

EXCEPTIONALLY PRESERVED LATE ALBIAN (CRETACEOUS) ARCELLACEANS (THECAMOEBIANS) FROM THE DAKOTA FORMATION NEAR LINCOLN, NEBRASKA, USA

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ABSTRACT

Thousands of exceptionally well-preserved Arcellaceans (Thecamoebians) have been recovered from a Late Albian (Cretaceous) deposit. Sedimentary samples were obtained from a clayey-silt leaf bed in the Dakota Formation, outcropping in a clay pit excavated by the Yankee Hill Brick Company, located near Lincoln, Nebraska. Based on recovered freshwater macrophyte spore and fossil remains, the leaf bed is a lagerstätten of paleobotanical remains in which the paleoenvironment has been interpreted as a quiescent freshwater setting. The large number of recovered thecamoebians revealed a high intraspecific variability in test morphology that is comparable to Holocene thecamoebian populations. Consequently, we employ the thecamoebian strain taxonomic framework, a first for ancient thecamoebians. Extant species contained in this collection include *Diffflugia oblonga*, *Diffflugia protaeiformis*, *Diffflugia urens*, *Pontigulasia compressa*, *Lagenodiffflugia vas*, *Cucurbitella tricuspis*, *Lesquereusia spiralis* and the cysts of environmentally stressed protozoans—with only one new species reported, *Diffflugia baukalabastron*. The well-preserved nature of the taxa, suggesting little taphonomic bias, and the lack of significant new species supports the current hypothesis of minimal evolution in thecamoebian lineages through geologic time.

INTRODUCTION

Thecamoebians are cosmopolitan in most modern freshwater habitats from moist tree bark, to soils, wetlands and lakes. However, detailed knowledge of their evolutionary history and paleoecology is minimal due to their scarce fossil record. Thecamoebians are a polyphyletic group of rhizopods that flourish in fresh-to-brackish water regimes. Throughout their life, thecamoebians maintain a simple secreted (autogenous) or agglutinated (xenogenous) test that may become a constituent of the sedimentary record following death. As thecamoebian populations are ecologically sensitive to environmental conditions, they are a valuable proxy in paleolimnological and paleoenvironmental reconstructions (e.g., Asioli and Medioli, 1993; McCarthy and others, 1995; Medioli and others, 1995; Asioli and others, 1996; Burbridge and Schröder-Adams, 1998; Reinhardt and others, 1998; Dallimore and others, 2000; Lloyd, 2000; Patterson and Kumar, 2002; Patterson and others, 2002; Reinhardt and others, 2005). This utility

is diminished, however, because some of the fragile autogenous tests are susceptible to post-depositional destruction, and the fossil record is usually skewed in favor of the agglutinated forms. This bias is pronounced in deep-time deposits, in which taphonomic processes can severely bias or eliminate any thecamoebian record, although in ideal circumstances, deep-time geologic fossil thecamoebians can be found and provide important data on evolutionary trends (e.g., Medioli and others 1990a, 1990b; Schönborn and others, 1999; Porter and Knoll, 2000; Schmidt and others, 2004).

Thecamoebians have been studied and classified for over two centuries, but significant taxonomic confusion has developed because the group exhibits high intraspecific variability. This has resulted in many synonymies, misnomers and inconsistencies in the literature. However, the taxonomic framework established by Medioli and Scott (1983) revitalized the paleontological usefulness and applicability of the thecamoebian group through standardization of the taxonomy, and micropaleontologists working with lacustrine thecamoebians generally accept this classification. Such a taxonomic framework is applied to the recovered Cretaceous individuals described herein. Further subdivision of this classification is based on ecophenotypes (strains), which are recognized through the repeated observation of specific morphological variants of the same species in similar modern environments (e.g., Asioli and others, 1996). Although the International Code of Zoological Nomenclature does not formally accept this trinomial taxonomic framework, ecophenotypes designated as strains now often facilitate the interpretation of thecamoebian assemblages (e.g., *Diffflugia oblonga* “triangularis,” *Centropyxis aculeata* “aculeata;” see Kumar and Dalby, 1998 and Patterson and others, 2002 for additional examples). Thecamoebians from pre-Quaternary lacustrine deposits, however, are rarely identified with confidence to the specific level, let alone characterized as a strain.

Eight of the modern thecamoebian families to date have a fossil record: *Arcellidae*, *Centropyxidae*, *Plagiopyxidae*, *Diffflugidae*, *Hyalophenidae*, *Phyrganellidae*, *Euglyphidae* and *Cyphoderiidae* (Fig. 1). These taxa were found in various modes of preservation which include autogenous tests encased in ancient tree amber (e.g., Waggoner, 1996a), compressed euglyphid siliceous plates in bulk sediment (e.g., Porter and Knoll, 2000), and pristine test preservation in wet-sediment residues (e.g., Medioli and others, 1990a; this study). The best examples of fossil thecamoebians are those preserved in ancient amber (i.e., Schmidt and others, 2004; Waggoner, 1996a), whereas examples from other modes of preservation require more critical evaluation (see Medioli and others, 1990b for a detailed review). Porter and Knoll (2000) documented Neoproterozoic marine thecamoebians that are assigned to modern freshwater genera,

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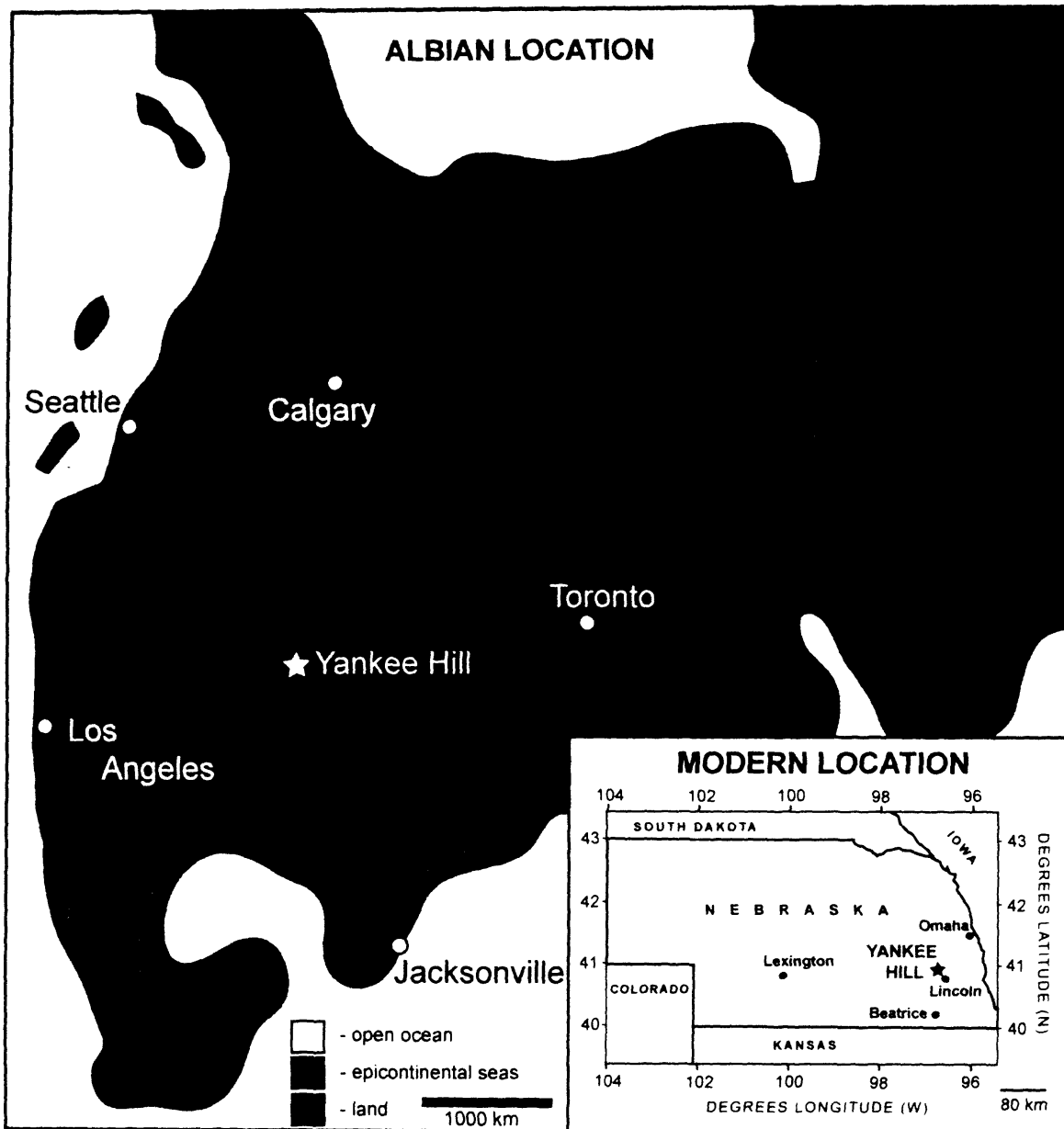


FIGURE 2. A paleogeographic map of North America during the late Early Cretaceous, illustrating the Western Interior Seaway and Yankee Hill site (adapted from White and others, 2001). The outcrop location is also noted on the modern geographic inset. Present-day co-ordinates of the outcrop are $40^{\circ} 45' 34.8''$ N and $096^{\circ} 47' 37.2''$ W.

bian tests were abundant in the residue, and exceptional tests were selected for scanning electron microscopy (SEM). Individuals were mounted and gold sputter-coated to increase electrical conductivity for SEM with a Philips 515 SEM equipped with a lanthanum hexaboride filament at the Canadian Centre for Electron Microscopy at McMaster University.

Within this sample set, some of the thecamoebians retained their original test characteristics, whereas others had undergone some post-depositional compression and flattening. Medioli and others (1990a) described a similar preservation state in assemblages of Cretaceous-age thecamoebians. Despite compression of the test, however, many test and aperture characteristics were preserved. Depending upon

the final orientation of the test with respect to the bedding plane, the subsequent sediment overburden has the potential to compress the test differently. This compression creates variability in the final appearance of the test and can create some confusion when describing different taxa. To facilitate communication and for clarity of descriptions, the following terms were used to describe the taxa.

Apertural-fundal compression. This occurs when the tectum has settled vertically in the sediment, and subsequent sedimentation has vertically compressed the tectum. The resultant two-dimensional tectum can potentially preserve apertural characteristics and the plan-view terminal outline of the tectum. With this type of compression, tests that are asymmetrical about their long axis are difficult

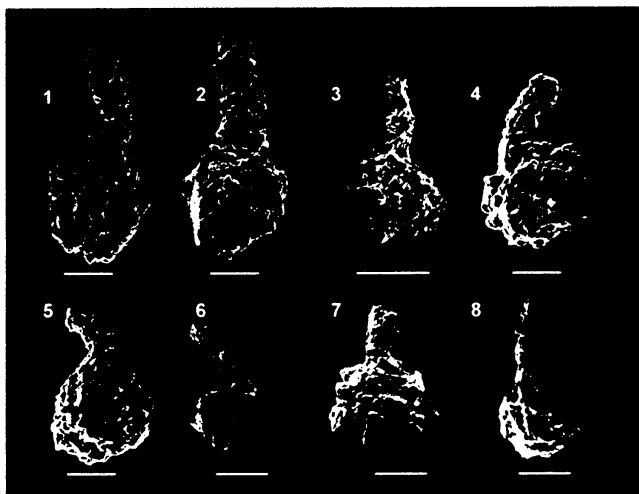


PLATE 1

Type series for the new species *Diffflugia baukalabastron*. 1 Holotype specimen with Royal Ontario Museum (ROM) catalogue #57863, X482. 2–5 Paratype specimens: 2 ROM #57863, X482; 3 ROM #57863, X600; 4 ROM #57864, X745; 5 ROM #57865, X720. 6–8 Additional examples: 6 X503; 7 X503; 8 Side view of specimen with lateral compression X503. Scale bar represents 50 μm .

to identify to the species level (i.e., *Lesquereusia spiralis*) and fundal characteristics—such as tapering, spines, and spinous processes—are potentially impossible to interpret.

Lateral compression. This occurs when the tectum has come to rest on its side (the body axis parallel to the bedding plane) and has been subsequently compressed by the sediment overburden. The preserved fossil can potentially retain the outline of the tectum. However, three-dimensional diagnostic features for modern thecamoebians will be distorted (i.e., subtle lateral compression in *Diffflugia bidens*). Elongated taxa will be easier to identify with this type of compression.

Oblique compression. This occurs when the tectum has come to rest at an angle oblique to the long axis of its tectum, either on the aboral (fundal) or the apertural terminus. Subsequent sediment deposition compresses the tectum at an angle, often obscuring the apertural and fundal features. This form of compression is the most awkward type when attempting to identify specimens, especially if rare or new taxa are present in the fossil collections. Elongated tests will be highly deformed by this type of compression (i.e., *Diffflugia oblonga* “oblonga”) and are most susceptible to fragmentation.

SYSTEMATIC PALEONTOLOGY

Giving official taxonomic names to intraspecific variations in phenotype is not considered valid according to the International Code of Zoological Nomenclature. However, the practice of dividing thecamoebians into strains continues because of its utility for paleoecological applications: researchers continue to find variants that dominate specific environmental conditions (see ecophenotypes of Reinhardt and others, 1998, 2005; Patterson and Kumar, 2002; Patterson and others, 2002; Kumar and Patterson, 2000). Where relevant, detailed observations of the fossil specimens are provided to aid future workers in identifying similar fossil

taxa, but only limited taxonomic details are provided for each established taxon. For full taxonomic information, we refer the reader to Medioli and Scott (1983, 1985).

Before addressing the systematic paleontology, there are several general observations that apply equally to all the fossils preserved in the investigated unit. There is no apparent agglutination of diatom frustules or other biogenic mineral remains: xenosomes are only made of clastic materials, such as quartz and platy minerals. In Plates 1 and 2, we give a scale for individual specimens, but actual variation in specimen size is highly variable. Additionally, due to post-depositional sediment compression, preservation of the original spherical structure is rare in specimens $>50 \mu\text{m}$ in diameter. The notable exception is the shape of encysted forms, which remain spherical. Spinous processes also seem to suffer during the fossilization process, becoming bent and broken. As a result, care was taken not to over-interpret the preserved morphology of a single specimen, and multiple specimens were observed under light and scanning electron microscopy to generate a taxonomic classification for a group exhibiting similar external morphology. Due to high intraspecific variability, we advocate that thecamoebian identification should always be based on relatively large numbers of individuals where possible in both recent and ancient collections. Multiple scanning electron micrographs of highly variable groups (i.e., *Diffflugia oblonga*) have been provided to better illustrate the high level of intraspecific variability. The exceptions are *Pontigulasia compressa* and *Diffflugia urens*. The V-shaped neck restriction in *P. compressa* and apertural characteristics of *D. urens* were not discernable when using SEM, but were visible when using light microscopy.

Phylum PROTOZOA Goldfuss, 1818
 Subphylum SARCODINA Schmarda, 1871
 Class RHIZOPODA von Siebold, 1845
 Subclass LOBOSA Carpenter, 1861
 Order ARCELLINIDA Kent, 1880
 Superfamily ARCELLACEA Ehrenberg, 1830
 Family DIFFLUGIDAE Stein, 1859
 Genus *Diffflugia* Leclerc in Lamarck, 1816
Diffflugia baukalabastron n. sp.
 Pl. 1, figs. 1–8

Diagnosis. A rounded and bulbous fundus continues into an elongated neck that exhibits minor curvature, as best illustrated in the holotype. Variability in the curvature of the neck gives rise to much of the intraspecific variation, with some individuals displaying a completely straight neck, whilst others appear to make an almost complete turn after emerging from the fundus. The ratio of the neck length to total test length is consistently 0.6–0.7. Frequent use of platy minerals for xenosomes was observed. The aperture does not appear to be crenulated, and many specimens exhibited lateral compression. However, it is not uncommon to see only the neck or body flattened.

Origin of name. Amalgamation of the Greek word for an ointment storage vase, “alabastron,” and the Latin word for a narrow-necked flask, “baukalion.” Thus, the name means a narrow-necked storage flask, which describes the morphology of this specimen.

Holotype. Plate 1, figure 1, deposited in the Royal Ontario Museum with Catalogue Number #57863.

Paratypes. Plate 1, figures 2–6, deposited in the Royal Ontario Museum with Catalogue Numbers #57864, #57865, #57866, #57867, #57868, respectively.

Remarks. This species is very similar to *Diffflugia bacillifera* as presented in McCarthy and others (1995, Figs. 2, 3–9). However, the occurrence of the elongated, curved and narrow neck in most

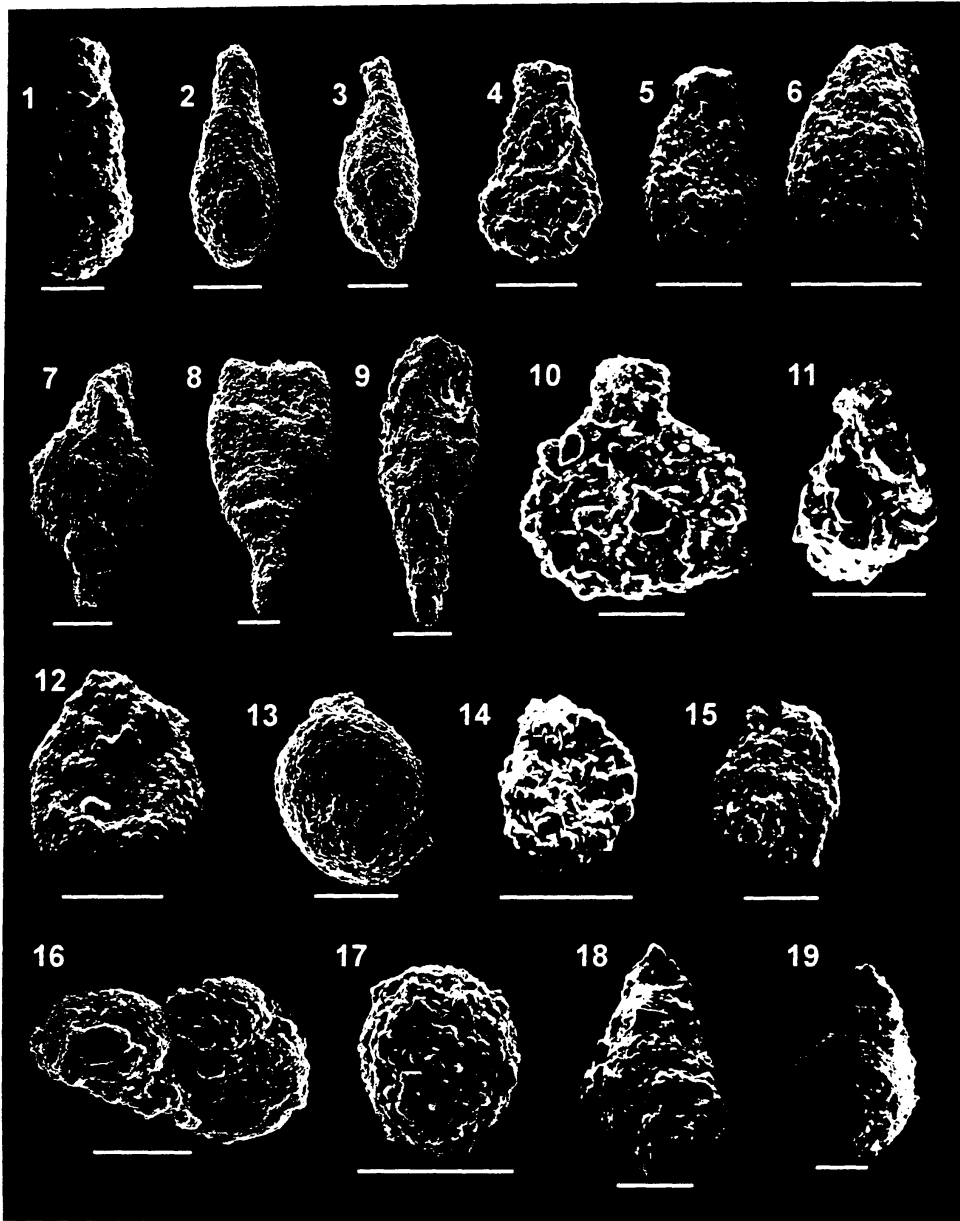


PLATE 2

1-7 Intraspecific variation observed in *Diffflugia oblonga*: 1 *Diffflugia oblonga* "oblonga," X482; 2 *Diffflugia oblonga* "oblonga," X406 3 *Diffflugia oblonga* "spinosa," X326; 4 *Diffflugia oblonga*, morphotype exhibiting a more triangular test, X406; 5 *Diffflugia oblonga* "tenuis," X745; 6 *Diffflugia oblonga* "tenuis," X526; 7 *Diffflugia oblonga* "spinosa," X241, note the heavily deformed apertural region. 8 *Diffflugia protaeiformis*, X252; 9 *Diffflugia protaeiformis*, X241. 10 *Diffflugia urens*, X625. 11 *Lagenodiffflugia vas*, X710. 12-15 *Cucurbitella tricuspis*: 12 Specimen with oblique compression, X775; 13 Specimen with test shape preserved, X600; 14 Specimen highly laterally compressed obscuring the aperture, X965; 15 Specimen with lateral compression with apertural lobes flattened outwards, X775. 16 Two *Cucurbitella* specimens fused together, X424. 17 The cystic test of a protist "cyst," X925. 18 *Lesquereusia spiralis* "cusplabrum," laterally flattened, obscuring the test shape, X573; 19 *Lesquereusia spiralis* "cusplabrum," with original shape, X503. Scale bar represents 50 μ m.

specimens of *D. haukalabastron* differentiates this species from *D. bacillifera*.

Diffflugia oblonga Ehrenberg, 1832

Pl. 2, figs. 1-7

Diffflugia oblonga Ehrenberg, 1832, p. 90.

Diffflugia oblonga Ehrenberg in Medioli and Scott, 1983, pl. 2, figs. 1-27.

Remarks. This species exhibits the highest intraspecific variation observed in the collection and is very common. In Holocene environments, up to eleven readily identifiable strains can be discerned in the same sample residue. Although we could not identify eleven strains in this sample set, it is not surprising that we have

recovered four: *Diffflugia oblonga* "oblonga," *Diffflugia oblonga* "spinosa," *Diffflugia oblonga* "tenuis" and *Diffflugia oblonga* "undifferentiated." Many specimens were laterally compressed (Pl. 2, fig. 5), with only a few that retained their original shape (Pl. 2, fig. 1). The similarity to Holocene individuals is striking (see Patterson and Kumar, 2002).

Diffflugia protaeiformis Lamarck, 1816

Pl. 2, figs. 8-9

Diffflugia protaeiformis Lamarck, 1816, p. 95 (with reference to material by LeClerc).

Diffflugia protaeiformis Lamarck in Medioli and Scott, 1983, pl. 1, figs 15-20.

Remarks. Very few representatives were found in the samples. The fundus of specimens tapered into a single spinous process, and the aperture was wide in comparison to some of the Holocene material observed (i.e., Fig. 4 from Medioli and Scott, 1983). The neck was repeatedly absent in these specimens. Xenosomes were always fine-grained. Extremely narrow strains of this species retained the original test shape. Incidentally, there was an increase of lateral compression with an increase in overall test width. Tests displaying oblique compression were highly deformed and could potentially be mistaken for *Diffflugia oblonga*. Although different strains were not designated, variability in this species was second only to *Diffflugia oblonga*.

Diffflugia urens Patterson, MacKinnon, Scott and Medioli, 1985

Diffflugia urens Patterson, MacKinnon, Scott and Medioli, 1985, p. 130, pl. 3, figs. 5–14.

Remarks. Recovered specimens are morphologically similar to Holocene specimens, except that the majority exhibit lateral compression. One specimen was observed with apertural-fundal compression and had a well-preserved aperture, providing a positive identification for this taxon. *Diffflugia urens* are very rare in the Yankee Hill collection, and the collar is fragile and susceptible to breakage.

Pontigulasia ? cf. *compressa* (Carter, 1864)

Diffflugia compressa Carter, 1864, p. 22, pl. 1, figs 5, 6.

Pontigulasia compressa (Carter, 1864) in Rhumbler, 1895, p.105, pl. 4, figs. 13a, b.

Pontigulasia compressa (Carter, 1864) in Medioli and Scott, 1983, pl. 6, Figs. 5–14.

Remarks. This species is very rare in the collection—less than ten individuals were recovered. The V-shaped restriction below the neck was only visible through light microscopy, and it is not observable under scanning electron microscopy. All specimens exhibit lateral compression. Additional specimens are needed to confirm this taxon in the Late Albian.

Lagenodifflugia ? cf. *vas* (Leidy, 1874)
Pl. 2, fig. 11

Diffflugia vas Leidy, 1874, p. 155.

Lagenodifflugia vas (Leidy, 1874) Medioli and Scott, 1983.

Remarks. This species was common, and the circular restriction in the neck around the circumference was apparent. Most individuals exhibit lateral compression.

Family HYALOSPHEIIDAE Schulze, 1877
Genus *Cucurbitella* Penard, 1902
Cucurbitella tricuspis (Carter, 1856)
Pl. 2, figs. 13–16

Diffflugia tricuspis Carter, 1856, p. 221, fig. 80.

Cucurbitella tricuspis (Carter) Medioli, Scott and Abbott, 1987, p. 42, pls. 1–4, text figs. 1, 4.

Remarks. This group displayed all types of test compression. Lateral compression often projected the cusped lobes upward, a deformity that aided the taxonomic classification (Pl. 2, fig. 15). When oblique compression occurred, then the aperture was often visible in its entirety (Pl. 2, fig. 12). Fundal-apertural compression often obscured the aperture completely, thus making the tests frequently indiscernible from cysts.

Genus *Lesquereusia* Schlumberger, 1845
Lesquereusia spiralis (Ehrenberg, 1840)
Pl. 2, figs. 18, 19

Diffflugia spiralis Ehrenberg, 1840, p. 199.

Lesquereusia spiralis (Ehrenberg) Schlumberger, 1845, p. 225.

Lesquereusia spiralis (Ehrenberg) in Patterson, MacKinnon, Scott and Medioli, 1985.

Remarks. Two general morphotypes were observed: (1) *Lesquereusia spiralis* “cusplabrum,” which has a pointed lip located at the lateral extreme of the neck and pointing in the body plane and (2) *Lesquereusia spiralis* “undifferentiated,” which is morphologically alike to modern specimens. It was decided that it was not necessary

to erect a new species to account for the strain *Lesquereusia spiralis* “cusplabrum” based on the species concept employed in this analysis (Reinhardt and others, 1998). This is supported by the rarity of recovered specimens (less than ten) and the possibility for natural phenotypic variation in the ancient population. This taxon was found with only lateral compression, albeit we did find a sole specimen with the original spherical shape preserved (Pl. 2, fig. 19).

Incerta Sedis
(Pl. 2, fig. 17)

Diagnosis. Sphere of agglutinated xenosomes that is hollow upon breakage. An aperture is not discernable.

Remarks. These spheres are interpreted as encysted protozoa. The appearance is very similar to that of Holocene (i.e., Belmonte and others, 1997; Dalby and others, 2000) and Carboniferous specimens (Wightman and others, 1994). Because both ciliate and amoeboid protozoans are known to encyst under environmentally harsh conditions, we can only surmise that this is a cyst and are uncertain if it is, indeed, a thecamoebian (as it could be a tintinnid cyst). However, for paleoenvironmental interpretations, a general increase in the abundance of cysts could indicate environmentally stressed protist populations (see discussions about cysts in Corliss and Esser, 1974; Belmonte and others, 1997; Müller and others, 2002).

DISCUSSION AND CONCLUSIONS

An exceptionally well-preserved Cretaceous thecamoebian assemblage was documented from a sedimentary outcrop of the Dakota Formation in southeastern Nebraska. Excluding the new species, *Diffflugia baukalabastron*, all other specimens were assigned to extant species within the following genera: *Diffflugia*, *Lagenodifflugia*, *Pontigulasia*, *Lesquereusia* and *Cucurbitella*. High intraspecific morphological variability was observed, particularly in the “oblonga” and “tenuis” strains of *Diffflugia oblonga*, and suggests that the modern strain concept is applicable to ancient thecamoebians. The intraspecific variations that were observed in *Diffflugia oblonga* and *D. protaeiformis* are comparable to those of modern populations. Typical thecamoebian taxonomists erect new species based on subtle morphological variation (i.e., compare *Diffflugia corona* Wallich, 1864 and *Diffflugia tuberspinifera* Hu, Shen, Gu, and Gong, 1997), with little consideration of the natural morphological variability that exists within the individual species themselves. This case study (1) applies the strain concept to the oldest fossil thecamoebians to date, (2) accurately describes individuals comparable to modern taxa and (3) exemplifies the applicability of this taxonomic method. The intraspecific variation observed here demonstrates that thecamoebian species in the geologic past were as variable as modern species.

Thecamoebians indiscriminately acquire available material from their benthic environment for use as xenosomes, and modern individuals frequently use diatom frustules. Consequently, it was readily recognized that diatom frustules were not used as xenosomes in this Cretaceous collection. Although diatoms have a marine fossil record that stretches potentially back to the Jurassic, their adaptation and migration to freshwater habitats only occurred during the Eocene in North America (Wolfe and Edlund, 2005; Krebs, 1994). The lack of agglutinated frustules as xenosomes is supporting evidence for the current understanding of diatom evolution.

The documentation of Neoproterozoic thecamoebians by Porter and Knoll (2000) from marine strata suggests

a marine origin for the thecamoebian group, as they are almost exclusively documented in modern fresh to brackish water. Our well-developed, freshwater thecamoebian community from the Cretaceous and others from the Mesozoic (Fig. 1) suggest a possible migration from marine to freshwater in the early Paleozoic. However, this issue will only be resolved through additional fossil thecamoebian finds from the Paleozoic (e.g., Vasicek and Rusicka, 1957; Thibudeau and others, 1987; Wightman and others, 1994).

We cannot explain the lack of centropxyid fauna in this collection. In modern lacustrine environments, difflugid communities are consistently accompanied by taxa such as *Centropxyxis aculeata*. Medioli and others (1990a) report a centropxyid-like taxon from Cretaceous strata, so their presence would be expected in this collection as well. Lack of preservation is not a satisfactory explanation because the recovered taxa have the same preservation potential as centropxyid taxa today.

Finally, although we cannot be certain that the cysts presented here are in fact even members of the Sarcodina, the preservation of cysts holds important paleoecological potential in reconstructing ancient lacustrine environments. Thecamoebians are not the only protist taxon capable of encysting under stressed conditions; other Sarcodina, ciliates, and flagellates use this mechanism to enable the organism to survive numerous years without additional nutrition. Although the cysts presented here are different from the modern cysts of *Difflugia urceolata* of Scott and others (1983), they are identical to those recovered by Dalby and others (2000). The consistent lack of a discernible aperture, presence of a hollow, spherical structure, and frequency of their recovery suggest that they are protozoan cysts. It is likely that high abundances of cysts relative to complete tests can be used as a paleoenvironmental tool: high abundances of cysts suggest environmentally harsh conditions that have forced a portion of the protist population into a cystic state of dormancy.

The results of this study do not extend the fossil record for any of the thecamoebian lineages. However, this study demonstrates that exceptionally preserved thecamoebians can be extracted from deep-time sedimentary outcrops and provide the promising potential of using thecamoebians as an ancient proxy in terrestrial and freshwater environments. Questions surrounding the evolution and early ecology of thecamoebians will only be resolved through the continued documentation of well-preserved individuals in the geologic record.

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