
Early Silurian microfossil plants from the upper part of the Xiushan Formation in Guizhou Province, China and their palaeobotanical significance

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The upper part of the Xiushan Formation outcropped at Fenggang, N. Guizhou, China, containing the megafossil plant *Pinnatiramosus qianensis* Geng, yields a remarkable assemblage of trilete spores (12 species referred to 5 genera), tetrads and acritarchs (11 species referred to 8 genera), tubular elements (6 species referred to 3 genera), leiosphere clusters and cuticle-like fragments (3 types). Evidence from a variety of fossil animal groups indicates that this stratum should be late Llandovery (Telychian). The discovery of trilete and retusoid spores and dispersed tubular elements provide reliable clues to suppose that vascular plants had come into existence in the Early Silurian. The presence of tracheids with bordered pits suggests that *Pinnatiramosus qianensis* is most likely the oldest known vascular plant.

Key words—Microfossil plants, Palaeobotanical significance, Early Silurian.

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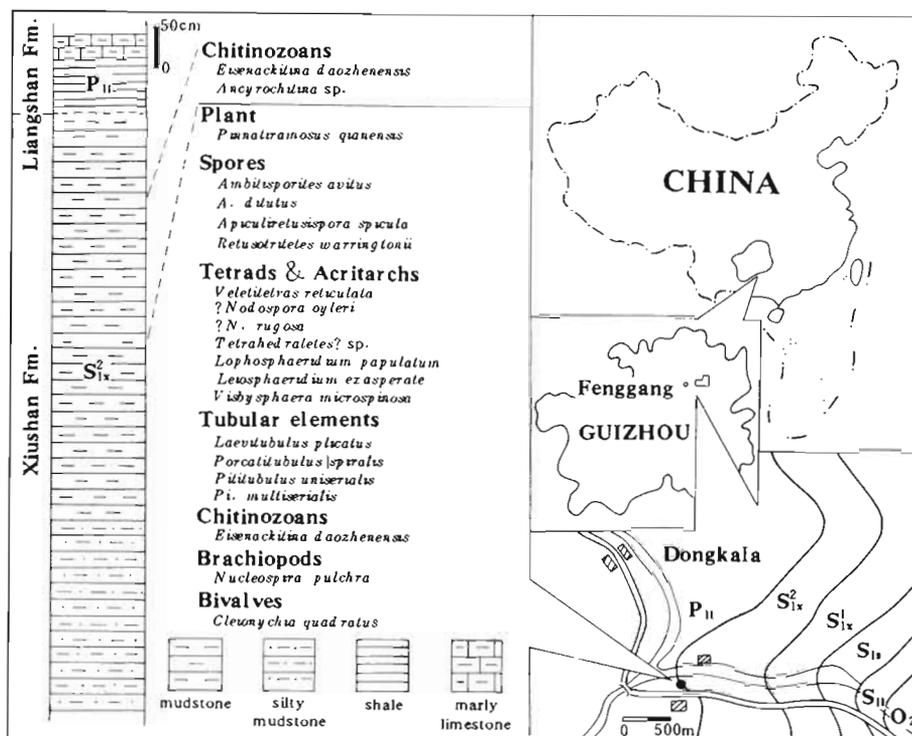
चीन में गुईझाऊ प्रान्त में जिउशान शैल-समूह के ऊपरी भाग से प्रारम्भिक सिलूरियन सूक्ष्मजीवाश्म तथा इनका पुरावनस्पतिक महत्व

वाँग यी, ऊयाँग शु एवं काई चौंगयाँग

चीन में उत्तरी गुईझाऊ में फैनगैंग में अनावरित जिउशान के ऊपरी भाग से गुरुपादपाश्र्मों के साथ-साथ एक महत्वपूर्ण समुच्चय उपलब्ध हुई है। इस समुच्चय में त्रिअरीय बीजाणुओं की 5 प्रजातियाँ एवं 12 जातियाँ, चतुष्को एवं एक्रीटाको की 8 प्रजातियाँ एवं 11 जातियाँ, नालाकार अवयवों की 3 प्रजातियाँ एवं 6 जातियाँ, लिओस्फेरिडों एवं उपचर्म-सदृश अवयवों के तीन रूप विद्यमान हैं। उपलब्ध जीवाश्मों के प्रमाणों से व्यक्त होता है कि यह संस्तर टेलाइसियन आयु का होना चाहिये। उपलब्ध पादपाश्र्म समुच्चय से पता चलता है कि प्रारम्भिक सिलूरियन काल में वाहिनीका युक्त पौधे पदार्पण कर चुके थे। *पिन्नेटिरेमोसस क्वियानेन्सिस* प्रायः सबसे पुराना वाहिनीका युक्त पौधा है।

THE origin and early evolution of vascular plants has long been one of the most interesting topics among botanists. To solve this kind of problems findings of relevant megafossil plants are dependable. However, in the rock formation such as Silurian, where complete plants are rare, the study of microfossil plants can be used to form initial hypotheses about the origin and early evolution of vascular plant. The utility of microfossil plants may be of more value than incomplete plants. Gensel *et al.* (1990) considered that the importance of early land plant debris lies in its message for the future of palaeobotanical research.

The Xiushan Formation outcropped at the locality Dongkala, Fenggang County, N. Guizhou (Text-figure 1) is well-known due to its containing the presumed vascular plant *Pinnatiramosus qianensis* Geng 1986. The "Wenlock" age of this formation was doubted by some palaeobotanists (e.g., Edwards, 1990) for the complexity of internal structure of this peculiar plant. In December 1991, and May 1995, the present authors and several colleagues from the Nanjing Institute went to the locality to make more detailed biostratigraphic investigation and systematically collected fossils and rock samples for microfossil



Text-figure 1—Showing the fossil locality, stratigraphic column and distribution.

sil plants study. The samples below the plant bed have yielded trilete spores, obligate tetrads and acritarchs, tubular elements, leiosphere clusters and cuticle-like fragments in association with chitinozoans. Moreover, some brachiopods are associated with the fossil plants, and some brachiopods and bivalves are found below the plant-bearing bed. These new findings provide direct evidence for dating the Xiushan Formation as discussed in the following.

STRATIGRAPHY

The Xiushan Formation exposed in Fenggang County, Guizhou is represented by a set of marine

clastic deposits, mainly consisting of yellowish green, greyish green mudstones, shales and siltstones, occasionally intercalated with thin-bedded sandstones, and calcareous mudstones or limestone lens, and is about 170.2 m in total thickness. The rock samples were collected from the uppermost part of this formation. It is overlain disconformably by the Liangshan Formation (Lower Permian), with the lower part composed of grey, dark mudstones and siltstones, intercalated with black carbonaceous shales, and locally a coal-seam (0.3-1.0 m thick). The Liangshan Formation is a transgressive series and probably represents lacustrine and swamp deposits near the coast. It is underlain conformably by the Rongxi Formation,

PLATE 1

All figures are X 800 unless otherwise indicated. The specimens are curated at Nanjing Institute of Geology & Palaeontology, Academia Sinica, and from the upper part of Xiushan Formation of Fenggang, Guizhou, China.

- 1, 11. *Ambitisporites avitus* Hoffmeister
2. *Apiculiretusispora sparsa* Wang et Ouyang
3. *Apiculiretusispora spicula* Richardson et Lister
4. *Retusotriletes warringtonii* Richardson et Lister
5. *Retusotriletes* cf. *warringtonii* Richardson et Lister
6. *Ambitisporites dilutus* (Hoffmeister) Richardson et Lister
7. *Leiotriletes* sp.
8. *Ambitisporites* cf. *dilutus* (Hoffmeister) Richardson et Lister
- 9, 12. *Retusotriletes* cf. *triangulatus* (Stree) Stree
10. Fragment of animal
13. Trilete spores broken away from tetrads, part of tetrad still attached.
- 14, 15. Leiosphere clusters.

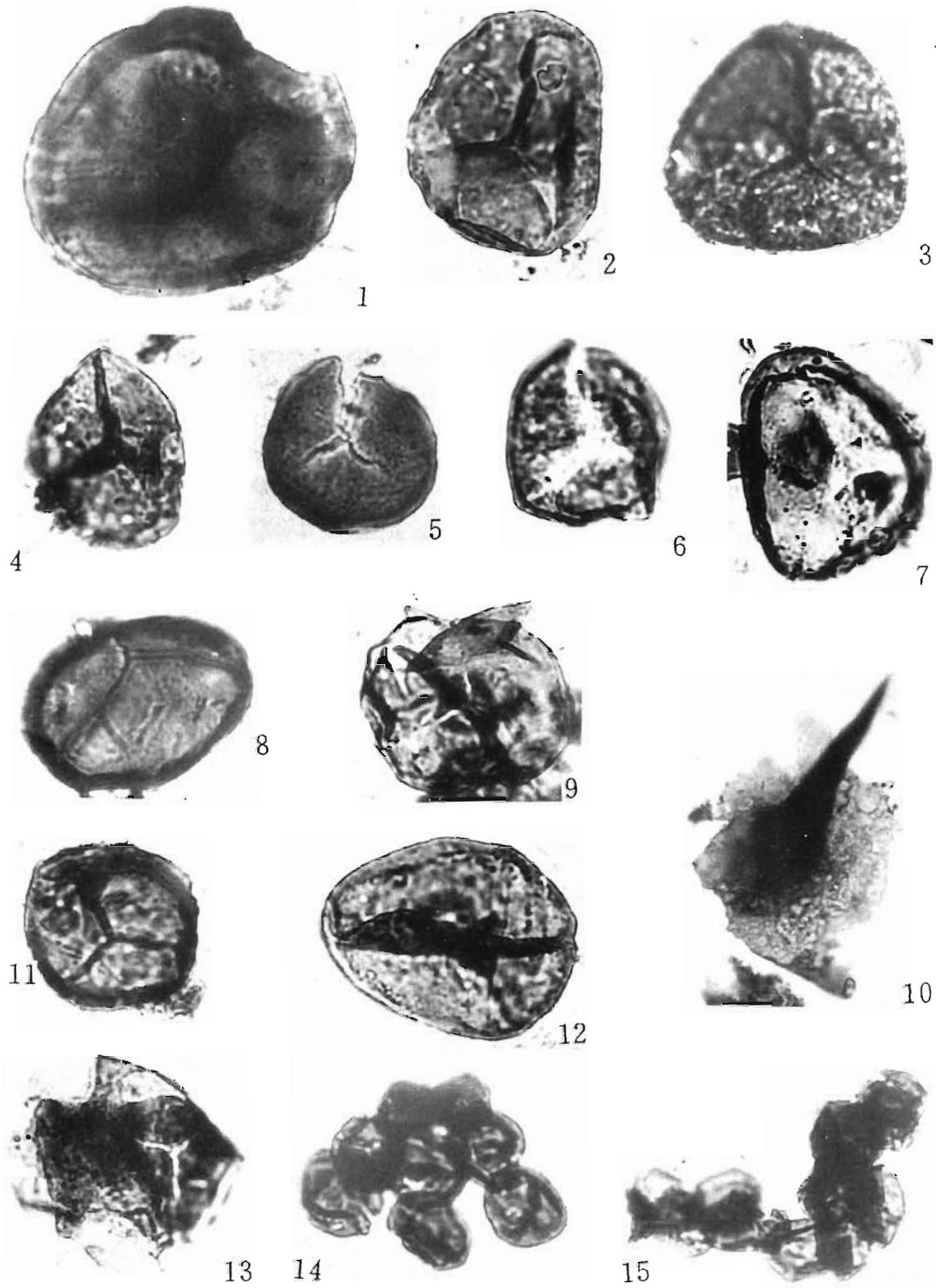


PLATE 1

composed of purple mudstones and silty mudstones intercalated with greyish and yellowish green siltstones, silty mudstones and a thin-bedded fine-grained sandstone, representing shallow-water deposits near the shore.

GEOLOGIC AGE

Other fossils, immediately above or beneath the microfossil plants-bearing bed, found in the upper part of Xiushan Formation (Cai *et al.*, 1995) include chitinozoans: *Eisenackitina daozhensis* Geng, *Ancyrochitina* sp. and *Conochitina* sp.; brachiopods *Nucleospira pulchra* Rong *et al.*, *Naliukinia* sp., *Protomegastrophia* sp. and *Lingula* sp.; bivalves *Cleionychia quadratus* (Hind), *Pterinopecten* cf. *cybele* (Barrande), *Parallelodon* sp. and *Leptodesma* sp.

Geng Liangyu (pers. comm.) considered that the chitinozoans may be assigned to the *Ancyrochitina brevicollis* zone established by Geng (1990) from the Yangtze Platform. This chitinozoan zone is referable to the graptolites *turriculatus/crispus* zone and partly covers the higher *griestoniensis* zone. The chitinozoans-bearing strata are corresponding to Early Telychian, late Llandovery.

The fannule of brachiopods was studied by Rong Jiayu. According to him (pers. comm.), stratigraphic range of *Naliukinia* is mainly Llandoveryan. *Nucleospira pulchra* Rong *et al.* has been known to occur in the Rongxi and Xiushan Formation elsewhere in NE Guizhou and SE Sichuan. *Protomegastrophia* sp. is also common in the Lower member of the Xiushan Formation in NE Guizhou and SE Sichuan. Both the Rongxi and Xiushan formations may be correlated with the upper part of the graptolite *Spirograptus turriculatus* zone of early Telychian, late Llandovery (Rong *et al.*, 1990).

The faunal of the bivalves was studied by Fang Zongjie (pers. comm.). The age significant *C. quadratus* was reported from the Llaneilo-Llandovery interval in Girvan, Scotland although the genus may range from the Middle Ordovician to Silurian. *P. cf. cybele* is quite similar to the type material from the *Pristograptus transgrediens* zone of Bohemia, but differs from the latter in the weaker radial ornament and the convex outline of anterior margin of the anterior ear. Specimens similar to *P. cf. cybele* are widespread in the Lower Silurian in the Yangtze Platform.

Thus different lines of faunal evidence point to the conclusion that the Xiushan Formation should be late Llandovery (Telychian) of Early Silurian in age.

CHARACTERISTICS OF MICROFOSSIL PLANTS

Characteristics of trilete spores and age implication

The sporomorph assemblage obtained from the Upper Xiushan Formation is dominated by obligate tetrads (70% of the total assemblage in quantity) together with less (ca. 20%) but quite diverse single trilete spores, the latter include some 12 species (forms) referred to 5 genera (Wang & Ouyang, 1996), they are: *Ambitisporites avitus* Hoffmeister (Pl. 1, figs 1, 11), *A. dilutus* (Hoffmeister) Richardson et Lister (Pl. 1, fig. 6), *A. cf. dilutus* (Hoffmeister) Richardson et Lister (Pl. 1, fig. 8), *Retusotriletes warringtonii* Richardson et Lister (Pl. 1, fig. 4), *R. cf. warringtonii* Richardson et Lister (Pl. 1, fig. 5); *R. cf. triangulatus* (Streel) Streel (Pl. 1, figs 9, 11), *R. minor*, *R. cf. abundo*, *Apiculiretusispora spicula* Richardson et Lister (Pl. 1, fig. 3), *A. sparsa* Wang et Ouyang (Pl. 1, fig. 2), *Leiotriletes* sp. (Pl. 1, fig. 7) and *Punctatisporites* sp. The trilete spore association shares the following features:

PLATE 2

All figures are X 800 unless otherwise indicated. The specimens are curated at Nanjing Institute of Geology & Palaeontology, Academia Sinica, and from the upper part of Xiushan Formation of Fenggang, Guizhou, China.

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| 1, 2, 4, 13. <i>Velatitetras</i> sp. A | 10. <i>Lophosphaeridium papulatum</i> Martin |
| 3, 6. ? <i>Nodospora rugosa</i> Strother et Traverse | 11. <i>Leiosphaeridia exasperate</i> Jahnsen |
| 5. <i>Tetrahedraletes</i> sp. | 12. <i>Retisphaeridium</i> ? sp. |
| 7. ? <i>Nodospora oyleri</i> Strother et Traverse | 14. <i>Visbysphaera microspinosa</i> (Eisenack) Lister |
| 8. <i>Cymatiosphaera</i> sp. B of Priedwalder | 15. <i>Velatitetras</i> sp. B |
| 9. <i>Velatitetras reticulata</i> Burgess | |

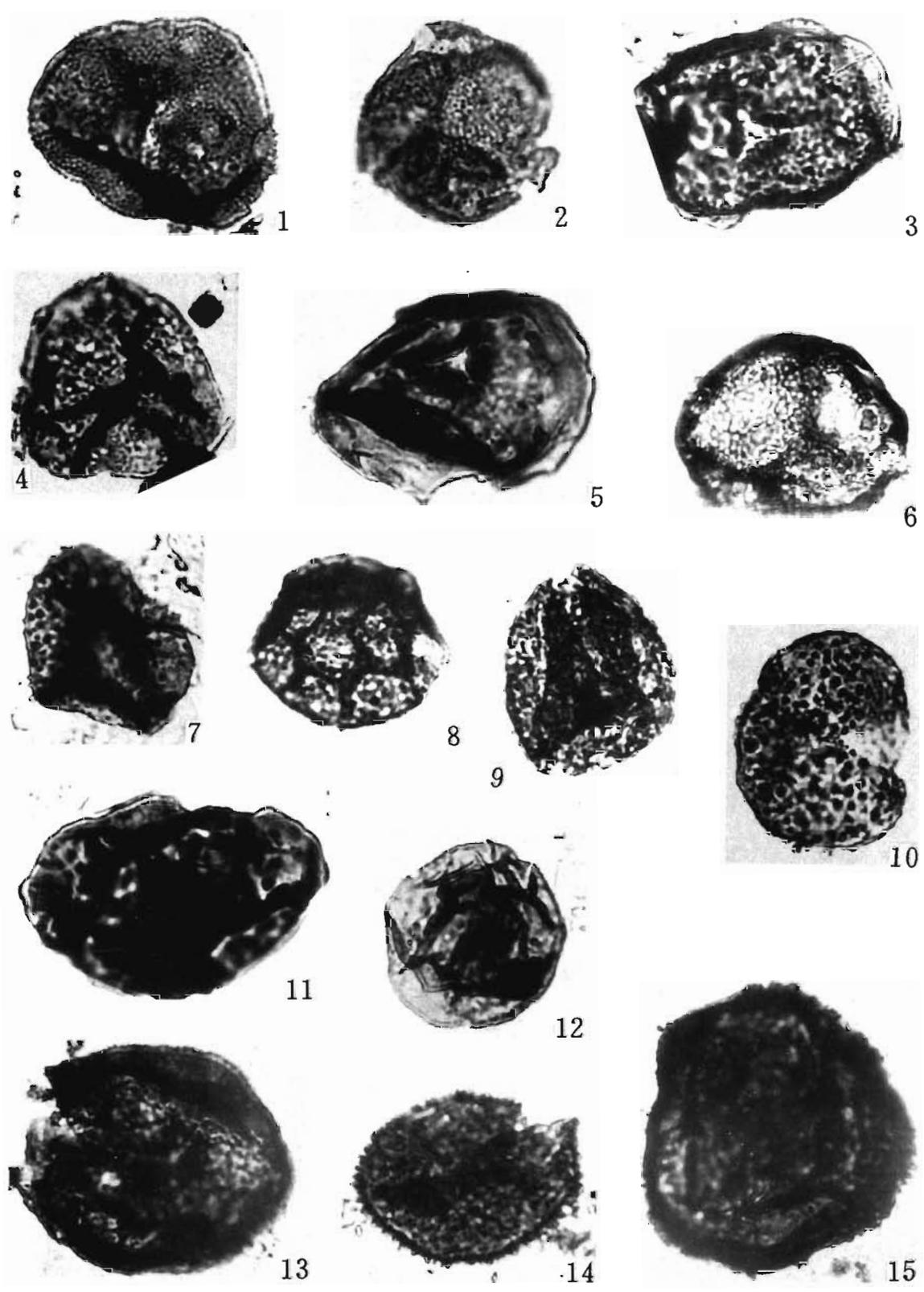


PLATE 2

1. *Ambitisporites* with quasi-curvedness is the main component, occupying about + 50 per cent of the Triletes in quantity, mainly represented by *A. cf. dilutus*, while *A. avitus* and *A. dilutus* are relatively low in proportion.
2. Retusoid spores are abundant, in which *Retusotriletes* stands first, nearly up to 40 per cent in content. Worthy of note and somewhat surprising is the occurrence of *Apiculiretusispora* for the earliest known record of this genus was from the Lower Ludlovian (Richardson & Lister, 1969). After figure 152 of Richardson and Edwards (1989) in the evolutionary events of spores, the first appearance of *Apiculiretusispora* was originally placed at the base of their Zone IV, now it has been descended down to the base of Zone III.
3. Compared with the roughly contemporaneous assemblages known in the world, the present one displays a comparatively high diversity. For instance, the Llandovery assemblages recorded from Libya (Hoffmeister, 1959), SW Wales (Late Aeronian-Telychian) (Burgess, 1991) and the United States (Pratt *et al.*, 1978; Strother & Traverse, 1978; Johnson, 1985; Miller & Eames, 1982) are all monotonous in trilete spore composition, mainly represented by 2 or 1 species of *Ambitisporites*, although in the USA assemblages may occur rich acritarchs, tetrads and dyads.

The palynoassemblage of Wenlock to Ludlov strata in England and South Wales first recorded by Richardson and Lister (1969) comprises *Ambitisporites dilutus*, *A. cf. dilutus*, *A. cf. avitus*, *Retusotriletes warringtonii*, *Archaeozonotriletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*, *Ar. chulus* var. *inframurinus*, *Ar. cf. divellomedian*, cf. *Synorisporites verrucatus*, cf. *S. downtonensis*, cf. *Streelispora granulatus*, *Apiculiretusispora synorea* and *Apiculiretusispora* sp. C-D. The assemblage of

Late Wenlock to Late Ludlov from Libya studied by Richardson and Ioannides (1973) shows much higher diversity than that of middle Llandovery of Libya by Hoffmeister (1959) and contains *Ambitisporites dilutus*, *A. avitus*, *Retusotriletes warringtonii*, *R. cf. warringtonii*, *R. minor*, *Archaeozonotriletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*, *Emphanisporites* cf. *protophanus*, cf. *Synorisporites verrucatus* and *S. cf. verrucatus*. Smith (1975) reported the presence of *Ambitisporites* in the early Wenlockian of Ireland. Based on the plant microfossils (acritarchs, tetrads and trilete spores), Burgess and Richardson (1991) have recognized two assemblages in the Wenlock strata of England. The early Wenlockone is characterized by the presence of *Ambitisporites avitus*, *A. dilutus*, *Archaeozonotriletes chulus* var. *chulus* and *Ar. chulus* var. *nanus*, and the late Wenlock by the appearance of *Synorisporites* cf. *S. libycus* and *Emphanisporites* cf. *protophanus*, in addition to the extending-up forms. The assemblages known from the late Wenlock to early Ludlov in Scotland (Wellman, 1993) contains abundant coherent tetrads in association with the trilete spores, such as *Ambitisporites avitus*, *A. dilutus*, *Archaeozonotriletes chulus*, *Chelinospora* sp. and *Cymbosporites* sp. A.

According to the palynological data accumulated since 1959, Richardson and McGregor (1986), and Richardson and Edwards (1989) have established some assemblage zones for Late Ordovician to Silurian, including 4 zones for the Early Silurian, in ascending order they are: III. *murusattenuata-murudensa*, IV. *avitus-dilutus*, V. *chulus-nanus*, VI. *protophanus-verrucatus*. Of these, the Zone III is largely represented by tetrads and dyads with few trilete spores, ranging from Rhuddanian (early Llandovery) to the lowest Aeronian, whereas Zone IV, V and VI are mainly composed of trilete spores, ranging from Aeronian to early Gorstian.

PLATE 3

All figures are X 800 unless otherwise indicated. The specimens are curated at Nanjing Institute of Geology & Palaeontology, Academia Sinica, and from the upper part of Xiushan Formation of Fenggang, Guizhou, China.

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| 1, 2. | <i>Pititubulus multiserialis</i> Wang et Cai | 8. | Cuticle-like fragment, Type-B |
| 3, 4. | <i>Porcatitubulus spiralis</i> Burgess et Edwards | 9. | Cuticle-like fragment, Type-C |
| 5, 5a. | <i>Pititubulus uniserialis</i> Wang et Cai | 10. | <i>Porcatitubulus annulatus</i> Burgess et Edwards, 1991. X 400 |
| 6. | <i>Porcatitubulus reticulatus</i> Wang et Cai | 11. | <i>Laevitubulus plicatus</i> Burgess et Edwards, 1991. X 400 |
| 7. | Cuticle-like fragment, Type-A | | |

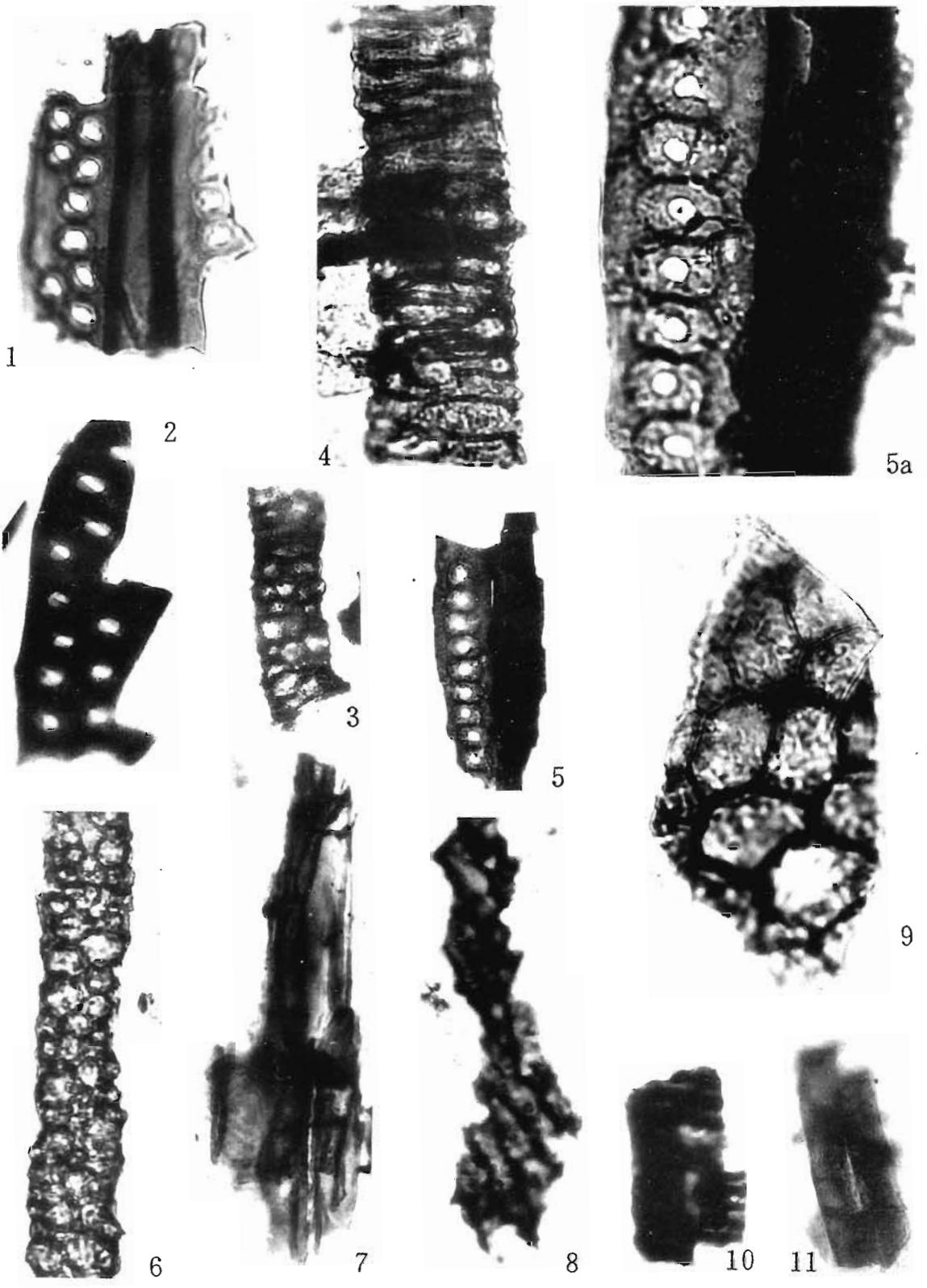


PLATE 3

It is difficult to exactly correlate the present assemblage with those zones as listed above. One of the reasons seems to be derived from the empirical character of the generalization and zonation which was made on the basis of a few known assemblages, implying that the very low diversity in the Early Silurian is possibly apparent than real. On the other hand, of course we must be very cautious about the relatively high diversity which may be resulted from a "splitter" stand point in classification as adopted here following other most palynologists, or from contamination during the sample-maceration process. However, the latter possibility can be excluded because the processing was done very carefully. And judging from the assemblage itself, some of the species have already been known in the Early Silurian, thus we believe these components are indigenous.

Amongst the 12 species or morpho-types of these trilete spores, several indeed reveal an aspect of Early Silurian, for instance, *Ambitisporites avitus*, *A. dilutus*, *A. cf. dilutus*, *Retusotriletes warringtonii* and *R. cf. warringtonii* have been known to occur down to Early Silurian: in Llandovery (Hoffmeister, 1959) and late Wenlock (to late Ludlov) (Richardson & Ioannides, 1971) in Libya; in Wenlock of England (Burgess & Richardson, 1991). On the other hand, several peculiar and characteristic forms have never been recorded below Ludlov. The earliest known occurrence of *Retusotriletes cf. triangulatus* with thickened apical area was from the base of Geddinian although similar spores (e.g., *R. cf. goensis* Lele & Strel) have been reported in the upper Ludlov (Richardson & Ioannides, 1971), and *Apiculiretusispora* was from the lower Ludlov. If special emphasis is just laid upon these two forms, one would assume that the present assemblage should not be older than Late Silurian (Ludlov) in age. However, some forms with more complex morphology and sculptures from late Wenlock to Ludlov have not been observed in our assemblage, for instance, "*Emphanisporites*" cf. *protophanus* and cf. *Synorisporites verrucatus* of the Zone VI (late Wenlock) as well as *Synorisporites lybicus*, *Lophozonotriletes? poicilomorphus*, "*Emphanisporites*" *protophanus*, *E. neglectus* and *Brochotriletes?* sp. of Zone VII (Ludlov). Consequently, the absence of these forms sug-

gests that the Fenggang assemblage is most likely older than late Wenlock-Ludlov.

The present assemblage is definitely younger than the lower part of *avitus-dilutus* Zone (IV) for its higher diversity than that of Libya (Hoffmeister, 1959) and some forms displaying a younger aspect; on the other hand, because of the absence of *Synorisporites* and "*Emphanisporites*", etc., it should be older than the late Wenlock (upper part of Zone V and VI Zone). Therefore, if one consider the age solely based on the palynological evidence, it seems appropriate to date the Fenggang assemblage as late Llandovery (Telychian) to early Wenlock. However, as stated above, the definition of Early Silurian (especially Llandovery to early Wenlock) seems far from complete because the Zones IV and V of Richardson and Edwards (1989) are based on rare known records. The Zone V not only has a very long range (from late Llandovery to late Wenlock), but contains few typical forms, only comprising 6 species, including two varieties (viz. *Ar. chulus* var. *chulus* and *Ar. chulus* var. *nanus*) with the earliest record in upper part of Telychian, the other 4 species have been known in the Zone IV. In other words, there is not any typical forms for the late Llandovery.

The chitinozoans, brachiopods and bivalves from the same bed as the spore assemblage, or from beds immediately above or beneath it indicate the Upper Xiushan Formation to be late Llandovery age. From the palynological stand point as discussed before, we have no ample grounds to object this dating. If the dating is reliable, it means that the present assemblage has made important supplementary content of the Llandovery, i.e., corresponding to the upper part of Zone IV or the lower part of Zone V, and throws light on the appearance of vascular plants during the Llandovery time.

Characteristics of tetrads and acritarchs and age implication

The obligate tetrads and acritarchs are composed of some 11 species (forms) referred to 8 genera. They are: *Velatitetras reticulata* Burgess (Pl. 2, fig. 9), *Velatitetras* sp. A (Pl. 2, figs 1, 2, 4, 13), *Velatitetras* sp. B (Pl. 2, fig. 15), ?*Nodospora oyleri* Strother et Traverse (Pl. 2, fig. 7), ?*N. rugosa* Strother et Traverse (Pl. 2, figs 3, 6), *Tetrahedraletes?* sp. (Pl. 2, fig. 5),

Lophosphaeridium papulatum Martin (Pl. 2, fig. 10), *Visbysphaera microspinosa* (Eisenack) Lister (Pl. 2, fig. 14), *Leiosphaeridia exasperata* Johnson (Pl. 2, fig. 11), *Retisphaeridium?* sp. (Pl. 2, fig. 12), *Cymatiosphaera* sp. B of Priwalder, 1987 (Pl. 2, fig. 8). There are some leiosphere clusters (Pl. 1, figs 14, 15).

The tetrads are represented by *Tetraedraletes*, *Nodospora* and *Velatitetras*, and acritarchs by *Leiosphaeridia* and *Visbysphaera*. Gray (1985) suggested that the change from spore tetrads to single trilete spores occurs in the mid-late Early Silurian. The present assemblage is dominated by tetrads and acritarchs associated with less but quite diverse single trilete spores. It means that it is possibly mid-especially late Early Silurian in age. *Leiosphaeridia exasperata*, *?Nodospora oyleri*, *?N. rugosa* have been found from the Tuscarora Formation (Llandovery) of U.S.A. (Johnson, 1985; Strother & Traverse, 1979), although the former has a longer range. The Tuscarora Formation was originally determined as Llandovery in age, but it may be older. *Visbysphaera microspinosa* has a long vertical distribution, but the specimens identified as this species are quite similar to those identified by Smelor (1987) from Llandovery to the earliest Wenlock strata of Norway. *Lophosphaeridium papulatum* and *Cymatiosphaera* sp. B of Priwalder have been found from the strata of late Llandovery to early Wenlock of Canada and SW-Carinthia (Priwalder, 1987). *Velatitetras reticulata* was established by Burgess (1991), they are found from the Early Llandovery (Rhuddanian-Aeronian) of South-west Wales. Leiosphere clusters are very similar to the specimens from the Tuscarora Formation of Llandovery in central Pennsylvania (Johnson, 1985, pl. 13, fig. 5).

The above evidence and discussions lead us to conclude that this palynomorph assemblage is Llandovery in age.

Characteristics of the tubular elements

The dispersed tubular elements obtained from the Upper Xiushan Formation are composed of some 6 species (forms) referred to 3 genera (types) (Wang & Cai, 1995), they are described and classified using the Artificial Anteturma system (Burgess & Edwards, 1991). The *Porcatitubulus reticulatus* Wang et Cai (Pl. 3, fig. 6) was erected within *Porcatitubulus* of

Infraturma, Endomurali. The Infraturma, Foveatimurali, was erected to include one genus, *Pititubulus* Wang et Cai with two species: *Pi. uniserialis* Wang et Cai (Pl. 3, figs 5, 5a) and *Pi. multiserialis* Wang et Cai (Pl. 3, figs 1, 2). The consistent components of the dispersed tubular elements are *Laevitubulus plicatus* Burgess et Edwards (Pl. 3, fig. 11), *Porcatitubulus annulatus* Burgess et Edwards (Pl. 3, fig. 10) and *Po. spiralis* Burgess et Edwards (Pl. 3, figs 3, 4). The dispersed tubular elements show the following features:

1. Smooth-walled tubes are the less component, as there are only one species.
2. Tubes with internal and external thickenings are the main component, mainly represented by *Porcatitubulus spiralis*, while *Po. plicatus* and *Po. reticulatus* are relatively low in proportion. Spiral thickenings are abundant.
3. Worthy of note and somewhat surprising is the occurrence of *Pititubulus*. There are uniseriate and multiseriate bordered pits on the wall. The tubes with bordered pits on the wall are the earliest known record.

Burgess and Edwards (1991) studied the dispersed tubes and filaments from the uppermost Ordovician, Silurian and Lower Devonian of Anglo-welsh Basin of Great Britain. Two assemblages of tubes and filaments were recognized. The older is found in uppermost Ordovician through to middle Silurian strata and is typified by a low diversity of smooth-walled tubes; the younger ranges from the middle Silurian at least to the Lower Devonian and is typified by various smooth-walled tubes, tubes with internal and external thickenings, and filaments. Based on the result of Burgess and Edwards (1991), tubular elements from Fenggang, Guizhou should be analogous to the upper assemblage at most. The age is possibly late Wenlock to Lower Devonian. Because of the appearance of the bordered pits, the tubular elements should not be older than upper assemblage of Burgess and Edwards (1991) in age. However, through a study of the biostratigraphy, these tubular elements are considered as a late Llandovery (Telychian) age.

In addition, there are three types of cuticle-like fragments (Pl. 3, figs 7-9). The Type C is very similar to the specimens from Llandovery to Wenlockian of

U.S.A. and Scotland (Pratt *et al.*, 1978; Strother & Traverse, 1979; Wellman, 1995), which possesses a reticulum comprising isodiametric polygonal units. The Type A is closely to the specimen from Lochkovian of Scotland (Wellman, 1995), which is characterised by the reticulum comprising elongate units. Wellman (1995) considered that these cuticle-like fragments probably derive from a higher land plant.

PALAEOBOTANICAL SIGNIFICANCE

Palaeobotanical significance of spores

The first appearance of trilete spores in strata is one of the important events in plant evolution, although their bearing on the origin of vascular plants does not seem beyond dispute. Because trilete spores are not only known in pteridophytes but also in some bryophytes. Just as Banks (1975) pointed out, we have no simple clue to distinguish the bryophytic or vascular plants.

Gray (1985) arrived at the following inference after surveying the relevant data: "The trilete configuration in living bryophytes is not so typical as it does in the modern vascular cryptogamic plants, and the actualise of comparison between ancient and modern analogies is practical and the conclusion of trilete spores representing vascular plants is less conjectural". We can discuss this subject further, and the conclusion arrived at is : even if not all triletes were produced by vascular plants, at least those retusoid spores (*Retusotriletes*, *Apiculiretusispora* and to some extent *Ambitisporites*) of pre-Devonian were derived from vascular plants. The arguments are as follows:

1. Among the 900-1000 genera of living bryophytes, trilete spores are mainly seen in Musci-Anthocerotales, Sphagnales and some of Andreales; while in liverworts, only a few trilete spores occur in Marchantiales (Hepaticae), Pottiales, Funariales and Isobryales. In both cases, there are not retusoid spores or their analogies (Boros *et al.*, 1975; Gray, 1985).
2. No reliable retusoid trilete spores have been known in the *in situ* spores of non-vascular plants. The only possible exception is the strange plant *Protosahvania* of Devonian age, however, much dispute and various assumptions have been arisen about its botanical affinity: euglenid?, red alga?, bryophyte?, fern? or certain kind of algae with some features of vascular plant? -not any of these assumptions has been firmly demonstrated, even its spore morphology is still unclear: Niklas and Phillips (1976) mentioned the *in situ* spores often in tetraspores or tetrads are larger than 200 μm across, and morphologically similar to *Retusotriletes*, but Taylor (1988) suggests these spores have no trilete, and are very close to spores of some living euglenids and red algae in morphology.
3. *In situ* retusoid trilete spores have been widely reported from Late Silurian to Early Devonian vascular plants, for instance, *Ambitisporites*, *Retusotriletes* and *Aneurospora*-type spores in *Cooksonia pertonia* Lang (Fanning *et al.*, 1988); *Retusotriletes*-type has also been recorded by Lang (1937) in *Cooksonia*, and it is very similar to *R. warringtonii*. Retusoid spores are also documented from *Rhynia major* (Kidston & Lang, 1917). *Renalia huebei* produced *Apiculiretusispora*-type spores (Gensel, 1976); *Psilophyton dawsoni* contains *Retusotriletes* (Banks *et al.*, 1975) and *Psilophyton crenulatus* bears *Apiculiretusispora*. Almost all *in situ* spores found in zosterophyllids which are widely developed in Early Devonian of the globe have been shown to be retusoid. For instance, *Zosterophyllum cf. fertile*, *Z. llanoveranum*, *Z. yunnanense*, *Discalis longistipa*, *Sawdonia ornata* and *Rebuchia ovata*, etc. produced *Retusotriletes*-type spores (Edwards, 1969; Hao Shougang, 1985; Fanning *et al.*, 1990). Spore comparable with *R. cf. triangulatus* have been known in *Sawdonia scanthotheca* (Gensel, 1982). More examples can be listed. As Fanning *et al.* (1990) summarized: there is a close relationship between retusoid spores and vascular plants.
4. Judging from the known dispersed spores, retusoid forms such as *Ambitisporites*, *Retusotriletes* and *Apiculiretusispora* had come into existence in the Early Silurian (Llandovery). However, their high development and differentiation was started from Siegenian (Fanning *et al.*, 1990). The earliest record of megafossil vascular plant has been known in the late Early Silurian

(Wenlock), such as the sporangia of *Cooksonia*-type from Ireland (Edwards, 1990), and towards Siegenian the vascular plants became progressively diverse in composition and showed different evolutionary trends in morphology, indicating the onset of great radiation and development. Thus it can be seen that the first appearance, development and differentiation of both retusoid spores and vascular plants are basically parallel.

The evidence as discussed above are much in favour of the assumption that there is a close connection between retusoid spores and vascular plants. Even Banks (1975) who is most cautious with reasonable reservation about the botanical significance of dispersed spores also mentioned: "Although generally one can not determine the dispersed trilete spores derived from what kind of plants, however, some of them are comparable to the in situ spores found in organically connected sporangia, and the similarity is so high, can not be casual.....". The same can be applied to the Fenggang spores. In other words, the retusoid spores in the present assemblage are highly probably produced by vascular plants. This implies that vascular plants had already appeared in Llandovery (Telychian) time provided that the dating is correct. This conclusion lends support to explain *Pinnatiramosus qianensis* as a vascular plant. In addition, the rather high diversity seems to indicate not only a single species of vascular plants existed during that time in SW China although this inference needs more evidence to be substantiated.

Palaeobotanical significance of tubular elements

The evidence for the appearance of the early vascular plant lies in the vascular bundle mainly consisting of tracheids. Gensel *et al.* (1990), Kenerick and Crane (1991) showed that the differences between the tubular elements and tracheids lie in the ultrastructure of the water-conducting cells and the biochemistry of walls. Kenerick and Crane (1991) termed that it is an important character of the tracheids of vascular plant with lignin. Niklas and Smocovitis (1983) considered that the differences of tubular elements and tracheids are in the lateral wall

thickenings appearing to be internal and the polyphenols (lignin-like moiety) in former but in the secondary wall and lignin in later. The study of plant anatomy takes a clear-cut stand that lignin is a mixed polymer containing phenolic derivatives of phenylpropane and commonly found in secondary thickened cell walls. It means that the difference of the tubulus elements and tracheids mainly lies in the secondary wall which does not appear in the former but in the later. According to plant anatomy, a certain portion of the cell wall of the vascular plant remains thin, even as the secondary wall is formed and, therefore, the thin areas consist only of primary wall material. These areas, which are variable in shape, are called pits; a bordered pit is formed by a thin area on the secondary wall. In other words, if bordered pits appear on the wall, it means that the wall contains the secondary wall and this tube belongs to the tracheids of vascular plant.

The wall of dispersed tubes from Fenggang, Guizhou displays indeed bordered pits, such as *Pittitubulus uniserialis*, *Pi. multiserialis*. Because of the appearance of bordered pits on the wall, it is most possible that the tubes with such pits contain the secondary wall. They probably represent the tracheids of vascular plant. In other words, the early vascular plants had appeared in Early Silurian (Telychian) judging from the view of plant anatomy.

Pinnatiramosus qianensis Geng, from the strata above this microfossil plant's horizon, is the only valuable macrofossil plant. According to the description of Geng Baoyin (1985), this plant consists of a creeping prostrate axis and an erect pinnate branching system, mostly the axes and branches possess a centrally conducting impression, among which one prostrate axis bears anatomical structure. Most tubular elements bear scalariform and alternate pits and occasionally laevitubes with no ornamentation. Geng Baoyin (1985) proposed that *Pinnatiramosus* "does not belong to a primitive group of vascular plant", and represents "a group of new plants with remarkably nontracheophyte morphology but tracheophyte-like anatomy", "it most probably represents an extinct group in the evolution of algae, which intended to live on land but failed to do so". Geng Baoyin (1985) also proposed that the pits on the tubular wall were possibly simple pits but actually

they are bordered pits. Hao Shougang and Beck (1990) assured that the tubular elements possessed circular bordered pits like those of the tracheids of typical vascular plants and suggested that this plant "was probably aquatic and subaquatic and exhibits some characteristics of both thallose nonvascular plants (in the case, algae) and primitive terrestrial vascular plant"; and considered that it may represent either a vascular plant ancestor or a very primitive vascular plant. Cai Chongyang and Li Xingxue (1994) held that the tubular elements were possibly tracheids because they had bordered pits. The pits of *Pinnatiramosus* are alternately arranged in 3-4 rows and polygonal in form by the close contact of each other (Geng Baoyin, 1985, pl. 4, figs 3, 5, 10), which is somewhat similar in arrangement to the pits of some *Callixylon* species of Late Devonian. In the transverse section of *Pinnatiramosus* (Geng Baoyin, 1985, pl. 3, figs 5-8) the secondary wall with bordered pits is clearly shown. It means that the vascular bundle of *P. qianensis* consists of the tracheids. Because of the unknown structure of its reproductive organ and the absence of cuticle with stomata, the systematic position of this plant remains hard to determine. However, their pitting structure indicates that this plant might have water-conducting and supporting functions. Based on the appearance of tracheids with bordered pits on vascular bundle, *P. qianensis* may represent the oldest known vascular plant in the world.

The derivation of *Porcatitubulus* remains equivocal. The conducting bundle of the non-vascular plants, such as *Nematoplexus rhyniensis*, *Nematasketum diveriforme*, *Protaxites hicksii*, *P. storriei*, *P. taitii*, *P. loganii*, etc. has been found to contain tubular elements, which are similar to *Porcatitubulus annulatus* and *P. spiralis*. Burgess and Edwards (1991) considered that the *Porcatitubulus* is probably from the Nematophytales Lang. Is it possible that *Porcatitubulus* derived from the vascular bundle of earliest vascular plants? Niklas and Smocovitis (1983) considered that leavitubes were from the conducting bundle of non-vascular plant. However, a few leavitubes are associated with bordered pits-bearing tracheids in the vascular bundle of *Pinnatiramosus qianensis* and in the dispersed tubes (Pl. 3, fig. 1). It implies that tubular elements are not exclusively of

non-vascular plant origin. The vascular bundle of the presumed earliest vascular plant in the Lower Silurian is of a special type, which consists of a few tubular elements (*Laevitubulus*, *Porcatitubulus*, etc.) and tracheids.

CONCLUSIONS

Evidence from a variety of fossil animal groups indicates that the Xiushan Formation yielding *Pinnatiramosus* should be late Llandovery (Telychian) in age, and the microfossil plants lend support to, or at least does not be in contradiction with such a dating. The discovery of trilete and retusoid spores and dispersed tubular elements provide reliable clues to suppose that vascular plants had come into existence in the Early Silurian. The presence of *in situ* tracheids with bordered pits suggests that *Pinnatiramosus qianensis* is most likely the oldest known vascular plant.

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