**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 Difflugidae Stein, 1859 more than 300 species and 200 sub-species have been attributed to the genus *Difflugia* 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 *Difflugia*, *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 *Difflugia*, explaining its polyphyletic status. We reclassify *Difflugia bidens* Penard, 1902 as type species of *Erugomicula*, a new genus within the Difflugidae, which is distinguished from other taxa within *Difflugia* by its broad, ovoid test, and distinct compression. Based on the compressed morphology of the test, which is not a characteristic of the Difflugiidae, we tentatively assign *Erugomicula* to the family Hyalo-spheniidae.

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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; Štepánek, 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 Diffugidae Stein, 1859. Diffugia 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 Diffugia several researchers have attempted to subdivide Diffugia 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 infrasubspecific nomenclature, which became known as ‘strains’ (Medioli et al., 1987; Asili 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 Diffugia 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 Diffugia (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 *Difflugia*, Gomaa et al. (2012, 2017) showed that the group is polyphyletic. Other phylogenetic reconstructions based on the NAD9/NAD7 gene have also shown that *Difflugia* 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 *Difflugia*. 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 *Difflugia*, 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 confirm relationships of the different species of *Difflugia* 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 *Difflugia*, require to have their systematic taxonomic placements re-evaluated (e.g., Nasser and Patterson, 2015; Patterson et al., 2015).

*Difflugia 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 PALAEONTOLOGY**

Phylum AMOEBOZOA (Lühe, 1913) Corliss, 1984
Class TUBULINEA Smirnov et al., 2005 emend. [Lobosea (Carpenter, 1861) Cavalier-Smith, 1993]
Subclass NEOLOBOSIA Cavalier-Smith et al., 2016
Superorder EULOBOSIA Cavalier-Smith et al., 2016
Order ARCELLINIDA Kent, 1880
Family HYALOSPHENIIDAE Schulze 1877
Genus *Erugomicula* n. gen.

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**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-compressed, 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-
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 *Difflugia 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 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.
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 taking using a Tes- can 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 as 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; Gomaa et al., 2017).

**Remarks.** *Erugomicula*, n. genus, differs from *Difflugia* 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 apertature 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 characterize 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 Kaup- pila, 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 *Difflugia biconcava*
Ertl, 1965 and the possible junior synonym of that species *Difflugia balcanica* Ogden and Zivovich, 1983 in *Erugomicula*. *Difflugia 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 *Difflugia 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 chitinoid, 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 Difflugiidae 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 *Difflugia*. 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

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**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 Leman, 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          |
relationship between the species of Diffugia, 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 Diffugia 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).

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