Fottea, Olomouc, 22(2): 228–237, 2022
DOI: 10.5507/fot.2022.004

New chrysophyte stomatocysts from high mountain lakes in Three Parallel Rivers of Yunnan Protected Areas, China

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Abstract: During a survey of the chrysophyte stomatocyst flora in surface sediments of 34 lakes in Three Parallel Rivers of Yunnan Protected Areas, 14 new stomatocysts were observed. These new cysts were described based on scanning electron microscopy (SEM) observations. Their morphology was compared with the most similar morphotypes worldwide. The obtained records improve our knowledge on the stomatocyst diversity in low latitude high mountain lakes of the world.

Key words: cyst, alpine lake, chrysophyte, Yunnan

Introduction

Three Parallel Rivers of Yunnan Protected Areas (E98°–100°30′, N25°30′–29°), located at the intersection of East Asia, South Asia and Qinghai Tibet Plateau, has always been a hotspot of Chinese biodiversity and is, in terms of biodiversity, also considered being one of the richest temperate regions of the world. The outstanding topographic and climatic diversity of this area made it retain a high degree of natural character (UNESCO 2021). There are 118 snow mountains with an altitude exceeding 5000 meters. These mountain peaks are year–round covered with snow and have constantly very low temperatures, making them belong to the cold climate or polar climate zone. Mountain lakes in this high altitude areas are barely influenced by human activity. Therefore, the area is home to more than 20% of all higher plants and more than 25% of all animal species in China. Despite this high diversity in flora and fauna, only four chrysophyte species have been reported so far from this area (Shi et al. 1994; Němcovà et al. 2015).

The Chrysophyta comprise a diverse group of heterokont microorganisms, occurring in a wide variety of freshwater and marine habitats. Although the species number was estimated at only –1200, clear quite low compared to the total number of described algal species, chrysophytes have very different occurrence spectra that determine their value as indicators (Kristiasen 2005). Fossil chrysophytes, mainly conserved by their scales, bristles, spines and cysts, are useful paleolimnological markers because they are well–preserved in sedimentary deposits. But only ca. 20% of chrysophyte species belong to siliceous scale–bearing genera (*Chrysosphaerella* Lauterborn, *Clathromonas* Scoble et Cavalier–Smith, *Mallomonas* Perty, *Neotessella* Jo et al., *Paraphysomonas* De Saedeleer, *Polylepidomonas* Presig et Hibberd, *Spinifermonas* Takahashi, *Synura* Ehrenberg). And these groups are rare in high Arctic and high altitude lakes (Duff et al. 1995).

Chrysophycean stomatocysts form the silicified resting stage in the life history of some Chrysophyceae and Synurophyceae. As most of these cysts are characterized by a distinct morphology of their siliceous structure, they are relatively easily identified and therefore can be used as excellent indicators of environmental change (Duff et al. 1995). Since the nomenclature and terminology of chrysophycean stomatocysts was standardized by the International Statospore Working Group (ISWG) in 1986 (Cronberg & Sandgren 1986), more than 2000 different stomatocysts have been described worldwide from diverse climatic regions, although most of them were reported from the middle to high latitudes (Duff et al. 1995; Facher & Schmidt 1996; Van de Vijver & Beyens 1997a, 1997b, 2000; Hansen 2001; Wilkinson et al. 2001; Firsova & Likhoshway 2006; Coradeghini & Vigna 2008; Firsova et al. 2019; Pang & Wang 2016, 2017; Pang & Van de Vijver 2021). Only a few cysts were reported from low latitudes such as Costa Rica, the Caribbean region, Cameroon, Egypt, Guinea and central Mexico (Zeeb & Smol 1996; Rull & Vegas–Vilarŕubia 2000; Piatek et al. 2009; Vilaclara et al. 2005; Piatek et al. 2012; Piatek & Piatek 2014; Piatek 2017).

In the present study, analysing the surface sediments of 34 lakes in Three Parallel Rivers of Yunnan Protected Areas, 14 new chrysophyte stomatocysts are described based on observations of their morphology using scanning electron microscopy (SEM). These records increase our limited knowledge on the diversity of chrysophyte stomatocyst in low latitude areas.

Material and Methods

Surface sediments of lakes (upper 1 cm) have been sampled with a Kajak gravity corer. Table 1 lists all samples together with their habitat characteristics. Lake water pH and specific conductance were measured in the field using a YSI 650 multi–parameter display system (650 MDS, YSI Incorporated 1700/1725 Brannum Lane, Yellow Springs, OH 45387 USA)

Table 1. Habitat characteristics of the sampling sites.

Lakes	Altitude (m a.s.l.)	Depth (m)	pH	Conductivity (µS.cm^{-1})	Water temperature (°C)
GS1–1	3907	90	6.5	6	11.4
GS2–2	4101	32	6.7	3	7.1
GS3–1	3503	18.5	6.5	5	15.0
GS3–2	3711	44	5.9	4	14.5
GS3–3	3655	9.5	6.3	7	15.0
GS3–4	3505	12.4	8.9	9	14.1
GS3–5	3448	6.3	8.6	6	10.4
GS4–1	3463	7.4	6.6	12	16.8
GS4–2	3860	35.3	6.9	7	12.4
GS4–3	3758	5	6.7	8	7.6
GS5–1	3686	23.5	7.0	10	14.5
TM	3507	13.5	6.9	8.3	6.3
XHH–1	3467	6	6.3	4	11.5
XHH–2	3603	10	7.0	8	10.6
XHH–3	3244	4.1	6.2	6	11.0
XHH–4	3605	4	6.8	4	10.3
XHH–5	3713	4.1	6.6	3	9.2
DQB–1	4634	37	8.0	64	7.7
DQB–2	4834	5.6	8.2	114	9.2
DQD–5	4712	12.7	8.2	182	7.2
DQD–7	4694	4.1	8.0	149	8.5
GK	3566	4	8.3	236	14.8
BM–2	4748	8.1	7.1	30	7.1
BM–3	4641	12.5	7.6	41	8.6
SSCN	4483	27.7	7.1	28	8.4
WD–1	3839	14.5	8.3	72	7.6
WD–2	3843	19	7.5	99	11.1
GZ–3	4325	10.4	7.7	166	6.
GZ–4	4011	6.8	7.6	76	7.1
CGD	4251	2.5	6.9	17	4.8
NB	4012	33	6.8	18	10.0
NB–1	4271	3.4	8.5	14	7.8
DR	3971	3.2	9.0	87	8.7
SDH	3538	7.5	7.1	44	14.2

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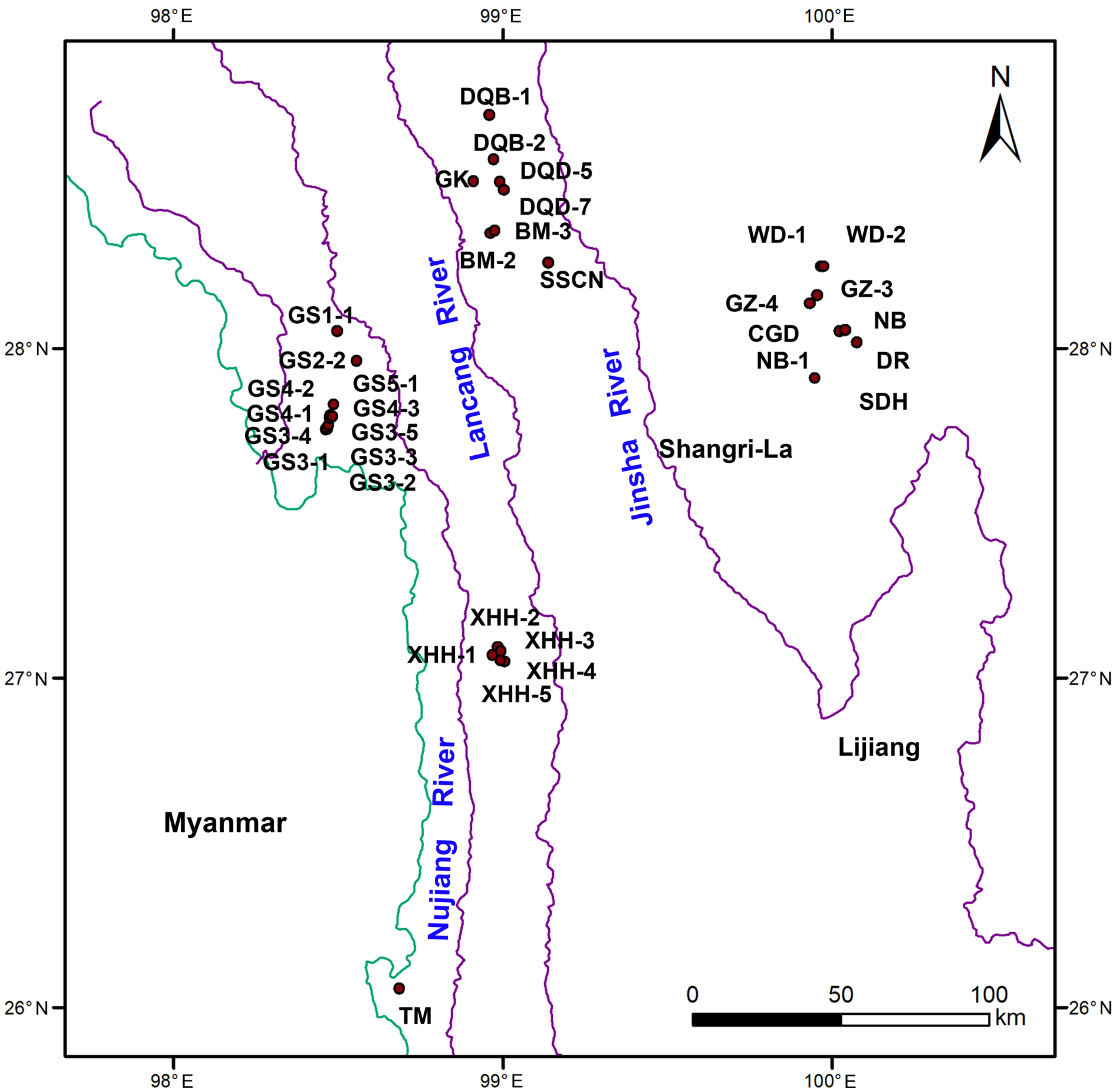

Fig. 1. Study sites locations.

with a 600XL probe. Samples were kept under 4 °C before laboratory treatment with HCl and H_2O_2, following the method in Battarbee (1986). Cleaned material for scanning electron microscope (SEM) analysis was air dried onto cover glasses, mounted onto aluminum stubs, and coated with 20 nm of Au. Stubs were subsequently analysed using a LEO 1530 scanning electron microscope (SEM). At least 200 cysts were counted in each surface sediment sample.

Samples and slides are preserved in the Herbarium of Yunnan University, China.

Results

Stomatocyst 1 W.Pang et Y.Li (Figs 2–3)
Number of observed specimens: 5.
SEM description: Body spherical, diameter 9.6–12.0 µm; pore regular, diameter 1.5 µm; collar conical, inner margin sloping, outer margin gradual and continuous with the body surface, apical diameter 2.8–4.1 µm; body surface smooth.
Locality: DQD–7.
Comments: This stomatocyst is similar to Stomatocyst 60 (Pang & Wang 2014), but the latter collar is relatively wider (body diameter 9.3–10.9 µm, collar apical diameter 2.8–4.0 µm) and is ornamented with conula. The new cyst collar is also similar to that of S346 (Pla 2001), but the latter collar apex is rounded and has a straight inner collar margin.

Stomatocyst 2 W.Pang et Y.Li (Figs 4–5)
Number of observed specimens: 16.
SEM description: Body spherical, diameter 5.1–6.3 µm; pore regular, diameter 0.3–0.4 µm; collar cylindrical and low, apex round, wide and irregular, apical diameter 1.5–1.8 µm, apex width 0.4–0.6 µm, height 0.3–0.4 µm; body surface smooth.

Localities: CGD, GZ–3, GZ–4, DQB–2, SDH, WD–1.
Comments: This stomatocyst is similar to Stomatocyst 276, Gilbert et Smol (GILBERT et al. 1997), but the latter collar is formed with rectangularly–shaped projections. The new cyst is also similar to *Cysta minima* Nygaard (GRITTEN 1977), but the latter collar is wider (body diameter 3.5 µm, collar diameter 1.5 µm).

Stomatocyst 3 W.Pang et Y.Li (Figs 6–10)
Number of observed specimens: 20.
SEM description: Body semilunar, spherical, diameter 4.3–4.8 µm; pore regular, diameter 0.5–0.7 µm; collar complex, primary collar low and cylindrical, apical diameter 0.8–0.9 µm, inner margin abrupt; secondary collar on one–third of the anterior hemisphere, wide and obconical, basal diameter 4.2–4.5 µm, apical diameter 4.5–5.3 µm, height 0.6–1.1 µm, inner and outer margin smooth or with irregular ribs, inner margin sloping, a flat wide annulus between the primary and secondary collar; body smooth or ornamented with conula (basal diameter 1.0–1.4 µm, height 0.3–0.6 µm) on the posterior hemisphere.
Localities: GS3–1, GS3–3, GS3–4, GS4–2, XHH–2, XHH–3.
Comments: At present, similar morphotypes could not be found in the literature.

Stomatocyst 4 W.Pang et Y.Li (Figs 11–12)
Number of observed specimens: 11.
SEM description: Body spherical, diameter 11.1–12.3 µm; pore regular, diameter ca. 0.9µm; collar complex, primary collar conical (basal diameter 2.3–3.2 µm, apical diameter 3.1–3.8 µm, height 0.9–1.4 µm), inner margin sloping; secondary collar wide and cylindrical, diameter 6.0–8.6 µm, height 0.9–1.5 µm, inner margin abrupt, separate from the primary collar with sloping annulus, width ca. 1.0 µm; body surface ornamented with scabrae, verrucae or small conula, diameter <0.5 µm, height <0.3 µm.
Locality: GK.
Comments: This stomatocyst is similar to Stomatocyst 204 (Duff & Smol 1994), but the latter secondary collar is significantly higher than the primary collar. The new cyst is also similar to Stomatocyst 294 (GILBERT et al. 1997, but differs in ornamentation, with the latter ornamented with ridges.

Stomatocyst 5 W.Pang et Y.Li (Figs 13–14)
Number of observed specimens: 32.
SEM description: Body oblate, diameter 5.0–5.9 × 4.5–5.2 µm; pore regular, ca. 0.5µm; collar cylindrical, diameter 1.4–1.5 µm, height ca. 0.5 µm; body and collar surface ornamented with scabrae, diameter <0.1 µm, scabrae connect and form equidistantly arranged ridges
Localities: BM–2, CGD, GS3–4, GS5–1, NB, NB–1, SSCN, TM, WD–2, XHH–1.
Comments: This stomatocyst is similar to Stomatocyst 117 (ZEEB et al. 1990), but the latter is ornamented with rounded, regularly arranged scabrae.

Stomatocyst 6 W.Pang et Y.Li (Figs 15–18)
Number of observed specimens: 20.
SEM description: Body spherical, diameter 9.7–13.0 µm; pore concave, inner diameter ca. 0.8 µm, outer diameter 2.8–3.2 µm; no collar; body smooth or ornamented with a few irregularly scattered conula, basal diameter 0.4–0.8 µm..
Localities: GS2–2, GS3–1, GS3–4, GS3–5, GS5–1, SSCN, CGD, WD–2.
Comments: This stomatocyst is similar to Stomatocyst 75 (VAN DE VIJVER & BEYENS 2000), but the latter has a very low collar and a second "hole" next to the collar.

Stomatocyst 7 W.Pang et Y.Li (Figs 19–20)
Number of observed specimens: 243.
SEM description: Body spherical to oval, diameter 6.6–9.3 µm; pore regular, diameter 0.6–0.9 µm; collar low and cylindrical, diameter 1.6–1.8 µm, height ca. 0.3 µm, thin and flat annulus extending outward in the middle of the outer margin, width to 1.2 µm, apex eroded; body ornamented with irregularly arranged conula or spines, basal diameter 0.1–0.8 µm, length to 4.1 µm; area near to the collar smooth or ornamented with scabrae.
Localities: GS1–1, GS3–1, GS3–2, GS3–3, GS3–4, GS3–5, GS4–1, GS4–2, GS4–3, GS5–1, XHH–4, XHH–5.
Comments: This stomatocyst is similar to Stomatocyst 82 (PANG & WANG 2014), but the latter has no annulus extending outward on the outer margin. The new cyst is also similar to S369 (PLA 2001), but the latter surface is ornamented with bent rib–like spines.

Stomatocyst 8 W.Pang et Y.Li (Figs 21–23)
Number of observed specimens: 110.
SEM description: Body spherical, diameter 9.4–10.3 µm; collar cylindrical, long, apical part obconical, basal diameter 2.0–2.3 µm, apical diameter 2.7–3.0 µm, length 3.5–7.8 µm; body and collar surface ornamented with echinate and wide–based spines, length to 2.7 µm, spines occasionally connect with each other by ridges.
Localities: DQD–5, GS3–1, GS3–3, GS3–4, GS3–5, GS4–1, GS4–2, GS4–3, GS5–1, XHH–2.
Comments: This stomatocyst is similar to Stomatocyst 35 (DUFF & SMOL 1989), but the latter has a surface ornamented with a triangular reticulum and echinate spines.

Stomatocyst 9 W.Pang et Y.Li (Figs 24–25)
Number of observed specimens: 10.
SEM description: Body spherical, diameter 3.6–4.6 µm; pore regular 0.2–0.3 µm; collar low and obconical, apex round, apical diameter 0.7–1.5 µm, height ca. 0.2 µm; body ornamented with short spines, basal diameter 0.3–0.5 µm, length to 0.3 µm.
Locality: BM–3.
Comments: This stomatocyst is similar to Cyst #4 (CARNEY et al. 1992), but the latter possesses an abrupt cylindrical collar.

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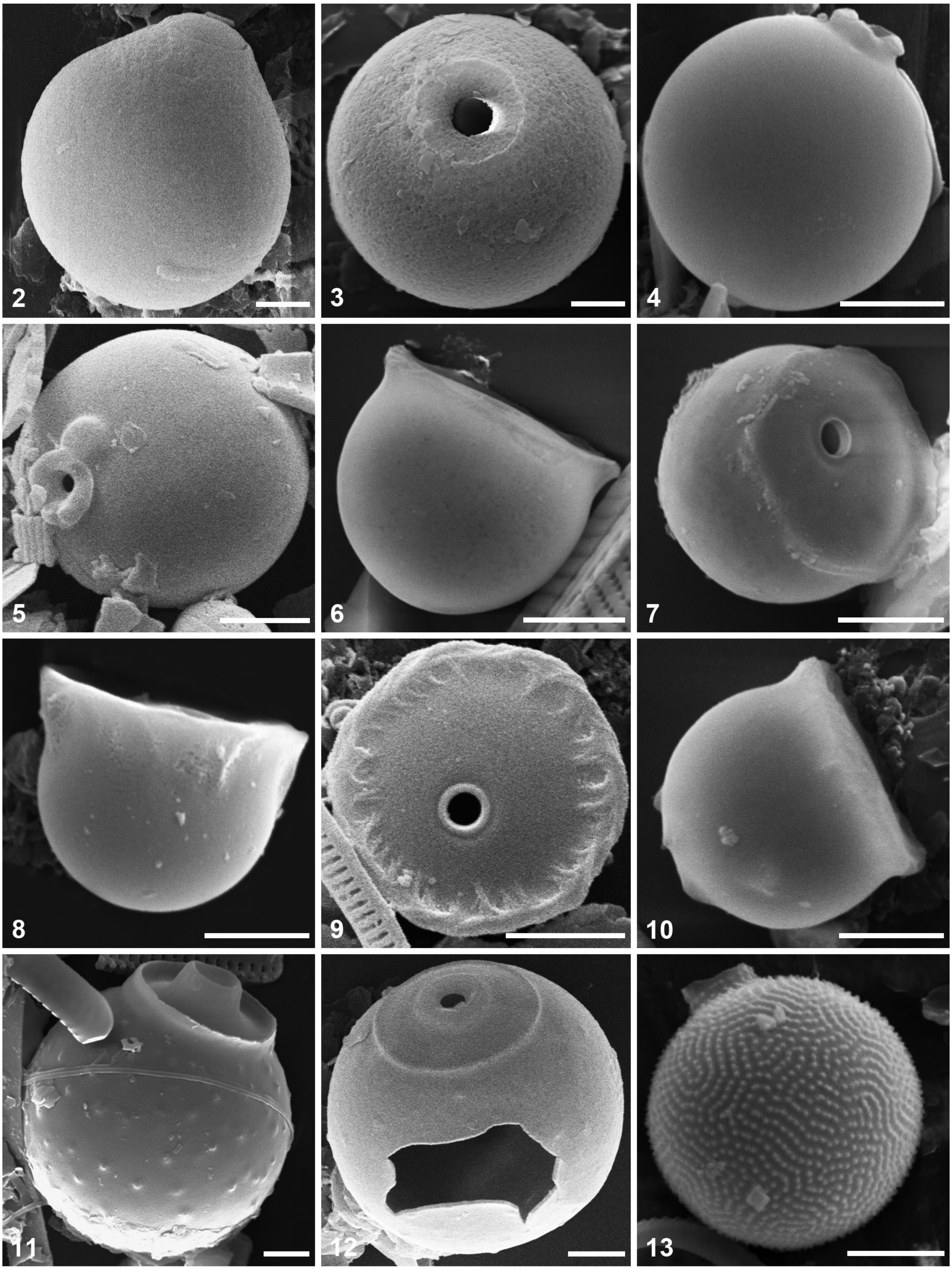
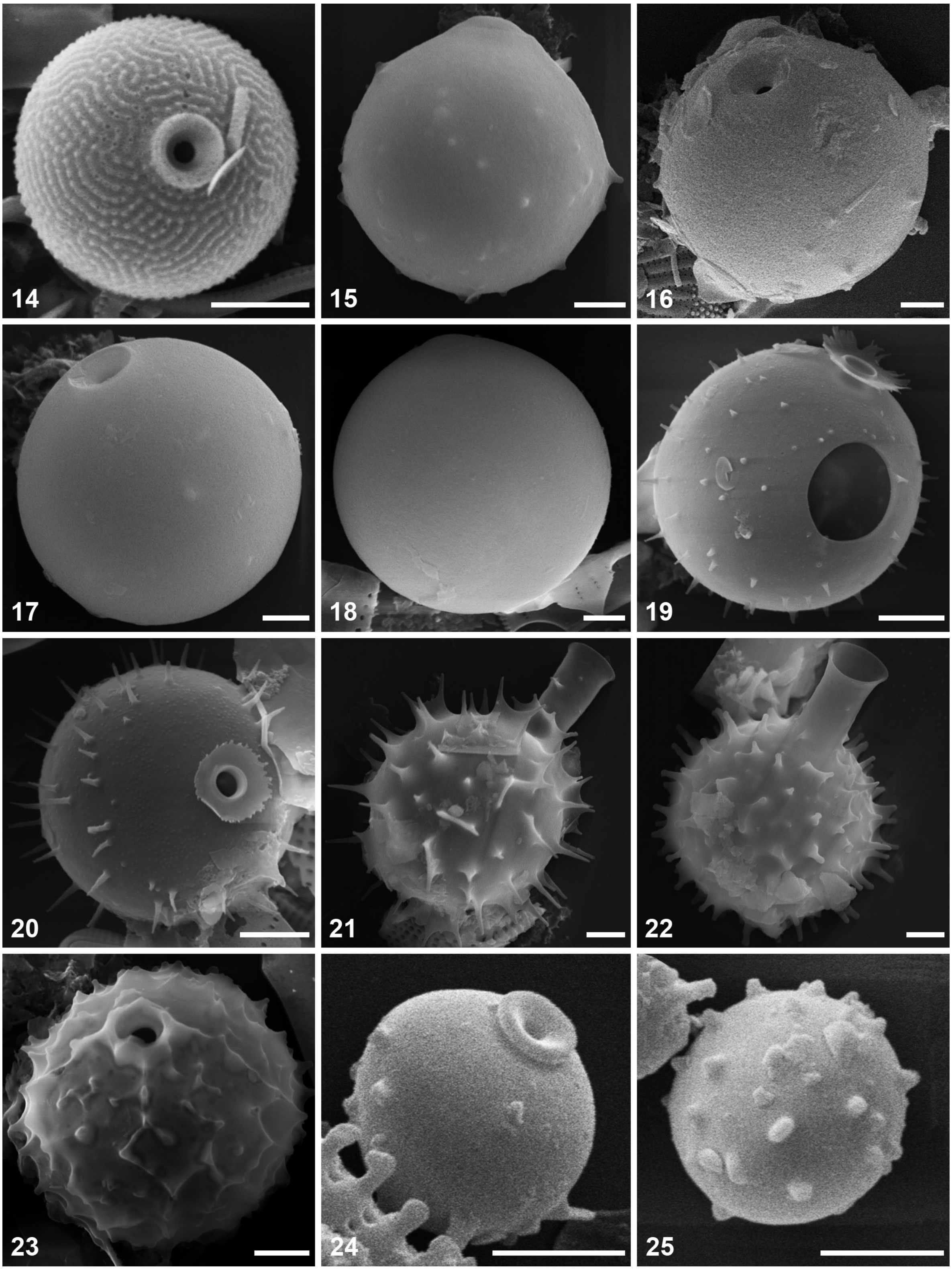
DOI: 10.5507/fot.2022.004



Figs 2–13. New stomatocysts from Three Parallel Rivers of Yunnan Protected Areas: (2–3) Stomatocyst 1; (4–5) Stomatocyst 2; (6–10) Stomatocyst 3; (11–12) Stomatocyst 4; (13) Stomatocyst 5. Scale bar 2µm.

Stomatocyst 10 W.Pang et Y.Li (Figs 26–27)
Number of observed specimens: 6.
SEM description: Body spherical, diameter 4.6–5.8 µm; pore regular, diameter ca. 0.7 µm; collar wide and obconical, basal diameter 2.5–3.5 µm, apical diameter 2.7–3.7 µm, height 0.4 µm; posterior hemisphere ornamented with three to ten echinate or bifurcating spines, basal diameter 0.2–0.7 µm, length to 3.6 µm.
Localities: WD–1, XHH–2.
Comments: This stomatocyst is similar to Stomatocyst



Figs 14–25. New stomatocysts from Three Parallel Rivers of Yunnan Protected Areas: (14) Stomatocyst 5; (15–18) Stomatocyst 6; (19–20) Stomatocyst 7; (21–23) Stomatocyst 8; (24–25) Stomatocyst 9. Scale bar 2µm.

132 (DUFF et al. 1992), but the latter surface is smooth.

Stomatocyst 11 W.Pang et Y.Li (Figs 28–30)
Number of observed specimens: 16.
SEM description: Body spherical, diameter 5.9–6.3 µm; pore regular 0.5–0.6 µm; collar complex, primary collar low and slightly conical (apical diameter 1.1–1.2 µm), secondary collar cylindrical (diameter 2.3–2.9 µm, height ca. 0.5 µm), flat planer interannulus between the primary and secondary collar; body surface ornamented with

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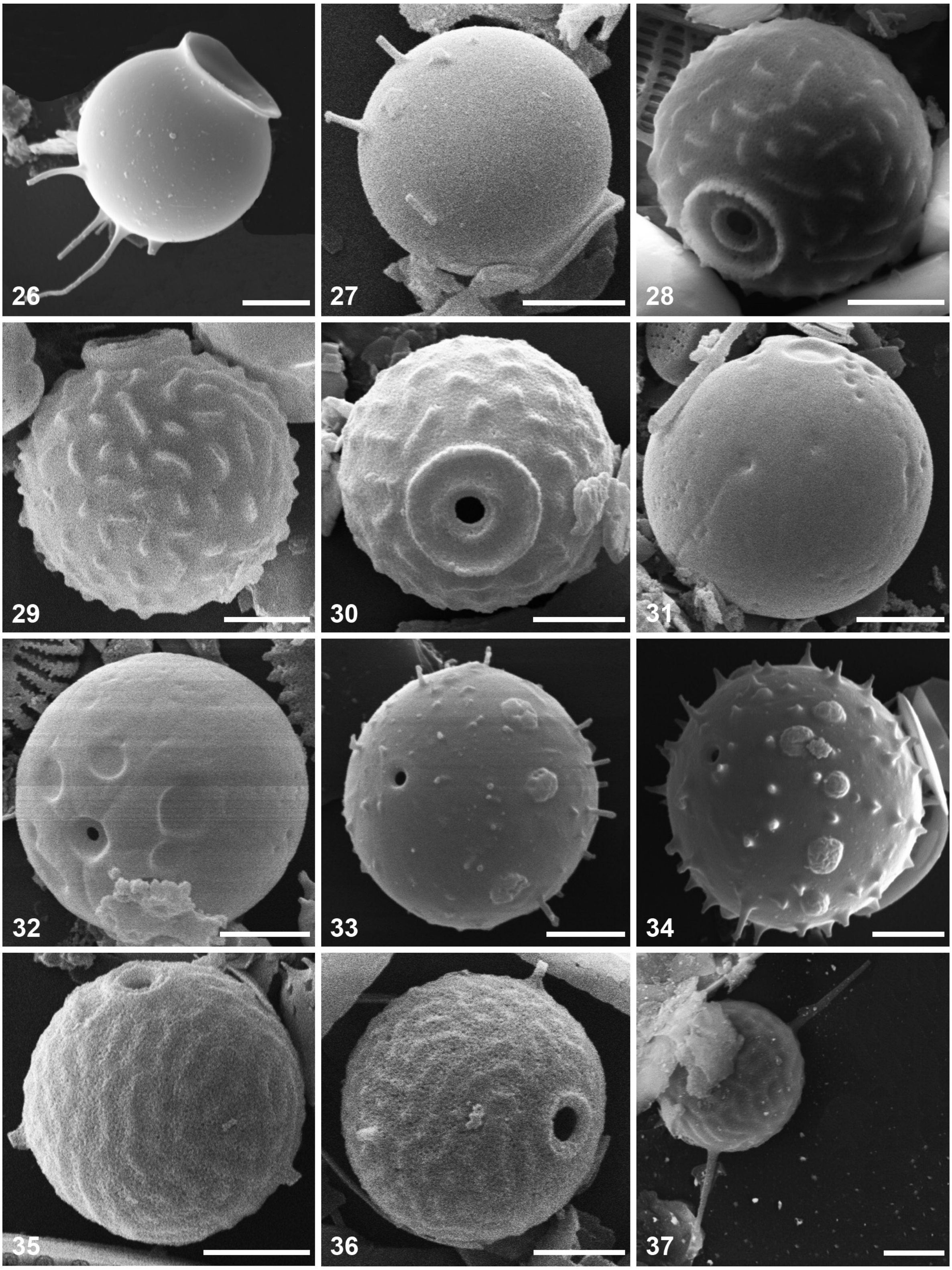

Figs 26–37. New stomatocysts from Three Parallel Rivers of Yunnan Protected Areas: (26–27) Stomatocyst 10; (28–30) Stomatocyst 11; (31–32) Stomatocyst 12; (33–34) Stomatocyst 13; (35–37) Stomatocyst 14. Scale bar 2µm.

short thin ridges, length 0.3–1.6 µm, height ca. 0.2 µm.
Locality: DR.
Comments: This stomatocyst is similar to Stomatocyst 111 (Zeeb et al. 1990), but the latter lacks the secondary collar.

Stomatocyst 12 W.Pang et Y.Li (Figs 31–32)
Number of observed specimens: 5.
SEM description: body spherical, diameter 6.4–6.5 µm; pore regular, diameter 0.3 µm; collar conical, apical diameter 1.0–1.4 µm, no boundary between collar base and body,

inner margin sloping, circular depressions surrounding the base, diameter 0.3–1.0 µm; body ornamented with circular depressions and shallow longitudinal fossae.
Localities: DQB–1, NB, SDH.
Comments: This stomatocyst is similar to Stomatocyst 253 (Wilkinson et al. 1997), but the latter has no circular depressions.

Stomatocyst 13 W.Pang et Y.Li (Figs 33–34)
Number of observed specimens: 30.
SEM description: Body spherical or slightly oblate, diameter 5.9–7.2 µm; pore regular, diameter 0.3–0.5 µm; collar cylindrical and low, diameter 0.5–0.8µm, apical apex round, inner margin slopping; body ornamented with narrow spines (length up to 1.2 µm) and plates (diameter 0.7–1.2 µm, height ca. 0.2 µm).
Localities: GS3–2, XHH–2, XHH–4, XHH–5.
Comments: This stomatocyst is similar to Stomatocyst 102 (Pang & Wang 2014), but the latter has a conical to obconical collar.

Stomatocyst 14 W.Pang et Y.Li (Figs 35–37)
Number of observed specimens: 55.
SEM description: Body spherical or slightly oblate, diameter 4.6–5.4 µm; pore regular, diameter 0.4–0.7 µm; collar cylindrical, low, diameter 1.2–1.4 µm, height, 0.3 µm, apical margin with notch–like indentation or not, inner margin sloping; body ornamented with short lunate to long wave ridges run randomly; one to three long, narrow spines present on equatorial position or absent, basal diameter 0.4–0.6 µm, length to 3.5 µm.
Locality: GK.
Comments: This stomatocyst is similar to L4 (Huber et al. 2009), but the later was ornamented with more or less regularly arranged conula and long, echinate spines.

Discussion

The new chrysophycean stomatocysts are unevenly distributed in various lakes (Supplementary table 1). Conductivity and pH are two important factors, determining the distribution of chrysophytes (Hartmann & Steinberg 1989; Kristiansen 2005). The relative abundance of the new morphotypes in the 34 lakes in this study ranges from 0.3 (only present in 1 lake) to 35% (present in 12 lakes) (Supplementary table 1). Stomatocyst 7 is the most frequent of all new morphotypes (35%) having a high relative abundance in most of those sites where it occurred (Table 1, Supplementary Table S1). It seems to tolerant a relatively wide pH range but only a low conductivity. Stomatocyst 8, the second most frequent new morphotype (30%), was mostly found in lakes with low conductivity and always showed a high abundance in these lakes. Most likely, it has the same habitat preferences as Stomatocyst 7. Stomatocyst 14 only appeared in one lake (GK), but it was the second most dominant morphotype in this lake (relative abundance 21%), indicating that it most likely prefers alkaline high mountain lakes with a high conductivity (236 $\mu S.cm^{-1}$).

Geographic restrictions are one of the factors that determine the biogeographical distributions of siliceous algae (Potapova & Charles 2002). Stomatocysts 1, 4, 9, 10, 11 and 14 were only found in one or two lakes. On the other hand, stomatocysts 2, 3, 7, 12, 13 were found in lakes located on adjacent areas, separated by one river. The frequency and relative abundance of stomatocyst 3, 7, 13 are obviously biased to the lakes on one side. Metabarcoding studies of European lakes revealed that mountain lakes act as biogeographic islands. Protist community composition in high mountain regions were affected by geographic distance more pronouncedly than that in lowland lakes (Boenigk et al. 2018). In Three Parallel Rivers of Yunnan Protected Areas, the mountains are intersected by the Jinsha River, the Lancang River, the Nu River and their crisscross tributaries, creating isolated area with different degree and shapes. Geographic distance and geographic barriers might be other factors responsible for the uneven distribution of these new stomatocysts.

Chrysophytes, in general, are known to have a worldwide distribution (Kristiansen 2005, 2008). *Chromulina* Cienkowsky, *Chrysosphaerella*, *Dinobryon* Ehrenberg, *Paraphysomonas*, *Polylepidomonas* and *Ochromonas* Vysotskii, are generally considered being cosmopolitan (Finlay & Clark 1999; Kristiansen & Preisig 2001)." But this statement must be reconsidered based on the presented hidden diversity of these genera through the study on their biogeography or phylogeny (Bock et al. 2014; Jiang et al. 2018, 2019; Scoble & Cavalier–Smith 2013, 2014; Škaloudova & Škaloud 2013; Andersen et al. 2017). Since stomatocysts are formed by a number of Chrysophyceae and Synurophyceae representing an obligate and characteristic stage in their life history, these two classes should have a similar biogeographic distribution as their stomatocysts. Therefore, chrysophyte stomatocysts could provide a more complete record of the entire chrysophyte community (Duff et al. 1995), making them interesting objects for biogeographical studies of chrysophytes. However, based on all currently available data, it is still difficult to understand the dispersal form of stomatocyst on a global scale. Nevertheless, they are at present far less reported from low latitude areas, as most of the stomatocysts are reported from temperate and cold zones. During the survey of silica scaled chrysophytes from tropical and subtropical areas, such as southern China (Wei et al. 2013, 2014; Němcovà et al. 2015), Vietnam (Gusev & Martynenko 2022; Gusev et al. 2015, 2016, 2017, 2018, 2019, 2020, 2021), Indonesia (Kapustin et al. 2019) and Cameroon (Piatek & Lukaszek 2016), more and more new species were reported. It confirmed that mountain lakes and generally water bodies in poorly studied tropical and subtropical areas from East Asia are rich with chrysophytes and many new species can be found there. Three Parallel Rivers of Yunnan Protected

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Areas is located at the intersection of East Asia, South Asia and Qinghai Tibet Plateau. In this area, the special geographical location and large elevation drop, result in a broad variety of climate and environment types, ranging from the south subtropical zone to the frigid zone. The 34 lakes in this study are all located above 3200 meters a.s.l., which explains most likely the high diversity of stomatocyst morphotypes that were found in this study. In this preliminary study, in total, 187 different morphotypes were identified (Supplementary table 2.). This high number clearly shows that the stomatocyst diversity in low latitude high mountain lakes is underestimated worldwide.

Acknowledgements
We thank Yulan Luo for her work of SEM photo shooting, and Kexin Gong for her valuable help during the material collection. This work has been supported by the National Natural Science Foundation of China (No. 41877296 & 32070227). The authors thank the anonymous reviewers and the editor for their useful comments that greatly improve this manuscript.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Relative abundances (%) of new stomatocysts in each sites.

Table S2. List of the stomatocysts identified from the high mountain lakes in Three Parallel Rivers of Yunnan Protected Areas.

Supplementary references

This material is available as part of the online article (http://fottea.czechphycology.cz/contents)

Received November 11, 2021
Accepted March 21, 2022