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

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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 0-4 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.

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48 **Key words**

49 Amazon; Peru; lacustrine; limnology; Arcellineda; testate lobose amoebae

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54 **Introduction**

55 Arcellinida Kent 1880, also variously known as thecamoebians (e.g. Vazquez  
56 Riveiros et al. 2007), testate lobose amoebae (Macumber et al. 2014) testate amoebae  
57 (Swindles et al. 2014), or arcellaceans (Patterson et al. 2013; Roe and Patterson 2014)  
58 are a group of unicellular protozoans commonly found in freshwater and brackish  
59 environments, including peatlands, saltmarshes, soils, ponds and lakes (Ogden and  
60 Hedley 1980; Medioli and Scott 1983; Patterson et al., 1985; Patterson and Kumar  
61 2002a). The potential of arcellinidans as bio-indicators of lake conditions has been  
62 demonstrated in several studies (e.g. Roe et al. 2010; Patterson et al. 2013; Roe and  
63 Patterson 2014); however, most studies have focused on temperate-latitude lakes  
64 (Patterson and Kumar 2002a). Most early research carried out in tropical zones was  
65 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 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. 2010, 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 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 Zaidenweg 1975). Research from elsewhere in South

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75 America has been much less detailed with only a handful of studies from Colombia  
76 (Grabandt 1983); Paraguay (Bonnet 1979); and Venezuela (Delcoitre 1955; Oye 1956).

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

86 Anthropogenic activity is having major impacts on biodiversity across Amazonia, and  
87 current extinction rates may result in irreversible loss of biodiversity (Chapin III et al.  
88 2000). Despite the global importance of microbial diversity it has been inadequately  
89 documented in Amazonia, with the ecology of the organisms being even less well  
90 understood (Hoorn et al. 2010). In this study we present new ecological data on  
91 Arcellinida fauna from Lake Quistococha in the central part of western (Peruvian)  
92 Amazonia. In the absence of previous research on Amazonian lacustrine arcellinidans  
93 this study is an important first step in determining the utility of the group as ecological  
94 indicators in this region.

95 **Study Area**

96 Lake Quistococha (AKA Laguna de Quistococha; 3°82894' S, 73°31843' W; Google  
97 Maps, 2014a) is located within the Quistococha Reserve environmental conservation

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98 area, 1.4 km west of the Rio Itaya, 10 km west of the main channel of the Amazon River  
99 and 10 km southwest of the city of Iquitos (Aniceto et al. 2014; Kelly et al. 2014;  
100 Roucoux et al. 2013; Fig. 1). This small lake is roughly circular, with a surface area of 1  
101 km<sup>2</sup> and is up to ~5 m deep (Räsänen et al. 1991; Roucoux et al. 2013). It is located  
102 between the flood plain and a 15 m high terrace, which demarcates the western  
103 boundary of the Amazon River floodplain and the Rio Itaya (Räsänen et al. 1991). Lake  
104 Quistococha is 104 m above mean sea, approximately the same elevation as the  
105 surrounding Amazon tributaries and floodplain (Roucoux et al. 2013). The area around  
106 the lake is swampy and heavily vegetated, with trees overhanging the shoreline. An  
107 area of peatland borders the edge of the lake, and areas of collapsed shoreline  
108 observed during the current research suggests that the margin may be erosive. Three  
109 tree species account for 82% of the vegetation canopy over the peatland; *Mauritia*  
110 *flexuosa*, *Mauritiella armata*, and *Tabebuia insignis* (Roucoux et al. 2013; Kelly et al.  
111 2014).

112 The Iquitos area is one of the wettest areas of Amazonia with average annual  
113 rainfall in excess of 3,000 mm (Marengo, 1998). Precipitation levels are relatively high  
114 even during the dry June-August dry season, averaging ~100 mm (Espinoza Villar et al.,  
115 2009). Due to these seasonal changes in precipitation, water levels in the Amazon  
116 River near Iquitos vary by ~10 m through the year (Kalliola and Puhakka, 1993). The  
117 flood regime defines two distinct landscapes in the western Amazon region with “terra  
118 firme” forests developed on unflooded uplands, and a variety of floodplain forests (e.g.  
119 “várzea”, “igapó”) in areas that are at least partially flooded during the rainy season  
120 (Prance, 1979; Kaandorp et al. 2003).

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121 Lake Quistococha is located very close to the “terra firme” boundary at the edge of  
122 the alluvial plain and is not typically prone to riverine flooding (Aniceto et al., 2014; Kelly  
123 et al. 2014). The lake and surrounding peatlands overlie an impermeable substrate of  
124 ancestral Amazon River riverine or lacustrine clay (Lawson et al., 2014), and the  
125 eastern site margin is defined by a levee of impermeable silty clay. Hydraulic  
126 conductivity tests and hydrological models have also shown that subsurface flow is not  
127 capable of shedding the large amount of rainfall from the peatland surrounding the lake,  
128 which suggests that groundwater flow into and out of the lake is minimal (Kelly et al.,  
129 2014). Even during rare floods events, as occurred at Lake Quistococha during the wet  
130 season of 2012 (Lawson et al., 2014) the source of water was believed to be primarily  
131 rainwater that had ‘backed up’ behind the river water, rather than overbank river water  
132 flooding the site (e.g. Mertes 1997). An analysis of the peat surface around Lake  
133 Quistococha following the 2012 flood supported this interpretation as there was no  
134 depositional evidence of clastic fluvial sediments (Lawson et al. 2014).

135 Lake Quistococha is characterized by clear water with low conductivity (Hegewald  
136 and Schnepf, 1978; Rasanen et al. 1991). Present-day deposition in the lake is primarily  
137 composed of fine organic sediments with virtually no minerogenic input. These  
138 sediments are characterized by a high (c. 50%) loss-on-ignition (LOI), 10-30% total  
139 organic carbon (TOC), and high (c. 20) C/N ratio (Aniceto et al. 2014), typical of organic  
140 sediments derived primarily from C<sub>3</sub> plants (Aniceto et al. 2014; Meyers P.A. 1993,  
141 2003). Sedimentation rates in the lake are low (0.2 mm yr<sup>-1</sup>). Riverine derived silts  
142 ceased to contribute to lake sedimentation roughly 2100-2600 yBP (Räsänen et al.



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1991; Roucoux et al. 2013; Aniceto et al. 2014). The current organic-rich depositional environment has prevailed since then.

**Materials 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 0-4 cm in each core, 28 subsamples in all, were used for this study. These subsamples ranged in volume from 1.1-2.6 cm<sup>3</sup>. 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 297µm sieve to remove coarse particles, and then a 37µm sieve to remove any fine clay, silt

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4 166 and organics. All observed arcellinidans from each sample were counted using an  
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6 167 Olympus SZH10 dissecting light binocular microscope, usually at x40-80 magnification.  
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9 168 The C:N ratios were obtained from the 1-2 and 3-4 cm intervals at eight core locations  
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11 169 within the lake basin, including all seven analyzed for arcellinidans (Fig. 1; Table 2).  
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14 170 Aliquots for C:N analysis were dried at 105°C and milled to ensure homogenization.  
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16 171 Each sub-sample was weighed and analyzed with a Eurovector Turboflash CNS  
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19 172 combustion analyzer at Leeds University using vanadium pentoxide as a catalyst. The  
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21 173 peat standard NJV942 was used with all sample batches. The experimental values for  
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24 174 carbon and nitrogen were within 95% of the certified value for NJV942 for all sample  
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26 175 runs.

## 27 28 176 **Results**

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31 177 A total of only 48 specimens, which included ten species and strains of Arcellinida  
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33 178 were observed in the Lake Quistococha samples. Centropyxid taxa were the most  
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36 179 common species observed (Table 1). *Diffflugia difficilis* Thomas 1954 was also  
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38 180 relatively abundant in most samples. Sediments from most stations were comprised of  
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41 181 gyttja while samples from the shallow, 1.5 m water depth, stations 1 and 9 near the  
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43 182 eastern shore were composed of decomposed peaty lake sediment (Fig. 1; Table 1).  
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46 183 The Troels-Smith descriptor code for the gyttja was Th2Dh1Ld1 while the peaty lake  
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48 184 sediment is described as Ld3As1 (Troels-Smith 1955).

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51 185 Arcellinida concentrations were very low in all samples, ranging from 0.4-1.1  
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53 186 specimens per cm<sup>3</sup> in the lake peat substrate to a similar 0.6-1.5 specimens per cm<sup>3</sup> in  
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55 187 gyttja. We therefore grouped the four 0-1 cm subsamples from each core into a single  
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188 0-4 cm sample, which still yielded relatively low counts. As total specimen counts were  
189 low, only a semi-quantitative analysis of the data was possible.

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

### 197 **Discussion and Conclusions**

198 Species compositions observed in both the gyttja and peaty lake sediment samples  
199 from Lake Quistococha are significantly different than faunal populations typical of  
200 Amazonian terrestrial peatlands (Swindles et al. 2014). Although *Centropyxis aculeata*  
201 (Ehrenberg 1832), *C. ecornis* (Ehrenberg 1841) and *Lesquereusia spiralis* (Ehrenberg  
202 1840) are common to both environments, the diversity and overall abundance of taxa is  
203 significantly higher in terrestrial peatland environments than in either the gyttja or peaty  
204 lake sediments sampled in Lake Quistococha (cf. Swindles et al. 2014). Aside from *C.*  
205 *aculeata*, *C. ecornis* and *L. spiralis* none of the other species observed in lacustrine  
206 settings were found in the peatland. These observations suggests that, despite high  
207 precipitation levels in the area, runoff from the adjacent terrestrial peatlands does not  
208 carry significant allochthonous specimens into the lake, and that terrestrial and lake  
209 peats comprise distinct arcellinidan habitats.

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7 211 sediments found in Lake Quistococha, analyses would typically yield hundreds of  
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9 212 specimens per 1-3 cm<sup>3</sup> aliquot (e.g. Boudreau et al. 2005; Patterson and Kumar 2002;  
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11 213 Roe et al. 2010; Roe and Patterson 2014). The results of this research and other  
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14 214 studies in adjacent Brazil, where at most only a few specimens per cm<sup>3</sup> were observed  
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16 215 (Table 1), suggest that the carrying capacity for arcellinidans in tropical lakes in the  
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19 216 region may be significantly lower than in temperate areas. As the ecology of  
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21 217 Amazonian arcellinidans is so poorly known it is only possible to speculate as to what  
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24 218 limiting factors (e.g. nutrient supply, predation pressure, competition; after Mächler and  
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26 219 Altermatt, 2012; Hardoim and Heckman, 1996) might be reducing population size by an  
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29 220 order of magnitude relative to that observed in temperate environments. Post-mortem  
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31 221 taphonomic factors might be a contributing factor to the low concentration of tests  
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34 222 observed in the core samples (Farooqui et al., 2012). To overcome this difficulty  
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36 223 researchers studying the group in Brazil (e.g. Alves et al. 2010, 2012; Lansac-Tôha et al.  
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38 224 2014; Corrêa et al. 2015) generally process very large 100 cm<sup>3</sup> sediment samples to  
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41 225 obtain enough specimens for statistical analysis. Processing such a large volume of  
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43 226 sediment is unheard of in research carried out elsewhere and the Brazilian research  
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46 227 was not known to us when this study was carried out.

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48 228 In the only previous study of arcellinidans carried out in Peru, a low diversity, low  
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51 229 abundance fauna was reported from a single sample obtained from Lake Cocococha  
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53 230 over 1000 km to the SE of Lake Quistococha (Haman and Kohl, 1994). Although not  
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55 231 formally in Amazonia, the Lake Cocococha region (Haman and Kohl, 1994) has a  
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58 232 similar climate to that of the Lake Quistococha area (Weatherspark.com, 2014). Both  
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4 233 lakes are also heavily vegetated along the shoreline (Google Maps 2014b). With the  
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7 234 exception of the common occurrence of *Mediolus corona* (Wallich 1864) and *L. spiralis*  
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9 235 in both lakes the fauna is otherwise completely different, with *Lagenodifflugia vas* (Leidy  
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11 236 1874), *Cucurbitella tricuspis* (Carter 1856) and *Diffflugia oblonga* (Ehrenberg 1832)  
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14 237 dominating at Lake Cocococha. A possible explanation for the observed faunal  
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16 238 differences may be found in the contrasting limnology and substrate characterizing each  
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19 239 lake. Whereas Lake Quistococha is permanently isolated from riverine influence with  
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21 240 an organic rich substrate, Lake Cocococha, a relatively young oxbow lake subject to  
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24 241 flooding from the nearby Rio Tambopata, is characterized by sediments that are much  
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26 242 siltier (Haman and Kohl 1994).

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29 243 Gyttja substrates in temperate lakes generally support a diverse and abundant  
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31 244 arcellinidan fauna (Patterson and Kumar, 2002a). The reason for the very low  
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33 245 arcellinidan productivity in Lake Quistococha may be related to the relatively low pH 4  
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36 246 values in the lake, resulting from the high volume of dissolved organic acids seeping  
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38 247 into the lake from the adjacent peatlands in addition to runoff following precipitation  
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41 248 events, where pH 4 values were also observed (Kelly et al. 2013). In an analysis of  
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43 249 arcellinidan response to pH in temperate James Lake from northeastern Ontario,  
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46 250 Canada it was observed that arcellinidan concentration and diversity were greatly  
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48 251 reduced in low pH environments (Patterson et al. 2013). Another possible contributor to  
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51 252 the low arcellinidan abundances in Lake Quistococha may be the general lack of  
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53 253 suitable fine minerogenic material used for arcellacean test construction in many taxa.  
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55 254 Many species, particularly difflugids, require allochthonous grains to build their tests  
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58 255 (Haman, 1990; Scott et al. 1991). Lake Quistococha has been isolated from a regular  
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4 256 source of clastic sedimentation for more than 2100 years (Lawson et al., 2014; Aniceto  
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7 257 et al. 2014), and even during rare flood events receives little or no silt input (Kelly et al.  
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9 258 2014). Diffflugids were generally successful in procuring an adequate supply of grains to  
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12 259 construct their tests (e.g. Figs. 2r-s, v-y; 3a), but centropyxid taxa were generally very  
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14 260 poorly agglutinated, often relying entirely on diatom frustules as a source of  
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16 261 allochthonous grains, which only partially covered the secreted test wall (e.g. Fig. 2h-k).  
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19 262 Some specimens of *Centropyxis discoides* Penard 1890 were entirely devoid of  
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21 263 agglutination (Fig. 2g). The lack of agglutinating particles made preparation of  
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24 264 specimens for SEM imaging particularly difficult as many would simply collapse upon  
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26 265 themselves under vacuum (e.g Fig. 2g). Poorly agglutinated specimens were observed  
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29 266 in the organic rich sediments in Lake Sentani, Indonesia (Dalby et al. 2000). Dalby et al.  
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31 267 (2000) attributed the centropyxid dominated fauna of Lake Sentani to the organic rich  
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34 268 substrate characterizing all samples analyzed. Dalby et al. (2000) noted that since  
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36 269 arcellids entirely produce autochthonous tests, and as centropyxids were able to  
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38 270 construct tests relying on little agglutination (often comprised of only a few diatom  
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41 271 frustules here and there), this group had a competitive advantage over diffflugids in that  
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43 272 lake. Specimens of *M. corona* (Fig. 3d-j) from Lake Quistococha, which secrete certain  
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46 273 portions or their tests, notably the apertural crenulations and basal spines, were  
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48 274 indiscriminate in sourcing allochthonous material to construct their tests, using a  
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51 275 combination of clastic grains, diatoms, and even pollen grains.

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53 276 The apparent low arcellinidan productivity in many tropical South American  
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55 277 lacustrine environments has implications for their use as bioindicators, as well as for  
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58 278 paleolimnological research in the region. Standard corers used in temperate areas  
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279 (Glew gravity corer (Patterson and Kumar 2002); or freeze corers (Macumber et al.  
280 2011) would generally provide inadequate sediment volume to carry out high-resolution  
281 paleolimnological research. Paleolimnological research utilizing arcellinidan in many  
282 Amazonian lakes will thus either require very large freeze corers generally used for  
283 marine research (e.g. Patterson et al. 2013), or wide bore “Big Ben” type piston corers  
284 (Patmore et al. 2014).

### 285 **Systematics**

286 Accepted practice within the limnological research community is to designate  
287 informal infrasubspecific strain names for ecophenotypic morphotypes (Asioli et al.  
288 1996; Kumar and Dalby, 1998; Patterson and Kumar 2002). These strain names have  
289 no formal taxonomic status (ICZN) but they are useful for delineating environmentally  
290 significant populations within lacustrine environments (Escobar et al. 2008; Kihlman and  
291 Kaupila 2009; Patterson and Kumar 2000a; Patterson, et al. 2012, 2013; Roe and  
292 Patterson 2006; Reinhardt et al. 1998).

293 Arcellinidan taxa are found from the tropics to the poles (Patterson and Kumar,  
294 2002). This has led many researchers to attribute ecological constraints on the  
295 distribution of taxa in one climate zone to apparent occurrences in very different  
296 environments (Patterson, 2014). This practice has been supported by genetic and  
297 morphometric research that has drawn a close correlation between test morphology and  
298 genetic clades (e.g. Gomaa et al., 2012; 2015; Macumber et al. 2014). Caution must be  
299 taken before drawing sweeping conclusions though as other research suggests that  
300 many morphologically indistinguishable species may actually be cryptospecies (e.g.  
301 Mitchel and Meisterfeld, 2005; Alizon, et al., 2008; Heger, et al., 2013; Oliverio, et al.,

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302 2014). It is obvious that due to the morphological plasticity within lineages, a  
303 combination of morphometric and molecular analyses will be required to eventually  
304 provide a more complete understanding of arcellinidan biodiversity (Oliverio, et al.,  
305 2014). The ramifications of this taxonomic uncertainty in the context of the research  
306 presented herein is that although the observed taxa are all attributed to well known  
307 species and strains based on morphology (e.g. shape and size) it is conceivable that  
308 genetic analysis would reveal at least some types to be distinct cryptotaxa.

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

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**Figures in text**

**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.

**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). **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-l, 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 during preparation for imaging. Spines are visible along test margin. **h.** Dorsal view specimen 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

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4 605 are hollow bifurcating tubes. **m-o.** *Centropyxis aculeata* (Ehrenberg 1832). **m.** ventral  
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7 606 view of well agglutinated specimen showing circular outline, arrangement of spines on  
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9 607 test postero-margin, and subterminal position of aperture. **n.** apertural view of specimen,  
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11 608 which has made extensive use of diatoms as agglutination building material. **o.** close up  
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14 609 of a portion of the postero-margin of (**n**) showing how diatoms are arranged on test  
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16 610 surface. **p.** *Centropyxis spinosa* Cash 1905. Oblique ventral view of specimen showing  
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19 611 typically long spines on postero-margin. **q-s.** *Diffflugia claviformis* Penard 1899. **q.** Side  
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21 612 view of typical specimen characterized by agglutinating particles, which are highly  
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24 613 variable in size. **r.** Side view of similar specimen show variation in the size and  
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26 614 orientation of basal process. **s.** Enlargement of neck of (**r**) showing sharply angular  
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29 615 grains used to agglutinate test. **t,u.** *Lesquereusia spiralis* (Ehrenberg 1840). **t.** Oblique  
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31 616 apertural showing circular aperture. **u.** Side view showing diagnostic asymmetrical neck.  
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34 617 **v-y.** *Diffflugia difficilis* Thomas 1954. **v.** Side view showing ovoid test shape, narrow  
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36 618 aperture with raised rim and characteristic aboral process. **w.** enlargement of (**v**)  
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38 619 showing irregularly sized and shaped agglutinating particles making up test wall. **x.** Side  
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41 620 view of specimen with a nearly spherical profile. **y.** Oblique apertural view showing  
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43 621 finely grained material bordering small circular aperture. All scale bars are 50 µm unless  
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46 622 otherwise indicated.

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51 624 **Fig. 3. a-j.** Scanning electron micrographs of Lake Quistococha arcellaceans. **a.**  
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53 625 *Diffflugia difficilis* Thomas 1954. Oblique apertural view showing finely grained material  
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55 626 bordering small circular aperture and ovoid test shape. **b,c.** *Diffflugia cf. scalpellum*  
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58 627 Pénard 1899. **b.** Side view of specimen showing elongate cylindrical test tapering  
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628 sharply to elongate fundus. **c.** Enlargement of specimen (b) showing hair-like structures  
629 embedded in an amorphous coating covering entire test wall. **d-j.** *Mediolus corona*  
630 (Wallich 1864). **d.** Side view of specimen with atypically broad apertural opening and  
631 typical basal spines. Test wall comprised of clastic grains, pollen grains and diatom  
632 frustules. **e.** Oblique side view of specimen with showing diagnostic raised apertural rim.  
633 **f.** Apertural view of specimen showing circular aperture with crenulated opening. **g.**  
634 Oblique apertural view showing basal spines. **h.** Enlargement of aperture of (**g**) showing  
635 that the raised apertural rim is secreted rather than comprised of finely agglutinated  
636 particles. **i.** Further enlargement of (**h**) showing that each apertural crenulation is  
637 characterized by a series of sharp spikes. **j.** Enlargement of basal process showing that  
638 they are secreted but may have minor agglutination.

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**640 Tables in text**

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

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



Figure 1  
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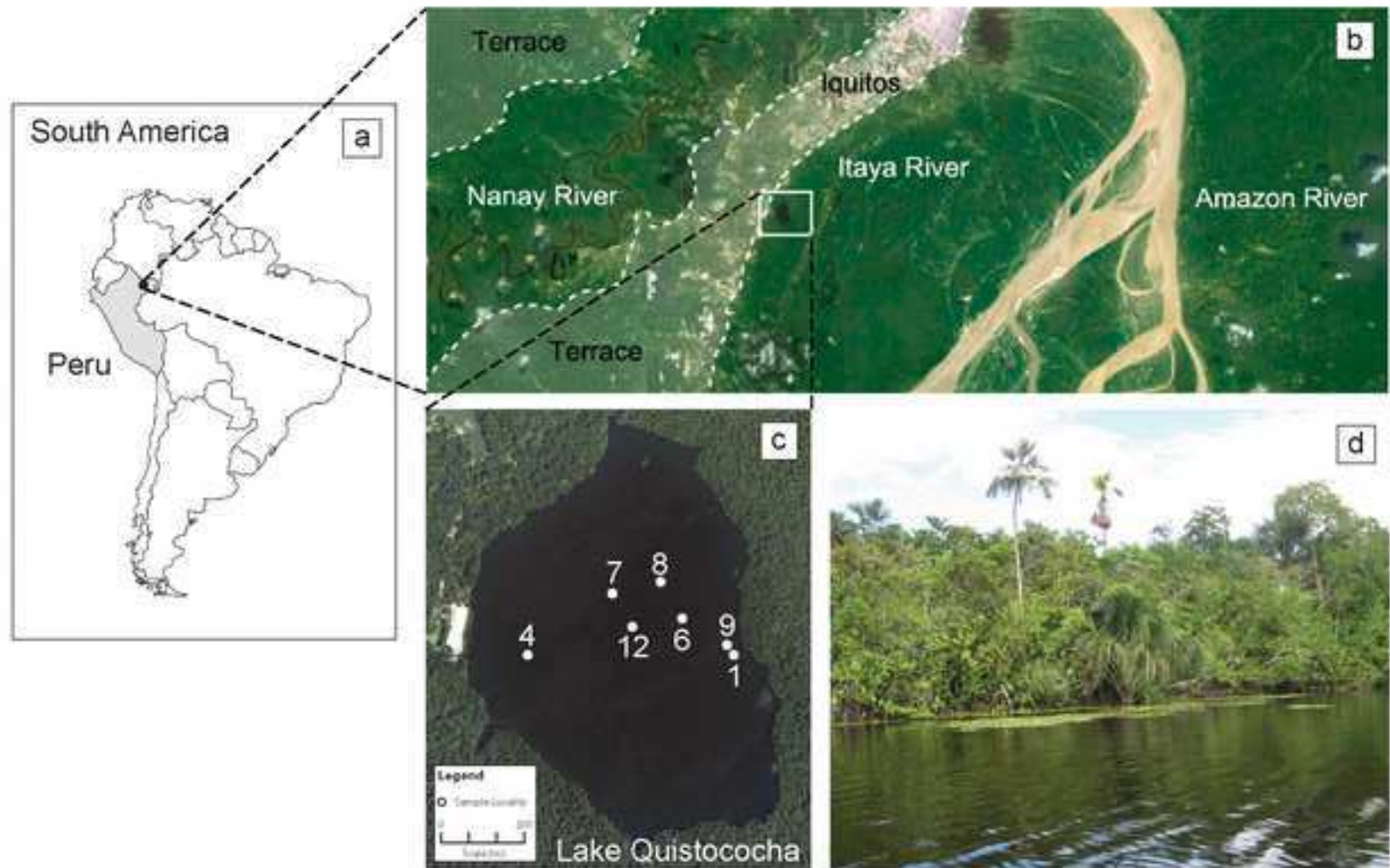


Figure 2  
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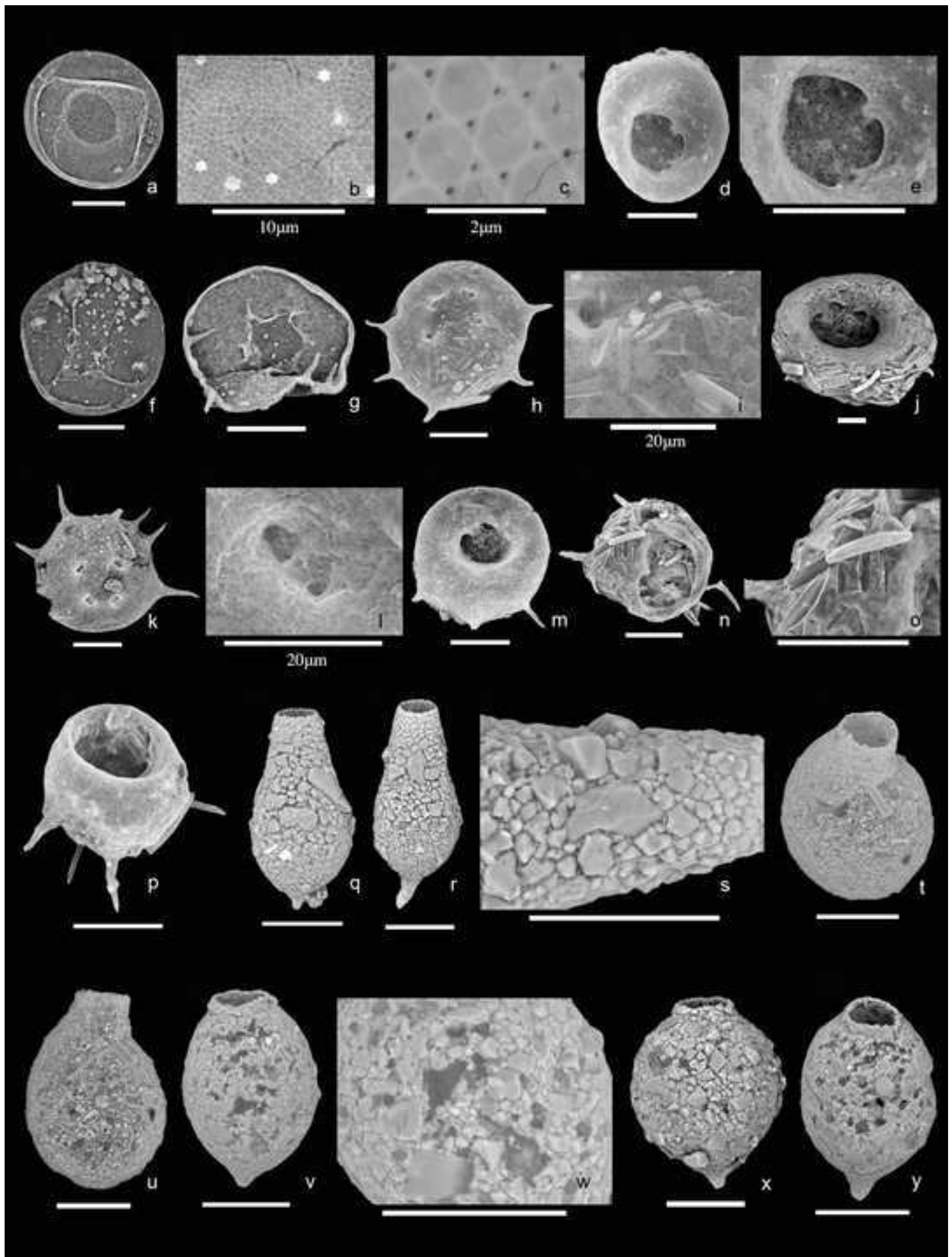
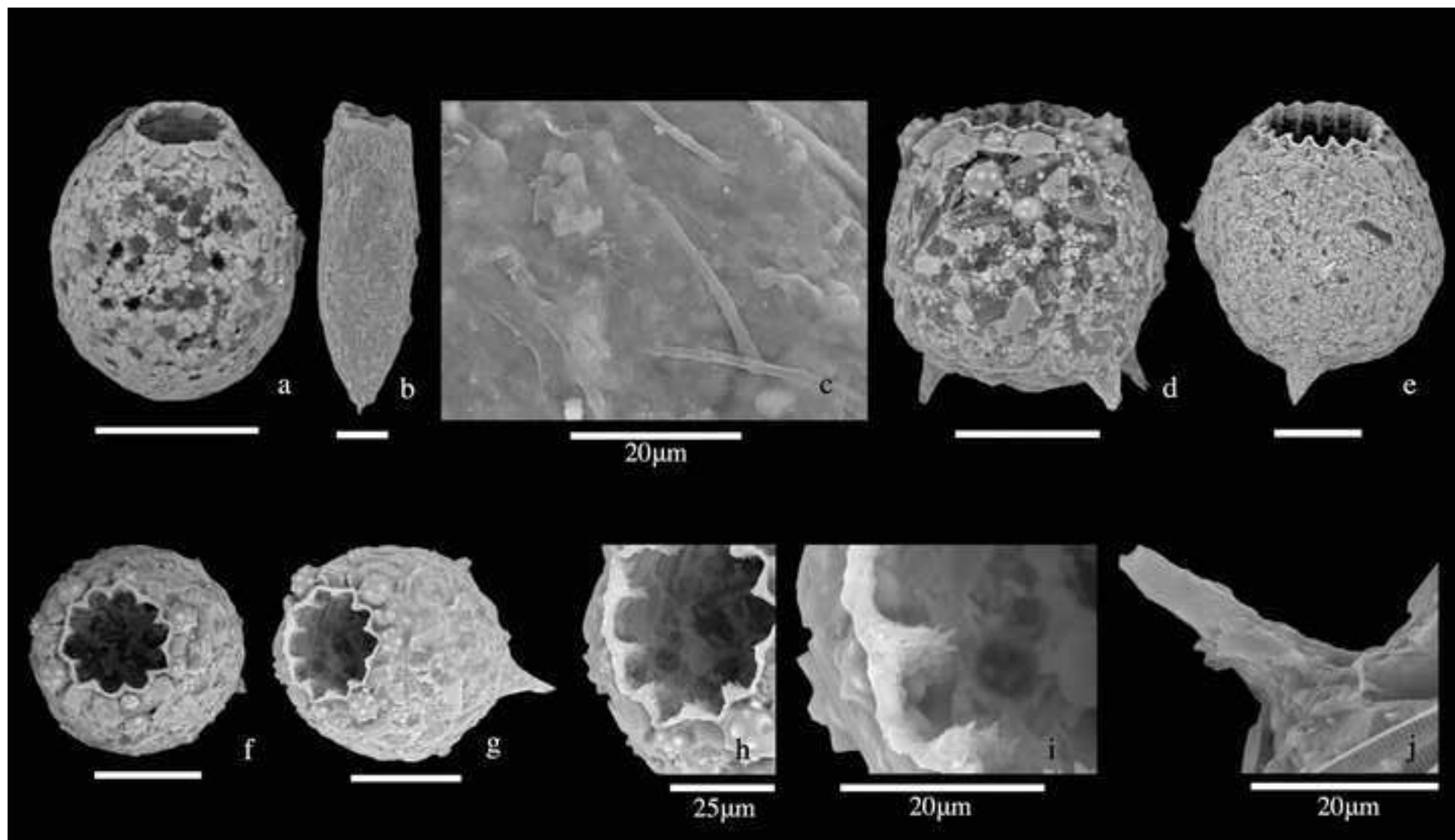


Figure 3  
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Revised Table 1

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	
Diffugia difficilis		0.44	0.29	0.25	0.25		0.33
Diffugia claviformis		0.22					
Mediolus corona	0.10	0.11	0.14	0.25	0.13		
Diffugia cf. scalpillum					0.13		
Lesquereusia spiralis	0.10				0.13		0.17

**Table 2**

Core Station Horizon	Sediment Type	N	C	C/N
Average	Gyttja	3.09	34.03	11.02
Median	Gyttja	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	Gyttja	2.44	27.32	11.19
Core 6: 0-1 cm	Gyttja	3.30	36.72	11.13
Core 7: 2-4 cm	Gyttja	3.14	34.38	10.96
Core 8: 0-1 cm	Gyttja	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	Gyttja	3.20	34.94	10.92
Core 12: 2-4 cm	Gyttja	3.21	35.15	10.95

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