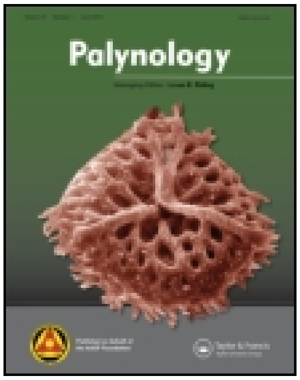

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Latest Permian acritarchs from South China and the Micrhystridium/Veryhachium complex revisited

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Latest Permian acritarchs from South China and the *Micrhystridium/Veryhachium* complex revisited

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Diverse and well-preserved latest Permian phytoplankton assemblages are described from four sections of the Yangtze Block, South China from localities in Zhongzhai (Guizhou Province), Shangsi (Sichuan Province), Xiakou (Hubei Province) and Dongpan (Guangxi Province). Most of the species have been reported previously from other upper Permian sections worldwide. The South Chinese phytoplankton taxa are generally very small in size, usually displaying diameters of about 20 μm and commonly include the genera *Micrhystridium*, *Veryhachium* and *Leiosphaeridia*. However, larger taxa with vesicles often exceeding 80 μm in diameter, such as *Dictyotidium*, are also abundant in the Shangsi section. Due to the presence of large populations of *Micrhystridium* and *Veryhachium*, a simple classification scheme for the *Micrhystridium/Veryhachium* complex is proposed, based on the geometrical shape of the vesicle. We propose dividing the complex into five groups: the *Veryhachium cylindricum* group, representing all ellipsoidal specimens; the *Veryhachium trispinosum* group, all with triangular-shaped vesicles; the *Veryhachium lairdii* group, all with rectangular forms; the *Micrhystridium pentagonale* group, all with pentagonal specimens; and the *Micrhystridium breve* group, which includes all spherical forms.

Keywords: phytoplankton; *Micrhystridium/Veryhachium* complex; Late Permian; Yangtze Block; China

1. Introduction

The group Acritarcha was created by Evitt (1963) as an informal grouping of all organic-walled microfossils with unknown or uncertain biological affinities (Servais 1996; Strother 1996). They first appeared in the Proterozoic and reached maximum diversity during the early and middle Palaeozoic, especially during the Ordovician and Early Devonian (Strother 1996; Servais et al. 2004, 2008). However, acritarch diversity dropped dramatically in the late Palaeozoic, particularly between the Late Devonian and Carboniferous, with very low diversities in the Carboniferous and Permian, leading to almost a complete absence of organic-walled microplankton, that was named by Riegel (1996, 2008) the 'Phytoplankton Blackout'. Servais et al. (2006) questioned the existence of a 'phytoplankton blackout', because the absence of resting cysts in the fossil record does not necessarily imply the absence of phytoplanktonic cyst-producing organisms in the late Palaeozoic oceans. Subsequently, Mullins and Servais (2008) reviewed the diversity of the Carboniferous phytoplankton, and noted that phytoplankton diversity was still high in the earliest Carboniferous, but declined significantly from the Tournaisian to the Serpukhovian. Phytoplankton diversity in the Late Carboniferous was generally very low, with typically only one to three species being documented in each assemblage (Mullins & Servais 2008). Subsequently, Lei et al. (2013) similarly reviewed the diversity of the phytoplankton of the Permian, and pointed out that phytoplankton diversities were much more higher than previously assumed, with highest diversities in the Early Permian and the latest Permian, where more than 30 phytoplankton genera have been reported.

Chinese acritarch studies, like elsewhere, have focused mainly on the early and middle Palaeozoic, with only a few studies in the Permian (Li et al. 2002, 2004). In the Late Permian of South China, most palynological investigations were focused on the taxonomy and biostratigraphy of spores and pollen grains. Only four papers (Ouyang 1982, 1986; Ouyang & Utting 1990; Li et al. 2004) have described acritarchs from the Permian–Triassic boundary (PTB), documenting the presence of 13 genera of acritarchs and related forms: *Archaeodinium*, *Baltisphaeridium*, *Cymatiosphaera*, *Dictyotidium*, *Leiosphaeridia*, *Micrhystridium*, *Psiloschizosporis*, *Veryhachium*, *Reduviasporonites*, *Schizosporis*, *Solisphaeridium*, *Tasmanites* and *Tunisphaeridium*. In these studies, the small taxa (with diameters ca. of 20 μm, such as *Micrhystridium*, *Veryhachium* and some species of *Leiosphaeridia*) are the most common.

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This paper documents the Late Permian acritarch populations from four sections of the Yangtze Block, South China, with special focus on the dominant group of taxa belonging to the *Micrhystridium*/*Veryhachium* complex, for which we propose a simple classification scheme of five informal groups.

2. Geological setting

The Yangtze Block of South China displays numerous continuous sections of Upper Permian and Lower Triassic strata from different palaeoenvironments, ranging from nearshore to platform and slope settings (Figure 1C). In the present study, four sections have been investigated in the Guizhou, Sichuan, Hubei and Guangxi provinces (Figure 1A, B). For each of these sections, the reader is referred to the relevant geological and palaeontological studies.

2.1. *Zhongzhai section*

The Zhongzhai section (26°09.110N; 105°17.113E) is located about 5 km north of Zhongzhai Village, near Langdai Town, Liuzhi County, Guizhou Province (He et al. 2008). The section is located in the western Yangtze Block (Figure 1); the uppermost Longtan Formation (beds 1 to 27) and the lowermost Yelang Formation (beds 28 to 37) are investigated in this study. The Longtan Formation is mainly composed of brownish sandstones and mudstones with a few limestones. The lowermost Yelang Formation is dominated by yellowish green or purplish red silty calcareous mudstones, and a few limestones and claystones at its base. According to the conodont zonation, Metcalfe and Nicoll (2007) considered that the PTB in the Zhongzhai section is in bed 28 (Figure 2). Based on uranium-lead (U-Pb) dates, the absolute age of the claystone in bed 29 indicates an age of 252.24 ± 0.13 Ma (Shen et al. 2011).

2.2. *Shangsi section*

The Shangsi section is located near Guangyuan City in the northern part of Sichuan Province, and belongs to the northwestern corner of the Yangtze Block (Lai et al. 1996; Figure 1). Both the Dalong (upper Wuchiapingian to Changhsingian) and the Feixianguan formations (Induan) are exposed here. The geology of the Shangsi section was first described by Li et al. (1986). Beds 17 to 22 are dominated by interbedded carbonaceous-siliceous rocks and siliceous limestones with a few mudstones. The interval from beds 23 to 29 is

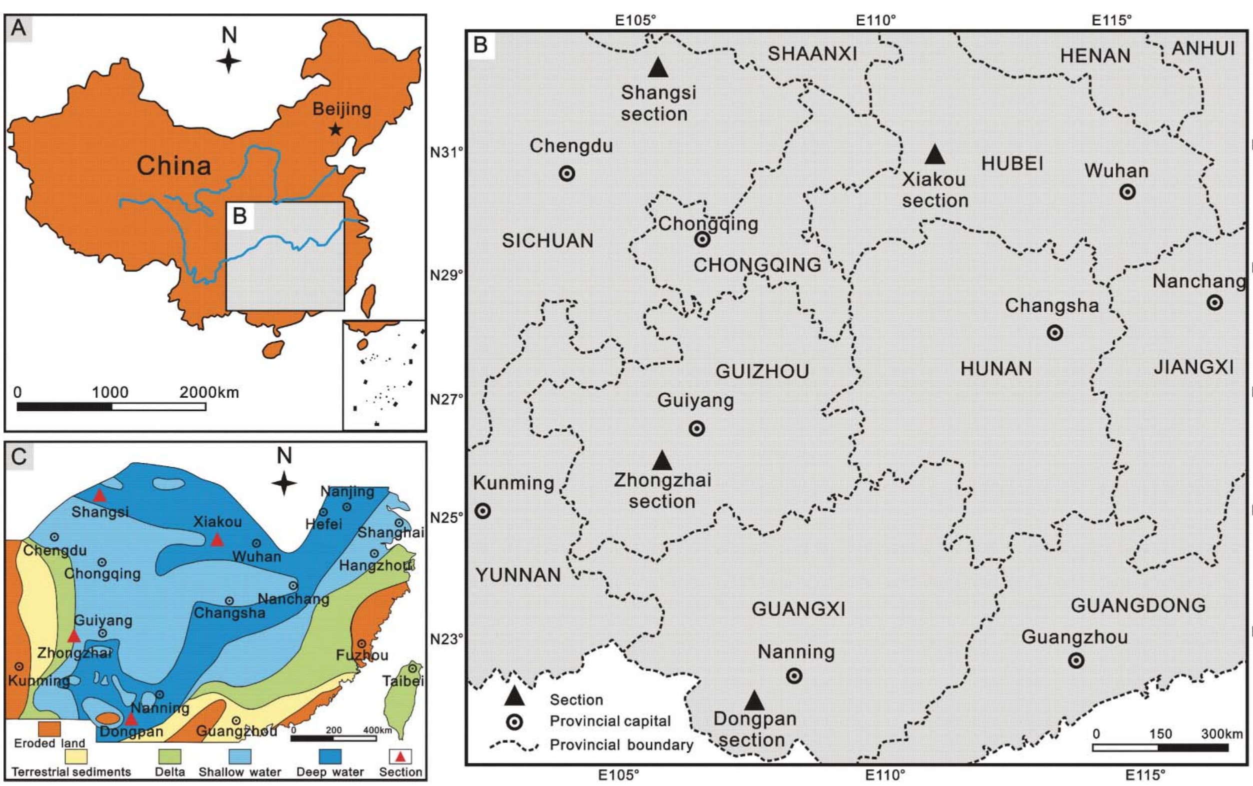


Figure 1. Location of the four sections studied in South China (Zhongzhai section, Shangsi section, Xiakou section and Dongpan section) (A and B), and the latest Permian palaeogeography of South China (C, modified after Feng & Gu 2002).

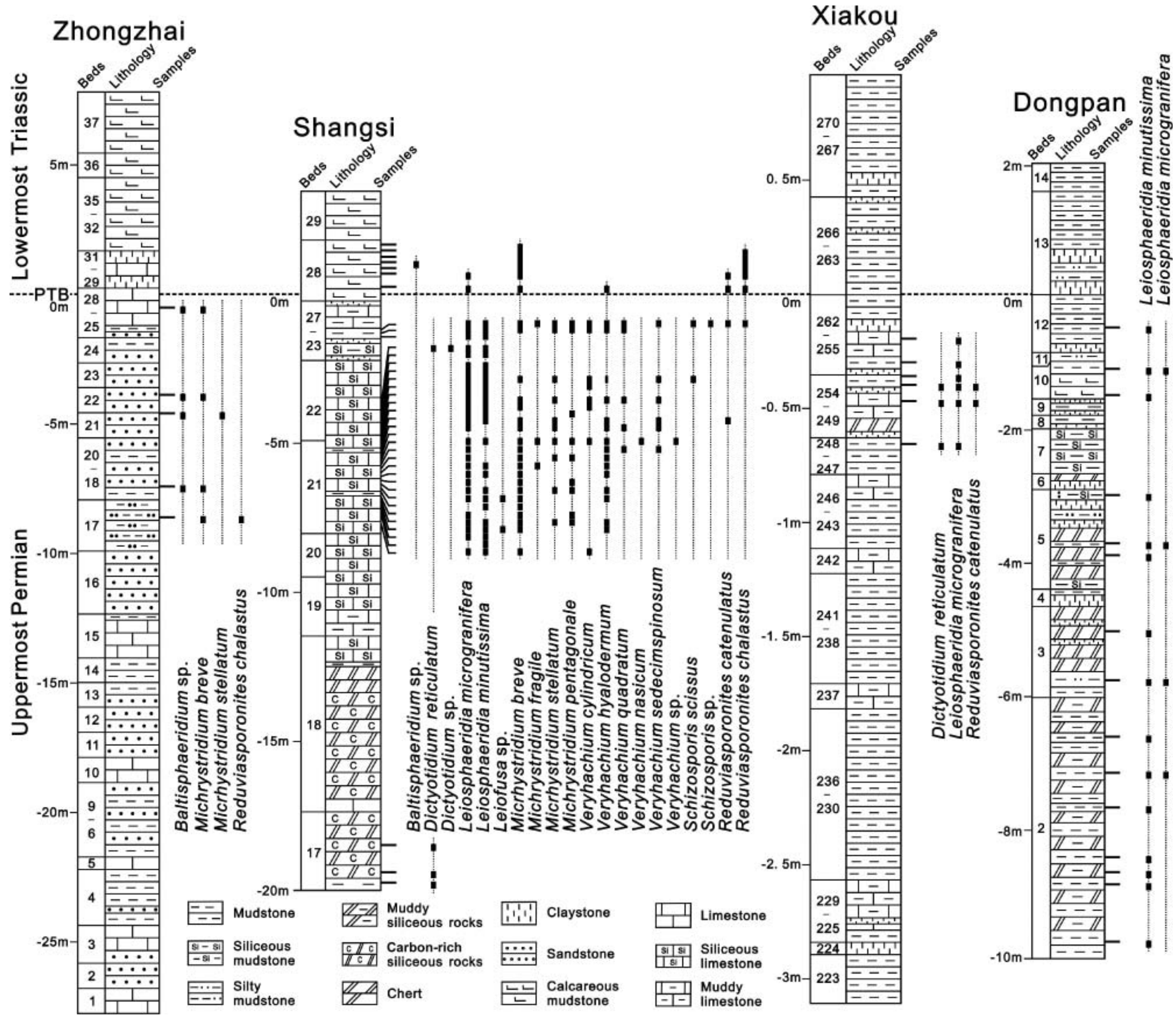


Figure 2. Phytoplankton distribution in the four sections investigated.

mainly composed of siliceous mudstones and calcareous mudstones with few claystones. Recently, Jiang et al. (2011) suggested that the PTB be placed 22 cm above the base of bed 28, based on hindeodid and gondolellid conodont taxa. Similarly to the Zhongzhai section, an absolute age (252.28 ± 0.13 Ma) was determined from the claystones of bed 27 by Shen et al. (2011).

2.3. *Xiakou section*

The Xiakou section (31°06.874 N; 111°48.221E) is situated near the town of Xiakou, in Xingshan County, Yichang City, Hubei Province. It is located in the north of the Yangtze Block (Wang & Xia 2004; Figure 1) and comprises the uppermost Changxing Formation (beds 223 to 256), which is dominated by mudstones and muddy limestones, and the lowermost Daye Formation (beds 257 to 270), which is dominated by mudstones with rare claystones. According to the conodont biozonation, the PTB is placed in bed 262 (Shen et al. 2012a), rather than in bed 266 (Wang & Xia 2004; Hong et al. 2008, 2011).

2.4. *Dongpan section*

The Dongpan section, located at 22°16.196 N and 107°41.505 E (Shen et al. 2012b), is situated 80 km southwest of Nanning, Guangxi Province, in the southern area of the Yangtze Block (He et al. 2007b) (Figure 1). Here, the Dalong Formation (beds 2 to 12) and the Luolou Formation (beds 13 to 14) are exposed.

The interval from beds 2 to 8 is mainly composed of well-bedded siliceous rocks, muddy siliceous rocks and mudstones. The interval from beds 9 to 14 is dominated by mudstones and silty mudstones with thin claystone intercalations (Feng et al. 2007). According to He et al. (2005, 2007a, 2007b) and Feng et al. (2007), beds 2 to 12 are late Changhsingian, and bed 13 is considered to be early Induan.

3. Materials and methods

Two hundred and sixty nine samples were collected from the four sections (45 samples from the Zhongzhai section, 141 samples from Shangsi, 60 samples from Xiakou and 23 samples from Dongpan). All of the samples were processed for palynological analysis.

Fifty grams of each sample were prepared using standard palynological methods. After treatment with hydrochloric acid (33%) and hydrofluoric acid (40%), the samples were concentrated by treatment with zinc bromide solution (s.g. 2.2). The samples were not oxidised or sieved. The residue was studied using light microscopy and scanning electron microscopy (SEM). All residues are stored in the collections of the China University of Geosciences, Wuhan.

4. Results

The present investigation indicates that diverse and abundant phytoplankton occur in the latest Permian of the Yangtze Block, South China, from the four sections investigated (Figure 2). The highest diversity is observed in the Shangsi section, with 20 species and eight genera recorded in 37 samples, including *Baltisphaeridium* sp., *Dictyotidium reticulatum*, *D.* sp., *Leiofusa* sp., *Leiosphaeridia microgranifera*, *L. minutissima*, *Micrhystridium breve*, *M. fragile*, *M. pentagonale*, *M. stellatum*, *Reduviasporonites catenulatus*, *R. chalastus*, *Schizosporis scissus*, *S.* sp., *Veryhachium cylindricum*, *V. hyalodermum*, *V. nasicum*, *V. quadratum*, *V. sedecimspinosum* and *V.* sp.

In the Zhongzhai and Xiakou sections, only a few species occur in several samples, including *Baltisphaeridium* sp., *Dictyotidium reticulatum*, *Leiosphaeridia microgranifera*, *Micrhystridium pentagonale*, *M. stellatum*, *Reduviasporonites catenulatus* and *R. chalastus*. In addition, only two species of *Leiosphaeridia* occur in the Dongpan section. However, they are abundant in 15 samples (Figure 2). The palynofacies changes in the Shangsi section are described by a Lei et al. (unpublished data), and the palaeoenvironmental distribution of the different was phytoplankton taxa interpreted by (2012). The present paper describes the systematic palaeontology of the assemblages investigated, with special focus on the *Micrhystridium*/*Veryhachium* complex.

5. The *Micrhystridium*/*Veryhachium* complex revisited

The genera *Micrhystridium* Deflandre 1937 and *Veryhachium* Deunff 1954 are amongst the most widely recorded acritarch genera throughout the entire Phanerozoic. Fensome et al. (1990) listed more than 200 species of them. With a wide range of diagnoses, they became typical 'waste-basket' genera, similar to other genera such as *Baltisphaeridium* (Eisenack 1958) Eisenack 1969, *Multiplicisphaeridium* Staplin 1961, and *Polygonium* Vavrdová 1966 (see Servais et al. 2007). Many palynologists described new species of small spherical acanthomorth acritarchs and placed them in *Micrhystridium*, whereas numerous new small polygonal acritarch species were attributed to *Veryhachium*. However, because the interspecific variability is very great, it is commonly difficult if not impossible to distinguish the different species, as well as differentiating the two genera. These genera and their species thus form a large plexus with a continuum of intermediate morphotypes.

Generally, the Permian specimens attributed to *Micrhystridium* display a spherical or oval vesicle, bearing many proximally open spines with closed tips, most often simple, and rarely branching. The vesicle diameter is usually less than 20 μm (larger species were usually attributed to the genera *Baltisphaeridium* and/or *Multiplicisphaeridium*). However, *Veryhachium* embraces all smaller acritarchs with polygonal body outlines and less than eight spines.

In the Permian, the two genera *Micrhystridium* and *Veryhachium* are very common. According to a recent literature search, 27 species of *Micrhystridium* were recorded 55 times in 26 publications, whereas 22 species of *Veryhachium* were documented 46 times (Lei et al. 2013). At the species level, *Micrhystridium breve*, *M. stellatum* and *Veryhachium reductum* are the most frequently reported species of the *Micrhystridium*/*Veryhachium* complex (Lei et al. 2013).

The genera *Micrhystridium* and *Veryhachium* have a complex taxonomic history and both have been revised and reviewed by many authors (see Sarjeant & Stancliffe 1994; Servais et al. 2007). The taxonomy is still being debated, and it remains difficult to identify some of the individual species. This problem of identification was noted very early, and some authors used the term '*Micrhystridium*/*Veryhachium* complex' several decades ago (e.g. Wall & Downie 1963; Visscher and Brugman 1981; Sarjeant & Stancliffe 1994; Eshet et al. 1995; Li et al. 2004; Van de Schootbrugge et al. 2005; Riegel 2008).

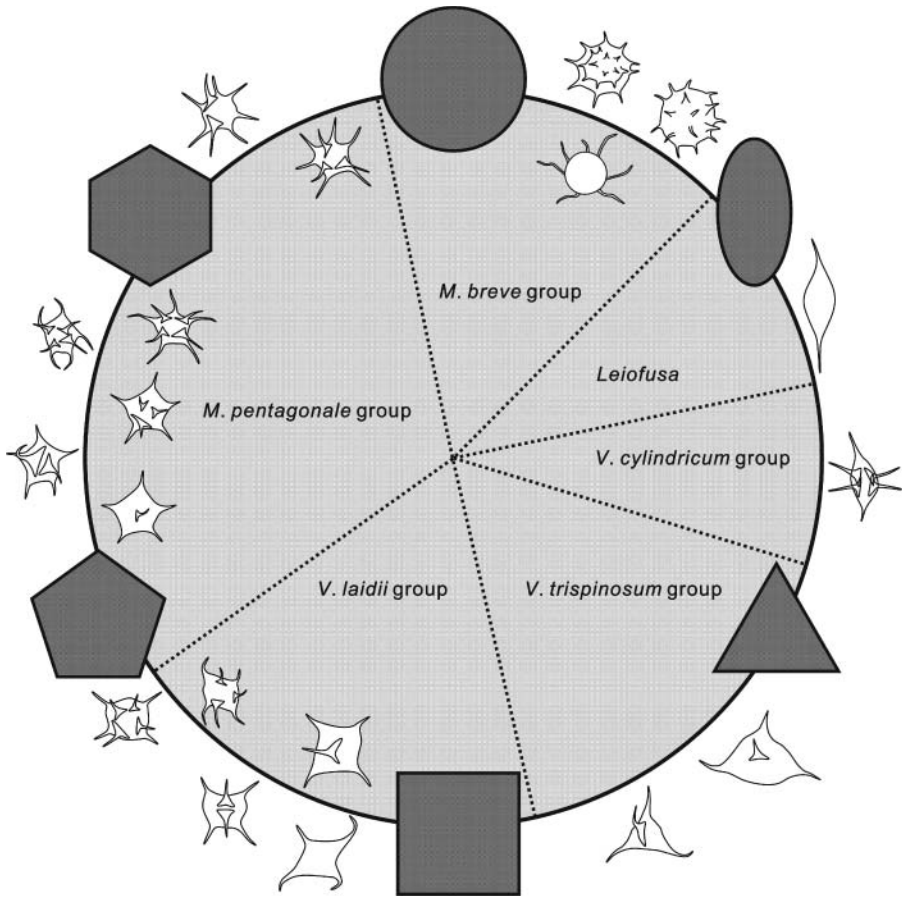


Figure 3. Idealised line drawings of the simplified classification scheme of the *Micrhystridium/Veryhachium* complex.

It is not the objective of this paper to fully review the classification scheme of the two genera, or to emend their diagnoses which have been modified several times already. A full revision, including population analyses with biometric studies, of all described taxa of the genera *Micrhystridium* and *Veryhachium* is necessary in order to understand the taxonomy of these taxa, and to provide synonymy lists. Our objective is to propose a simple classification scheme that can easily be used for analyses of latest Permian phytoplankton assemblages, especially by palynologists who do not describe the acritarch taxonomy in detail. However, the simplified classification scheme presented here does not consider all previously described taxa as synonyms.

In the present study of Late Permian phytoplankton assemblages from South China, 10 morphotypes within the *Micrhystridium/Veryhachium* complex are recognised, and are here tentatively attributed to formerly described species. However, interspecific and intergeneric variability is large and it is difficult to draw clear lines between species. For identifying this complex more easily, we propose to divide them into five informal categories, which are based on the geometric shape of the vesicle and do not take into account the morphologies of the spines (or appendices) (Figure 3).

Servais et al. (2007) revised the oldest morphotypes of *Veryhachium* that first appeared in the Ordovician and, following the informal usage of several authors, proposed two informal groups for the genus *Veryhachium* in order to facilitate their classification. The *Veryhachium trispinosum* group was proposed for triangular specimens, and the *Veryhachium lairdii* group for rectangular forms.

Compared to the Ordovician, the Permian morphotypes of *Veryhachium* are even more variable and include morphological transients that range into *Micrhystridium*. Therefore, we continue the reasoning of Servais et al. (2007) and propose three additional informal groupings to facilitate the classification of these morphotypes in the late Palaeozoic. The informal *Veryhachium cylindricum* group is here proposed to include all ellipsoidal specimens of *Veryhachium*, whereas two informal groups for *Micrhystridium* are

Table 1. South Chinese species of the *Micrhystridium*/*Veryhachium* complex recorded in the present study and their attribution to five informal groups, based on their general central body outline.

Group name	Shape of the vesicle	Included in this paper
V. cylindricum group	ellipsoidal	*V. cylindricum*
V. trispinosum group	triangular	*V. hyalodermum V. sp.*
V. laidii group	rectangular	*V. nasicum V. quadratum V. sedecimspinosum*
M. pentagonale group	pentagonal & hexagonal	*M. pentagonale M. stellatum*
M. breve group	spherical	*M. fragile M. breve*

proposed. These correspond to the *Micrhystridium pentagonale* group for all pentagonal and hexagonal specimens, and the *Micrhystridium breve* group for all spherical specimens.

In our study, the *Veryhachium cylindricum* group includes the previously described species *Veryhachium cylindricum* (Table 1). The *Veryhachium trispinosum* group includes all triangular specimens, amongst them *Veryhachium hyalodermum* and *Veryhachium* sp. The *Veryhachium lairdii* group includes all morphotypes with rectangular or square vesicles, such as *Veryhachium nasicum*, *V. quadratum* and *V. sedecimspinosum*. The *Micrhystridium pentagonale* group includes the two species *Micrhystridium pentagonale* and *M. stellatum*, whereas the *Micrhystridium breve* group includes both *Micrhystridium fragile* and *M. breve*. It is clear that this proposal is a tentative classification into an informal subgeneric scheme, and other geometric shape-like groupings could be added if necessary. The idealised line drawings of Figure 3 illustrate that all vesicle shapes from triangular to square, pentagonal to polygonal, round and ellipsoidal may exist, and Plate 2 shows that morphotypes with such vesicles shapes are actually present in the Permian assemblages. It is obvious that these specimens belong to a *Micrhystridium*/*Veryhachium* complex, and that the determination at the specific level becomes problematical when dealing with larger populations, such as those recorded from the Chinese Permian.

The objective of this tentative classification into informal groupings is simply to propose a rapid classification scheme of the *Micrhystridium*/*Veryhachium* complex. We do not know if these morphotypes actually represent the cysts of a single biological species, or of a greater number of taxa. It is beyond the scope of this paper to answer that question. However future research, such as analysis of the biomarkers or biochemistry of the vesicle walls, would help facilitate a better understanding of the generic relationships of the different taxa. Interestingly, Grice et al. (2005) and Hays et al. (2011) analysed the biomarkers of sediments from Greenland at the Permian–Triassic boundary, and suggested that the C33 *n*-alkylcyclohexane may be a potential biomarker for the *Micrhystridium*/*Veryhachium* complex. So far, these data result from the analyses of both *Micrhystridium* and *Veryhachium*. Future research of separated *Micrhystridium* and *Veryhachium* populations may provide more precise interpretations.

6. Systematic palaeontology

Acritarchs are, by definition organic-walled microfossils of unknown biological affinities (Evitt 1963; Servais 1996). Several authors have suggested, mostly based on morphological comparisons with extant phytoplankton, biological relationships with various microalgal groups. According to various authors (e.g. Colbath & Grenfell 1995; Le Hérissé et al. 2009), the genera *Dictyotidium*, *Leiosphaeridia* and *Schizosporis* could be related to the green algae (Prasinophyceae and Zygnematophyceae). We follow this suggestion, without providing arguments for or against this interpretation. In addition, the vigourous debate of whether *Reduviasporonites* is of algal origin or a fungal spore continues (Eshet et al. 1995; Visscher et al. 1996, 2011; Afonin et al. 2001; Foster et al. 2002; Sephton et al. 2009). We do not discuss herein the biological affinity of *Reduviasporonites*, and tentatively place it in the acritarchs. All acritarchs are classified as 'Incertae sedis', and listed in alphabetical order.

Algae
Division Chlorophyta Pascher 1914
Class Prasinophyceae Christensen 1962
Order Not assigned
Family Pterosphaeridiaceae Mädler 1963

Dictyotidium Eisenack 1955 emend. Staplin 1961
Type species. *Dictyotidium dietyotum* (Eisenack 1938) Eisenack 1955

Dictyotidium reticulatum Schulz 1965
Plate 1, figures 1–12

Dictyotidium reticulatum Schulz 1965, p. 278, pl. 23, figs. 12–14

Description. The vesicle is spherical to subspherical, and covered by a reticulate ornamentation. The ornamentation includes irregular and interconnected fields, with four to six ridges. The width of each ridge is ca. 4–10 μm. The wall is approximately 2–5 μm thick

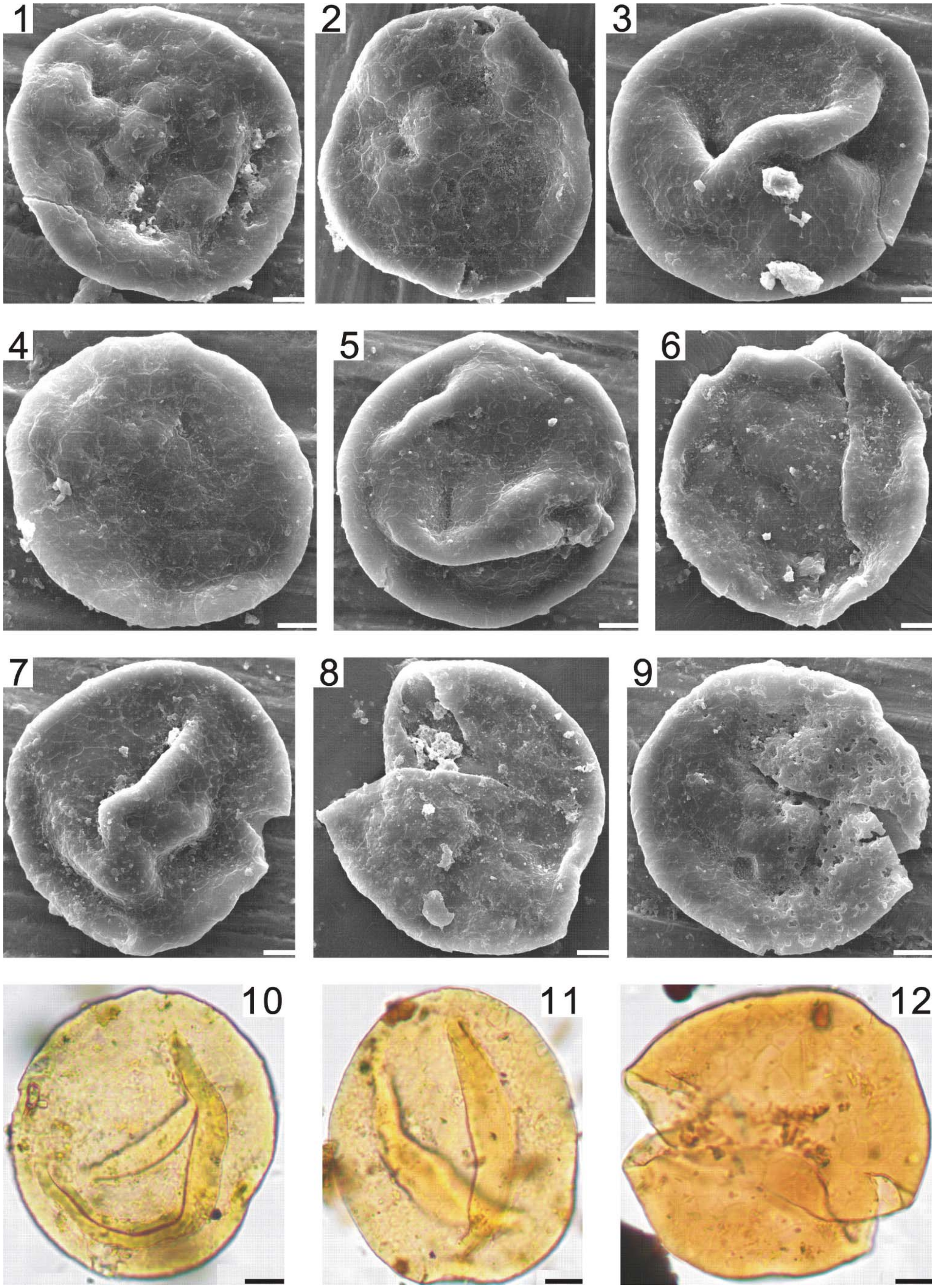


Plate 1. Phytoplankton from the latest Permian of South China. Each scale bar is 10 μm. Figures 1–9 were taken using SEM; figures 10–12 were taken using the transmitted light microscope. Figures 1–12: *Dictyotidium reticulatum*. All specimens are from Shangsi section/SS292-4.

and usually folded. Folds are straight or slightly sinuous. The wall occasionally splits open.
Dimensions. Vesicle diameter 52 (76) 110 μm, 45 specimens measured.
Remarks. In Permian strata, the morphology and size of *Dictyotidium reticulatum* are comparable to those of *Leiosphaeridia changxingesis* Ouyang & Utting 1990. However, the surface of the two species is very different. The former is covered by an ornamentation of irregular ridges, whereas the latter is nearly laevigate to slightly scabrate, or punctuate with locally developed ridges.
Previous records. Permian, China (Ouyang & Utting 1990); Norway (Mangerud 1994); Triassic, Germany (Schulz 1965); Spain (Besems 1981).
Stratigraphical occurrence. Abundant in beds 15 to 22 of the Shangsi section, and present in the Xiakou section.

Dictyotidium sp.
Plate 3, figures 11–12

Description. The vesicle is spherical. The surface of the vesicle is covered by irregular and interconnected fields, four to six-sided with ridges commonly 2–4 μm long, the fields are mostly hollow.
Dimensions. Vesicle diameter 30 (36) 42 μm, five specimens measured.
Remarks. The vesicle of this species is nearly spherical in shape, and generally not folded. The fields are much smaller than those of *Dictyotidium reticulatum*.
Stratigraphical occurrence. Present in bed 22 of the Shangsi section.

Leiosphaeridia Eisenack 1958 emend. Downie & Sarjeant 1963
Type species. *Leiosphaeridia baltica* Eisenack 1958

Leiosphaeridia micrograniferа (Staplin 1961) Downie & Sarjeant 1963
Plate 3, figures 19–21

Protoleiosphaeridium micrograniferа Staplin 1961, p. 405, pl. 48, fig. 4
Leiosphaeridia micrograniferа (Staplin 1961) Downie & Sarjeant 1963, p. 124

Description. The vesicle is ellipsoidal to spherical in outline, commonly folded, with a dense granulose wall. The granules are rounded, clearly separated, and about 0.5 μm in diameter.
Dimensions. Vesicle diameter 25 (32) 40 μm, 14 specimens measured.
Remarks. This species is similar to *Leiosphaeridia granulosa* Staplin 1961. However, the vesicle of the former is much larger and the granules are much smaller (0.5 μm in diameter) than on the latter (1 μm diameter).
Previous records. Lower Silurian, Pennsylvania (Johnson 1985); Upper Devonian, Canada (Staplin 1961).
Stratigraphical occurrence. Abundant in the Shangsi and Xiakou sections.

Leiosphaeridia minutissima (Naumova 1949) Jankauskas 1989
Plate 3, figures 13–18

Leiosphaeridia minutissima Naumova 1949, p. 52–53, pl. 1, figs. 1–2, pl. 2, figs. 1–2
Leiosphaeridia minutissima (Naumova 1949) Jankauskas 1989, p. 79–80, pl. 9, figs. 1–4, 11

Description. The vesicle is spherical to subspherical, smooth, single-layered, always folded with the folds being straight or slightly sinuous.
Dimensions. Vesicle diameter 25 (31) 40 μm, 23 specimens measured.
Remarks. The outline of this species is similar to that of *Leiosphaeridia micrograniferа*, and both of them are generally folded. However, the surfaces of the two species are usually very different. *L. minutissima* has a smooth vesicle wall, whereas *L. micrograniferа* displays dense granules.
Previous records. Neoproterozoic, Canada (Butterfield & Chandler 1992); Congo (Gaucher & Germs 2006); Czech Republic (Vavrdová 2008); India (Bhat et al. 2009); Russia (Maslov 2004; Stanevich et al. 2007; Vorob'eva et al. 2009); Ediacaran, Poland (Moczydlowska 2008); Ukraine (Leonov & Ragozina 2007); Uruguay (Gaucher et al. 2008); Cambrian, Czech Republic (Konzalová 1995; Steiner & Fatka 1996); Russia (Naumova 1949)
Stratigraphical occurrence. Abundant in the Shangsi and Dongpan sections.

Class Zygnematophyceae Round 1971
Order Zygnematales Borge & Pascher 1913
Family Zygnemataceae Kützing 1843

Schizosporis Cookson & Dettmann 1959 emend. Pierce 1976
Type species. *Schizosporis reticulatus* Cookson & Dettmann 1959

Schizosporis scissus (Balme & Hennelly 1956) Hart 1965
Plate 3, figures 8–10

Laevigatosporites scissus Balme & Hennelly 1956, p. 56, pl. 1, figs. 6–9
Spheripollenites scissus (Balme & Hennelly 1956) Jansonius 1962, p. 82, pl. 16, fig. 8
Schizosporis scissus (Balme & Hennelly 1956) Hart 1965, p. 14

Description. The vesicle is subspherical. The laevigate wall is 0.5–1 μm thick, and occasionally splits open or into two halves.
Dimensions. Vesicle diameter 25 (36) 45 μm, five specimens measured.
Remarks. The wall of this species is much thicker than that of other taxa, such as *Micrhystridium*, *Veryhachium*, *Leiosphaeridia* and other genera, but it is much smaller and thinner than that of *Dictyotidium*. Generally, the vesicle splits into two halves and is not folded.
Previous records. Permian, Antarctica (Balme & Playford 1967; Farabee et al. 1991); Australia (Balme & Hennelly 1956; Segroves 1967); Pakistan (Balme 1970); Triassic, Canada (Jansonius 1962).
Stratigraphical occurrence. Recorded from beds 22 and 25, Shangsi section.

Schizosporis sp.
Plate 3, figures 1–7

Description. The vesicle is spherical. Wall occasionally splits open or into two halves. Dense short spines (ca. 0.5 μm long) present along the surface of the vesicle, well distributed, simple, hollow and acuminate, closed distally.
Dimensions. Vesicle diameter 20 (23) 25 μm, eight specimens measured.
Remarks. Similar to *Schizosporis scissus*, the wall of *Schizosporis* sp. splits open. Compared with *Leiosphaeridia microgranifera*, it has a similar vesicle (wall thickness and dense spines). However, whereas *L. microgranifera* has a generally ellipsoidal and folded vesicle, that of *Schizosporis* sp. is spherical and rarely folded.
Stratigraphical occurrence. Present in bed 25, Shangsi section.

Group Acritarcha Evitt 1963

Gorgonisphaeridium Staplin et al. 1965
Type species. *Gorgonisphaeridium winslowiae* Staplin et al. 1965

Gorgonisphaeridium sp.
Plate 2, figure 20

Description. The thin and single-layered vesicle is spherical to subspherical, and covered by dense short spines that are not pointed.
Dimensions. Vesicle diameter 25 (35) 42 μm, process length 2–4 μm, four specimens measured.
Remarks. This species is very different from *Micrhystridium* and *Veryhachium*, because of the spines and the general outline. The vesicle is clearly much larger than those of *Micrhystridium*, with dense spines on the surface of the vesicle that are solid and not pointed.
Stratigraphical occurrence. Occurs in the Zhongzhai and Shangsi sections.

Leiofusa Eisenack 1938
Type species. *Leiofusa fusiformis* Eisenack 1938

Leiofusa sp.
Plate 2, figure 13

Description. The central body is elliptical. The thin wall is laevigate. Two long spines are present at both ends of the central body.
Dimensions. Vesicle diameter 35 μm, spine length 17–20 μm, one specimen measured.
Remarks. The central body is much bigger than that of *Micrhystridium* and *Veryhachium*, but the spines are similar. As only one specimen is recorded, it is left in open nomenclature.
Stratigraphical occurrence. Present in bed 21, Shangsi section.

Micrhystridium Deflandre 1937 emend. Sarjeant & Stancliffe 1994
Type species. *Micrhystridium inconspicuum* (Deflandre 1935) Deflandre 1937

Micrhystridium breve Jansonius 1962
Plate 2, figures 21–25

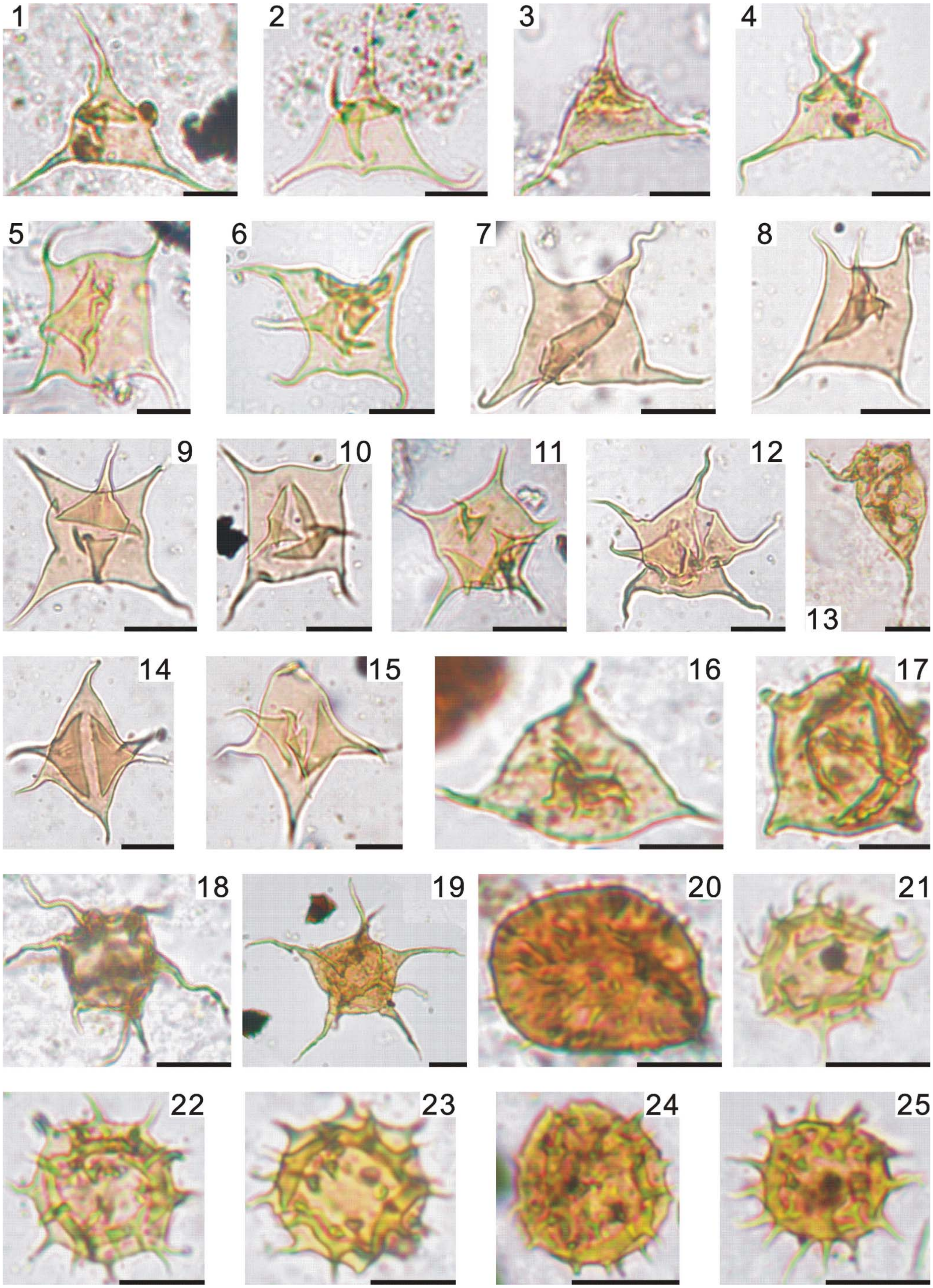
Micrhystridium breve Jansonius 1962, p. 85, pl. 16, figs. 62, 63, 66

Description. The vesicle is ellipsoidal to spherical in outline. The wall is single-layered and thin. About 20–40 processes are present along the surface of the vesicle, they are simple, hollow and acuminate, closed distally. Vesicle and process surfaces are laevigate.
Dimensions. Vesicle diameter 15 (17) 21 μm, process length 2–5 μm, 23 specimens measured.
Remarks. Sarjeant et al. (1970) suggested that *Micrhystridium breve* and *M. recurvatum* forma *brecispinosa* Valensi 1953 are possibly the same species. Because of its numerous, short spines it is easily recognised.
Previous records. In Permian, Pakistan (Sarjeant et al. 1970); Canada (Utting 1978); Australia (McMinn 1982); USA (Jacobson et al. 1982); Brazil (Quadros 2002); In Triassic, Canada (Jansonius 1962; Utting et al. 2004; Utting et al. 2005; Zonneveld et al. 2010); Siberia (Ilyina & Egorov 2008); Cretaceous, Canada (Collom & Hills 1999).
Stratigraphical occurrence. Abundant in beds 20 to 28, Shangsi section.

Micrhystridium fragile Deflandre 1947
Plate 2, figure 18

Micrhystridium fragile Deflandre 1947, p. 8, fig. 13–18

Description. The vesicle is spherical to subspherical, with a thin wall covered by tiny spines that are pointed and generally flexible. Most of these spines are longer than the diameter of the central body.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Dimensions. Vesicle diameter 9 (11) 12 μm, process length 11–15 μm, four specimens measured.
Remarks. The vesicle of this species is the smallest in our samples, only about 10 μm in diameter. The spines are more flexible than those of other species of *Micrhystridium*.
Previous records. Permian, Uruguay (Mautino et al. 1998); England (Sarjeant 1962); Triassic, England (Van de Schootbrugge et al. 2007); Jurassic, England (Wall 1965; Porter 1988; Stancliffe 1990); Israel (Sarjeant 1962).
Stratigraphical occurrence. Recorded from beds 21 to 25, Shangsi section.

Micrhystridium pentagonale Stockmans & Willière 1963
Plate 2, figures 11–12

Micrhystridium pentagonale Stockmans & Willière 1963, p. 470–471, pl. 3, fig. 32

Description. The thin-walled vesicle is pentagonal in outline. Five prominent spines are present along each corner. The other one to four spines arise from the central area of the vesicle. All spines are pointed.
Dimensions. Vesicle diameter 12 (14) 17 μm, process length 4–10 μm, 15 specimens measured.
Remarks. The outline of the vesicle is similar to that of *Micrhystridium stellatum*, but it has a more pentagonal shape. Moreover, the spines of the former are much shorter.
Previous records. Carboniferous, Turkey (Higgs et al. 2002); Silurian, Belgium (Stockmans & Willière 1963).
Stratigraphical occurrence. Present in beds 21 to 25 of the Shangsi and Zhongzhai sections.

Micrhystridium stellatum Deflandre 1945
Plate 2, figure 19

Micrhystridium stellatum Deflandre 1945, p. 65, pl. 3, figs. 16–19

Description. The vesicle is polyangular in outline. The thin wall is single-layered. About eight to 12 strong but simple processes are present around the vesicle, they are relatively long, tapering, with sharp points and hollow.
Dimensions. Vesicle diameter 13 (16) 18 μm, process length 6–15 μm, 15 specimens measured.
Remarks. Common in Permian strata, the species can easily be distinguished because of its polyangular vesicle and the long spines.
Previous records. Ordovician, USA (Eley & Legault 1988); Silurian, England (Dorning 1981); France (Deflandre 1945); Sweden (Gelsthorpe 2004; Stricanne et al. 2006); Devonian, Libya (Moreau-Benoit 1984); Poland (Filipiak 2009); Carboniferous, China (Gao 1986); Turkey (Higgs et al. 2002); Permian, Britain (Wall & Downie 1963); China (Ouyang & Utting 1990); Germany (Schaarschmidt 1963); Israel (Horowitz 1973); Triassic, England (Van de Schootbrugge et al. 2007).
Stratigraphical occurrence. Common in beds 21 to 28, Shangsi section, and present in the Zhongzhai section.

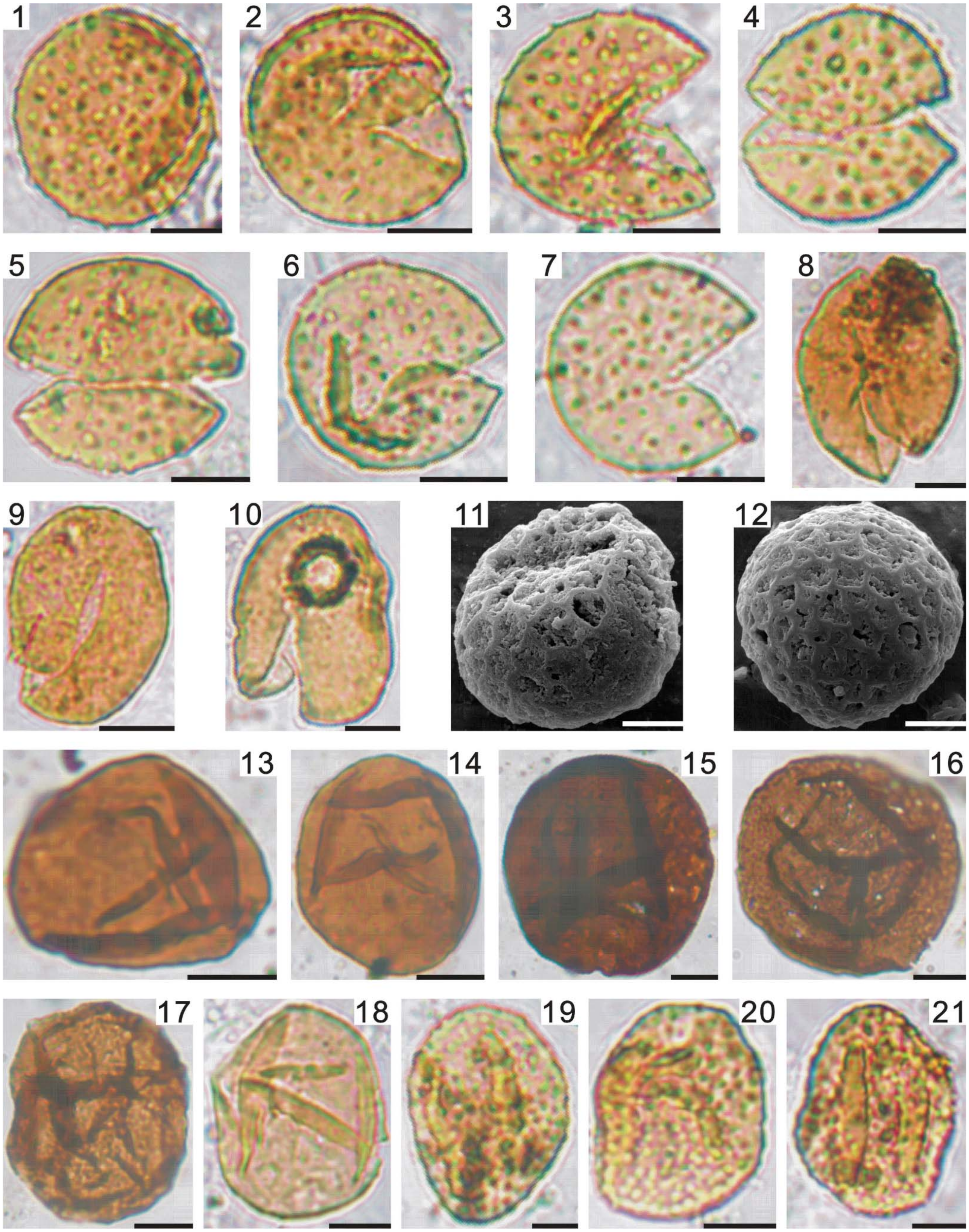
Reduviasporonites Wilson 1962 emend. Foster et al. 2002
Type species. *Reduviasporonites catenulatus* Wilson 1962

Remarks. *Reduviasporonites* has been considered by several authors to be a fungal spore. However, several authors (e.g. Afonin et al. 2001; Foster et al. 2002) questioned a fungal affinity, and suggested that it is green algae. Because the biological affinity is unknown, we place it here within the acritarchs. Interestingly, many authors pointed out that the 'spike' of *Reduviasporonites* occurs at the PTB (e.g. Eshet et al. 1995; Visscher et al. 1996). Indeed, around the PTB strata of South China, the relative abundances of *Reduviasporonites* are much higher than that in other strata, but they never exceed 14% of an assemblage, which clearly indicates that a 'spike' does not occur in the present study.

Reduviasporonites catenulatus Wilson 1962
Plate 4, figures 12–17

Description. The vesicle is circular or oval in outline, sometimes folded, wall laevigate. Many cells connect together usually like a chain, but sometimes they are present as pairs of cells or as a single cell. The length/width ratio of the vesicle ranges between 1:1 and 2:1.

Plate 2. Phytoplankton from the latest Permian of South China. Each scale bar is 10 μm. All figures were taken using the transmitted light microscope. 1–4: *Veryhachium hyalodermum*; 5–8: *Veryhachium nasicum*; 9–10: *Veryhachium sedecimspinosum*; 11–12: *Michrystridium pentagonale*; 13: *Leiofusa* sp.; 14–15: *Veryhachium cylindricum*; 16: *Veryhachium* sp.; 17: *Veryhachium quadratum*; 18: *Michrystridium fragile*; 19: *Michrystridium stellatum*; 20: *Baltisphaeridium* sp.; 21–25: *Michrystridium breve*. The section/sample numbers for all specimens are as follows. 1–12: Shangsi section/SS25-E; 13: Shangsi section/SS289-1-2; 14–15, 17: Shangsi section/SS290-7; 16: Shangsi section/SS291-6; 18: Shangsi section/SS290-4; 19, 21–25: Shangsi section/TS28-18; 20: Zhongzhai section/ZZ22-2.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Dimensions. Vesicle diameter 8 (15) 20 μm, 17 specimens measured.
Remarks. Foster et al. (2002) described this species in detail, indicating that many characteristics are shared between *Reduviasporonites catenulatus* and *Reduviasporonites chalastus*. We simply distinguish them on the basis that the former is much smaller than the latter.
Previous records. Permian, Australia (Foster et al. 2002); USA (Wilson 1962; Elsik 1999); Cretaceous, Canada (Kalgutkar & Braman 2008).
Stratigraphical occurrence. Common in the Shangsi section, and present in the Xiakou section.

Reduviasporonites chalastus (Foster 1979) Elsik 1999
Plate 4, figures 1–11, 18–23

Chordecystia chalasta Foster 1979, p. 109–110, pl. 41, figs. 3–9
?*Brazilea helbyi* forma *gregata* Foster 1979, p. 112, pl. 41, figs. 1–2
Tympanicysta stoschiana Balme 1979, p. 22–24, pl. 1, figs. 3–7
Tympanicysta stoschiana Afonin et al. 2001, p. 484–486, figs. 1, 2A–C, E, F
Reduviasporonites stoschianus (Balme 1979) Elsik 1999, p. 40, pl. 1, figs. 1–24.
?*Reduviasporonites stoschianus* (Balme 1979) Elsik 1999, Wood & Elsik 1999, p. 46–48, pl. 1, figs. 1–9, pl. 2, figs. 1–7

Description. The vesicle is subcircular or subrectangular, sometimes folded, smooth. Many cells connect together, usually forming a chain, but sometimes they are present as pairs of cells or isolated as a single cell. The length/width ratio of the vesicle varies between 2:1 and 6:1.
Dimensions. Vesicle diameter 15 (36) 65 μm, 19 specimens measured.
Remarks. The species is distinguished based on the characteristic chain-forming cells, the vesicle being much larger than that of *Reduviasporonites catenulatus*.
Previous records. Permian, Australia (Foster 1979; Foster et al. 2002); China (Ouyang & Utting 1990); Denmark (Balme 1979); Iraq (Stolle 2007); Kenya (Hankel 1992); Paraguay (Pérez Loinaze et al. 2010); Peru (Wood & Elsik 1999); Russia (Afonin et al. 2001); Turkey (Stolle 2010); USA (Elsik 1999).

Stratigraphical occurrence. Common in the Shangsi and Zhongzai sections.

Veryhachium Deunff 1954 emend. Sarjeant & Stancliffe 1994

Type species. *Veryhachium trisulcum* (Deunff 1954) Deunff 1959

Veryhachium cylindricum Schaarschmidt 1963
Plate 2, figures 14, 15

Veryhachium cylindricum Schaarschmidt 1963, p. 64, pl. 18, figs. 8–10

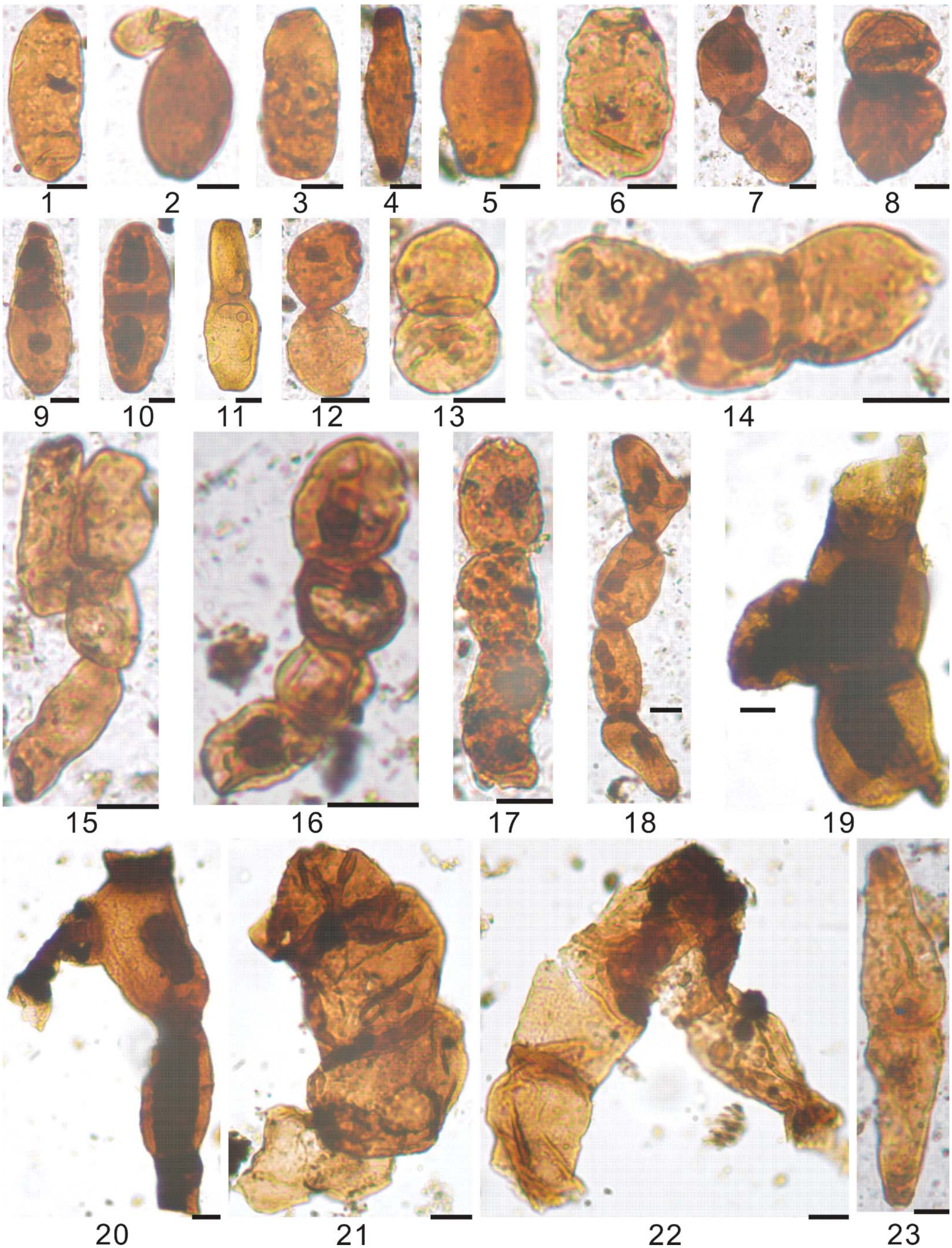
Description. The vesicle is ellipsoidal in outline. The thin wall is single-layered. Six prominent but simple processes are present around the vesicle, they are proximally wide (about 5 μm in width), and the tips are acuminate, and closed distally.
Dimensions. Vesicle diameter 15 (18) 22 μm, process length 8–12 μm, 13 specimens measured.
Remarks. This species is easily recognisable, because of its six spines that are arranged symmetrically around the vesicle. Two of them prolong the long axis of the vesicle, and the other four spines are displayed symmetrically around the short axis of the vesicle.
Previous records. Permian, Germany (Schaarschmidt 1963).
Stratigraphical occurrence. Recorded from beds 21 to 25, Shangsi section.

Veryhachium hyalodermum (Cookson 1956) Schaarschmidt 1963
Plate 2, figures 1–4

Veryhachium hyalodermum Cookson 1956, p. 188–189, pl. 1, figs. 12–16
Veryhachium hyalodermum (Cookson 1956) Schaarschmidt 1963, p. 62–63

Description. The vesicle is triangular in outline, with four processes. Three processes are present along each angle of the vesicle, and another process is attached on the central body. The processes are simple, long, and distally closed. The thin wall is single layered.
Dimensions. Vesicle diameter 10 (12) 14 μm, process length 9–15 μm, 25 specimens measured.
Remarks. Many species of *Veryhachium* with four spines or a triangular vesicle have been described, such as *V. ceratioides* Stockmans & Willière 1962,

Plate 3. Phytoplankton from the latest Permian of South China. Each scale bar is 10 μm. Figures 11–12 were taken using scanning electron microscopy (SEM); figures 1–10 and 13–21 were taken using the transmitted light microscope.1–7: *Schizosporis* sp.; 8–10: *Schizosporis scissus*; 11–12: *Dictyotidium* sp.; 13–18: *Leiosphaeridia minutissima*; 19–21: *Leiosphaeridia micrograniferа*. The section/sample numbers for all specimens are as follows. 1–10: Shangsi section/SS25-E; 11–12: Shangsi section/SS292-4; 13–14: Dongpan section/DP2-G; 15–16: Dongpan section/DP3-A; 17: Dongpan section/DP5-B; 18: Shangsi section/SS290-8-1; 19–21: Shangsi section/SS291-2.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V. europaeum Stockmans & Willière 1960, *V. leonense* Cramer 1964 and others. It is difficult to distinguish *V. hyalodermum* and *V. europaeum* solely by their vesicle outline. However, the spines of the former are obviously much longer than those of the latter.
Previous records. Permian, China (Ouyang & Utting 1990); Germany (Schaarschmidt 1963); Israel (Horowitz 1974); South Africa (Horowitz 1990); Eocene, Australia (Cookson 1956).
Stratigraphical occurrence. Common in beds 21 to 28, Shangsi section.

Veryhachium nasicum (Stockmans & Willière 1960) Stockmans & Willière 1962
Plate 2, figures 5–8

Stellinium nasicum Stockmans & Willière 1960, p. 3, pl. 1, fig. 3
Veryhachium nasicum (Stockmans & Willière 1960) Stockmans & Willière 1962, p. 52

Description. The vesicle is rectangular in outline, with five processes. Four of these processes are present at each corner of the vesicle, and another process arises from the central body; the processes are simple, short, and distally closed. The thin wall is single layered.
Dimensions. Vesicle diameter 17 (19) 22 μm, process length 5–9 μm, 21 specimens measured.
Remarks. There are many species of *Veryhachium* with a rectangular vesicle and Servais et al. (2007) attributed them to the *Veryhachium lairdii* group. *V. nasicum* is easily recognised with its characteristic four spines present at each corner, and a further spine attached on the surface of the vesicle.
Previous records. Devonian, Belgium (Stockmans & Willière 1960); China (Gao 1986); Libya (Moreau-Benoit 1984); Carboniferous, Russia (Marhoumi & Rauscher 1984); Permian, Germany (Schaarschmidt 1963).
Stratigraphical occurrence. Common in beds 21 to 25, Shangsi section.

Veryhachium quadratum Schaarschmidt 1963
Plate 2, figure 17

Veryhachium quadratum Schaarschmidt 1963, p. 63, pl. 17, figs. 8–10

Description. The vesicle is polyangular in outline. The thin wall is single-layered, with about five to eight short spines that are 2 μm wide at their base, and 1–2 μm long.
Dimensions. Vesicle diameter about 20 μm, process length 1–2 μm, one specimen measured.
Remarks. This species is very different from the other species of *Veryhachium*, because of its short spines, generally only 1–2 μm in length.
Previous records. Permian, Germany (Schaarschmidt 1963).
Stratigraphical occurrence. Present in bed 21, Shangsi section.

Veryhachium sedecimspinosum Staplin 1961
Plate 2, figures 9–10

Veryhachium sedecimspinosum Staplin 1961, p. 414, pl. 49, figs. 9–11

Description. The thin wall is single-layered, and the outline is rectangular, with five to eight processes. Four of these processes arise from each corner of the vesicle, and the other processes (two to four in number) arise from the central body. All of the processes are simple, short, and distally closed.
Dimensions. Vesicle diameter 15 (16) 17 μm, process length 7–13 μm, four specimens measured.
Remarks. Similar to *Veryhachium nasicum*, the rectangular vesicle of *V. sedecimspinosum* has four spines that arise from each corner. However, there are more (generally two to four) additional spines attached on the surface of the vesicle.
Previous records. Devonian, Canada (Staplin 1961); Permian, Germany (Schaarschmidt 1963).
Stratigraphical occurrence. Common in the Shangsi section.

Veryhachium sp.
Plate 2, figure 16

Description. The vesicle is triangular with a smooth wall. Three short spines are present at each of the angles. One or two short additional spines arise from the central body.
Dimensions. Vesicle diameter 25 μm, process length about 5 μm, one specimen measured.
Remarks. Similar to *Veryhachium hyalodermum*, *Veryhachium* sp. has a triangular vesicle, but it is much larger than the latter, and the spines are much shorter. Because only one specimen has been recovered, the species is left in open nomenclature.
Stratigraphical occurrence. Present in bed 21, Shangsi section.

Plate 4. Phytoplankton from the latest Permian of South China. Each scale bar is 10 μm. All figure images were taken using the transmitted light microscope. 1–11, 18–23: *Reduviasporonites chalastus*; 12–17: *Reduviasporonites catenulatus*. The section/sample numbers for all specimens are as follows. 1–6, 11, 14, 23: Shangsi section/TS28-17; 12–13: Xiakou section/XK254-1; 16–17: Zhongzhai section/ZZ19-3; 7–10, 15, 18–22: Shangsi section/ TS28-18.

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