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**HOLOCENE ARCELLACEA (THECAMOEBIANS)
FROM EASTERN CANADA**

by

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ABSTRACT

A previous geological study of bottom and core samples of fossilized Holocene freshwater thecamoebians, involving the study of thousands of specimens belonging almost entirely to the superfamily Arcellacea, has prompted us to revise some of the rather confused taxonomy of several common genera. The Arcellacea present numerous cases of morphological test intergradation between main phenetic clusters. This has led specialists to propose classifications that recognize almost every rare morphotype as a distinct taxon (species or "variety"). We believe that such intergradation, which is at the basis of the confusion in these genera, is mainly due to the rarity of sexual events. We discuss the rationale and practical criteria for recognizing "species" among such uniparental or almost uniparental organisms. Apart from the problem of intergradation in fossil thecamoebians, taxonomic difficulties also arise from the absence of basic diagnostic characteristics (such as pseudopodia and others). We discuss how the importance of pseudopodial types in thecamoebian microclassification may have been exaggerated. More difficulties stem from the fact that in the past many arcellacean species and varieties have been defined according to the nature of their xenosomes (foreign agglutinated particles). While the shape of idiosomes (test particles secreted by the organism) may be a valid taxonomic characteristic, in most cases the

nature of the xenosomes depends on the availability of inorganic particles and not on genome-based selectivity.

The discussion of these problems leads us to define arcellacean species as wide phenetic clusters in which specimens are linked to each other through intergradation. In most cases the intergradational series were selected from large contiguous populations. We have organized accordingly the taxonomy of fourteen species (some of which can themselves be linked to each other by scarcer intermediate specimens) instead of the several dozens of species in which the same organisms were divided by earlier authors. The fourteen species (in five genera) are: *Diffflugia protaeiformis* Lamarck, *D. bacilliarum* Perty, *D. bidens* Pénard, *D. corona* Wallich, *D. fragosa* Hempel, *D. globulus* (Ehrenberg), *D. oblonga* Ehrenberg, *D. urceolata* Carter, *D. tricuspis* Carter, *Lagenodiffflugia vas* (Leidy), *Pontigulasia compressa* (Carter), *Heleopera sphagni* (Leidy), *Centropyxis aculeata* (Ehrenberg), and *C. constricta* (Ehrenberg). These species are redescribed, discussed, and their fossilized forms illustrated. The literature indicates that these species are cosmopolitan and usually form a large percentage of the lacustrine faunas everywhere. Hence the taxonomy presented here is potentially applicable universally.

INTRODUCTION

The thecamoebians are an artificial array of testatean rhizopods or shelled amoebas (Deflandre, 1953). They include forms of two or three classes and two or three orders of the current protozoan classifications; only a small fraction of one order (the Arcellinida) appears to be common in the fossil state. The vast majority of forms included in the thecamoebians have little or no paleontological importance.

From 1816 on, many species of Arcellacea have been described, often uncritically and with very little con-

sideration for the rules of nomenclature or for the previous literature. While the taxonomy of lacustrine species dominated the literature from 1816 to the 1930s, recent decades have seen a shift of emphasis towards the taxonomy of soil and mesopsammic forms and towards ecological studies in general. Fossilized and subfossil material has been almost completely ignored although Arcellaceans can be quite conspicuous in Holocene lacustrine sediments. They have been reported, although we have some reservations about these records, in older deposits, some as old as Carboniferous (Vašíček and Růžička, 1957).

A recent, comprehensive and exquisitely illustrated book by Ogden and Hedley (1980) updates and illustrates numerous taxa within the frame of a somewhat traditional taxonomy. The microclassification of the group remains, despite this excellent effort, in a chaotic state and only a systematic, thorough and critical review of the entire superfamily will gradually bring some order. We have based our taxonomy on a review of the literature as thorough as possible and on a unique study of large populations of thousands of specimens. From those large populations material was drawn for the intergradational series illustrated in the plates at the end of this paper. In cases where the material of a particular morphotype was scarce (e.g., *Lecquereusia*-like specimens) we have made no changes in the general taxonomy although we feel that some will be necessary when more information becomes available.

This paper is our contribution to the solution of the problem of arcellacean taxonomy. Its objective is that of stabilizing, on a reasonably critical basis, a number of Holocene species of arcellaceans which are of micropaleontological interest. The study is centered on material collected from Lake Erie, but also includes material from numerous lakes in Atlantic Canada and the western shores of James and Hudson Bays.

METHODS OF COLLECTION AND PREPARATION

Most of the samples studied were collected in Lake Erie by personnel from the Canadian Center for Inland Waters (cruises directed by R. Thomas) aboard the research vessel C.S.S. *Limnos*. Surface samples from the central and eastern basins were collected in October, 1978; surface samples in the western basin and all cores were obtained in October, 1979 (see Scott and Medioli, 1983).

Surface samples were collected using a grab sampler; at each station a couple of 20 cc replicate samples were removed from the grab. Cores were obtained using a Benthos gravity corer.

Surface samples were fixed in formalin subsequent to collection. Following shipment to Halifax, 20 cc samples were sieved using a .5 mm screen to retain coarse organics and shells and a .063 mm screen to retain arcellaceans. Fine organics were separated from arcellaceans by decantation. Following the concentration procedure a mixture of formalin and rose Bengal (a stain used to detect living matter) was added to the sample and, after standing overnight, samples were rinsed and placed in denatured ethanol.

Core samples were treated in a similar manner but no formalin was added; the samples were simply placed

in ethanol. Some samples contained excessive sand, they were dried and the arcellacean tests floated with carbon tetrachloride. These samples were subsequently resuspended in ethanol. Samples were examined using a dissecting microscope.

Occasionally material from James Bay and from various ponds in Nova Scotia and New Brunswick has been used; this material has been treated as described above.

GENERAL CHARACTERISTICS OF ARCELLACEA

The animal consists of a test with an aperture and a cytoplasmic amoeboid body with nucleus, inclusions, and pseudopods which branch out from the aperture like those of the Foraminifera.

Arcellacean tests, although there are many exceptions, are roughly sack-shaped (generally similar to that of the foraminiferan *Saccamina*) and are either made of purely organic matter or they grade into a test made of variable proportions of foreign material agglutinated in an organic matrix. Deflandre (1953) gave a detailed description of the biology of thecamoebians with an excellent coverage of the Arcellacea.

The vast majority of the Arcellacea belongs to the microfauna of freshwaters and of sufficiently moist places (soils, etc.) but a few forms live in more or less "oligohaline" waters (as defined in Reid, 1961).

Numerous authors have shown that different ecological niches are often characterized by different thecamoebian faunules. This was predictable for a group that inhabits such diverse environments as soil, sphagnum, ponds, lakes, ditches, tree bark and, in general, any sufficiently wet area. This characteristic of the group has already proven to be useful in the study of Holocene paleocology (Scott and Medioli, 1983).

The Arcellacea, so far as we know, are cosmopolitan. Mechanisms of distribution have been suggested by Pénard (1902) and further elaborated by Decloître (1953). As the Arcellacea can encyst and withstand prolonged desiccation, winds and aquatic birds can carry them around the globe alive.

Arcellaceans, with exceptions, reproduce once every two to eleven days by simple asexual fission of the parent cell (Ogden and Hedley, 1980). Sexuality appears to be rare but not absent (Valkanov, 1962a, b, 1966).

CLASSIFICATION

This paper is essentially concerned with the generic and specific classification of fossilized Arcellacea, but

we shall occasionally extend outside the limits of the superfamily Arcellacea in the course of the discussions that follow.

CRITERIA FOR THE CLASSIFICATION OF THECAMOEBIANS

Ideally, a suprageneric classification of protists should be based on a variety of ultrastructural characteristics, not only on those revealed by the light microscope. Practical reasons, however, seldom permit this and the fact that the light-microscopic features utilized to classify thecamoebians are poor in taxonomically significant information (e.g., test shape, the debatable presence or absence and nature of xenosomes, nature of the pseudopodia) is probably the source of much confusion.

Thecamoebians have often been divided, according to the usual aspect of their pseudopods, into "lobose," "filose" and "granuloreticulose" forms, although the supposed granuloreticulose thecamoebians (e.g., *Lieberkuehnia*) are often considered to be primitive foraminifera (Loeblich and Tappan, 1964).

That the characteristics of the pseudopodia alone are bad taxonomic guides is strongly suggested by the fact that pseudopodia of somewhat similar morphology have apparently arisen independently in widely separated lineages. The lobose pseudopodia of many naked amoebae and a number of thecamoebians are matched by more or less similar pseudopodia in vertebrate leucocytes. The trichomonad flagellates have produced one lobose amoeboid genus, *Dientamoeba* (Camp and others, 1974). Furthermore, many sarcodine individuals display two or several kinds of pseudopodia, simultaneously or successively. Such a peculiar phenomenon has been described and illustrated for *Vannella*, *Polychaostimidum*, *Amoeba proteus* and other forms by Page (1976), for *Yalodiscus* by Hoogenraad (1907b), Hausmann (1975) and Sawyer (1975), for *Vampyrella* by Leidy (1879) and Hoogenraad (1907a), for *Pseudoparamoeba pagei* by Page (1979), etc. As for the thecamoebians themselves, Schouteden (1906, p. 328) noted that, in some filose forms, there can be, in alternation or simultaneously, lobated or filiform pseudopods. *Diffugiella*, usually considered as lobose, has both lobose and filose pseudopods. Yet, pseudopodial features have been emphasized in thecamoebian macroclassification because they are the only characteristics of the cell proper that have been observed in many species and that can be used to build a moderately coherent and comprehensive classification. We accept, mainly because this has a negligible

effect on this paper, a pseudopodial macroclassification, but with many reservations.

Other data potentially useful for macrotaxonomy (e.g., ultrastructures of the organic part of the test and of the perinuclear area, etc.) are known so far in too few species (Hedley and Bertaud, 1962; Joyon and Charret, 1962; Hedley and Wakefield, 1969; Griffin, 1972; Eckert and McGee-Russell, 1973; Hedley and Ogden, 1973; Harrison and others, 1976; Hedley and others, 1977; Bonnet and others, 1979; Ogden, 1979a, b; Ogden and Fairman, 1979; Netzel, 1980) to be immediately usable.

OUR CLASSIFICATION AND ITS PROBLEMS

In recent decades suprageneric classifications were proposed by de Saedeleer (1934), Deflandre (1953), Loeblich and Tappan (1964), Bovee and Jahn (1966), Jahn and others (1974), Ogden and Hedley (1980), and, in more abbreviated form, Levine and others (1980), and Starobogatov in Krylov and others (1980). All of these classifications are based, at their higher rank, mainly on pseudopodial characteristics.

We have no strong opinion as to which one of the various classifications is the best. Four of the most recent systems (all derived from de Saedeleer's) are quite similar to each other (de Saedeleer, 1934; Deflandre, 1953; Loeblich and Tappan, 1964; Ogden and Hedley, 1980). We have adopted the last one with a few minor changes.

In our modified classification we have used the following rules: for the taxa above superfamily rank we have recognized a name as available from date of first publication (at any rank); we have accepted its first latinized spelling; we did not use uniform endings to denote rank. The resulting classification is as follows:

- Phylum SARCODARIA Milne-Edwards, 1850
 - Superclass RHIZOPODA Dujardin, 1835
 - Class LOBOSA Carpenter, 1861
 - Subclass TESTACEALOBOSA de Saedeleer, 1934
 - Order THECOLOBOSA Haeckel, 1878
 - (=ARCELLINIDA *auctorum*)
 - Superfamily ARCELLACEA Ehrenberg, 1830
 - Family DIFFLUGIDAE Stein, 1859
 - Genus *Diffugia* Leclerc in Lamarck, 1816
 - Diffugia protaeiformis* Lamarck, 1816
 - Diffugia bacillariorum* Perty, 1849
 - Diffugia bidens* Pénard, 1902

- Diffflugia corona* Wallich, 1864
Diffflugia fragosa Hempel, 1898
Diffflugia globulus (Ehrenberg, 1848)
Diffflugia oblonga Ehrenberg, 1832
Diffflugia tricuspis Carter, 1856
Diffflugia urceolata Carter, 1864
 Genus *Lagenodiffflugia* n.gen.
Lagenodiffflugia vas (Leidy, 1874)
 Genus *Pontigulasia* Rhumbler, 1895
Pontigulasia compressa (Carter, 1864)
 Family HYALOSPHEIIDAE Schulze, 1877
 Genus *Heleopera* Leidy, 1879
Heleopera sphagni (Leidy, 1874)
 Family CENTROPYXIDIDAE De-flandre, 1953 *ab* Jung, 1942
 Genus *Centropyxis* Stein, 1859
Centropyxis aculeata (Ehrenberg, 1832 *ab* Ehrenberg, 1830)
Centropyxis constricta (Ehrenberg, 1843)
 Superfamily CRIPTODIFFLUGIACEA Loeblich and Tappan, 1964 *ab* Jung, 1942
 Family PHRYGANELLIDAE Loeblich and Tappan, 1964 *ab* Jung, 1942
 Genus *Phryganella* Pénard, 1902
 Class FILOSA Leidy, 1879
 Order TESTACEAFILOSA de Saedeleer, 1934 (=GROMIDA *auctorum*)
 Family GROMIIDAE Claparède and Lachmann, 1859
 Genus *Pseudodiffflugia* Schlumberger, 1845

COMMENT

In the above taxonomic scheme we designate the lobose and filose thecamoebians respectively by de Saedeleer's names Testacealobosa and Testaceafilosa (accepted by various recent authors almost always with identical meanings) rather than by the terms Arcellina Ehrenberg, 1830 (=Arcellinida *auctorum*) and Gromida Claparède and Lachman, 1859, which were given numerous different meanings in the literature.

We delimit the Difflogiidae more or less as it is usually done. Within the Difflogiidae, however, we separate from *Pontigulasia* (as usually circumscribed) the new genus *Lagenodiffflugia* for the well known species *Pontigulasia vas* (Leidy).

The xenosomic-globulose tests of *Diffflugia globulus*, the genus *Phryganella*, forms of the filose genus *Pseudodiffflugia*, and forms of *Centropyxis* with axial symmetry cannot be separated from each other when the

pseudopodia cannot be inspected (as it is the case with fossil forms). We suspect that our *Diffflugia globulus*, which we treat as a legitimate species in this paper, might contain specimens belonging to all of those taxa.

NOMENCLATURE

We abided by the International Code of Zoological Nomenclature, 2nd edition (Stoll, 1964) and additions (Anonymous, 1974), hereafter designated as "the Code."

For the exact spelling of family names, we do not apply Art. 29(d) of the Code, enacted in 1972 (see Anonymous, 1974), which apparently will be suppressed in the third edition of the Code (Sabrosky, 1980).

The Code unfortunately does not offer clear guidance for some of the problems encountered in the works of Wallich (1864) and Leidy (1879). Some of the binomina used by them might remain unavailable in their works depending on how one interprets articles 11, 5, 45d-e which are unclear to us. We shall not try to solve this problem ourselves; for the time being we consider those two papers as nomenclaturally acceptable (as did most of our predecessors) and all new names of subspecies and varieties as available, provided that all criteria of availability (except those of art. 5 and art. 45) have been fulfilled.

A number of taxonomic names were first published in a way that left them unavailable (e.g., *nomina nuda*), and only in a later work did they become available. The literature is often confused as to the correct authorship of such names and, to clarify these cases (G. Merinfeld, personal communication, 1982), we introduce the use of the latin preposition *ab*, as in the following example:

Arcella aculeata Ehrenberg, 1832 *ab* Ehrenberg, 1830

in which "Ehrenberg, 1830" designates the work in which the epithet *aculeata* was first published but not made available. "Ehrenberg, 1832" designates the work in which the epithet became available and is thus the valid authorship. In such cases, which in our experience are common, some previous authors have used the term *ex*. The use of *ex* is also prescribed by the International Code of Nomenclature of Bacteria, but it is confusing in this context because botanists have already used it in an opposite sense.

Our synonymy lists follow these rules: 1) the name structure is that utilized in the works quoted and it may display characteristics conflicting with the Code, i.e., the use of binomina for subspecific and infrasubspecific taxa and the use of pre-1961 "formae" and

“varieties” (the latter have been frequently and incorrectly recognized as valid in numerous post-1960 works); 2) spelling is that used by the author, when misspellings have been noticed they have been underlined either by (sic), or by (misspelled); 3) authors and dates are those required by the Code and not necessarily those cited in the work quoted (we usually indicate where there is a conflict).

The literature on thecamoebians often lists binomina without illustrations. As the accuracy of such identifications is at best questionable we did not report them in our synonymies without compelling reasons.

TYPE SPECIES, HOLOTYPE AND LECTOTYPES

In 1964 Loeblich and Tappan listed the type species of all the genera discussed in this paper. We have very little to add to that, except for some marginal comments in the text. We report the appropriate Loeblich and Tappan type species before every genus.

So far as we know, however, holotypes have never been specifically designated for any of the species discussed in this paper. So far as we could ascertain, no specimens were ever deposited for this purpose in public collections (Pénard did leave a small collection with the British Museum but, apparently, he did not designate types out of that material).

Consequently all that the modern micropalaeontologist can do to improve the definition of these species, is to designate lectotypes by means of figures (as permitted by the Code [art. 74 (b), rec. 74 B]), as Loeblich and Tappan did for *D. protaeiformis* (1964). This is beyond the scope of the present paper and so we have decided not to erect lectotypes at this time. Representative specimens of our material are deposited with the Smithsonian Institution in Washington, D.C.

FOSSIL ARCELLACEA AND THE SPECIES PROBLEM

Except for very few reports from older terrains, fossil arcellaceans are consistently recorded from the Holocene only, a very short time span during which arcellacean genotypic evolution presumably has been minimal at the species level. Arcellaceans are therefore customarily classified in a purely phenetic frame.

In an ideal phenetic classification all characters of the organism, including those of its genome, should be considered. In fact, the phenetic taxonomy of species and subspecies is generally based on the hope (often unexpressed) that all phenotypic differences should re-

flect genotypic differences. This hope is probably realistic for many or most phenotypic characters, and is the basis of much biological taxonomy. This may have underlain much of the minute splitting that has occurred in thecamoebian taxonomy at the species, subspecies and variety levels. But, particularly in lower, simple organisms, the phenotypic characters are often external and usually adaptative ones, whose very evolutionary success may often be due to the fact that they can be switched “on” and “off” by a single given genotype in response to environmental circumstances.

The absolute ranking (genus, family, etc.) of phenetic taxa is normally defined on the basis of intuitive or numerical perceptions of phenetic differences, often coupled with other vague motivations (traditions, etc.). The phenetic species rank is, however, an exception to that custom. Generally for organisms with at least occasional sexuality (i.e., the majority of organisms, some thecamoebians as well), phenetic taxonomists hope that the phenetic species that they define will correspond to the quite different, non-phenetic notion of *biological species* or “biospecies,” i.e., Mendelian populations with usually intense interbreeding and very little or no genetic recombinations with other populations. Surprisingly, this pious hope often corresponds to reality, but in most cases it is not supported by any data. The immense majority of accepted phenetic species in which recent organisms are usually classified have never been submitted to any breeding experiments (although these are often possible and easy to perform), and indeed have been based only on dead material. It should be noted that paleontologists too, when defining morphospecies of heterogamic organisms, hope that such species corresponded to the biospecies alive at any given point in time along the single paleontological lineage under consideration, although in this case verification is objectively impossible. In other words, the biospecies concept is applied, in more or less peculiar and indirect ways, to both living and fossil material: but there are exceptions.

It so happens that the biospecies concept probably cannot universally apply to thecamoebians because only few of these organisms have been shown to interbreed at all and it is more than legitimate to suspect that most of them do not.

Among the lobose and filose thecamoebians, sexual reproduction is known with certainty only in the genus *Gromia* (Arnold, 1966), whose taxonomic position, relative to the other thecamoebians, remains debatable, and which is certainly not an arcellacean. The literature does report, in a few other lobose and filose genera, some rare, curious, ill-understood phenomena that do evoke copulation, and which are summarized

and rejected by Deflandre (1953, pp. 118–120); but whether such phenomena are actually sexual is still uncertain. Even the unquestionable cases of thecamoebian copulation presented by Valkanov (1962a, b, 1966) cover, in our opinion, too few species to change the “uniparental” status of the majority of the group. It is prudent, although not necessarily accurate, to admit that most thecamoebians certainly reproduce “. . . so far as is known, by replication of the parent during asexual binary fission to form an identical daughter cell,” as generalized by Ogden and Hedley (1980, p. 8).

If the concept of biospecies is not applicable, then the *usual* paleontological concept of “morphological species” does not apply to ancient Arcellacea either, since it implies the existence of a biological species, at any given time, in the paleontological lineage under consideration.

Under such circumstances the Arcellacea could be organized into species only by using another, arbitrary, *ad hoc* definition of the concept. For instance, it would be tempting, and apparently easy, to equate uniparental species with clones. But clones are unmanageable in taxonomy. Since we cannot hope to ever reconstitute the precise sexual and genetic history of the Arcellacea, we will never know how many clones are included in the group. All Arcellacea are perhaps members of one single, enormously diversified, giant clone; or the group is perhaps made of a few, or of dozens, thousands or millions of clones, depending on the frequency of heterogamy in the history of the group (Fig. 1).

One author who seems to have equated species and clone is Wallich (1864), who apparently believed that most of what we call today the Arcellacea were members of a single giant clone. He thought that the huge but intergraded phenotypic variations within that clone were due to environmental influences and considered such a unit one single, multiform species, *Diffflugia protaeiformis*. In reality even the presence of intergradational forms between two or more morphological types does not guarantee that they all belong to the same clone. Such intergradational forms, in the Arcellacea, could probably be produced by weakly or strongly different genotypes derived from the same or from different clones and reacting to environmental stimuli.

We noted that most taxonomists hope that their practical units correspond to distinct genotypes or to distinct groups of almost similar genotypes. There is probably an immense number of different genotypes among the Arcellacea; even if one could identify them all, considering each one of them a separate “species” would lead to utter taxonomic chaos. It would appear

more reasonable to regroup them into a finite number of taxa. In practice, such grouping of genotypes, unless done arbitrarily, is impossible. In order to establish the genotypic distances between the many arcellaceans, one should submit them to such a number of comparative experiments under strictly controlled conditions that chaos would probably follow once more. So far as we know such experiments have never been done and they will probably never be carried out on a scale sufficient to give a satisfactory picture of the “genotypic taxonomy” of the group.

Having run out of options we are forced by practical reasons to base our taxonomic distinctions on *phenotypes alone*. We could hope that distinct phenotypes might grossly correspond to genotypes or to groups of similar nature. But a few culturing experiments that have been done suggest an enormous phenotypic plasticity of the genotypes in uniparental protists (which may go far explaining their success in extremely variable microenvironments). Examples of that plasticity have been shown by Jennings (1916) and by Arnold (1954, 1968). Their experiments did not determine the exact source of such plasticity, but part of it objectively must have been caused by purely environmental factors. Jennings (1937), for instance, showed that the number of teeth in *D. corona* is “inherited” not genetically but by a unique mechanical interaction between the “parent” and the “daughter” tests. Similar mechanisms, presumably, can control size and apertural details in other arcellacean species.

In addition, Jollos' (1921, 1934) often forgotten “dauermodifikazionen” could, and probably do, play havoc with arcellacean phenotypes. Unfortunately his experiments were not concentrated on morphology and we can only speculate on how important this factor might be.

Even in cases in which uniparental broods have not been studied in the laboratory, there can be strong indications of enormous phenotypic plasticity either of a single genotype, or of a collection of genotypes that probably differ little between each other. For instance, Schönborn (1962) showed that, in what he considers the “species” *Diffflugia limnetica*, the benthic and planktonic populations that succeed each other seasonally, strongly differ in the morphology of their tests. Spring benthic forms are covered with quartz grains and have no collar. Summer planktonic individuals agglutinate diatom frustules and develop a collar. Later summer planktonic forms again agglutinate quartz grains and develop a collar.

How can such a phenotypic plasticity be explained? Sonneborn (1957) ascribes those rapid variations to two possible mechanisms, 1) mutations, which are like-

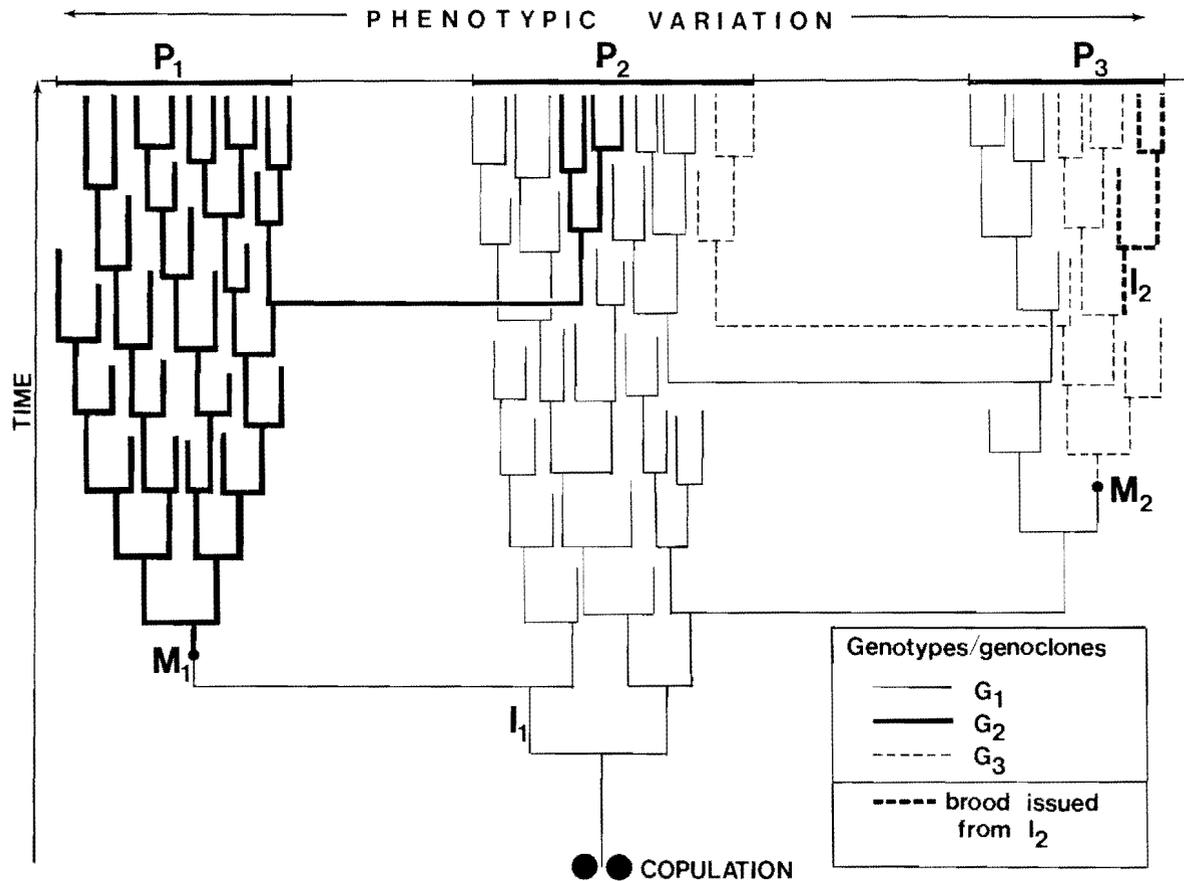


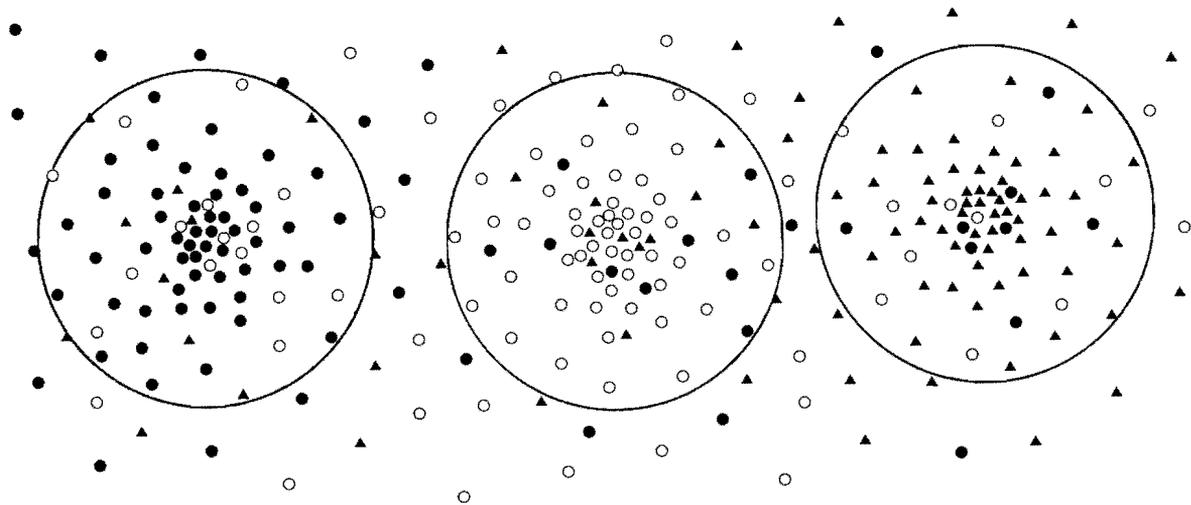
FIGURE 1. Theoretical examples of clones, genotypes, genoclines and broods in uniparental organisms. The figure shows an entire clone issued, through repeated asexual bipartitions, from one hypothetical, original copulation. Every vertical segment is one organism. Abscissa: field of phenotypic variation (simplified to one dimension only). All members of the clone are grouped within three distinct phenotypic clusters P_1 , P_2 , P_3 (in reality, many thecamoebian phenotypic clusters are not so sharply separated, but linked to each other by more scattered intermediate individuals). G_1 : original genotype/genocline, from which genotypes/genoclines G_2 and G_3 arose respectively through mutations M_1 and M_2 . The brood issued from individual I_2 is part of genocline G_3 and is represented by thickened dashes for clarity. The complex brood issued from individual I_1 is not distinguished by a special drafting pattern; it includes part of genocline G_1 and the entire genocline G_2 . The figure assumes that each of the three genotypes will mostly limit itself to one of the three phenotypic clusters, but will nevertheless produce stray individuals in other phenotypic clusters. Fig. 2 will show a more realistic representation of phenotypic scattering in the arcellaceans.

ly to be relatively rare and usually irreversible, and 2) presence in the genotype of multiple loci controlling mutually exclusive characters (e.g., elongated versus rounded test). Each of these loci can be easily activated or inhibited by environmental stimuli. Different, discrete phenotypes, produced by the same genotype through this mechanism, should ideally be classified within the same "species" and be considered, at best, as ecophenotypes.

In laboratory cultures, which are normally maintained only for a short time, and for which only a minute fraction of the natural environmental variation can be imagined and duplicated (but usually is not), broods will tend to show a minimum variability. But if the degree of phenotypic plasticity already found in

such cultures (Jennings, 1916) actually characterizes all the Arcellacea, one can justifiably speculate that under natural conditions that plasticity must be extremely, sometimes almost unimaginably, high in the whole group. In a lake, pond or bog, a more or less infinite number of conditions vary continuously on an hourly, daily and monthly basis, thus challenging the phenotypic flexibility of the arcellaceans, which (as our material seems to indicate) must be tremendous, or the group would have become extinct long ago.

Given this phenotypic plasticity, we may expect that considerable phenotypic overlapping may exist (especially in natural assemblages) between different genotypes (Fig. 1). Mayr (1970, p. 18) rather optimistically stated that uniparental assemblages fortunately



● ○ ▲ three different genotypes

FIGURE 2. Theoretical example of phenotypic scattering in the arcellaceans. For simplicity's sake, the field of phenotypic variation is simplified here to the variability of only two characters: in nature the number of variable characters is several orders of magnitude larger. Each graphic mark represents one specimen. Each of the three symbols represents a different genotype. In terms of phenotype, most specimens are concentrated within three clusters, but intermediate individuals exist between the clusters, which are thus not sharply separated from each other. More than 75% of all specimens are included in the three circles which represent the limits of arcellacean species as understood here. As in Fig. 1, it is assumed that each of the three phenotypic clusters mostly corresponds to one different genotype, although each of the three genotypes can include stray individuals outside its main cluster and all over the phenotypic field.

present well-defined morphological discontinuities which can be used to define "uniparental species." This statement certainly does not apply to the arcellaceans in which "discontinuities" are indeed present but not at all well defined especially if the field material is plentiful, sufficiently representative, and submitted to a general study of the population of the sample. Our impression, although we did not perform biometric studies, is that a number of individuals are tightly clustered around the center of the variability spectrum of each taxon and that between such clusters there is indeed morphological discontinuity. A majority of individuals, however, are scattered in the space between clusters, so that the variability spectra intergrade into each other in various directions in the "taxonomic field." As a result, it is often difficult to place a given individual in one of *several* possible taxa (Fig. 2).

In face of such a continuous intergradational field with its clusters and its numerous extra-cluster individuals, different investigators inevitably develop different attitudes. For instance, most specialists, for well over a century, have almost ignored whole populations while focusing their attention on new species. Often, lamentably, these new species are based on isolated

specimens of *relatively rare* intercluster phenotypes, individually and arbitrarily selected out of their natural intergradational assemblages. Many of them have been based on characteristics (such as spines, details of apertural teeth, etc.) which, as Jennings (1916, 1937) and others have clearly shown, are certainly individual characters that widely vary within single laboratory broods. We consider that such an attitude is unjustifiable and impracticable for uniparental organisms because of the resulting extreme "morphological splitting." Besides, this philosophy leads to an interesting, practical consequence: the narrower the definition of the recognized "species" becomes, the higher the proportion of individuals (in natural assemblages) that becomes unidentifiable (Fig. 2).

If this method of randomly selecting specimens on which to base new "species" is continued indefinitely the result (given the scattering of innumerable phenotypes and perhaps genotypes throughout the arcellacean taxonomic field) will inevitably be that the species concept will narrow to the point that one species per individual will become necessary, that is, the species will no longer exist.

Other investigators have hoped that the mass of phenotypes and perhaps genotypes could be sorted into biotypes through laboratory cultures, and that each of the innumerable biotypes could then be considered as a taxon of a given level (e.g., "species"). Perhaps, but we have seen that, *in practice*, comparative rearing experiments are not done, and, if they were, so many "species" would be erected that taxonomic chaos would ensue.

This dilemma, real as it is, is very difficult to accept for many workers. A few have given suggestions for a reasonable and practical delimitation of the elusive "uniparental species." Sonneborn (1957, p. 313) wrote, "... genetically simple morphological differences ... are ... inadmissible as species differentials if species are to represent equivalent evolutionary divergences in sexual and asexual organisms. Many criteria now used in asexual organisms to distinguish species are comparable to individual differences in sexual organisms." This, to us, sounds as a warning not to over-emphasize the usually narrow genetic or random differences in the genotypes observed in laboratory cultures and also to be wary of the numerous, supposedly stable, but probably environment-induced, isolated variations observed in natural assemblages. Mayr (1963, p. 433) suggested that similarities should not be overlooked either, he proposed to consider "... each morphologically distinct clone a microspecies ... Even though between strains there are morphological differences ... there is usually so much morphological agreement ... that it is justifiable to treat them as components of collective species."

Since for the moment any kind of large-scale comparative culturing for circumscribing genotypes is out of the question, we propose here a practical compromise solution to the elusive problem of the uniparental arcellacean species. If an interbreeding "population" is the basic material for defining a biological species, it would be logical to base the definition of the "uniparental species" not on carefully and arbitrarily selected specimens, nor on artificially isolated laboratory lineages, but on the general, if necessary statistical study of phenotypic variations in total *natural* assemblages, recognizing as "variation centre" of a distinct species each one of those proportionally important phenotypic clusters in which many, more or less similar, individuals are grouped within narrow variation limits. If a relatively low number of species are reasonably delimited in such a way, the percentage of unclassifiable individuals will be relatively low, and the classification produced will be quite manageable in practical work. Nothing prevents other workers using such a solution

from continuing to recognize, if so wished, within relatively few species and subspecies, a large number of infraspecific and infrasubspecific units which would not be considered as real taxa, but as ecotypic formae which could even keep many of the Latin epithets of the traditional taxonomy. At this stage of our work we have not distinguished any formae, nor subspecies.

One could object that the wide intergradational phenospecies built on such criteria would not necessarily correspond to genotypic similarity groupings. Of course we do not know and arguing back and forth would solve nothing because, in practice, this criticism is not amenable to mass experimental refutation. We strongly suspect that, could the necessary experiments be carried out, it would be found that the natural assemblage-based phenospecies would largely (though perhaps not perfectly) correspond to the actual clustering of the genotypic affinities. As this is nothing more than an educated guess we expect many of our colleagues to enthusiastically disagree with us on this point.

These are, in any event, the criteria that we have decided to follow to arrive at our own concept of arcellacean species. The transposition of this solution to fossil material, which is our real goal, requires a few more simple words of introduction.

Taxonomic complications are particularly annoying to the paleontologists who have stratigraphy and paleoecology as first priorities and require unequivocal species that are relatively easy to identify. With this in mind we have studied our Holocene material on the assumption that arcellaceans have experienced no important evolution during this period and therefore we could fully refer our material to the recent forms described in the literature.

We have also assumed, however, that fossil arcellacean assemblages are even more variable than living assemblages that are sampled at one particular point in time. Indeed, in a surficial or core sample, the assemblage of dead tests, covering at least several years of reproduction, will have to be an integration of all possible variations that have occurred during hundreds of generations each of which has been subjected to the vagaries of everchanging natural conditions. In such fossil samples one normally finds an immense variety of phenotypes which must have been overlooked by previous authors.

We have applied to our fossils our concept of "*natural-assemblage species*" which may be somewhat unorthodox, but the paleontological concept of "species" is, of necessity, remarkably flexible and gives us ample freedom. Arkell (1956) advises that paleon-

tological species are legitimate whenever they are geologically useful. We feel we have already demonstrated the usefulness of our species (Scott and Medioli, 1983). In addition, not to abuse the freedom, we placed very strong constraints on our species by using, as our major test of validity, the concept of intergradation (Mayr and others, 1953; Medioli and Scott, 1978). As we have mentioned before this test alone is not sufficient in the Arcellacea to prove the species valid, but it provides good circumstantial evidence, which is more than has been used for the creation of the vast majority of zoological species.

Based on the ideas discussed so far we have attempted in defining our own "arcellacean species" to use as much common sense as we could muster and compromise between extreme "splitting" and extreme "lumping." We circumscribed our "species" strictly on the basis of our study of *whole* assemblages (both recent and fossil) and with the purpose of making these species fit the *entire* complex of different assemblages. This more or less dictated that we place into our species all the forms that were clearly interconnected by a series of gradual shifts in gross morphology. In some of the descriptions we specify the maximum amount of variability that we allow to each species, which is consistent with the material, and which does not lead to a complete conceptual breakdown. We constructed our units with the proviso that, collectively, they had to accommodate 75% or more of the entire assemblage of the sample. In most cases this percentage ran as high as 90–95%, only the few extreme deviants being left out.

The results of our taxonomic method are not entirely consistent and satisfactory, but we unilaterally believe that they represent an improvement over the excessively restricted "species" in use at the present time. This statement too is likely to generate enthusiastic disagreement. It is of some comfort to know that our species, although arrived at quite independently, are in surprisingly good agreement with the classical ones recognized by Leidy (1879).

Also encouraging is the thought that in 1928, Defflandre, after a long and well documented discussion, reached conclusions that, except for details, were almost identical to ours. Unfortunately, in the taxonomic part of the same paper, he either forgot what he had said a few pages before (which, of course, we do not believe) or he underwent a spectacular loss of self confidence (which is also rather uncharacteristic of Defflandre). Being this as it may, in that paper he certainly did not attempt to simplify the taxonomy of the Ar-

cellacea in accordance with his own carefully stated principles (Fig. 3).

"XENOSOME SELECTION" AND TAXONOMY IN THE ARCELLACEA

Another problem that further complicates the taxonomy of the Arcellacea, but has received very little attention, is that of the complex and variable nature of the arcellacean test. The inorganic particles present in many such tests (Hoogenraad, 1936, p. 404) are of two types: 1) idiosomes, secreted by the thecamoebian itself and extremely variable in shape, size and composition; 2) xenosomes, minute objects collected by the animal in the environment: grains of quartz, diatom frustules, siliceous sponge spicules, glass fragments in culture vessels (Stump, 1936; Netzel, 1976) and even, in *Nebela* and *Heleopera*, idiosomes of other thecamoebians on which they prey (MacKinlay, 1936; Thomas and Gauthier-Lièvre, 1959).

Tests whose inorganic fraction is entirely made of idiosomes are called here "autogenous;" those entirely made of xenosomes are called "xenogenous." Some tests are "mixed." In general, only xenogenous tests fossilize, although some autogenous forms can be found in Holocene sediments.

It has long been customary to distinguish species, genera and even families of thecamoebians according to the presence of either xenosomes or idiosomes, the shape of those particles, and the origin and nature of the xenosomes. These "microtextural" criteria have led to the highly formal taxonomy of many of the modern specialists.

Microtextural taxonomic criteria assume that the either xenogenous or autogenous structure of a test is determined purely by the genotype, independently of any environmental circumstances, and that a given xenogenous genotype will always select from the environment a given type of xenosomes, presumably irrespective of its availability. This general assumption may well be justified for some genotypes under specific circumstances, but we have very serious reservations concerning its applicability to the entire arcellacean complex.

By contrast, it does seem intuitively correct to expect that idiosome shape and size are largely determined by the genotype, and indeed, these characteristics seem to be constant in given broods maintained in culture (Netzel, 1976, 1977a). Idiosome morphology could thus be a good taxonomic criterion, but not very useful to us as autogenous forms hardly ever fossilize.

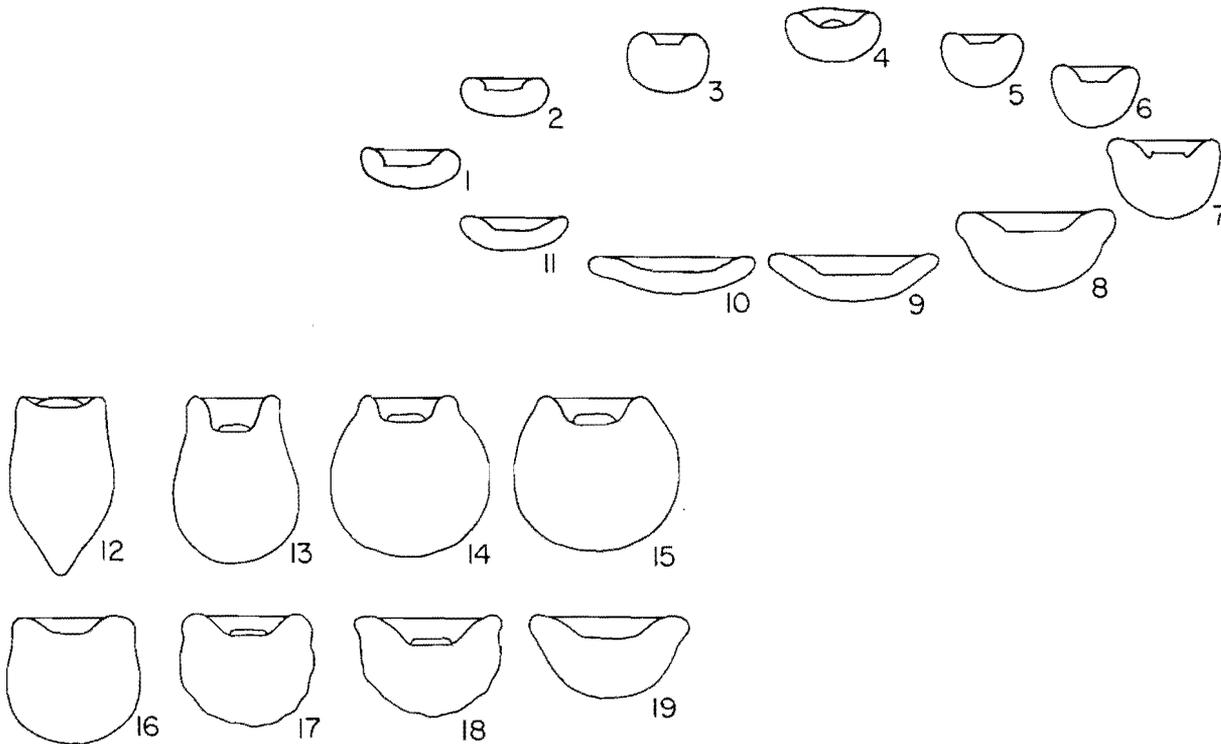


FIGURE 3. Figures of *Arcella* (redrafted and rearranged from Deflandre, 1928, p. 205, 207). 1—*A. rotundata* var. *aplanata*; 2—*A. rotundata*; 3—*A. rotundata* var. *alta*; 4—*A. atava*; 5—*A. hemisphaerica*; 6—*A. hemisphaerica* var. *intermedia*; 7—*A. gibbosa* var. *levis*; 8—*A. vulgaris*; 9—*A. discoides* var. *pseudovulgaris*; 10—*A. discoides*; 11—*A. discoides* var. *scutelliformis*; 12—*A. apicata*; 13—*A. mitrata* var. *pyriformis*; 14—15—*A. mitrata*; 16—*A. jeanelli*; 17—*A. gibbosa* var. *mitriformis*; 18—*A. gibbosa*; 19—*A. vulgaris*.

Deflandre himself felt the need to present those nine "species" and eight "varieties" in two intergradational arrangements. In the first example (1–11), the intergradation is circular: the author obviously did not know where to start and end the sequence. Notice that *A. vulgaris* (8, 19) and *A. gibbosa* (7, 17, 18) fit equally well in both series.

Absence vs. presence of xenosomes does not seem to be a good taxonomic criterion either. Often, forms with identical outlines, but usually ascribed to different and sometimes distant species or genera, offer smooth intergradational series between wholly autogenous and wholly xenogenous tests. This suggests that the same genotype may develop an autogenous or xenogenous test depending on circumstances. A good example is that of the autogenous "*D. oviformis*" and the xenogenous *D. tricuspis* which we consider as the very same species. (Our limited experiments seem to support this point of view.) The literature suggests that many more such cases probably exist.

The nature of xenosomes does not seem to provide a reliable taxonomic criterion either. Xenogenous tests often display all degrees of mixture of xenosomes between certain extremes that have been given formal taxonomic status. For instance, we find countless intermediate forms between the wholly "sandy" *Difflu-*

gia elegans auctorum and some specimens of the almost wholly "diatomaceous" *Difflugia bacilliarum auctorum*. An example of change of xenosomes during the year is the already mentioned case of *Difflugia limnetica*, as studied by Schönborn (1962).

In conclusion, we strongly suspect that in a number of arcellacean genotypes the genotypic affinities are indicated, at the phenotypic level, by the general test shape (and in particular the aperture) and the shape of idiosomes, if they are present.

Some genotypes, however, would be able to build xenogenous, mixed or autogenous tests according to a number of circumstances (not only the availability of xenosomes, but perhaps temperature, pH, availability of dissolved silica, food, planktonic versus benthic phases, etc.).

Xenogenous tests of a given genotype apparently may be built with any available material; this means with a mixture of materials in some cases or with one class

of material in others, depending on environmental conditions. Consequently the taxonomic units based on the presence and nature of xenosomes only reflect environmental circumstances and are not likely to be justified.

It is quite extraordinary that this central problem of thecamoebian taxonomy has almost never been attacked through proper experimentation. Of the few authors who have reared thecamoebians, some (Netzel, 1976, 1977a; Eckert and McGee-Russell, 1974) cultured broods in xenosome-free media that, under those conditions, built autogenous tests. They did not investigate whether those broods would have built xenogenous tests in the presence of xenosomes (although Netzel's "*Diffflugia oviformis*" was capable of integrating glass fragments in its otherwise autogenous tests).

Conversely other authors (Jennings, 1916, 1937; Stout and Walker, 1976) regularly provided their broods with natural water or soil and obtained xenogenous tests. They did not investigate what would have happened to their broods in the absence of available xenosomes. The only apparently decisive experiments known to us are those of Stump (1936), who elegantly showed that, under the environmental conditions that he imposed, "*Pontigulasia vas*" *auctorum* (= our *Lagenodiffflugia vas*) would reproduce if the medium contained xenosomes, but would not reproduce if deprived of them. In other words, under his culture conditions, his broods were incapable to form idiosomes. Simple experiments of this kind (with broods being offered or deprived of xenosomes) repeated for the various species would be invaluable in clarifying the taxonomy of the Arcellacea.

CONCLUSIONS

The above comments were necessary to place the following taxonomic review into proper perspective and to make it understandable to those not specifically familiar with the subject. We hope that the following pages will clarify to some extent the taxonomy of our species. We are painfully aware, however, that much remains to be done.

With some of the largest and more complex taxonomic problems somewhat simplified, it should become possible for many to routinely examine fossil arcellaceans and report on them. The authors have shown that arcellaceans do occur in natural fossil assemblages that appear to align well with environmental factors (Scott and Medioli, 1983). These organisms are well preserved in core material and can provide useful information on the benthic paleoenvironment, a unique

feature since other freshwater benthic indicators (ostracodes, molluscs) are often poorly preserved in highly organic, often low-pH lake sediments.

ACKNOWLEDGMENTS

Although it is not customary to give special acknowledgment to long-deceased authors, we must express our gratefulness and admiration to Joseph Leidy (1823–1891) for his 1879 monograph and for being a constant source of inspiration. Our work is essentially a modernization of Leidy's: our taxonomic units are basically those he arrived at some 100 years ago. Leidy's work will probably never be duplicated. He covered North America on horseback, and he apologized, in the introduction to his monograph, for spending \$222 of Geological Survey money to complete his massive study. Without his enormous contribution to this field, our study would have been virtually impossible.

Among our contemporaries we thank C. G. Ogden (British Museum) for many helpful comments and criticisms; A. Loeblich, Jr. and H. Tappan (UCLA), and H. Hernandez-Lena (Florida State Univ.) for carefully and critically reading and revising the manuscript; R. V. Melville (Secretary, International Commission on Zoological Nomenclature) and G. Merinfeld for supplying nomenclatural advice; R. Thomas (Canada Centre for Inland Waters) who provided us with samples from Lake Erie; I. P. Martini (University of Guelph) who supplied us with samples from James Bay; A. Miller who patiently and diligently checked every detail in the final version of the manuscript; B. Abbot who assisted with preliminary culturing experiments; B. Angeloff-Cossar and M. Robinson who patiently and repeatedly typed this manuscript; L. Sapienza who redrafted illustrations from Leidy and other works. Last, but not least, a special thanks goes to our wives, Caterina and Ann, for their patience. Financial support came from Natural Sciences and Engineering Research Council (Canada) operating grants to Medioli and Scott.

SYSTEMATIC TAXONOMY

Family DIFFLUGIIDAE Stein, 1859

Test usually with axial symmetry, elongated, ovoid, globose or rarely depressed ("acrostome" or "arcella" type of Bonnet, 1976a), sometimes with slight lateral compression, never coiled. Aperture terminal; test made of hard organic matter and entirely covered with siliceous xenosomes (and possibly idiosomes, see *D. tricuspis*) of highly varied, mineral and/or biological origin (quartz grains, diatom frustules, etc.). In some

genera, an internal diaphragm with one or two (rarely more) openings separates the main part of the test from a narrower neck which bears the aperture.

Our delimitation of this family is essentially that of Deflandre (1953), Loeblich and Tappan (1964) and Ogden and Hedley (1980). Our difflugiid material is distributed in three genera: *Diffflugia* with a simple acrostome test devoid of diaphragm; *Lagenodifflugia* n.gen., erected for *Pontigulasia vas auctorum*, characterized by a diaphragm with one opening; and *Pontigulasia* (except for *P. vas auctorum*) with a diaphragm pierced by two (rarely more) openings.

Genus DIFFFLUGIA Leclerc in Lamarck, 1816

Type species. *Diffflugia protaeiformis* Lamarck, 1816.

Diagnosis. Test simple, without an internal diaphragm; sack-like, either globular or more or less elongated, rarely depressed. Aperture circular, lobated or crenulated; simple or complicated by constrictions; either at the end of a more or less complicated collar or opening directly into the test. We circumscribe *Diffflugia* more or less as done by Loeblich and Tappan (1964) but we keep in it, at least temporarily, *D. tricuspis* (= *lobostoma auctorum*) and *D. corona*, which they had transferred to *Loboforamina*.

Discussion. For the authorship of this genus we follow Loeblich and Tappan (1964, p. C35). From data in Lamarck (1816), Ehrenberg (1838), Cash and Hopkinson (1909), and Loeblich and Tappan (1964), we reconstitute the nomenclatural history of this genus as follows. Lamarck (March 1816, a date indicated on his title page but often misquoted as 1815) established and described, simultaneously and without illustrations, the genus *Diffflugia* (which he credited to a manuscript by [sic] Le Clerc) and one single species in it, *D. protaeiformis*, which he credited to no one. Hence the type species of *Diffflugia* Leclerc in Lamarck 1816 formally is *D. protaeiformis* Lamarck 1816, by original monotypy. In September 1816 Leclerc published on this genus a work (which most authors date as 1815) in which he described the genus without a latin name but under the french term "difflugie." According to Loeblich and Tappan (1964), it is on the manuscript of this paper by Leclerc that Lamarck's description of *Diffflugia*, published slightly earlier, had been based: Lamarck's description does undoubtedly follow that of Leclerc very closely. Leclerc (1816) commented that he had found two or three species of this genus; he gave six figures but he did not name them. Lamarck's text shows that his variable species *D. protaeiformis* most probably refers to all of Leclerc's figures. Later

authors ascribed each of Leclerc's figures to various species of *Diffflugia* named later than *D. protaeiformis*. Loeblich and Tappan (1964) clarified the nomenclatural situation by designating, as lectotype of *D. protaeiformis*, Leclerc's figure 5, which they also consider conspecific (as did Ehrenberg, 1838, and Leidy, 1879) with *D. acuminata* Ehrenberg, 1830. Thus they consider *D. protaeiformis* as a senior subjective synonym of *D. acuminata*. Although we feel somewhat uncertain as to whether Leclerc's figure 5 represents a *D. acuminata* or a *D. oblonga* Ehrenberg, 1832 (which could force us to declare *D. protaeiformis nomen dubium* with possible disastrous consequences), we prefer, at least until some substantial new information becomes available, to accept the competent opinion of Loeblich and Tappan and consider the lectotype of *D. protaeiformis* as conspecific and, as such, a senior subjective synonym of *D. acuminata*.

The name *D. protaeiformis*, which because of the vagueness of the early descriptions (Lamarck, 1816; Ehrenberg, 1838) has not enjoyed much popularity during this century (its last use known to us being that by Bergonzini, 1883), is thus revived by Loeblich and Tappan (1964) for one of the most common species of *Diffflugia*.

Diffflugia protaeiformis Lamarck, 1816

Pl. 1, Figs. 15–20

We have not attempted to compile a list of the early synonyms of this species because the remarkable confusion surrounding it would have made the exercise unprofitable.

- Diffflugia protaeiformis* LAMARCK, 1816, p. 95 (with reference to material in a manuscript by LeClerc). LOEBLICH and TAPPAN, 1964, p. C35, fig. 13, no. 3. HAMAN, 1982, p. 367, pl. 4, figs. 1–3.
- Diffflugia acuminata* EHRENBURG, 1830, p. 95. EHRENBURG, 1832a, p. 75. EHRENBURG, 1838 (part), p. 131, pl. 9, fig. 3. CARTER, 1864, p. 29, pl. 1, fig. 10. LEIDY, 1879, p. 109, pl. 12, figs. 24–29; pl. 13, figs. 1–26. PÉNARD, 1890, p. 139, pl. 3, fig. 54. PÉNARD, 1902, p. 233, text-figs. 1–11. CONN, 1904, p. 15, pl. 5, fig. 27. EDMONDSON, 1906, p. 14, pl. 2, fig. 13. CASH and HOPKINSON, 1909, p. 19, text-figs. 42, 43; pl. 18, figs. 12–14. RAMPI, 1947, p. 74, text-fig. 1. DECLOÏTRE, 1953, p. 41, text-figs. 105, 106. GROSPIETSCH, 1958, p. 45, text-fig. 39a. GREEN, 1975, p. 549, text-fig. 7. OGDEN and HEDLEY, 1980, p. 118, pl. 48. SCOTT and MEDIOLI, 1983, p. 818, fig. 9d.
- Diffflugia acaulis* PERTY, 1849a, p. 167.
- Diffflugia acuminata* var. *acaulis* PERTY, 1852, p. 187, pl. 9 (upper part), fig. 6. CASH and HOPKINSON, 1909, p. 22, text-fig. 44. THOMAS, 1954, p. 250, pl. 1, figs. 14, 15; pl. 3, figs. 2, 3.
- Diffflugia bicornis* PÉNARD, 1890, p. 141, pl. 4, figs. 12–14.
- (?) *Diffflugia lanceolata* PÉNARD, 1890, p. 145, pl. 4, figs. 59, 60.

- SCHOUTEDEN, 1906, p. 343. CASH and HOPKINSON, 1909, p. 31, pl. 19, figs. 9–11.
- Diffugia pyriformis* var. *claviformis* PÉNARD, 1899, p. 25, pl. 2, figs. 12–14. PÉNARD, 1902, p. 218, text-figs. 3, 4 on p. 219. PÉNARD, 1905, p. 19, text-fig. HARNISCH, 1958, p. 40, pl. 8 (after Pénard, 1902), fig. 1.
- Diffugia curvicaulis* PÉNARD, 1899, p. 36, pl. 3, figs. 2–6. PÉNARD, 1902, p. 242, text-figs. 1–4. PÉNARD, 1905, p. 16, text-fig. on p. 17. (?) SCHOUTEDEN, 1906, p. 342, 346, pl. opposite p. 336, fig. 18. CASH and HOPKINSON, 1909, p. 29, pl. 19, fig. 8. OGDEN and HEDLEY, 1980, p. 130, pl. 54.
- Diffugia scalpellum* PÉNARD, 1899, p. 38, pl. 3, figs. 15, 16. PÉNARD, 1902, p. 243, 244, text-figs. 1–7. PÉNARD, 1905, p. 23, text-fig. on p. 24.
- Diffugia acuminata* var. *umbilicata* PÉNARD, 1902, p. 233, text-fig. 3.
- (?) *Diffugia praestans* PÉNARD, 1905, p. 24–25, text-fig.
- Diffugia acuminata* var. *curvata* CASH in CASH and HOPKINSON, 1909, p. 24, pl. 21, figs. 1–2. DECLÔTRE, 1953, p. 47, text-figs. 107, 108.
- Diffugia acutissima* DEFLANDRE, 1931, p. 84, pl. 12, figs. 1–3.
- Diffugia smilion* THOMAS, 1953, p. 132, text-figs. 6–13. THOMAS, 1954, p. 259, pl. 3, figs. 6, 7. GREEN, 1975, p. 549, text-fig. 11.
- Diffugia pyriformis* Perty. BIERNACKA, 1956, pl. 1, fig. 10. Not Perty, 1849a, p. 168, nor Perty, 1852, p. 187, pl. 9 (upper part), fig. 9.
- Diffugia claviformis* Pénard. OGDEN and HEDLEY, 1980, p. 126, pl. 52.

Lectotypes. Designated by Loeblich and Tappan, 1964, p. C35, as being the specimen illustrated on pl. 17, fig. 5, of Leclerc, 1816.

Diagnosis. Test shape extremely variable; amphora-like to elongate oval, cylindroconical, pyriform. Fundus more or less tapering, acute, either acuminate or prolonged into one or more blunt spine processes. The test blends into these processes with smooth curves. Neck long, short or absent. Aperture large, terminal, subcircular. Test composed of quartz grains of variable size and abundance, at times mixed with variable amounts of diatom frustules that, when abundant, completely obscure the shape of the test. Generalized dimensions for our material were the following: length from 84 to 520 μm , width from 36 to 184 μm , diameter of aperture from 24 to 100 μm .

Differs from *D. oblonga* in having smoother transition from test to spines and for its larger ratio of *aperture diameter : maximum diameter* which is about 0.7 to 0.5 for *D. protaeiformis* and 0.5 to 0.2 for *D. oblonga*.

Discussion. This extremely variable species (Fig. 4) includes, in our definition, a large number of taxa recognized by many authors but which we consider as conspecific. We list the most obvious synonyms, but we made no attempt to evaluate critically the less obvious cases. Our list is but a fraction of what we believe to be the complete one. We discuss only the most

important cases. Many of the early authors listed almost anything under the sun under *D. protaeiformis*. We made no attempt to analyze critically those early identifications.

Leidy (1879) had already listed nine synonyms of this species and had noted its amazing variability commenting that the shape is like an ancient Roman amphora, or is oblong oval, gradually narrowing toward the oral extremity, or it is pyriform, or it is cylindroid. He added that the amphora-like specimens of his *D. acuminata* grade into *D. urceolata*, and the pyriform ones into *D. pyriformis* (=our *D. oblonga*), while the drop-tube-like forms are the most peculiar or characteristic. He described the shell of his *D. acuminata* as ordinarily composed of clear quartz sand, not infrequently of a colorless chitinous membrane (*D. curvicaulis auctorum*, *D. scalpellum auctorum*) with quartz sand or with intermingled diatoms. Certain specimens consist entirely of diatoms (*D. bacilliarium auctorum* ?), the fundus presents various degrees of acuteness, passing into a more or less acuminate condition or prolonged into a nipple-like process which can be short and thick, or long and narrow. Considerable also is the size range of Leidy's *D. acuminata*.

We agree with Leidy's comprehensive interpretation of this species and we feel that most of the splitting that has taken place during the last 100 years must have been caused by the inadequacy of the study material. It is quite understandable that forms like *D. curvicaulis* and *D. claviformis* (*sensu* Pénard, 1899), for example, were kept separated by authors who never dealt with a really large population of intermediate specimens connecting the two apparently different forms. Pénard himself, who is responsible for many varieties of this species, admitted that *D. protaeiformis* is very difficult to study (Pénard, 1902). The group, he admitted, contains a series of forms distinguished from each other by means of characteristics so poorly defined that it is nearly senseless to make subdivisions. The results of his splitting were, as one could have anticipated, rather confusing. For instance, he claimed that his *D. curvicaulis* and *D. scalpellum* could be differentiated at first sight on the basis of a horn which is present in *D. curvicaulis* but is replaced by a slightly bent, sharp point in *D. scalpellum*. This last feature, however, is unmistakably present in his own figure of *D. curvicaulis* on p. 243. Judging from his figures and comments, the two species, in our opinion, should never have been separated from each other or from *D. protaeiformis* to which they are linked by a long series of intermediate forms.

We admit nevertheless that there are, within this

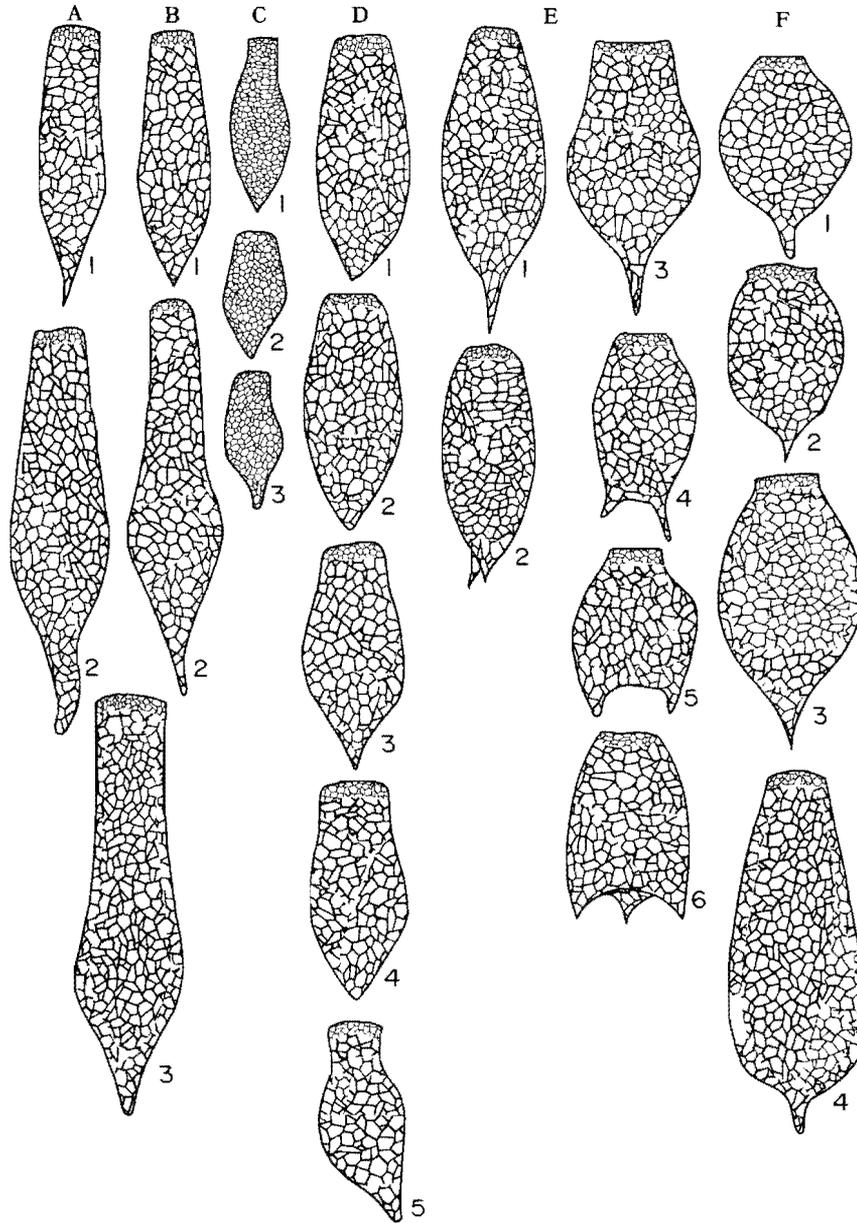


FIGURE 4. Figures of *Difflugia protaeiformis* (redrafted and rearranged from Leidy, 1879, pls. 12, 13. All drawings with approximately the same magnification). These forms of our *D. protaeiformis* are here presented in an intergradational arrangement in which they could be linked in many different sequences without changing the external limits of the intergradational field. Some of these sequences, instead of being open, could be circular like those of Deflandre (1928) for *Arcella* (for instance: D1-B1-A1-E1-E2-E4-E5-E3-D3-D2, or many other combinations). No matter how those specimens are sequenced, the fact remains that A1 and E6, F1 and A-B3, F4 and D5, for example, are so different from each other that taken in isolation they would appear to belong to two different "species." In comparison, when studied in the context of an entire population, they seem to fit into the same species rather naturally.

species, a number of conspicuous and relatively consistent morphotypes which may conceivably be attributed to ecophenotypic variations or to genotypic differences. Whether or not this is indeed the case cannot be determined. At the present level of knowledge, in

our opinion, it would still be premature to attempt any morphological differentiation within this complex.

Occurrence. Ditches, ponds, swamps and lakes.

Observations on material illustrated in this paper. Five specimens are illustrated here. Most show the

basic characteristics of the group except the specimen displayed in Figure 18 which closely resembles Pénard's (1890) *D. bicornis*. The latter, however, is figured so poorly that it cannot be attributed to any species. Many specimens were so fragile that they disintegrated before a photograph could be obtained. Text-figure 4, obtained by outlining and rearranging Leidy's (1879) figures, shows a compressed intergradational series of this species.

Diffugia bacilliarum Perty, 1849

Pl. 5, Figs. 16–19; Pl. 6, Figs. 1–4

- Diffugia bacilliarum* PERTY, 1849b, p. 27. PERTY, 1852, p. 187, pl. 9, fig. 7. CASH and HOPKINSON, 1909, p. 25, text-figs. 45–47. WAILES, 1931, pl. 2, fig. 26. HOOGENRAAD and DE GROOT, 1952, p. 239, text-fig. 8. DECLÔTRE, 1953, p. 48, text-figs. 109, 110. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 327, text-figs. 45b, c. HARNISCH, 1958, p. 41, pl. 8, fig. 26 (after Pénard, 1902). (?) OGDEN and HEDLEY, 1980, p. 122, pl. 50.
- Diffugia acuminata* Ehrenberg. LEIDY, 1879 (part), p. 109, pl. 13, figs. 10–17, (23–26?). CONN, 1904, p. 15, pl. 5, fig. 27. GROSPICHTSCH, 1972, p. 14, text-fig. 31. SMAGOWICZ, 1975, p. 408, text-fig. 8.
- Diffugia elegans* Pénard, 1890 (epithet invalid; junior primary homonym of *Diffugia elegans* Leidy, 1874a = *Hyalosphenia elegans auctorum*), p. 140, pl. 4, figs. 4–11. PÉNARD, 1902, p. 236, text-figs. on p. 237 (1–5 and 11–13). STEINECKE, 1914, p. 304, text-fig. 1. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 338, text-figs. 49a, b, c. CHARDEZ, 1964, p. 36, pl. 3, fig. 8. GREEN, 1975, p. 549, text-fig. 9. SCHÖNBORN, 1975, p. 130, text-fig. 1f. OGDEN and HEDLEY, 1980, p. 132, pl. 55.
- Diffugia mamillaris* PÉNARD, 1893, p. 176, pl. 3, figs. 18, 19. PÉNARD, 1899, p. 37, pl. 3, figs. 13, 14. PÉNARD, 1902, p. 255, text-figs. 1–4. CHARDEZ, 1964, p. 37, pl. 4, fig. 6 (misspelled *D. mamillaris*).
- Diffugia elegans* var. *teres* PÉNARD, 1899, p. 27, pl. 2, figs. 16–20. PÉNARD, 1902, p. 239, text-fig. 9. PÉNARD, 1905, p. 15, text-fig. on p. 16. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 335, text-fig. 50.
- Diffugia acuminata* var. *inflata* PÉNARD, 1899 (last epithet invalid; junior primary homonym of *Diffugia bacillifera* var. *inflata* Pénard, 1890), p. 29, pl. 3, fig. 1. PÉNARD, 1902, p. 234, text-fig. 10. PÉNARD, 1905, p. 14, text-fig. on p. 15. CASH and HOPKINSON, 1909, p. 23, pl. 18, fig. 14. WAILES, 1931, pl. 2, fig. 25.
- Diffugia acuminata* var. *elegans* Pénard. WEST, 1901, p. 319, pl. 28, figs. 11, 12.
- Diffugia bacilliarum* var. *elegans* Pénard. CASH and HOPKINSON, 1909, p. 28, text-fig. 48, pl. 20, figs. 2–5.
- Diffugia elegans* var. *angustata* DEFLANDRE, 1926, p. 523, text-fig. 10. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 335, text-figs. 49c, f, g. GREEN, 1963, p. 505, text-fig. 20.
- Diffugia elegans* forma *tricornis* JUNG, 1936a, p. 45. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 335, text-fig. 49d.
- Diffugia curvicaulis* var. *inflata* DECLÔTRE, 1951 (last epithet invalid; junior primary homonym of *Diffugia bacillifera* var. *inflata* Pénard, 1890), p. 105, text-fig. 16. DECLÔTRE, 1953, p. 50, text-fig. 113. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 331, text-fig. 47c.

Diagnosis. Test normally transparent and covered with sand grains. Judging from the literature, the xenosomes often include a very conspicuous fraction of diatom frustules (not found in our specimens from James Bay) which often obscure the basic shape of the test. Test broad in proportion to its length; at times the maximum width is reached at the aperture or, more often, a constriction forms a sort of broad collar under the aperture. In the latter case, the maximum width is reached at approximately $\frac{2}{3}$ of the length from the aperture. Fundus always somewhat conical, often terminated either by a blunt protuberance or a hollow spine.

Differs from *D. protaeiformis* by 1) the larger ratio of *aperture diameter: maximum diameter* (0.4 to 0.6 for *D. bacilliarum* and 0.5 to 0.7 for *D. protaeiformis*), 2) the larger *width: length* ratio (about 0.5 to 0.9 versus 0.2 to 0.6), and 3) the funnel-like collar that sometimes flares out almost perpendicularly to the main axis of the test (in some cases it appears to become vestigial).

Discussion. The material for this species, which was not recorded in Lake Erie, comes from James Bay where it is relatively scarce. Consequently, the comments that follow should be taken as somewhat tentative.

Cash and Hopkinson (1909) had already realized that *D. bacilliarum* and its varieties formed a group as difficult to identify as the multitudinous forms of *D. constricta* (=our *Centropyxis constricta*). We agree that this is a variable group although we do not think that it is one of the most variable.

The species grades into *D. protaeiformis* at one extreme of its spectrum of variability and into *D. urceolata* at the other extreme. In our material, however, considering the entire assemblage, the percentage of intermediate forms that leave serious doubts as to their specific identification is unusually low for an arcellaean group. The central part of the spectrum, possibly because of the relative scarcity of material, is heterogeneous with a number of clearly visible clusters (morphotypes). The number of intermediate forms, however, is sufficiently high to make it impossible to keep such clusters separated from each other.

The variations, either observed by us in our material or reported in the literature, seem to affect particularly 1) the overall shape of the test, from roughly conical, to distinctly pear-shaped, to urceolate; 2) the nature of the agglutinated material, from mainly diatomaceous to wholly non-biological; and 3) the structure of the fundus that can either be rounded or carry a very conspicuous hollow spine or a blunt protuberance. Various combinations of these characteristics create a large va-

riety of morphotypes, all clearly belonging to this species. Apart from the basic morphological variability of the test, another factor that in our opinion contributed to the taxonomic confusion surrounding this group is the variable nature of the xenosomes. *D. bacillariarum*, in fact, at times selects diatom frustules as xenosomes. Authors have tended, in our opinion, to pay more attention to the presence or absence of highly visible diatom frustules than to the basic shape of the test.

H. Lena-Hernandez (personal communication, 1981) suggests that the forms that we illustrate (Pl. 5, Figs. 16–19; Pl. 6, Figs. 1–4) may represent freshwater tintinnids (such as *Tintinnopsis rioplatensis* Souto, 1973). Generally speaking, this is a distinct possibility, the tests of the two types of organisms show an uncanny similarity and, in the literature, there appears to be a marginal overlapping of dimensions between the tests of both (see for instance the small specimens of *D. elegans* with diameters of 30–40 μm described by Pénard, 1890). On the other hand our samples were separated with a 63 μm opening sieve. Such openings are significantly larger than the maximum diameters quoted for *T. rioplatensis* (e.g., 49 μm in Souto, 1973), which makes it very unlikely that our material could contain tintinnids at all. Furthermore, the diameters of most of our specimens of *D. bacillariarum* are clustered around 70–80 μm .

Occurrence. Deep parts of the great alpine lakes, bog-pools in England and Wales. Pénard (1905) claims that in the great alpine lakes the morphotype that he calls var. *teres* dominates the group below 30 m depth. Ditches, ponds, and swamps.

Observations on material illustrated in this paper. This is the only species discussed in this paper that is not found in Lake Erie. We have illustrated five specimens. Even in this relatively stable species considerable variability of lip development can be observed (Pl. 5, Figs. 16–19; Pl. 6, Figs. 1–4).

***Diffugia bidens* Pénard, 1902**

Pl. 1, Figs. 1–5

Diffugia bidens PÉNARD, 1902, p. 264, text-figs. 1–8. SCHOUTEDEN, 1906, p. 342, 345, fig. 16a opposite p. 336. THOMAS, 1954, p. 250, pl. 4, figs. 5, 6. HARNISCH, 1958, p. 41, pl. 8, fig. 9 (after Pénard, 1902). SCOTT and MEDIOLI, 1983, p. 818, figs. 9h, i. (?) *Diffugia bicurvis* GAUTHIER-LIÈVRE and THOMAS, 1958, p. 328, text-figs. 45d, e, f. *Diffugia* sp. Y GREEN, 1963, p. 510, text-fig. 13.

Diagnosis. Shell regularly ovoid, usually laterally compressed; transversal cross section ovoid. Fundus

obtusely and evenly rounded, usually furnished with two to three short and blunt hollow spines. In our material the shell appears to be composed of small, reasonably well sorted quartz grains. Mouth wall thickened internally; no external neck; aperture round and well defined.

This species differs from *D. corona* in 1) being laterally compressed whereas the latter never is, 2) having a smooth apertural rim quite different from the strongly crenulated one of *D. corona*, and 3) being always somewhat elongated while most specimens of *D. corona* tend to be characteristically spheroidal. Rare, extreme specimens of *D. bidens* and *D. bacillariarum* could be confused. They can be easily separated because the former species is flattened and has a smaller *aperture diameter: maximum diameter* ratio (0.3 to 0.4, versus 0.4 to 0.6).

Discussion. This form was originally described by Pénard (1902) from Lake Lemán, Switzerland. Our specimens correspond perfectly to his original figures.

Thomas (1954) reported the same species from the Bordeaux region of France without describing it in detail. He did, however, elaborate on the structure of the spines which he described as hollow, very transparent, and not in communication with the interior of the shell. Closer examination revealed a floor at the base of the spines which is a continuation of the fundus of the shell.

It is surprising that this species, which we have found as relatively common in Lake Erie and numerous lakes in Atlantic Canada, appears so seldom in the literature. Vaguely similar forms, however, have been reported by several authors. Leidy (1879, p. 109, pl. 12, figs. 24–29) described and figured, as *D. acuminata*, a form with 2–3 spines and an ovoidal-compressed outline. Despite the obvious similarity, Leidy's forms differ from ours by having a short, sometimes rimmed neck.

Pénard himself (1890, p. 141, pl. 4, figs. 12–14) described and figured, as *D. bicornis*, a form somewhat similar to *D. bidens*. His 1890 figures, however, are too poor to be of any help in deciding whether or not the two forms are conspecific. In 1902, in the work in which he first described *D. bidens*, Pénard stated that his 1890 *D. bicornis* were really two-horned specimens of his *D. elegans*. He did not mention any affinity between *D. bicornis* and *D. bidens*.

D. bidens, as we circumscribe it, appears to be a comparatively uniform species which does not seem to present any of the taxonomic problems so characteristic of most other species of this genus.

Occurrence. Lake Lemán (Pénard, 1902), and in a swamp near Bordeaux, France (Thomas, 1954). We

found it in Lake Erie and in several lakes in New Brunswick.

Observations on material illustrated in this paper. Except for the relatively small spines at the fundus, *D. bidens* showed the least variability of any of our species. Our figured specimens (Pl. 1, Figs. 1–5) look almost exactly as those in Pénard (1902).

Diffflugia corona Wallich, 1864

Pl. 1, Figs. 6–14

D. proteiformis (sic) (Ehrenberg) subspecies *D. globularis* (Dujardin) var. *D. corona* (Wallich). WALLICH, 1864, p. 244, pl. 15, figs. 4b, ?4a, ?4c; pl. 16, figs. 19, 20.

Diffflugia corona Wallich. ARCHER, 1866a, p. 186. ARCHER, 1866b, p. 266. LEIDY, 1874b, p. 14. LEIDY, 1879, p. 177, pl. 18, figs. 1–14. PÉNARD, 1890, p. 141, pl. 4, figs. 15–19. PÉNARD, 1902, p. 287, text-figs. 1–6, on p. 288. CONN, 1904, p. 15, pl. 4, fig. 22. EDMONDSON, 1906, p. 16, pl. 3, fig. 16. SCHOUTEDEN, 1906, p. 344–348, fig. 21. CASH and HOPKINSON, 1909, p. 49, text-fig. 65, pl. 22, figs. 3–7. JENNINGS, 1916, p. 407–534, text-figs. 1–3, 6a–b, 7, 13–15, 19. DEFLANDRE, 1953, p. 121, text-figs. 85, 86. GROSPIETSCH, 1958, p. 44, text-fig. 37c. HARNISCH, 1958, p. 41, pl. 8, fig. 13 (after Pénard, 1902). GREEN, 1963, p. 504, text-figs. 6–9. CHARDEZ, 1964, p. 35, pl. 6, fig. 1. GROSPIETSCH, 1972, p. 14, text-fig. 28. OGDEN and HEDLEY, 1980, p. 128, pl. 53. HAMAN, 1982, p. 367, pl. 3, figs. 7–14. SCOTT and MEDIOLI, 1983, p. 818, fig. 9p.

Diagnosis. Shell subspherical, ovoid to spheroid, circular in transversal cross section. Fundus furnished with a variable number of spines (1 to 10 or more); mouth central, roughly circular but crenulated by 6 to 20 regular indentations forming a thin collar. Test composed of fine, angular quartz grains of varied sizes; smaller pieces fill the gaps in between larger ones. Spines delicate and very easily broken, composed of the same material. Although highly variable in size and shape, *D. corona* is a distinctive and easily recognized species (Fig. 5).

D. corona is easily differentiated from xenosomic specimens of *D. tricuspis* because the former usually has a much higher number of apertural indentations (minimum of 6) than the latter (maximum of 6 clear indentations, sometimes more but in that case the indentations are irregular and poorly defined). There are rare specimens that are intermediate between the two taxa (Leidy, 1879, who used the binomen *D. lobostoma* for our *D. tricuspis*) and cannot be attributed with certainty to either one. *D. corona* differs from *D. urceolata* by its usually smaller size, the apertural crenulation, and the lack of a collar.

Discussion. Leidy (1879) wrote that in this species the shell is one of the smoothest of the genus, although composed of angular particles of quartz. The mouth truncates the shell, or it continues its curvature, or it

projects from it. The lip is crenulated with thick, angular processes in number from 6 to 16, but more frequently 12 or more rather than less. The notches are as deep as they are wide, and rounded at the bottom. The fundus carries a variable number of spines, generally 3 to 7 but ranging from 1 to 11; often they form a circle at the fundus third of the shell. We seldom noticed more than five spines. The species is distinctive and relatively stable.

Loeblich and Tappan (1964) defined the genus *Loeboforamina* as having only 3 to 6 lobes in the aperture and no collar. For reasons that are not clear to us they listed under it *D. corona*, despite the fact that this species is normally described as having a larger number of lobes.

Leidy (1879, p. 119, pl. 17, fig. 12) illustrated an intermediate form that he had difficulties placing in either *D. corona* or *D. lobostoma*. We agree with Leidy that in some cases the limit between the two taxa is not clearly defined.

It is unfortunate that Jennings (1916) chose this rather uncontroversial and stable form for his study on heredity and variation in uniparental organisms, because the figures that we report from his paper only show what we believe to be a low level of variability for an arcellacean species. Had Jennings chosen a group with spectacular variability, such as *D. oblonga* or *D. protaeiformis*, much more would have been learned about the problem.

Occurrence. The literature reports *D. corona*, seldom very commonly, in ditches and ponds, we found it also in lakes.

Observations on material illustrated in this paper. We illustrate a wide range of variability in this species (Pl. 1, Figs. 6–14). The most “typical” specimen is that shown on Figure 11. Our material shows variation limits much wider than those illustrated by Jennings (1916) which, in our opinion, proves our point that a population produced through a laboratory culture can only show a *minimum* of variability, the *maximum* being visible only in wild populations and when the numbers are sufficiently high.

The consistent feature throughout the species is the crenulated aperture. Shape, size, number, and position of spines are all highly variable.

Diffflugia fragosa Hempel, 1898

Pl. 1, Figs. 21–27

Diffflugia fragosa HEMPEL, 1898, p. 320, text-figs. 1, 2. PÉNARD, 1902, p. 573, fig. 2 on p. 572. AVERINTSEV, 1906, p. 216 and table opposite p. 180. SCHOUTEDEN, 1906, p. 344, 348 (misspelled

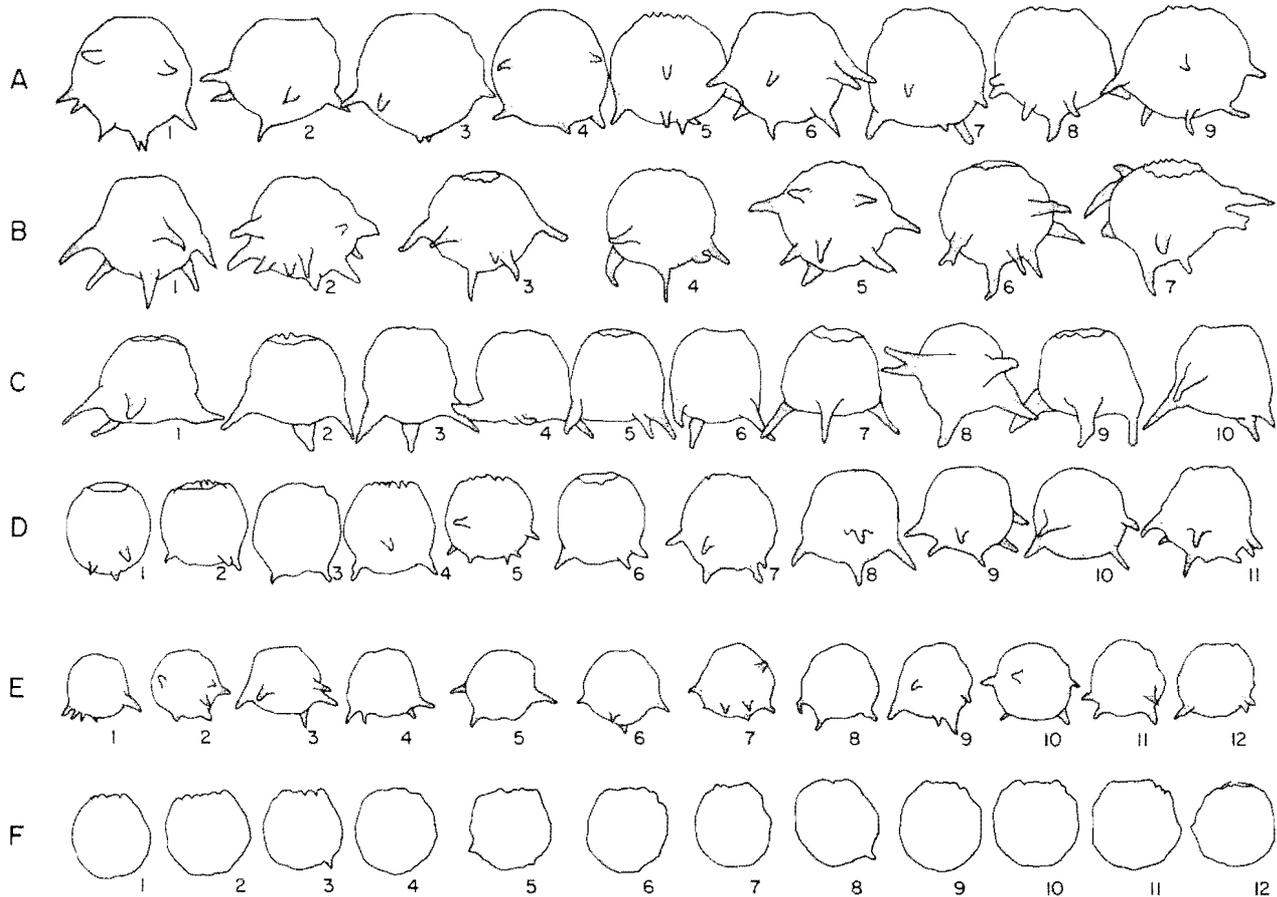


FIGURE 5. Figures of *Diffflugia corona* (redrafted and rearranged from Jennings, 1916). Six of Jennings' broods, chosen to show the gradual decrease in size and spinosity from A to F. The characteristics of the parent specimen (first from left) vary somewhat between each brood but basically descendants remain similar to ancestors. The differences, however, between broods A and F are such that any specimen of A, taken in isolation, could not be matched to any isolated specimen of F. The diagram illustrates the absolute need for assemblage studies.

D. fragosa). HARNISCH, 1958, p. 40, pl. 8, fig. 21 (after Pénard, 1902). SCOTT and MEDIOLI, 1983, p. 818, fig. 9o.

(?) *Pentagonia maroccana* GAUTHIER-LIÈVRE and THOMAS, 1958, p. 349, text-fig. 56.

(?) *Maghrebina spatulata* GAUTHIER-LIÈVRE and THOMAS, 1958, p. 351, pl. 13. LOEBLICH and TAPPAN, 1964, p. 36, text-fig. 16.1.

(?) *Diffflugia maroccana* (Gauthier-Lièvre and Thomas). LOEBLICH and TAPPAN, 1964, p. C35, text-fig. 15.

Diagnosis. Shell composed of agglutinated sand grains. The overall outline, in side view, is roughly drop-shaped but the general appearance is dominated by one to eight large ribs running from roughly the middle of the test to the fundus, and past it, and often extending into blunt spines or tubercles. In most cases, when viewed from the apertural or from the fundus side, the test shape is from triangular to octagonal or totally irregular, depending on the number and shape of the ribs. Aperture rounded or irregular, usually sur-

rounded by a single row of regularly arranged sand grains. This species is not likely to be confused with any other.

Discussion. This peculiar and distinctive species is very seldom reported in the literature. It was described by Hempel (1898) from the Illinois River. Pénard (1902) reported that it was absent from Lake Lemane; his figure appears to have been redrafted from Hempel's original drawing. Averintsev (1906) and Schouteden (1906) summarized Hempel's description without showing any figures but did not observe this species directly. The only unquestionable and direct observations known to us (Hempel's and ours) are from eastern North America.

We found no other mention of this form but our material fits quite well into Hempel's species. As far as we know, *D. fragosa* does not appear to present the

usual problems of differentiation from neighboring species. We do not know whether the presence of ribs is genetically determined and we feel that, should these ribs disappear or be modified under the influence of environmental factors, the validity of the species would become very questionable. Conceivably, the ribs could be an accidental feature that could affect different species of *Diffugia* either at random or in response to some set of environmental circumstances.

Ogden and Hedley (1980, p. 102, pl. 40) described and figured under the name *Nebela griseola* Pénard, 1911, a form which shows a striking resemblance in general shape with *D. fragosa*. It apparently differs from our form by being laterally compressed, by having the test largely composed of small idiosome-like particles, and by having 11–12 ribs instead of 8.

Gauthier-Lièvre and Thomas (1958) established the two species *Pentagonia maroccana* and *Maghrebica spatulata* respectively as type species for their new genera *Pentagonia* and *Maghrebica*. Each of these two forms might be junior synonyms of *D. fragosa*; they seem to differ from it mainly in the characters of their collar. Due to the scarcity of material we cannot reach an intelligent decision on this matter.

Occurrence. So far reported from the Illinois River and neighboring small lakes and, in this paper, Lake Erie. Perhaps, but we have serious doubts, recorded by Gauthier-Lièvre and Thomas from ponds in northwestern Africa as *Pentagonia maroccana* and *Maghrebica spatulata*.

Observations on material illustrated in this paper. Our material conforms fairly closely with the original description but shows a significant amount of variability (Pl. 1, Figs. 21–27). The extreme specimens (Figs. 21, 22) are close to Hempel's (1898) original forms but others appear almost rounded (Fig. 25).

***Diffugia globulus* (Ehrenberg, 1848)**

Pl. 5, Figs. 1–15

- (?) *Diffugia proteiformis* (sic) Lamarck. EHRENBURG, 1838, p. 131 (part), pl. 9, figs. 1a, b.
- Arcella*? *globulus* EHRENBURG, 1848, p. 379. EHRENBURG, 1856, p. 333, fig. 4 of unnumbered plate.
- D. proteiformis* (sic) (Ehrenberg) subspecies *D. globularis* (Dujardin). WALLICH, 1864, p. 241, pl. 15, fig. 4h; pl. 16, figs. 1, 2, 2a, 17, 21.
- Diffugia globulosa* Dujardin. LEIDY, 1879, p. 96, pl. 15, figs. 25–31; pl. 16, figs. 1–23. RHUMBLER, 1895, p. 74, pl. 4, fig. 21. (?) WEST, 1901, p. 320 (part), (?) pl. 29, figs. 17, 18. PÉNARD, 1902, p. 259, unnamed varieties, text-figs. 5, 6 on p. 258. CONN, 1904, p. 15, pl. 2, fig. 14 (miswritten *D. globosa* in text and *D. globostoma* in caption). HARNISCH, 1958, p. 44, pl. 8, fig. 18 (after Pénard, 1902). OGDEN and HEDLEY, 1980, p. 134, pl. 56. SCOTT and MEDIOLI, 1983, p. 818, figs. 9j, n.

Diffugia globulosa var. *globularis* Wallich. PÉNARD, 1902, p. 257, text-figs. 1–6 on p. 258, fig. 18 on p. 213.

Diffugia globulosa forma *genuina* PÉNARD, 1902, p. 257.

Diffugia globulus (Ehrenberg). CASH and HOPKINSON, 1909, p. 33, text-figs. 52–54, pl. 21, figs. 5–9.

Diagnosis. Shell spheroidal to ellipsoidal (up to 20% longer than wide) with the oral pole truncated by a circular, occasionally slightly invaginated aperture which is usually large but can decrease in diameter to as little as $\frac{1}{4}$ of maximum width. Overall shape resembling that of the sea urchin *Echinus*. At times the aperture is slightly protruding or slightly invaginated. Shell composed of a chitinous membrane covered by agglutinated quartz particles and/or diatom frustules. The species differs from *D. corona* by the complete lack of apertural crenulation and spines, and from *D. urceolata* by the lack of a pronounced collar and by the relatively shorter main axis.

Discussion. Although we have not seen them, we conclude from the literature that *D. globulus* should be characterized by typical arcellate pseudopods. This species has been recognized by many authors under that name and two others *D. globulosa* Dujardin and *D. globularis* Wallich.

D. globularis has a globular test with large xenosomes and fits without any doubt into our own definition of this species. Dujardin (1837) described and figured as *D. globulosa* a thecamoebian with arcellate pseudopods. The test was markedly oval, smooth, xenosomes free, "corneous," apparently translucent, with a very small aperture figured only in profile and not described in the text. Because of those characteristics Dujardin's organism cannot be a specimen of *D. globulus* as defined by us, and its exact taxonomic nature remains unclear.

In 1841 Dujardin widened his definition of *D. globulosa* to include more globular specimens, but even this new unit does not seem to be related to our species. Thus *D. globulosa* cannot be the valid name for our mainly globular *Diffugia* species.

Leidy (1879), who was quite familiar with Dujardin's species, figured numerous specimens of what he called *D. globulus* without showing the pseudopods. Leidy's specimens very likely belong to our species.

Pénard (1902) included in his *D. globulosa* Dujardin's "corneous" forms (which Pénard apparently never observed directly), in addition to other forms that we would include in our *D. globulus*. Many authors have used the name *D. globulosa* in Leidy's or Pénard's sense, mainly to redescribe and illustrate large, heavily xenosomic specimens (e.g., Ogden and Hedley, 1980), with pseudopods either of arcellate aspect or unknown, all probably belonging to this species.

Cash and Hopkinson (1909) were the first to recognize a unit strictly similar to ours (they rejected from it Dujardin's specimens of *D. globulosa*) which they correctly named *D. globulus*.

Ehrenberg (1848) described, but never illustrated, as "*Arcella ? globulus*" a subglobose form with a simple aperture and a diameter of about 45 μm . We believe that this form might have been either a globular *Difflugia* or some type of *Centropyxis*; from the dimensions it might even have been our *D. globulus*. In 1856, however, the same author showed in his figure 4 a specimen that clearly fits into our description and this reinforces our suspicion that the previous report was also dealing with this species.

We unite, in *Difflugia globulus*, all the arcellacean tests found in our samples that correspond to the above diagnosis. We recognize, however, that some of such forms could conceivably belong not only to *D. globulus* but also to the genera *Phryganella*, *Pseudodifflugia* and *Centropyxis* (forms with axial symmetry, which some call *Cyclopyxis*).

As already pointed out by Cash and Hopkinson (1909), these groups of organisms, in fact, cannot be distinguished in the fossil state because they are differentiated mainly by means of their pseudopods, which are 1) lobose, wide and finger-like, never anastomosing in *D. globulus* proper and in *Centropyxis*; 2) lobose, very narrow, sometimes anastomosing in *Phryganella*; and 3) filose in *Pseudodifflugia*. The tests of those three groups are largely similar and their respective size ranges, while different for various groups, overlap (range of test diameter in our material: 63 μm to about 190 μm).

Except for *Centropyxis*, however, these groups consist almost entirely of tests which, according to the literature, are either too small to be retained by our sieves (aperture 63 μm) or that, in some forms of *Pseudodifflugia*, are covered only with sparse and very tiny xenosomes. The probability that they may fossilize is next to nil. In practical terms, then, the problem is reduced mainly to the genus *Centropyxis*.

According to the literature "*Cyclopyxis*" can be identified by its invaginated aperture. In our rare fossils with some sort of invagination, the structure is ill defined and possibly deformed or eroded (our best invaginated specimen is shown in Pl. 5, Figs. 13, 14). This blurs further what to us is already an excessively tenuous distinction between fossil *D. globulus* and *Centropyxis*. Very early in this study we abandoned the futile struggle to keep the two units separated. This means that in our studies the species *D. globulus*, as we define it, in the fossil state may contain a few misidentified forms.

Occurrence. Ooze of ditches, ponds and bogs, lakes.

Observations on material illustrated in this paper.

Our Lake Erie specimens often were attached to huge sand grains (Pl. 5, Figs. 1–4, 10). A few of the attached specimens and all the unattached ones, with a somewhat depressed shape, had the aperture closed by a porous plate made of numerous small xenosomes (Pl. 5, Figs. 5–7, 9–11) and similar to the epiphragm reported in cyst-containing tests of "*Cyclopyxis*" by Bonnet (1964). The nature and function of such a structure is unknown to us. We found no tests with epiphragms outside Lake Erie. Specimens from Nova Scotia (Pl. 5, Figs. 13, 14) have a slightly invaginated aperture reminiscent or, possibly, indicative of "*Cyclopyxis*." Some of the variability in shape of the Lake Erie material can be linked, to variable degrees, to the attached habit (Medioli and Scott, 1978).

Difflugia oblonga Ehrenberg, 1832

Pl. 2, Figs. 1–17, 24–26

- Difflugia oblonga* EHRENBERG, 1832b, p. 90. EHRENBERG, 1838, p. 131, pl. 9, figs. 2a–d. CASH and HOPKINSON, 1909, p. 4, pl. 17, figs. 1–3, 7, 8; pl. 19, figs. 3, 4, 33. THOMAS, 1954, p. 254, pl. 3, fig. 1. GROSPIETSCH, 1958, p. 44, pl. 1, fig. 3. FEYLING-HANSSSEN, 1964, p. 217, pl. 1, figs. 4–6. GREEN, 1975, p. 550, text-figs. 14, 15. OGDEN and HEDLEY, 1980, p. 148, pl. 63. HAMAN, 1982, p. 367, pl. 3, figs. 19–25. SCOTT and MEDIOLI, 1983, p. 818, figs. 9a, b.
- Difflugia pyriformis* PERTY, 1849a, p. 168. PERTY, 1852, p. 187, pl. 9 (upper part), fig. 9. CARTER, 1864, p. 21, pl. 1, fig. 1. LEIDY, 1879, p. 98, pls. 10, 11; pl. 12, figs. 1–18; pl. 15, figs. 32, 33; pl. 16, fig. 38; pl. 19, figs. 24–26. CERTES, 1889, p. 12, pl. 1, fig. 2. PÉNARD, 1890, p. 136, pl. 3, figs. 30–38. BLANC, 1892, p. 380, pl. 2, figs. 11, 12. WEST, 1901, p. 317, pl. 28, figs. 13, 14. PÉNARD, 1902, p. 214, text-figs. 1–8 on p. 216, text-fig. 3 on p. 213. EDMONDSON, 1906, p. 12 (part), pl. 2, fig. 9. SCHOUTEDEN, 1906, p. 343, 346, fig. 17 opposite p. 336. TODD and BRONNIMANN, 1957, p. 21, pl. 1, fig. 2. HARNISCH, 1958, p. 42, pl. 8, fig. 3 (after Pénard, 1902). HAMAN, 1982, p. 367, pl. 4, figs. 4–12.
- Difflugia entochloris* LEIDY, 1874c, p. 79. LEIDY, 1878, p. 307.
- Difflugia compressa* Carter. LEIDY, 1879, p. 99, pl. 11, figs. 1–6; pl. 12, figs. 10–16.
- Difflugia cornuta* var. of *pyriformis* LEIDY, 1879, p. 99, pl. 12, figs. 17, 18.
- Difflugia nodosa* var. of *pyriformis* LEIDY, 1879, p. 99, pl. 11, figs. 7–22.
- Difflugia pyriformis* var. *nodosa* Leidy. PÉNARD, 1890, p. 136, pl. 3, figs. 45, 46. PÉNARD, 1902, p. 218, text-figs. 1–8.
- Difflugia pyriformis* var. *linearis* PÉNARD, 1890, p. 137, pl. 3, figs. 42–44.
- Difflugia pyriformis* var. *tenuis* PÉNARD, 1890, p. 138, pl. 3, figs. 47–49.
- (?) *Difflugia bacillifera* PÉNARD, 1890, p. 146, pl. 4, figs. 61–66. PÉNARD, 1902, p. 230, text-figs. 1–4 on p. 231. GROSPIETSCH, 1958, p. 44, text-fig. 38c, pl. 1, fig. 2. OGDEN and HEDLEY, 1980, p. 124, pl. 51.
- Difflugia pyriformis* var. *claviformis* PÉNARD 1899, p. 25, pl. 2, figs. 12–15.

- Diffugia pyriformis* var. *lacustris* PÉNARD, 1899, p. 24, pl. 2, fig. 11. PÉNARD, 1905, p. 21, text-fig. on p. 22.
- Diffugia capreolata* PÉNARD, 1902, p. 222, text-figs. 1–6 on p. 223, text-fig. 6 on p. 213. TODD and BRONNIMANN, 1957, p. 21, pl. 1, figs. 3, 4. FEYLING-HANSEN, 1964, p. 217, pl. 1, figs. 1–3. SCOTT, 1977, p. 163, pl. 1, figs. 4–7. SCOTT and others, 1977, p. 1578, pl. 1, figs. 3, 4. SCOTT and others, 1980, p. 224, pl. 1, figs. 4–7. HAMAN, 1982, p. 367, pl. 3, figs. 1–3.
- Diffugia pyriformis* var. *venusta* PÉNARD, 1902, p. 220, text-fig. 5 on p. 218. CASH and HOPKINSON, 1909, p. 10, pl. 17, figs. 4, 5.
- Diffugia pyriformis* var. *bryophila* PÉNARD, 1902, p. 221, text-fig. 7 on p. 218.
- Diffugia pyriformis* var. *atricolor* PÉNARD, 1902, p. 218, text-fig. 6.
- Diffugia oblonga* Ehrenberg 1832, forma *bryophila* Pénard 1902. SMAGOWICZ, 1976, p. 91, text-fig. 1.
- Diffugia oblonga* var. *claviformis* Pénard. CASH and HOPKINSON, 1909, p. 11, pl. 17, figs. 6–9.
- Diffugia oblonga* var. *lacustris* Pénard. CASH and HOPKINSON, 1909, p. 12, text-fig. 40, pl. 19, figs. 1, 2. DECLOÏTRE, 1953, p. 52, text-fig. 120.
- (?) *Proteonina longicollis* WIESNER, 1931, p. 82, pl. 6, fig. 55. (?) CUSHMAN and McCULLOCH, 1939, p. 42, pl. 1, figs. 7a, b, 8a, b, 9a, b.
- (?) *Diffugia pyriformis longicollis* GASSOWSKY, 1936, p. 103–119, text-fig. 8. [Last epithet invalid: junior homonym of *D. longicollis* Ehrenberg 1872 ab 1854.]
- Diffugia oblonga* var. *bryophila* Pénard. DECLOÏTRE, 1953, p. 52, text-fig. 119.
- (?) *Diffugia longicollis* Gassowsky. OGDEN and HEDLEY, 1980, p. 144, pl. 61.

Diagnosis. Test extremely variable in shape and size, pyriform to compressed and flask-shaped (Fig. 6). In cross section rounded to compressed. Fundus rounded to subacute or expanded into one to three blunt, rounded conical processes. Neck subcylindrical, more or less long, gradually narrowed toward the oral end. Aperture terminal, circular to slightly oval. Test made of sand particles sometimes mixed with a variable amount of diatom frustules which, if large, can partly or completely obscure the overall shape of the specimen.

Differs from *D. protaeiformis* by often being compressed and by lacking the acute spinal process that is so characteristic of that species. The ratio *apertural diameter*: *maximum diameter* varies between 0.5 and 0.2 while in *D. protaeiformis* it varies from 0.5 to 0.7. The test ranges from 60 to 580 μm in length, 40 to 240 μm in width, 16 to 120 μm in apertural diameter.

Discussion. This extremely common and variable species, like *D. protaeiformis*, has been split with abandon by the various authors. We list in synonymy only the units that most obviously fit into the species as we define it. We made no attempt to critically evaluate the less obvious cases, consequently our list is far from complete. Furthermore, only the synonyms that we consider important are discussed in the text.

After Ehrenberg (1832b) established *D. oblonga*, Perty (1849a) erected his species *D. pyriformis* on the

basis of material that we place in *D. oblonga*. During the last hundred years the epithet *pyriformis* has been more popular than *oblonga*, despite the fact that it is a junior synonym. Ehrenberg (1872, p. 256) was the first to notice that the two species might be synonymous, and that in this case the name *D. pyriformis* had to be rejected. Leidy (1879) doubted the relationship between *D. pyriformis* and *D. oblonga*. He considered that the latter was absent from his material and was more probably related to *D. acuminata* (=our *D. protaeiformis*). Cash and Hopkinson (1909, p. 8) reproduced Perty's original figure of *D. pyriformis* and noted that, while that figure could represent a *Nebela*, Perty's comment that the texture is coarse makes it more probable that it was a *Diffugia* and thus, in their opinion, a junior synonym of *D. oblonga*.

The oldest figures published by Ehrenberg for this species (Ehrenberg, 1838, pl. 9, figs. 2a–d) show that the specimens figured had a smooth but xenosomic test. Xenosomic tests can indeed be very smooth if the xenosomes are thin and flat (e.g., mica flakes or recycled thecamoebian plates) as visible, for example, in the SEM pictures of *D. lanceolata* published by Ogden and Hedley (1980).

Several of the forms that we regroup under *D. oblonga* were distributed by Leidy (1874a, b, c) into three species, *D. pyriformis* Perty, *D. compressa* Carter and *D. entochloris* Leidy. In 1879, however, the same author, having acquired a better knowledge of the assemblages, recognized all such forms as constituting only one species in which he differentiated five varieties (which he designated by binomina), *D. pyriformis* Perty, 1849, *D. compressa* Carter, 1864, *D. nodosa* Leidy, 1879 (a new name that he proposed to substitute for his former epithet *entochloris*), *D. cornuta* Leidy, 1879, *D. vas* Leidy, 1874. Leidy concluded that, given the graduality with which each of these varieties leads into the next, none of them could be considered as an independent taxon.

Cash and Hopkinson (1909), in discussing the variability of *D. oblonga* (= *D. pyriformis*), remarked that Leidy regarded these variations as accidental, whereas, in their opinion, the frequent recurrence justifies the conclusion that they point to some organic distinction. The two authors were of the opinion that between the pyriform and oblong examples of this variable species there are intermediate forms which cannot be classified. They suggested that their own figures may be taken as showing the limits of variation in the species. In fact, Leidy (1879) did not seem to mean that the varieties are accidental; he seemed to have considered (as did Cash and Hopkinson, 1909) that the species is

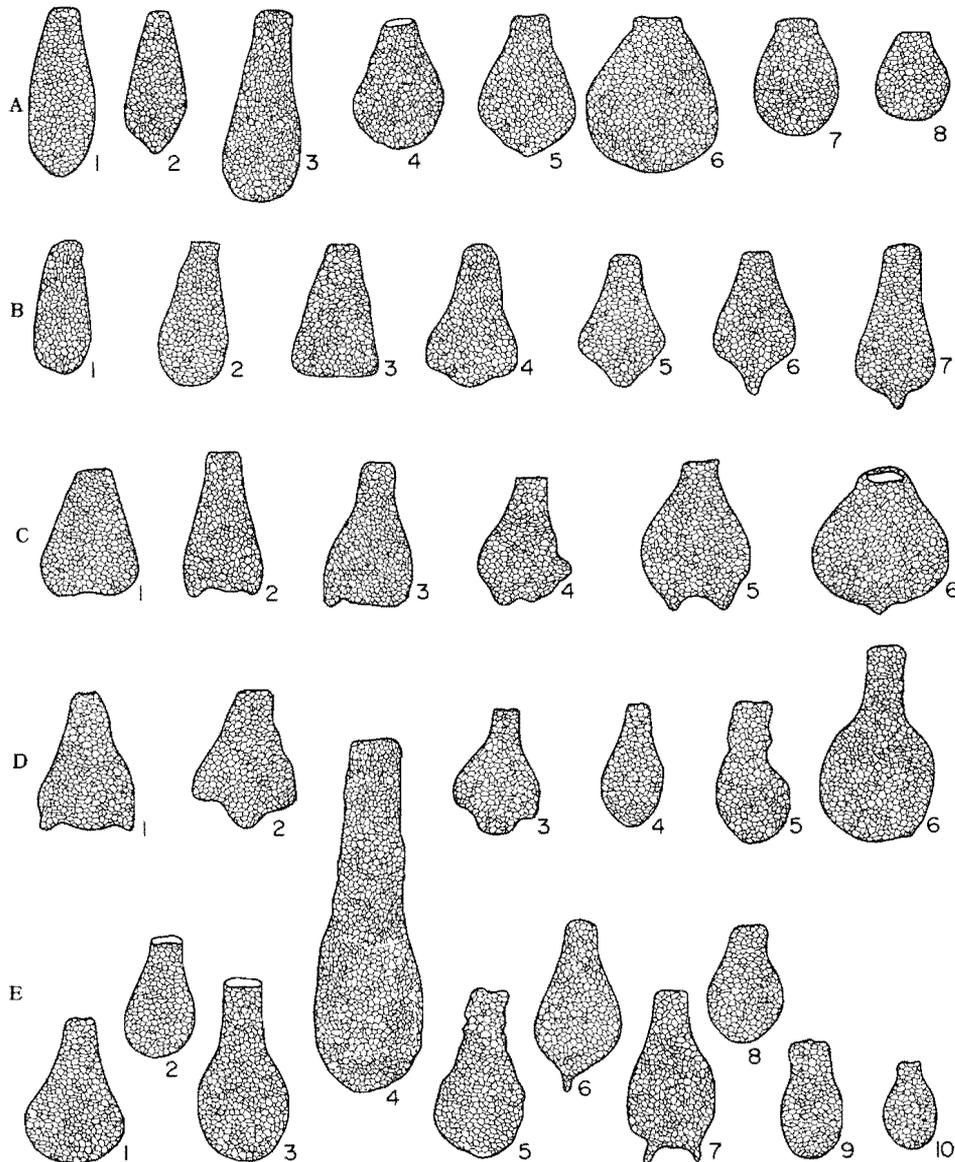


FIGURE 6. Figures of *Diffugia oblonga* (redrafted and rearranged from Leidy, 1879, pls. 10–11). Leidy's figures are rearranged here in five very simplified and shortened horizontal intergradational series. The same figures can easily be sequenced in a number of other ways (including circular sequences, as for example: A1-B2-E2-E1-B4-B6-B5-A5-A4-D4-B1-A1). The excessive number of intermediate forms in *D. oblonga* makes it impossible to present a detailed intergradational arrangement. From any specimen one can follow several different series radiating in various directions and merging with each other again at various points of the network.

so variable, and the variations so gradual, that distinct varieties cannot be separated from each other. Only a small minority of extreme specimens are so distinctly different from the most common ones that they can be identified by different varietal names, while intermediate forms, which represent the vast majority, cannot be so classified.

Pénard (1890, 1902, 1905) also recognized several

varieties within *D. pyriformis*. However, he commented (1905) that his variety *claviformis* appears to be clearly derived from *D. pyriformis*, and more precisely from the largest form which, in turn, appears to grade into var. *nodosa* Leidy. Leidy (1879) himself felt that his var. *nodosa* graded into the typical *D. pyriformis*. Talking about his var. *lacustris*, Pénard (1905) admitted that among his varieties of *D. pyriformis*, to

be rigorous, some could be assimilated to var. *lacustris*. Thus, Pénard too realized that there is gradual variation throughout this species.

We suspect that at least part of *D. bacillifera* Pénard and its "varieties" may fall into *D. oblonga* as defined above. "*D. bacillifera*" represents a serious problem: we feel that parts of it fall into more than one species of *Diffugia*. The forms illustrated by Pénard and subsequent authors are characterized by a test coated with large diatom frustules. Such frustules, because of their large size, tend to obscure the shape of the test which can only be guessed. Some figured specimens of *D. bacillifera* appear to belong to this species, others to *D. protaeiformis* and often they cannot be distinguished from our *D. bacilliarum* Perty when the latter is obscured by diatom frustules too. We feel that *D. bacillifera* is not a valid species but rather an artifact that will never be interpreted correctly until we are able to shed some light on the mechanisms governing the building of the test in the Arcellacea. In any event we have not seen a sufficient number of specimens to make an intelligent taxonomic decision on this point.

In conclusion, it appears that Leidy (1879) was justified in considering that *D. pyriformis*, despite its immense variability, cannot be split into clearly separated units. As illustrated by Leidy and redrafted and rearranged by us (Fig. 6), this species indeed represents an extreme example of a giant intergradational series radiating tridimensionally. Lack of space prevents us from showing on one plate its entire variability spectrum. The iconography in the literature, for the same reason, gives an impression of discontinuity that does not exist in nature. We have delimited this species according to Leidy's concept of *D. pyriformis* (=our *D. oblonga*). Our only serious reservation about Leidy's concept of this species concerns the fact that he placed in it what he called variety *D. vas* Leidy, 1874. We place the same form in the new genus *Lagenodiffugia* as *Lagenodiffugia vas*. An apparent intergradation may exist between *D. oblonga* and specimens of *L. vas* provided that very large xenosomes in the area of the neck hide the constriction (see our discussion of *L. vas*). This is why Leidy placed his taxon *D. vas* in *D. pyriformis*.

Occurrence. Oozes of all sorts of freshwater bodies.

Observations on material illustrated in this paper. Our material indicates (Pl. 2) the usual variability of this species already shown by Leidy, although our specimens come from only two lakes (mainly Lake Erie) while Leidy's material spanned the continent.

An attached specimen is shown for the first time for this species (Pl. 2, Figs. 13, 16).

Diffugia tricuspis Carter, 1856

Pl. 4, Figs. 5–19

- Diffugia tricuspis* CARTER, 1856b, p. 221, pl. 7, fig. 80. SCOTT and MEDIOLI, 1983, p. 818, figs. 9q, r.
- (?) *Diffugia bombayensis* CARTER, 1864, p. 27, pl. 2, fig. 16.
- Diffugia proteiformis* (sic) (Ehrenberg) subspecies *D. globularis* (Dujardin) var. *D. tuberculata* WALLICH, 1864, p. 241, pl. 15, fig. 4g; pl. 16, fig. 18.
- Diffugia tuberculata* Wallich. ARCHER, 1867, p. 177. PÉNARD, 1902 (part), p. 292, text-figs. 1–3 on p. 293. SCHOUTEDEN, 1906, p. 341, 345, fig. 14 on pl. opposite p. 336. CASH and HOPKINSON, 1909, p. 159, text-figs. 105, 106. DECLÔTRE, 1953, p. 53, text-figs. 125, 126. GAUTHIER-LIÈVRE and THOMAS, 1958, p. 279, text-figs. 14a, b. GREEN, 1963, p. 509, text-fig. 23. OGDEN, 1980, p. 130, text-figs. 18–22. OGDEN and HEDLEY, 1980, p. 156, pl. 67.
- Diffugia lobostoma* LEIDY, 1874c, p. 79. LEIDY, 1879, p. 112, pl. 15, figs. 1–24; pl. 16, figs. 25–29. PÉNARD, 1890, p. 147, pl. 4, figs. 72–90, 96. PÉNARD, 1902, p. 276, text-figs. 1–7 on p. 277. CONN, 1904, p. 15, pl. 2, fig. 16 (ascribed to Ehrenberg on caption). EDMONDSON, 1906, p. 15, pl. 2, figs. 10, 11. SCHOUTEDEN, 1906, p. 341, 345, fig. 20 on pl. opposite p. 336. CASH and HOPKINSON, 1909, p. 44, text-figs. 58, 59, 61, 62, 64, pl. 21, figs. 14–17. DECLÔTRE, 1953, p. 57, text-figs. 141–145. HARNISCH, 1958, p. 43, pl. 8, fig. 14 (after Pénard, 1902). GREEN, 1963, p. 506, text-figs. 25, 26. CHARDEZ, 1964, p. 37, pl. 6, figs. 6a, b, c. GROSPIETSCH, 1972, p. 17, text-fig. 24.
- Diffugia amphora* Leidy (epithet invalid; junior primary homonym of *Diffugia amphora* Ehrenberg, 1872). PÉNARD, 1902, p. 289, text-figs. 1–8 on p. 290. PÉNARD, 1905, p. 26, text-fig. SCHOUTEDEN, 1906, p. 341, 345, fig. 15 opposite p. 336. GROSPIETSCH, 1958, text-fig. 39b, pl. 1, fig. 6. HARNISCH, 1958, p. 42, pl. 8, fig. 11 (after Pénard, 1902).
- Diffugia lithoplites* PÉNARD, 1902, p. 284, text-figs. 1–10 on p. 285. THOMAS, 1954, p. 256, pl. 1, fig. 2; pl. 4, fig. 1. HARNISCH, 1958, p. 41, pl. 8, fig. 10 (after Pénard, 1902).
- Diffugia gramen* PÉNARD, 1902, p. 281, text-figs. 1–3 on p. 282. DECLÔTRE, 1953, p. 50, text-figs. 114–116. HARNISCH, 1958, p. 43, pl. 8, fig. 29 (after Pénard, 1902). GROSPIETSCH, 1972, p. 16, text-fig. 27. OGDEN and HEDLEY, 1980, p. 136, pl. 57.
- Diffugia gramen* var. *achlora* PÉNARD, 1902, p. 283, text-fig. 9 on p. 282. DECLÔTRE, 1953, p. 51, figs. 117, 118.
- (?) *Diffugia oviformis* CASH in CASH and HOPKINSON, 1909, p. 52, pl. 20, figs. 8–12. NETZEL, 1976, p. 321–339, pls. 63–70. NETZEL, 1977, p. 1–30, pls. 1–14. OGDEN and HEDLEY, 1980, p. 150, pl. 64.
- Diffugia labiosa* WAILES, 1919, p. 39, pl. 51, fig. 11. OGDEN and HEDLEY, 1980, p. 138, pl. 58.
- (?) *Nebela tuberculata* (Wallich). OWEN and JONES, 1976, p. 486, text-figs. 1–9.
- (?) *Netzelia oviformis* (Cash). OGDEN, 1979a, p. 206.
- Diffugia corona* Wallich (part). HAMAN, 1982, p. 367, pl. 3, figs. 11, 12.

Diagnosis. Test of variable shape, from subspherical to oval, without a neck. Aperture usually deeply indented by three to six (or more) lobes; these lobes are rounded to somewhat angular and usually regularly distributed around a center (the degree of regularity,

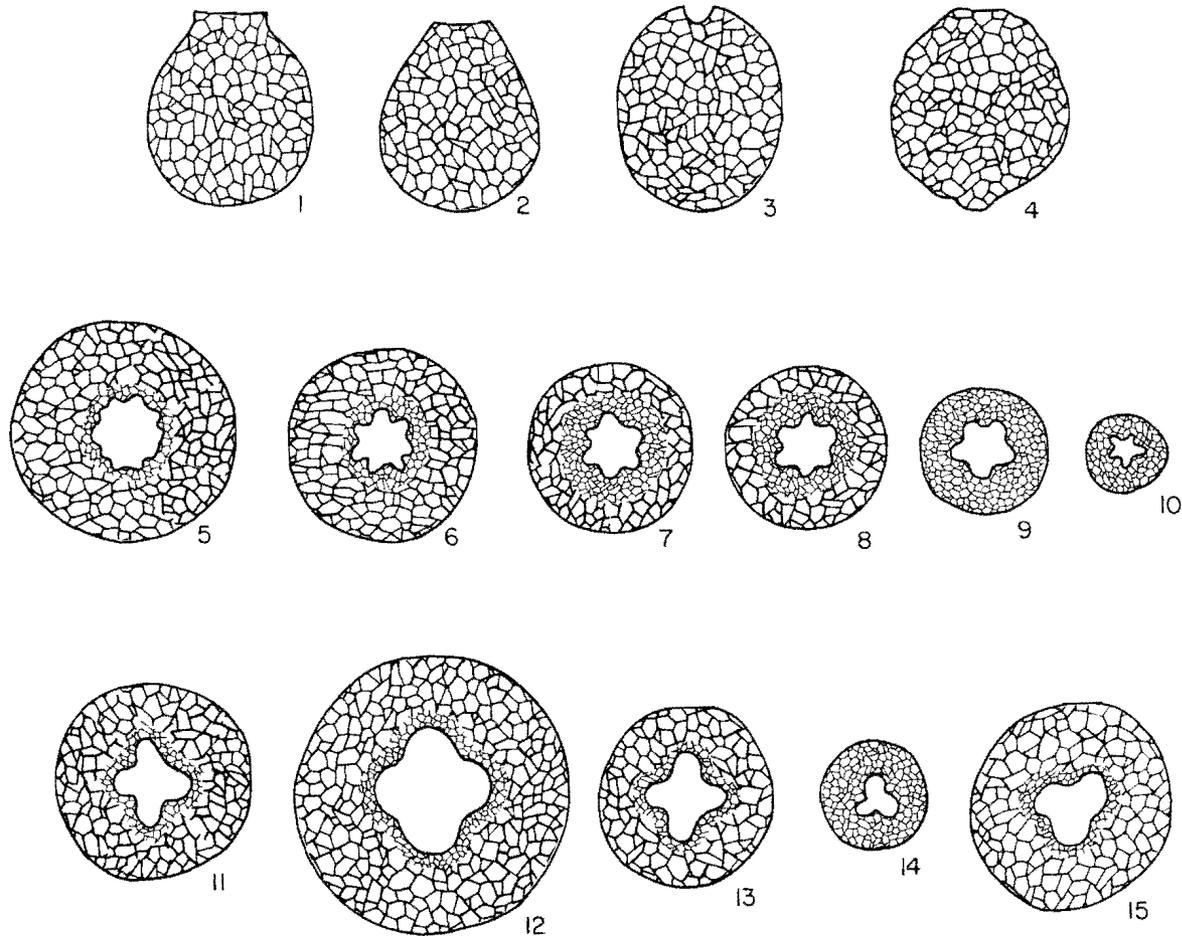


FIGURE 7. Figures of *Diffflugia tricuspis* (redrafted and rearranged from Leidy, 1879, pl. 15). The variability of our *D. tricuspis* is comparable in both general shape and structure of the aperture. The number of lobes in the aperture usually varies from three to six but forms with up to 12 *irregular* lobes are not rare. Irregular, multi-lobated apertures could be the result of an accident that occurred to a recent ancestor. The results of such an accident could have been *non-genetically* transmitted to the descendants (Jennings, 1937) and would, of course, be taxonomically meaningless.

however, tends to decrease as the number of lobes increases) (Fig. 7). Test texture difficult to observe: often, in fossil samples the test is composed of fine, agglutinated quartz grains, and is more or less smooth in overall appearance; rarely the test is composed wholly or partly of diatoms. We suspect very strongly that in many cases it is wholly autogenous which could put this species outside the genus *Diffflugia*, as it is defined now. We have this problem under investigation.

Differs from *D. corona* because the latter normally has more than six indentations in the aperture. Not infrequently, however, forms can be found with intermediate numbers of lobes, in these cases identification becomes impossible.

Discussion. Carter (1856a) first ascribed this form to "*Diffflugia protaeiformis*" (*sensu* Lamarck) and subsequently (1856b), on the basis of the trilobate structure of the aperture in his material, distinguished it as a separate species, *Diffflugia tricuspis*. Leidy (1879), quite correctly, considered *D. tricuspis* Carter as a synonym of his own *D. lobostoma*, but he rejected the senior epithet *tricuspis* in favor of the junior epithet *lobostoma* because he had observed forms of this species with up to six or more apertural lobes instead of just three, as the epithet implies (Leidy was in the habit of changing species epithets when he disliked them). Carter's senior epithet is often semantically inappropriate, this is not a unique case and it does not make the

epithet invalid [Code, art. 18(a)], thus the correct name of the species remains *D. tricuspis* Carter, 1856. During the last hundred years, however, most authors maintained the name *D. lobostoma*. Cash, cited posthumously in Cash and Hopkinson (1909), had certainly not overlooked the mistake, but Hopkinson (who finished the manuscript after Cash's death) suspected some differences between Carter's *D. tricuspis* and Leidy's *D. lobostoma* and decided to retain the name of the latter with the unacceptable excuse that the species had been universally known with that name for thirty-five years.

The nomenclatural situation was for a long time made more complicated by authors who stated or suggested the existence of a connection between this species and the most confused of all arcellacean species, *D. protaeiformis* Lamarck, 1816 as redescribed by Ehrenberg (1838). Carter (1856a) first ascribed to "*D. protaeiformis*" what he would soon afterwards (1856b) rename *D. tricuspis*. Leidy (1879) and Cash and Hopkinson (1909) suspected that Ehrenberg's "*D. protaeiformis*" might be a *D. lobostoma* because of its general shape in lateral view, but they could not confirm such a synonymy since Ehrenberg (1838) neither described nor illustrated the aperture of his form. Ehrenberg himself (1872b, p. 238) had discussed Carter's *D. tricuspis* but did not point to any connection between it and his own species. In fact, "*D. protaeiformis*," as redescribed by Ehrenberg (1838), could correspond to several species of the later taxonomists. The name, according to Leidy (1879), was of exceedingly indefinite application.

D. gramen Pénard, 1902 differs from the usual forms of *D. tricuspis* only in being smaller, with a rougher test, and, we might add, in always having a three-lobed mouth (while *D. tricuspis* as defined by us may have more than three lobes). Pénard (1902) suggested that *D. gramen* could be a synonym of Carter's *D. tricuspis* but felt that the data available on the latter species were insufficient to decide whether this synonymy was real. Cash and Hopkinson (1909) added to Pénard's original description that the size was variable; they also suspected that a small specimen with a five-lobed mouth, illustrated by Leidy (1879, pl. 15, figs. 23, 24), belonged to *D. gramen*. It appears that the criteria used to separate the two units are far too variable and far too subjective to warrant species status to the form "*D. gramen*" and its varieties. What Ogden and Hedley (1980) refer to as *D. gramen* Pénard appears to us, on the basis of the aperture, to be more or less identical to Carter's original figures of *D. tricuspis* as reproduced by Cash and Hopkinson (1909, p. 48). In conclusion, we consider *D. gramen* as a junior synonym of *D. tricuspis*.

D. amphora, as described originally (Leidy, 1874c; see also Leidy, 1879), is here placed into *D. urceolata*. However, starting with Pénard (1902), several authors (Pénard, 1905; Schouteden, 1906; Grospietsch, 1958) misapplied the name *D. amphora* to a clearly different form, which, on the basis of its lobulated aperture and partly recessed collar, we place in *D. tricuspis*. Wailes (1919), recognizing the difference between *D. amphora* as described by Leidy (1874c) and *D. amphora* as described by Pénard (1902), gave to the latter form the new name *D. labiosa*. While Wailes' (1919) description of *D. labiosa* is in agreement with that given by Pénard (1902) for *D. amphora*, Wailes' figure shows none of the essential characters of the aperture. Ogden and Hedley (1980) gave a description and figure of *D. labiosa* which agree with Wailes' (1919) text and with Pénard's (1902) text and figures. We feel that *D. amphora* sensu Pénard and *D. labiosa*, as redescribed by Ogden and Hedley (1980), should be moved into *D. tricuspis*. Because of Wailes' (1919) figure of *D. labiosa*, we list his work only with a question mark.

D. lithoplites Pénard does not appear to differ from *D. tricuspis* in any meaningful respect and we have kept the two together.

Leidy (1879) also argued that multilobated forms of *D. lobostoma* are very difficult to differentiate from the simpler specimens of *D. corona* and that possibly the transition is gradual. This problem is dealt with in more detail under *D. corona*.

The literature mentions two species which are very similar to *D. tricuspis* and to each other in overall morphology, but differ from it in the composition of the test which is made, unlike *D. tricuspis*, entirely or largely of idiosomes.

For the first one of these species, *D. oviformis* Cash in Cash and Hopkinson 1909, Ogden (1979a) proposed the genus *Netzelia*, which he defined as having a shell composed of idiosomes but with possible incorporated grains of quartz.

The other species, *Diffflugia tuberculata* Wallich, seems to have either a totally autogenous (Owen and Jones, 1976) or an apparently totally xenogenous test (Ogden and Hedley, 1980). In the literature these two forms are often confused, given their most conspicuous character, a tuberculated surface. Many authors described and illustrated, under *D. tuberculata*, tests that we would interpret as autogenous; only occasionally (Pénard, 1902; Cash and Hopkinson, 1909; Gauthier-Lièvre and Thomas, 1958) did the literature report xenogenous tests.

If it could be proven that *D. oviformis*, or *D. tuberculata*, or both can develop, according to circumstances, xenogenous, autogenous or mixed tests, then

both species should be included in our *D. tricuspis*. Similarly, should it be proved that the "*D. tuberculata*" group produces auto/xenogenous/intermediate tests depending on the circumstances, then the whole group will have to remain within *D. tricuspis*.

The conspecificity of these forms with auto/xenogenous/intermediate tests has not been demonstrated experimentally (although data from our recent cultures, which we have not entirely analyzed yet, seem to prove it beyond any doubt). Culture data known to us (Heal, 1964; Stout and Walker, 1976; Netzel, 1977a) are inconclusive from this point of view. Heal (1964) did not describe his specimens of "*D. tuberculata*," so it is not clear whether or not he had xeno- or autogenous tests at any stages of his experiments. Netzel's "*D. oviformis*" cultures started with undescribed material and, kept free of foreign mineral particles, produced, of course, only specimens with autogenous tests, which proves nothing. The author, however, mentions the occasional presence of what appear to be foreign particles in some tests (p. 324, fig. 2). The problem could be solved only by applying to *Diffflugia* the experimental strategy by which Stump (1936) proved that *Pontigulasia vas auctorum* was unable to produce idiosomes.

Should it be proved that some groups of "*Diffflugia*" can produce the three types of tests depending on circumstances, then either the usual definition of *Diffflugia* will have to be modified, or another genus (presumably *Netzelia*) will have to be found to accommodate this new category.

Occurrence. According to the literature, the species is common in ponds, ditches and swamps, in the ooze or among the algae. Found in wet moss at pond sites, on trees, near the water edge.

Observations on material illustrated in this paper. We have illustrated this species extensively to show the different apertural forms (Pl. 4, Figs. 5–19). As Leidy (1879) observed, the aperture in this species is often not trilobate; in our material it tended towards being more rounded than more lobate. We have assembled a complete intergradational series starting with a specimen which has more than three lobes (Fig. 5) and ending with one that has a completely round aperture and tends to be about twice the size of the other specimens. A few specimens develop spinosity (Figs. 12, 19); apertural lip development varies greatly (compare Figs. 7, 9, 11).

***Diffflugia urceolata* Carter, 1864**

Pl. 3, Figs. 1–23; Pl. 4, Figs. 1–4

Diffflugia urceolata CARTER, 1864, p. 27, pl. 1, fig. 7. LEIDY, 1879, p. 106, pl. 14, figs. 1, 2, 5–10, 14; pl. 16, fig. 33; pl. 19, fig. 27.

- BLANC, 1892, p. 378, pl. 2, figs. 1–3, 21, 22. PÉNARD, 1902, p. 266, text-figs. 1, 2 on p. 267. EDMONDSON, 1906, p. 15, pl. 3, fig. 19. SCHOUTEDEN, 1906, p. 344, 348. CASH and HOPKINSON, 1909, p. 39, text-figs. 56, 57, pl. 21, figs. 10–12. DECLOÏTRE, 1953, p. 56, text-figs. 136, 137. TODD and BRONNIMANN, 1957, p. 21, pl. 1, fig. 1. GROSPIETSCH, 1958, p. 44, text-fig. 37a, pl. 1, fig. 7. HARNISCH, 1958, p. 42, pl. 8, fig. 4 (after Pénard, 1902). GROSPIETSCH, 1972, p. 13, 19, text-fig. 22. SCOTT, 1977, p. 163, pl. 1, figs. 8, 9. SCOTT and others, 1977, p. 1578, pl. 1, fig. 9. OGDEN and HEDLEY, 1980, pl. 158, p. 68. SCOTT and others, 1980, p. 224, pl. 1, figs. 8, 9. HAMAN, 1982, p. 367, pl. 4, figs. 13–26. SCOTT and MEDIOLI, 1983, p. 818, figs. 9f, g.
- Diffflugia amphora* LEIDY, 1874c (epithet invalid; junior homonym of *Diffflugia amphora* Ehrenberg, 1872b), p. 79. LEIDY, 1879, pl. 14, figs. 3, 4; pl. 16, fig. 34 (binomen used for a variety of *Diffflugia urceolata* Carter, 1864 in the caption of pl. 14). (?) PÉNARD, 1890, p. 139, pl. 3, figs. 57, 58, 64.
- Diffflugia olla* LEIDY, 1874a, p. 156. LEIDY, 1879, p. 107, pl. 14, figs. 10–13; pl. 16, fig. 32; pl. 19, figs. 28, 29 (binomen used for a variety of *D. urceolata* in the caption of pl. 19, figs. 28, 29).
- Diffflugia amphora* var. *minor* PÉNARD, 1890, p. 140, pl. 4, figs. 1–3.
- Diffflugia urceolata* var. *lebes* PÉNARD, 1893, p. 177, pl. 3, fig. 17.
- Diffflugia lebes* PÉNARD. PÉNARD, 1899, p. 30, pl. 3, figs. 7, 8, 12. PÉNARD, 1902, p. 270, text-fig. 1 on p. 271.
- Diffflugia lebes* var. *elongata* PÉNARD, 1899 (epithet invalid; junior primary homonym of *Diffflugia constricta* var. *elongata* Pénard, 1890), p. 34, pl. 3, fig. 9. PÉNARD, 1902, p. 272, text-figs. 2, 3 on p. 271.
- Diffflugia olliformis* LAGERHEIM, 1901, p. 512, text-figs. 1–5.
- Diffflugia binucleata* PÉNARD, 1902, p. 262, text-fig. 23 on p. 213, text-figs. 1–5 on p. 263.
- Diffflugia gramen* var. *achlora* PÉNARD, 1902, p. 283, text-fig. 8 on p. 282.
- Diffflugia elongata* PÉNARD, 1905, p. 33, text-fig. on p. 34.
- Diffflugia amphoralis* HOPKINSON in CASH and HOPKINSON, 1909, p. 43, pl. 21, fig. 13.
- Lagunculina vadescens* CUSHMAN and BRONNIMANN, 1948a, p. 15, pl. 3, figs. 1, 2. PARKER, 1952a, p. 451, pl. 1, fig. 8. (?) PARKER and others, 1953, p. 10, pl. 1, fig. 1.
- Lagunculina* sp. (?) PARKER and others, 1953, p. 10, pl. 1, fig. 2.

Diagnosis. Test spheroid to acutely ovate; general appearance amphora-like to cauldron-like. Fundus rounded to acuminate, at times provided with blunt protuberances. Neck short, terminating in an evaginated, sometimes recurved or straight collar of variable shape and size (Fig. 8). Mouth wide, circular, terminal. Test xenosomic, usually composed of sand grains of variable coarseness.

Differs from *D. corona*, with which it could be confused in few, extreme cases, by the pronounced collar and the lack of apertural crenulation.

Discussion. Relatively little confusion surrounds this species. This is probably due to the distinctive evaginated collar and to the relatively large size that make it difficult to confuse the typical specimens with any other *Diffflugia*, although the shape and size of this collar vary exceedingly.

The shape of the rest of the test also varies consid-

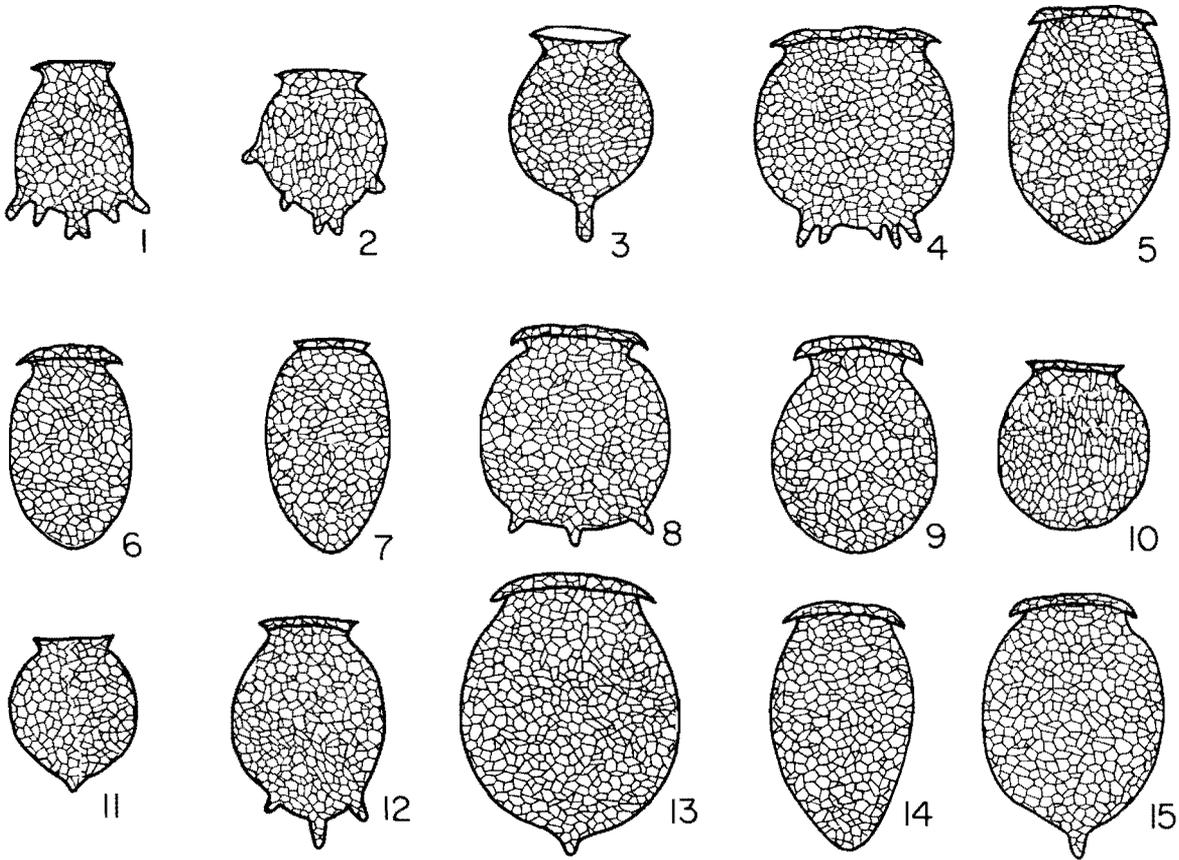


FIGURE 8. Figures of *Diffugia urceolata* (redrafted and rearranged from Leidy, 1879, pls. 14, 16). This is a rather stable and uncontroversial species. Intermediate specimens between this and other species are less numerous than elsewhere in the Arcellaea, but not easier to identify with some degree of confidence. This is particularly true when the very characteristic collar becomes less evident as in 7, or disappears altogether. Intergradational series in this species can be organized on the basis of the structure of the collar (e.g., 3, 2, 12, 14, 9, 5, 4, 11, 7) or on the basis of overall shape (e.g., 14, 7, 6, 5, 15, 13, 9, 8). More variability is illustrated in our material (Plates 3, 4).

erably, from globular to olive-shaped. This variability has generated some problems. In extreme cases, rounded forms, especially those with blunt spines, develop a "witch cauldron" appearance which many authors identify with that of *D. urceolata* Carter sensu stricto. The very elongated forms develop a general aspect which is almost exactly that of a Roman amphora and have often been called *D. amphora* Leidy. These two extremes, however, are connected by a completely gradual series of intermediate specimens.

Occasionally some confusion also arises from the variability of the more or less pronounced collar. Here too, an intergradational series between the extremes (i.e., between the almost collarless *D. lebes* sensu Pénard, 1902 and the typical *D. urceolata* sensu Carter with marked evaginated collar) is present.

D. amphora, as originally described (Leidy, 1874c)

and discussed by Leidy (1879) and probably Pénard (1890), belongs, in our opinion, to *D. urceolata*. The "*D. amphora*" discussed and illustrated by several later authors (Pénard, 1902, 1905; Schouteden, 1906; Grospietsch, 1958) on the basis of its lobulated, partly recessed collar is a clearly different form, possibly very close to *D. tricuspis*.

A few authors have ascribed to the genus *Lagunculina* Rhumbler, 1893 some forms that we attribute, with various degrees of uncertainty, to *D. urceolata* (see also Bolli and Saunders, 1954). As for the genus *Lagunculina* itself, Loeblich and Tappan (1964) had placed it in the Testaceafilosa because of the filiform, branched pseudopods of its type species *Ovulina urnula* Gruber, 1884. We believe that this genus belongs to the Foraminifera because, according to Gruber (1884), *O. urnula* has a typical foraminiferan nucleus.

Occurrence. *Diffflugia urceolata*, as defined here, is reported in the literature mainly from ponds, ditches and swamps, and also from shore and deep waters in Lake Leman.

Observations on material illustrated in this paper. The detailed illustration of this species (Pl. 3, Figs. 1–23; Pl. 3, Figs. 1–10; Pl. 4, Figs. 1–4) shows the gradation between the “*lebes*” form and the more typical form illustrated as *D. urceolata* in the literature. We also illustrate what appears to be a cyst. Cysts were observed free (Pl. 4, Figs. 1–3) or encased in a test (Pl. 3, Figs. 16, 17, 20–23).

Genus **LAGENODIFFLUGIA** n. gen.

Type species. *Diffflugia vas* Leidy, 1874a, designated here.

Diagnosis. Difflogiids with overall elongated, roughly pyriform tests divided into a bulbous main part and a neck. The main part and the neck are separated by an internal diaphragm pierced by a single, central, usually large orifice. The external side of the test is normally marked by a continuous constriction corresponding to the internal diaphragm. Aperture at the extremity of the neck.

Discussion. We establish this new genus for the single species *Diffflugia vas* Leidy, 1874. Pénard (1902) suggested that this species be placed in genus *Pontigulasia* Rhumbler, 1895. He also widened the definition of *Pontigulasia* in order to include not only the difflogiids with a diaphragm with two perforations (as originally defined by Rhumbler), but also those with a single perforation. In his 1902 work, Pénard did not use the binomen *Pontigulasia vas* for the former *D. vas* but proposed instead the new name *Pontigulasia spectabilis*. Schouteden (1906) corrected Pénard by pointing out that the valid binomen for the species was *P. vas*: the species has generally been so designated since. We re-adopt here Rhumbler’s original definition of *Pontigulasia*, that is, difflogiids whose diaphragm has two orifices, thus forming a bridge through the neck. This definition excludes *Diffflugia vas*, for which a new genus is established here.

The nebelid *Nebela vas* Certes, 1889 is largely similar in shape to *D. vas* Leidy (=our *Lagenodiffflugia vas*) and has been described mainly from the southern hemisphere (Certes, 1889; Pénard, 1911; Jung, 1942a; Grospietsch, 1971; Boltovskoy and Lena, 1971). It is often laterally compressed, but this also occurs, although to a lesser degree, in some specimens of *D. vas* Leidy. Jung (1942b) figured a specimen of *N. vas* (his *Apodera vas*) without lateral compression, that is, with

the circular cross section usual in *D. vas* Leidy. The inorganic test platelets of *N. vas* are of various shapes and sizes and their origin is partly uncertain (as usual in *Nebela*) although they do include idiosomes of (ingested?) filose thecamoebians. It is not known whether *N. vas* can secrete idiosomes, but if it could, it would not be related to *D. vas* Leidy, which is incapable of secreting them (Stump, 1936, 1943; Freeman, 1974). If, however, all platelets of *N. vas* Certes were xenosomes (in that case, most probably corroded diatoms frustules and/or plates of ingested thecamoebians), *N. vas* Certes and *D. vas* Leidy might be congeneric or even conspecific nominal taxa in a purely xenosomic genus. This genus would no longer be *Lagenodiffflugia* but *Apodera* Loeblich and Tappan, 1961 *ab* Jung, 1942. *Apodera* was proposed by Jung (1942a, b) for two nebelid species including *N. vas* Certes, and *N. vas* Certes was designated as type species of *Apodera* by Loeblich and Tappan (1961).

Lagenodiffflugia vas (Leidy, 1874a) comb. nov.

Pl. 2, Figs. 18–23, 27, 28

Diffflugia pyriformis Perty. EDMONDSON, 1906, p. 12 (part), pl. 2, fig. 12.

Diffflugia vas LEIDY, 1874a, p. 155. LEIDY, 1879 (binomen used for a variety of *Diffflugia pyriformis* Perty, 1849a), p. 99, pl. 12, figs. 2–9.

(?) *Pontigulasia spiralis* Rhumbler. PÉNARD, 1902, p. 317, text-figs. on p. 318.

Pontigulasia spectabilis PÉNARD, 1902, p. 318, text-figs. on p. 319.

Pontigulasia bryophila PÉNARD, 1902, p. 324, text-figs. on p. 324.

Pontigulasia vas (Leidy) SCHOUTEDEN, 1906, p. 338, footnote. CASH and HOPKINSON, 1909, p. 59, pl. 23, fig. 1, text-figs. 70, 71. STUMP, 1935, p. 136. STUMP, 1936, p. 142, text-figs. 1a, b. STUMP, 1943, p. 14, pl. 1, fig. 1a. FREEMAN, 1974, p. 10–66 (*passim*), pl. 2, figs. 1, 5.

Diffflugia oblonga forma *A* SCOTT and MEDIOLI, 1983, p. 818, fig. 9c.

Diagnosis. Main part of the test usually ovoid, with the neck arising from its narrower extremity, and with a wide fundus. Neck usually slightly higher than wide, with the shape of a cone truncated by the aperture and the constriction. Constriction not always conspicuous: some specimens have an almost continuous, pyriform outline from the fundus to the aperture. The constriction is sometimes more or less hidden by xenosomes; only sand grains have been reported as xenosomes.

Discussion. Despite our speculations to the contrary, the neck of this species is formed during asexual reproduction, at the same time as the rest of the test and it is not a sort of second chamber resulting from a later outgrowth (Stump, 1943). Numerous questions concerning the function of the peculiar neck structure of *L. vas* remain unanswered. The whole test is usually

circular in cross section, but can be slightly flattened. Leidy (1879, pl. 19, fig. 24) illustrated an exceptional case with horns on the fundus.

It is likely that the diaphragm always exists, but the constriction is not always visible. In some specimens the outline of the neck is almost continuous with that of the main part of the test (the groove can be covered with flat sand grains as shown by Pénard, 1902, text-figs. on p. 319) so that, in external view, an apparent intergradation exists between *D. oblonga* (pyriform specimens) and *L. vas* (Leidy, 1879, p. 101–102, pl. 12, fig. 4; pl. 19, fig. 24). Stump (1935) always found that all the little-constricted specimens that he examined had a diaphragm.

Occurrence. Not as common as *D. oblonga* but found sporadically in Lake Erie. More common in some New Brunswick lakes.

Observations on material illustrated in this paper. Our material too contains the apparently “intermediate” tests mentioned above (Pl. 2, Figs. 18–23, particularly Figs. 19, 22). Sometimes the constriction, however pronounced, is partly or entirely masked by large sand grains (Pl. 2, Figs. 19, 22). These cases of unobvious constriction make it difficult with fossil material to sharply distinguish *L. vas* from *D. oblonga*. This is why Leidy (1879) and many later authors considered *D. vas* as a variety of *Diffugia pyriformis* (which is itself, in our opinion, a synonym of *Diffugia oblonga*), and why Scott and Medioli (1982), in their study of the Arcellacea of Lake Erie sediments, have designated this species as *Diffugia oblonga* forma *A*.

Genus PONTIGULASIA Rhumbler, 1895

Type species. *Pontigulasia compressa* Rhumbler, 1895 [*Pontigulasia rhumbleri* Hopkinson in Cash and Hopkinson, 1909; not *Pontigulasia compressa* (Carter, 1864)].

Diagnosis. Test ovoid to pyriform; aperture rounded and resting on a more or less elongated neck. The main characteristic of the genus is a constriction of the base of the neck marking the position where a perforated, internal diaphragm often extends across the neck. Such an internal diaphragm is seldom present in fossilized forms. At times a bent neck, combined with the constriction, simulates a spiral arrangement. Test composed of agglutinated foreign particles.

Discussion. Rhumbler (1895) erected the genus to accommodate three new species, *P. incisa*, *P. spiralis* and *P. compressa*, the latter nominal species differing from *Diffugia compressa* Carter, 1864. Cash and Hopkinson (1909, p. 59) mistakenly stated that the genus was created to accommodate *Diffugia vas* Leidy, 1874.

Diffugia compressa Carter, 1864 was transferred to *Pontigulasia* by Cash and Hopkinson (1909). The binomen *Pontigulasia compressa* (Carter, 1864) was utilized by many later authors; as it is a senior secondary homonym of *Pontigulasia compressa* Rhumbler, 1895, Hopkinson replaced the latter name by an objective synonym that he created for that purpose, *P. rhumbleri* Hopkinson in Cash and Hopkinson, 1909. Loeblich and Tappan (1964) designated *P. compressa* Rhumbler, 1895 (= *P. rhumbleri* Hopkinson in Cash and Hopkinson 1909) as type species of *Pontigulasia* (the date of Rhumbler's *compressa* was mistakenly recorded as “1905”).

We believe that this nominal type species, *P. compressa* Rhumbler, 1895 (= *P. rhumbleri*), must be included (as a junior subjective synonym) into *P. compressa* (Carter, 1864). Only the latter name remains valid, because of its priority.

As for *Diffugia vas* Leidy, 1874, which Cash and Hopkinson (1909) had called *Pontigulasia vas* and considered as “typical” of *Pontigulasia*, we consider it the type species of the new genus *Lagenodiffugia*.

Our material contains an intergradational series of entirely xenogenous specimens, from the typical symmetrical *Pontigulasia compressa* to typical asymmetrical pseudocoiled, xenogenous “*Lecquereusia*-like” forms (Pl. 6, Figs. 5–12).

The relationships between *Pontigulasia* Rhumbler, 1895 and *Lecquereusia* Schlumberger, 1845 represent a complex problem. Both genera are characterized by a constriction at the base of the neck which corresponds to an internal diaphragm, usually with two or more openings in a more or less central position in *Pontigulasia*, or with one opening in a peripheral position in *Lecquereusia*. The overall outline of the two forms is ovoid to pyriform but, in the case of *Lecquereusia*, the neck is often asymmetrical because of the asymmetrical position of the diaphragm (or vice versa, if you will). This lack of symmetry produces the rather characteristic “pseudocoiled” appearance of the typical *Lecquereusia* forms. However, asymmetrical necks and diaphragms are not rare in *Pontigulasia* either, such that, in a sufficiently large population, a morphological intergradation exists between the two genera (this is visible both in our material and in the literature).

The only remaining difference between the two genera (which is also, according to many authors, the main difference between the families Hyalospheniidae Schulze, 1877 and Diffugiidae Stein, 1859) resides in the fact that the test of *Lecquereusia* is usually composed of siliceous idiosomes shaped like curved rods

or platelets (sometimes mixed with or totally replaced by xenosomes), whereas the test of *Pontigulasia* is always reported to be composed of xenosomes.

This criterion is insufficient to separate these two genera, since intermediate and wholly xenogenous tests of *Lecquereusia* (*auctorum*) are well known. The two genera, therefore, do not seem to be separable on any account and possibly they should be fused in which case *Lecquereusia*, being the senior synonym, would displace *Pontigulasia*.

However, as we have dealt with only a few xenogenous "Lecquereusia-like" forms and we have no autogenous *Lecquereusia* tests in our material, we have taken no action on this matter at least until more information (i.e., large populations) is available.

***Pontigulasia compressa* (Carter, 1864)**

Pl. 6, Figs. 5–14

- Diffugia compressa* CARTER, 1864, p. 22, pl. 1, figs. 5, 6. (Not *Diffugia compressa* Carter, 1864 as a variety of *Diffugia pyriformis* Perty, 1849a, in LEIDY, 1879, p. 99, pl. 11, figs. 1–6; pl. 12, figs. 10–16.)
- Diffugia elisa* PÉNARD, 1893, p. 177, pl. 3, fig. 7.
- Pontigulasia compressa* RHUMBLER, 1895, p. 105, pl. 4, figs. 13a, b. AVERINTSEV, 1906, p. 169. SCHOUTEDEN, 1906, p. 338, 339. DEFLANDRE, 1953, p. 129, text-figs. 91f–h.
- Pontigulasia incisa* RHUMBLER, 1895, p. 105, pl. 4, figs. 5, 22a. PÉNARD, 1902, p. 315, text-figs. 1–6. SCHOUTEDEN, 1906, p. 338, 339, fig. 9, on plate opposite p. 336.
- Diffugia pyriformis* var. *vas* Leidy, subvar. *bigibbosa* (last epithet is infrasubspecific and thus not made available here). PÉNARD, 1899, p. 26, pl. 2, fig. 10.
- Pontigulasia bigibbosa* PÉNARD, 1902 (*ab* Pénard, 1899), p. 322, text-figs. 1–3 on p. 323. PÉNARD, 1905, p. 35, text-fig.
- Pontigulasia compressa* (Carter). AVERINTSEV, 1906, p. 169. SCHOUTEDEN, 1906, p. 338, 339. CASH and HOPKINSON, 1909, p. 62, text-fig. 72, pl. 23, figs. 3–5. DEFLANDRE, 1953, p. 129, figs. 91f–h. TODD and BRONNIMANN, 1957, p. 21, pl. 1, fig. 5. CHARDEZ, 1964, p. 39, pl. 8, fig. 1. FEYLING-HANSEN, 1964, p. 217, pl. 1, figs. 7, 8. SCOTT, 1977, p. 163, pl. 1, figs. 10–12. SCOTT and others, 1977, p. 1578, pl. 1, figs. 5, 6. OGDEN and HEDLEY, 1980, p. 162, pl. 20. SCOTT and others, 1980, p. 224, pl. 1, figs. 10–12. SCOTT and MEDIOLI, 1983, p. 819, fig. 9m.
- Pontigulasia elisa* (Pénard). SCHOUTEDEN, 1906, p. 339, footnote. CASH and HOPKINSON, 1909, p. 161, text-figs. 107, 108. OGDEN and HEDLEY, 1980, p. 164, pl. 71.
- Pontigulasia compressa* (Carter) var. *flexa* HOPKINSON in CASH and HOPKINSON, 1909, p. 64, pl. 23, figs. 6, 7.
- Pontigulasia rhumbleri* HOPKINSON in CASH and HOPKINSON, 1909, p. 162. WAILES, 1919, p. 49, pl. 63, figs. 1, 2.
- (?) *Proteonina compressa* CUSHMAN and McCULLOCH, 1939, p. 42, pl. 1, figs. 10a, b.
- (?) *Proteonina hancocki* CUSHMAN and McCULLOCH, 1948, p. 76.
- (?) PARKER, 1952a, p. 454, pl. 1, fig. 3.
- (?) *Diffugia avellana* Pénard. HAMAN, 1982, p. 367, pl. 3, figs. 1–3.

Diagnosis. Test usually large, rounded to pyriform,

laterally compressed. Neck well defined, tapering regularly towards the narrow aperture. Mouth truncated, rounded or broadly elliptical in cross section. The junction between the neck and the test proper is marked usually by a clearly visible constriction (which may not be visible when diatoms are agglutinated in the test). This constriction marks the position of what is described in the literature as a doubly perforated internal diaphragm which is often missing in fossil forms (we have never been able to satisfactorily observe such a structure). The test appears to be composed of minute quartz grains arranged so as to give a rough appearance to the main part of the test; the neck is usually smoother.

Discussion. Carter (1864) originally assumed that this species belonged to the genus *Diffugia*. The overall appearance of *P. compressa* is indeed quite similar to one of the many varieties of *Diffugia pyriformis* from which it can be differentiated only by the presence, at times difficult to ascertain, of the usually doubly perforated diaphragm which is considered typical of *Pontigulasia*. Rhumbler (1895) instituted the latter genus into which this species was transferred from *Diffugia* by Averintsev (1906). In routine investigations of fossil material the diaphragm is particularly difficult to observe accurately because it is missing or damaged most of the time. When the diaphragm cannot be observed two associated characteristics usually help differentiate this species at first glance, 1) the flattened appearance, and 2) the constriction at the base of the neck. Neither characteristic is visible in all specimens, the two of them are present in the same specimen at the same time about 50–60% of the time.

The forms figured by Leidy (1879) as "variety *D. compressa*" in species *D. pyriformis*, and which he considered as identical to Carter's *D. compressa*, do not appear at all to be the same forms that Carter originally described. The neck constriction is neither mentioned nor figured by Leidy and we believe that his material was a genuine, compressed variety of his *D. pyriformis* (=our *D. oblonga*, our Pl. 2, Figs. 24–26).

Pénard (1902) described six species of *Pontigulasia*, 1) *P. incisa* Rhumbler (synonym: *Diffugia elisa* Pénard, 1893), 2) *P. compressa* Rhumbler, 3) *P. spiralis* Rhumbler, 4) *P. bigibbosa* Pénard, 5) *P. bryophila* Pénard, and 6) *P. spectabilis* Pénard. The first four of these species appear to grade into each other and Pénard's separations seem to us to be quite unjustified. In our opinion, only two of those six units must be separated from *P. compressa* (Carter); that is the units containing the non-compressed forms *P. spectabilis* and *P. bryophila* (both = *D. vas* Leidy, 1879 = *Pontigulasia vas*

in Schouteden, 1906 and Cash and Hopkinson, 1909 = *Lagenodifflugia vas* in this paper).

P. compressa var. *flexa* Hopkinson does not appear to be justified as an independent unit either; the only difference with *P. compressa* (Carter) being a slightly curved neck and a smoother appearance.

Nor does *P. rhumbleri* Hopkinson, as described by Wailes (1919), appear to be acceptable, its only peculiar characteristics being agglutinated diatom frustules in the test and a central diaphragm with openings on either side. Wailes himself admitted that *P. compressa* (Carter) and *P. rhumbleri* showed external similarity.

Presently, and until more information becomes available, we will keep all the species and varieties mentioned above (except *P. spectabilis* = *D. vas*) within *P. compressa* (Carter) because we see no good reason for splitting the group.

We must also put in proper perspective the taxonomic importance of the internal diaphragm at the species level, particularly in fossil material. In our samples this diaphragm is present only occasionally and we can only consider its absence as taxonomically insignificant, or we would not be able to identify any specimens at all. The constriction in the neck, marking the position where the diaphragm should have been at some stage, is, on the contrary, more consistent and therefore of greater importance for the routine differentiation of *Pontigulasia* from *Diffflugia*.

A few authors have ascribed to the foraminiferal genus *Proteonina* the species *Proteonina hancocki* which we tentatively attribute to *Pontigulasia compressa* (see also Bolli and Saunders, 1954).

Our *Lecquereusia*-like specimens (Pl. 6, Figs. 5, 6) are few and sparse, and do not represent the centre of a statistical phenotypic cluster. They are linked to the *Pontigulasia compressa* phenotypic cluster by a series of intermediate specimens. Nevertheless, we do not have sufficient data to decide what their real taxonomic position is.

Occurrence. *P. compressa* has been reported in the literature as occurring from sphagnum bogs to deep parts of lakes (over 200 m deep).

Observations on material illustrated in this paper. The problem of *Lecquereusia* versus *Pontigulasia* has been mentioned before. In our Plate 6 we show what appears to be intergradation between the two morphotypes (Pl. 6, Figs. 5–14). Figures 5 and 6 are typical *P. compressa* while Figure 7 is already beginning to show torsion in the lower right part of the neck. Figures 10–12 show various degrees of torsion. Figures 13 and 14 show, to the best of our ability with the SEM, the diaphragm. In Figure 13 the diaphragm is the black

shadow through the middle inside the specimen, while in Figure 14 the diaphragm occurs above the fracture (notice how the neck naturally broke uniformly through the constrictions).

Family HYALOSPHEINIIDAE Schulze, 1877
Genus HELEOPERA Leidy, 1879

Type species. *Heleopera picta* Leidy, 1879. [Objective synonym of *Diffflugia sphagni* Leidy, 1874a. By not citing the latter nominal species as type species of *Heleopera*, we violate the Code's art. 67(e) but conform to a new rule that will be enacted in the third edition of the Code (see Sabrosky, 1980).]

Diagnosis. Test more or less compressed, ovoid; in broad view, more or less convex and truncated at the aperture. Aperture terminal, transversely elliptical, more or less narrow, usually notched in narrow lateral view. Fundus regularly rounded, but this shape is often obscured by large xenosomes. Test composed of siliceous shell plates, often more or less masked by relatively fine xenosomes.

Discussion. Leidy (1879) instituted this rather uncontroversial genus for two species, 1) what he designated as its type species *H. picta* Leidy, 1879, and 2) *H. petricola* Leidy, 1879. In that same work Leidy commented that, in *H. picta*, occasional particles of quartz are incorporated in the shell at the fundus, whereas *H. petricola* has the fundus loaded with quartz-sand. His plate 26, however, shows that there is a completely gradual transition from what appears to be a fully autogenous *H. picta* (pl. 26, figs. 1–4) to completely xenogenous forms of *H. petricola* (pl. 26, fig. 20). This is a rather important point because almost all the scarce specimens found in Lake Erie are completely xenogenous and the few autogenous tests found were far too delicate to survive the treatment of gold coating for SEM observation. We want to underline, therefore that *Heleopera*, as interpreted in this paper, can be, and indeed often is, completely covered with xenosomes. When this happens the specimens become completely unrecognizable as conspecific with the largely autogenous forms shown in the literature, particularly when only few xenogenous specimens are available. Presumably it is only when autogenous and xenogenous forms are found together in approximately equal amounts and can be arranged in an intergradational series of sorts, that the conspecificity of the two types becomes obvious. Agglutination, somehow, affects the shape of the aperture which usually becomes wider and less notched than that of non-agglutinated forms.

Deflandre (1953) described the test of this genus as being made of irregular plates, autogenous or, rather, sutured with the fundus almost always carrying quartz grains at times quite large. His figures 92a, b show a specimen that was perhaps completely agglutinated.

Ogden (personal communication, 1981) suggests that what we interpret as xenogenous *Heleopera* might be a form of compressed *Difflugia*. He may be correct, but having seen some of the intermediate forms of this species we are very reluctant to change our identification. Although our plates are pitifully inadequate for the moment, we feel justified in keeping our material within *Heleopera*, at least until better documentation becomes available.

***Heleopera sphagni* (Leidy, 1874a)**

Pl. 6, Figs. 15–18

Difflugia (Nebela) sphagni LEIDY, 1874a, p. 157.

Nebela sphagni (Leidy). LEIDY, 1876, p. 118, text-figs. 16, 17.

Heleopera picta LEIDY, 1879, p. 162, pl. 26, figs. 1–11. SCHOUTEDEN, 1906, p. 356, 357. HOOGENRAAD, 1935, text-figs. 30, 31.

Heleopera petricola LEIDY, 1879, p. 165, pl. 26, figs. 12–20. PÉNARD, 1890, p. 167, pl. 7, figs. 56–58. PÉNARD, 1902, p. 382, text-figs. 1–6. SCHOUTEDEN, 1906, p. 357. CASH and HOPKINSON, 1909, p. 137, pl. 29, figs. 13–19. HOOGENRAAD, 1935, text-fig. 26. JUNG, 1936b, p. 104, text-fig. 4. HARNISCH, 1948, p. 552, pl. 1, fig. f. GROSPIETSCH, 1952, p. 220, text-fig. 6. GROSPIETSCH, 1953, p. 339. GROSPIETSCH, 1958, p. 46, fig. 42a.

Heleopera petricola var. *amethystea* PÉNARD, 1899, p. 53, pl. 5, figs. 1–5. PÉNARD, 1902, p. 382, text-figs. 7, 8. PÉNARD, 1905, p. 36, text-fig. on p. 37. CASH and HOPKINSON, 1909, p. 140, pl. 29, fig. 22. JUNG, 1936b, p. 105, fig. 5.

Heleopera sphagni (Leidy). CASH and HOPKINSON, 1909, p. 143, pl. 30, figs. 4–9. GROSPIETSCH, 1953, p. 339. GROSPIETSCH, 1958, p. 46, text-fig. 42b, pl. 2, fig. 15. OGDEN and HEDLEY, 1980, p. 80, pl. 29 (misspelled *H. sphangi*). SCOTT and MEDIOLI, 1983, p. 819, fig. 9e.

Heleopera petricola var. *major* CASH in CASH and HOPKINSON, 1909, p. 139, pl. 29, figs. 20, 21.

Diagnosis. Shell strongly compressed, ovoid; oral pole narrower in broadside view. In those tests that are apparently autogenous, the terminal mouth forms an elongated, narrow ellipse with acute commissures. Tests that are totally or mainly xenosomic usually have a wider, oval aperture that becomes almost subcircular in extreme cases. Tests composed of siliceous idiosomes (Deflandre, 1953), substituted more or less extensively by xenosomes. The xenogenous part of the test varies in area; often it is completely absent, or it covers only the fundus or, less commonly, it coats the entire test obscuring completely the autogenous plates. In fossil samples, strongly xenogenous forms appear to be selectively preserved while forms with abundant autogenous plates are almost completely absent.

Discussion. Leidy (1874a) instituted the species *Difflugia (Nebela) sphagni* which he later (1879) renamed *Heleopera picta* without explaining why. He clearly indicated, however, that *D. sphagni* was a senior objective synonym of *H. picta*. The valid name of this species is thus *Heleopera sphagni* (Leidy, 1874a).

In 1879 Leidy described two species of *Heleopera*, *H. picta* and *H. petricola*. His basis for discriminating the two species is not clear to us. Almost the only difference is apparently an abrupt variation in ratio between idiosomes and xenosomes. Leidy's plate 26 shows, however, that such a criterion cannot be used. We have condensed Leidy's plate in our Figure 9 which shows that the transition from completely autogenous to completely xenogenous forms is so gradual that any division appears to be completely arbitrary (Fig. 9). Our material, despite its limitations, confirms our conclusions on this point. We consider *H. picta* and *H. petricola* as synonyms, and thus both names fall under *H. sphagni*.

We suspect that, in general, the fossilization processes produce fossil assemblages that are very heavily biased in favor of the totally xenogenous forms. The xenogenous forms are particularly enhanced in this species in which, even before the destruction associated with SEM sample preparation, we observed a very strong dominance of xenogenous over autogenous forms. Our impression is that previous workers studying recent samples found few or no totally xenogenous forms. If they did find them, they must have experienced insurmountable difficulties in identifying their material as *H. sphagni*.

We see no reason to keep *H. petricola* var. *amethystea* Pénard and *H. petricola* var. *major* Cash separated from *H. sphagni*. The former was instituted mainly on the basis of its purple colour and the latter on the basis of its slightly larger size. Neither reason appears sufficient in zoology as well as, *a fortiori*, in paleontology for separation from *H. sphagni*.

Our synonymic list does not include *H. sylvatica* Pénard, 1890 nor *H. rosea* Pénard, 1890. Different authors seem to describe and figure, under each of those two names, different forms, some of which undoubtedly belong to *H. sphagni* whereas others might genuinely belong to other species. We have very serious doubts, however, about the validity of both species.

Occurrence. Reported in the literature as common in *Sphagnum* swamps, rare in Lake Erie.

Observations on material illustrated in this paper. We had few forms left to photograph and could not adequately illustrate this species from our material alone (Pl. 6, Figs. 15–18). The photographs we do have il-

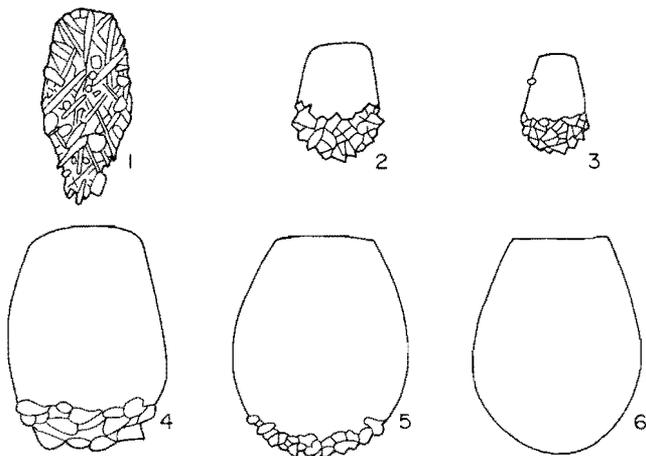


FIGURE 9. Figures of *Helicoperla sphagni* (redrafted and rearranged from Leidy, 1879, pl. 26). Leidy (1879), in his plate 26, identified the specimens 1, 2, 3 and 4 of our figure as *H. petricola* and 5 and 6 as *H. picta*. The dividing line between Leidy's two units (based on the amount of material agglutinated on the fundus) was originally intended to fall between our Figs. 4 and 5.

illustrate some of the basic characteristics such as increase in size of xenosomes towards the fundus and the elliptical aperture. Figure 18 shows an attached specimen. The characteristic "V" slit in side view of the aperture is not apparent in our illustrations (except for a slight notch in Fig. 15) and it is possible that the slit does not develop in strongly xenogenous specimens.

Family CENTROPYXIDIDAE Jung, 1942
Genus CENTROPYXIS Stein, 1859

Type species. *Arcella aculeata* Ehrenberg, 1830.

Diagnosis. Test plagiostome (Bonnet, 1976a) bilaterally symmetrical and with distinct ventral, dorsal, posterior, anterior, right and left sides (Fig. 10). We define as *apertural side* the one bearing the aperture and in contact with the substrate (the aperture, seldom central, is usually more or less anterior). The rest of this side, always posterior, may or may not be in contact with the substrate. If it is, we consider it the continuation of the apertural side; if it is not, then we define it as the *ventral side*. In dorsal view, test discoid to irregularly ovoid. In lateral view, the test may, at times, rest flat on the apertural side. In these cases apertural and ventral sides coincide (Fig. 10c). In other forms the test stands on the aperture so that apertural and ventral sides form a more or less obtuse angle (Fig. 10a). The anterior angle (defined as the angle between the tangent to the dorsal side and the apertural side)

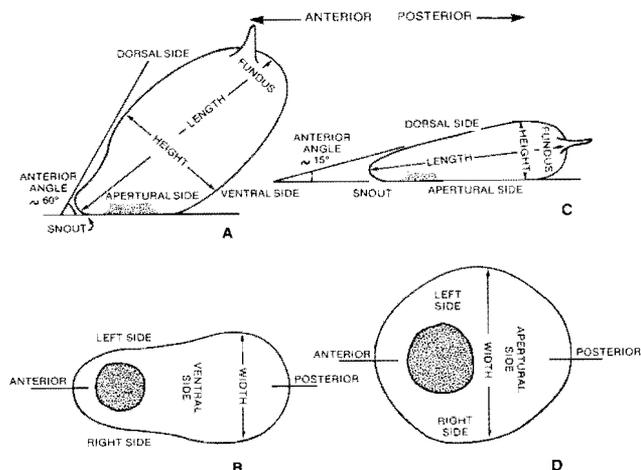


FIGURE 10. General geometry and terminology of the genus *Centropyxis*. Test plagiostome (Bonnet, 1976), more or less elongated vertically, bilaterally symmetrical and with obvious ventral, dorsal, posterior, anterior, right and left sides. We define as *apertural side* the one bearing the aperture and in contact with the substrate. The aperture, seldom central, is usually more or less anterior. The rest of this side, always posterior, may or may not be in contact with the substrate. If it is, we consider it the continuation of the apertural side; if it is not, then we define it as the *ventral side*. In dorsal view, test discoid to irregularly ovoid. In lateral view, the test is from flat on the apertural side to vertical (=fundus uppermost), with a large majority of intermediate forms which are inclined backwards, with somewhat convex anterior and posterior slopes. On a sagittal cross-section we call the angle between the tangents to the dorsal side and the apertural side the *anterior angle*. This angle varies from about 60 degrees in almost vertical forms to about 15 degrees in flat forms. The dorso-posterior curved area which is the part of the test furthest from the aperture, and which joins the anterior and posterior slopes, is the *fundus*. The fundus migrates in response to the changes in geometry experienced by the test. A variable number of more or less conical spines is sometimes present at the posterolateral margins (due to the displacement of the fundus from uppermost position to marginal position). We define as the *snout* the area connecting the anterior margin of the aperture with the dorsal side. The center of the snout is the most anterior part of the test. The *length* is the maximum distance between snout and fundus; the *height* is the maximum distance perpendicular to it.

can, exceptionally, be close to 90 degrees, but usually it varies between approximately 60 and 15 degrees (Fig. 10a, c). The dorso-posterior curved area which is the part of the test further away from the aperture, and which joins the anterior and posterior slopes, is the *fundus*. The fundus migrates in response to the changes in geometry experienced by the test. A variable number of more or less conical spines is sometimes present at the posterolateral margins (this is simply due to the displacement of the fundus from uppermost position to marginal position).

We define the area connecting the anterior margin

the aperture with the dorsal side as the *snout*. The center of the snout is the most anterior part of the test. The *length* is the maximum distance between snout and fundus; the *height* is the maximum distance perpendicular to it. The aperture is invaginated and round or irregular or even polygonal.

Test composed of organic material; often, but not always, more or less completely covered with agglutinated mineral particles of various nature. A variable number of conical spines is sometimes present at the lateral margin (which represents the fundus migrated to a marginal position).

Discussion. In 1859 (often misdated "1857") Stein created *Centropyxis* to accommodate the single species *Arcella aculeata* Ehrenberg, 1830. Calparède and Lachmann (1859), erected the genus *Echinopyxis* for the same single species. Today neither work can be dated more accurately than 1859, which makes *Centropyxis* and *Echinopyxis* simultaneous, objective synonyms. Ehrenberg (1872b, p. 241, 245) listed them as synonymous names and made a first-revisor choice in accepting *Centropyxis* as the valid name of this subgenus [Code, art. 24 (a)(i)]. The name *Echinopyxis* is thus invalid forever.

Deflandre (1929) divided *Centropyxis* into two subgenera, *Centropyxis sensu stricto* and *Centropyxis (Cyclopyxis)*. The former was characterized by dorso-ventral symmetry and an excentric aperture; the latter by axial symmetry and a central aperture. Loeblich and Tappan (1964) accepted *Cyclopyxis* as an independent genus and even placed it outside the Centropyxididae in their family Trigonopyxididae. We reject *Cyclopyxis* because we find, in the same populations, forms that are obviously conspecific, but that according to their axial or dorso-ventral symmetry, would belong to one or the other of those two genera.

The genus *Centropyxis*, at the two ends of its spectrum of variability, cannot be clearly differentiated from *Diffflugia* at one end and *Arcella* at the other. The species that contain the extreme transitional forms are also the two main species of the genus, *C. constricta* at the near-*Diffflugia* end and *C. aculeata* at the near-*Arcella* end. Deflandre (1929), in his monograph on *Centropyxis*, wrote that he had tried to make some sense out of the chaotic array of forms grouped by previous authors under the two nominal species *D. constricta* and *C. aculeata*. In an attempt to achieve his goal, although he fully realized the danger involved in this project, he felt compelled to follow his instinct that told him that there were numerous forms that had to be separated. We understand Deflandre's caution, considering the chaos in the literature. However, despite our re-

spect for his work and for his judgement, we believe that breaking the group down into numerous species and varieties, as he did, is neither justified nor, above all, practical. We believe almost exactly the opposite: the genus is obviously divided into only two distinct clusters covering almost all its possible forms. Although such units tend to grade into other genera and into each other at the extremes of their spectra, the vast majority of our *Centropyxis* specimens fall unmistakably into one or the other. These two units, *C. constricta* and *C. aculeata auctorum*, are not entirely satisfactory but they are enormously less confusing than the 33 elusive species and varieties recognized in *Centropyxis* by Deflandre. We thus regretfully reject the second part of Deflandre's 1929 work almost completely, mainly on the grounds that his taxonomic units are far too restrictive and impossible to handle. Ironically, with these 33 species, Deflandre contradicted his own very lucid essay (contained in the first part of the same paper and with which we agree) on the concept of thecamoebian species.

***Centropyxis aculeata* (Ehrenberg, 1832)**

ab Ehrenberg, 1830

Pl. 7, Figs. 10–19

- Arcella aculeata* EHRENBERG, 1832b (*ab* Ehrenberg, 1830, p. 60, *nomen nudum*; or Ehrenberg, 1832a, p. 40, *nomen nudum*), p. 91. EHRENBERG, 1838, p. 133, pl. 9, figs. 6a–c.
- Arcella cornis* EHRENBERG, 1843, p. 410, pl. 1, part IV, fig. 9; pl. 3, part I, fig. 46.
- Centropyxis aculeata* (Ehrenberg). STEIN, 1859, p. 43. LEIDY, 1879, p. 180, pl. 31, figs. 1–32, 35; pl. 32, figs. 29–34, 37. PÉNARD, 1890, p. 149, pl. 5, figs. 21–37. WEST, 1901, p. 315, pl. 29, figs. 15, 16. PÉNARD, 1902, p. 302, text-figs. 1–4 on p. 303. CASH and HOPKINSON, 1905, p. 132, pl. 16, figs. 10–14. SCHOUTEDEN, 1906, p. 349. EDMONDSON, 1906, p. 18, pl. 4, figs. 27, 28. DEFLANDRE, 1929, p. 344, text-figs. 80–92. JUNG, 1936b, p. 98. RAMPL, 1947, p. 74, pl. 1, text-fig. 17. GROSPIETSCH, 1958, p. 42, text-fig. 33c. GROSPIETSCH, 1972, p. 11, text-fig. 15. SCHÖNBORN, 1975, p. 127, text-figs. 3a, b. OGDEN and HEDLEY, 1980, p. 46, pl. 12. HAMAN, 1982, p. 365, pl. 1, figs. 1–5. SCOTT and MEDIOLI, 1983, p. 819, fig. 91.
- Echinopyxis aculeata* (Ehrenberg). CLAPARÈDE and LACHMANN, 1859, p. 447. CARTER, 1864, p. 29, pl. 1, fig. 8.
- Echinopyxis hemispherica* BARNARD, 1876, p. 242. BARNARD, 1879, p. 84, pl. 8, fig. 2.
- Diffflugia constricta* (Ehrenberg). LEIDY, 1879, p. 120, pl. 18, figs. 1–7. PÉNARD, 1902, p. 298, text-figs. 6, 7, 9, 10, 14. RIOJA, 1942, p. 515, text-figs. 7a, b.
- Centropyxis cornis* (Ehrenberg). LEIDY, 1879, p. 180, pl. 30, figs. 20–34. DEFLANDRE, 1929, p. 359, text-figs. 123–138. GROSPIETSCH, 1958, p. 42, text-fig. 33a. GROSPIETSCH, 1972, p. 12. OGDEN and HEDLEY, 1980, p. 56, pl. 17. HAMAN, 1982, p. 365, pl. 1, figs. 15–19.
- Centropyxis aculeata* var. *cornis* (Ehrenberg). PÉNARD, 1890, p. 150, pl. 5, figs. 45–48. CASH and HOPKINSON, 1905, p. 136, pl. 16, fig. 16.

- Centropyxis aculeata* var. *discoides* PÉNARD, 1890, p. 150, pl. 5, figs. 38–41. WAILES, 1919, p. 34, pl. 61, figs. 1, 2.
- Centropyxis aculeata* var. *spinosa* CASH in CASH and HOPKINSON, 1905, p. 135, text-figs. 26a–c, pl. 16, fig. 15.
- Centropyxis hemisphaerica* (sic) (Barnard). DEFLANDRE, 1929, p. 356, text-figs. 116, 117.
- Centropyxis spinosa* Cash. DEFLANDRE, 1929, p. 353, text-figs. 108–111. GROSPIETSCH, 1972, p. 12, text-fig. 13. OGDEN and HEDLEY, 1980, p. 62, pl. 20.
- Centropyxis aculeata* var. *grandis* DEFLANDRE, 1929, p. 349, text-fig. 93.
- Centropyxis hirsuta* DEFLANDRE, 1929, p. 354, text-figs. 112–115. GROSPIETSCH, 1958, p. 42, text-fig. 33b. GREEN, 1975, p. 548, text-fig. 6. OGDEN and HEDLEY, 1980, p. 58, pl. 18.
- Centropyxis minuta* DEFLANDRE, 1929, p. 366, text-figs. 148–152.
- Centropyxis aculeata* var. *oblonga* DEFLANDRE, 1929, p. 349, text-figs. 96–103.
- Centropyxis aculeata* var. *tropica* DEFLANDRE, 1929, p. 348, text-figs. 94, 95.
- (?) *Pseudarcella arenata* CUSHMAN, 1930, p. 15, pl. 1, figs. 3a, b. (?) CUSHMAN and McCULLOCH, 1939, p. 43, 48, pl. 2, figs. 4a, b.
- Millettella glabrella* CUSHMAN and McCULLOCH, 1939, p. 43, pl. 2, figs. 3a, b.
- (?) *Leptodermella salsa* CUSHMAN and BRONNIMANN, 1948a, p. 15, pl. 3, figs. 3, 4.
- (?) *Leptodermella excentrica* CUSHMAN and BRONNIMANN, 1948b, p. 37, pl. 7, figs. 1, 2.
- (?) *Leptodermella variabilis* PARKER, 1952a, p. 452, pl. 1, figs. 11a, b, 12. PARKER and others, 1953, p. 10, pl. 1, fig. 3.
- Centropyxis (Cyclopyxis) arenatus* (sic) (Cushman). TODD and BRONNIMANN, 1957, p. 22, pl. 1, figs. 8a, b. (?) FEYLING-HANSEN, 1964, p. 217, pl. 1, figs. 9–11.
- Centropyxis (Cyclopyxis) salsus* (sic) (Cushman and Bronnimann). TODD and BRONNIMANN, 1957, p. 22, pl. 1, figs. 10, 11.
- (?) *Centropyxis excentricus* (sic) (Cushman and Bronnimann). TODD and BRONNIMANN, 1957, p. 22, pl. 1, fig. 9. SCOTT, 1976, p. 230, pl. 1, figs. 1, 2. SCOTT, 1977, p. 163, pl. 1, figs. 1–3. SCOTT and others, 1977, p. 1577, pl. 1, figs. 1, 2. SCOTT and others, 1980, p. 224, pl. 1, figs. 1–3.
- Centropyxis (Centropyxis) sp. A.* TODD and BRONNIMANN, 1957, p. 22, pl. 1, fig. 12.
- Centropyxis constricta* (Ehrenberg). BOLTOVSKOY and BOLTOVSKOY, 1968, p. 140, pl. 1, figs. 1a, b. HAMAN, 1982, p. 365, pl. 1, figs. 6–14.
- Centropyxis discoides* Pénard. GREEN, 1975, p. 548, text-fig. 1.

Diagnosis. Test depressed; although quite variable it can be described as beret-shaped; in dorsal view, usually large and more or less circular; anterior slope large, with small (mostly 15 to 40 degrees) anterior angle; posterior slope ill-defined, practically absent, fusing into the fundus, the latter being quite posterior; *height : length* ratio usually low (mostly 0.4 to 0.5). Aperture subcentral, usually slightly anterior, invaginated. Spines not always present; when present, mostly concentrated along the posterior and postero-lateral margins (Fig. 11). Test basically organic, mature specimens usually covered with somewhat loose, amorphous, siliceous particles, in most cases completely covering the membrane.

Discussion. Through the years the various authors seem to have been unable to accept a simple remark by Leidy (1879, p. 81), "... (This group) ... is exceedingly variable in character, but I have not been able to distinguish more than one species. This is to be sure not always aculeate, as expressed by the name ..." (Leidy's figures are redrafted in our Fig. 11). In fact, throughout the past century various authors have split, regrouped, redefined, etc., this species *ad nauseam* with singularly unsatisfactory results. In our opinion, the failure to reach a reasonable taxonomic definition of the species is due to the fact that the species is usually rare in normal freshwater environments: we had the opportunity to observe large and diverse natural populations in slightly brackish coastal lakes where the species flourishes. We believe that we are dealing here with one species only, and we have treated it as such. Ogden (personal communication, 1981) is probably not alone in strongly disagreeing with us.

In 1929 Deflandre stated that the aperture of this species is highly variable and has no taxonomic importance. Ogden (personal communication, 1981) is of the opposite opinion. On the basis of the material discussed in this paper, as well as of material from all over North America, we must emphatically agree with Deflandre.

Forms that we rather tentatively ascribe to this species have been attributed by various authors to the genera *Pseudarcella*, *Leptodermella* and *Millettella*, all considered by their respective first describers as foraminiferal genera. The genus *Leptodermella*, however, has for its type species *Pseudarcella arenata* Cushman, 1930, which we place in synonymy with *Centropyxis aculeata*. Hence, *Leptodermella* becomes a junior synonym of *Centropyxis*. *Pseudarcella*, we believe, is a genuine foraminiferal genus. Whether *Millettella* is a thecamoebian or a foraminiferal genus is still uncertain (see Bolli and Saunders, 1954).

Occurrence. Deflandre (1929) reported that Levander (no reference given) found this species in marine water (probably, we suspect, in the brackish waters of the Baltic Sea or adjacent gulfs, on which Levander frequently published). Whether Levander's marine specimens were alive or not, Deflandre did not say, but he commented that the species appears to be extremely undemanding. From this last comment we concluded that Levander's forms must have been alive. Whatever the exact limits of its salinity tolerance, *Centropyxis aculeata* is the only thecamoebian that we consistently find fossilized in our cores at the transition between marine and lacustrine deposits in raised and

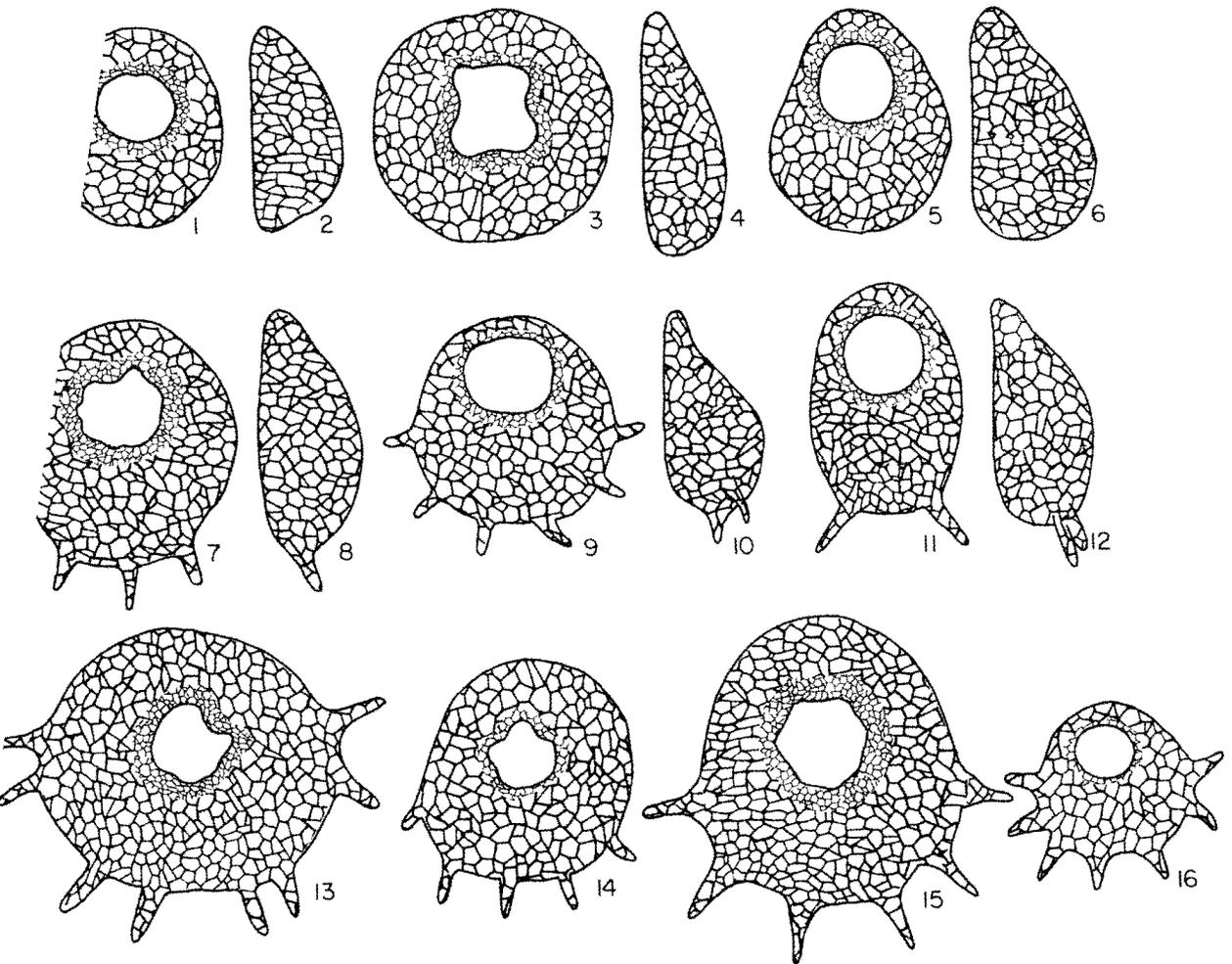


FIGURE 11. Figures of *Centropyxis aculeata* (redrafted and rearranged from Leidy, 1879, pl. 31). The figure shows some of the morphotypes we would include in our *C. aculeata*. The characteristics that vary most frequently are 1) number and shape of spines, 2) shape and position of the aperture, 3) outline of the dorso-ventral cross section of the shell.

merged lakes in Atlantic Canada (Scott and Miller, 1980; Miller and others, 1982).

This seems to be the first species of the Arcellacea to colonize emerging coastal basins while they evolve from marine, to brackish, to freshwater systems. Once freshwater conditions are firmly established, all other species can move in.

Observations on material illustrated in this paper. This species is not very common in purely lacustrine environments (e.g., Lake Erie) and here we illustrate a great variety of morphotypes (Pl. 7, Figs. 10–19). However, even these few illustrations show considerable variability in many aspects; number of spines (Figs. 10–13), degree of agglutination (all figures), shape (Fig. 18 compared to others), and types of xenosomes (Fig.

18 compared to others). We observed only specimens with round apertures in Lake Erie and Atlantic Canada and we place all these in the same species. We have observed different apertures in specimens from other parts of the world.

Centropyxis constricta (Ehrenberg, 1843)

Pl. 7, Figs. 1–9

Arcella constricta EHRENBURG, 1843, p. 410, pl. 4, fig. 35; pl. fig. 1.

Diffflugia proteiformis (sic) (Ehrenberg) subspecies *D. marsupifera* (Wallich) var. *D. cassis* WALLICH, 1864, p. 241, pl. 15, figs. 10, 11; pl. 16, figs. 6, 6a (binomen *D. cassis* used for a variety of subspecies: epithet *cassis* is, therefore, not available).

Diffflugia proteiformis (sic) (Ehrenberg) subspecies *D. marsupij*

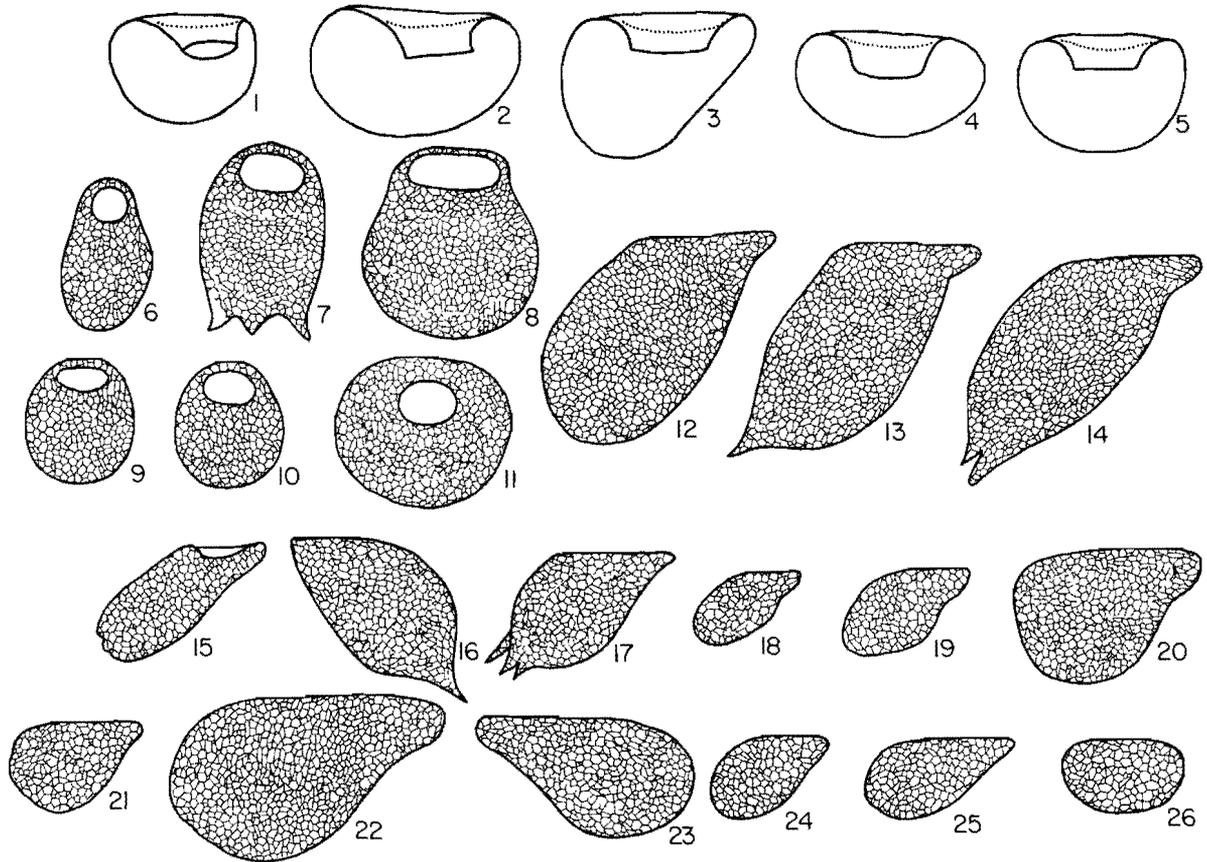


FIGURE 12. Figures of *Centropyxis constricta* (redrafted and rearranged after Leidy, 1879, pl. 18). The figure shows some of the morphotypes that Leidy attributed to *D. constricta*. The separation of this species from *D. aculeata* is relatively easy in those cases (6 to 19) in which the flat ventral side is small and represents a small fraction of the total outer surface. When the ventral side increases in size (20 to 26) the separation of the two species at first glance becomes more problematic and subjective. A certain number of specimens in every assemblage cannot be attributed to one species rather than the other.

(Wallich) 1864, p. 241. PÉNARD, 1890, p. 142, pl. 4, figs. 22, 23, 30, 31, 33.

Diffugia constricta (Ehrenberg). LEIDY, 1879, p. 120, pl. 18, figs. 8–55. PÉNARD, 1890, p. 148, pl. 5, figs. 1–16. PÉNARD, 1902, p. 298, text-figs. 1–3, 5, 8, 11, 12. EDMONDSON, 1906, p. 14, pl. 3, fig. 17. SCHOUTEDEN, 1906, p. 340, 348. CASH and HOPKINSON, 1909, p. 54, text-figs. 66–69, pl. 19, figs. 14–20; pl. 22, figs. 12–14.

Diffugia constricta var. *elongata* PÉNARD, 1890, p. 149, pl. 5, figs. 17–20.

Diffugia platystoma PÉNARD, 1890, p. 143, pl. 4, figs. 35–37.

Centropyxis constricta (Ehrenberg). DEFLANDRE, 1929, p. 340, text-figs. 60–67. DECLOÏTRE, 1953, p. 62, text-figs. 164–166. BOLLI and SAUNDERS, 1954, p. 48, text-fig. 2, no. 6a, b. TODD and BRONNIMANN, 1957, p. 21, pl. 1, figs. 6, 7 (misspelled *C. constrictus*). GROSPIETSCH, 1958, p. 40, text-fig. 32a. GREEN, 1975, p. 547, text-fig. 4. SCHÖNBORN, 1975, p. 127, text-fig. 3e. SCOTT and MEDIOLI, 1983, p. 819, fig. 9k.

Centropyxis marsupiformis (Wallich). DEFLANDRE, 1929, p. 342, text-figs. 68–75. DECLOÏTRE, 1953, p. 64, text-figs. 167–171.

Centropyxis platystoma (Pénard). DEFLANDRE, 1929, p. 338, text-figs. 43–57. DECLOÏTRE, 1953, p. 62, text-figs. 161–163. SCHÖNBORN, 1975, p. 127, text-fig. 3k. SMAGOWICZ, 1975, p. 410, text-fig. 17. OGDEN and HEDLEY, 1980, p. 60, pl. 19.

Centropyxis platystoma var. *armata* DEFLANDRE, 1929, p. 340, text-figs. 58, 59.

Centropyxis cassis DEFLANDRE, 1929 (ab Wallich, 1864), p. 335, text-figs. 35–40. GREEN, 1975, p. 547, text-fig. 3. COUTEAUX, 1977, p. 564, text-fig. 1e.

Urnulina compressa CUSHMAN, 1930, p. 15, pl. 1, figs. 2a, b. PARKER, 1952b, p. 394, pl. 1, fig. 4. PARKER, 1952a, p. 460–461, pl. 1, fig. 9. PARKER and others, 1953, p. 5, pl. 1, figs. 7, 8. SCOTT, 1977, p. 163, pl. 1, figs. 13–15. SCOTT and others, 1977, p. 1578, pl. 1, figs. 7, 8. SCOTT and others, 1980, p. 224, pl. 1, figs. 13–15.

Millettella spinata CUSHMAN and CAHILL, 1933, p. 5, pl. 1, figs. 3a–c. CUSHMAN and McCULLOCH, 1939, p. 43, pl. 2, figs. 1a, b, 2.

Urnulina difflugaeformis (sic) Gruber. (?) PARKER, 1952a, p. 461, pl. 1, fig. 10.

Urnulina sp. A. PARKER and others, 1953, p. 5, pl. 1, fig. 9.

- Urnulina* sp. B. PARKER and others, 1953, p. 5, pl. 1, fig. 10.
Centropyxis capucina BONNET, 1976b, p. 302, text-figs. 6, 7.
 COUTEAUX, 1977, p. 566, text-fig. 2.
Centropyxis elongata (Pénard). COUTEAUX, 1977, p. 564, text-figs. li, m-p.

Diagnosis. Test much less depressed than in *C. aculeata* and usually elliptical in dorsal view, with a profile usually raised posteriorly. Anterior angle larger than in *C. aculeata* (mostly 40 to 65 degrees) and posterior angle normally well defined. Fundus raised in uppermost position. Ventral side often relatively small, with invaginated aperture in antero-marginal position. The degree of invagination of the mouth varies. *Height : length* ratio high (usually 0.5 to 1.1). When this ratio is very high and the anterior angle rises to about 80 degrees or more, the plagiostome aspect intergrades into an acrostome one; the ventral face becomes limited to the aperture alone, which thus ceases to be "anterior" or "antero-marginal" and becomes terminal. Forms with this type of aperture seem to grade into acrostome, elongated forms of *Diffflugia* from which *C. aculeata* cannot be easily separated (except for the invagination of the pseudostome).

The fundus often carries two or more spines, as is common in most forms of *Centropyxis*. Test largely organic, often completely covered with mineral particles of various nature.

Discussion. This usually abundant species is extremely variable in size and shape; very seldom are two specimens really alike. This is, no doubt, the cause for much of the confusion that has plagued the taxonomic literature on this species for well over a century. Leidy (1879) already had to group seven synonyms into his *Diffflugia constricta* (essentially the same as our *C. constricta*) and, in order to adequately illustrate the spectrum of variability, had to devote to it an entire plate with 57 figures. Later authors split Leidy's unit into numerous species and varieties. As supporting evidence that *C. constricta* is, in fact, one species, one can easily arrange Leidy's figures into a complex but quite complete intergradational series (Fig. 12).

Cash and Hopkinson (1905) were quite perplexed by this variety of forms and commented that, as the species is cosmopolitan, it is more than probable that its variable character is induced by the surrounding conditions (i.e., ecophenotypes?). They left the problem at that with the wise remark that the task of separating the varieties of such a species would be endless and unprofitable. Their comment did not seem to deter Deflandre (1929) from splitting the group into about twenty taxa. Most of Deflandre's "species" and "varieties" occur in our material from eastern Canada, but

unfailingly together with uncategorizable, intermediate forms that unmistakably link each variety to the next. This makes it impossible and indeed "unprofitable" to divide the group into discreet units, informal as they may be. As far as we are concerned, until a very convincing case to the contrary is made, we strongly agree with Leidy that the entire group falls into *C. constricta*.

Forms that we more or less tentatively ascribe to this species have, in the past, been interpreted as Foraminifera and placed in the genus *Millettella*.

Occurrence. Very common in the ooze of all sorts of freshwater bodies and in most wet places.

Observations on material illustrated in this paper. This species was relatively common in Lake Erie and we have been able to adequately illustrate its variability (Pl. 7, Figs. 1-9). Most distinct variations here occur in the number of spines on the fundus. Considerable variability is also present in the neck region with a distended collar (Fig. 5) in some specimens and virtually a simple aperture in others (Fig. 8). In other areas we have observed specimens very close to *C. aculeata* (i.e., resting almost flatly on the apertural side).

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PLATE 1

(All specimens from Lake Erie unless otherwise specified. Magnifications approximated.)

1-5 *Diffflugia bidens*. 1. Apertural view; $\times 175$. 2. Side view; $\times 145$. 3. Front view; $\times 113$. 4. Front view of specimen from Gibson Lake, New Brunswick (note very small spines at fundus); $\times 102$. 5. Apertural view of Gibson Lake specimen; $\times 128$. **6-14** *Diffflugia corona*. 6. Side view of specimen with single basal spine; $\times 144$. 7. Close-up of aperture of specimen in Fig. 6; $\times 484$. 8. Apertural view of regular specimen; $\times 193$. 9. Enlargement of aperture in Fig. 8; note secondary cement on aperture; $\times 574$. 10. Apertural view of specimen with several spines; $\times 180$. 11. Side view of specimen with several spines; $\times 150$. 12. Side view of oblong specimen; $\times 143$. 13. Side view of oblong specimen with many spines; $\times 180$. 14. Side view showing position of spines at fundus; $\times 184$. **15-20** *Diffflugia protaeiformis*. 15. Apertural view of normal specimen; $\times 244$. 16. Enlargement of Fig. 15 showing detail of the aperture; $\times 514$. 17. Side view of compressed specimen; $\times 193$. 18. Side view of specimen with two spines and a rough surface; $\times 231$. 19. Side view of typical specimen; $\times 175$. 20. Side view of specimen tending toward *Diffflugia oblonga*; $\times 98$. **21-27** *Diffflugia fragosa*. 21. Side view of multi-faceted specimen; $\times 184$. 22. Apertural view of specimen in Fig. 21; $\times 248$. 23. Apertural view of specimen with less accentuated ribs; $\times 351$. 24. Side view of specimen in Fig. 23; $\times 227$. 25. Side view of more rounded specimen with several small spines; $\times 291$. 26. Top side view of typical specimen; $\times 218$. 27. Side view of specimen with several spines; $\times 291$.

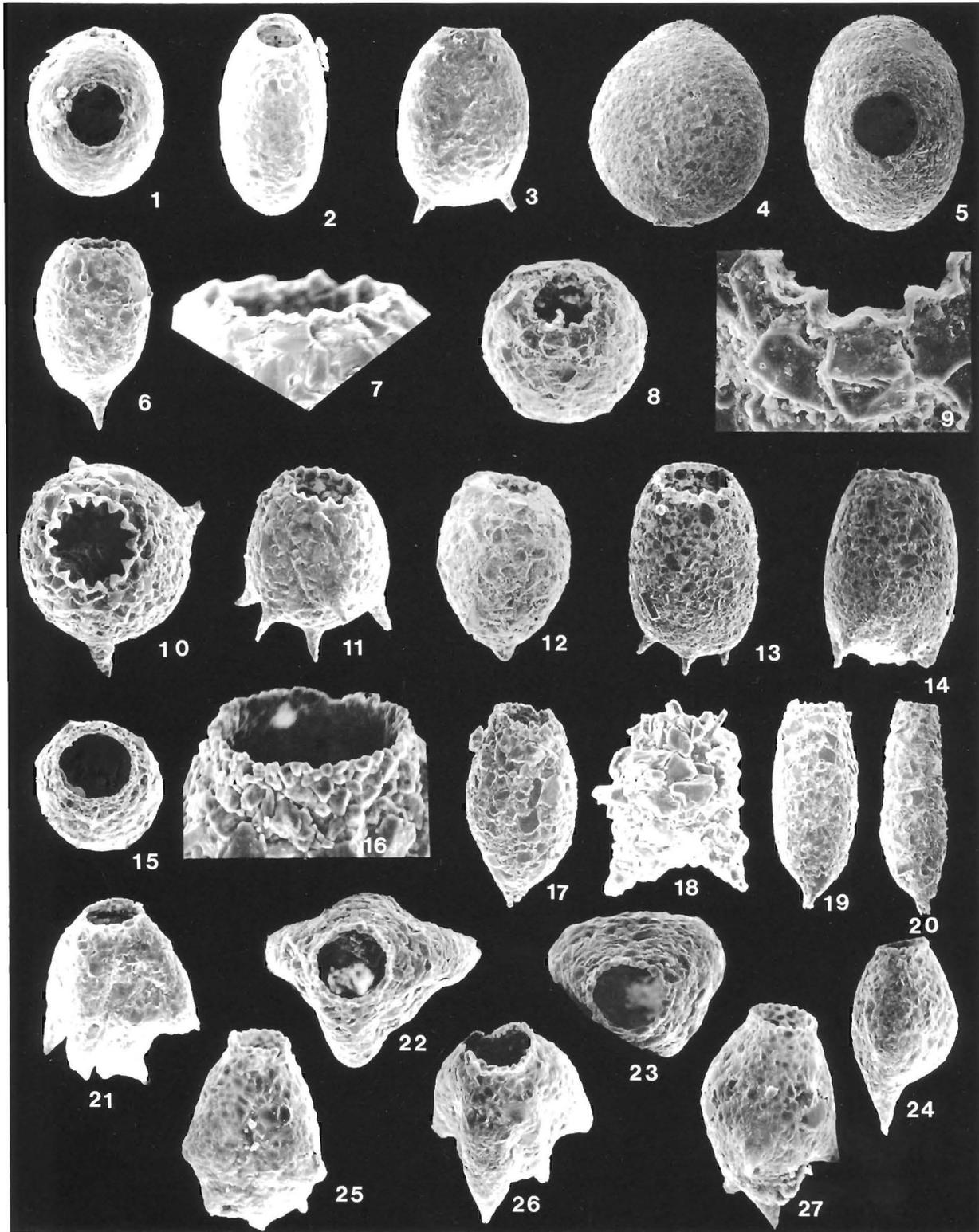


PLATE 2

(All specimens from Lake Erie unless otherwise specified. Magnifications approximated.)

1-17 *Diffflugia oblonga*. 1. Side view of pyriform type with large grains; $\times 105$. 2. Side view of specimen with coarser agglutination at apertural neck; $\times 135$. 3. Side view of smooth pyriform type; $\times 180$. 4. Side view of smaller specimen with neck developing; $\times 283$. 5. Side view of specimen with well-developed neck; $\times 184$. 6. Side view of large-necked specimen; $\times 100$. 7. Side view of typical specimen with spine; $\times 95$. 8. Side view of specimen with straight spine; $\times 98$. 9. Side view of vase-shaped specimen; $\times 94$. 10. Side view of U-shaped specimen; $\times 130$. 11. Side view of laterally compressed specimen; $\times 114$. 12. Apertural view of typical specimen; $\times 300$. 13. Side view of pyriform specimen attached to sand grain; $\times 120$. 14. Apertural view of compressed specimen; $\times 201$. 15. Two typical forms fused into one specimen; $\times 102$. 16. Pyriform type attached to sand grain; $\times 88$. 17. Apertural view of compressed specimen; $\times 138$. **18-23** *Lagenodiffflugia vas*. 18. Side view of specimen with prominent constriction; $\times 266$. 19. Side view of constricted specimen with coarser agglutination at the constriction; $\times 144$. 20. Apertural view of specimen in Fig. 19; $\times 278$. 21. Side view of typical specimen; $\times 248$. 22. Side view of specimen with heavy agglutination at neck; $\times 144$. 23. Apertural view of specimen in Fig. 22; $\times 253$. **24-26** *Diffflugia oblonga* from Gibson Lake, New Brunswick. 24. Apertural view of compressed form, $\times 87$. 25. Side view of compressed form with angular fundus; $\times 80$. 26. Side view of compressed form with basal spines; $\times 100$. **27, 28** *Lagenodiffflugia vas*, Gibson Lake. 27. Side view, note large main chambers and narrow neck; $\times 130$. 28. Apertural view; $\times 130$.

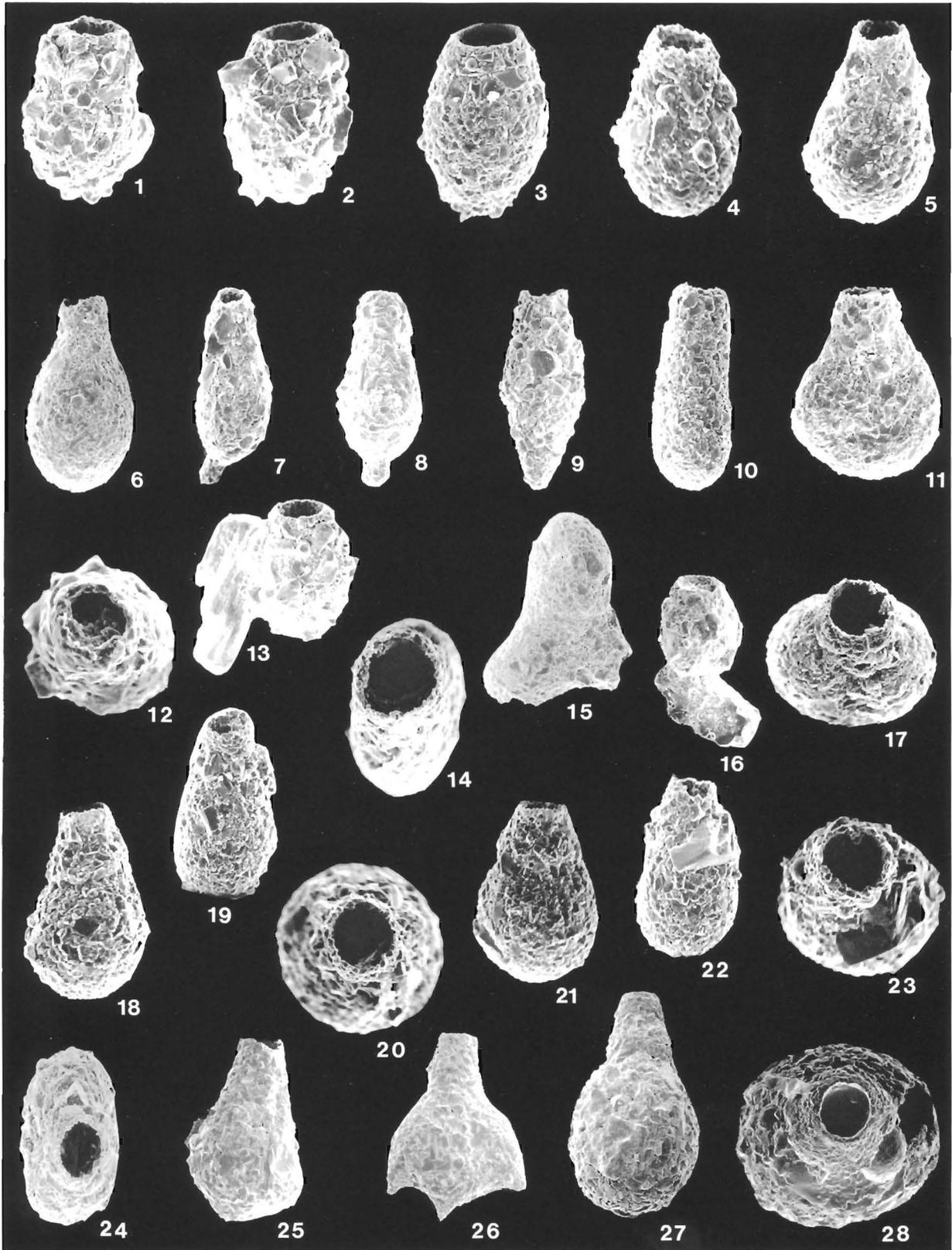


PLATE 3

(All specimens from Lake Erie unless otherwise specified. Magnifications approximated.)

1-23 *Diffugia urceolata*. 1. Side view of *D. lebes*-like form, note neck; ×85. 2. Apertural view of “*lebes*” form; ×78. 3. Side view of a “*lebes*” form with coarser agglutination at aperture; ×87. 4. Side view of more oblong “*lebes*” form; ×85. 5. Side view of “*lebes*” specimen with longer neck; ×64. 6. Side view of “*lebes*” specimen with long neck; ×68. 7. Side view of specimen with neck just slightly curved over; ×80. 8. Side view of specimen with curved lip; ×104. 9. Side view of specimen with lip incomplete; ×71. 10. Side view of specimen with thickened neck; ×88. 11. Side view of “*D. amphora*”-like specimen; ×130. 12. Apertural view of typical specimen; ×137. 13. Side view of “*amphora*”-like specimen; ×94. 14. Side view of specimen with narrow neck; ×95. 15. Side view of typical specimen; ×283. 16. Apertural view of encysted specimen showing cyst cover with unidentified foreign particle; ×283. 17. Enlargement of connection between cyst cover and test wall; ×338. 18. Side view of specimen with thickened lip; ×100. 19. Side view of specimen with asymmetric thickened lip; ×88. 20. Top side view of specimen in Fig. 16; ×108. 21. Top side view of specimen in Fig. 17; ×117. 22. Side view of specimen with round cyst chamber inside (test broken open); ×95. 23. Enlargement of cyst wall area of specimen in Fig. 22; ×400.

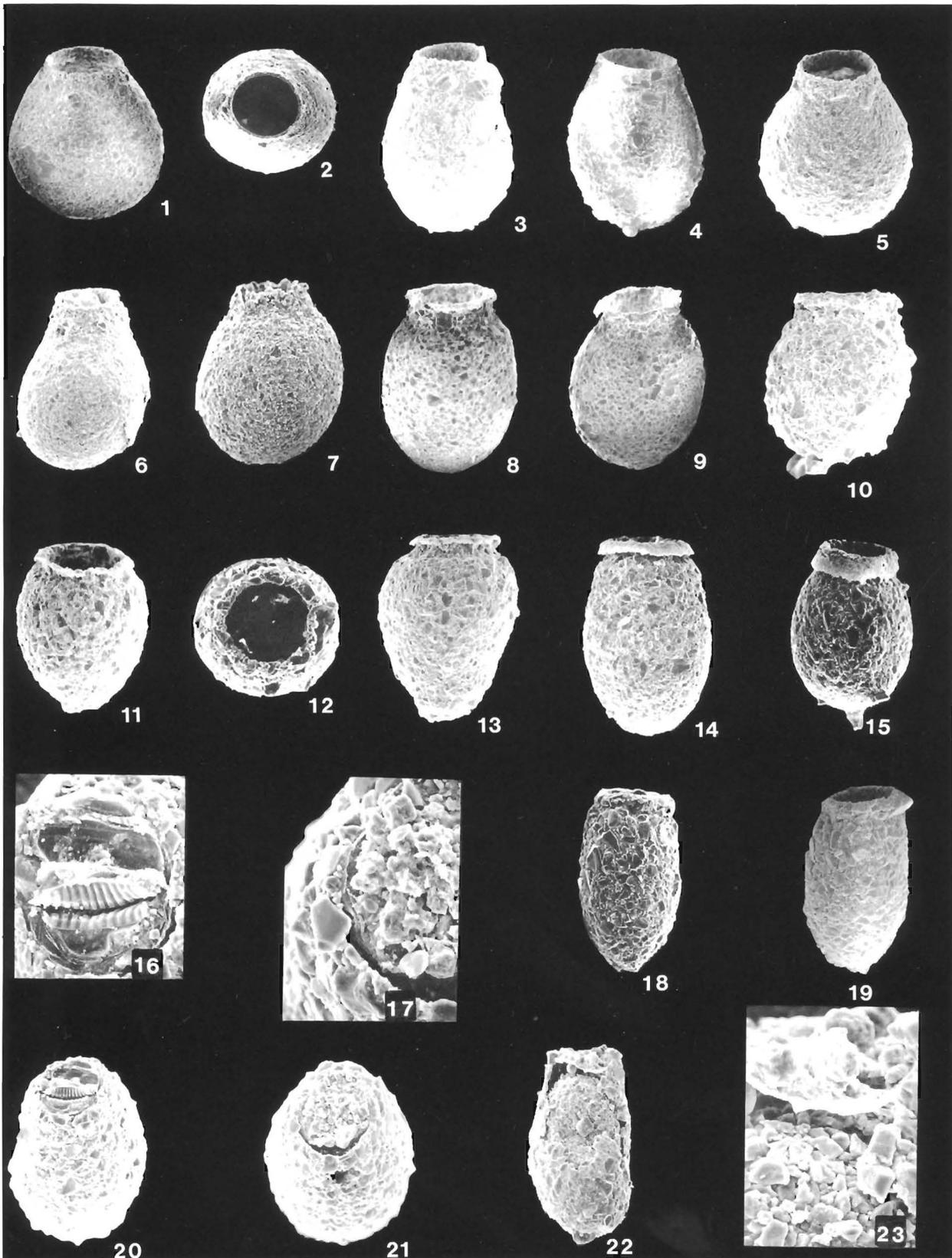


PLATE 4

(All specimens from Lake Erie unless otherwise specified. Magnifications approximated.)

1-4 *Diffflugia urceolata*. 1. Spherical cyst commonly seen in some cores from Lake Erie: these were often observed naked as shown here; $\times 113$. 2. Cyst with what appears to be an apertural opening; $\times 134$. 3. Enlargement of aperture of specimen in Fig. 2; $\times 411$. 4. Cyst partially encased in larger test; $\times 105$. 5-19 *Diffflugia tricuspis*. 5. Side-apertural view of specimen with pluri-lobate aperture; $\times 257$. 6. Side-aperture view of form with mildly indented aperture; $\times 248$. 7. Side-apertural view of accentuated lobate aperture; $\times 398$. 8. Side-apertural view of strongly heart-shaped aperture; $\times 398$. 9. Enlargement of apertural lip in Fig. 8; $\times 1,037$. 10. Side view of specimen with discontinuous lip edge at the aperture; $\times 377$. 11. Enlargement of straight lip edge of specimen in Fig. 10; $\times 1,628$. 12. Side view of specimen with triangular aperture and spines; $\times 317$. 13. Side view of typical specimen with sub-triangular aperture; $\times 377$. 14. Apertural view of specimen with thickened apertural lip; $\times 433$. 15. Side-apertural view of specimen with virtually no lip; $\times 411$. 16. Side-apertural view of specimen with round aperture (note slight indentation); $\times 171$. 17. Side-aperture view of specimen with completely round aperture and reduced lip size; $\times 283$. 18. Side view of elongated specimen with round aperture and coarse agglutination; $\times 270$. 19. Side view of elongated specimen with spines; $\times 288$.

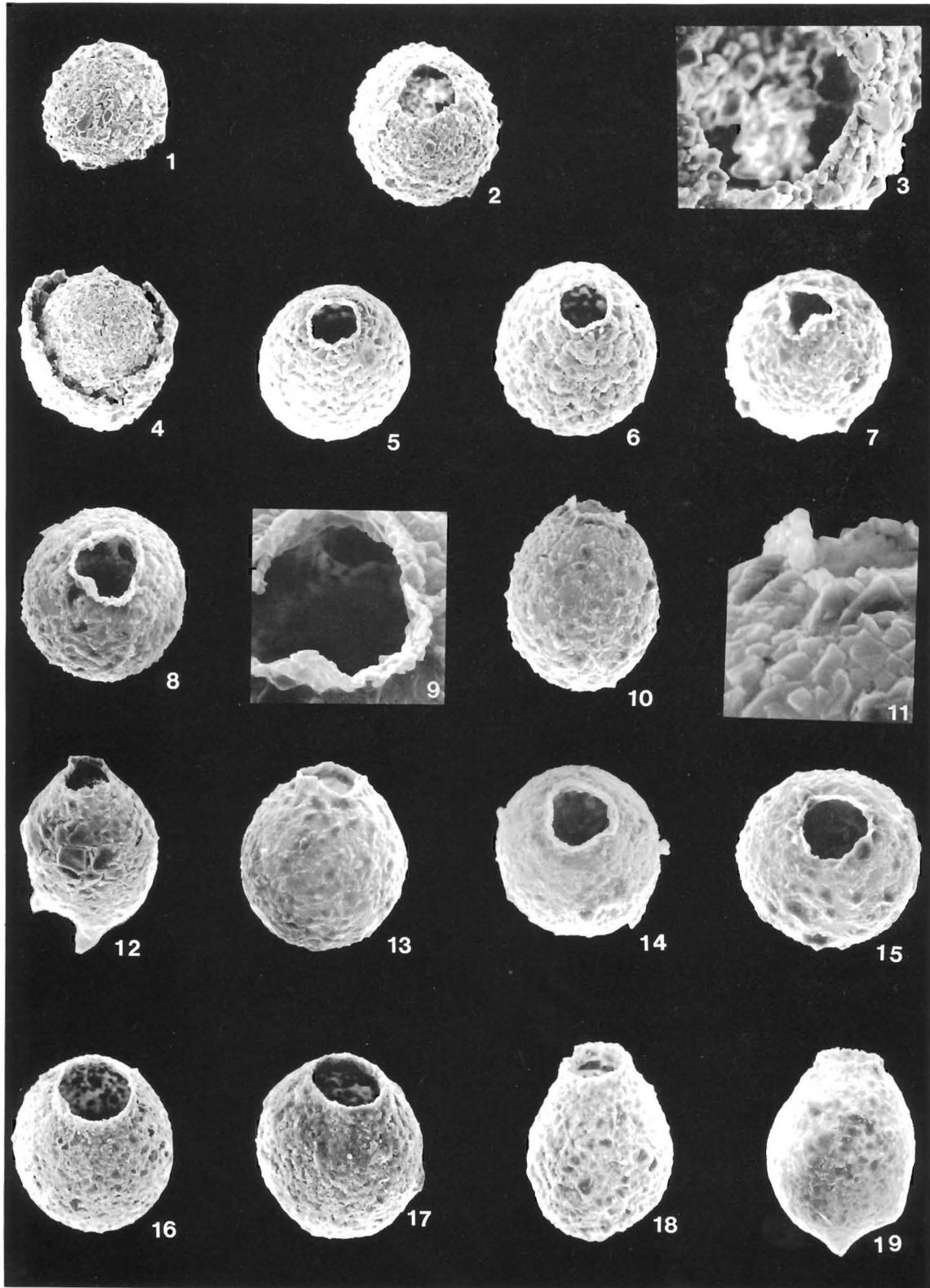


PLATE 5

(All specimens from Lake Erie unless otherwise specified. Magnifications approximated.)

1-15 *Diffflugia globulus*. 1. Top view of specimen attached to larger sand grain; $\times 171$. 2. Side view of attached specimen; $\times 140$. 3. Side view of large specimen; $\times 64$. 4. Enlargement of attachment area of specimen in Fig. 3; $\times 145$. 5. Apertural view of specimen with sieve-plate; $\times 185$. 6. Enlargement of contact between test wall and sieve plate of specimen in Fig. 5; $\times 485$. 7. Side view of specimen in Fig. 5; $\times 185$. 8. Enlargement of test wall of specimen in Fig. 5; $\times 770$. 9. Enlargement of sieve plate of specimen in Fig. 5; $\times 770$. 10. Side view of specimen attached but also exhibiting an apertural area with sieve plate; $\times 111$. 11. Apertural view of specimen with sieve-plate partially broken; $\times 135$. 12. Top view of attached specimen; $\times 163$. 13. Side view of specimen from Framboise Cove, Nova Scotia with no evidence of sieve plate; note slight invagination of aperture; $\times 257$. 14. Apertural view of Framboise Cove specimen; $\times 193$. 15. Enlargement of wall area of specimen in Fig. 12 showing some pores in cement areas; $\times 497$. **16-19** *Diffflugia bacilliarum* from James and Hudson Bays marsh areas. 16. Apertural view; $\times 591$. 17. Side view of specimen in Fig. 16; $\times 304$. 18. Side view; note reduced lip compared to that in Fig. 17; $\times 390$. 19. Fundus view; $\times 450$.

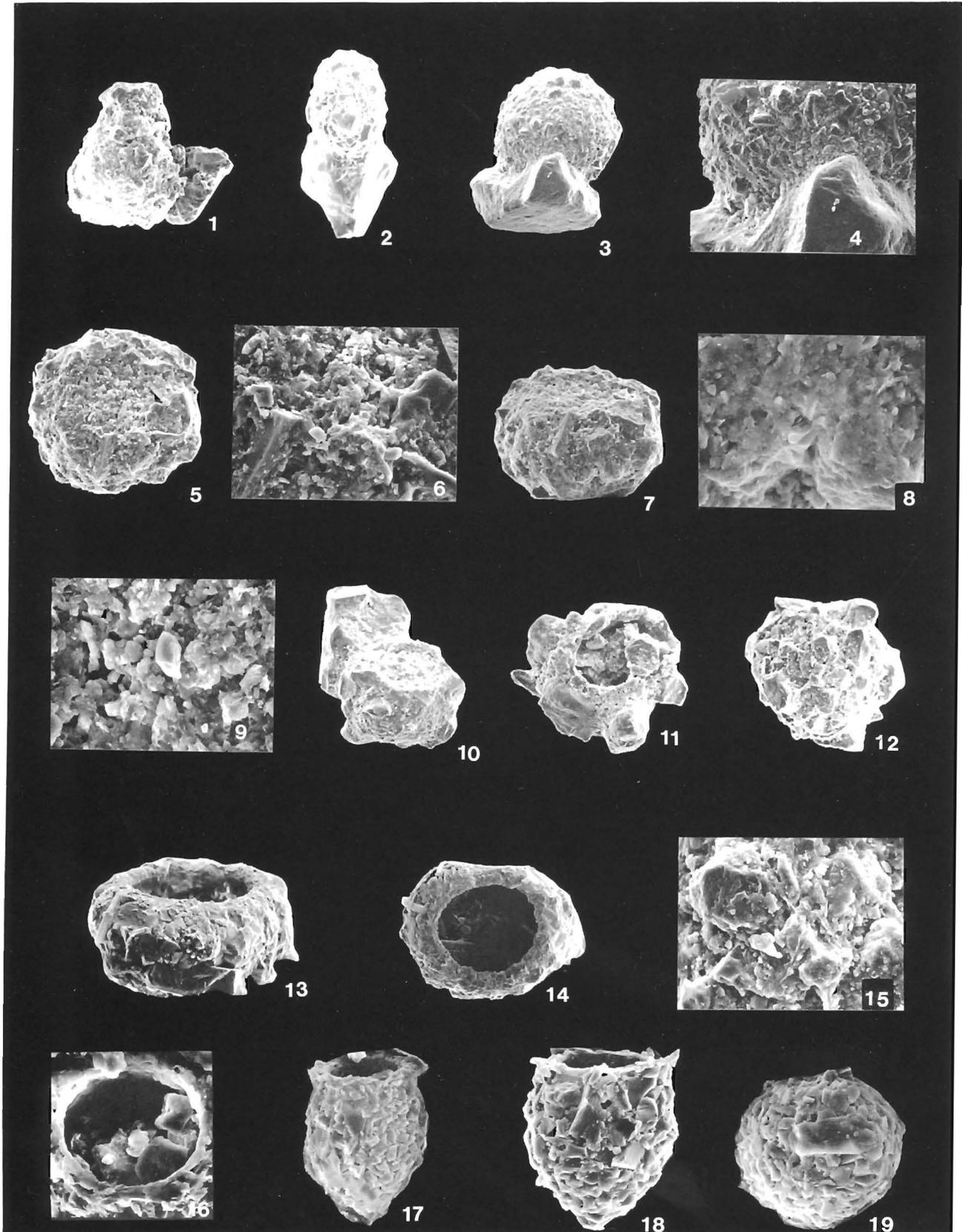


PLATE 6

(All specimens are from Lake Erie unless otherwise specified. Magnifications approximated.)

1-4 *Diffugia bacilliarum* from Hudson and James Bays marshes. 1. Side view of specimen with poor lip development; $\times 373$. 2. Enlargement of lip area of specimen in Fig. 1; $\times 677$. 3. Side view of specimen with well developed lip; $\times 330$. 4. Apertural view of specimen in Fig. 3; $\times 643$. **5-14** *Pontigulasia compressa*. 5. Side view of typical specimen; note V-shaped constriction just at the middle in the apertural neck region; this is the position of the diaphragm; $\times 253$. 6. Side view of specimen with more marked constriction; $\times 134$. 7. Side view of specimen beginning to show some torsion; $\times 167$. 8. Side view of specimen showing torsion in the neck area; $\times 257$. 9. Apertural view of specimen in Fig. 8; $\times 296$. 10. Side view of specimen with both strong constriction and torsion; $\times 231$. 11. Apertural view of specimen in Fig. 10; $\times 257$. 12. Side view of specimen showing torsion; $\times 223$. 13. Apertural view of specimen in Fig. 12; $\times 650$. 14. Neck of specimen broken at constriction to show remains of diaphragm on the inside lower parts of figure; $\times 270$. **15-18** *Heleopera sphagni*. 15. Side view of specimen; note slight notch in aperture and also increased grain size in agglutination near the fundus; $\times 197$. 16. Apertural view, note elliptical shape of aperture; $\times 197$. 17. Front view of specimen, again note increased agglutination at fundus; $\times 184$. 18. Apertural view of specimen attached to large sand grain; $\times 151$.

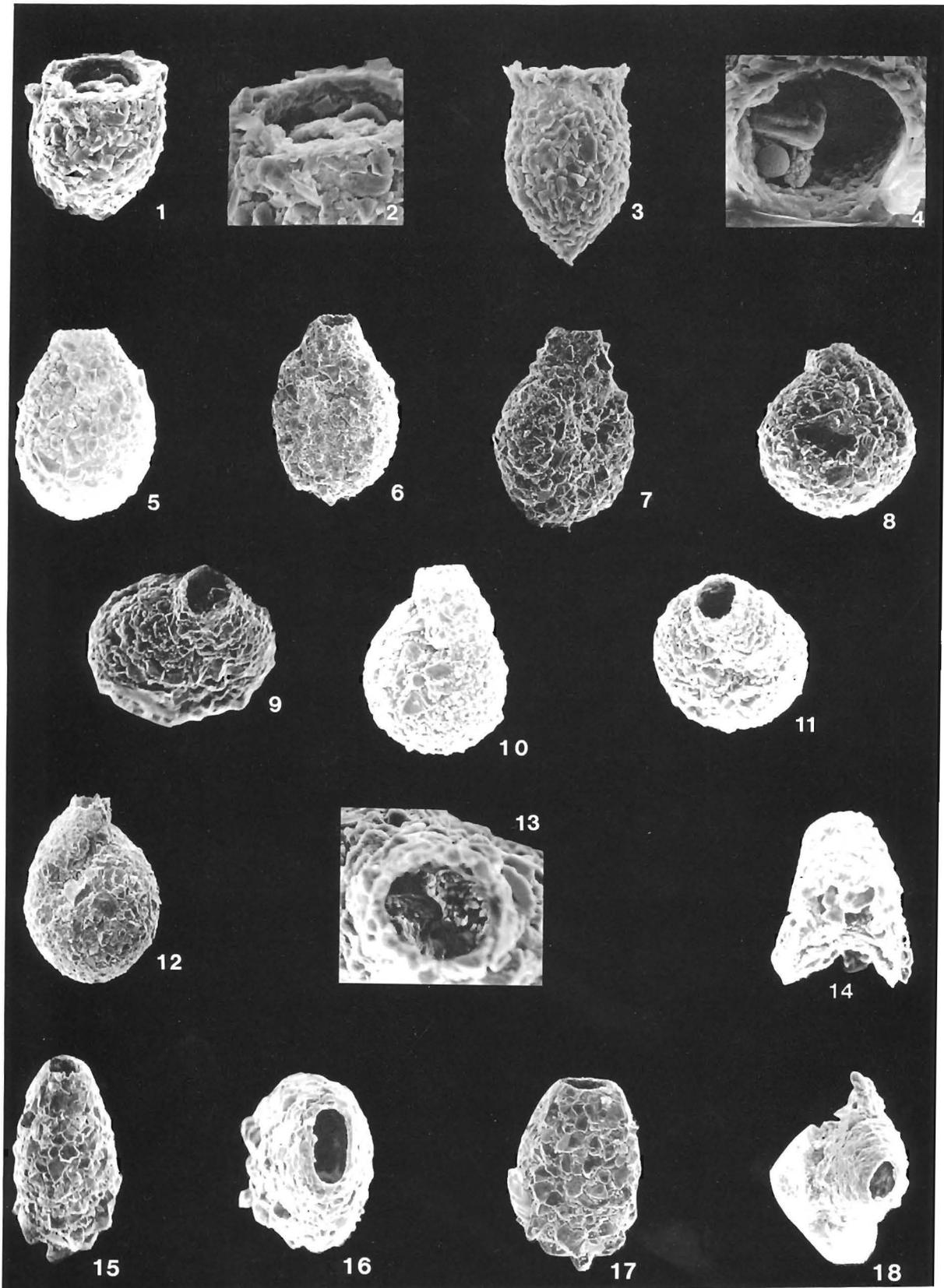


PLATE 7

(All specimens from Lake Erie unless otherwise specified. Magnifications approximated.)

1-9 *Centropyxis constricta*. 1. Ventral view of specimen with two spines; $\times 201$. 2. Apertural view of specimen in Fig. 1, note invaginated aperture; $\times 248$. 3. Ventral view of three-spined specimen; $\times 184$. 4. Ventral view of flattened specimen with three spines; $\times 188$. 5. Ventral view of specimen with no spines; $\times 176$. 6. Ventral view of specimen with four spines; $\times 180$. 7. Ventral view of specimen with aperture slightly inclined; $\times 210$. 8. Ventral view of specimen with five spines and small aperture; $\times 218$. 9. Apertural view of specimen in Fig. 8; $\times 248$. **10-19** *Centropyxis aculeata*. 10. Ventral view of specimen with two complete spines and several broken ones; $\times 261$. 11. Ventral view of specimen with no spines; note increased agglutination near periphery of specimen; $\times 257$. 12. Dorsal view of specimen with spines; note flattened area near the top of specimen; $\times 248$. 13. Ventral view of specimen which is almost circular; $\times 278$. 14. Side view of specimen with little agglutination; this specimen is also much broader than usual; $\times 202$. 15. Enlargement of test wall of specimen in Fig. 14; $\times 548$. 16. Ventral view of specimen from Framboise Cove, Nova Scotia; $\times 87$. 17. Dorsal view of specimen from Framboise Cove, Nova Scotia; $\times 88$. 18. Dorsal view of broken specimen from Framboise Cove; note the agglutinated diatoms; $\times 223$. 19. Ventral view of specimen from Hudson and James Bays showing spines and increased agglutination at periphery; $\times 240$.

