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1 **Palaeoecology of testate amoebae in a tropical peatland**

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21 **Abstract**

22 We present the first detailed analysis of subfossil testate amoebae from a tropical
23 peatland. Testate amoebae were analysed from a 4-m peat core from western Amazonia
24 (Peru) and a transfer function developed from the site was applied to reconstruct changes in
25 water table over the past ca. 8,000 years. Testate amoebae were in very low abundance in the
26 core, especially in the lower 125 cm, due to a combination of poor preservation and
27 obscuration by other organic matter. A modified preparation method enabled at least 50
28 testate amoebae to be counted in each core sample. The most abundant taxa preserved include
29 *Centropyxis aculeata*, *Hyalosphenia subflava*, *Phryganella acropodia* and *Trigonopyxis*
30 *arcula*. *Centropyxis aculeata*, an unambiguous wet indicator, is variably present and indicates
31 several phases of near-surface water table. Our work shows that even degraded, low-
32 abundance assemblages of testate amoebae can provide useful information regarding the long-
33 term ecohydrological developmental history of tropical peatlands.

34
35 **Keywords:** Amazonia; Palaeoecology; Peatlands; Testate amoebae; Tropical rainforest

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38 Introduction

39 Tropical peatlands represent one of the largest pools of terrestrial organic carbon (C)
40 on Earth and are found in Asia, Africa and South America (Page et al., 2011; Lahteenoja and
41 Page, 2011). The ~89 Pg of C held in tropical peatlands (Page et al., 2011) is similar in
42 amount to that stored in the total aboveground live biomass of the entire Amazon rainforest
43 (93 ± 23 Pg C; Malhi et al., 2006). Despite the importance of tropical peatlands in the global
44 carbon cycle, relatively little is known about the ecohydrological dynamics of these systems
45 and the sensitivity of their carbon stocks to climate change. A greater understanding of long-
46 term hydrological change in tropical peatlands, whether driven by autogenic or allogenic (e.g.
47 climate) factors is needed, as enhanced drought is predicted for many tropical areas in future
48 climate change scenarios.

49 Testate amoebae are established as important hydrological indicators in mid- and high latitude
50 peatlands (e.g., Charman and Warner, 1992; Tolonen et al., 1994; Charman et al., 2000) as
51 development of transfer functions have enabled quantitative reconstruction of bog
52 palaeohydrology from subfossil tests (Charman et al., 2007; Lamentowicz et al. 2008;
53 Amesbury et al., 2013; Turner et al., 2013; Swindles et al., 2014). Recent research suggests
54 that testate amoebae show distinct responses across hydrological gradients in a tropical
55 peatland in Amazonia and therefore may have potential as palaeohydrological indicators in
56 tropical peatlands (Swindles et al., 2014). However, no detailed studies of subfossil testate
57 amoebae preserved in tropical peats exist at present. In this paper we examine the utility of
58 testate amoebae assemblages preserved in a core collected from the same Amazonian peatland
59 where modern testate amoebae were investigated (Swindles et al., 2014) to evaluate their
60 potential in palaeoecological studies of tropical peatlands.

61

62 **Material and Methods**

63 **Study site**

64 Aucayacu (meaning “water of the natives” or “water of the warriors” in the language
65 of indigenous people) is an ombrotrophic peat dome in Peruvian Amazonia (Lähteenoja et al.,
66 2012). It is situated on alluvial sediments between the Tigre River and a stream of the Pastaza
67 fan (Figure 1). The peatland formed as a nutrient-rich minerotrophic system that gradually
68 developed into an ombrotrophic raised bog (Lähteenoja et al., 2012). Aucayacu represents the
69 deepest and oldest peatland discovered in the Amazon basin (~7.5 m thick in the centre). Peat
70 initiation at the centre of the site is dated to c. 8870 cal. BP (Lähteenoja et al., 2012). The
71 vegetation of Aucayacu is characterised by 'pole' and 'dwarf' forest communities (Figure 2;
72 Swindles et al., 2014). For further information on the vegetation and geochemistry of the site
73 see Swindles et al. (2014). In Iquitos (120 km east of the study site), average annual rainfall of
74 up to 3,000 mm is typical, with a wetter period between the months of November to March
75 (Martinez et al., 2011). The average annual temperature at Iquitos is 26°C, with a diurnal
76 range of approximately 10°C (30-32°C daytime temperatures and 21-22°C at night) (Met
77 Office, 2011).

79 **Methods**

80 A 4-m long core was extracted from a litter flat between pools in the interior of
81 Aucayacu peatland using a Russian D-section corer with a 50-cm long chamber (Jowsey
82 1966; De Vleeschouwer et al. 2010; Figure 2). Core samples were transported to the
83 laboratory at the University of Leeds, UK, and stored in refrigeration at 4°C. Three AMS ¹⁴C
84 dates were retrieved from sieved acid-alkali-acid treated peat with rootlets picked out. ¹⁴C
85 dating was carried out at NERC Radiocarbon Facility (East Kilbride) and dates were

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86 calibrated using IntCal13 (Reimer et al. 2013). Testate amoebae were prepared using a
87 modified version of Booth et al. (2010). As testate amoebae were extremely rare at depth in
88 the core material, a fine sieve of 35 μm was used instead of the standard 15 μm to improve
89 sample clarity. No small specimens were found in the <35 μm fraction. Samples were stored
90 in deionised water before analysis. Testate amoebae were counted under transmitted light at
91 200-400 \times magnification and identified using test morphology, composition, size and colour to
92 distinguish taxa following Ogden and Hedley (1980), Charman et al., (2000), Meisterfeld
93 (2000a,b), and Mazei and Tsyganov (2006). The taxonomy uses a morpho-species approach
94 in some circumstances, where a name that includes several species has been classed as a
95 "type". A count of at least 50 specimens was achieved for all samples. The weighted-
96 averaging partial least squares (component 3) transfer function of Swindles et al. (2014) was
97 applied to the subfossil testate amoebae to generate a water-table reconstruction. This model
98 has the following performance statistics: $r^2_{(\text{apparent})} = 0.81$; $\text{RMSE} = 3.81$; $r^2_{(\text{leave-one-out cross}$
99 $\text{validation})} = 0.65$, $\text{RMSEP} = 5.24$, water-table depth range = 49 to -12 cm. As the transfer
100 function is based on one-time water table measurements the reconstruction was detrended by
101 linear regression following Swindles et al. (2015). Peat loss-on-ignition and humification
102 were determined following Chambers et al. (2011) and Roos-Barraclough et al. (2004),
103 respectively. Humification determinations were carried out on the same samples as those
104 analysed for testate amoebae. Statistical analyses were carried out using C2 (Juggins, 2007)
105 and R v. 3.1.2 (R Core Team, 2014).

107 **Results and Discussion**

108 Testate amoebae were in extremely low abundance in the core, which may be related
109 to relatively poor preservation (Swindles and Roe, 2007; Mitchell et al., 2008). However, a
110 count of 50 or more was achieved in all cases (Figure 3). Payne and Mitchell (2009) showed

111 that meaningful palaeoenvironmental signals can still be obtained from testate amoebae with
112 counts as low as 50 specimens. The transfer function was applied to the subfossil data and
113 there were no missing modern analogues. The subfossil testate amoebae diagram (Figure 3)
114 was zoned by visual inspection as follows:

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116 **Z1 (300-180 cm)** - This zone is characterised by a high relative abundance of *Hyalosphenia*
117 *subflava* (major and minor). *Phryganella acropodia* occurs up to the middle of the zone.
118 *Centropyxis aculeata* appears in the bottom of the zone and in the top – suggesting wet
119 conditions at this time. The total number of taxa fluctuates but remains below 10. The water
120 table depth curve exhibits a humpbacked profile changing from ~0 to 10 cm, and then getting
121 wetter again towards the top of the zone.

122 **Z2 (180-120 cm)** – The number of taxa increases slightly in this zone. *Hyalosphenia subflava*
123 “major” has a similar percentage to zone Z1; however, *H. subflava* “minor” decreases
124 considerably. *Centropyxis aculeata* reaches ~20%, but disappears towards the top of the zone.
125 Water table decreases to ~11 cm.

126 **Z3 (120-50 cm)** – The number of taxa is higher than in the former zone but fluctuates. Several
127 new species appear such as: *Arcella arenaria*, *Argygnia caudata*, *Centropyxis aerophila*,
128 *Diffflugia pulex*, *Padaungiella langeniformis* and *Tracheleuglypha dentata*; however, none of
129 these species are very abundant. The abundance of *Trigonopyxis arcuata* “polygon aperture”
130 increases considerably suggesting drier conditions. There is also an increase in *Phryganella*
131 *acropodia*. Reconstructed water-table increased from ~11 cm to ~7 cm and then decreased to
132 ~15 cm in top of the zone.

133 **Z4 (50-0 cm)** - Relative abundance of *Hyalosphenia subflava* (major and minor) is high (over
134 50%) in this zone. The percentage of *Centropyxis aculeata* increased towards the top of the
135 peat profile, suggesting wetter conditions. Additionally *Cryptodiffugia oviformis* has a high
136 abundance compared to the rest of the profile which may be related to better preservation at
137 the top of the profile. *Phryganella acropodia* reached ~40 % at the top of the core which
138 might be an artefact of better preservation in the core top. In general, the testate amoebae
139 assemblage indicates rising water table from ~13 to 2 cm. Species diversity is also highest in
140 this zone – providing evidence that the lower levels are being affected by poor preservation.
141 One specimen of the new species *Arcella peruviana* was found in this zone (Reczuga et al.,
142 2015).

143 The relationship between selected species of modern testate amoebae and water-table
144 depth in Aucayacu peatland is shown in Figure 4 (data are from Swindles et al., 2014). It is
145 apparent that the species *Centropyxis aculeata* is an important indicator of near-surface water
146 tables, supporting previous observations (e.g. Charman et al., 2000 and references therein).
147 The relationship between water-table depth and the abundance of the other taxa is more
148 ambiguous. There is general agreement between the level of humification and testate amoeba-
149 derived water-table reconstruction ($r = -0.48$, $p < 0.05$, $n = 25$) (Figure 5), suggesting that
150 both proxies are responding to a common hydrological driver. Radiocarbon dating shows that
151 the peatland began to develop ~ 7700 cal. BP and was characterised by near-surface water
152 tables, potentially as a swamp (Figure 5). The peatland then became drier as the peat dome
153 developed before entering a phase at ~ 6400 cal. BP characterised by a wetter peat surface
154 driven by high river levels. Flooding at this time is indicated by suppressed loss-on-ignition
155 values associated with increased deposition of minerogenic material. There is also a shift to
156 increased surface wetness near the top of the profile that may relate to recent increased

157 wetness in western Amazonia (Gloor et al., 2013). However, further detailed dating of the
1 recent peats is needed to clarify this.

159 Tropical peatlands are globally-important climate carbon stores (Page et al., 2011) that
160 are under threat from human impacts and climate change. However, there is a lack of
161 information regarding the ecohydrological dynamics and Holocene development pathways of
162 these systems. Our work shows that even highly degraded, low-abundance assemblages of
163 testate amoebae can be recovered from tropical peats and provide important
164 paleoecohydrological information. While subfossil testate amoebae in tropical peatlands may
165 never provide the level of information that can be gained from mid-high latitude peatlands
166 they nonetheless provide insight into the hydrological variability of tropical peatlands that
167 needs to be considered in global climate models and feedback mechanisms. This information
168 alongside other proxy evidence, e.g., pollen (plant functional types), humification (degree of
169 decomposition), bulk density (carbon and peat accumulation) is important for testing the
170 outputs of peatland development models (Frolking et al., 2010; Morris et al., 2011; Swindles
171 et al., 2012) modified for tropical peatland ecosystems. In the case of Amazonian peatlands,
172 testate amoebae also provide information regarding long-term hydrological change and
173 floodplain dynamics in Amazonia (Figure 5).

174

175 **Conclusions**

176 [1] Testate amoebae were analysed in a core from a tropical peat dome in western Amazonia
177 (Peru). Subfossil tests were sparse, although a minimum count of 50 specimens was achieved
178 for each sample.

179 [2] The most abundant testate-amoeba taxa in the core include *Centropyxis aculeata*,
180 *Hyalosphenia subflava*, *Phryganella acropodia* and *Trigonopyxis arcula*. *Centropyxis*

181 *aculeata* is an important indicator of standing water in tropical peatlands. A transfer function
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2 182 developed from the same site was applied to the subfossil assemblages to reconstruct
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5 183 fluctuations in water-table depth from ~7700 cal. BP to present.

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8 184 [3] Our work shows that testate amoebae can provide useful information regarding
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10 185 ecohydrological changes in tropical peatlands during the Holocene, despite the problems of
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12 186 low abundance and poor preservation.

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321 **Figure captions**

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323 **Figure 1.** Map showing the location of the Aucayacu peatland, Loreto region, Peruvian

324 Amazonia. False colour Landsat TM RGB image (Orthorectified, WRS-2, Path 007, Row

325 063). Band 4 was assigned to red, band 5 was assigned to green and band 7 was assigned to

326 blue. Landsat Data are available from the U.S. Geological Survey

327 (<http://earthexplorer.usgs.gov/>).

328

329 **Figure 2.** Photographs of (A) Pole forest typical of the Aucayacu peatland; (B) Dry 'litter

330 flat' area; (C) Peat pool.

331

332 **Figure 3.** Relative abundance of subfossil testate amoeba preserved in the Aucayacu core.

333 Also shown are the total count of tests, number of slides analysed to achieve the total count,

334 the number of taxa in each sample, Shannon diversity index, water-table depth reconstruction

335 (with errors derived from bootstrapping), and the water-table depth residuals (detrended

336 following Swindles et al., 2015).

337

338 **Figure 4.** Contemporary hydrological distribution of selected testate amoeba species present

339 in the Aucayacu core. The data are from Swindles et al. (2014). The red line represents

340 calculated optima from a simple Gaussian species packing model, based on weighted

341 averaging (ter Braak and van Dam, 1989); the thin blue lines represent the tolerance (standard

342 deviation).

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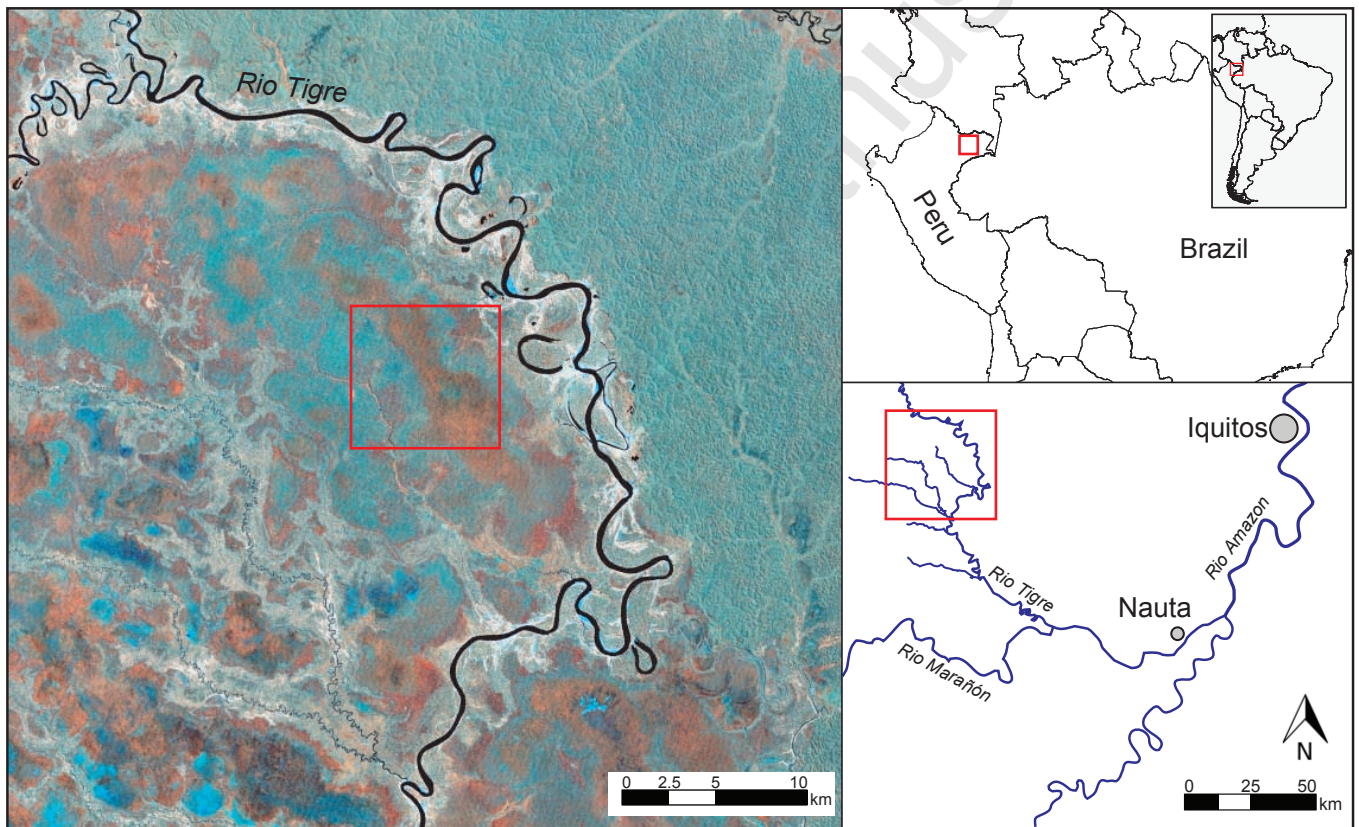
344 **Figure 5.** Detrended water-table depth reconstruction, plotted alongside humification (%
1 transmission) and loss-on-ignition data. Radiocarbon dates and hydrological interpretations
2 345 are illustrated.
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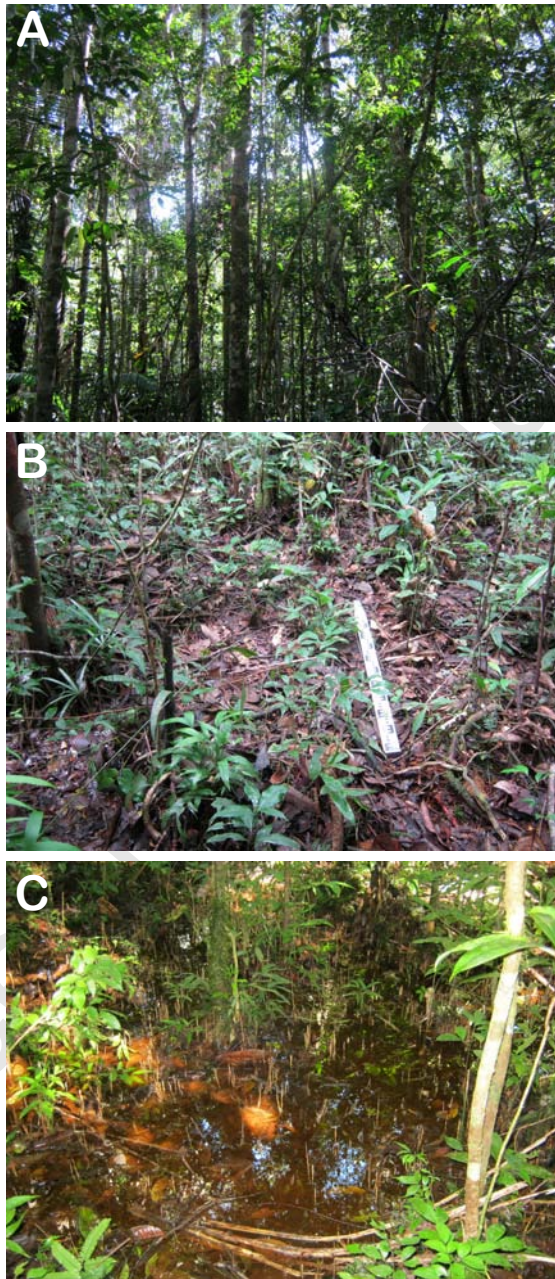
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9 **Table 1.** Taxa names and taxonomic authorities. All taxa shown are from the contemporary
10 348 training set from Aucayacu (Swindles et al., 2014). Those marked with an asterisk (*) were
11 349 found in the Aucayacu core samples.
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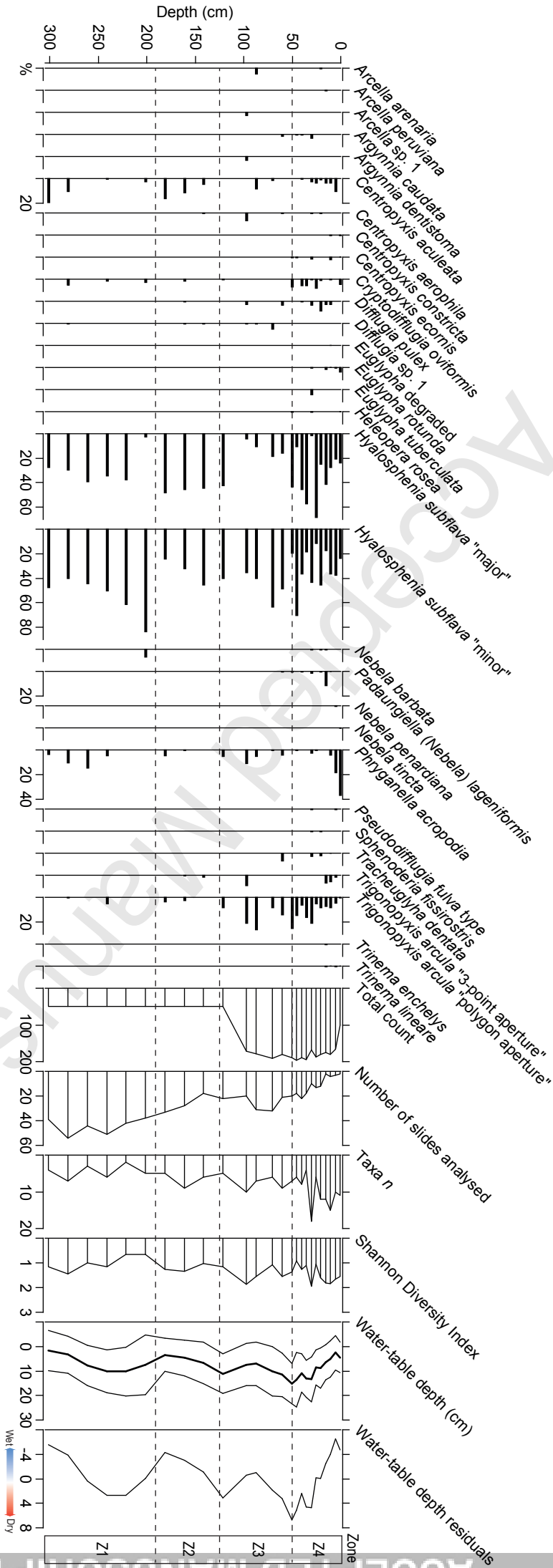
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18 **Table 2.** ^{14}C dates. AMS ^{14}C dates calibrated using IntCal13 (Reimer et al., 2013), including
19 352 2σ calibrated ages.
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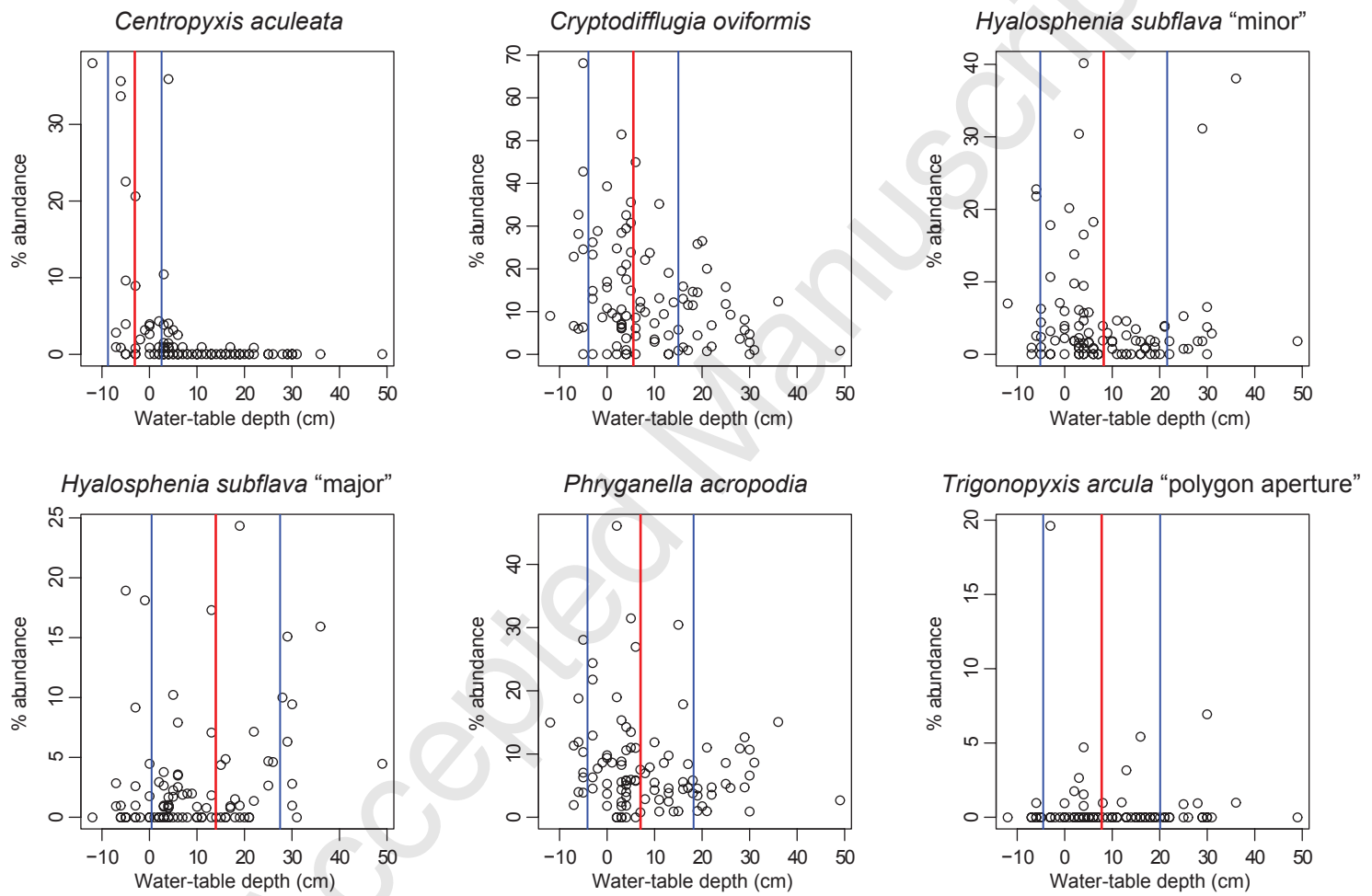
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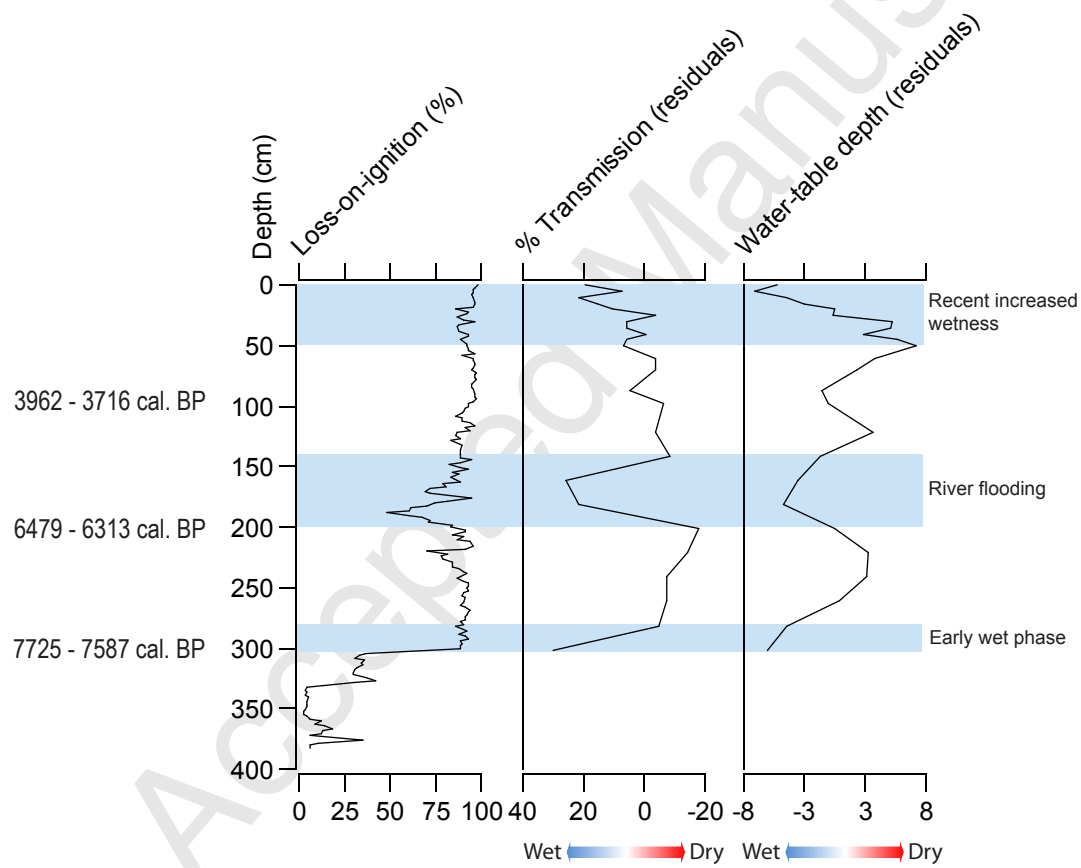
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SYSTEMATIC PALAEOONTOLOGY

Species name	Authority
<i>Arcella arenaria</i> *	Greeff 1866
<i>Arcella peruviana</i> *	Reczuga <i>et al.</i> 2015
<i>Arcella</i> spp.*	n/a
<i>Argygnia caudata</i> *	Leidy 1879
<i>Argygnia dentistoma</i> *	Penard 1890
<i>Argygnia spicata</i>	Wailes 1913
<i>Assulina muscorum</i>	Greeff 1888
<i>Centropyxis aculeata</i> *	Ehrenberg 1838
<i>Centropyxis aerophila</i> *	Deflandre 1929
<i>Centropyxis constricta</i> *	Ehrenberg 1841
<i>Centropyxis ecornis</i> *	Ehrenberg 1841
<i>Cryptodiffugia oviformis</i> *	Penard 1890
<i>Cryptodiffugia oviformis</i> “narrow”	Penard 1890
<i>Diffugia pulex</i> *	Penard 1902
<i>Diffugia</i> spp.*	n/a
<i>Euglypha crenulata</i>	Wailes 1912
<i>Euglypha cristata</i>	Leidy 1874
<i>Euglypha degraded</i> *	n/a
<i>Euglypha rotunda</i> type*	Wailes and Penard 1911
<i>Euglypha strigosa</i>	(Ehrenberg 1872); Leidy 1878
<i>Euglypha tuberculata</i> *	Dujardin 1841
<i>Heleopera rosea</i> *	Penard 1890
<i>Heleopera sylvatica</i>	Penard 1890
<i>Hyalosphenia subflava</i> “major”*	Cash and Hopkinson 1909
<i>Hyalosphenia subflava</i> “minor”*	Cash and Hopkinson 1909
<i>Lesqueresia spiralis</i>	Ehrenberg 1840
<i>Nebela barbata</i> *	Leidy 1874
<i>Nebela militaris</i>	Penard 1890
<i>Nebela penardiana</i> *	Deflandre 1936
<i>Nebela tincta</i> *	(Leidy 1979); Awerintzew 1906
<i>Padaungiella (Nebela) lageniformis</i> *	(Penard 1890); Lara et Todorov
<i>Padaungiella (Nebela) tubulata</i>	(Brown 1911); Lara et Todorov
<i>Phryganella acropodia</i> type*	(Hertwig and Lesser 1874); Cash and Hopkinson 1909
<i>Physochila cratera</i>	Wailes 1912
<i>Physochila griseola</i>	Wailes and Penard 1911
<i>Pseudodiffugia fulva</i> type*	Archer 1870
<i>Pyxidicula operculata</i>	Ehrenberg 1838
<i>Quadrullella symmetrica</i>	(Wallich 1863); Schulze 1875
<i>Sphenoderia fissirostris</i> *	Schlumberger 1845
<i>Tracheolocorythion pulchellum</i>	Penard 1890
<i>Tracheleuglypha dentata</i> *	Deflandre 1929
<i>Trigonopyxis arcula</i> “3-point aperture”*	Penard 1912
<i>Trigonopyxis arcula</i> “polygon aperture”*	Penard 1912
<i>Trinema complanatum</i>	Penard 1890
<i>Trinema enchelys</i> *	Leidy 1878
<i>Trinema grandis</i>	Chardez 1960
<i>Trinema lineare</i> *	Penard 1890

Code	Depth	Conventional ^{14}C age (years BP $\pm 1\sigma$)	Material	$\delta^{13}\text{C}_{\text{VPDB}} \pm 0.1$	Carbon content (% by weight)	Calibrated age (2σ)
SUERC-59689	90 - 91 cm	3549 \pm 37	Peat, sieved and roots removed	-29.4	58.3	3962 - 3716 cal. BP (Median probability = 3842 cal. BP)
SUERC-59691	200 - 201 cm	5625 \pm 37	Peat, sieved and roots removed	-29.8	52.1	6479 - 6313 cal. BP (Median probability = 6404 cal. BP)
SUERC-59693	300 - 301 cm	6825 \pm 39	Peat, sieved and roots removed	-29.9	14.7	7725-7587 cal. BP (Median probability = 7656 cal. BP)

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