



## ***Erugomicula*, a new genus of Arcellinida (testate lobose amoebae)**

**Nawaf A. Nasser, Braden R.B. Gregory, David Singer,  
R. Timothy Patterson, and Helen M. Roe**

### **ABSTRACT**

Testate lobose amoebae of the order Arcellinida are a diverse, cosmopolitan group of shelled protists found in many environments, including freshwater habitats, peatlands, and soils. Their decay-resistant tests make them an important fossil group for reconstructing Quaternary environments. Within the family Diffugiidae Stein, 1859 more than 300 species and 200 sub-species have been attributed to the genus *Diffugia* Leclerc, 1815. Although carried out on only a few taxa, molecular evidence has demonstrated that test morphology is more important than test composition in categorizing distinct taxa within the Arcellinida. The type species of *Diffugia*, *D. proteiformis* Lamarck, 1816, is characterized by a terminal aperture and an elongate acuminate test. The morphology of *D. proteiformis* is vastly different from most species assigned to *Diffugia*, explaining its polyphyletic status. We reclassify *Diffugia bidens* Penard, 1902 as type species of *Erugomicula*, a new genus within the Diffugiidae, which is distinguished from other taxa within *Diffugia* by its broad, ovoid test, and distinct compression. Based on the compressed morphology of the test, which is not a characteristic of the Diffugiidae, we tentatively assign *Erugomicula* to the family Hyalospheniidae.

Nawaf A. Nasser. Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa K1S 5B6, Canada. [nawaf.nasser@carleton.ca](mailto:nawaf.nasser@carleton.ca)

Braden R.B. Gregory. Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa K1S 5B6, Canada. [GregorBRB@gmail.com](mailto:GregorBRB@gmail.com)

David Singer. Department of Zoology, Institute of Biosciences, University of São Paulo, São Paulo, Brazil and Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa K1S 5B6, Canada. [david.singer.bio@outlook.com](mailto:david.singer.bio@outlook.com)

R. Timothy Patterson. Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa K1S 5B6, Canada. [tim.patterson@carleton.ca](mailto:tim.patterson@carleton.ca)

Helen M. Roe. School of Natural and Built Environments, Queen's University Belfast, Belfast, United Kingdom, BT7 1NN. [h.roe@qub.ac.uk](mailto:h.roe@qub.ac.uk)

<https://zoobank.org/4BFD1CBC-4668-4431-A4FB-F0D2468108C9>

Nasser, Nawaf A., Gregory, Braden R.B., Singer, David, Patterson, R. Timothy, and Roe, Helen M. 2021. *Erugomicula*, a new genus of Arcellinida (testate lobose amoebae). *Palaeontologia Electronica*, 24(1):a16. <https://doi.org/10.26879/807> [palaeo-electronica.org/content/2021/3356-erugomicula-a-new-genus-of-arcellinida](https://palaeo-electronica.org/content/2021/3356-erugomicula-a-new-genus-of-arcellinida)

Copyright: April 2021 Paleontological Society.

This is an open access article distributed under the terms of Attribution-NonCommercial-ShareAlike 4.0 International (CC BY-NC-SA 4.0), which permits users to copy and redistribute the material in any medium or format, provided it is not used for commercial purposes and the original author and source are credited, with indications if any changes are made. [creativecommons.org/licenses/by-nc-sa/4.0/](https://creativecommons.org/licenses/by-nc-sa/4.0/)

Keywords: Arcellinida; testate lobose amoebae; Quaternary; new genus

Submission: 24 July 2017. Acceptance: 27 April 2021.

## INTRODUCTION

Arcellinida (testate lobose amoebae) are a diverse cosmopolitan group of shelled amoebae (Medioli et al., 1990). They are abundant in many environments including freshwater habitats (Patterson and Kumar, 2002), peatlands, and soils (Mitchell et al., 2008). Their ability to encase their cellular bodies in a robust and decay resistant test (Swindles and Roe, 2007) make Arcellinida an important fossil group, particularly in Quaternary paleoenvironments (McCarthy et al., 1995; Patterson and Kumar, 2002) and through the Phanerozoic into the Neoproterozoic (Porter and Knoll, 2000). They are important environmental proxies due to their short life spans and high sensitivity to environmental changes; e.g., water quality (Roe et al., 2010), water table fluctuation (Charman et al., 1998), pH variability (Patterson et al., 2013), lake acidity (Kumar and Patterson, 2000), land-use change (Patterson et al., 2002), nutrient loading (Patterson et al., 2012), seasonal environmental changes (Neville et al., 2011; Farooqui et al., 2012), ecosystem health (Neville et al., 2011), road salt contamination (Cockburn et al., 2020), and the impact of metal contaminants (Nasser et al., 2016, 2020).

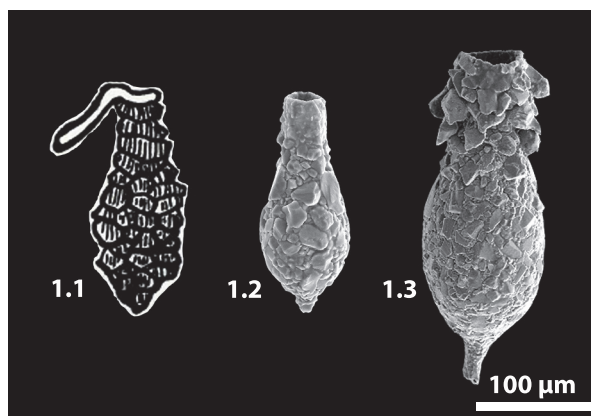
Taxonomic discrimination of arcellinidan taxa at the genus and species level has been variously based on several criteria, including differences in test shape, size (e.g., Bonnet, 1975; Medioli et al., 1987; Beyens and Meisterfeld, 2001) and, to a lesser extent, test composition, and shape and number of nuclei (Penard, 1902; Awerinzew, 1907; Štěpánek, 1952; Ogden and Meisterfeld, 1989; Chardez, 1991). This varied approach, coupled with the considerable morphologic variability observed within some taxa has resulted in the description of many new species with little regard to previous literature, the value of characters used, or even the rules of nomenclature (see discussions in Ogden and Hedley, 1980; Medioli and Scott, 1983; Tolonen, 1986; Medioli et al., 1987; Bobrov et al., 1999; Charman et al., 2000; Mazei and Warren, 2012). Meisterfeld (2000) carried out the last comprehensive taxonomic revision of the Arcellinida, grouping taxa primarily by test wall composition within the arcellinidan family Diffflugidae Stein, 1859. *Diffflugia* Leclerc, 1815 is by far the largest genus, comprised of more than 300 species and

200 subspecies (Leclerc, 1815; Meisterfeld, 2000; Meisterfeld and Mitchell, 2008; Gomaa et al., 2012). Although many of these taxa are legitimate species, the great taxonomic diversity has been partially attributed to inadequate descriptions, type material not being designated or preserved, and/or lack of diagnostic features (Lahr et al., 2008; Mazei and Warren, 2012). In efforts to rationalize the disparate species attributed to *Diffflugia* several researchers have attempted to subdivide *Diffflugia* into smaller, more manageable groups. For example, Medioli and Scott (1983) proposed a possible solution by suggesting that species be considered as widely variable groups that collectively accommodate 75% or more of the morphological variability within the entire population. This approach was refined with the establishment of an informal infra-specific nomenclature, which became known as 'strains' (Medioli et al., 1987; Asioli et al., 1996; Reinhardt et al., 1998). The 'strain' approach came out of the recognition that certain specimen morphologies, not necessarily linked to specific taxa, could be associated with specific environmental stressors, which during multivariate statistical analysis permitted the recognition of subtler environmental subdivision than would be otherwise possible (Patterson et al., 1996; Patterson and Kumar, 2002). In parallel, Gauthier-Lièvre and Thomas (1958), and more recently Mazei and Warren (2012, 2014, 2015), conducted surveys of the genus *Diffflugia* that resulted in the unofficial subdivision of the genus into small subgroups based on test morphology. There have also been more formal efforts to describe new genera based on taxa formerly attributed to *Diffflugia* (e.g., Patterson, 2014; Nasser and Patterson, 2015).

During the last decade, a revolution in the field of molecular research has resulted in this approach being used as a valuable taxonomic tool that has challenged many classical approaches to taxonomy (DeSalle and Goldstein, 2019). For example, molecular studies have been used to discriminate closely related species (Singer et al., 2015, 2019), as well as to improve upon, and correct the taxonomic placement of many iconic testate amoeba species (Duckert et al., 2018). For example, molecular research, albeit on a limited number of taxa, has provided evidence that test morphology closely aligns with natural phylogenetic relationships within

the group (Lahr et al., 2012, 2013, 2019; Kosakyan et al., 2016). Phylogenetic reconstruction using single cell transcriptomic data has also provided evidence that the shape of the test is a key element to determine and characterize the relation between higher taxonomic ranks (Lahr et al., 2019). In an analysis of the SSU rRNA gene in species attributed to the genus *Diffflugia*, Gomaa et al. (2012, 2017) showed that the group is polyphyletic. Other phylogenetic reconstructions based on the NAD9/NAD7 gene have also shown that *Diffflugia* species can be definitively separated in different clades that correspond closely to morphologic features (Macumber et al., 2020). Based on molecular research, several morphologic characters including apertural shape, presence or absence of a neck, test shape (e.g., elongate, compressed, size, girth), test composition, and mixotrophy have been determined to be useful for discriminating separate arcellinidan species and genera (Macumber et al., 2020; Marcisz et al., 2020). These results indicate that a convergence has developed between the morphometric characters used in conventional systematics, and the similar characters recognized to be of systematic importance based on molecular-based approaches (e.g., Marcisz et al., 2020; Steele et al., 2020). This is fortunate considering the relatively few taxa that have been to date analyzed using molecular methodologies.

An important starting point before initiating any taxonomic revision is to consider the underlying taxonomic basis for *Diffflugia*. The type species of the genus is *D. proteiformis* Lamarck, 1816 (lectotype designated by Loeblich Jr. and Tappan, 1964, p. C35, as the specimen illustrated in Lamarck, 1816, pl. 17, figure 5), which is characterized by an acuminate test with a terminal aperture and a fundus tapering to a point (see typical specimens in Figure 1). Morphologically *D. proteiformis* differs significantly from many taxa presently attributed to *Diffflugia*, and thus based on the molecular research described above many species presently attributed to the genus should be split into multiple morphological shape groups at the genus level (Gomaa et al., 2012; Kosakyan et al., 2012, 2016). Unfortunately, molecular sequencing of arcellinidan taxa has proven challenging due to the presence of an obscuring test, resulting in very few species having been sequenced. Therefore, characterizing new genera and species using the conventional methodology remains a fundamental taxonomic tool within the Arcellinida. Until such time as the large number of required barcode and transcriptome analyses have been carried to con-



**FIGURE 1.** Original line drawings and SEM images of *Diffflugia proteiformis* (Penard, 1902). Scale bar equals 100  $\mu\text{m}$ . 1.1, Reproduction of original line drawing of *D. proteiformis* from Lamarck, 1816. 1.2, *D. proteiformis* from lake near Yellowknife, NWT, Canada. 1.3, *D. proteiformis* from Bell's Lake, ON, Canada.

firm relationships of the different species of *Diffflugia* in the tree of life, it seems that traditional approaches to determining phylogenetic relations will continue to play an important role.

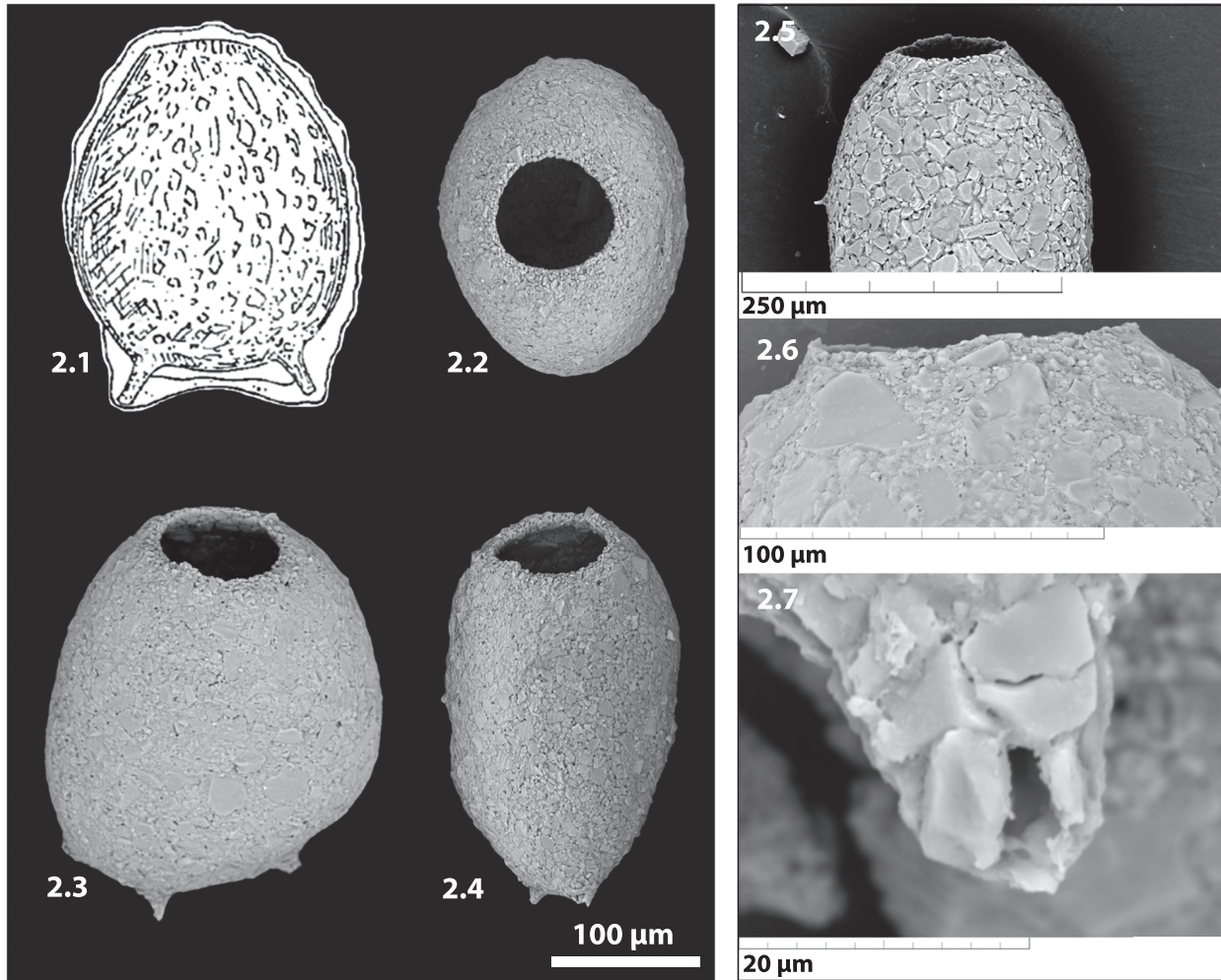
As part of ongoing research to determine the positioning of arcellinidans within lake ecosystems (e.g., Patterson et al., 2013, 2015; Macumber et al., 2014; Nasser et al., 2016, 2020; Roe et al., 2017), we aim to integrate apparent taxonomic relationships into the work, which has resulted in the determination that many taxa, particularly many attributed to *Diffflugia*, require to have their systematic taxonomic placements re-evaluated (e.g., Nasser and Patterson, 2015; Patterson et al., 2015).

*Diffflugia bidens* Penard 1902 is a distinctive arcellinidan taxon characterized by a laterally-compressed, ovoid test, a circular aperture, and it may have a varying number of laterally aligned spines on the fundus (see typical specimens in Figures 2, 3). Aside from both sharing the general arcellinidan characteristics of being unilocular and having an agglutinated test, *D. bidens* bears little similarity to the type species *D. proteiformis*. We therefore propose that *D. bidens* be recognized as the type species of the new genus *Erugomicula* n. gen.

**Institutional abbreviation.** CANA: Canadian Museum of Nature

## SYSTEMATIC PALAEOLOGY

Phylum AMOEBOZOA (Lühe, 1913) Corliss, 1984  
 Class TUBULINEA Smirnov et al., 2005 emend.  
 [Lobosea (Carpenter, 1861) Cavalier-Smith, 1993]



**FIGURE 2.** SEM images of *Erugomicula bidens* showing typical morphology; images 2.1-2.4 are all relative to a 100  $\mu\text{m}$  scale bar. 2.1, Original drawing of *E. bidens* reproduced from Penard, 1902. This specimen has been designated herein as the lectotype for *E. bidens* (Penard 1902). 2.2, Apertural view of *E. bidens* showing circular aperture and lateral compression. 2.3, *E. bidens* showing ovoid shape and three spines in a slightly angled face view. 2.4, Oblique view of *E. bidens* specimen showing lateral compression from side view. 2.5, *E. bidens* specimen showing slightly raised collar around aperture. Scale bar equals 250  $\mu\text{m}$ . 2.6, Enlarged view of *E. bidens* collar. Scale bar equals 100  $\mu\text{m}$ . 2.7, Broken basal process from a *E. bidens* specimen showing that these processes are hollow. Scale bar equals 20  $\mu\text{m}$ .

Subclass NEOLOBOSIA Cavalier-Smith et al.,  
2016

Superorder EULOBOSIA Cavalier-Smith et al.,  
2016

Order ARCELLINIDA Kent, 1880

Family HYALOSPHEIIDAE Schulze 1877

Genus *Erugomicula* n. gen.

zoobank.org/A42A7EB9-B8CC-45E6-867E-2CDBCA038B23

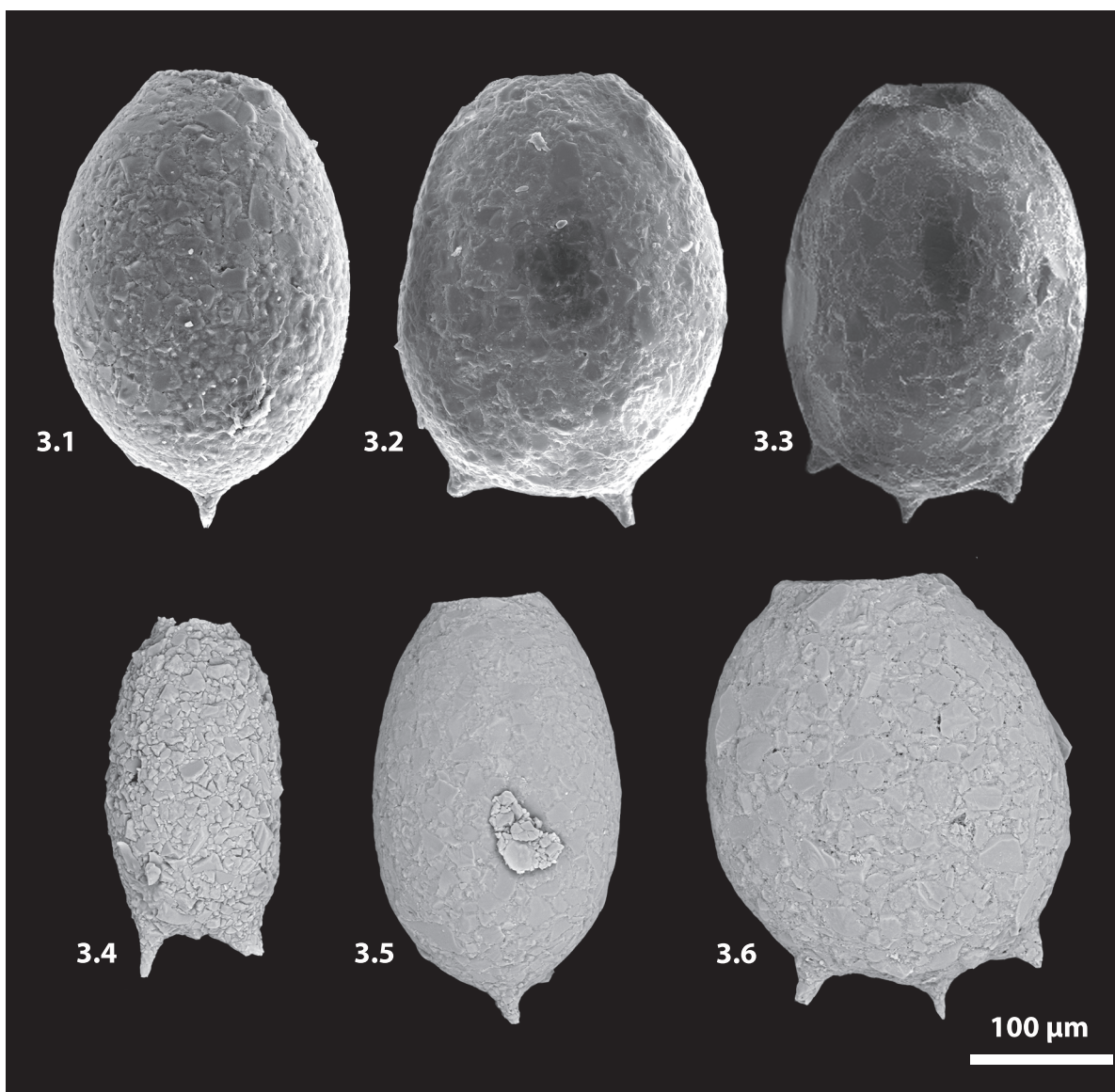
**Type species.** *Diffugia bidens* Penard, 1902, p. 264, figures 1-8 (figure 1 is re-illustrated here as Figure 2.1)

**Diagnosis.** A genus tentatively assigned to the Hyalospheniidae characterized by laterally-com-

pressed, ovoid test, typically comprised of agglutinated particles, but is relatively smooth, generally with short hollow spines (Figure 2.7) oriented along the line of compression on the fundus (Figure 3); aperture round, simple (never slit-like) (Figure 2.2), occasionally with slight raised collar about the aperture (Figure 2.6).

**Description.** Test free, unilocular, wide, and ovoid in face view with a smooth outline (Figure 2.2); compressed in section (Figure 2.3-4); test wall comprised of finely agglutinated xenogenous particles, attached with an organic cement; anterior positioned circular aperture occasionally sur-



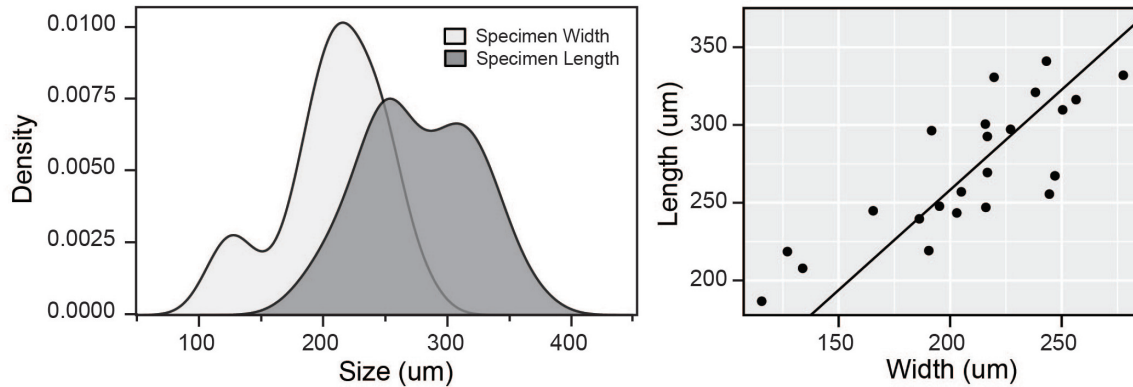


**FIGURE 3.** SEM images of *Erugomicula bidens* specimens from Bell's Lake, ON, Canada, showing morphological variability. Scale bar equals 100 µm. 3.1-3.3, A series of *E. bidens* specimens displaying the varying number of basal processes typical of the species. The number of basal processes present, including specimens with no processes present is highly variable, although morphologies with two basal processes are most common. When present the basal processes are arranged along the fundus. 3.4-3.6, A series of *E. bidens* specimens in side view demonstrating variations in the length-to-width ratio.

rounded by slight raised collar; delicate hollow spines ranging in number from zero to three (two most common), aligned along the line of compression, generally characterize the fundus (Figure 3.1-3).

**Types and occurrence.** In his description of *Diffugia bidens*, based on specimens collected from Lake Geneva, Switzerland, Pernard (1902) illustrated four distinct syntypes on page 265 (figures 1-4), but did not designate any as the holotype of the new species. Penard's figure 1 (re-illustrated

here as Figure 2.1) is the most typical morphotype of the species, being characterized by two basal processes from which the species name '*bidens*' is derived. The specimen in Penard's figure 2 is characterized by three basal processes, and figures 3 and 4 have no basal processes. As per Article 74.1 of the International Code of Zoological Nomenclature (1999) we designate Penard's figure 1 as the lectotype for the species. The additional hypotypes illustrated here are included to provide higher quality scanning electron microscope (SEM) images of



**FIGURE 4.** Morphological parameters of *Erugomicula bidens* measured using specimens retrieved from Bell's Lake (ON) Scott's Pond (ON) and Yellowknife (NT) (n=24). Left, Density distribution plot of length and width of *E. bidens*; specimen width is represented by the light grey curve, and specimen length with the dark grey curve. Right, Scatterplot of length versus width of measured *E. bidens* specimens; the black line represents the median length:width ratio of 1.3.

the morphologic variability within the species. They were obtained recently from Bell's Lake, Schomberg, Ontario, Canada (43°56.597' N, 79°39.762' W), Figure 2.2-4 (CANA 129300), Figure 3.1-6 (CANA 129301). The SEM images of the specimens illustrated here were taken using a Tescan Vegall XMU SEM in the Nano Imaging Facility, Carleton University.

**Dimensions.** Hypotype specimens measured for this study (n = 24) were from Bell's Lake, Ontario, Canada (length: 219 – 341 µm [mean = 274 µm]; width: 127 – 250 µm [mean = 207 µm]), with an average length:width ratio of 1.33 (Table 1, Figure 4). Specimens from Bell's Lake showed little morphological variability, with only minor deviation about the mean length:width ratio, despite large size variation between specimens (Figure 4). Specimens of *E. bidens* measured by Penard (1902) from Lake Geneva, Switzerland, ranged from 250-270 µm in length, within the observed range of specimens from Bell's Lake. Specimens retrieved from ditches in Naardermeer, Netherlands (Siemensma, 2017) were slightly larger than *E. bidens* found in Canada and Switzerland, ranging from 307-366 µm in length. The average apertural width of the Bell's Lake hypotypes was 83 µm (50 – 103 µm), or approximately 40% of specimen width. Most specimens observed had two spines on the fundus, which was why the type species is named '*bidens*', although specimens with zero, one, and three spines were also observed. It is likely that the presence or absence of spines is due to phenotypic plasticity and is not a suitable classification criterion (Jennings, 1916; Lahr et al., 2008; Gooma et al., 2017).

**Remarks.** *Erugomicula*, n. genus, differs from *Diffflugia* Leclerc, 1815 in the distinct compression of a wide ovoid test (Figures 2-3). *Erugomicula* is distinguished by having a simple round aperture in contrast to *Awerintzewia* Schouteden, 1906, which has a compressed to oval aperture and inhabits forest soils, and sphagnum and peat bogs. The new genus is also distinct from *Heleopera* Leidy, 1879, which is characterized by a slit like aperture and roughly agglutinated aboral region. *Erugomicula* differs from *Nebela* (Leidy, 1874; sensu Kosakyan et al., 2016) by being composed of finely agglutinated xenogenous mineral particles, while *Nebela* is composed primarily of oval and circular siliceous plates or organic cement. *Nebela* species are also characterized by distinctive apertures which can be either linear, slightly or strongly curved.

The type species of the new genus, *E. bidens*, is usually present in small numbers in most lacustrine assemblages. *Erugomicula bidens* has been observed in lakes across Canada, including eastern Canada (Medioli and Scott, 1983; McCarthy et al., 2012; Patterson et al., 2012; Macumber et al., 2014), western Canada (Torigai et al., 2000; Neville et al., 2010), and the Northwest Territories (Nasser et al., 2016, 2020). It has also been found in Europe in Bulgaria (Serafimov et al., 1995; Golemansky et al., 2003), Estonia (Lokko et al., 2014), Finland (Kauppila et al., 2006; Kihlman and Kauppila, 2012), France (Thomas, 1954), Lithuania (Šatkauskienė, 2014), Portugal (Camacho et al., 2015), and of course Switzerland (Penard, 1902; Golemansky et al., 2003), where the species was first described. Based on the similarly compressed test we also tentatively place *Diffflugia biconcava*

**TABLE 1.** Measurements of morphological parameters of *Erugomicula bidens*. Measurements are presented in micrometers; specimens measured using light photos and SEMs.

Length (L) (microns)	Width (W) (microns)	Aperture width (microns)	No. of Spines (#)	L:W (ratio)	Location
250-270	-	-	-	-	Lake Lemán, Switzerland
307-366	-	-	-	-	Ditches in Naardermeer, Netherlands
257	205	77	3	1.25	Bell's Lake, Ontario, Canada
247	216	77	2	1.14	Bell's Lake, Ontario, Canada
247.76	195.21	72.83	2	1.27	Bell's Lake, Ontario, Canada
269.42	216.68	75.01	2	1.24	Bell's Lake, Ontario, Canada
255.53	244.46	100.01	3	1.05	Bell's Lake, Ontario, Canada
186.65	115.54	53.33	2	1.62	The Hollows, Ontario, Canada
244.81	165.50	75.86	2	1.48	Scott Pond, Ontario
219.20	190.43	63.02	2	1.15	Scott Pond, Ontario
239.64	186.19	72.41	3	1.29	Yellowknife, Northwest Territories
243.43	202.98	63.67	2	1.20	Yellowknife, Northwest Territories
309.74	250.43	102.37	2	1.24	Bell's Lake, Ontario, Canada
331.97	277.59	101.25	2	1.20	Bell's Lake, Ontario, Canada
292.60	216.66	87.81	2	1.35	Bell's Lake, Ontario, Canada
300.55	215.77	74.42	2	1.39	Bell's Lake, Ontario, Canada
267.29	246.96	75.10	1	1.08	Bell's Lake, Ontario, Canada
320.99	238.22	81.37	2	1.35	Bell's Lake, Ontario, Canada
296.35	191.69	88.98	2	1.55	Bell's Lake, Ontario, Canada
330.68	219.69	72.74	1	1.51	Bell's Lake, Ontario, Canada
297.19	227.08	99.06	2	1.31	Bell's Lake, Ontario, Canada
341.04	243.15	103.21	2	1.40	Bell's Lake, Ontario, Canada
334.49	-	-	2	-	Bell's Lake, Ontario, Canada
207.82	133.90	55.66	1	1.55	Bell's Lake, Ontario, Canada
218.57	127.06	50.96	2	1.72	Bell's Lake, Ontario, Canada
316.29	256.42	97.72	2	1.23	Bell's Lake, Ontario, Canada

Ertl, 1965 and the possible junior synonym of that species *Diffflugia balcanica* Ogden and Zivovich, 1983 in *Erugomicula*. *Diffflugia lucida* Penard, 1890 is not placed in *Erugomicula* as that very coarsely agglutinated taxa has a very compressed aperture and due to the presence of a neck. Similarly, the compressed and coarsely agglutinated *Diffflugia nodosa* Leidy, 1879 is also excluded from the new genus due to the presence of a pronounced neck.

*Erugomicula* is here tentatively placed in the family Hyalospheniidae based on recent molecular studies that suggest that test shape is an inherited fundamental trait of deep time ancestral phylogenetic importance (Lahr et al., 2019). Although genera of the family Hyalospheniidae are compressed, tests of current genera within that family are variously identified as chitinous, clear, completely organic, or if agglutinated, comprised of the shell

plates of small euglyphids. As *E. bidens* is comprised of mineral agglutinated particles further research will be required to determine whether *Erugomicula* is actually attributable to the Hyalospheniidae or Diffugiidae Stein 1859 where many agglutinated test genera are placed, or neither. If proven to be the case, then the test composition description of the Hyalospheniidae will require amendment. The work of Macumber et al. (2020) may provide additional support for placing the new genus in the Hyalospheniidae, based on recognition in that study of two distinct morphologically-based clades (lanceolate and pyriform) within *Diffflugia*. Interestingly the "pyriform" clade of Macumber et al. (2020) was determined to be a sister clade of *Hyalosphenia papilio* Leidy, 1874 (Family Hyalospheniidae). Nevertheless, these recent studies provide only a preliminary indication of the

relationship between the species of *Diffflugia*, with much additional research required (Gomaa et al., 2012). *Erugomicula* be a key genus that requires particular attention in future molecular investigations of the group.

*Erugomicula bidens* is considered to be an indicator of increased terrigenous erosion of minerals and organic matter associated with land-use change (Patterson et al., 1985; Kihlman and Kauppila, 2012; Macumber et al., 2014). However, Patterson et al. (2002) did not observe an increase in *D. bidens* abundance in Swan Lake, Ontario in a stratigraphic section where an increase in sediment runoff into the lake was observed. The sediment runoff was predominantly a nutrient poor glacial clay; the lack of nutrients is most likely an additional important limiting factor on the distribution for *D. bidens*. An association of *D. bidens* with nutrient status was further supported by Patterson et al. (2012) as it was observed to have one of the higher optima and tolerances for Olsen's phosphorus (150-400 ppm). It has also been observed in

mesotrophic and hypereutrophic lakes (Neville et al., 2010) and lakes impacted by industrial contaminants (Kauppila et al., 2006; Neville et al., 2011; Nasser et al., 2016).

**Etymology.** From the Latin *Erugo*, clear of wrinkles, smooth; and *mico*, shine, sparkle, f. dim., with reference to the relatively smooth surface of the type species *Diffflugia bidens* Penard, 1902.

**Stratigraphic range.** Although some arcellinidan species have been found in sediments dating as far back as the Permian (Singh et al., 2015), the type species of the new genus *Erugomicula bidens* has, to date, only been observed in Holocene lacustrine sediments (Medioli and Scott, 1983).

#### ACKNOWLEDGEMENTS

The authors acknowledge funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grant to RTP, (#RGPIN05329) and the Swiss National Science Foundation project (P2NEP3\_178543 to DS).

---

#### REFERENCES

- Asioli, A., Medioli, F.S., and Patterson, R.T. 1996. Thecamoebians as the tool for reconstruction of paleoenvironments in some southern Alpine Lakes (Orta, Varese and Candia). *Journal of Foraminiferal Research*, 26:248-263. <https://doi.org/10.2113/gsjfr.26.3.248>
- Awerinzew, S. 1907. Über einige Arten gehäusetragender Rhizopoden des Süßwassers. *Archiv für Protistenkunde*, 8:86-94.
- Beyens, L. and Meisterfeld, R. 2001. Protozoa: testate amoebae, p. 121-153. In Smol, J.P., Birks, H.J.B., and Last, W.M. (eds.), *Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators*. Kluwer Academic Press, Dordrecht, the Netherlands. [https://doi.org/10.1007/0-306-47668-1\\_7](https://doi.org/10.1007/0-306-47668-1_7)
- Bobrov, A., Charman, D.J., and Warner, B.G. 1999. Ecology of testate amoebae (Protozoa: Rhizopoda) on peatlands in western Russia with special attention to niche separation in closely related taxa. *Protist*, 150:125-136. [https://doi.org/10.1016/s1434-4610\(99\)70016-7](https://doi.org/10.1016/s1434-4610(99)70016-7)
- Bonnet, L. 1975. Types morphologiques, écologie et évolution de la thèque chez les thécamoebiens. *Protistologica*, 11:363-378.
- Camacho, S., Connor, S., Asioli, A., Boski, T., and Scott, D.B. 2015. Testate amoebae and tintinnids as spatial and seasonal indicators in the intertidal margins of Guadiana Estuary (southeastern Portugal). *Ecological Indicators*, 58:426-444. <https://doi.org/10.1016/j.ecolind.2015.05.041>
- Carpenter, W.B. 1861. On the systematic arrangement of the Rhizopoda. *Natural History Review*, 1:456-472.
- Cavalier-Smith, T. 1993. Kingdom protozoa and its 18 phyla. *Microbiological Reviews*, 57:953-994. <https://doi.org/10.1128/membr.57.4.953-994.1993>
- Cavalier-Smith, T., Chao, E.E., and Lewis, R. 2016. 187-gene phylogeny of protozoan phylum Amoebozoa reveals a new class (Cutosea) of deep-branching, ultrastructurally unique, enveloped marine Lobosa and clarifies amoeba evolution. *Molecular Phylogenetics and Evolution*, 99:275-296. <https://doi.org/10.1016/j.ympev.2016.03.023>
- Chardez, D. 1991. Note sur *Diffflugia humilis* sp. n. (Protozoa: Rhizopoda: Testacea). *Acta Protozoologica*, 1:45-47.



- Charman, D.J., Roe, H.M., and Gehrels, W.R. 1998. The use of testate amoebae in studies of sea-level change: a case study from the Taf Estuary, south Wales, UK. *The Holocene*, 8:209-218. <https://doi.org/10.1191/095968398676389446>
- Charman, D.J., Hendon, D., and Woodland, W.A. 2000. *The Identification of Peatland Testate Amoebae. Technical Guide*. Quaternary Research Association, London.
- Cockburn, C.F., Gregory, R.B., Nasser, N.A., Patterson, R.T. 2020. Intra-lake Arcellinida (testate lobose amoebae) response to winter de-icing contamination in an eastern Canada road-side 'Salt Belt' lake. *Microbial Ecology*, 80:366-383. <https://doi.org/10.1007/s00248-020-01513-w>
- Corliss, J.O. 1984. The kingdom Protista and its 45 phyla. *BioSystems*, 17:87-126. [https://doi.org/10.1016/0303-2647\(84\)90003-0](https://doi.org/10.1016/0303-2647(84)90003-0)
- DeSalle, R. and Goldstein, P. 2019. Review and interpretation of trends in DNA barcoding. *Frontiers in Ecology and Evolution*, 7:302. <https://doi.org/10.3389/fevo.2019.00302>
- Duckert, C., Blandenier, Q., Kupferschmid, F.A., Kosakyan, A., Mitchell, E.A., Lara, E., and Singer, D. 2018. En garde! Redefinition of *Nebela militaris* (Arcellinida, Hyalospheniidae) and erection of *Alabasta* gen. nov. *European Journal of Protistology*, 66:156-165. <https://doi.org/10.1016/j.ejop.2018.08.005>
- Ertl, M. 1965. Zur Kenntnis der Testaceenfauna der slowakischen Reifelder. *Hydrobiologia*, 26:13-20. <https://doi.org/10.1007/bf00142249>
- Farooqui, A., Kumar, A., and Swindles, G.T. 2012. Thecamoebian communities as proxies of seasonality in Lake Sadatal in the Ganga-Yamuna Plains of North India. *Palaeontologia Electronica*, 15.1.3A:1-19. <https://doi.org/10.26879/200>
- Gauthier-Lièvre, L. and Thomas, R. 1958. Les genres *Diffflugia*, *Pentagonia*, *Maghrebica* et *Hoogenraadia* (Rhizopodes testacés) en Afrique. *Archiv für Protistenkunde*, 103:241-370.
- Golemansky, V.G., Todorov, M.T., and Zhecheva, A. 2003. A check-list of the Rhizopods (Amoebida and Testacea) in the collection of Dr P Pateff deposited at the Institute of Zoology (Sofia). *Acta Zoologica Bulgarica*, 55:95-104.
- Gomaa, F., Todorov, M., Heger, T.J., Mitchell, E.A.D., and Lara, E. 2012. SSU rRNA phylogeny of Arcellinida (Amoebozoa) reveals that the largest Arcellinid genus, *Diffflugia* Leclerc 1815, is not monophyletic. *Protist*, 163:389-399. <https://doi.org/10.1016/j.protis.2011.12.001>
- Gomaa, F., Lahr, D.J.G., Todorov, M.T., Lin, J.H., and Lara, E. 2017. A contribution to the phylogeny of agglutinating Arcellinida (Amoebozoa) based on SSU rRNA gene sequences. *European Journal of Protistology*, 59:99-107. <https://doi.org/10.1016/j.ejop.2017.03.005>
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*. Fourth Edition. The Natural History Museum, London.
- Jennings, H.S. 1916. Heredity, variation and the results of selection in the uniparental reproduction of *Diffflugia corona*. *Genetics*, 1:407-534. <https://doi.org/10.1093/genetics/1.5.407>
- Kauppi, T., Kihlman, S., and Mäkinen, J. 2006. Distribution of arcellaceans (testate amoebae) in the sediments of a mine water impacted bay of Lake Retunen, Finland. *Water, Air, and Soil Pollution*, 172:337-358. <https://doi.org/10.1007/s11270-006-9099-9>
- Kent, W.S. 1880. *A Manual of the Infusoria: including a Description of all known Flagellate, Ciliate, and Tentaculiferous Protozoa, British and Foreign, and an Account of the Organization and Affinities of Sponges*, vol. 1. Bogue, London.
- Kihlman, S. and Kauppi, T. 2012. Effects of mining on testate amoebae in a Finnish lake. *Journal of Paleolimnology*, 47:1-15. <https://doi.org/10.1007/s10933-011-9541-x>
- Kosakyan, A., Heger, T.J., Leander, B.S., Todorov, M., Mitchell, E.A.D., and Lara, E. 2012. COI barcoding of nebelid testate amoebae (Amoebozoa: Arcellinida): extensive cryptic diversity and redefinition of the Hyalospheniidae Schultze. *Protist*, 163:415-434. <https://doi.org/10.1016/j.protis.2011.10.003>
- Kosakyan, A., Gomaa, F., Lara, E., and Lahr, D.J.G. 2016. Current and future perspectives on the systematics, taxonomy and nomenclature of testate amoebae. *European Journal of Protistology*, 55:105-117. <https://doi.org/10.1016/j.ejop.2016.02.001>
- Kumar, A. and Patterson, R.T. 2000. Arcellaceans (Thecamoebians): new tools for monitoring long- and short-term changes in lake bottom acidity. *Environmental Geology*, 39:689-697. <https://doi.org/10.1007/s002540050483>
- Lahr, D.J.G., Bergmann, P.J., and Lopes, S.G.B.C. 2008. Taxonomic identity in microbial eukaryotes: A practical approach using the testate amoeba *Centropyxis* to resolve conflicts between old and new taxonomic descriptions. *Journal of Eukaryotic Microbiology*, 55:409-416. <https://doi.org/10.1111/j.1550-7408.2008.00339.x>

- Lahr, D.J.G., Lara, E., and Mitchell, E.A.D. 2012. Time to regulate microbial eukaryote nomenclature. *Biological Journal of the Linnean Society*, 107:469-476. <https://doi.org/10.1111/j.1095-8312.2012.01962.x>
- Lahr, D.J.G., Grant, J.R., and Katz, L.A. 2013. Multigene phylogenetic reconstruction of the Tubulinea (Amoebozoa) corroborates four of the six major lineages, while additionally revealing that shell composition does not predict phylogeny in the Arcellinida. *Protist*, 164:323-339. <https://doi.org/10.1016/j.protis.2013.02.003>
- Lahr, D.J., Kosakyan, A., Lara, E., Mitchell, E.A., Morais, L., Porfirio-Sousa, A.L., Ribeiro, G.M., Tice, A.K., Pánek, T., Kang, S., and Brown, M.W. 2019. Phylogenomics and morphological reconstruction of Arcellinida testate amoebae highlight diversity of microbial eukaryotes in the Neoproterozoic. *Current Biology*, 29:991-1001. <https://doi.org/10.1016/j.cub.2019.01.078>
- Lamarck, J.B. 1816. *Naturelle des Animaux sans Vèrtebres Tome 2*. Verdière, Paris.
- Leclerc, M. 1815. Note sur la Diffflugie, nouveau genre de polype amorphe. *Memoires du (Paris) Museum D'Histoire Naturelle*, 2:474-479.
- Leidy, J. 1874. Notice of some new freshwater rhizopods. *Journal of Natural History*, 14:383-385.
- Leidy, J. 1879. *Fresh-Water Rhizopods of North America*. United States Geological Survey of the Territories, Washington, D.C.
- Loeblich Jr., A.R. and Tappan, H. 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida, p. 1-900. In Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part C, Protista 2*. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- Lokko, K., Virro, T., and Kotta, J. 2014. Taxonomic composition of zoopsammon in fresh and brackish waters of Estonia, a Baltic province ecoregion of Europe. *Estonian Journal of Ecology*, 63:242-261. <https://doi.org/10.3176/eco.2014.4.04>
- Lühe, M. 1913. Faunistische Untersuchung der Moore Ostpreußens. *Schriften der physikalisch-ökonomischen Gesellschaft Königsberg*, 54:84-86.
- Macumber, A.L., Patterson, R.T., Roe, H.M., Reinhardt, E.G., Neville, L.A., and Swindles, G.T. 2014. Autoecological approaches to resolve subjective taxonomic divisions within Arcellacea. *Protist*, 165:305-316. <https://doi.org/10.1016/j.protis.2014.03.004>
- Macumber, A.L., Blandenier, Q., Todorov, M., Duckert, C., Lara, E., Lahr, D.J., Mitchell, E.A., and Roe, H.M. 2020. Phylogenetic divergence within the Arcellinida (Amoebozoa) is congruent with test size and metabolism type. *European Journal of Protistology*, 72:125645. <https://doi.org/10.1016/j.ejop.2019.125645>
- Marcisz, K., Jassey, V.E.J., Kosakyan, A., Krashevskaya, V., Lahr, D.J.G., Lara, E., Lamentowicz, Ł., Lamentowicz, M., Macumber, A., Mazei, Y., Mitchell, E.A.D., Nasser, N.A., Patterson, R.T., Roe, H.M., Singer, D., Tsyganov, A.N., and Fournier, B. 2020. Testate amoeba functional traits and their use in paleoecology. *Frontiers in Ecology and Evolution*, 8:575966. <https://doi.org/10.3389/fevo.2020.575966>
- Mazei, Y. and Warren, A. 2012. A survey of the testate amoeba genus *Diffflugia* Leclerc, 1815 based on specimens in the E. Penard and C.G. Ogden collections of the Natural History Museum, London. Part 1: Species with shells that are pointed aborally and/or have aboral protuberance. *Protistology*, 7:121-171.
- Mazei, Y. and Warren, A. 2014. A survey of the testate amoeba genus *Diffflugia* Leclerc, 1815 based on specimens in the E. Penard and C.G. Ogden collections of the Natural History Museum, London. Part 2: Species with shells that are pyriform or elongate. *Protistology*, 8:133-171.
- Mazei, Y. and Warren, A. 2015. A survey of the testate amoeba genus *Diffflugia* Leclerc, 1815 based on specimens in the E. Penard and C.G. Ogden collections of the Natural History Museum, London. Part 3: Species with shells that are spherical or ovoid. *Protistology*, 9:1-49.
- McCarthy, F.M.G., Collins, E.S., McAndrews, J.H., Kerr, H.A., Scott, D.B., and Medioli, F.S. 1995. A comparison of postglacial arcellacean ("Thecamoebian") and pollen succession in Atlantic Canada, illustrating the potential of arcellaceans for paleoclimatic reconstruction. *Journal of Paleontology*, 69:980-993. <https://doi.org/10.1017/s0022336000035630>
- McCarthy, F.M.G., Tiffin, S., Sarvis, A., McAndrews, J.H., and Blasco, S. 2012. Early Holocene brackish closed basin conditions in Georgian Bay, Ontario, Canada: microfossil (thecamoebian and pollen) evidence. *Journal of Paleolimnology*, 47:429-445. <https://doi.org/10.1007/s10933-010-9415-7>
- Medioli, F.S. and Scott, D.B. 1983. Holocene Arcellacea (Thecamoebians) from eastern Canada. *Cushman Foundation for Foraminiferal Research Special Publication*, 21:1-63.

- Medioli, F.S., Scott, D.B., and Abbott, B.H. 1987. A case study of protozoan intracolon variability: taxonomic implications. *Journal of Foraminiferal Research*, 17:28-47. <https://doi.org/10.2113/gsjfr.17.1.28>
- Medioli, F.S., Scott, D.B., Collins, E.S., and McCarthy, F.M.G. 1990. Fossil thecamoebians: present status and prospects for the future, p. 813-840. In Hemleben, C., Kaminski, M.A., Kuhnt, W., and Scott, D.B. (eds.), *Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of Agglutinated Foraminifera*. NATO Advanced Study Institute Series, Series C, Mathematical and Physical Sciences. Springer, The Netherlands.
- Meisterfeld, R. 2000. Arcellinida, 2nd ed., p. 690-1432. In Lee, J.J., Leedale, G.F., and Bradbury, P. (eds.), *An Illustrated Guide to the Protozoa Volume II*. Society of Protozoologists, Lawrence, Kansas.
- Meisterfeld, R. and Mitchell, E.A.D. 2008. *Diffflugia* Leclerc, 1815. The Tree of Life Web Project. Retrieved from <http://tolweb.org/Difflugia/124487/2008.09.02>
- Mitchell, E.A.D., Charman, D.J., and Warner, B. 2008. Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present and future. *Biodiversity and Conservation*, 17:2115-2137. <https://doi.org/10.1007/s10531-007-9221-3>
- Nasser, N.A. and Patterson, R.T. 2015. *Conicocassis*, a new genus of Arcellinina (testate lobose amoebae). *Palaeontologia Electronica*, 18.3.46A:1-11. <https://doi.org/10.26879/538>
- Nasser, N.A., Patterson, R.T., Roe, H.M., Galloway, J.M., Falck, H., Palmer, M.J., Spence, C., Sanei, H., Macumber, A.L., and Neville, L.A. 2016. Lacustrine Arcellinina (testate amoebae) as bioindicators of arsenic contamination. *Microbial Ecology*, 72:130-149. <https://doi.org/10.1007/s00248-016-0752-6>
- Nasser, N.A., Patterson, R.T., Roe, H.M., Galloway, J.M., Falck, H., and Sanei, H. 2020. Use of Arcellinida (testate lobose amoebae) arsenic tolerance limits as a novel tool for biomonitoring arsenic contamination in lakes. *Ecological Indicators*, 113:106177. <https://doi.org/10.1016/j.ecolind.2020.106177>
- Neville, L.A., Christie, D.G., McCarthy, F., and MacKinnon, M.D. 2010. Biogeographic variation in Thecamoebian (Testate amoeba) assemblages in lakes within various vegetation zones of Alberta, Canada. *International Journal of Biodiversity and Conservation*, 2:215-224.
- Neville, L.A., McCarthy, F.M.G., MacKinnon, M.D., Swindles, G.T., and Marlowe, P. 2011. Thecamoebians (testate amoebae) as proxies of ecosystem health and reclamation success in constructed wetlands in the Oil Sands of Alberta, Canada. *The Journal of Foraminiferal Research*, 41:230-247. <https://doi.org/10.2113/gsjfr.41.3.230>
- Ogden, C.G. and Hedley, R.H. 1980. *An Atlas of Freshwater Testate Amoebae*. British Museum (Natural History), London and Oxford University Press, Oxford.
- Ogden, C.G. and Meisterfeld, R. 1989. The taxonomy and systematics of some species of *Cucurbitella*, *Difflugia* and *Netzelia* (Protozoa: Rhizopoda); with an evaluation of diagnostic characters. *European Journal of Protistology*, 25:109-128. [https://doi.org/10.1016/s0932-4739\(89\)80022-7](https://doi.org/10.1016/s0932-4739(89)80022-7)
- Ogden C.G. and Živković A. 1983. Morphological studies on some Difflugiidae from Yugoslavia (Rhizopoda, Protozoa). *Bulletin British Museum Natural History (Zoology)*, 44:341-375.
- Patterson, R.T. 2014. *Mediolus*, a new genus of Arcellacea (testate lobose amoebae). *Palaeontologia Electronica*, 17.1.28A:1-8. <https://doi.org/10.26879/440>
- Patterson, R.T., MacKinnon, M.D., Scott, D.B., and Medioli, F.S. 1985. Arcellaceans ("thecamoebians") in small lakes of New Brunswick and Nova Scotia: Modern distribution and Holocene stratigraphic changes. *Journal of Foraminiferal Research*, 15:114-137. <https://doi.org/10.2113/gsjfr.15.2.114>
- Patterson, R.T., Baker, T., and Burbidge, S.M. 1996. Arcellaceans (thecamoebians) as proxies of arsenic and mercury contamination in northeastern Ontario lakes. *Journal of Foraminiferal Research*, 26:172-183. <https://doi.org/10.2113/gsjfr.26.2.172>
- Patterson, R.T., Dalby, A.P., Kumar, A., Henderson, L.A., and Boudreau, R.E.A. 2002. Arcellaceans (thecamoebians) as indicators of land-use change: settlement history of the Swan Lake area, Ontario as a case study. *Journal of Paleolimnology*, 28:297-316.
- Patterson, R.T. and Kumar, A. 2002. A review of current testate rhizopod (thecamoebian) research in Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 180:225-251. [https://doi.org/10.1016/s0031-0182\(01\)00430-8](https://doi.org/10.1016/s0031-0182(01)00430-8)

- Patterson, R.T., Roe, H.M., and Swindles, G.T. 2012. Development of a thecamoebian (testate amoebae) based transfer function for sedimentary phosphorous in lakes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 348-349:32-44. <https://doi.org/10.1016/j.palaeo.2012.05.028>
- Patterson, R.T., Lamoureux, E.D.R., Neville, L.A., and Macumber, A.L. 2013. Arcellacea (testate lobose amoebae) as pH indicators in a pyrite mine-acidified lake, Northeastern Ontario, Canada. *Microbial Ecology*, 65:541-554. <https://doi.org/10.1007/s00248-012-0108-9>
- Patterson, R.T., Huckerby, G., Kelly, T.J., Swindles, G.T., and Nasser, N.A. 2015. Hydroecology of Amazonian lacustrine Arcellinida (testate amoebae): A case study from Lake Quistococha, Peru. *European Journal of Protistology*, 51:460-469. <https://doi.org/10.1016/j.ejop.2015.06.009>
- Penard, M.E. 1902. Faune rhizopodique du bassin du Lemman. (H. Kundig, Ed.). Librairie de L'Institut, Geneva.
- Penard, E. 1890. Etudes sur les Rhizopodes d'eau douce. *Memoires de la Societe de Physique et d'Histoire Naturelle de Geneve*, 2:1-230.
- Porter, S.A. and Knoll, A.H. 2000. Testate amoeba in the Neoproterozoic Era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. *Paleobiology*, 26:360-385. [https://doi.org/10.1666/0094-8373\(2000\)026<0360:TAITNE>2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)026<0360:TAITNE>2.0.CO;2)
- Reinhardt, E.G., Dalby, A.P., Kumar, A., and Patterson, R.T. 1998. Arcellaceans as pollution indicators in mine tailing contaminated lakes near Cobalt, Ontario, Canada. *Micropaleontology*, 44:1-18.
- Roe, H.M., Patterson, R.T., and Swindles, G.T. 2010. Controls on the contemporary distribution of lake thecamoebians (testate amoebae) within the Greater Toronto Area and their potential as water quality indicators. *Journal of Paleolimnology*, 43:955-975. <https://doi.org/10.1007/s10933-009-9380-1>
- Roe, H.M., Elliot, S.M. and Patterson, R.T. 2017. Re-assessing the vertical distribution of testate amoeba communities in surface peats: implications for palaeohydrological studies. *European Journal of Protistology*, 60:13-27. <https://doi.org/10.1016/j.ejop.2017.03.006>
- Šatkauskienė, I. 2014. Testate amoebae (Testaceae) of Lithuania. *Biologija*, 60, 59-69. <https://doi.org/10.6001/biologija.v60i2.2906>
- Schouteden, H. 1906. Les Rhizopodes testaces d'eau douce, d'apres la Monographie du Prof. A. (Sic) Awerintzew. *Annales de Biologie Lacustre*, 1(3):327-382.
- Schultze, F.E. 1877. Rhizopodenstudien VI. *Archiv für mikroskopische Anatomie*, 13:9-30.
- Serafimov, B.L., Golemansky, V.G., and Todorov, M.T. 1995. Testacean taxocenoses (Rhizopoda, Testacea) in two quarry lakes of Sofia district. *Acta Zoologica Bulgarica*, 48:23-33.
- Siemensma, F.J. 2017. Microworld, world of amoeboid organisms. Retrieved from <http://www.arcella.nl>
- Singer, D., Kosakyan, A., Pillonel, A., Mitchell, E.A., and Lara, E. 2015. Eight species in the *Nebela collaris* complex: *Nebela gimlii* (Arcellinida, Hyalospheniidae), a new species described from a Swiss raised bog. *European Journal of Protistology*, 51:79-85. <https://doi.org/10.1016/j.ejop.2014.11.004>
- Singer, D., Mitchell, E. A., Payne, R. J., Blandenier, Q., Duckert, C., Fernández, L. D., Fournier, B., Hernández, C.E., Granath, G., Rydin, H., Bragazza, L., Koronatotova, N.G., Goia, I., Harris, L.I., Kajukalo, K., Kosakyan, A., Lamentowicz, M., Kosykh, N.P., Vellak, K., and Lara, E. 2019. Dispersal limitations and historical factors determine the biogeography of specialized terrestrial protists. *Molecular Ecology*, 28(12):3089-3100. <https://doi.org/10.1111/mec.15117>
- Singh, V., Pandita, S.K., Tewari, R., van Hengstum, P.J., Pillai, S.S., Agnihotri, D., Kumar, K., and Bhat, G.D. 2015. Thecamoebians (testate amoebae) straddling the Permian-Triassic boundary in the Guryul Ravine section, India: evolutionary and palaeoecological implications. *PLoS One*, 10:e0135593. <https://doi.org/10.1371/journal.pone.0135593>
- Smirnov, A., Nassonova, E., Cedric, B., Fahrni, J., Bolivar, I., and Pawlowski, J. 2005. Molecular phylogeny and classification of the lobose amoebae. *Protist*, 156:129-142. <https://doi.org/10.1016/j.protis.2005.06.002>
- Steele, R.E., Patterson, R.T., Hamilton, P.B., Nasser, N.A., and Roe, H.M. 2020. Assessment of FlowCam technology as a potential tool for rapid semi-automatic analysis of lacustrine Arcellinida (testate lobose amoebae). *Environmental Technology & Innovation*, 17:100580. <https://doi.org/10.1016/j.eti.2019.100580>



- Stein, S.F.N. 1859. Über die ihm aus eigener Untersuchung bekannt gewordenen Süßwasser-Rhizopoden. Königliche Böhmisches Gesellschaft der Wissenschaften Abhandlungen, Ser. 5, 10:41-43.
- Štěpánek, M. 1952. Testacea of the pond of Hrádek at Kunratice (Prague). Acta Musei Nationalis Pragae, Series B - Historia Naturalis Praha: Národní Muzeum, 8:1-55.
- Swindles, G.T. and Roe, H.M. 2007. Examining the dissolution characteristics of testate amoebae (Protozoa: Rhizopoda) in low pH conditions: Implications for peatland palaeoclimate studies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 252:486-496. <https://doi.org/10.1016/j.palaeo.2007.05.004>
- Thomas, R. 1954. Thécamoebiens de la région bordelaise. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 89:245-264.
- Tolonen, K. 1986. Rhizopod analysis, p. 645-666. In Berglund, B.E. (ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley and Sons, New York.
- Torigai, K., Schröder-Adams, C.J., and Burbridge, S.M. 2000. A variable lacustrine environment in Lake Winnipeg, Manitoba: evidence from modern thecamoebian distribution. *Journal of Paleolimnology*, 23:305-318. <https://doi.org/10.1023/A:1008148027142>