

## DISTRIBUTION OF THECAMOEBIANS (TESTATE AMOEBAE) IN SMALL LAKES AND PONDS, BARBADOS, WEST INDIES

HELEN M. ROE<sup>1</sup> AND R. TIMOTHY PATTERSON<sup>2</sup>

### ABSTRACT

Thecamoebian faunas identified from 15 small permanent and ephemeral lakes and ponds on Barbados, West Indies, are characterized by low numbers of individuals and low species diversities (Shannon-Wiener Diversity Index = 0–1.4). Four lakes and ponds were found to contain no thecamoebians. The faunas were dominated by *Centropyxis aculeata*, with lesser numbers of *Arcella vulgaris*, *Cucurbitella tricuspis*, *Centropyxis constricta* and *Cyclopyxis kahli*. Very low numbers of the small idiosomic species *Euglypha rotunda* and an undifferentiated *Corythion-Trinema* type were also reported; the first records from a tropical region. Centropyxid-dominated faunas have been reported from other tropical areas and may indicate stressed environmental conditions. Additional important ecological controls on these faunas include substrate characteristics, the nature of bankside and aquatic vegetation and water depth. Land use characteristics do not appear to have a significant influence on faunal distribution, although the soil indicator thecamoebian species *C. kahli* seems to have been introduced into at least one pond through erosion from adjacent fields. Significant numbers of the salt marsh foraminiferid *Jadammina macrescens*, and lesser numbers of *Polysaccamina ipohalina* and *Miliammina fusca*, were found in one coastal pond, with a few specimens of *J. macrescens* found in another. The presence of this unusual, nonmarine foraminiferal fauna may relate to the intrusion of salt water into local ground waters, or possibly the introduction of sea salt from the prevailing Atlantic winds. Foraminiferal and thecamoebian colonization into the ponds may have been avian mediated.

### INTRODUCTION

Thecamoebians (Protozoa: Rhizopoda), also known as testate amoebae, are unicellular protozoans that occur commonly worldwide in a variety of freshwater and slightly brackish environments (Medioli and Scott, 1983, 1988; Warner, 1990; Tolonen and others, 1992; Charman and others, 1998, 2000; Patterson and Kumar, 2002). Research on the group has largely been descriptive in nature, although in recent years an increasing number of studies have focused on the utility of thecamoebians as environmental and paleoenvironmental indicators. This work has considered faunas from peat bogs (e.g., Warner, 1987; Tolonen and others, 1992; Woodland and others, 1998; Charman and others, 2000), lakes (e.g., Patterson, 1987; Reinhardt and others, 1998; Lloyd, 2000; Patterson and Kumar, 2002; Boudreau and others, 2005) and more

recently, salt marshes (Charman and others, 1998, 2002; Gehrels and others, 2001; Roe and others, 2002). Thecamoebians have proven ideal in this capacity, because 1) their tests tend to be resistant to dissolution and preserve well in sediments; and 2) they are sensitive to a wide variety of environmental variables (Warner, 1990; Warner and Charman, 1994; Warner and Bunting, 1996; Charman and others, 2000; Patterson and Kumar, 2002; Patterson and others, 2002). It is now known that distinct assemblages of thecamoebian species can be correlated to a variety of environmental and climatic parameters, including metal and organic pollutant contamination, substrate type, salinity, levels of organics, oxygen concentration, water temperatures, water table fluctuations, humification, changes in intertidal flooding and land use change (e.g., Scott and Medioli, 1983; Patterson and others, 1985; Medioli and others, 1990; Collins and others, 1990; Tolonen and others, 1992; McCarthy and others, 1995; Asioli and others, 1996; Patterson and others, 1996; Charman and others, 1998, 2002; Reinhardt and others, 1998; Patterson and Kumar, 2000a, 2000b; Patterson and Kumar, 2002; Patterson and others, 2002; Booth and Jackson, 2003).

Most research on thecamoebians has focused on faunas found at higher latitudes (see Tolonen and others, 1992; Patterson and Kumar, 2002). Only a handful of studies have been carried out in the tropical zone, with the majority of that research being descriptive in nature. Examples of low-latitude studies on thecamoebians include: faunas from the wetlands of central Brazil (Green, 1975); Lake Cocococha, Peru (Haman and Kohl, 1994); the Sokoto River in Nigeria (Green, 1963); lakes in Java, Sumatra, and Irian Jaya, Indonesia (van Oye, 1949; Dalby and others, 2000); lakes in Malaysia (Sudzuki, 1979); and brackish and freshwater lakes and ponds on the islands of Bombay (Carter, 1856a, 1856b, 1864, 1865). Javaux (1999) studied the occurrence of thecamoebians and foraminifera from ponds in Bermuda. There have been no other previous studies carried out in the Caribbean region.

The purpose of this research is to contribute to this scant database by documenting the thecamoebian faunas from 15 small lakes and ponds on the island of Barbados in the southeastern Caribbean, and correlating faunal variation to measured limnological parameters. In the course of this research, a nonmarine occurrence of marsh-type foraminifera was also documented in a coastal pond. Although not unique (see Patterson and others, 1990; Boudreau and others, 2001), such a nonmarine occurrence of foraminifera is of sufficient rarity to warrant discussion here.

### STUDY AREA

The island of Barbados (latitude 13°02'–13°10'N; longitude 59°25'–59°39' W) is located in the southeastern

<sup>1</sup>School of Geography, Queen's University of Belfast, Belfast, Northern Ireland, BT7 1NN, UNITED KINGDOM.  
E-mail: h.roe@qub.ac.uk

<sup>2</sup>Department of Earth Sciences, Carleton University, and Ottawa-Carleton Geoscience Centre, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6, CANADA. E-mail: tpatters@ccs.carleton.ca

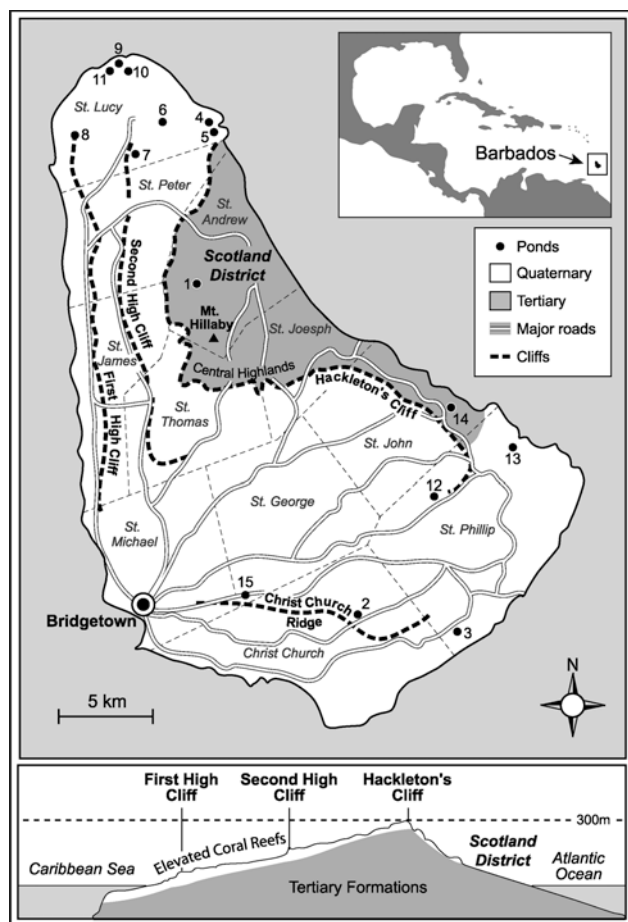


FIGURE 1. Map showing location of sampled Barbados lakes and ponds.

Caribbean Sea, 150 km east of the Lesser Antilles. Covering 430 km<sup>2</sup>, the island extends 32 km from north to south and is 24 km wide. Barbados is relatively low-lying with the highest point being Mt. Hillaby at 343 m above sea level (Schellmann and others, 2002).

## CLIMATE

Barbados has a humid to sub-humid, tropical maritime climate (Randall, 1970). There is little seasonal temperature variability with mean daily temperatures ranging from 28–31°C. Temperatures seldom fall below 20°C at night. Mean annual precipitation averages 1,100 to 1,200 mm on the island but due to orographic effects there is considerable regional variability. For example, up to 1,750 mm of rain falls in the central highlands (Fig. 1). The driest areas are along the south to southeastern coast in the lee of the central highlands. With the exception of the central highlands, the island has a pronounced dry season from January to May and a rainy season from September to December. Barbados lies within the belt of northeast trade winds (Randall, 1970). As a result, most winds come from the northeast, east, or southeast and have a significant control on local wave direction (James and others, 1977). This in turn influences coastal lakes and ponds on the windward side of the island.

## LAKE PHYSIOGRAPHY

The Quaternary coral reef cap that covers 86% of Barbados is easily soluble in the tropical climate that prevails on the island (Fermor, 1972; Radtke and Grün, 1990). The resultant karst morphology is notable for its large numbers of dolines that are typically round, small, discrete, and contain sinkholes (Day, 1983). Approximately 2830 dolines, averaging 6 m in depth, have been mapped in total (Wandelt, 2000). Based on fieldwork carried out for this research, the island supports approximately 20 dolines that are large enough to be classified as small permanent lakes and ephemeral ponds.

The extremely permeable coral limestone forms the only aquifer on the island. Groundwater flow within the aquifer is determined by the higher porosity and permeability of the coral cap in respect to underlying Tertiary rocks and precipitation (Banner and others, 1994). Recharge to the small lakes and ponds is also highly dependent on precipitation, as well as local groundwater flow. In areas near the coast, sedimentary layers are lower than sea level. In these areas, a coastal phreatic wedge and freshwater-saltwater mixing zone occur (Humphrey, 1997). In some places saltwater has infiltrated freshwater reservoirs. This contamination is the result of ongoing sea-level rise and salination resulting from the over-pumping of aquifers, and may explain heightened salinity readings in some coastal lakes and ponds.

## MATERIAL AND METHODS

### SAMPLE COLLECTION

Fifteen small lakes and ponds were sampled during November 2002 from the northern, southern and western areas of Barbados (Fig. 1). The sampling period followed three days of heavy rain which had resulted in localized flooding and elevated water tables. The ponds sampled represent the full range of lake and pond types that exist on the island, and show considerable variation in size, depth and surrounding land use (Table 1). This sample set represents approximately 90% of the inland water bodies recorded on local 1:60,000 maps. Samples were collected with a trowel from the readily accessible, shallower areas of the lakes. Approximately 200 g of surface sediment (i.e., the uppermost 1–2 cm of the sedimentary infill) was collected from each site. Sample water depths were noted. The samples were transferred to sealed sample bags and refrigerated at 4°C. In addition to the sediment samples, the following characteristics were noted for each site: 1) pond diameter; 2) approximate maximum water depth; 3) the general character of any bankside and aquatic vegetation; 4) surrounding land use; and 5) evidence for artificial modification of the ponds (e.g., the presence of inflow pipes).

### SEDIMENT ANALYSES

In the laboratory, the sediment samples were described and the color noted using a Munsell soil color chart. Sediment composition was further described using the classification scheme of Troels-Smith (1955), which pro-

TABLE 1. Locations and physical characteristics of sampled ponds.

Pond	Latitude / Longitude	Location / Parish	Geological setting	Approximate Maximum Water Depth	Pond Diameter	Permanent (P) / Ephemeral (E)	Natural (N) / Modified (M)	Land use	Vegetation Emergent	Bankside	Floating
1	59° 36' 15" N 13° 14' 77" W	Bawdens, St. Andrew	Tertiary sandstone	1 - 2 m	25 m	P	M	Undeveloped	Sparse	Grasses only	-
2	59° 31' 50" N 13° 5' 62" W	Lowland, Christ Church	Pleistocene coral	2 - 3 m	24 m	P	N	Commercial	Present	Diverse	-
3	59° 29' 23" N 13° 5' 54" W	Hopfield, St. Philip	Pleistocene coral	2 m	22 m	P	N	Commercial	Sparse	Diverse	Some algae
4	59° 35' 54" N 13° 18' 53" W	Cuckold Point, St. Lucy	Pleistocene coral	0.25 m	8 m	E	N	Undeveloped / Pasture	-	Grasses only	-
5	59° 35' 46" N 13° 18' 39" W	Corbens Bay, St. Lucy	Pleistocene coral	0.5 - 1.0 m	7 m	E	N	Undeveloped / Pasture	-	Grasses only	Some algae
6	59° 37' 54" N 13° 18' 85" W	Chance Hall, St. Lucy	Pleistocene coral	1 - 2 m	14 m	P	N	Agricultural	Present	Diverse	Sparse
7	59° 38' 19" N 13° 17' 62" W	Church Hill, St. Lucy	Pleistocene coral	0.5 m	19 m	E	N	Residential / Agricultural	Present	Grasses only	-
8	59° 39' 46" N 13° 18' 15" W	Bromfield Plantation, St. Lucy	Pleistocene coral	2 m	24 m	P	M	Residential	Sparse	(None - artificial bank)	-
9	59° 38' 23" N 13° 20' 15" W	near Cluffs, St. Lucy	Pleistocene coral	0.75 m	9 m	E	N	Undeveloped	Sparse	Grasses only	-
10	59° 38' 08" N 13° 20' 12" W	near Cluffs, St. Lucy	Pleistocene coral	1 m	14 m	P	N	Agricultural	Sparse	Grasses only	-
11	59° 38' 39" N 13° 20' 00" W	near Cluffs, St. Lucy	Pleistocene coral	<0.25 m	5 m	E	N	Undeveloped / Pasture	-	Grasses only	-
12	59° 29' 89" N 13° 8' 15" W	near Summerville, St. Philip	Pleistocene coral	1 m	7 m	P	N	Agricultural	Present	Diverse	Abundant pondweed
13	59° 27' 70" N 13° 10' 39" W	Bayfield Pond, St. Philip	Pleistocene coral	>3 m?	19 m	P	N	Residential	Present	Diverse	Present (lilies)
14	59° 29' 46" N 13° 11' 39" W	Codrington College, Sealy Hall, St. John	Tertiary sandstone	0.8 m	23 m	P	M	Residential	-	(None - artificial bank)	Present (lilies)
15	59° 34' 62" N 13° 6' 46" W	Lower Birneys, St. George	Pleistocene coral	0.4 m	19 m	E	N	Residential	Present	Grasses only	-

vides a simple, semiquantitative means of recording the main sediment constituents. To provide insights into other potential controls on thecamoebian distribution, the sediment samples were also subject to loss-on-ignition analysis and sediment-derived conductivity and pH analyses. Loss-on-ignition analysis, which was used to examine the possible influence of lake organics on faunal composition, was undertaken following the method of Allen and others (1974), with ignition of the samples to 450°C. Sediment-derived conductivity readings were taken to gain insights into lake water conductivity, and particularly salinity. The method used was an extraction procedure that is more typically applied to soils (Rowell, 1994). This involved mixing 20 g of air-dried sample (20 g) vigorously with 100 ml parts of distilled water, filtering the mixture and taking a reading of the supernatant with a conductivity meter. This method was considered to provide the best available proxy for lake water salinity in the absence of field-based conductivity measurements on the lake water itself. For ease of analysis, and to facilitate comparisons with other sites, the conductivity readings were converted to salinity values (both in mg per liter of sediment and parts per thousand) using the conversion algorithms of George and others (1996). Sediment pH was measured in a similar way to conductivity using a 1:2 part dilution of sediment to distilled water (Allen and others, 1974).

#### THECAMOEBIAN PREPARATION AND COUNTING

A 10 cc subsample of sediment was used for thecamoebian analysis. Prior to preparation, each sample was soaked in rose Bengal solution to stain remnants of protoplasm and aid in the identification of live specimens (Walton, 1952; Murray and Bowser, 2000). The samples were then agitated for one hour using a Burrell wrist shaker. They were subsequently screened with a 250 µm sieve to remove coarse organic particles and then with a 37 µm screen to remove fine organic and mineral detritus. The residues on the 37 µm sieves were retained for thecamoebian analysis. To further examine whether very small thecamoebians were present in the samples, the <37 µm fraction was also retained. The 37–259 µm fraction samples were then subdivided into aliquots for quantitative analysis using a wet splitter (Scott and Hermelin, 1993). Wet aliquots were examined under a dissecting binocular microscope, usually at 40–80X magnification, until an entire split was quantified for each sample. Any foraminifera present in these samples were also recorded.

The technique used to examine the smaller thecamoebians in the <37 µm size fraction was similar to that developed for peatland samples (Hendon and Charman, 1997) and recently applied to salt marsh samples (Charman and others, 1998, 2002; Roe and others, 2002). The <37 µm residues were subject to a further stage of sieving through a 15 µm mesh to remove fine mineral material. This additional sieving stage has proved particularly important in the treatment of clay-rich samples from salt-marsh environments and was considered to be important for the clay-dominated samples of the present study. After sieving, the residues were mixed with glycerol, mounted under a 22 × 50 mm coverslip and counted using a high power light

microscope at 400–1000X magnification. All specimens under two coverslips were recorded for each sample.

Scanning electron micrographs were obtained using JEOL 6400 scanning electron microscopes at the Carleton University Research Facility for Electron Microscopy and the Electron Microscope Unit, Queen's University, Belfast, Northern Ireland, United Kingdom.

#### THECAMOEBIAN DATA ANALYSIS

The thecamoebian counts in the 37–250 µm fraction were expressed as percentages of the total thecamoebians in this fraction (Table 2). It was considered inappropriate to merge these counts with those of the smaller size fraction because of the different approaches used for counting, although total species diversity from the combined fractions was noted (Table 2). To facilitate comparisons with other lake-based thecamoebian studies, the Shannon–Wiener Diversity Index (SDI) was also calculated for the 37–250 µm fraction using the equation:

$$SDI = - \sum_{i=1}^S \left( \frac{X_i}{N_i} \right) \times \ln \left( \frac{X_i}{N_i} \right) \quad (2)$$

where  $X_i$  = the abundance of each taxon in a sample,

$N_i$  = the total abundance of the sample, and

$S$  = the species richness of the sample.

The SDI is a rough measure of faunal diversity and is useful in indicating the relative health of the community from which the sample was taken. In multiple regression analyses, SDI has been determined to be one of the most powerful explanatory variables and is as useful a paleoecological tool as individual taxa (Dalby, 2002).

## RESULTS

### POND DESCRIPTIONS

Of the 15 small lakes and ponds examined in this study (referred to hereafter as 'ponds'), 13 were contained within the area of the Pleistocene coral outcrop, whilst two, Ponds 1 and 14, were located within the Tertiary sediments of the Scotland District (Fig. 1; Table 1). As most of the ponds are positioned within small, karstic dolines, they tend to be rounded in character and have a maximum diameter of less than 30 m. These ponds can be subdivided into nine permanent and six semipermanent or ephemeral bodies. Although both types of pond overlap in diameter, the permanent ponds are generally much deeper (0.8 – >3.0 m) than the ephemeral ponds (0.25 – 1.0 m; Table 1). The ponds can be further subdivided on the basis of the surrounding land use, which ranges from open pasture land to land used for crops and commercial activities. The settings of the ponds are summarized below:

- *Pond 1* (unnamed pond in Bawdens, St. Andrew Parish, Scotland District, northeast Barbados). This permanent pond was 25 m in diameter and rounded, with an approximate maximum water depth of 2 m. There was a large inflow pipe carrying water from surrounding agricultural land and some evidence of localized

TABLE 2. Sample locations; sediment pH, conductivity, salinity values and water depth; Troels-Smith sediment descriptions; Munsell sediment color descriptions; foraminiferal counts, thecamoebian specimen counts divided into the 15-37  $\mu\text{m}$  and 37-250  $\mu\text{m}$  fractions; number of live specimens indicated by brackets; thecamoebian percentage data 37 - 250  $\mu\text{m}$  fraction; and Shannon Diversity Index (SDI) values for 37-250  $\mu\text{m}$  fraction.

Pond	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Water depth of sample (cm)	30	50	28	25	40	50	25	50	25	40	15	30	50	35	20
pH	7.84	7.60	7.33	8.14	7.49	7.65	7.53	8.09	7.33	7.19	7.00	7.26	8.16	7.82	7.46
Conductivity ( $\mu\text{S}$ )	826	342	246	464	331	296	261	290	128	288	179	367	803	571	196
Sediment salinity (mg/L)	454	188	135	255	182	163	144	160	70	158	96	202	442	314	108
Sediment salinity (ppt)	0.45	0.19	0.14	0.26	0.18	0.16	0.14	0.16	0.07	0.16	0.10	0.20	0.44	0.31	0.11
Loss-on-ignition	3.83	8.45	14.02	13.9	12.44	15.06	13.59	2.61	13.4	13.62	15.17	18.13	8.11	2.59	12.86
Sediments	olive brown silty clay	dark brown silty clay	dark brown silty clay with line sand	olive brown silty clay	yellow grey silty clay	yellow grey silty clay	dark brown silty clay	yellow brown silty sand	yellow grey silty clay	yellow grey silty clay	yellow grey silty clay	dark brown silty clay	grey silty clay with fine sand	olive grey silty sand	yellow grey silty clay
Troels-Smith sediment description	Ag2, As2	Ag2, As2	Ag3, As1, Ga++	As2, Ag2	As3, Ag1, Ga+	As3, Ag1, Ga+	As3, Ag1, Ga+	Ga2, Gs1, Ag1	As3, Ag1	As3, Ag1	As3, Ag1	As2, Ag2	As2, Ag2, Ga++	Gs2, Gs1, Ag1	Ag2, As2
Munsell color	5Y 5/3	2.5Y 5/3	2.5Y 3/2	2.5Y 3/3	2.5Y 4/1	2.5Y 4/1	2.5Y 3/2	2.5Y 5/3	2.5Y 5/1	2.5Y 5/1	2.5Y 5/1	2.5Y 3/2	2.5Y 4/2	5Y 5/2	2.5Y 4/2
Total Thecamoebians (15 - 37 $\mu\text{m}$ )	17	46	37	Void	5	11	8	Void	5	2	Void	Void	123	3	1
Total Thecamoebians (37 - 250 $\mu\text{m}$ )	32	147	173	Void	51	175	36	Void	Void	Void	4	Void	101	Void	3
Total Thecamoebian Counts	49	183	210	-	56	186	44	-	Void	Void	4	-	224	Void	4
Foramifera counts (37 - 250 $\mu\text{m}$ )	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SDI (Thecamoebians: 37 - 250 $\mu\text{m}$ fraction)	1.4	0.3	1	-	0.3	0.9	1.1	-	0	0	0	-	390	0	0.6
Total Thecamoebian Taxa	8	8	7	-	4	6	5	-	2	1	1	-	10	2	2
<b>Thecamoebians (15 - 37 <math>\mu\text{m}</math>) Raw counts</b>															
<i>Ammonia</i>	2	1	1	-	1	1	1	-	-	-	-	-	1	-	-
<i>Ammonia</i> spp.	1	1	1	-	1	1	1	-	-	-	-	-	1	-	-
<i>Centropyxis aculeata</i>	5	5	4	-	1	1	1	-	-	-	-	-	2	-	-
<i>Centropyxis aculeata</i> "aculeata"	2	5	1	-	1	1	1	-	-	-	-	-	2	-	-
<i>Centropyxis aculeata</i> "discoides"	2	23	16	-	4	4	6	-	-	-	-	-	14	-	-
<i>Centropyxis kahli</i>	7	13	9	-	3	3	4	-	4	-	-	-	94	-	1
<i>Cucurbitella truncatus</i>	1	3	5	-	1	1	1	-	1	-	-	-	2	-	-
<i>Diffugia cf. gibbula</i>	1	3	5	-	1	1	1	-	1	-	-	-	6	-	1
<i>Diffugia oblonga</i> undifferentiated type	1	3	5	-	1	1	1	-	1	-	-	-	6	-	1
<i>Diffugia proteiformis</i>	1	3	5	-	1	1	1	-	1	-	-	-	6	-	1
<i>Lesquerella modesta</i>	1	3	5	-	1	1	1	-	1	-	-	-	6	-	1
Unknown idiosomic species	1	1	1	-	1	1	1	-	1	-	-	-	1	-	-
<b>Thecamoebians (37 - 250 <math>\mu\text{m}</math>) Raw counts</b>															
<i>Ammonia</i>	1	1	1	-	1	1	1	-	-	-	-	-	1	-	-
<i>Ammonia</i> spp.	1	1	1	-	1	1	1	-	-	-	-	-	1	-	-
<i>Centropyxis aculeata</i>	7	137	120	-	4	9	4	-	-	-	-	-	2	-	-
<i>Centropyxis aculeata</i> "aculeata"	14	1	15	-	4	14	16	-	16	-	-	-	50	-	1
<i>Centropyxis aculeata</i> "discoides"	1	1	4	-	47	17	14	-	14	-	-	-	10	-	-
<i>Centropyxis constricta</i> "aerophila"	5	8	10	-	128	2	2	-	2	-	-	-	14	-	-
<i>Cyclopyxis kahli</i>	5	5	10	-	7	7	7	-	7	-	-	-	24	-	-
<i>Cucurbitella truncatus</i>	5	5	10	-	1	1	1	-	1	-	-	-	1	-	-
<i>Diffugia oblonga</i> "oblonga"	5	5	10	-	1	1	1	-	1	-	-	-	1	-	-
<b>Thecamoebians (37 - 250 <math>\mu\text{m}</math>) Percent</b>															
<i>Ammonia</i>	3.1%	0.7%	8.7%	-	7.8%	5.1%	11.1%	-	-	-	-	-	2.0%	-	-
<i>Ammonia</i> spp.	21.9%	92.2%	69.4%	-	84.4%	44.4%	44.4%	-	-	-	-	-	49.5%	-	-
<i>Centropyxis aculeata</i>	43.8%	13.3%	2.3%	-	92.2%	9.8%	38.9%	-	-	-	-	-	9.9%	-	-
<i>Centropyxis aculeata</i> "discoides"	0.7%	0.7%	2.3%	-	92.2%	9.8%	38.9%	-	-	-	-	-	13.9%	-	-
<i>Centropyxis constricta</i> "aerophila"	15.6%	5.4%	5.8%	-	73.1%	5.6%	5.6%	-	-	-	-	-	23.8%	-	-
<i>Cyclopyxis kahli</i>	15.6%	0.0%	5.8%	-	4.0%	4.0%	4.0%	-	-	-	-	-	1.0%	-	-
<i>Cucurbitella truncatus</i>	15.6%	0.0%	5.8%	-	4.0%	4.0%	4.0%	-	-	-	-	-	1.0%	-	-
<i>Diffugia oblonga</i> "oblonga"	15.6%	0.0%	5.8%	-	4.0%	4.0%	4.0%	-	-	-	-	-	1.0%	-	-
<b>Foraminifera (Raw counts)</b>															
<i>Jadammina macrescens</i>	10	10	10	-	10	10	10	-	10	-	-	-	10	-	3
<i>Polysaccamina lippoliana</i>	6	6	6	-	6	6	6	-	6	-	-	-	6	-	-
<i>Millammina fusca</i>	48	48	48	-	48	48	48	-	48	-	-	-	48	-	-
Reworked fossil bolivinitids sp.	74	74	74	-	74	74	74	-	74	-	-	-	74	-	-



FIGURE 2. Photograph of Pond 3 showing disturbed soils and proximity of mill.

dredging, probably to enhance water storage capacity. This was only one of two ponds sampled within the Scotland District. The substrate of this pond comprised coarse silty sand reflecting the underlying early Tertiary sandstones. Two samples, 1A and 1B, were collected from this pond, the former from the margin of the lake near the inflow pipe.

- *Pond 2* (unnamed pond in Lowland, Christ Church Parish, southern Barbados). This permanent, round pond, 24 m in diameter, was contained within a doline, with a maximum approximate water depth of 3 m. The pond was bordered by a diverse bankside and emergent aquatic vegetation. Several houses bordered the pond as well as a junkyard.
- *Pond 3* (unnamed pond in Hopefield, St. Philip Parish, Southern Barbados; Fig. 2). This permanent pond, 22 m in diameter, was also rounded and contained within a doline, with an approximate maximum water depth of 2 m. The pond was immediately adjacent to mills and completely surrounded by bare, disturbed, bull-dozered soil with a few scrubby palms on one side (Fig. 2). At the margins the water was tinged slightly green with algae.
- *Pond 4* (unnamed pond from Cuckold Point near Pie Corner, St. Lucy Parish, northeast Barbados). This shallow (0.25 m), ephemeral pond, which filled a small doline, was located 30 m from a high (>50 m) coastal cliff. The 8-m-diameter pond was surrounded by palms and used as a water source for cattle. The water was a yellow-brown color, reflecting disturbance of the silty clay substrate by wading animals. There was an extensive algal scum on the margin of the pond, as well as abundant water beetles and leeches.
- *Pond 5* (unnamed pond from Corbens Bay, St. Lucy Parish, northeast Barbados). This small, ephemeral pond was also positioned only 30 m from a high coastal cliff. The pond was located in an open, grassy area and used as a water source for cattle. The cattle had also disturbed the silty clay substrate in this pond while wading, resulting in yellow-brown-colored water. The pond contained abundant grass in the shallows along the edges that matched that of the surrounding pasture (Fig. 3), suggesting that much of the water in the pond



FIGURE 3. Photograph of ephemeral Pond 5 located in a shallow doline depression.

may have originated from the heavy rains that had occurred only a few days earlier. The pond had apparently not been completely dry, as there were abundant swimming leeches.

- *Pond 6* (unnamed pond from Chance Hall, St. Lucy Parish, northeast Barbados). This round and permanent pond had a maximum depth of 2 m. It was also contained within a doline and was completely surrounded by sugarcane fields. The dark, organic-rich substrate and the dark waters of the pond may reflect input from agricultural runoff.
- *Pond 7* (unnamed pond from Church Hill, St. Lucy Parish, north Barbados). Vegetation choked this very small and only 0.5-m-deep ephemeral pond adjacent to buildings and cane fields. The pond had a muddy soil substrate, with peripheral areas being covered by pasture grass. It is likely that the pond was larger than normal following recharge during heavy rains only a few days before.
- *Pond 8* (unnamed heavily modified pond from Bromefield Plantation House, Bromefield, St. Lucy Parish, northwest Barbados). This permanent, 2-m-deep doline pond was heavily modified, as it had been dredged and lined with fine gravel.
- *Pond 9* (unnamed pond near Cluffs, St. Lucy Parish, north Barbados). This shallow, undisturbed, ephemeral pond, up to 0.75 m deep and 9 m in diameter, filled a topographic hollow in the corner of a pasture field. Pasture grass was growing in the area submerged by water, suggesting that water levels were abnormally high. The substrate was composed of clay.
- *Pond 10* (unnamed pond 100 m inland from Pond 9, near Cluffs, St. Lucy Parish, north Barbados). This permanent pond was only 20 m in diameter and 1 m deep. There was only a thin veneer of sediment in the pond overlying the fossil coral substrate.
- *Pond 11* (unnamed pond near Cluffs, St. Lucy Parish, north Barbados). This shallow, ephemeral depression, containing less than 25 cm of water, was located in a field. The water may have originated entirely from heavy rains that fell only a few days prior to sampling.
- *Pond 12* (unnamed pond near Summervale, St. Philip Parish). This 1-m-deep pond was surrounded by a sugar cane field and buildings. The water was odiferous and totally covered by *Lemna*, a fine pond weed.



FIGURE 4. Photograph of Pond 13 located in a karstic doline depression. The well-zoned bankside vegetation is visible.

- *Pond 13* (Bayfield Pond, St. Philip Parish, southeast Barbados). This permanent pond (Fig. 4) was one of the largest (23 m diameter) and deepest (>3 m) examined in the study. It was positioned in a flat and exposed area on one of the lowest Pleistocene terraces in the eastern part of the island that is subject to almost continuous winds coming in from the Atlantic Ocean. There was an extensive 3-m-wide area of zoned vegetation completely surrounding the pond (Fig. 4). An abundant snail population was also noted. The pond waters were somewhat stagnant in appearance and the surface supported a large community of lilies. The substrate comprised a mixture of organic mud and coral rubble. Several homes border the pond.
- *Lake 14* (Codrington College Pond, Sealy Hall, St. John Parish, southeast Barbados). This shallow (0.8 m deep) pond was heavily modified and lined with concrete. There were abundant water lilies and snails visible. There was only a thin veneer of organic-rich substrate mixed with sand over concrete.
- *Lake 15* (unnamed pond, Lower Birneys, St. George Parish, southwest Barbados). This 19-m-wide and very shallow (<0.5 m), pond-like depression was floored by grass in a low area of derelict land in a residential region. It was undoubtedly ephemeral and had been filled during heavy rains that fell only a few days prior to sampling.

#### SEDIMENT CHARACTERISTICS

The majority of the samples were dominated by silts and clays, with a few showing subsidiary levels of sand (Table 2). Only two samples—those from the artificially modified Ponds 8 and 14—were notably different, both displaying a high sand content. The loss-on-ignition values, which range from 3.83 – 23.03%, are generally consistent with the high mineral content of the sediments, with only four ponds, Ponds 3, 6, 11 and 12, registering values of greater than 15% (Table 2). In the case of Ponds 2 and 3, the elevated organic levels may be related to the occurrence of

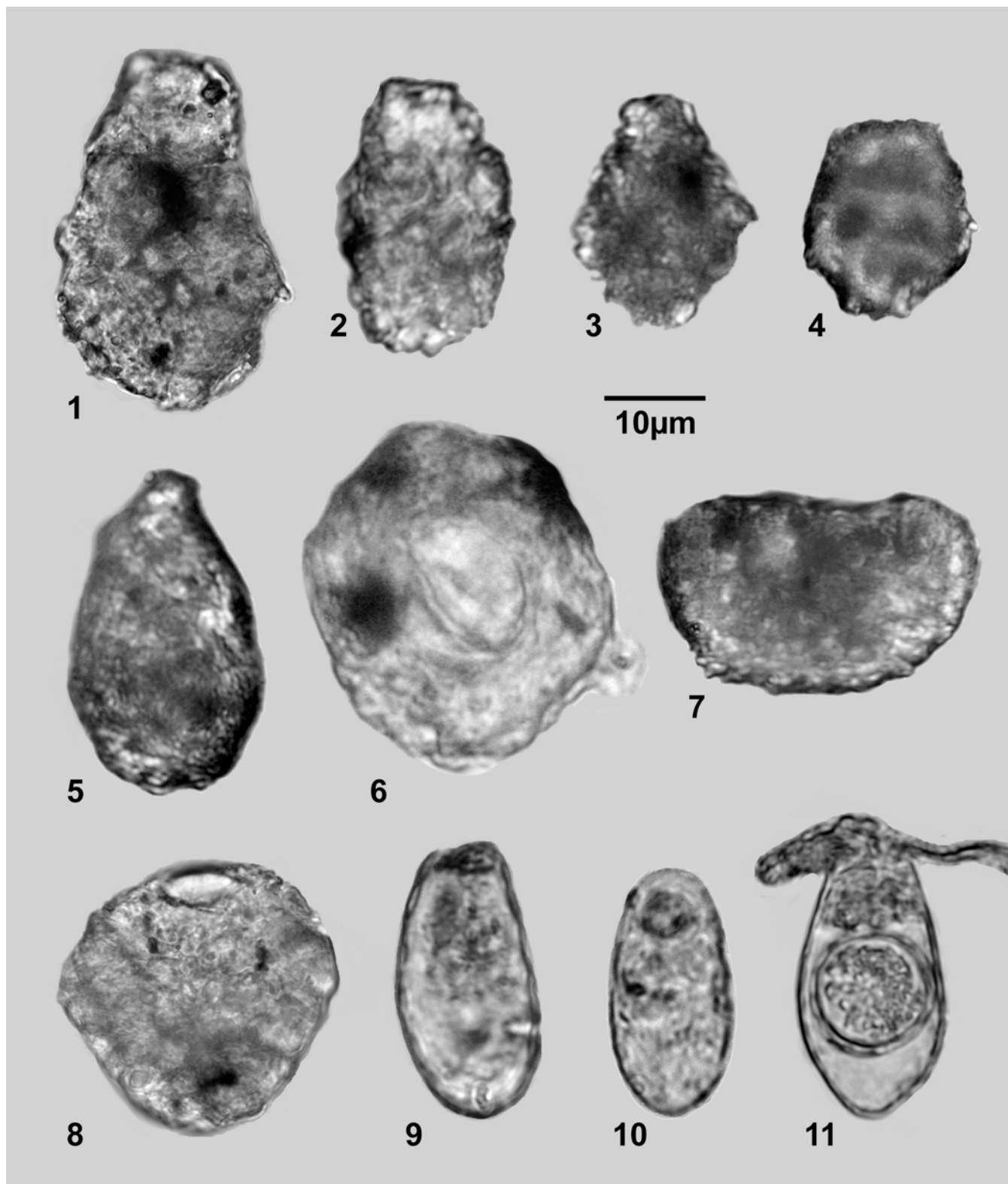
diverse bankside and aquatic plant communities and the deeper character of the ponds (Table 1). Pond 12 also supported diverse bankside vegetation and floating plants, but was substantially shallower. No clear relationship was observed between sediment composition and surrounding land use.

The sediment pH values show a strong degree of similarity between all the ponds, with each yielding a neutral to slightly alkaline pH (Table 2). This is consistent with the calcareous nature of the Quaternary coral substratum. The pH values for the two ponds overlying the Tertiary sandstones of the Scotland District did not differ from those on the coral outcrop.

The sediment-derived salinity values (in mg/L) are generally low and would be classified as being within the freshwater range (Table 2), which extends up to 500 mg/L for total dissolved salts (George and others, 1996). The conductivity values, which range from 128–826  $\mu$ S, are slightly higher than those recorded for “natural [fresh] waters” which range from 85–120  $\mu$ S (Allen and others, 1974). The samples from Ponds 13 and 3 and sample A from Pond 1 yielded the highest values of >800  $\mu$ S (Table 2). The converted values for salinity in parts per thousand are low for all the samples, and again fall within the oligotrophic (freshwater) range. Some caution must, however, be exercised in interpreting all these values, as variations in sediment texture are known to influence determinations of total salt content using the extraction method (Landon, 1991).

#### THECAMOEBIAN ASSEMBLAGES

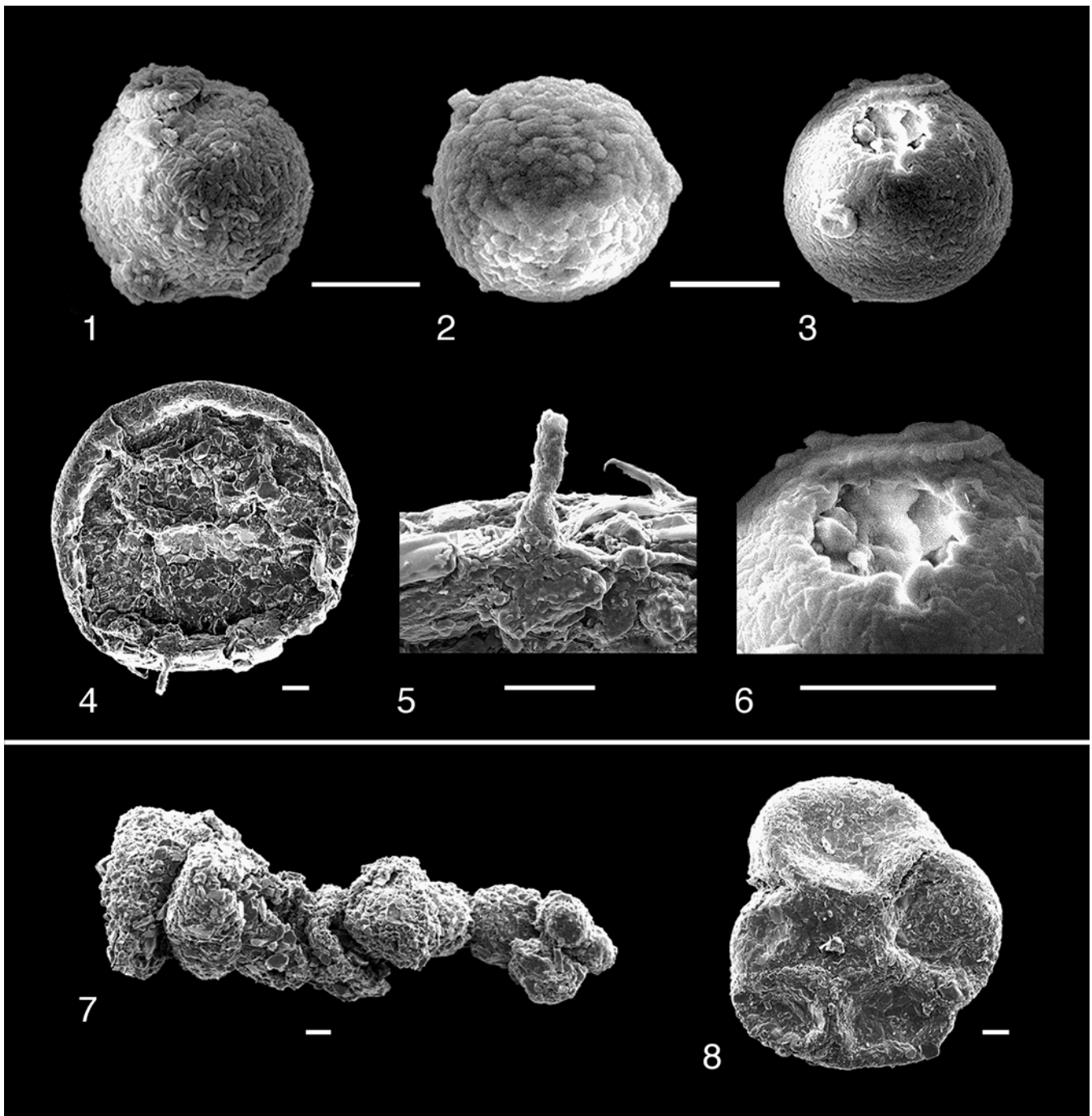
Thecamoebian distribution showed considerable variability between the 15 samples, with four samples (from Ponds 2, 3, 6 and 13) yielding moderate to high numbers of individuals (>100) and seven or more species and ‘strains’ (Patterson and Kumar, 2002), and eight samples yielding lower numbers of individuals (<100) and generally fewer species (Table 2). Four samples, from Ponds 1A, 4, 8 and 12, were barren. Fourteen species were recorded in total, whilst SDI values ranged from 0 to 1.4. Very low numbers



## PLATE 1

Scale bar = 10 µm. 1–3 *Diffflugia oblonga* Ehrenberg undifferentiated strain type. 1. Side view of pyriform specimen (Pond 13). 2. Side view of more elongated specimen (Pond 2). 3. Side view of heavily agglutinated specimen (Pond 13). 4. *Diffflugia* cf. *globula* (Ehrenberg), Side view of specimen with typical very wide aperture (Pond 13). 5. *Lesquereusia modesta* Rhumbler, side view of specimen showing difflugid-like morphology of species (Pond 10). 6. *Centropyxis aculeata* (Ehrenberg) undifferentiated strain type, Ventral view showing elongate invaginated aperture (Pond 2). 7. *Cyclopyxis kahli* Deflandre, edge view of hemispherical test (Pond 13). 8. *Cucurbitella tricuspis* Carter, oblique apertural view of specimen showing small round aboral aperture with crenulated margin (Pond 2). 9. *Euglypha rotunda* Wailes and Penard, side view of ovoid specimen with typical apertural teeth (Pond 1, Sample b). 10. *Corythion-Trinema* undifferentiated sp., side view of delicate test (Pond 1, Sample b). 11. Incerta sp. A, side view of specimen showing internal biological structures and extended pseudopodia (Pond 2).





## PLATE 2

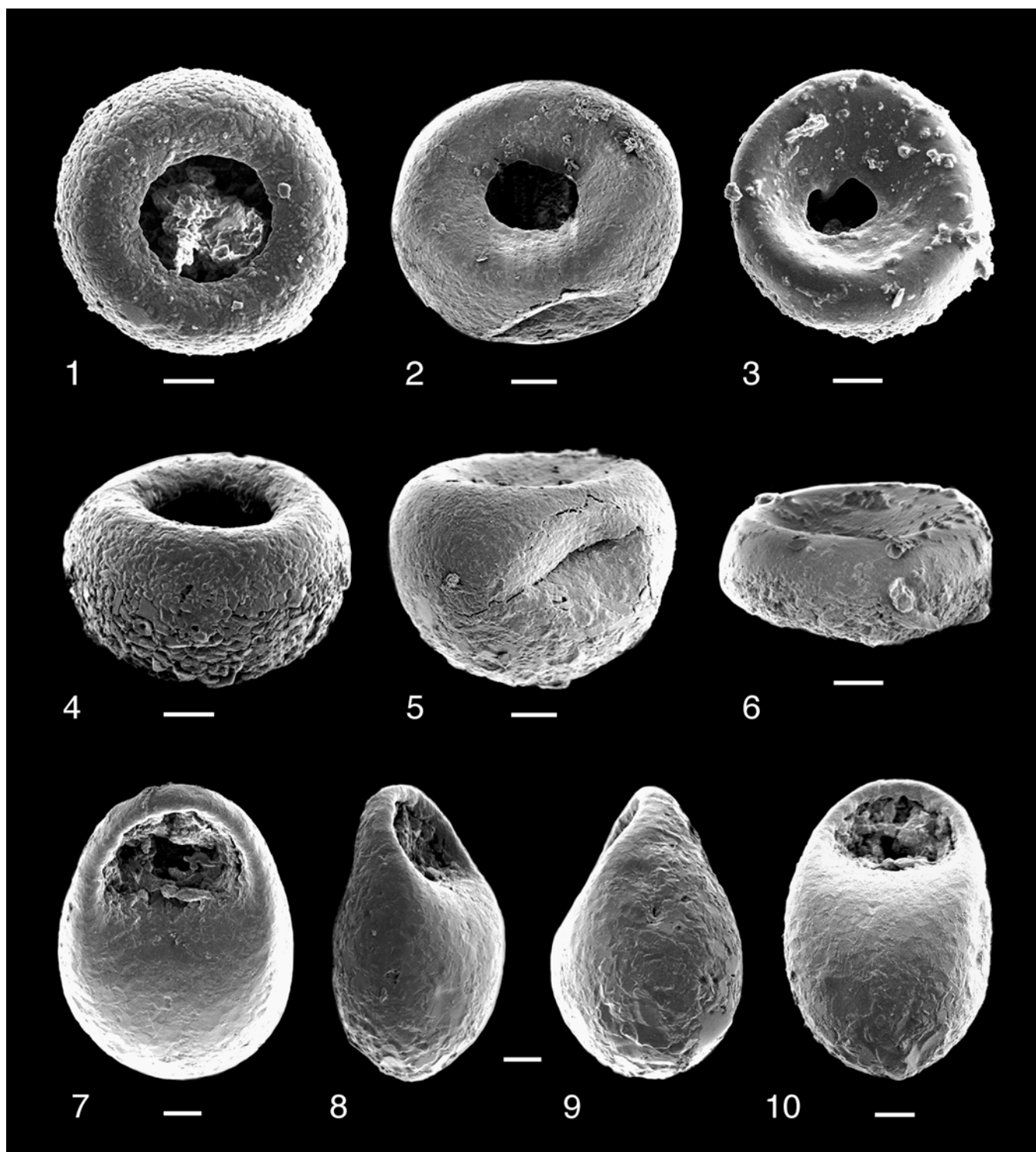
Scale bar = 10  $\mu\text{m}$ . 1–3, 6 *Cucurbitella tricuspis* Carter. All specimens from Pond 13. 1. Side view of tiny specimen with visible idiosomes. Coccolith plates are attached to the test in several places. 2. Edge view of specimen with attached coccoliths that give the appearance of basal processes under light microscopy. 3. Oblique apertural view of specimen showing small round aboral aperture. 4. Enlarged apertural view of same specimen showing crenulated aperture. 4,5. *Centropyxis aculeata* strain type “*aculeata*”. 4. Dorsal view of weakly agglutinate typical circular specimen that collapsed upon itself when removed from water; evidence of aperture on undersurface visible in central portion of test; single spine visible on lower edge (Pond 2). 5. Enlargement of spine showing nature of attachment to test surface. 7. *Polysaccamina ipohalina* Scott. Side view of typical specimen (Pond 13). 8. *Jadammina macrescens* (Brady). Dorsal view of typical weakly agglutinated specimen that has become compressed upon removal from later (Pond 13).

of live specimens (1–2 per sample) were recorded in five of the samples (Ponds 2, 3, 5, 6, and 7).

Interestingly, eleven samples yielded thecamoebians in the smaller (15–37  $\mu\text{m}$ ) size fraction. Eleven species were recorded. In some cases, notably in Ponds 9, 10 and 11,

small specimens were present when larger ones were absent. However, only in the case of Pond 13, were the numbers on a par with those in the larger fraction.

In terms of species composition, the dominant species were centropyxids, particularly *Centropyxis aculeata* (Eh-



## PLATE 3

Scale bar = 10  $\mu$ m. All specimens from Pond 13. 1–6. *Cyclopyxis kahlī* Deflandre. 1. Apertural view of typical specimen showing radially symmetrical test and large aperture. 4. Edge view of same specimen showing details of invaginated aperture; 2. Apertural view of specimen with much smaller aperture. 5. Edge view of same specimen showing hemispherical test morphology. 3. Apertural view of specimen with even smaller aperture and very smooth test surface on ventral face. 6. Edge view of same specimen showing atypical compressed morphology. 7–10. *Centropyxis constricta* strain type “*aerophila*”. 7. Apertural view showing details of invaginated aperture; 8. Oblique edge view of same specimen showing the thick apertural lip. 9. Edge view of same specimen showing distinctive sloping angle of aperture and pear shape of test, and outlines of morphology of xenosomes in the test well. 10. Face view of same specimen showing position of eccentric elliptical aperture in aboral region of test.

renberg 1832), which achieved the greatest totals in 6 of the 15 samples and dominated the assemblages of the larger size fraction. Three separate 'strains' were identified, *C. aculeata* "aculeata" (Pl. 2, figs 4, 5), *C. aculeata* "discoides" and *C. aculeata* "aerophila" (Table 1). Other common species included *Cyclopyxis kahli* Deflandre 1929 (Pl. 3, figs, 1–6), which comprised 92.2% of the >37 µm size fraction of Pond 6, and *Cucurbitella tricuspis* (Carter 1856b), which was present in eight samples in the larger fraction (Pl. 2, figs. 1–3, 6). *Arcella vulgaris* Ehrenberg 1830 was also commonly recorded, whilst *Diffflugia oblonga* Ehrenberg 1832 occurred in low numbers.

Not surprisingly, the species in the 15–37 µm size fraction included many smaller specimens of species represented in the larger fraction, notably small centropxyxids, although due to the restrictions imposed by the counting method (see discussion on Systematics below) it was often not possible to identify species strains. This fraction also included a number of species not noted in the larger fraction, including *Lesquereusia modesta* Rhumbler 1985, two small diffflugids, *Diffflugia protaeiformis* Lamarck 1816 and *Diffflugia* cf. *globula* (Ehrenberg 1848), and two idiosomic species, *Corythion-Trimema* type (Charman and others, 2000) and *Euglypha rotunda* Wailes and Penard 1911 (Pl. 3). All were represented at sparse levels of abundance. The four specimens of *E. rotunda* showed some degree of test degradation (see, for example, Pl. 1, fig. 9). Only one live specimen was encountered in this size fraction, a fresh, unidentified idiosomic specimen from Pond 13 (Pl. 1, fig. 11).

Notable in the thecamoebian assemblages of the individual ponds are the higher species (>6 species) diversities recorded in Ponds 1 (Sample 1B), 2, 6 and 13. In all of these ponds the centropxyxids showed a particularly strong presence, with varying dominances of *C. aculeata* "aculeata" and *C. aculeata* "discoides". Significantly, these four ponds were deeper and wider than many of the others, and generally showed a better development of bankside vegetation (Table 1). Only Pond 1 was exceptional in that it was characterized by relatively impoverished bankside plant communities. Nevertheless, it was similar in depth to the other ponds. Interestingly, sample 1A from Pond 1 was taken only 4 m away from sample 1B, but was barren. The proximity of this sample to an inflow pipe, its reduced organic content or the shallower depth of the water at the sampling point (20 cm in contrast to 50 cm), may account for the observed differences in thecamoebian distribution.

The assemblages from Ponds 6 and 13 are also worthy of particular note. In Pond 6 the faunas included significantly higher levels of *C. kahli* than at the other sites, which comprised 73.1% of the total in the >37 µm size fraction (Table 1). This species never exceeded 24% in the other sites, even though the remaining elements of the fauna were similar. Pond 13 was noteworthy in that it yielded high numbers of *Cucurbitella tricuspis* in the smaller size fraction (94 specimens), although this species was absent in the larger fraction (Table 2). Individual specimens were typically 19–20 µm in diameter (Pl. 2, figs. 1–3). This pond was also only one of two ponds examined in the study which yielded foraminifera (Table 2). These included a few undifferentiated and obviously reworked fossil species of

planktic foraminifera and bolivinids. Other species present included *Jadammina macrescens* (Brady) (252 individuals) and *Polysaccamina ipohalina* Scott 1976. Both are characteristic of high salt-marsh environments (Scott, 1976; Patterson, 1990). Three specimens of *J. macrescens* were also noted in Pond 15.

In general, the shallower, more ephemeral ponds, which were often characterized by impoverished bankside vegetation and more clay-rich substrates, showed poor thecamoebian preservation. Ponds 4 and 11, for example, both fell into this category. There are some notable exceptions, however. For example, Pond 7, which had a water depth of only 30 cm (estimated to be 50 cm at time of maximum flooding) yielded five species (44 specimens). The two artificially modified ponds, Ponds 8 and 14, which had very sandy substrates, were both devoid of thecamoebians, even though the latter clearly supported other larger invertebrates (see above).

## DISCUSSION

When considered as a whole, the thecamoebian assemblages described in this study show many similarities with those reported previously from other tropical and subtropical regions in that they 1) generally occur in low abundances and show only moderate to low species diversities; and 2) are dominated by centropxyxids and other faunal elements which appear to be indicative of sub-optimal environmental conditions (Green, 1963, 1975; Dalby and others, 2000; Patterson and Kumar, 2000a). The comparatively impoverished character of the faunas is confirmed by the SDI values (0–1.4), which are considerably lower than those reported in limnological studies at higher latitudes (Patterson and Kumar, 2002). In these regions, healthy thecamoebian faunas usually have SDI values >2.5 and abundances of over 500 specimens/cc (Patterson and Kumar, 2000a; Patterson and Kumar, 2002). In unfavorable environments, the SDI generally falls below 0.5 and abundances are generally between 30 – 150 specimens/cc, a trend noted in several of the Barbados samples (Patterson and Kumar, 2000a; Patterson and Kumar, 2002).

The dominance of *Centropxyxis aculeata* in the Barbados samples, and the associated occurrences of *Arcella vulgaris*, *Diffflugia oblonga* and *Cucurbitella tricuspis*, show striking similarities to the faunas reported by Dalby and others (2000) in tropical Lake Sentani in Indonesia, a 22-m-deep, oligiomictic lake which is subject to seasonal variations in fluvial inflow. Here, the prevalence of *C. aculeata* and *A. vulgaris* were considered to reflect locally stressed conditions, possibly afforded by reduced levels of oxygen, or related to other environmental variables, for example, anthropogenic activity or "conditions peculiar to tropical lakes" (Dalby and others, 2000). Interestingly, as in the present study, the faunas from Lake Sentani were also dominated by the two 'strains' *C. aculeata* "aculeata" and *C. aculeata* "discoides", although three other 'strains' were also reported. Further paleoecological work is required to examine whether or not these 'strains' have any ecological significance in tropical and other regions.

Faunas dominated by centropxyids and including several of the species recorded in the present study (notably *C. tricuspis* and *D. oblonga*) have also been reported in other tropical and subtropical sites (e.g., Haman and Kohl, 1994). One species, which has been notably absent in these previous investigations, however, is *Cyclopyxis kahli*, which dominated the fauna of Pond 6. This species is typically most common in soils and forest litter (Ogden, 1988; Wanner, 1994a, b; Wanner and Meisterfeld, 1994; Foissner, 1995; Todorov, 2002).

Arguably, one of the most significant findings of the present study is the record of eleven species of smaller thecamoebians in the 15–37  $\mu\text{m}$  size fraction. Although numbers were generally very low (often significantly less than 50 specimens counted under two  $22 \times 50$  mm coverslips), this fraction included several species that were absent in the larger fraction, including several small difflugids and rare occurrences of the idiosomic species *Corythion-Trinema* undifferentiated type and *Euglypha rotunda*. In the case of the difflugids, this finding is somewhat surprising given that the species recorded (for example, *D. protaeiformis* and *D. cf. globula*) would normally be expected to occur in the larger size range. The small nature of the specimens may imply that conditions were suboptimal for the survival of these species in the ponds under investigation. The occurrence of very high numbers of small specimens of *C. tricuspis* in Pond 13 and the absence of this species in the larger fraction may warrant a similar explanation.

To our knowledge, smaller thecamoebian species, and certainly idiosomic species such as *E. rotunda*, have never previously been reported in tropical regions, and indeed are rarely described in limnological studies in general (Roe and others, 2002; D. Charman, oral communication, 2003). This is probably not a reflection of their absence in these environments, but an artifact of the preparation and counting procedures. Since most small tests cannot be easily detected using the lower powered stereomicroscopes favored by many micropaleontologists, the smaller size fractions are generally not examined. Only in peatland studies and, more recently, in some salt marsh studies, have smaller fractions been examined using high-power, light microscopy (Warner, 1990; Hendon and Charman, 1997; Charman and others, 1998). For example, 15–63  $\mu\text{m}$  is the range typically examined in peatland studies, whilst some workers have adopted 15–300  $\mu\text{m}$  when treating salt-marsh and coastal sediments (Gehrels and others, 2001; Charman and others, 2002; Roe and others, 2002). Given the lack of previous work on equivalent size fractions in lacustrine environments, it is difficult to draw inferences based on the smaller species described in the present study as no comparable data exist. However, these results may provide some preliminary justification for modifying preparation and counting techniques in lake-based thecamoebian studies.

#### ECOLOGICAL CONTROLS ON THECAMOEBIAN DISTRIBUTION

In order to evaluate the limnological significance of the Barbados faunas, it is important to consider potential controls on their ecology, distribution and preservation, and in particular to examine possible explanations for 1) the

impoverished character of the assemblages; and 2) the variations in species composition between the ponds. As the findings of this study are based on only one or two samples per pond, any inferences that can be drawn can only be tentative, but should serve as a starting point for future investigations.

Impoverished, centropxyid-dominated faunas have previously been reported in other tropical and subtropical sites, and have been attributed, at least in the case of the Lake Sentani study of Dalby and others (2000), to stressed or suboptimal conditions. Centropxyids such as *Centropxyxis aculeata* are opportunistic species which are able to colonize environments that are unfavorable to other thecamoebian species, such as brackish environments (Declôte, 1953; Patterson and others, 1985; Guilbault and others, 1996; Boudreau and others, 2001), those with low nutrient levels and oligotrophic conditions (Schönborn, 1984), and contaminated sites (Reinhardt and others, 1998). Because comparatively few studies have been undertaken in the tropics, however, the causes of the observed centropxyid dominance and limited faunal composition remain poorly understood. It is not clear, for example, whether the faunas described reflect conditions that are unique to the sites which have been investigated (e.g., pH characteristics, substrate type, vegetation or reduced oxygen levels), or whether they are related to a wider set of variables such as high water temperatures, which are common to tropical regions in general. The issue of test preservation in tropical environments is also uncertain, but remains a key consideration when interpreting faunal distribution.

Previous research has indicated that centropxyids are intolerant of low-pH (<5.5) conditions (Patterson and others, 1996; Reinhardt and others, 1998). The results of the present study confirm that centropxyid-dominated faunas prefer neutral to slightly alkaline conditions (pH 7.0–8.2), and that pH is not a limiting factor controlling thecamoebian distribution on Barbados. The ponds reported here are similar in character to centropxyid-dominated Lake Sentani, which gave pH readings of 6.2–7.2 (Dalby and others, 2000).

Substrate characteristics appear to have had a significant influence on faunal distribution in the Barbadian samples. The absence of thecamoebians in the very sandy samples from the two artificially modified ponds, for example, indicates that particle size, and in particular the presence of coarse substrates, is a limiting factor. This finding is consistent with the results of studies in higher latitude regions, where thecamoebian faunas have been found to be considerably reduced on coarser substrates (Patterson and Kumar, 2002). The presence of depauperate faunas under these coarse substrate conditions may be linked to either a lack of nutrients in the winnowed substrate, or an absence of sufficient fine sediment to support test construction.

The near absence of difflugids from the ponds may also be substrate-related. Most samples examined were clay- or silt-dominated and sometimes included low proportions of organic matter. Since difflugids require slightly coarser (i.e., fine sand-sized) mineral grains to construct their tests, they may be rare or absent on very fine substrates (Haman, 1982; Medioli and Scott, 1983; Patterson and others, 1985). Interestingly, slightly higher difflugid numbers were re-

ported from Ponds 13 and 3, which both included some fine sand (Table 2).

Sediment organic content also appears to have had an impact on faunal composition and species numbers. The ponds with the highest species diversities and numbers of individuals were nearly always associated with samples that yielded loss on ignition values  $>8\%$ , or were noticeably more organic in appearance (Table 2). Not surprisingly, many of these ponds were also associated with richer bankside and obligate aquatic vegetation. These results are consistent with findings from many other regions where a strong association between vegetation and species abundance has been noted (Medioli and Scott, 1983; Scott and Medioli, 1983; Patterson and others, 1996).

One particular element of the fauna which may be closely associated with pond vegetation is *Cucurbitella tricuspis*. This species has been described previously in lakes with high levels of green algae and is often associated with eutrophic conditions (Medioli and others, 1987; Patterson and Kumar, 2002). It was present in low frequencies in seven of the ponds studied, and was particularly prevalent in the small size fraction of Pond 13. This pond, which is illustrated in Fig. 4, did not have noticeably high levels of algae, although the waters were somewhat stagnant in appearance (see above). Interestingly, Pond 3, which yielded 5.8% of *C. tricuspis* in the 37–250  $\mu\text{m}$  size fraction, supported algae in the shallow bankside areas, although the very shallow Pond 4, which was characterized by a wide algal scum around its margins, included no record of this species and was indeed devoid of thecamoebians. It is worthy of note that this species has also been linked to high amounts of algae in New Brunswick, Canada (Honig and Scott, 1987) and in Lake Erie (Scott and Medioli, 1983). Further research is required to assess the potential utility of *C. tricuspis* as an algal indicator species in the Caribbean region.

It is more difficult to evaluate the role of water depth on the Barbados pond faunas, because only one sample was taken from most of the ponds and this was rarely at the deepest point. The water levels of the ponds also appear to fluctuate quite dramatically even over short timescales (hours to days) in association with highly variable seasonal rainfall. Very heavy rains in the days prior to sampling may have resulted in many ponds being somewhat over-full, and hence not typical, at the time of sampling. Notwithstanding these problems, it is clear that the deeper, more permanent ponds generally support the richest faunas. Of arguably greater significance is the finding that thecamoebians are able to survive in even the shallowest ( $<0.5$  m), ephemeral ponds, albeit with depressed faunal diversities and low abundances. This result may imply that these ponds never completely dry out, or if they do, the soil must remain moist all year round. Alternatively, the thecamoebians may encyst during dry phases. Further analysis of the relationship between pond depth, seasonal rainfall intensities and faunal composition is required. The method of pond colonization by thecamoebians is also a related consideration. This may be linked to avian transport (Patterson and others, 1997), although given the significantly high rainfall on the island, input via surface runoff may provide an additional colonization vector.

The role played by land use on the pond faunas is generally difficult to determine because of the considerable variety of land use types reported, even around individual ponds. The various commercial activities noted (e.g., the presence of a mill next to Pond 3, and the junkyard near to Pond 2) appear to have left no directly detectable imprint on the faunas. Soil erosion related to agricultural activities may, however, have had an impact on the faunal composition of Pond 6. The dominant thecamoebian in that small water body was the soil indicator species *Cyclopyxis kahli*. The water in that pond was very dark from the input of sediment from the surrounding fields following the heavy rains prior to sampling. *Cyclopyxis kahli* was probably transported into the pond with the eroding sediment.

A further potential control on the faunal composition of the ponds that is worthy of note is the role played by salt inputs, which appear to be a consideration for Pond 13. This yielded significant numbers of foraminiferal species, notably *J. macrescens* and *P. ipohalina*, which both typically occur in brackish, high salt-marsh environments (Scott, 1976; Scott and Martini, 1982; Patterson, 1990). Although Pond 13 also contained significant numbers of obviously reworked planktic foraminiferal species and bolivinids probably derived from the adjacent Tertiary highlands, the sparsely agglutinated *J. macrescens* and even more delicate *P. ipohalina* would not withstand significant transport. Although rose Bengal staining detected no living foraminiferal specimens, the presence of another typical marsh foraminiferal species, *Miliammina fusca*, in Pond 13 also supports the hypothesis that this population is endemic. Such a nonmarine occurrence of foraminifera would not be unique as there are many documented occurrences of this type (e.g., Patterson and others, 1990; Boudreau and others, 2001; Javaux and Scott, 2003). Unfortunately, no direct measurement of pond-water salinity was taken at the time of collection. Although the results of the sediment-derived conductivity and salinity analyses suggest that dissolved salts were slightly higher here than in some of the other ponds, they did not indicate that the lake was characterized by brackish waters (i.e., above 5‰; Table 2). However, the actual levels of dissolved salts in the sediment may have been slightly undercalculated because of problems associated with the extraction methodology (see above). Salinity values may also have become depressed in the pond following several days of torrential rains just prior to sampling. If Pond 13 is indeed very slightly brackish, then the salt water is most probably related to the development of a fresh-water - salt water mixing zone that is known to have penetrated many more low-lying coastal areas around the island and has significantly influenced the salinity of local groundwaters (Humphrey, 1997). The input of airborne salts from Atlantic winds also provides an alternative explanation.

## SUMMARY

1. Fifteen shallow ponds were sampled from a variety of environmental settings on the island of Barbados in order to examine thecamoebian distribution and

preservation in a Caribbean setting. Seven of the ponds yielded faunas, which were characterized by moderate to low numbers of individuals (>150) and generally low species diversities. Fourteen species were recorded in total. Four samples were barren. Shannon–Wiener Diversity Index values ranged from 0–1.4.

2. The faunas were dominated by centropyxids, particularly *Centropyxis aculeata*, with subsidiary levels of *Arcella vulgaris*, *Cucurbitella tricuspis* and *Diffflugia oblonga*. Some species not previously described in tropical regions were noted, including the small idiosomic species *E. rotunda* and *Corythion-Trinema* undifferentiated type. This record may be an artifact of sample preparation (which included analysis of the 15–37  $\mu\text{m}$  size fraction) rather than the absence of these species in other regions. The record of these and several other very small species in this study may provide some preliminary justification for modifying preparation and counting procedures in lake-based thecamoebian studies.
3. Preliminary results, based on a sampling set of 16 samples, suggest that the most important ecological controls on thecamoebian distribution on the island are 1) substrate characteristics (including both particle size and organic content); 2) the character of bankside vegetation; and 3) water depth. The role of high annual temperatures is less certain. In general, however, the faunas are indicative of stressed, suboptimal environments. No significant relationship appears to exist between thecamoebian faunas and land use, although some types of agriculture may have an impact in introducing reworked species from damp soils. Further work on the ecological controls on thecamoebian distribution and preservation is required.
4. At two inland pond localities, thecamoebians were found to co-exist with salt-marsh foraminifera. Reworking of these foraminiferal specimens can be overruled. In the case of one of these ponds, numbers were substantive (>250). The occurrence of favorable conditions for foraminifera in the ponds may be related to 1) a saltwater wedge that has invaded local ground water bodies in coastal regions; or to 2) input of salts from Atlantic winds. Foraminifera may have been directly introduced into the ponds by avian transport (Patterson and others, 1990, 1997). Additional research is required to investigate this.
5. The results of the study suggest that thecamoebians may hold some potential as environmental indicators in tropical environments, particularly for the assessment of climate-induced vegetation or precipitation (e.g., water table) changes.

#### SYSTEMATIC PALEONTOLOGY

Thecamoebians are an artificial, polyphyletic grouping of testate amoeboid protozoans within the subphylum Sarcodina Schmarida, 1871, that includes the orders Gromida Claparede and Lachmann, 1859, Arcellinida Kent 1880 and part of the suborder Allogromiina Loeblich and Tappan,

1961, of the Order Foraminifera Eichwald, 1830 (Loeblich and Tappan, 1964). They are classified into species based on the nature of their pseudopodia (filose or lobose), and especially for fossil material, the nature of the generally very simple sac-like or cap-like test that protects the amoeboid sarcodine cell (Bonnet, 1975; Mediolli and Scott, 1983; Mediolli and others, 1987, 1990; Beyens and Meisterfeld, 2001).

Considerable taxonomic confusion surrounds the group due to the proliferation of species names. These difficulties have partly arisen because a considerable proportion of systematic research on the group has concentrated on describing new species of regional interest without wider consideration of previous work elsewhere (Mediolli and others, 1987; Patterson and Kumar, 2002). Different methods of sample preparation and analysis have also contributed to the taxonomic problems.

In peatlands research, for example, sample residues are typically mounted under cover slips and analyzed using high-power, bright-field microscopy (Warner, 1990; Hendon and Charman, 1997; Charman and others, 2000). The approach provides an optimal method for identifying the smaller species (typically idiosomic species) that dominate in these environments (Charman and others, 2000), but poses problems for identification of larger, agglutinated specimens, which cannot be readily turned under coverslips or viewed in three dimensions. As a result, peatlands researchers place an increased emphasis on morphometric criteria (e.g., length: breadth ratios) as a basis for species classification (Charman and others, 2000). “The (typical) taxonomic approach adopted is to divide the assemblages into the largest number of taxa (species) possible, in order to give more detailed ecological information on each morphotype” (Bobrov and others, 1999). This numerical taxonomic methodology may provide a rigorous method for the classification of species in two dimensions, but creates difficulties when used in combination with natural classification schemes.

For thecamoebians from lacustrine environments, Mediolli and Scott (1983) proposed a possible solution to the taxonomic ‘over-splitting’ problem. They considered thecamoebian species to be widely variable groups that collectively, for any given wild population, accommodate at least 75% of the entire population. Although this approach is somewhat subjective, it does make allowance for the considerable observed morphological variability in the group and does not preclude designation of informal infraspecific strains (e.g., Mediolli and Scott, 1988; Mediolli and others, 1987; Asioli and others, 1996; Reinhardt and others, 1998; Dalby and others, 2000; Kumar and Patterson, 2000; Patterson and Kumar, 2000a, 2000b, 2002). Although such infraspecific strains are not considered valid according to the International Code of Zoological Nomenclature (ICZN), their informal use is often useful in paleoecological studies (Patterson and Kumar, 2002; Dalby, 2002) and is the approach followed here. For consistency, the smaller specimens analyzed in the 15–37  $\mu\text{m}$  size fraction were, where possible, described using the same nomenclature. In cases where identification of ‘distinct’ strains was not possible, specimens were classified

only to species level. Only abbreviated systematic descriptions are included.

Subphylum SARCODINA Schmarda 1871  
Class RHIZOPODEA von Siebold 1845  
Subclass LOBOSA Carpenter 1861  
Order ARCELLINIDA Kent 1880  
Superfamily ARCELLACEA Ehrenberg 1830

Family ARCELLIDAE Ehrenberg 1830  
Genus *Arcella* Ehrenberg 1830  
*Arcella vulgaris* Ehrenberg 1830

*Arcella vulgaris* EHRENBERG 1830, p. 40, pl. 1, fig. 6

*Diagnosis*: Test depressed, hyaline, and autogenous, with an invaginated aperture.

Family CENTROPYXIDIDAE Deflandre 1953  
Genus *Centropyxis* Stein 1859  
*Centropyxis aculeata* (Ehrenberg 1832)  
Strain type "aculeata"  
(Pl. 2, figs. 4,5)

*Arcella aculeata* EHRENBERG 1832, p. 91

*Diagnosis*: Test depressed, circular, with 1–8 spines on posterolateral margin.

*Centropyxis aculeata* (Ehrenberg 1832)  
Strain type "discooides"

*Arcella discooides* EHRENBERG 1843, p. 139  
*Arcella discooides* Ehrenberg, EHRENBERG 1872, p. 259, pl. 3, fig. 1  
*Arcella discooides* Ehrenberg, LEIDY 1879, p. 173, pl. 28, figs. 14–38  
*Centropyxis aculeata* var. *discooides* PENARD 1890, p. 150, pl. 5, figs. 38–41

*Centropyxis discooides* Penard [sic], OGDEN and HEDLEY 1980, p. 54, pl. 16, figs. a–e

*Diagnosis*: Test depressed, circular (almost 'doughnut shaped'), without spines.

*Centropyxis aculeata* (Ehrenberg 1832)  
Strain type: undifferentiated  
(Pl. 1, fig. 6)

*Arcella aculeata* EHRENBERG 1832, p. 91

*Remarks*: Due to the problems associated with manipulating agglutinated thecamoebians under coverslips (see above), it was not possible to identify strains for many of the smaller specimens of *C. aculeata* counted within the 15–37  $\mu$ m size fraction.

*Centropyxis constricta* (Ehrenberg 1843)  
Strain type: "aerophila"  
(Pl. 3, figs. 7–10.)

*Arcella constricta* EHRENBERG 1843, p. 410, pl. 4, fig. 35; pl. 5, fig. 1  
*Centropyxis aerophila* DEFLANDRE 1929

*Centropyxis aerophila* Deflandre OGDEN and HEDLEY 1980, p. 48–49  
*Cucurbitella* [sic.] *constricta* REINHARDT et al. 1998, pl. 1, fig. 6

*Diagnosis*: Test shape varies from spherical to subspherical and elongated. It is characterized by an invaginated aperture in antero-marginal position with a very high, thick, apertural lip.

Genus *Cyclopyxis* Deflandre 1929  
*Cyclopyxis kahli* (Deflandre 1929)  
(Pl. 1, fig. 7, Pl. 3, figs. 1–6)

*Centropyxis kahli* Deflandre, 1929, p. 330  
*Cyclopyxis kahli* (Deflandre) OGDEN and HEDLEY 1980, p. 70–71, Pl. 24, Figs. a–e

*Diagnosis*: Planoconvex, radially symmetrical, hemispherical test. Aperture circular, large and symmetrical.

Family DIFFLUGIDAE Stein 1859  
Genus *Diffflugia* Leclerc in Lamarck 1816  
*Diffflugia* cf. *globula* (Ehrenberg 1848)  
(Pl. 1, fig. 4)

*Arcella globulus* EHRENBERG 1848, p. 379

*Diffflugia globulus* (Ehrenberg) MEDIOLI and SCOTT 1983, p. 24–25, Pl. 5, Figs. 1–15

*Diagnosis*: Test spheroidal to ellipsoidal (up to 20% longer than wide) with terminal and generally wide, slightly invaginated aperture.

*Remarks*: Identification is not entirely certain due to problems associated with manipulating agglutinated thecamoebians 15–37  $\mu$ m in size under coverslips (see above). The species was not identified in the larger 37–250  $\mu$ m size fraction.

*Diffflugia oblonga* Ehrenberg 1832  
Strain type: "oblonga"

*Diffflugia oblonga* EHRENBERG 1832, p. 90

*Diffflugia oblonga* Ehrenberg OGDEN and HEDLEY 1980, p. 148, pl. 63, figs. a–c

*Diffflugia oblonga* Ehrenberg HAMAN 1982, p. 367, Pl. 3, Figs. 19–25  
*Diffflugia oblonga* Ehrenberg SCOTT and MEDIOLI 1983, p. 818, figs. 9a–b

*Diagnosis*: Test elongated, pyriform, flask-shaped, or ovoid; fundus subrounded to rounded; tapered neck; aperture narrow and circular with crenulated lip; test made of generally medium to fine sand grains.

*Diffflugia oblonga* Ehrenberg 1832  
Strain type: undifferentiated  
(Pl. 1, figs. 1–3)

*Diffflugia oblonga* EHRENBERG 1832, p. 90

*Remarks*: Due to problems associated with manipulating agglutinated thecamoebians under coverslips it was not possible to identify strains of *D. oblonga* with confidence within the 15–37  $\mu$ m size fraction.

*Diffflugia protaeiformis* Lamarck 1816  
Strain type: undifferentiated

*Diffflugia protaeiformis* LAMARCK 1816, p. 95 (with reference to material in a manuscript by Leclerc).

*Description*: Test elongated, almost cylindroconical; fundus acuminate, tapering to occasionally form a blunt spine; neck absent; aperture circular, narrow, without lip.

Family HYALOSPHEINIIDAE Schulze 1877  
Genus *Cucurbitella* Penard, 1902  
*Cucurbitella tricuspis* (Carter 1856b)  
(Pl. 2, figs. 1–3, Pl. 3, fig. 8)

*Diffflugia tricuspis* CARTER 1856b, p. 221, fig. 80  
*Cucurbitella tricuspis* (Carter) MEDIOLI, SCOTT, and ABBOTT 1987, p. 42, pls. 1–4, text figs. 1, 4

*Diagnosis*: Test egg- to vase-shaped, comprised of small to large, rounded to elongate idiosomes, or a mixture of idiosomes and xenosomes of varying composition. The crenulated aperture has a variable number of teeth ranging from three to twenty, depending on the number of teeth on the parent test.

Genus *Lesquereusia* Schlumberger 1845  
*Lesquereusia modesta* Rhumbler 1985  
(Pl. 1, fig. 5)

*Lesquereusia modesta* RHUMBLER 1895

*Diagnosis*. Shell primarily of xenosomes with very few idiosomic plates. Has *Diffflugia*-like appearance; neck short and broad, slightly turned to one side.

Class RETICULAREA Lankester 1885  
Subclass FILOSIA Leidy 1879  
Order GROMIDIA Claparede and Lachmann 1859  
Superfamily EUGLYPHACEA Wallich 1864  
Family EUGLYPHIDAE Wallich 1864  
Genus *Euglypha* Dujardin 1841  
*Euglypha rotunda* Wailes and Penard 1911  
(Pl. 1, fig. 9)

*Euglypha rotunda* WAILES AND PENARD 1911, p. 41, Pl. 4, fig. 19

*Diagnosis:* Test ovoid, varies in transverse section from circular to oval as it tapers from the mid-body region to the aboral region; test comprised of approximately 120 oval shell-plates; aperture circular and surrounded by 8–14 evenly spaced apertural plates. Each apertural plate is ovoid, thickened at the denticulate margin, and with a large median tooth bordered by two or three smaller teeth.

Family **TRINEMATIIDAE** Hoogenraad and Groot, 1940  
Subfamily **TRINEMATINAE** Hoogenraad and de Groot, 1940  
Genera *Trinema* Dujardin 1841 and *Corythion* Taránek 1882  
*Corythion-Trinema* undifferentiated sp.  
(Pl. 1, fig. 10)

*Corythion-Trinema* type CHARMAN, HENDON, and WOODLAND 2000 p. 106, 107, fig. 31a

*Diagnosis:* Test elongate, ovoid in lateral view. Circular aperture. Test composed of siliceous plates, not visible under light microscopy. Almost translucent in appearance.

*Remarks:* Trinematinae, particularly in the 15–37 µm size range observed here, are difficult to differentiate. This is because the tests of species in the group are often very delicate with thin walls, and are comprised of fine plates, which are difficult to see. The specimens observed here are either referable to *Trinema* sp. or *Corythion* sp.

Order Foraminiferida Eichwald 1830  
Suborder TEXTULARIINA Delage and Hérouard 1896  
Superfamily ASTROORHIZACEA Brady 1881  
Family Polysaccamminidae Loeblich and Tappan 1984  
Genus *Polysaccammina* Scott 1976  
*Polysaccammina ipohalina* Scott 1976  
(Pl. 2, fig. 7)

*Polysaccammina ipohalina* SCOTT 1976, p. 319, 320, text figure 4, pl. 2 figs. 1–4

*Diagnosis:* Agglutinated test characterized by irregularly shaped chambers that increase in size as added.

Superfamily RZEHAKINACEA Cushman 1930  
Family RZEHAKINIDAE Cushman 1930  
Genus *Miliammina* Heron-Allen and Earland 1930  
*Miliammina fusca* (Brady) 1870

*Quinqueloculina fusca* BRADY in BRADY and ROBERTSON 1870, p. 286, pl. 11, fig. 2

*Miliammina fusca* (Brady) PATTERSON 1990, p. 240, pl. 1, fig. 4

Superfamily TROCHAMMINACEA Schwager 1877  
Family TROCHAMMINIDAE Schwager 1877  
Subfamily JADAMMININAE Saidova 1981  
*Jadammina* Bartenstein and Brand 1938  
*Jadammina macrescens* (Brady) 1870  
(Pl. 2, fig. 8)

*Trochammina inflata* Montagu var. *macrescens* BRADY in BRADY and ROBERTSON 1870, p. 290, pl. 11, fig. 5a–c

*Jadammina polystoma* BARTENSTEIN and BRAND 1938, p. 381, figs. 1a–c, 2a–l, 3

*Trochammina macrescens* Brady SCOTT and MEDIOLI 1980b, p. 44, pl. 3, figs. 1–8

*Jadammina macrescens* (Brady) PATTERSON 1990, p. 239, pl. 2, figs. 7–9

## INCERTA

*Incerta* sp. A  
(Pl. 1, fig. 11)

*Remarks:* Unknown idiosomic thecamoebian species with pseudopods and internal biological structures visible.

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## REFERENCES

- ALLEN, S. E., GRIMSHAW, H. M., PARKINSON, J. A., and QUARMBY, C., 1974, Chemical analysis of ecological materials: Blackwell Scientific Publications, Oxford, 565 p.
- ARCHER, W., 1866, Quarterly Journal of Microscopical Science, new series, v. 6, p. 185–188.
- ASIOLI, A., MEDIOLI, F. S., and PATTERSON, R. T., 1996, Thecamoebians as a tool for reconstruction of paleoenvironments in some Italian lakes in the foothills of the southern Alps (Orta, Varese and Candia): Journal of Foraminiferal Research, v. 26, no. 3, p. 248–263.
- BANNER, J. L., MUSGROVE, M. L., and CAPO, R. C., 1994, Tracing ground-water evolution in a limestone aquifer using Sr isotopes: Effects of multiple sources of dissolved ion and mineral-solution reactions: Geology, v. 22, p. 687–690.
- BARTENSTEIN, H., and BRAND, E., 1938, Die Foraminiferen-Fauna des Jade-Gebietes; 1. *Jadammina polystoma* n. g., n. sp. aus dem Jade-Gebiet: Senckenbergiana, Frankfurt on Main, v. 20, p. 381–385.
- BEYENS, L., and MEISTERFELD, R., 2001, Protozoa: testate amoebae, in Smol, J. P., Birks, H. J. B., and Last, W. M. (eds.), Tracking Environmental Change Using Lake Sediments: Biological Techniques and Indicators (v. II): Dordrecht, Kluwer, p. 121–153.
- BOBROV, A. A., CHARMAN, D. J., and WARNER, B. G., 1999, Paleoecology of testate amoebae (Protozoa: Rhizopoda) on peatlands in western Russia with special attention to niche separation in closely related taxa: Protist, v. 150, p. 125–136.
- BONNET, L., 1975, Types morphologiques, écologie et évolution de la thèque chez les thécamoebiens: Protistologica, v. 11, p. 363–378.
- BOOTH, R. K., and JACKSON, S. T., 2003, A high-resolution record of late-Holocene moisture variability from a Michigan raised bog, USA: Holocene, v. 13, p. 863–876.
- BOUDREAU, R. E. A., PATTERSON, R. T., MCKILLOP, W. B., and DALBY, A. D., 2001, Non-Marine occurrence of the foraminifer *Cribroelphidium gunteri* in Lake Winnipegosis, Manitoba: Journal of Foraminiferal Research, v. 32, p. 108–119.
- , GALLOWAY, J. M., PATTERSON, R. T., KUMAR, A., and MICHEL, F. A., 2005, A paleolimnological record of Holocene climate and environmental change in the Temagami region, northeastern Ontario: Journal of Paleolimnology, v. 33, p. 445–461.
- BRADY, G. S., and ROBERTSON, D., 1870, The ostracoda and foraminifera of tidal rivers with an analysis and description of the foraminifera: Annual Magazine of Natural History, v. 6, p. 273–309.
- CANADIAN INTERNATIONAL DEVELOPMENT AGENCY (CIDA), 1985, Sentani Lake Hydro Electric Development Assessment: Government of Canada Report.
- CARTER, H. J., 1856a, Notes on the fresh water Infusoria of the island of Bombay. No 1 Organization: Annals and Magazine of Natural History, ser. 2, v. 18, no. 104, p. 115–132.
- , 1856b, Notes on the freshwater Infusoria of the island of Bombay. No. 1. Organization: Annals and Magazine of Natural History, ser. 2, v. 18, no. 105, p. 221–249.
- , 1864, On fresh water rhizopoda of England and India: Annals and Magazine of Natural History, ser. 3, v. 13, p. 18–39.
- , 1865, On the fresh and salt water Rhizopoda of England and India: Annals and Magazine of Natural History, ser. 3, v. 15, p. 277–293.
- CASH, J., and HOPKINSON, J., 1905, The British freshwater Rhizopoda and Heliozoa: Vol. II: Rhizopoda, Part II: Ray Society, London, 151 p.
- CHARMAN, D., ROE, H. M., and GEHRELS, W. R., 1998, The use of testate amoebae in studies of sea-level change: a case study from the Taf Estuary, south Wales, UK: Holocene, v. 8, p. 209–218.



- , HENDON, D., and WOODLAND, W., 2000, The identification of peatland testate amoebae: Quaternary Research Association Technical Guide no. 9, London, 147 p.
- , ROE, H. M., and GEHRELS, W. R., 2002, Modern distribution of saltmarsh testate amoebae: regional variability of zonation and response to environmental variables: *Journal of Quaternary Science*, v. 17 (5–6), p. 387–409.
- COLLINS, E. S., MCCARTHY, F. M., MEDIOLI, F. S., SCOTT, D. B., and HONIG, C. A., 1990, Biogeographic distribution of modern thecamoebians in a transect along the eastern North American coast, in Hemleben, C., Kaminski, M. A., Kuhnt, W., and Scott, D. B. (eds.), *Paleoecology, Biostratigraphy, Paleocyanography and Taxonomy of Agglutinated Foraminifera: North Atlantic Treaty Organization Advanced Study Institute Series, Series C, Mathematical and Physical Sciences*, v. 327, p. 783–791.
- DALBY, A. P., 2002, Application of multivariate statistical and analytical techniques in the examination of lacustrine acellacean data from southwestern New Brunswick: Unpublished Carleton University Ph.D. Dissertation, 278 p.
- , KUMAR, A., MOORE, J. M., and PATTERSON, R. T., 2000, Utility of arcellaceans (thecamoebians) as paleolimnological indicators in tropical settings: Lake Sentani, Irian Jaya, Indonesia: *Journal of Foraminiferal Research*, v. 30, p. 135–142.
- DAY, M. J., 1983, Doline morphology and development in Barbados: *Annals of the Association of American Geographers*, v. 73, p. 206–219.
- DECLÔTRE, L., 1953, Recherches sur les Rhizopodes thecamoebiens d'A.O.F. (Suite). Faune du Lac Tamna (Senegal): *Bulletin Institut Français d'Afrique Noire*, v. 31, 249 p.
- DEFLANDRE, G., 1928, Le genre *Arcella* Ehrenberg. Morphologie - Biologie. Essai phylogénétique et systématique. *Archiv fuer Protistenkunde: Protozoen-Algen-Pilze*, v. 64, p. 152–287.
- , 1929, Le genre *centropyxis* Stein: *Archiv fur Protistenkunde*, v. 67, p. 323–375.
- DUJARDIN, F., 1841, Sur une nouvelle espèce de *Gromia* et sur les Difflogies: *Annales des Sciences Naturelles*, ser. 2, v. 8, p. 310–313.
- EHRENBERG, C. G., 1830, Organisation, Systematik und Geographisches Verhältnis der Infusionstierchen: *Druckerei der Könlichen Akademie der Wissenschaften*, Berlin, 108 p.
- , 1832, Über die Entwicklung und Lebensdauer der Infusionstiere, nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme: *Königliche Akademie der Wissenschaften zu Berlin Physikalische Abhandlungen*, v. 1831, p. 1–154.
- , 1843, Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord Amerika: *Königliche Akademie der Wissenschaften zu Berlin Physikalische Abhandlungen*, v. 1841, p. 291–446.
- , 1848, Fortgesetzte Beobachtungen über jetzt herrschende atmosphärische mikroskopische Verhältnisse: Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, v. 13, p. 370–381.
- , 1872, Nachtrag zur Übersicht der organischen Atmosphärien: *Königliche Akademie der Wissenschaften zu Berlin Physikalische Abhandlungen*, v. 1871, p. 233–275.
- FERMOR, J., 1972, The dry valleys of Barbados: *Transactions of the Institute of British Geographers*, v. 57, p. 153–165.
- FOOD AGRICULTURAL ORGANIZATION (FAO), Inland Fisheries Development in West Irian: Report on Project Results, Conclusions and Recommendations, KW: Irian Jaya.
- FOISSNER, W. M., 1995, Redescription of three testate amoebas (Protozoa: Rhizopoda) from a Caucasian soil: *Centropyxis Plagiostoma* Bonnet and Thomas, *Cyclopyxis kahli* (Deflandre) and *Cyclopyxis intermedia* Kufferath: *Archiv für Protistenkunde*, v. 146, p. 1328.
- GEHRELS, W. R., ROE, H. M., and CHARMAN, D. J., 2001, Foraminifera, testate amoebae and diatoms as sea-level indicators in UK saltmarshes: a quantitative multiproxy approach: *Journal of Quaternary Science*, v. 16, no. 3, p. 201–220.
- GEORGE, R. J., WEAVER, D., and TERRY, J., 1996, Environmental water quality: a guide to sampling and measurement: Agriculture Western Australia, Perth, Publication no. 16.
- GREEN, J., 1963, Zooplankton of the River Sokoto, the Rhizopoda Testacea: *Proceedings of the Zoological Society*, London, v. 141, p. 497–514.
- , 1975, Fresh water ecology in the Mato Grasso, Central Brazil, IV: Associations of Testate Rhizopoda: *Journal of Natural History*, v. 9, p. 545–560.
- GUILBAULT, J.-P., CLAGUE, J. J., and LAPOINTE, M., 1996, Foraminiferal evidence for the amount of coseismic subsidence during a late Holocene earthquake on Vancouver Island, west coast of Canada: *Quaternary Science Reviews*, v. 15, p. 913–937.
- HAMAN, D., 1982, Modern Thecamoebians (Arcellinida) from the Balize Delta, Louisiana: *Transactions of the Gulf Coast Association of Geological Societies*, v. 32, p. 353–376.
- , and KOHL, B., 1994, A thecamoebian assemblage from Lake Cocococha, Tambopata reserve, Madre de Dios province south-eastern Peru: *Journal of Foraminiferal Research*, v. 24, p. 226–232.
- HAYWARD, B. W., GRENEL, H., CAIRNS, G., and SMITH, A., 1996, Environmental controls on benthic foraminiferal and thecamoebian associations in a New Zealand tidal inlet: *Journal of Foraminiferal Research*, v. 26, no. 2, p. 150–171.
- HENDON, D., and CHARMAN, D., 1997, The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat: *The Holocene*, v. 7, p. 199–205.
- HONIG, C. A., and SCOTT, D. B., 1987, Post glacial stratigraphy and sea-level change in southwestern New Brunswick: *Canadian Journal of Earth Science*, v. 24, p. 354–364.
- HOOGENRAAD, H. R., and GROOT, A. A., 1940, Moosbewhnende thekamoebe rhizopoden von Java und Sumatra: *Treubia*, no. 17, p. 209–256.
- , and ———, 1946, Thekamoebe sphagnumrhizopoden van Buitenzorg (Java): *Biologische Jaarboek, Dodonea (Gent)*, no. 13, p. 112–126.
- HOWARD, K. T., 1987, Inland Fisheries Development Irian Jaya: Government of Indonesia UNDP/IRBD Regional Planning Investigation, Preparation and Experimental Area Development Project, Nusa Tenggara, Southeast Sulawesi and Irian Jaya.
- HUMPHREY, J. D., 1997, Geology and hydrogeology of Barbados, in Vacher, H. L., and Quinn, T. M. (eds.), *Geology and Hydrogeology of Carbonate Islands: Developments in Sedimentology*, v. 54, p. 381–406.
- JAMES, N. P., STEARN, C. W., and HARRISON, R. S., 1977, Field Guidebook to Modern and Pleistocene Reef Carbonates, Barbados, West Indies: Third International Symposium on Coral Reefs, Miami Beach, Florida, 31 p.
- JAVAUX, E. J., 1999, Benthic foraminifera from the modern sediments of Bermuda: implications for Holocene sea-level studies: unpublished Ph.D. dissertation, Dalhousie University, N.S., Canada.
- , and SCOTT, D. B., 2003, illustration of modern benthic foraminifera from Bermuda and remarks on distribution in other subtropical/tropical areas: *Palaeontologia Electronica*, v. 6, no. 1, 29p.
- KUMAR, A., and PATTERSON, R. T., 2000, Arcellaceans (Thecamoebians): new tools for monitoring long and short term changes in lake bottom acidity: *Environmental Geology*, v. 39, p. 689–697.
- , and DALBY, A. P., 1998, Identification key for Holocene lacustrine arcellacean (thecamoebian) taxa: *Palaeontologia Electronica*. (<http://www-odp.tamu.edu/paleol/>) v. 1, no. 1, 33p.
- , and PATTERSON, R. T., 1997, Arcellaceans (thecamoebians) as proxies of lake bottom acidity: An example from James Lake, northeastern Ontario: Abstract, GAC/MAC Annual Meeting, May 19–21, 1997, Ottawa, Canada, p. A-150.
- LONDON, J. R. (ed.), 1991, *Booker Tropical Soil Manual. A handbook for soil survey and agricultural land evaluation in the tropics and subtropics*: Longman Scientific and Technical, Essex, England, 474 p.
- LAMARCK, J. B., 1816, *Histoire Naturelle des Animaux sans Vertèbres*: Verdiers, Paris, v. 2, p. 1–568.
- LAMINGER, H., 1972, Notes on some terrestrial Testacea (Protozoa, Rhizopoda) from Nepal, Himalaya (Lhotse Shar): *Archiv für Protistenkunde*, v. 114, no. 4, p. 486–488.
- LLOYD, J., 2000, Combined foraminiferal and thecamoebian environmental reconstruction from an isolation basin in NW Scotland: implications for sea-level studies: *Journal of Foraminiferal Research*, v. 30, no. 4, p. 294–305.
- MCCARTHY, F. M. G., COLLINS, E. S., McANDREWS, J. H., KERR, H. A., SCOTT, D. G., and MEDIOLI, F. S., 1995, A comparison of postglacial arcellacean (“thecamoebian”) and pollen succession in

- Atlantic Canada, illustrating the potential of arcellaceans for paleoclimatic reconstruction: *Journal of Paleontology*, v. 69, p. 980–993.
- MEDIOLI, F. S., and SCOTT, D. B., 1983, Holocene Arcellacea (Thecamoebians) from eastern Canada: Cushman Foundation for Foraminiferal Research Special Publication no. 21, 63 p.
- , and ABBOTT, B. H., 1987, A case study of protozoan interclonal variability: taxonomic implications: *Journal of Foraminiferal Research*, v. 17, p. 28–47.
- , and ———, 1988, Lacustrine thecamoebians (mainly arcellaceans) as potential tools for palaeolimnological interpretations: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 62, p. 361–386.
- , COLLINS, E. S., and MCCARTHY, F. M. G., 1990, Fossil thecamoebians: present status and prospects for the future, in Hemleben, C., Kaminski, M. A., Kuhnt, W., and Scott, D. B. (eds.), *Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of Agglutinated Foraminifera*: North Atlantic Treaty Organization Advanced Study Institute Series, Series C, Mathematical and Physical Sciences, v. 327, p. 813–840.
- MOORE, J. M., ROCCHI, A., and RENYAAN, S. J., 1995, Lake Systems in Irian Jaya: Unpublished poster presentation, Biological Society of New Guinea, Annual Meeting, Tabubil, Papua New Guinea, August 27–31, 1995.
- MURRAY, J. W., and BOWSER, S. S., 2000, Mortality, protoplasm decay rate, and reliability of staining techniques to recognize “living” foraminifera: a review: *Journal of Foraminiferal Research*, v. 30, no. 1, p. 66–70.
- NAIR, K. N., and MUKHERJEE, R. N., 1968, On some testacean rhizopods (Protozoa: Sarcodina) of the ground and tree mosses from Calcutta and its environs: *Proceedings of the National Academy of Sciences of India*, v. 38b, p. 185–193.
- OGDEN, C. G., 1988, Fine structure of the shell wall in the soil testate amoeba *Cyclopyxis kahli* (Rhizopoda): *Journal of Protozoology*, v. 35, p. 537–540.
- , and HEDLEY, R. H., 1980, *An Atlas of Freshwater Testate Amoeba*: British Museum (Natural History), Oxford University Press, 222p.
- PATTERSON, R. T., 1987, Arcellaceans and foraminifera from Lake Tecopa, and eastern California Pleistocene Lake: *Journal of Foraminiferal Research*, v. 17, p. 333–343.
- , 1990, Intertidal benthic foraminiferal biofacies on the Fraser River Delta, British Columbia: modern distribution and paleoecological importance: *Micropaleontology*, v. 36, p. 183–199.
- , and FISHBEIN, E., 1989, Re-examination of the statistical methods used to determine the number of point counts needed for micropaleontological quantitative research: *Journal of Paleontology*, v. 63, no. 2, p. 245–248.
- , and KUMAR, A., 2000a, Assessment of arcellacea (thecamoebian) assemblages, species and strains as contaminant indicators in variably contaminated James Lake, north Eastern Ontario: *Journal of Foraminiferal Research*, v. 30, p. 310–320.
- , and ———, 2000b, Use of arcellacea to gauge levels of pollution and remediation of industrially polluted lakes, in Martin, R. E. (ed.), *Environmental Micropaleontology: Topics in Geobiology*. v. 15, Kluwer Academic/Plenum Publication, New York, p. 257–278.
- , and ———, 2002, A review of current testate rhizopod (thecamoebian) research in Canada: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 180, p. 225–251.
- , BARKER, T., and BURBIDGE, S. M., 1996, Arcellaceans (thecamoebians) as proxies of arsenic and mercury contamination in northeastern Ontario lakes: *Journal of Foraminiferal Research*, v. 26, p. 172–183.
- , DALBY, A., KUMAR, A., and HENDERSON, L. A., 2002, Arcellaceans as indicators of land-use change: settlement history of the Swan Lake area, Ontario as a case study: *Journal of Paleolimnology*, v. 28, p. 297–316.
- , MCKILLOP, W. B., KROKER, S., NIELSON, E., and REINHARDT, E. G., 1997, Evidence for rapid avian-mediated foraminiferal colonization of Lake Winnipegosis, Manitoba, during the Holocene Hypsithermal: *Paleolimnology*, v. 18, p. 131–143.
- , MACKINNON, K. D., SCOTT, D. B., and MEDIOLI, F. S., 1985, Arcellaceans (Thecamoebians) in small lakes of New Brunswick and Nova Scotia: modern distribution and Holocene stratigraphic changes: *Journal of Foraminiferal Research*, v. 15, p. 114–137.
- , SCOTT, D. B., and MCKILLOP, W. B., 1990, Recent marsh-type agglutinated foraminifera from Lake Winnipegosis, Manitoba: *Proceedings of the Third International Advanced Course on Paleocology, Biostratigraphy, Paleoceanography, and Taxonomy of Agglutinated Foraminifera*: NATO Advanced Study Institutes Programme, Tübingen, West Germany, 17–28 September, 1989, p. 765–781.
- PENARD, E., 1890, Études sur les Rhizopodes d’eau douce: *Mémoires de la Société de Physique et d’Histoire Naturelle de Genève*, v. 31, no. 2, p. 1–230.
- , 1899, Les Rhizopodes de faune profonde dans le lac Léman: *Revue Suisse de Zoologie*, v. 7, p. 1–142.
- , 1907, On some Rhizopods from the Sikkim Himalayas: *Royal Microscopical Society of London Journal*, p. 274–278.
- RADTKE, U., and GRÜN, R., 1990, Revised reconstruction of Middle and Late Pleistocene sea-level changes based on new chronologic and morphologic investigation in Barbados, West-Indies: *Journal of Coastal Research*, v. 6, p. 699–708.
- RANDALL, R. E., 1970, Vegetation and environment on the Barbados coast: *Journal of Ecology*, v. 58, p. 155–172.
- REINHARDT, E. G., DALBY, A. P., KUMAR, A., and PATTERSON, R. T., 1998, Utility of arcellacean phenotypic variants as pollution indicators in mine tailing contaminated lakes near Cobalt, Ontario, Canada: *Micropaleontology*, v. 44, p. 1–18.
- RHUMBLER, L., 1895, Beiträge zur Kenntnis der Rhizopoden (Beitrag III, IV, und V): *Zeitschrift für Wissenschaften Zoologie*, v. 61, p. 38–110.
- ROE, H. M., CHARMAN, D., and GEHRELS, W. R., 2002, Fossil testate amoebae in coastal deposits in the UK: implications for studies of sea-level change: *Journal of Quaternary Science*, v. 17 (5–6), p. 411–429.
- ROWELL, D. L., 1994, *Soil Science: Methods and Applications*: Longman Scientific & Technical, Essex, England, 350 p.
- SCHHELLMANN, G., RADTKE, U., and WHELAN, F., 2002, *The Coral Reef Terraces of Barbados: a Guide*: Barbados 2002- International Conference on Quaternary Sea Level Change with Field Trips and Fourth Annual Meeting of IGCP Project 437 “Coastal Environmental Change during Sea Level Highstands: A Global Synthesis with Implications for Management of Future Coastal Change”, Bamberg, 120 p.
- SCHÖNBORN, W. E., 1984, Studies on remains of Testacea in cores of the Great Warty Lae (NE Poland): *Limnologica*, v. 16, p. 185–190.
- SCOTT, D. B., 1976, Brackish-water foraminifera from southern California and description of *Polysaccamina ipohalina* n. gen., n. sp.: *Journal of Foraminiferal Research*, v. 6, p. 312–321.
- , and HERMELIN, J. O. R., 1993, A device for precision splitting of micropaleontological samples in liquid suspension: *Journal of Paleontology*, v. 67, p. 151–154.
- , and MARTINI, I. P., 1982, Marsh foraminifera zonation in western James and Hudson Bays: *Le Naturaliste Canadien*, v. 109, p. 399–414.
- , and MEDIOLI, F. S., 1980a, Post-glacial emergence curves in the Maritimes determined from marine sediments in raised basins: *Proceedings of Coastlines '80*, National Science and Engineering Research Council, p. 428–449.
- , and ———, 1980b, Quantitative studies of marsh foraminiferal distributions in Nova Scotia: implications for sea level studies: Cushman Foundation for Foraminiferal Research, Special Publication, no. 17, 57p.
- , and ———, 1983, Testate rhizopods in Lake Erie: modern distribution and stratigraphic implications: *Journal of Paleontology*, v. 57, p. 809–820.
- SUDZUKI, M., 1979, Marine interstitial Testacea from Plau Pinang, Malaysia: *Annot. Zool. Japan*, v. 52, no. 1, p. 50–53.
- TARÁNEK, K. J., 1882, *Monographie der Nebeliden Böhmen's: Ein Beitrag zur Kenntniss der Süßwasser Monothalamien*: Abhandlungen der königlichen Böhmisches Gesellschaft der Wissenschaften, v. 6, p. 1–56.
- TODD, R., and BRONNIMANN, P., 1957, Recent Foraminifera and Thecamoebina from the eastern Gulf of Paria: Cushman

- Foundation for Foraminiferal Research, Special Publication, no. 3, p. 1–25.
- TODOROV, M., 2002, Morphology, biometry and ecology of *Nebela bigibbosa* Penard, 1890 (Protozoa: Rhizopoda): *Acta Protozoologica*, v. 41, p. 239–244.
- TOLONEN, K., WARNER, B. G., and VASANDER, H., 1992, Ecology of testaceans (Protozoa: Rhizopoda) in mires in southern Finland: I. Autoecology: *Archiv für Protistenkunde*, v. 142, p. 119–138.
- TROELS-SMITH, J., 1955, Karakterisering af løse jordeter. Characterisation of unconsolidated sediments: Danmarks Geologiske Undersøgelse, ser. IV, v. 3, no. 10, 73p.
- VAN OYE, P., 1949, Rhizopodes de Java: *Bijdragen tot de Dierkunde*, v. 28, p. 327–352.
- WAILES, G. H., and PENARD, E., 1911, Clare Island Survey: Rhizopoda: *Proceedings of the Royal Irish Society*, v. 31, p. 1–64.
- WALLICH, G. C., 1864, On the extent, and some of the principal causes, of structural variation among the difflugian rhizopods: *Annals and Magazine of Natural History*, ser. 3, v. 13, p. 215–245.
- WALTON, W. R., 1952, Techniques for recognition of living Foraminifera: *Contributions from the Cushman Foundation for Foraminiferal Research*, v. 3, p. 56–60.
- WANDEL, B., 2000, Geomorphologische Detail-kartierung und chronostratigraphische Gliederung der quartären Korallenriffe auf Barbados (West Indies) unter besonderer Berücksichtigung des Karstformenschatzes: Unpublished Thesis, University of Cologne (German).
- WANNER, M., 1994a, Effects of light, fertilizers and pesticides on shell size of the common freshwater and soil species *Cyclopyxis kahli* (Rhizopoda, Testacealobosia): *Limnologica*, v. 24, p. 333–338.
- , 1994b, Biometrie der Schalen von *Cyclopyxis kahli* Deflandre (Rhizopoda, Testacealobosia) - eine Möglichkeit zur Bioindikation? *Verhandlungen Deutsche Zoologische Gesellschaft*, v. 87, p. 317.
- , and MEISTERFELD, R., 1994, Effects of some environmental factors on the shell morphology of testate amoebae (Rhizopoda, Protozoa): *European Journal of Protistology*, v. 30, p. 191–195.
- WARNER, B. G., 1987, Abundance and diversity of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum* peatland in southwestern Ontario, Canada: *Archiv für Protistenkunde*, v. 133, p. 173–189.
- , 1990, *Methods in Quaternary Ecology #5. Testate Amoebae* (Protozoa): *Geoscience Canada*, v. 5, p. 56–74.
- , and BUNTING, M. J., 1996, Indicators of rapid environmental change in northern peatlands, in Berger, A. R., and Iams, W. J. (eds.), *Geoindicators, assessing rapid environmental changes in earth systems*: A.A. Balkema, Rotterdam, p. 235–246.
- , and CHARMAN, D. J., 1994, Holocene changes on a peatland in northwestern Ontario interpreted from testate amoebae (Protozoa) analysis: *Boreas*, v. 23, p. 270–279.
- WOODLAND, W. A., CHARMAN, D. J., and SIMS, P. C., 1998, Quantitative estimates of water tables and soil moisture in Holocene peatlands from testate amoebae: *The Holocene*, v. 8, p. 261–273.

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