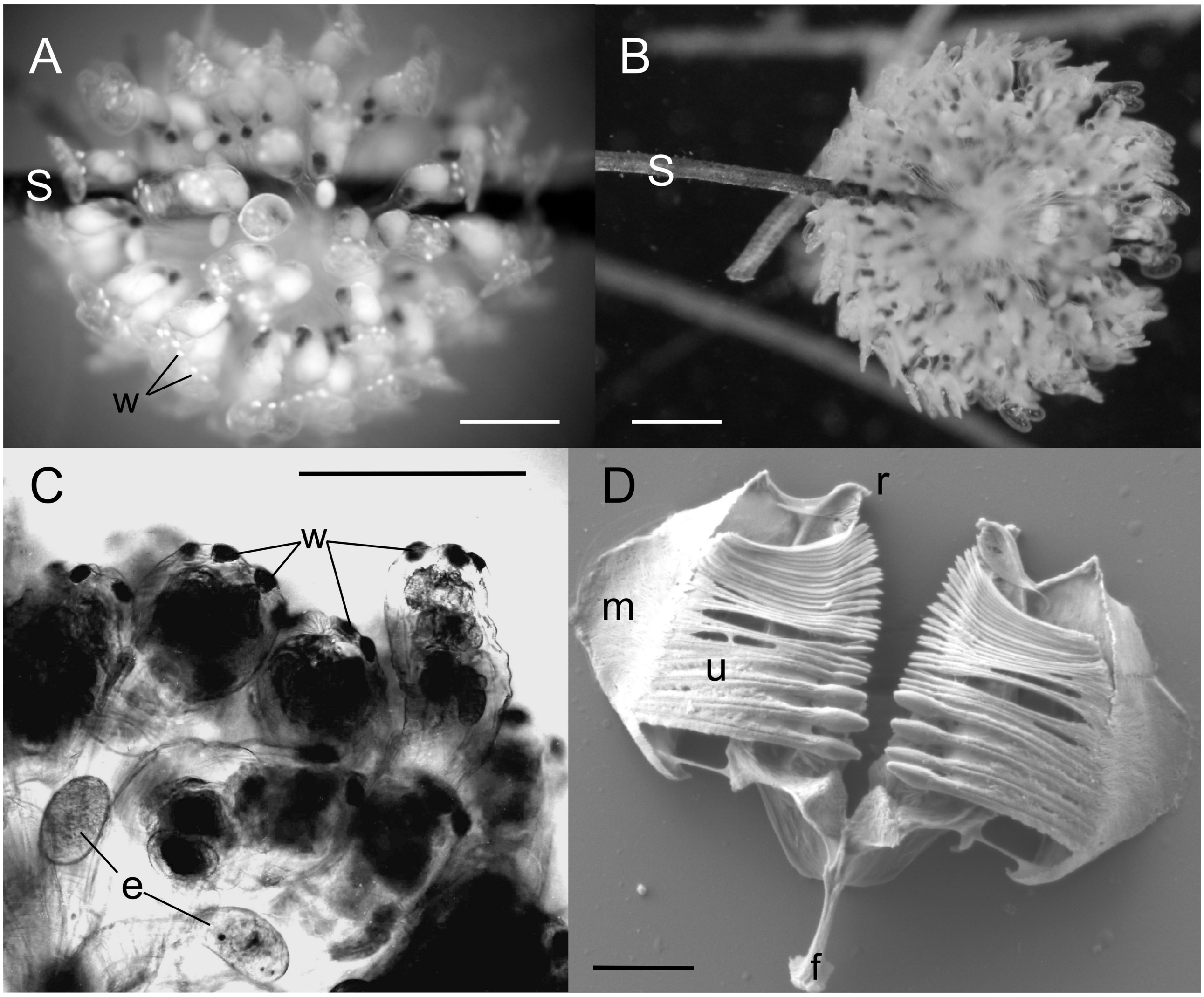

FIGURE 7. *Sinantherina socialis*. A. Expanded colony with warts (white spots). B. Expanded colony: warts not visible. C. Colony with the individuals contracted with warts (dark spots). D. Trophi, frontal view. (A. epi-illumination; B. transmitted illumination.) Symbols: e = embryos; f = fulcrum; m= manubrium; r = ramus; S = substratum; u = uncus; w = warts. Bars: A,B = 500 µm; C = 250 µm; D = 10 µm.

Conclusions

We suggest that research be undertaken to document colony formation (Garcia 2004; Surface 1906; Wallace 1987; Wallace & Snell 2010; Wallace *et al.* 2006) and morphology of their trophi. Further analysis of the tendency for amphoteric production of embryos (Champ & Pourriot 1977a; Rico-Martínez & Walsh 2013) and the presence of compounds that are thought to be unpalatable should be undertaken (Felix *et al.* 1995; Wallace *et al.* 2023; Walsh *et al.* 2006).

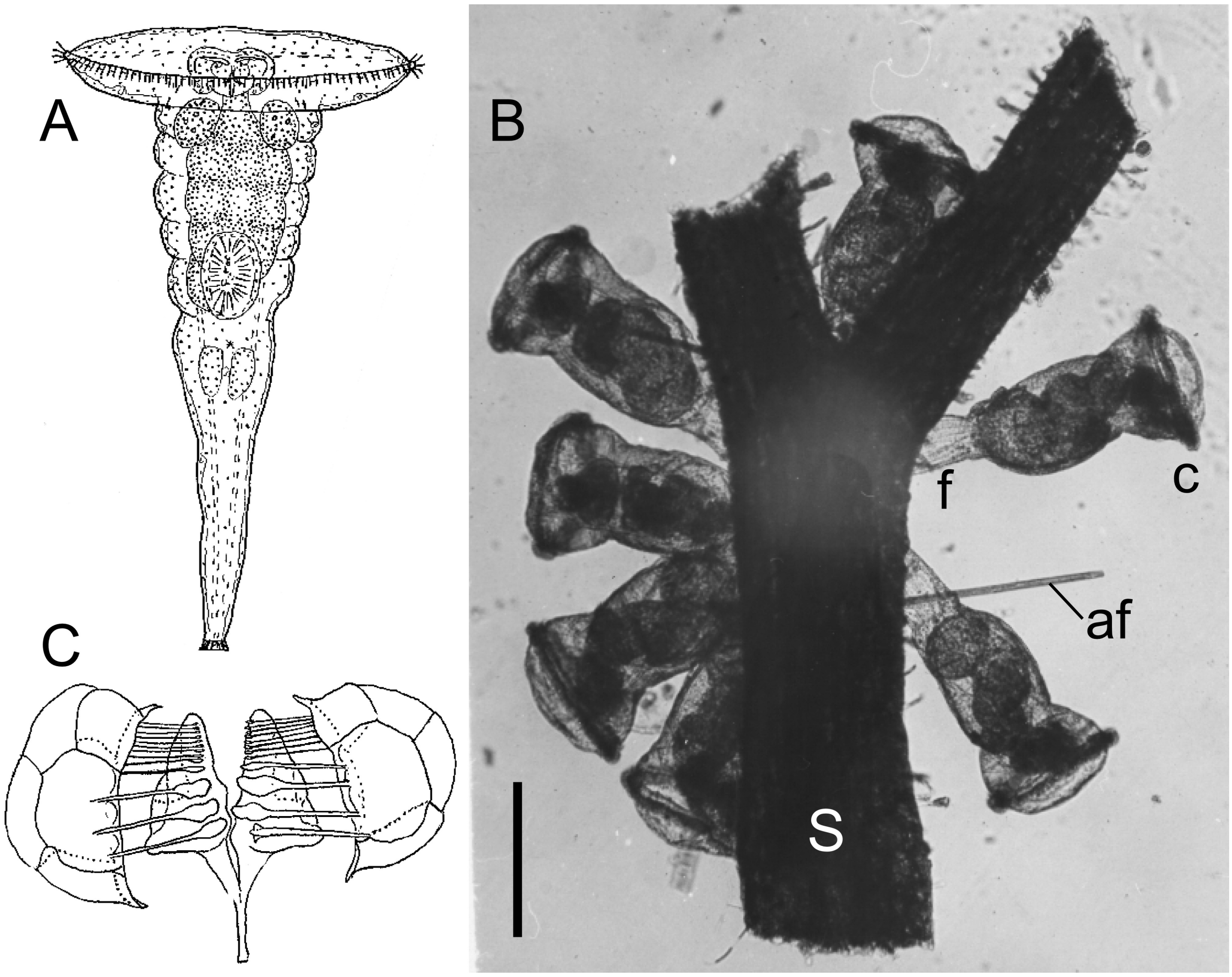

FIGURE 8. *Sinantherina ariprepes*. A. Adult. B. Trophi. C. Small colony attached to *Ceratophyllum*. Symbols: af = algal filament; c = corona; f = foot; S = substratum. Bar = 250 µm. (Reproduced from art provided by W.T. Edmondson. No scale was provided for C).

Declarations

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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.

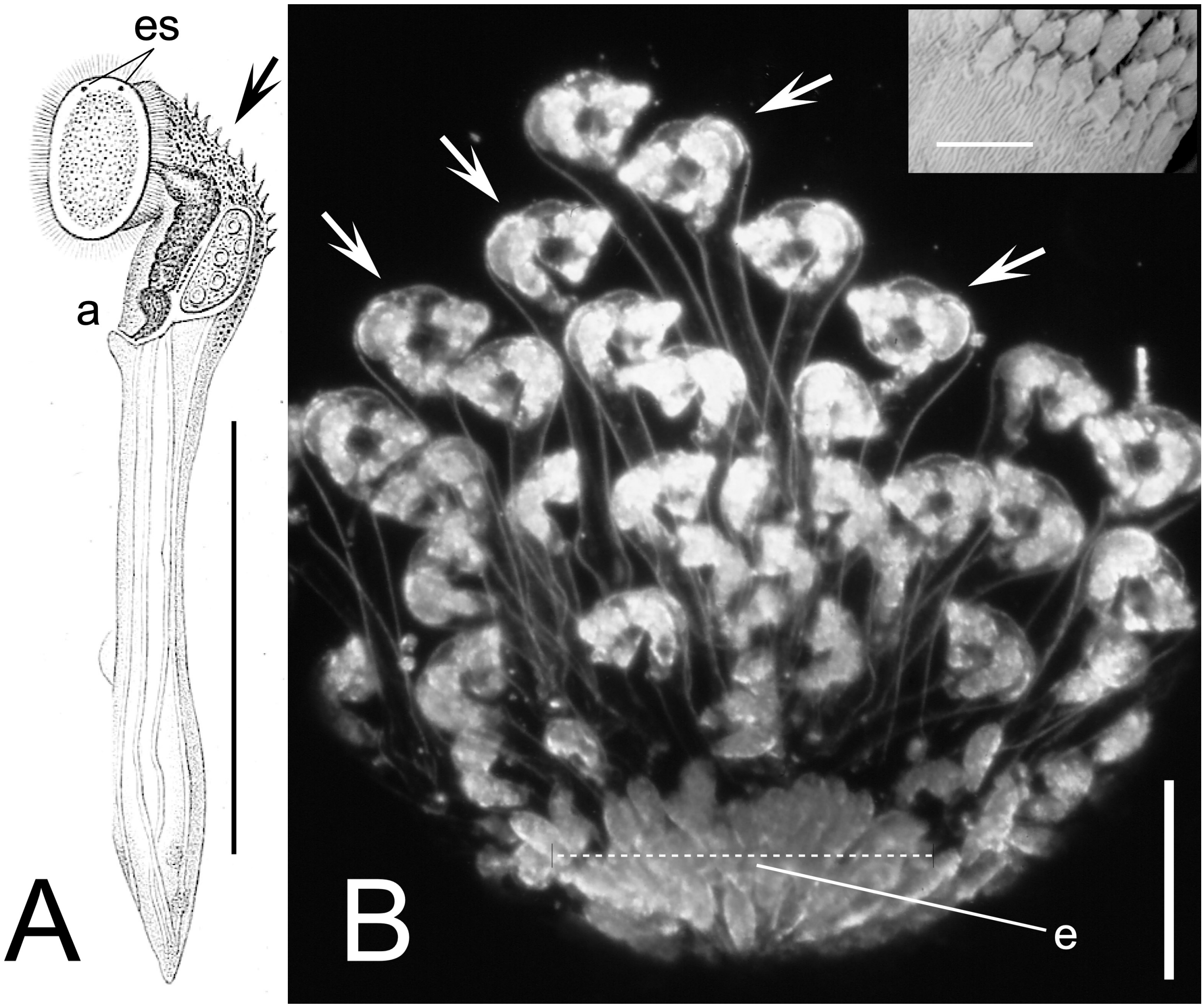

FIGURE 9. *Sinantherina spinosa*. A. Individual. B. Colony. Inset: SEM of junction of spined field and the ventral body side. Symbols: Arrows indicate the position of minute spines; a = anus; e = embryos; es = eyespots. Bars: A = 500 µm; B = 250 µm; insert = 5 µm. (A. Single animals, not completely flexed: from Weber (1898); B. Photomicrograph of a preserved colony courtesy of M.F. Vidrine).

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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