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Hydroecology of Amazonian lacustrine Arcellinida (testate amoebae): A case study from Lake Quistococha, Peru

R. Timothy Patterson[a,*], Gail Huckerby[a], Thomas J. Kelly[b], Graeme T. Swindles[b], Nawaf A. Nasser[a]

[a] Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario K1S 5B6, Canada
[b] School of Geography, University of Leeds, Leeds LS2 9JT, United Kingdom

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Abstract

Organic rich sediments were obtained from seven core tops taken in Lake Quistococha, near the city of Iquitos in the Peruvian Amazon. Subsamples from 0 to 4 cm depth in each core were analyzed under dissecting light microscopy to carry out the first investigation of Arcellinida (testate lobose amoebae) from a lacustrine environment in this ecologically important region. The fauna was characterized by a low diversity, low abundance community dominated by centropyxids. This fauna is similar to 'stressed' assemblages reported from temperate latitudes, except that test concentrations were two orders of magnitude lower than typical in temperate lakes. Principle arcellinidan stressors in Lake Quistococha likely include the low pH 4 conditions in the lake, and a general lack of suitable minerogenic material to construct tests in the organic rich lake substrate. The low pH conditions are the result of runoff and seepage of water high in dissolved organic carbon from the adjacent similarly low pH 4 terrestrial peatland. The dearth of minerogenic material is the result of the lake being isolated from riverine input for the past ∼2000 years, even during flooding events. Other limiting factors contributing to depressed arcellinidan populations may include nutrient supply, predation pressure, competition, and post-mortem taphonomic factors.

Keywords: Amazon; Peru; Lacustrine; Limnology; Arcellineda; Testate lobose amoebae

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Introduction

Arcellinida Kent 1880, also variously known as thecamoebians (e.g. Vázquez-Riveiros et al. 2007), testate lobose amoebae (Macumber et al. 2014) testate amoebae (Swindles et al. 2014), or arcellaceans (Patterson et al. 2013; Roe and Patterson 2014) are a group of unicellular protozoans commonly found in freshwater and brackish environments, including peatlands, saltmarshes, soils, ponds and lakes (Ogden and Hedley 1980; Medioli and Scott 1983; Patterson et al. 1985; Patterson et al. 1996; Patterson and Kumar 2002). The potential of arcellinidans as bio-indicators of lake conditions has been demonstrated in several studies (e.g. Roe et al. 2010; Patterson et al. 2013; Roe and Patterson 2014); however, most studies have focused on temperate-latitude lakes (Patterson and Kumar 2002). Most early research carried out in tropical zones was descriptive in nature, with little attention paid to relationships between taxa and their limnological environment (see Roe and Patterson 2006 for a review). It was

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*Corresponding author. Tel.: +1 613 520 2600x4425; fax: +1 613 520 5613.
E-mail address: tim.patterson@carleton.ca (R.T. Patterson).

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difficult to directly compare the results of this research with more recent studies in tropical South America, as very little work has been carried out on arcellinidans in lacustrine environments (e.g. Green 1975; Dabés 1995; Alves et al. 2007; Alves et al. 2010; Alvest et al. 2012; Morais Costa et al. 2011; Lansac-Tôha et al. 2014). In South America most arcellacean studies have focused on riverine environments, particularly the Paraná River flood plain of southern Brazil (see Schwind et al. 2013 for a detailed review of 36 published papers from that nation). Similarly there have been several papers published on Arcellinida faunas from Argentina (see Lena and Zaidenwersg 1975). Research from elsewhere in South America has been much less detailed with only a handful of studies from Colombia (Grabandt 1983); Paraguay (Bonnet 1979); and Venezuela (Decloitre 1955; Oye 1956).

There is no existing literature on the distribution of lacustrine Arcellinida in any part of Amazonia, although Walker (1982) did examine arcellinidan distributions in an Amazonia stream in Brazil. The only previous research carried out on arcellinidans in Peru was based on material from Lake Cocococha, in the Tambopata Reserve, in the SE part of the country near the Bolivian border (Haman and Kohl 1994). There have also been some studies on the group in litter and soil in tropical rainforests in Ecuador (e.g. Krashevska et al. 2007). Swindles et al. (2014) and Reczuga et al. (2015) recently published the first study on the ecology of arcellinidans and other testate amoebae from a peatland in Peruvian Amazonia.

Anthropogenic activity is having major impacts on biodiversity across Amazonia, and current extinction rates may result in irreversible loss of biodiversity (Chapin III et al. 2000). Despite the global importance of microbial diversity it has been inadequately documented in Amazonia, with the ecology of the organisms being even less well understood (Hoorn et al. 2010). In this study we present new ecological data on Arcellinida fauna from Lake Quistococha in the central part of western (Peruvian) Amazonia. In the absence of previous research on Amazonian lacustrine arcellinidans this study is an important first step in determining the utility of the group as ecological indicators in this region.

Study area

Lake Quistococha (AKA Laguna de Quistococha; 3°82894′ S, 73°31843′ W; Google Maps 2014a) is located within the Quistococha Reserve environmental conservation area, 1.4 km west of the Rio Itaya, 10 km west of the main channel of the Amazon River and 10 km southwest of the city of Iquitos (Aniceto et al. 2014; Kelly et al. 2014; Roucoux et al. 2013; Fig. 1). This small lake is roughly circular, with a surface area of 1 km^2 and is up to ∼5 m deep (Räsänen et al. 1991; Roucoux et al. 2013). It is located between the flood plain and a 15 m high terrace, which demarcates the western boundary of the Amazon River floodplain and the Rio Itaya (Räsänen et al. 1991). Lake Quistococha is 104 m above mean sea, approximately the same elevation as the surrounding Amazon tributaries and floodplain (Roucoux et al. 2013). The area around the lake is swampy and heavily vegetated, with trees overhanging the shoreline. An area of peatland borders the edge of the lake, and areas of collapsed shoreline observed during the current research suggests that the margin may be erosive. Three tree species account for 82% of the vegetation canopy over the peatland; *Mauritia flexuosa*, *Mauritiella armata*, and *Tabebuia insignis* (Roucoux et al. 2013; Kelly et al. 2014).

The Iquitos area is one of the wettest areas of Amazonia with average annual rainfall in excess of 3000 mm (Marengo 1998). Precipitation levels are relatively high even during the dry June–August dry season, averaging ∼100 mm (Espinoza Villar et al. 2008). Due to these seasonal changes in precipitation, water levels in the Amazon River near Iquitos vary by ∼10 m through the year (Kalliola and Puhakka 1993). The flood regime defines two distinct landscapes in the western Amazon region with “terra firme” forests developed on unflooded uplands, and a variety of floodplain forests (e.g. “várzea”, “igapó”) in areas that are at least partially flooded during the rainy season (Prance 1979; Kaandorp et al. 2003).

Lake Quistococha is located very close to the “terra firme” boundary at the edge of the alluvial plain and is not typically prone to riverine flooding (Aniceto et al. 2014; Kelly et al. 2014). The lake and surrounding peatlands overlie an impermeable substrate of ancestral Amazon River riverine or lacustrine clay (Lawson et al. 2014), and the eastern site margin is defined by a levee of impermeable silty clay. Hydraulic conductivity tests and hydrological models have also shown that subsurface flow is not capable of shedding the large amount of rainfall from the peatland surrounding the lake, which suggests that groundwater flow into and out of the lake is minimal (Kelly et al. 2014). Even during rare floods events, as occurred at Lake Quistococha during the wet season of 2012 (Lawson et al. 2014) the source of water was believed to be primarily rainwater that had ‘backed up’ behind the river water, rather than overbank river water flooding the site (e.g. Mertes 1997). An analysis of the peat surface around Lake Quistococha following the 2012 flood supported this interpretation as there was no depositional evidence of clastic fluvial sediments (Lawson et al. 2014).

Lake Quistococha is characterized by clear water with low conductivity (Hegewald and Schnepf 1978; Räsänen et al. 1991). Present-day deposition in the lake is primarily composed of fine organic sediments with virtually no minerogenic input. These sediments are characterized by a high (c. 50%) loss-on-ignition (LOI), 10–30% total organic carbon (TOC), and high (c. 20) C/N ratio (Aniceto et al. 2014), typical of organic sediments derived primarily from C_3 plants (Aniceto et al. 2014; Meyers 1994, 2003)). Sedimentation rates in the lake are low (0.2 mm yr^{-1}). Riverine derived silts ceased to contribute to lake sedimentation roughly 2100–2600 yBP (Räsänen et al. 1991; Roucoux et al. 2013; Aniceto et al. 2014). The current organic-rich depositional environment has prevailed since then.

Material and Methods

Field sampling

Twelve cores were collected from Lake Quistococha in 2011 using a Kajak-type gravity corer (Renberg 1991; Fig. 1), and seven of these were used in this research. Coring station locations were determined using a Garmin E-trex high-sensitivity GPS unit, and as the lake was small, positioning was also mapped by visually estimating station locations against shoreline features (Fig. 1c). Each core was extruded and subsampled at 1 cm intervals. Subsamples from 0 to 4 cm in each core, 28 subsamples in all, were used for this study. These subsamples ranged in volume from 1.1 to 2.6 cm^3. The subsamples were transported to Carleton University for subsequent analysis and were refrigerated at 4 °C when not in use.

Water depths at each station were determined using a standard depth sounding line, and ranged from 1.5 to 5.3 m (Table 1). The lake was shallow and the water column well-mixed, therefore water property data (e.g. pH, temperature) were only collected from a single station and extrapolated to the entire basin.

Laboratory analyses

In the laboratory, the sediment subsamples were stained using Rose Bengal (acid red 94) protoplasmic stain and left overnight to detect any live specimens (after Patterson and Kumar 2000b). The samples were subsequently screened with a 297 μm sieve to remove coarse particles, and then a 37 μm sieve to remove any fine clay, silt and organics. All observed arcellinidans from each sample were counted using an Olympus SZH10 dissecting light binocular microscope, usually at ×40–80 magnification.

The C:N ratios were obtained from the 1 to 2 and 3 to 4 cm intervals at eight core locations within the lake basin, including all seven analyzed for arcellinidans (Fig. 1; Table 2). Aliquots for C:N analysis were dried at 105 °C and milled to ensure homogenization. Each sub-sample was weighed and analyzed with a Eurovector Turboflash CNS combustion analyzer at Leeds University using vanadium pentoxide as a catalyst. The peat standard NJV942 was used with all sample batches. The experimental values for carbon and nitrogen were within 95% of the certified value for NJV942 for all sample runs.

Results

A total of only 48 specimens, which included ten species and strains of Arcellinida were observed in the Lake Quistococha samples. Centropyxid taxa were the most common species observed (Table 1). *Difflugia difficilis* Thomas 1954 was also relatively abundant in most samples. Sediments from most stations were comprised of gyttja while samples from the shallow, 1.5 m water depth, stations 1 and 9 near the eastern shore were composed of decomposed peaty lake

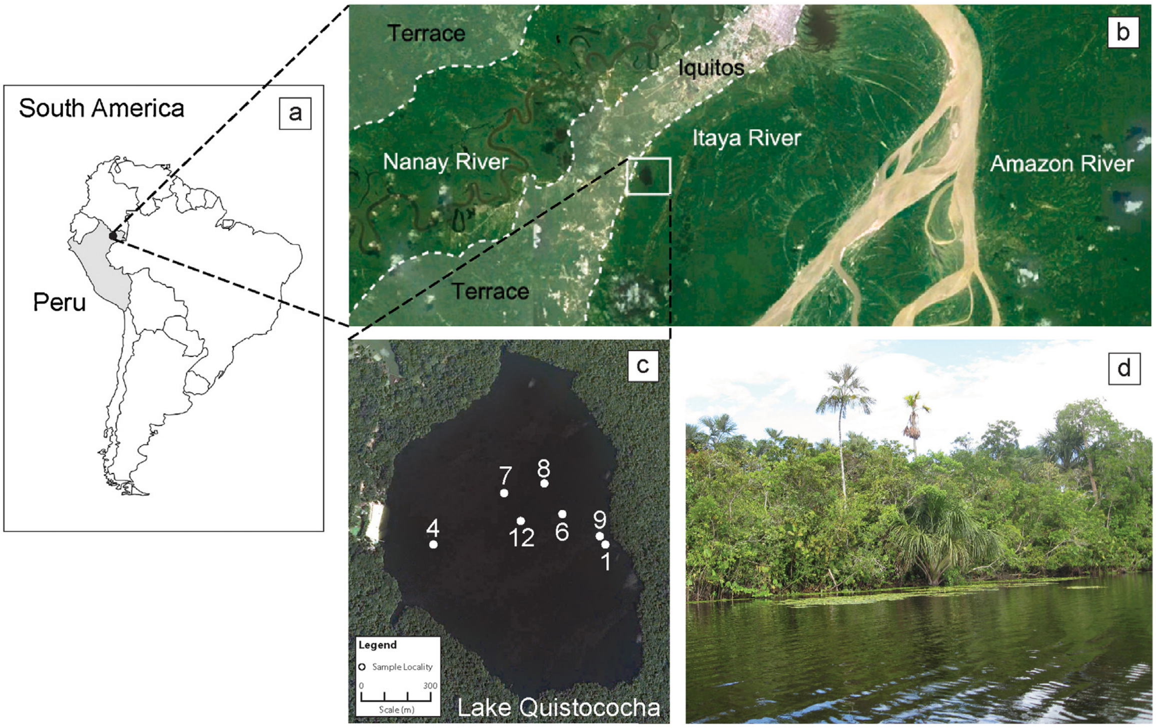

Fig. 1. Location map showing (a) relative position of Lake Quistococha in Peru; (b) position of the lake relative to Iquitos and the raised 'terra firma' terrace; (c) sample stations where samples were collected, and (d) the typical vegetation bordering the lake.

Table 1. Total and percent arcellacean abundances obtained from 0 to 4 cm core top samples from each sampling station. Samples were quantitatively analyzed and are recorded as fractional abundances.

Taxa/Station	Core 1	Core 4	Core 6	Core 7	Core 8	Core9	Core 12
Latitude: south	3.82962	3.82982	3.82914	3.82885	3.82874	3.82952	3.82924
Longitude: west	73.31589	73.32041	73.31682	73.31782	73.3172	73.31592	73.31749
Water depth: meters	1.5	3.6	2.7	5.3	5.3	1.5	3.6
Sediment type	Peaty seds	Gyttja	Gyttja	Gyttja	Gyttja	Peaty seds	Gyttja
Sediment volume: cc	9.3	6.1	5.0	6.7	8.9	9.6	7.3
Total taxa	6	5	5	4	7	3	4
Total specimens	10	9	7	4	8	4	6
Arcellid/Centropyxids	0.90	0.22	0.57	0.50	0.38	1.00	0.50
Arcella vulgaris	0.20			0.25			
Centropyxis aculeata	0.10	0.11	0.14		0.13	0.25	0.17
Centropyxis discoides	0.40		0.29		0.13	0.25	0.33
Centropyxis ecornis				0.25			
Centropyxis spinosa	0.20	0.11	0.14		0.13	0.50	
Difflugia difficilis		0.44	0.29	0.25	0.25		0.33
Difflugia claviformis		0.22					
Mediolus corona	0.10	0.11	0.14	0.25	0.13		
Difflugia cf. *scalpellum*					0.13		
Lesquereusia spiralis	0.10				0.13		0.17

sediment (Fig. 1; Table 1). The Troels-Smith descriptor code for the gyttja was Th2Dh1Ld1 while the peaty lake sediment is described as Ld3As1 (Troels-Smith 1955).

Arcellinida concentrations were very low in all samples, ranging from 0.4 to 1.1 specimens per cm^3 in the lake peat substrate to a similar 0.6 to 1.5 specimens per cm^3 in gyttja. We therefore grouped the four 0–1 cm subsamples from each core into a single 0–4 cm sample, which still yielded relatively low counts. As total specimen counts were low, only a semi-quantitative analysis of the data was possible.

The gyttja and peaty lake samples yielded very different fauna and C:N values. Fauna observed in the peaty lake sediment samples comprised 90–100% centropyxid taxa and relatively high C:N ratios (20–31) typical of the upper peats in the adjacent peatland area (Lawson et al. 2014). In contrast, 22–57% centropyxids were found in the gyttja substrate (Table 1), and much lower C:N ratios (~11), typical of gyttja derived from algae and phytoplankton (e.g. Hecky et al. 1993; Meyers 1994; Moreira-Turcq et al. 2004; Sifeddine et al. 2004).

Table 2. Concentration (in wt%) of total organic carbon (C), nitrogen (N), and molar organic C/N ratios for selected core samples.

Core station horizon	Sediment type	N	C	C/N
Average	Gyttjja	3.09	34.03	11.02
Median	Gyttjja	3.20	35.05	10.97
Average	Lake peat	2.03	51.56	26.21
Median	Lake peat	1.91	52.03	27.70
Core 1: 2–4 cm	Lake peat	2.50	49.89	19.99
Core 4: 2–4 cm	Gyttjja	2.44	27.32	11.19
Core 6: 0–1 cm	Gyttjja	3.30	36.72	11.13
Core 7: 2–4 cm	Gyttjja	3.14	34.38	10.96
Core 8: 0–1 cm	Gyttjja	3.25	35.66	10.97
Core 9: 0–1 cm	Lake peat	1.91	52.76	27.70
Core 9: 2–4 cm	Lake peat	1.68	52.03	30.95
Core 12: 0–1 cm	Gyttjja	3.20	34.94	10.92
Core 12: 2–4 cm	Gyttjja	3.21	35.15	10.95

Discussion and Conclusions

Species compositions observed in both the gyttja and peaty lake sediment samples from Lake Quistococha are significantly different than faunal populations typical of Amazonian terrestrial peatlands (Swindles et al. 2014). Although *Centropyxis aculeata* (Ehrenberg 1832), *C. ecornis* (Ehrenberg 1841 [1843]) and *Lesquereusia spiralis* (Ehrenberg 1840) are common to both environments, the diversity and overall abundance of taxa is significantly higher in terrestrial peatland environments than in either the gyttja or peaty lake sediments sampled in Lake Quistococha (cf. Swindles et al. 2014). Aside from *C. aculeata*, *C. ecornis* and *L. spiralis* none of the other species observed in lacustrine settings were found in the peatland. These observations suggests that, despite high precipitation levels in the area, runoff from the adjacent terrestrial peatlands does not carry significant allochthonous specimens into the lake, and that terrestrial and lake peats comprise distinct arcellinidan habitats.

In temperate gyttja lake environments, most analogous to the organic rich sediments found in Lake Quistococha, analyses would typically yield hundreds of specimens per 1–3 cm^3 aliquot (e.g. Boudreau et al. 2005; Patterson and Kumar

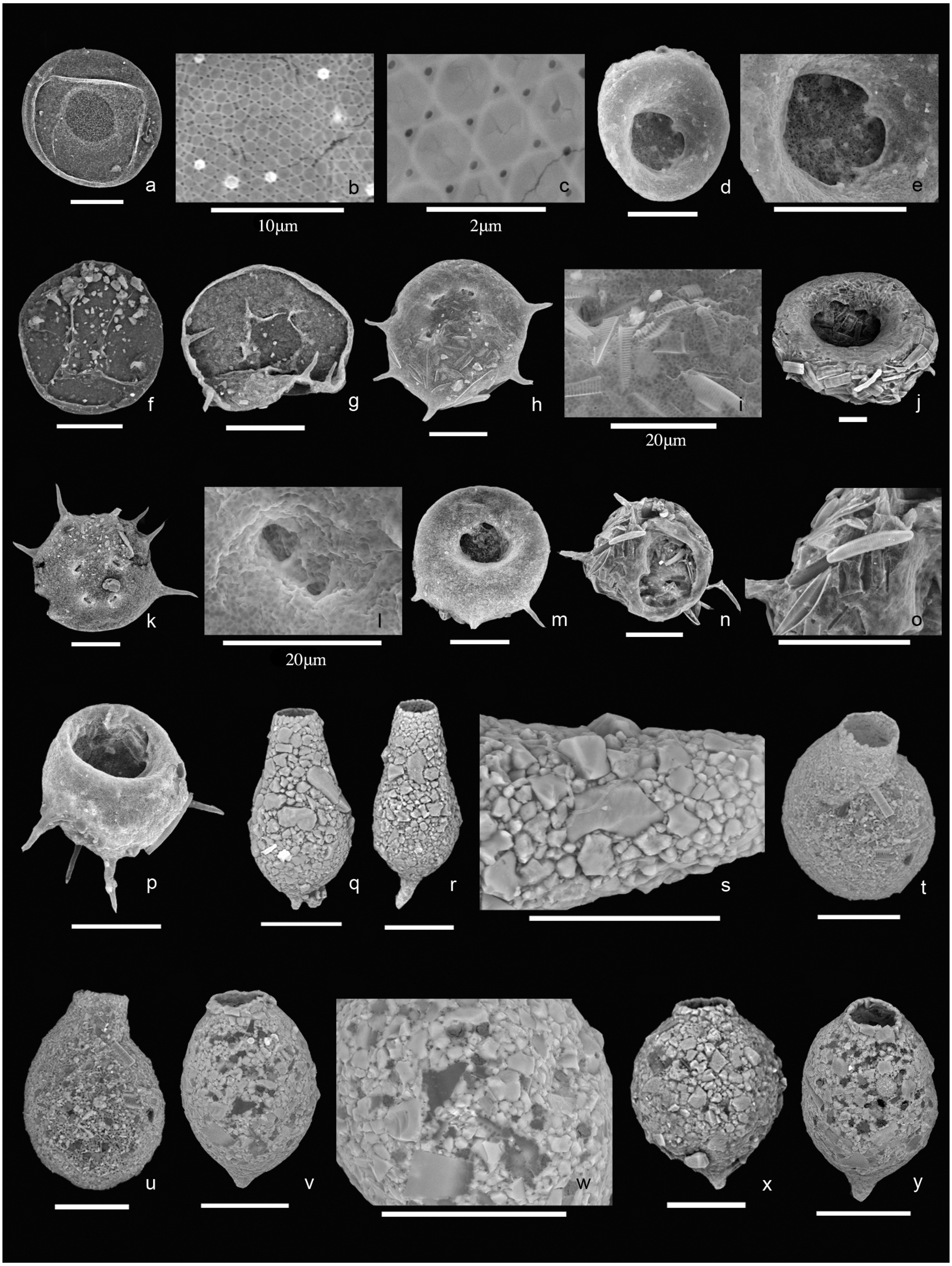

Fig. 2. **a–y.** Scanning electron micrographs of Lake Quistococha arcellaceans. **a–c.** *Arcella vulgaris* Eherenberg 1830. **a.** Dorsal view of specimen. **b.** Ventral view of a different specimen wall showing repeating hexagram pattern. **c.** Further enlargement of **(b)** showing relative position of pores in relation to hexagram vortices. **d,e,j.** *Centropyxis ecornis* (Ehrenberg 1841 [1843]). **d.** Ventral view showing relative position of aperture and characteristic lack of spines. **e.** Enlargement of **(d)** showing details of small pillars that connect its invaginated apertural margin to dorsal side of test. (j) Ventral view of specimen that primarily utilized diatoms in test construction. **f–I, k,l** *Centropyxis discoides* Penard 1890. **f.** Dorsal view of poorly agglutinated specimen that became compressed when put under a vacuum for SEM imaging. Short spines visible along test margin. **g.** Ventral view of a different poorly agglutinated specimen that also became very compressed under vacuum

2002; Roe et al. 2010; Roe and Patterson 2014). The results of this research and other studies in adjacent Brazil, where at most only a few specimens per cm^3 were observed (Table 1), suggest that the carrying capacity for arcellinidans in tropical lakes in the region may be significantly lower than in temperate areas. As the ecology of Amazonian arcellinidans is so poorly known it is only possible to speculate as to what limiting factors (e.g. nutrient supply, predation pressure, competition; after Mächler and Altermatt 2012; Hardoim and Heckman 1996) might be reducing population size by an order of magnitude relative to that observed in temperate environments. Post-mortem taphonomic factors might be a contributing factor to the low concentration of tests observed in the core samples (Farooqui et al. 2012). To overcome this difficulty researchers studying the group in Brazil (e.g. Alves et al. 2010, 2012; Lansac-Tôha et al. 2014; Corrêa et al. 2015) generally process very large 100 cm^3 sediment samples to obtain enough specimens for statistical analysis. Processing such a large volume of sediment is unheard of in research carried out elsewhere and the Brazilian research was not known to us when this study was carried out.

In the only previous study of arcellinidans carried out in Peru, a low diversity, low abundance fauna was reported from a single sample obtained from Lake Cocococha over 1000 km to the SE of Lake Quistococha (Haman and Kohl 1994). Although not formally in Amazonia, the Lake Cocococha region (Haman and Kohl 1994) has a similar climate to that of the Lake Quistococha area (Weatherspark.com 2014). Both lakes are also heavily vegetated along the shoreline (Google Maps 2014b). With the exception of the common occurrence of *Mediolus corona* (Wallich 1864) and *L. spiralis* in both lakes the fauna is otherwise completely different, with *Lagenodifflugia vas* (Leidy 1874), *Cucurbitella tricuspis* (Carter 1856) and *Difflugia oblonga* (Ehrenberg 1832) dominating at Lake Cocococha. A possible explanation for the observed faunal differences may be found in the contrasting limnology and substrate characterizing each lake. Whereas Lake Quistococha is permanently isolated from riverine influence with an organic rich substrate, Lake Cocococha, a relatively young oxbow lake subject to flooding from the nearby Rio Tambopata, is characterized by sediments that are much siltier (Haman and Kohl 1994).

Gyttja substrates in temperate lakes generally support a diverse and abundant arcellinidan fauna (Patterson and Kumar 2002a). The reason for the very low arcellinidan productivity in Lake Quistococha may be related to the relatively low pH 4 values in the lake, resulting from the high volume of dissolved organic acids seeping into the lake from the adjacent peatlands in addition to runoff following precipitation events, where pH 4 values were also observed (Kelly et al. 2013). In an analysis of arcellinidan response to pH in temperate James Lake from northeastern Ontario, Canada it was observed that arcellinidan concentration and diversity were greatly reduced in low pH environments (Patterson et al. 2013). Another possible contributor to the low arcellinidan abundances in Lake Quistococha may be the general lack of suitable fine minerogenic material used for arcellacean test construction in many taxa. Many species, particularly difflugids, require allochthonous grains to build their tests (Haman 1990; Scott et al. 1991). Lake Quistococha has been isolated from a regular source of clastic sedimentation for more than 2100 years (Lawson et al. 2014; Aniceto et al. 2014), and even during rare flood events receives little or no silt input (Kelly et al. 2014). Difflugids were generally successful in procuring an adequate supply of grains to construct their tests (e.g. Figs 2r–s, v–y, 3a), but centropyxid taxa were generally very poorly agglutinated, often relying entirely on diatom frustules as a source of allochthonous grains, which only partially covered the secreted test wall (e.g. Fig. 2h–k). Some specimens of *Centropyxis discoides* Penard 1890 were entirely devoid of agglutination (Fig. 2g). The lack of agglutinating particles made preparation of specimens for SEM imaging particularly difficult as many would simply collapse upon themselves under vacuum (e.g. Fig. 2g). Poorly agglutinated specimens were observed in the organic rich sediments in Lake Sentani, Indonesia (Dalby et al. 2000). Dalby et al. (2000) attributed the centropyxid dominated fauna of Lake Sentani to the organic rich substrate characterizing all samples analyzed. Dalby et al. (2000) noted that since arcellids entirely produce autochthonous tests, and

during preparation for imaging. Spines are visible along test margin. **h.** Dorsal view speciment that used diatoms as the primary source of xenogenous agglutination. Apertural pillar structures are expressed as depressions on the dorsal test surface. **i.** Enlargement of agglutinated specimen with four apertures situated directly behind the attachment points in the ventral aperture. **k.** Dorsal view of poorly agglutinated specimen with very clear view of dorsal expression of apertural pillar structures. **l.** Enlargement of apertural pillar structure from (k) showing that depressions are hollow bifurcating tubes. **m–o.** *Centropyxis aculeata* (Ehrenberg 1832). **m.** Vertral view of well agglutinated specimen showing circular outline, arrangement of spines on test postero-margin, and subterminal position of aperture. n. apertural view of specimen, which has made extensive use of diatoms as agglutination building material. **o.** Close up of a portion of the postero-margin of **(n)** showing how diatoms are arranged on test surface. **p.** *Centropyxis spinosa* Cash 1905. Oblique ventral view of specimen showing typically long spines on postero-margin. **q–s.** *Difflugia claviformis* Penard 1899. **q.** Side view of typical specimen characterized by agglutinating particles, which are highly variable in size. **r.** Side view of similar specimen show variation in the size and orientation of basal process. **s.** Enlargement of neck of **(r)** showing sharply angular grains used to agglutinate test. **t,u.** *Lesquereusia spiralis* (Ehrenberg 1840). **t.** Oblique apertural showing circular aperture. **u.** Side view showing diagnostic assymetrical neck. **v–y.** *Difflugia difficilis* Thomas 1954. **v.** Side view showing ovoid test shape, narrow aperture with raised rim and characteristic aboral process. **w.** Enlargement of **(v)** showing irregularly sized and shaped agglutinating particles making up test wall. **x.** Side view of specimen with a nearly spherical profile. **y.** Oblique apertural view showing finely grained material bordering small circular aperture. All scale bars are 50 μm unless otherwise indicated.

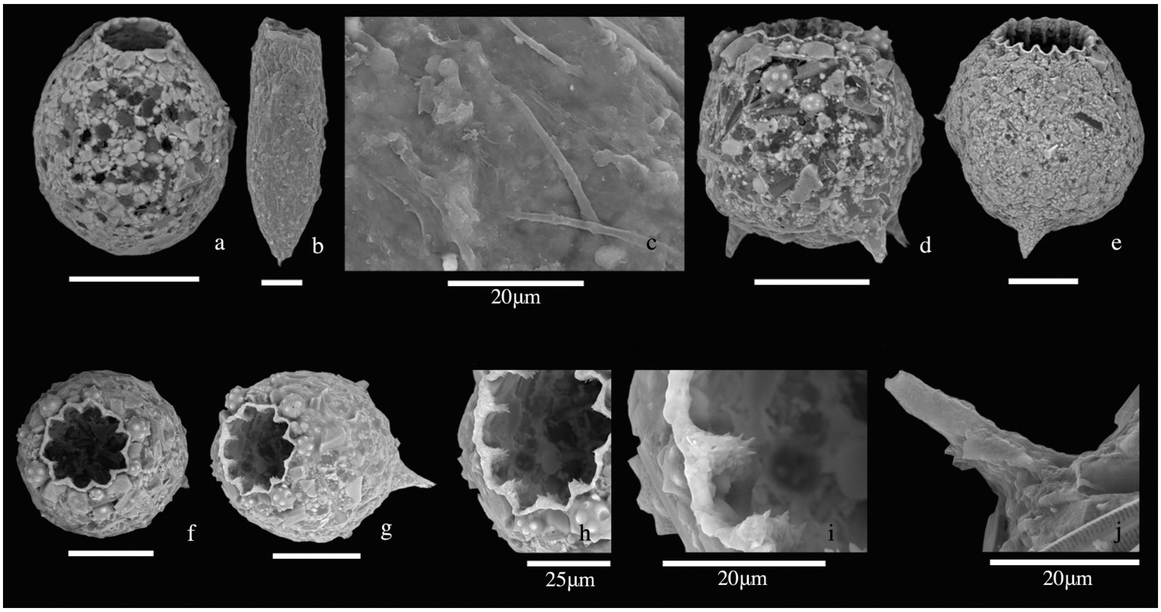

Fig. 3. **a–j.** Scanning electron micrographs of Lake Quistococha arcellaceans. **a.** *Difflugia difficilis* Thomas 1954. Oblique apertural view showing finely grained material bordering small circular aperture and ovoid test shape. **b,c.** *Difflugia* cf. *scalpellum* Pénard 1899. **b.** Side view of specimen showing elongate cylindrical test tapering sharply to elongate fundus. **c.** Enlargement of specimen (b) showing hair-like structures embedded in an amorphous coating covering entire test wall. **d–j.** *Mediolus corona* (Wallich 1864). **d.** Side view of specimen with atypically broad apertural opening and typical basal spines. Test wall comprised of clastic grains, pollen grains and diatom frustules. **e.** Oblique side view of specimen with showing diagnostic raised apertural rim. **f.** Apertural view of specimen showing circular aperture with crenulated opening. **g.** Oblique apertural view showing basal spines. **h.** Enlargement of aperture of **(g)** showing that the raised apertural rim is secreted rather than comprised of finely agglutinated particles. **i.** Further enlargement of **(h)** showing that each apertural crenulation is characterized by a series of sharp spikes. **j.** Enlargement of basal process showing that they are secreted but may have minor agglutination.

as centropyxids were able to construct tests relying on little agglutination (often comprised of only a few diatom frustules here and there), this group had a competitive advantage over difflugids in that lake. Specimens of *M. corona* (Fig. 3d–j) from Lake Quistococha, which secrete certain portions or their tests, notably the apertural crenulations and basal spines, were indiscriminate in sourcing allochthonous material to construct their tests, using a combination of clastic grains, diatoms, and even pollen grains.

The apparent low arcellinidan productivity in many tropical South American lacustrine environments has implications for their use as bioindicators, as well as for paleolimnological research in the region. Standard corers used in temperate areas (Glew gravity corer (Patterson and Kumar 2002); or freeze corers (Macumber et al. 2011) would generally provide inadequate sediment volume to carry out high-resolution paleolimnological research. Paleolimnological research utilizing arcellinidan in many Amazonian lakes will thus either require very large freeze corers generally used for marine research (e.g. Patterson et al. 2013), or wide bore “Big Ben” type piston corers (Patmore et al. 2014).

Systematics

Accepted practice within the limnological research community is to designate informal infrasubspecific strain names for ecophenotypic morphotypes (Asioli et al. 1996; Kumar and Dalby 1998; Patterson and Kumar 2002). These strain names have no formal taxonomic status (ICZN) but they are useful for delineating environmentally significant populations within lacustrine environments (Escobar et al. 2008; Kihlman and Kaupila 2009; Patterson and Kumar 2000a; Patterson et al. 2012, 2013; Roe and Patterson 2006; Reinhardt et al. 1998).

Arcellinidan taxa are found from the tropics to the poles (Patterson and Kumar 2002). This has led many researchers to attribute ecological constraints on the distribution of taxa in one climate zone to apparent occurrences in very different environments (Patterson 2014). This practice has been supported by genetic and morphometric research that has drawn a close correlation between test morphology and genetic clades (e.g. Gomaa et al. 2012, 2015; Macumber et al. 2014). Caution must be taken before drawing sweeping conclusions though as other research suggests that many morphologically indistinguishable species may actually be cryptospecies (e.g. Mitchell and Meisterfeld 2005; Alizon et al. 2008; Heger et al. 2013; Oliverio et al. 2014). It is obvious that due to the morphological plasticity within lineages, a combination of morphometric and molecular analyses will be required to eventually provide a more complete understanding of arcellinidan biodiversity (Oliverio et al. 2014). The ramifications of this taxonomic uncertainty in the context of the research presented herein is that although the observed taxa are all attributed to well known species and strains based on morphology (e.g. shape and size) it is conceivable that genetic analysis would reveal at least some types to be distinct cryptotaxa.

Images of all observed taxa were obtained using a Texcan Vega-II XMU VP scanning electron microscope at the Carleton Nano Imaging Facility (Figs 2, 3). The name of each observed taxa, author and year described is provided in the figure caption. A more detailed taxonomic treatment of each taxon is provided in Supplementary Information Document 1.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ejop.2015.06.009.

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