A new seed-bearing leaf from the Permian of China

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Seed-bearing leaves of the pterosperms are not common but a few Palaeozoic examples have been useful in understanding the diversity of these plants and their importance in the evolution of several Mesozoic seed plants. *Eophyllogonium cathayense* gen. et sp. nov. is instituted for recently discovered seed-bearing taeniopteroid leaves from the Permian Leping Formation of China. The seeds are abundant along the margin of the leaves lying in the grooves of the crenulate margin at the terminus of a reticulate network of veins. This new seed fern is compared and contrasted with other seed-bearing Permian age foliage of China. This seed fern may have produced as many as 160 seeds on an individual leaf thus illustrating its extensive potential for seed production. The micropyles are unique structures, appearing as inverted cones extending outward from the distal end of the seed. Many specific features of *Eophyllogonium cathayense* are discussed.

Key-words—Pterosperms, Seed-bearing leaves, Permian, China.

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सारांश

चीन के परमी कल्प से एक नई बीज-धारक पत्ती

मी मी-ताँग, डेविड एल० दिल्चर एवं वान झइ-हुइ

टेरीडोस्पर्मी पौधों की बीज-धारक पत्तियाँ सामान्यतः नहीं मिलती लेकिन कुछ पुराजीवी प्ररूपों से इन पौधों की विविधता तथा कई मध्यजीवी बीज युक्त पौधों के विकास में इनका महत्व जानने में सहायता मिली है। अभी हाल में चीन के परमी लेपिंग शैल-समूह से प्राप्त बीज-धारक टीनिऑप्टेरॉयडी पत्तियों हेतु **ईओफ़िल्लोगोनियम कैथेयेन्से** नव प्रजाति व जाति बनाई गई है। पत्तियों के किनारों के संग-संग पर्याप्त संख्या में बीज विद्यमान हैं। इस बीज युक्त फ़र्न की तुलना चीन के परमी कल्प से प्राप्त एक अन्य बीज-धारक अवयव से की गई है। ऐसा लगता है कि इस पत्ती से लगभग 160 बीज बने होंगे। **ईओफ़िल्लोगोनियम कैथेयेन्से** के कई विशेष लक्षणों की भी विवेचना की गई है।

THIS is a report of seed-bearing leaves that were found in Permian age sediments in South China. The seeds are located at the margin of the leaf. The leaves are taeniopteroid in shape with simple anastomosing venation.

These seed-bearing fossils are found associated with *Gigantopteris dictyophylloides* and *Gigantonoclea acuminatiloba* in the same fossiliferous bed, but their characteristic elongate polygonal anastomosing venation is different from all known gigantopterid genera. The shape, the venation of the leaf and the characters of the seeds, when taken all together, strongly suggest that these seed-bearing leaves probably represent an undescribed type of gymnosperm.

MATERIAL AND METHODS

The fossils described here are found in coal-bearing strata exposed in a prospect tunnel that belongs to the 226th Coal Geology Team of Jiangxi Coal Geology and Exploration Corporation. The locality is situated near Yichun City, Jiangxi Province. The sediments belong to the Permian Guanshan Member of the Leping Formation (Mei *et al.*, 1987). There are several fossil plants, such as *Pecopteris* sp., *Fascipteris (Ptychocarpus) densata* Gu & Zhi, *Compsopteris contracta* Gu & Zhi, *Gigantonoclea*

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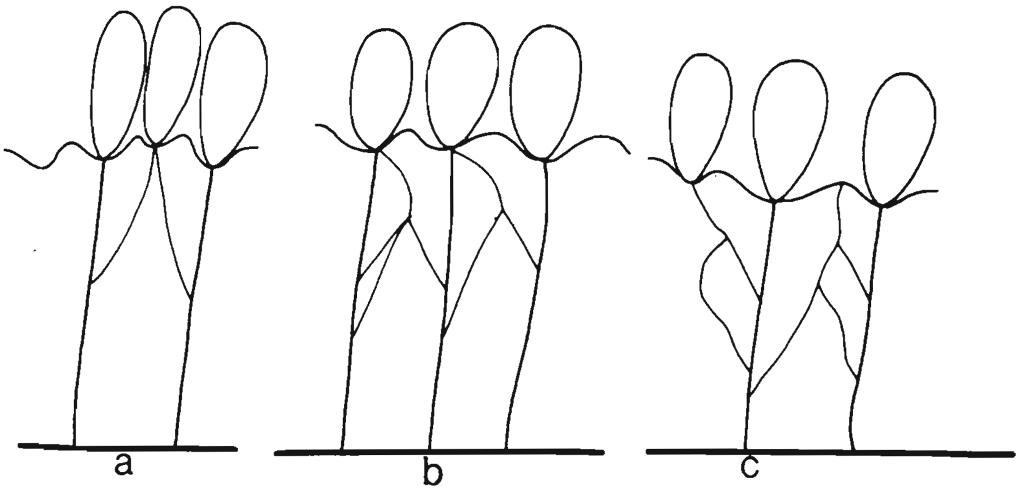

Text-figure 1—Idealized diagram of a fertile leaf margin of *Eophyllogonium cathayense*. The different diagrams, a, b and c, illustrate the different ways that the tertiary veins of the leaf form reticulations.

acuminatiloba (Shim.) Gu & Zhi, *Gigantopteris dictyophylloides* Gu & Zhi and *Taeniopteris* sp. associated together in these beds with the seed-bearing leaves.

More than forty specimens of seed-bearing leaves have been collected. All of them are preserved as impressions and most of them show morphological details. Because no organic material is preserved, only external morphological characters can be observed. The specimens were photographed using Linhof camera and oblique lighting to accentuate the details of the impressions. Other details of some specimens were best revealed by latex casts which were then observed with SEM.

SYSTEMATICS

Eophyllogonium gen. nov.

Diagnosis—Seed-bearing leaf, lanceolate, gradually narrowing distally. Leaf margin bearing regular symmetrical crenulations. Midrib stout, narrowing towards the apex. Veins pinnate, in three orders. Secondary veins fine, branching dichotomously at their bases. Tertiary veins anastomose forming elongate, polygonal meshes. Seeds elongate-oval to round-oval, borne abaxially along the leaf margins, inserted in convex areas of the crenulations, directed outward and at an oblique angle to the midrib. Some seeds bearing a cone-like elongation extending from the distal end, directed upward, toward the adaxial surface of the leaves.

Derivation of the name—Eo—old, phyll—relating to leaves, gono—female reproductive organs; thus, old leaves bearing-seeds.

Type species—*Eophyllogonium cathayense* sp. nov.

Number of specimens examined : 45.

Eophyllogonium cathayense sp. nov.

Pl. 1, figs 1-5; Pl. 2, figs 1-4; Pl. 3, fig. 2; Pl. 4, figs 1-5; Pl. 5, figs 1-4

Diagnosis—Same as for the genus with the following additions. Leaves somewhat more than 70 mm long, 10 mm wide near the apex, the lower part 15 mm wide; margins crenulate, h = 0.4 mm, w = 1.2 mm. Midrib up to 0.68 mm wide. Branches of secondary veins slightly arching, running parallel to each other, extending to the margin. Tertiary veins located between two lateral veins, joining them together forming a reticulate pattern. Elongate polygonal areoles occupy 2/3 length of secondary veins. Seeds 1.2 × 0.8 mm to 1.9 × 1.9 mm, in size, attached at angles of 68-72 degrees in relation to the midrib. Each seed joining a branch of a secondary vein.

Holotype—× 9-005. Paratypes: × 9-147, × 9-282.

Number of specimens examined : 45.

Occurrence—Guanshan Member, Leping Formation (Permian), Jiangxi Province, South China.

Derivation of the name—*cathayense* refers to China where the fossils occur.

DESCRIPTION

These seed-bearing leaves are characterized by their shape, their venation and the presence of attached seeds. The lanceolate shape shown in Plate 1, figures 1 and 2 is a typical taeniopteroid-type leaf commonly found in the Palaeozoic.

Characters of the venation include formation of a reticulate network (Text-figure 1; Pl. 4, figs 1, 2; Pl. 5, figs 2, 3). The elongate polygonal areoles are formed as a result of the dichotomous branching of the secondary veins and their subsequent anastomosing by means of the tertiary veins.

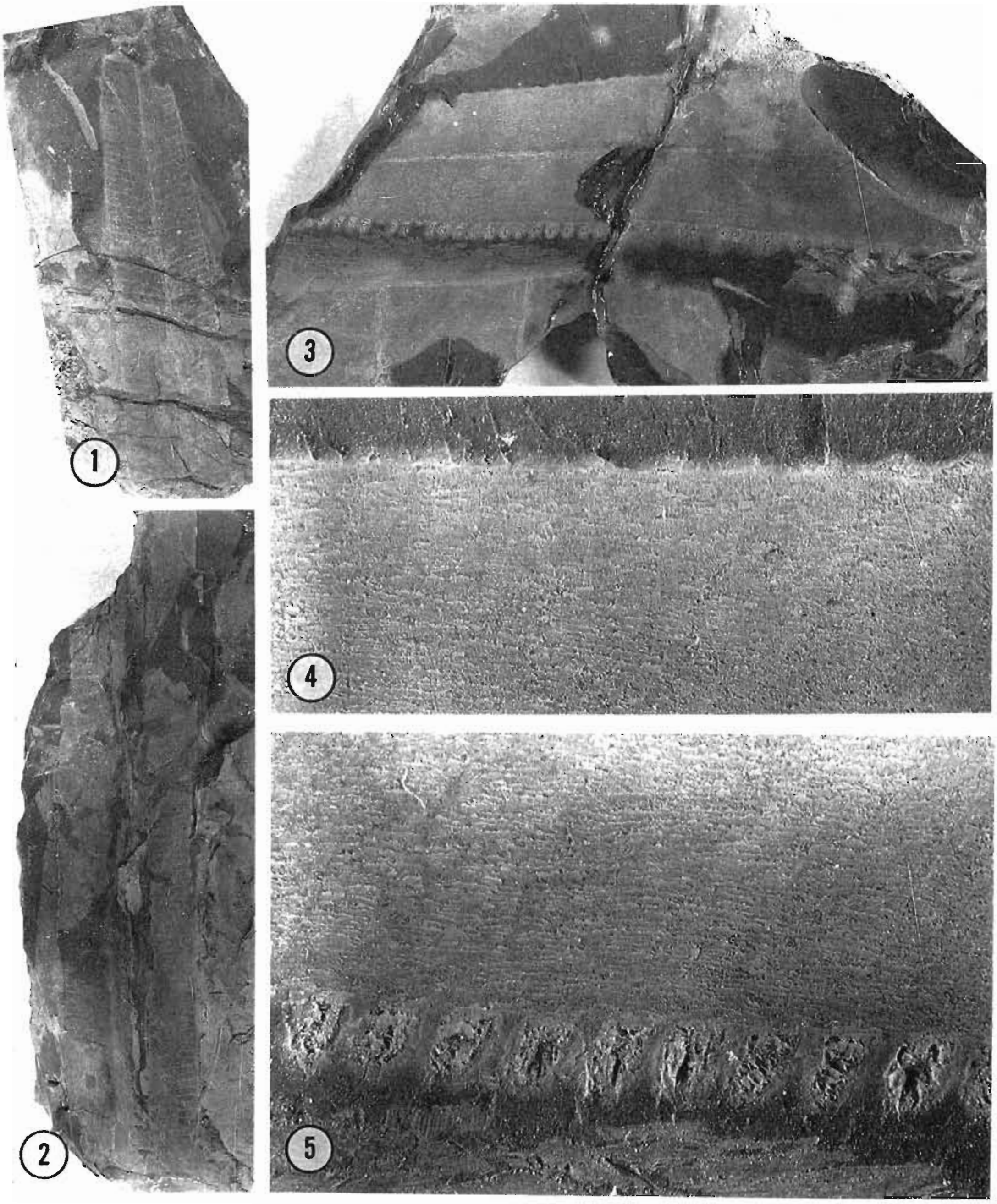

PLATE 1

1. The upper part of the seed-bearing leaf. × 1.4, no. X9-025.
2. The lower part of the seed-bearing leaf. × 1.4, no. X9-017. Figures 1 and 2 show the whole shape of the seed-bearing leaf.
3. The margin of the seed-bearing leaf, the upper side showing a row of attached seeds. (the lower part of the specimen shows association with a gigantopterid.). × 1.5, no. X9-005 (Holotype).
4. Portion of figure 3 enlarged showing the crenulate margins. × 7.5, no. X9-005.
5. Portion of figure 3 enlarged showing the attached seeds. × 7.5, no. X9-005.

Due to the incomplete preservation we cannot be certain that the seeds were borne along the full length of the leaf margins. The seeds are closely and regularly spaced on both margins of the leaf (Pl. 1, figs 3, 5). When the seeds are lost, the leaf margin is crenulate (Pl. 1, figs 3, 4). The estimated length of

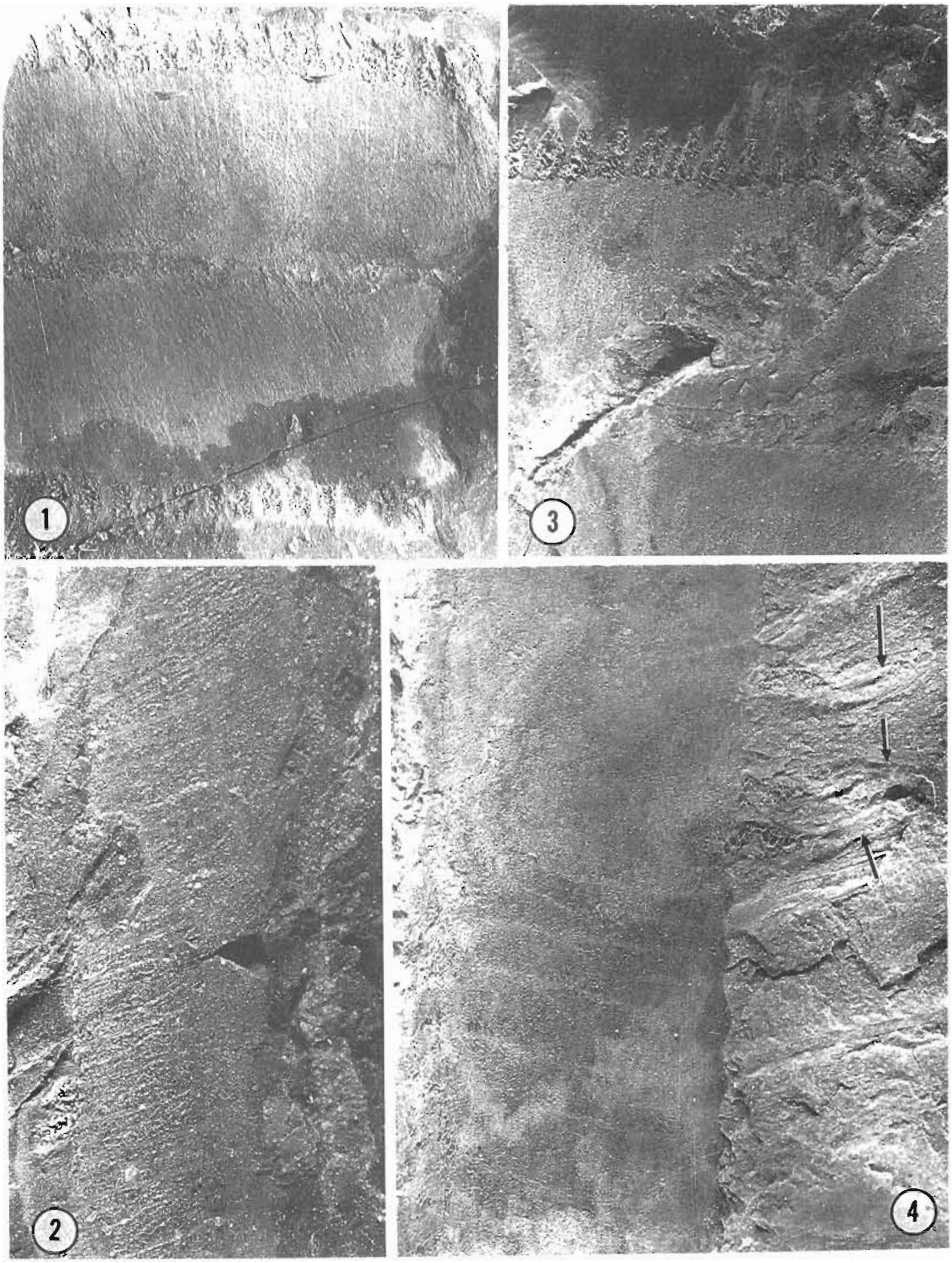

PLATE 2

1. Portion of leaf showing elongate-polygonal reticulate meshes. Each secondary vein extends to a seed. ×4, no. X9-282 (Paratype).
2. The complex net venation, two attached seeds seen in the lower left leaf margin. ×5, no. X9-001 (Paratype)
3. Seeds attached along the margin of a leaf. The seeds in the right area have elongate micropyles. Impressions of trichomes are scattered on the midvein. ×6, no. X9 147 (Paratype).

4 Three attached seeds with long micropyles (arrows) and crenulate margin where seeds have fallen away. Impressions of trichomes scattered on midvein. ×5.5, no. X9-353.

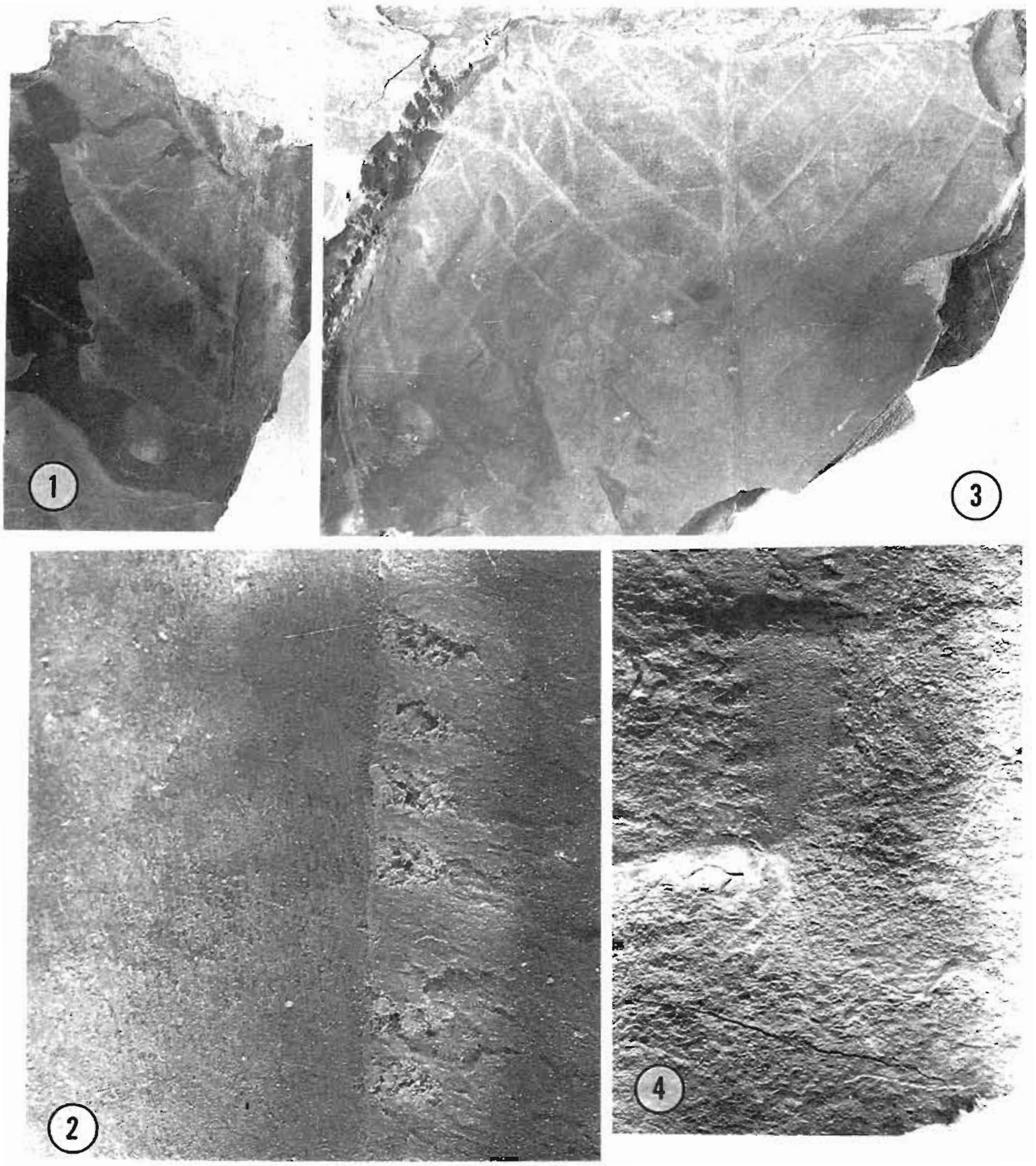

PLATE 3

1. *Gigantonoclea* sp. × 1.5, no. X9-140.
2. Portion of Plate 2, figure 3, enlarged showing attached seeds with long micropylar ends. × 8.2. no. X9-147 (Paratype).
3. *Gigantopteris dictyophylloides* Gu & Zhi. × 1.5, no. X9-037.
4. *Gigantonomia* Li & Yao. × 4.5, no. X1-001.

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the leaf is about 10 cm, and it had the potential to bear a maximum of about 160 seeds (21 seeds/2.8 cm).

The seeds are orientated at a slightly acute angle in relation to the midrib, and rotated to form a slightly imbricate pattern (Pl. 1, fig. 3; Pl. 4, figs 3, 4; Pl. 5, fig. 1). Some of the seeds may be spaced widely enough apart so that they do not actually overlap (Pl. 4, figs 1, 3). Each seed joins a branching secondary vein (Pl. 4 figs 1, 2, 5; Pl. 5, figs 1, 2, 4). Upon careful observation and measurement of the seeds, obvious differences in their form, size and the stage of the development of conical elongations borne at their apices became apparent (Table 1). Several of the seeds are attached together along the leaf margins so that any changes in their size and form, correlated with their position on the leaf, from the apex to the base, can be examined. There is a

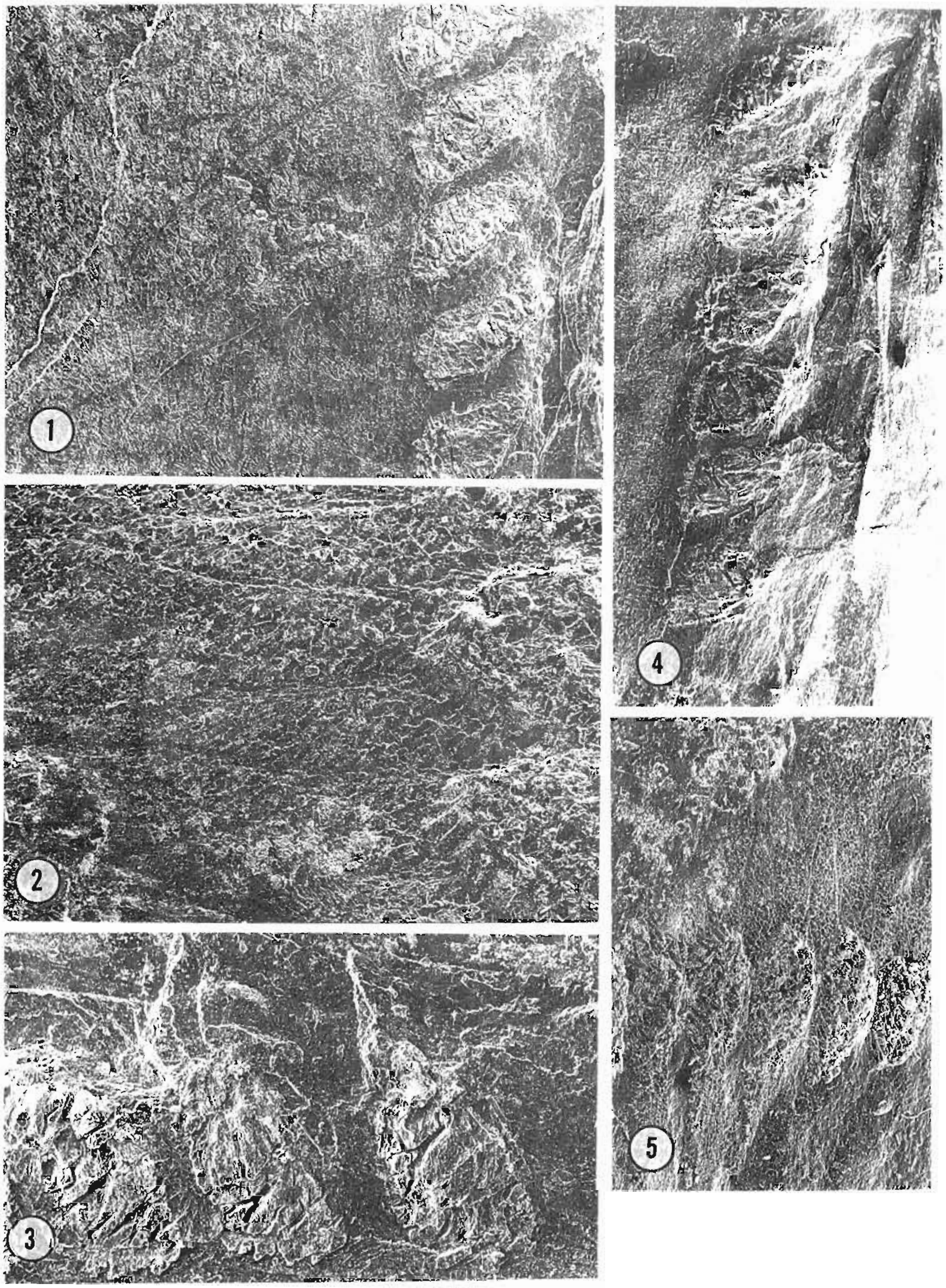
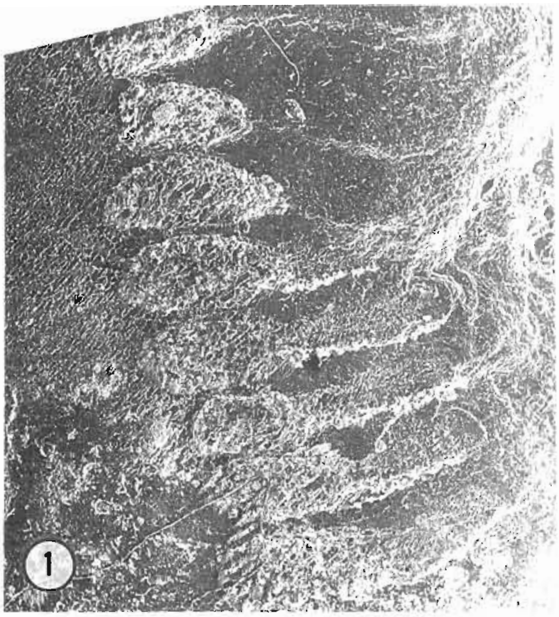


PLATE 4

1. Scanning electron micrograph showing each secondary vein connected to a seed. × 10, no. X9-002.
2. Scanning electron micrograph showing portion of figure 1 enlarged demonstrating the elongate polygonal nets. × 30, no. X9-002.
3. Portion of figure 1 enlarged showing the seeds arranged at an oblique angle in relation to the midvein. × 20, no. X9-002.
4. The arrangement of the seeds—oblique and slightly overlapped. × 10, no. X9-002.
5. Scanning electron micrograph showing the elongated polygonal nets of the veins attached to the seeds. × 10, no. X9-002.



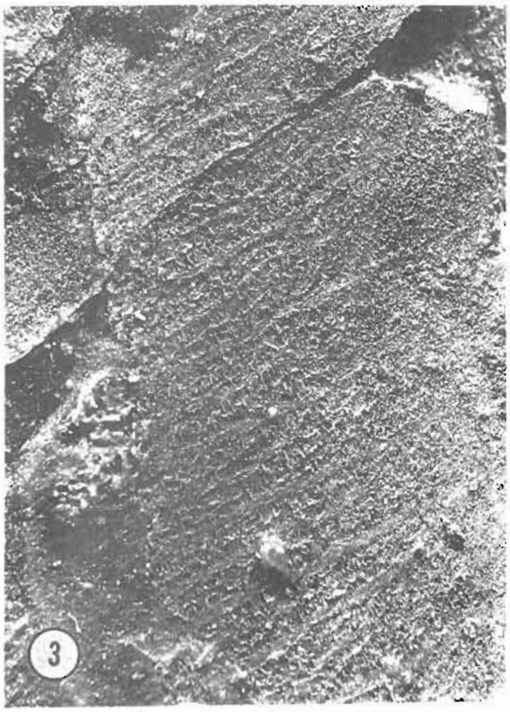


PLATE 5

1. Scanning electron micrograph showing the seeds with long micropylar ends. × 10, no. X9-147 (Paratype)
2. The simple reticulate venation extending to the seeds. × 10, no. X9-282
3. The complex netted venation of the leaf. × 8, no X9-001
4. A row of seeds attached The upper part of the specimen shows seeds with long micropylar ends × 8, no. X9-147 (Paratype).

Table 1—Measurements show the relationship between the size of attached seed and the length of the cone-like elongation at the apex of the seeds. Measurements are listed from near the apex of the leaf towards the base of the leaf.

SPECIMEN NUMBER	SEED SIZE	CONE-LIKE (LENGTH)	ELONGATION	SEEDS SPACED
×9-005	1.1 × 1.6 mm	0.3 mm	(very narrow)	
Leaf apex	1.2 × 1.6 mm	0.2 mm	(very narrow)	regularly (0.4-0.5 mm)
	1.9 × 1.9 mm	none		
	1.6 × 2.0 mm	none		
	1.3 × 1.9 mm	none		
Leaf base	1.5 × 2.0 mm	none		
	1.6 × 1.8 mm	none		
	(length of the leaf margin 6.1 cm, number of attached seeds = 27)			
			(width of enlarged end)	
×9-147	1.6 × 0.8 mm	1.6 mm	0.64 mm	
	1.2 × 0.8 mm	2.0 mm	0.64 mm	regularly
Leaf apex				(0.2-0.3 mm)
	1.6 × 0.8 mm	1.7 mm	0.56 mm	
	1.6 × 0.9 mm	1.9 mm	0.56 mm	
	1.6 × 1.0 mm	1.3 mm		
Leaf base	1.8 × 1.0 mm	none		
	1.8 × 1.0 mm	none		
	(length of the leaf margin 1.4 cm, number of attached seeds = 16)			
xy-353	1.7 × 0.7 mm	0.9 mm		
	1.5 × 0.7 mm	0.8 mm		
	1.6 × 0.7 mm	0.6 mm		
		(incompletely preserved)		

gradient in the size and form of the seeds from the leaf base to the leaf apex (Table 1). The seeds at the leaf base are slightly larger. The length of the conical elongations of the seed apices changes also. Towards the leaf apex they are slightly longer (Table 1). In specimen ×9-005, the proximal seeds are larger and more oval (1.6 × 1.8 mm to 1.5 × 2.0 mm) and lack conical elongations, while the distal seeds have short conical elongations and are narrow and smaller (1.2 × 1.6 mm to 1.1 × 1.6 mm). In specimen xy-353, the attached seeds have long conical elongations (0.8 mm length, 0.9 mm length) and are elongate-oval in shape and smaller in size (1.5 × 0.7 mm, 1.7 × 0.7 mm). The conical elongations may have served for trapping pollen and directing it towards the micropyle. The reduction in seed size apically suggests that the individual seeds mature acropetally. Probably, the conical elongations were lost as the seeds matured.

Stages of maturation are proposed as follows:

1. Early Stage—seeds elongate-oval in shape, small in size, with long conical elongations at seed apex.
2. Middle Stage—seeds oval in shape, medium in size, conical elongations shorter.
3. Nearly Mature Stage—seeds round-oval in shape, largest in size, conical elongations missing.
4. Mature Stage—seeds shed from the leaf margins, leaving crenulate leaf margins.

DISCUSSION

One of the basic questions to be answered regarding this taxon is whether the seeds are attached to leaves or to leaflets. Conclusive evidence is not available because the fossils studied do not provide any suggestion of leaflet attachment to a rachis or any indication of compound leaves. The sample size was small (*ca* 45 specimens) and the overall size of the rock specimens collected was not large (usually under 15 cm); it would be difficult with the available data to support labeling of these organs as either leaves or leaflets. Also, no entire margined leaves with this venation pattern have been found. This is based upon the assumption that the crenate margin relates to seed attachment areas. Thus, we do not know the nature of the sterile foliage. Because we have found the seed-bearing specimens only as individual units and have no reason to assume they were leaflets of a compound leaf we use the term leaf in this paper. This is open to further interpretation.

The specimens are incompletely preserved. Most of them represent the middle-basal portion of the lamina to near the apex of the lamina. This partial preservation may indicate that the leaves were broken from the parent plant by accident. The attachment of the seeds coincides with the indentations of the crenulations along the margins of the leaf lamina.

The seeds have a regular distribution, they are outwardly directed from the abaxial margin of the leaf at an angle to the midrib and slightly imbricate, oval in shape and of moderate size (1.9 × 1.9 to 1.6 × 2.0 mm). Each seed joins a branching secondary vein (Pl. 5, fig. 2). These are facts that suggest to us that these objects are seeds.

The conical elongations are organically connected to the apex (micropyle) of the seeds, and extend outward, sometimes bending upward, from the distal end of the seeds. An enlarged opening extends away from the seed. These conical elongations are attached to the seed apex by their narrow end (Pl. 2, fig. 4). The length of this cone changes from the distal part to the proximal part (see Table 1) of the leaf, and is closely tied to the size and shape of the seed. This change in size as the seed matures supports the idea that the conical elongations may have functioned as pollen traps. We propose that, upon fertilization, these conical elongations may have lost a pollination droplet (Rothwell, 1977) they may have contained, and may have begun to dry and shrink in size. When we consider that on these specimens different stages of seeds seem to occur simultaneously, it becomes apparent that these leaves may have spread out the timing of seed maturation over a period of days or weeks. This would have provided for lengthening the overall time of pollen receptivity, which would have the effect of increasing the chances of successful pollination of at least some of the seeds produced, and increasing the possibility for outcrossing with a variety of pollen sources.

Halle (1929) described some fern-like fronds with attached seeds from the Permian of China, and illustrated the geological distribution of different types of attachment of the seeds known at that time. In the Permian there are two types: i) Seeds marginal to subabaxial on normal or slighly reduced pinnules (e.g., *Dicksonites pluckenetii* (Schl.) Sterzel); ii) Seeds not terminal or marginal, but on the abaxial surface (rachis or lamina) of ordinary pinnae or pinnules (e.g., *Alethopteris norinii* Halle, *Sphenopteris tenuis* Halle, *Emplectopteris triangularis* Halle). These two basic types of seed attachment are still recognized today. Neither the location of the seeds nor the form of the pinnae or pinnules are similar to the fossils described in this paper.

Asama (1959) wrote: "The seeds of *Bicoemplectopteris halle (Bicoemplectopteris halle* Asama (1959) = *Gigantopteris nicotianaefolia* Halle 1927) (Pl. 4, Figs. 2, 3) are ovate and very small (Pl. 7, Figs. 2, 3)". When carefully examined, the morphology of the seeds shown in Plate 7, figures 2, 3 (Asama, 1959) is very unclear and it is difficult to accept that they actually are the impressions of seeds.

Gigantonomia (Gigantonoclea) fukiensis (Yabe & Oishi) Li & Yao 1983 was presented as the first discovery of seed-bearing leaflets of gigantopterids in China. The fertile leaves or leaflets are linear, with three orders of veins. The anastomosing veins are generally indistinct. Seeds are arranged in two rows at the ends of the secondary veins, not extending to the leaf margin. The fertile leaves or leaflets are reconstructed, showing them arranged in the upper part of the plant with *Gigantonoclea fukiensis* attached below in the lower part of the reconstruction by Li and Yao (1983). The seeds are elliptical, covered with glandular dots and are borne on the lower surface to both sides of the midvein. The seeds are reported to have the micropylar region directed upwards and inserted into a groove on the upper surface of the leaf lamina. Several important differences exist between *Gigantonomia* and our specimens, such as the position of the seeds along the leaf margins, the nature of the micropyle, and the orientation of the seeds.

Gigantopteridium americana (White) Koidzumi is the species which is most closely related to gigantopterids from the United States. White (1912) described a type of seed that he considered linked to "*Gigantopteris americana*" because of its "abundant and intimate" association with "*G. americana*". The seeds are small and obovate and lie in the concave face of a winged-bract. It is still unknown if they are the actual seeds of "*Gigantopteris americana*" but they are not similar to *Eophyllogonium*.

In recent years, several advances in the research of very early seed-bearing plants from the Palaeozoic have been made in the United States (Andrews, 1963; Pettitt & Beck, 1967, 1968; Scheckler, 1975; Rothwell, 1977; Taylor & Millay, 1979; Gillespie, Rothwell & Scheckler, 1981). Except for the seed-bearing leaves assigned to the Cycadales from the Lower Permian, only *Tinsleya texana* Mamay (Mamay, 1966) and *Padgettia readi* Mamay (Mamay, 1960) have been reported as belonging to the Pteridospermales. *Tinsleya* was collected from the Wichita Group (Lower Permian), Texas. The frond is of a callipteroid form, with open venation. Seeds are urn-shaped, borne one or two to a fertile pinnule, have a cupuliform sheath, and terminate in a narrowed neck with several digitate apical projections. *Padgettia* was found in the Lower Permian (Wolfcamp) of Texas. The pinnules are of a neuropterid form, some of them contain one to several seeds. Seeds are arranged parallel to the midrib and apparently embedded within the tissues of the pinnules. The apices of the seeds are truncated, exactly at the pinnule margins. These two genera are different from the genus described in this paper.

Spermopteris (Cridland & Morris, 1960) is a genus which has seeds borne in a similar position to *Eophyllogonium*. *Spermopteris* is from the Upper Pennsylvanian Series and Permian (Mamay, 1976) of Kansas. The fertile leaves also belong to the form genus *Taeniopteris* as in *Eophyllogonium*. A row of seeds borne on the abaxial surface is confined to the margin of the leaf in *Spermopteris*. The seeds are oriented at right angles to the midvein, having a distinct central region surrounded by an outer zone, which is enlarged above, and they have a notch in the micropylar region. Both the arrangement of the seeds and the existence of micropyles are somewhat similar to *Eophyllogonium*. But in *Spermopteris*, the *Taeniopteris* leaf has open venation, and the seeds lack the apical conical elongations typical in *Eophyllogonium*.

The comparisons which are made above indicate that *Eophyllogonium* is a new type of seed-bearing leaf. It is different from Cycadales (*Archaeocycas, Phasmatocycas* and *Primocycas*) and Pteridospermales (*Dicksonites, Alethopteris, Sphenopteris, Emplectopteris, Tinsleya, Padgettia*) mainly because of the particularly simple reticulate veins in the leaves, and several characters of the seeds (Zhu & Du, 1981, Gillespie & Pfefferkorn, 1986).

The potential affinity of this seed-bearing leaf found in Jiangxi Province in China is best analyzed by considering the leaf venation and fossils associated with it. The seed-bearing leaf is characterized by the elongate polygonal areoles. Most of the gigantopterid genera have closely spaced reticulate veins. In some specimens (e.g., ×9·005) there appear to be trichome bases as impressions scattered on the midrib. *Gigantonoclea acuminatiloba* has the same character also. The reproductive organs occur together with *Gigantonoclea acuminatiloba* and *Gigantopteris dictyophylloides* in the Permian sediments. All these show that the seed-bearing leaf is closely associated with gigantopterids.

Three gigantopterid genera, *Cathaysiopteris, Gigantonoclea* and *Gigantopteris*, are found in the Permian in China. *Gigantopteridium americanum* (White) Koidzumi, *Delnortea abbottii* Mamay, *Cathaysiopteris yochelsonii* Mamay, *Zeilleropteris wattii* Mamay and *Gigantonoclea* sp. are gigantopterid genera described from Lower Permian strata in Texas (Mamay, 1986; Mamay *et al.*, 1988). These genera are compared in Table 2.

The nature of the leaf type (taeniopteroid) and course reticulate venation of *Eophyllogonium* may be considered primitive compared to the finer reticulate venation and leaf form of *Gigantonoclea* and *Gigantopteris* (Pl. 3, figs 1, 3, 4). But

Table 2—The main features in the leaf and venation among gigantopterid genera and *Eophyllogonium*

GENUS	LEAF	VENATION PATTERNS	RETICULATE VENATION
Cathaysiopteris	compound leaf (*C. yochelsonii* Mamay dichotomously divided)	pinnate 3 orders sutural veins	None
Gigantonoclea	compound leaf	pinnate 2-4 orders	simple reticulate, secondary veins extend to the margin or near the margin.
Gigantopteris	simple leaf (large)	pinnate 4 orders	compound reticulate.
Gigantopteridium	compound leaf (large) forked	pinnate 4 orders	ultimate veins "herringbone weave," variably forking and anastomosing
Delnortea	simple leaf, petiolate, regularly crenate margins	pinnate 4 orders secondary veins terminated at a marginal sinus	ultimate vein forms a dense network of oblong meshes
Zeilleropteris	compound leaf (large) dichotomously divided	pinnate 4 orders	small narrow triangular to polygonal meshes
Eophyllogonium	simple or compound leaf	pinnate 3 orders	elongate polygonal meshes

Eophyllogonium represents a fertile leaf and is characterized by its taeniopteroid shape, the branching secondary veins and the elongate polygonal reticulation.

It is important to point out that the venation of *Glossopteris communis* Feistmantel, a typical element of Gondwana Flora, is characterized by its pinnate form, dichotomous secondary veins anastomosing to form a simple reticulum. These characters are similar to *Eophyllogonium. Mexiglossa varia* Person & Delevoryas has the similar elongate reticulate veins also (Delevoryas, 1969; Person & Delevoryas, 1975). *Mexiglossa* is a *Glossopteris*-like foliage collected from the Middle Jurassic of Oaxaca, Mexico. In morphology, *Eophyllogonium* is intermediate between *Taeniopteris* and *Glossopteris.* It is important to note that we have a *Glossopteris*-like element in a gigantopteroid assemblage, and further research is needed to understand its significance.

The leaves of *Eophyllogonium* are quite well adaptated for the production of large number of seeds. The elongate conical micropylar extension may have carried pollination droplets and been directed upward, as indicated by one specimen (Pl. 3, fig. 2; Pl. 5, fig. 4). This would have been suited for pollination by either wind or flying insects feeding on the fluid in the conical elongation. The differing stages of ovule and seed development present on an individual leaf at one time suggest that each fertile leaf was receptive to pollination over a long period of time. These conical elongated structures attached to the seeds may have served as pollen traps or pollen chambers. *Ephedra, Ginkgo* and conifers are extant gymnosperms that possess pollen chambers (Foster & Gifford, 1974).

The discovery of this seed-bearing leaf indicates that the Permian is an important transitional period in the biostratigraphy and evolution of plants. The Pteridosperms are quite a diverse group of plants by the end of the Palaeozoic. The fossil record of taeniopteroid lamina on *Phasmatocycas* megasporophylls (Cycadales) corroborated Mamay's hypothesis that the cycads were derived from the Pteridosperms (Mamay, 1969; Mamay, 1973). However, it should be realised that the form-genus *Taeniopteris* also accommodates two divergent groups of seed plants—Pteridosperms and Cycads. For further comments on the evolution of Cycads also see Krasilov (1988).

Eophyllogonium seems to represent a group or evolutionary lineage not currently recognized as belonging to any group during the Late Carboniferous or the Early Permian.

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