



***Mediolus*, a new genus of Arcellacea (Testate Lobose Amoebae)**

R. Timothy Patterson

ABSTRACT

Mediolus, a new arcellacean genus of the Diffflugidae (informally known as thecamoebia, testate rhizopods, or testate lobose amoebae) differs from other genera of the family in having distinctive tooth-like inward oriented apertural crenulations and tests generally characterized by a variable number of hollow basal spines.

R. Timothy Patterson. Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario, K1S 5B6, Canada. Tim.Patterson@carleton.ca

Keywords: Arcellacea; thecamoebian; testate lobose amoebae; Quaternary, new genus

INTRODUCTION

Arcellacea (also informally known as thecamoebians, testate amoebae, testate rhizopods, or testate lobose amoebae; Patterson et al., 2012) are a diverse group of unicellular testate rhizopods that occur in a wide array of aquatic and terrestrial environments (Patterson and Kumar, 2002) from the tropics to poles (Dalby et al., 2000). Although most common in Quaternary sediments fossil arcellaceans have been found preserved in sediments deposited under freshwater and brackish conditions spanning the Phanerozoic and into the Neoproterozoic (Porter and Knoll, 2000; Van Hengstum, 2007).

Within the Arcellacea the genus *Diffflugia* Leclerc, 1815 is the most species rich, being comprised of more than 300 species and 200 subspecies (Meisterfeld and Mitchell, 2008). At the species level, especially for fossil material, the most important characteristics for systematic placement, has generally been the shape and size

of the simple unilocular test (e.g., Bonnet, 1975; Medioli et al., 1987, 1990; Beyens and Meisterfeld, 2001), although some researchers have placed more emphasis on test composition (e.g., Anderson, 1988). The proliferation of species descriptions within the *Diffflugia*, often based on subtle test differences, has resulted in considerable taxonomic confusion (Patterson and Kumar, 2002). Researchers have often described new species based on regional interest, often with little consideration of the previous literature or the systematic value of distinguishing characters (see discussions in Medioli and Scott, 1983; Medioli et al., 1987; Ogden and Hedley, 1980; Tolonen, 1986; Bobrov et al., 1999; Charman et al., 2000). On the other hand recent research suggests that many morphologically indistinguishable species may actually be cryptospecies (Mitchell and Meisterfeld, 2005; Alison et al., 2008; Heger et al., 2013; Oliverio et al., 2014). Species ascribed to *Diffflugia* are characterized by a wide variety of morphologies, some bear-

www.zoobank.org/E43633B7-2017-48CB-B887-849D86D3F230

PE Article Number: 17.2.28A

Copyright: Paleontological Society July 2014

Submission: 15 November 2013. Acceptance: 19 June 2014

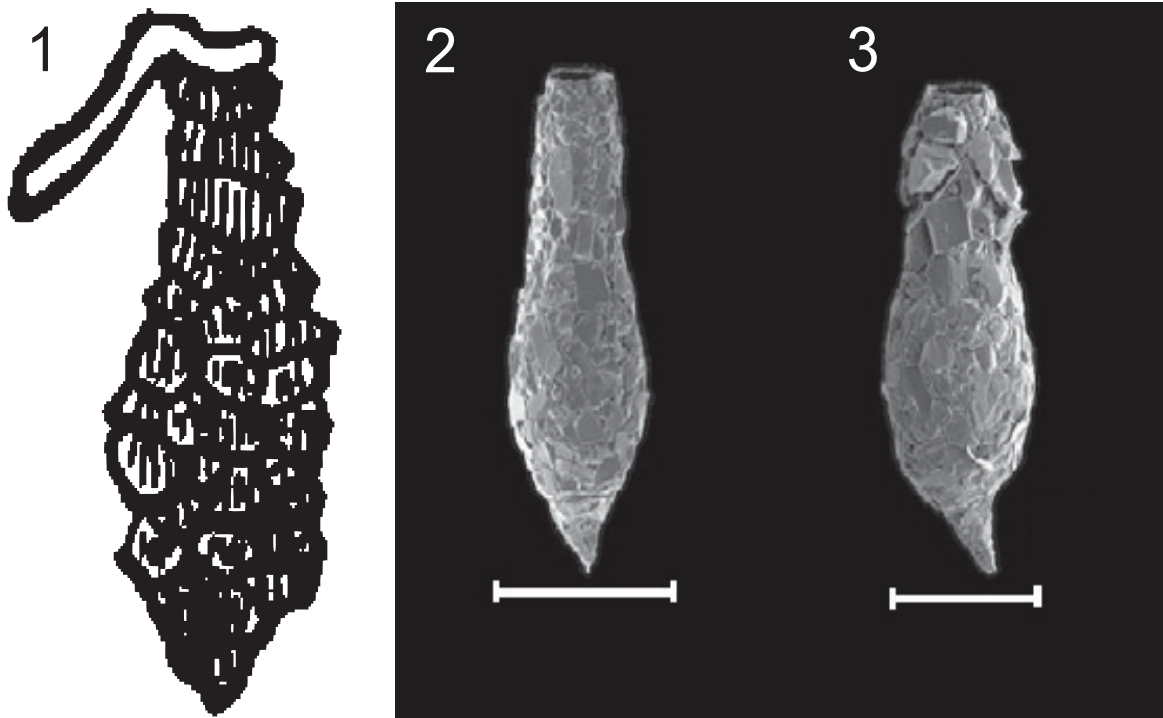


FIGURE 1. Specimens of *Diffflugia protaeiformis* Lamarck, 1816, the type species of *Diffflugia*. 1. *Diffflugia protaeiformis* Lamarck, 1816 as illustrated in Lamarck, 1816, pl. 17, figure. 5. 2. and 3. Scanning electron micrographs of hypotypes of *Diffflugia protaeiformis* Lamarck strain “protaeiformis” from Mytopo Lake, eastern Ontario (Latitude 44°40.179N, Longitude 77°3.397W). Scale bar equals 100 μm . 2. side view of typical specimen with characteristic broad base and narrow, elongate neck; 3. side view of a relatively common morphology characterized by heavy agglutination on neck.

ing little resemblance to the type species *Diffflugia protaeiformis* Lamarck, 1816 (lectotype designated by Loeblich and Tappan, 1964, p. C35, as the specimen illustrated in Lamarck, 1816, pl. 17, figure. 5), which is characterized by an amphora-shaped test with narrow aperture and tapering at the base to a point (Figure 1.1-3).

There have been various attempts to subdivide this large genus into more manageable subgroups. For example, Gauthier-Lièvre and Thomas (1958) divided the genus into 10 artificial groups based on morphologic test variability (e.g., elongate, globose, ovoid, urceolate, pyriform, and compressed tests; lobate, collared, and toothed apertures; presence or absence of spiked processes). Mazei and Warren (2012) carried out a similar survey of *Diffflugia* species, informally subdividing the genus into groupings based on morphology. The newest available systematic tool to potentially study the systematics of *Diffflugia* is the application of molecular systematics. Unfortunately, due to the difficulty of sequencing protists with agglutinated tests, only a handful of studies have been carried out on thecamoebian taxa (e.g., Nikolaev et al., 2005; Lara et al., 2008; Kudryavt-

sev et al., 2009), and only a single study has been carried out on *Diffflugia* (Gomaa et al., 2012). In an analysis of five taxa (*Diffflugia bacilliarum* Perty, 1849, *D. hiraethogii* Ogden, 1983, *D. acuminata* Ehrenberg, 1838; *D. lanceolata* Penard, 1890; *D. achlora* Penard, 1902) Gomaa et al. (2012) determined that *Diffflugia* is not monophyletic, and as suggested in previous morphologic studies, shell shape, and not test composition, most closely correlates with genetic clades. Genetic analysis of Arcellacea is in its infancy, and it will be many years before such analysis is routine. It is obvious though, that due to the morphological plasticity within lineages across evolutionary time scales, it will be a combination of morphometric and molecular analysis that will eventually provide a more complete understanding of arcellacean biodiversity (Oliverio et al., 2014). New advances in morphometric analysis techniques may also provide guidance as to the validity of at least morphologically distinct taxa. For example, Macumber, et al. (2014) employed a novel statistical approach to determine that two strains of Arcellacea, *Diffflugia protaeiformis* Lamarck strain ‘acuminata’ and *Diffflugia*

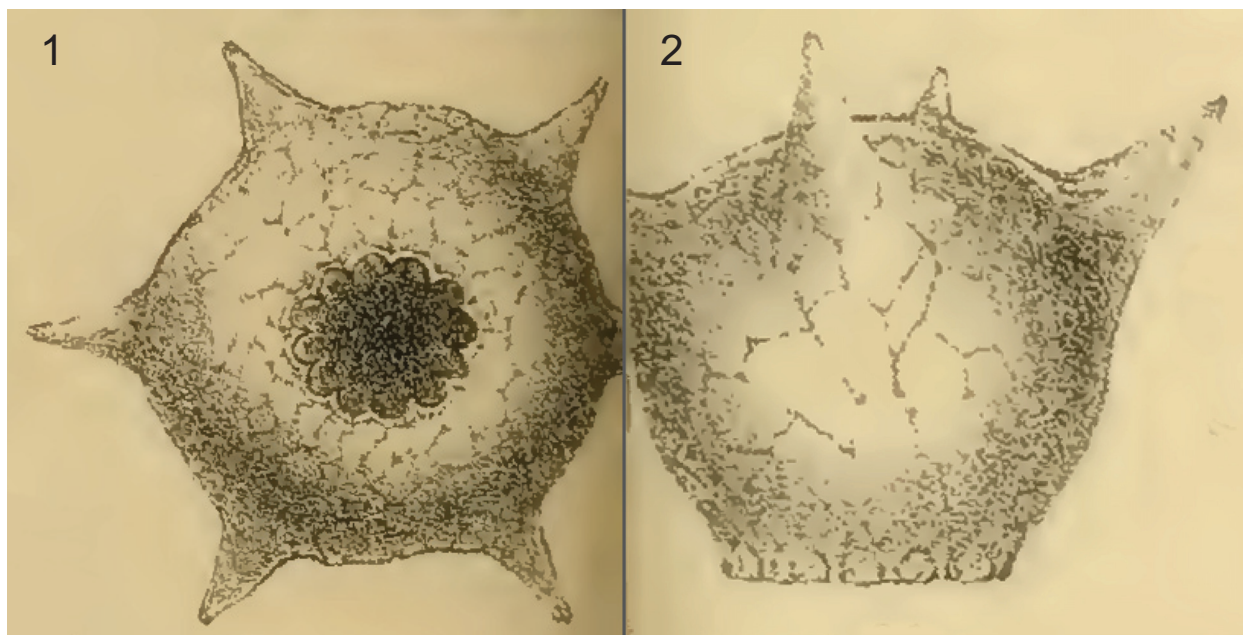


FIGURE 2. Specimens of *Mediolus corona* from Wallich, 1864. 1. illustrated as figure 19 in the original publication, Wallich described the specimen as “front view, showing crenulate margin of aperture; a six-horned variety”; 2. illustrated as figure 20 in the original publication, Wallich described the specimen as “a somewhat smaller four-horned variety; side view.”

protaeiformis Lamarck strain ‘claviformis’ most likely represent distinct species.

One of the most distinctive and easily recognizable arcellacean taxa is *D. corona*, Wallich, 1864, which is characterized by an agglutinated subspheroidal test, a fundus covered with a variable number of processes and a round aperture bordered by numerous crenulations or teeth (Figure 2.1-2; Figure 3.1-12). Aside from both being unilocular and characterized by an agglutinated test this species bears no resemblance to the *Diffflugia* type species, *D. proteaiformis* (Figure 1.1-3). In an attempt to make a start at formally breaking *Diffflugia* into more systematically realistic groups it is proposed that *D. corona* be recognized as the type species of the new genus *Mediolus* n. gen.

TAXONOMY

Subkingdom PROTOZOA
 Phylum AMOEBOZOA Lühe, 1913
 Class LOBOSIA Carpenter, 1861
 Order ARCELLINIDA Kent, 1880
 Superfamily ARCELLACEA Ehrenberg, 1830
 Family DIFFLUGIDAE Stein, 1859
 Genus *Mediolus* n. gen.

www.zoobank.org/E43633B7-2017-48CB-B887-849D86D3F230

Type species. *Diffflugia proteaiformis* (sic) (Ehrenberg) subspecies *D. globularis* (Dujardin) var. *D.*

corona (Wallich) WALLICH 1864 p. 244, pl. 16, figures 19, 20 (reillustrated here as Figure 2.1-2).

Diagnosis. A genus of Diffflugidae characterized by a symmetrical globular test, a test most typically comprised of agglutinated particles from the environment, round aperture with multiple inward-oriented angular tooth-line crenulations, and a test typically characterized by a variable number of spines extending outward on the test.

Description. Test free, unilocular; ovoid to subspherical to spheroid; circular in section, about the vertical aperture through the fundus; test wall comprised of agglutinating particles variously composed of xenogenous mineral grains and/or organic material derived from the ambient environment; agglutinating particles attached together with an organic cement; circular aperture characterized by thin collar of secreted cement with variable number of inward-oriented angular crenulations also composed of cement; delicate spines may be present, spines long and narrow, hollow, and composed of very fine agglutinating particles.

Types and occurrence. Hypotype (Canadian Museum of Nature (CANA 87186), recent from “Lake 10” near Yellowknife, Northwest Territories, Canada (62°30.924’N, 113°46.817’W); Hypotype (CANA 91905), recent from Mew Lake, Algonquin Park, Ontario (45°34.575’N, 78°31.087’W); Hypotype (CANA 87197), recent from Bell’s Lake, municipality of King (Greater Toronto Area),

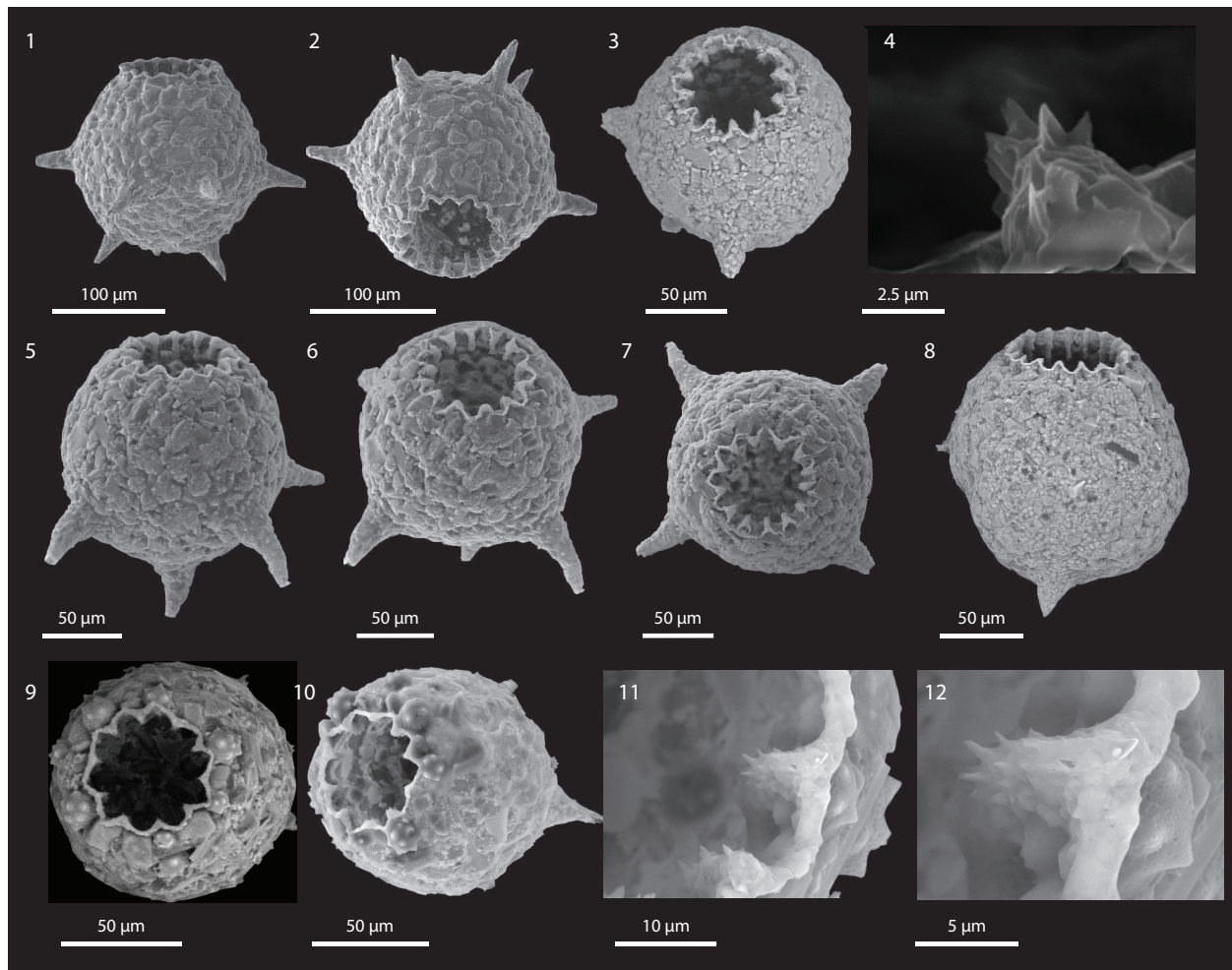


FIGURE 3. Specimens of *Mediolus corona* from lakes in the Subarctic ("Lake 10" near Yellowknife, Northwest Territories; 62°30.924'N, 113°46.817'W); temperate region (Mew Lake, Algonquin Park, Ontario; 45°34.575'N, 78°31.087'W, Bell's Lake, King (Greater Toronto Area), Ontario; 43°N56.597, 79°39.762W); and equatorial regions (Holocene core from Laguna de Quistococha, Iquitos, Peruvian Amazon; 3°49.746'N, 73°19.157'W). 1. side view of typical spheroidal hypotype (CANA 91905) from sediment-water interface in Mew Lake showing orientation of basal spines and thin narrow apertural rim; 2. oblique apertural view of same specimen showing crenulated aperture; 3. apertural view of hypotype (CANA 87197) from sediment-water interface in Bell's Lake showing round aperture; 4. Closeup of individual crenulation in Bell's Lake specimen showing spiny projections; 5. Side view of globular hypotype (CANA 87186) from "Lake 10" showing distribution of spines; 6. oblique apertural view of same specimen showing narrow apertural rim; 7. apertural view of same specimen showing rounded apertural opening and regular distribution of basal spines; 8. Globular hypotype (CANA 87198) from Holocene core collected from Laguna de Quistococha with relatively few short spines; 9. apertural view of different hypotype (CANA 87199) from Laguna de Quistococha showing typical rounded and crenulated aperture but with considerably reduced basal spines than shown in "Lake 10" specimen (7 above); 10. oblique apertural view of same specimen showing typical narrow crenulated apertural lip; 11. close up of apertural region on same specimen showing regular spacing and uniform structure of crenulations; 12. close up of a single crenulation showing typical spiny ultrastructure, which are nearly identical to those of temperate latitude specimens (4 above).

Ontario, Canada (43°N56.597, 79°39.762W); Hypotypes (CANA 87198 and CANA 87199), Holocene from Laguna de Quistococha, Iquitos, Peruvian Amazon (3°49.746'N, 73°19.157'W).

Dimensions. 100-400µm; mean ~ 150 µm (Medioli and Scott, 1983; Hu et al., 1997; Yang et al., 2004; Lahr and Lopes, 2006).

Remarks. The genus is readily distinguished from *Protocurbitella* Gauthier-Liévre and Thomas, 1960, as *Mediolus* lacks the distinctive diaphragm around

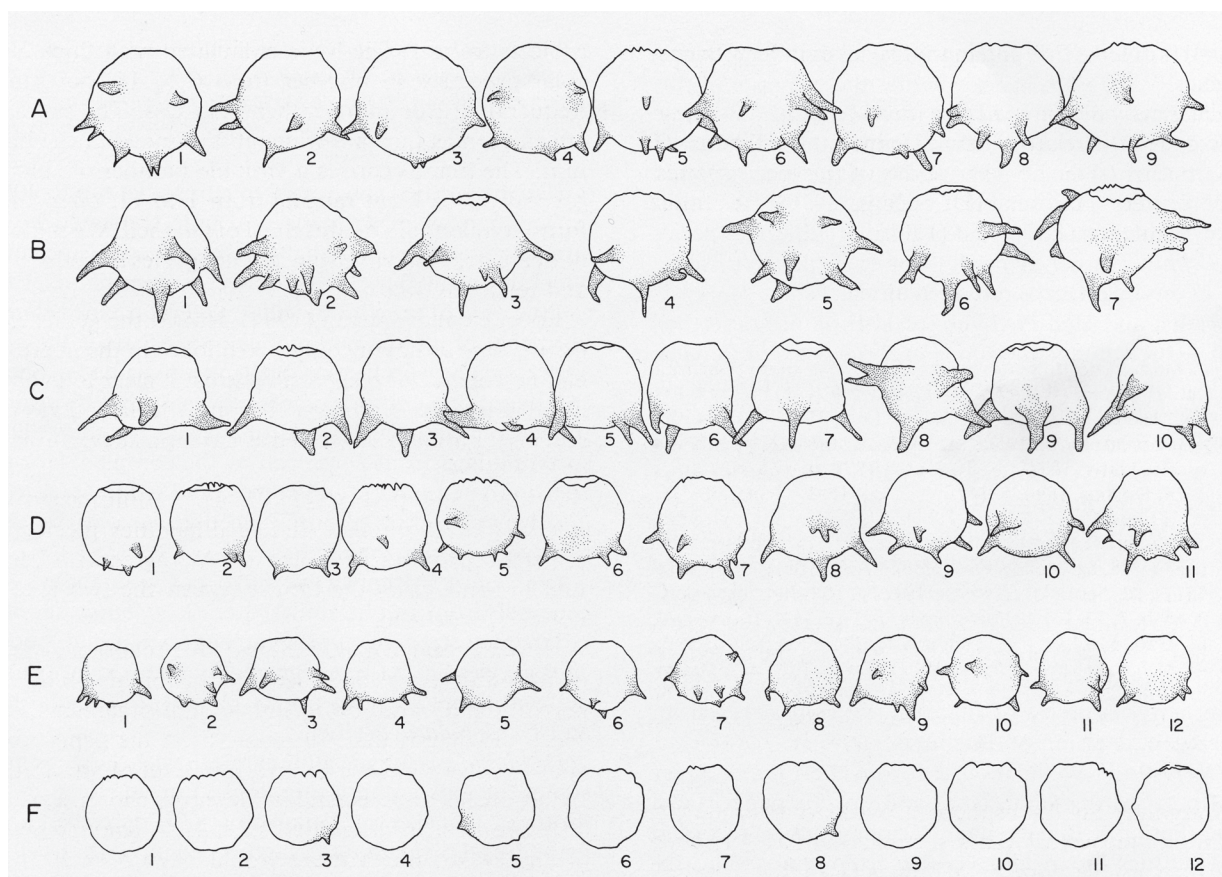


FIGURE 4. Line drawings of *Mediolus corona* clones produced within six of Jennings (1916) broods, redrafted and rearranged by Medioli and Scott (1983). The figure shows that although there is little variation within broods through only a few generations there is considerable variation in both size and process number and arrangement between broods. The research of Jennings (1916) indicated that although the crenulated aperture was a constant feature in all clones, some morphotypes can be processless.

the peristome. The peristomal diaphragm of *Proto-cucurbitella* is similar to a similar structure characterizing *Cucurbitella* Penard, 1902. In addition, the pronounced lobed apertural collar of *Cucurbitella* is also very distinct from the apertural crenulations characterizing *Mediolus*. *Cucurbitella* is distinct from most other arcellaceans with regard to its distinctive relationship with some algal species. As the spring and summer growing season progresses and algae begins to grow into the water column *Cucurbitella* individuals go with it. In the absence of xenogenous grains to construct their test, late season specimens of this genus have the ability to produce idiosomic particles, which they use to construct their shell (Schönborn, 1984; Medioli et al., 1987). *Mediolus* differs from *Loboforamina* Jung, 1942 in that the latter is characterized by a lobate apertural region similar to that found in *Cucurbitella*.

As illustrated in this paper living representatives of *Mediolus* are found from the tropics to the

poles. It is relatively common in mesotrophic to eutrophic lakes where it is often found attached to water plants (Medioli and Scott, 1983; Roe et al., 2010; Patterson et al., 2012; Roe and Patterson, 2014). It is less common in ponds and ditches and has also been reported from sphagnum bogs. Individuals are heterotrophic using its lobose pseudopods to engulf organic material or smaller prey (e.g., diatoms and bacteria) (Medioli and Scott, 1983).

The crenulated aperture typical of the type species *D. corona* is much more diagnostic of the genus than the spines. Using broods of *D. corona*, Jennings (1916) carried out what is now recognized as a classic experiment on heredity in uniparental organisms. He found that although clones differed greatly in overall size and the number of spines produced through many generations, there was an almost perfect correlation between the number of apertural teeth produced within brood lineages. As the spines would sometimes disap-

pear entirely in some broods it is the apertural teeth that are the single most distinguishing characteristic of *Mediolus* (Figure 4). The seasonally planktic species *Diffflugia tuberspinifera* Hu, Shen, Gu, and Gong, 1997, a species endemic to east Asia, is morphologically similar to *D. corona*, differing in that the toothed aperture in *D. tuberspinifera* tends to be contained within a protruding apertural flange, and that the conical spines are restricted to the upper equatorial region (Yang et al., 2004; Han et al., 2008). Yu et al. (2014) have recognized that, as also observed in *D. corona*, spineless strains also exist. Based on the general similarity of the apertural crenulations in both *D. corona* and *D. tuberspinifera*, the latter species is tentatively assigned to *Mediolus*.

The extreme range of habitat observed for the type species of *Mediolus* may provide indirect evidence that it may encompass two or more cryptospecies. A possible non-genetic analysis approach to eventually test this hypothesis has been demonstrated using planktic foraminifera (Morard et al., 2013). Using transfer functions Morard et al. (2013) modeled the temperature dependence of several species of planktic species in the southern hemisphere and determined that several morphologically indistinguishable morphotypes are most likely distinct species.

Etymology. In honor of the late Professor Emeriti Franco Mediolini (1935-2014), Department of Earth Sciences, Dalhousie University, in recognition of his extensive research on the ecology, systematics, and biostratigraphy of Arcellacea and related groups.

Stratigraphic Range. Quaternary, but particularly common in Holocene deposits.

ACKNOWLEDGEMENTS

This research was supported by a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to RTP.

REFERENCES

- Alizon, S., Kucera, M., and Janser, V.A.A. 2008. Competition between cryptic species explains variations in rates of lineage evolution. *Proceedings of the National Academy of Sciences*, 105:12382-12386.
- Anderson, O.R. 1988. Testate Amoebae (Classes: Lobosea and Filosea), p. 63–65. In Anderson, O.R. (ed.), *Comparative Protozoology: Ecology, Physiology, Life History*. Springer-Verlag, Berlin, New York.
- Beyens, L.D. and Meistefeld, R. 2001. Testate protozoa, p. 121-153. In Smol, J.P., Birks, H.J.B., and Last, W.M. (eds.), *Tracking Environmental Change Using Lake Sediments: Biological Techniques and Indicators. v. II*, Kluwer Academic Press.
- Bobrov, A.A., Charman, D.J., and Warner, B.G. 1999. Paleocology of testate amoebae (Protozoa: Rhizopoda) on peatlands in western Russia with special attention to niche separation in closely related taxa. *Protist*, 150:125-136.
- Bonnet, L. 1975. Types morphologiques, écologie et évolution de la thèque chez les thécamoebiens. *Protistologica*, 11:363-378.
- Carpenter, W.B. 1861. On the systematic arrangement of the Rhizopoda. *Natural History Review New Series*, 1:456-472.
- Charman, D.J., Hendon, D., and Woodland, W. 2000. The identification of peatland testate amoebae. *Quaternary Research Association Technical Guide no. 9*, London, 147 pp.
- Dalby, A.P., Kumar, A., Moore, J.M., and Patterson, R.T. 2000. Utility of arcellaceans (thécamoebians) as paleolimnological indicators in tropical settings: Lake Sentani, Irian Jaya, Indonesia. *Journal of Foraminiferal Research*, 30:135-142.
- Ehrenberg, C.G. 1830. *Organisation, Systematik und geographisches Verhältnis der Infusionstierchen*. Druckerei der Königl. Akademie der Wissenschaften, Berlin.
- Ehrenberg, G.C. 1838. *Die Infusionstierchen als Vollkommene Organismen*. Verlag von Leopold Voss, Leipzig.
- Gauthier-Lièvre, L. and Thomas, R. 1958. Les genres *Diffflugia*, *Pentagonia*, *Maghrebica* et *Hoogenraadia* (Rhizopodes testaces) en Afrique. *Archiv Protistenkunde*, 103:241-370.
- Gauthier-Lièvre, L. and Thomas, R. 1960. Le genre *Cucurbitella* Penard. *Archiv Protistenkunde*, 104:569-602.
- 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.
- Han, P.-P., Wang, T., Lin, Q.-Q., and Dumont, H.J. 2008. Carnivory and active hunting by the planktonic testate amoebae *Diffflugia tuberspinifera*. *Hydrobiologia*, 596:197-201.
- Heger, T.J., Mitchell, E.A., and Leander, B.S. 2013. Holarctic phylogeography of the testate amoeba *Hyalosphenia papilio* (Amoebozoa: Arcellinida) reveals extensive genetic diversity explained more by environment than dispersal limitation. *Molecular Ecology*, 22:5172-5184.
- Hu, D.L., Shen, Y.F., Gu, M.R., and Gong, X.J. 1997. New species and new records of protozoa from Wuling Mountains Area p. 40-72. In Song, D.X. (ed.), *Invertebrates of Wuling Mountains Area, Southwestern China*. Science Press, Beijing (in Chinese).

- Jennings, H.S. 1916. Heredity, variation and the results of selection in the uniparental reproduction of *Diffugia corona*. *Genetics*, 1:407-534.
- Jung, W. 1942. Südchilenische Thekamöben (aus dem südchilenischen Küstengebiet, Beitrag 10). *Archiv Protistenkunde*, 95:253-356.
- 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.
- Kudryavtsev, A., Pawlowski, J., and Hausmann, K. 2009. Description and phylogenetic relationships of *Spumochlamys perforate* n. sp and *Spumochlamys bryora* n. sp (Amoebozoa, Arcellinida). *Journal Eukaryotic Microbiology*, 56:495-503.
- Lahr, D.J.G. and Lopes, S.G.B.C. 2006. Morphology, biometry, ecology and biogeography of five species of *Diffugia* Leclerc, 1815 (Arcellinida: Diffugiidae), from Tiete River, Brazil. *Acta Protozoologica*, 45:77-90.
- Lamarck, J.B. 1816. *Histoire Naturelle des Animaux sans Vêrtebres*. Verdière, Paris, tome 2, p. 1-568.
- Lara, E., Heger, T.J., Ekelund, F., Lamentowicz, M., and Mitchell, E.A.D. 2008. Ribosomal RNA genes challenge the monophyly of the Hyalospheniidae (Amoebozoa: Arcellinida). *Protist*, 159:165-176.
- Leclerc, L. 1815. Note sur la Diffugie, nouveau genre de polype amorphe. *Mémoires du Muséum d'Histoire Naturelle* 2, 474-478.
- Loeblich, A.R., Jr., and Tappan, H. 1964. Sarcodina, chiefly "Thecamoebians" and Foraminiferida, p. C1-900. In Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part C, Protista 2*, Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- Lühe, M. 1913. Faunistische Untersuchung der Moore Ostpreußens. *Schriften 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. Autecological approaches to resolve subjective taxonomic divisions within Arcellacea. *Protist*, 165:305-316.
- Mazei, Y. and Warren, A., 2012. A survey of the testate amoeba genus *Diffugia* 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 protuberances. *Protistology*, 7:121-171.
- Medioli, F.S. and Scott, D.B. 1983. *Holocene Arcellacea (Thecamoebians) from eastern Canada*. *Cushman Foundation For Foraminiferal Research Special Publication* 21.
- Medioli, F.S., Scott, D.B., and Abbott, B.H. 1987. A case study of protozoan interclonal variability: taxonomic implications. *Journal of Foraminiferal Research*, 17:28-47.
- 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 327.
- Meisterfeld, R. and Mitchell, E.A.D. 2008. *Diffugia*, Leclerc 1815 Version 02 September 2008. The Tree of Life Web Project, tolweb.org/Diffugia/124487/2008.09.02. Retrieved 4 Nov. 2013.
- Mitchell, E.A.D. and Meisterfeld, R. 2005. Taxonomic confusion blurs the debate on cosmopolitanism versus local endemism of free-living protists. *Protist*, 156:263-267.
- Morard, R., Quillévéré, F., Escarguel, G., de Garidel-Thoron, T., de Vargas, C., and Kucera, M. 2013. Ecological modeling of the temperature dependence of cryptic species of planktonic foraminifera in the southern hemisphere. *Palaogeography, Palaeoclimatology, Palaeoecology*, 391:13-33.
- Nikolaev, S.I., Mitchell, E.A.D., Petrov, N.B., Berney, C., Fahrni, J., and Pawlowski, J. 2005. The testate lobose amoebae (order Arcellinida Kent, 1880) finally find their home within Amoebozoa. *Protist*, 156:191-202.
- Ogden C.G. 1983. Observations on the systematics of the genus *Diffugia* in Britain (Rhizopoda, Protozoa). *Bulletin British Museum (Natural History)*. Zoology, 44:1-73.
- Ogden, C.G. and Hedley, R.H., 1980. *An Atlas of Fresh Water Testate Amoeba*. British Museum (Natural History), Oxford University Press, Oxford.
- Oliverio, A.M., Lahr, D.J., Nguyen, T., and Katz, L.A., 2014. Cryptic diversity within morphospecies of testate amoebae (Amoebozoa: Arcellinida) in New England bogs and fens. *Protist*, 165:196-207.
- Patterson, R. Timothy. 2014. IN MEMORIAM: Dr. Franco Medioli, April 1, 1935 – January 31, 2014. *Palaeontologia Electronica* Vol. 17, Issue 2;4E; 4p; palaeo-electronica.org/content/2014/783-in-memoriam-dr-franco-medioli
- Patterson, R.T. and Kumar, A., 2002. A review of current testate rhizopod (thecamoebian) research in Canada. *Palaogeography, Palaeoclimatology, Palaeoecology*, 180:225-251.
- Patterson, R.T., Roe, H.M., and Swindles, G.T. 2012. Development of an Arcellacea (testate lobose amoebae) based transfer function for sedimentary phosphorus in lakes. *Palaogeography, Paleoclimatology, Palaeoecology*, 348-349:32-44.
- Penard, E. 1890. Études sur les Rhizopodes d'eau douce. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, 31:1-230.
- Penard, E. 1902. *Faune Rhizopodique du Bassin du Lemán*. Henry Kundig, Geneve.

- Perty, M. 1849. Mikroskopische Organismen der Alpen und der Italienischen Schweiz. *Naturforschende Gesellschaft in Bern Mittheilungen*, 164-165:153-176.
- 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.
- Roe, H.M. and Patterson, R.T. 2014. Arcellacea (testate amoebae) as bio-indicators of road salt contamination in lakes. *Microbial Ecology*, DOI: 10.1007/s00248-104-0408-3.
- 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.
- Schöneborn, W.E. 1984. Studies on Remains of Testacea in cores of the Great Warty Lae (NE Poland): *Limnologia*, 16:185-190.
- Stein, S.F.N. 1859. Über die ihm aus eigener Untersuchung bekannt gewordenen Süßwasser-Rhizopoden. *Königliche Böhmsche Gesellschaft der Wissenschaften Abhandlungen*, ser. 5, 10:41-43.
- 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.
- Van Hengstum, P.J., Reinhardt, E.G., Medioli, F.S., and Gröcke, D.R. 2007. Exceptionally preserved Late Albian (Cretaceous) arcellaceans (Thecamoebians) from the Dakota Formation near Lincoln, Nebraska, USA. *Journal of Foraminiferal Research*, 37:300-308.
- Wallich, G.C. 1864. On the extent, and some of the principal causes of structural variation among the difflugian rhizopods. *Annals and Magazine of Natural History Series 3*, 13:215-245.
- Yang, J., Beyens, L., Shen, Y.F., and Feng, W.S. 2004. Redescription of *Difflugia tuberspinifera* Hu, Shen, Gu et Gong, 1997 (Protozoan: Rhizopoda: Arcellinida: Difflugiidae) from China. *Acta Protozoologica*, 43:281-289.
- Yu, Z., Zhang, W., Liu, L., and Yang, J. 2014. Evidence for two different morphotypes of *Difflugia tuberspinifera* from China. *European Journal of Protistology*, 50:205-211.