

## Palaeoecological and palaeoenvironmental significance of some important spores and micro-algae in Quaternary deposits

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Spores of ferns and allied plants, and micro-algae frequently occur in abundance in Quaternary deposits, but their palaeoenvironmental significance is seldom evaluated. This paper presents morphological descriptions of spores of *Selaginella sinensis* (Desv.) Spring, 1843 (Selaginellaceae) and *Ceratopteris* cf. *thalictroides* (L.) Brongniart, 1821 (Parkeriaceae) and the algae *Pediastrum boryanum* (Turpin) Meneghini, 1840, *P. simplex* Meyen, 1829, *P. integrum* Nägeli, 1849 (all Hydrodictyaceae), *Spiniferites* Mantell, 1850, emend. Sarjeant, 1970 (Spiniferitaceae) and *Concentricystes* Rossignol, 1962, emend. Jiabo, 1978 (systematic position unclear), and discusses their occurrence in mostly Quaternary sedimentary successions. All are closely associated with aquatic habitats. Extant *Selaginella sinensis* often colonizes fairly wet hillsides and gaps between rocks, and shady sides of ravines and slopes; it is also found within thickets of trees and shrubs (boscages) and in forests with calcareous soils. *Ceratopteris thalictroides*, *Pediastrum* and *Concentricystes* inhabit freshwater lakes and both natural and artificial wetlands, such as paddy fields and ditches. *Spiniferites* is a salt-water genus and usually associated with the marine realm. Fossil and subfossil representatives of all of these taxa can be useful proxies of biodiversity and, therefore, also important for determining environmental conditions during the Quaternary period.

**pteridophyte spores, micro-algae, hydrophytes, lakes, wetlands, Quaternary deposits**

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Abundant pteridophyte spores and algal palynomorphs (micro-algae) occur frequently in Quaternary deposits owing to their wide distribution. Although ferns and allied plants may be found in habitats that vary considerably in temperature, amount of precipitation received and soil composition, they are usually most numerous and diverse in warm, shady, humid environments and, as a result, are commonly key elements of understorey herbs in forests. It has been

demonstrated on many occasions in the past that the distribution of spores of pteridophytes that are preserved in sediments and sedimentary rocks can indicate the palaeoecology of their parent plants. Most algae are aquatic. Many occur in fresh and brackish habitats, such as species of *Pediastrum* in freshwater lakes, as well as in salt water, such as *Spiniferites* offshore in the marine realm. In a recent palynological study on lake sediments from drill cores on the Tibetan plateau, we found *Pediastrum* in freshwater to slightly brackish sediments, species compositions altering

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according to locality and varying depositional conditions. In addition, species richness and abundance of this genus varies with depth of water and even in different cores from the same lake; thus, both can be indicative of past aquatic-ecosystem changes.

The significance of pteridophyte spores and micro-algae in palaeoclimatic and palaeoecological reconstructions of Quaternary sedimentary successions has been generally under-evaluated hitherto, despite their frequent occurrence in deposits of this age. The reasons for this are unclear, but may include identification problems or unrecognized types of, for example, meadow or marsh vegetation. By not taking into account their occurrence, palaeoenvironmental conclusions drawn mainly on the basis of the angiosperm pollen record may not be as accurate as they might have been had this information been taken into account. Since many studies of pre-Quaternary sediments have shown that some pteridophyte spores can be useful indicators of environmental changes through time, there is no reason why their occurrence in Quaternary successions should not prove equally useful.

For example, fossil spores of the extant species *Selaginella sinensis* have been recorded from the Zhoukoudian site of ape man in the Beijing area of China, indicating a warm climate. This determination is at variance with previous interpretations of cold, damp conditions because *S. sinensis* spores were incorrectly identified as *Botrychium* or *Pteris*. Kong et al. [1] corrected these mistakes and interpreted the occurrence of *S. sinensis* to indicate not only a warm but also a generally dry climate.

Our current palynological investigation of Holocene deposits at Anxin in northern China has revealed that *Ceratopteris* cf. *thalictroides* is richly represented. However, the modern distribution of this species is limited to the south of

the Huaihe and Yangtze rivers in eastern China, which is a subtropical region. Hence, the subfossil record indicates that conditions at Anxin were warmer and more humid during the Holocene than they are now.

Zhu et al. [2] and Wang et al. [3–5] reported fossil and subfossil algae in eastern China during the 1970s and 1980s, and Mao et al. [6] recently evaluated the potential significance of abundant pteridophyte spore and micro-algal records from deltaic sediments of the Yangtze River recovered by drilling into early Holocene deposits at Fengxian in Shanghai. However, because of limited work on the ecology of many extant pteridophytes and micro-algae and the relationship between their occurrence and the deposition of their spores and other remains in sediments, palaeoecological and palaeoenvironmental determinations have been limited to a very few situations or have merely focused on arbitrarily selected species.

In this paper we present morphological descriptions and data on, and the palaeoecological significance of, fossil and subfossil remains of seven types of spores and micro-algae in China in a geological context (location, epoch and distribution) in order to refine Quaternary biological proxies and improve palaeoecological and palaeoenvironmental interpretation.

## 1 Fossil and subfossil spores and micro-algae, and their morphological description

We summarize below the fossil and subfossil records of spores of two pteridophyte species and remains of five types of micro-algae based on both published and our own, recently acquired data. The material reviewed and examined is from many parts of China, as shown in Table 1, which

**Table 1** Data on fossil and subfossil spores of *Selaginella sinensis* and *Ceratopteris*, and of the algae *Pediastrum* (three species), *Spiniferites* and *Concentricystes*

Fossil-subfossil	Location	<sup>14</sup> C date (cal ka BP) or geological epoch	Reference
<i>Selaginella sinensis</i>	Fula'erji in Heilongjiang	late Cenozoic	[7]
	Qian'an in Jilin	late Tertiary	[8]
	Hohhot, Gu'aohan in Inner Mongolia	Holocene	[9]
	Daqingshan in Inner Mongolia	7.5–6.2	[10]
	Xinglongwa in Inner Mongolia	8.3–8.1	[11]
	Chifeng in Inner Mongolia	8.9–6.8	[11]
	Qarhan Salt Lake, Tsaidam Basin in Qinghai	33.0–28.7	[12]
	Qinghai lake	Holocene	[13]
	Zhoukoudian in Beijing	Pleistocene, Holocene	[1]
	Fenzhuang in Beijing	Holocene	[14]
	Beijing	late Tertiary–Holocene	[15]
	West coast of Bohai Bay	Holocene	[16]
	Dalianhuapao in Dalian	1.8	[17]
	Baiyangdian in Hebei	Holocene	[18]
	Anxin in Hebei	Pleistocene	This paper
	Coast of Qingdao in Shangdong	Holocene	[19]
	Linyi in Shandong	Holocene	
	Mianyang in Sichuan	Holocene	
	Xinghua in Jiangsu	Pleistocene	This paper
Lianyungang in Jiangsu	Holocene		

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Fossil-subfossil	Location	<sup>14</sup> C date (cal ka BP) or geological epoch	Reference
<i>Ceratopteris cf. thalictroides</i>	Xinglongwa in Inner Mongolia	7.47–6.90	[11]
	Yanqin, Shunyi in Beijing	8.1–5.7	[10]
	Tangu, Jinghai, Beitang in Tianjin	8.1–5.7	[10]
	Anxin in Hebei	Pleistocene–Holocene	This paper
	Huanghua in Hebei	Holocene	[10]
	Baiyangdian in Hebei	8.1–6.8	[18,20]
	Mengcun in Hebei	8.9–5.7	[10]
	Shenxian, Jingxian, Renxian in Hebei	8.9–3.3	[10]
	Heilonghong, Cangzhou in Hebei	8.9	[10]
	Hills of Jibei, Guanzhong Plain in Hebei	8.3–5.7	[11]
	Bohai Bay in Hebei	8.9–5.7	[21]
	Continental shelf of East China Sea, coast of Bohai in Hebei	late Tertiary	[22]
	Zhengzhou in Henan	Holocene	This paper
	Xinzheng Jiahu, Dazhengzhuang in Henan	8.9–5.7	[10]
	Peiligang in Henan	8.9–8.1	[10]
	Coast of Qingdao in Shandong	8.9–5.7	[10]
	Nansihu, Cuixian, Humin in Shandong	8.9–5.7	[10]
	Yellow River Delta	8.3–5.7	[10]
	Jiaozhou Bay in Shandong	Holocene	[23]
	Rizhao in Shandong	8.7–5.7	[10]
	Wangyin in Yanzhou, Shandong	5.7	[10]
	Linyi in Shandong	Holocene	This paper
	Tancheng in Shandong	5.9	[10]
	Congyang in Anhui	8.9	[24]
	Lüsi in Jiangsu	Holocene	
	Xinghua and Taizhou in Jiangsu	Pleistocene	This paper
	Guangfulin, Chongming Island in Shanghai	Holocene	
	Fengxian in Shanghai	Holocene	[6]
	Hemudu, Yuyao, Linshan in Zhejiang	Holocene	This paper
	Baohuashan, Nanjing in Jiangsu	5.8	[25]
	Basin of southern Yellow Sea	Pleistocene, late Tertiary	[26]
	Leizhou Peninsula in Guangdong	Pleistocene, late Tertiary	[27]
	Continental shelf, northern South China Sea	late Tertiary	[28]
<i>Pediastrum</i> spp.	Fula'erji in Heilongjiang	late Cenozoic	[7]
	Qian'an in Jilin	late Tertiary	[8]
	Yinming River, Hunlunbuir in Inner Mongolia	5.2	[9]
	Anxin in Hebei	Holocene	This paper
	Duantouliang, Tengger Desert	Late Pleistocene	[29]
	Shallow lake, Badanjilin Desert	Late Pleistocene	[29]
	Qarhan Salt Lake, Qaidam Basin in Qinghai	33.0–28.7	[12]
	Eastern Qaidam Basin in Qinghai	37.8–21.5	[30]
	Hurleg Lake in Qinghai	10.8–0.1	[31]
	Nam Co in Tibet	17.8–10.96	This paper
	Gongzhu Co in Tibet	Holocene	
	Pumoyum Co in Tibet	19.0–0.5	[32]
	Ahung Co, Co Ngion in Tibet	8.3–1.8; 6.3–1.8	[33]
	La'ang Co in Tibet	Holocene	This paper
	Ren Co in Tibet	8.5–6.0	[34]
	Hidden Lake in Tibet	14.0–0.5	[33]
	Zigetang Lake in Tibet	Holocene	[35]
	Tanggulashan (Tgsh) Co in Tibet	4.3–38	[33]
	Yidun Glacial Lake in Sichuan	11.0–0.5	[34]
	Wulungu Lake in Xinjiang	9.55–3.62	[36,37]
	Bosten Lake in Xinjiang	8.0–0.1	[38]
Kuming Lake in Beijing	(1750–1960 AD)	[15]	

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Fossil-subfossil	Location	<sup>14</sup> C date (cal ka BP) or geological epoch	Reference
<i>Pediastrum</i> spp.	Qian'an in Hebei	8.3–6.8	[20]
	Anxin in Hebei	Pleistocene–Holocene	This paper
	Peat layer on continental shelf of East China Sea, Yellow Sea	Late Pleistocene	[39]
	Guangfulin, Chongming Island in Shanghai	Holocene	This paper
	Taizhou, Lüsi, Xinhua in Jiangsu	Pleistocene, Holocene	
	Fengxian in Shanghai	Holocene	[6]
	Yangchenghu in Jiangsu	Late Pleistocene	[39]
	Yangtze River Delta	Recent	[40]
	Xihu, Ningbo in Zhejiang	Late Pleistocene, Holocene	[40]
	Hemudu, Yuyao, Linshan in Zhejiang	Holocene	This paper
	Dianchi in Yunnan	Holocene	[41]
	Shuangchi Maar Lake, Hainan Island	1.7–0.7	[42]
Huguangyan Maar Lake in Guangdong	4.5	[43]	
#7 core, continental shelf, South China Sea	Late Pleistocene	[39]	
<i>Spiniferites</i>	Basin of South Yellow Sea	Pleistocene, late Tertiary	[44,26]
	Coast of Bohai, Longjin Basin on the continent shelf, East China Sea	late Tertiary	[45,46]
	Continental shelf, East China Sea	Cenozoic	[47,48]
	Dongying in Shandong	Late Pleistocene	[49]
	Continental shelf, north South China Sea	late Tertiary	[28]
	Lianyungang, Lüsi in Jiangsu	Holocene	This paper
	Taizhou, Xinghua in Jiangsu	Late Pleistocene	
	Fengxian in Shanghai	Holocene	[6]
	Baiyangdian in Hebei	Holocene	This paper
	Guangfulin, Chongming Island in Shanghai	Holocene	
Hemudu, Yuyao, Linshan in Zhejiang	Holocene		
<i>Concentricystes</i>	Mudanjiang in Helongjiang	Holocene	This paper
	Liaoning, Shandong and Bohai	Tertiary	[45]
	Tianjin, Shandong (Dongying Formation), Bohai (Minghuazhen Formation)	Tertiary	[47]
	Loess Plateau	Late Pleistocene	[50]
	Anxin in Hebei	Pleistocene	This paper
	Linyi in Shandong	Holocene	
	Hefei in Anhui	Holocene	[25]
	Lianyungang, Lüsi in Jiangsu	Holocene	This paper
	Taizhou, Xinghua in Jiangsu	Late Pleistocene	
	Nantong in Jiangsu	Pleistocene	[51]
	Tailake in Jiangsu	Holocene	[40]
	Ducunin Jiangsu	Holocene	[52]
	Yangtze River Delta	Modern sediment	[40]
	Jinshan, Fengxian in Shanghai	Holocene	[3,6]
	Hemudu, Yuyao, Linshan in Zhejiang	Holocene	This paper
	Baiyangdian in Hebei	Holocene	
	Chongqing	Holocene	
	Hanzhou Bay in Zhejiang	Pleistocene, Holocene	[5]
	Coasts of Yellow Sea and East China Sea	Late Pleistocene	[53,39]
	Ningbo in Zhejiang	Holocene	[53]
	Xishanxiyaohu, Lushan in Jiangxi	Holocene	[54]
	Nanyang in Henan	Holocene	This paper
	Mianyang in Sichuan, Chongqing	Holocene	
	Jinjiang in Fujian	Holocene	[5]
	Dianchi in Yunnan	Modern sediment	[41]
	Foshan in Guangdong	Holocene	This paper
	Beibu Gulf in Guangxi	Pleistocene	[28]
Hong Kong	Late Pleistocene	[55]	
Houhai, Shenzhen in Guangdong	Late Pleistocene	[56]	
Sunda Shelf, South China Sea	16.5	[57]	
Jilin	Holocene	[58]	

provides information on locality, age, and source of data.

### 1.1 *Selaginella sinensis* (Desv.) Spring, 1843

In China, spores of *Selaginella* have been reported from late Cretaceous deposits in the Beijing area, but the earliest records of the products of *Selaginella sinensis* date back to the late Tertiary–Quaternary [14] in the form of specimens from Pliocene sandstone at Qian'an in Jilin and the Middle Pleistocene at Fula'erji in Heilongjiang [7, 8]. They have been recorded frequently from sediments of Pleistocene and/or Holocene age at Anxin in Hebei, Linyi in Shandong, Xinhua and Lianyungang in Jiangsu, and Mianyang in Sichuan (Table 1) during our recent palynological investigations (Figure 1).

Spores of *Selaginella sinensis* recovered during our study of Pleistocene and Holocene deposits show morphological consistency. They are rounded triangular to sub-circular in polar view, oblong in equatorial view, and ca. 33.3–41.1  $\mu\text{m}$  in maximum diameter. A somewhat meandering trilete suture extends almost to the equator. The exine is thin and sculptured with verrucae. The irregular trilete mark, which lacks a margo, and comparatively large verrucae distinguish the spores of this species from those of *Pteris* and *Botrychium* (e.g. *Botrychium lunaria* (L.) Sw.), which are otherwise similar [58].

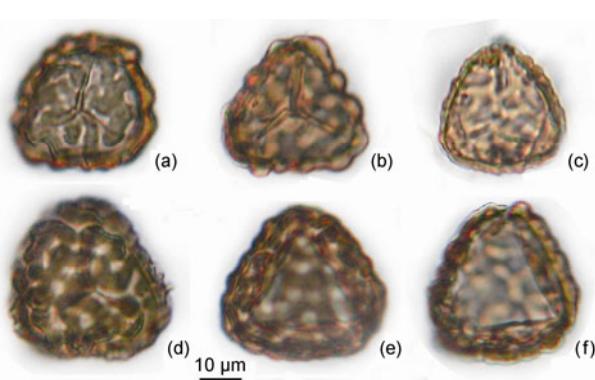
*Selaginella sinensis* is a perennial lycopsid and endemic to China. Its habitat is often fairly wet hillsides and gaps between rocks, shady sides of ravines and slopes, and within thickets of trees and shrubs (boscages) and forests with calcareous soils [59]. The genus *Selaginella* is widely distributed throughout the world, but in China it is mainly associated with temperate forests, forest-steppe and steppe areas to the north of the Yangtze River.

### 1.2 *Ceratopteris* cf. *thalictroides* (L.) Brongniart, 1821

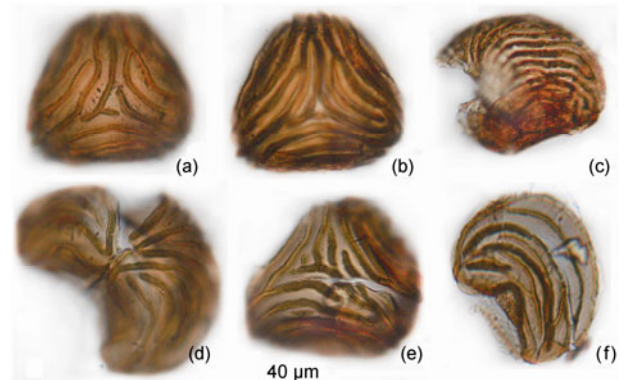
In our study, spores of *Ceratopteris* cf. *thalictroides* have been found in Holocene deposits at Hemudu, Yuyao and

Linshan in Zhejiang, Guangfulin, Fengxian and Chongming Island in Shanghai, and Linyi in Shandong, and in Pleistocene and Holocene deposits at Anxin in Hebei, and Taizhou and Lüsü in Jiangsu (Table 1). Fossil-subfossil spores of *Ceratopteris* cf. *thalictroides* are also well documented from some other localities (e.g. Kong et al. [10,11]; see Table 1). They are very similar to the spores of extant *C. thalictroides* in being large (ca. 95–162.5  $\mu\text{m}$  in maximum diameter), trilete and rounded triangular to sub-circular in polar view with a strongly convex distal surface. The laesurae of the trilete mark extend to approximately two-thirds of the radius of the spore. The exine is ca. 4.8  $\mu\text{m}$  thick and consists of two-layers; the outer layer is the thicker of the two and distinctly murornate. There are up to 6–7 muri on the distal surface arranged approximately parallel to the sides of the spore, but no more than 3–4 on each side of the trilete suture on the proximal face (Figure 2).

Fossil spores of *Ceratopteris* cf. *thalictroides* that have been recorded from late Tertiary deposits have commonly been referred to *Magnastriatites* and also sometimes to *Cicatricosisporites*, species of which are often especially numerous in early Cretaceous deposits in many parts of the world, but which also occur in younger Cretaceous and Tertiary strata [15,60–62]. These two genera are generally easy to distinguish and have different familial origins, with *Cicatricosisporites* representing the families Schizaeaceae and Pteridaceae and *Magnastriatites* referable to the Parkeriaceae. The latter genus was erected by Germeraad et al. [63] from mid Tertiary deposits in Colombia and has been found in early Oligocene–Pliocene strata there and in China, Nigeria, Indonesia and India. In China, the earliest fossil records of spores of *Ceratopteris* cf. *thalictroides* have been attributed to species of *Magnastriatites* in late Tertiary sediments in many regions [22,26,28,44,45,64], such as *M. howardii* Germeraad, Hopping and Muller in the middle part of the Longjing Formation in the continental-shelf basin of the East China Sea, *M. granulastriatatus* Li and *M. minutus* Li from the Longjing through to the Yuquan formations of later Tertiary age [47] and *M. leizhouensis*



**Figure 1** Fossil-subfossil spores of *Selaginella sinensis* (Desv.) Spring, 1843. (a)–(c) Pleistocene, Anxin in Hebei; (d)–(f) Holocene, Linyi in Shandong.



**Figure 2** Fossil-subfossil spores of *Ceratopteris* cf. *thalictroides* (L.) Brongniart, 1821. (a)–(c) Pleistocene, Anxin in Hebei; (d)–(f) Holocene, Linyi in Shandong.

Zhang in the late Miocene Weizhou Formation on the continental shelf of the northern South China Sea.

Both *Ceratopteris* cf. *thalictroides* and *Magnastriatites* are, therefore, classified in the pteridophyte family Parkeriaceae. Modern *Ceratopteris thalictroides* is an aquatic fern that is commonly found in ponds, paddy fields and ditches. In China it is widely distributed in Guangdong, Taiwan, Fujian, Jiangsu, Zhejiang, Anhui, Hubei, Sichuan, Guangxi and Yunan [65]. It also occurs in tropical and subtropical regions of Africa, Europe and other parts of Asia.

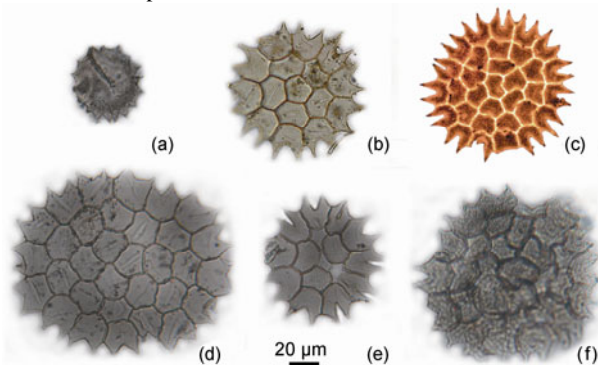
### 1.3 *Pediastrum boryanum* (Turpin) Meneghini, 1840

The earliest fossil record of *Pediastrum boryanum* is from the Cretaceous in Europe [66,67]. The oldest variety of this species to have been reported from China is *P. boryanum* var. *undulatum* Wille, 1879 from the Shahejie Formation in the Bohai area, which was dated as early Eocene–late Oligocene [46]. *Pediastrum boryanum* has also been recorded from Early Pleistocene sediments at Fula'erji in Heilongjiang [7]. Our records of this species come from Holocene sediments at Yuyao, Hemudu and Linshan in Zhejiang, Guangfulin, Fengxian and Chongming Island in Shanghai, and Pleistocene deposits at Taizhou and Lüsi in Jiangsu, and Anxin in Hebei (Table 1).

The coenobia of *P. boryanum* are disc-shaped oval or circular in outline, usually with 16–64 cells but sometimes comprising as many as 256. The cells are irregular, 5–6-sided polygons that are closely arranged, typically in 2–4 concentric circles. Marginal cells have two lobes that are ca. 2–10  $\mu\text{m}$  in length. These are in the plane of the coenobium and separated from each other by U- or V-shaped invaginations. They become narrower outwards and have pointed tips. The cell wall is regularly granular. The coenobia and cells are usually ca. 50–160  $\mu\text{m}$  and ca. 10–30  $\mu\text{m}$  in maximum diameter, respectively (Figure 3).

### 1.4 *Pediastrum simplex* Meyen, 1829

*Pediastrum simplex* has been found in Holocene sediments



**Figure 3** Fossil-subfossil *Pediastrum boryanum* (Turpin) Meneghini, 1840. (a) Pleistocene–Holocene, Anxin in Hebei; (b), (d), (e) Pleistocene–Holocene, Nam Co in Tibet; (c) Holocene, Ahung Co in Tibet; (f) Holocene, Gongzhu Co in Tibet.

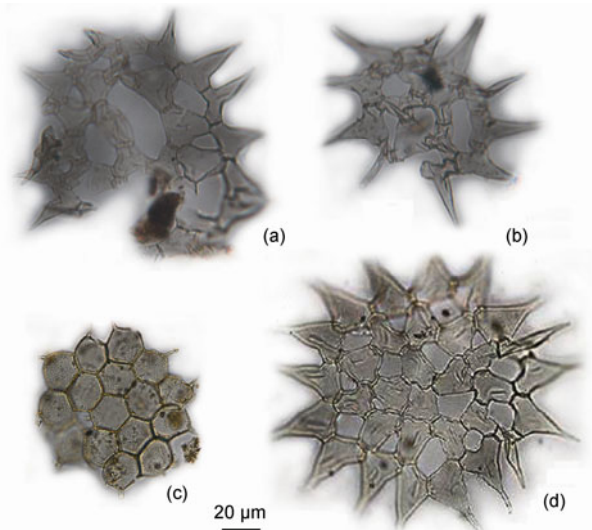
at Lüsi in Jiangsu, and Yuyao, Hemudu and Linshan in Zhejiang, Guangfulin, Fengxian and Chongming Island in Shanghai; in Pleistocene sediments at Taizhou and Lüsi in Jiangsu and Anxin in Hebei; and in Pleistocene–Holocene deposits in Ahung Co, Tanggula Shan (Tglsh) Co, La'ang Co, Gongzhu Co and Nam Co in Tibet, and Yidun Glacial Lake in Sichuan (Table 1).

The coenobia of the specimens examined consist of 18–56 cells that are commonly partly separated by intercellular spaces. The inner cells are irregular, 5–6-sided polygons. The marginal cells have one narrowing lobe (Figure 4). In other respects, the morphology of this species is closely comparable to that of *P. boryanum*.

### 1.5 *Pediastrum integrum* Nägeli, 1849

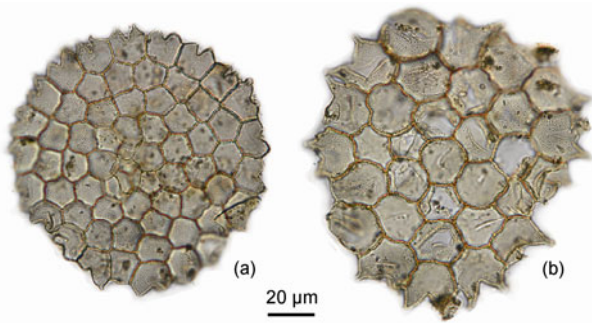
Specimens of *Pediastrum integrum* were collected from Pleistocene–Holocene deposits in Nam Co and La'ang Co, Tibet (Table 1). The coenobia of those examined comprise 32–64 cells that, as for *P. boryanum*, are all connected, i.e. there are no intercellular spaces. The inner cells are irregular, 5–6-sided polygons. The marginal cells extend into two short lobes that are separated by only a shallow indentation. The cell wall is regularly granular. The dimensions of the cells are ca. 12–18  $\mu\text{m}$  and the maximum diameter of the coenobium is 120  $\mu\text{m}$  (Figure 5).

Other species of fossil *Pediastrum* have also been found in Chinese sediments. For example, in addition to *P. boryanum* and *P. simplex*, *P. duplex* Meyen has been recovered from Holocene sediments of Shuangchi Maar Lake on Hainan Island [68]. Zhang et al. [39] found specimens of *P. simplex*, *P. duplex*, *P. boryanum*, *P. kawraiskyi* Schmidle, *P. biradiatum* Meyen, *P. integrum*, *P. mulicum* Kuetz, *P. clathratum* (Schröder) Lemmermann and *P. araneosum*



**Figure 4** Fossil-subfossil *Pediastrum simplex* Meyen, 1829. (a) Holocene, Anxin in Hebei; (b) Holocene, Lüsi in Jiangsu; (c) Pleistocene–Holocene, Nam Co in Tibet; (d) Holocene, Fengxian in Shanghai.





**Figure 5** *P. integrum* Nägeli, 1849. (a), (b) Pleistocene-Holocene, Nam Co in Tibet.

(Racib.) Smith in drill core No.7 on the continental shelf of the South China Sea. Further afield, among other records of *Pediastrum*, Zamalao and Tell [69] reported several species of different ages from South America: the oldest, *P. boryanum* var. *boryanum*, was recorded from late Cretaceous deposits of Rio Guaco, Venezuela; *P. tetras* (Ehrenberg) Ralfs from early Eocene deposits of Cerro La Huitrera, Argentina; and *P. boryanum* var. *brevicornis* Braun, *P. boryanum* var. *longicornis* Reinsch, *P. duplex*, *P. integrum*, *P. kawraiskyi*, *P. leonensis* Tell and Zamalao, *P. mustersii* Tell and Mataloni and *P. simplex* from Miocene sediments of Monte Leon, Argentina.

### 1.6 *Spiniferites* Mantell, 1850, emend. Sarjeant, 1970

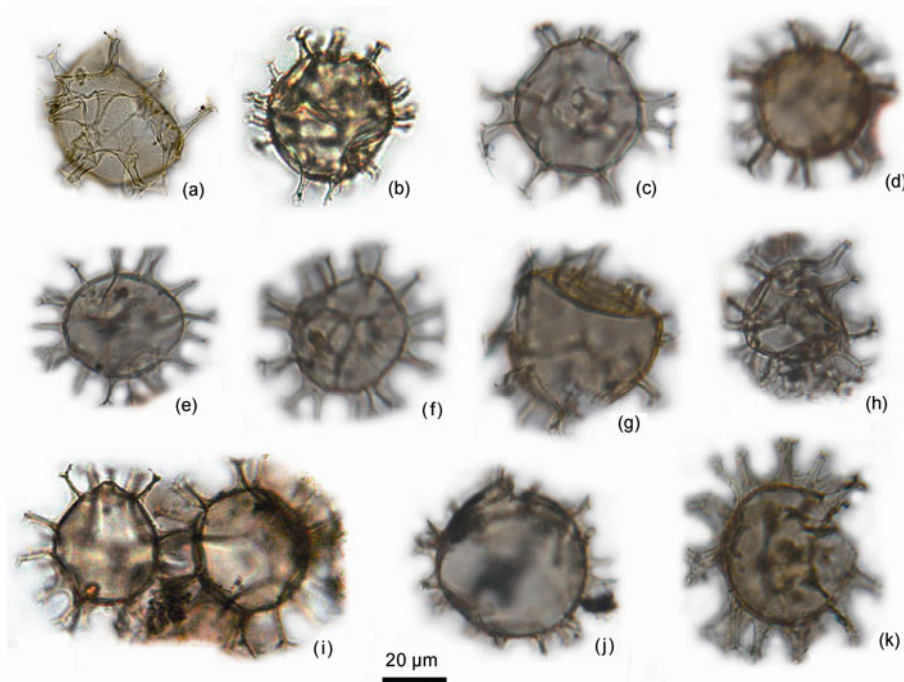
Fossil-subfossil micro-algae referred to *Spiniferites* were not identified to species in this study. The genus is known from the Cretaceous Period onwards in many parts of the

world, e.g. [70], almost all representatives clearly indicating a marine environment. In China, they have been recovered from Holocene and/or Pleistocene sediments at Hemudu, Linshan and Yuyao in Zhejiang, Guangfulin, Fengxian and Chongming Island in Shanghai, and Lüsi, Taizhou, Lian-yungang and Xinghua in Jiangsu, and are also well documented elsewhere (e.g. Zhu, 2004 [49]; Table 1).

*Spiniferites* is a spiniferate, chorate cyst with both sutural and gonal processes that delineate a paratabulation which reflects the tabulation of the living dinoflagellate. Many of the processes have broad bases and bifid or trifid terminations. The archeopyle is precingular. The dimensions of the cyst excluding the processes of the specimens examined are generally in the region of 30–40 µm (Figure 6).

Before the mid 1960s, spinose micro-algae of the same morphology were identified as *Hystrochosphaera*, but the research of Evitt [66], Rossignol [71] and others proved that these supposed fossil dinoflagellates were cysts and not the remains of motile thecae; hence, micro-algae with demonstrably dinoflagellate characters that had been described as “hystrochospheres” were considered to be dinoflagellate cysts and those lacking such characters were termed ‘acritarchs’. For most of the time since then *Hystrochosphaera* has been regarded as a synonym of *Spiniferites*.

Around ten species of *Spiniferites* have been reported from the lower part of the Longjin Basin on the continental shelf of the East China Sea. Frequently occurring in Early Pleistocene deposits, they include *S. bentorii* (Rossignol) Wall and Dale, *S. cf. bulloides* (Deflandre and Cookson) Sarjeant, *S. cingulatus* var. *spinatus* Song, *S. cf. hyperacanthus* (Deflandre and Cookson) Cookson and Eisenack,



**Figure 6** Fossil-subfossil *Spiniferites*. (a) Holocene, Fengxian in Shanghai; (b), (i) Pleistocene, Lianyungang in Jiangsu; (c), (g) Holocene, Guangfulin in Shanghai; (d)–(f), (j) Holocene, Lüsi in Jiangsu; (h), (k) Holocene, Hemudu in Zhejiang.

*S. membranaceus* (Rossignol) Sarjeant, *S. nodosus* (Wall) Sarjeant and *S. ramosus* (Ehrenberg) Mantell, the identifications being based on general morphology and size, and the dimensions and morphology of the processes [44–47]. Yu [48] and Zhu [49] reported *S. bentorii* subsp. *truncatus* (Rossignol) Lentin and Williams, 1973, from early Eocene deposits in the upper Oujiang and lower Wenzhou formations in the continental-shelf basin of the East China Sea. *Spiniferites bentorii* has also been reported from the Eocene–early Oligocene Shahejie Formation on the Bohai coast: these are among the earliest fossil records of Chinese *Spiniferites*.

### 1.7 *Concentricystes* Rossignol, 1962, emend. Jiabo, 1978

The body of fossil-subfossil *Concentricystes* is subcircular

or oval in polar view and may separate into two parts along the equator. Both parts are sculptured with narrow muri, most of which are orientated parallel to the equator so that they appear as essentially concentric rings, but at varying distances towards the poles they have a more broken appearance, reminiscent of a finger print (Figure 7). A thin outer membrane may also be present.

*Concentricystes* is of unclear systematic position. Wolff first recorded it from Pliocene lignite in Germany as *Sporites* [72]. It was described as *Sporites circulus* by Downie et al. [73] but later renamed by Rossignol [74] as *Concentricystes rubinus*. Rossignol treated *Concentricystes* as a freshwater alga and found abundant representatives in the bed of Wadi Kutin in Israel and in Quaternary alluvial deposits in North America and Australia [71]. Spores of *Trachelomonas onulifera* (Fritsch and Rich) Huberpestalozzyi and *T. stokesiana* Palmer of the flagellate aquatic-algal



**Figure 7** Fossil-subfossil *Concentricystes* Rossignol 1962, emend. Jiabo, 1978. (a)–(c) Pleistocene–Holocene, Anxin in Hebei; (d), (k), (l) Pleistocene–Holocene, Lianyungang in Jiangsu; (e) Pleistocene–Holocene, Taizhou in Jiangsu; (f) Holocene, Foshan in Guangdong; (g), (m), (q) Holocene, Nanyang in Henan; (h), (i) Holocene, Hemudu in Zhejiang; (j) Holocene, Linyi in Shandong; (n) Holocene, Lüsi in Jiangsu; (o), (p) Holocene, Fengxian in Shanghai; (r) Holocene in Chongqing ((r-1), (r-2) different views).



phylum Euglenophyta have an annular ornamentation similar to that of *Concentricystes* [46], but a systematic relationship between these taxa is unproven. Wu et al. [56] reported similar specimens from upper-Mid Pleistocene peat at Houhai, Shenzhen in Guangdong and identified them as *Trachelomonas* sp. Also similar are the specimens identified as *Pseudoschizaea* sp. by Medanic [75]. These were reported from coastal peat and lagoonal sediments in Rio Grande, Brazil.

Species of *Concentricystes* have been based on the presence or absence of a thin outer membrane and the structure of the ornament. In China, they include *Concentricystes membranaceus* Jiabo and *C. panshanensis* Jiabo [45,47], the former from late Tertiary deposits in Liaoning, Shandong and Bohai [45], and the latter from early Tertiary beds in the southern suburbs of Tianjin and the Dongying Formation in Shandong, and from the Minghuazhen Formation of late Tertiary age in Bohai [47].

*Concentricystes* occurs frequently in Quaternary lacustrine deposits, e.g. in Pleistocene lake muds at Yuanrangshanxia village, Dongyong, Dapu and Qingshuidao in Hong Kong [55]; Late Pleistocene peat at Houhai, Shenzhen in Guangdong [56]; Pleistocene–Holocene lacustrine sediments at Duncuo in Jiangsu [52]; Holocene sediments in the Mudanjiang area of Heilongjiang; Early Pleistocene deposits in Jilin [58]; and Holocene peat in Haidian, Beijing [76], but it has rarely been found in northwestern China and Tibet. Fossil-subfossil records in our study are from Pleistocene and Holocene deposits on the delta of the Yangtze River and Lianyungang and Lüsi in Jiangsu; the Pleistocene of Taizhou and Xinghua in Jiangsu; the Holocene of Chongming Island in Shanghai; and the Pleistocene and Holocene of Anxin in Hebei (Table 1).

## 2 Results and discussion

### 2.1 *Selaginella sinensis* indicating an understory component of forests in a warm, humid climate

In addition to the records of *Selaginella sinensis* from the Mid Pleistocene site of Beijing ape man at Zhoukoudian [1] and other Tertiary–Quaternary localities mentioned above, this species has also been found at the Palaeolithic site of Zhaowudameng Aohanqi in the Inner Mongolia Autonomous Region [9], and in the Pleistocene of Qarhan Salt Lake in the Qaidam Basin [12] and the Holocene of the Qingdao coast [38]. However, as noted in the introduction, the occurrence of spores of this species (along with the other taxa we discuss) and, hence, their stratigraphic and palaeoenvironmental significance, are often ignored in Quaternary pollen analyses. We attempt to remedy this situation here.

According to the Flora of China [65], the northernmost occurrence of *Selaginella sinensis* today is in the Daxing'an Mountain range (50.24°N, 124°E) and the southernmost is

in the Wudang Mountains (31.6°N, 113.8°E). This area of distribution has a mean annual temperature range of –2–15.6°C and 20.1–28°C, with an annual precipitation that ranges from ca. 473 to 988 mm. Hence, *S. sinensis* prefers a humid habitat and moderately high temperatures [59]. The westernmost occurrence of fossil-subfossil spores of *S. sinensis* is in the Qaidam Basin in Qinghai, the northernmost in Liaoning, the easternmost in Dalian and the south-easternmost in Ganyu. Thus, Pleistocene–Holocene spores of this species in Qinghai Lake and the Qaidam Basin (36°40'–37°10'N, 94°10'–95°10'E) indicate that the plant was distributed more widely in the past than it is today, namely 2° further north and 10° further west. This implies that the climate was significantly warmer and more humid than [59].

Spores of *Selaginella sinensis* account for 80.2% of the palynological assemblage from the Mid Pleistocene deposits of Zhoukoudian, indicating warm interglacial conditions [58]. Abundant pteridophyte spores have been reported in the Dalianhua profile at Dalian [17], with those of *S. sinensis* comprising an extremely high percentage (90%), indicating that the climate was warm and wet at around 1.7 cal. Ka BP. We have found abundant spores of this species in Pleistocene and Holocene lacustrine, wetland and tidal-flat deposits at Anxin in Hebei, Linyi in Shandong, and Xinghua and Lianyungang in Jiangsu. Hence, abundant spores of *S. sinensis* in sediments may be strongly associated with forest or forest-steppe vegetation, and linked mostly to warm, wet conditions.

### 2.2 *Ceratopteris* cf. *thalictroides* indicating a warm to hot, humid climate and lacustrine and fluvial sedimentary environments

During the late 1970s and early 1980s *Ceratopteris* cf. *thalictroides* was recorded (as *Magnastriatites*) from early Tertiary deposits of the Bohai Coast [46], the continental-shelf basin in the East China Sea [47] and the South Yellow Sea Basin [28], and from Pleistocene deposits on the Leizhou Peninsula [27].

*Ceratopteris* probably originated during the Late Eocene in tropical Asia and spread to other tropical regions during the Oligocene and also northwards later. Spores attributable to the genus have been recorded from deposits ranging in age from Oligocene to Quaternary in tropical regions [47], including the Caribbean, Nigeria and coastal Bay of Bengal. They have also been reported to occur frequently in sediments of late Tertiary–Quaternary age, but less commonly in early Tertiary deposits of the Bohai coast and Yangtze River Basin of eastern China.

As a monotype genus of Parkeriaceae, in common with the occurrence of the fossil-subfossil spores attributed to it, *Ceratopteris* is widely distributed in tropical and subtropical zones of the world. There are two species in China, namely *Ceratopteris thalictroides* and *C. pteridodes* (Hook) Hieron.

These are mainly found in the southern Yangtze River area, growing in ponds, marshes, paddy fields and ditches, often floating on the water. Warm, still water is obviously a suitable habitat. The northernmost occurrence of *Ceratopteris* in China today has been recorded from Nansi Lake in Shandong (34.5°N) according to biogeographic data on the genus [65]. Southernmost occurrences are in Yunnan and Hainan Island. However, palynological studies have shown that mid Holocene sites (ca. 8.9–5.9 cal ka BP) 1–6 degrees of latitude further north than the current distribution of the genus have yielded spores attributable to *C. cf. thalictroides*, the northernmost occurrences being in Yanqing (40.5°N) and Shunyi (40.1°N) in Beijing [10]. If temperature changes by 0.6°C per degree of latitude, as is generally accepted, it can be inferred that the annual mean temperature at these sites during the mid Holocene would have been 0.6–3.6°C higher than today, i.e. the climate of Hebei and Shandong was much warmer and wetter than it is now. We have recently found spores of *C. cf. thalictroides*, pollen of Cyperaceae and Typha, and freshwater algae indicative of a warmer and wetter climate than at present in Pleistocene–Holocene sediments in the Anxin and Baiyangdian areas. Another example is from the ruins of Wangyin in Yanzhou, Shandong: abundant spores of *C. cf. thalictroides* have been logged, indicating that the mean annual temperature of the Huanghuai area in central eastern China (i.e. between the Yellow and Huai rivers) was 2°C higher than at present and that large areas of lakes and bogs probably developed there [11]. The extremely rich assemblages of *C. cf. thalictroides* in deposits dated to 6.8 cal ka BP at Baiyangdian in Hebei [18] and to 5.9 cal ka BP at Tancheng in Shandong, indicate that the mean January temperature of the Haihe area at 5.9 cal ka BP was  $5 \pm 2^\circ\text{C}$ , which is  $9 \pm 2^\circ\text{C}$  higher than at present in Baoding, Hebei, and the mean January temperature at Tancheng in Shandong was  $3.5 \pm 1^\circ\text{C}$  higher than today [24, 25].

The occurrence of *C. cf. thalictroides* in early to mid Holocene (about 8.9–5.9 cal ka BP) deposits of the Haihe River Basin, the Yellow River Delta and the coast of Bohai Bay, as well as in the southern Yangtze River area where *Ceratopteris* still exists, has palaeoenvironmental significance [10]. The pollen assemblages are dominated by *Quercus*, *Ulmus* and *Betula*; however, several tropical and subtropical pollen types have been recovered from sediments dated at 8.3 to 5.7 cal ka BP in Haihe, the Yellow River Delta, Beijing, Tianjin, eastern Hebei, the Guanzhong plain and the northern Hebei hills, including *Fagus*, *Liquidambar*, *Carya* and *Ceratopteris* [16], probably indicating that the climate was fairly humid. Some pollen of trees, shrubs and other plants that inhabit the subtropics, such as *Quercus* (including evergreen type), *Symplocos*, *Myrica*, *Liquidambar*, *Ilex*, *Fagus*, *Ceratopteris* and *Pteris*, are indicative of vegetation that is transitional between temperate broadleaf forests and subtropical evergreen and deciduous broadleaf forests, linking it to a much warmer and wetter

climate than at present [21,23].

Numbers of *Ceratopteris* plants may increase abruptly when the water temperature and quality are suitable. Such increases have a significant impact on the ecology and hydrologic conditions of a lake. Therefore, the presence of *Ceratopteris* spores in sediments can be a valuable proxy of the depositional environment in lakes, bogs and other wetlands, and slow-moving rivers in a warm to hot, humid climate.

### 2.3 Abundance of *Pediastrum* indicating changes in lake water levels

Species of extant *Pediastrum* occur worldwide in still or slow-moving water bodies and typically occur in freshwater or slightly brackish lakes, ponds and river channels, especially in hard water [77]. Fossil occurrences are similarly world-wide. Those reported from marine sediments are usually attributable to transport by streams and rivers from non-marine environments into the marine realm, but they may also be present as a result of reworking of sediments during marine incursions.

Boudreau et al. [78] reported abundant specimens of *Pediastrum* and other freshwater algae in the sediments of Lake Temagami in northeastern Ontario, Canada, and interpreted warm conditions associated with the Holocene Hypsithermal climate that prevailed in the study area during 6.25–4.115 ka BP (uncalibrated  $^{14}\text{C}$  age) based on both pollen and algal data [78]. The palynomorph assemblage of *Pediastrum*, *Carpinus*, *Corylus* and *Alnus* in late interglacial deposits of the Baltic Sea, offshore Poland, indicates both a warm climate and a freshwater invasion into the marine realm [79]. A pollen analysis of Altiplano lake sediments in Bolivia consisting of interbedded lake muds and halite that accumulated during 90–21.5 cal ka BP reflects the alternating humid and arid conditions that are indicated by the sediments [80]. Remarkable fluctuations in the abundance of *Pediastrum* and the aquatic plant assemblage also indicate an arid environment dominated by salt deposition; however, humid conditions prevailed during 54–30.5 cal ka BP and the Last Glacial Maximum (LGM) and the period after that [80]. The freshwater algae *Pediastrum*, *Zygnema* and *Spirogyra* have been found in Holocene peat on the Rio Grande coastal plain, Brazil, indicating a lagoonal environment that was affected by marine transgressions and regressions [75]. In the Kerala Basin of western coastal India, an assemblage of *Pediastrum* and *Botryococcus* in Holocene sediments proved freshwater invasion and the development of lagoons [81]. In China, specimens of fossil and subfossil *Pediastrum* are commonly encountered in sediments from the very south of the country at Shuangchi Maar Lake on Hainan Island [42] and the continental shelf of the South China Sea [39] to the very north at Qian'an in Jilin [8] and Fula'erji in Heilongjiang [7]; from the bottom of the East China Sea [39] and the Yangtze Delta [6] to the alpine lakes

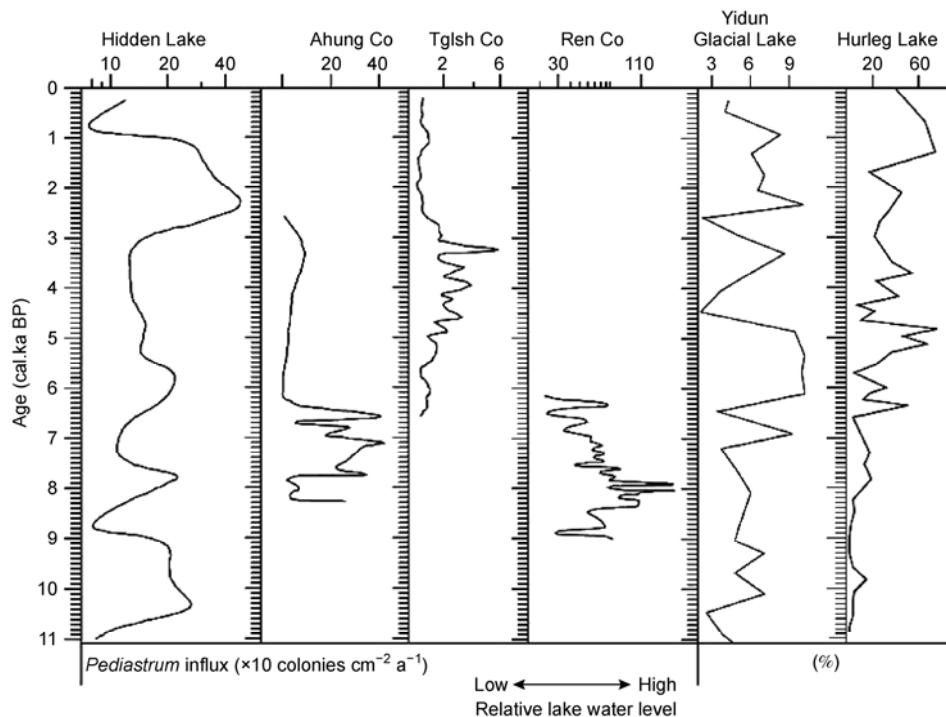
of the Tibetan Plateau [33,34], Wulungu Lake in Xinjiang [36, 37], and lakes in the Tengger Desert of Inner Mongolia [29].

Abundances and water-depth relationships of occurrences of living *Pediastrum* in shallow freshwater or slightly salty lakes on the Tibetan Plateau and in western China have been investigated. Colonies of this alga have been found to increase with increasing depth of water. In Hurleg Lake in the Qaidam Basin (maximum water depth 8.6 m), colonies gradually increased in number from depths of 0.6 m to 8 m, but were absent below 8 m [31]. Numbers of colonies in bottom-surface sediment from Dianchi Lake in Yunnan (water depth 6.5 m) dramatically increased from 2000 colonies g<sup>-1</sup> (gram of dried sediment) at a depth of 4.5 m to 10000 colonies/g at 6.4 m [41]. Chen et al. [38] did not find any, or encountered only a very few, *Pediastrum* colonies in shallow-water sediments of Bosten Lake in Xinjiang, whereas concentrations of this alga gradually increased with depth down to 10 m. For lakes that are less than 15 m deep [2], there seems to be a clear relationship between abundances in bottom-surface sediments and depth of water, which in turn can indicate changes in water level. Whether such a relationship is also apparent in deep lakes has yet to be investigated. In alpine lakes 20–90 m deep (e.g. Gongzhu Co, Mapeng Co, Beng Co, Mapangyon Co, Bangong Co), *Pediastrum* is commonly found in bottom-surface sediments. At least three species of *Pediastrum* have been found in such sediments in Nam Co and Pumoyon Co, which are more than 90 and 60 m deep respectively (Figures 5–7).

According to palynological records from Pleistocene–Holocene lake sediments of the Tibetan Plateau, quite a few

specimens of *Pediastrum* have been encountered, with especially high flux (colonies cm<sup>-2</sup> a<sup>-1</sup>: yearly abundance and accumulation rate per unit area) in the middle-late Holocene deposits [69]. *Pediastrum* flux during 8.5–6.0 cal ka BP in Ren Co and Ahung Co reached 300–2000 colonies cm<sup>-2</sup> a<sup>-1</sup>, and between 10.8–9.0 and 2.0–1.5 cal ka BP in Hidden Lake it reached 500–700 colonies cm<sup>-2</sup> a<sup>-1</sup>. In Tglsh Co *Pediastrum* peak values of 300–400 colonies cm<sup>-2</sup> a<sup>-1</sup> occurred after 4.2 cal ka BP [33,82], and flux peaks of 2000–2500 colonies cm<sup>-2</sup> a<sup>-1</sup> in Nam Co took place between 10.96–12.71 and 17.8 cal ka BP, respectively. In Hurleg Lake, Qaidam Basin, *Pediastrum* gradually increased to 76% of the palynomorph assemblage after 5.5 cal ka BP (Figure 8) [31] and in Wulungu Lake, Xinjiang, it reached 43.4% during 5.21–3.62 cal ka BP and 15.6%–43.3% between 9.55 and 7.74 cal ka BP [36,37]. In Shuangchi Maar Lake on Hainan Island and Huguangyan Maar Lake in Guangdong it reached 2000–6000 colonies g<sup>-1</sup> during 1.7–2.4 and 4.5 cal ka BP, respectively [42,43].

*Pediastrum* influx values in Tglsh Co and Ahung Co reached peak values of 60 colonies cm<sup>-2</sup> a<sup>-1</sup> during 4.5–3.0 cal ka BP and 400 colonies cm<sup>-2</sup> a<sup>-1</sup> during 7.8–6.5 cal ka BP, respectively (Figure 8). These coincide with the highest total pollen influx values, the Po/Ar (Poaceae/Artemisia) ratio and the highest percentage of Cyperaceae pollen [33,34]. The increasing pollen influx values suggest that monsoon rainfall in the vicinity of the lakes also increased at that time. However, there is no evidence of a change in the composition of the vegetation and carbonate δ<sup>18</sup>O values remain very low. This suggests that the lakes overflowed in



**Figure 8** *Pediastrum* influx values (colonies cm<sup>-2</sup> a<sup>-1</sup>) in Holocene sediments of alpine lakes, Tibet [31].

response to the higher rainfall [33]. In other lake sediments, increasing numbers of *Pediastrum* colonies also imply higher monsoon rainfall. Numbers of *Pediastrum* colonies in Shuangchi Maar Lake on Hainan Island dramatically increased during 2.4–1.8 cal ka BP. This was 5–8 times more than during the period 1.7–1.3 cal ka BP and is interpreted to reflect enhanced monsoon rainfall and an enlarged lake area [42]. In arid northwest China, numbers of *P. boryanum* in drill core CK2022 in Qarhan Saline Lake reached 14.8% during 31.8–25.6 ka BP, indicating that the lake water was fresher during this period than it had been previously [12]. In the Yimin Basin, Inner Mongolia Autonomous Region, the occurrence of *P. boryanum* in sediments dated to 4.5 ka BP showed that moisture levels were higher at that time than previously [9]. In the Duantouliang sedimentary succession in the Tengger Desert, *Pediastrum* averages 31.5% of the palynomorph assemblage between 28 and 30 cal ka BP. This suggests that increased rainfall led to the formation of a lake in the desert [29].

Similar observations have been reported from other countries. In the State of Victoria, Australia, *Pediastrum* reached 81.7% of the palynomorph assemblage in Kelabit Crater Lake during 6.5–5.0 cal ka BP, indicating a humid climate and freshening of previously more saline conditions [73]. In Holocene deposits of Bollinger So, Denmark, the concentration of eight species of *Pediastrum* increased to 20000 colonies  $\text{cm}^{-2} \text{a}^{-1}$ , indicating a rise in alkaline water level [83].

In common with relative abundances of *Pediastrum*, changes in the abundance of Cyperaceae pollen in a palynomorph assemblage can be an indicator of varying lake levels in the alpine meadow-steppe ecotone on the central Tibetan Plateau. For a small lake like Xuguo Co, most Cyperaceae pollen comes from the swamp meadows that surround it. If the lake area becomes smaller these meadows may be enlarged, with the result that more Cyperaceae pollen is produced and deposited locally. In sediments younger than 8.5 cal ka BP, no specimens of *Pediastrum* have been recorded whereas the Cyperaceae pollen content gradually increases. This suggests that the lake water was fresh prior to 8.5 cal ka BP but as water levels lowered and the lake became smaller, conditions for the growth of *Pediastrum* were no longer suitable, although the presence of Cyperaceae pollen indicates that the water was still fresh [33,34].

#### 2.4 *Spiniferites* indicating offshore, foreshore or marine-transgressive conditions

As reported previously in numerous publications [e.g. 84] *Spiniferites* is typical of marine palynomorph assemblages and commonly dominates those recovered from sediments that accumulated in the open sea. A few examples follow. The brackish to brackish-marine species *Spiniferites puyangensis* He, Zhu and Jin has been encountered in early Oligocene sediments of coastal areas of Bohai and *S. hexatypicus* Matsuoka, *S. pseudofurcatus* (Klump) Sarjeant

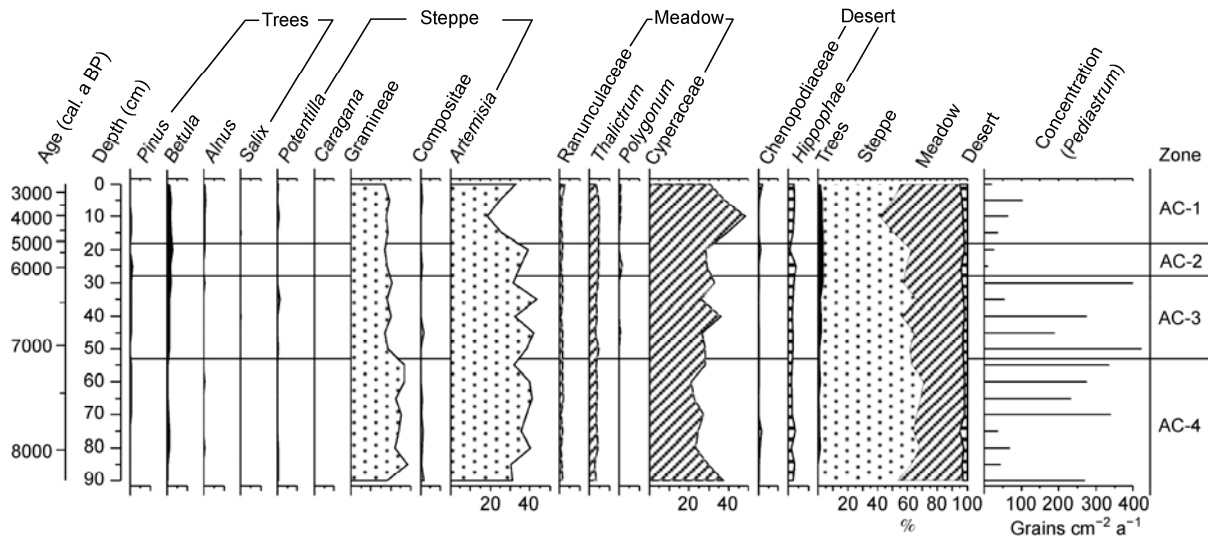
and *S. ramosus* were found in Miocene sediments of Niigata, Japan and the Qiongdong Basin on the northern continental shelf of the South China Sea [14]. There are continuous fossil records of *Spiniferites* from the Oligocene to the Early Pleistocene in the Bay of Biscay in the North Atlantic Ocean, and in Italy and Niigata, Japan: commonly recorded in abundance are *S. membranaceus* and *S. ramosus*. During the Pleistocene, species of *S. mirabilis* (Rossignol) Sarjeant and *S. frigidus* Harland and Reid were dominant in the North Pacific and North Atlantic oceans. In common with Pleistocene sediments in the Bering Sea, the northern North Pacific and the Rockall Plateau, Holocene deposits have also yielded numerous specimens of *S. elongatus* Reid, *S. membranaceus*, *S. mirabilis* and *S. ramosus* [70,85]. De Vernal and Mudie [86] linked *Spiniferites*-dominated assemblages with marine interglacial sediments; however, Edwards et al. [87] found it difficult to relate assemblages of this taxon to sea temperature and depth.

Our records of Holocene *Spiniferites* from Lüsi in Jiangsu, Hemudu and Linshan in Zhejiang, and Guangfulin, Fengxian and Chongming Island in Shanghai indicate offshore or near-shore/foreshore sedimentary environments in marine successions. The Pleistocene deposits at Taizhou and Xinghua in Jiangsu mainly reflect deposition in fresh water, but a few horizons have yielded *Spiniferites*, which must reflect occasional marine incursions.

#### 2.5 Abundant *Concentricystes* in lacustrine sediments commonly indicating a warm, humid climate

*Concentricystes* is an alga that appears to have been able to adapt to a diverse range of freshwater habitats. It is widely distributed in Quaternary strata in China and elsewhere, mostly in lacustrine sediments and peats. Wall reported it to occur frequently in deep marine deposits and on the continental shelf [88]. However, there are no such anomalous records in China.

Abundant specimens of *Concentricystes* occur in Holocene peat and black lacustrine silts in eastern coastal areas of China in association with representatives of aquatic plants referable to the Cyperaceae, *Typha*, *Potamogeton*, *Alisma* and *Lemna*, and with species of other freshwater algae including *Pediastrum*, *Zygnema* and *Cosmarium*. The pollen assemblages in these areas reflect evergreen *Quercus*-dominated vegetation, and are indicative of a warm, humid climate in which freshwater lakes or alluvial flats with back-swamps prevailed [5]. *Concentricystes* has also been found in early Miocene deposits of the Longjin Formation in the continental-shelf basin of the East China Sea, the Shidi Formation in Taiwan and the Ainoura Formation in Japan. It has often been found together with the pollen *Sporotrapoidites* and *Rutaceoipollis* and spores referable to *Magnastriatites* in Miocene lacustrine sediments in eastern China and Taiwan, here indicating a humid, warm temperate-subtropical climate [47,89]. It has also been reported from Pleistocene sediments in the southernmost of the



**Figure 9** An example of numerical calculation: percentages of the main pollen and spore taxa and concentration of *Pediastrum* from Ahung Co, Tibet [33].

Nansha Islands in the South China Sea.

The relative abundance of *Concentricyastes* shows a consistent increase in association with an increase in the variety of pollen types derived from tropical lowland rainforest on the Sunda Shelf since the last deglaciation. This may be linked to the onset of a rise in sea level [57]. In coastal Pleistocene sediments of the Beibu Gulf, China, it shows similar increasing trends associated with a greater variety of tropical and subtropical pollen representatives of such families as Lauraceae, Moraceae, Proteaceae and Sapindaceae, indicating a humid subtropical to tropical climate [5].

That *Concentricyastes* has a wide tolerance of different climates is apparent from palynological records from the south to the north of China in Pleistocene–Holocene deposits. It has been recovered from Quaternary sediments on the Yellow Sea coast and in Helongjiang, North China, and from the Quaternary loess plateau of western China. Hence, regardless of whether conditions favoured a forest dominated by broadleaf trees in a warm, humid climate or a coniferous forest in a cold, relatively dry climate, fossil-subfossil *Concentricyastes* occurs abundantly in lacustrine and other freshwater deposits, enabling the history of freshwater lake and associated environmental conditions to be determined.

## 2.6 Estimation of concentrations of algae in palynological preparations

Algae such as *Pediastrum*, *Zygnema* and *Concentricyastes* are frequently identified and counted in Quaternary pollen analyses and can be helpful in determining conditions of deposition. Their occurrences should be recorded separately from those of pollen and spores. If percentages or concentrations of algae are included in total palynomorph counts, they reduce the amount of spore and pollen data upon which environmental conclusions pertaining to terrestrial vegeta-

tion are based. Indeed, some of the observations on occurrences noted in this paper have relied on relative percentages of algae of this sort and not on separate counts, which we prefer. If algal concentrations are calculated independently, then algal flux (colonies  $\text{cm}^{-2} \text{a}^{-1}$  or grains  $\text{cm}^{-2} \text{a}^{-1}$ ) can be estimated (Figure 9), thus improving palaeoecological conclusions and palaeoenvironmental determinations.

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