

ORIGINAL ARTICLE

Open Access



Fruits of *Scirpus* (Cyperaceae) from the early Miocene of Weichang, Hebei Province, North China and their palaeoecological and palaeobiogeographical implications

Ping Lu¹, Ya Li², Jian-Wei Zhang³, Xiao-Qing Liang^{1*}, Yue-Zhuo Li⁴ and Cheng-Sen Li⁵

Abstract

This paper describes the fossil fruits of *Scirpus weichangensis* X.Q. Liang, sp. nov. from the early Miocene of Guangyongfa Village, Weichang County, Hebei Province, North China. The fossil fruits are obovate in shape and their lateral sections are plumply trigonous. The cell walls of the surface are straight. The persistent stout bristles have downward-directed barbellae in distal 1/2. The occurrence of the fossil *Scirpus* indicates that Guangfayong was a wetland in the early Miocene. Based on the fossil data, the genus likely originated in Western Siberia in the Oligocene, spread during the Miocene, and was finally distributed worldwide in the Holocene.

Keywords: *Scirpus*, Early Miocene, Palaeoecology, Palaeobiogeography, Weichang

1 Introduction

Cyperaceae Juss. is a cosmopolitan family, with 106 genera and approximately 5400 species (Dai et al. 2010; Spalink et al. 2016). The family is in a range from sea level up to 5475 m, covering large areas of swamp and arctic vegetation (Goetghebeur 1998). The family may have originated in the Late Cretaceous South America, and may have spread in the southern hemisphere via Antarctica (Spalink et al. 2016). Many fossils of Cyperaceae are mainly fruits or pollen. The biogeography of some genera of the family has been discussed based on fossil data, e.g. *Cladium* (Liang et al. 2017). Here, we report on the fruit fossils of *Scirpus* Linnaeus.

Scirpus Linnaeus (Cyperaceae) consists of herbs or perennials. The perianth has zero to six bristles. Nutlets with the beaked apices are obovoid to ellipsoid and are biconvex to compressed 3-sided. They have smooth surfaces. *Scirpus* is distributed in North America, Mexico, Eurasia, Australia, and Pacific Islands (Whittemore and Schuyler 2002; Dai et al. 2010).

Fossil fruits of *Scirpus* have been collected in Europe, Asia, and North America. *Scirpus foveolatus* was found in the early Oligocene Siberia (Nikitin 2006). *S. microcarpus* Presl appeared in the Pliocene Canadian Arctic (Matthews and Ovenden 1990). *S. atroviroides* was collected in the Pliocene Czarnucha and the Pleistocene Łuków of eastern Poland (Stachowicz-Rybka 2005, 2015). *Scirpus* sp. occurred in the Holocene Rapa Nuii, Polynesia (Horrocks et al. 2012).

Here we describe fossil fruits of *Scirpus* found from the early Miocene Weichang, North China; and further assign these fossil fruits to a new species, compare them with extant and fossil species, and discuss their biogeographical implications.

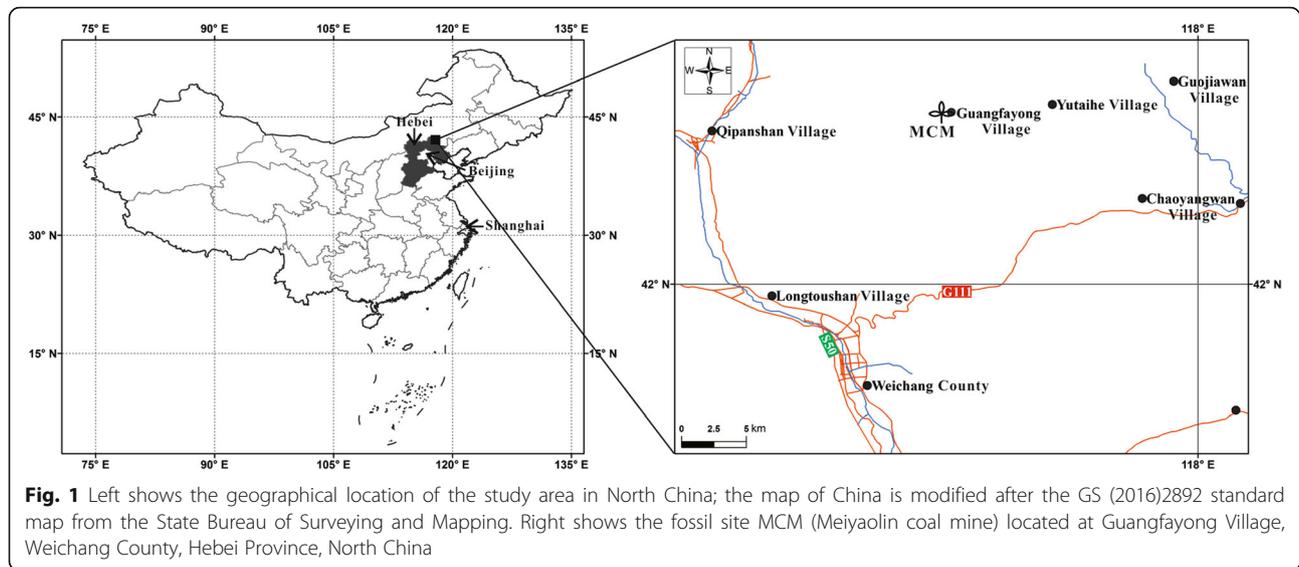
2 Locality and stratigraphy

The studied section is located in the Meiyaolin coal mine (42°07'34"N, 117°50'27"E, 1396 m), near the Guangfayong Village of Weichang County, Hebei Province, North China (Fig. 1). The sediments mostly consist of mudstone, lignite, conglomerate, and shale. These sediments are similar to those developed in the Wuluogong section (Hannuoba Formation), and their geological age has been placed in the early Miocene

* Correspondence: liangxq@yxnu.edu.cn

¹School of Chemistry, Biology, Environment, Yuxi Normal University, Yuxi 653100, Yunnan Province, China

Full list of author information is available at the end of the article



(about 22.1 Ma) using the K–Ar dating method (Li and Xiao 1980).

Many leaf and fruit fossils have been found in the Meiyaolin coal mine, including fossil examples such as *Comptonia*, *Dusembaya*, *Lepidium*, *Medicago*, *Pinus*, *Ulmus*, and *Weigela* (Liang 2009; Liang et al. 2010, 2013). Based on a palynological study, the early Miocene vegetation of Weichang can be characterized as a mixed temperate forest of conifers (e.g. *Pinus*, *Picea*, *Tsuga*) and broad-leaved trees (e.g. *Betula*, *Alnus*), with some subtropical plants (e.g. *Carya*). Its climate was warm temperate to subtropical (Li et al. 2009).

3 Material and methods

For this study, fossil fruits of *Scirpus* were collected from the 8th layer of the section (see Li et al. 2009), which consists of mudstone and lignite. The fruits were isolated from the sediment using a procedure described by Wellman and Axe (1999), and were observed and scanned with a light microscope and scanning electron microscope (SEM) (ZEISS/EVO LS10). The terminology used is based on Berggren (1969).

4 Systematics

Family: Cyperaceae Juss.

Genus: *Scirpus* L.

Species: *Scirpus weichangensis* X.Q. Liang, sp. nov. (Plate 1).

Holotype: WCF-1-1 (Plate 1a).

Paratypes: WCF-1-2 (Plate 1b).

Type locality: Guangfayong Village, Weichang County, Hebei Province, North China.

Type formation and age: Hannuoba Formation, early Miocene.

Etymology: The specific name, *weichangensis*, is derived based on the fossil site in Weichang County.

Repository: National Museum of Plant History, Institute of Botany, Chinese Academy of Sciences, Beijing, China.

Diagnosis: Nut obovate. Lateral section slightly 3-sided. Persistent bristles 3 with downward-directed barbellae in the upper part. The style-base is point-like. Surface glabrous; epidermal cells distinct.

Description: Fossil fruits of *Scirpus* are obovate in outline, with a length of 0.88 ± 0.04 mm and width of 0.65 ± 0.05 mm (Plate 1). Their bases are cuneate (Plate 1a-d), and apices are obtuse or apiculus (Plate 1b, f). Their lateral sections are plumply trigonous (Plate 1a-d). The cell walls of the surface are straight (Plate 1). Three broken persistent bristles in the base are stout and have downward-directed barbellae in distal 1/2 (Plate 1a, d). The longest one is 0.73 mm in length and is as long as 0.85 times the length of the fruit (Plate 1a).

5 Discussion

5.1 Comparison of *Scirpus weichangensis* X.Q. Liang, sp. nov. with extant and fossil species

The fossil fruits from the early Miocene of Weichang are obovate with a slightly 3-sided lateral section (Fig. 2). They have three stout persistent bristles with downward-directed barbellae (Fig. 2). They share similar characteristics with Cyperaceae with respect to the fruit outline, the lateral section, and bristles. As such, they belong to the family, with more than ninety genera. Among the genera, fruits of *Scirpus* L., *Phylloscirpus* C.B. Clarke, and *Pseudoschoenus* (C.B. Clarke) Oteng-Yeb. have persistent stout bristles with downward-directed barbellae. However, the fruits of *Phylloscirpus* have six bristles, and the cell walls of their

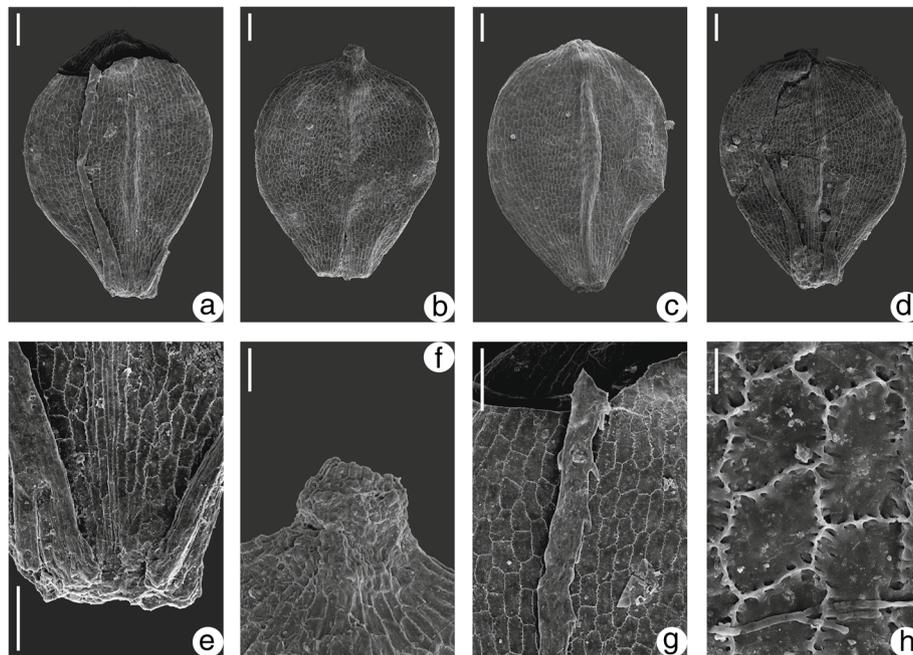


Plate 1 The fossil fruits of *Scirpus weichangensis* X.Q. Liang, sp. nov. from the early Miocene of Weichang, Hebei Province, North China. **a-d** - Fruits (WCF-1-1, WCF-1-2, WCF-1-3, WCF-1-4); **e** - Base of **a**; **f** - Apex of **b**; **g** - Bristle of **a**; **h** - Surface of fruit of **c**. Scale bars: **a-d** = 100 μ m; **e-g** = 60 μ m; **f** = 30 μ m; **h** = 9 μ m

surfaces are minutely reticulate–foveolate. *Pseudoschoenus* have fruits with 3–5 (6) bristles (Goetghebeur 1998). Fruits of *Schoenoplectus* (Reichenbach) Palla have the faintly to prominently rugose or with transverse wavy ridges, and are 2.5–3.5 mm in length (Whittemore and Schuyler 2002). Fruits of *Bolboschoenus* (Ascherson) Palla are 2.3–5.5 mm long (Whittemore and Schuyler 2002). Nutlet surface of *Schoenoplectiella* Lye is smooth or transversely rugulose to sharply ridged, and epidermal cells are narrowly oblong to linear (Hayasaka 2012). Consequently, fossil fruits are ascribed as being part of *Scirpus*.

Within the genus, nineteen species have fruits with four, five or up to six bristles (e.g. *S. orientalis*, *S. radicans*, *S. polyphyllus*) (Oh and Ham 1998; Whittemore and Schuyler 2002; Dai et al. 2010) (Table 1). Fruits of *S. atrocinctus* Fernald, *S. congdonii* Britton, *S. diffusus* Schuyler, *S. flaccidifolius* (Fernald) Schuyler, *S. lineatus* Michaux, and *S. longii* Fernald have six slender bristles (Whittemore and Schuyler 2002). The fruits of *S. polyphyllus* Muell. and *S. wichureae* Boeckeler have filiform and silk-like bristles, respectively (Healy and Edgar 1980; Oh and Ham 1998; Wilson 1994; Dai et al. 2010) (Table 1).

Fruits of *S. microcarpus* Presl & Presl have bristles with barbellae arranged almost to the base (Whittemore and Schuyler 2002) (Table 1). The bristles of *S. georgianus* Harper are much shorter than the fruit (Yu 2003) (Table 1). The fruit barbellae of *S. chunianus* Tang & Wang are near the apex of the bristles (Dai et al. 2010) (Table 1). Fruits of the *S. rosthornii* Diels are elliptic to subspherical in outline, and are smaller than the fossil fruits (Dai et al. 2010) (Table 1). The fruits of *S. ternatanus* Reinwardt ex Miquel are biconvex (Dai et al. 2010) (Table 1).

Many fossil fruits of *Scirpus* are obovate, e.g. *S. foveolatus* Nikitin from the early Oligocene Tyumen, *S. clavatus* Nikitin from the Oligocene Novosibirsk, *S. chandlerae* Nikitin from the late Oligocene, *S. nagorskyi* Dorofeev from the Miocene Tomsk, *S. atroviroides* Wieliczka from the Pliocene Czamucha and Pleistocene

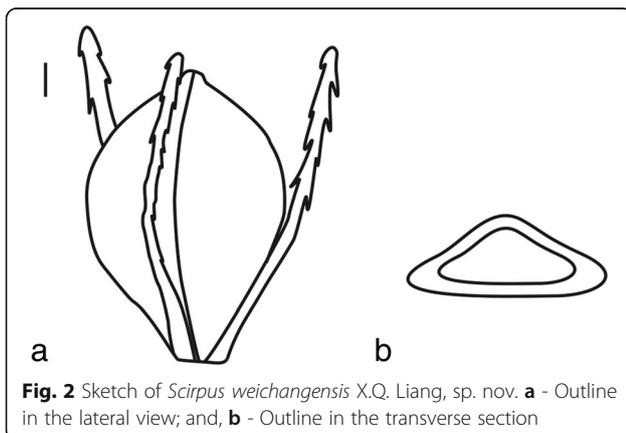


Fig. 2 Sketch of *Scirpus weichangensis* X.Q. Liang, sp. nov. **a** - Outline in the lateral view; and, **b** - Outline in the transverse section

Table 1 Comparison of *Scirpus weichangensis* X.Q. Liang, sp. nov. with extant species

Species	Shape	3-sided	Length (mm)	Width (mm)	Surface	Bristle	Barbellae (μ)	Reference
Fossil	Obovate	+	0.88 \pm 0.04	0.65 \pm 0.05	Net	3	Apical half	This study
<i>S. orientalis</i> Ohwi	Obovate to elliptic	Compressed				5–6	+	Oh and Ham 1998; Dai et al. 2010
<i>S. radicans</i> Schkuhr	Obovate	Compressed	0.9	0.5		6	Near apex	Oh and Ham 1998; Pignotti and Mariotti 2004; Dai et al. 2010
<i>S. karuisawensis</i> Makino	Oblong to obovate	Compressed	1			6	Near apex	Oh and Ham 1998; Pignotti and Mariotti 2004; Dai et al. 2010
<i>S. lushanensis</i> Ohwi	Elliptic	Compressed	1.5	0.5		6	Near apex	Dai et al. 2010
<i>S. wichurae</i> Boeckeler	Elliptic to obovate	+	1.3			6 (silk-like)	Apical half	Oh and Ham 1998; Pignotti and Mariotti 2004; Dai et al. 2010
<i>S. ternatanus</i> Reinwardt ex Miquel	Elliptic, obovate, subspherical	Biconvex	0.7–1			2–3	Apical half	Pignotti and Mariotti 2004; Dai et al. 2010
<i>S. chunianus</i> Tang & Wang	Elliptic to subspherical	Biconvex	1.5		Verruculose	2–3	Near apex	Dai et al. 2010
<i>S. rosthornii</i> Diels	Elliptic to subspherical	Biconvex	0.6–0.7			2–3	Apical half	Dai et al. 2010
<i>S. filipes</i> Clarke	Obovate	Compressed				6	+	Dai et al. 2010
<i>S. hainanensis</i> Huang	Obovate to broadly obovate	+	1.5			6	Apically pubescent	Dai et al. 2010
<i>S. maximowiczii</i> Clarke	Narrowly obovate	+	1.8–2	1		6	Near apex	Dai et al. 2010
<i>S. paniculato-corymbosus</i> Kükenthal	Narrowly obovate	+	1.5			6		Dai et al. 2010
<i>S. ancistrochaetu</i> Schuyler	Elliptic to obovate	Plano-convex	1.1–1.7	0.6–0.8		6	In distal 0.6–0.9	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. atrocinctus</i> Fernald	Elliptic or obovate	Plumply trigonous or plano-convex	0.7–0.9	0.4–0.5		6 (slender)		Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. atrovirens</i> Willdenow	Elliptic or obovate	Plumply trigonous or plano-convex	(0.8-) 1.0–1.3	0.4–0.6		(5-) 6	In distal 0.3–0.6	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. congdonii</i> Britton	Obovate or elliptic	Plumply trigonous or plano-convex	0.9–1.3	0.6–0.8		6 (slender)	In distal 0.5	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. cyperinus</i> (Linnaeus) Kunth	Elliptic or obovate	Plumply trigonous or plano-convex	0.6–0.9	0.3–0.5		6		Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. diffuses</i> Schuyler	Obovate or elliptic	Plano-convex	0.9–1.3	0.7–0.8		6 (slender)	In distal 0.5	Whittemore and Schuyler 2002
<i>S. divaricatus</i> Elliott	Elliptic-obovate	Strongly trigonous with very strong angles and concave sides	0.8–1.0	0.6–0.8		6	In distal 0.5	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. expansus</i> Fernald	Oblong-elliptic to broadly elliptic or obovate	Plano-convex or sometimes plumply trigonous	1.0–1.6	(0.6-) 0.8–1.0		6	Almost to base	Whittemore and Schuyler 2002

Table 1 Comparison of *Scirpus weichangensis* X.Q. Liang, sp. nov. with extant species (Continued)

Species	Shape	3-sided	Length (mm)	Width (mm)	Surface	Bristle	Barbellae (μ)	Reference
<i>S. flaccidifolius</i> (Fernald) Schuyler	Elliptic or obovate	Plano-convex or plumply trigonous	1.0–1.2	0.4–0.6		6 (slender)	In distal 0.2–0.5	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. georgianus</i> Harper	Elliptic or obovate	Plumply trigonous or plano-convex	0.6–1.2	0.4–0.5		0–3		Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. hattorianus</i> Makino	Elliptic or obovate	Plumply trigonous	(0.6–) 0.7–1.1	0.3–0.5		(4–) 5–6	In distal (0.1–) 0.2–0.4	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. lineatus</i> Michaux	Elliptic	Plano-convex or plumply trigonous	0.1–1.5	0.6–0.7		6 (slender)		Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. longii</i> Fernald	Elliptic or obovate	Plano-convex or plumply trigonous	0.7–1.0	0.4–0.5		6 (slender)		Whittemore and Schuyler 2002
<i>S. microcarpus</i> Presl & Presl	Ovate to obovate	Biconvex to plano-convex	0.7–1.6	0.8–1.0		(3–) 4 (–6)	Arranged almost to base	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. pallidus</i> (Britton) Fernald	Oblong-elliptic to elliptic or obovate	Plumply trigonous or plano-convex	0.8–1.2	0.4–0.6		6	In distal 0.3–0.5	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. pedicellatus</i> Fernald	Elliptic or obovate	Plumply trigonous or plano-convex	0.7–0.9	0.4–0.5		6		Whittemore and Schuyler 2002
<i>S. pendulus</i> Muhlenberg	Elliptic	Plano-convex or plumply trigonous	1.0–1.2	0.6–0.8		6		Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. polyphyllus</i> Vahl	Obovate or nearly obtriangular	Plumply trigonous or plano-convex	1.1–1.4(–1.8)	0.8–1.0		6	In distal 1/2	Whittemore and Schuyler 2002; Pignotti and Mariotti 2004
<i>S. polystachyus</i> Muell.	Ellipsoid to obovoid	Plano-convex or with a distinct dorsal angle	1.2–1.5	0.6–0.8		Many, filiform		Healy and Edgar 1980; Wilson 1994

Kathmandu (Dorofeev 1963; Stachowicz-Rybka 2005; Nikitin 2006; Bhandari et al. 2009). Moreover, fossil fruits of these species are commonly larger than fossil fruits from Weichang, e.g. *S. foveolatus* Nikitin from the early Oligocene Tyumen, *S. clavatus* Nikitin from the Oligocene Novosibirsk, and *S. nagorskyi* Dorofeev from the Miocene Tomsk (Dorofeev 1963; Nikitin 2006) (Table 2). Fruits of *S. novorossicus* Doweld from the late Miocene Odessa, Ukraine are ovate but also larger (Doweld 2018). *S. nagorskyi* Dorofeev from the Miocene Tomsk and *S. atroviroides* Wieliczka from the Pliocene Czamucha have fruits without bristles (Dorofeev 1963; Stachowicz-Rybka 2005). *Scirpus* sp. from the Pleistocene Kathmandu has fruits with the longitudinal epidermal cells and six to eight bristles (Bhandari et al. 2009).

No further more information about fossil fruits without bristles can be compared with materials from Weichang, e.g. *S. microcarpus* Presl from the Pliocene Ellesmere, and

Scirpus sp. from the Holocene Niederweningen (Switzerland), Rapa Nui (Polynesia), Connecticut (USA), Colorado (USA), and Jiangsu (China) (Pierce and Tiffney 1986; Matthews and Ovenden 1990; Drescher-Schneider et al. 2007; Li et al. 2008; Horrocks et al. 2012; Strickland et al. 2014). Thus, we ascribed fossil fruits from the early Miocene of Weichang to a new species, *Scirpus weichangensis* X.Q. Liang, sp. nov.

5.2 Palaeoecological and palaeobiogeographical implication of *Scirpus weichangensis*

Extant plants of *Scirpus* usually grow in wetlands, swamps, and marshes (Goetghebeur 1998). *Scirpus weichangensis* appeared in the early Miocene deposit in Weichang, with *Weigela* (Liang et al. 2013), indicating that Guangfayong was a wetland in the early Miocene, and then the wetland gradually disappeared as a result of land uplift.

Table 2 Comparison of *Scirpus weichangensis* X.Q. Liang, sp. nov. with other fossil species

Species	Shape	3-sided	Length (mm)	Width (mm)	Surface	Bristle	Barbellae (μ)	Site	Epoch	Reference
Fossil	Obovate	+	0.88 ± 0.04	0.65 ± 0.05	Net	3	Apical half	Weichang, China	Miocene	This study
<i>S. foveolatus</i> Nikitin	Obovate	+	2.5–3.4	1.2–2.0	Polygonal and isodiametric			Tyumen	Oligocene	Nikitin 2006
<i>S. clavatus</i> Nikitin		+	1.6–2.1	0.5–0.7				Novosibirsk	Oligocene	Nikitin 2006
<i>S. chandlerae</i> Nikitin	Ovate-obovate	+	1.2–1.6	0.9–1.1				Tomsk	Oligocene	Nikitin 2006
<i>S. nagorskyi</i> Dorofeev			0.9–1.0	0.3–0.5				Tomsk	Miocene	Dorofeev 1963
<i>S. novorossicus</i> Doweld	Ovate	+	1.4–2.1	0.6–1.0				Odessa, Ukraine	Miocene	Doweld 2018
<i>S. atroviroides</i> Wieliczka	Obovate		0.9	0.55	Small-celled			Czarnucha	Pliocene	Stachowicz-Rybka 2005
<i>Scirpus</i> sp.	Obovate				Longitudinal rows of cells	6–8		Kathmandu, Nepal	Pleistocene	Bhandari et al. 2009

The fruit fossils of *Scirpus* were firstly found in the early Oligocene of Tyumen (Nikitin 2006). And, a noticeable point here is that we inclined to keep Nikitin’s fossil species of *Scirpus* based on the fossil morphological information, although many fossil species of the genus have been ascribed to other genera (Doweld 2018). They appeared in the Miocene of Tomsk, Odessa and Weichang (Dorofeev 1963; Doweld 2018; and this study). They were collected in the Pliocene of Ellesmere Island, Echigawa, Prince Patrick Island, and Czarnucha (Matthews and Ovenden 1990;

Stachowicz-Rybka 2005; Yamakawa et al. 2008). They were found in the Pleistocene of Kathmandu, and Łuków (Bhandari et al. 2009; Stachowicz-Rybka 2015); and in the Holocene of Niederweningen, Rapa Nuiis, Hamden, Ziegler Reservoir, Sacramento-San Joaquin Delta, and Tangnan (James-West 1977; Pierce and Tiffney 1986; Drescher-Schneider et al. 2007; Li et al. 2008; Horrocks et al. 2012; Strickland et al. 2014).

Based on genus fossil data, *Scirpus* originated in the Oligocene of Siberia, and then migrated widely into

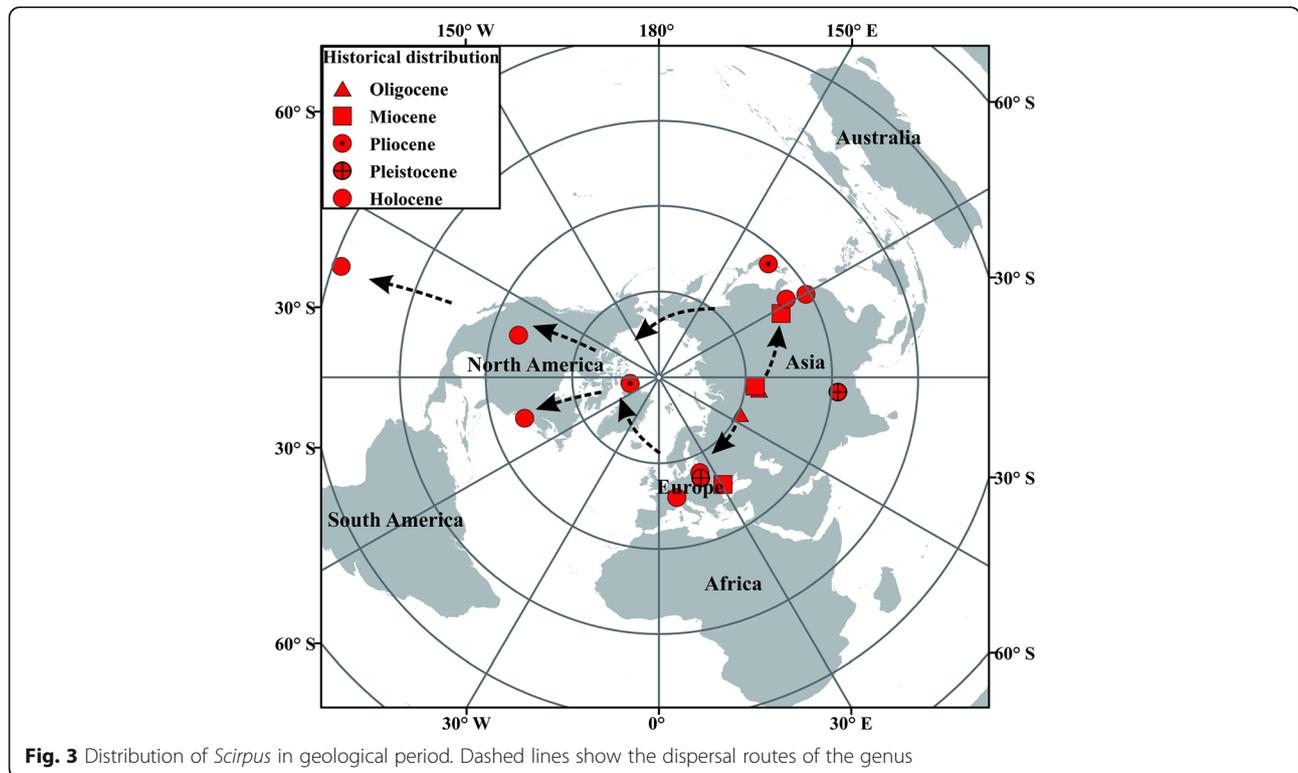


Fig. 3 Distribution of *Scirpus* in geological period. Dashed lines show the dispersal routes of the genus

Europe and Eastern Asia during the Miocene. It occurred in North America through transoceanic dispersal in the Pliocene. *Scirpus* then spread widely around the world in the Holocene (Fig. 3).

6 Conclusions

Fossil fruits of *Scirpus* were first reported from Weichang County, Hebei Province, North China. They were obovate in the lateral view and trigonous in the transverse section, and had three stout persistent bristles with downward-directed barbellae in the apical half. Compared with extant and fossil species of the genus, they were ascribed to *Scirpus weichangensis* X.Q. Liang, sp. nov. Based on the systematic research of fossil fruits of *Scirpus*, this study could infer that its plants first occurred in the early Oligocene Siberia (*S. foveolatus*), and then appeared in the Miocene Asia (e.g. *S. weichangensis*), subsequently grew in North America in the Pliocene (e.g. *S. microcarpus* from Ellesmere Island, Canada) and in South Hemisphere in the Holocene (e.g. *Scirpus* sp. from Rapa Nuiis, Polynesia). And finally, distribution of the genus was nearly cosmopolitan.

Acknowledgements

The authors are grateful to the Central Lab of the Xishuangbanna Tropical Botanical Garden for their helps in SEM. Thanks are also expressed to two anonymous reviewers for their helpful comments.

Funding

This research was supported by grants from the National Natural Science Foundation of China (Nos. 31760057, 31860049, 41502017, 41072022).

Availability of data and materials

Information of data and material(s) was in figures, plate(s) and tables of the manuscript.

Author contributions

X-QL and C-SL collected the materials. PL and X-QL carried out the experiment and wrote the manuscript. YL, J-WZ, Y-ZL and C-SL helped modify the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Author details

¹School of Chemistry, Biology, Environment, Yuxi Normal University, Yuxi 653100, Yunnan Province, China. ²CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing 210008, Jiangsu Province, China. ³Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, 818 South Beijing Road, Urumqi 830011, Xinjiang Uygur Autonomous Region, China. ⁴Qian-Dao-Hu Museum of Natural History, Hangzhou 311700, Zhejiang Province, China. ⁵State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.

Received: 18 September 2018 Accepted: 18 March 2019

Published online: 11 April 2019

References

- Berggren, G. 1969. *Atlas of seeds and small fruits of northwest European plant species with morphological descriptions. Part 2: Cyperaceae*. Sweden: Berlingska Boktryckeriet.
- Bhandari, S., A. Momohara, and K.N. Paudyal. 2009. Late Pleistocene plant macro-fossils from the Gokarna formation of the Kathmandu Valley, Central Nepal. *Bulletin of the Department of Geology* 12: 75–88.
- Dai, L.-K., L. Song-Yun, L. Song-Jun, Z. Shu-Ren, T. Yan-Cheng, T. Koyama, G.C. Tucker, D.A. Simpson, H.J. Noltie, M.T. Strong, J.J. Bruhl, K.L. Wilson, and A.M. Muasya. 2010. Cyperaceae. In *Flora of China*, ed. Z.-Y. Wu, P.H. Raven, and D.-Y. Hong, vol. 23. Beijing, Science Press: (Acoraceae through Cyperaceae).
- Dorofeev, P.I. 1963. *The Tertiary floras of Western Siberia*. Leningrad: Izdatelstvo Akademii Nauk SSSR.
- Doweld, A.B. 2018. New names of fossil Cyperaceae of northern Eurasia. *Phytotaxa* 356: 131–144.
- Drescher-Schneider, R., C. Jacquat, and W. Schoch. 2007. Palaeobotanical investigations at the mammoth site of Niederweningen (Kanton Zürich), Switzerland. *Quaternary International* 164-165: 113–129.
- Goetghebeur, P. 1998. Cyperaceae. In *The families and genera of vascular plants IV flowering plants — Monocotyledons*, ed. K. Kubitzki. Berlin: Springer.
- Hayasaka, E. 2012. Delineation of *Schoenoplectiella* lye (Cyperaceae), a genus newly segregated from *Schoenoplectus* (Rchb.) Palla. *Journal of Japanese Botany* 87: 169–186.
- Healy, A.J., and E. Edgar. 1980. *Flora of New Zealand. Vol. III. Adventive cyperaceous, Petalous and Spathaceous monocotyledons*. Wellington: Government Printer.
- Horrocks, M., W.T. Baisden, J. Flenley, D. Feek, L.G. Nualart, S. Haoa-Cardinali, and T.E. Gorman. 2012. Fossil plant remains at Rano Raraku, Easter Island's statue quarry: Evidence for past elevated lake level and ancient Polynesian agriculture. *Journal of Paleolimnology* 48: 767–783.
- James-West, G. 1977. *Late Holocene vegetation history of the Sacramento-san Joaquin Delta*. California: Cultural heritage section, California Department of Parks and Recreation.
- Li, J., and Z.G. Xiao. 1980. *Introduction of Qipanshan section (K-50-16), 1/200000 geological map of People's Republic of China*. Beijing: Geological Map Printing Plant of China (in Chinese).
- Li, J.-F., D.K. Ferguson, J. Yang, G.-P. Feng, A.G. Ablav, Y.-F. Wang, and C.-S. Li. 2009. Early Miocene vegetation and climate in Weichang District, North China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 280: 47–63.
- Li, L., C. Zhu, L.-G. Lin, Q.-H. Zhao, G.-Y. Shi, and H.-B. Zhu. 2008. Transgression records between 7500-5400BC on the stratum of the Luotuodun site in Yixing, Jiangsu Province. *Acta Geographica Sinica* 63: 1189–1197.
- Liang, X.-Q. 2009. *The Early Miocene Flora of Weichang, Hebei, China*. Ph.D. thesis, Institute of Botany. In *Chinese Academy of Sciences*. China: Beijing.
- Liang, X.-Q., Y. Li, Z. Kvaček, V. Wilde, and C.-S. Li. 2013. Seeds of Weigela (Caprifoliaceae) from the Early Miocene of Weichang, China and the biogeographical history of the genus. *Taxon* 62: 1009–1018.
- Liang, X.-Q., P. Lu, A. Tiwari, T. Su, and Z.-K. Zhou. 2017. New fossil record of Cladium (Cyperaceae) from the middle Miocene of Zhenyuan, SW China, and the palaeobiogeographical history of the genus. *Review of Palaeobotany and Palynology* 237: 1–9.
- Liang, X.Q., V. Wilde, D.K. Ferguson, Z. Kvaček, A.G. Ablav, Y.F. Wang, and C.S. Li. 2010. *Comptonia naumannii* (Myricaceae) from the early Miocene of Weichang, China, and the palaeobiogeographical implication of the genus. *Review of Palaeobotany and Palynology* 163: 52–63.
- Matthews, J.V., and L.E. Oviden. 1990. Late tertiary plant macrofossils from localities in Arctic/subarctic North America: A review of the data. *Arctic* 43: 364–392.
- Nikitin, V.P. 2006. *Paleocarpology and stratigraphy of the Paleogene and Neogene strata in Asian Russia*. Novosibirsk: Academic publishing house.
- Oh, Y.C., and E.J. Ham. 1998. A taxonomic study on *Scirpus* Linn. (Cyperaceae) of Korea. *Korean Journal of Plant Taxonomy* 28: 217–247.
- Pierce, L.S., and B.H. Tiffney. 1986. Holocene fruit, seed and leaf flora from riverine sediments near New Haven, Connecticut. *Rhodora* 88: 229–252.
- Pignotti, L., and L.M. Mariotti. 2004. Micromorphology of *Scirpus* (Cyperaceae) and related genera in South-West Europe. *Botanical Journal of the Linnean Society* 145: 45–58.
- Spalink, D., B.T. Drew, M.C. Pace, J.G. Zaborsky, J.R. Starr, K.M. Cameron, T.J. Givnish, and K.J. Sytsma. 2016. Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants. *Journal of Biogeography* 43: 1893–1904.

- Stachowicz-Rybka, R. 2005. Reconstruction of climate and environment in the Augustovian interglacial on the basis of select plant macrofossil taxa. *Polish Geological Institute Special Papers* 16: 127–132.
- Stachowicz-Rybka, R. 2015. Record of environmental and climatic changes in middle Pleistocene sediments from Łuków (eastern Poland) on the basis of plant macroremains analysis. *Acta Palaeobotanica* 55: 68–93.
- Strickland, L.E., R.G. Baker, R.S. Thompson, and D.M. Miller. 2014. Last interglacial plant macrofossils and climates from Ziegler reservoir, Snowmass Village, Colorado, USA. *Quaternary Research* 82: 553–566.
- Wellman, C.H., and L. Axe. 1999. Extracting plant Mesofossils and Megafossils by bulk acid maceration. In *Fossil plants and spores: modern techniques*, ed. T.P. Jones and N.P. Rowe, 11–14. London: Geological Society of London.
- Whittemore, A.T., and A.E. Schuyler. 2002. *Scirpus* Linnaeus. In: Committee, F.o.N.A. E. (Ed.). *Flora of North America Vol. 23: Magnoliophyta: Commelinidae (in part): Cyperaceae*. New York: Oxford University Press, pp. 8–21.
- Wilson, K.L. 1994. Cyperaceae. In *Flora of Victoria Vol. 2, ferns and allied plants, conifers and monocotyledons*, ed. N.G. Walsh and T.J. Entwisle. Melbourne: Inkata Press.
- Yamakawa, C., A. Momohara, T. Nunotani, M. Matsumoto, and W. Yasuyuki. 2008. Paleovegetation reconstruction of fossil forests dominated by *Metasequoia* and *Glyptostrobus* from the late Pliocene Kobiwako group, Central Japan. *Paleontological Research* 12: 167–180.
- Yu, Z.-C. 2003. Late Quaternary dynamics of tundra and forest vegetation in the southern Niagara escarpment, Canada. *New Phytologist* 157: 365–390.

Submit your manuscript to a SpringerOpen[®] journal and benefit from:

- ▶ Convenient online submission
- ▶ Rigorous peer review
- ▶ Open access: articles freely available online
- ▶ High visibility within the field
- ▶ Retaining the copyright to your article

Submit your next manuscript at ▶ [springeropen.com](https://www.springeropen.com)
