

Agora Paleobotanica

Revisiting the spore assemblages from the Lower Devonian Posongchong Formation of Wenshan, Yunnan Province, southwestern China

B. Cascales-Miñana^{1*†}, J. Z. Xue^{2*}, G. Rial¹, P. Gerrienne¹, P. Huang² and P. Steemans¹

¹ Palaeobiogeology-Palaeobotany-Palaeopalynology, Department of Geology, University of Liège, Allée du 6 Août, B18 Sart Tilman, B4000 Liège, Belgium.

Email: borja.cascales-minana@univ-lille.fr

² The Key Laboratory of Orogenic Belts and Crustal Evolution, School of Earth and Space Sciences, Peking University, Beijing 100871, People's Republic of China.

Email: pkuxue@pku.edu.cn

*Corresponding author

†Current address: Evo-Eco-Paleo, UMR 8198, CNRS, University of Lille, Villeneuve d'Ascq F-59655, France.

ABSTRACT: The Lower Devonian Posongchong Formation (Wenshan, Yunnan Province, southwestern China) consists of a series of continental deposits with an outstanding plant megafossil diversity. More than 20 years ago, this formation was interpreted as 'Siegenian' (~Pragian) in age based on palynology. However, such interpretation needs further evidence because of the known differences between the dispersed spore assemblages from South China and Euramerica/northwestern Gondwana. Here, we present new dispersed spore assemblages recently recovered from the Posongchong Formation. The isolated spore diversity is highly diverse, with 18 genera and 32 species. The recognised taxa include, among others, *Ambitisporites avitus*, *Aneurospora conica*, *Aneurospora posongchongensis* sp. nov., *Aneurospora xujiachongensis*, *Apiculiretusispora plicata*, *Archaeozonotriletes chulus*, *Concentricosporites agradabilis*, *Dibolisporites echinaceus*, *Emphanisporites rotatus*, *Gneudnasporea divellomedia*, *Latosporites ovalis*, *Retusotriletes triangulatus*, *Tetrahedraletes medinensis* and *Verrucosporites polygonalis*, with *Aneurospora* and *Retusotriletes* being the most abundant forms. The known Posongchong palynoflora (previous spore data included) suggests that the Posongchong Formation assemblages can be correlated with the Pragian interval of the *polygonalis*–*wetteldorfensis* Opper Zone (PoW). This age determination is supported by the presence of index species of PoW, such as *Verrucosporites polygonalis*, *Dictyotriletes subgranifer* and *Camarozonotriletes parvus* (*sensu* Steemans, 1989), the latter being known only from the Pragian of Belgium and Germany. Recent advances in the study of the marine faunas in the overlying sequences also indicate a Pragian age for the Posongchong Formation. This new investigation of the Posongchong palynoflora highlights differences of abundance at species level between the Gondwanan–Laurussian floras during the Early Devonian.



KEY WORDS: palynoflora, phytogeography, Pragian, South China.

The Lower Devonian Posongchong Formation (Wenshan, Yunnan Province, southwestern China) comprises a series of continental clastic deposits, from which 28 vascular plant genera have been described to date (Hao & Xue 2013, table 5.1). This plant megafossil flora represents a key part of the Early Devonian diversity. Zhu *et al.* (1994) considered the Posongchong Formation to be late Pragian in age on the basis of fish assemblages. This age assignment was later supported by Gerrienne (1996) based on a biostratigraphic coefficient analysis applied to plant megafossils. The latest reviews of the Posongchong Formation also consider a Pragian age for those deposits, the middle–late Pragian time interval being the most probable datation (Hao & Xue 2013, pp. 23–24, and references therein).

Spore data are good stratigraphic indicators for correlating marine–terrestrial deposits as well providing an accurate

temporal assignment to plant megafossils. From the 1980s, this has been routinely done using the spore zonation schemes from the Old Red Sandstone Continent (Richardson & McGregor 1986) and the Ardenne-Rhenish region (Streel *et al.* 1987). Before the present study, the spore evidence from the Posongchong and Pojiao formations at the Zhichang section (Gumu Town, Wenshan) came from Wang's (1994) investigation. The author concluded that the *Apiculiretusispora plicata*–*Dictyotriletes emsiensis* assemblage zone can be recognised in the Posongchong Formation, and assigned a 'Siegenian' age (according to the original nomenclature) to this formation. To reach this conclusion, Wang (1994) correlated the relevant palynological zones of China and Laurussia (North America and Western Europe). However, the spore zonation of the Chinese formations is preliminary due to the limited data and the complexity of the geological series.

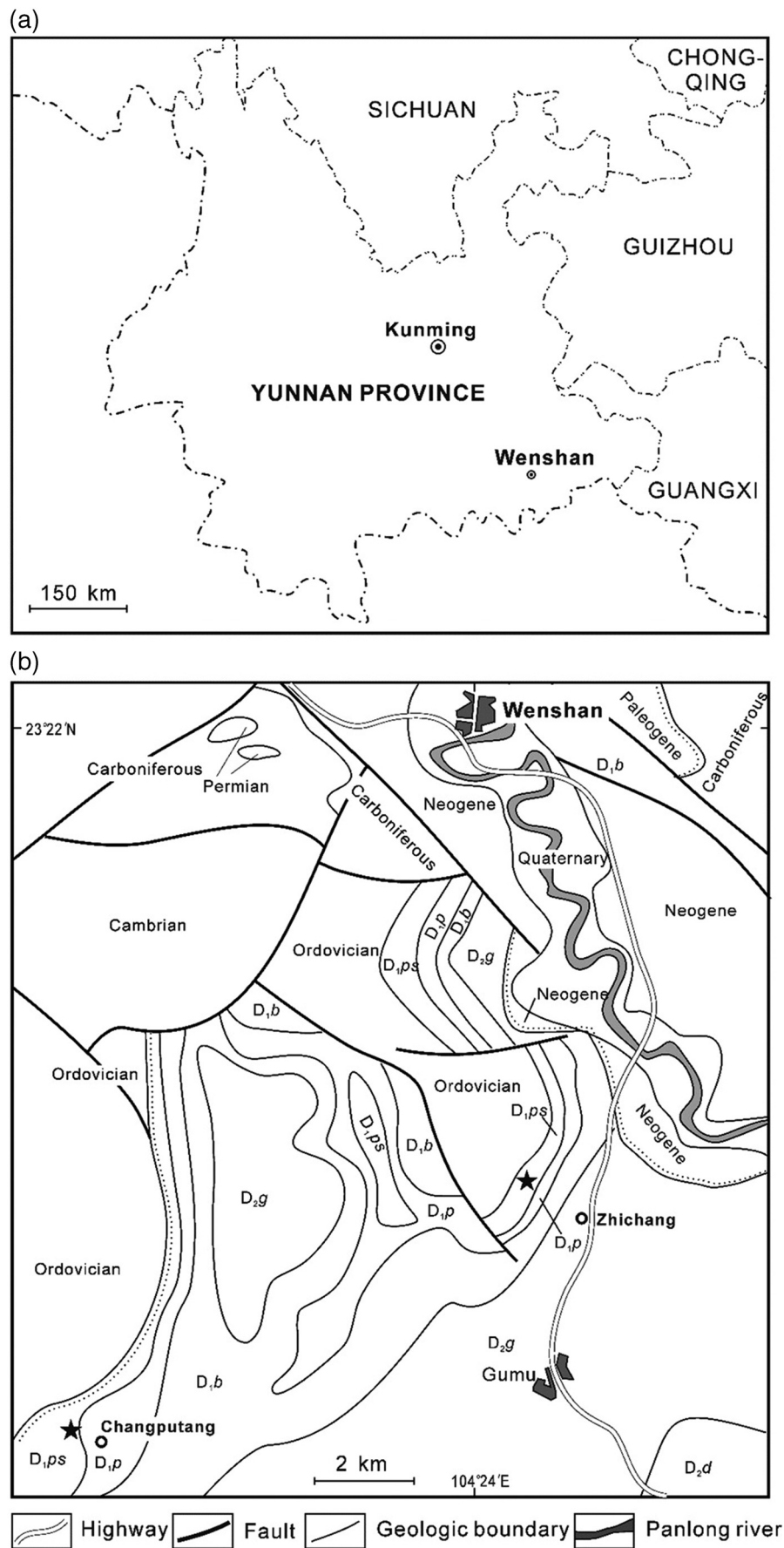


Figure 1 Map showing location of studied section: (a) general view of Yunnan Province (southwestern China) showing position of study area (Wenshan), modified from Hao & Xue (2013, fig. 2.1); (b) location of the Zhichang and Changputang sections in the Wenshan area, modified from Hao & Xue (2013, fig. 2.3). Abbreviations: D_{2d} = Middle Devonian Donggangling Formation; D_{2g} = Middle Devonian Gummu Formation; D_{1b} = Lower Devonian Bajiaoqing Formation; D_{1p} = Lower Devonian Pojiao Formation; D_{1ps} = Lower Devonian Posongchong Formation.

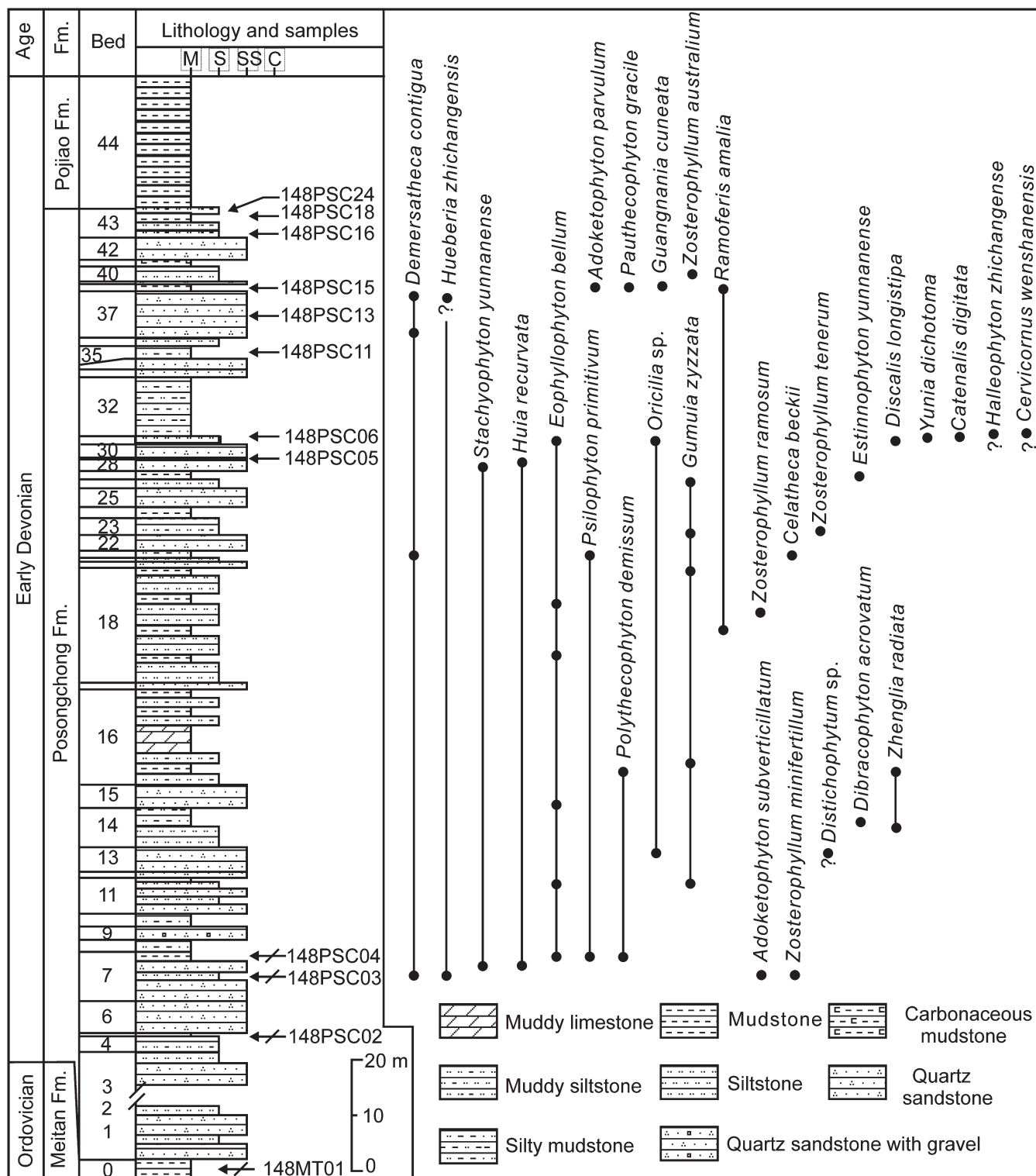


Figure 2 Stratigraphy of the Lower Devonian Posongchong Formation at the Zhichang section, Wenshan, Yunnan, southwestern China. Sampled levels indicated by arrows. Plant fossils recovered from this section are also indicated. Modified from Hao & Xue (2013, fig. 3.4).

Here, we present a new spore assemblage recently collected from the Posongchong Formation from the Zhichang and Changputang sections (Wenshan area, Yunnan Province). A new spore species is described (*Aneurospora posongchongensis* sp. nov.). This palynoflora is of significance in that (i) evidence comes from northeastern Gondwana, a palaeogeographical area where the spore diversity is less known in comparison with Laurussia, (ii) the sampled deposits correspond to the most diverse Early Devonian plant megafossil assemblages and (iii) a complex early terrestrial landscape appears well represented in the Posongchong Formation. The aim of this

study is to provide new insights into the known spore diversity and phytogeography of the Early Devonian floras, especially from northeastern Gondwana, and to reduce uncertainties about the temporal assignment of the Posongchong flora.

1. Stratigraphy, material and methods

The Lower Devonian strata of Wenshan area (southeastern Yunnan, Fig. 1a) are well exposed (Fig. 1b). The strata at the Zhichang section (Zhichang slope) include, in ascending order,

Table 1 Details of studied samples from the Posongchong Formation.

| Sample name | Grid reference | Posongchong section | Sampled level | Details | Result |
|-------------|-------------------|---------------------|-----------------------------------|-------------------------------------------------------------------------------------|----------|
| 148PSC14 | 74479/74651 | Changputang | Upper part of the Posongchong Fm. | Mudstone; <i>Zosterophyllum australianum</i> horizon of Hao & Gensel (1998, fig. 1) | Positive |
| 148PSC24 | 74475/74476/74650 | Zhichang | Bed 43 (Posongchong Fm.) | Muddy siltstone | Positive |
| 148PSC18 | 74484/74654 | Zhichang | Bed 43 (Posongchong Fm.) | Mudstone | Positive |
| 148PSC16 | 74482/74483/74653 | Zhichang | Bed 43 (Posongchong Fm.) | Gray muddy siltstone | Positive |
| 148PSC15 | 74480/74481/74652 | Zhichang | Bed 38 (Posongchong Fm.) | Dark gray mudstone; fossil site 17 of Hao & Xue (2013, table 3.2). | Positive |
| 148PSC13 | 74477/74478 | Zhichang | Bed 37 (Posongchong Fm.) | Muddy siltstone | Positive |
| 148PSC11 | 74473/74474/74649 | Zhichang | Bed 35 (Posongchong Fm.) | Dark gray laminated silty mudstone | Positive |
| 148PSC06 | 74470/74471/74648 | Zhichang | Bed 31 (Posongchong Fm.) | Mudstone; fossil site 14 of Hao & Xue (2013, table 3.2) | Positive |
| 148PSC05 | 74468/74469/74647 | Zhichang | Bed 29 (Posongchong Fm.) | Dark grey silty mudstone | Positive |
| 148PSC04 | 74467 | Zhichang | Bed 7 (Posongchong Fm.) | Silty mudstone | Negative |
| 148PSC03 | 74466 | Zhichang | Bed 7 (Posongchong Fm.) | Greenish muddy siltstone; fossil site 2 of Hao & Xue (2013, table 3.2) | Negative |
| 148PSC02 | 74465 | Zhichang | Bed 4 (Posongchong Fm.) | Greenish gray muddy siltstone | Negative |
| 148MT01 | 74472 | Zhichang | Bed 0 (Meitan Fm.) | Greenish gray mudstone | Negative |

the Posongchong, Pojiao, Bajiaoqing and Gumu formations (Fig. 1b). Details of the stratigraphic sequence of the Posongchong Formation are provided in Figure 2. The samples analysed in this study were mainly collected from this section (Figs 1b, 2). The Posongchong Formation at the Zhichang section unconformably overlies the quartzose sandstone of the marine Lower Ordovician Meitan Formation, and has a conformable contact with the overlying marine Pojiao Formation (Jin *et al.* 2005; Hao & Xue 2013). Various endemic Early Devonian plants have been discovered from this section, e.g., *Adoketophyton subverticillatum* (Hao *et al.* 2003), *Gumuiia zyzzata* (Hao 1989), *Guangnania cuneata* (Wang & Hao 2002), *Ramoforis amalia* (Hao & Xue 2011) and *Zhenglia radiata* (Hao *et al.* 2006; Fig. 2). The Changputang section (Tiechan slope) was also investigated (Fig. 1b). The stratigraphy and the lithology of this section are similar to those of the Zhichang section (Hao & Gensel 1998; Jin *et al.* 2005). Several endemic plants have also been described from the Changputang section, e.g., *Catenalis digitata* (Hao & Beck 1991) and *Celatheca beckii* (Hao & Gensel 1995).

Altogether, we collected 12 palynological samples from the Zhichang section and one from the Changputang section (see sample details in Table 1). Rock samples (approximately 30 g each) were treated using standard HF-HCL-HF acid maceration. Following maceration, the remaining residue was briefly oxidised in HNO₃ and KClO₃ and sieved through a 12 µm mesh to remove particles of organic matter and fine mineral matter. Afterwards, a 25 % HCl hot bath was used to eliminate the remaining fine mineral particles. All samples were finally rinsed through a 12 µm mesh. The remaining organic residue was rich in well-preserved palynomorphs dominated by spores and phytodebris. No acritarchs were found.

2. Systematic palaeontology

Genus *Aneurospora* Strel emend. Richardson *et al.*, 1982

Type species. *Aneurospora goensis* Strel, 1964

Aneurospora posongchongensis sp. nov.
(Plate 1, 4–8)

Holotype. Plate 1, 8 (slide 74482, England Finder M43/2).

Paratype. Plate 1, 7 (slide 74482, England Finder H43/1).

Type locality and horizon. Zhichang section, Wenshan, Yunnan Province, southwestern China; upper part of the Posongchong Formation.

Age. Lower Devonian; Pragian (but not early).

Derivation of name. From the formation name.

Diagnosis. Trilete spore ornamented distally by regularly distributed baculae with a conical top. The base of the baculae is polygonal, 0.5–1.0 µm in diameter and separated by more than 0.5–3.0 µm. The cingulum is 2.0–3.5 µm wide.

Description. Trilete spore with subcircular to subtriangular amb, with an equatorial cingulum of 2–3.5 µm. Laesurae straight, simple, 2/5 to 7/10 of the length of spore radius. Proximal face laevigate. Distal and equatorial regions are sculptured with evenly distributed conical baculae, 0.5–1.0 µm wide and 1.0–1.5 µm high. The base of the baculae is polygonal and the distance between sculptures is irregular, ranging from 0.5 to 3.0 µm. The sculptures tend to be concentrated in the centre of the distal face. On some specimens, the cingulum is not clearly visible.

Dimensions. 27–(33)–43 µm; 20 specimens measured.

Comparison and remarks. Some specimens are similar in size and number of baculae to *Aneurospora conica* (Lu & Ouyang) Wellman *et al.*, 2012. However, the new species bears a cingulum and the base of the baculae is polygonal. *Aneurospora posongchongensis* sp. nov. is close to *Aneurospora* cf. *tojoides* (Cramer) Steemans, 1989, but it is smaller, with a smaller number and a lower density of baculae; furthermore, it lacks prominent labra.

Aneurospora sp. A
(Plate 1, 10–11)

Description. Trilete spore with sub-circular amb. Equatorial cingulum up to 2 µm wide. Laesurae straight and simple, and extending up to the margin of the amb. Proximal face laevigate. Distal and equatorial regions are sculptured with irregularly distributed conical baculae separated by up to 5 µm. The base of the cone is polygonal/rounded, 1.0–1.5 µm wide and 1.0–1.5 µm apart.

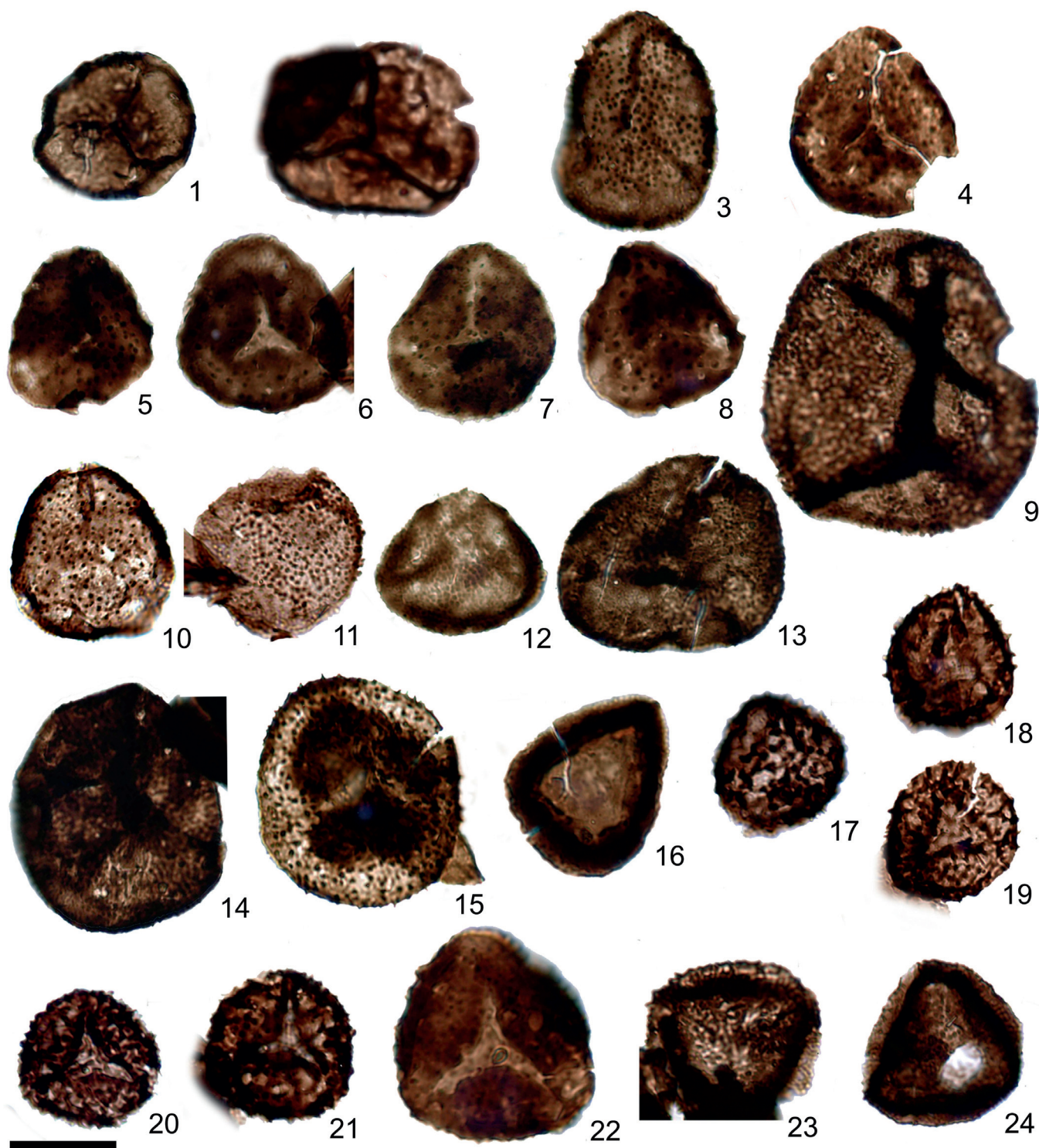


Plate 1 Posongchong spore diversity (I). 1–2. *Ambitisporites avitus* Hoffmeister, 1959 (74474 V36/1, 74469 M39/2). 3. *Aneurospora conica* (Lu & Ouyang) Wellman *et al.*, 2012 (74473 N36/2, 74474 H45/2). 4–8. *Aneurospora posongchongensis* sp. nov. (74482 H39/0, 74482 C50/0, 74482 H43/1, 74482 D38/2, 74482 M43/2-Holotype). 9. *Aneurospora xuchiachongensis* Wellman *et al.*, 2012 (74480 D49/3). 10–11. *Aneurospora* sp. A (74473 E29/1, 74474 P47/1, 74474 H45/2). 12. *Aneurospora* sp. B (74475 E37/0). 13–14. *Apiculiretusispora plicata* (Allen) Streeel, 1967 (74468 G52/0–4, 74470 G41/0). 15. *Apiculiretusispora* cf. *arabiensis* Al-Ghazi, 2009 (74473 S5/0 4). 16. *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, 1969 (74477 U40/2). 17–21. *Biornatispora* cf. *dubia* (McGregor) Steemans 1989 (74473 L51/0, 74473 R35/4, 74474 D44/1, 74480 H47/0, 7448/0 D48/4). 22. *Camarozonotriletes parvus* Owens, 1971 (*sensu* Steemans, 1989) (74477 J32/3). 23–24. *Camarozonotriletes* sp. A (74469 G35/4, 74473 O41/4). Slides housed in the Palaeobiogeology–Palaeobotany–Palaeopalynology Unit, Liege University collections. Scale bar = 20 μ m.

Dimensions. 30–(33)–37 µm; three specimens measured.

Comparison. *Cymbosporites proteus* McGregor & Camfield, 1976 has more dense and regular ornamentation than *Aneurospora* sp. A. *Aneurospora* cf. *tojoides* (Cramer) Steemans, 1989 has prominent labra and the separation between the conii is regular. *Aneurospora* sp. A and *Aneurospora posonchongensis* are similar in amb and size, but differ in the ornamentation. The base of the conii in *Aneurospora* sp. A is slightly larger (1.0 to 1.5 µm) than in *Aneurospora posonchongensis* (0.5 to 1.0 µm).

Dimensions. 30–(33)–37 µm; three specimens measured.

Aneurospora sp. B
(Plate 1, 12)

Description. Trilete spore with subtriangular amb. Equatorial cingulum up to 2.5 µm wide. Laesurae straight, simple, extending 2/5 to 7/10 of the length of the spore radius. Proximal face laevigate. Distal and equatorial regions sculptured with grana. The base of the sculptures is rounded to polygonal, 0.5 µm wide, up to 0.5 µm high and 0.5 µm apart. The verrucae are connected at their base, forming convoluted muri, up to 4.0 µm long.

Dimensions. 35 µm; one specimen measured.

Genus *Camarozonotriletes* Naumova ex Naumova, 1953

Type species. *Camarozonotriletes devonicus* Naumova, 1953
Camarozonotriletes sp. A
(Plate 1, 23–24)

Description. Trilete spores with amb sub-circular with rounded corners. Laesurae visible in one of the specimens, simple, straight and extending to the inner margin of the equatorial cingulum, 2.5 µm wide. The exine is equatorially and distally granulate. The sculptural elements are less than 1.0 µm high. Some sculptures are connected, forming rugulate ornaments of no more than five elements.

Dimensions. 30–(31)–32 µm; two specimens measured.

Genus *Chelinospora* Allen emend. McGregor & Camfield, 1976

Type species. *Chelinospora concinna* Allen, 1965
Chelinospora sp. A
(Plate 2, 2)

Description. Amb sub-circular. Laesurae thick, extending to the end of the inner body. Patina sculptured with broad reticulum. Muri 0.5 µm wide and 1.0 µm high. At junctions, the muri widen and form rounded verrucae.

Dimensions. 21.5 µm; one specimen measured.

Genus *Convolutispora* Hoffmeister et al., 1955

Type species. *Convolutispora subtilis* Owens, 1971
Convolutispora sp. A
(Plate 2, 4)

Description. Amb circular. Distal face with convoluted ornamentation. The ornamentation is formed by grana closely attached together and forming rugulae, 0.5 µm apart and 1.0 µm high.

Dimensions. 42 µm; one specimen measured.

Convolutispora? sp. B
(Plate 2, 5)

Description. Amb circular. Distal face densely ornamented. The sculpture is formed by grana closely attached together of no more than five or six elements forming rugulae, up to 0.5 µm wide, up to 0.5 µm apart and 1.0 µm high.

Comparison. *Convolutispora?* sp. B and *Convolutispora* sp. A are similar in size, but in *Convolutispora?* sp. B, the size of the grana is larger and the number of attached elements does not exceed six.

Dimensions. 44 µm; one specimen measured.

Genus *Dibolisporites* Richardson, 1965

Type species. *Dibolisporites echinaceus* (Eisenack)
Richardson, 1965
Dibolisporites sp. A
(Plate 2, 8)

Description. Trilete spores with amb sub-triangular. The exine is 3.0–3.5 µm thick equatorially. Equatorial and distal region is ornamented. The sculptures consist of biform ornaments with a cone 3.5–4.0 µm wide at base, 2.5–3.0 µm high and surmounted by a spine 0.5 µm long.

Dimensions. 50 µm; one specimen measured.

Dibolisporites sp. B
(Plate 2, 9)

Description. The preservation of the spore does not allow for the precise defining of the amb. Equatorial and distal regions ornamented. The sculptures consist of biform ornaments: cones 1.0 µm wide at the base, 2.0–3.0 µm high and surmounted by spines 0.5 µm high. The specimen presents zones where the ornamentation is widely separated or absent.

Comparison. *Dibolisporites* sp. A is covered by a dense ornamentation and the sculptures are wider at their base. It is possible that *Dibolisporites* sp. A and *Dibolisporites* sp. B represent the same species because they show comparable size and sculptures, but this is not possible to ascertain because there is currently only one specimen for each.

Dimensions. 50 µm; one specimen measured.

Genus *Grandispora* Hoffmeister et al. emend.
Neves & Owens, 1966

Type species. *Grandispora spinosa* Hoffmeister et al., 1955
Grandispora sp. A
(Plate 2, 13–14)

Description. Camerate spore with a sub-circular amb. Laesurae not visible. The inner body diameter is 2/3 to 4/7 of the total diameter. Inner body is laevigate. The outer layer is sculptured by grana. Elements are up to 1.0 µm wide, round to polygonal at the base and up to 0.5 µm apart.

Comparison. *Grandispora* sp. A as described in Steemans et al. (2008) is similar but smaller in size (25–(29)–32 µm).

Dimensions. 30–(40)–50 µm; two specimens measured.

Genus *Retusotriletes* Naumova emend. Strel, 1964

Type species. *Retusotriletes simplex* Naumova, 1953
Retusotriletes sp.
(Plate 3, 2)

Description. Amb sub-circular. Laesurae straight and thin, up to 0.5 µm wide, extending up to the end of the amb. Proximal and distal faces are laevigate.

Dimensions. 27–(32.5)–40 µm; six specimens measured.

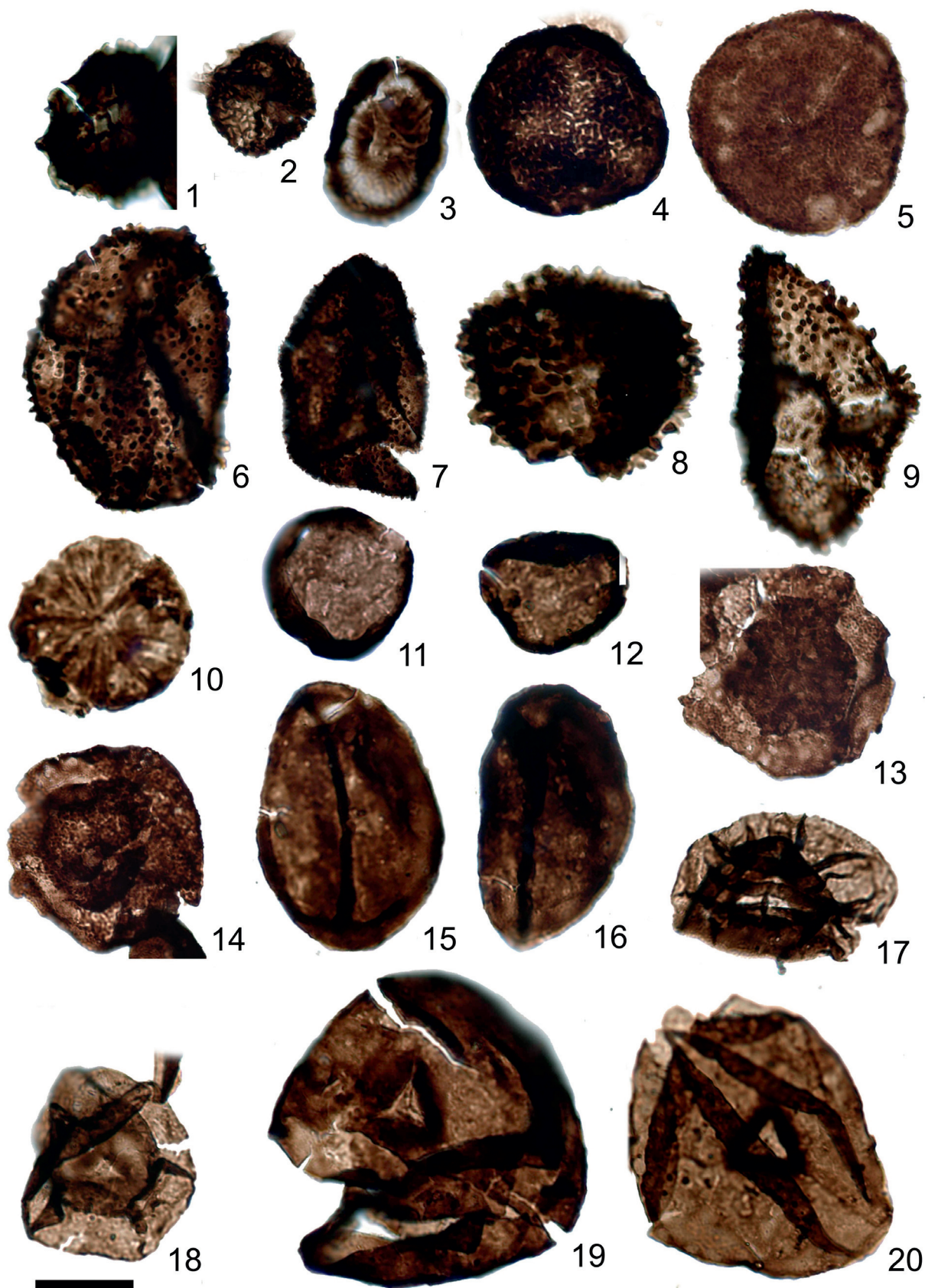


Plate 2 Posongchong spore diversity (II). 1. *Camarozonotriletes?* cf. *luii* Wellman *et al.*, 2012 (74481 Q43/2). 2. *Chelinospora* sp. A. (74481 L44/1). 3. *Concentricosporites agradabilis* (Rodríguez) Rodríguez, 1983 (74649 H39/1). 4. *Convolutispora* sp. A (74474 G33/2). 5. *Convolutispora?* sp. B (74474 L46/3). 6–7. *Dibolisporites echinaceus* (Eisenack) Richardson, 1965 (74470 M36/3, 74471 F33/2). 8. *Dibolisporites* sp. A (74482 Q37/1). 9. *Dibolisporites* sp. B (74482 K30/0). 10. *Emphanisporites rotatus* (McGregor) McGregor, 1973 (74482 E41/2). 11–12. *Gneudnaspora divellomedia* (Chibrikova) Balme, 1988 (74468 T51/1, 74473 O39/4). 13–14. *Grandispora* sp. A (74481 E49/2, 74481 Q37/4). 15–16. *Latosporites ovalis* Breuer, 2007 (74480 K40/4, 74470 P42/0). 17–18. *Leiozonospora xichongensis* Wellman *et al.*, 2012 (74481 Q43/2, 74474 E36/03). 19–20. *Retusotriletes triangulatus* (Streel) Streel, 1967 (74473 D28/0, 74471 H28/1). Slides housed in the Palaeobiogeology–Palaeobotany–Palaeopalynology Unit, Liege University collections. Scale bar = 20 μ m.

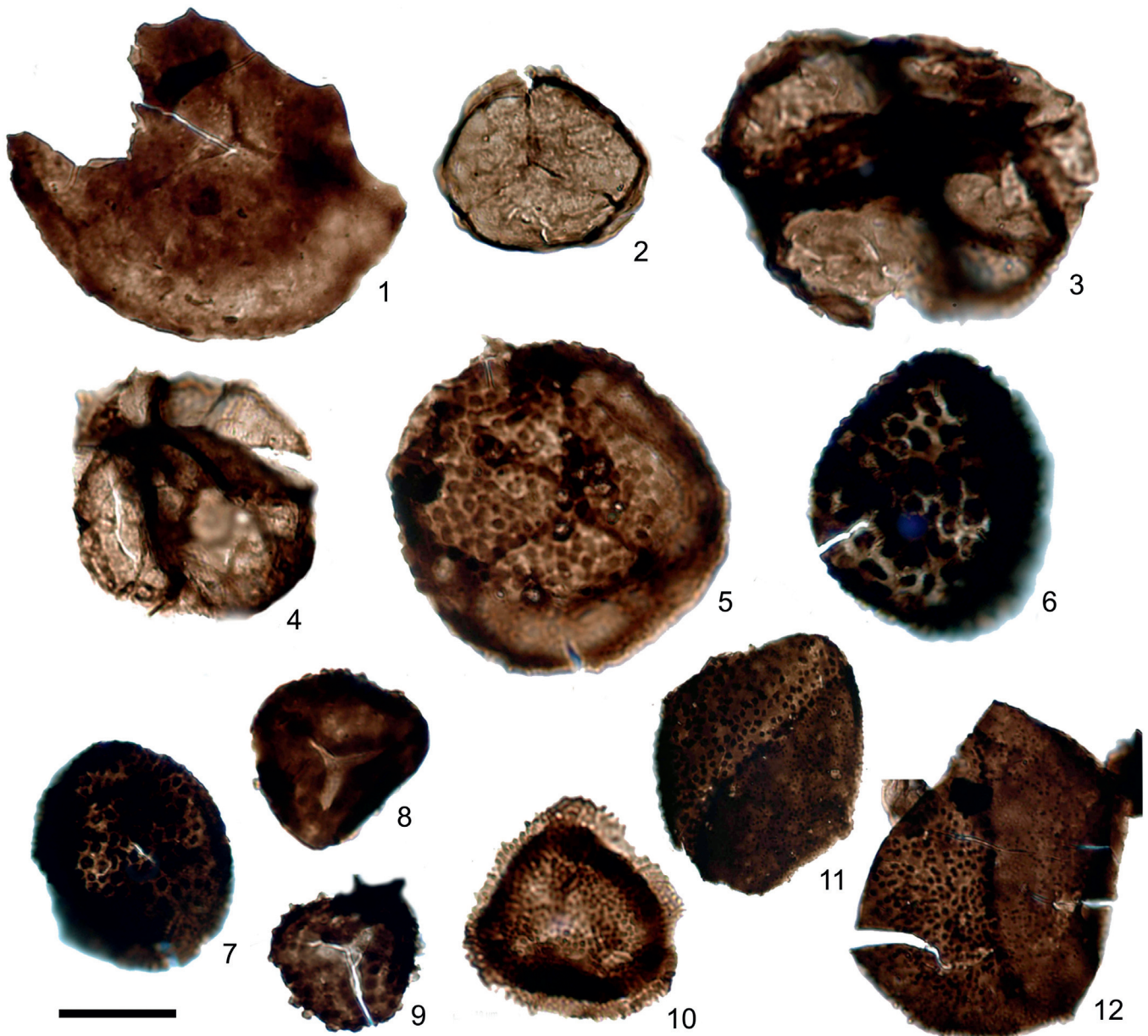


Plate 3 Posongchong spore diversity (III). 1. *Retusotriletes* cf. *rotundus* Streele emend. Lele & Streele, 1969 (74475 H38/3). 2. *Retusotriletes* sp. (74474 G37/04). 3–4. *Tetraedraletes medinensis* Strother & Traverse emend. Wellman & Richardson, 1993 (74474 N39/4, 74477 R35/4). 5. *Verrucosporites polygonalis* Lanninger, 1968 (74482 H50/2). 6–7. *Verrucosporites* cf. *polygonalis* Lanninger, 1968 (74480 N47/4, 74480 H33/1). 8–9. *Verrucosporites* sp. (74470 V30/0, 74473 Q40/0–4). 10. Specimen 74483 X48/4 (zonate spore). 11–12. Fragment of spore showing distinct types of ornament on two distinct parts (74474 F47/2, 74474 Q51/1). Wellman *et al.* (2012, fig. 8N) illustrated and commented on a similar phenomenon. Slides housed in the Palaeobiogeology–Palaeobotany–Palaeopalynology Unit, Liege University collections. Scale bar = 20 μ m.

Genus *Verrucosporites* Ibrahim emend. Smith, 1971

Type species. *Verrucosporites verrucosus* (Ibrahim)
Ibrahim, 1933
Verrucosporites sp.
(Plate 3, 8–9)

Description. Amb sub-triangular. Laesurae curved and 2.5 μ m thick, 2/5 to 3/5 of the length of the amb radius. Proximo-equatorial and distal regions are sculptured with verrucae and pilae, 2.5 to 5.0 μ m wide, 2.0 to 3.5 μ m high and up to 0.5 μ m apart.

Dimensions. 30–(31)–32 μ m; two specimens measured.

3. Spore diversity from the Posongchong Formation

Nine of the 13 samples were productive (Table 1). The palynological analysis shows a high spore diversity, with 18 genera and 32 species. The dispersed spores include: *Ambitisporites avitus* (Plate 1, 1–2), *Aneurospora conica* (Plate 1, 3), *Aneurospora posongchongensis* sp. nov. (Plate 1, 4–8), *Aneurospora xuchiachongensis* (Plate 1, 9), *Aneurospora* sp. A (Plate 1, 10–11), *Aneurospora* sp. B (Plate 1, 12), *Apiculiretusispora plicata* (Plate 1, 13–14), *Apiculiretusispora* cf. *arabiensis* (Plate 1, 15), *Archaeozonotriletes chulus* (Plate 1, 16), *Biornatispora* cf. *dubia* (Plate 1, 17–21), *Camarozonotriletes parvus* (Plate 1, 22), *Camarozonotriletes* sp. A (Plate 1, 23–24), *Camarozonotriletes?* cf. *huii* (Plate 2, 1), *Chelinospora* sp. A. (Plate 2, 2), *Concentrico-*

Table 2 Spore taxa reported by Wang (1994) from the Posongchong Formation, Wellman *et al.* (2012) from the Xujiachong Formation and this study (including those common to Wang 1994).

| This study | Posongchong Formation | Xujiachong Formation |
|---------------------------------------------------------------------------------------|-------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| | Wang 1994 | Wellman <i>et al.</i> 2012 |
| <i>Ambitisporites avitus</i> Hoffmeister 1959 | <i>Apiculiretusispora plicata</i> (Allen) Streele 1967 | <i>Ambitisporites avitus</i> Hoffmeister 1959 |
| <i>Aneurospora conica</i> (Lu & Ouyang) Wellman <i>et al.</i> 2012 | <i>Apiculiretusispora pygmaea</i> McGregor 1973 | <i>Aneurospora conica</i> (Lu & Ouyang) comb. nov. |
| <i>Aneurospora posongchongensis</i> sp. nov. | <i>Apiculiretusispora wenshanensis</i> sp. nov. | <i>Aneurospora xuchiachongensis</i> sp. nov. |
| <i>Aneurospora xuchiachongensis</i> Wellman <i>et al.</i> 2012 | <i>Brochotriletes</i> sp. B of McGregor 1973 | <i>Apiculiretusispora brandtii</i> Streele 1964 |
| <i>Aneurospora</i> sp. A | <i>Brochotriletes?</i> <i>foveolatus</i> Naumova 1953 | <i>Apiculiretusispora plicata</i> (Allen) Streele 1967 |
| <i>Aneurospora</i> sp. B | <i>Calamospora</i> cf. <i>microrugosa</i> (Ibrahim) Schopf <i>et al.</i> 1944 | <i>Archaeozonotriletes chulus</i> (Cramer) Richardson & Lister 1969 |
| <i>Apiculiretusispora plicata</i> (Allen) Streele 1967 | <i>Calamospora</i> cf. <i>panucea</i> Richardson 1965 | ? <i>Brochotriletes rarus</i> Arkhangelskaya 1978 |
| <i>Apiculiretusispora</i> cf. <i>arabiensis</i> Al-Ghazi 2009 | <i>Camarozonotriletes sextantii</i> McGregor & Camfield 1976 | <i>Camarozonotriletes?</i> cf. <i>lunii</i> sp. nov. |
| <i>Archaeozonotriletes chulus</i> (Cramer) Richardson & Lister 1969 | <i>Camptozonotriletes</i> cf. <i>caperatus</i> McGregor 1973 | <i>Cheilotetras caledonica</i> Wellman & Richardson 1993 |
| <i>Biornatispora</i> cf. <i>dubia</i> (McGregor) Steemans 1989 | <i>Camptozonotriletes</i> sp. G. of Streele <i>et al.</i> 1981 | <i>Chelinospora ouyangii</i> sp. nov. |
| <i>Camarozonotriletes parvus</i> Owens 1971 (sensu Steemans 1989) | <i>Crissisporites guangxiensis</i> Gao 1978 | <i>Dibolisporites</i> cf. <i>echinaceus</i> (Eisenack) Richardson 1965 |
| <i>Camarozonotriletes</i> sp. A | <i>Cyclogranisporites</i> sp. | <i>Dictyotriletes emsiensis?</i> (Allen) McGregor 1973 |
| <i>Camarozonotriletes?</i> cf. <i>lunii</i> Wellman <i>et al.</i> 2012 | <i>Cymbosporites echinatus</i> Richardson & Lister 1969 | ? <i>Dictyotriletes favosus</i> McGregor & Camfield 1976 |
| <i>Chelinospora</i> sp. A. | <i>Cymbosporites raistrickiaeformis</i> (Schultz) Steemans 1982 | <i>Dictyotriletes</i> sp. A |
| <i>Concentricosisporites agradabilis</i> (Rodriguez) Rodriguez 1983 | <i>Dibolisporites echinaceus</i> (Eisenack) Richardson 1965 | <i>Latosporites ovalis</i> Breuer <i>et al.</i> 2007 |
| <i>Convolutispora</i> sp. A | <i>Dibolisporites eifeliensis</i> (Lanninger) McGregor 1973 | <i>Leiozosterospora xichongensis</i> sp. nov. |
| <i>Convolutispora?</i> sp. B | <i>Dictyotriletes emsiensis</i> (Allen) McGregor 1973 | <i>Pseudodyadospora petasus</i> Wellman & Richardson 1993 |
| <i>Dibolisporites echinaceus</i> (Eisenack) Richardson 1965 | <i>Dictyotriletes gorgoneus</i> Cramer 1967 | <i>Retusotriletes</i> cf. <i>triangulatus</i> (Streele) Streele 1967 |
| <i>Dibolisporites</i> sp. A | <i>Dictyotriletes subgranifer</i> McGregor 1973 | <i>Retusotriletes</i> cf. <i>rotundus</i> Streele emend. Lele & Streele 1969 |
| <i>Dibolisporites</i> sp. B | <i>Emphanisporites</i> cf. <i>decoratus</i> Allen 1965 | <i>Retusotriletes</i> sp. A |
| <i>Emphanisporites rotatus</i> (McGregor) McGregor 1973 | <i>Emphanisporites</i> cf. <i>neglectus</i> Vigran 1964 | <i>Tetraedraletes medinensis</i> Strother & Traverse emend. Wellman & Richardson 1993 |
| <i>Gneudnaspora divellomedia</i> (Chibrikova) Balme 1988 | <i>Punctatisporites</i> sp. | <i>Verrucosisporites megaplatyverruca</i> Lu and Ouyang 1976 |
| <i>Grandispora</i> sp. A | <i>Raistrickia</i> sp. | <i>Verrucosisporites polygonalis</i> Lanninger 1968 |
| <i>Latosporites ovalis</i> Breuer <i>et al.</i> 2007 | <i>Retusotriletes rotundus</i> Streele emend. Lele & Streele 1969* | |
| <i>Leiozonospora xichongensis</i> Wellman <i>et al.</i> 2012 | <i>Retusotriletes warringtonii</i> Richardson & Lister 1969 | |
| <i>Retusotriletes triangulatus</i> (Streele) Streele 1967 | <i>Retusotriletes</i> cf. <i>triangulatus</i> (Streele) Streele 1967 | |
| <i>Retusotriletes</i> cf. <i>rotundus</i> Streele emend. Lele & Streele 1969 | <i>Verrucosisporites polygonalis</i> Lanninger 1968 | |
| <i>Retusotriletes</i> sp. | | |
| <i>Tetraedraletes medinensis</i> Strother & Traverse emend. Wellman & Richardson 1993 | | |
| <i>Verrucosisporites polygonalis</i> Lanninger 1968 | | |
| <i>Verrucosisporites</i> cf. <i>polygonalis</i> Lanninger 1968 | | |
| <i>Verrucosisporites</i> sp. | | |

* *Retusotriletes rotundus* (Streele) Streele 1967 in original source.

sisporites agradabilis (Plate 2, 3), *Convolutispora* sp. A (Plate 2, 4), *Convolutispora?* sp. B (Plate 2, 5), *Dibolisporites echinaceus* (Plate 2, 6–7), *Dibolisporites* sp. A (Plate 2, 8), *Dibolisporites* sp. B (Plate 2, 9), *Emphanisporites rotatus* (Plate 2, 10), *Gneudnaspora divellomedia* (Plate 2, 11–12), *Grandispora* sp. A (Plate 2, 13–14), *Latosporites ovalis* (Plate 2, 15–16), *Leiozonospora xichongensis* (Plate 2, 17–18), *Retusotriletes triangulatus* (Plate 2, 19–20), *Retusotriletes* cf. *rotundus* (Plate 3, 1), *Retusotriletes*

sp. (Plate 3, 2), *Tetraedraletes medinensis* (Plate 3, 3–4), *Verrucosisporites polygonalis* (Plate 3, 5), *Verrucosisporites* cf. *polygonalis* (Plate 3, 6–7) and *Verrucosisporites* sp. (Plate 3, 8–9). Interestingly, a zonate spore (Plate 3, 10) and several small fragments of spores showing distinct types of ornamentation are also observed (Plate 3, 11–12) – a phenomenon previously illustrated and commented upon by Wellman *et al.* (2012, fig. 8N).

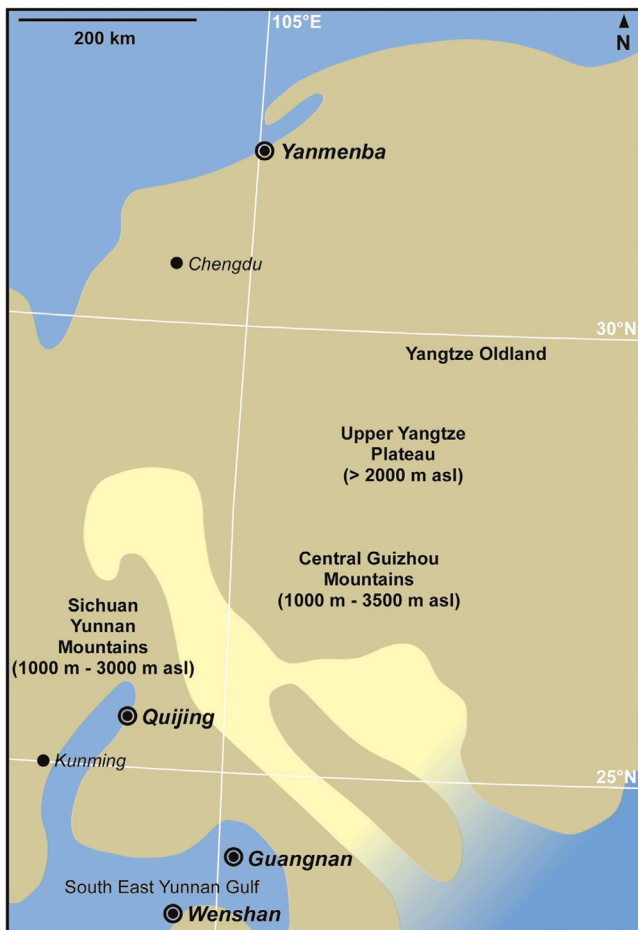


Figure 3 Palaeogeographical map showing the distribution of the major outcrops of fossil floras (Whenshan and Guangan, Posongchong Formation; Quijing, Xujiachong Formation; Yanmenba, Pingyipu Group) of the South China Plate. Green, blue and yellow colours represent land, shallow seas and estuarine conditions, respectively. Modified from Edwards *et al.* (2016).

Wang (1994) previously documented 27 spore taxa from the Posongchong Formation (Table 2). Our palynoflora shares three species (*Apiculiretusispora plicata*, *Dibolisporites echinaceus*, *Verrucosporites polygonalis*) with Wang's result. Amongst the spores described by Wang (1994), we think that seven of his taxa could be re-interpreted as follows: *Brochotriletes* sp. B (=cf. *Biornatispora dubia* in the present study), *Camptozonotriletes* cf. *caperatus* (= ?*Camptozonotriletes* cf. *caperatus*), *Camptozonotriletes* sp. G (=cf. *Camptozonotriletes macrospinus*), *Crissisporites guangxiensis* (= ?*Crissisporites guangxiensis*), *Cyclogranisporites* sp. (= ?*Cyclogranisporites* sp.), *Cymbosporites raistrickiaeformis* (= *Dibolisporites wetteldorfensis*) and *Punctatisporites* sp. (= *Retusotriletes* spp.). The spore diversity of the Posongchong Formation also includes 17 other taxa from Wang's (1994) study, namely: *Apiculiretusispora pygmaea*, *Apiculiretusispora weenshanensis*, *Brochotriletes? foveolatus*, *Calamospora* cf. *microrugosa*, *Calamospora* cf. *panucea*, *Camarozonotriletes sextantii*, *Cymbosporites echinatus*, *Dibolisporites eifeliensis*, *Dictyotriletes emsiensis*, *Dictyotriletes gorgoneus*, *Dictyotriletes subgranifer*, *Emphanisporites* cf. *decoratus*, *Emphanisporites* cf. *neglectus*, *Raistrickia* sp., *Retusotriletes* cf. *triangulatus*, *Retusotriletes rotundus* and *Retusotriletes warringtonii*. Thus, combining the results of this study and Wang (1994), the currently known Posongchong spore diversity is composed of at least 56 different morphological species belonging to 28 genera (see supplementary material for the list (available at <https://doi.org/10.1017/S1755691018000233>),

which is consistent with the impressive plant diversity and disparity documented from this formation (Fig. 2).

Wellman *et al.* (2012) recently studied the spore diversity of the Xujiachong Formation from Yunnan Province (see Table 2), which is more or less coeval with the Posongchong Formations (Hao & Xue 2013, table 2.1). Moreover, outcrops of the Xujiachong and Posongchong formations (Quijing and Wenshan, respectively) are located in adjacent zones within the South China Plate (Fig. 3). At least 12 spore species (*Ambitisporites avitus*, *Aneurospora conica*, *Aneurospora xujiachongensis*, *Apiculiretusispora plicata*, *Archaeozonotriletes chulus*, *Camarozonotriletes? cf. luii*, *Latosporites ovalis*, *Leiozosterospora xichongensis*, *Retusotriletes* cf. *triangulatus*, *Retusotriletes* cf. *rotundus*, *Tetrahedraletes medinensis* and *Verrucosporites polygonalis*), which represents around 52 % of observed spore diversity from the Xujiachong Formation, have also been collected from the Posongchong Formation.

4. Description of palynomorph assemblages

The distribution and abundance of the spore taxa within the studied samples are shown in Table 3. The spore assemblages are dominated by crassitate apiculate spores (*Aneurospora* spp.). This spore group represents the maximum observed values of abundances (e.g., 77.5 % in sample 148PSC24). Three *Aneurospora* species are present, *Aneurospora conica*, *Aneurospora posongchongensis* sp. nov. and *Aneurospora xujiachongensis*, but only one of them (*Aneurospora posongchongensis*) shows high abundance values (25.5 % and 29.5 % in samples 148PSC16 and 148PSC18, respectively). The second dominant group includes laevigate retusoid spores (*Retusotriletes* spp.). Because of its morphological simplicity, this spore group is difficult to discriminate. Indeed, only a well-defined species (*Retusotriletes triangulatus*) was identified. It shows high abundance values (14.5–24 % in samples 148PSC11, 148PSC13 and 148PSC14). The third most characteristic group consists of the apiculate retusoid spores (*Apiculiretusispora* spp.). Two species are recognised (*Apiculiretusispora* cf. *arabiensis* and *Apiculiretusispora plicata*), but only the latter is quantifiable. *Dibolisporites*, *Verrucosporites* or *Archaeozonotriletes* are uncommon. For instance, *Archaeozonotriletes chulus* is only quantifiable in a single sample (2.5 % in sample 148PSC13). Interestingly, some specimens of the simple laevigate monolete spore, *Latosporites ovalis*, are present. They occur in four samples (148PSC5, 148PSC6, 148PSC11, 148PSC15; 0.5–1.5 %). Cryptospores are also present, but the only representatives are hilate cryptospores (*Gneudnaspora divellomedia*) and permanent tetrads (*Tetrahedraletes medinensis*).

5. Biostratigraphical interpretation

The *Apiculiretusispora plicata*–*Dictyotriletes emsiensis* (PE) zone recognised from the Posongchong Formation by Wang (1994) correlates with the Pragian of the Old Red Sandstone Continent (Streel 1967; Steemans 1981, 1989; Streel *et al.* 1981, 1987; Richardson & McGregor 1986; Fig. 4). Definitively, the PE zone according to Wang (1994) correlates with the *polygonalis*–*emsiensis* Spore Assemblage Biozone (PE) *sensu* Richardson & McGregor (1986) and the equivalent *polygonalis*–*wetteldorfensis* Opperl Zone (PoW) *sensu* Streel *et al.* (1987) (Fig. 4). The PE/PoW spore assemblage is considered early (but not earliest) Pragian to? earliest Emsian in age (Wellman 2006; Wellman *et al.* 2012).

The temporal distribution of the key Posongchong spores is presented in Figure 5. Our results suggest that the time interval covered by the Posongchong spore assemblages corresponds to

Table 3 Distribution and abundance (in percentage) of the spore taxa in the studied samples. P, present but not featured in counts.

| Spore taxon | 148PSC | 148PSC | 148PSC | 148PSC | 148PSC | 148PSC | 148PSC | 148PSC | 148PSC |
|-------------------------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | 5 | 6 | 11 | 13 | 14 | 15 | 16 | 18 | 24 |
| <i>Ambitisporites avitus</i> | 5 | 6 | 1.5 | 6.5 | P | 4 | 4 | | 0.5 |
| <i>Ambitisporites</i> spp. | 14 | 14 | | 6 | | 11.5 | 4.5 | | 4 |
| <i>Aneurospora conica</i> | 1.5 | 0.5 | P | | | P | | | |
| <i>Aneurospora posongchongensis</i> | | | P | | | 2 | 25.5 | 29.5 | 16 |
| <i>Aneurospora xujiachongensis</i> | 5 | 5 | 1.5 | 4 | 2 | 6.5 | 1 | 0.5 | |
| <i>Aneurospora</i> sp. A | | | P | | | | | | |
| <i>Aneurospora</i> sp. B | | | | P | | | | | |
| <i>Aneurospora</i> spp. | 19 | 25.5 | 19.5 | 29 | 30 | 25.5 | 40 | 70 | 77.5 |
| <i>Apiculiretusispora plicata</i> | 6 | P | P | 2 | 6 | 1.5 | | | |
| <i>Apiculiretusispora</i> cf. <i>arabiensis</i> | | | P | | | | | | |
| <i>Apiculiretusispora</i> spp. | 9 | 1 | 6 | | 9 | | | | |
| <i>Archaeozonotriletes chulus</i> | | P | | 2.5 | | | | | |
| <i>Biornatispora</i> cf. <i>dubia</i> | 3.5 | 0.5 | 2 | 2.5 | | 8 | 3 | | |
| <i>Camarozonotriletes parvus</i> | | | | P | | | | | |
| <i>Camarozonotriletes</i> sp. A | P | | | | | | | | |
| <i>Camarozonotriletes?</i> cf. <i>lunii</i> | | | P | | | P | | | |
| <i>Camarozonotriletes</i> spp. | 1 | 1 | P | | | | P | | |
| <i>Chelinospora</i> sp. A | | | | | | P | | | |
| <i>Chelinospora</i> spp. | | 1 | | | | P | | | |
| <i>Concentricosporites agradabilis</i> | | | | P | | | | | |
| <i>Convolutispora</i> sp. A | | | P | | | | | | |
| <i>Convolutispora?</i> sp. B | | | P | | | | | | |
| <i>Convolutispora</i> spp. | | | 1 | | | | | | |
| <i>Dibolisporites echinaceus</i> | P | 3 | 1 | | | 4 | 5 | | |
| <i>Dibolisporites</i> sp. A | | | | | | | P | | |
| <i>Dibolisporites</i> sp. B | | | | | | | P | | |
| <i>Dibolisporites</i> spp. | 7.5 | 9 | 4 | | | 6 | 1.5 | | |
| <i>Emphanisporites rotatus</i> | | | | | | | 0.5 | | |
| <i>Gneudnaspora divellomedia</i> | 7 | 3 | 4.5 | 4 | | 2.5 | 1.5 | | |
| <i>Grandispora</i> sp. A | | | | | | | | P | |
| <i>Latosporites ovalis</i> | 1 | 1.5 | 0.5 | | | 1 | | | |
| <i>Leiozonospora xichongensis</i> | | | | | | 1.5 | P | | |
| <i>Retusotriletes triangulatus</i> | 8 | 5 | 18.5 | 14.5 | 24 | 7.5 | 5.5 | | |
| <i>Retusotriletes</i> cf. <i>rotundus</i> | | | | | | | | | P |
| <i>Retusotriletes</i> sp. | | | P | | | | | | |
| <i>Retusotriletes</i> spp. | 12 | 24 | 38.5 | 27 | 27 | 18.5 | 8 | | 2 |
| <i>Tetraedraletes medinensis</i> | 0.5 | | 1.5 | 2 | 2 | | | | |
| <i>Verrucosporites polygonalis</i> | | | | | | P | P | | |
| <i>Verrucosporites</i> cf. <i>polygonalis</i> | P | | | | | P | P | | |
| <i>Verrucosporites</i> sp. | | P | P | | | | | | |
| <i>Verrucosporites</i> spp. | | P | P | | | | | | |
| Zonate spore | | | | | | | P | | |
| Spores counted per sample | 176 | 200 | 200 | 48 | 47 | 200 | 200 | 200 | 200 |

the Pragian. This age assignment is supported by the presence of index species of the PoW zone, such as *Verrucosporites polygonalis*, *Dictyotriletes subgranifer* and *Camarozonotriletes parvus* (*sensu* Steemans, 1989) (Table 2; supplementary material). Importantly, *Camarozonotriletes parvus* (*sensu* Steemans, 1989) has only been described from the Pragian of Belgium and Germany, and is characteristic of the Pa Interval Zone of Streeel *et al.* (1987), i.e., the Pragian (but not early) horizons of

the PoW zone. This view is also in agreement with the presence of *Aneurospora conica*, *Aneurospora xujiachongensis* and *Leiozonospora xichongensis*, three spore species documented only from the Xujiachong Formation of Qujing, Yunnan, a sequence correlative to the PE/PoW spore assemblage from Euramerica (Wellman *et al.* 2012). To summarise, the presence of the aforementioned taxa, together with *Latosporites ovalis*, a taxon that ranges from the Pragian to the Emsian (Breuer & Steemans

| SERIES | STAGE | LAURUSSIA (North America and Western Europe) | | SOUTH CHINA | | | |
|-------------------|---------------------|-------------------------------------------------|------------------------------------|--------------------|----------------|-------------------------------|--|
| | | SPORE BIOZONES | | PLANT BIOZONES | SPORE BIOZONES | INDEX PLANTS | |
| MIDDLE DEV. | EIFELIAN (Lower) | AP* | <i>velatus-langii</i> | <i>Hyeria</i> | V** | VL**** | |
| | | | <i>dauglastownense-enrypterota</i> | <i>Psilophyton</i> | IV** | ES**** | |
| LOWER DEVONIAN | EMSIAN | FD* | <i>annulatus-sexanii</i> | | | | |
| | | AB* | | | | | |
| | PRAGIAN | PoW* | <i>polygonalis-emsiensis</i> | II** | NC*** | | |
| | | BZ* | | | | <i>breconensis-zavallatus</i> | |
| LOCHKOVIAN | MN* | <i>micromatus-newportensis</i> | I** | SN*** | | | |
| | PRIDOLI | | | | | <i>tripapillatus-spicula</i> | |

Figure 4 Comparison of the uppermost Silurian–lowermost Middle Devonian spore and plant zonations from Laurussia and South China. *Miospore zones based on Strel *et al.* (1987): MN = *micromatus-newportensis* Opper Zone; BZ = *breconensis-zavallatus* Opper Zone; PoW = *polygonalis-wetteldorfensis* Opper Zone; AB = *annulatus-bellatulus* Opper Zone; FD = *foveolatus-dubia* Opper Zone; AP = *apiculatus-proteus* Opper Zone. **Miospore zones based on Gao (1981): I = *Synorisporites verrucatus-Streelisporea newportensis* Assemblage Zone; II = *Streelisporea granulate-Archaeozonotrites chulus* Assemblage Zone; III = *Emphanisporites neglectus-Brochotrites* sp. Assemblage Zone; IV = *Emphanisporites annulatus-Dictyotrites emsiensis* Assemblage Zone; V = *Rhabdosporites langii-Grandispora velata* Assemblage Zone. ***Miospore zones according to Fang *et al.* (1994): SN = *Apiculiretusispora spicula-Emphanisporites neglectus* Assemblage Zone, Yulongsi Formation, Qujing (Yunnan); NC = *Emphanisporites micromatus-Streelisporea newportensis* Assemblage Zone, Xiaishacun Formation, Qujing (Yunnan). ****Miospore zones according to Wang (1994): PE = *Apiculiretusispora plicata-Dictyotrites emsiensis* Assemblage Zone, Posongchong Formation, Wenshan (Yunnan); ES = *Dibolisporites eifeliensis-Camarozonotrites sextantii* Assemblage Zone, Pojiao Formation, Wenshan (Yunnan). *****Miospore zone according to Hsü & Gao (1991): VL = *Calyptosporites velatus-Rhabdosporites langii* Assemblage Zone, Chuandong Formation, Qujing (Yunnan). Spore and plant biozones from Laurussia are based on Edwards *et al.* (2000, fig. 2). Abbreviations: DEV = Devonian.

2013; Cascales-Miñana *et al.* 2016; Breuer, pers. comm. 2016), is consistent with a middle–late Pragian age for the Posongchong Formation (Fig. 5).

The Posongchong spore assemblage is very similar to that of the PE/PoW (Stemans 1981, 1989; Strel *et al.* 1981, 1987; Richardson & McGregor 1986; see also Wellman 2006 and references therein). The Posongchong assemblage is dominated by crassitate apiculate spores, laevigate retusoid spores (*Retusotrites*), with a noticeable presence of apiculate forms (*Apiculiretusispora*) and with biform sculpture (*Dibolisporites*) (Table 3). Some species of the PE/PoW spore assemblage from Euramerica, such as *Verrucosporites polygonalis*, *Dictyotrites emsiensis* and *Dibolisporites wetteldorfensis*, are present in South China from Xujiachong and Posongchong assemblages (Wellman *et al.* 2012; Table 2; supplementary material). A close spore comparison with the previous study from the Xujiachong Formation shows that the main difference is in the spore dominance: retusoid spores in all of the levels in the Xujiachong Formation (Wellman *et al.* 2012) and crassitate apiculate spores for this study. Morphotypes such as *Dictyotrites* and *Brochotrites* present in Wang's (1994) study have not been found in the assemblage, and the diversity of *Emphanisporites* in the Posongchong Formation is limited to *Emphanisporites rotatus* only (Table 2). This fact supports the observations of Wellman *et al.* (2012) from the Xujiachong Formation, who showed that (i) *Dictyotrites*, *Brochotrites* and *Emphanisporites* are rare in South China, whereas they are common in Euramerica; (ii) other common taxa in Euramerica (e.g., *Clivosispora* and *Breconisporites*) are absent from the Posongchong spore assemblages; and (iii) cryptospore

dyads that are often observed in Euramerica assemblages have also not been found in the Posongchong assemblages.

In the Wenshan area, the Posongchong Formation is overlain by the Pojiao and Bajiaoqing formations (Jin *et al.* 2005; Hao & Xue 2013, table 3.1). Updated studies of the faunas from the marine Pojiao and Bajiaoqing formations (Lu & Chen 2016; Lu *et al.* 2016) provide further constraints for dating the Posongchong spores. Lu & Chen (2016) re-examined the conodonts obtained from the Bajiaoqing Formation and concluded that the previously reported *Polygnathus dehiscens abyssus* and *Polygnathus dehiscens dehiscens* from the base of the formation should rather be identified as *Polygnathus excavatus*. This means that the Bajiaoqing Formation may be correlated with the *Polygnathus excavatus* Zone (i.e., the second Emsian conodont zone). The level of the boundary of the first Emsian conodont zone, the *Polygnathus kitabicus* Zone, remains unknown. The Pojiao Formation is characterised by the *Acrospirifer tonkinensis*, now called *Rostrospirifer tonkinensis* brachiopod fauna (Jin *et al.* 2005). This fauna has also been found from the lower part of the Yujiang Formation at the Liujing section of Guangxi, China (Wang & Rong 1986), where the Pragian–Emsian boundary most probably is in the lower part of the Yujiang Formation (Shizhou Member; Lu *et al.* 2016). This means that, at Liujing, the *Rostrospirifer tonkinensis* fauna probably ranges from the latest Pragian to early Emsian. In northern Vietnam, similar brachiopods, called *Euryspirifer tonkiensis* (= *Rostrospirifer tonkinensis*) fauna, have also been reported from the Pragian Mia Le Formation (Racheboeuf & Tong-Dzuy 2000). Thus, faunal evidence suggests that the Pojiao Formation ranges

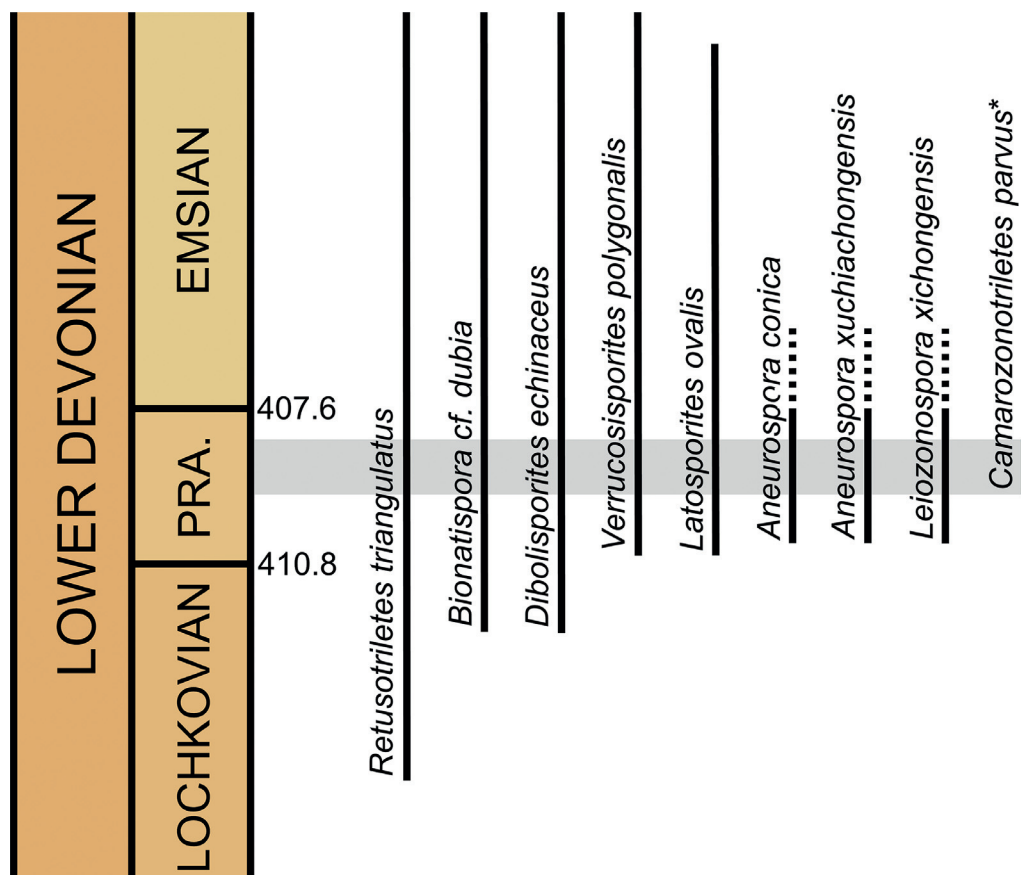


Figure 5 Stratigraphic ranges of key spore taxa encountered in this study for dating the Posongchong Formation. Grey boxes indicate the assigned temporal interval. Absolute ages according to the International Chronostratigraphic Chart (v2016/12). Abbreviations: PRA = Pragian. **Camarozonotriletes parvus* (sensu Steemans, 1989).

from the late (or latest) Pragian to earliest Emsian in age. This scenario indicates that the Posongchong spore assemblages are, therefore, older than Emsian, which reinforces a Pragian assignment for the Posongchong Formation.

6. Palaeobotanical implications

A comparison of the most representative Early Devonian floras is shown in Table 4, including the Posongchong, Xujiachong and Pingyipu floras from South China. With *ca.* 33 species, the Posongchong flora is the most diverse Early Devonian flora from the fossil record (Table 4). However, only three Posongchong species (*Guangnania cuneata*, *Hedeia sinica* and *Zosterophyllum australianum*) are shared with the Xujiachong Formation (Table 4), and a single species (*Zosterophyllum australianum*) together with *Zosterophyllum* sp. are shared with the upper *Baragwanathia* flora from Victoria, Australia (Table 4). Indeed, the Posongchong flora does not share any species with other coeval floras from the Old Red Sandstone Continent, nor with any other floras from Laurussia, which shows a high level of endemism of the South China fossil floras during the Early Devonian. The absence of paratracheophytes (plants with S-type water-conducting cells, formerly called Rhyniaceae; Gerienne *et al.* 2006) and the diversity of euphyllophytes from the Posongchong and Xujiachong floras are also noticeable (Wellman *et al.* 2012; Table 4). These data are quite difficult to reconcile with the evidence supplied by the dispersed spore fossil record. The different palynoflora comparators contain similar

spore morphotypes, especially the PE palynofloras (i.e., the coeval Posongchong, Xujiachong, Anglo-Welsh and Rhynie spore assemblages), independently of the known plant diversity. Furthermore, the Xujiachong and Posongchong palynofloras are dominated by *Retusotriletes* spp. and *Apiculiretusispora* spp. or *Aneurospora* spp. respectively, which also occur in Euramerican assemblages. It has to be noted that some spore species are only documented from the Lower Devonian of South China, as in the case of *Aneurospora conica*, *Aneurospora posongchongensis*, *Aneurospora xujiachongensis* or *Leiozonospora xichongensis*. This fact also suggests an isolated palaeogeographic position of the South China Plate during the Early Devonian, as do the plant megafossil data. Likewise, differences of species-level abundance between taxa would also support this view (e.g., the poor presence of *Camarozonotriletes*, *Emphanisporites* or *Verrucosisporites* in South China compared to their high abundance in Euramerica).

7. Acknowledgements

We thank Charles Wellman and Deming Wang for their valuable comments on the earlier version of this manuscript. BCM thanks the support provided by a Marie Curie COFUND Postdoctoral Fellowship, University of Liege (grant no. 600405). JZX and PH are supported by the National Natural Science Foundation of China (no. 41722201) and the Yunnan Key Laboratory for Palaeobiology, Yunnan University (no.

Table 4 Comparison of the main Early Devonian floras from northeastern Gondwana and Laurussia. Modified from Hao & Xue (2013, table 5.2).

| Flora | Age | Spore/graptoline biozone(s) | Locality(ies) | Plant diversity | References |
|----------------------------|---------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------|
| Posongchong | Pragian (but not early) | <i>Apiculiretusispora plicata</i> - <i>Dictyotriletes emisiensis</i> Spore Assemblage; <i>polygonalis-emsienensis</i> Spore Assemblage (equivalent to <i>polygonalis-wetteldorfensis</i> Oppel Zone) | Wenshan, Guangnan and Mengzi, Yunnan (China) | <i>Adoketophyton parvulum</i> (I), <i>Adoketophyton subverticillatum</i> (I), <i>Baragwanathia</i> sp. (L), <i>Catenalis digitata</i> (I), <i>Celatheca beckii</i> (I), cf. <i>Halleophyton</i> sp. (L), cf. <i>Hicklingia</i> sp. (Z), <i>Demersatheca contigua</i> (I), <i>Dibracophyton acrovatum</i> (Ba?), <i>Discalis longistipa</i> (Z), <i>Distichophyton</i> sp. (Z), <i>Eophyllophyton bellum</i> (E), <i>Estinnophyton yunnanense</i> (S), <i>Guangnania cuneata</i> (Z), <i>Gumuia zyzzata</i> (Z), <i>Hedeia sinica</i> (E), <i>Hueberia zhichangensis</i> (L), <i>Huia recurvata</i> (R), <i>Oricilla</i> sp. (Z), <i>Pauthecophyton gracile</i> (E), <i>Polythecophyton demissum</i> (I), <i>Psilophyton primitivum</i> (E), <i>Ramoferis amalia</i> (Z), <i>Ramoferis</i> sp. (Z), <i>Stachyophyton yunnanense</i> (Ba?), <i>Wenshania zhichangensis</i> (Z), <i>Yunia dichotoma</i> (Z), <i>Yunia guangnania</i> (Z), <i>Zhenglia radiata</i> (L), <i>Zosterophyllum australianum</i> (Z), <i>Zosterophyllum minifertillum</i> (Z), <i>Zosterophyllum ramosum</i> (Z), <i>Zosterophyllum tenerum</i> (Z) | Wang 1994; Hao & Xue 2013; this study |
| Xujiachong | Pragian (but not earliest)-?earliest Emsian | <i>polygonalis-emsienensis</i> Spore Assemblage (equivalent to <i>polygonalis-wetteldorfensis</i> Oppel Zone) | Qujing, Yunnan (China) | <i>Bracteophyton variatum</i> (I), <i>Drepanophycus qujingensis</i> (L), <i>Guangnania cuneata</i> (Z), <i>Hedeia sinica</i> (E), <i>Hsüa deflexa</i> (R), <i>Hsüa robusta</i> (R), <i>Huia gracilis</i> (R), <i>Zosterophyllum australianum</i> (Z), <i>Zosterophyllum yunnanicum</i> (Z) | Wang <i>et al.</i> 2002; Wang 2007; Wellman <i>et al.</i> 2012 |
| Pingyipu | Lochkovian-Pragian | <i>Streelispora newportensis</i> - <i>Synorisporites verrucatus</i> Spore Assemblage; <i>Brochotriletes</i> spp.- <i>Synorisporites downtonensis</i> Spore Assemblage | Yanmenba, Jiangyou, Sichuan (China) | <i>Amplectosporangium jiangyouensis</i> (I), <i>Drepanophycus spinaeformis</i> (L), <i>Drepanophycus spinosus</i> (L), <i>Drepanophycus</i> sp. (L), <i>Eogaspesia gracilis</i> (I), <i>Guangnania minor</i> (Z), <i>Hicklingia</i> cf. <i>edwardii</i> (Z), <i>Oricilla unilateralis</i> (Z), <i>Psilophyton</i> sp. (E), <i>Sciadocillus cuneiformis</i> (I), <i>Uskiella</i> sp. (R), <i>Yanmenia longa</i> (L?), <i>Zosterophyllum myretonianum</i> (Z), <i>Zosterophyllum sichuanensis</i> (Z), <i>Zosterophyllum yunnanicum</i> (Z) | Gao 1988; Geng 1992a, 1992b; Edwards <i>et al.</i> 2016 |
| Upper <i>Baragwanathia</i> | middle Pragian | <i>Monograptus thomasi</i> Graptolite Zone | Wilson Creek Shale, Victoria (Australia) | <i>Baragwanathia longifolia</i> (L), <i>Baragwanathia</i> sp. (L), <i>Dawsonites subarcuatus</i> (E), <i>Hedeia</i> sp. (E), <i>Salopella australis</i> (R), <i>Salopella caespitosa</i> (R), <i>Yarravia oblonga</i> (I), <i>Zosterophyllum australianum</i> (Z), <i>Zosterophyllum</i> sp. (Z) | Lang & Cookson 1935; Garrat 1978; Tims & Chambers 1984 |
| Anglo-Welsh | Pragian | <i>polygonalis-emsienensis</i> Spore Assemblage (equivalent to <i>polygonalis-wetteldorfensis</i> Oppel Zone) | Pembrokeshire, Walsh, South Wales (United Kingdom) | <i>Cooksonia pertoni</i> (R), <i>Cooksonia</i> sp. (R), <i>Dawsonites</i> sp. (E), <i>Deheubarthia splendens</i> (Z), <i>Drepanophycus spinaeformis</i> (L), <i>Goslingia breconensis</i> (Z), <i>Krithodeophyton croftii</i> (Ba?), <i>Salopella</i> sp. (R), <i>Sennicaulis hippocrepiformis</i> (R), <i>Sporogonites exuberans</i> (B), <i>Taeniocrada</i> sp. (I), <i>Tarella trowenii</i> (Z), <i>Thrinakophyton formosum</i> (Z), <i>Uskiella spargens</i> (R), <i>Zosterophyllum ?australianum</i> (Z), <i>Zosterophyllum</i> cf. <i>fertile</i> (Z), <i>Zosterophyllum llanoveranum</i> (Z), <i>Zosterophyllum</i> sp. (Z) | Wellman <i>et al.</i> 1998; Edwards & Richardson 2004 |
| Rhynie | latest Pragian-?earliest Emsian | <i>polygonalis-emsienensis</i> Spore Assemblage (equivalent to <i>polygonalis-wetteldorfensis</i> Oppel Zone) | Rhynie outlier, Aberdeenshire, Scotland (United Kingdom) | <i>Aglaophyton major</i> (R), <i>Asteroxylon mackiei</i> (L), <i>Horneophyton lignieri</i> (H), <i>Kidstonophyton discoides</i> (G), <i>Langiophyton mackiei</i> (G), <i>Lyonophyton rhyniensis</i> (G), <i>Nothia aphylla</i> (Z), <i>Remyophyton delicatum</i> (G), <i>Rhynia gwynne-vaughanii</i> (R), <i>Trichopherophyton teuchansii</i> (Z), <i>Ventarura lyoni</i> (Z) | Kerp <i>et al.</i> 2004; Wellman 2004, 2006 |
| Wépion | early Emsian | <i>annulatus-bellatulus</i> Oppel Zone | Estinnes-au-Mont, Blinche (Belgium) | <i>Dawsonites arcautus</i> (E), <i>Drepanophycus spinaeformis</i> (L), <i>Estinnophyton gracile</i> (S), <i>Forgesia currata</i> (Z), <i>Krithodeophyton</i> sp. (Ba?), <i>Psilophytites</i> sp. (I), <i>Psilophyton</i> cf. <i>crenulatum</i> (E), <i>Psilophyton forbesii</i> (E), <i>Psilophyton gensehae</i> (E), “ <i>Psilophyton</i> ” <i>burnotense</i> (E?), cf. <i>Psilophyton princeps</i> (E?), <i>Rebuchia? pendula</i> (Z), cf. <i>Sawdonia ornata</i> (Z?), <i>Sciadophyton laxum</i> (G), <i>Sporogonites exuberans</i> (B), <i>Stockmansella langii</i> (R), <i>Zosterophyllum</i> cf. <i>fertile</i> (Z), <i>Zosterophyllum deciduum</i> (Z) | Streel <i>et al.</i> 1987; Gerrienne 1993 |
| Wahn-bachschichten | late Pragian | Below <i>Dictyotriletes subgranifer</i> -palynozone | Wahnbachschichten, Siegburg, Rhineland (Germany) | <i>Drepanophycus spinaeformis</i> (L), <i>Estinnophyton wahnbachense</i> (E), <i>Hicklingia</i> sp. (Z), <i>Psilophyton burnotense</i> (E), <i>Sartilmania jonbachensis</i> (Z?), <i>Sawdonia ornata</i> (Z), <i>Sciadophyton laxum</i> (G), <i>Sporogonites exuberans</i> (B), <i>Stockmansella langii</i> (R), <i>Taeniocrada decheniana</i> (I), <i>Taeniocrada dubia</i> (R), <i>Taeniocrada longisporangiata</i> (I), <i>Wahnbachella bostrychioides</i> (I), <i>Zosterophyllum deciduum</i> (Z), <i>Zosterophyllum rhenanum</i> (Z) | Stemans 1989; Schweitzer 1990 |

Notes: The capital letter in brackets indicates taxonomic or morphological groups as most appropriate. B: Bryophyte; Ba: Barinophyte; E: Euphyllophyte; G: Gameotophyte; H: Horneophytopsoid; I: *Incertae sedis*; L: Lycopsid; R: Rhyniopsid and related plants; S: Sphenopsid; Z: Zosterophyllopsid. Northeastern Gondwanan floras: Posongchong, Xujiachong, Pingyipu, Upper *Baragwanathia*. Laurussian floras: Anglo-Welsh, Rhynie, Wépion, Wahnbachschichten.

2015DG007-KF04). PG and PS are FRS–FNRS Senior Research Associates.

8. Supplementary material

Supplementary material is available online at <https://doi.org/10.1017/S1755691018000233>.

9. References

- Al-Ghazi, A. 2009. *Apiculiretusispora arabiensis*, new name for *Apiculiretusispora densa* Al-Ghazi, 2007. *Revue de Micropaléontologie* **52**, 193.
- Arkhangel'skaya, A. D. 1978. Spores from the Lower Devonian of the Lithuanian SSR. *Paleontologicheskii Zhurnal* **2**, 113–20. [In Russian.]
- Balme, B. E. 1988. Miospores from Late Devonian (Early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B* **209**, 109–66.
- Breuer, P. 2007. Devonian miospore palynology in Western Gondwana: an application to oil exploration. PhD Thesis, University of Liege, Belgium.
- Breuer, P. & Steemans, P. 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy. *Special Papers in Palaeontology* **89**, 1–163.
- Cascales-Miñana, B., Gerrienne, P., Moreno-Domínguez, R., Xue, J. Z., Valenzuela-Ríos, J. I., Díez, J. B., Rial, G. & Steemans, P. 2016. A new highly diverse palynoflora from the Lower Devonian Nogueras Formation of the Iberian Peninsula. *Historical Biology* **28**, 1118–24.
- Edwards, D., Fairon-Demaret, M. & Berry, C. M. 2000. Plant megafossils in Devonian stratigraphy: a progress report. *Courier Forschungsinstitut Senckenberg* **220**, 25–37.
- Edwards, D., Geng, B. Y. & Li, C. S. 2016. New plants from the Lower Devonian Pingyipu Group, Jianguo County, Sichuan Province, China. *PLoS ONE* **11**, e0163549.
- Edwards, D. & Richardson, J. B. 2004. Silurian and Lower Devonian plant assemblages from the Anglo-Welsh Basin: a palaeobotanical and palynological synthesis. *Geological Journal* **39**, 375–402.
- Fang, Z. J., Cai, C. Y., Wang, Y., Li, X. X., Wang, C. Y., Geng, L. Y., Wang, S. Q., Gao, L. D., Wang, N. Z. & Li, D. Y. 1994. New advance in the study of the Silurian–Devonian boundary in Qujing, east Yunnan. *Journal of Stratigraphy* **18**, 81–90. [In Chinese with English Abstract.]
- Gao, L. D. 1978. The Early Devonian spores and acritarchs from the Nakaoling Stage of Liuqing, Kwangsi. In *The Institute of Geology, Mineral Resources, Chinese Academy of Geological Sciences (ed.) Symposium on the Devonian strata of South China*, 346–58. Beijing: Geological Publishing House. [In Chinese.]
- Gao, L. D. 1981. Devonian spore assemblages of China. *Review of Palaeobotany and Palynology* **34**, 11–23.
- Gao, L. D. 1988. Spore biostratigraphy. In Hou, H. F., Wan, Z. Q., Xian, S. Y., Fan, Y. N., Tang, D. Z. & Wand, S. T. (eds) *Devonian stratigraphy, paleontology and sedimentary facies of Longmenshan*, 99–106. Beijing: Geological Publishing House. [In Chinese with English Abstract.]
- Garratt, M. J. 1978. New evidence for a Silurian (Ludlow) age for earliest *Baragwanathia* flora. *Alcheringa* **2**, 217–24.
- Geng, B. Y. 1992a. *Amplectosporangium* a new genus of plant from the Lower Devonian of Sichuan, China. *Acta Botanica Sinica* **34**, 450–55. [In Chinese with English Abstract.]
- Geng, B. Y. 1992b. Studies on Early Devonian flora of Sichuan. *Acta Phytotaxonomica Sinica* **30**, 97–211. [In Chinese with English Abstract.]
- Gerrienne, P. 1993. Inventaire des végétaux éodévonien de Belgique. *Annales de la Société Géologique de Belgique* **116**, 105–17. [In French with English Abstract.]
- Gerrienne, P. 1996. A biostratigraphic method on a quantification of fossil tracheophyte characters – its application to the Lower Devonian Posongchong flora (Yunnan Province, China). *The Palaeobotanist* **45**, 194–200.
- Gerrienne, P., Dilcher, D. L., Bergamaschi, S., Milagres, I., Pereira, E. & Rodrigues, M. A. C. 2006. An exceptional specimen of the early land plant *Cooksonia paranensis*, and a hypothesis on the life cycle of the earliest eutracheophytes. *Review of Palaeobotany and Palynology* **142**, 123–30.
- Hao, S. G. 1989. *Gumuia zyzzata*. A new plant from the Lower Devonian of Yunnan, China. *Acta Botanica Sinica* **31**, 954–61. [In Chinese with English Abstract.]
- Hao, S. G., Wang, D. M. & Beck, C. B. 2003. Observations on anatomy of *Adoketophyton subverticillatum* from the Posongchong Formation (Pragian, Lower Devonian) of Yunnan, China. *Review of Palaeobotany and Palynology* **127**, 175–86.
- Hao, S. G., Wang, D. M., Wang, Q. & Xue, J. Z. 2006. A new lycopsid, *Zhenglia radiata* gen. et sp. nov., from the Lower Devonian Posongchong Formation of Southeastern Yunnan, China, and its evolutionary significance. *Acta Geologica Sinica* **80**, 11–19.
- Hao, S. G. & Beck, C. B. 1991. *Catenalis digitata* gen. et sp. nov., a plant from the Lower Devonian of Yunnan, China. *Canadian Journal of Botany* **69**, 873–82.
- Hao, S. G. & Gensel, P. G. 1995. A new genus and species, *Celatheca beckii*, from the Siegenian (Early Devonian) of southeastern Yunnan, China. *International Journal of Plant Science* **156**, 896–909.
- Hao, S. G. & Gensel, P. G. 1998. Some new plant finds from the Posongchong Formation of Yunnan, and consideration of a phytogeographic similarity between south China and Australia during the Early Devonian. *Science in China: Earth Science* **41**, 1–13.
- Hao, S. G. & Xue, J. Z. 2011. A new zosterophyll plant, *Ramopheris* gen. nov., from the Posongchong Formation of Lower Devonian (Pragian) of Southeastern Yunnan, China. *Acta Geologica Sinica* **85**, 765–76.
- Hao, S. G. & Xue, J. Z. 2013. *The Early Devonian Posongchong flora of Yunnan – a contribution to an understanding of the evolution and early diversification of vascular plants*. Beijing: Science Press.
- Hoffmeister, W. S. 1959. Lower Silurian plant spores from Libya. *Micropaleontology* **5**, 331–34.
- Hoffmeister, W. S., Staplin, F. L. & Malloy, R. E. 1955. Mississippian plant spores from the Hardinsburg Formation of Illinois and Kentucky. *Journal of Paleontology* **29**, 372–99.
- Hsü, J. & Gao, L. D. 1991. Middle and early Upper Devonian miospore zonations in eastern Yunnan and the significance in stratigraphy. *Acta Botanica Sinica* **33**, 304–13.
- Jin, S. Y., Shen, A. J., Chen, Z. L., Lu, J. M., Wei, M., Wang, Y. Q. & Xie, F. 2005. *Mixed biostratigraphy of Devonian in Wenshan, Yunnan*. Beijing: Petroleum Industry Press.
- Kerp, H., Trewin, N. H. & Hass, H. 2004. New gametophytes from the Early Devonian Rhynie chert. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**, 411–28.
- Lang, W. H. & Cookson, I. C. 1935. On a flora, including vascular land plants, associated with *Monographus*, in rock of Silurian age, from Victoria, Australia. *Philosophical Transactions of the Royal Society of London* **224**, 421–49.
- Lanninger, E. P. 1968. Sporen-Gesellschaften aus dem Ems der SW-Eifel (Rheinisches Schiefergebirge). *Palaeontographica Abteilung B* **122**, 95–170. [English Abstract.]
- Lele, K. M. & Streel, M. 1969. Middle Devonian (Givetian) plant microfossils from Goé (Belgium). *Annales de la Société Géologique de Belgique* **92**, 89–121.
- Lu, J. F., Qie, W. K. & Chen, X. Q. 2016. Pragian and lower Emsian (Lower Devonian) conodonts from Liuqing, Guangxi, South China. *Alcheringa* **40**, 275–96.
- Lu, J. F. & Chen, X. Q. 2016. New insights into the base of the Emsian (Lower Devonian) in South China. *Geobios* **49**, 459–67.
- McGregor, D. C. 1973. Lower and Middle Devonian spores of eastern Gaspé, Canada. I. Systematics. *Palaeontographica Abteilung B* **142**, 1–77.
- McGregor, D. C. & Camfield, M. 1976. Upper Silurian? To Middle Devonian spores of the Moose River Basin, Ontario. *Geological Survey of Canada, Bulletin* **263**, 1–63.
- Naumova, S. N. 1953. Spore-pollen assemblages of the Upper Devonian of the Russian Platform and their stratigraphic significance. *Transactions of the Institute of Geological Sciences, Academy of the Sciences of the USSR* **143**, 1–154. [In Russian.]
- Neves, R. & Owens, B. 1966. Some Namurian spores from the English Pennines. *Pollen et Spores* **8**, 337–60.
- Owens, B. 1971. Spores from the Middle and Early Upper Devonian rocks of the Western Queen Elizabeth Island, Arctic Archipelago. *Geological Survey of Canada, Paper* **70–38**, 1–157.
- Racheboeuf, P. R. & Tong-Dzuy, T. 2000. Lower Devonian chonetoid brachiopods from Bac Bo, North Viêt Nam. *Palaeontology* **43**, 1039–68.
- Richardson, J. B. 1965. Middle Old Red Sandstone spore assemblages from the Orcadian basin north-east Scotland. *Palaeontology* **7**, 559–605.

- Richardson, J. B., Streef, M., Hassan, A. & Steemans, P. 1982. A new spore assemblage to correlate between the Breconian (British Isles) and the Gedinian (Belgium). *Annales de la Société Géologique de Belgique* **105**, 135–43.
- Richardson, J. B. & Lister, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh borderland and South Wales. *Palaeontology* **12**, 201–52.
- Richardson, J. B. & McGregor, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Bulletin of the Geological Survey of Canada* **364**, 1–79.
- Rodríguez, R. M. 1983. *Palinología de las Formaciones del Silúrico Superior–Devónico Inferior de la Cordillera Cantábrica*. León: Servicio de Publicaciones, Universidad de León.
- Schopf, J. M., Wilson, L. R. & Bentall, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Illinois State Geological Survey, Report of Investigations* **91**, 1–66.
- Schweitzer, H. J. 1990. *Pflanzen erobern das Land. Kleine Senckenberg-Reihe 18*. Senckenberg: Forschungsinstitut und Natur-Museum.
- Smith, A. V. H. 1971. Le genre *Verrucosiporites* Ibrahim 1933 emend. In Alpern, B. & Neves, R. (eds) *Microfossiles organiques du Paleozoique, les spores*, 35–87. Paris: Centre National de la Recherche Scientifique.
- Steeemans, P. 1981. Etude stratigraphique des spores dans les couches de transition “Gedinien-Siegenien” a Nonceveux et à Spa (Belgique). *Annales de la Société Géologique de Belgique* **104**, 41–59. [English Abstract.]
- Steeemans, P. 1982. Gedinian and Siegenian spore stratigraphy in Belgium. *Courier Forschungsinstitut Senckenberg* **55**, 165–80.
- Steeemans, P. 1989. Etude palynostratigraphique de Dévonien inférieur dans l’Ouest de l’Europe. *Mémoires et Explication des Cartes Géologiques et Minières de Belgique* **27**, 1–453. [English Abstract.]
- Steeemans, P., Rubinstein, C. & Melo, J. H. G. 2008. Siluro-Devonian spore biostratigraphy of the Urubu River area, western Amazon Basin, northern Brazil. *Geobios* **41**, 263–82.
- Streef, M. 1964. Une association de spores du Givetien inférieur de la Vesdre, à Goé (Belgique). *Annales de la Société Géologique de Belgique* **87**, 1–30. [English Abstract.]
- Streef, M. 1967. Associations de spores du Dévonien Inférieur belge et leur signification stratigraphique. *Annales de la Société Géologique de Belgique* **90**, 11–53. [English Abstract.]
- Streef, M., Fairon-Demaret, M., Otazo-Bozo, N. & Steemans, P. 1981. Etude stratigraphique des spores du Dévonien Inférieur au bord sud du synclinorium de Dinant (Belgique) et leurs applications. *Annales de la Société Géologique de Belgique* **104**, 173–91. [English Abstract.]
- Streef, M., Higgs, K., Loboziak, S., Riegel, W. & Steemans, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. *Review of Palaeobotany and Palynology* **50**, 211–29.
- Tims, J. D. & Chambers, T. C. 1984. Rhyniophytina and Trimerophytina from the early land flora of Victoria, Australia. *Palaeontology* **27**, 265–79.
- Vigran, J. O. 1964. Spores from Devonian deposits, Mimerdalen, Spitsbergen. *Norsk Polarinstitut, Skrifter* **132**, 1–30.
- Wang, D. M. 2007. Two species of *Zosterophyllum* from South China and dating of the Xujiachong Formation with a biostratigraphic method. *Acta Geologica Sinica* **81**, 525–38.
- Wang, D. M., Hao, S. G. & Liu, Z. 2002. Researches on plants from the Lower Devonian Xujiachong Formation in the Qujing District, Eastern Yunnan. *Acta Geologica Sinica* **76**, 393–407.
- Wang, D. M. & Hao, S. G. 2002. *Guangnania cuneata* gen. et sp nov from the Lower Devonian of Yunnan Province, China. *Review of Palaeobotany and Palynology* **122**, 13–27.
- Wang, Y. 1994. Lower Devonian miospores from Gumu in the Wenshan District, Southeastern Yunnan. *Acta Micropalaeontologica Sinica* **11**, 319–32.
- Wang, Y. & Rong, J. Y. 1986. Yukiangian (Early Emsian, Devonian) brachiopods of the Nanning-Liujing district, central Guangxi, South China. *Palaeontologia Sinica* **22**, 1–282. [In Chinese with English Abstract.]
- Wellman, C. H. 2004. Palaeoecology and palaeophytogeography of the Rhynie chert plants: evidence from integrated analysis of *in situ* and dispersed spores. *Proceedings of the Royal Society B* **271**, 985–92.
- Wellman, C. H. 2006. Spore assemblages from the Lower Devonian ‘Lower Old Red Sandstone’ deposits of the Rhynie outlier, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **97**, 167–211.
- Wellman, C. H., Thomas, R. G., Edwards, D. & Kenrick, P. 1998. The Cosheston Group (Lower Old Red Sandstone) in southwest Wales: age, correlation and palaeobotanical significance. *Geological Magazine* **135**, 397–412.
- Wellman, C. H., Zhu, H., Marshall, J. E. A., Wang, Y., Berry, C. M. & Xu, H. 2012. Spore assemblages from the Lower Devonian Xujiachong Formation from Qujing, Yunnan, China. *Palaeontology* **55**, 583–611.
- Wellman, C. H. & Richardson, J. B. 1993. Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology* **36**, 155–93.
- Zhu, M., Wang, J. Q. & Fan, J. H. 1994. Early Devonian fishes from Gujiatun and Xujiachong Formations of Qujing, Yunnan, and related biostratigraphic problems. *Vertebrata Palasiatica* **32**, 1–20.

MS received 9 November 2016. Accepted for publication 7 December 2017