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中国一中新世湖泊的古生态：根据山旺盆地植硅体的初步解释

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摘要：山东山旺中新世山旺组湖相沉积中富含保存精美的古生物化石。对于湖相沉积中的昆虫、植物和哺乳动物化石，前人已经做了大量的研究工作。其中植物大化石和孢粉的研究结果表明，中新世山旺组在沉积期间，山旺湖周围的植被处于湿润的暖温带到亚热带的古生态环境下。哺乳动物蝙蝠和貘化石的研究结果也支持这个结论。然而，迄今为止，还没有关于草本植物的种类组成及含量的研究报道。本文首次对山旺组样品中的植硅体进行了研究，为山旺中新世植被的研究提供了新的证据。对从6块山旺组样品中分析出的植硅体进行研究的结果表明，山旺中新世植硅体组合含有丰富的保存极好的草本植物植硅体，代表森林成分的双子叶植物植硅体，以及偶尔出现的棕榈科植硅体。草本植物的植硅体主要来自于C_3/C_4禾本科的PACCAD类群和早熟禾亚科的植物，少数可能来自于在林下封闭生活环境中生长的草本植物。山旺中新世植硅体组合显示，在湖边森林生活环境下，伴生大量的适合沼生到中生环境的草本植物，在较干旱的地区生长着早熟禾（和PACCAD）的草本植物。本文的研究结果进一步支持山旺中新世气候比现在更加湿润而且变动较小的观点。山旺中新世植硅体组合与土耳其和北美大平原中新世湖相沉积中的植硅体组合不同，后者的植硅体组合主要是由多种C_3早熟禾亚科草本和不同种类的PACCAD类群草本植物组成。今后的研究工作将进一步揭示这种差异是否反映了草本植物群落在大尺度的生物地理上的差异，或者是由于地区性的局部气候不同所导致。

关键词：中国山旺，中新世，禾本科，植硅体分析，古生态

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PALAEOECOLOGY OF AN EARLY-MIDDLE MIOCENE LAKE IN CHINA: PRELIMINARY INTERPRETATIONS BASED ON PHYTOLITHS FROM THE SHANWANG BASIN

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Abstract The lacustrine Early to Middle Miocene Shanwang Formation contains an exceptionally well-preserved biota including insects, plants, and vertebrates that has been subject to intense study. Palaeoecological work on plant macrofossils and palynofloras indicate that the locality represents a forest under a humid, warm-temperate to subtropical climate that remained rather stable during the deposition of the formation. This interpretation is supported by fossil vertebrates such as bats and tapirs discovered in the Shanwang section. However, to date no information has been available on the presence, abundance, and taxonomic composition of grasses at this locality. Here, we report on phytoliths extracted from six samples from the Shanwang Formation, providing new evidence of the vegetation that grew around the lake. The phytolith assemblages contain well-preserved and abundant grass phytoliths, forest indicator phytoliths from dicotyledonous plants, and infrequent palm phytoliths. The grass phytoliths consist of forms produced by C_3/C_4 PACCAD grasses and pooids, with a minor component of morphotypes thought to derive from closed-habitat grasses. Our preliminary interpretation of these phytolith assemblages is that they reflect a lake-side wooded habitat and abundant helophytic to mesophytic grasses, with drier areas supporting pooid (and PACCAD) grasses. The data support the reconstruction of the Miocene Shanwang region as more humid and equable than presently. The Shanwang phytolith assemblages contrast with Miocene lacustrine phytolith assemblages from Turkey and the Great Plains of North America, which indicate grass communities characterized by diverse C_3 pooids and different types of PACCAD grasses. Future research will determine whether this variability reflects large-scale biogeographic differences in grass communities or local, microclimate-related variation.

Key words Shanwang, China; Miocene; Poaceae; phytolith analysis; palaeoecology

1 Introduction

The Shanwang locality in the Shandong Province, eastern China (Fig. 1), considered to be latest Early Miocene to early Middle Miocene in age (~17 - 14 Ma, Qiu et al., 1999; Liang, 2004; Deng, 2006), has the status of *Konservat-Lagerstätte* due to its extraordinarily well-preserved and rich fossil biota. Over 500 hundred species of fungi, diatoms, insects, ostracodes, fishes, amphibians, reptiles, birds, mammals, and vascular plants have been excavated from the diatomaceous lacustrine shales of the Shanwang Formation (e.g., Li, 1982; Yan et al., 1983; Wang, 1989; Leopold et al., 1992; Yang and Yang, 1994; Zhang et al., 1994; Liang, 2004; Wang et al., 2005; Wang et al., 2006); the exquisitely preserved fossil material boasts non-mineralized organic tissues with detailed ultra-structure of plants and animals, original coloration of plants and insects, and fully articulated animals with skin and stomach contents (Yang and Yang, 1994). The area was discovered in the early 1800s and since the 1930s, intense research on the fauna, flora, stratigraphy, petrology, palaeomagnetism, and radiometric dating has been conducted (for review, see Yang and Yang, 1994; Sun et al., 2002; Liang, 2004). The wealth of data that has emerged from this work has played a fundamental role in our understanding of the vegetation, climate, and ecological interactions in eastern Asia during the Miocene.

Based on palaeoecological analysis [coexistence approach (CoA), leaf margin analysis (LMA) and Climate Leaf Analysis Multivariate Programme (CLAMP)] of detailed plant macrofossil and palynological data, the Shanwang ecosystem has been reconstructed as a closed, mixed mesophytic forest growing in a humid, warm-temperate to subtropical climate (Sun et al., 2002; Liang et al., 2003; Liang, 2004). The middle and lower Yangtze River Valley, ~750 km south of the Shanwang Basin, have been suggested as a reasonable modern analogue for this habitat (e. g., Hu and Chaney, 1940; Liu and Leopold, 1992; Sun et al., 2002; Liang et al., 2003). This interpretation is supported by the vertebrate fauna, recording the presence of bats, tapirs, and tree squirrels (Deng et al., 2003; Qiu and Yan, 2005; Fortelius, 2006). All proxies further indicate that climate and vegetation remained fairly stable throughout the deposition of the Shanwang Formation (Sun et al., 2002; Liang et al., 2003; Liang, 2004).

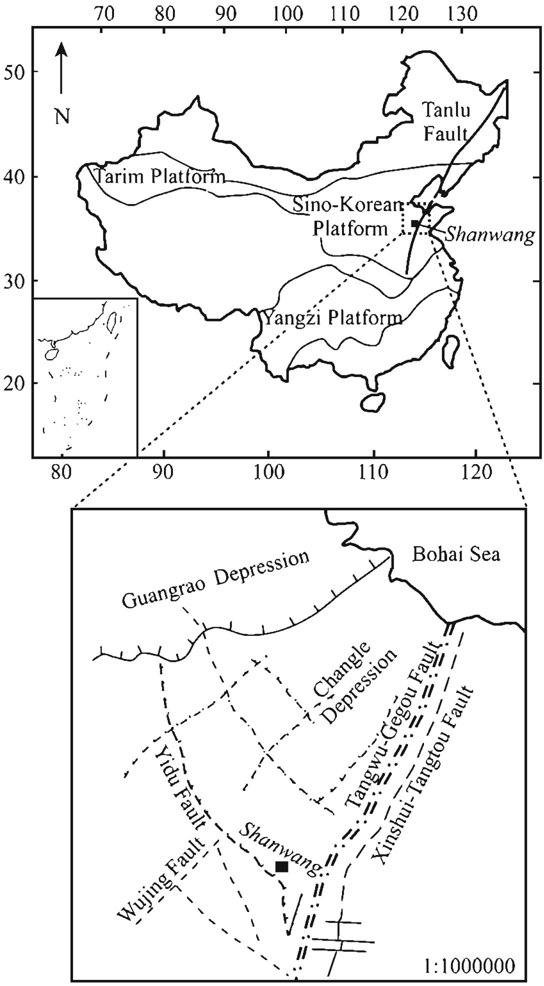

Fig. 1　Regional tectonic map of China showing the geographic location of the Shanwang locality (top, modified after Zhang et al., 1984) and the geologic structure of the Shanwang area (bottom, after Sha, 1978)

Despite the amount of detailed information about this diverse ecosystem, essential pieces of information are missing. Based on palynological and faunal data, the Miocene of China is thought to have seen the rise to ecological dominance of grasses, in particular open-habit grasses (Leopold et al., 1992; Li et al., 1995; Qiu and Qiu, 1995; Jacobs et al., 1999; Sun and Wang, 2005). Rare pollen and macrofossils of grasses show that these also formed part of the vegetation in Shanwang (Liu and Leopold, 1992; Liang et al., 2003; Liang, 2004). However, the preservation of the macrofossils has generally been too poor for precise identification and grass pollen are ubiquitous within Poaceae, prohibiting closer taxonomic discrimination (Li et al., 1995; Jacobs et al., 1999). Knowledge of the taxonomic composition and abundance of grasses at Shanwang, which may provide vital information about ecology, as well as grass evolution and biogeography, has therefore not previously been available.

In this study we investigate phytoliths (silica bodies from vascular plants) from the Miocene Shanwang section and discuss the environmental implications of the phytolith analysis in light of the accumulated knowledge of the Shanwang lake system. Phytoliths are known to provide vital clues for habitat reconstruction (Piperno, 1988, 2006; Strömberg, 2004; Lu et al., 2006). In particular, grass phytoliths can be highly specific and allow fairly detailed taxonomical and ecological characterization of grass communities (Piperno and Pearsall, 1998; Lu and Liu, 2003; Prasad et al., 2005; Piperno, 2006).

2 Materials and methods

2.1 Locality and geologic framework

The Shanwang Formation is thought to represent a small (< 1 km^2), shallow, stratified freshwater mountain lake, formed as a maar or in a similar volcanic or tectonic setting (e. g., Zhang and Shan, 1994; Liang, 2004; Wang et al., 2005). The soft-tissue preservation of the fossils and the lack of bioturbation indicate periods of anoxia during lake formation (Wang et al., 2005; Yang and Yang, 1994). Radiometric dating of basaltic layers above and below fossil-

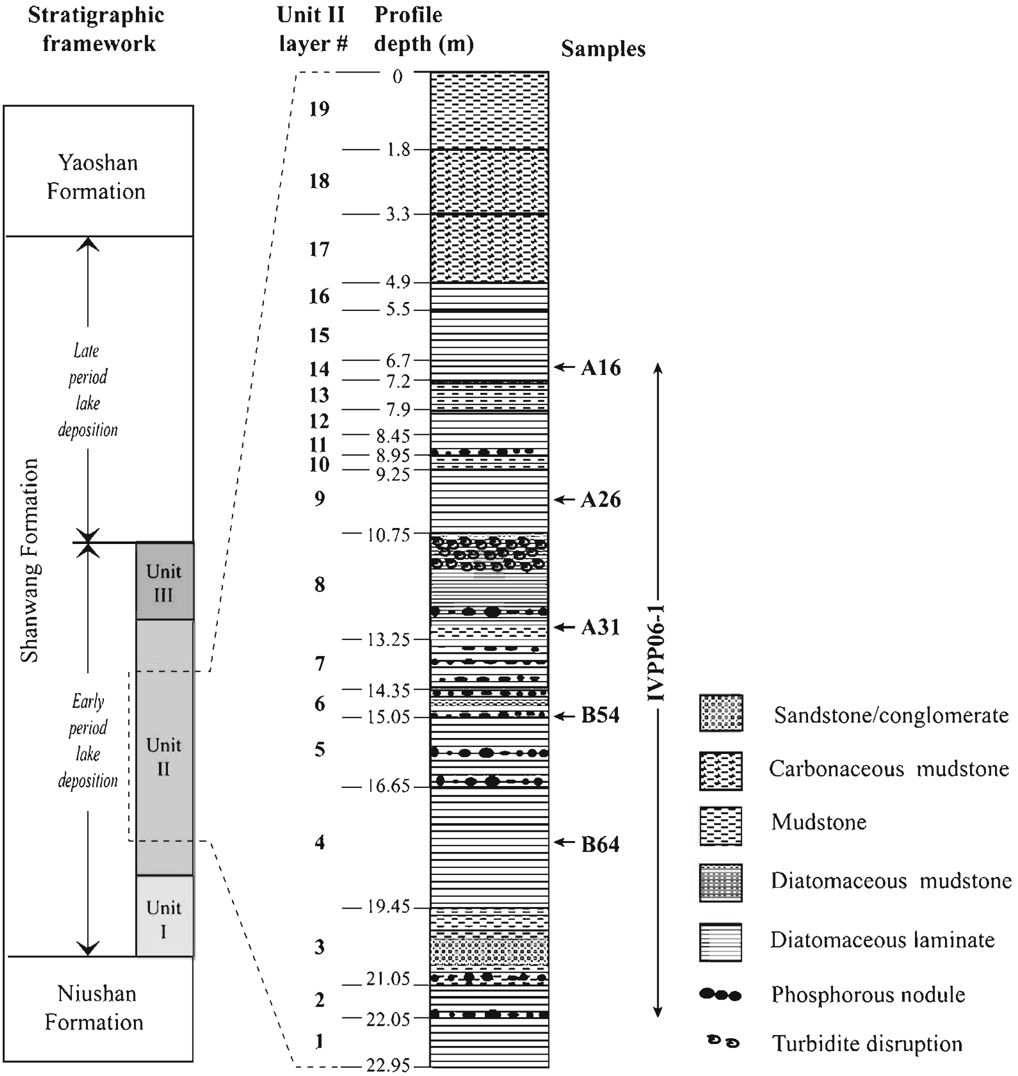

Fig. 2 Stratigraphic framework (left) and lithology (right) of the sampled section in Unit II of the Shanwang Formation

Placement of studied samples indicated on the far right bearing horizons together with biostratigraphical data provides an age of about 17 – 14 million years for the biota (Chen and Peng, 1985; Jin, 1985; Zhu et al., 1985; see reviews in Liang, 2004; Deng, 2006). The Cenozoic sedimentary deposits of the Shanwang Basin have been described in detail elsewhere (e. g., Yang and Yang, 1994; Zhang and Shan, 1994; Sun et al., 2002; Liang, 2004; Liang et al., 2003). In this preliminary study, we have selected five samples previously analyzed for pollen and spores from the fossiliferous Unit II of the lower part of the Shanwang Formation (Table 1; Fig. 2) (Liang, 2004; Liang et al., 2003). This unit represents deposition in the established, early-stage lake, and is divided into 19 lithologically distinct layers numbered from the bottom up (Liang, 2004; Liang et al., 2003). The samples included in this study derive from layers in which, aside from palynomorphs, leaf and animal fossils have been found (Table 1). The sample labelled IVPP06-1 was provided by Z. Q. Zhang and M. M. Chang and comes from a fish collection housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP). The collection stems from an unidentified layer within Unit II of the lower Shanwang Formation. Judging from the lithology of IVPP06-1, it is most likely from either of layers 2, 4, 5, 7, 9, 11, 12, or 14, but its absolute (and relative) position in the section is unknown.

Table 1　Samples studied from Unit II of the lower part of the Shanwang Formation

Sample	Layer	Lithology	Other fossils	References
B64*	4	Grey-white muddy diatomaceous shale with black-white lamination	Pollen/spores, leaves, fish, insects, mammals	Liang et al., 2003; Liang, 2004
B54	5	Grey-white muddy diatomaceous shale with black-white lamination	Pollen/spores, leaves, fish, insects	Liang et al., 2003; Liang, 2004
A31	8	Thickly-stratified grey muddy diatomaceous shale with black-white lamination, folded; 20 cm thick yellow-green mudstone at the base of the layer	Pollen/spores, leaves, fish, insects, mammals	Liang et al., 2003; Liang, 2004
A26	9	Grey-black diatomaceous shale with black and white lamination	Pollen/spores, leaves, fish, insects, mammals	Liang et al., 2003; Liang, 2004
A16*	14	Grey-black diatomaceous shale with black and white thin lamination	Pollen/spores, leaves, fish	Liang et al., 2003; Liang, 2004
IVPP06-1	?	Grey-white muddy diatomaceous shale with black-white lamination	Fish	Z. Q. Zhang, M. M. Chang, pers. comm.

* Assemblages not included in quantitative analysis because of low phytolith concentration.

2.2 Extraction and analysis

The sediment samples were processed using standard methods (Strömberg, 2004; Strömberg et al., in press). The extracted phytolith morphotypes were identified using a comprehensive reference collection of phytoliths from modern plants (Strömberg, 2003; Strömberg et al., in press; Strömberg, unpublished data) and the literature (e. g., Twiss et al., 1969; Postek, 1981; Mulholland, 1989; Piperno, 1988, 2006; Bozarth, 1992; Kondo et al., 1994; Kealhofer and Piperno, 1998; Piperno and Pearsall, 1998; Blinnikov, 2005). In each sample, more than 230 (231 – 305) phytoliths considered diagnostic for vegetation inference were counted. Employing the classification of Strömberg et al. (in press; Table 2), the following main phytolith classes were used (Fig. 3):

1) Forest indicator total (FI TOT) phytoliths, including phytoliths typically produced by (a) palms, and (b) woody or herbaceous dicotyledons, conifers, and ferns;

2) Grass silica short cells (GSSC), which are found exclusively in grasses (Poaceae), divided into GSSC morphotypes typical of (a) closed-habitat grasses [in the (Bambusoideae + Ehrhartoideae) (BE) clade, and a variety of basal grasses (GPWG, 2001)] (CH TOT),

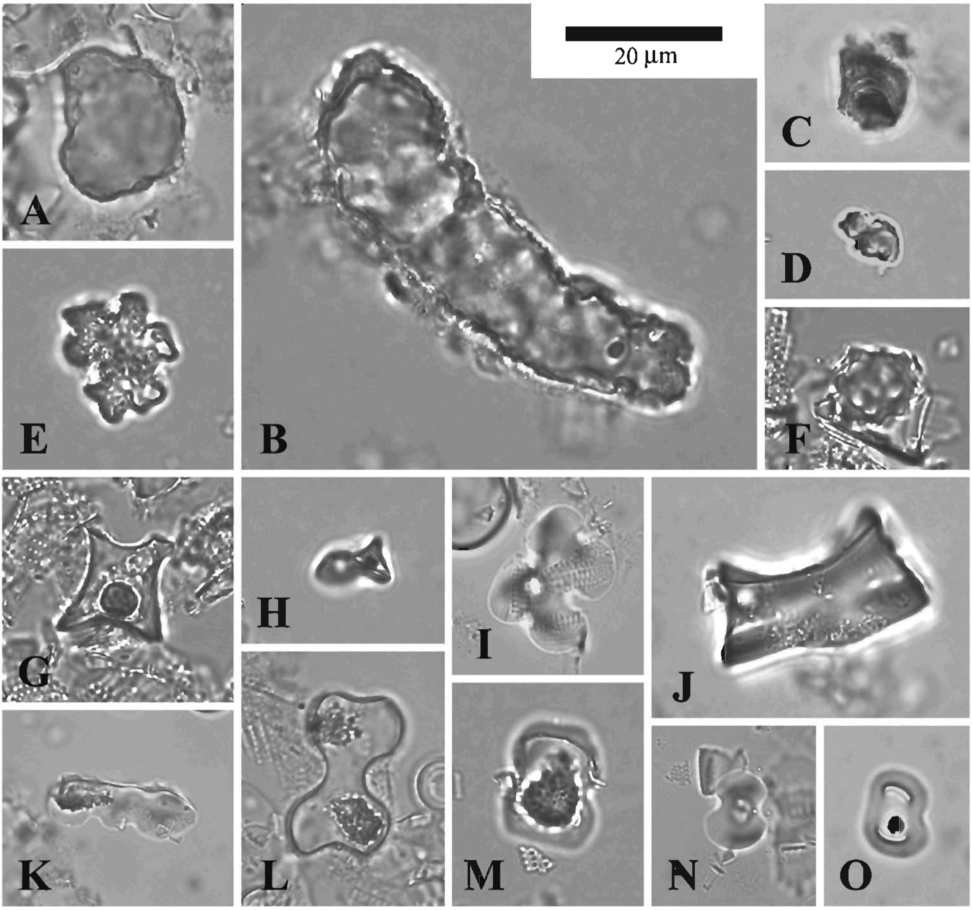

Fig. 3 Selected phytolith morphotypes used herein

A – F. Forest indicator total (FI TOT) morphotypes, A. Globular verrucate, common in Ulmaceae/Moraceae (A31); B. *Eucommia*-type irregular verrucate body (A26); C. Non-spherical laminar vesicular infilling, general forest indicators (A31); D. Globular granulate, general forest indicators (IVPP06-1); E. Lacunose anticlinal epidermis, found in Ulmaceae/Moraceae (B54); F. Globular echinate, diagnostic of palms (A26); G – O. Grass silica short cell (GSSC) morphotypes, G. Chusquoid body with a top consisting of a concave, often ornamented plate (BB-1 in Table 2), potentially produced by closed-habitat grasses (A26); H. Chusquoid body (BB-3), closed-habitat grasses; I. Cross, typical of PACCAD grasses (A31); J. Unusually wide collapsed saddle (BB-2), closed-habitat grasses (B54); K. Crenate GSSC, pooids (A31); L. Near-panicoid bilobate, PACCAD grasses (A31); M. *Stipa*-type bilobate, commonly produced in pooids (A26); N – O. Rondel-bilobate base with saddle top (Saddle-bilobate in Table 2); N. Fossil (A31); O. Modern, extracted from *Phragmites* leaf

(b) C_3 open-habitat grasses in the Pooideae [highly diagnostic forms (POOID-D) and less diagnostic, but abundantly produced forms (POOID-ND)], (c) C_3 and C_4 open-habitat grasses in the PACCAD clade (Panicoideae + Arundinoideae + Chloridoideae + Centothecoideae + Aristidoideae + Danthonioideae) (PACCAD TOT), and (d) other (unidentified) Poaceae (OTHG);

3) Phytoliths produced by wetland plants, primarily sedges (Cyperaceae) (AQ);

4) Non-diagnostic “grass” phytoliths (NDG);

5) Non-diagnostic and unclassified phytoliths (NDO).

Table 2　Assemblage data for Miocene biosilica assemblages from Shanwang, China

			FI TOT (%)		GSSC (%)							GSSC morphotypes (presence) 3)					FI-t ratio		FI forms (% of FI TOT)		Other biosilica 4)		
Sample 1)	Preservation 2)	AQ (%)	Palm	Other FI	CH TOT	POOID-D	POOID-ND	Panicoid	Chloridoid	PACCAD general	OTHG	Highly diagnostic of closed-habitat grasses	Saddle-bilobate	NDG (%)	NDO (%)	Total number of phytoliths counted	FI TOT/(FI TOT + GSSC) (%)	95% confidence interval (±%)	Ulmaceae/ Moraceae-type	*Eucommia*-type	Diatoms	Chrysophyte cysts	Sponge spicules
B64*	G	n.o.	n.o.	p	n.o.	n.o.	n	n.o.	n.o.	p	n.o.	—	—	p	p	n/a	n/a	n/a	p	n.o.	vab	p	p
B54	G	0,0	0,2	32,7	5,2	4,5	5,8	3,0	1,4	8,0	7,0	BB-1, BB-2, BB-3	x	5,8	26,3	449	48,5	5,9	38,5	0,0	ab	p	p
A31	G	0,2	0,0	31,3	2,0	2,9	1,1	4,0	1,1	7,5	1,6	BB-1,BB-3	x	4,8	43,4	546	60,6	5,7	5,3	4,7	vab	vab	p
A26	G	0,0	1,6	25,9	3,0	8,9	5,2	4,1	0,5	7,3	5,9	BB-1,BB-3	(x)	6,6	31,1	440	44,2	6,0	10,7	6,6	vab	n.o.	n.o.
A16*	G	n.o.	n.o.	p	p?	n.o.	p	n.o.	n.o.	p	n.o.	—	—	p	p	n/a	n/a	n/a	p	p	vab	n.o.	n.o.
IVPP06-1	G(-P)	0,3	p	39,2	0,8	6,0	1,6	1,0	1,0	6,8	3,6	BB-3	x	6,0	33,8	385	65,4	6,2	12,6	11,9	vab	mab	mab

1) Samples: * assemblages not included in quantitative analysis because of low phytolith concentration (n. o. = not observed; p = present; mab = moderately abundant; ab = abundant; vab = very abundant).

2) Preservation: G = good - pristine; P = poor (Strömberg et al., in press).

3) Grass silica short cell (GSSC) morphotypes: BB - 1 = chusquoid body with top consisting of a concave, often ornamented plate (BE? or basal? grass); BB - 2 = collapsed saddle (BE grasses, certain basal grasses); BB - 3 = chusquoid body (likely BE or basal grasses); (x) = single specimen only.

4) Semi - quantitative assessment of abundances of diatoms, chrysophyte cysts, and sponge spicules.

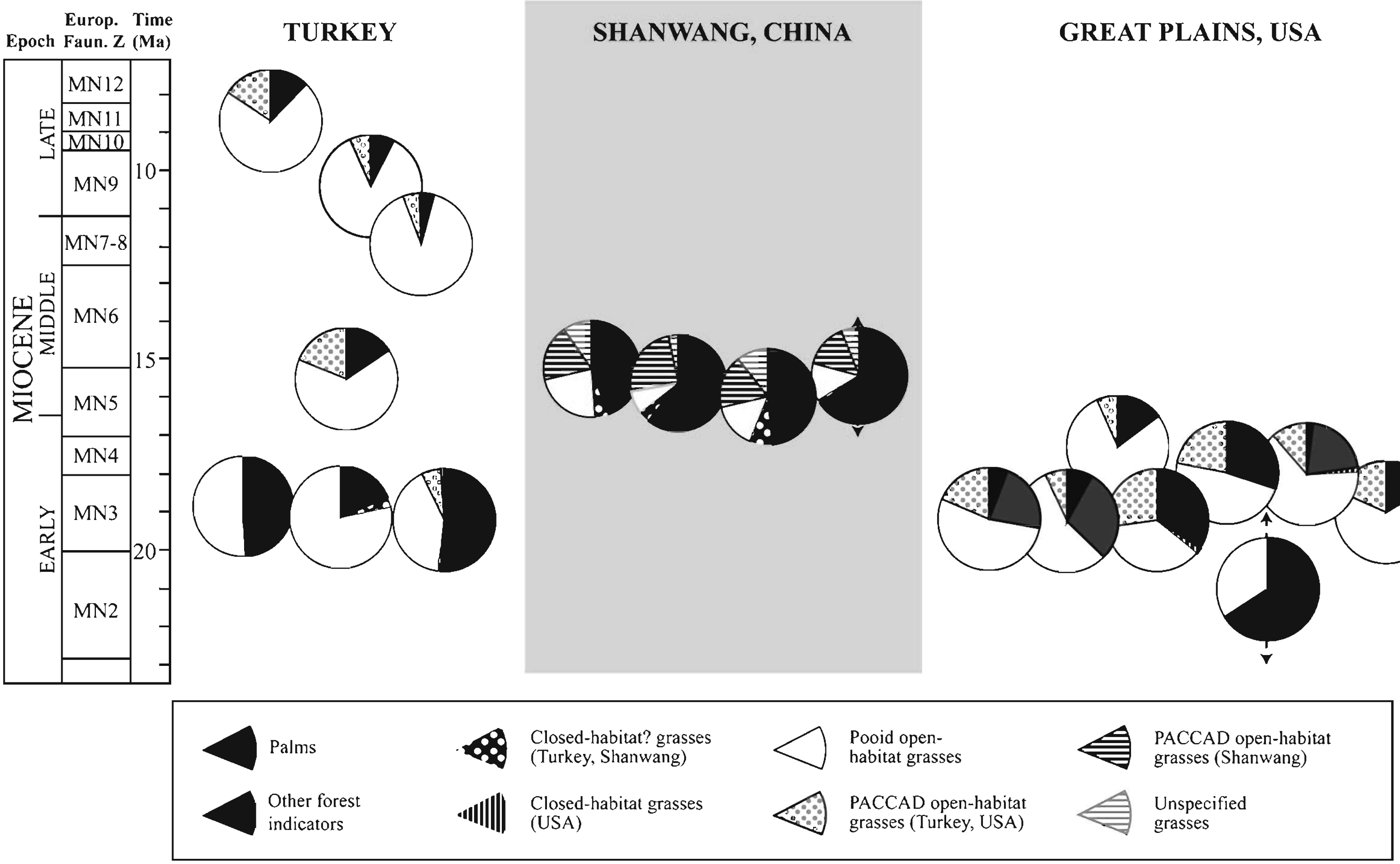

Fig. 4 The record of vegetation in the Miocene of Shanwang based on phytolith assemblages (represented as pie charts in the center) compared to records from lacustrine deposits from Turkey (left) and Great Plains, USA (right)

The comparison indicates that different PACCAD morphotypes dominate in Shanwang assemblages compared to Turkey and the Great Plains; vertical arrows denote uncertainty in the absolute age of the phytolith assemblages (see text for further explanation)

Vegetation type was reconstructed through quantitative and qualitative comparison of different phytolith morphotype classes using methods described in detail elsewhere (Strömberg, 2005; Strömberg et al., in press).

3 Results

All samples yielded abundant diatoms, rare to moderately abundant sponge spicules and chrysophyte cysts, as well as phytoliths (Table 2). Relative to other forms of biosilica, phytoliths range from being common (number of phytoliths on the same order of magnitude as number of diatoms) in sample B54, to too rare for counting (phytoliths several magnitudes less common than diatoms) in samples B64 and A16. The preservation of phytoliths is overall good, with delicate ornamentation and intact organic inclusions in many GSSCs (Table 2). However, the assemblages contain few larger phytoliths such as bulliform cells, and elongate morphotypes are commonly fragmented. Therefore, some degree of size sorting during the formation of the sediment cannot be ruled out (see below for discussion).

All phytolith assemblages that were analyzed quantitatively, B54, A31, A26, and IVPP06-1 (heretofore referred to simply as "all assemblages"; B64 and A16 will not be discussed unless specifically mentioned) consist of relatively high abundances of forest indicator phytoliths (expressed as the FI-t ratio = FI TOT/(FI TOT + GSSC)%) such as globular granulate, polyhedral epidermis, laminar vesicular infilling, silicified sclerenchyma and similar, and "blocky polyhedrons" (44% -65%; Table 2). In A31 and IVPP06-1, FI TOT forms dominate over GSSC, whereas in B54 and A26, GSSCs are slightly more abundant (Fig. 4). Among the FI TOT phytoliths, it can be noted that morphotypes commonly produced by Ulmaceae and Moraceae (globular verrucate, lacunose anticlinal epidermis, and cystoliths, Bozarth, 1992; Kealhofer and Piperno, 1998; Strömberg, 2003; Piperno, 2006) are present in all samples and occasionally very abundant (39% of FI TOT phytoliths in B54); forms described from *Eucommia* wood (elongate and irregular forms made up of light, transparent, opaque silica with small, black dots in the interior and with a verrucate, somewhat diffuse surface, Strömberg, 2003) are distinct elements of certain assemblages (12% of FI TOT forms in IVPP06-1). Rare palm phytoliths are found in three samples.

The grass short cell assemblages are diverse and dominated by phytoliths produced primarily by open-habitat grasses, including forms typical of stipoid pooids (*Stipa*-type bilobate and crenates, Fredlund and Tieszen, 1994; Strömberg, 2005) and certain PACCAD grasses. The PACCAD morphotypes encompass several kinds of crosses and bilobates, in particular simple lobates, inverted bilobates, panicoid bilobates, and near-panicoid bilobates found in various C_3 and C_4 PACCADs (Fredlund and Tieszen, 1994; Strömberg, 2003). Near-panicoid bilobates/crosses (Fig. 3L) are particularly common in the Shanwang samples. Morphotypes with a rondel-bilobate base (the surface facing the exterior of the leaf, cf. Strömberg et al., in press) and a saddle top, characteristic of *Phragmites* (Ollendorf et al., 1988; Mulholland, 1989; Piperno and Pearsall, 1998; Strömberg, unpublished data), are found in low frequencies in all samples. Bootstrap analysis of the assemblages (data not shown) indicate low to moderate frequencies of basal or BE grasses, as does an inventory of observed, diagnostic GSSC morphotypes, such as chusquoid bodies and collapsed saddles (Table 2) (Piperno and Pearsall, 1998; Prasad et al., 2005). Among these forms are GSSCs with a chusquoid base and a top consisting of a concave, often ornamented plate, which are herein tentatively assigned to basal/BE grasses (BB-3 in Table 2; Fig. 3G). These bodies show some resemblance to morphotypes dominating certain grass communities in the Eocene of Turkey that are interpreted as coming from bamboo relatives (Strömberg et al., in press).

Phytoliths of sedges and other wetland plants are very rare.

4 Discussion

Lu and Liu (2003) documented the variation in bilobate grass silica short cells (GSSCs) of PACCAD grasses from a range of modern habitats in China and found a correlation between bilobate morphology and autecology. More precisely, grasses inhabiting moist habitats tended to produce bilobates with short shanks, while long-shanked bilobates were found predominantly in arid-land grass taxa. Although it is somewhat speculative to extrapolate this relationship into the Miocene, it can be noted that the bilobates recorded in the Shanwang phytolith assemblages correspond most closely to the range of bilobate morphotypes that are found in modern helophytic to mesophytic C_3/C_4 PACCADs (a rigorous morphometric study is needed to verify this quantitatively). For example, near-panicoid bilobates are abundantly produced in the C_3 grass *Arundo donax* (giant reed), which, similarly to *Phragmites* (common reed), forms tall, dense stands in riparian habitats and wetlands (Watson and Dallwitz, 1992 onwards; Bell, 1997; Meyerson et al., 2000). In addition, stable carbon isotopic data from tooth enamel and palaeosol carbonates from localities north and slightly south of Shanwang (Yushe Basin, Baode and Lantian) indicate that C_4 grasses became common only in the Late Miocene (after ~8 – 7 Ma, Fortelius et al., 2005; Passey et al., 2006, this issue). This suggests that the bilobate-producing PACCAD grasses in the Shanwang assemblages were most likely C_3, supporting an interpretation of these grasses as water or shade-loving, rather than indicators of open, dry habitats.

The high abundance of GSSCs typical of these grasses may therefore indicate vegetation in close proximity to water. The relatively high frequencies of forest indicator (FI TOT) morphotypes point to a wooded habitat or closed dicotyledonous forest with rare palms, as does the implied presence of basal and BE grasses (Strömberg, 2004). Accordingly, we interpret the Shanwang phytolith assemblages as reflecting primarily a lake-side, wooded habitat, with abundant water-loving grasses, as well as low frequencies of basal or BE grasses and rare palms.

The FI TOT morphotype spectra support this interpretation. Liang (2004) identified four different vegetation associations (clusters A-D) in her palynological analysis of samples from Unit II of the Shanwang Formation. These associations of taxa were thought to represent upland *Fagus* forest (A), *Liquidambar-Pterocarya* lake-side forest (B), *Ulmus-Zelkova* calcareous lake-side forest (C), and mixed mesophytic forest (D), presumably representing habitats away from the lake margin. Aside from the dominant representatives *Liquidambar* and *Pterocarya*, cluster B includes pollen produced by *Eucommia*, and we hypothesize that the *Eucommia*-type FI TOT phytoliths derive from this lake-side vegetational association. Similarly, it seems reasonable to assume that the Ulmaceae/Moraceae-type phytolith morphotypes reflect the *Ulmus-Zelkova* calcareous lake-side forest. The other, relatively non-diverse FI TOT phytoliths are more or less ubiquitous within forest indicator taxa, or present in such low abundances in the fossil assemblages that it is presently difficult to discern patterns that would tie them to any specific plant or taxonomic assemblage in Liang's (2004) scheme. Thus, they could derive either from the lake-margin vegetation or from more distal habitats. Nevertheless, several of the plants assumed to have been growing abundantly in the more upland areas are well-known phytolith producers (e. g., *Fagus*, *Quercus*, *Acer*, *Carpinus*, *Juglans*, *Carya*), and their phytoliths distinctive enough (Rovner, 1971; Geis, 1973; Bozarth, 1992; Strömberg, 2003) to suggest that these plants did not contribute substantially to the phytolith assemblages studied here (but see discussion on phytolith taphonomy below).

The palm phytoliths confirm the rare occurrence of palms implied by a single grain of the pollen taxon *Arecipites* documented from the Shanwang section (Liang, 2004). Combined with the presence of BE or basal grasses these data support earlier interpretations of the Miocene Shanwang region as more humid and equable than today (e. g., Hu and Chaney, 1940; Song et al., 1964; Zhou, 1990; Liu and Leopold, 1992; Sun et al., 2002; Wang et al., 2003, 2005;

Liang, 2004), perhaps more similar to the Lower Yangtze River Valley where bamboos and palms co-occur today (Moore, 1973; Ohrnberger and Goerrings, 1986). However, the phytolith assemblages also contain GSSCs produced by stipoid pooids. The modern representatives of this clade are mesophytic to xerophytic and typical of open habitats (Watson and Dallwitz, 1992 onwards). These grasses (and potentially also the PACCADs, see above) may indicate drier patches in the lake-side vegetation, as inferred previously based on the presence of pollen produced by *Ephedra* and Chenopodiaceae (Liang, 2004).

The rare occurrence of sedges in the Shanwang lakeshore flora, inferred from phytoliths (Table 2), is notable, given the importance and diversity of Cyperaceae in Miocene lakeshore floras in Europe and western Asia (e. g., Dorofeev, 1963; Friis, 1985; Mai, 1995). An explanation for this low representation of sedges at Shanwang could perhaps be the suggested presence of abundant reed grasses. Reeds are aggressive invaders of disturbed wetland habitats in many ecosystems today, where they are known to competitively exclude other hydrophytic plants (Galatowitsch et al., 1999; Zedler and Kercher, 2004).

There is some compositional variation among the assemblages, such as in the relative abundance of FI TOT phytoliths and the frequency of closed-habitat vs. pooid vs. PACCAD grasses (Fig. 4). This pattern points to differences in tree cover, and in grass community composition, respectively. No major changes in regional climate during the deposition of the Shanwang Formation are apparent from previous studies (Liang, 2004; Liang et al., 2003; Sun et al., 2002), suggesting that the observed compositional variability is more likely due to differences in local climate and soil conditions (pH, porosity, hydrology etc.). However, given the low number of stratigraphically constrained samples currently available, it is difficult to test whether this represents variation due to temporal or spatial heterogeneity in vegetation or if it is a result of phytolith taphonomy in lakes, as will be discussed below.

4.1 Phytolith taphonomy

As can be expected, the amply documented macrofossil floras and palynofloras of Shanwang (Hu and Chaney, 1940; Song, 1959; Song et al., 1964; WGCPC, 1978; Wang, 1981, 1991; Liu and Leopold, 1992; Sun et al., 2002; Liang, 2004; Wang, 2006; Wang et al., 2006) provide palaeobotanical information at different spatial resolutions. Thus, the well-preserved leaves of the Shanwang macrofloras represent primarily the proximal, lake-side vegetation, while the pollen and spores appear to mirror both the regional and the local vegetation (see Liang et al., 2003). Generally speaking, phytoliths, which behave roughly like silt-sized soil particles after deposition, fall somewhere between macrofossils and palynomorphs in terms of the catchment area represented in an assemblage (for review, see e. g., Piperno, 1988, 2001, 2006; Fredlund and Tieszen, 1994; Strömberg, 2004). Moreover, research on phytoliths in lake cores has shown that the spatial scale relevant for phytolith deposition depends largely on the hydrological conditions in the lake (for review, see Piperno, 2001). In lakes with a large fluvial input, phytoliths are carried from farther away, resulting in lake phytolith assemblages reflecting relatively regional vegetation. Such assemblages show very diverse non-grass phytoliths deriving from the different habitats present in the lake watershed (Piperno, 1993, 2001). In addition, major fires can lead to long-distance, aeolian transport of phytoliths into lakes (Piperno, 1988). In contrast, in relatively closed lakes surrounded by dense forest, where fluvially-transported material, as well as erosion and wind-transport are less important, the phytolith record tends to mirror very local, shoreline vegetation (Piperno, 2001). The marked representation in the Shanwang phytolith assemblages of forms hypothesized to derive from lake-side plants (grasses, rare sedges, and dicotyledons) would support a lake system with a fairly limited fluvial input. This is consistent with geologic evidence (grain size, lamination of sediments), suggesting deposition under low energy, potentially anoxic conditions in a structurally confined lake (Li et al., 2000).

Another important issue to consider is the previously mentioned, potential size bias of the Shanwang phytolith assemblages. Although it is possible that the predominantly narrow size range of the observed morphotypes faithfully mirrors the pytolith output of the source vegetation, it could also be a consequence of size sorting relating to water transport in the lake. Indeed, the low energy environment inferred for the Shanwang lake during most of the deposition of Unit II strata (Li et al., 2000), implies that phytoliths larger than coarse silt (~63 micrometers) would not be transported far from the shore. Such a bias would select against certain large, diagnostic dicotyledonous morphotypes, such as hair bases and sclerenchyma (often >100 micrometers, see discussion in Strömberg, 2004). Smaller, and often less diagnostic, FI TOT phytoliths, such as globular granulate, single polyhedral epidermal cells, and vesicular infillings would more likely be deposited away from the lake margin along with diagnostic grass phytoliths (GSSCs). Size sorting may thus produce phytolith assemblages where the non-grass component is not only underrepresented, but also provide less taxonomic detail. This may explain why some of the taxa that apparently grew close to the lake, as judged by pollen and macrofossils (e. g., *Magnolia*, Liang et al., 2003), are so poorly represented in the phytolith assemblages, despite being ample producers of highly diagnostic phytolith morphotypes (e. g., Postek, 1981; Piperno, 2006). Note that an increase in fluvial input, linked to higher water velocities (at least close to deltas), should not just lead to higher input of phytoliths from upland elements, but also allow larger phytoliths to be carried farther out into the lake.

An investigation of phytolith assemblages from modern lake sediment from the middle Yangtze River Valley (i. e., the often proposed climatic analogue for the Miocene of Shanwang, see Liang, 2004) by Zhao and Piperno (2000), serves as a useful reference point for the present study. These authors found that grass phytoliths likely originating from the lakeshore herbaceous vegetation are dominant in the phytolith assemblages. However, although less abundant, non-grass phytoliths are diverse and include many morphotypes indicative of woody plants and associated forest indicator taxa growing further away from the lake (e. g., Annonaceae, Fagaceae). This signal of the upland forest could thus be used to determine a regional catchment area for the phytoliths deposited in the lake. Many of the non-grass phytoliths that Zhao and Piperno (2000) recorded are generally very large (>100 micrometers, Piperno, 2006), further supporting higher energy conditions associated with ample fluvial influence and thus, longer transport.

4.2 Biogeographic comparisons

A comparison of the Shanwang phytolith assemblages with Miocene lacustrine phytolith assemblages from other parts of the world (Fig. 4) raises some intriguing questions that are worth a brief discussion. Specifically, there appears to be important differences between Miocene wetland grass communities in different parts of Eurasia (Fig. 4). Thus, Middle-Late Miocene lake deposits of western Eurasia (Turkey) have yielded GSSC assemblages that are consistently dominated by pooid types, rather than PACCAD morphotypes (Strömberg et al., in press). Furthermore, the PACCAD GSSCs that are common in the Turkish assemblages are different from the PACCAD forms that dominate the Shanwang samples. The Turkish phytolith assemblages are more similar overall, and in terms of PACCAD GSSCs, to Early Miocene lacustrine assemblages from the Great Plains of North America (Strömberg, 2004, 2005). On the other hand, the BE and basal GSSCs of Shanwang and Turkey, characterized primarily by chusquoid bodies with elaborate tops (Strömberg et al., in press), are more similar to each other than either is to those recorded from the Cenozoic of the Great Plains.

A speculative interpretation of this preliminary pattern is that it suggests different biogeographic affinities for grasses with different ecologies (open-habitat vs. closed-habitat). If this holds up to closer scrutiny (more data), it may relate to the timing and nature (light, temperature, moisture, physical continuity) of different dispersal routes during the Cenozoic, as has been suggested by Tiffney and Manchester (2001) for other plants. However, because of the restricted number of currently known fossil phytolith assemblages from the Cenozoic, in particular from Asia and Europe, we only have a rudimentary understanding of Miocene grass communities in this climatically complex part of the world. Therefore, it remains to be tested whether the observed differences between these remote regions is instead due to local environmental or taphonomic variation.

5 Conclusions

Preliminary analysis of phytolith assemblages from the Shanwang Formation indicates that the near lakeshore vegetation contained abundant dicotyledonous trees and rare palms. Open-habitat grasses from the Pooideae and the PACCAD clade were also diverse and abundant in these local habitats, whereas BE or basal grasses were less frequent. The abundance of open-habitat grasses suggests open patches in the wooded vegetation, either on better-drained soils or water-logged areas at the lake margin (e. g., giant reed).

Comparison between Miocene lacustrine phytolith assemblages from Shanwang, Turkey, and the Great Plains of North America indicates biogeographical differences in grass communities between eastern and western Eurasia, but the data are still too scarce for rigorous analysis. Future research will seek to expand the Miocene phytolith dataset in Eurasia to get a fuller understanding of the function of grasses in Cenozoic ecosystems of China, as well as potential biogeographic differences in grass communities. In particular, we hope to focus our sampling on localities thought to represent arid, grass-dominated habitats, to investigate the role that pooids and PACCAD grasses played in the expansion of open, arid-land vegetation that characterize the Neogene of eastern Asia.

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