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ORIGINAL PAPER

Ecology of testate amoebae (thecamoebians) in subtropical Florida lakes

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Abstract Fifty-seven surface sediment samples from 35 Florida lakes were collected to study testate amoebae. Seven genera, 17 species, and 28 strains were identified in the 46 sediment samples from 31 lakes that contained testate rhizopods. Seven species accounted for ≥90% of the individuals in all samples. Sediment total phosphorus (TPsed), organic matter (OM), and total carbon:total nitrogen ratio (TC:TN) were measured to assess the effect of these variables on thecamoebian assemblages. OM content was the only sediment variable that influenced presence/absence of thecamoebians. Samples with <5% OM contained no thecamoebians. Lakes with multiple surface sediment samples showed high Morisita–Horn similarity values (0.74–0.99), indicating that all sites at which samples were collected in a lake provided representative thecamoebian assemblages. No relationship was observed between thecamoebian diversity indices and sediment variables. Lake trophic state and pH were examined to explore potential water column influences on thecamoebian communities. Highest thecamoebian diversity indices were found in mesotrophic to eutrophic lakes with pH near 8.0. These results suggest that water column conditions have a greater influence on thecamoebian assemblages than do sediment variables. We used multivariate analysis to evaluate the relations between water quality variables and testate rhizopod assemblages. Canonical correspondence analysis (CCA) showed that alkalinity and pH are the water column variables that most influence the relative abundance of species. Thecamoebians thus hold promise as bioindicators of acidification in Florida lakes. Thecamoebian remains in lake sediment cores should be useful to infer past anthropogenic shifts in lake pH.

Key words Testate amoebae · pH · Florida lakes · Water quality · Lake sediment

Introduction

Lacustrine and marine sediment cores have been used to study historical environmental changes brought about by natural processes and anthropogenic activities. Assessments of human impacts on aquatic biota are sometimes hindered by a lack of baseline studies

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on ecosystem variability, species diversity, and organism response to water quality changes and sediment alteration. Among the most common biological indicators in paleolimnological studies are the diatoms (e.g. Werner and Smol 2005), ostracods (e.g. Altinsacli and Griffiths 2001), chironomids (e.g. Zhang et al. 2007), cladocera (e.g. Bredesen et al. 2002) and pollen (e.g. Clerk et al. 2000). Other potentially useful microfossils have often been overlooked.

Testate amoebae, commonly called "thecamoebians" (e.g. Medioli and Scott 1983), are benthic organisms characterized by an agglutinated or autogenous shell in the form of a sack. Thecamoebians are generally present in peat deposits, sediments of freshwater lakes and rivers, and in some brackish water deposits (Medioli and Scott 1988). Testate amoebae can be very useful as environmental and paleoenvironmental indicators because of their high abundance and species diversity, widespread distribution, easy identification, and good preservation in sediments. Until recently, these microorganisms were neglected in both modern and paleoenvironmental studies despite their potential advantages over other bioindicator groups. For instance, thecamoebians may serve as reliable indicator species in low-pH environments where remains of other groups such as molluscs and ostracods tend to dissolve.

In the last three decades thecamoebian species assemblages have been used as bioindicators of: (1) sea level change (e.g. Scott and Medioli 1980; Charman et al. 1998; Scott et al. 2001), (2) paleohydrology and paleoclimate (e.g. Tolonen 1986; Warner and Charman 1994), and (3) limnological variables such as temperature, pH, oxygen concentrations, and heavy metal content (e.g. Reinhardt et al. 1998; Patterson and Kumar 2002). Most studies have focused on lakes from temperate latitudes. The few thecamoebian investigations in low-latitude lakes (e.g. Green 1963; Lena 1983) listed the taxa found, but paid little attention to the environmental controls on organism distribution. Clearly, further studies of thecamoebians in the tropics and subtropics are needed. Until more detailed calibration studies are completed, ecological and paleoecological interpretations remain tentative. Once the ecological requirements of modern thecamoebian taxa have been defined, it will be possible to use their

Fig. 1 Map of study area showing the location of the 35 study lakes

Table 1 Water quality data for the surveyed lakes

Lake	P (μg/l)	N (μg/l)	CHLA (μg/l)	pH	Cond (μS/cm)	Chlo (mg/l)	Talk (mg/l)	Ca (mg/l)	Na (mg/l)	SO_4 (mg/l)	Mg (mg/l)	K (mg/l)
AA	16	570	10.7	5.9	70	15.3	1.4	2.9	7.6	6.3	1.5	0.8
AB	5	373	3.6	5.8	40	7.8	0.6	1.6	3.8	5.4	0.7	0.7
AC	37	870	12.7	8.4	276	18.0	106.0	48.0	6.9	6.9	1.9	2.2
AD	3	182	1.3	5.8	18	3.2	1.4	1.1	1.6	5.4	0.2	0.3
AE	15	811	7.6	7.0	177	27.0	12.0	13.0	12.0	25.0	3.0	4.0
AF	39	2,256	74.2	8.7	293	26.4	104.9	32.7	13.6	14.0	30.8	6.0
AG	3	230	1.7	5.1	15	2.8	0.6	0.6	1.7	5.6	0.4	0.2
AH	26	3,317	5.6	6.7	102	24.3	5.5	4.8	11.0	7.5	1.2	1.0
AI	75	3,251	163.0	8.6	292	26.8	100.9	31.2	14.8	16.6	30.2	5.5
AJ	15	360	6.0	6.7	26	5.2	3.4	1.9	2.0	3.5	0.8	0.2
AK	35	1,851	66.8	8.6	257	19.6	101.0	31.6	10.1	10.2	19.1	3.2
BA	15	904	4.5	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
BB	8	219	3.2	4.8	37	7.0	0.0	N.D.	N.D.	N.D.	N.D.	N.D.
BC	100	1,300	77.0	7.4	152	N.D.	64.0	28.7	5.4	N.D.	4.7	1.1
AL	44	950	33.6	6.4	99	16.0	3.8	5.5	7.7	14.8	3.2	1.7
AM	9	339	1.7	6.1	148	24.4	1.8	8.2	12.3	23.0	5.9	0.8
AN	51	984	21.6	6.5	63	13.7	3.4	2.5	6.0	5.5	1.5	2.5
AO	59	2,356	106.9	7.4	90	11.6	24.4	9.7	6.1	3.9	5.1	0.4
AP	5	488	2.2	4.9	19	3.1	0.8	0.3	1.4	0.1	0.2	0.2
AQ	16	564	6.0	8.1	247	21.0	80.0	35.0	10.0	19.0	1.3	1.1
AR	121	3,561	233.7	6.9	67	11.4	12.4	5.7	6.8	3.8	6.9	0.4
AS	50	1,670	53.0	7.1	74	10.8	19.4	7.5	6.7	3.3	5.6	0.2
AT	28	745	12.2	8.3	259	10.5	102.9	40.3	5.7	23.1	16.6	0.2
BE	13	199	4.2	5.9	28	5.0	0.4	N.D.	N.D.	N.D.	N.D.	N.D.
BF	12	441	3.6	8.1	218	12.0	93.7	N.D.	N.D.	1.6	N.D.	N.D.
AU	11	429	6.7	5.9	60	12.7	1.8	2.5	7.3	6.1	2.7	0.6
AV	32	928	26.7	8.0	144	12.0	35.4	11.6	6.2	12.4	9.3	2.3
AW	11	754	11.4	7.1	168	30.1	19.7	4.0	16.8	8.4	14.8	2.0
AX	7	243	2.9	4.6	45	9.6	0.6	0.8	4.3	5.5	2.2	0.1
AY	25	1,506	35.1	8.3	284	26.4	114.8	27.4	20.1	7.0	45.2	3.6

Time frame for water data 1986-2001. Water data were obtained from the Florida Lakewatch database. Identification codes from lakes used in the multivariate analysis start with the letter "A". Abbreviations: N.D., no data. P, Phosphorus. N, Nitrogen. CHLA, Chlorophyll-a. Cond, Specific Conductance. Chlo, Chloride. Talk, Total alkalinity. Ca, Calcium. Na, Sodium. SO_4, Sulfate. Mg, Magnesium. K, Potassium. Lake abbreviations: Alto, AA; Annie, AB; Charles, AC; Compass, AD; Crystal, AE; Eustis, AF; Gap, AG; Green, AH; Griffin, AI; Hall, AJ; Harris, AK; Hunters, BA; Johnson, BB; Johnson Pond, BC; Josephine East, AL; Kerr, AM; Little Orange, AN; Lochloosa, AO; Loften, AP; Lutz, AQ; Newnans, AR; Okeechobee, BD; Orange, AS; Panasoffkee, AT; Pebble, BE; Saddleback, BF; Santa Fe, AU; Wales, AV; Weir, AW; Wildcat, AX; Yale, AY

well-preserved remains in fossil records to infer past environmental conditions and assess ecosystem change.

Little is known about the ecology of thecamoebians and their response to different limnological variables. When Tolonen (1986) reviewed the use of thecamoebians as lacustrine bioindicators, it was assumed that the principal environmental control on species distribution was trophic state acting through the influence of the C:N ratio, grain size, oxygen concentration and surrounding vegetation. Recent work however, has suggested that thecamoebian response to environmental variables may be more complex. They may be sensitive to pollution (e.g. arsenic, mercury), pH, and temperature changes (e.g. Patterson et al. 1996; Reinhardt et al. 1998).

Therefore, this study addresses the geographic distribution and ecology of thecamoebians in subtropical Florida lakes.

Study sites

Despite the large number (~7,800) and diversity of lakes in Florida, few thecamoebian studies have been carried out in the state. Lena (1982, 1983) studied the taxonomy and distribution of thecamoebians in several Florida water bodies and showed that species assemblages are related to substrate type and water depth rather than temperature, with highly organic sediments displaying greater thecamoebian abundance and diversity. The testacean fauna from these Florida water bodies did not differ from assemblages found in lakes of other regions (i.e. Canada) with similar substrates. Collins et al. (1990) studied the thecamoebian assemblage from southern Florida, on the border of the outer coastal plain and the Everglades. Based on their findings and comparisons with other thecamoebian assemblages from the eastern North American coast, they concluded that modern thecamoebian distribution can be linked to climate conditions, which in turn control limnological variables such as water level, water chemistry, and trophic state.

Only one thecamoebian-based paleoecological study has been conducted in Florida (Schrumm 2001). The objective of that study was to examine whether thecamoebians could be used as indicators of the marine/freshwater transition in south Florida. Results showed that thecamoebians could be used to detect fine-scale environmental changes in mangrove peat environments.

For this study we collected 57 surface sediment samples from 35 north and central Florida lakes (Fig. 1) that display a broad range of physical and chemical variables. Water chemistry data (Table 1) were obtained from the Florida Lakewatch database (Florida LAKEWATCH 2002, 2006). Study lakes were chosen to reflect a broad range of limnological characteristics, from acidic, ultra-oligotrophic water bodies, to alkaline, hypereutrophic lakes (Table 2). Florida displays high diversity with respect to lake water variables, making it an excellent natural laboratory for investigating potential bio-indicators, and providing opportunities to develop limnological calibration studies and carry out paleoenvironmental research.

Table 2 Classification of calibration lakes with respect to mean water column total phosphorus and pH

pH	Trophic state (TP µg/l)				
	Ultraoligo 0–5	Oligo 5–10	Meso 10–30	Eu 30–60	Hypereu >60
Alkaline			Saddleback	Wales	Griffin
>7.5			Lutz	Harris	
			Yale	Charles	
			Panasoffkee	Eustis	
Circumneutral			Weir	Orange	Newnans
6.5–7.5			Crystal	L. Orange	Johnson Pond
			Hall	Lochloosa	
			Green		
Acidic	Gap	Wildcat	Santa Fe	Josephine East	
<6.5	Annie	Kerr	Alto		
	Loften	Johnson	Pebble		
	Compass				
N.D.			Hunters		

Abbreviations: N.D., no data. Ultraoligo, Ultraoligotrophic. Oligo, Oligotrophic. Meso, Mesotrophic. Eu, Eutrophic. Hypereu, Hypereutrophic

Methods

Field sampling

Surface sediment samples were collected in 2003 and 2004 with an Ekman dredge. Topmost sediment (0–2 cm) in each sample was removed for micropaleontological analysis. These uppermost sediments are thought to represent the last 2–10 years of deposition based on ^{210}Pb dating of cores from Florida basins (Brenner and Binford 1988). Sample locations within each lake were determined with a hand-held Global Positioning System and bathymetric maps from Florida Lakewatch (Florida LAKEWATCH 2002, 2006). Multiple samples (21 total) were collected from six morphometrically diverse lakes to test the spatial homogeneity of thecamoebian assemblages in each basin.

Laboratory methods

Sediment sub-samples of 10-cm^3 wet volume were prepared for thecamoebian counting. Sub-samples were sieved through a 707-µm screen (sieve # 25) to remove coarse particles and through a 53-µm screen (sieve # 270) to retain thecamoebians. The smallest (<53 µm) walled rhizopods were lost during the sieving process and were not counted in this study. Each sediment fraction between 707 µm and 53 µm was subdivided into aliquots using a wet splitter (Scott and Hermelin 1993), preserved with isopropyl alcohol, and stored wet at 4°C. Wet aliquots were examined under a stereomicroscope until at least 300 thecamoebians per sample were identified. Both living and dead thecamoebians were counted. Because of their rapid generation time of several days, assemblages provide an accurate estimate of recent community composition (Scott and Medioli 1983; Medioli and Scott 1988). Medioli and Scott (1983), Kumar and Dalby (1998) and Reinhardt et al. (1998) were used as key taxonomic references. A complete list of taxonomic references used in this study can be found in the appendix.

Sediment chemical analysis

Wet 5-g sub-samples were used for sediment chemical analyses. Sub-samples were freeze-dried and crushed with a mortar and pestle. Total carbon:total nitrogen weight ratio (TC:TN) was measured using a Carlo Erba NA 1500 C/N/S analyzer. Total phosphorus in sediments (TPsed) was analyzed by combining 20 ml of 0.53 M sulfuric acid and 10 ml of 0.062 M potassium persulfate with a weighed amount of dry sediment between 0.0425 and 0.0525 g. Samples were sonicated for 10 min and placed in an autoclave for 35 min at 100°C. Finally, 10 ml of 0.1325 N NaOH was added to each sample before centrifuging at 1500 revolutions per minute (rpm). Total P in solution was measured on a Bran–Luebbe Autoanalyzer. Total organic matter (OM) content in sediments was estimated by weight loss on ignition (LOI) (Håkanson and Jansson 1983).

Water chemistry

Water quality data (i.e. total phosphorus, total nitrogen, chlorophyll *a*, pH, conductivity, chloride, total alkalinity, calcium, sodium, sulfate, magnesium, potassium) used in this study were obtained from the Florida Lakewatch database, in which detailed descriptions of analytical methods can be found (Florida LAKEWATCH 2002, 2006).

Numerical analyses

The Shannon–Wiener diversity index (*H*') was calculated on all samples containing testate rhizopods. This index assumes that all individuals are represented in the sample and are randomly sampled from an "infinitely large" population (Magurran 1988). Shannon–Wiener diversity values usually fall between 1.5 and 3.5 (Margalef 1972). Diversity index data were correlated with both sediment and water variables.

The Morisita–Horn similarity index was calculated to test the homogeneity of thecamoebian assemblages in lakes from which multiple surface sediment samples were collected. This index assesses the similarity of two compared samples with respect to both the number and relative abundance of species (e.g. Wolda 1981). The index value equals 1 in cases of perfect similarity (i.e. the same species and equal relative abundance of each species in the two samples) and is 0 if the two compared assemblages have no species in common.

Table 3 Thecamoebian occurrences in samples from Florida lakes

Lake counts(%)	AA	AB	AC	AD	AE	AF	AG	AH(1)	AH(2)	AH(3)	AI	AJ	AK	BA(1)	BA(2)	BA(3)
arcvulg	7.0		5.7		0.7											2.0
arcdent			0.3								0.3					0.7
ceimpre														0.3	0.3	
ceacuac		32.7	24.0	44.0	3.3	10.0	14.7	1.7	4.0	1.7	39.3	24.0	20.3	3.3	3.0	20.7
ceacudi			0.3	0.3												
ceconae		2.0			1.7											
ceconco		1.7	2.0	1.0	12.0	38.7	2.7	7.3	9.0	9.3	3.0	1.0	21.3	46.0	48.7	23.7
lespira	27.0	23.0	1.3	14.0	9.0	1.3	5.0	9.0	7.0	6.7		10.0	10.3	4.0	4.7	8.0
cucutri	42.3	14.0	16.3	10.3	27.0	4.0	2.3	49.7	47.0	38.7	14.3	24.7	7.0	19.0	8.7	13.0
diproam	8.7	1.3	29.0	5.0	6.7	7.0	5.0	2.3	7.0	4.7	18.7	13.0	17.3	7.0	14.0	4.7
diprocl																
diproac		2.3	6.7	7.7	7.7	0.7	11.0	6.7	5.7	9.0	1.3	4.7	2.7	1.0	0.7	4.0
diurcur		0.3	0.7		1.7	7.0	0.3		1.7	0.7		0.7	4.0	3.0	3.3	1.7
diurcel														0.3		
dioblla								0.3								
dioblli	1.7		4.3		0.3	1.0	1.0	7.0	5.0	5.7		0.3				
dioblgl		13.3									18.7	7.0	5.7			
dioblob	12.0	3.3	7.0	17.0	18.3	27.0	54.7	5.3	3.3	8.7	0.3	9.0	10.7	12.0	10.3	10.7
dioblte						2.7	2.7	4.3	1.0	1.7						
dioblbr					2.3		0.7	0.7		1.0				0.3	0.3	
dioblsp			2.0		0.7			1.3		0.7						0.3
diobltr				0.7	1.0			2.3	1.0	1.7				0.7		
diurens								0.3	0.3							
dicoron	1.3	1.3	0.3		5.0	0.7		1.7	8.0	10.0	3.7	5.3	0.7	3.0	6.0	10.7
difrafr											0.3	0.3				
diflspy					1.3											
euacant		3.7														
necarin		1.0														
incersp					1.3											

Lake counts(%)	BB	BC(1)	BC(2)	BC(3)	BC(4)	BC(5)	AL	AM	AN	AO	AP	AQ	AR	BD(1)	BD(K8)	BD(Kr)
arcvulg	1.0	0.7	0.3			1.7				4.0		0.3	5.3			
arcdent			0.3						0.3							
ceimpre																
ceacuac	5.7	24.0	13.3	15.7	21.3	37.0	10.0	0.7	20.3	24.0	7.0	8.3	36.7	15.7	25.3	9.0
ceacudi			0.7						2.3	4.3	0.7		0.7			
ceconae												3.0		6.0	1.7	7.7
ceconco	1.7	1.0					0.3		5.3	5.0	20.3	6.3	1.3	12.3	5.3	13.7
lespira	7.0	2.3	0.3		0.3		13.3	3.0	7.0	1.7	10.0	7.7	6.7			
cucutri	40.3	32.7	75.7	73.3	68.3	24.0	57.0	44.7	28.3	36.3	7.7	22.3	32.0	4.7	0.3	2.0
diproam	3.3	1.3	2.0	0.7	1.0	0.3	13.7	7.0	5.0	16.0	7.3	24.7	14.0	25.7	18.7	41.7
diprocl						0.3										
diproac	1.0	5.0	2.7	5.0	3.7	8.3	0.7	0.7		1.7	3.7	3.3	0.3	1.7	0.7	1.3
diurcur		6.3			0.3	2.0	0.3			1.7	2.7	0.7	0.3			
diurcel								3.0						0.7		
dioblla		0.7														
dioblli	6.7	5.0				0.3			0.3	1.0		1.7				
dioblgl	1.3							6.3						29.7	42.0	11.0
dioblob	28.7	13.3	1.0	1.0	1.3	11.7	2.7	34.7	29.0	2.7	40.0	11.0	0.7	3.7	5.0	13.3
dioblte		0.3														
dioblbr		0.3														
dioblsp		0.3										0.3				
diobltr												1.3				

Table 3 continued

Lake counts(%)	BB	BC(1)	BC(2)	BC(3)	BC(4)	BC(5)	AL	AM	AN	AO	AP	AQ	AR	BD(1)	BD(K8)	BD(Kr)
diurens											0.3	0.7				
dicoron		5.7	3.7	4.3	3.7	14.0			1.3	1.7	0.3	7.0	2.0			
difrafr							2.0								1.0	0.3
diflspy	1.0					0.3										
euacant																
necarin																
incersp	2.3	1.0							0.7			1.3				

Lake counts(%)	BD(M9)	BD(O11)	AS	AT(1)	AT(2)	AT(3)	BE	BF	AU	AV(1)	AV(2)	AW	AX	AY
arcvulg				1.0	1.0	0.3	2.3		1.0	7.7	3.7			
arcdent	0.3			1.3		0.7		0.7						0.3
ceimpre														
ceacuac	13.7	22.7	51.7	93.0	56.0	88.0	10.7	10.3	8.7	39.3	23.0	22.7	5.0	48.7
ceacudi														
ceconae	5.3	1.7			37.7	3.7		5.3						1.7
ceconco	15.0	4.7	9.0	1.3	2.7	3.3	2.3	10.0	1.3	3.3	5.0	1.7	0.3	26.3
lespira	0.3		3.0				4.0	2.7	31.0	5.0	5.3	12.3	9.7	2.0
cucutri		0.7	14.3				53.7	13.3	21.0	11.3	11.7	2.0	63.3	1.3
diproam	29.0	41.7	14.7	0.3	0.7		6.3	20.7	2.0	16.0	15.0	1.7	3.0	9.7
diprocl														
diproac	0.7		1.3	2.0	1.7	2.7		9.3	9.3	7.0	11.0	5.7		1.7
diurcur	0.3		0.3				2.0	8.7		1.3	7.0	1.7	0.7	1.7
diurcel											0.3			
dioblla									0.3					
dioblli							5.7	1.0	10.3	0.7	4.3			
dioblgl	28.3	26.7			0.3	0.7	0.3	1.3				3.0	4.3	2.0
dioblob	6.7	1.7	3.7	1.0		0.7	12.0	9.0	12.3	4.0	8.0	48.3	13.7	4.0
dioblte											0.3			
dioblbr								0.3		0.3	0.3			
dioblsp								1.3						
diobltr								0.3			1.0	0.3		
diurens							0.3			0.3				
dicoron			2.0				0.3	5.3	2.7	3.7	4.0	0.7		0.7
difrafr	0.3	0.3												
diflspy														
euacant														
necarin														
incersp								0.3						

Samples were quantitatively analyzed and are presented as fractional abundances. Abbreviations: *Arcella vulgaris*, ARCVULG; *Arcella dentata*, ARCDENT; *Centropyxis impressa*, CEIMPRE; *Centropyxis aculeata* "aculeata", CEACUAC; *Centropyxis aculeata* "discoides', CEACUDI; *Centropyxis constricta* "aerophila", CECONAE; *Centropyxis constricta* "constricta", CECONCO; *Lesquereusia spiralis*, LESPIRA; *Cucurbitella tricuspis*, CUCUTRI; *Difflugia protaeiformis* "amphoralis", DIPROAM; *Difflugia protaeiformis* "claviformis", DIPROCL; *Difflugia protaeiformis* "acuminata", DIPROAC; *Difflugia urceolata* "urceolata", DIURCUR; *Difflugia urceolata* "elongata", DIURCEL; *Difflugia oblonga* "lanceolata", DIOBLLA; *Difflugia oblonga* "linearis", DIOBLLI; *Difflugia oblonga* "glans", DIOBLGL; *Difflugia oblonga* "oblonga", DIOBLOB; *Difflugia oblonga* "tenuis", DIOBLTE; *Difflugia oblonga* "bryophila", DIOBLBR; *Difflugia oblonga* "spinosa", DIOBLSP; *Difflugia oblonga* "triangularis" DIOBLTR; *Difflugia urens*, DIURENS; *Difflugia corona*, DICORON; *Difflugia fragosa* "fragosa", DIFRAFR; Difflugia sp.Y (Green, 1962), DIFLSPY; *Euglypha acantaphora*, EUACANT; *Nebela carinata*, NECARIN; Incerta sp, INCERSP. Lake abbreviations: Alto, AA; Annie, AB; Charles, AC; Compass, AD; Crystal, AE; Eustis, AF; Gap, AG; Green, AH; Griffin, AI; Hall, AJ; Harris, AK; Hunters, BA; Johnson, BB; Johnson Pond, BC; Josephine East, AL; Kerr, AM; Little Orange, AN; Lochloosa, AO; Loften, AP; Lutz, AQ; Newnans, AR; Okeechobee, BD; Orange, AS; Panasoffkee, AT; Pebble, BE; Saddleback, BF; Santa Fe, AU; Wales, AV; Weir, AW; Wildcat, AX; Yale, AY. Numbers within parentheses designate sample number within the lake

Only 25 lakes had complete water chemistry data (Table 1) and were used for multivariate analysis. Both indirect and direct gradient analysis techniques were used to investigate relationships between sites (i.e. lakes), environmental variables, and thecamoebians. Species data were first subjected to detrended correspondence analysis (DCA) in an exploratory analysis. This indirect ordination method assumes a modal response of species distribution along environmental gradients, and it combines species data into linear ordination axes that best explain the variance among species. Canonical correspondence analysis (CCA), a direct ordination technique, was then used to determine the environmental factors that had a greater influence on thecamoebian assemblages.

Results and discussion

Fifty-seven sediment samples from 35 lakes were counted for thecamoebians. Seven genera, 17 species, and 28 strains (Table 3, Figs. 2 and 3) were identified in the 46 sediment samples from 31 lakes that contained testate rhizopods. Seven species accounted for >90% of the counts in all samples. We used the thecamoebian size fraction > 53 µm and < 707 µm. Although this size selection introduces some bias in evaluating the total testate rhizopod community, it allowed us to make comparisons with studies from temperate lakes, in which the focus has been on thecamoebians > 53 µm.

Most thecamoebian research in lakes has dealt with multiple samples from single lakes. These lakes have typically had a large surface area (e.g. Scott and Medioli 1983), complex morphometry (e.g. Scott and Medioli 1983), or had environmental degradation along one shore (Kumar and Patterson 2000). These spatially variable environmental conditions contribute to variable faunal composition from site to site within the lake. Most of the lakes in this study were small, shallow, and well mixed. The water bodies thus presented relatively homogenous environmental conditions. Nevertheless, multiple sediment samples from six lakes were collected to test the homogeneity of thecamoebian assemblages within lakes. Lowest Morisita–Horn similarity values were obtained from Lake Okeechobee and Johnson Pond (Table 4). Among the study basins, they displayed, respectively, the largest surface area (Okeechobee = 1,732km^2) (Beaver and Havens 1996) and greatest maximum depth (Johnson Pond = 17.5 m) (Whitmore et al. 1991). Other lakes showed high Morisita–Horn similarity values (0.74–0.99), suggesting that any site within those basins is suitable for collecting a representative thecamoebian assemblage.

Presence/absence and diversity of thecamoebians

Organic matter content in sediment emerged as the only variable that influenced presence/absence of thecamoebians in Florida lakes. All barren samples but the peaty Lake Okeechobee sample (M17) and the low-density Lake Wauberg sample contained <5% OM (Table 5). Organic-rich sites contained large numbers of thecamoebians, whereas sites characterized by sandy substrates yielded few or no thecamoebians. These results are similar to findings in high (Patterson and Kumar 2000) and low (Roe and Patterson 2006) latitude lakes, in which sandy substrates contained small, allochthonous thecamoebian assemblages.

Shannon–Wiener diversity index values ranged from 0.37 to 2.37 (Table 6). Thecamoebian assemblages from the tropics and subtropics have relatively low diversity index values. Shannon diversity values in Lake Sentani, Indonesia ranged from 0.65 to 1.44 (Dalby et al. 2000). Roe and Patterson (2006) reported diversity values from several ponds in Barbados ranging from 0 to 1.4. There was no significant relation between diversity index values and variables TPsed, OM or TC:TN. Lakes in this study with the highest diversity indices are in the mesotrophic to eutrophic range (Table 6, Fig. 4a). The relation between water column pH data and thecamoebian diversity index values shows a significant trend. The Shannon–Wiener diversity index is generally higher in alkaline waters compared to acid water bodies (Fig. 4b). Highest thecamoebian diversity index values ($\sim$2.5) occur at pH values close to 8.0. Few taxa are tolerant of low-pH environments. These data are consistent with results of Kumar and Patterson (2000) in James Lake, Ontario, Canada where highest diversity indices were found in near-neutral waters. These results, together with the lack of significant correlations between assemblages and sediment variables, suggest that although testate rhizopods are benthic microorganisms, water-column conditions strongly influence thecamoebian communities.

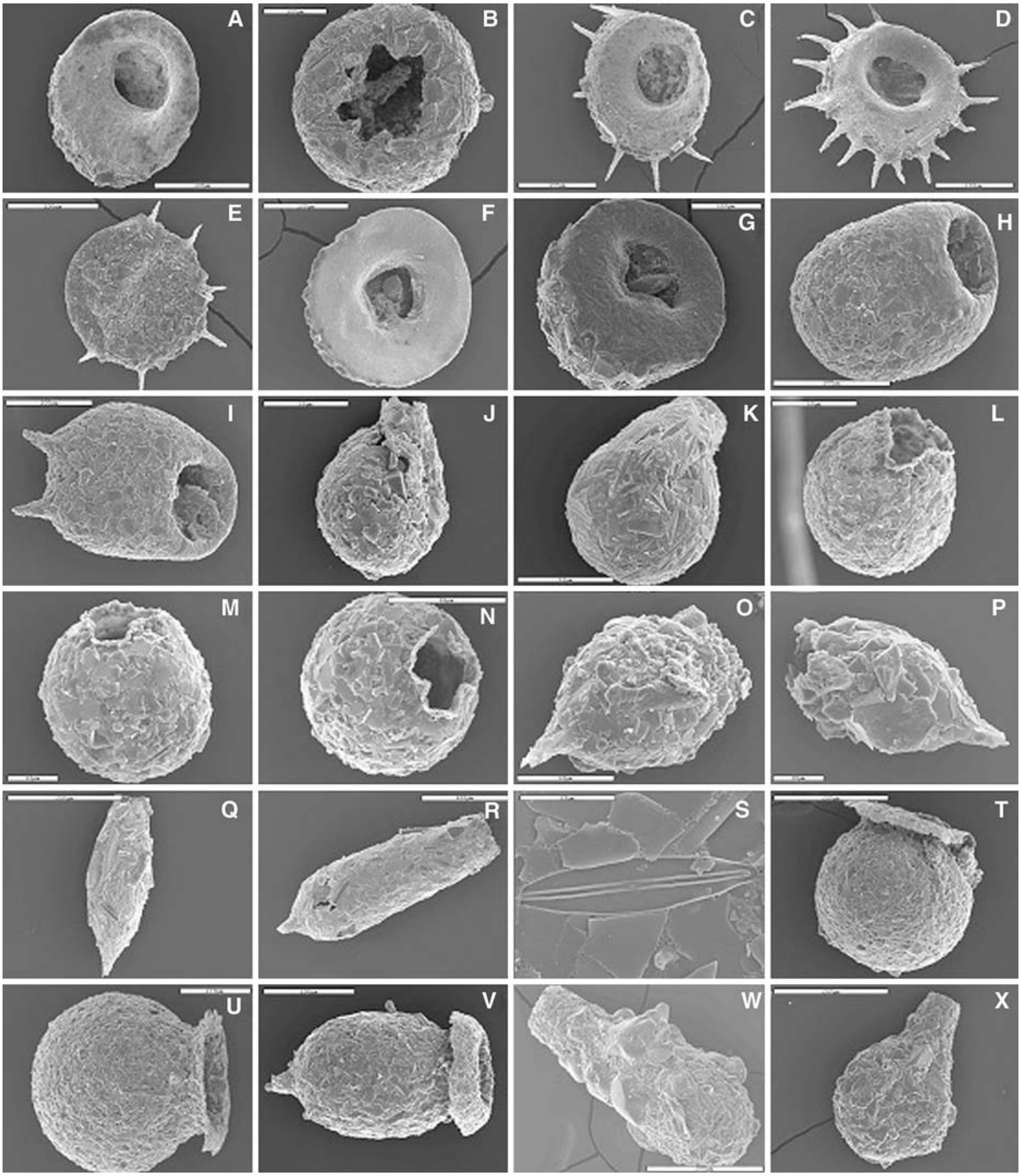

Fig. 2 SEM photographs of thecamoebian specimens from Florida Lakes. (**a**) *Arcella vulgaris;* Ehrenberg 1830. (**b**) *Centropyxis impressa;* Daday 1905. (**c**, **d**, **e**) *Centropyxis aculeata* "aculeata"; Ehrenberg 1832. (**f**, **g**) *Centropyxis aculeata* "discoides"; Ehrenberg 1832. (**h**) *Centropyxis constricta* "aerophila"; Ehrenberg 1843. (**i**) *Centropyxis constricta* "constricta"; Ehrenberg 1843. (**j**, **k**) *Lesquereusia spiralis;* Ehrenberg 1840. (**l**, **m**, **n**) *Cucurbitella tricuspis;* Carter 1856. (**o**, **p**) *Difflugia protaeiformis* "amphoralis"; Lamarck 1816. (**q**) *Difflugia protaeiformis* "claviformis"; Lamarck 1816. (**r**) *Difflugia protaeiformis* "acuminata"; Lamarck 1816. (**s**) Diatom frustule as part of a thecamoebian shell. (**t**, **u**) *Difflugia urceolata* "urceolata"; Carter 1864. (**v**) *Difflugia urceolata* "elongata"; Carter 1864. (**w**) *Difflugia oblonga* "lanceolata"; Ehrenberg 1832. (**x**) *Difflugia oblonga* "linearis"; Ehrenberg 1832

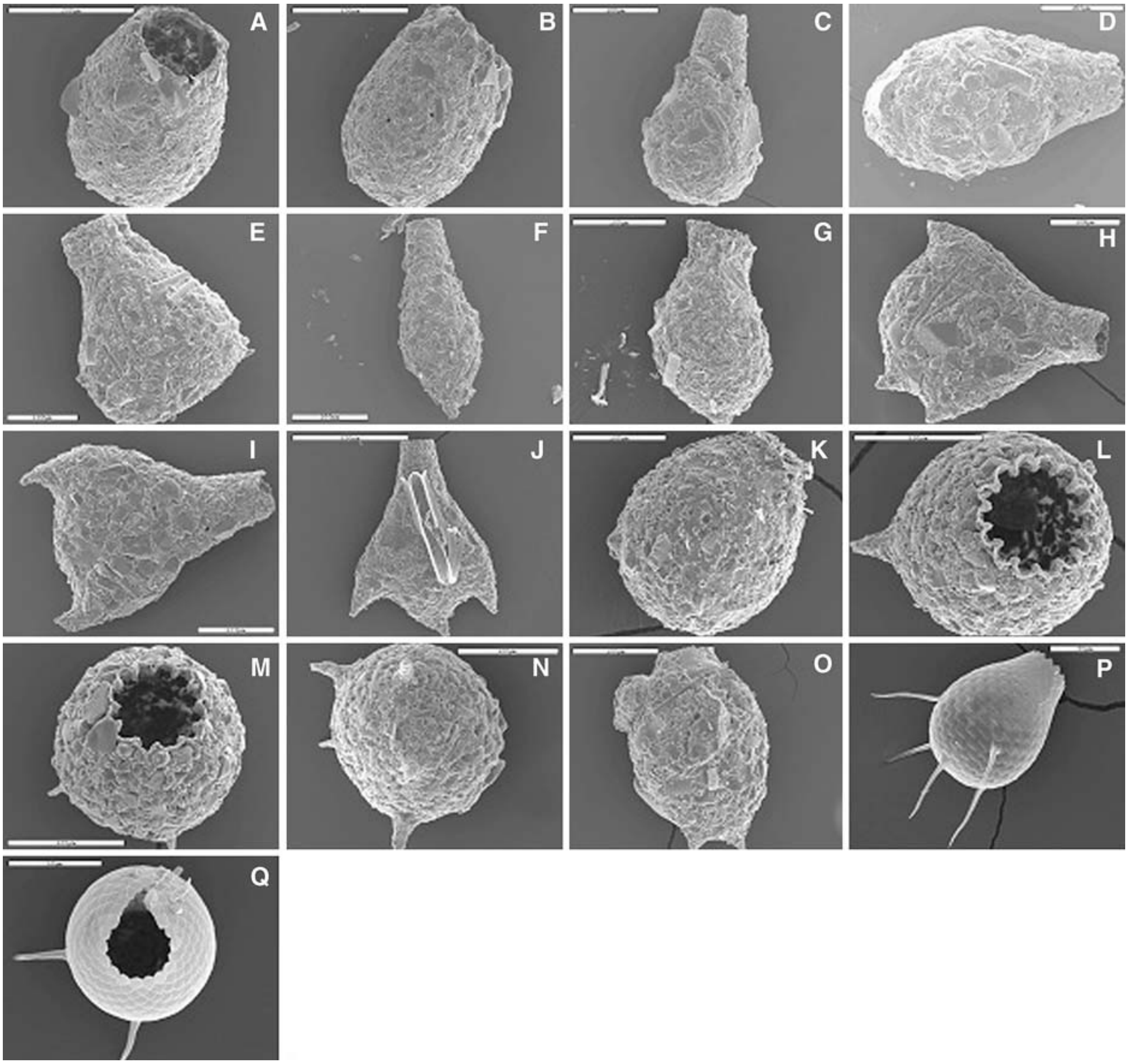

Fig. 3 SEM photographs of thecamoebian specimens from Florida Lakes. (**a**, **b**) *Difflugia oblonga* "glans"; Ehrenberg 1832. (**c**) *Difflugia oblonga* "oblonga"; Ehrenberg 1832. (**d**) *Difflugia oblonga* "tenuis"; Ehrenberg 1832. (**e**) *Difflugia oblonga* "bryophila"; Ehrenberg 1832. (**f**, **g**) *Difflugia oblonga* "spinosa"; Ehrenberg 1832. (**h**, **i**, **j**) *Difflugia oblonga* "triangularis"; Ehrenberg 1832. (**k**) *Difflugia urens;* Patterson et al., 1985. (**l**, **m**, **n**) *Difflugia corona;* Wallich 1864. (**o**) *Difflugia fragosa* "fragosa"; Hempel 1898. (**p**, **q**) *Euglypha acantaphora;* Ehrenberg 1843

Multivariate analysis

Twenty-five lakes had complete water chemistry data (Table 1) and were selected for multivariate analysis. *Difflugia protaeiformes* "claviformis", and *Centropyxis impressa* have been reported from only a few sites and in small numbers in tropical ecosystems (e.g. Green 1963, 1975). In this study the taxa were present in only one lake each and in low abundances, and were therefore omitted from the data set. Few specimens of *Euglypha acantaphora* and *Nebela carinata* were found in only one lake as well and were deleted to reduce the total variation in the matrix. This reduced the number of thecamoebian taxa to 24 strains.

Species ordination based on DCA shows that total alkalinity (0.94, $P < 0.01$) and pH (0.921, $P < 0.01$) are both strongly correlated with axis 1 (Table 7,

Table 4 Morisita–Horn (MH) similarity index for lakes with multiple sediment sampling sites

Samples	MH	Samples	MH	Samples	MH
Green (1-2)	98.0	Johnson pond (2-3)	99.8	Okeechobee (K8-011)	86.5
Green (1-3)	95.1	Johnson pond (2-4)	98.9	Okeechobee (K8-M9)	89.1
Green (2-3)	97.2	Johnson pond (2-5)	57.9	Okeechobee (Kr-K8)	62.6
Hunters (1-2)	96.8	Johnson pond (3-5)	61.2	Okeechobee (Kr-M9)	88.0
Hunters (1-3)	77.8	Johnson pond (4-5)	67.3	Okeechobee (Kr-O11)	87.1
Hunters (2-3)	74.7	Johnson pond (3-4)	99.5	Okeechobee (O11-M9)	92.4
Johnson pond (1-2)	72.1	Okeechobee (1-Kr)	82.8	Panasoffkee (1-2)	78.9
Johnson pond (1-3)	74.4	Okeechobee (1-K8)	92.0	Panasoffkee (1-3)	99.7
Johnson pond (1-4)	78.9	Okeechobee (1-M9)	98.6	Panasoffkee (2-3)	82.3
Johnson pond (1-5)	91.2	Okeechobee (1-O11)	91.7	Wales (1-3)	89.0

It equals 100 in cases of complete similarity and 0 if the assemblages have no species in common. Designations in parentheses are the sampling stations compared within a lake

Table 5 Thecamoebian presence/absence and percent organic matter for all surface sediment samples in this survey

Lake	%OM	P/A	Lake	%OM	P/A	Lake	%OM	P/A
Okeechobee (fc)	0.2	–	Okeechobee (K8)	28.3	+	Harris	56.9	+
Sheelar	0.4	–	Panasoffkee (2)	28.6	+	Alto (2)	57.9	+
Wales (2)	0.7	–	Okeechobee	32.3	+	Hunters (3)	58.0	+
Okeechobee (J5)	0.8	–	Okeechobee (O11)	35.3	+	Eustis	58.7	+
Okeechobee (J7)	0.9	–	Hall	37.7	+	Weir	59.0	+
Okeechobee (TC)	0.9	–	Lutz	38.0	+	Lochloosa	59.1	+
Hamilton (1)	3.2	–	Compass	38.7	+	Green (1)	59.4	+
Sampson	3.2	–	Johnson Pond (2)	40.5	+	Gap	60.3	+
Hamilton (2)	4.4	–	Johnson Pond (1)	40.6	+	Griffin	62.8	+
Santa Fe	12.7	+	Panasoffkee (3)	41.6	+	Yale	63.1	+
Johnson	17.6	+	Wales(3)	42.1	+	Loften	64.7	+
Okeechobee (M9)	17.9	+	Wales (1)	42.3	+	Okeechobee (M17)	65.7	–
Green (3)	18.6	+	Johnson Pond (4)	44.0	+	Orange (2)	67.4	+
Pebble	19.8	+	Johnson Pond (3)	45.7	+	Hunters (1)	68.3	+
Okeechobee (Kr)	21.0	+	Hunters (2)	45.8	+	Johnson Pond (5)	71.3	+
Kerr	21.8	+	Wildcat	46.8	+	Wauberg	72.4	–
Crystal	24.1	+	Green (2)	49.2	+	Little Orange	86.4	+
Saddleback	26.8	+	Annie	50.1	+	Charles	N.D.	
Panasoffkee (1)	27.7	+	Newnans	56.0	+	Josephine East	N.D.	

Data were sorted by percent organic matter in the sediment. Abbreviations: OM, organic matter; P/A, presence/absence; +, presence; −, absence

Fig. 5). Axis 2 is significantly negatively correlated with total phosphorus (−0.941, $P < 0.05$) and chlorophyll *a* (−0.797, $P < 0.1$) (Table 7, Fig. 5).

The ordination of species based on CCA shows that 68% of the variance in the testate rhizopod weighted averages is accounted for by the environmental data at hand (Table 8). There is little variation between CCA eigenvalues and those from the CA and DCA analyses. This suggests that the measured environmental variables explain the main gradients in the testate rhizopod data. Although the full CCA model is significant, only variables pH, total alkalinity, calcium, total phosphorus and chlorophyll *a* have a significant relationship with the species data (Table 9).

Tolonen (1986) made one of the first attempts to test the utility of thecamoebians as lacustrine bioindicators. Results suggested that major environmental variables controlling thecamoebian distribution were sediment C:N ratio, grain size, oxygen concentration, and surrounding vegetation. The present results together with other research (e.g. Patterson et al.

Table 6 Shannon–Wiener diversity index (*H*') values in lakes containing at least 300 testate rhizopods

Lake	*H*'	Lake	*H*'	Lake	*H*'
Alto	1.50	Johnson	1.72	Okeechobee(O11)	1.39
Annie	1.90	Johnson Pond(1)	1.97	Okeechobee(M9)	1.72
Charles	1.97	Johnson Pond(2)	0.91	Okeechobee(mean)	1.62
Compass	1.62	Johnson Pond(3)	0.88	Orange	1.50
Crystal	2.25	Johnson Pond(4)	0.97	Panasoffkee(1)	0.37
Eustis	1.72	Johnson Pond(5)	1.67	Panasoffkee(2)	0.96
Gap	1.53	Johnson Pond(mean)	1.28	Panasoffkee(3)	0.56
Green(1)	1.86	Josephine East	1.34	Panasoffkee(mean)	0.63
Green(2)	1.88	Kerr	1.37	Pebble	1.60
Green(3)	2.05	Lutz	2.19	Saddleback	2.37
Green(mean)	1.93	Little Orange	1.75	Santa Fe	1.91
Griffin	1.61	Lochloosa	1.83	Wales(1)	1.93
Hall	2.00	Loften	1.78	Wales(2)	2.30
Harris	2.04	Newnans	1.59	Wales(mean)	2.12
Hunters(1)	1.70	Okeechobee(1)	1.79	Weir	1.55
Hunters(2)	1.67	Okeechobee(Kr)	1.72	Wildcat	1.23
Hunters(3)	2.08	Okeechobee(K8)	1.50	Yale	1.53
Hunters(mean)	1.82				

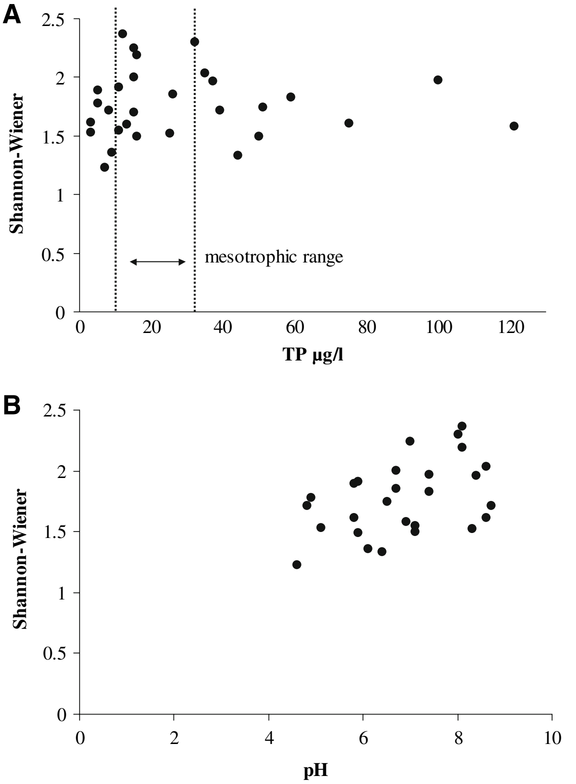

Fig. 4 Shannon–Wiener index in relation to (**a**) water column TP, (**b**) water column pH

Table 7 Characteristics of axes 1 and 2 and correlation coefficients following a detrended correspondence analysis

	DCA1	DCA2	r^2	Pr (>*r*)
Total phosphorus	0.336	−0.941	0.28	0.020
Total nitrogen	0.587	−0.808	0.1	0.285
Chlorophyll *a*	0.602	−0.797	0.24	0.060
pH	0.921	−0.388	0.34	0.010
Conductivity	0.802	−0.596	0.09	0.36
Chloride	−0.379	0.925	0.01	0.865
Total alkalinity	0.94	−0.34	0.35	0.005
Calcium	0.756	−0.654	0.25	0.050
Sodium	0.134	−0.99	0.01	0.88
Sulfate	0.162	−0.986	0.04	0.635
Magnesium	0.964	−0.263	0.17	0.13
Potassium	0.402	0.915	0.01	0.83

1996; Reinhardt et al. 1998; Kumar and Patterson, 2000) suggest that thecamoebian response to environmental variables might be more complex. Organic matter in sediments, pH, total alkalinity, limnetic total phosphorus, and chlorophyll *a* influence thecamoebian distribution in Florida lakes.

The species *Centropyxis aculeata* is adapted to both eutrophic (Asioli et al. 1996) and oligotrophic

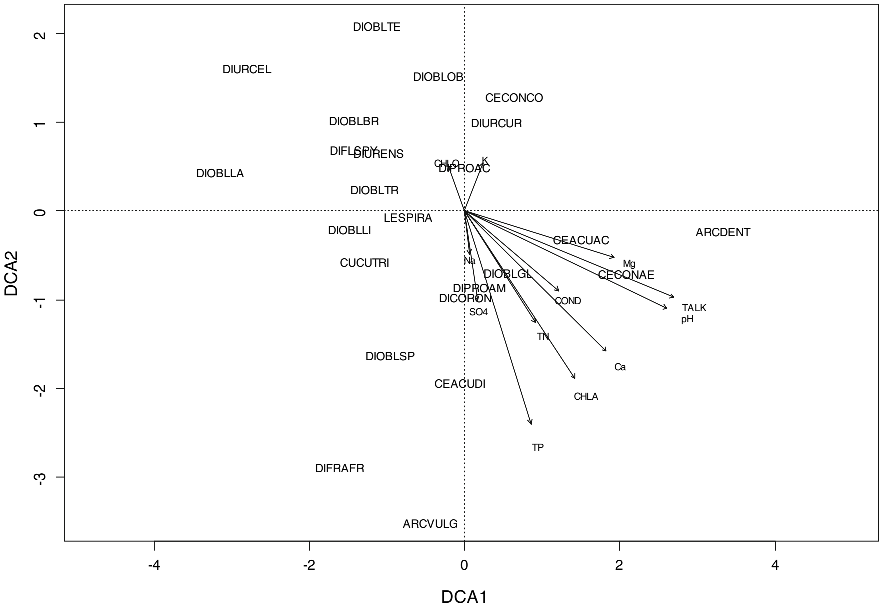

Fig. 5 Detrended correspondence analysis (DCA) for Florida thecamoebians and environmental variables (arrows)

Table 8 Axes comparison between a correspondence analysis, detrended correspondence analysis and canonical correspondence analysis

	CA (%)	DCA (%)	CCA		
			Total inertia 1.1221	Constrained 0.6817 (%)	Unconstrained 0.4405
Axis 1	25.73	25.49		21.13	
Axis 2	21.26	19.23		14.12	
Axis 3	12.14	11.95		6.42	
Axis 4	9.46	8.09		5.74	

Table 9 Characteristics of the canonical correspondence analysis

Variable	Total variance (%)	*P*
Full CCA model		0.01333*
Total phosphorus	9.34	0.0175*
Total nitrogen	7.34	0.0645
Chlorophyll *a*	8.98	0.02 *
pH	12.97	<0.005***
Conductivity	6.00	0.16
Chloride	6.11	0.65
Total alkalinity	13.43	<0.005***
Calcium	9.9	0.005**
Sodium	2.62	0.82
Sulfate	2.23	0.88
Magnesium	7.22	0.06563
Potassium	4.37	0.35

conditions (McCarthy et al. 1995; Schonborn 1984). A CCA on the testate rhizopod community in Florida lakes (Fig. 6) shows that this species prefers eutrophic rather than oligotrophic conditions. These findings are in agreement with results from paleolimnological studies in Lake Varese, Italy where Asioli et al. (1996) showed an upcore increase in the dominance of *C. aculeata* as water column nutrient concentrations increased.

Scott and Medioli (1983) were the first to associate high relative abundance of *Cucurbitella tricuspis* with areas of high nutrient input in Lake Erie. Similar results were found in other temperate lakes such as Lake Varese (Asioli et al. 1996), Lake Ontario (Patterson et al. 1996), and Lake Winnipeg (Torigai et al. 2000). A perpendicular projection of *C. tricuspis* on the CCA total phosphorus arrow shows that

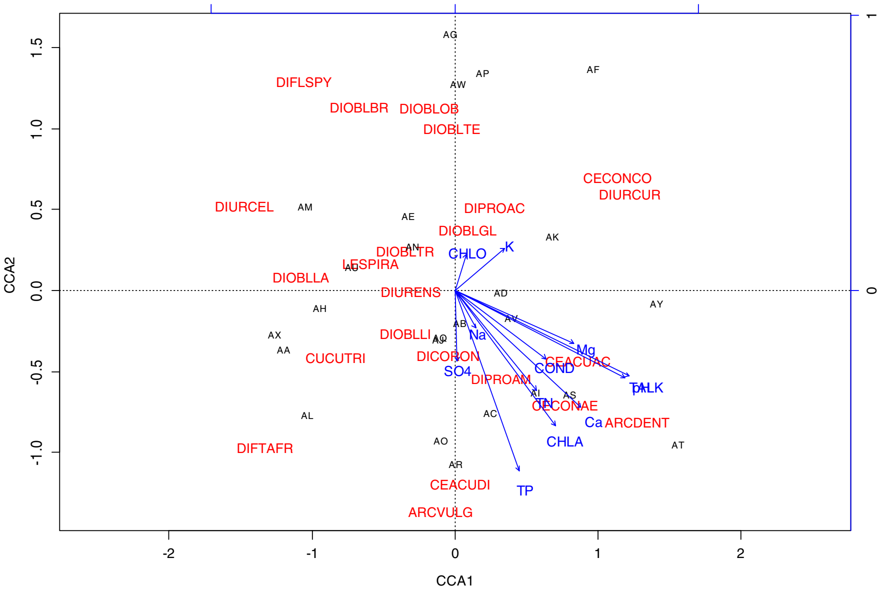

Fig. 6 Canonical correspondence analyses (CCA) for Florida thecamoebians, lakes and environmental variables (arrows)

its weighted average crosses the origin of the CCA plot (i.e. TP average value, 29.5 µg/l, mesotrophic state). These contrasting results suggest that *C. tricuspis* responds to TP values differently in temperate versus subtropical environments.

Ellison (1995) clustered a number of thecamoebian taxa into two main categories, those found in waters with pH values <6.2 and those thriving in waters with higher pH values. In Florida lakes, pH seems to have a large influence on particular species abundances. Affinity of *C. tricuspis* and *Difflugia protaeiformis* "amphoralis" for low and high pH environments, respectively (Fig. 6), is in agreement with the findings of Kumar and Patterson (2000) that showed strains of *D. protaeiformis* are absent from low-pH environments. Asioli et al. (1996) reported, however, that *D. protaeifomis* is abundant in industrially polluted, low-pH environments. It is not yet clear to what extent ecological factors such as pH and industrial pollutants influence the abundance of *D. protaeiformis*. Association of *D. protaeiformis* with industrial pollutants and pH requires further research.

Arcella vulgaris is known to inhabit stressed environments such as lakes with high levels of heavy metal contamination or brackish conditions (Medioli and Scott 1988; Patterson and Kumar 2000; Patterson et al. 1996; Reinhardt et al. 1998). *A. vulgaris* has been reported to thrive in environments with high metal concentrations (Fe and Al) and low pH (Kumar and Patterson 2000). In James Lake (Canada), which was impacted by a pyrite mine, *A. vulgaris* is the dominant species in areas with low-pH values (<5.5), but accounts for <5% of thecamoebian populations in near-neutral waters (Kumar and Patterson 2000). In Florida lakes, *A. vulgaris* abundance never surpasses 8% of the total thecamoebian assemblage (Table 3) even though several of the lakes where it is found have low-pH values. This suggests that the abundance of *A. vulgaris* may be controlled by metal concentrations rather than pH in heavily polluted lacustrine environments.

Conclusions

The broad ranges for physical and chemical variables in Florida lakes and the high number of testate rhizopods found in the majority of surveyed basins suggest that the Florida Peninsula is an appropriate region for thecamoebian-based biological calibration studies. Canonical correspondence analysis (CCA) shows that total alkalinity and pH are the environmental variables that most influence the distribution of species.

These results suggest that thecamoebians hold promise as potential water quality bio-indicators in Florida lakes. Use of multiple bio-indicators (e.g. diatoms and thecamoebians) in stratigraphic samples from sediment cores will make it possible to infer past human-induced pH changes in Florida's freshwater aquatic ecosystems.

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Appendix

As this paper is not of taxonomic nature, only an abbreviated taxonomy of all the species and strains found is provided. Some of the strain names we used are based on organisms described as species in the scientific literature

Subphylum Sarcodina; Schmarda 1871
Class Rhizopodea; von Siebold 1845
Subclass Lobosa; Carpenter 1861
Order Arcellinida; Kent 1880
Superfamily Arcellacea; Ehrenberg 1880
Family Arcellidae; Ehrenberg 1880
Genus *Arcella*; Ehrenberg 1880
Arcella vulgaris; Ehrenberg 1830
Arcella dentata; Ehrenberg 1830
Family Centropyxididae; Deflandre 1953
Genus *Centropyxis*; Stein 1859
Centropyxis aculeata; Ehrenberg 1832
Strain: *Centropyxis aculeata* "aculeata"
Other literature
Arcella aculeata; Ehrenberg 1832
Strain: *Centropyxis aculeata* "discoides"
Other literature
Arcella discoides; Ehrenberg 1843, 1872; Leidy 1879
Centropyxis discoides; Ogden and Hedley 1980
Centropyxis constricta; Ehrenberg 1843
Strain: *Centropyxis constricta* "constricta"
Other literature
Arcella constricta; Ehrenberg 1843
Strain: *Centropyxis constricta* "aerophila"
Centropyxis impressa; Daday 1905
Lesquereusia spiralis; Ehrenberg 1840
Family Hyalosphenidae; Schulze 1877
Genus *Cucurbitella*; Penard 1902
Cucurbitella tricuspis; Carter 1856
Family Difflugidae
Genus *Difflugia*; Leclerc in Lamarck 1816
Difflugia protaeiformis; Lamarck 1816
Strain: *Difflugia protaeiformis* "acuminata"
Other literature
Difflugia acuminata; Ehrenberg 1830; Ogden and Hedley 1980; Scott and Medioli 1983
Strain: *Difflugia protaeiformis* "amphoralis"
Other literature
Difflugia amphoralis; Cash and Hopkinson 1909
Strain: *Difflugia protaeiformis* "claviformis"
Other literature
Difflugia pyriformis "claviformis"; Penard 1899
Difflugia urceolata; Carter 1864
Strain: *Difflugia urceolata* "urceolata"
Strain: *Difflugia urceolata* "elongata"
Difflugia oblonga; Ehrenberg 1832
Strain: *Difflugia oblonga* "lanceolata"
Other literature
Difflugia lanceolata; Penrad 1890; Ogden and Hedley 1980
Strain: *Difflugia oblonga* "linearis"
Other literature
Difflugia pyriformis "linearis"; Penard 1890
Strain: *Difflugia oblonga* "glans"
Other literature
Difflugia glans; Penard 1902
Strain: *Difflugia oblonga* "oblonga"
Other literature
Difflugia oblonga; Ehrenberg 1832; Ogden and Hedley 1980; Haman 1982; Scott and Medioli 1983
Strain: *Difflugia oblonga* "tenuis"
Other literature
Difflugia pyriformis "tenuis"; Penrad 1890
Strain: *Difflugia oblonga* "bryophila"
Other literature
Difflugia pyriformis "bryophila"; Penard 1902
Difflugia bryophila; Ogden and Ellison 1988
Strain: *Difflugia oblonga* "spinosa"
Strain: *Difflugia oblonga* "triangularis"
Difflugia urens; Patterson et al., 1985
Difflugia corona; Wallich 1864
Difflugia fragosa; Hemperl 1898
Strain: *Difflugia fragosa* "fragosa"

References

Altinsacli S, Griffiths HI (2001) Ostracoda (Crustacea) from the Turkish Ramsar site of Lake Kus (Manyas Golu). Mar Freshwat Ecosyst 11:217–225

Asioli A, Medioli FS, Patterson RT (1996) Thecamoebians as a tool for reconstruction of paleoenvironments in some Italian lakes in the foothills of the southern Alps (Orta, Varese and Candia). J Foramin Res 26:248–261

Beaver J, Havens K (1996) Seasonal and spatial variation in zooplankton community structure and their relation to possible controlling variables in Lake Okeechobee. Freshwater Biol 36:45–56

Bredesen EL, Bos DG, Laird KR, Cumming BF (2002) A cladoceran-based paleolimnological assessment of the impact of forest harvesting on four lakes from the central interior of British Columbia, Canada. J Paleolimnol 28:389–402

Brenner M, Binford MW (1988) Relationships between concentrations of sedimentary variables and trophic state in Florida lakes. Can J Fish Aquat Sci 45:294–300

Clerk S, Hall R, Quinlan R, Smol JP (2000) Quantitative inferences of past hypolimnetic anoxia and nutrient levels from a Canadan Precambrian Shield lake. J Paleolimnol 23:319–336

Collins ES, McCarthy FM, Medioli FS, Scott DB, Honig CA (1990) Biogeographic distribution of modern thecamoebians in a transect along the eastern North American coast. In: Hemleben C, Kaminski MA, Kuhnt W, Scott DB (eds) Paleoecology, biostratigraphy, paleoceanography and taxonomy of agglutinated Foraminifera. NATO Advanced Studies Institute Series, Series C, pp 783–791

Charman DJ, Roe HM, Gehrels WR (1998) The use of testate amoebae in studies of sea level change: a case study from the Taf estuary, South Wales, UK. The Holocene 8:209–218

Dalby AP, Kumar A, Moore JM, Patterson RT (2000) Preliminary survey of arcellaceans (Thecamoebians) as limnological indicators in tropical lake Sentani, Irian Java, Indonesia. J Foram Res 30:135–142

Ellison RL (1995) Paleolimnological analysis of Ullεswater using testate amoebae. J Paleolimnol 13:51–63

Florida LAKEWATCH (2002) Florida LAKEWATCH Annual Data Summaries for 1986 through 2001. Department of Fisheries and Aquatic Sciences, University of Florida/Institute of Food and Agricultural Sciences. Library, University of Florida. Gainesville, Florida

Florida LAKEWATCH (2006) Florida LAKEWATCH Annual Data Summaries 2005. Department of Fisheries and Aquatic Sciences, University of Florida/Institute of Food and Agricultural Sciences. Library, University of Florida. Gainesville, Florida

Green J (1975) Fresh water ecology in Mato Grasso, Central Brazil IV: Associations of testate Rhizopoda. J Nat Hist 9:545–560

Green J (1963) Zooplankton of the river Sokoto, the rhizopoda testacea. Proc Zool Soc Lond 141:497–514

Håkanson L, Jansson M (1983) Principles of lake sedimentology. Springer-Verlag, New York, p 316

Kumar A, Patterson RT (2000) Arcellaceans (thecamoebians): new tools for monitoring long- and short-term changes in lake bottom acidity. Environ Geol 39:689–697

Kumar A, Dalby AP (1998) Identification key for Holocene lacustrine arcellacean (thecamoebian) taxa. Paleontologia Electronica. 1. http://palaeo-electronica.org/: 1–39

Lena H (1983) Testaceolobosia (Protozoa, Rhizopoda) of Melbourne, Florida, USA. Revista Española de Micropaleontología 15:317–328

Lena H (1982) Observations on the ecology of benthic aquatic testaceans (Protozoa, Rhizopoda, Testacecealobosia). J Protozool 29:288

Magurran AE (1988) Ecological diversity and its measurements. Princeton University Press, New Jersey, p 179

Margalef R (1972) Homage to Evelyn Hutchinson, or why is there an upper limit to diversity. Trans Conn Acad Arts & Sci 44:211–235

McCarthy FMG, Collins ES, McAndrews JH, Kerr HA, Scott DB, Medioli FS (1995) A comparison of postglacial Arcellacean (Thecamoebian) and pollen succession in Atlantic Canada, illustrating the potential of arcellaceans for palaeoclimatic reconstruction. J Paleontol 69: 980–993

Medioli FS, Scott DB (1988) Lacustrine thecamoebians (mainly Arcellaceans) as potential tools for palaeolimnological interpretations. Palaegeogr Palaeoclimatol Paleoecol 62:361–386

Medioli FS, Scott DB (1983) Holocene Arcellacea (Thecamoebians) from Eastern Canada. Cushman Foundation Editorial, Washington, DC, 63pp

Patterson RT, Kumar A (2002) A review of current testate rhizopod (thecamoebian) research in Canada. Palaegeogr Palaeoclimatol Palaeoecol 180:225–251

Patterson RT, Kumar A (2000) Assessment of arcellacean (thecamoebian) assemblages, species, and strains as contaminant indicators in James lake, northeastern Ontario, Canada. J Foramin Res 30:310–320

Patterson RT, Barker T, Burdidge S (1996) Arcellaceans (thecamoebians) as proxies of arsenic and mercury contamination in northeastern Ontario lakes. J Foramin Res 26:172–183

Reinhardt E, Dalby AP, Kumar A, Patterson RT (1998) Arcellaceans as pollution indicators in mine tailing contaminated lakes near Cobalt, Ontario, Canada. Micropaleontology 44:131–148

Roe HM, Patterson RT (2006) Distribution of thecamoebians (testate amoebae) in small lakes and ponds, Barbados, West Indies. J Foramin Res 36(2):116–134

Scott DB, Hermelin JOR (1993) A device for precision splitting of micropaleontological samples in liquid suspension. J Paleontol 67:151–154

Scott DB, Medioli FS (1983) Agglutinated rhizopods in Lake Erie: modern distribution and stratigraphic implications. J Paleontol 54:809–820

Scott DB, Medioli FS (1980) Post-glacial emergence curves in the Maritimes determined from marine sediments in raised basins. Proceedings of Coastlines 80 (Canada). Ed. NERSC 428–446

Scott DB, Medioli FS, Schafer CT (2001) Monitoring in coastal environments using Foraminifera and thecamoebian indicators. Cambridge University Press, New York, p 177

Schonborn W (1984) Studies on remains of testacea in cores of the Great Woryty Lake (NE-Poland). Limnologica 16: 185–190

Schrumm L (2001) Use of Foraminifera and Thecamoebians as reliable indicators of marine/freshwater transition zones in South Florida. Honor Undergraduate Thesis. Dalhousie University

Tolonen K (1986) Rhizopod analysis. In: Berglund BE (eds) Handbook of holocene palaeoecology and palaeohydrology. Wiley, Chichester, pp 645–666

Torigai K, Schroder-Adams CJ, Burdridge SM (2000) A variable lacustrine environment in Lake Winnipeg, Manitoba: evidence from modern thecamoebian distribution. J Paleolimnol 23:305–318

Warner BG, Charman DJ (1994) Holocene soil moisture changes on a peatland in northwestern Ontario based on fossil testate amoebae (protozoa) analysis. Boreas 23: 270–279

Werner P, Smol JP (2005) Diatom–environmental relationships and nutrient transfer functions from contrasting shallow and deep limestone lakes in Ontario, Canada. Hydrobiologia 533:145–173

Whitmore TJ, Brenner M, Rood BE, Japy KE (1991) Deoxygenation of a Florida Lake during winter mixing. Limnol Oceanogr 36:577–585

Wolda H (1981) Similarity indices, sample size and diversity. Oecologia 50:296–302

Zhang E, Jones R, Bedford A, Langdon P, Tang H (2007) A chironomid-based salinity inference model from lakes on the Tibetan Plateau. J Paleolimnol 38:477–491