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

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Running head: Spores from the Lower Devonian Posongchong Formation

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. We here 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 recognized taxa include, among others, *Ambitisporites avitus*, *Aneurospora conica*, *Aneurospora posonchongensis* sp. nov., *Aneurospora xujiachongensis*, *Apiculiretusispora plicata*, *Archaeozonotriletes chulus*, *Concentricosisporites agradabilis*, *Dibolisporites echinaceus*, *Emphanisporites rotatus*, *Gneudnaspora 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 only known from the Pragian of Belgium and Germany. Recent advances on the marine faunas in the overlying sequences also indicate a Pragian age for the Posongchong Formation. This new investigation of the Posongchong palynoflora highlights also differences of abundance at species level between the Gondwanan-Laurussian floras during the Early Devonian.

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

The Lower Devonian Posongchong Formation (Wenshan, Yunnan Province, southwestern China) comprises a series of continental clastic deposits, from which twenty-eight 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 on plant megafossils. The latest reviews about 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, p. 23–24, and references therein).

Spore data are good stratigraphic indicators used to correlate marine-terrestrial deposits as well as to provide 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 Pojjiao formations at the Zhichang section (Gumu Town, Wenshan) came from Wang's (1994) study. The author concluded that the PE assemblage zone (based on the presence of *Apiculiretusispora plicata* and of *Dictyotriletes emsiensis*) can be recognized 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.

In this study, 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; (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, 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), *Gumuia zyzata* (Hao 1989), *Guangnania cuneata* (Wang & Hao 2002), *Ramofaris amalia* (Hao & Xue 2011), *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 been also 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 sample 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 techniques. Following maceration, the remaining residue was briefly oxidized in HNO₃ and KClO₃ and sieved through a 12 µm mesh to remove particles of organic matter and fine mineral matter. Afterwards, a hot bath in 25% HCl 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* Streele emend. Richardson *et al.* 1982

Type species *Aneurospora goensis* Streele 1964

Aneurospora posongchongensis sp. nov.

(Pl. I, 4-8)

Holotype: Plate I, 9 (slide 74482, England Finder M43/2).

Paratype: Plate I, 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

(Pl. I, 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 coni 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.

Dimensions: 30-(33)-37 μm ; 3 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 coni is regular. *Aneurospora* sp. A and *Aneurospora posonchongensis* are similar in amb and size, but differ in the ornamentation. The base of the coni 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 ; 3 specimens measured.

Aneurospora sp. B

(Pl. I, 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 ; 1 specimen measured.

Genus *Camarozonotriletes* Naumova ex Naumova 1953

Type species *Camarozonotriletes devonicus* Naumova 1953

Camarozonotriletes sp. A

(Pl. I, 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 5 elements.

Dimensions: 30-(31)-32 µm; 2 specimen measured.

Genus *Chelinospora* Allen emend. McGregor & Camfield 1976

Type species *Chelinospora concinna* Allen 1965

Chelinospora sp. A

(Pl. II, 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; 1 specimen measured.

Genus *Convolutispora* Hoffmeister *et al.* 1955

Type species *Convolutispora subtilis* Owens 1971

Convolutispora sp. A

(Pl. II, 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; 1 specimen measured.

Convolutispora? sp. B

(Pl. II, 5)

Description: Amb circular. Distal face densely ornamented. The sculpture is formed by grana closely attached together of no more than 5 or 6 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 6.

Dimensions: 44 μm ; 1 specimen measured.

Genus *Dibolisporites* Richardson 1965

Type species: *Dibolisporites echinaceus* (Eisenack) Richardson 1965

Dibolisporites sp. A

(Pl. II, 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 ; 1 specimen measured.

Dibolisporites sp. B

(Pl. II, 9)

Description: The preservation of the spore does not allow defining the amb precisely. 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 it is not possible to ascertain because there is currently one specimen for each only.

Dimensions: 50 µm; 1 specimen measured.

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

Type species *Grandispora spinosa* Hoffmeister *et al.* 1995

Grandispora sp. A

(Pl. II, 13-14)

Description: Camerate spore with a sub-circular amb. Laesurae not visible. The inner body diameter 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; 2 specimen measured.

Genus *Retusotriletes* Naumova emend. Streeel 1964

Type species *Retusotriletes simplex* Naumova 1953

Retusotriletes sp.

(Pl. III, 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; 6 specimen measured.

Genus *Verrucosisporites* Ibrahim emend. Smith 1971

Type species *Verrucosporites verrucosus* (Ibrahim) Ibrahim 1933

Verrucosporites sp.

(Pl. III, 8-9)

Description: Amb sub-triangular. Laesurae curved and 2.5 µm 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 µm wide, 2.0 to 3.5 µm high and up to 0.5 µm apart.

Dimensions: 30–(31)-32 µm; 2 specimen measured.

3. Spore diversity from the Posongchong Formation

Nine of the thirteen 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* (Pl I, 1-2), *Aneurospora conica* (Pl I, 3), *Aneurospora posongchongensis* sp. nov. (Pl I, 4-8), *Aneurospora xuchiachongensis* (Pl I, 9), *Aneurospora* sp. A (Pl I, 10-11), *Aneurospora* sp. B (Pl I, 12), *Apiculiretusispora plicata* (Pl I, 13-14), *Apiculiretusispora* cf. *arabiensis* (Pl I, 15), *Archaeozonotriletes chulus* (Pl I, 16), *Biornatispora* cf. *dubia* (Pl I, 17-21), *Camarozonotriletes parvus* (Pl I, 22), *Camarozonotriletes* sp. A (Pl I, 23-24), *Camarozonotriletes?* cf. *lunii* (Pl II, 1), *Chelinospora* sp. A. (Pl II, 2), *Concentricosisporites agradabilis* (Pl II, 3), *Convolutispora* sp. A (Pl II, 4), *Convolutispora?* sp. B (Pl II, 5), *Dibolisporites echinaceus* (Pl II, 6-7), *Dibolisporites* sp. A (Pl II, 8), *Dibolisporites* sp. B (Pl II, 9), *Emphanisporites rotatus* (Pl II, 10), *Gneudnaspora divellomedia* (Pl II, 11-12), *Grandispora* sp. A (Pl II, 13-14), *Latosporites ovalis* (Pl II, 15-16), *Leiozonospora xichongensis* (Pl II, 17-18), *Retusotriletes triangulatus* (Pl II, 19-20), *Retusotriletes* cf. *rotundus* (Pl III, 1), *Retusotriletes* sp. (Pl III, 2), *Tetrahedraletes medinensis* (Pl III, 3-4), *Verrucosporites polygonalis* (Pl III, 5), *Verrucosporites* cf. *polygonalis* (Pl III, 6-7), *Verrucosporites* sp. (Pl III, 8-9). Interestingly, a zonate spore (Pl. III, 10) and several small fragments of spores showing distinct types of ornamentation are also observed (Pl. III, 11-12), a phenomenon previously illustrated and commented by Wellman *et al.* (2012, Fig. 8N).

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 macrospinosus*), *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 by, at least, 56 different morphological species belonging to 28 genera (see Appendix for the list), 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 xuchiachongensis*, *Apiculiretusispora plicata*, *Archaeozonotriletes chulus*, *Camarozonotriletes? cf. luyi*, *Latosporites ovalis*, *Leiozosterospora xichongensis*, *Retusotriletes* cf. *triangulatus*, *Retusotriletes* cf. *rotundus*, *Tetraedraletes 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 recognized (*Apiculiretusispora* cf. *arabensis* and *Apiculiretusispora plicata*), but only the latter is quantifiable. *Dibolisporites*, *Verrucosisporites* or *Archaeozonotriletes* are not common at all. 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 only hilate cryptospores (*Gneudnaspora divellomedia*) and permanent tetrads (*Tetrahedraletes medinensis*).

5. Biostratigraphical interpretation

The *Apiculiretusispora plicata*-*Dictyotriletes emsiensis* (PE) zone recognized from the Posongchong Formation by Wang (1994) correlates with the Pragian of the Old Red Sandstone continent (Streel 1967; Streel *et al.* 1981, 1987; Steemans 1981, 1989; Richardson & McGregor 1986; Fig. 4). Concretely, 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* Opper 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 the Pragian. This age assignation is supported by the presence of index

species of PoW zone, such as *Verrucosporites polygonalis*, *Dictyotriletes subgranifer* and *Camarozonotriletes parvus* (*sensu* Steemans 1989) (Table 2, Appendix). Importantly, *Camarozonotriletes parvus* (*sensu* Steemans 1989) has been only 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 only documented from the Xujiachong Formation of Qujing, Yunnan, a sequence correlative to the PE/PoW spore assemblage from Euramerica (Wellman *et al.* 2012). To summarize, the presence of the above-mentioned taxa together with *Latosporites ovalis*, a taxon that ranges from the Pragian to the Emsian (Breuer & Steemans 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 (Richardson & McGregor 1986; Streeel *et al.* 1981, 1987; Steemans 1981, 1989; see also Wellman 2006 and references therein). The Posongchong assemblage is dominated by crassitate apiculate spores, laevigate retusoid spores (*Retusotriletes*), 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*, *Dictyotriletes emsiensis*, and *Dibolisporites wetteldorfensis* are present in South China from Xujiachong and Posongchong assemblages (Wellman *et al.* 2012; Table 2, Appendix). A close spore comparison with the previous study from the Xuajiachong Formation shows that the main difference is in the spore dominance: retusoid spores in all of the levels in Xujiachong Formation (Wellman *et al.* 2012) and crassitate apiculate spores for this study. Morphotypes such as *Dictyotriletes* and *Brochotriletes* present in Wang's (1994) study have not been found in the assemblage, and the diversity of *Emphanisporites* in 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 (i) that *Dictyotriletes*, *Brochotriletes* and *Emphanisporites* are rare in South China, whereas they are common in Euramerica; (ii) that other common taxa in Euramerica (e.g. *Clivosispora* and *Breconisporites*) are absent from the Posongchong spore assemblages; and (iii) that cryptospore dyads that are often observed in Euramerica assemblages have also not been found in the Posongchong assemblages.

In 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* Mawson and *Polygnathus dehiscens dehiscens* from the base of formation should rather be identified as *Polygnathus excavatus*. It 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 characterized 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 Liujiang 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 Liujiang, 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 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 assignation 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; Gerrienne *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 palynofloras compared 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 however to be noted that some spore species are only documented from the Lower Devonian of South China, as it is the case of *Aneurospora conica*, *Aneurospora posongchongensis*, *Aneurospora xujiachongensis* or *Leiozonospora xichongensis*. This fact also suggests an isolated palaeogeographic position of South China Plate during the Early Devonian, as do the plant megafossil data. Likewise, differences at the 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).

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Figure legends

Figure 1. Map showing the location of the studied section. (a) General view of Yunnan Province (southwestern China) showing the position of study area (Wenshan). Modified from Hao & Xue (2013, fig. 2.1). (b) Map showing the location of the Zhichang and Changputang sections in Wenshan area. Modified from Hao & Xue (2013, fig. 2.3). Abbreviations: D_{2d}, Middle Devonian Donggangling Formation; D_{2g}, Middle Devonian Gumu Formation; D_{1b}, Lower Devonian Bajioqing 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).

Figure 3. Palaeogeographical map showing the distribution of the major outcrops of fossil floras (Whensan and Guangnan, 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).

Figure 4. Comparison of the uppermost Silurian-lowermost Middle Devonian spore and plant zonation from Laurussia and South China. Note: *Miospore zones based on Streeel *et al.* (1987): MN, *micrornatus-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 granulata-Archaeozonotriletes chulus* Assemblage Zone; III, *Emphanisporites neglectus-Brochotriletes* sp. Assemblage Zone; IV, *Emphanisporites annulatus-Dictyotriletes emsiensis* Assemblage Zone; V, *Rhabdosporites langii-Grandisporea velata* Assemblage Zone. ***Miospore zones according to Fang *et al.* (1994): SN, *Apiculiretusispora spicula-Emphanisporites neglectus* Assemblage Zone, Yulongsi Formation, Quijing (Yunnan); NC, *Emphanisporites micrornatus-Streelisporea newportensis* Assemblage Zone, Xiaxisacun Formation, Quijing (Yunnan). ****Miospore zones according to Wang (1994): PE, *Apiculiretusispora plicata-Dictyotriletes emsiensis* Assemblage Zone, Posongchong

Formation, Wenshan (Yunnan); ES, *Dibolisporites eifeliensis-Camarozonotriletes sextantii* Assemblage Zone, Pojiao Formation, Wenshan (Yunnan). *****Miospore zone according to Hsü & Gao (1991): VL, *Calytosporites 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.

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).

Plate legends

Plate I. 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) Strel 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 µm.

Plate II. Posongchong spore diversity (II).

1. *Camarozonotriletes?* cf. *lunii* 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 *et al.* 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 µm.

Plate III. Posongchong spore diversity (III).

1. *Retusotriletes* cf. *rotundus* Streel emend. Lele & Streel 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 µm.

Tables

Table 1. Details of studied samples from the Posongchong Formation.

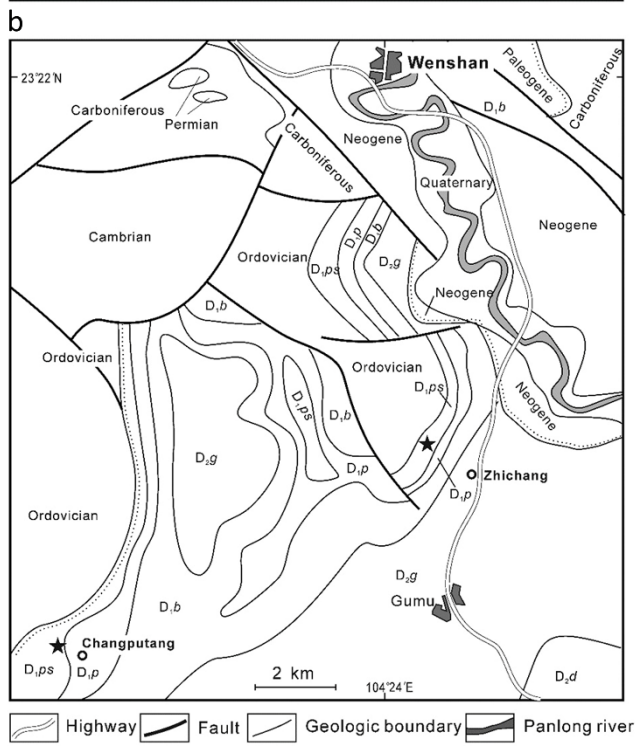
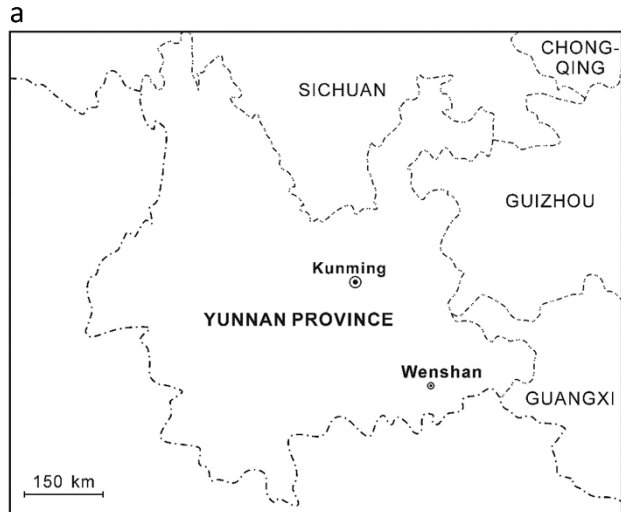
Table 2. Spore taxa reported by Wang (1994) from the Posongchong Formation, Wellman *et al.* (2012) from the Xujiachong Formation and this study (including those common to Wang 1994).

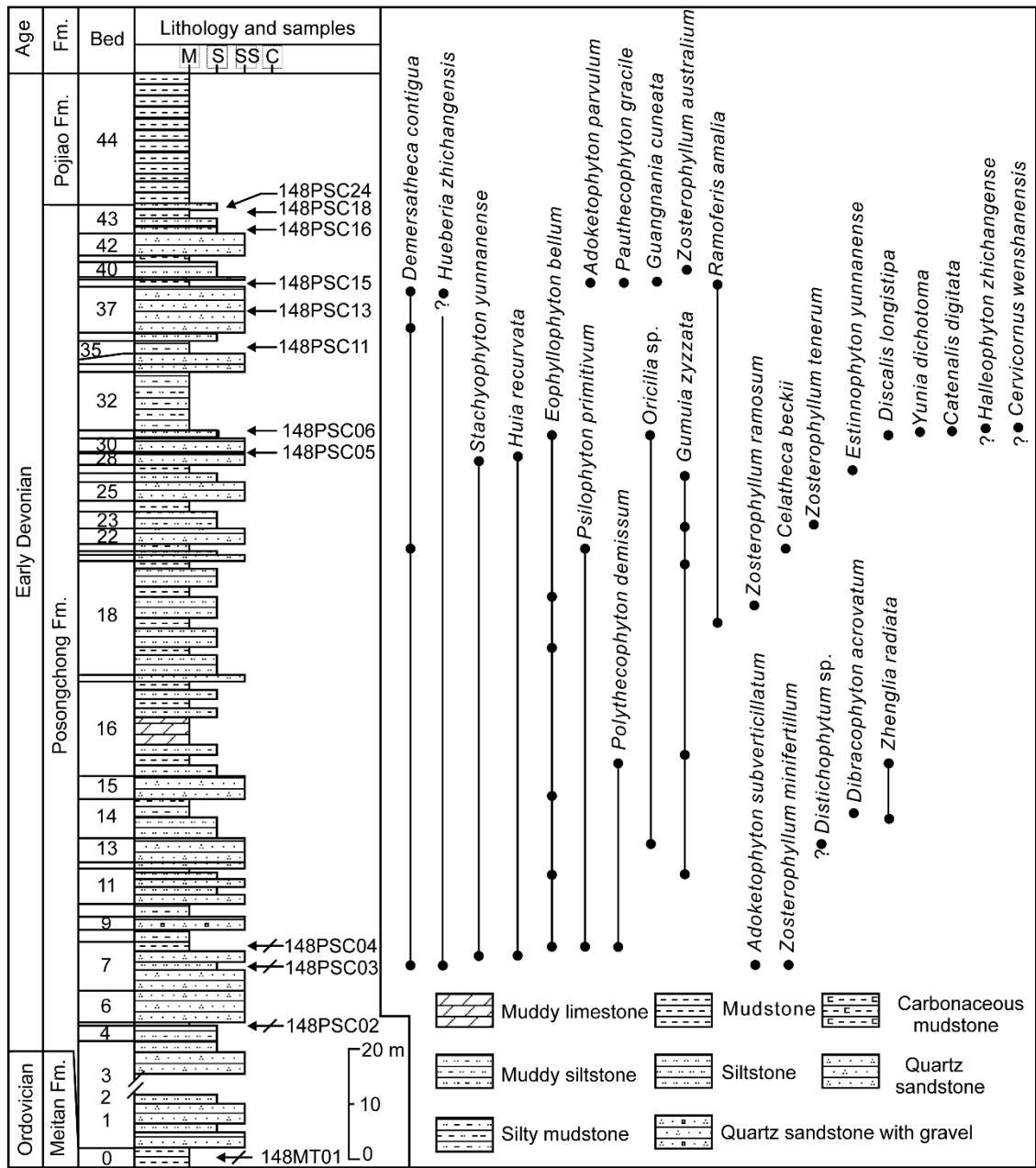
Table 3. Distribution and abundance (in percentage) of the spore taxa in the studied samples. P, present but not featured in counts.

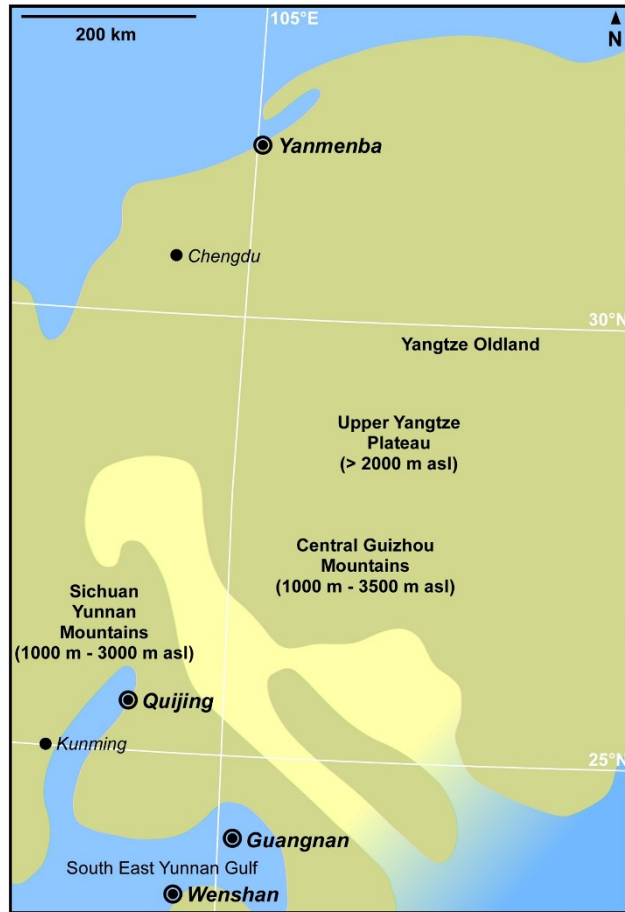
Table 4. Comparison of the main Early Devonian floras from northeastern Gondwana and Laurussia. Modified from Hao & Xue (2013, table 5.2).

Supplementary online material

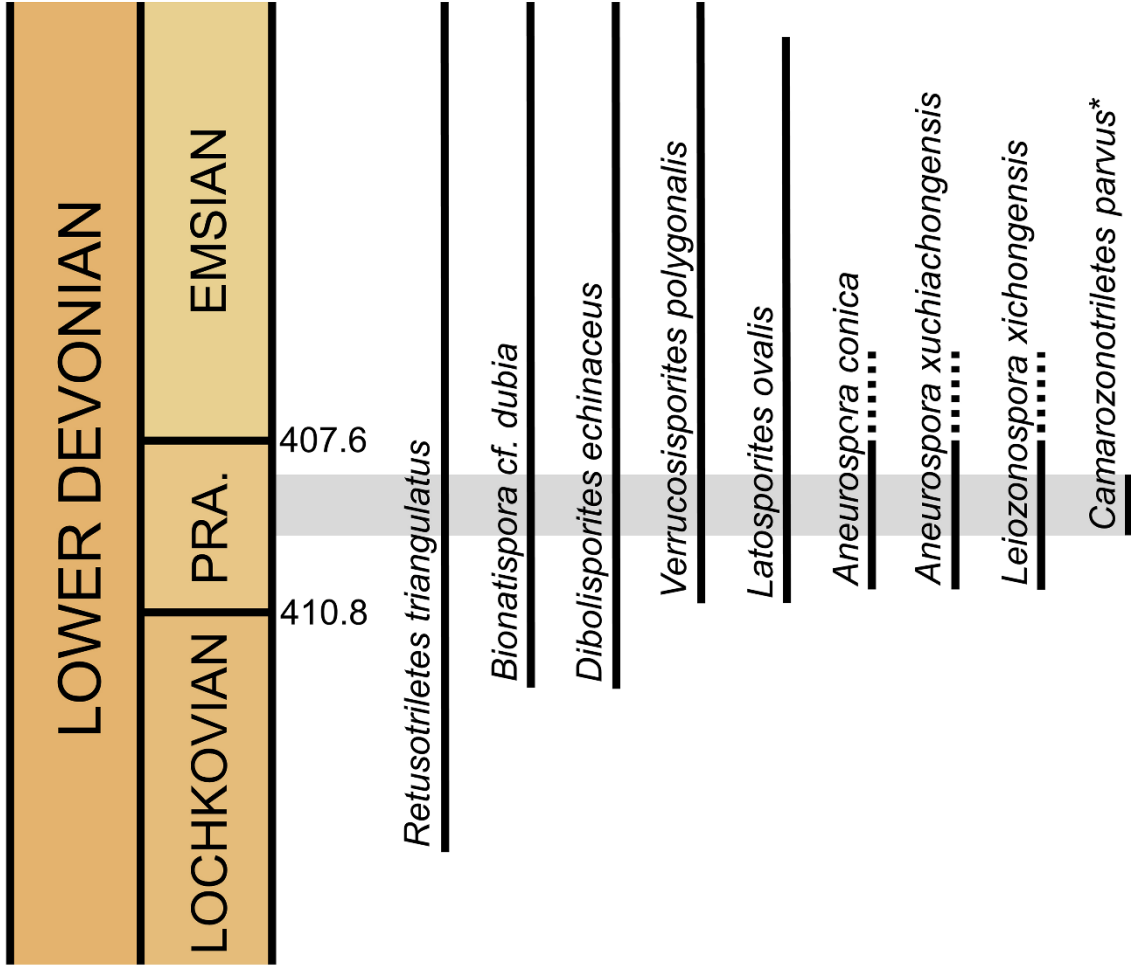
Appendix. Known Posongchong spore diversity.

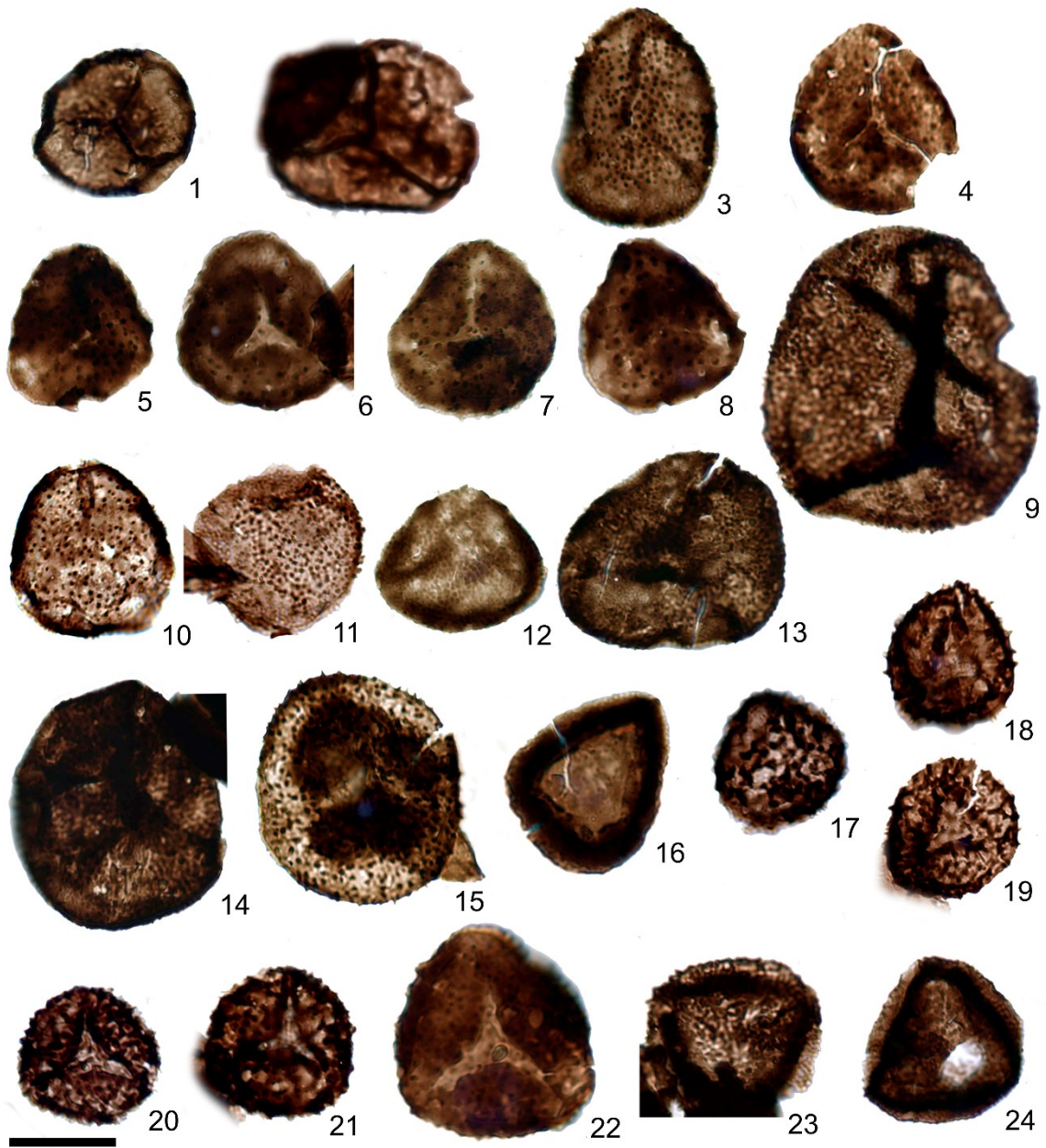


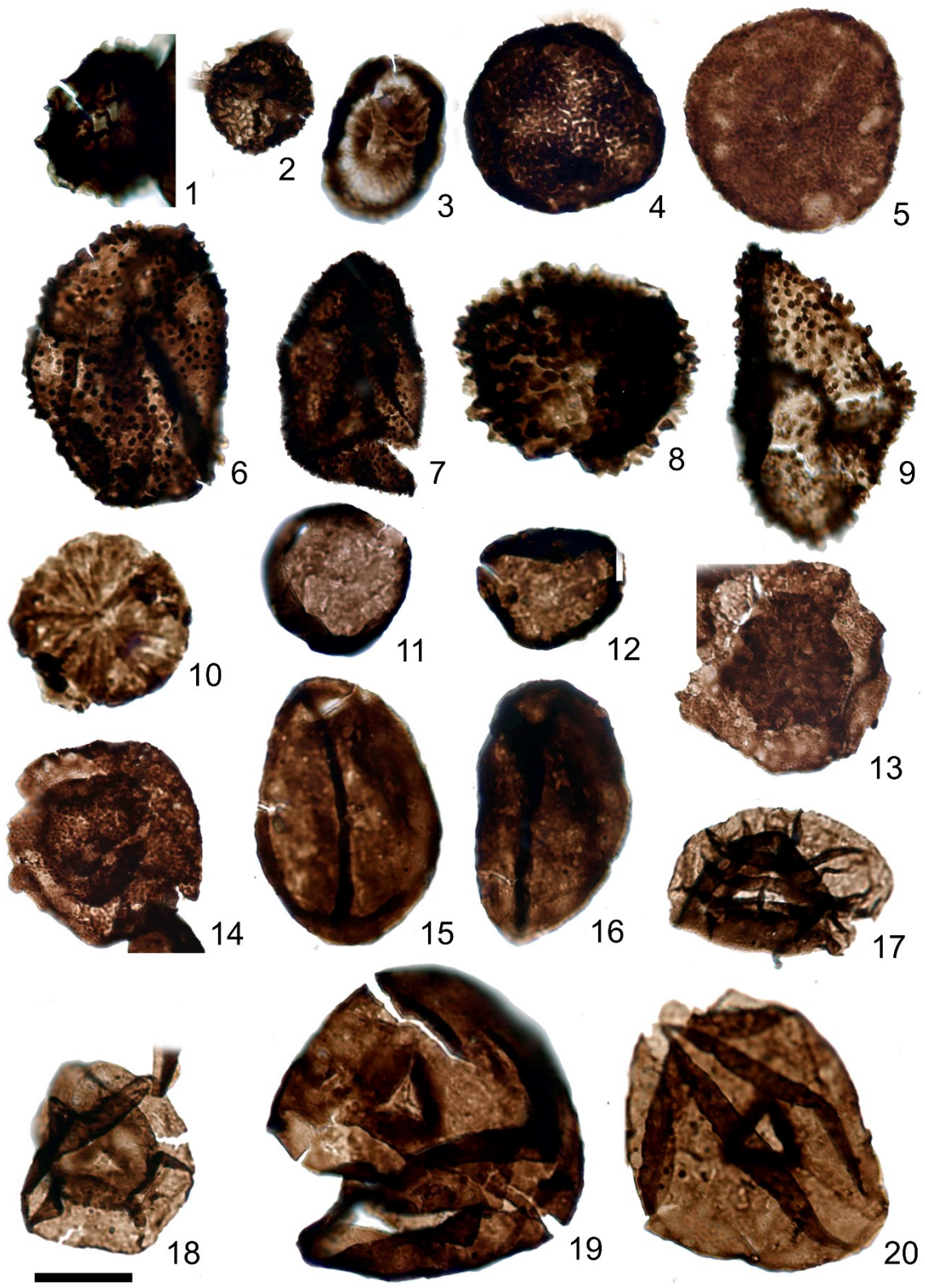




SERIES	STAGE	LAURUSSIA (North America and Western Europe)		SOUTH CHINA			
		SPORE BIOZONES	PLANT BIOZONES	SPORE BIOZONES		INDEX PLANTS	
MIDDLE DEV.	EIFELIAN (Lower)	AP*	<i>velatus-langii</i>	<i>Hyenia</i>	V**	VL*****	<div style="display: flex; flex-direction: column; align-items: center;"> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px; margin-bottom: 5px;"></div> <div style="border-left: 1px solid black; border-right: 1px solid black; width: 10px; height: 100px;"></div> </div>
LOWER DEVONIAN	EMSIAN		<i>dauglastownense-enrypterota</i>	<i>Psilophyton</i>	IV**	ES****	
		FD*	<i>annulatus-sexanii</i>				
		AB*					
	PRAGIAN	PoW*	<i>polygonalis-emiensis</i>	<i>Zosterophyllum</i>	III**	PE****	
	LOCHKOVIAN	BZ*	<i>breconensis-zavallatus</i>		II**		
MN*		<i>micromatus-newportensis</i>	I**		NC***		
PRIDOLI			<i>Cooksonia</i> (extending into the Wenlock)		SN***		







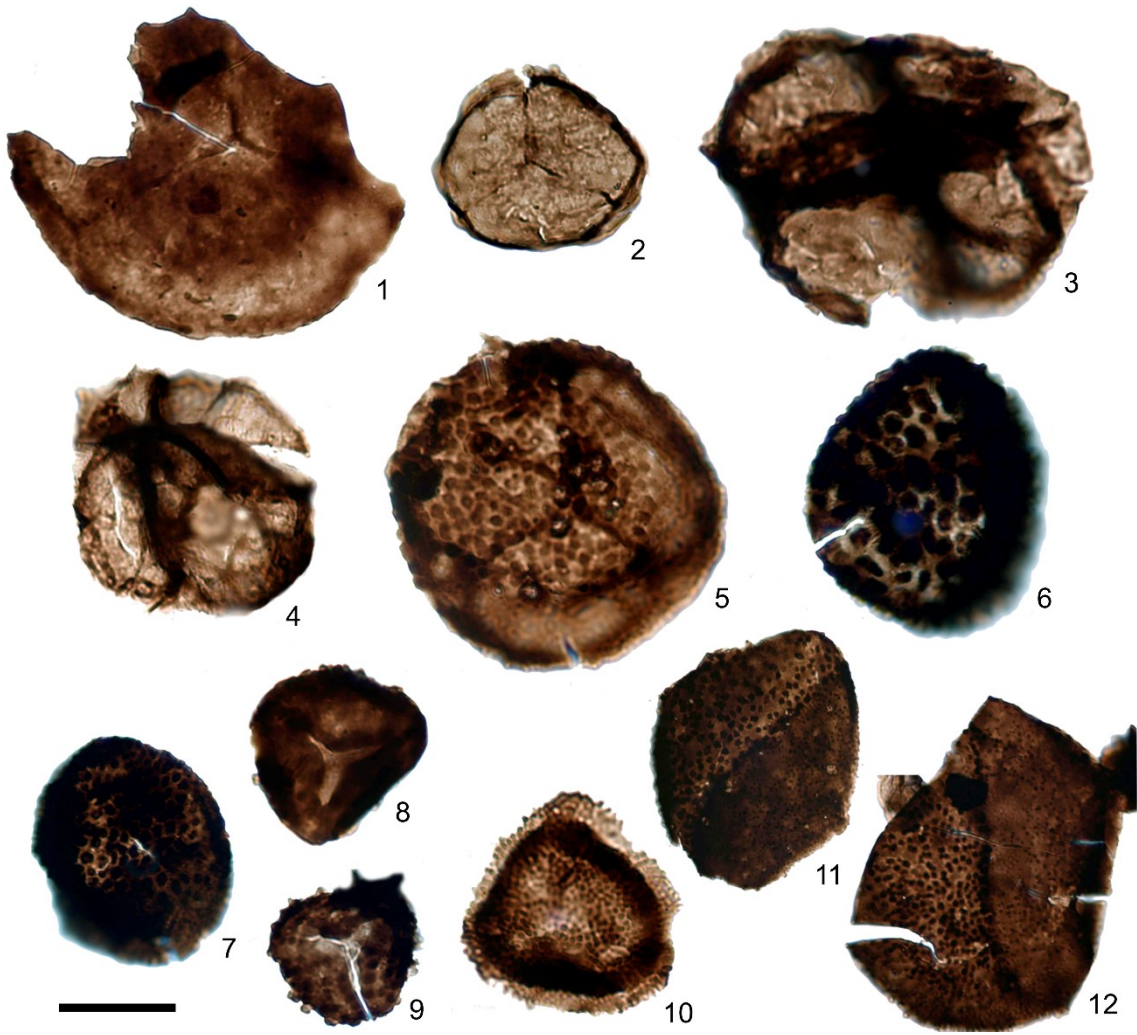


Table 1. Details of studied samples from the Posongchong Formation.

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.)	Drak 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 siltone	Negative
148MT01	74472	Zhichang	Bed 0 (Meitan Fm.)	Greenish gray mudstone	Negative

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).

	Posongchong Formation		Xujiachong Formation
	This study	Wang 1994	Wellman <i>et al.</i> 2012
<i>Ambitisporites avitus</i> Hoffmeister 1959		<i>Apiculiretusispora plicata</i> (Allen) Strel 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 xujiachongensis</i> sp. nov.
<i>Aneurospora xujiachongensis</i> Wellman <i>et al.</i> 2012		<i>Brochotriletes</i> sp. B of McGregor 1973	<i>Apiculiretusispora brandtii</i> Strel 1964
<i>Aneurospora</i> sp. A		<i>Brochotriletes?</i> <i>foveolatus</i> Naumova 1953	<i>Apiculiretusispora plicata</i> (Allen) Strel 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) Strel 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>luii</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 Strel <i>et al.</i> 1981	<i>Chelinospora ouyangii</i> sp. nov.
<i>Camarozonotriletes parvus</i> Owens 1971 (<i>sensu</i> 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>luii</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> (Lanning) 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> (Strel) Strel 1967
<i>Dibolisporites</i> sp. A		<i>Dictyotriletes subgranifer</i> McGregor 1973	<i>Retusotriletes</i> cf. <i>rotundus</i> Strel emend. Lele & Strel 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>Tetrahdraletes 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> Lanning 1968
<i>Latosporites ovalis</i> Breuer <i>et al.</i> 2007		<i>Retusotriletes rotundus</i> Strel emend. Lele & Strel 1969*	
<i>Leiozonospora xichongensis</i> Wellman <i>et al.</i> 2012		<i>Retusotriletes warringtonii</i> Richardson & Lister 1969	
<i>Retusotriletes triangulatus</i> (Strel) Strel 1967		<i>Retusotriletes</i> cf. <i>triangulatus</i> (Strel) Strel 1967	
<i>Retusotriletes</i> cf. <i>rotundus</i> Strel emend. Lele & Strel 1969		<i>Verrucosisporites polygonalis</i> Lanning 1968	
<i>Retusotriletes</i> sp.			
<i>Tetrahdraletes medinensis</i> Strother & Traverse emend. Wellman & Richardson 1993			
<i>Verrucosporites polygonalis</i> Lanning 1968			
<i>Verrucosisporites</i> cf. <i>polygonalis</i> Lanning 1968			
<i>Verrucosisporites</i> sp.			

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

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>Concentricosisporites 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>Tetrahedraletes 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

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-Dictyotriletes emisiensis</i> Spore Assemblage; <i>polygonalis-emsiensis</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 zhichangesis</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-emsiensis</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-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 thomasii</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-emsiensis</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>Thrinophyton 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-emsiensis</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

Table 4. Continued.

Flora	Age	Spore/graptoline biozone(s)	Locality(ies)	Plant diversity	References
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 genseliae</i> (E), " <i>Psilophyton</i> " <i>burnotense</i> (E?), cf. <i>Psilophyton princeps</i> (E?), <i>Rebuchia?</i> <i>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
Wahnbachschichten	late Pragian	Below <i>Dictyotriletes subgranifer</i> -palynozones	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: Gametophyte; H: Horneophytosid; I: *Incertae sedis*; L: Lycopsid; R: Rhyniopsid and related plants; S: Sphenopsid; Z: Zosterophylloids. Northeastern Gondwanan floras: Posongchong, Xujiachong, Pingyipu, Upper *Baragwanathia*. Laurussian floras: Anglo-Welsh, Rhynie, Wépion, Wahnbachschichten.

Appendix. Known Posongchong spore diversity

Ambitisporites avitus Hoffmeister 1959
Aneurospora conica (Lu & Ouyang) Wellman *et al.* 2012
Aneurospora posongchongensis sp. nov.
Aneurospora sp. A
Aneurospora sp. B
Aneurospora xuchiachongensis Wellman *et al.* 2012
Apiculiretusispora plicata (Allen) Strel 1967
Apiculiretusispora pygmaea McGregor 1973
Apiculiretusispora weenshanensis Wang 1994
Apiculiretusispora cf. *arabiensis* Al-Ghazi 2009
Archaeozonotriletes chulus (Cramer) Richardson & Lister 1969
Biornatispora cf. *dubia* (McGregor) Steemans 1989
cf. *Biornatispora dubia* (McGregor) Steemans 1989
Brochotriletes? *foveolatus* Naumova 1953
Calamospora cf. *microrugosa* (Ibrahim) Schopf *et al.* 1944
Calamospora cf. *panucea* Richardson 1965
Camarozonotriletes parvus Owens 1971 (*sensu* Steemans 1989)
Camarozonotriletes sextantii McGregor & Camfield 1976
Camarozonotriletes? cf. *luii* Wellman *et al.* 2012
cf. *Camptozonotriletes macrospinosus* Steemans 1986
?Camptozonotriletes cf. *caperatus* McGregor 1973
Camarozonotriletes sp. A
Chelinospora sp. A.
Concentricosisporites agradabilis (Rodriguez) Rodriguez 1983
Convolutispora sp. A
Convolutispora? sp. B
?Crissisporites guangxiensis Gao 1978
Cymbosporites echinatus Richardson & Lister 1969
?Cyclogranisporites sp.
Dibolisporites echinaceus (Eisenack) Richardson 1965
Dibolisporites eifeliensis (Lanninger) McGregor 1973
Dibolisporites wetteldorfensis (Lanninger) McGregor 1973
Dibolisporites sp. A
Dibolisporites sp. B
Dictyotriletes emsiensis (Allen) McGregor 1973
Dictyotriletes gorgoneus Cramer 1967
Dictyotriletes subgranifer McGregor 1973
Emphanisporites rotatus (McGregor) McGregor 1973
Emphanisporites cf. *decoratus* Allen 1965
Emphanisporites cf. *neglectus* Vigran 1964
Gneudnaspora divellomedia (Chibrikova) Balme 1988
Grandispora sp. A
Latosporites ovalis Breuer *et al.* 2007
Leiozonospora xichongensis Wellman *et al.* 2012
Raistrickia sp.

Appendix. Known Posongchong spore diversity (continued)

Retusotriletes rotundus Strel emend. Lele & Strel 1969

Retusotriletes triangulatus (Strel) Strel 1967

Retusotriletes warringtonii Richardson & Lister 1969

Retusotrilete cf. *triangulatus* (Strel) Strel 1967

Retusotriletes cf. *rotundus* Strel emend. Lele & Strel 1969

Retusotriletes sp.

Retusotriletes spp.

Tetraedraletes medinensis Strother & Traverse emend. Wellman & Richardson 1993

Verrucosporites polygonalis Lanninger 1968

Verrucosporites cf. *polygonalis* Lanninger 1968

Verrucosporites sp.
