

Composition and palaeogeographic position of the Early Permian Jambi flora from Sumatra

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A preliminary taxonomic revision of the Early Permian Jambi flora results in a lower number of taxa, a number of new determinations and several new combinations (*Dicranophyllum molle* (Jongmans & Gothan) comb. nov., *Oligocarpia posthumii* (Jongmans & Gothan) nov. comb., *Callipteridium strictinervis* (Jongmans & Gothan) comb. nov.). Cones containing the bicuspidate seeds *Tobleria bicuspis* are recorded for the first time. The exact stratigraphic position of the Jambi flora is unknown, but brachiopods and fusulinids indicate an Early Permian age. Comparisons with the East Asian Permian floras of the Cathaysian realm indicate that the Jambi palaeoflora can best be compared to a relatively xeric Cathaysian flora, possibly indicative of relatively high latitude.

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Introduction

A change from a cool to a much warmer and partly drier climate took place at the Pennsylvanian-Permian transition. It was characterized by a period of warming that started near the Moscovian-Kasimovian (Late Pennsylvanian) boundary, after which glacial conditions reappeared in last stage of the Pennsylvanian, the Gzhelian. Non-glacial conditions were only fully established at the end of the Early Permian (Artinskian).

This climate change went hand in hand with a change in precipitation pattern in the palaeoequatorial belt and affected its everwet floral facies, the Amerosinian Flora. This flora had a rather similar composition from North and Central America (Odreman-Rivas & Wagner, 1979; also including northern South America) to China passing across Europe, part of North Africa (Morocco and part of Algeria) and central Asia. Its distribution

pattern changed in the Permian, indicating that the everwet areas became gradually more restricted in size; simultaneously, drier areas became increasingly more common (Wagner, 1993, 2004; Gastaldo *et al.*, 1996; Rees *et al.*, 2002). Everwet floras remained in the equatorial belt. The Chinese Cathaysia flora represents such a Permian everwet flora (Halle, 1937; Ziegler, 1990).

In south-central Sumatra, on the fringe of southeast Asia and its Permian everwet floras, lies the Jambi province that has yielded Early Permian deposits holding floral remains. Jongmans & Gothan (1925, 1935) published a full description of this flora and attributed a (late) Stephanian age to it. Halle (1927) published the description of the Cathaysia flora just after the earlier description of Jongmans & Gothan (1925) and stated that the Jambi flora was Permian. Posthumus (1927), who thought that the *Lepidodendroides* from the Jambi flora were *Walchia* remains, considered the Jambi flora to be Early Permian.

A revision of the descriptions by Jongmans & Gothan (1925, 1935) is long overdue, particularly now that Permian floral taxa have been recorded from other parts of south-east Asia (Asama *et al.* 1975), the Middle East (Wagner, 1962; Archangelsky & Wagner, 1983; El Khayal & Wagner, 1985; Hill *et al.*, 1985; Rigby, 1996, 1998; Broutin *et al.*, 1995; Berthelin *et al.*, 2003) and many new localities in the Far East (Asama *et al.*, 1975; Halle, 1927; Kawasaki, 1931; Kon'no *et al.*, 1970; Li, 1995; Stockmans & Mathieu, 1939, 1957). The numerous, newly described species and specimens, from which fertile remains have also been described (sporangia and synangia), can be compared to the (fertile) specimens described earlier by Jongmans & Gothan (1925, 1935).

The detailed stratigraphic position of the Jambi succession is unknown, but the brachiopods (Suyoko, 1996) and fusulinids (Vachard, 1989) indicate an Early Permian age. In the past (Jongmans & Gothan, 1935), the Permian Jambi flora caused some problems with respect to its palaeogeographical position because neither the walchian conifers typical of the Euramerian Early Permian were found, nor glossopterids, characteristic of the Gondwana realm. Further, no Angara elements were found. Cathaysian plants were observed, but the European components were believed to be dominant.

In a taxonomic study Laveine *et al.* (2003) suggested that Indochina, east Malaysia, and South and North China were closely connected during the Carboniferous. Barber & Crow (2003) even considered that central Sumatra was linked to east Malaysia during the Late Palaeozoic and must have been part of Cathaysia, but also stressed the need to gain insight into the positions of central Sumatra and the West Sumatra block (with the Mengkarang Formation) relative to east Malaysia and Cathaysia.

Comparisons are made with the East Asian Permian floras of the Cathaysian realm herein (Asama *et al.*, 1975; Halle, 1927; Kawasaki, 1931; Kon'no *et al.*, 1970; Li, 1995; Stockmans & Mathieu, 1939, 1957). Moreover, references to European taxa of Jongmans & Gothan (1935) are critically reviewed. Our results on the taxonomic revision lead us to conclude that the age of the deposits in which the Jambi flora was found is most probably Asselian or Sakmarian. The presence of mesomorphic plants (including peltasperms, but also taeniopterids, sphenopterids and *Dicranophyllum*) suggests that the drier areas typical of the Early Permian were represented in the sedimentary rocks of the West Sumatra Block.

Materials and methods

The plant fossils were collected during an expedition held in 1925 to the province of Jambi in Sumatra (Indonesia) near the town of Bangko (Fig. 1). This material is curated at the Nationaal Natuurhistorisch Museum in Leiden. Material assembled earlier by A. Tobler (Jongmans, 1925) was also considered. These latter plant fossils are kept at the Naturhistorisches Museum Basel, Switzerland.

The material consists of 1848 impressions with some compression material that yielded a few spores. The material is fragmentary and usually small in size (100 mm commonly, but rarely up to 400 mm, large fragments are 3500 mm long). Fossil plants are found in the Mengkarang Formation, which is the oldest formation in this area and believed to be Early Permian. The exact age of the formation is uncertain; brachiopods indicate a Sakmarian age (Suyoko, 1996), whereas fusulinids suggest it is Asselian (Vozzenin Serra, 1989). The Mengkarang Formation is a regressive sequence (Suyoko,

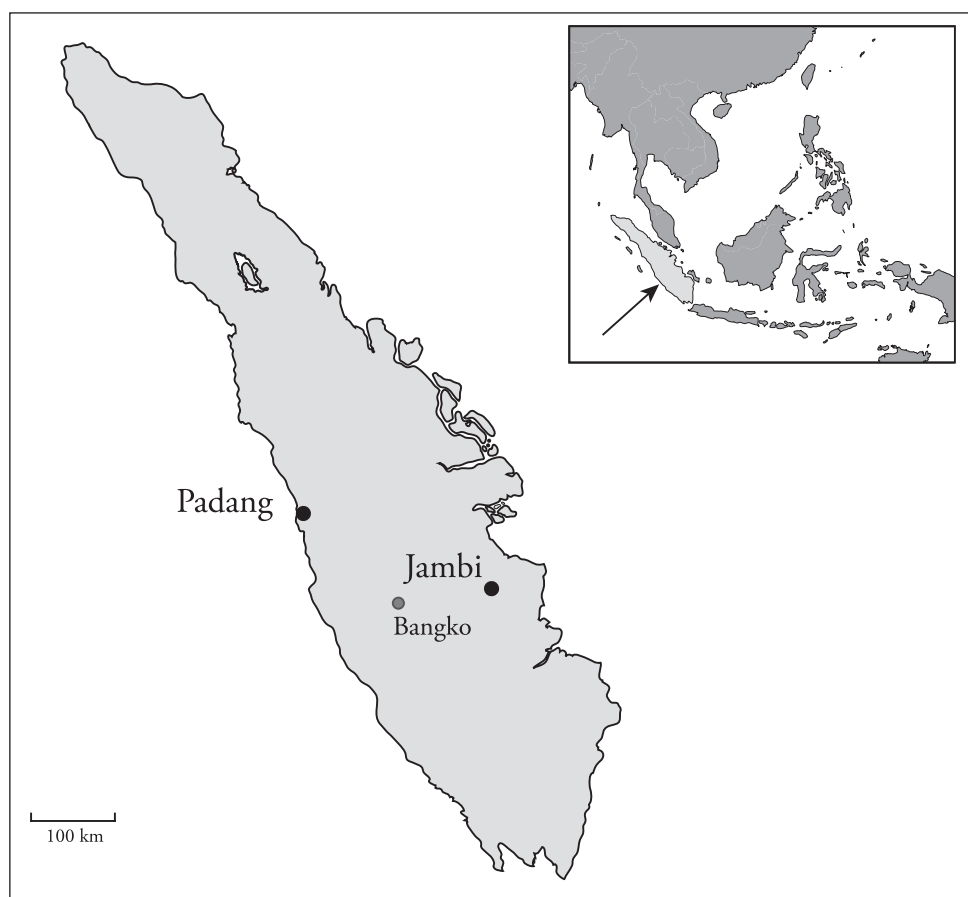


Fig. 1. Outline map of the island of Sumatra (arrowed on inset map of southeast Asia). Plant fossils discussed herein were collected from the Lower Permian Mengkarang Formation, exposed in the vicinity of Bangko.

1996) composed of alternating sandstones, siltstones, claystones, shales, tuffs and conglomerates, with limestone at its base and coal intercalations. It is a time equivalent to the Palepat Formation composed of andesites, dacites and dolerites, with intercalations of tuff, volcanic breccia, shales, siltstones, sandstones, claystones, and locally conglomerates and limestones (Suwarna *et al.*, 1994). The Palepat Formation outcrops in the northwestern part of the Bangko area, along the Mesumai River. The Mengkarang Formation outcrops along the Merangin and Mengkarang rivers and their tributaries, but also along the tributaries of the Mesumai River in the north (Fig. 2). The Triassic in this area consists of intrusive granitic bodies. The Pliocene Kasai Formation discordantly overlies the Permian and Triassic deposits. It is composed of tuff, pumiceous tuff, intercalations of tuffaceous sandstone and claystone, conglomerates and silicified wood.

The structure of the area consists of an anticline with a granitic intrusion at its core (Zwierzycki, 1935). The sedimentary rocks are slightly thermally altered in the vicinity of a Triassic granitic body. The coal rank is bituminous, but highly volatile; the spore reflection is dark orange.

Provenance studies based on grain composition of the sedimentary rocks of the Mengkarang Formation suggest a rather long distance to the source area because of the high relative purity of the quartzitic sandstones (Suyoko, 1996). The presence of dacites and andesites seems to indicate an Andean-type magmatic arc. Barber & Crow (2003) suggested this subduction arc was formed on Cathaysia when the Sibumasu Block sep-

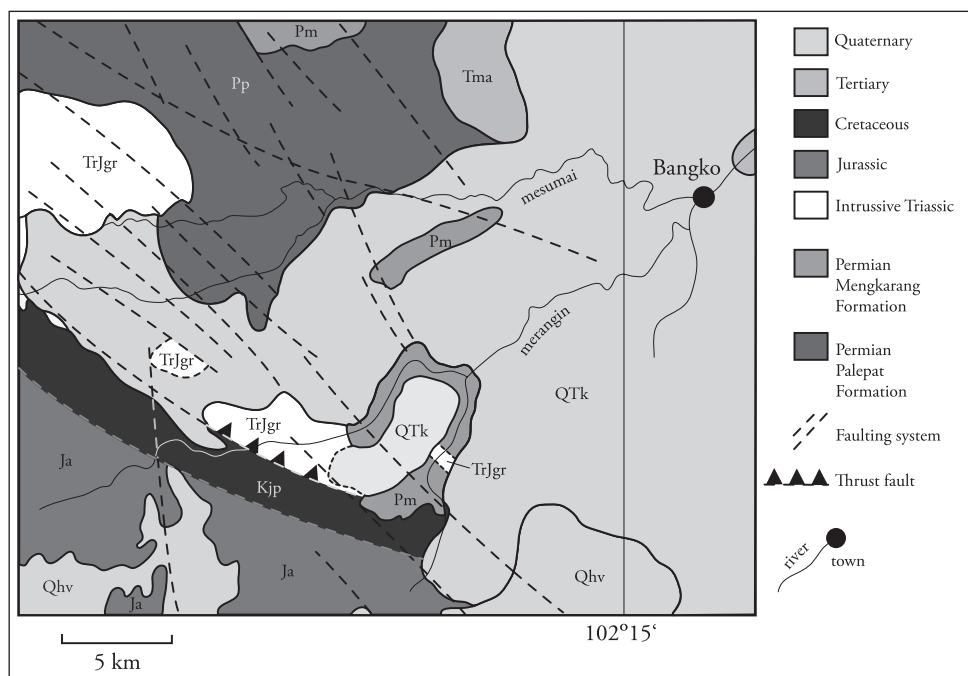


Fig. 2. Geological map of the Bangko area: Pp = Early Permian Palepat Formation; Pm = Early Permian Mengkarang Formation; TrJgr = Triassic granite; Ja = Jurassic Asai Formation; Kjp = Cretaceous Peneta Formation; Tma = Miocene Airbenakat Formation; Qtk = Pliocene Kasai Formation. Black triangles: thrust front. Redrawn from Suwarna *et al.* (1994; Geological map GRDC 0913).

arated from Gondwana through extensional rifting. Subduction was induced on Cathaysia and then was placed alongside the Sibumasu Block through oblique subduction in the Late Permian or Early Triassic.

There are at least three river sections that are about 500 m long and provide continuous exposure of the Mengkarang Formation (Fig. 2). The localities are named after the rivers or the tributaries. Exact localities of the samples in the collections held in Leiden and Basel from along these rivers and tributaries are not known, as each river or tributary holds many localities. The river sections can be reached through the town of Bangko, at the village of Dusunbaru, at 02° 11' 03.1" S 102° 10' 25.0" E

Herein, we present a preliminary revision of the flora in the form of comparative tables, using the species of Jongmans & Gothan (1935) and our proposed new names. These results are compared to coeval floras from Johore (Kon'no *et al.*, 1970), north, northwest and south Cathaysia (Li, 1995), the European Early Permian flora (Josten & van Amerom, 1999; Remy & Remy, 1977) and coeval floras of the Middle East (El Khayal & Wagner, 1985; Hill *et al.*, 1985; Broutin *et al.*, 1995; Berthelin *et al.*, 2003). A comprehensive taxonomic analysis is planned, but is not the objective of the present paper.

Preliminary systematic revision of the Jambi flora

Equisetaleans

Table 1.

Remarks – We did not find any differences between our review of the equisetaleans and the identifications of Jongmans & Gothan (1935), except for their *Annularia* sp., which they considered might have been a new species. Unfortunately, the single piece on which the determination was based has disappeared, but, judging from the illustration in Jongmans & Gothan (1935, pl. 2, fig. 6), this *Annularia* has a spatulate leaf, reminiscent of *A. mucronata* Schenk, but with fewer leaves on the whorl.

Table 1. Preliminary review of the equisetaleans comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Calamites jubatus</i> Lindley & Hutton	<i>Calamites (Crucicalamites) jubatus</i> L. & H.
<i>Calamites suckowi</i> Brongniart	<i>Calamites suckowii</i> Brongniart
<i>Annularia stellata</i> (Schlotheim) Wood	<i>Annularia</i> cf. <i>stellata</i> (Schlotheim) Wood
<i>Annularia</i> sp.	<i>Annularia</i> sp.
<i>Asterophyllites</i> sp.	<i>Asterophyllites</i> sp.
<i>Palaeostachya incrassata</i> J. & G.	<i>Palaeostachya incrassata</i> J. & G.

Sphenophylls

Table 2; Figs. 3, 4.

Remarks – Asama (1970) reclassified the *Sphenophyllum* species from Cathaysia based on the venation and the arrangement of the leaves. Genera with trizygoid leaves and straight veins were transferred from *Sphenophyllum* to *Trizygia*. Non-trizygoid curved veined genera, that is, with equal sized leaves, were transferred from *Sphenophyllum* to *Parasphenophyllum*. *Parasphenophyllum* in the Jambi flora was considered conspecific with

Table 2. Preliminary review of the sphenophylls comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Sphenophyllum thoni</i> Mahr	<i>Parasphenophyllum thonii</i> (Mahr) Asama (Fig. 3)
<i>Sphenophyllum verticillatum</i> (Schlotheim) Zeiller	<i>Sphenophyllum verticillatum</i> (Schlotheim) Zeiller (Fig. 4)
<i>Sphenophyllum oblongifolium</i> (Germar & Kaulfuss) Unger	<i>Trizygia oblongifolia</i> (Germar & Kaulfuss) Asama
<i>Sphenophyllum</i> cf. <i>emarginatum</i> Brongniart	<i>Sphenophyllum</i> cf. <i>emarginatum</i> Brongniart
<i>Sphenophyllostachys</i> sp.	<i>Bowmanites</i> sp.

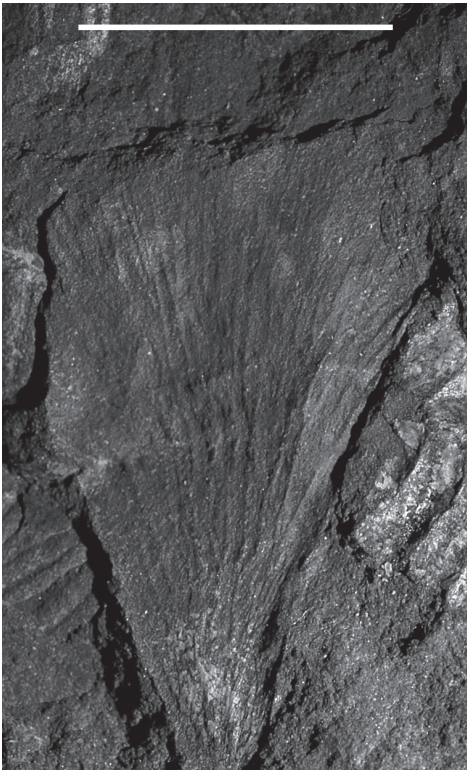


Fig. 3. *Parasphenophyllum thonii* (Mahr) Asama, sample DJ 45836 (bar represents 10 mm).



Fig. 4. *Sphenophyllum verticillatum* (Schlotheim) Zeiller, sample DJ 45861 (bar represents 10 mm).

P. thonii from Cathaysia (Halle, 1927, pl. 8 fig. 19), which also has relatively short dentations. *Parasphenophyllum thonii* var. *minor* (Halle, 1927, pl. 9, fig 2), which also has less pronounced dentations, does not resemble our species as the whole leaf is more rounded and less triangular, and the straight venation in the middle of the leaf seems to form a depressed midvein, sometimes even leading to a constriction at the leaf margin. The latter feature is not observed in our leaves.

The generic name *Bowmanites* Binney, 1871, has priority over *Sphenophyllostachys* Seward, 1898, as was pointed out by Hoskins & Cross (1943).

Lycopsids
Table 3; Fig. 5.

Remarks – We generally agree with the identifications of lycopsids by Jongmans & Gothan (1935). Nevertheless, we draw attention to *Lepidodendron molle* (Fig. 5). The finely striate leaves are flat, 1 to 3 mm wide and often more than 200 mm long. A similar leaf structure is observed in *Dicranophyllum striatum* (Brongniart, 1828, pl. 30, figs. 1, 2); these leaves are slightly wider (4 to 5 mm), but are about the same length. In the Jambi material, thin and striate leaves are attached to a stem and form bushy leaf bundles placed at an angle of 30 to 60° to a branch. The features of the branch are hard to detect, but a rhomboidal, helically-arranged scar pattern underlays the leaves. Because the leaves form dense bundles, it is impossible to see leaves bifurcating at the base; however, at the ends of some leaves bifurcations, as described by Brongniart (1828), are present.

Table 3. Preliminary review of the lycopsids comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Lepidodendron mesostigma</i> J. & G.	<i>Lepidodendron mesostigma</i> J. & G.
<i>Lepidodendron posthumi</i> J. & G.	<i>Lepidodendron posthumii</i> J. & G.
<i>Lepidodendron molle</i> J. & G.	<i>Dicranophyllum molle</i> (J. & G.) comb. nov. (Fig. 5)
<i>Maroesia rhomboidea</i> J. & G.	<i>Maroesia rhomboidea</i> J. & G.
<i>Lycopodites</i> sp.	<i>Lycopodites</i> sp.
<i>Stigmaria ficoides</i> Brongniart	<i>Stigmaria</i> sp.
<i>Stigmaria asiatica</i> J. & G.	<i>Stigmaria asiatica</i> J. & G.

Similar leaf length, scar arrangement and bifurcations of the leaves are observed on *Dicranophyllum hallei* from the Permian of Germany (Barthel & Noll, 1999, figs. 2, 4, 5). These beautifully preserved fossils hold small female cones. Small, detached cones (*Tobleria* cones) occur in the Jambi flora. They might belong to a primitive conifer like *Dicranophyllum*. Our *Tobleria* cones (see below) have the same size and scaled structure as the immature cones attached to *Dicranophyllum hallei* (Barthel & Noll, 1999, fig. 3), but their shape is slightly different.

All these considerations indicate that *L. molle* might not be a Cathaysian *Lepidodendron*, but an early conifer. Remarkably, *Dicranophyllum hallei* was also mistaken for a *Lepidodendron* (Barthel & Noll, 1999). Because of these considerations, we propose *Dicranophyllum molle* (Jongmans & Gothan) comb. nov. A similar



Fig. 5. *Dicranophyllum molle* (Jongmans & Gothan) comb. nov., detail of leaves, sample DJ 45664 (bar represents 10 mm).

type of bushy *Dicranophyllum* sp. is known from the flora of Kaiping (Stockmans & Mathieu, 1939, pl. 23, fig. 4).

The rhomboidal scars from *Maroesia rhomboidea* Jongmans & Gothan strongly resemble the *Omphalophloios* stems as figured most recently from the Stephanian C of Spain (Wagner *et al.*, 2003), especially because of the absence of parychnos, a feature that was observed in many Late Carboniferous and Early Permian lycophytes. The *Stigmaria* specimens in the collection showed too few properties to allow us to differentiate at species level. According to Jongmans & Gothan (1935), *S. asiatica* has finer roots than *S. ficoides*, but no precise data were given. They pointed out that the *Stigmaria* illustrated by Halle (1927, pl. 49, figs. 11, 12) is also relatively small and must be a different Asiatic species, possibly related to the Late Carboniferous and Permian *Lepidodendrales* based on picture comparison of illustrations. We tentatively support this interpretation.

Sphenopterid ferns

Table 4; Fig. 6.

Remarks – We consider that *Sphenopteris* cf. *mathetii* Zeiller was wrongly identified by Jongmans & Gothan (1935), because *Sph. mathetii* has more acute pinnae with fewer pinnules on each pinna than in the specimens observed here. The Jambi fossils fit the description by Halle (1927) of *Sphenopteris grabau* with broad pinnae and 3 to 5 pinnules on each pinna, with the lowermost pinnule more dissected than the others and the midvein distinct, but second order veins less distinct.

Oligocarpia posthumii (Jongmans & Gothan) comb. nov. is re-assigned from the genus *Monocarpia posthumii* (Jongmans & Gothan, 1935). Several specimens were described as *Monocarpia posthumii* in Jongmans & Gothan (1935, pl. 21, figs. 2-4, pl. 22, figs. 1-3), but *Monocarpia* was already in use for extant plants. Only one specimen from Jambi allows a fairly reasonable description because the other two show the main rachis and the pinna rachis only. This species shows rounded, possibly stalked, sori with several sporangia in a sorus. These characters fit the genus *Oligocarpia*. According to Jongmans & Gothan's description (1935), the sporangia would be single and not forming a sorus, which led them to attribute the genus to the Schizaeaceae. We observed clearly that several sporangia form a sorus and attribute the species to the morphogenus *Oligocarpia*.

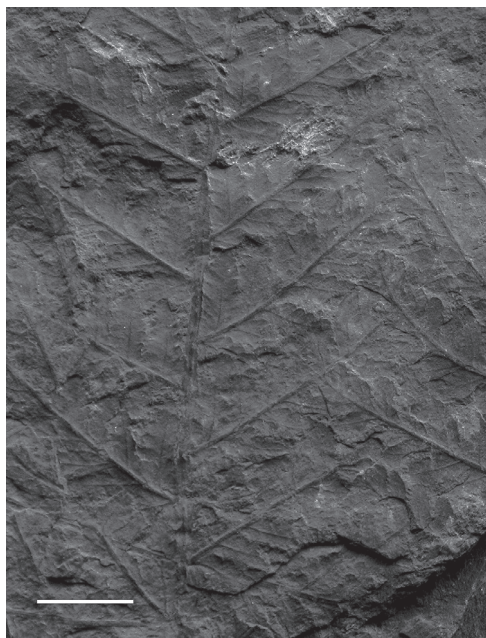


Fig. 6. *Sphenopteris grabau* Halle, sample DJ 45789 (bar represents 10 mm).

Table 4. Preliminary review of the sphenopterids comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Sphenopteris</i> cf. <i>matheti</i> Zeiller	<i>Sphenopteris grabau</i> Halle (Fig. 6)
<i>Sphenopteris zwierzyckii</i> J. & G.	<i>Sphenopteris zwierzyckii</i> J. & G.
<i>Sphenopteris</i> cf. <i>gothani</i> Halle	<i>Sphenopteris</i> (<i>Oligocarpia</i>) <i>gothanii</i> Halle
<i>Sphenopteris</i> cf. <i>grabau</i> Halle	<i>Sphenopteris grabau</i> Halle
cf. <i>Sphenopteris tinggii</i> Halle	<i>Sphenopteris tinggii</i> Halle
<i>Monocarpia posthumii</i> J. & G.	<i>Oligocarpia posthumii</i> (J. & G.) comb. nov.
<i>Sphenopteris</i> spp. A, C, D	<i>Sphenopteris</i> (<i>Oligocarpia</i>) <i>gothanii</i> Halle
<i>Sphenopteris</i> sp. B	cf. <i>Sphenopteris zwierzyckii</i> J. & G.
<i>Schuetzia</i> sp.	<i>Schuetzia</i> sp.

Sphenopteris species A, C and D (Jongmans & Gothan, 1935, pl. 23, figs. 1-4) represent fern fragments with small pinnules similar to *Sph. gothani*, but with fewer lobes on the pinnule. In spite of the smaller number of lobes these specimen are assigned to *Sph. gothanii* because the specimens are apical fragments. *Sphenopteris* sp. B is reminiscent of *Sph. zwierzyckii*, but it is a small specimen with only a few features and, therefore, only a tentative attribution is made.

Pecopterid ferns

Table 5; Figs. 7-15.

Remarks – These new identifications of the pecopterids from the Jambi collection are based on fragmented material allowing little more than the description of pinna and their pinnules. The basic properties that were considered were pinnules free or (basally) adnate, margin morphology, length/width ratio of pinnules, shape of the pinnule, angle and forking of secondary veins, density of the secondary veins and fructification type.

The Jambi palaeoflora includes five main groups of pecopterids: (1) pecopterids with unforked secondary veins and free pinnules; (2) pecopterids with unforked secondary veins and (basally) adnate pinnules; (3) pecopterids with bifurcating secondary veins, individualized pinnules and non-decurrent midveins; (4) pecopterids with bifurcating secondary veins, individualized pinnules, and decurrent midveins; and (5) pecopterids with bifurcating secondary veins and pinnules with a constricted base.

(1) *Pecopterids often with unforked secondary veins and free pinnules* - In this first group we see pecopterids with moderately long pinnules (length/width ratio varies between 2.0 and 4.5), the secondary veins are placed at an angle between 45 and 70°, and the secondary veins are mostly straight, but sometimes slightly curved backwards or forwards. Pinnules are adjacently attached. There are few features that really differentiate the pecopterids from this group, namely the presence of a specialized basiscopic pinnule and the fertile form being either *Scolecopteris*- or *Danaeites*-like, the place of the pinna rachis on the leaf rachis and the shape of the apical pinnule.

Pecopteris arborescens was not observed. On all pecopterids with unforked secondary veins these arise at an angle of 55-60° and not 90° as in *P. arborescens* (Rémy & Rémy, 1977).

Table 5. Preliminary review of the pectopterids comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Pecopteris arborescens</i> (Schlotheim) Brongniart	cf. <i>Rajahia pseudohemiteloides</i> (Brongniart) K. & A. (Figs. 7, 8)
<i>Pecopteris hemiteloides</i> Brongniart	<i>Pecopteris hemiteloides</i> Brongniart
<i>Pecopteris mengkarangensis</i> J. & G. <i>pro parte</i>	<i>Pecopteris</i> (<i>Danaeites</i>) <i>mengkarangensis</i> J. & G. (Fig. 12)
<i>Pecopteris candolleana</i> Brongniart	<i>Pecopteris candolleana</i> Brongniart
<i>Pecopteris oreopteridia</i> Schlotheim	<i>Pecopteris orientalis</i> (Schenk) Potonié (Fig. 9)
<i>Pecopteris oreopteridia</i> Schlotheim	<i>Pecopteris</i> sp. A
<i>Pecopteris densifolia</i> Goeppert	<i>Pecopteris densifolia</i> Goeppert
<i>Pecopteris polymorpha</i> Brongniart	<i>Acitheca polymorpha</i> (Brongniart) Wagner
<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>verbeeki</i> J. & G. <i>pro parte</i>	<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>verbeekii</i> J. & G. (Fig. 14)
<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>verbeeki</i> J. & G. <i>pro parte</i>	<i>Scolecopteris</i> sp. B
<i>Pecopteris daubreei</i> Zeiller	<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>daubreei</i> Zeiller
<i>Pecopteris</i> cf. <i>cistii</i> Brongniart	<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>daubreei</i> Zeiller
<i>Pecopteris</i> (<i>Ptychocarpus</i>) <i>unita</i> Goeppert	<i>Diplazites unitus</i> (Brongniart) Goeppert (Fig. 13)
<i>Pecopteris feminaeformis</i> Schlotheim	<i>Nemejcopteris feminaeformis</i> (Schlotheim) Barthel (Fig. 10, 11)
<i>Pecopteris unitaeformis</i> J. & G.	<i>Pecopteris unitaeformis</i> J. & G.
<i>Pecopteris djambiensis</i> J. & G.	<i>Pecopteris djambiensis</i> J. & G.
<i>Asterotheca</i> sp. A, B <i>pro parte</i>	<i>Dizeugotheca</i> sp. A (Fig. 15)
<i>Asterotheca</i> sp. A, B <i>pro parte</i>	<i>Scolecopteris</i> sp. A

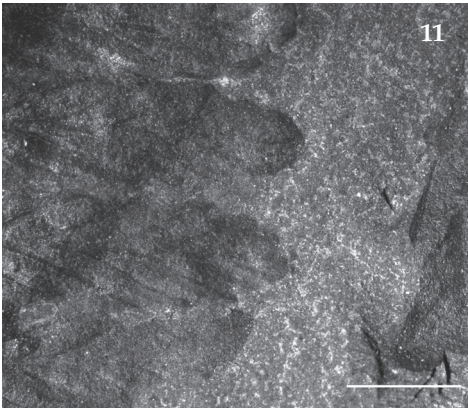
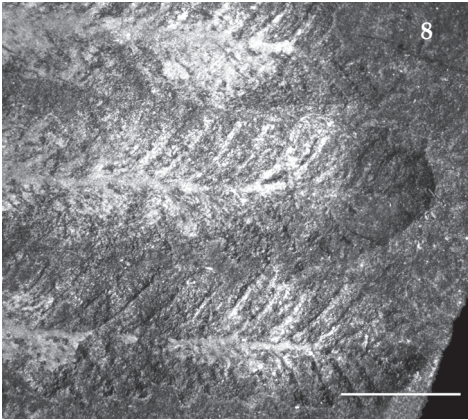
Pectopterids without a specialized basiscoppic pinnule and a *Scolecopteris*-type of fertile form fit in the description of *P. hemiteloides* Brongniart (1828) and the drawings of Grand'Eury (1877, pl. 8, fig. 9).

Some pectopterids with a special basiscoppic pinnule and a *Daneites*-type of fertile form tentatively fit into *Rajahia pseudohemiteloides* Kon'no *et al.* (1970). Although our material (Figs. 7, 8) might fit into the description of *Rajahia pseudohemiteloides* by Kon'no *et al.* (1970), the lack of fertile material precludes confident attribution.

Some of the pectopterids without bifurcating secondary veins sometimes have an elongated apical pinnule, are slightly lobate and have a pinna rachis laterally attached to the leaf rachis. These are typical features of *Pecopteris mengkarangensis*. A single character only seems to separate *Rajahia pseudohemiteloides* from *Pecopteris mengkarangensis*; that is, the attachment of the pinna rachis high on the frond rachis, rather than on the side of it. Kon'no *et al.* (1970) already mentioned that *P. hemiteloides*, *P. mengkarangensis* and *R. pseudohemiteloides* were hardly distinguishable.

(2) *Pecopterids often with unforked secondary veins and (basally) adnate pinnules* - Three species in the Jambi palaeoflora belong to the group with adnate pinnules. One has rela-

- Fig. 7. cf. *Rajahia pseudohemiteloides* (Brongniart) Kon'no & Asama, sample Basel 2206 (bar represents 10 mm).
- Fig. 8. cf. *Rajahia pseudohemiteloides* detail of the pinnule (Brongniart) Kon'no & Asama, sample DJ 45324 (bar represents 2 mm).
- Fig. 9. *Pecopteris orientalis* (Schenk) Potonié, sample DJ 127 e (bar represents 10 mm).
- Fig. 10. *Nemejcopteris feminaeformis* (Schlotheim) Barthel, sample DJ 45587 (bar represents 10 mm).
- Fig. 11. *Nemejcopteris feminaeformis* (Schlotheim) Barthel, detail of the pinnule, sample DJ 45587 (bar represents 2 mm).



tively short pinnules (L/W 1.5 to 2.5) with thick secondary veins that are clearly paired, but not completely opposed. These pectopterids belong to *P. unita* Brongniart, from which the fertile was placed in the separate genus *Diplazites* by Goeppert (1841). This species uncommonly shows also partially adnate pinnules similar to those of *Pectopteris arcuata* Halle, 1927, although according to Halle the secondary veins of *P. arcuata* bifurcate once while *Pectopteris unita* Brongniart has a midvein giving off unforked veins on each side. Halle (1927, p. 96) also mentioned the resemblance between *P. unita* and *P. arcuata*. We suspect that the variability of *P. arcuata* is rather large and might comprise two species. The illustrations in Halle (1927, pl. 19, figs. 1-4, pl. 20, figs. 8-12) compare closely to the specimen described here as *Diplazites unitus*.

A single specimen was observed with confluent and relatively short pinnules (L/W ratio: 1.48- 2.27), but with bifurcating secondary veins. We call this species *Pectopteris* sp. A.

A third species of this category has relatively long pinnules (L/W 3 to 4), also showing stronger secondary, seemingly paired veins. The pinnules are delicately dentate at the end of each secondary vein. Pectopterids with this morphology belong to *Nejmecopteris feminaeformis* (Schlotheim) Barthel (Figs. 10, 11).

(3) *Pectopterids with bifurcating secondary veins, individualized pinnules and non-decurrent midveins* - Pectopterids of the third group have pinnules with variable length/width ratios (L/W 1.3 to 6.3) and bifurcating secondary veins, but no basally adnate pinnules. *Pectopteris candolleana* is quite typical with its secondary veins bifurcating regularly at some distance from the midrib. *Pectopteris candolleana* has a strongly variable L/W ratio. In *P. verbeeki*, the angle at which the secondary veins are placed is relatively high (60-80°).

(4) *Pectopterids with bifurcating secondary veins, individualized pinnules and decurrent midveins* - The fourth category of *Pectopteris* species is characterized by secondary veins bifurcating once or twice, with unconstricted, individualized pinnules and decurrent midveins. Three species with decurrent midveins were originally identified by Jongmans & Gothan (1935) and fit into this category: *P. orientalis*, *P. unitaeformis* and *P. djambiensis*.

The holotype of *P. unitaeformis* was found in the collection and can clearly be recognized as a separate species. *Pectopteris djambiensis* was not observed in the collection, but was illustrated by Jongmans & Gothan (1935, pl. 34, figs. 2, 3), where this species and *P. unitaeformis* were compared with *P. unita* and *P. arcuata* (respectively, *Diplazites unitus* and *D. arcuatus*). They considered *P. unitaeformis* to have steeper secondary veins and *P. djambiensis* to possess denser venation than *Diplazites unitus*. We agree that the individualized pinnules, the pronounced midvein and the vein density make both species distinct from *Diplazites unitus*, but there is too little information to support or reject the differentiation between *P. unitaeformis* and *P. djambiensis* recognized by Jongmans & Gothan (1935).

Halle (1927, p. 74) pointed out that the pectopterids which Jongmans & Gothan (1935) considered to be *Pectopteris oreopteridia* are better identified as *P. orientalis* (Schenk) Potonié based on the thickness of the rachis of the ultimate pinna and its slight bending forwards at the end. Jongmans & Gothan (1935) did not mention a possible identification as *P. orientalis*, while Halle (1927) considered and rejected identification as *P. oreopteridia*.

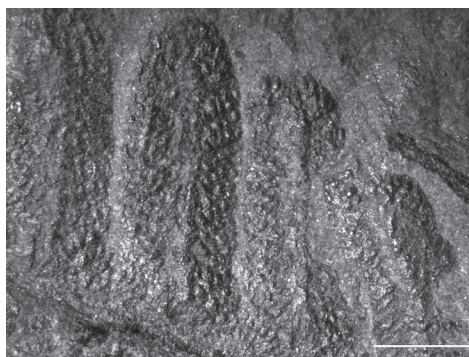


Fig. 12. *Pecopteris (Danaeites) mengkarangensis*, sample DJ 45512 (bar represents 2 mm).

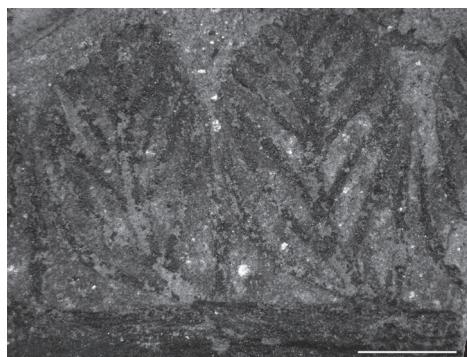


Fig. 13. *Diplazites unitus*, sample DJ 45612 (bar represents 2 mm).

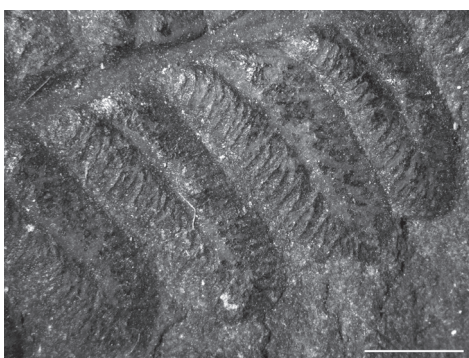


Fig. 14. *Pecopteris verbeekii*, sample DJ 45583 (bar represents 10 mm).



Fig. 15. *Dizeugotheca* sp. A, sample DJ 45332 (bar represents 2 mm).

(5) *Pecopterids with bifurcating secondary veins and pinnules with a constricted base* - Pecopterids of the fifth group have a small constriction at the pinnule base. *Pecopteris densifolia* shows secondary veins bifurcating only once. The second species, *Pecopteris polymorpha*, has secondary veins that bifurcate at least twice. Wagner (1959) transferred *P. polymorpha* to the genus *Polymorphopteris*. A review of *Polymorphopteris* indicated that all *P. polymorpha* have *Acitheca*-type of sporangia, so it was revised to *Acitheca polymorpha* (Cleal, 2005, pers. comm.).

Two other species that were originally identified fit in this category. The species that have relatively short pinnules, smaller at the base than at the pinnule apex and a midvein arising at an acute angle, are *P. daubreei* and *P. cf. cistii*. These species can be

differentiated by the clarity and the strong recurving of the secondary veins (Jongmans & Gothan, 1935). The density of the secondary veins in *P. cistii* is low and the veins clearly bifurcate twice (Brongniart, 1828). Further specimens with a dense secondary venation, with backwards curving secondary veins, bifurcating once and sometimes more are also observed. These specimens have a pronounced midvein. These features fit *Pecopteris daubreei*, a single fragment of which was observed with a scolecopterid type of sporangia. This indicates a subgeneric classification of *P. (Scolecopteris) daubreei*.

Special fructification types - The typical synangia of *Dizeugotheca* sp. A. (Fig. 15) with sporangia arranged in two pairs of two (two uppermost overlapping the two lowermost) were observed on the counterpart of the specimen holding the *Scolecopteris* sp. A with synangia of 3 to 5 (usually 4) sporangia.

Aphlebia specimens have not been examined.

Possible seedferns, including Gigantopterids

Table 6; Figs. 16-19.

Remarks – *Alethopteris strictinervis* Jongmans & Gothan, 1935 (pl. 40, fig. 1) showed bilateral symmetry and bifurcating, very dense secondary veins (straight and hard to see when they bifurcate twice); the rachis is rather thick and the pinnules have a slightly falcate shape, properties belonging to the genus *Callipteridium*. The pinnules are attached almost perpendicularly, as is also typical for *Callipteridium*. The width of the pinna is approximately 40 mm. This species was also identified earlier by Halle as *C. trigonum* in China. Jongmans & Gothan (1935, p. 129) compared their specimens with *C. trigonum*, but considered “Die Stücken sind ziemlich feinaderig, von unserer Art aber sicher verschieden durch die meist schlank-dreieckigen, mehr getrennt stehenden und stark gewolbten Blättchen.” The pinnules of *C. trigonum* are clearly more triangular and the venation is steeper (Franke, 1912) than in the specimens of *Alethopteris strictinervis* and the *C. trigonum* described in Halle (1927). Hence, the new combination

Table 6. Preliminary review of the seedferns comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Alethopteris strictinervis</i> J. & G.	<i>Callipteridium strictinervis</i> (J. & G.) comb. nov. (Figs. 16, 17)
<i>Macralethopteris hallei</i> J. & G.	<i>Macralethopteris hallei</i> J. & G.
<i>Callipteridium mengkarangense</i> J. & G.	<i>Callipteridium mengkarangense</i> J. & G.
<i>Callipteridium sumatranum</i> J. & G.	cf. <i>Lescuropteris moorii</i> (Lesquereux) Schimper
<i>Callipteridium</i> cf. <i>gigas</i> (Gutbier) Weiss	<i>Callipteridium strictinervis</i> (J. & G.) comb. nov.
<i>Dictyocallipteridium sundaicum</i> J. & G.	<i>Emplectopteridium alatum</i> Kawasaki (Fig. 18, 19)
<i>Gigantopteris bosschana</i> J. & G.	<i>Gothanopteris bosschana</i> (J. & G.) Koidzumi
<i>Gigantopteris</i> sp.	cf. <i>Gothanopteris bosschana</i> (J. & G.) Koidzumi
<i>Gigantopteris mengkarangkensis</i> J. & G.	<i>Paleogoniopteris mengkarangensis</i> (J. & G.) Koidzumi
<i>Neuropteris</i> cf. <i>gleichenoides</i> (Stur) Sterzel	cf. <i>Neurocallipteris neuropteroides</i> (Goeppert) Cleal
<i>Neuropteridium</i> vel <i>Neuropteris</i> sp.	<i>Neuropteris</i> sp.
<i>Cyclopteris</i> sp.	<i>Cyclopteris</i> sp.



Fig. 16. *Callipteridium strictinervis* (Jongmans & Gothan) comb. nov., pinna, sample DJ 45390 (bar represents 10 mm).



Fig. 17. *Callipteridium strictinervis* (Jongmans & Gothan) comb. nov., detail pinnule at rachis, sample DJ 45399 (bar represents 10 mm).

Callipteridium strictinervis (Jongmans & Gothan) comb. nov. (Figs. 16, 17). The specimens attributed to *Callipteridium? gigas* (Gutbier) Weiss by Jongmans & Gothan (1935) are also referable to *C. strictinervis*.

Macraethopteris is a possible seed fern, also recorded from Kaiping (Stockmans & Mathieu, 1939, 1957), but as *Alethopteris hallei*. Whether or not certain species of *Alethopteris*, such as *A. schneideri* Sterzel from the Rotliegend in Europe, may be compared with *Macraethopteris* is uncertain.

The few fragments of *Callipteridium sumatranum* Jongmans & Gothan, 1935 (pl. 44, figs. 1, 2) found in the collection have the same size, lobate pinnule shape and secondary bifurcating of veins as occurs in *Lescuropteris moorii* (Lesquereux) Schimper. The pinnules in the Sumatran species are slightly more rounded than in *Lescuropteris moorii*, as was also observed by Jongmans & Gothan (1935). This seems to be a preservational artefact, as some pinnules show the triangular shape typical of *L. moorii*. Jongmans & Gothan (1935) considered *L. moorii* to be more 'odontopterid' than their species. They were implying that several secondary veins in *L. moorii* enter the pinnule from the rachis, which they did not see in *C. sumatranum*. We observed secondary veins entering the pinnule from the rachis in the Jambi material and believe that the specimens should be identified as *L. moorii*.

Koidzumi (1936) erected *Gothanopteris* and *Paleogoniopteris* in order to express the primitive character of these two distinct gigantopterid genera. Jongmans & Gothan

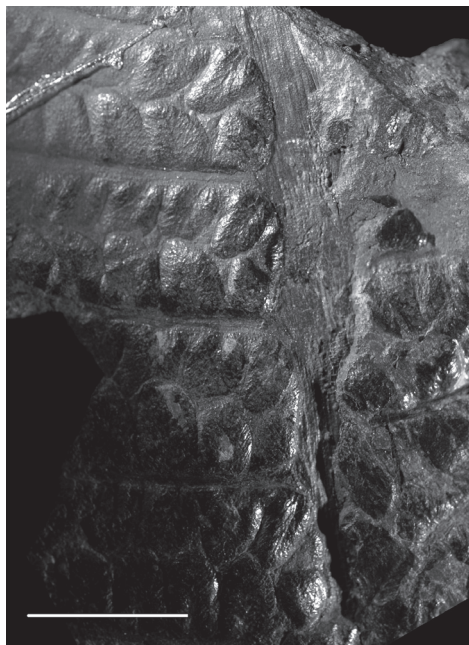


Fig. 18. *Emplectopteridium alatum* Kawasaki, rachis with pinnae, sample DJ 45401 (bar represents 10 mm).



Fig. 19. *Emplectopteridium alatum* Kawasaki, detail of pinnule, sample DJ 45401 (bar represents 10 mm).

(1935) treated *Gigantopteris* sp. separately because the pinnules are slightly more separate than in *G. bosschana*. This was probably overly cautious because measurements indicate a difference of only about 10 % in the incision between each pinnule in *Gigantopteris* sp. and in *G. bosschana*. The specimen of *Gigantopteris* sp. is clearly more apical than the other fragments, which could explain the difference.

Dictyocallipteridium sundaicum was identified as *Emplectopteridium alatum* Kawasaki because of the very small pinnule on the rachis placed between two normal pinnules (Figs. 18, 19). This property is characteristic of *E. alatum*.

Neuropteris gleichenoides is a junior synonym of *Neuropteris neuropteroides*. This species was reassigned to *Neurocallipteris neuropteroides* (Goeppert) by Cleal *et al.* (1990).

Neuropteridium vel *Neuropteris* was reduced to *Neuropteris* sp. because we observed only one pinnule with strong radiating secondary veins and possibly attached through the middle part of the pinnule to the rachis. *Neuropteridium* is a mainly Mesozoic genus with simply pinnate fronds. *Cyclopteris* is not reassessed herein.

Taeniopterids

Table 7; Figs. 20, 21.

Remarks – The original material described by Jongmans & Gothan (1935) was analyzed and speciated anew using measurable characters where appropriate. Only a few characters could be measured because the material was very fragmentary; the characters were vein density, leaf width, midrib width and number of vein bifurcations. Other

Table 7. Preliminary review of the taeniopterids comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Taeniopteris</i> cf. <i>multinervia</i> Weiss	<i>Taeniopteris</i> cf. <i>multinervia</i> Weiss (Fig. 20)
<i>Taeniopteris</i> cf. <i>norini</i> Halle	<i>Taeniopteris</i> cf. <i>multinervia</i> Weiss (Fig. 20)
<i>Taeniopteris nystroemi</i> Halle	<i>Taeniopteris nystroemii</i> Halle
<i>Taeniopteris taiyuanensis</i> Halle	<i>Taeniopteris taiyuanensis</i> Halle
<i>Taeniopteris densissima</i> Halle	<i>Taeniopteris densissima</i> Halle
<i>Taeniopteris latecostata</i> Halle	<i>Taeniopteris latecostata</i> Halle (Fig. 21)
<i>Taeniopteris incrassata</i> J. & G.	<i>Taeniopteris nystroemii</i> Halle
<i>Taeniopteris camptoneura</i> J. & G.	<i>Taeniopteris camptoneura</i> J. & G.
<i>Taeniopteris crassicaulis</i> J. & G.	<i>Taeniopteris</i> cf. <i>multinervia</i> Weiss

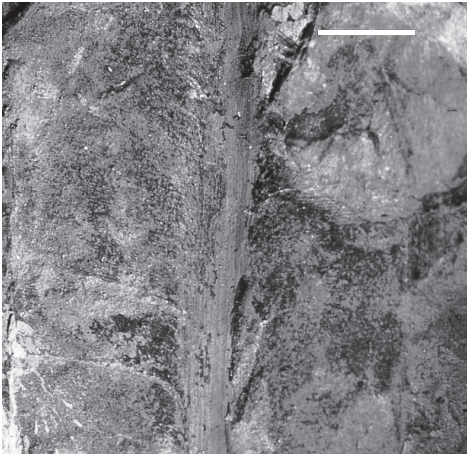


Fig. 20. *Taeniopteris* cf. *multinervia* Weiss, sample DJ 45252 (bar represents 10 mm).

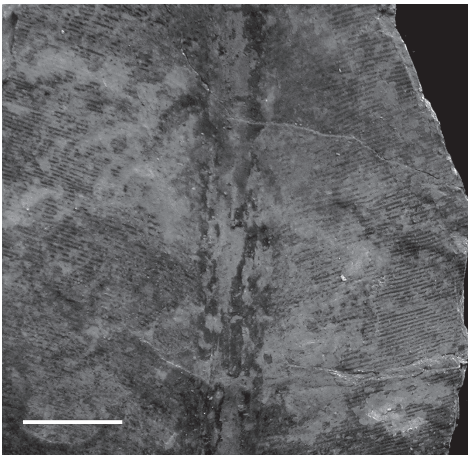


Fig. 21. *Taeniopteris latecostata* Halle, sample DJ 45211 (bar represents 10 mm).

qualitative characters were considered as well to support the identification of discrete groups based on relevant properties. These qualitative characters were decurrentness (the degree to which a vein that reaches the mid-rib will be tangential or at an angle) and relief of veins at the midrib, shape of the leaf at the apex or at the base, and leaf length. These qualitative characters could rarely be observed.

These properties gave four clear specimen groups that compared to the properties of the holotypes as described by their authors (Halle, 1927; Weiss, 1869). The groups are:

- (1) *Taeniopteris latecostata* Halle (Fig. 21) - Leaf fragments with a ratio of midrib width to leaf width < 40 and less than 25 veins/cm.
- (2) *Taeniopteris multinervia* Weiss (Fig. 20) - Leaf fragments with a ratio of midrib width to leaf width < 40 and with 25 to 35 veins/cm.
- (3) *Taeniopteris densissima* Halle - Leaf fragments with a ratio of midrib width to leaf width < 40 and with 35 to 40 veins/cm.
- (4) *Taeniopteris nystroemii* Halle - Leaf fragments with a ratio of midrib width to leaf width > 40 and < 25 veins/cm.

A single specimen had two distinct properties that singled it out, that is, the very dense venation and a very thick midrib cf. *Taeniopteris taiyuanensis* Halle.

The specimen identified by Jongmans & Gothan (1935) as *T. norinii* did not have the rounded apex typical for this species. This and the other properties of this specimen more closely resemble *T. multinervia* to which it is reassigned.

Taeniopteris incrassata described by Jongmans & Gothan falls within the group of *T. nystroemii* because of its relatively thin midrib and low vein density. According to Jongmans & Gothan, it is characterized by the relief the secondary veins have near the midrib; this was also mentioned by Halle (1927, pp. 148, 149) in the description of *T. nystroemi*. *Taeniopteris camptoneura* falls in the *T. latecostata* group and is only differentiated by strongly recurving secondary veins. *Taeniopteris crassicaulis* fits the description of *T. multinervia* Weiss.

Cordaites

Table 8; Figs. 22, 23.

Remarks – *Cordaites* leaf fragments cannot be reasonably identified without cuticle characters (Ledran, 1966), which are absent in our material. Šimůnek & Libertin (2006) demonstrated that the stomatal pattern in *Cordaites* also varies considerably. To review the *Cordaites* leaves, we examined all the material in search for criteria that would help to support the species described earlier by Jongmans & Gothan (1935), supplemented by the information Halle (1927) provided on the Cathaysia flora. Halle (1927) demonstrated that the vein patterns in the different parts of the species *C. schenkii* varied from 5 to 8 small veins between two wider ones, via a single small vein alternating with a wide one, to exclusively wide veins without smaller veins in between. In the light of the variation in venation pattern observed in *C. schenkii* (Halle, 1927), it was clear that only shape and size had to be used as identification criteria.

For the Permian Jambi specimens, leaf length was hard to determine because the specimens are fragmentary, but their width was often measurable. Vein density was measured for 30 specimens (ten belonging to what was identified by Jongmans & Gothan, 1935, as *C. principalis*, ten specimens identified originally as *C. borassifolium* and a further ten identified as *C. palmaeformis*); vein density for most specimens had a normal distribution between 18 and 50 veins/cm. We also measured the width of all specimens;

Table 8. Preliminary review of the cordaites comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
<i>Cordaites principalis</i> Germar	<i>Cordaites principalis</i> Germar
<i>Cordaites simplicinervius</i> J. & G.	<i>Cordaites principalis</i> Germar
<i>Cordaites borassifolius</i> (Sternberg) Unger	<i>Cordaites principalis</i> Germar
<i>Poacordaites</i> sp.	<i>Cordaites palmaeformis</i> (Goeppert) Grand'Eury (Fig. 22)
<i>Cordaites lingulatus?</i> Grand'Eury	<i>Cordaites lingulatus?</i> Grand'Eury (Fig. 23)
<i>Artisia</i> sp.	not observed
<i>Cordaitanthus</i> sp.	<i>Cordaitanthus</i> sp.
<i>Cordaicladus</i> sp	stem

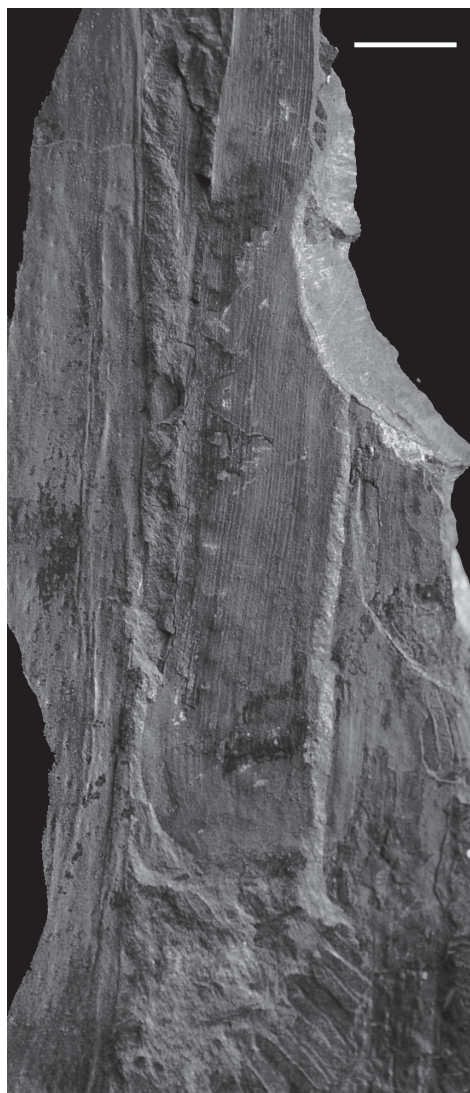


Fig. 22. *Cordaites palmaeformis* Goeppert, sample DJ 45278 (bar represents 10 mm).

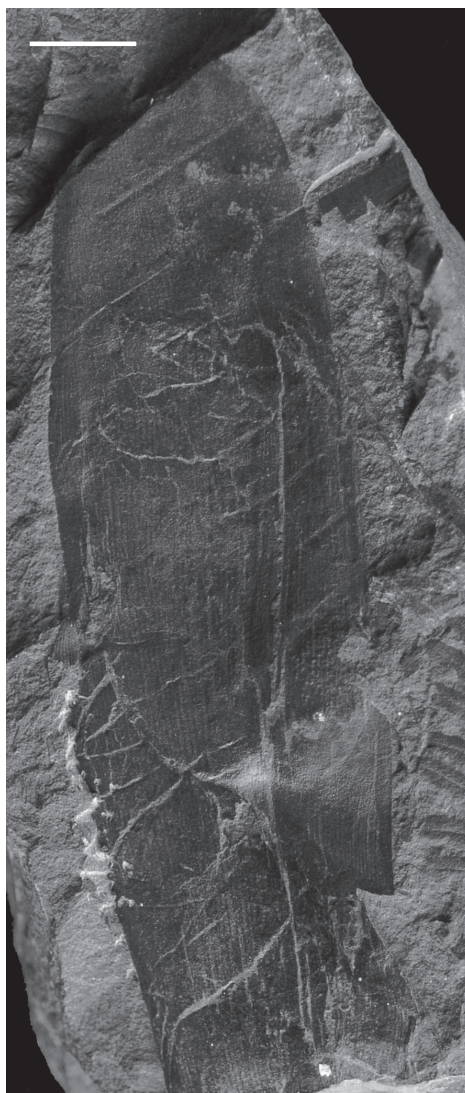


Fig. 23. *Cordaites lingulatus* Grand'Eury, sample DJ 4527c (bar represents 10 mm).

leaf width also had a normal distribution between 10 and 70 mm in our material.

It was not possible to differentiate between the three species identified by Jongmans & Gothan (1935) because the venation patterns varied within a leaf, and the vein density and the leaf width, both had a normal distribution and could very well represent different growth stages of a leaf.

The basal scar in what was described by Jongmans & Gothan (1935, pl. 57, figs. 1, 2) shows it is more correctly identified as *Poacordaites* sp.; we believe that in the collection we also see a *Cordaites palmaeformis* (Goeppert) (Fig. 22). The specimen identified as

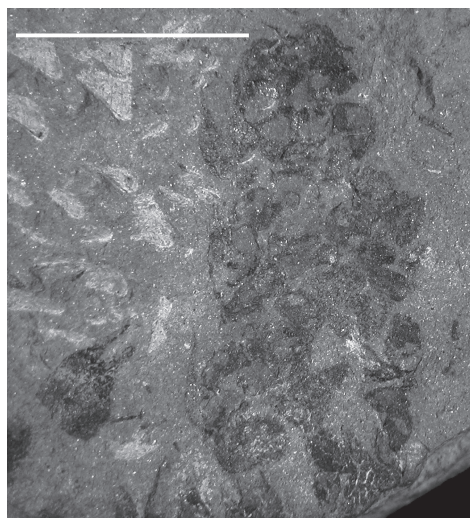
Cordaites lingulatus Grand'Eury (Fig. 23) has the rounded, finely veined leaves of this species, but there is only one specimen in the Jongmans collection and it agrees with the tentative identification of Jongmans & Gothan (1935). The *Cordaicladus* sp. of Jongmans & Gothan (1935, p. 159) consists of a little stem with no other feature than a few scars. The material did not allow more precise identification.

Artisia sp. was not observed in the collection. Illustrations of Jongmans & Gothan (1935, pl. 56, fig. 4) did not allow further systematic differentiation.

Gymnosperm cones and seeds

Table 9; Figs. 24, 25.

Remarks – Three *Tobleria* cones (Fig. 24) were observed in association with *Tobleria bicuspidis* seeds. Jongmans & Gothan (1935) did not record these specimens and they may well have missed them due to their small size. Seeds and bracts can be observed along the side of the cone and the organisation of the scales on the cone seems to be helical. The cones are small, 30 mm in length and were not observed associated with a particular leaf. Possible candidates in the Jambi flora for being parent plants to these cones are *Dicranophyllum* or *Cordaites*. *Cordaites* leaves are numerous in the Jambi flora, *Dicranophyllum* is rare. We observed that the three cones were seemingly axillary placed at the same angle, which suggests an organisation like in *Cordaitanthus*. Nevertheless, the seed (Fig. 25) are very distinct in shape and size from those seeds associated with *Cordaites* (*Cordaicarpus* seeds, also found in the collection).



▲ Fig. 24. *Tobleria* cone, sample DJ 45308 (bar represents 10 mm).



► Fig. 25. Seeds and bract of *Tobleria bicuspidis* Jongmans & Gothan, sample DJ 45311 (bar represents 10 mm).

Table 9. Preliminary review of the seeds comparing the systematic determinations of Jongmans & Gothan (1935) and the present authors.

Jongmans & Gothan (1935)	Present review
Not observed by J. & G.	<i>Tobleria</i> cone (Fig. 24)
<i>Tobleria bicuspis</i> J. & G.	<i>Tobleria bicuspis</i> J. & G. (Fig. 25)
<i>Cordaicarpus cordai</i> Geinitz	<i>Cordaicarpus cordai</i> Geinitz
<i>Cordaicarpus ovalis</i> J. & G.	<i>Cordaicarpus ovalis</i> J. & G.
<i>Cordaicarpus crassimarginatus</i> J. & G.	<i>Cardiocarpus crassimarginatus</i> J. & G.
<i>Rhynchogonium permo-carbonicum</i> J. & G.	<i>Rhynchogonium permo-carbonicum</i> J. & G.
<i>Trigonocarpus</i> sp.	<i>Rhynchogonium</i> sp.
<i>Carpolithus</i> sp.	<i>Carpolithus</i> sp.
<i>Carpolithus coffeoides</i> J. & G.	<i>Carpolithus</i> sp.
<i>Carpolithus multigranosus</i> J. & G.	<i>Carpolithus multigranosus</i> J. & G.
<i>Carpolithus granulosus</i> J. & G.	<i>Carpolithus granulosus</i> J. & G.
<i>GigantospERMum posthumi</i> J. & G.	<i>GigantospERMum posthumii</i> J. & G.

Trigonocarpus depicted by Jongmans & Gothan (1935, pl. 55, fig. 7) was not found in the collection. Their seed was approximately 15 mm long with six apices at the end of six long, slender leaf-shaped envelopes. Considering the size and the shape of this seed, and also the slender envelopes and apices, we suggest it might be related to *Rhynchogonium permo-carbonicum* and suggest that *Rhynchogonium* sp. might be a better name.

Similarly, specimens of *Carpolithus coffeoides* do not form part of the Jambi collection at the Nationaal Natuurhistorisch Museum and the picture (Jongmans & Gothan 1935, pl. 53, fig. 9) show few features.

Discussion and conclusions

Table 10.

The Jambi flora is composed of 60 taxa, 18 of which have been recorded only from this flora. Seven also occur in Malaysia (Johore), 23 are Euramerican, 31 are Chinese species (including south, north and northwest China), and 16 have been recorded from both China and Euramerica (see Table 10). Most of the taxa in common with the Euramerican floras are generalized morphotaxa, so the flora can be considered Cathaysian in character.

A more detailed comparison with the three Early to early Late Permian Chinese provinces of Cathaysian floras (Li, 1995, p. 202) shows a great similarity with the north-west Chinese province where four localities yielded a total of 214 species, 24 of which were also found in the Jambi Flora. In the North Chinese province ten localities yielded 513 species from which a relatively low number of 31 species also occurred in the Jambi flora. Peltasperms(?) have been found in the palaeofloras from north China. The south Chinese province is represented by seven localities only, yielding 243 species, of which 13 also were found in the Jambi Flora. In South China the peltasperms are present also. Peltasperms in the Jambi flora are limited to *Callipteridium strictinervis* and *Emplectopteridium alatum*.

Jongmans & Gothan (1935, p. 185) thought the Jambi flora was mainly European in character though showing links with the *Gigantopteris* flora. This statement should be

Table 10. Comparison between the species occurring in the Early Permian of Jambi (Sumatra), China and Malaysia.

*1 *Annularia* cf. *stellata*: we consider the distribution of *Annularia stellata*.*2 *Dicranophyllum molle*: we considered the occurrences of *D. hallei* and *Dicranophyllum* sp. described by Stockmans & Mathieu (1957).*3 *Maroessia* sp.: we consider the distribution of *Omphalophloios*.*4 *Callipteridium strictinervis*: we consider it equivalent of *Callipteridium trigonum* as illustrated in Halle (1927).*5 cf. *Neurocallipteris neuropteroides*: we consider it as *Neurocallipteris neuropteroides*.

Species in the Jambi flora	Euram	Johore	S China	N China	NW China
<i>Calamites</i> (<i>Crucicalamites</i>) <i>jubatus</i> L. & H.	x	-	-	-	-
<i>Calamites suckowii</i> Brongniart	x	x	x	x	x
<i>Annularia</i> cf. <i>stellata</i> (Schlotheim) Wood	x	-	*1	x	x
<i>Palaeostachya incrassata</i> J. & G.	-	-	-	-	-
<i>Parasphenophyllum thonii</i> (Mahr) Asama	x	-	-	x	x
<i>Sphenophyllum verticillatum</i> (Schlotheim) Zeiller	x	-	-	x	x
<i>Trizygia oblongifolia</i> (G. & K.) Asama	x	-	-	x	x
<i>Sphenophyllum</i> cf. <i>emarginatum</i> Brongniart	x	-	-	x	x
<i>Lepidodendron mesostigma</i> J. & G.	-	-	-	-	-
<i>Lepidodendron posthumii</i> J. & G.	-	-	-	x	x
<i>Dicranophyllum molle</i> (J. & G.) comb. nov.	*2	-	-	x	-
<i>Maroesia rhomboidea</i> J. & G.	*3	-	-	-	-
<i>Stigmara asiatica</i> J. & G.	-	-	-	x	-
<i>Sphenopteris grabau</i> Halle	-	-	x	x	x
<i>Sphenopteris zwierzyckii</i> J. & G.	-	-	-	-	-
<i>Sphenopteris</i> (<i>Oligocarpia</i>) <i>gothanii</i> Halle	-	-	-	x	-
<i>Sphenopteris tinggii</i> Halle	-	-	x	x	-
<i>Oligocarpia posthumii</i> (J. & G.) comb. nov.	-	-	-	-	-
cf. <i>Rajahia pseudohemiteloides</i> (Brongniart)					
Kon'no & Asama	-	x	x	-	-
<i>Pecopteris hemiteloides</i> Brongniart	x	-	x	x	x
<i>Pecopteris</i> (<i>Danaeites</i>) <i>mengkarangensis</i> J. & G.	-	-	-	-	-
<i>Pecopteris candolleana</i> Brongniart	x	-	-	x	x
<i>Pecopteris orientalis</i> (Schenk) Potonié	-	-	x	x	x
<i>Pecopteris densifolia</i> Goeppert	x	-	x	x	x
<i>Polymorphopteris polymorpha</i> (Brongniart) Wagner	x	-	x	x	x
<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>verbeekii</i> J. & G.	-	-	-	-	-
<i>Pecopteris</i> (<i>Scolecopteris</i>) <i>daubreei</i> Zeiller	x	-	-	-	-
<i>Diplazites unita</i> (Brongniart) Goeppert	x	-	-	x	x
<i>Nemejcopteris feminaeformis</i> (Schlotheim) Barthel	x	-	-	x	x
<i>Pecopteris unitaeformis</i> J. & G.	-	-	-	-	-
<i>Callipteridium strictinervis</i> (J. & G.) comb. nov.	-	-	-	*4	-
<i>Macralethopteris hallei</i> J. & G.	-	-	-	x	-
<i>Callipteridium mengkarangense</i> J. & G.	-	-	-	-	-
cf. <i>Lescuropteris moorii</i> (Lesquereux) Schimper	x	-	-	-	-
<i>Emplectopteridium alatum</i> Kawasaki	-	-	-	x	x
<i>Gothanopteris bosschana</i> (J. & G.) Koidzumi	-	-	-	-	-
<i>Paleogoniopteris mengkarangensis</i> (J. & G.) Koidzumi	-	-	-	-	-
cf. <i>Neurocallipteris neuropteroides</i> (Goeppert) Cleal	x	-	-	*5	-
<i>Taeniopteris</i> cf. <i>multinervia</i> Weiss	x	x	x	x	x
<i>Taeniopteris nystroemii</i> Halle	-	x	x	x	x

Species in the Jambi flora	Euram	Johore	S China	N China	NW China
<i>Taeniopteris taiyuanensis</i> Halle	-	x	x	x	x
<i>Taeniopteris densissima</i> Halle	-	-	x	x	x
<i>Taeniopteris latecostata</i> Halle	-	x	-	x	x
<i>Taeniopteris camptoneura</i> J. & G.	-	-	-	-	-
<i>Cordaites principalis</i> Germar	x	-	-	-	-
<i>Cordaites palmaeformis</i> Goeppert	x	-	x	x	x
<i>Cordaites lingulatus?</i> Grand'Eury	x	-	-	-	-
<i>Tobleria</i> cone	-	-	-	-	-
<i>Tobleria bicuspis</i> J. & G.	-	-	-	-	-
<i>Cordaicarpus cordai</i> Geinitz	x	x	x	x	x
<i>Cordaicarpus ovalis</i> J. & G.	-	-	-	-	-
<i>Cardiocrarpus crassimarginatus</i> J. & G.	-	-	-	-	-
<i>Rhynchogonium permo-carbonicum</i> J. & G.	-	-	-	-	-
<i>Carpolithus multigranosus</i> J. & G.	-	-	-	-	-
<i>Carpolithus granulosus</i> J. & G.	-	-	-	-	-
<i>Gigantospermum posthumii</i> J. & G.	-	-	-	-	-

read in the context of the knowledge available in the 1930s. Jongmans & Gothan's perception of a European floral composition reflects the recognition of a floral composition of Stephanian-Permian age in everwet conditions within the palaeoequatorial belt. A direct link with the European area is not implied, but instead it recognises that the everwet floras of Late Pennsylvanian and Early Permian age are of similar composition everywhere in the same palaeolatitudinal area. Within this general context, the presence of a number of species described from Sumatra and not yet recorded elsewhere in the 1930s may be regarded as being due, at least in part, to the paucity of fossil records in southeast Asia at that time. Of course, some of the species encountered in the Jambi palaeoflora might have been endemic, but too little is known of the palaeogeographical and stratigraphical position of this part of Sumatra to rely on such an argument.

It has been noted that the waning of the late Pennsylvanian ice age brought a climate change that produced an increased number of drier habitats in the palaeoequatorial belt with a more limited and rather different floral composition (Gastaldo *et al.*, 1996). This is the Euramerian flora, which is well known from Europe and eastern North America. The most characteristic elements in the drier Euramerian floras are the 'calopterids' (Peltaspermales) and, above all, the walcchian conifers. The latter, though present throughout the Pennsylvanian, are usually absent in the Permian everwet floras of Cathaysia. A few walcchian conifers have been described from China (Halle, 1927, p. 198; Li, 1995). Nevertheless, the presence of other mesomorphic plants (amongst other peltasperms, but also taeniopterids, sphenopterids and *Dicranophyllum*) suggests that the drier areas typical of the Early Permian are represented in the sedimentary rocks of the West Sumatra block. These possibly indicate a higher latitude than purely equatorial as was suggested by Metcalfe (2002). The absence of these characteristically Euramerian Early Permian floral elements probably influenced Jongmans & Gothan in their belief that the Jambi flora was Stephanian in age rather than Permian, a point of view not shared by Posthumus (1927).

Halle (1927) noted taxonomic similarities between the east Asian Cathaysia and the Jambi flora based on Jongmans & Gothan (1925). In various publications, including Asama *et al.* (1975), the Jambi flora was recognized as being Cathaysian in aspect, the relative age being the only bone of contention. The geographically closest Cathaysian flora is in Johore, Malaysia (Kon'no *et al.*, 1970), just across the Strait of Malacca (separating the Malaysian Peninsula and Sumatra). The flora in Johore is Late Permian and it has only seven species in common with the Jambi flora (Table 10). A Late Permian flora was also described from the Jenka Pass in west Malaysia. Out of 24 species, four also occur in the Jambi flora (Kon'no & Asama, 1970). Kon'no and Asama (1970) considered the similarity strikingly low, even when considering that their flora is younger than that of Jambi and few similarities were expected.

Cathaysian type floras, though occurring mainly in east Asia, are also found in Permian everwet areas in the Middle East (Berthelin *et al.*, 2003) and Central America, from the southern United States across Mexico into Venezuela (Archangelsky & de la Sota, 1960). Of particular importance is the record from the Early Permian of Texas (DiMichele *et al.*, 2001), which is ecotonal with the Euramerian area, containing gigantopterids as well as callipterid peltasperms and conifers.

Jongmans & Gothan (1935) considered the Sumatran species *Pecopteris mengkarangensis*, *Alethopteris strictinervis* (= *Callipteridium strictinervis*), *Lepidodendron mesostigma* and *L. posthumii* to have European affinities. *Lepidodendron posthumii* was recorded from China (Halle, 1927; Li, 1995). So far, *Lepidodendron mesostigma* and *Pecopteris mengkarangensis* are known only from Sumatra. *Callipteridium strictinervis* is sufficiently similar to *Callipteridium trigonum* Franke, as recorded from east Asia, to raise doubts about its recognition as an unequivocally separate species. Callipterids, together with *Gigantopteris*, *Macraethopteris* and the large number of *Taeniopteris* species, were regarded by Jongmans & Gothan (1935, pp. 183, 184) as quite different from European Permo-Carboniferous floral elements.

Although *Taeniopteris* has been recorded from strata as old as Moscovian, it is known that a profusion of *Taeniopteris* taxa generally denotes Permian rather than Pennsylvanian deposits. The presence of the gigantopterid genera *Paleogoniopteris* and *Gothanopteris* is of evolutionary and temporal significance. They are considered the most primitive equivalents of the other gigantopterids (Asama, 1959), a group of seed ferns that developed a typical angiosperm-type of leaves with net venation and that we see developing during the Permian in various localities (for example U.S.A., Cathaysia). Their presence could mean that our deposits are older than those holding the Chinese flora.

According to Asama *et al.* (1975), the Jambi flora may be best compared with that of the Chinese Yuehmenkou beds (incorporating the Taiyuan and Shansi formations). However, our data suggest that a greater similarity exists with the Lower Shihhotse beds in north China. According to a widely accepted subdivision (Liu *et al.* 2003, p. 371), the Shansi Formation and Lower Shihhotse beds are assigned to Artinskian-Kungurian and Kungurian-Wordian ages, respectively. Asama *et al.* (1975) considered the Jambi flora to be Artinskian, based on the comparison of plant species associations. In Jambi, marine strata bearing fusulinids and brachiopods occur both below and above the beds with plant fossils. The identification of the brachiopod *Stereochia semireticula-*

tus (Martin) in the Mengkarang Formation (see Fig. 2) resulted in an assignment of Artinskian (Suyoko, 1996), whereas earlier research on the fusulinids by Vachard (1989) suggested an Asselian age. *Stereochia semireticulatus* (Martin) is an incorrect systematic assignment, but the generic determination is probably correct (C. F. Winkler Prins, pers. comm.), referring to the Permian of Timor as *Productus semireticulatus* Martin (Broili, 1916). However, that species (now *Dictyoclostus semireticulatus* (Martin)) is from the Mississippian (Viséan) of England. Grant (1976) stated that Broili's specimen belongs to his genus *Stereochia*, the type species of which, *S. litostyla*, is from the Artinskian of Thailand, whilst the genus to which the new brachiopod from Jambi most probably belongs, ranges from Sakmarian to Kungurian. Interestingly, Jongmans & Gothan (1935) mentioned that the best match between the flora of the Mengkarang Formation and that from Shansi, north China, would be that of the Lower Shihhotse beds of Kungurian-Wordian age.

Laveine *et al.* (2003) suggested that during the Carboniferous, Indochina, east Malaysia, south China and north China were closely connected. Barber & Crow (2003) even considered that central Sumatra must have been part of the Indochina Block of Cathaysia and stressed the need to gain insight into the position of Central Sumatra, the West Sumatra Block, on which the Mengkarang Formation was deposited, relative to the Indochina and the two Cathaysia blocks.

Inferences on climate drawn from floral composition provide useful constraints to plate tectonic reconstructions. In a recent discussion of the plate tectonic model adopted for the geological history of Sumatra, Barber & Crow (2003) accepted the presence of different blocks, West Sumatra, Sibumasu and East Malaysia, presently situated from southwest to northeast. The Jambi locality on Sumatra belongs to the West Sumatra Block. It is now believed that this block would have become separated from Cathaysia in the Late Permian or Early Triassic through strike-slip faulting, but the position of the West Sumatra Block during the Early Permian still is not clear. We believe that the age of the deposits in which the plant fossils were found is Sakmarian or older, because of the rather simple, probably primitive gigantopterids (Asama, 1959). The presence of mesomorphic plants (such as peltasperms, but also taeniopterids, sphenopterids and *Dicranophyllum*) suggests that the drier areas typical of the Early Permian were represented in these sedimentary rocks of the West Sumatra Block. A relatively high palaeolatitude for the West Sumatra Block on the southern hemisphere as was presented in Barber *et al.* (2005) cannot be excluded here, in spite of a clearly Cathaysian affinity of the Jambi palaeoflora.

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