

## Euryhaline, Sand-dwelling, Testate Rhizopods in the Great Lakes

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**ABSTRACT.** Rich and highly specialized communities of sand-dwelling testate rhizopods (amoebae, mainly of the subclass Testaceafilosia) are known from marine and brackish waters of the world's oceans, but no representatives of these communities have been reported previously from the Great Lakes. Beach sand samples were collected in September, 2002 at 37 locations in Lake Superior, Lake Huron (including the North Channel and Georgian Bay), Lake Erie, and Lake Ontario and were examined for the presence of psammobiont (obligate sand-dwelling) testate rhizopods. Four species were found, three of which belong to the genus *Psammonobiotus* that may have their origins in the Ponto-Caspian region of Eurasia. *Psammonobiotus communis* Golemansky was originally described in the late 1960s as a marine relict from Lake Ohrid, Macedonia and from the Black Sea, but has since become the most widely reported *Psammonobiotus* species in marine/brackish water beach sands. It was abundant and widely distributed in the Great Lakes samples, as was a presently unnamed species of *Psammonobiotus* known previously only from the Polish coast of the Baltic Sea. A third species, *P. linearis* Golemansky, also widely known from oceanic and brackish beach sands, was found at the eastern end of Lake Ontario and in Rondeau Bay, Lake Erie. The fourth psammobiont, *Corythionella golemanskyi* Nicholls is apparently an exclusively freshwater form that was common in many of our Great Lakes samples. Based on published accounts, the three *Psammonobiotus* species have wide salinity tolerances that may have facilitated their establishment in the Great Lakes, perhaps after introduction in ships' ballast water.

**INDEX WORDS:** Black Sea, invasive species, Laurentian Great Lakes, Ponto-Caspian, psammobiont testate amoebae, salinity tolerance, sand-dwelling Testaceafilosia.

### INTRODUCTION

Establishment of more than 160 non-indigenous and exotic species of fish, mollusks, crustaceans and other animals and plants in the Laurentian Great Lakes during the past 1–2 centuries (Mills *et al.* 1993, Ricciardi 2001) has undoubtedly altered ecosystem structures and functions of these lakes (Vanderploeg *et al.* 2002). Lack of information on species representing some protozoan groups has, however, precluded development of an understanding of changes in some communities resulting from the possible introduction of protozoan species from areas outside the Great Lakes, as mediated by, for example, ships' ballast water (MacIsaac *et al.* 2002).

Wailes (1927) described the first known sand-

dwelling testate rhizopod (*Pseudocorythion acutum* (Wailes) Valkanov) from beach sands on the west coast of British Columbia, Canada. This shoreline biotope was largely ignored, however, for the next four decades until the late 1960s when renewed investigations in the Black Sea, the Baltic Sea, and the North Sea by Golemansky (1970a, 1970b), Chardez (1971) and others contributed descriptions of many new supralittoral marine genera and species. Most species known today are included in the family *Psammonobiotidae* Golemansky emend Meisterfeld and the family *Cyphoderiidae* de Saedeleer. A morphological feature shared by many species is a thin organic shell or test (the origin of the descriptor, "testate") that is covered either in endogenously-produced, small, siliceous scales (*Cyphoderiidae*), or in thin, irregularly-shaped quartz particles assembled by the amoeboid organ-

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ism (Psammonobiotidae). The aperture through which filose pseudopodia extend for locomotion and feeding often is at the end of a bent neck-like extension of the test that possesses a terminally flared collar. The collar, which in many species is a large flared disc-like structure, may facilitate attachment of the organism to a sand grain (Golemansky 1990). Marine associations of sand-dwelling rhizopods comprise uniquely specialized species that can be referred to as obligate psammobionts (exclusively sand-dwellers), which were believed to inhabit the littoral zone sands of seas but not of freshwater lakes. In particular, *Psammonobiotus communis* Golemansky, is well known from beach sands in virtually all oceans including the Antarctic, where it is often a component of a very rich community of a score or more of species representing several exclusively marine genera of testate rhizopods (e.g., Golemansky 1998a, 2000).

Although some limited information exists for testate rhizopod communities in Great Lakes basin wetlands (Booth 2001), there have been no previous investigations of the testate rhizopod species of Great Lakes beaches. During a preliminary survey in the fall of 2001, one of us (K.N.) discovered *Psammonobiotus communis* in a sample of beach sand at Dorcas Bay on the east side of Lake Huron. This discovery was not reported, pending a broader search of other Great Lakes beaches for other marine and brackish water species. This expanded search was undertaken in September 2002 and included sites representing all of the Great Lakes except Lake Michigan. The purpose of this paper is to report the findings of that search.

## METHODS

Samples (100–1,000 cc) of shoreline sand from the wave zones of Great Lakes beaches were collected 5 September 2001 from Dorcas Bay, Lake Huron and from this and 36 other beaches in Lake Superior, Lake Huron (including Georgian Bay and the North Channel), Lake Erie, and Lake Ontario between 2–9 September 2002 (Fig. 1). Sand samples were collected with a clean garden trowel and placed in a clean plastic pail with about 1 L of lake water from the same location. After thorough mixing to dislodge and suspend micro-organisms presumed attached to sand grains, the supernatant was poured off into 500 mL polycarbonate screw-capped bottles for transportation on ice to the laboratory. Another portion (25 mL) was immediately

preserved with formalin (about 1.5% formaldehyde).

Living and preserved samples were examined with an inverted microscope using a 10× objective under dark-field illumination for initial detection and high power (40× and 100× oil immersion objectives) with Zernike phase-contrast for measurements and examination of structure of rhizopod tests. Isolation of single specimens was done with a micro-pipette (drawn out in a flame). Optimal orientation for measurement was achieved by manual manipulation of isolated specimens with a single hair brush. For *P. communis*, which has a propensity to come to rest on its ventral or dorsal surface in water, a 50% solution of glycerol helped maintain specimens oriented in lateral view while measurements could be made. Test dimensions and terminology were as portrayed in Figure 2. Statistical data describing test morphology (mean, standard deviation, median, minimum, maximum, coefficient of variation) and Mann-Whitney *U*-tests of significant difference between populations were done in *CoStat* (CoHort Software 1995). Specimens were mounted in Canada Balsam for permanent preservation. Drawings were made from tracings from microscope projections or digital images. Additional 20 mL aliquots from the original living sample bottles were preserved after several weeks of growth in the laboratory in semi-darkness at about 18°C. Typically, these cultured bottles contained about 0.5 cm of sand and 10 cm of overlying water (500 mL) from the original collection site. Investigation of testate amoebae during an incubation period of up to several months following initial collection is a common practice with this group of organisms (e.g., Golemansky 2002). Extreme care was taken to ensure that cross contamination among the sample containers did not occur. All containers retained their original caps for the duration of the investigation and a disposable plastic pipette was used to sample each container.

## RESULTS

Filose testate amoebae were not abundant in samples examined within the first week of collection. Only after several weeks of incubation in the original sample collection bottles did substantial populations of several taxa develop. The main conclusions about relative abundance and distributions of species discussed here are based on 1–3 month-old cultures.

Although the emphasis in this study was on ob-

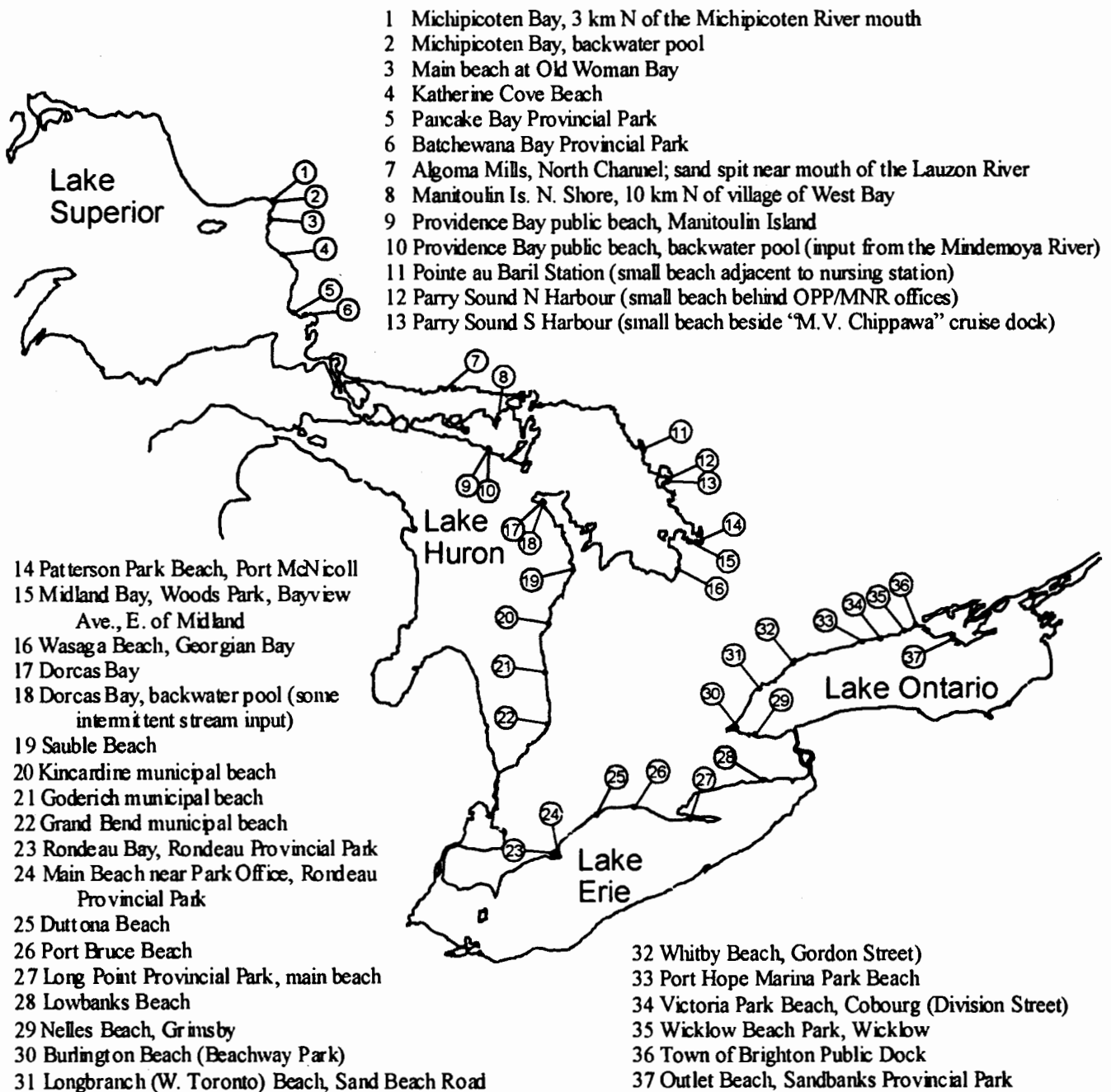


FIG. 1. Sites along the Great Lakes where beaches were sampled for sand-dwelling testate rhizopods.

ligate psammobionts, many other testate rhizopods were recorded also, but the identification of several of these was preliminary and incomplete. Still, because the beach sand Great Lakes biotope had not been examined previously for any of these taxa, it is instructive to present our preliminary list of the non-psammobionts. Of the locally abundant testate rhizopods found in our beach sand collections, sev-

eral are apparently ubiquitous, with world-wide occurrence in a wide variety of freshwater habitats including damp soils and mosses (Chardez and Lambert 1981). In our samples, these included species of the arcellids *Arcella*, *Centropyxis*, *Diffugia*, *Hyalosphenia* (notably *H. cuneata* Stein), and *Schoenbornia*, and of the euglyphids, *Campascus minutus* Penard (Nicholls 2003a), *Cyphoderia am-*

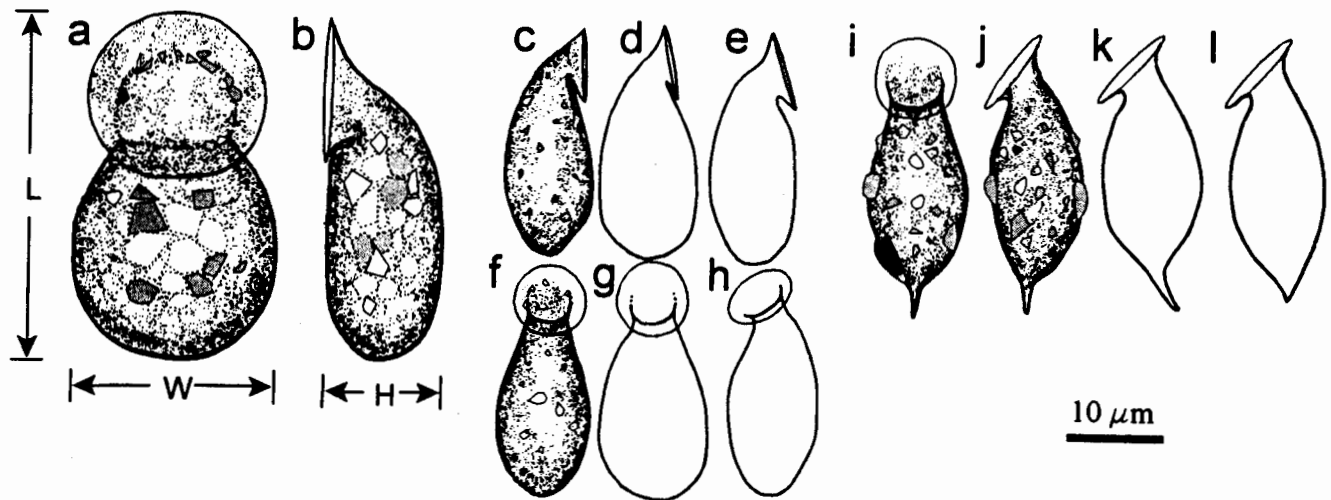


FIG. 2. Drawings of the tests of three species of sand-dwelling *Psammonobiotus* found in Great Lakes samples. a-b: *P. communis* ventral view (a) and lateral view (b) depicting conventional measurement axes for test length (L), width (W) and height (H). c-h: *Psammonobiotus* sp. # 2 showing variations in test shape in lateral view (c-e) and in ventral view (f-h). i-l: *P. linearis* showing typical ventral view (i) and variations in test shape in lateral views (j-l).

*pulla* Ehr., *Cyphoderia trochus* Penard, *Cyphoderia laevis* Penard, *Tracheleglypha dentata* (Vejd.) Deflandre, *Pareuglypha reticulata* Penard, *Paulinella chromatophora* Lauterborn, *Trinema enchelys* (Ehr.) Leidy, *Trinema lineare* Penard, *Euglypha filifera* Penard, and other small *Euglypha*, *Sphenoderia*, and *Scutiglypha* species. Because the emphasis in this project was on species of testate rhizopods of previously-known marine/brackish water distribution, no further taxonomic or distributional data pertaining to the above mentioned taxa were therefore generated.

Our search for any of the 37 known marine or brackish water, sand-dwelling species of the genera *Alepiella*, *Chardezia*, *Corythionella*, *Mesemvriella*, *Micramphora*, *Micropsammella*, *Ogdeniella*, *Popsammonobiotus*, *Psammonobiotus*, and *Pseudocorythion* revealed only three species of *Psammonobiotus* in the Great Lakes samples. In addition, the apparently exclusively freshwater psammobiotic species *Corythionella golemanskyi* Nicholls (Fig. 3x-z) was also well represented at several Great Lakes sites (Table 1).

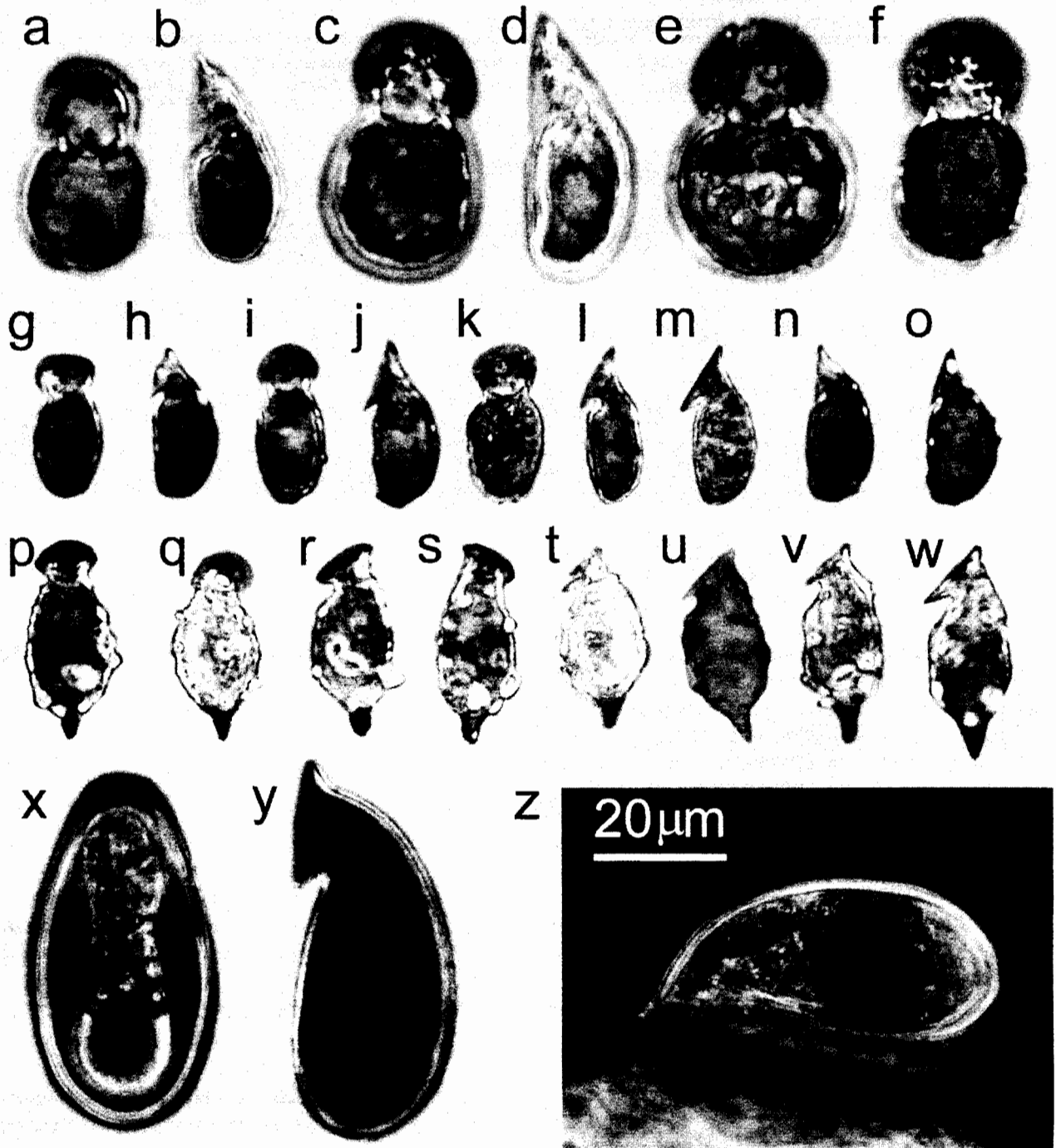
*Psammonobiotus communis* Golemansky, 1967; Figs. 2a, 2b, 3a-f

Of the three *Psammonobiotus* species found, *P. communis* was the most common with occurrences in all of the Great Lakes. More specifically, it was

present at two locations in Lake Superior, six locations in Lake Huron, four locations in Lake Erie, and five locations in Lake Ontario (Table 1). Possibly more than one hundred specimens of *P. communis* were observed, many of which were living specimens with active filopods. Measurements of 20 specimens (Table 2) from a single location (Rondeau Bay, Lake Erie) were believed representative of the species from other locations harboring this species. Relatively small ranges separated the minima and maxima of test lengths, widths, heights, and L-to-W ratios of the Rondeau Bay specimens; coefficients of variation for these four test dimensions were all low, ranging between 5.3 and 8.5% (Table 2). The most obvious component of variability was the shape of the aboral region of the test in ventral and/or dorsal views. In most specimens, this portion of the test was slightly elliptical in outline, being longer than wide; however, occasional tests were found with an aboral test section that was nearly circular in outline (compare Figs. 3e and 3f).

*Psammonobiotus* sp #2; Figs. 2c-h, 3g-o

This species was much more difficult to detect than *P. communis*, owing to its small size. Measurements of 47 specimens (Table 2) revealed median test length, width, and height of only 23, 11, and 10  $\mu$ m, respectively. Measurements were made on two widely separated populations, one at Provi-



**FIG. 3.** Digital images showing the range of form in four species of psammobiont testate rhizopods found in the Great Lakes. *a-f*: *Psammonobiotus communis* in ventral views (*a, c, e* and *f*) and lateral views (*b* and *d*); note that *a* and *b* represent different views of the same specimen, as do *c* and *d*. *g-o*: *Psammonobiotus* sp. # 2 in ventral views (*g, i* and *k*) and lateral views (*h, j* and *l-o*); *g* and *h* represent the same specimen as do *i* and *j*. *p-w*: *Psammonobiotus linearis* in ventral views (*p* and *q*) and lateral views (*r-w*). *x-z*: *Corythionella golemanskyi*. (*x*), living specimen in ventral view showing typical hour-glass-like shape of the cytoplasm of a cell preparing for encystment; (*y*), test in lateral view; (*z*), living cell showing ventral attachment to a sand grain. The scale bar applies to all images, *a-z*.

**TABLE 1.** Distribution of four psammobiotic species of testate rhizopods in the Great Lakes. The location codes refer to Figure 1.

Location code	<i>Psammonobiotus communis</i>	<i>Psammonobiotus</i> sp. # 2	<i>Psammonobiotus linearis</i>	<i>Corythionella golemanskyi</i>
2	✓			
6	✓	✓		
9	✓	✓		✓
16				✓
18	✓			✓
19	✓			✓
20	✓			
21	✓	✓		✓
22	✓	✓		✓
23	✓	✓	✓	
24	✓			✓
27	✓			
28	✓	✓		✓
29	✓			
30	✓			
32	✓	✓		✓
33				✓
34	✓	✓		
35	✓	✓		
36			✓	

dence Bay, and the other at Rondeau Bay in Lake Erie (sampling locations 9 and 23 in Fig. 1). Mann-Whitney *U*-tests revealed a high likelihood of no significant differences (two-tailed tests,  $P > 0.05$ ) between the lengths, widths and heights of the tests in the two populations, but the L/W ratios of the two populations, although very similar (medians of 2.18 and 2.09 for those from Rondeau Bay and Providence Bay, respectively), were significantly different ( $P = 0.013$ ).

In addition to its much smaller size, *Psammonobiotus* sp. # 2 has a median length-to-width ratio that averages about 20% greater than that for *P. communis*, a manifestation of its more narrow, oblong shape in both dorsal views (Figs. 2f–h, 3g, 3i, and 3k) and in lateral views (Figs. 2c–e, 3h, 3j, 3l–o). The oral aperture (pseudostome) is at the end of a bent neck-like anterior extension of the test and is surrounded by a flared collar (Figs. 2c, 2f). In lateral view, the angle of the plane of the pseudostome collar ranges from near zero degrees (i.e., it is parallel to the long axis of the test), through angles of 20–30° to a maximum of about 45° (compare e.g., Figs. 3n and 3m).

Specimens fitting our description of *Psammonobiotus* sp. #2 were reported by Golemansky (1973) from samples of beach sand collected in 1969 in the Baltic Sea. There have been no other reports of this

taxon in the intervening three decades (V. Golemansky, Zoological Institute, Sofia, Bulgaria, personal communication, 14 December 2002).

*Psammonobiotus linearis* Golemansky, 1971;  
Figs. 2i–l, 3p–w

This is a highly distinctive species, the only one of the nine known *Psammonobiotus* species with a posterior “tail;” it was found only at the eastern end of Lake Ontario (our location # 36) and in Rondeau Bay of Lake Erie (location # 23). Specimens showed a propensity to accumulate some remarkably large irregularly shaped particles on their tests (Figs. 3p, 3r, 3v). Although few in number, there was no apparent preferred location on the tests for these to appear. The overall effect was to lend a “camouflaged” appearance to tests of this species that made detection difficult owing to the distorted outlines of tests possessing these large particles, especially when such tests were accompanied in the microscope field of view by similarly sized bits of detritus. The posterior tail was nearly always well developed (Figs. 2i–k) with the exception of just a couple of specimens that lacked a typical tail and whose aboral extremity of the test could best be described as “pointed” (Fig. 2l).

**TABLE 2.** Descriptive statistics for critical test dimensions of the three *Psammobiotus* species found in the Great Lakes beach sand samples. Units of measurement are  $\mu\text{m}$ ; L = length; W = width; H = height (see Fig. 2). St. dev. = standard deviation; co.var (%) = coefficient of variation (%).

	<i>P. communis</i> (location # 23)				<i>P. sp. # 2</i> (location # 23)				<i>P. sp. # 2</i> (location # 9)				<i>P. linearis</i> (location # 36)			
	L	W	H	L/W	L	W	H	L/W	L	W	H	L/W	L	W	H	L/W
mean	34.5	19.4	14.9	1.78	23.3	10.6	10.2	2.21	23.5	11.3	10.5	2.09	28.4	13.2	12.9	2.15
median	35	19	15	1.83	23	11	10	2.18	23	11	11	2.09	28	13	13	2.17
minimum	31	18	13	1.55	22	9	9	1.83	22	10	9	1.71	26	12	12	1.73
maximum	37	22	17	1.94	25	12	11	2.56	27	14	12	2.36	32	15	14	2.5
st. dev.	1.79	1.14	1.25	0.12	0.97	0.72	0.57	0.17	1.67	1.12	0.93	0.14	1.71	0.89	0.65	0.18
co.var.(%)	5.26	5.96	8.51	6.67	4.22	6.88	5.73	7.63	7.17	10.0	8.97	6.61	6.12	6.80	5.15	8.66
N	20	20	20	20	23	23	23	23	24	24	24	24	21	21	21	21

Note: the values of the mean, median, minimum, maximum, st. dev. and co.var (%) for the original measurements of the *Psammobiotus* sp. # 2 tests in the two populations combined (N = 47) were as follows: for L, 23.4, 23, 22, 27, 1.36, 5.85; for W, 11.0, 11, 9, 14, 1.0, 9.17; for H, 10.3, 10, 9, 12, 0.79, 7.66; and for L/W, 2.15, 2.2, 1.17, 2.56, 0.16, and 7.56

## DISCUSSION

Compared to marine beaches, the sand beach biotope of the Great Lakes apparently contains relatively few psammobiont testate rhizopods. Our investigation revealed just four species: *Psammobiotus communis* Golemansky, *Psammobiotus* sp. # 2, *P. linearis* Golemansky, and *Corythionella golemanskyi* Nicholls. *C. golemanskyi* is the only known exclusively freshwater psammobiotic species of *Corythionella* (Nicholls 2003b); all five other known species are marine-brackish water. In contrast, the beaches of coastal Japan contain at least 21 genera (Sudzuki 1979a, b); but not including genera such as "Micramphoraopsis," "Pseudocyphoderia," "Pseudowallesella," "Corythionelloides," and "Micropsammeloides" which were described rather superficially (Sudzuki 1979b) and which await more critical study before authentication. Similarly, the total testate amoeban beach fauna of the Baltic Sea included 23 genera and 51 species (Golemansky 1998a), while similar investigations of the Mediterranean revealed 57 species, of which 29 were psammobionts (Golemansky 1990). Understandably, smaller, more localized areas of marine beach habitat hold fewer taxa. Ogden and Coûteaux (1989) found seven genera and 11 species at locations on the east coast of England, and Vucetich and Escalante (1983) found 11 species in six genera in beach sand near Buenos Aires, Argentina. Other similar examples include Golemansky's (2000) find of 11 species in nine genera in samples from two sand beaches near Rio de Janeiro, Brazil. In a summary of the knowledge

of marine sand-dwelling testate rhizopod community structure, Chardez and Lambert (1981) identified 28 genera and 66 species as characteristic of the world's beaches.

The morphology of Great Lakes specimens of *P. communis* was very similar to those observed in a collection of specimens from the Black Sea received in December, 2002 from Dr. V. Golemansky of Sofia, Bulgaria. Test morphology was also in good agreement with most descriptions of this species from other marine and brackish-water habitats from other parts of the world, although a considerably wider range of test size apparently exists in some other locations. For example, Golemansky (1970a) provided a test length range of 28–50  $\mu\text{m}$  for the Black Sea, but only 23–25  $\mu\text{m}$  for Cuba. The only other reports of this species from the western hemisphere are from the west coast of Canada (Golemansky 1971; test lengths = 33–44  $\mu\text{m}$ ), from coastal Argentina (Vucetich and Escalante 1983; test lengths = 38.4–49.2  $\mu\text{m}$ ), and from the southwest Atlantic near Rio de Janeiro (Golemansky 2000; no test sizes given). Test lengths of specimens from the Antarctic were 30–42  $\mu\text{m}$  (Golemansky and Todorov 1999). Incidentally, the specimen represented in Figure 3e, from our location #22 in Lake Huron, with a width of 26  $\mu\text{m}$ , was the widest one observed, but it was not one of the 20 individuals measured for statistical representation and so was not included in our Table 2 summary of test morphology for this species.

*P. linearis* has a more limited world distribution than *P. communis* and descriptions of test shapes and sizes are limited to just three reports. Gole-



mansky (1970b) provided the original description of specimens from the Black Sea that included test length, width, and height measurements of 21–24  $\mu\text{m}$ , 10–12  $\mu\text{m}$ , and 7–9  $\mu\text{m}$ , respectively. Subsequently, Golemansky (1973) gave similar measurements for specimens from the Polish coast of the Baltic Sea (21–24, 9–11, and 8  $\mu\text{m}$ , respectively). Although there are nine other published occurrences of this species from many different localities, only Chardez and Thomas (1980) included a drawing of a test and provided measurements of test length (16–17  $\mu\text{m}$ ) for specimens from the French Atlantic (Bay of Biscay region). Because of the much smaller size and an apparently atypically large pseudostomal collar relative to the oral aperture (their Fig. 8), there is some doubt as to whether or not the Bay of Biscay taxon is really *P. linearis*. It was with some hesitation that our Great Lakes specimens were assigned to *P. linearis*, because they all had greater test lengths than Golemansky's original material. But, in other respects, notably the posterior tail of the test and the absence of more data on sizes of specimens in other populations that would improve our understanding of the range in form and size, *P. linearis* appears to be the most appropriate name for our material at the present time.

Although no quantitative estimates were made, the largest populations of psammobiont testate rhizopods in our Great Lakes samples developed in Lake Huron and Rondeau Bay (Lake Erie) samples. Only a few specimens were encountered in samples from Lake Superior beaches. These, and the other Lake Superior samples where *P. communis* was not found, were the "cleanest" of all the Great Lakes samples. It is possible that there is a limited supply of suitable food (bacteria, other particulate organic materials) to allow development of detectable populations of *P. communis* and other related species in this lake. Its absence from central Lake Erie may relate to an observed preponderance of very fine clay particles in the beach sands at these locations owing to ongoing erosion of the bluffs on the north shore of central Lake Erie. Grain size in beach sands is critical, as it determines interstitial water movement and the supply of dissolved oxygen—two factors important in the establishment and survival of sand-dwelling rhizopods (Golemansky 1994a). Further investigations of psammobiont rhizopods in the Great Lakes should attempt to relate distribution and abundance of species to these physical-chemical variables.

Of the three *Psammobiotus* species found in

the Great Lakes, only *P. communis* was known previously from freshwater—Lakes Ohrid and Prespa in Macedonia where it is thought to be a marine relict (Golemansky 1967, 1994b); these ancient lakes are considered to have had preglacial links to the Sarmatian Sea (Naumoski 1990). *P. communis* has a wide range of salinity tolerance, from 35–37‰ on the east coast of England (Ogden and Coûteaux 1989) to that in oligotrophic Lake Ohrid which has only negligible salinity (Stanković 1960). There is no evidence that the Laurentian Great Lakes were saline at any point in their geologic history (Reid and Orlova 2002). Present-day levels of chloride and specific conductance in the Great Lakes range from 2 to 24 mg/L and from 100 to 320  $\mu\text{mhos/cm}$ , respectively (Ontario Ministry of the Environment, unpublished). Populations of *Psammobiotus communis* now resident in the Great Lakes clearly exist in freshwater habitats.

Similar euryhaline tendencies are evident for *P. linearis*. Its distribution includes locations with salinities near full-strength sea water, such as the Turkish Sea of Marmora with a salinity of 31‰ (Golemansky 1998b), and the Gulf of Aber in the French Atlantic near Roscoff with a salinity of 26‰ (Golemansky 1992) to low salinity locations such as the Russian Baltic coast (Finn Bay) with a salinity of 1.7‰ (Golemansky 1983). Less is known of the salinity tolerances of *Psammobiotus* sp. # 2. Its original discovery on the Polish Baltic Sea coast, and only known location outside of the Great Lakes, was at a location with a salinity of only about 2‰ (Dr. V. Golemansky, Zoological Institute, Sofia, Bulgaria, personal communication, 14 December 2002). Like *P. communis*, its widespread occurrence in the Great Lakes suggests that it can adapt well to freshwater habitats.

The requirement for a wide salinity tolerance has been recognized as a prerequisite for species of Ponto-Caspian origin (endemic to the Black, Caspian and Azov Seas) that are potentially invasive in the North American Great Lakes (Ricciardi and MacIsaac 2000, Reid and Orlova 2002). The euryhaline eco-physiology of these *Psammobiotus* species together with their microscopic size suggests a certain ease of translocation from their nascent habitats. Both *Psammobiotus communis* and *P. linearis* were originally described from the Black Sea and nearby waters (Golemansky 1967, 1970a). The only previous report of *Psammobiotus* sp. # 2 was from the Baltic Sea (Golemansky 1973, as *Psammobiotus* "sp."). Reid and Orlova (2002) have described the geologic and evolution-



ary history of Ponto-Caspian species and their selection for euryhalinity over hundreds of thousands of years. Their account of geologic, bioevolutionary, and human societal change in the region can explain why *P. communis* is found in the ancient Lakes Ohrid and Prespa (Golemansky 1994b) near the Black Sea. The extensive development and use of Eurasian shipping canals during the past several centuries has served as invasion corridors for Ponto-Caspian species establishment in the Baltic Sea. More recently, the development of maritime commerce, and specifically the completion of the St. Lawrence Seaway in 1959, has facilitated the trans-Atlantic transfer of nonindigenous species in ships' ballast water from both the Baltic and North Seas and possibly the Black Sea (Reid and Orlova 2002). Given the occurrence of *Psammonobiotus* species in the Black Sea and in other marine and brackish water systems, and the well-established euryhalinity of these species, the three species found in the Great Lakes may have originated in the Ponto-Caspian basin. That these species may have been introduced directly into the Great Lakes in ships' ballast water in relatively recent times is also possible, given the large number of Ponto-Caspian taxa that arrived here by that means (Ricciardi and Rasmussen 1998, Ricciardi and MacIsaac 2000). It is also possible that gulls and other aquatic birds may have introduced these testate rhizopods from the Atlantic seaboard at any time during the post-glacial history of the Great Lakes.

The discovery of just three euryhaline psammonobionts in the Great Lakes is surprising, given the diversity of genera and species with similar environmental tolerances in the Ponto-Caspian region and their widespread occurrence at other marine/brackish water beach locations. This pattern might suggest that *Psammonobiotus* species in the Great Lakes may have arrived relatively recently and that other species of these and related genera have yet to become established.

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