Morphology of Chrysophycean stomatocysts in three peatlands in central China

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SUMMARY

Chrysophytes are sensitive to environmental changes in alpine peatlands, within which acidic and oligotrophic conditions favour the proliferation of chrysophytes. Previous investigations of chrysophyte stomatocysts in temperate and boreal regions provide basic knowledge on their morphology and distribution; however, subtropical areas have been less thoroughly explored. Twelve *Sphagnum* samples collected from three subtropical montane peatlands (central China) were analysed to reveal the morphotypes of stomatocysts in this less investigated region. Twenty-three morphotypes of chrysophyte stomatocysts were identified in these samples following the International Statospore Working Group (ISWG) guidelines, and illustrated by SEM and LM micrographs. They include nineteen previously described cysts and four newly described stomatocysts. The results of canonical correspondence analysis (CCA) indicated that the cyst assemblage was related to depth to water table (DWT), pH, oxidation reduction potential (ORP) and electrical conductivity (EC). These results improve our knowledge of the taxonomy and autecology of stomatocysts, highlighting the potential of stomatocysts as bioindicators in peatlands.

KEY WORDS: chrysophyte, environmental gradient, stomatocyst morphotype, subtropical peatland

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INTRODUCTION

Chrysophytes, known as ‘golden brown algae’ due to their predominant carotenoid pigments (mostly xanthophyll fucoxanthin) and other accessory pigments (phycochrysin) (Duff *et al*. 1995, Wilkinson *et al*. 2001), are a diverse group of freshwater algae consisting of over 1000 described species (Duff *et al*. 1995, Pla 2001). They live primarily in oligotrophic fresh water bodies with low temperature and slight acidity, such as montane lakes (Pla 2001, Cabała & Piątek 2004, Kamenik & Schmidt 2005, Soróczki-Pintér *et al*. 2014) and boreal peatlands (Gilbert *et al*. 1997, Wilkinson *et al*. 1997, Cabała 2003, Cabała 2005a, Piątek *et al*. 2009, Cambra 2010). They are typically planktonic but several epiphytic, epilithic and epipelic species also exist (Wilkinson *et al*. 1997, Pla 2001). Amongst benthic species, epiphyton and epilithon are more common than epipelon (Douglas & Smol 1995, Gilbert *et al*. 1997). Many chrysophytes have narrow ecological optima and tolerances along gradients of environmental factors such as pH and electrical conductivity (EC) (Van De Vijver & Beyens 1997, Smol & Cumming 2000). All chrysophytes are believed to produce siliceous stomatocysts, a special stage in chrysophyte propagation characterised by hollow, typically globose structures (Wilkinson *et al*. 1997), which can be well preserved in sediments (Kamenik & Schmidt 2005, Piątek *et al*. 2009, Soróczki-Pintér *et al*. 2014). The chrysophyte stomatocyst wall is morphologically diverse and different morphologies are thought to be species-specific (Duff *et al*. 1995, Pla 2001, Kamenik & Schmidt 2005, Piątek *et al*. 2009). All the characteristics mentioned above suggest that chrysophycean stomatocysts are potentially sensitive bioindicators of environmental conditions (Duff *et al*. 1995, Van De Vijver & Beyens 1997, Wilkinson *et al*. 2001, Pang 2012) such as nutrient concentration (Smol 1985, Chen *et al*. 2013), air temperature (Kamenik & Schmidt 2005, Lara *et al*. 2011) and hydrochemistry (Betts-Piper *et al*. 2004).

Peatlands are typically wet, nutrient-poor and acidic habitats that host distinctive fauna and flora (Rydin & Jeglum 2013). Although microorganisms (e.g. algae) play vital roles in biodiversity conservation and the biogeochemical cycles of peatlands, they have been less investigated than peatland macroorganisms (e.g. *Sphagnum* and vascular plants) (Rydin & Jeglum 2013, Chen *et al*. 2016). Chrysophytes, one important type of algae occurring within peatlands, have been investigated in temperate and boreal regions during recent decades. In North America, Alaska and Hawaii, more than 750 morphotypes were identified in montane lakes, wet meadows, ephemeral ponds and *Sphagnum* bogs (Adam & Mahood 1981). In north-eastern Siberia, 161 morphotypes were recorded from a forest peat core (Gilbert *et al*. 1997). On Ellesmere Island, Canada, 137 morphotypes were described (Wilkinson *et al*. 1997). In Polish peatlands, more than 30 morphotypes were discovered (Cabała 2003, 2005a). In the eastern Pyrenees, a total of 34 chrysophyte taxa were identified from lakes and peat bogs (Cambra 2010). On the subantarctic island of South Georgia, a total of 46 morphotypes were found in Strømness Bay (Van De Vijver & Beyens 1997).

China's peatlands cover about 7,000 km^2 and are distributed across diverse climate zones ranging from tropical in the far south to boreal in the far north (Chai 1990, Joosten & Clarke 2002). Until recently there had been few investigations of stomatocysts in China's peatlands (Pang & Wang 2017). More than 70 morphotypes of chrysophycean stomatocysts were observed in wetlands on the south-west flank of the Great Xing'an Mountains (Pang *et al*. 2012), and 171 morphotypes in an alpine peatland located in Inner Mongolia (Pang & Wang 2014). These pioneering studies conducted in temperate peatlands expanded our knowledge of stomatocysts in China.

In the subtropical region of central China, some patches of natural peatland have developed in topographic lowlands of mountains (Chen *et al*. 2014, 2016). These peatlands are hotspots of biodiversity (Joosten & Clarke 2002) and some of them, such as Dajiuhu Peatland, have been designated by the Chinese government as wetlands of international importance under the Ramsar Convention (Chen *et al*. 2017). Stomatocysts, potential bioindicators of modern and past environmental change in these subtropical peatlands, have received far less attention. This study aims to reveal morphotypes of chrysophycean stomatocysts and their distribution in three montane peatlands of the subtropical region of central China. The results will enhance our understanding of stomatocyst distribution and related environmental drivers, manifesting the potential of chrysophyte cysts as bioindicators in peatlands.

METHODS

The study area including Dajiuhu, Erxianyan and Qizimeishan peatlands is located in western Hubei Province, central China (Figure 1) and characterised by limestone and dolomite bedrock. It is situated in the subtropical monsoonal climate zone with a mean annual rainfall of ~1500–1800 mm and a mean annual temperature of ~7–14 °C. The peatlands are characterised by *Sphagnum* plants, slight acidity and low ionic strength (Table 1). Qizimeishan Peatland remains in a relatively natural environmental condition due to low levels of human disturbance (Cao *et al*. 2017) and was designated as a natural reserve immediately after its discovery in 2005 (Wang *et al*. 2005).

A total of 12 surface *Sphagnum* samples (four from each peatland) were collected in July 2014 by cutting with scissors. The sampling sites spanned three habitat types, namely hummocks, hollows and ditch edges (see the Appendix for details). At each

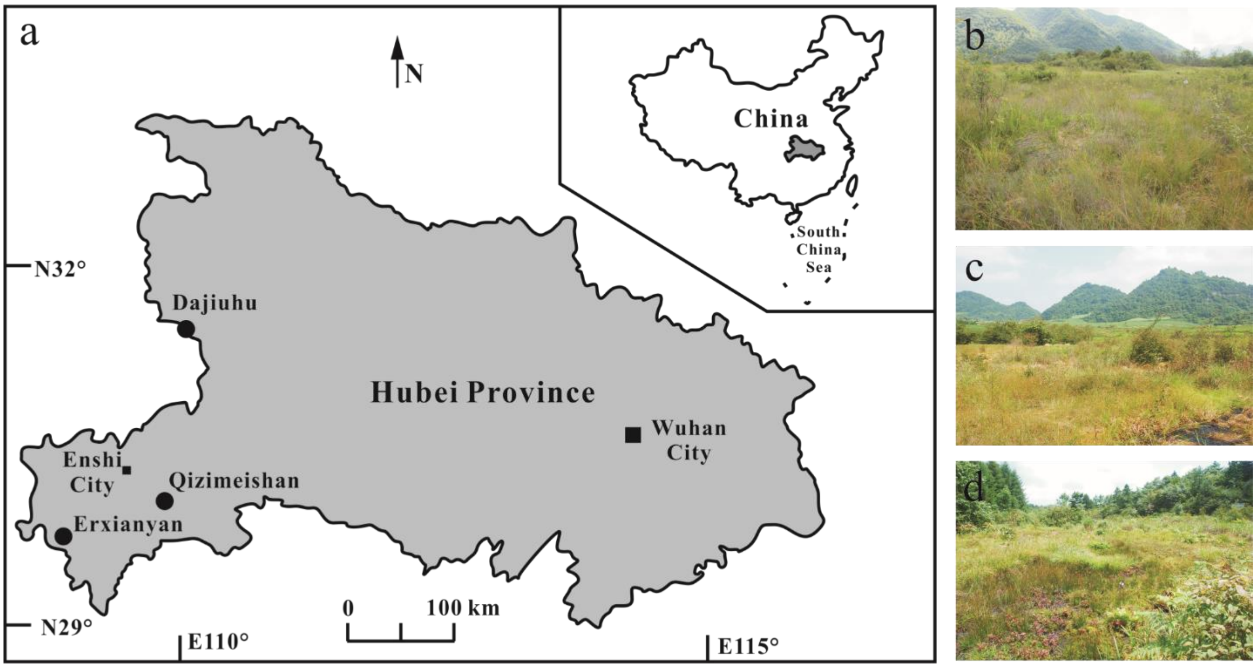

Figure 1. Locations of the three sampling sites in the study area (a) and landscape views of the Dajiuhu (b), Erxianyan (c) and Qizimeishan (d) peatlands.

Table 1. Summary information on the Dajiuhu, Erxianyan and Qizimeishan peatlands. For the environmental factors pH, EC (electrical conductivity) and ORP (oxidation reduction potential), ranges are shown in brackets.

	Dajiuhu	Erxianyan	Qizimeishan
Coordinates	31° 28′ 56″ N 109° 59′ 07″ E	29° 43′ 31″ N 108° 48′ 12″ E	29° 57′ 50″ N 109° 45′ 11″ E
Altitude (m a.s.l.)	~1760	~1550	~1800
Sample size	4	4	4
pH	5.2 (4.8–5.5)	5.7 (4.8–6.2)	4.8 (4.3–5.3)
EC (µS cm^{-1})	31.3 (17.5–56.7)	69.8 (32.0–113.5)	11.8 (7.6–21.4)
ORP (mV)	419.6 (402.3–443.8)	264.2 (218.5–350.8)	345.5 (331.5–371.3)

sampling site, geographical coordinates were determined using a Garmin Etrex GPS and depth to water table (DWT) was measured in a ~5 cm diameter hole using a graduated ruler. Electrical conductivity (EC), pH and oxidation reduction potential (ORP) were measured *in situ* using portable electrodes (Sanxin PD-501 for EC and pH, Thermo ORION 3-STAR for ORP). All electrodes were calibrated before use.

The treatment of stomatocyst samples is identical to the techniques used for diatoms (Barttarbee *et al*. 2001), because stomatocysts and diatoms have similar siliceous structures (Zeeb & Smol 2001). Samples were put into polythene bags and brought to the laboratory, where they were washed out in 100 ml of distilled water and thoroughly squeezed to collect the water. The contents of this *Sphagnum* wash (water with cysts and mud) were transferred into a beaker and heated to 80 °C with 10 % HCl and 30 % H_2O_2 in order to remove carbonate and organic matter (Chen *et al*. 2014). After the digestion, the aliquot suspensions were evaporated on cover slips and embedded in Naphrax^{TM} (RI = 1.7). For light microscope (LM) analyses, an Olympus BX53 microscope with 100 Plan N equipped with an Olympus DP27 digital camera was used. For the scanning electron microscope analyses (SEM), cleaned material was allowed to air-dry on microscope slides then sputter-coated with gold-palladium using a MSP-2S magnetron sputter for 1.4 minutes. SEM analyses were performed with a HITACHI SU8010 SEM operated at 15.0 kV. Cysts were identified mainly according to the taxonomy of Duff *et al*. (1995), Pla (2001), Wilkinson *et al*. (2001) and Pang & Wang (2017). New stomatocysts were measured and described according to the ISWG guidelines (Cronberg & Sandgren 1986), and they were assigned numbers beginning with Stomatocyst #1 and cited as “this article”. Picture-file number and number of specimens referred to the number of scanning electron micrographs used for description of new stomatocysts. At least 300 specimens were counted *per* sample, and cyst relative abundances were calculated for each sample.

In the ordination analyses, only those taxa with ≥ 2 % abundance in at least one sample were included. A unimodal ordination technique (canonical correspondence analysis, CCA) was chosen to explore the relationships between cyst composition and measured environmental variables (i.e. DWT, pH, EC and ORP), because the gradient length of cyst composition was more than three standard deviations, as assessed by an earlier detrended correspondence analysis (DCA) (ter Braak and Šmilauer 2002). All ordinations were performed using CANOCO 4.5 (ter Braak and Šmilauer 2002).

RESULTS

Stomatocysts were well preserved and cyst morphotypes could be distinguished on the basis of body surface ornamentation, cyst shape, collar type and pore type. A total of 23 morphotypes were identified using SEM, with 19 previously described cysts and four new stomatocysts (Table 2 and Figure 2). All of these morphotypes could be distinguished, at least tentatively, using LM (Figure 3). Detailed descriptions of the four new stomatocysts are given below.

Stomatocyst #1, Bai & Chen (Figures 2i, 3e).

SEM description: Spherical cyst (diameter 5.23–7.16 μm) with a smooth surface, a regular pore (diameter 0.37 μm) and a conical collar (basal diameter 1.64–1.86 μm; apical diameter 1.36–1.54 μm; apical diameter : cyst diameter ratio 0.22–0.29). The collar apex is irregular and slightly wavy with height 0.41–0.57 μm. The collar apex is acute and the outer collar base is gradual.

SEM Picture file number: Q13-19_i392.

Number of SEM specimens: 3.

Biological affinity: Unknown.

Locality: Qizimeishan Peatland.

Ecology: Sampled from a relatively dry hummock (DWT 13 cm) with pH 4.7, EC 10.1 μS cm^{-1} and ORP 342.9 mV.

Comments: Similar to Stomatocyst 181, Brown & Smol in Brown *et al*. 1994 (diameter 6.1–7.5 μm), especially under the LM, but our stomatocyst is smaller. Otherwise, the shape of the outer collar wall is steeper than in Stomatocyst 181 but the irregular collar apex is indistinguishable under the LM. Both Stomatocyst #1 and Stomatocyst 183, Brown & Smol have an irregular collar apex, but the acute apex of Stomatocyst #1 is different from the thickened apex of Stomatocyst 183 (Brown *et al*. 1994). Stomatocyst #1 is also similar in size to Stomatocyst 234, Duff *et al*. 1995 (diameter 5.3–7.9 μm, collar diameter/cyst diameter 0.22–0.35), but Stomatocyst 234 has a flat collar apex and a lower collar (height 0.1–0.3 μm). Stomatocyst 146, Zeeb & Smol (Pienitz *et al*. 1992) is also similar to Stomatocyst #1, but the former has a regular and rounded apex, and relatively larger collar (diameter 2.2–2.7 μm) and pore (0.6 μm).

Table 2. List of previously identified and newly observed stomatocysts in Dajiuhu (D), Erxianyan (E) and Qianzimeishan (Q) peatlands and their frequencies (+ rare; ++ moderate; +++ abundant).

Morphotypes		Figures	Peatlands		
			D	E	Q
Unornamented stomatocyst without a collar	**Stomatocyst 1**, Duff & Smol 1988 *emend*. Zeeb & Smol 1993a	2a, 3a			+
	Stomatocyst 9, Duff & Smol 1988 *emend.* Zeeb & Smol 1993a	2b, 3n		+	+++
	Stomatocyst 19, Duff & Smol 1988	2c, 3o	+++		+
	Stomatocyst 42, Duff & Smol 1989	2e, 3t			+
	Stomatocyst 120, Duff & Smol in Duff *et al*. 1992 *emend*. Zeeb & Smol 1993a	2d, 3b	+		+
Unornamented stomatocyst with a conical collar	**Stomatocyst 110**, Zeeb *et al*. 1990	2f, 3c	+	+++	
	Stomatocyst 134, Duff & Smol in Duff *et al*. 1992	2g, 3d, 3l	++	+	+
	Stomatocyst 181, Brown & Smol in Brown *et al*. 1994	2h, 3p	+	+++	+
	Stomatocyst #1, Bai & Chen (this article)	2i, 3e			+
Unornamented stomatocyst with a cylindrical collar	**Stomatocyst 52**, Duff & Smol 1991 *emend*. Duff *et al*. 1995	2j, 3f	+		+
	Stomatocyst 183, Brown & Smol in Brown *et al*. 1994	2k, 3g		+	
	Stomatocyst 234, Duff *et al*. 1995	2l, 3q	+	+	+

continued overleaf

Table 2: continuation

Morphotypes		Figures	Peatlands		
			D	E	Q
Unornamented stomatocyst with an obconical collar	**Stomatocyst 41**, Pang & Wang 2017	2m, 3r	+	+	
Unornamented stomatocyst with a complex or false collar	**Stomatocyst 16**, Duff & Smol 1988	2n		+	
	Stomatocyst 135, Duff & Smol in Duff *et al*. 1992	2o, 3u	+	+	+
	Stomatocyst 136, Duff & Smol in Duff *et al*. 1992	2p, 3m			+
	Stomatocyst 187, Brown and Smol in Brown *et al*. 1994	2q, 2r, 3s	+	+	+
	Stomatocyst #2 Bai & Chen (this article)	2s, 3h	+++	+	++
	Stomatocyst #3 Bai & Chen (this article)	2t, 3i	+	+++	+
Ornamented stomatocyst with spines	**Stomatocyst 80**, Hansen 2001	2u, 3v, 3w	+++	++	+++
	Stomatocyst #4, Bai & Chen (this article)	2v, 3x	+	+	+
Ornamented stomatocyst with ridges	**Stomatocyst 334**, Wilkinson & Smol 1998	2w, 3j			+
Ornamented stomatocyst with reticula	**Stomatocyst 86**, Duff & Smol in Duff *et al*. 1995	2x, 3k	++		

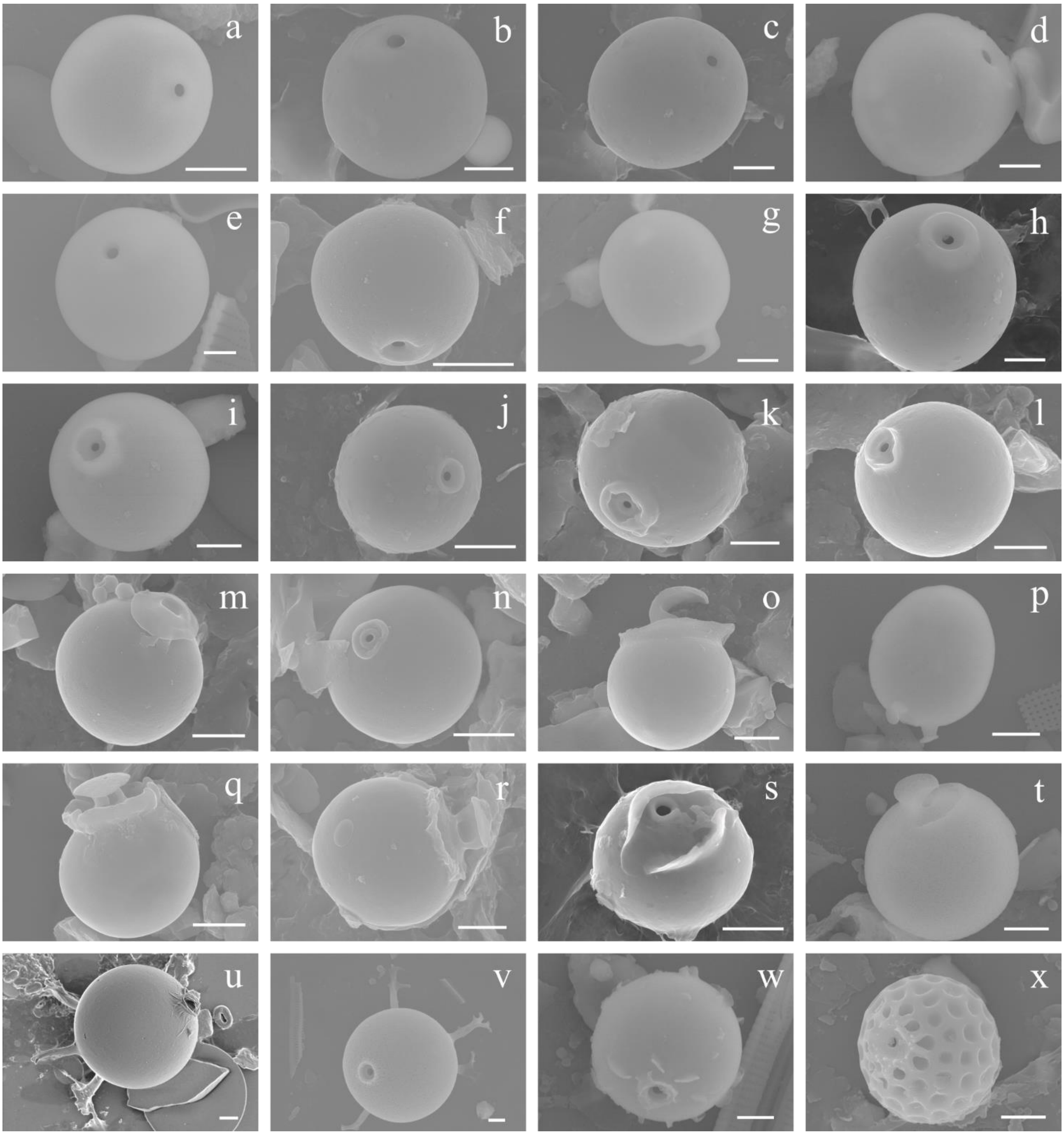

Figure 2. SEM pictures of chrysophyte stomatocysts. a: Stomatocyst 1, Duff & Smol 1988 *emend*. Zeeb & Smol 1993a; b: Stomatocyst 9, Duff & Smol 1988 *emend*. Zeeb & Smol 1993a; c: Stomatocyst 19, Duff & Smol 1988; d: Stomatocyst 120, Duff & Smol in Duff *et al*. 1992 *emend*. Zeeb & Smol 1993a; e: Stomatocyst 42, Duff & Smol 1989; f: Stomatocyst 110, Zeeb *et al*. 1990; g: Stomatocyst 134, Duff & Smol in Duff *et al*. 1992; h: Stomatocyst 181, Brown & Smol in Brown *et al*. 1994; i: Stomatocyst #1, Bai & Chen (this article); j: Stomatocyst 52, Duff & Smol 1991 *emend*. Duff *et al*. 1995; k: Stomatocyst 183, Brown & Smol in Brown *et al*. 1994; l: Stomatocyst 234, Duff *et al*. 1995; m: Stomatocyst 41, Pang & Wang 2017; n: Stomatocyst 16, Duff & Smol 1988; o: Stomatocyst 135, Duff & Smol in Duff *et al*. 1992; p: Stomatocyst 136, Duff & Smol in Duff *et al*. 1992; q and r: Stomatocyst 187, Brown & Smol in Brown *et al*. 1994; s: Stomatocyst #2, Bai & Chen (this article); t: Stomatocyst #3, Bai & Chen (this article); u: Stomatocyst 80, Hansen 2001; v: Stomatocyst #4, Bai & Chen (this article); w: Stomatocyst 334, Wilkinson & Smol 1998; x: Stomatocyst 86, Duff & Smol in Duff *et al*. 1995. Scale bars = 2 µm.

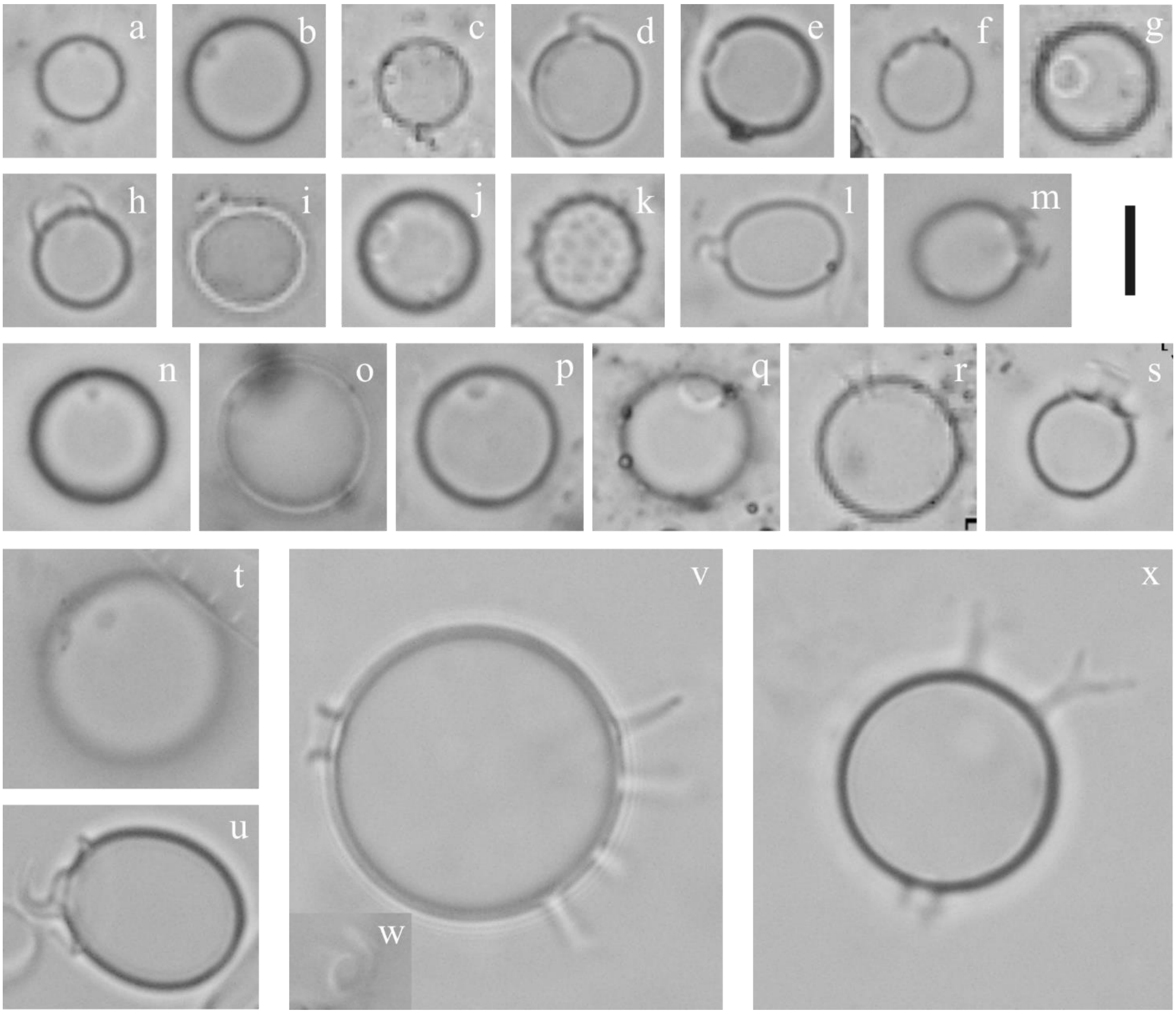

Figure 3. LM pictures of chrysophyte stomatocysts. a: Stomatocyst 1, Duff & Smol 1988 *emend*. Zeeb & Smol 1993a; b: Stomatocyst 120, Duff & Smol in Duff *et al*. 1992 *emend*. Zeeb & Smol 1993a; c: Stomatocyst 110, Zeeb *et al*. 1990; d and l: Stomatocyst 134, Duff & Smol in Duff *et al*. 1992; e: Stomatocyst #1, Bai & Chen (this article); f: Stomatocyst 52, Duff & Smol 1991 *emend*. Duff *et al*. 1995; g: Stomatocyst 183, Brown & Smol in Brown *et al*. 1994; h: Stomatocyst #2, Bai & Chen (this article); i: Stomatocyst #3, Bai & Chen (this article); j: Stomatocyst 334, Wilkinson & Smol 1998; k: Stomatocyst 86, Duff & Smol in Duff *et al*. 1995; m: Stomatocyst 136, Duff & Smol in Duff *et al*. 1992; n: Stomatocyst 9, Duff & Smol 1988 *emend*. Zeeb & Smol 1993a; o: Stomatocyst 19, Duff & Smol 1988; p: Stomatocyst 181, Brown & Smol in Brown *et al*. 1994; q: Stomatocyst 234, Duff *et al*. 1995; r: Stomatocyst 41, Pang & Wang 2017; s: Stomatocyst 187, Brown & Smol in Brown *et al*. 1994; t: Stomatocyst 42, Duff & Smol 1989; u: Stomatocyst 135, Duff & Smol in Duff *et al*. 1992; v: Stomatocyst 80, Hansen 2001; w: spiral ridge ornamentation on the base of the outer collar of Stomatocyst 80, Hansen 2001; x: Stomatocyst #4, Bai & Chen (this article). Scale bar = 5 µm.

Stomatocyst #2, Bai & Chen (Figures 2s, 3h).

SEM description: This stomatocyst can have different shapes of cyst body. It is spherical, oval or obovate (diameter 4.92–8.47 µm) with a smooth surface and a regular pore (diameter 0.45–0.48 µm). The pore margin may be swollen (width of the swollen annulus 0.14 µm). Two long wing-like ridges (distance between ridges 2.36–5.08 µm; length of ridges 2.16–5.85 µm; height 0.34–1.74 µm) surround the pore to form a false collar. In general, the ridges are asymmetric and the apices are flexed inwards, but there are also some irregularly-flexed apices.

SEM Picture file number: E12-20_i368.

Number of SEM specimens: 31.

Biological affinity: Unknown.

Localities: Dajiuhu Peatland, Erxianyan Peatland and Qizimeishan Peatland.

Ecology: This may be a widespread morphotype with broad tolerance along gradients of water level (DWT 2–32 cm), pH (4.7–6.2), EC (7.6–113.5 µS cm^{-1}) and ORP (218.5–420.7 mV).

Comments: The side profile of the false collar under the LM is just like animal tentacles, and the apical profile is usually asymmetric. The pore can be observed in an apical view. This stomatocyst looks very similar to Stomatocyst 204, Duff & Smol 1994 in Cabała & Piątek 2004 under the LM, but the latter has a true complex collar and a complete secondary collar. Some specimens look similar to Stomatocyst 65, Pang & Wang, but Stomatocyst 65 is larger (diameter 10.9–13.1 µm) and ornamented with tuberculate projections (Pang & Wang 2014).

Stomatocyst #3, Bai & Chen (Figures 2t, 3i).

SEM description: This stomatocyst has different shapes of cyst body; it may be spherical, ovate or sometimes oblate (diameter 6.52–7.13 µm). A vertical cap-like projection rises from one side of the pore and inflates terminally (size and morphology of the pore are not visible). The projection is flat and rounded at the apex (diameter 1.49–2.25 µm; height 0.56–1.55 µm). On the other side of the pore, there is a low semicircular collar with an irregular apex (diameter 1.69–3.66 µm; height 0.31–0.68 µm).

SEM Picture file number: E14-25_i334.

Number of SEM specimens: 12.

Biological affinity: Unknown.

Localities: Erxianyan Peatland and Qizimeishan Peatland.

Ecology: This may be a widespread morphotype with broad tolerance along gradients of water level (DWT 8–32 cm), pH (4.3–6.2), EC (21.4–74.4 µS cm^{-1}) and ORP (218.5–371.3 mV).

Comments: Stomatocyst #3, Bai & Chen is very similar to Stomatocyst 187, Brown & Smol in Brown *et al*. 1994 under the LM, but the former is not so rounded as the latter. This morphotype looks like Stomatocyst 61, Van De Vijver & Beyens 1997, but the apex of the secondary collar is more developed and thickened in Stomatocyst 61. It is also similar to Stomatocyst 54, Hansen 2001 which, however, lacks the semicircular collar and has a longer projection.

Stomatocyst #4, Bai & Chen (Figures 2v, 3x).

SEM description: Spherical cyst (diameter 12.16–15.81 µm) with a regular pore (diameter 0.68–1.08 µm) and a cylindrical collar (diameter 2.27–3.38 µm). The collar height is quite different (up to 1.08 µm) and the collar apex may be irregular. A flat planar annulus (width 0.34–0.80 µm) separates the pore and the collar. There are several broken spines on the posterior (length up to 5.95 µm; width at the base ~ 0.20–1.02 µm). The spines may be bifurcated.

SEM Picture file number: D12-29_i151.

Number of SEM specimens: 16.

Biological affinity: Unknown.

Localities: Dajiuhu Peatland, Erxianyan Peatland and Qizimeishan Peatland.

Ecology: This may be a widespread morphotype with broad tolerance along gradients of water level (DWT 2–32 cm), pH (4.7–6.2), EC (10.1–59.2 µS cm^{-1}) and ORP (246.4–420.7 mV).

Comments: This morphotype is similar to Stomatocyst 80, Hansen 2001 (cyst diameter 11.9–15.9 µm; pore diameter 0.8–1.0 µm; basal collar diameter 2.5–3.6 µm; height 1.0–1.8 µm), but the latter has distinctive features including out-flexed collar apices, a few swollen annuli on inner collar walls, and spiral ridges on the bases of collars and spines (cf. Pang & Wang 2017). Indeed, Stomatocyst #4, Bai & Chen cannot be distinguished from Stomatocyst 80, Hansen 2001 under LM if the latter does not display an obvious outwardly flexed collar apex.

Two subgroups were identified on the basis of body surface ornamentation; there were 19 morphotypes without ornamentation and four morphotypes with reticula, ridges and spines on their body surfaces (Table 2). Cyst sizes ranged from 3.6 to 17.3 µm, primarily within the range 6–9 µm. Among the 23 morphotypes, both Stomatocyst 52, Duff & Smol *emend*. Duff *et al*. and Stomatocyst 110, Zeeb *et al*. were small (≤ 5 µm), while Stomatocyst 42, Duff & Smol, Stomatocyst 80, Hansen and Stomatocyst #4, Bai & Chen were relatively large (> 9 µm). Four collar shapes were found in our samples, namely cylindrical (three morphotypes), conical (five morphotypes), obconical (one morphotype) and complex or false (six morphotypes). Both regular and concave pores were observed, with pore size ranging from 0.3 to 1.1 µm.

A total of 15, 14 and 18 morphotypes were identified in Dajiuhu, Erxianyan and Qizimeishan Peatlands, respectively. Overall, 4014 cysts were enumerated in the 12 samples, with 17 morphotypes occurring at relative abundance ≥ 2 % in at least one sample. Stomatocyst 80, Hansen (19.5 %), Stomatocyst 181, Brown & Smol (18.7 %) and Stomatocyst #2, Bai & Chen (10.5 %) were the dominant cysts in the three peatlands. Most cysts (69.5 %) had unornamented body surfaces.

The first two CCA axes explained 26.5 % of the variance in cyst composition, and the cysts displayed clear variations along the measured environmental gradients (Figure 4a). For example, Stomatocyst 80, Hansen preferred wet habitats along the water level gradient, while Stomatocyst 41, Pang & Wang was a drought-tolerant cyst and abundant in dry hummocks. Along the acidity gradient, both Stomatocyst 42, Duff & Smol and Stomatocyst 134, Duff & Smol preferred more acidic habitats than Stomatocyst #3, Bai & Chen, which was mainly found in slightly acidic environments (pH 6–7). Along the ORP gradient, Stomatocyst 19, Duff & Smol preferred habitats with higher ORP while Stomatocyst 181, Brown & Smol thrived in more reducing conditions. In addition, Stomatocyst 9, Duff & Smol preferred extremely low ionic strength environments while Stomatocyst #3,

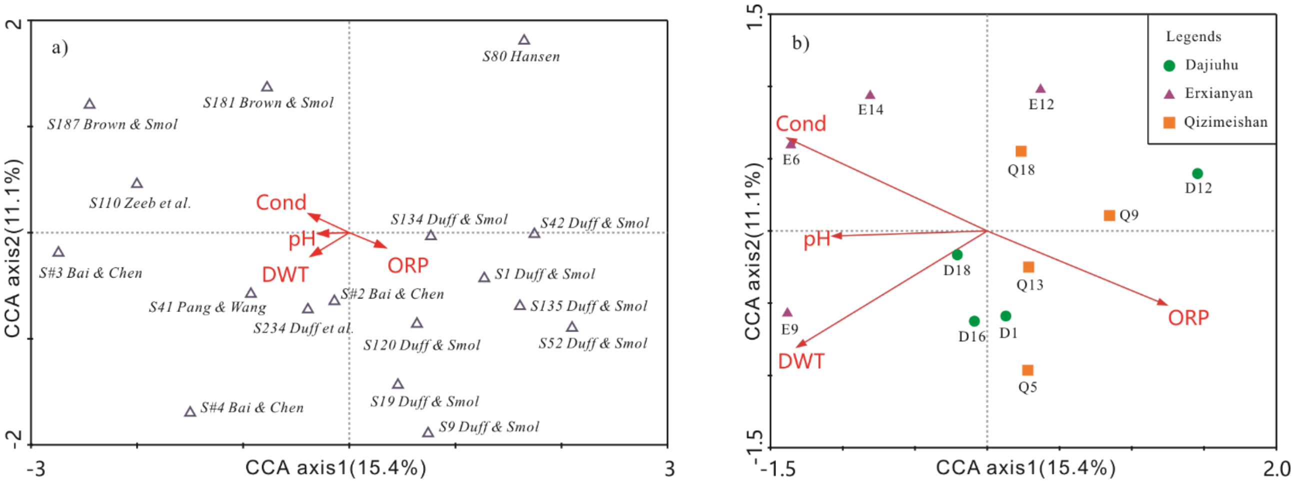

Figure 4. The results of canonical correspondence analysis (CCA): a) ordination of cysts and b) ordination of sampling sites with selected environmental variables. In a), ‘S’ is an abbreviation for ‘Stomatocyst’.

Bai & Chen proliferated in habitats with relatively high EC (> 50 µS cm^{-1}). Samples from Dajiuhu Peatland were similar to those from Qizimeishan Peatland, as indicated by their overlapping locations in the biplot (Figure 4b). Compared with Dajiuhu and Qizimeishan, Erxianyan Peatland was characterised by high pH and conductivity.

DISCUSSION

Stomatocysts have been studied mostly in boreal peatlands and alpine lakes characterised by cool and humid climatic conditions. Most (19) of the 23 morphotypes identified in our study have been reported in other places around the world. Stomatocyst 1, Duff & Smol has been found in Ellesmere Island (Duff & Smol 1988, Wilkinson *et al*. 1997), Minnestota (Zeeb & Smol 1993a, 1993b), northeastern Siberia (Gilbert *et al*. 1997), Kraków-Częstochowa Upland (Cabała 2002), Svalbard archipelago (Betts-Piper *et al*. 2004), Tatra National Park (Cabała 2005a), the Southern Carpathians (Soróczki-Pintér *et al*. 2014); the Great Xing'an Mountains (Pang & Wang 2014) and Xinjiang Province in China (Pang & Wang 2016). Stomtocyst 9, Duff & Smol has been found in Ellesmere Island (Duff & Smol 1988, Duff *et al*. 1992, Wilkinson *et al*. 1997), Minnestota (Zeeb & Smol 1993a), northwestern Greenland (Brown *et al*. 1994), northeastern Siberia (Gilbert *et al*. 1997), Svalbard archipelago (Betts-Piper *et al*. 2004), Małopolska Upland (Wołowski *et al*. 2004), Tatra National Park (Cabała & Piątek 2004, Cabała 2005a, b) and the Southern Carpathians (Soróczki-Pintér *et al*. 2014). Stomatocyst 16, Duff & Smol has been found in Ellesmere Island (Duff & Smol 1988), northeastern Siberia (Gilbert *et al*. 1997), Svalbard archipelago (Betts-Piper *et al*. 2004) and Tatra National Park (Cabała & Piątek 2004). Stomatocyst 19, Duff & Smol has been found in Ellesmere Island (Duff & Smol 1988, Duff *et al*. 1992, Wilkinson *et al*. 1997), northeastern Siberia (Gilbert *et al*. 1997), Kraków-Częstochowa Upland (Cabała 2002), Svalbard archipelago (Betts-Piper *et al*. 2004) and Tatra National Park (Cabała 2005a). Stomatocyst 41, Pang & Wang has been found in the Great Xing'an Mountains in China (Pang & Wang 2014, 2017). Stomatocyst 42, Duff & Smol has been found in Ellesmere Island (Duff *et al*. 1992, Wilkinson *et al*. 1997), Baffin Island (Duff & Smol 1989), northeastern Siberia (Gilbert *et al*. 1997), Svalbard archipelago (Betts-Piper *et al*. 2004), Małopolska Upland (Wołowski *et al*. 2004), the Great Xing'an Mountains (Pang & Wang 2014) and Xinjiang Province in China (Pang & Wang 2016). Stomatocyst 52, Duff & Smol has been found in northwestern Greenland (Brown *et al*. 1994), northeastern Siberia (Gilbert *et al*. 1997) and Tatra National Park (Cabała & Piątek 2004). Stomatocyst 80, Hansen has been found in the Azores archipelago (Hansen 2001), Tatra National Park (Cabała 2005a) and the Great Xing'an Mountains in China (Pang & Wang 2014). Stomatocyst 86, Duff & Smol has been found in Svalbard archipelago (Betts-Piper *et al*. 2004), Tatra National Park (Cabała & Piątek 2004, Cabała 2005a) and the Great Xing'an Mountains in China (Pang & Wang 2014). Stomatocyst 110, Zeeb *et al*. has been found in Ellesmere Island (Duff *et al*. 1992), northeastern Siberia (Gilbert *et al*. 1997) and Svalbard archipelago (Betts-Piper *et al*. 2004). Stomatocyst 120, Duff & Smol has been found in Ellesmere Island (Duff *et al*. 1992, Wilkinson *et al*. 1997), Minnestota (Zeeb & Smol 1993a, 1993b), northwestern Greenland (Brown *et al*. 1994), northeastern Siberia (Gilbert *et al*. 1997), Kraków-Częstochowa Upland (Cabała 2002), Svalbard archipelago (Betts-Piper *et al*. 2004), Małopolska upland (Wołowski *et al*. 2004), Tatra National Park (Cabała & Piątek 2004) and the Southern Carpathians (Soróczki-Pintér *et al*. 2014). Stomatocyst 134, Duff & Smol has been found in Ellesmere Island (Duff *et al*. 1992), northeastern Siberia (Gilbert *et al*. 1997), Kraków-Częstochowa Upland (Cabała 2002), Svalbard archipelago (Betts-Piper *et al*. 2004) and the Great Xing'an Mountains in China (Pang & Wang 2014). Stomatocyst 135, Duff & Smol has been found in Ellesmere Island (Duff *et al*. 1992), northeastern Siberia (Gilbert *et al*. 1997), Tatra National Park (Cabała & Piątek 2004, Cabała 2005a), the Southern

Carpathians (Sorócki-Pintér *et al*. 2014), the Great Xing'an Mountains (Pang & Wang 2014) and Xinjiang Province in China (Pang & Wang 2016). Stomatocyst 136, Duff & Smol has been found in Ellesmere Island (Duff *et al*. 1992), northeastern Siberia (Gilbert *et al*. 1997), the Southern Carpathians (Sorócki-Pintér *et al*. 2014), the Great Xing'an Mountains (Pang & Wang 2014) and Xinjiang Province in China (Pang & Wang 2016). Stomatocyst 181, Brown & Smol has been found in northwestern Greenland (Brown *et al*. 1994), northeastern Siberia (Gilbert *et al*. 1997), Kraków-Częstochowa Upland (Cabała 2002), Svalbard archipelago (Betts-Piper *et al*. 2004), Tatra National Park (Cabała & Piątek 2004) and the Great Xing'an Mountains in China (Pang & Wang 2014). Stomatocyst 183, Brown & Smol has been found in northwestern Greenland (Brown *et al*. 1994), northeastern Siberia (Gilbert *et al*. 1997), Tatra National Park (Cabała 2005a) and the Great Xing'an Mountains in China (Pang & Wang 2014). Stomatocyst 187, Brown & Smol has been found in northwestern Greenland (Brown *et al*. 1994) and northeastern Siberia (Gilbert *et al*. 1997). Stomatocyst 234, Duff *et al*. has been found in Ellesmere Island (Duff *et al*. 1992), northeastern Siberia (Gilbert *et al*. 1997) and Svalbard archipelago (Betts-Piper *et al*. 2004). Stomatocyst 334, Wilkinson & Smol has been found in south-central Ontario (Wilkinson & Smol 1998) and Svalbard archipelago (Betts-Piper *et al*. 2004). These morphotypes may be produced by cosmopolitan species. Stomatocyst 42, Duff & Smol was even discovered in a thermo-mineral spring in Ain Sukhna, an arid region of Egypt (Piątek *et al*. 2009), indicating that this morphotype has a broad environmental tolerance. The four new morphotypes discovered in this study may be produced by endemic species, and further study of their biological affinities is needed.

The relatively natural environmental condition of Qizimeishan Peatland probably accounted for its high species richness. Environmental conditions in Dajiuhu Peatland were similar to those in Qizimeishan Peatland, as indicated by the similar ranges of measured environmental variables. Erxianyan Peatland differed from Dajiuhu and Qizimeishan in that pH and EC were higher, probably as a result of *Sphagnum* harvesting which can increase nutrient and cation concentrations in the water column by accelerating peat decomposition (Wind-Mulder & Vitt 2000, Cao *et al*. 2017).

Stomatocyst 181, Brown & Smol, Stomatocyst 187, Brown & Smol and Stomatocyst 110, Zeeb *et al*. thrived in habitats with high pH and ionic strength (Figure 4a). Stomatocyst 110, Zeeb *et al*. also occurred in a Polish lake with pH ranging from 7.4 to 7.7 (Rybak 1987). Stomatocyst 52, Duff & Smol, Stomatocyst 42, Duff & Smol and Stomatocyst 135, Duff & Smol were abundant in highly acidic conditions with low ionic strength (Figure 4a). Stomatocyst 52, Duff & Smol and Stomatocyst 135, Duff & Smol were also observed in a Polish peat bog with low ionic strength (EC ~ 42 µS cm^{-1}) and low pH (~ 5) (Cabała & Piątek 2004). Stomatocyst 42, Duff & Smol increased with declining pH in a Polish lake (Rybak 1987). Stomatocyst 80, Hansen preferred wet hollows in this study and was also found in *Sphagnum* bogs in the Great Xing'an Mountains (Pang 2012). These results improve our knowledge of stomatocyst taxonomy, biodiversity and geographical distribution in subtropical montane areas, and expand the potential for further applications of stomatocyst analysis in modern environmental assessment and reconstruction of past environments.

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Appendix: Environmental information on the sampling sites. The Dajiuhu, Erxianyan and Qizimeishan peatlands are coded D, E and Q, respectively. Abbreviations: Alt = altitude a.s.l.; DWT = depth to water table; EC = electrical conductivity; ORP = oxidation reduction potential

Peatland	Sampling code	Latitude (N)	Longitude (E)	Alt (m)	DWT (cm)	pH	EC (µS cm^{-1})	ORP (mV)	Vegetation
Dajiuhu	D1	31° 28′ 57.80″	109° 59′ 09.94″	1762	25	4.8	21.1	443.8	*Carex sp., Veratrum sp., Polygonum senticosum*
	D12	31° 28′ 56.66″	109° 59′ 07.32″	1758	2	5.5	17.5	420.7	*Carex sp., Veratrum sp., P. senticosum*
	D16	31° 28′ 54.89″	109° 59′ 07.34″	1763	24	5.2	29.7	411.5	*Carex sp., Veratrum sp., Sanguisorba officinalis, P. senticosum*
	D18	31° 28′ 55.83″	109° 59′ 06.49″	1761	20	5.4	56.7	402.3	*Carex sp., Veratrum sp., P. senticosum*
Erxianyan	E06	29° 43′ 31.30″	108° 48′ 10.82″	1545	22	5.8	113.5	241.2	*Carex sp., Betula ovalifolia, P. senticosum*
	E09	29° 43′ 30.70″	108° 48′ 12.87″	1551	32	6.2	59.2	246.4	*Carex sp., Juncus setchuensis, Bidens sp., Hosta ventricosa, Sphagnum palustre*
	E12	29° 43′ 9.50″	108° 48′ 11.57″	1546	7	4.8	32.0	350.8	*J. setchuensis, Pteridium, S.palustre*
	E14	29° 43′ 30.42″	108° 48′ 10.24″	1547	8	6.0	74.4	218.5	*Carex sp., J. setchuensis, S. palustre*
Qizimeishan	Q05	29° 57′ 48.78″	109° 45′ 11.45″	1791	13	5.3	7.6	331.5	*Carex sp., Rhododendron sp., Pinus, S. palustre*
	Q09	29° 57′ 50.39″	109° 45′ 11.15″	1799	5	5.0	8.2	336.2	*Carex sp., J. setchuensis, H. ventricosa, S. palustre*
	Q13	29° 57′ 51.03″	109° 45′ 10.78″	1794	13	4.7	10.1	342.9	*Carex sp., Pteridium, S. palustre*
	Q18	29° 57′ 51.75″	109° 45′ 10.56″	1809	13	4.3	21.4	371.3	*Carex sp., Calamagrostis epigeios, S. palustre*