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Conicocassis, a new genus of Arcellinina (testate lobose amoebae)

Nawaf A. Nasser and R. Timothy Patterson

ABSTRACT

Superfamily Arcellinina (informally known as thecamoebians or testate lobose amoebae) are a group of shelled benthic protists common in most Quaternary lacustrine sediments. They are found worldwide, from the equator to the poles, living in a variety of fresh to brackish aquatic and terrestrial habitats. More than 130 arcellininid species and strains are ascribed to the genus *Centropyxis* Stein, 1857 within the family Centropyxidae Jung, 1942*,* which includes species that are distinguished by having a dorsoventral-oriented and flattened beret-like test (shell). *Conicocassis*, a new arcellininid genus of Centropyxidae differs from other genera of the family, specifically genus *Centopyxis* and its type species *C. aculeata* (Ehrenberg, 1932), by having a unique test comprised of two distinct components; a generally ovoid to subspherical, dorsoventral-oriented test body, with a pronounced asymmetrically positioned, funnel-like flange extending from a small circular aperture. The type species of the new genus, *Conicocassis pontigulasiformis* (Beyens et al., 1986) has previously been reported from peatlands in Germany, the Netherlands and Austria, as well as very wet mosses and aquatic environments in High Arctic regions of Europe and North America. The occurrence of the species in lacustrine environments in the central Northwest Territories extends the known geographic distribution of the genus in North America considerably southward.

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INTRODUCTION

Superfamily Arcellinina, also known as testate lobose amoebae (e.g., Macumber et al. 2014) or thecamoebians (e.g., Vázquez-Riveiros et al., 2007), are a group of well-preserved benthic protists common in most Quaternary lacustrine deposits (Loeblich and Tappan, 1964; Medioli and Scott, 1983; Scott and Medioli, 1983). This cosmopolitan group is found worldwide from the tropics to polar regions, living in a wide range of moist freshwater environments (e.g., lakes, rivers and peatlands: Ogden and Hedley, 1980; Medioli and Scott, 1983; Patterson et al., 1985; Medioli et al., 1990a; Medioli et al., 1990b; Patterson et al., 1996) as well as being found in low-salinity brackish habitats (Charman et al., 2000; Patterson and Kumar, 2002). The amoeboid body of the organism is protected by a beret- or sac-like test (shell) that is sometimes autogenous (secreted by the organism) and more commonly xenogenous (formed by agglutinating foreign materials like sand grains and/or diatoms frustules) (Patterson and Kumar, 2002). Although preserved arcellininid specimens are most common in Quaternary deposits, their fossil record extends through the Phanerozoic (Porter and Knoll, 2000) and into the Neoproterozoic (van Hengstum et al., 2007).

Centropyxidae Jung, 1942, a family within Arcellinina, includes the genus *Centropyxis* von Stein, 1857. Members of this family are distinguished by a chitinous, dorsoventrally symmetric test with a central to eccentric ventral aperture. Species and strains attributed to the genus *Centropyxis* are characterized by a generally flattened beret-like, discoid or oval test with a sub-terminal to central, circular to ovate, invaginated aperture located on the ventral side. The test is colorless to brown and may or may not be covered by agglutinating material, which varies from mineral grains to organic debris, particularly diatom frustules. Additionally, the test may or may not be ornamented with spines of varying number and length. As noted by several authors, this broad generic description permits considerable latitude in the morphology of species that can be attributed to the genus (e.g., Leidy, 1879; Root, 1918; Deflandre, 1929; Medioli and Scott, 1983; Ogden, 1988; Wanner, 1999). Centropyxid species have mainly been distinguished by variation in test size and shape, aperture size and form, as well as the number and length of spines. Of the more than 130 species and strains identified, the descriptions for many are inadequate (Meisterfeld, 2002). A particular problem within this group is that some of the more poorly agglutinated species are quite delicate creating difficulties in imaging them, particularly under

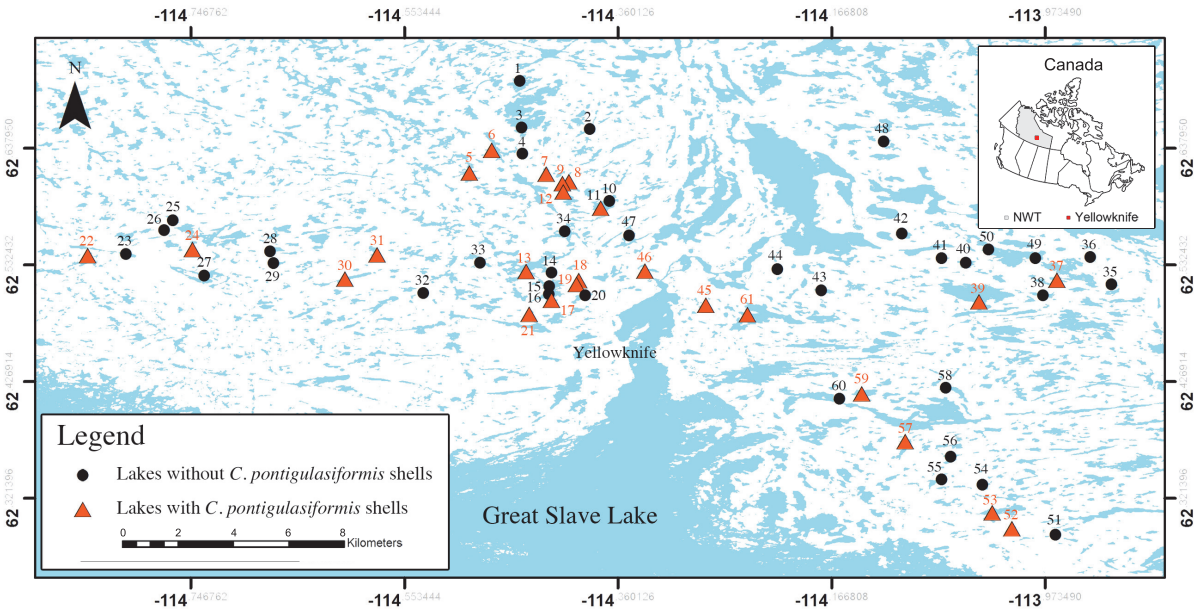

FIGURE 1. Map of the study region showing location of the sampled lakes (red triangles and black circles). The red triangles represent sample stations where *Centropyxis pontigulasiformis* was observed, while black circles characterize stations where the species was not detected. The numbers represent the sampling order, which corresponds to the sample identification codes shown in Table 1.

a vacuum as required for most scanning electron microscopes, as well as in preserving type material (Lahr et al., 2008). Additional difficulties arise because some centropyxid taxa are characterized by considerable morphologic variation, for example *Centropyxis aculeata* (Ehrenberg, 1832), resulting in various phenotypes being erroneously attributed to separate taxa (Medioli and Scott, 1983; Lahr, personal comun., 2014).

A potentially valuable new tool to determine the validity and taxonomic position of centropyxid taxa is molecular systematics. In an analysis of five difflugid taxa, Gomaa et al. (2012) determined that the group was not monophyletic and that shell morphology closely correlated with genetic clades. Genetic research has also revealed that testate lobose amoebae are characterized by numerous morphologically identical cryptospecies, inhabiting geographically diverse environments (Mitchell and Meisterfeld, 2005; Alizon et al., 2008; Heger et al., 2013; Oliverio et al., 2014). Based on these results Patterson (2014) has suggested that even iconic arcellininid taxa such as *Mediolus corona* (Wallich, 1864), found living in a range of habitats from the equator to poles, may be comprised of several crypto taxa, the morphology of which may be the product of convergent evolution. Unfortunately, genetic analysis of Arcellinina is still in its early stages. Only few studies have been successfully carried out on arcellininid taxa (e.g., Nikolaev et al., 2005; Lara et al., 2008; Kudryavtsev et al., 2009; Gomaa et al., 2015) due to the difficulty of sequencing protists with agglutinated tests. In addition to genetic analyses, novel morphometric approaches (e.g., Macumber et al., 2014 in an analysis of *Difflugia protaeiformis* Lamarck, 1816 strains) may provide an additional methodology to determine the systematic placement of taxa.

As part of a project mandated to determine the utility of arcellininids as a tool to monitor arsenic contamination in lakes from the Yellowknife region of the Northwest Territories, Canada, we have identified and quantified populations of *Centropyxis pontigulasiformis* Beyens et al., 1986, which is present in statistically significant numbers (between 4 and 62 shells) in many lakes within the studied region (Figure 1; Table 1; NAN, unpublished data; Patterson and Fishbein, 1989). This species was originally described from very wet terrestrial mosses, as well as from subaqueous mosses on Edgeøya (Edge) Island (77° 45' N, 22° 30' E) in the Norwegian Svalbard archipelago (Beyens et al., 1986). The species was subsequently reported from both wet terrestrial mosses and aquatic environments at high latitude throughout the Svalbard archipelago, West Greenland, islands in the Canadian Arctic Archipelago and the north coast of Alaska (Beyens and Chardez, 1995). Based on these occurrences the species was initially determined to be restricted to Arctic environments. However, specimens attributed to *C. pontigulasiformis* have also been identified in samples obtained from peat bogs in Het Hol, Netherlands, Rotes Wasser, Germany and Tirol, Austria (Siemensma, 2015). The occurrence of *C. pontigulasiformis* in lakes from the Yellowknife area of the central Northwest Territories significantly extends the known geographic distribution of the species southward in North America (Figure 1; Table 1).

Centropyxis pontigulasiformis is one of the most distinctive arcellininid species. Atypical of arcellininid species and strains of the genus *Centropyxis*, the test is comprised of two distinctive components: a semi-spherical to spherical main test body and a relatively large, open ended, conical, visor-like flange that extends from a small circular aperture (Figure 2). Aside from being unilocular, the species bears no similarity to *C. aculeata*, the type species of the genus *Centropyxis* (Figure 3), or any other species attributed to the genus. However, the tests of *C. pontigulasiformis* maintain the dorsoventral symmetry characterizing the family Centropyxidae. We, therefore, propose that *C. pontigulasiformis* be recognized as the type species of a new genus within the family Centropyxidae.

MATERIALS AND METHODS

Field Work

Sixty-one surface sediment samples were collected from 59 lakes from the Yellowknife region in August of 2012. The samples were collected along four, ~40 km long transects (north, south, east and west of the city of Yellowknife) from a float helicopter using an Ekman grab sampler (Figure 1). The onboard helicopter GPS system was used to record the position of each station (Table 1). The depth of each sampled lake was determined by deploying a commercial "fish finder" with bottom hardness indicator from a helicopter pontoon. Sample stations characterized by muddy substrates were preferentially sought out, as nutrient poor silt to sand substrates are generally characterized by depauperate allochthonous arcellininid populations (Patterson and Kumar, 2002).

TABLE 1. Coordinates, quantitative arcellininid information and Shannon Diversity Index (SDI) values of the samples containing specimens of *Centropyxis pontigulasiformis*.

Sample ID	Transect	Lat.	Long.	Total Arcellininid Counts	*C. pontigulasiformis*		SDI
					Absolute Abundance	Relative Abundance (%)	
BC 5	North	62.6158	-114.4944	338	4	1.1834	1.96
BC 6	North	62.6362	-114.4744	184	2	1.087	2.36
BC 7	North	62.6147	-114.4248	226	2	0.885	2.07
BC 8	North	62.608	-114.4045	317	13	4.1009	2.57
BC 9	North	62.6063	-114.4103	290	5	1.7241	2.6
BC 11	North	62.584	-114.3756	303	1	0.33	2.1
BC 12	North	62.5987	-114.4096	232	6	2.5862	2.23
BC 13	North	62.5269	-114.443	265	1	0.3774	2.16
BC 17	North	62.5007	-114.4201	291	2	0.6873	1.53
BC 18	North	62.5184	-114.3956	213	4	1.8779	1.84
BC 19	North	62.5152	-114.3974	222	9	4.0541	1.7
BC 21	North	62.4882	-114.4405	250	3	1.2	2.62
BC 22	West	62.5411	-114.84	143	41	28.6713	1.93
BC 24	West	62.5466	-114.7452	176	2	1.1364	1.64
BC 30	West	62.5199	-114.6072	264	1	0.3788	2.45
BC 31	West	62.5418	-114.578	278	5	1.7986	2.37
BC 37	East	62.5189	-113.9626	306	54	17.6471	1.89
BC 39	East	62.4992	-114.0331	284	2	0.7042	2.12
BC 45	East	62.4962	-114.2803	184	1	0.5435	2.25
BC 46	East	62.527	-114.3357	296	62	20.9459	1.93
BC 52	South	62.2941	-114.0033	266	2	0.7519	2.27
BC 53	South	62.3087	-114.0213	239	2	0.8368	2.31
BC 57	South	62.3729	-114.0998	264	1	0.3788	1.97
BC 59	South	62.4161	-114.1392	287	44	15.331	1.94
BC 61	South	62.4876	-114.2426	307	31	10.0977	2.11

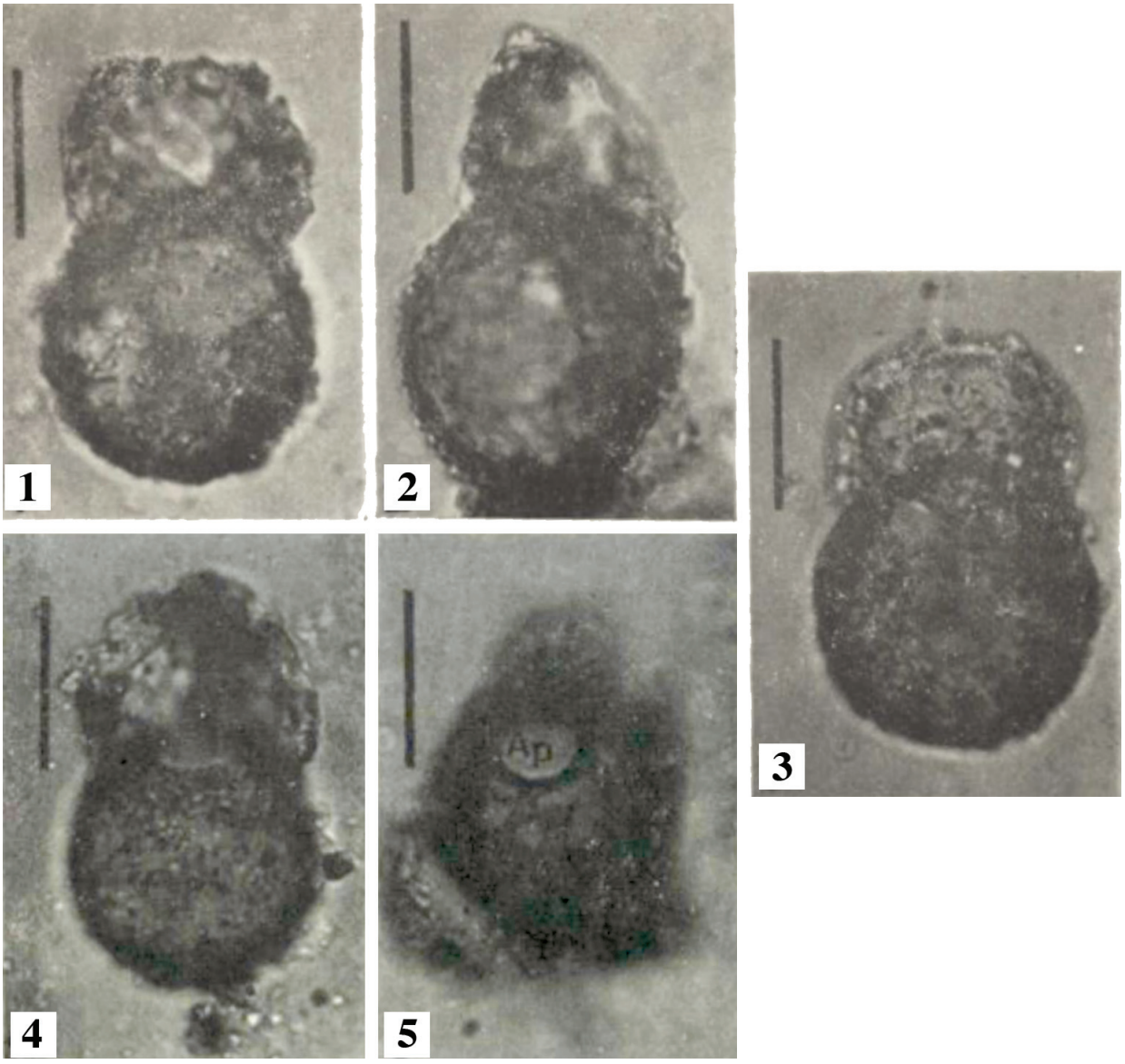

FIGURE 2. Light photomicrographs of the type illustrations of *Centropyxis pontigulasiformis* (as published by Beyens et al., 1986, plate 3, 1-5). **1**, apertural view of the test; **2**, lateral view of the test; **3**, apertural view of the test; **4**, apertural view of the test; and **5**, a close-up on the circular aperture without the flange. The length of the scale bars represent 40 µm. Permission to reprint Beyens et al. (1986, plate 3, 1-5) was granted by Acta Protozoologica.

Micropaleontological Analysis

The upper 0.5 cm of sediment from each Ekman grab was retained for micropaleontological and geochemical analysis. A 2.5 cc^3 sub samples was separated for micropaleontological analysis. These samples were first wet sieved through a 297-µm mesh to remove any coarse debris (e.g., coarse grains, grass and sticks) and subsequently passed through a 37-µm mesh to remove the clay-size fraction and retain arcellininids. Samples were immediately placed in isopropyl alcohol and refrigerated in order to avoid protoplasm decay. Prior to quantitative micropaleontological analysis the preserved sediment was subdivided into six aliquots using a wet splitter (after Scott and Hermelin, 1993). Each wet aliquot was then placed in a gridded Petri Dish and arcellininid specimens were counted using an Olympus SZH dissecting binocular microscope (at 7.5–64x magnification) until, whenever possible, a statistically significant number of specimens were quantified (Patterson and Fishbein, 1989). Identification of arcellininids primarily followed the descriptions and illustrations

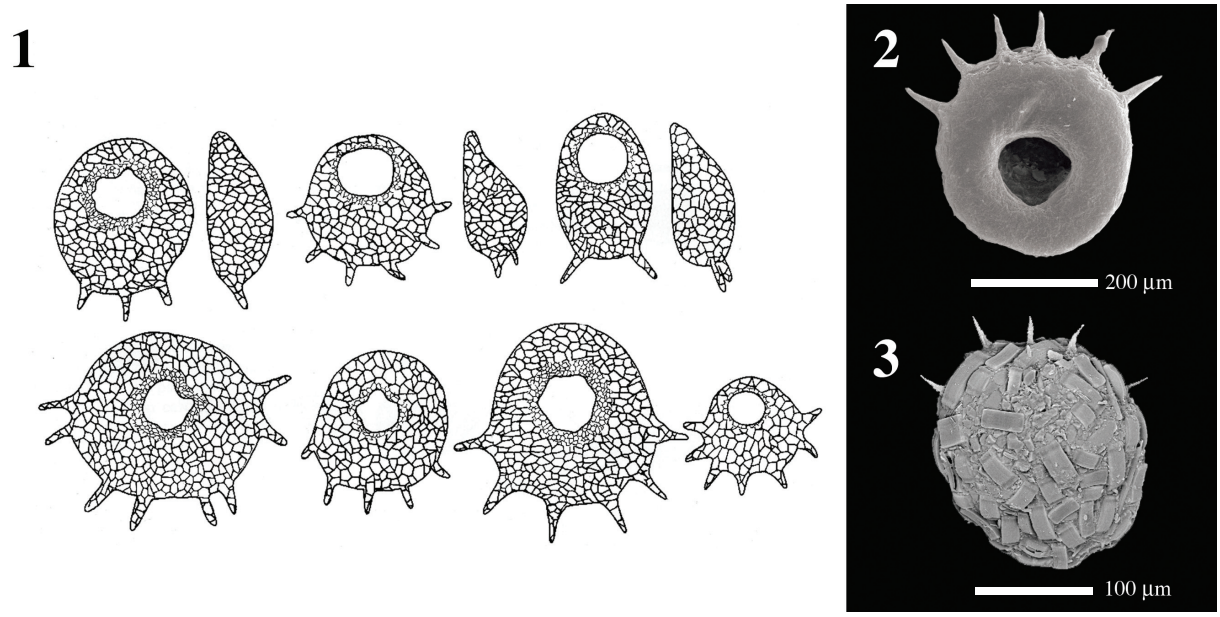

FIGURE 3. Specimens of *Centropyxis aculeata* (Ehrenberg, 1832), the type species of genus *Centropyxis*. **1**, redrafted sketches of *C. aculeata* from Leidy (1879, plate 31) (modified after Medioli and Scott, 1983, figure 11) showing some of the typical morphotypes within the species. **2** and **3**, scanning electron microscope of specimens from the lakes in the Yellowknife region, NT, Canada; ventral-apertural view showing the most common test morphology with semi-circular aperture and long spines extending from the fundus and very fine grained agglutination on ventral surface (**2**) and dorsal view showing xenogenous agglutination comprised both of diatom frustules and mineral grains (**3**).

found in various publications, notably Medioli and Scott (1983), Reinhardt et al. (1998), Roe et al. (2010), Patterson et al. (2012, 2013). Specimens of *C. pontigulasiformis* were identified in 25 lakes (Table 1). Light photomicrographs of arcellininids where taken using a Canon Rebel T1i, while Scanning electron microscope images were obtained using a Tescan Vega-II XMU VP scanning electron microscope at the Carleton University SEM facility.

TAXONOMY

Phylum AMOEBOZA (Lühe, 1913) Corliss, 1984
Subphylum LOBOSA Carpenter, 1861
Class TUBULINEA Smirnov et al., 2005
Subclass TESTACEALOBOSIA De Saedeleer, 1934
Order ARCELLINIDA Kent, 1880
Suborder ARCELLININA Haeckel, 1884
Superfamily DIFFLUGACEA Stein, 1859
Family CENTROPYXIDAE Jung, 1942
Genus *Conicocassis* gen. nov.

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Type Species. *Centropyxis pontigulasiformis* Beyens, Chardez and De Bock, 1986.

Diagnosis. A genus of Centropyxidae characterized by dorsoventrally symmetric, ovoid to subspherical test typically comprised of agglutinated particles obtained from the environment, round aperture and diagnostic very large and asymmetrically oriented conical to funnel-like apertural flange extending from a small circular aperture.

Description. Test free; unilocular; ovoid to subspherical to spherical; subcircular in cross section; test dorsoventrally symmetrical in most cases; test wall comprised of agglutinated particles derived from mineral or biologic sources bound together with an organic cement; aperture circular; proportionately very large conical to funnel-shaped and typically asymmetrically oriented flange extends from aperture; broad apertural rim recurved inward and comprised of fine agglutinated grains.

Types and Occurrence. Very wet mosses and aquatic environments in High Arctic regions of Europe and North America; lacustrine environments in the Central Northwest Territories of Canada; and peatlands in Germany, the Netherlands and Austria.

Dimensions. Length: 90–150 µm; width: 50–100 µm. Main test body: 50–100 µm across in all dimensions; funnel-shaped apertural flange: 25–50 µm across.

Remarks. Many of the diagnostic test features characterizing members of the family Centropyxi-

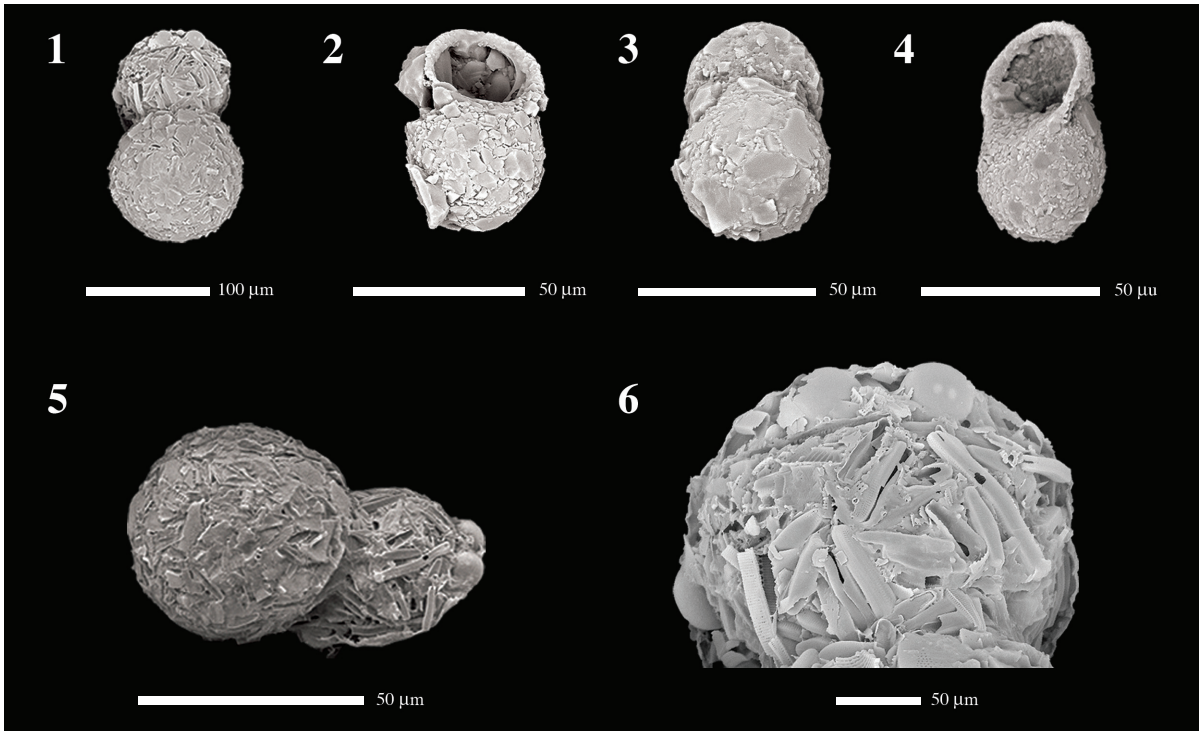

FIGURE 4. Specimens of *Conicocassis pontigulasiformis* gen. et comb. nov. from lakes in Yellowknife region, Northwest Territories, Canada. **1**, dorsal view of a specimen from sample BC8 showing the distinct main test body and distinctive upper funnel-like flange; **2**, apertural view of a specimen collected from sample BC12 showing large aperture; **3**, dorsal view of a specimen from sample BC12 with agglutination primarily comprised of large xenogenous particles; **4**, oblique view of a test collected from sample BC37 showing orientation of large flange relative to apertural opening; **5**, edge view of a specimen in sample BC12 showing the distinctive morphology of the main test body relative to asymmetric flange; and **6**, a close-up of the flange of a specimen collected from sample BC12 clearly showing that pennate diatoms, pollen grains and mineral particles are important components of the agglutination of this specimen.

dae (e.g., dorsoventral symmetry, chitinoid test and circular to oval aperture) are maintained in the new genus, *Conicocassis*. Therefore, *Conicocassis* is recognized as a member of the family Centropyxidae along with the genus *Centropyxis*. However, the new genus is readily distinguished from *Centropyxis* in having a two-component test comprised of an ovoid to subspherical main body, and a relatively very large conical to funnel-like and asymmetrically positioned flange extending out from a small circular aperture. In contrast *Centropyxis* tests tend to be beret-like to discoidal shaped with an invaginated ventral aperture. *Conicocassis* differs from some taxa of *Difflugia* (e.g., *D. urceolata* Carter, 1864, and *D. urens* Patterson et al., 1985), which are also characterized by apertural rims, in that the rim surrounding the aperture of the new genus tends to be asymmetrically placed and in most cases is nearly as large as the main test body.

The lower test body of *Conicocassis* is ovoid or subspherical to spherical with a wall composed of polymorphous mineral particles within an organic matrix. The colorless to brown main test body is topped by a cone-like flange, which extends out from a small circular aperture. The cone-like flange is mostly embossed with broken, or intact, diatoms frustules and quartz particles (Figure 4), and appears to be nearly as large as the main test body if observed from the apertural view. In some cases, the flange may be characterized by coloration distinct from the main test body. The attachment area of the apertural flange to the main test body produces a pronounced constriction in the test wall that is particularly diagnostic.

A statistically significant number of *Conicocassis* specimens (between 4 and 62 shells) was quantified in 12 surface sediment samples (Table 1) that were collected from lakes in the Yellowknife region in 2012 (personal observation). In addition to the stark morphological differences between specimens from *Conicocassis* and *Centropyxis*, it was possible to identify distinctive ecological preferences between differences between these gen-

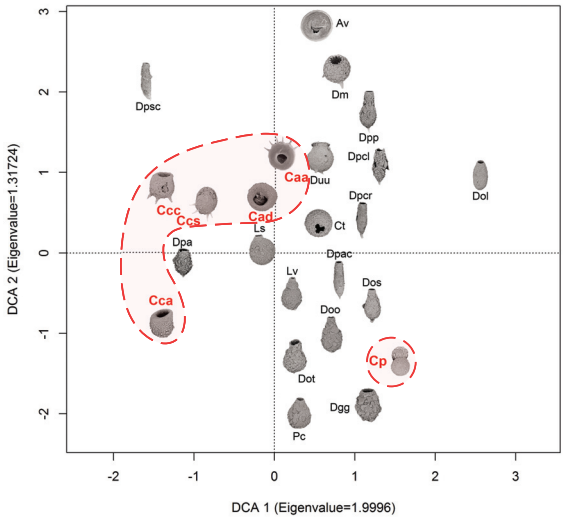

FIGURE 5. Detrended Correspondence Analysis (DCA) bi-plot based on species scores showing the faunal distribution of arcellininid species and strains in the Yellowknife region. Abbreviations: Av, *Arcella vulgaris*; Caa, *Centropyxis aculeata* "aculeata"; Cad, *Centropyxis aculeata* "discoides"; Cca, *Centropyxis constricta* "aerophila"; Ccc, *Centropyxis constricta* "constricta"; Ccs, *Centropyxis constricta* "spinosa"; Cp, *Conicocassis pontigulasiformis*; Ct, *Cucurbitella tricuspis*; Dgg, *Difflugia glans* "glans"; Dol, *Difflugia oblonga* "lanceolata"; Doo, *Difflugia oblonga* "oblonga"; Dos, *Difflugia oblonga* "spinosa"; Dot, *Difflugia oblonga* "tenuis"; Dpa, *Difflugia protaeiformis* "amphoralis"; Dpac, *Difflugia protaeiformis* "acuminata"; Dpcl, *Difflugia protaeiformis* "claviformis"; Dpcr, *Difflugia protaeiformis* "curvicaulis"; Dpp, *Difflugia protaeiformis* "protaeiformis"; Dpsc, *Difflugia protaeiformis* "scalpellum"; Duu, *Difflugia urceolata* "urceolata"; Ls, *Lesquereusia spiralis*; Lv, *Lagenodifflugia vas*; Mc, *Mediolus coron*; Pc, *Pontigulasia compressa*.

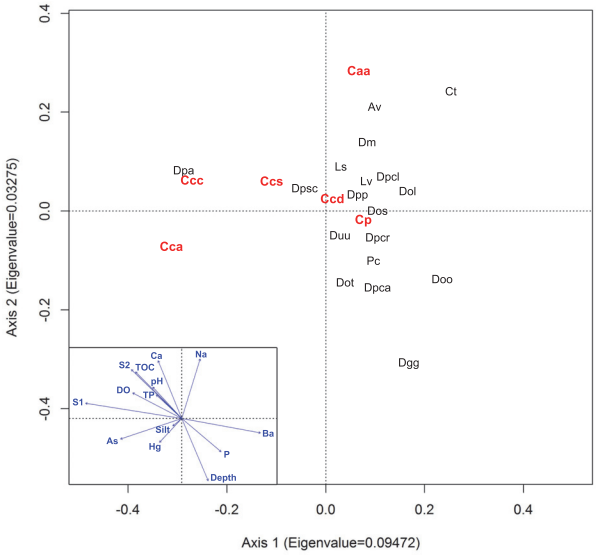

FIGURE 6. Redundancy Analysis (RDA) species-environment-sample tri-plot. Environmental variables (arrows) are shown in the inset to avoid a clutter. Abbreviations: As, arsenic; Ba, barium; Ca, calcium; DO, dissolved oxygen; Hg, mercury; Na, sodium; P, phosphorous; S1, S1 carbon; S2, S2 carbon; TOC, total organic carbon; TP, total phosphorous. See Figure 5 caption for other abbreviations.

era using multivariate analyses techniques like Detrended Correspondence Analysis (DCA) and Redundancy Analysis (RDA). The DCA results revealed *Conicocassis* plotting at a significant distance from the *Centropyxis* species and strains, which clustered closely together (Figure 5), indicating a fundamental difference in realized niche space for *Centropyxis* and *Conicocassis*. The RDA analysis results showed that *Conicocassis* is influenced by environmental variables associated with relatively healthy and productive environments (e.g., barium and phosphorous), whereas stress tolerant centropyxid taxa were most strongly associated with significant environmental stressors (e.g., elevated levels of arsenic; Figure 6).

Etymology. From the Latin *Conicus*, cone, cone-like + o, connective vowel + Latin *Cassis*, helmet, with reference to the distinct shape of the pronounced apertural flange. The gender for this new genus is feminine.

Stratigraphic Range. Holocene.

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