Zootaxa 4442 (2): 307–318
http://www.mapress.com/j/zt/

Article

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

https://doi.org/10.11646/zootaxa.4442.2.7
http://zoobank.org/urn:lsid:zoobank.org:pub:49141B92-B4B7-4594-B8B9-AC9F6DD52BCF

Key to the currently recognized species of *Limnias* Schrank, 1803 (Rotifera, Monogononta, Gnesiotrocha, Flosculariidae)

ROBERT LEE WALLACE[1,4], AZAR KORDBACHEH[2] & ELIZABETH J. WALSH[3]

[1]*ORCID 0000-0001-6305-4776*
Department of Biology, Ripon College, Ripon, WI, 54971, USA
[2]*ORCID 0000-0001-5804-4805*
Department of Biological Sciences, 500 W. University Ave., University of Texas at El Paso, El Paso, TX, 79968, USA
[3]*ORCID 0000-0002-6719-6883*
Department of Biological Sciences, 500 W. University Ave., University of Texas at El Paso, El Paso, TX, 79968, USA
[4]*Corresponding author. E-mail: wallacer@ripon.edu*

Abstract

Although the most widely used key to the Rotifera subsumes six species of the sessile genus *Limnias* within two species groups (*L. ceratophylli* and *L. melicerta*), the original descriptions of these forms are sufficiently different to recognize them as distinct entities. We used these descriptions and all available literature on these species to develop dichotomous and formula keys to the six species based on easily recognizable morphological characters. As part of our review we added relevant ecological information from published sources, as well as our own data. We also discuss the need for additional observations of morphological, behavioral, life history, and genetic features to better understand the diversity of this wide-spread genus.

Key words: biodiversity, distribution, morphology, taxonomy

Introduction

Genus *Limnias* Schrank, 1803 is one of nine genera of the gnesiotrochan family Flosculariidae within Rotifera. Species are diagnosed by their distinctive tube morphology, length of ventral antennae, and number of distinctive nodules located on the dorsal surface of the neck. Hlava (1908) produced a workable key to the species, but used the dorsal nodules as a primary character; these are difficult to see without taking great care. Seventy years later Koste (1978) subsumed all six species into either one of two species groups: *L. ceratophylli* and *L. melicerta*. We aver that Koste's interpretation was unwarranted, as he provided no detailed analysis of the variability of distinguishing characteristics used by Hlava to delineate the species. Moreover assigning all species within two groups leads to a loss of information regarding their ecological and genetic differentiation. On the other hand, viewing these taxa as separate species provides the basis for developing more robust hypotheses of relationships, permitting better phylogenetic assessment of the genus using additional morphological characters and molecular data.

Here we present two practical, morphologically based keys: dichotomous and formula. To do our analysis we reviewed descriptions from the original authorities and consulted previously published keys. As part of this contribution we included ecological information from published sources, as well as our own data. As appropriate we cite reference numbers for specimens deposited in The Academy of Natural Sciences of Philadelphia [ANSP] (now The Academy of Natural Sciences of Drexel University) and pictured in Jersabeck *et al.* (2003), and in the Rotifer World Catalog (http://www.rotifera.hausdernatur.at/Species/Index/387).

Accepted by H. Segers: 18 May 2018; published: 2 Jul. 2018

Genus *Limnias* Schrank, 1803

Type species. *Limnias ceratophylli* Schrank, 1803

Diagnosis. Elongate body (head, trunk, foot), sessile adults inhabiting a distinct tube in the shape of a pipe (Fig. 1). Juveniles (larvae) are free-swimming. Tube base often begins as a short, nearly featureless, hyaline (clear), plain cylinder, that abruptly changes above; tube widens from the base to the top (~2x base diameter). Tubes either straight, curved, or twisted, constructed with either annulated rings cemented on top of one another or as a continuous granular (stucco) matrix, sometimes with transverse rows of minute raised apices (points), with or without adhering debris, including sand grains. Adult tube length varies from ~400 to ≥1500 µm. Corona with one pair of distinct lateral lobes, each slightly wider than tall, with a ventral depression (concave sinus) usually present, either slight or strong: i.e., providing an illusion of a lemniscate (∞). A dorsal gap of varying width is apparently present in all species. Dorsal antenna short; ventral antennae short or long. Some species possess short nodules (protuberances) located anteriorly just beneath the corona on the dorsal side (n = 0–14). Foot long, peduncle absent, but a short adhesive disc may be present at its base.

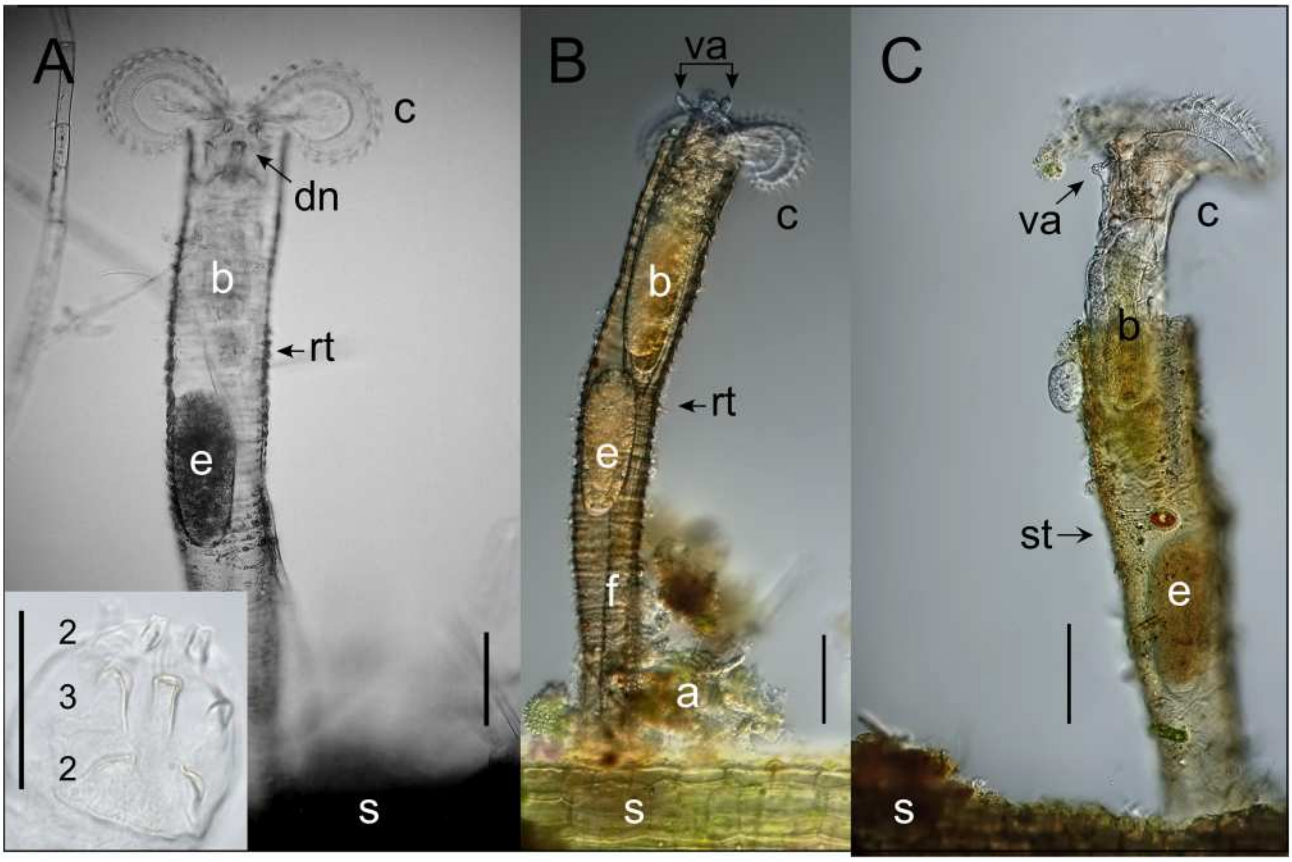

FIGURE 1. Representative morphology of two species of *Limnias*. (A) *Limnias melicerta* in ventral view. (NB: Ventral antennae on the opposite side obscured.) Inset: Region of dorsal nodules: (3 rows: 2,3,2). (B) *L. melicerta* in 3/4th ventral view. (C) *Limnias ceratophylli* in 3/4th ventral view. Symbols: a = algae and debris; b = adult body; c = corona; dn = dorsal nodules; e = amictic embryo; f = foot; rt = ringed tube; s = substratum; st = stucco-like tube (with adhering epiphytes and debris); va = ventral antennae; bars ~100 µm. (Photomicrographs B and C are courtesy of Michael Plewka.)

With one exception all populations that have been reported are sessile, solitary, occasionally forming small branching colonies of up to ~30 individuals. Larvae possess two red eyespots, lost in adults. Amictic reproduction is oviparous, oldest embryos most proximal to tube base. Males poorly described in one species. Diapausing embryos undescribed.

Trophi malleoramate: rami slightly asymmetrical; major teeth on unci reported as 3/3 or 4/4.

Comments. The etymon of this genus (L., *limnos*, lake) is an allusion to the general habitat of these animals. Two species groups are recognized based on tube structure: *L. ceratophylli* and *L. melicerta* (Koste 1978).

Enumeration of the dorsal nodules is from the anterior to the posterior. While they may be seen while the animal is feeding, determining their number, position, and shape is best done when the corona is retracted and the animal has been removed from its tube.

Dichotomous key to *Limnias* species

1	Tube annulated: a series of stacked rings (collars or girdles), often transparent, sometimes slightly colored; ventral antennae short or long; dorsal nodules present (4, 7, or 14) (Fig. 1A,B)	2
-	Tube not annulated: stucco-like, often opaque, with a granular matrix or covered with transverse, parallel rows of minute raised apices (points); tube may be coated with debris; ventral antennae short or long; dorsal nodules present or absent. (Fig. 1C)	4
2	Tube greatly curved and/or twisted, rarely straight; length ~400–500 µm; ventral antennae long; dorsal nodules present (n=4, in 2 rows: 2,2) (Fig. 2A)	*L. cornuella*
-	Tube straight or only slightly curved; tube length >500 µm; ventral antennae short; number and pattern of dorsal nodules varies	3
3	Dorsal nodules present (n=7, in 3 rows: 2,3,2) (Fig. 1A,B)	*L. melicerta*
-	Dorsal nodules present (n=14, in 3 rows (6,6,2) (Fig. 2B)	*L. nymphaea*
4	Ventral antennae short; dorsal nodules absent (Fig. 1C)	*L. ceratophylli*
-	Ventral antennae long; dorsal nodules present	5
5	Tube slightly curved; dorsal nodules present (n=2) (Fig. 3A)	*L. myriophylli*
-	Tube straight, surface covered with transverse, parallel rows of minute raised apices (points) (Fig. 3B); dorsal nodules present (n=7, in 4 rows: 1 [bifurcate], 2,2,2)	*L. shiawasseensis*

Formula key to *Limnias* species

1 Tube surface seen as annulated rings (Fig. 1A,B)
2 Tube surface seen as stucco-like (granular), with or without debris (Fig. 1C)
3 Ventral antennae short (Fig. 1B,C)
4 Ventral antennae long (Fig. 2A)
5 Dorsal nodules absent
6 Dorsal nodules (n=2)
7 Dorsal nodules (n=4 in 2 rows: 2,2) (Fig. 2A)
8 Dorsal nodules (n=7 in 3 rows: 2,3,2) (Fig. 1A)
9 Dorsal nodules (n=7 in 4 rows: 1 [bifurcate], 2,2,2)
10 Dorsal nodules (n=14 in 3 rows: 6,6,2) (Fig. 2B)

Species
L. cornuella 1, 4, 7
L. melicerta 1, 3, 8
L. nymphaea 1, 3, 10
L. ceratophylli 2, 3, 5
L. myriophylli 2, 4, 6
L. shiawasseensis 2, 4, 9

Limnias ceratophylli Schrank, 1803
Fig. 1C

Melicerta biloba Ehrenberg, 1832
Limnias socialis Leidy, 1874

Types: None designated
Type locality: Bayern (Germany).
Other material: Specimen Preparation ANSP 793.

Diagnosis. Base of tube straight or slightly curved, clear at base, abruptly changing to stucco-like granular surface to the top; tube may be light to dark brown (opaque), depending on water conditions. Solitary or colonial. Ventral antennae short. Dorsal nodules absent. Dorsal gap in corona less than neck width. Tube length ≤1500 µm. Trophi: unci longest tooth ~14 µm; 3 (4?) pairs of main teeth. Amictic embryos: ca. 257 x 88 µm. Males known; diapausing embryos not described. Considered to have a cosmopolitan distribution.

Measurements: Total length, ≤1500 µm; corona width, 125–183 µm; tube length, ≤800, tube width (at top), ≈80 µm; amictic egg, 40–50 x 100–110 µm. See also Koste (1978). Putative male poorly described by Hudson and Gosse (1886: 76).

Geographic range: Apparently cosmopolitan: Africa (Senegal), Australia, Europe (France, Russia, U.K.), North America (Canada, U.S.A., Mexico), South America (Brazil, Ecuador, Panama), Thailand.

Ecology: pH, 6–9.6; bicarbonate, 7.3–396 mg/L, conductivity, 77–663 µS/cm^2, temperature, 13–30 °C; colonizes inert materials (glass and stones), submerged logs, algae, aquatic moss (*Fontinalis*), several vascular hydrophytes, including *Ceratophyllum, Elodea, Myriophyllum, Potamogeton, Ranunculus, Utricularia*), and an animal (crocodile) (Edmondson 1944; Koste 1978; Magnusson 1985; Meksuwan *et al*. 2011; Nilsen and Larimore 1973; Sarma *et al*. 2017; Tiefenbacher 1972; pers. obs.). It sometimes forms moderately sized allorecruitive colonies, but its propensity to form colonies has not been studied. A planktonic population has been reported (see below).

Comments. The etymon of this genus is apparently a reference to the plant substratum on which Schrank (1803) found specimens. See Koste (1978) for additional synonyms. Tiefenbacher (1972) reported that he did not see the periodical production of tube material, as in the way that *Limnias melicerta* deposits its tube in rings (Wright 1954), and that colony formation occurred at high population levels.

Four curious habitats have been reported for *L. ceratophylli*: three sessile and one planktonic. (1) Leidy (1874) reported a population attached to stones in an undefined region of the Schuylkill River (Philadelphia, Pennsylvania, U.S.A.) where colonies of up to 50 individuals occurred. (2) Nilsen and Larimore (1973) reported population densities reaching 17 inds/cm^2 on submerged, bark-less logs. (3) Magnusson (1985) noted *L. ceratophylli* to be an epizootic on an Amazonian crocodile. (4) Although *L. ceratophylli* has always been considered to be sessile, Beach (1960) reported abundant planktonic populations in two lakes out of approximately 25 lotic and lentic habitats examined in the Ocqueoc River system, Presque Isle Co. (Michigan, U.S.A.). Regrettably Beach did not state whether he examine hydrophytes for sessile individuals, but he implied that: *L. ceratophylli* "… was always present and always free-swimming." In one lake the mean population level over three summers was ~900 inds/L. Beach suggested that his findings of *L. ceratophylli* as an "adventitiously planktonic" was not from the animals being dislodged from their sessile attachment by water movements, but rather that local factors of lake morphology and water chemistry accounted for this unusual condition. Unfortunately, no drawings or photomicrographs were provided to substantiate these observations. Without that level of documentation the possibility remains that Beach was mistaken and that the organisms he observed were tintinnids or another small, encapsulated planktonic organism. However, apparently Beach was familiar with tintinnids, such as *Codonella* sp., which he reported being present in the freshwater system he studied. Thus, while his report may be in error, it cannot simply be dismissed.

Limnias cornuella **Rousselet, 1889**
Fig. 2A

Types: None designated

Type locality: Hot-house tank; Gardens of the Royal Botanic Society, Regent's Park (U.K).

Diagnosis. Tube ringed as in *melicerta* species group, smaller (1/2x) in size then either *L. ceratophylli* (≤1500 µm) or *L. melicerta* (≤500 µm); curved or twisted; transparent at base and top and opaque between. Ventral antennae long. Dorsal gap in corona unknown. Koste (1978) reports dorsal nodules as either 4 or 10.

Comments. The etymon of this species (L., *cornu*, horn + L., *ella*, diminutive) is in reference to the shape of the tube. Trophi: no available information. Amictic, male, and diapausing embryos undescribed. Apparently this species has not been reported since the original description of Rousselet (1889). Placed as a subspecific taxon within the *L. melicerta* species group by Koste (1978). Although this species was presented as *species inquirenda* by Segers (2007), it may be distinguished from other members of the *L. melicerta* species complex by its long ventral antennae and the number of dorsal nodules (n=4).

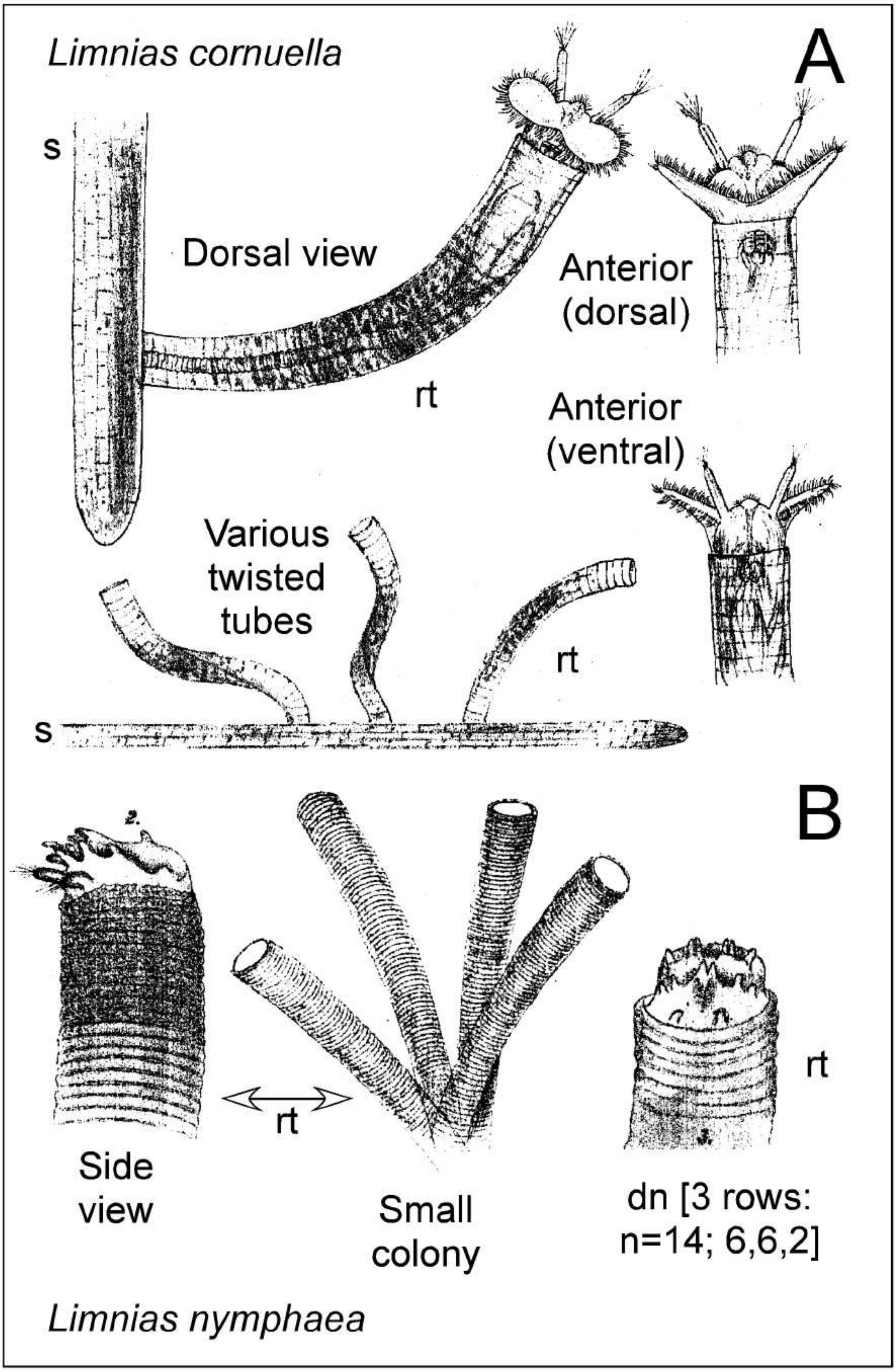

FIGURE 2. Two very rare *Limnias* species, each of which has been reported only once. (A) *Limnias cornuella* (Line art of four figures from Rousselet, 1889); (B) *Limnias nymphaea* (Line art of three figures from Stenroos, 1898). Symbols: dn = dorsal nodules; rt = ring tube; s = substratum.

***Limnias melicerta* Weisse, 1848**
Figs 1A,B; 4C

Cephalosiphon limnias Ehrenberg, 1853
Limnias corniculata Ehrenberg, 1853
Limnias annulatus Bailey, 1855; name amended to *annulata* to agree with feminine genus name
Limnias doliolum Schoch, 1868
Melicerta cubitti Cubitt, 1871; text refers to *M. annulata*, but plate 98 labels as *M. cubitti*
Limnias granulosa Weber, 1888
Limnias melicerta melicerta: Koste, 1978

Types: None designated

Type locality: Afrossimov Estate, St. Petersburg, Russia.

Other material: Specimen Preparation ANSP 1527.

Diagnosis. Base of tube clear, switching abruptly to a series of clear, stacked rings. Ventral antennae short; dorsal nodules present (n = 7 in 3 rows: 2,3,2). Dorsal gap in corona ciliation approximately equal to neck width. Trophi: rami asymmetrical; uncus with 3 strong main teeth.

Measurements: Total body length, ≤1550 µm; corona width, 160 µm; height, 70 µm; tube width (at top), ≈100 µm; amictic egg, 130–242 x 40–98 µm. See also Koste (1978).

Geographic range: Apparently cosmopolitan: Africa (Democratic Republic of the Congo), Australia, Europe (France, Germany, Ireland, Russia, U.K.), India, North America (Canada, U.S.A., Mexico), South America (Brazil, Ecuador), Thailand.

Ecology: pH, 4.1–8.9; bicarbonate, 57–305 mg/L; calcium, 5–38 mg/L; magnesium, ≤20 mg/L, conductivity, 81–686 µS/cm^2, temperature, 18–32 °C; colonizes a wide variety of substrata such as glass, charophyte algae (*Chara*, *Nitella*), aquatic mosses (*Fontinalis*, *Sphagnum*), and vascular hydrophytes including *Ceratophyllum*, *Elodea*, *Eriocaulon*, *Lemna*, *Ludwigia*, *Myriophyllum*, *Nuphar*, *Nymphaea*, *Potamogeton*, *Ranunculus*, and *Utricularia* (Bailey 1855; Francez 1984b; Kellicott 1888; Koste, 1978; Sarma *et al*. 2017; Wallace 1977; Yang & Hochberg 2018; pers. obs.). Edmondson (1944) suggests that flat surfaces provide suitable substrata.

Comments. The etymon of this species (G., *meli*, honey + G., *keras*, horn) is apparently in reference to the color that the tube of this species may take. Male and diapausing embryos undescribed. Construction of the ringed tube (rings ~5-10 µm in height) is by an elaborate behavior of the animal (Wright 1954).

***Limnias myriophylli* (Tatem, 1868)**
Fig. 3A

Limnioides myriophylli Tatem, 1868
Limnias myriophylli (Tatem): Western, 1891

Types: None designated.

Type locality: No locality indicated.

Diagnosis. Tube straight to slightly curved; base clear, abruptly changing to obscure to which debris adheres. Dorsal gap in corona slightly less than neck width. Ventral antennae long. Dorsal nodules present (n=2). Amictic, male, and diapausing embryos undescribed.

Measurements: Tube length ~340 µm; extended animal ~460 µm.

Comments. The etymon of this genus was not discussed by Tatem (1868). No type location is reported by Tatem (1868). Western (1891) discussed problems with Tatem's descriptions, offering the conclusion that the species Tatem described was a *Limnias* rather than a representative of the genus *Limnioides*. However, Western's record of *Limnias myriophylli* from an undefined location in Oxshott, U.K. is most likely erroneous.

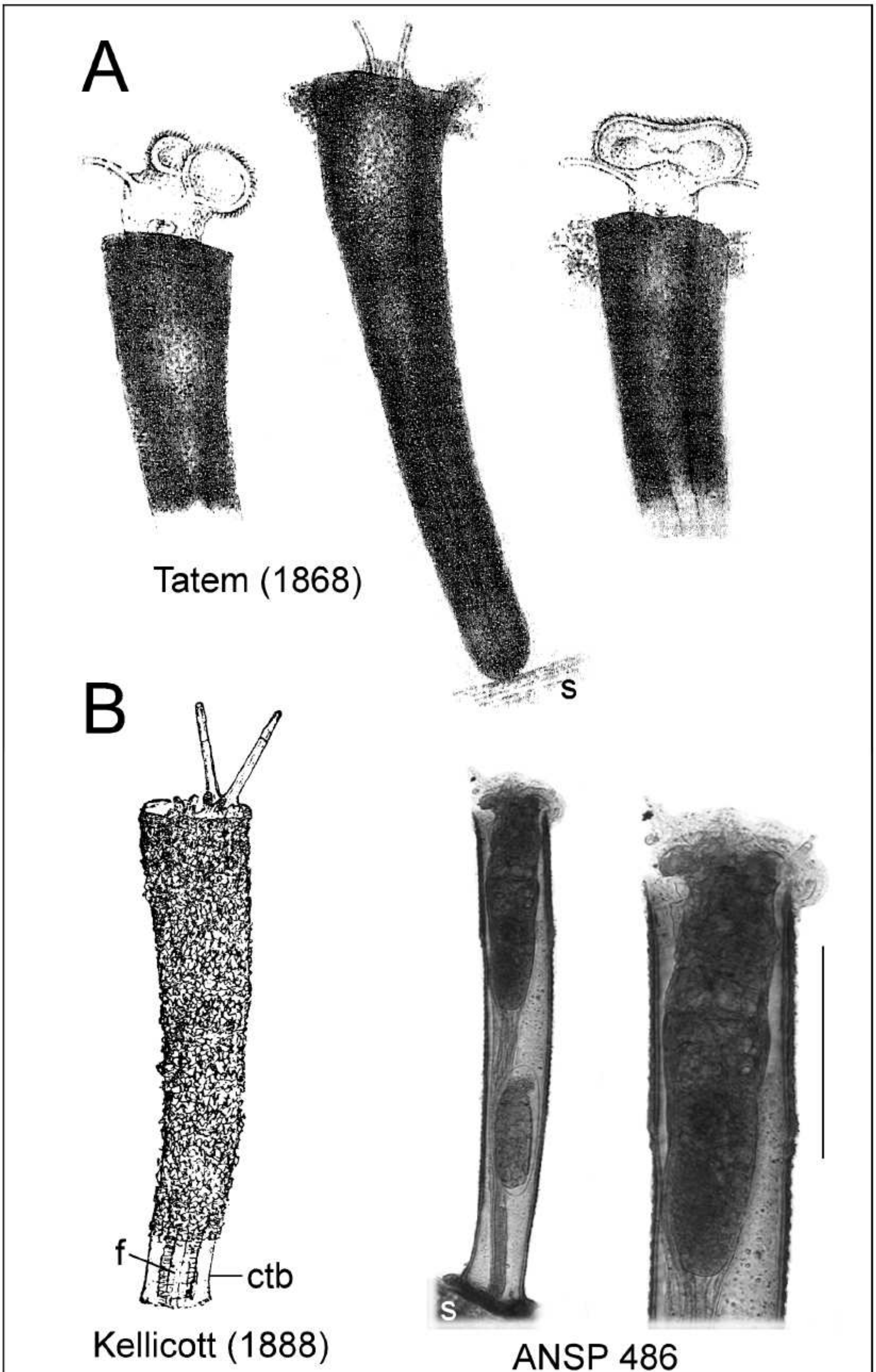

FIGURE 3. Two rare *Limnias* species. (A) *Limnias myriophylli*. (B) *Limnias shiawasseensis* (Line art as indicated; photomicrograph of Specimen Preparation ANSP 486 [collected by C.F. Rousselet] courtesy of C. Jersabek; The Academy of Natural Sciences of Drexel University). Symbols: ctb = clear tube base; f = foot; s = substratum; bar = 100 µm.

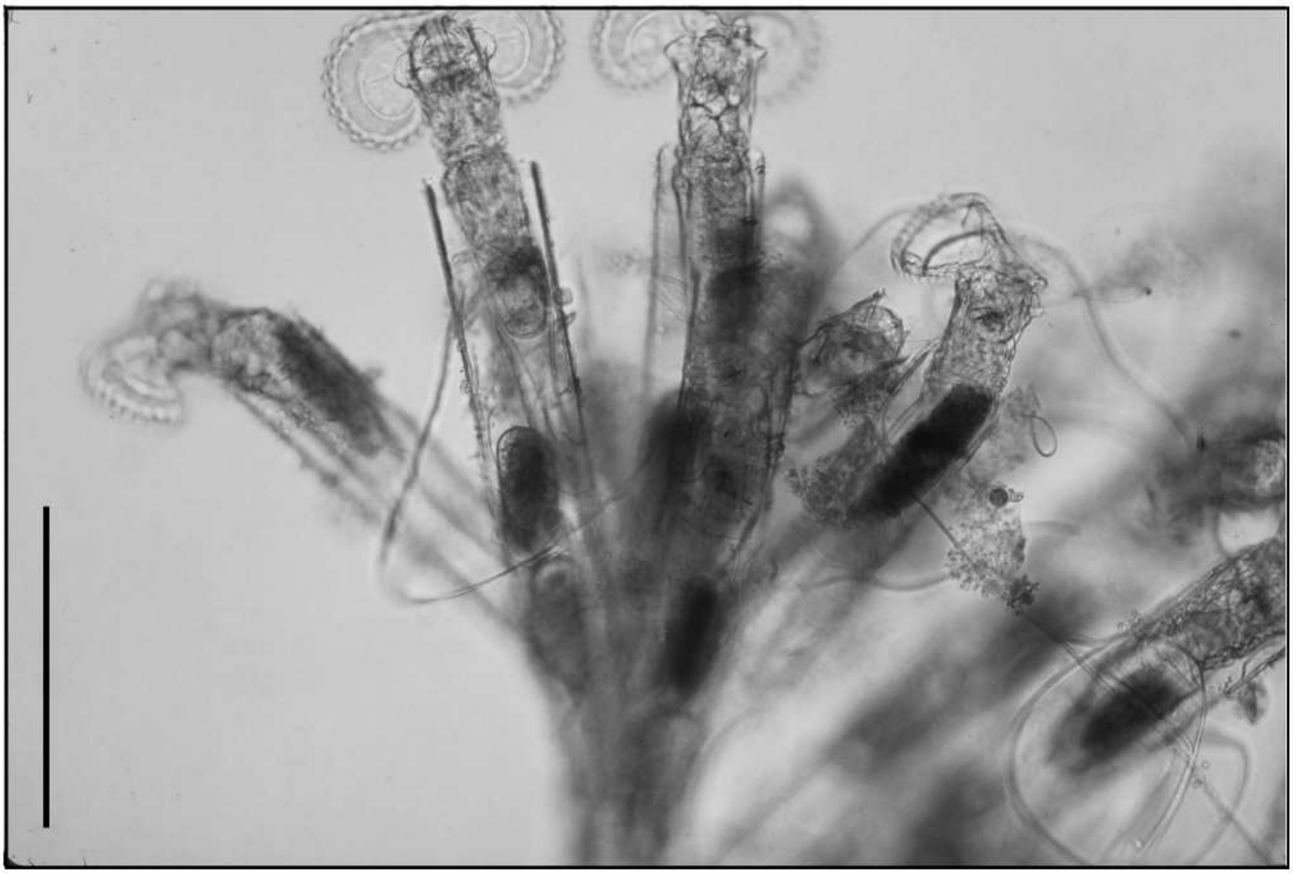

FIGURE 4. Coloniality in *Limnias*. Bar = 500 µm.

***Limnias nymphaea* Stenroos, 1898**
Fig. 2B

Limnias melicerta nymphae: Koste, 1978

Types: None designated.

Type locality: Lake Nurmijärvi (Finland).

Diagnosis. Tube dark gray, set with grains of sand. Ventral antennae short. Dorsal gap in corona unknown. Dorsal nodules present (n = 14 in 3 rows: 6,6,2).

Measurements: Total tube length 510–650 µm.

Comments. The etymon of this genus is apparently a reference to the plant substratum, *Nuphar*-Blätte (sic), on which Stenroos (1898) found specimens. Amictic, male, and diapausing embryos undescribed. This species was described from a single occurrence on the leaves of *Nuphar* sp. in Lake Nurmijärvi (Finland). Koste (1978) states that this species may be a form of *L. melicerta*.

***Limnias shiawasseensis* Kellicott, 1888**
Fig. 3B

Limnias Shiawasseënsis Kellicott, 1888
Limnias shiawasseensis Kellicott: Hudson & Gosse, 1889
Limnias shiawasseensis Kellicott: Harring, 1913
Limnias melicerta shiawasseensis Kellicott: Koste, 1978

Types: None designated.

Type locality: Shiawassee River, Shiawassee Co., Michigan, (U.S.A.).

Other material: Specimen Preparation ANSP 486

Diagnosis. Tube surface covered by transverse, parallel rows of tiny raised points. Ventral antennae long. Dorsal nodules n = 7 in 4 rows: 1 [bifurcate], 2,2,2). Dorsal gap present, undefined. Amictic, male, and diapausing embryos undescribed.

Measurements: None reported.

Geographic range: Very rare: Scotland (U.K.), Florida, and Michigan (U.S.A.).

Ecology: pH, 6.9–7.6; bicarbonate, 21.4–38.4 mg/L. Sessile on *Myriophyllum* and *Ranunculus*.

Comments. The etymon of this species refers to its poorly defined type location "… at the border of the …" Shiawassee River, Shiawassee Co. (Michigan, U.S.A.). Edmondson (1944) reported this species from a lake in Connecticut (U.S.A.); Ahlstrom (1934) listed this species as present in Florida (U.S.A.). Additionally, there is a mounted adult specimen (collected by C.F. Rousselet (1912.08.07), pond near Glasgow, Scotland and prepared by L. M. Dorsey: see Other material, above).

Kellicott's (1888) description offers ratios of certain features, but no dimensions are provided. To our knowledge the seven dorsal nodules have never been illustrated adequately. The original description of this species notes that specimens were found attached to *Myriophyllum* along with two congeners *L. ceratophylli* and *L. melicerta*, both of which were more common. Edmondson (1944) notes the occurrence of this species on hydrophytes that had the characteristics of "… predominantly flat or very gently convex leaves, whether finely divided or not" and certain other species that did not fit this categorization (e.g., *Ranunculus*). Kellicott (1888) noted two interesting behaviors. (1) The animals are said to pack flocculent debris against the rugose tube wall. Except for the placement of formed debris pellets in some *Floscularia* and fecal pellets in some *Ptygura,* no other sessile species actively augments their tubes. (2) The coronal discs are held in a near vertical position with the ventral antennae held at a sharp angle to the tube.

An additional taxon, *Limnias sphagnicola* Zacharias, 1886 has not been included in the present treatment of the genus as it is considered an unrecognizable *species inquirenda* (Segers 2007; Jersabek & Leitner 2013). In addition the name is included on the list of names to be removed from zoological nomenclature in the candidate part Phylum Rotifera of the List of Available Names in Zoology (see Segers *et al.* 2012).

Discussion

While the six species of *Limnias* can be recognized by morphological characteristics, much of their morphology, life history, and genetics remain unresolved.

Morphological features that need to be examined include the following. (1) Tube: Within the two species groups tube morphology is distinctive, with some interesting variations. In *L. melicerta*, tube length is increased by a series of discrete rings formed by the animal, one ring on top of another (Wright 1954; Yang & Hochberg 2018). Except for Kutikova's (1995) description of the early development of the tube ($\leq$7 hrs), no detailed analysis of tube construction in members of the *L. ceratophylli* species group has been reported. In *L. shiawasseensis*, the outer surface of the tube is covered with a transverse series of minute raised apices (points) that become coated with dark colored debris by a curious behavior (see below). The outer surface of the tube of *L. nymphaea* is embedded with minute particles of sand, but how that happens has not been determined. In some forms, the tube is slightly curved (*L. melicerta*) or even twisted (*L. cornuella*) (Fig. 4). (2) Corona: The presence and size of a dorsal gap in the corona has not been quantified among the six species. (3) Dorsal nodules: The number, position, and shape of the dorsal nodules, as well as their variability within each of the six morphospecies should be confirmed. (4) Ventral antennae: Variation in length of the ventral antennae across species needs to be examined. (5) Trophi: Details of the morphology of trophi in the species complexes need to be examined using SEM technologies (De Smet 1998; Kleinow *et al.* 1990) in combination with geometric morphometric analyses (Fontaneto *et al.* 2007; Fontaneto *et al.* 2004). (6) Embryos: No information regarding the size, shape, or surface characteristics of these embryos is available. (7) Larvae: No morphological analysis of the larvae of the six species has been undertaken (cf. Kutikova 1995). (8) Males: Details of male morphology is lacking. (9) Diapausing egg: No details of the surface morphology using either light microscopy or SEM techniques are available.

Life history features in need of resolution include the following. (1) Colony formation: Allorecruitive colony formation in seen in both species groups, including formation of both interspecific and interspecific colonies (Meksuwan *et al*. 2011; Wallace *et al*. 2015), and is probably a function of population density (Tiefenbacher 1972). However, we do not know the extent of colony formation in *Limnias* (Fig. 4). (2) Substratum selection: While some species of rotifer appear to exhibit strong specificities for a substratum to which larvae attach (Wallace 1978; Wallace & Edmondson 1986) or on which they attach their embryos (Walsh 1989), we know little about substrata preference for any species of *Limnias*. Of the six species, two (*L. ceratophylli* and *L. melicerta*) have been frequently reported to settle on a range of substrata (Francez 1984a, 1984b; Leidy 1874; Nilsen & Larimore 1973; Segers *et al*. 2010; Tiefenbacher 1972; Wallace 1977). *Limnias myriophylli* and *L. shiawasseensis* each have been reported twice, but only on *Myriophyllum*. The other two species, *L. cornuella* and *L. nymphaea*, have been reported to occur on *Trianoe Bogotensis* (sic) and *Nuphar* sp., respectively. In a 30-km^2 lake in Thailand, Meksuwan *et al*. (2011) found *L. ceratophylli* on 10 different substrata and *L. melicerta* on 12. Based on these limited records, we cannot be sure whether *Limnias* species possess little preference for substrata or that specificity or lack of specificity is an artifact of infrequent reporting. Alternatively, perceived preferences may be a result of identifying all specimens only by the general morphology of their tube: i.e., stucco = *L. ceratophylli* and ringed = *L. melicerta*. Additionally, we do not understand the edaphic conditions by which a substantial planktonic population might develop as reported for *L. ceratophylli* by Beach (1960). Unfortunately, it is not clear whether Beach examined hydrophytes for sessile rotifers in that study, and the possibility of misidentification is possible (see above). (3) Adult behaviors: Kellicott (1888) attributed an unusual behavior to the adults of *L. shiawasseensis*: use of its dorsal processes to pack the outer surface of its tube with floccose material. Hudson and Gosse (1886: 76) also report this behavior. Few sessile species are known to exhibit a behavior that incorporates exogenous materials into their tubes: e.g., *Floscularia ringens* (Linnaeus, 1758), *Ptygura pilula* (Cubitt, 1872). (4) Mating: If sexual individuals from various taxa were produced simultaneously, cross-mating experiments could be performed to delineate species boundaries. (The protocol for culturing *Limnias* species described by Sarma *et al*. (2017) will be useful.) However, cues that induce mixis are unknown. During four years of laboratory culture using crowding, as well as a variety of temperature and photoperiods, we were unable to induce mixis in either *L. ceratophylli* or *L. melicerta* (A.K. and E.J.W, pers. obs.).

Use of molecular tools has revealed hidden diversity (cryptic species complexes) within many taxa of rotifer (Fontaneto 2014; Fontaneto *et al*. 2009) including *Brachionus calyciflorus* Pallas, 1766 (Wen *et al*. 2016), *Brachionus plicatilis,* Müller, 1786 (Gómez *et al*. 2002; Gribble & Mark Welch 2012; Mills *et al.* 2017), and *Euchlanis dilatata* Ehrenberg, 1830 (Kordbacheh *et al.* 2017). Although morphological differences in some of these taxa were recognized prior to the use of molecular techniques, the extent of the diversity was difficult to appreciate applying morphological criteria alone (Fu *et al.* 1991; Segers 1995). In other taxa similar diversity was suspected, which was subsequently confirmed (e.g., Reyna-Fabián *et al.* 2010; Schröder & Walsh 2010). To date these studies have included only planktonic forms. To appreciate the extent of sessile rotifer genetic diversity, we have undertaken an analysis of cryptic species in two species of *Limnias*, as well as other species, which we will report elsewhere.

Acknowledgments

We thank H. Segers and the anonymous reviewers for their careful review of the manuscript. We also thank Michael Plewka for allowing us to use his photomicrographs of *Limnias ceratophylli* and *L. melicerta*. Funding was provided by the National Science Foundation DEB-1257068 (E.J. Walsh) and DEB-1257116 (R.L. Wallace) and by grant 5G12MD007592 from the National Institutes on Minority Health and Health Disparities (NIMHD), a component of the National Institutes of Health (NIH). The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health or the National Science Foundation.

Literature cited

Ahlstrom, E.H. (1934) Rotatoria of Florida. *Transactions of the American Microscopical Society*, 53 (3), 251–266.

https://doi.org/10.2307/3222102
Bailey, J.W. (1855) Notes on new species and localities of microscopical organisms. *Smithsonian contributions to knowledge*, 7 (Ar. III), 3, 1–16.
Beach, N.W. (1960) A study of the planktonic rotifers of the Ocqueoc River system, Presque Isle County, Michigan. *Ecological Monographs*, 30 (4), 339–358.
https://doi.org/10.2307/1948432
Delbecque, E.J.P. & Suykerbuyk, R.E.M. (1988) A comparison of the periphyton of *Nuphar lutea* and *Nymphaea alba*. Spatial and temporal changes in the occurrence of sessile microfauna. *Archiv für Hydrobiologie*, 112 (4), 541–566.
De Smet, W.H. (1998) Preparation of rotifer trophi for light and scanning electron microscopy. *Hydrobiologia*, 387/388, 117–121.
https://doi.org/10.1023/A:1017053518665
Edmondson, W.T. (1944) Ecological studies of sessile Rotatoria, Part I. Factors affecting distribution. *Ecological Monographs*, 14 (1), 32–66.
https://doi.org/10.2307/1961631
Fontaneto, D. (2014) Molecular phylogenies as a tool to understand diversity in rotifers. *International Review of Hydrobiology*, 99 (1–2), 178–187.
https://doi.org/10.1002/iroh.201301719
Fontaneto, D., Giordani, I., Melone, G. & Serra, M. (2007) Disentangling the morphological stasis in two rotifer species of the *Brachionus plicatilis* species complex. *Hydrobiologia*, 583 (1), 297–307.
https://doi.org/10.1007/s10750-007-0573-1
Fontaneto, D., Kaya, M., Herniou, E.A. & Barraclough, T.G. (2009) Extreme levels of hidden diversity in microscopic animals (Rotifera) revealed by DNA taxonomy. *Molecular Phylogenetics and Evolution*, 53 (1), 182–189.
https://doi.org/10.1016/j.ympev.2009.04.011
Fontaneto, D., Melone, G. & Cardini, A. (2004) Shape diversity in the trophi of different species of *Rotaria* (Rotifera, Bdelloidea): a geometric morphometric study. *Italian Journal of Zoology*, 71 (1), 63–72.
https://doi.org/10.1080/11250000409356552
Francez, A.-J. (1984a) Écologie des peuplements de rotifères sessiles des lac-tourbières D'Auvergne (France). *Bulletin d' Écologie*, 15 (4), 231–237. [in French]
Francez, A.-J. (1984b) Rotifères sessiles observés en Auvergne. *Cahiers des Naturalistes*, 40 (3/4), 73–80. [in French]
Fu, Y., Hirayama, K. & Natsukari, Y. (1991) Morphological differences between two types of the rotifer *Brachionus plicatilis* O. F. Müller. *Journal of Experimental Marine Biology and Ecology*, 151 (1), 29–41.
https://doi.org/10.1016/0022-0981(91)90013-M
Gómez, A., Serra, M., Carvalho, G.R. & Lunt, D.H. (2002) Speciation in ancient cryptic species complexes: evidence from the molecular phylogeny of *Brachionus plicatilis* (Rotifera). *Evolution*, 56 (7), 1431–1444.
https://doi.org/10.1111/j.0014-3820.2002.tb01455.x
Gribble, K.E. & Mark Welch, D.B. (2012) The mate recognition protein gene mediates reproductive isolation and speciation in the *Brachionus plicatilis* cryptic species complex. *BMC Evolutionary Biology*, 12 (1), 134.
https://doi.org/10.1186/1471-2148-12-134
Hlava, S. (1908) Böhmens Rädertiere. Monographie der Familie Melicertidae. *Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen*, 13, 1–83. [in German]
Hudson, C.T. & Gosse, P.H. (1886) *The Rotifera; or wheel-animalcules, both British and foreign. Vols. I & II.* Longmans, Green, and Co., London, 41 pp. & 48 pp.
Jersabek, C.D. & Leitner, M.F. (2013) *The Rotifer World Catalog*. World Wide Web electronic publication. Available from: http://www.rotifera.hausdernatur.at/ (accessed 13 March 2018)
Jersabek, C.D., Segers, H. & Dingmann, B.J. (2003) *The Frank J. Myers Rotifer Collection at The Academy of Natural Sciences: The whole collection in digital images. Special Publication 20.* The Academy of Natural Sciences of Philadelphia, Philadelphia. [ISSN 0097-3254, CD-ROM]
Kellicott, D.S. (1888) Partial list of Rotifera of Shiawassee River at Corunna, Michigan. *Proceedings of the American Society of Microscopists*, 10, 89–96.
https://doi.org/10.2307/3220439
Kleinow, W., Klusemann, J. & Wratil, H. (1990) A gentle method for the preparation of hard parts (trophi) of the mastax of rotifers and scanning electron microscopy of the trophi of *Brachionus plicatilis* (Rotifera). *Zoomorphology*, 109, 329–336.
https://doi.org/10.1007/BF00803573
Kordbacheh, A., Garbalena, G. & Walsh, E.J. (2017) Population structure and cryptic species in the cosmopolitan rotifer *Euchlanis dilatata*. *Zoological Journal of the Linnean Society*, 20 (4), 1–21.
https://doi.org/10.1093/zoolinnean/zlx027
Koste, W. (1978) *Rotatoria. Die Rädertiere Mitteleuropas begründet von Max Voigt. I. Textband*. Gebrüder Borntraeger, Stuttgart, 673 pp. [in German]
Leidy, J. (1874) Notes of some fresh water infusoria. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 26 (2), 140.
Kutikova, L.A. (1995) Larval metamorphosis in sessile rotifers. *Hydrobiologia*, 313/314 (1), 133–138.
https://doi.org/10.1007/BF00025942
Magnusson, W.E. (1985) Habitat selection, parasites and injuries in Amazonian crocodilians. *Amazoniana*, 9 (2), 193–204.

Meksuwan, P., Pholpunthin, P. & Segers, H. (2011) Diversity of sessile rotifers (Gnesiotrocha, Monogononta, Rotifera) in Thale Noi Lake, Thailand. *Zootaxa*, 2997, 1–18.

Mills, S., Alcántara-Rodríguez, J.A., Ciros-Pérez, J., Gómez, A., Hagiwara, A., Galindo, K.H., Jersabek, C.D., Malekzadeh-Viayeh, R., Leasi, F., Lee, J.-S., Mark Welch, D.B. Papakostas, S., Riss, S., Segers, H., Serra, M., Shiel, R., Smolak, R., Snell, T.W., Stelzer, C.-P., Tang, C.Q., Wallace, R.L., Fontaneto, D. & Walsh, E.J. (2017) Fifteen species in one: deciphering the *Brachionus plicatilis* species complex (Rotifera, Monogononta) through DNA taxonomy. *Hydrobiologia*, 796 (1), 39–58.
https://doi.org/10.1007/s10750-016-2725-7

Nilsen, H.C. & Larimore, R.W. (1973) Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois. *Ecology*, 54 (2), 366–374.
https://doi.org/10.2307/1934344

Reyna-Fabián, M.E., Laclette, J.P., Cummings, M.P. & García-Varela, M. (2010) Validating the systematic position of *Plationus* Segers, Murugan & Dumont, 1993 (Rotifera: Brachionidae) using sequences of the large subunit of the nuclear ribosomal DNA and of cytochrome C oxidase. *Hydrobiologia*, 644 (1), 361–370.
https://doi.org/10.1007/s10750-010-0203-1

Rousselet, C. (1889) Note on a new rotifer, "*Limnias cornuella.*" *Journal of the Quekett Microscopical Club*, Series 2, 3, 337–338.
https://doi.org/10.5962/bhl.part.2077

Sarma, S.S.S., Jiménez-Santos, M.A., Nandini, S. & Wallace, R.L. (2017) Demography of the sessile rotifers, *Limnias ceratophylli* and *Limnias melicerta* (Rotifera: Gnesiotrocha), in relation to food (*Chlorella vulgaris* Beijerinck, 1890) density. *Hydrobiologia*, 796 (1), 181–189.
https://doi.org/10.1007/s10750-017-3184-5

Schröder, T. & Walsh, E.J. (2010) Genetic differentiation, behavioural reproductive isolation and mixis cues in three sibling species of monogonont rotifers. *Freshwater Biology*, 55 (12), 2570–2584.
https://doi.org/10.1111/j.1365-2427.2010.02487.x

Schrank, F. (1803) Fauna Boica. Durchgedachte Geschichte der in Baiern einheimischen und zahmen Thiere. Dritten und lezten Bandes zweyte Abtheilung. *Fauna Boica*, 3/2, 1–372. [in German]

Segers, H. (1995) Nomenclatural consequences of some recent studies on *Brachionus plicatilis* (Rotifera, Brachionidae). *Hydrobiologia*, 313/314, 121–122.
https://doi.org/10.1007/978-94-009-1583-1_15

Segers, H. (2007) Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. *Zootaxa*, 1564, 1–104.

Segers, H., De Smet, W.H., Fischer, C., Fontaneto, D., Michaloudi, E., Wallace, R.L. & Jersabek, C.D. (2012) Towards a list of available names in zoology, partim phylum Rotifera. *Zootaxa*, 3179, 61–68.

Segers, H., Meksuwan, P. & Sanoamuang, L.-o. (2010) New records of sessile rotifers (Phylum Rotifera: Flosculariacea, Collothecacea) from Southeast Asia. *Belgian Journal of Zoology*, 140 (2), 235–240.

Stenroos, K.E. (1898) Das Thierleben im Nurmijärvi-See. *Acta Societatis pro Fauna et Flora Fennica*, 17, 1–259. [in German]

Tatem, J.G. (1868) On a new melicertian and some varieties of *Melicerta ringens. The Journal of the Quekett Microscopical Club*, 1, 124–125.
https://doi.org/10.5962/bhl.part.3580

Tiefenbacher, L. (1972) Beträge zur Biologie und Ökologie sessiler Rotatorien unter besonder Berücksichtigung des Gehäusebaues und der Regenerationsfähigkeit. *Archiv für Hydrobiologie*, 71 (1), 31–78. [in German]

Wallace, R.L. (1977) Distribution of sessile rotifers in an acid bog pond. *Archiv für Hydrobiologie*, 79 (4), 478–505.

Wallace, R.L. (1978) Substrate selection by larvae of the sessile rotifer *Ptygura beauchampi*. *Ecology*, 59 (2), 221–227.
https://doi.org/10.2307/1936366

Wallace, R.L. & Edmondson, W.T. (1986) Mechanism and adaptive significance of substrate selection by a sessile rotifer. *Ecology*, 67 (2), 314–323.
https://doi.org/10.2307/1938575

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, MA, pp. 225–271.
https://doi.org/10.1016/B978-0-12-385026-3.00013-9

Walsh, E.J. (1989) Oviposition behavior of the littoral rotifer *Euchlanis dilatata*. *Hydrobiologia*, 186/187 (1), 157–161.
https://doi.org/10.1007/BF00048908

Wen, X., Xi, Y., Zhang, G., Xue, Y. & Xiang, X. (2016) Coexistence of cryptic *Brachionus calyciflorus* (Rotifera) species: roles of environmental variables. *Journal of Plankton Research*, 38 (3), 478–489.
https://doi.org/10.1093/plankt/fbw006

Western, G. (1891) Notes on rotifers. *Journal of the Quekett Microscopical Club*, Series 2, 4, 320–322.

Wright, H.G.S. (1954) The ringed tube of *Limnias melicerta* Weisse. *Microscopy*, 10, 13–19.

Yang, H. & Hochberg, R. (2018) Ultrastructure of the extracorporeal tube and "cement glands" in the sessile rotifer *Limnias melicerta* (Rotifera: Gnesiotrocha). *Zoomorphology*, 137 (1), 1–12.
https://doi.org/10.1007/s00435-017-0371-x