A revision of the Late Triassic Bintan flora from the Riau Archipelago (Indonesia)

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In 1951, W.J. Jongmans published the description of a small flora from Bintan Island in the Riau Archipelago of Indonesia, based on material from one fossil locality in the Bintan Formation (Late Triassic). The complete fossil plant collection from Bintan includes specimens from four localities, all of which were examined for the first time in this study. Twenty-one taxa were determined, compared to an earlier four, and three earlier determinations were revised. Of these 21 taxa, 14 were attributed to the Bennettitales, including eleven leaf species, one *Williamsonia* sp., and two other fertile and stem organs. The other components of the flora were limited to twigs and cones of *Brachyphyllum* sp., leaves of *Podozamites* sp. and leaves of *Nilssonia* sp., in addition to some unusually large seeds. The Bintan Flora is exceptional compared to southeast Asian Late Triassic floras because of the complete absence of fern and sphenophyte remains, and the dominance of diminutive *Pterophyllum* and *Ptilophyllum* leaves. Since the Bintan flora lacks riparian elements, these differences are attributed to effects of taphonomy. Further, the similarities between the Bintan and southwest Asian floras support earlier palaeogeographical reconstructions for the Late Triassic.

Contents

Introduction

A small, unusual flora from the Indonesian island of Bintan, in the Riau Archipelago, was described by Jongmans (1951). The four leaf species that Jongmans identified from Bintan were quite diminutive and pertained exclusively to the cycadophytes, including one new taxon, *Pterophyllum bintanense* Jongmans. He considered the flora to be Mesozoic and a geologist of the Billiton mining company suggested that the source sedimentary rocks were Upper Triassic. The Bintan flora was the first of Mesozoic age to be described from Indonesia, but the original study considered fossils from only one of the four localities where material had been collected.

The Bintan Flora is just one of the many Triassic floras studied from southeast Asia, with the focus on southern China and Vietnam. The Upper Triassic floras from southern China are characterized by equally abundant cycadophytes and ferns, with the Dipteridaceae typifying the latter group (Dobruskina, 1994, p. 115). The same components are typical for the floras of Vietnam (Zeiller, 1903; Dobruskina, 1994, p. 115), and east Malaysia and Thailand (Kon'no & Asama, 1973). In this context, the exclusively cycadophyte flora of Bintan is quite exceptional.

Because of its unusual composition, some authors argued that the Bintan flora was much younger than stated by Jongmans (1951). Indeed, it was suggested that the flora should be dated as Early Cretaceous (Kon'no, 1972; Kon'no & Asama, 1973). The unique composition of the Bintan flora and the controversy over its age provided motivation to examine the additional fossil material from the three undescribed localities.

The objectives of this study were to describe all the specimens available from the Bintan Formation, and perform anatomical and palynological studies. However, neither anatomical nor palynological studies could be completed because of inferior preservation. Still, many additional taxa were encountered in the collection, which has allowed us to make new conclusions about the peculiar flora.

Material and methods

The fossil material consists of 61 compression specimens, of which 15 were previously described by Jongmans (1951). In addition, wood remains were found. The matrix of all four sites is quite similar; carbon-rich shale with some 'coaly bits,' with the shale ranging from fine-grained and dark grey to light grey with fine-grained sandstone. The material is stored at the Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands.

Each specimen was measured macroscopically, and examined under a dissecting microscope for meso- and micro-scale features. Thin layers of carbonaceous film were picked from several compression surfaces, mounted on stubs and observed directly with SEM. This method yielded some information on venation and epidermal patterns. The wood was thin sectioned, but did not show any cellular details.

The palaeogeographical reconstructions that are referenced in the discussion were obtained from Scotese (2006) using the draw map function, with research group "paleobotany", time interval "Upper Triassic" and reconstruction date "210 Mya."

Localities and geological information

The fossil material was collected from carbonaceous beds of the Bintan Formation at the west and south coasts of the small island Penjengat and at Batu Itam and Batu Litjin, two sites on the southeast coast of Bintan island, all of which are part of the Riau Archipelago, Indonesia (Fig. 1). The Bintan Formation contains alternating shale and sandstone layers, and is considered to be Triassic (Jongmans, 1951). At Batu Itam, the fossiliferous beds were exposed at low tide on a tidal platform. Representatives of the Billiton Company collected the material in the first half of the 20th Century during geological exploration for mining and further details of the localities are not available. Aside from the Bintan Formation, Bintan Island is composed of Jurassic granites compa-

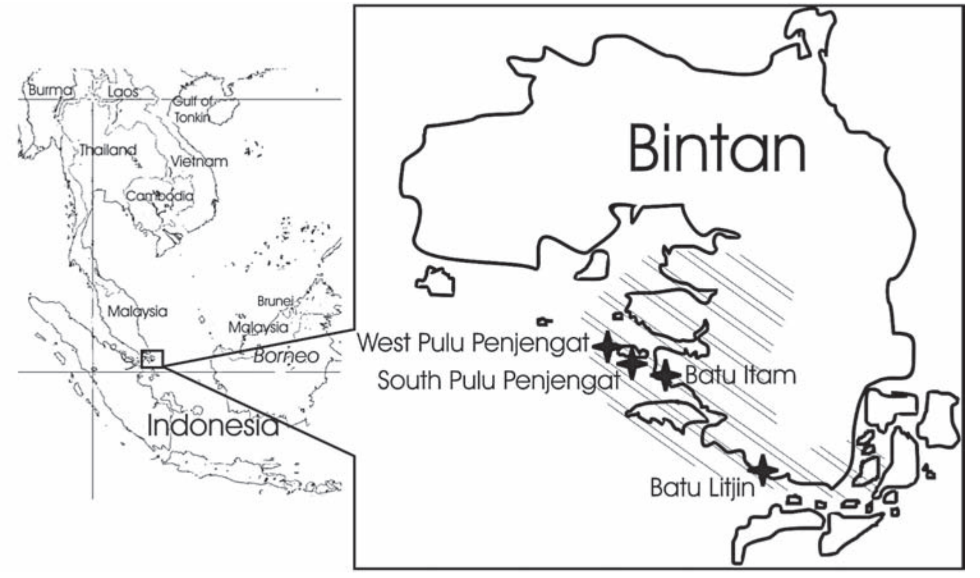

Fig. 1. The geography of southeast Asia including the location of Bintan Island, indicated by the small box on the map at left. On the map of Bintan at the right, the four localities are indicated by black stars and their names. The shaded area on the map of Bintan indicates the approximate extent of the Bintan Formation. Bintan map and geology after Jongmans (1951, p. 190).

rable to those found on Singapore, and Triassic metamorphosed and arenaceous shales that are similar to formations from Malaysia and Singapore (van Bemmelen, 1949).

Systematic palaeobotany

Cycadophyta
Cycadales
Genus *Nilssonia* Brongniart
***Nilssonia* sp.**
Pl. 1, fig. 1.

Material – JMS 52207-52208 (part and counterpart), JMS 52200.

Localities – One specimen was collected at South Pulu Penjengat and the other at Batu Itam.

Description – Both compressions are fragmentary and each shows a small part of a pinnate leaf. The more complete of the two fossils is 142 mm long by 56 mm wide at the central part. The leaf seems to narrow toward the apex. The rachis appears to be exposed on one side and covered by the bases of the pinnae on its other side. The rachis is 3 mm wide. There are no interspaces between the pinnae; indeed, in some examples they overlap. The angle of attachment is at least 70° at the centre, but 45° near the base.

The pinnae themselves are 22 to 40 mm long and always 6 to 7 mm wide. They are slightly lanceolate with a tip that is rounded to pointed. The veins are parallel with two to three per mm. The veins are not seen to fork. The pinna margin is entire. The pinnae are very similar between the two specimens, although the smaller has better preserved veins.

Discussion – An oxidized mineral has filled in the mesophyll of the pinnae of both specimens, which gives the impression that the plants had very thick leaves. Cuticle studies of JMS 52208 isolated one small piece (accidentally destroyed) that lacked sinuous epidermal cell outlines and showed simple haplocheilic stomata. As a result, this specimen is assigned to the Cycadales. Since the pinnae are attached over the whole rachis on one side and the veins do not fork (see Schweitzer *et al*., 2000), it is assigned to the genus *Nilssonia*.

Bennettitales
Genus *Anomozamites* Schimper
cf. *Anomozamites* sp.
Pl. 1, fig. 2.

Material – JMS 52190.

Locality – The leaf fossil is from West Pulu Penjengat.

Description – The Bintan collection contains an incomplete specimen of a pinnate leaf, 60 mm long by 15 mm wide. The width of the leaf does not seem to vary. The rachis is 1 mm wide and has three longitudinal striations. The pinnae are 7.0 to 8.0 mm long and 4.5 mm wide, and the length to wide ratio is less than 2. The pinnae are attached at about 90°. There is up to 1 mm of space between the pinnae at the pinna base, but the pinnae are about 1 mm wider at their outer edge than at the base. The apex and base of each pinna is truncate, with the upper corner of the outer edge slightly stretched, which gives an approximately rhomboid shape to the pinna. The pinnae have entire margins and parallel veins. The venation is very fine, with at least twelve veins per mm.

Discussion – The genus *Anomozamites* is suggested because the length to width ratio is less than 2. However, the relatively wide spacing of the pinnae and the slightly contracted pinna bases are unlike other examples from that genus, such as *Anomozamites minor*, described herein. The shape of the pinnae approaches that of the genus *Sphenozamites* Brongniart emend. Wesley, 1958, but leaves of that genus are much larger than this specimen. From the Upper Triassic of northeastern Sichuan (China), there is a taxon described as *Zamites jiangxiensis*, of which dissimilar small and large forms are figured (Ye *et al*., 1986). The small forms have pinnae with an average length to width ratio of just over 2 and the pinna base is often contracted (Ye *et al*., 1986, pl. 28, fig. 9, pl. 29, fig. 4, 4a). For comparison, the larger forms have elongated pinnae (length to width ratio of 4 or more) and straight pinnae bases (Ye *et al*., 1986, pl. 29, fig. 1, 2, pl. 30, fig. 1, 3). The pinnae of the smaller form have a similar appearance to those of the leaf figured here. See also the discussion of *Pterophyllum* sp. A, below. Finally, this specimen is vaguely similar to *Pterophyllum bintanense* and was collected at one of the locations where *P. bintanense* is abundant. It might also be an unusual example of *P. bintanense*.

Anomozamites minor Nathorst, 1878
Pl. 1, fig. 3.

Selected synonyms –

1878 *Anomozamites minor* sp. nov.; Nathorst, p. 19, pl. 2, fig. 12.
1932 *Anomozamites minor* Nathorst; Harris, p. 29, text-fig. 10, pl. 1, fig. 7, pl. 2, figs. 1, 6.
1973 *Anomozamites minor* Nathorst; Kon'no & Asama, p. 168, pl. 27, fig. 1, 1a.
2003 *Anomozamites minor* Nathorst; Schweitzer & Kirchner, p. 48, pl. 8, figs. 6-8.

Material – JMS 52189.

Locality – The specimen was collected at Batu Itam.

Description – The Bintan collection contains only one, incomplete specimen of a compound leaf, 31 mm long by 10 mm wide. The width of the leaf does not vary along the visible length. The rachis is 0.8 mm wide, but is not well preserved. The pinnae are 4.0 to 5.0 mm long and 2.5 mm wide. The length to width ratio is about 1.75. The pinnae are attached at about 70°. They are spaced directly next to one another without overlapping. The apex and base of each pinna is truncate, giving a rectangular shape to the pinna. The pinnae have entire margins and parallel veins, and the venation seems to be very fine.

Discussion – This specimen is quite small compared to the one figured by Nathorst (1878), but small specimens from Greenland were shown to have cuticles identical to larger leaves identified as *A. minor* (Harris, 1932). *Anomozamites minor* is also reported from the Upper Triassic Huai Hin Lat Formation of Khorat, Thailand (Kon'no & Asama, 1973). Neither the Khorat nor the Bintan specimen is identical to the northern European examples of *A. minor*. A better identification of this taxon would require more specimens.

Genus *Pterophyllum* Brongniart
Pterophyllum bintanense Jongmans, 1951
Pl. 1, figs. 4-6.

Selected synonym –

1951 *Pterophyllum bintanense* sp. nov., Jongmans, p. 187, pl. 1, figs. 1, 1a, 2, 2a, 3, 3a.

Material – JMS 52178-52182, 52184, 52185, 52189, 52194, 52195, 52196, 52197, 52200.

Localities – *Pterophyllum bintanense* occurs more commonly than any other species in the flora, but it was only collected at Batu Itam and West Pulu Penjengat. In these two localities it is the most common element.

Description – Fifteen fragments were examined to make this description. All are incomplete, but examples of the petiole, central leaf and apex were encountered. The species is a small, once pinnate leaf (Pl. 1, fig. 6). The fragments are 23 to 74 mm long. The width varies from 9 to 17 mm. Based on the specimen with the petiole attached (JMS 52197), the typical dimensions of a leaf are at least 60 mm long by 15 mm wide, although shorter and especially longer leaves do occur commonly. The dimensions of a leaf vary proportionally. The leaf is linear with a truncate base and an apex, which seems to end in one pinna placed as a continuation of the rachis, although the latter was observed in only one specimen (Pl. 1, fig. 4). The rachis is less than 1.8 mm wide and appears to have longitudinal striations. The rachis is always visible; when it is not preserved, it is seen as a gap between the two rows of pinnae (Pl. 1, fig. 5). These are attached at almost 90º and are closely placed, except toward the base of the leaf. The pinnae are up to 6.0 or 7.0 mm long and 2.0 to 3.0 mm wide, but can be as small as 4.5 mm by 2.0 mm. The length to width ratio is always greater than 2. The parallel veins occur with a frequency of 3 to 4 per mm and the pinna margin is entire. The pinnae are truncated or slightly rounded. The shape is like a rectangle with rounded corners.

Discussion – Having examined the entire Bintan collection, the original description of Jongmans (1951) is confirmed, with the addition that the pinnae are equally wide from the base nearly to the apex. Near the apex the leaf narrows and there is one terminal pinna (Pl. 1, fig. 4). Aside from the variation in size from very small to small leaves, all with equal proportions, the appearance is consistent. The small size of *P. bintanense* is notable since the other species of the Bintan flora are quite small as well, for example, as compared to similar species from the Tonkin flora (Zeiller, 1903). From the Rhaeto-Liassic Hsuchiaho Series (northern Sichuan), one leaf called *Otozamites* sp. was figured with a shape like that of *P. bintanense* (Lee, 1964, pl. 11, fig. 5, 5a). However, the Hsuchiaho leaf is even smaller than the Bintan specimens of *P. bintanense* and there is no written description of the leaf. Thus, it is impossible at this time to make a more informed comparison of these somewhat similar specimens.

Pterophyllum bavieri **Zeiller, 1903, emend. Schweitzer et Kirchner, 2003**
Pl. 1, figs. 7, 8.

Selected synonyms –

1903 *Pterophyllum bavieri* sp.nov. Zeiller, p. 198, pl. 44, figs. 1-3.
1934 *Pterophyllum bavieri* Zeiller; Prynada, p. 93, pl. 3, fig. 3.
1951 *Pterophyllum* cf. *contiguum* Zeiller; Jongmans, p. 188, pl. 2, fig. 4, 4a.
2003 *Pterophyllum bavieri* Zeiller; Schweitzer & Kirchner, p. 62, text-figs. 21a, b, 22a-f, pl. 13, figs. 1-8.

Material – JMS 52172, 52173, 52176, 52177, 52192.

Localities – These specimens are found at three of the four collection sites; two specimens at Batu Itam, two at Batu Litjin and one at West Pulu Penjengat.

Description – There are four specimens of this pinnate leaf, all incomplete, and one smaller fragment showing only five pinnae. The specimens are 46 mm to 84 mm long, with a width of 26 to 32 mm. The shortest of those four is an apical fragment, which narrows to a width of 12 mm at the apex (Pl. 1, fig. 8). The shape of the leaf is linear to elliptic because the apex is not pointed; the apex is a bit less than half as wide as the central part of the leaf. The rachis is 1.0 to 1.5 mm wide. The pinnae just overlap one side of the rachis and are spaced 0.5 mm apart; they arise at approximately 80° (Pl. 1, fig. 7). The pinna base is slightly expanded onto the rachis. The pinnae are 13 to 17 mm long and their width is 2 mm or less, with an average length to width ratio of 7.5. The pinnae are usually linear with slightly acute tips, although the pinnae can also be slightly convex toward the apex or have rounded tips. The venation is parallel with five to eight veins visible per pinna. The pinna margin is entire.

Discussion – Jongmans (1951) described this species as *Pterophyllum* cf. *contiguum* based only on the apical fragment (Pl. 1, fig. 8). Herein, it is observed that the central part of the leaf has linear pinnae and only the apex bears leaves where the pinnae curve toward the apex. It also seems that the pinnae tend to be narrower at the base than in the centre, giving the leaf a slightly elliptical shape. These specimens are comparable to *Pterophyllum bavieri* that Zeiller (1903) described from the Tonkin Flora. However, the leaves are smaller and the pinnae not as narrow as those of the Tonkin Flora. *Pterophyllum bavieri* was emended by Barnard (1967) and then by Schweitzer & Kirchner (2003). The newest description is largely in accord with the Bintan specimens, except in two respects. First, the length to width ratio of the pinnae is still slightly smaller than in that description. Second, the apices of the pinnae of these specimens are more pointed than the description notes. However, this appears to be a fairly plastic feature of this species, since the specimens in Schweitzer & Kirchner (2003, text-fig. 22a, b) show pinnae with both truncate and pointed apices on the same leaf.

***Pterophyllum* sp. A**
Pl. 1, fig. 9.

Material – JMS 52205.

Locality – The specimen was collected at West Pulu Penjengat.

Description – One incomplete fragment of the central part of the leaf was observed. This specimen is 67.5 mm long and 28.0 mm wide. The leaf has a narrow rachis of 1 mm with no visible features. The pinnae are attached to the rachis at 60° and overlap slightly on the rachis. The pinnae are closely spaced and nearly overlap. Their dimensions are 15 mm long and three times longer than wide. The pinnae are rectangular with a truncate pinna apex, parallel venation and three veins per mm. The leaf margin is entire. The leaf has a linear shape.

Discussion – The pinnae of the specimen have a smaller angle of attachment than those of the other specimens of *Pterophyllum* described herein. This specimen is distinguished from *P. inconstans* because its pinnae are 1.5 times longer, and their length to width ratio is 3.0 versus a consistent 2.5 for the other species. Further, the rachis of *Pterophyllum* sp. A is very narrow compared to those of *P. inconstans*. However, the base of the pinna is symmetrical, so the specimen is assigned to the genus *Pterophyllum*. With respect to its pinnae, this leaf is of a similar size and shape to the large forms of *Zamites jiangxiensis* described from the Upper Triassic of northeastern Sichuan (Ye *et al*., 1986, pl. 29, figs. 1, 2, pl. 30, figs. 1, 3). See also the discussion of cf. *Anomozamites* sp., above.

Pterophyllum inconstans **(Braun, 1843) Goeppert, 1844**
Pl. 1, fig. 10; Pl. 2, fig. 1.

Selected synonyms –
1843 *Pterozamites (Ctenis) inconstans* sp. nov., Braun, p. 30.
1843 *Ctenis inconstans* (Braun); Braun, p. 41, p. 100, pl. 11, figs. 6, 7.
1844 *Pterophyllum inconstans* (Braun); Goeppert, p. 54.
1903 *Pterophyllum (Anomozamites) inconstans* (Braun); Zeiller, p. 177, pl. 43, fig. 8, pl. 44, figs. 1-5.
1951 *Pterophyllum* sp.; Jongmans, p. 9, pl. 2, fig. 5, 5a.

Material – JMS 52168-52171, 52174, 52175.

Localities – One fragment with curved pinnae came from Batu Itam, one from South Pulu Penjengat and one from Batu Litjin. The specimens with rectangular pinnae were all found at Batu Litjin.

Description – The collection contains six fragments, all incomplete. Of these, four are of varying lengths and are approximately 20 mm wide with the width measured mid-length. The other two fragments are leaf apices, which narrow to 7-8 mm wide at the apex. The leaf tapers toward the apex, but ends rather bluntly even so (Pl. 1, fig. 10). For all fragments where the rachis is visible, it is 1.8 mm wide and seems to have small, raised features, but these may be artifacts of preservation. The pinnae are attached to the rachis at right angles and are spaced up to 1 mm apart. The pinnae are visibly separated except toward the apex, where they are closely spaced (Pl. 2, fig. 1). Each non-apical pinna is 8 to 10 mm long and 3 to 4 mm wide, with a length to width ratio of about 2.5. The base and apex of the pinna are bluntly truncate. The pinna is shaped like a rectangle or can be slightly curved toward the apex, as in three of the six specimens; this tendency occurs especially near the apex. The veins are parallel and rather dense, with five veins per mm. Some veins may dichotomize near the base. The pinnae margins are entire. In general, the fragments are alike, with the exception of the variability from rectangular to slightly curved pinnae.

Discussion – This species from Bintan was earlier described by Jongmans (1951) as *Pterophyllum* sp., based on one incomplete specimen. The new description is based on six incomplete specimens. Three of the six fragments, including the specimen previously described by Jongmans, have pinnae that curve slightly toward the apex. In the size of the fronds and rachis, this leaf is like the smaller specimens of *Pterophyllum inconstans* from the Tonkin Flora (Zeiller, 1903). That author gave the genus as *Pterophyllum* (*Anomozamites*); however, in these specimens the length to width ratio is just over 2, designating it as *Pterophyllum* according to the clarification made by Harris (1969). Schweitzer & Kirchner (2003, p. 68, text-fig. 23b, pl. 14, fig. 4) described an apical fragment from the Rhaetic of Alborz (Iran) as *P. nathorstii* Schenk, 1883 emend. Barnard, which is quite similar to the apical fragment attributed here to *P. inconstans* (Pl. 1, fig. 10). Their other examples of *P. nathorstii* are dissimilar from the apex they figure. Further, Schenk's (1883, p. 261, pl. 53, figs. 5, 7) original diagnosis and description of *P. nathorstii* does not mention the leaf apex. Thus, the apex illustrated by Schweitzer & Kirchner (2003) may pertain to *P. inconstans* rather than *P. nathorstii*.

***Pterophyllum* sp. B**
Pl. 2, fig. 2.

Material – JMS 52179, 52198.

Locality – One specimen was collected at West Pulu Penjengat. The other fragment came from South Pulu Penjengat.

Description – Two incomplete fragments of this leaf were observed. The fragments are 18 mm long by 14 mm wide and 12 mm long by 15 mm wide. The rachis is 1 mm wide with no visible features. The pinnae are attached laterally to the rachis at 80°. The pinnae are closely spaced with interspaces 0.2 mm wide. The pinnae are 7 mm long with a length to width ratio of 2.6. The pinnae are rectangular with a rounded truncate pinna apex and parallel venation. Individual veins are difficult to count because they are so fine, but an estimate is twenty veins per mm. The leaf margin is entire. The leaf seems to narrow toward the apex.

Discussion – The pinnae of the specimens are more elongated than those of *Pterophyllum bintanense* and the angle of attachment is also consistently smaller, although only by 10°. Since one fragment was collected at a site where no *P. bintanense* were found, these specimens are grouped apart from that species.

Genus *Ptilophyllum* Morris
***Ptilophyllum* sp. A**
Pl. 2, figs. 3, 4.

Material – JMS 52200, 52202, 52203.

Localities – Two specimens were collected at Batu Itam and one at South Pulu Penjengat.

Description – This is a simple pinnate leaf. Examples of the base and apex are present. The fragments are 61.0 mm long by 22.5 mm wide and 37.0 mm long by 11.0 mm wide (half of leaf present). The apical fragment is 12.0 mm long and 12.0 mm wide at the bottom, and it narrows to a point (Pl. 2, fig. 3). The leaf is narrower at the base than in the centre and narrows to a point at the apex, giving an overall lanceolate shape. The rachis is 1 to 2 mm wide and widest near the leaf base. The pinnae are attached at 50° with interspaces of 1 to 2 mm along the whole length. The pinnae found near the centre of the leaf are 13 mm long and 3 mm wide, and have an elongated, convex shape with a rounded pinnae apex and an asymmetric pinnae base (Pl. 2, fig. 4). There appear to be six parallel veins per pinna. The pinnae have entire margins.

Discussion – Jongmans (1951) tentatively labelled one of these specimens *Pterophyllum* sp. The pinnae, with asymmetric bases and an angle of attachment well under 90°, coincide better with *Ptilophyllum* than *Pterophyllum*, when juxtaposed with the comparison of the two genera made by Harris (1969). *Ptilophyllum* sp. A differs from *Ptilophyllum* cf. *vasekgahense* with respect to several characters of the pinnae. First, the pinnae interspaces are wider (1.0-2.0 mm versus less than 0.8 mm). Also, the pinnae are more elongated (larger length to width ratio), their bases are contracted and their apices are bluntly rounded instead of somewhat pointed. The three specimens of *Ptilophyllum* sp. A were quite similar in appearance, although one is not well preserved. The leaf has a delicate aspect, but the pinnae may have been very thick. An oxidized mineral seems to have built up in the former volume of the leaf mesophyll. In nearly all its features, this leaf is like *Ptilophyllum* cf. *pterophylloides* Yokoyama from Ulu Endan in the Pahang-Johore border region in Thailand (Kon'no, 1966, pp. 150-154, pl. 27, figs. 6-9). However, the veins are not preserved on the Bintan specimen, so the bifurcation and interstitial striations described by Kon'no (1966) cannot be confirmed in this specimen.

***Ptilophyllum* cf. *vasekgahense* Barnard et Miller, 1976**

Pl. 2, fig. 5.

Selected synonyms –

1976 *Ptilophyllum vasekgahense* sp. nov., Barnard & Miller, p. 50, text-fig. 7A-G, pl. 3, figs. 7-10, pl. 4, figs. 8, 9, pl. 11, fig. 6.

2003 *Ptilophyllum vasekgahense* Barnard & Miller; Schweitzer & Kirchner, p. 120, text-figs. 49-51, pl. 31, figs. 1-5, pl. 32, figs. 1-3.

Material – JMS 52189, 52206.

Locality – Both specimens were collected at Batu Itam.

Description – This description is based on two extremely fragmented specimens, although one has a preserved base of a slender, *Ptilophyllum*-type leaf. The fragments are 50 mm long by 16 mm wide and 10 mm long by 12 mm wide. The rachis has longitudinal striations and is 0.8 mm wide. The pinnae attach to it at 45°-60°; toward the centre of the leaf the angle of attachment is larger. Pinnae are spaced tightly next to each other, up to 0.8 mm apart. The base of the pinna is not contracted. A small pinna is 6.0 mm long by 1.5 mm wide, while the largest visible pinna is 8.0 mm long by 2.0 mm wide, giving a typical length to width ratio of 4. The pinnae apex is narrowed and rounded, and the base of a pinna is slightly extended down the rachis. The pinnae are curved in the central part of the leaf, and straighter toward the base and apex. The pinnae have parallel venation with six veins per mm. The pinna margin is entire. Each leaf is linear with a slightly narrower base.

Discussion – Both specimens examined herein are very similar in appearance. Schweitzer & Kirchner described several leaves as *P. vasekgahense*, but, in particular, they figured one of the smaller leaves, collected at Karkar, Afghanistan (lower Middle Jurassic) (Schweitzer & Kirchner, 2003, pl. 31, fig. 3), which is similar to the leaf fragments described herein. However, those specimens are significantly younger than the presumed Late Triassic Bintan flora. Further, the diagnosis of *P. vasekgahense* includes characteristics of the cuticle, which is not preserved.

Genus *Williamsonia* Carruthers emend. Harris
***Williamsonia* sp.**
Pl. 2, fig. 6.

Material – JMS 52170.

Locality – Collected at Batu Litjin.

Description – This description is based on one incomplete specimen of the female bennettitalean flower. The preservation is a medial compression with the proximal side of the receptacle of the inflorescence visible. The diameter of the receptacle is 24.0 mm and the peduncle scar has a diameter of 3.1 mm. No other surface features of the receptacle are preserved. Five scale leaves are visible and at least four more must have been attached to the receptacle of the inflorescence. The scale leaves are attached very close together and overlap. A scale leaf is 15 mm wide and at least 28 mm long. The venation of the scale leaves seems to have a frequency of two veins per mm.

Discussion – This specimen is an incomplete, but readily recognizable, example of *Williamsonia*. The occurrence of this reproductive organ upholds the idea that most leaves from Bintan correspond to the Bennettitales despite the absence of cuticle from all specimens. The unusual aspect of this organ is its large size; its overall size is comparable to that of *Williamsonia gigas* (Lindley et Hutton) Carruthers, but the leaf remains observed in the Bintan flora are significantly smaller than the *Zamites* leaves with which *W. gigas* is associated (summarized in Harris, 1969). Based on its size and scale leaves, it cannot be compared readily with any of the species of Bennettitales collected at Batu Litjin or at any other location.

Genus *Bennetticarpus* Harris
cf. *Bennetticarpus* sp.
Pl. 2, fig. 7.

Material – JMS 52175.

Locality – Collected at Batu Litjin.

Description – One specimen was found preserved as a lateral compression. It appears to have an incomplete gynoecium and a peduncle, but no bracts are preserved. The peduncle structure is 10 mm wide. The gynoecium is cup shaped, 18 mm wide and 25 mm long, but the apex is not preserved. The inner part of the gynoecium is coalified. Some of the interseminal scales are visible; they are quadrangular and around 0.8 mm by 0.8 mm.

Discussion – It is difficult to interpret whether some of the structures of this specimen are organic remains or fusite crystals. The lack of bracts means that it cannot be assigned to *Williamsonia*. However, the placement of the gynoecium on top of the peduncle is sufficient to associate it with *Bennetticarpus*.

Genus *Zamites* Brongniart
cf. *Zamites* sp.
Pl. 2, fig. 8.

Materials – JMS 52171, 52179, 52187, 52188.

Localities – Two of the specimens described here were found at Batu Litjin and the third at West Pulu Penjengat.

Description – The material consists of three very incomplete specimens. The fragments are 55.0 mm long by 11.0 mm wide, 28.0 mm long by 9.5 mm wide and 16.0 mm long by 6.5 mm wide. A petiole-like structure is preserved on the smallest fragment. This structure is 0.9 mm wide and visibly extends to 2 mm from the bottom of the leaf. This specimen narrows at the base and widens steadily toward the central part. The specimen has 1.5 veins per mm, with interstitial veins in between. The veins are at first parallel, but spread out with the widening of the leaf. It seems that some end in the leaf margin before the apex. The overall shape is lanceolate.

Discussion – These specimens may be large pinnae from the genus *Zamites* Brongniart. The arrangement of the veins, which seem to end in the leaf margin and not only in the leaf apex (Harris, 1926), gives evidence that the specimens may not pertain to the Coniferales. A few other small fragments of apparently similar leaves occur at South Pulu Penjengat. No similar lamina is seen at Batu Itam.

Genus *Bucklandia* Sternberg
***Bucklandia* sp.**
Pl. 2, fig. 9.

Material – JMS 52186.

Locality – Collected at West Pulu Penjengat.

Description – One example of this stem morphogenus was found in the flora. The stem is 10 mm wide and the preserved specimen is 26 mm long. The leaf scars occur at a frequency of about 25 cm^{-2} of the surface area. The leaf scars are scattered across the stem without any apparent pattern. Most scars have a diameter of 0.6 mm, but they are wider presumably toward the base of the stem, the widest visible having a diameter of 1.1 mm.

Discussion – This morphogenus applies to moderately thick stems that are often believed to belong to the bennettites (Harris, 1969). This stem fits the general description of the morphogenus, but was not directly associated with any leaves.

Genus *Otozamites* Braun
cf. *Otozamites* sp.
Pl. 3, figs. 1, 2.

Material – JMS 52209.

Locality – This fossil was collected at Batu Litjin.

Description – Of this taxon there are only the part and counterpart of a single pinna, 15 mm long by 10 mm wide. It seems to have a lobe (Pl. 3, fig. 2) which could be interpreted as an auricle. Otherwise, the shape of the pinna is relatively rectangular. The veins are only visible on the counterpart of the pinna fossil, where the auricle is not preserved. The veins are parallel. There are two per mm and they spread a bit toward the edge of the pinna (Pl. 3, fig. 1). The pinna margin is entire.

Discussion – There is so little material preserved that it is difficult to interpret this specimen. It might also be the pinna of a parallel-veined pteridosperm. However, no other pteridosperms have been identified in the Bintan flora, whereas bennettitalean morphogenera are abundant. Leaves of the genus *Otozamites* have been identified in Upper Triassic floras including the central Asian floras of Pamir (Prynada, 1934) and Alborz (Schweitzer & Kirchner, 2003), and the geographically nearer Baoding (Xu *et al*., 1979) and Tonkin floras (Zeiller, 1903).

Coniferophyta
Genus *Brachyphyllum* Brongniart
***Brachyphyllum* sp.**
Pl. 3, figs. 3, 4.

Material – JMS 52176, 52191-52193.

Locality – All of the specimens were collected at Batu Litjin.

Description – The material includes one branch fragment (Pl. 3, fig. 4) on which the shoots are 1.1 mm wide or less and two specimens consisting of many loose fragments, one with attached cones. The leaves are scale-like and helically arranged. Each leaf is about 1.2 mm long by 1.2 mm wide. The leaf apex is a broad point. The free part of the leaf is not clearly distinguished, but seems to occupy around one-quarter of the overall leaf length. The two cones are 12 mm long and 5 mm wide. There are seven visible sporophylls per cone and these are widely rhomboidal (Pl. 3, fig. 3). It appears that each cone is borne on the end of a shoot.

Discussion – Most of the material is fragmentary, but with the inclusion of the cones it is fairly certain that these specimens pertain to *Brachyphyllum*. It is not clear if the cones are male or young female cones. *Brachyphyllum* has been described from the Jurassic Phra Wihan Formation of Khorat, Thailand (Kon'no & Asama, 1973) and the Lower Jurassic of southwest Hunan, China (Zhou, 1984), both of which are presumably younger than this material. Prynada (1934) reported *Brachyphyllum* sp. from the Upper

Triassic Pamir flora (Tajikistan), but the figured material has a different aspect than the specimens described here. The only reported Upper Triassic *Brachyphyllum* from southeast Asia is from the Rhaetian of Guizhou, China (Bureau of Geology & Mineral Resources of Guizhou, 1987).

Genus *Podozamites* Braun
***Podozamites* sp.**
Pl. 3, fig. 5.

Selected synonym –
1951 *Cycadolepis* sp.; Jongmans, p. 189, pl. 3, fig. 8, 8a.

Material – JMS 52199, 52201.

Locality – These leaves were both collected at Batu Itam.

Description – This material consists of two simple, oval-shaped leaves. One is 23.0 mm by 12.5 mm and the second is 33.0 mm by 17.0 mm. No petiole is preserved, but the base of the leaf narrows slightly and then is truncate. The leaf apex is rounded. The veins are parallel with 1 per mm and interstitial veins in between. These interstitial veins seem to be very fine and could not be accurately counted due to indifferent preservation. The veins seem to converge towards the leaf apex. The leaf margin is entire.

Discussion – One of these two leaves was reported by Jongmans (1951) as *Cycadolepis* sp. However, specimens of *Cycadolepis* Saporta usually have a rather pointed apex and most have transverse wrinkles (Harris, 1969, p. 102). Given the characteristic venation and the general aspect of these leaves, the specimens are attributed here to the conifer morphogenus *Podozamites* Braun. The genus *Podozamites* is a common element in Upper Triassic floras in east and southeast Asia (Kon'no, 1972). For example, it is reported from the Tonkin flora (Zeiller, 1903), the Norian-Rhaetian strata from Fujian Province (China) (Zhou, 1978) and the Late Triassic Baoding flora (southwest Sichuan, China) (Xu *et al*., 1979). It was also noted by Prynada (1934) in the southwest Asian Pamir flora.

Fruits & seeds
Semina incertae sedis
Genus *Cardiocarpus* Brongniart
***Cardiocarpus* sp.**
Pl. 3, fig. 6.

Selected synonym –
1951 ?*Cycadolepis*; Jongmans, p. 189, pl. 3, fig. 7, 7a.

Material – JMS 52214.

Locality – Collected at Batu Itam.

Description – This specimen is 17 mm long and 11 mm wide. Its distal end is narrowed and the proximal end has two short lobes. The structure is ridged or grooved, with one ridge per mm.

Discussion – Jongmans (1951) expressed uncertainty as to whether this specimen was a scale or a seed. It appears to be a seed of the morphogenus *Cardiocarpus*, although the possibility remains that it is a small pinna of *Zamites* or a *Cycadolepis* scale.

Seed A
Pl. 3, fig. 7.

Selected synonym –
1951 ?*Cycadolepis*; Jongmans, p. 189, pl. 2, fig. 6, 6a.

Material – JMS 52181.

Locality – Collected at Batu Itam.

Description – This specimen is nearly round and very finely grooved or ridged. It is 8 mm long and 6 mm wide. The proximal end has two weak lobes. The distal end is not visible. All the grooves seem to terminate at the distal edge. It is somewhat similar in size and shape to bennettitalean seeds described from the Upper Triassic of East Greenland (Pedersen *et al*., 1989).

Discussion – Jongmans (1951) suggested this small object to be a scale or perhaps a seed. Based on its general appearance and shape, it is believed to be a seed.

Seed B
Pl. 3, fig. 8.

Material – JMS 52216.

Locality – Collected at West Pulu Penjengat.

Description – This bulbous, rounded object is 22 mm long by 16 mm wide. The compression itself is at least 2 mm thick. There are no visible surface features apart from what begins to resemble a pore at one end. If that is the proximal end, then the distal end is very smooth.

Discussion – The specimen is quite large for a seed of this age. No similar seeds were noted in the literature of the Triassic.

Seed C
Pl. 3, fig. 9.

Material – JMS 52215.

Locality – Collected at South Pulu Penjengat.

Description – This unusual, oval specimen has separated from the matrix. The specimen is 47 mm long by 36 mm wide and 7 mm thick at its thickest part. It narrows at one end and the other end is not preserved. On one side, near the narrow end, there is an elongated hump parallel to the long axis of the object. A scale pattern is observed in one area of its surface.

Discussion – The specimen is extremely large for a seed of this age. No similar seeds were noted in the literature of the Triassic.

Problematica
Problematicum
Pl. 3, fig. 10.

Material – JMS 52204.

Locality – Collected at Batu Itam.

Description – This incomplete specimen is 53 mm long. It is 19 mm wide at one end and 25 mm wide at the other end. It is not straight, but rather curves between the narrower and wider ends. It seems to have been somewhat thick. The specimen has reticulate-like markings, but it is not clear if these are veins, some other structure or the result of preservation.

Discussion – There is only one specimen with this appearance. It does not give the impression of a leaf. It may be a stem of some kind.

Discussion

Having examined the complete plant macrofossil collection from the Bintan Formation, it is clear that the original description by Jongmans (1951) of just four taxa of cycadophyte leaves and scales captured the general character of the flora. Indeed, the current study found that 90 % of the specimens of leaves and organs could be attributed to the cycadophytes (Table 1). However, with 21 taxa determined and three earlier determinations revised, this re-examination provides a much more complete picture of the fossil plants of Bintan Island (Table 2). We show that the fossil collection includes the bennettitalean reproductive organ *Williamsonia* sp. (Pl. 2, fig. 6) and the stem organ *Bucklandia* sp. (Pl. 2, fig. 9). Although the lack of cuticle preservation precludes anatomical evidence, the presence of these reproductive and stem organs points to a bennet-

Table 1. The percent of fossil specimens in the expanded Bintan flora from each taxonomic group. Fertile and stem organs were included, but seeds and problematica were excluded. The attribution of leaf genera to the Bennettitales was not based on anatomical evidence.

Taxonomical Group	Percent of specimens
Bennettitales	86 %
Coniferophytes	10 %
Cycadales	4 %
Equisetales	0 %
Ferns	0 %

titalean identity for most of the cycadophyte leaf genera. No reproductive organs of the Cycadales were encountered. The flora also contains sparse conifers, one cycad and several seeds of unknown affinities. In total, 56 specimens were examined, and no ferns, seed ferns, lycophytes, sphenophytes or ginkgophytes were identified in the flora.

Localities – In addition to having identified many more taxa, another notable difference between this study and the previous one was the number of localities considered. The specimens examined here were collected at four different carbonaceous shale beds of the Bintan Formation, which consists of layers of sandstone and shale, whereas the earlier study considered only one locality, Batu Itam (Jongmans, 1951) (Fig. 1). More specimens were collected at Batu Itam than at any other locality, but only eight of the 14 leaf genera determined here were found at Batu Itam (Table 2). Also, the fertile and stem organs figured here were collected at Batu Litjin (cf. *Bennetticarpus* sp. and *Williamsonia* sp.) and West Pulu Penjengat (*Bucklandia* sp.), which explains why they did not appear in the original description by Jongmans (1951). While some differences exist among the localities, they are still quite similar. For each locality, at least 50 % of the taxa found there also occur at one or more of the other localities. Further, leaves that likely pertain to the Bennettitales make up 75 % or more of the leaf fossils at each of the four locations (Table 2). Thus, all four localities appear to be of approximately the same age and to represent a single flora, the Bintan flora.

Table 2. The frequency of fossil specimen occurrences at each of the four localities. The taxon sum is the total number of specimens of each taxon in the fossil collection. Taxa with an asterisk were described by Jongmans (1951). Total specimens described = 56.

Group	**Taxa**	**Batu Itam**	**Batu Litjin**	**West Pulu Penjengat**	**South Pulu Penjengat**	**Taxon sum**
Bennettitales	*Anomozamites minor*	1				1
	cf. *Anomozamites* sp.			1		1
	*Pterophyllum bavieri**	2	2	1		5
	*Pterophyllum bintanense**	13		2		15
	*Pterophyllum inconstans**	1	4		1	6
	Pterophyllum sp. A			1		1
	Pterophyllum sp. B			1	1	2
	Ptilophyllum cf. *vasekgahense*	2				2
	Ptilophyllum sp. A*	2			1	3
	cf. *Otozamites* sp.		1			1
	cf. *Zamites* sp.		3	1		4
	Bucklandia sp.			1		1
	cf. *Bennetticarpus* sp.		1			1
	Williamsonia sp.		1			1
Cycadales	*Nilssonia* sp.	1			1	2
Coniferophytes	*Brachyphyllum* sp.		3			3
	Podozamites sp.*	2				2
Seeds	*Cardiocarpus* sp.*	1				1
	Seed A*	1				1
	Seed B			1		1
	Seed C				1	1
Problematica	Problematicum	1				1

Comparison with other floras – Jongmans (1951, p. 189) concluded very generally that "the small flora of Bintan is well comparable with other floras of approximately the same age from East Asia (Tonkin, China, Japan)." However, the composition of the fossil collection is truly unusual seen in the context of Upper Triassic floras of southeast Asia and beyond. The Chinese (Shuying, 1987) and Vietnamese (Zeiller, 1903) Upper Triassic floras are commonly dominated by cycadophytes, including especially the bennettites, but ferns of the Dipteridaceae are simultaneously ubiquitous in these floras. The Upper Triassic floras from Thailand and east Malaysia are reported to be dominated by sphenophytes and ferns, and bennettitalean leaves occur less frequently (Kon'no, 1972; Kon'no & Asama, 1973). Thus, the complete dearth of ferns and sphenophytes in the Bintan flora makes it exceptional.

The conifer component of the Bintan flora also distinguishes it from other southeast Asian Upper Triassic floras. One of the two leaves attributed to the coniferophytes is *Podozamites* sp. (Pl. 3, fig. 5); this genus is common in Upper Triassic floras from China and Vietnam (Table 3). The other conifer in the flora is *Brachyphyllum* sp., including two small cones (Pl. 3, fig. 3). The genus *Brachyphyllum* is rare in the Upper Triassic and the significance of this fossil will be discussed further.

Vietnam – The Tonkin flora of Vietnam was referenced by Jongmans (1951, p. 187) as a flora with which "it is quite natural to make a comparison," but there are notable differences between the Tonkin and Bintan floras. Two bennettitalean taxa are shared between the floras (Table 3), including *Pterophyllum bavieri*, which was first described from the Tonkin flora (Zeiller, 1903). However, the Tonkin flora has a large number of ferns, especially of the Dipteridaceae (Zeiller, 1903), which ally it with the other Upper Triassic Asian floras; these are entirely absent from the Bintan flora (Table 4).

China – Compared to the Upper Triassic floras of the southern province of China (Shuying, 1987), the Bintan flora has few taxa and a low diversity of fossil classes (Table 4). Still, several cycadophyte taxa are shared among the Chinese and this floras (Table 3). *Anomozamites minor* is one such example, although it is broad ranging and was originally described from northern Europe (Nathorst, 1878). The Upper Triassic floras of Sichuan province share a few common cycadophyte taxa with the Bintan flora. *Pterophyllum bavieri* also occurs in the Late Triassic of Baoding (southwest Sichuan), along with *A. minor* (Xu *et al*., 1979). The Hsuchiaho Formation of northeast Sichuan does not have any of the same species as the Bintan flora, but several of its leaf taxa are similar in appearance to fossil remains determined here. Leaf remains of *Pterophyllum* sp. A and cf. *Anomozamites* sp. of this flora are like *Zamites jiangxiensis* of the Hsuchiaho flora (Ye *et al*., 1986, pl. 28, fig. 9, pl. 29, figs. 1, 2, 4, 4a, pl. 30, figs. 1, 3). An earlier study of that formation figured a leaf shaped like *P. bintanense*, although the Hsuchiaho leaf is even more diminutive (Lee, 1964, pl. 11, fig. 5, 5a). Norian-Rhaetian deposits in Fujian province also share two leaf taxa with Bintan, namely *Anomozamites inconstans* (*Pterophyllum inconstans*) (Zhou, 1978, pl. 17, fig. 4) and again *P. bavieri* (Zhou, 1978, pl. 22, fig. 2). Still, the bennettitaleans of the Chinese floras are generally larger than those from Bintan. This suggests that the growth conditions of the plants found in the Chinese floras were more favourable than those of the plant remains collected from the Bintan Formation.

Other southeast Asian localities – Due to the relative geographical proximity of east Malaysia (Borneo), Malaysia and Thailand to Bintan Island, one might assume that the Upper Triassic floras from these locations would be more readily comparable to the

Table 3. Co-occurring bennettitalean and coniferophyte taxa between the Bintan and approximately coeval southeast Asian floras. The co-occurrences are indicated by the published age of the occurrence. Co-occurrence ages in parenthesis indicate the co-occurrence of a similar, but not identical, taxon, as assessed by the authors. The following abbreviations are used in the table: N-R = Norian-Rhaetian; Rhaet. = Rhaetian; U. Trias. = Upper Triassic; L. Cret. = Lower Cretaceous; Asama = Kon'no & Asama (1973); Kon'no 66 = Kon'no (1966, 1968); Kon'no 72 = Kon'no (1972); Lee = Lee (1964); Xu = Xu *et al*. (1979); Ye = Ye *et al*. (1986); Zeiller = Zeiller (1903); Zhou = Zhou (1978).

RIAU ARCHIPELAGO	**CHINA**				**VIETNAM**	**OTHER SOUTHEAST ASIA**		
Bintan Taxa	**Fujian**	**Baoding**	**Hsuchiaho**	**Hsuchiaho**	**Tonkin**	**Krusin**	**Khorat**	**Gagua**
	Zhou	Xu	Lee	Ye	Zeiller	Kon'no 72	Asama	Kon'no 66
Bennettites								
Anomozamites minor		U. Trias.					Norian	
cf. *Anomozamites* sp.				(U. Trias.)				
Pterophyllum bavieri	N-R	U. Trias.			Rhaet.			
Pterophyllum/								
Anomozamites inconstans	N-R				Rhaet.		(Norian)	
Pterophyllum bintanense			(U. Trias.)					
Pterophyllum sp. A				(U. Trias.)				
Pterophyllum sp. B								
Ptilophyllum cf. *vasekgahense*								
Ptilophyllum sp. A								L. Cret.
cf. *Otozamites* sp.								
cf. *Zamites* sp.								
Coniferophyte genera								
Podozamites	N-R	U. Trias.	U. Trias.	U. Trias.	Rhaet.			
Brachyphyllum							Jurassic	

Bintan flora. These floras were published after the original description of the Bintan flora and thus were not available to Jongmans for the initial comparison. Despite the geographical nearness, though, the floral assemblages are quite dissimilar. The fossil plants of the reportedly Upper Triassic Huai Hin Lat Formation from the poorly dated Khorat Group, Thailand, are primarily sphenophytes and ferns (Kon'no & Asama, 1973) (Table 4). The same fossil groups are dominant in the Krusin florula from Sarawak, east Malaysia (Kon'no, 1972) (Table 4).

Indeed, the Khorat and Krusin floras are exceptional in their own right among southeast Asian Upper Triassic floras because of the 38 and 29 % shares of sphenophyte taxa, respectively, and the high abundance of ferns versus few cycadophytes (Kon'no, 1972; Kon'no & Asama, 1973). In the Chinese southern province and Tonkin floras, cycadophyte taxa are the most abundant, followed by ferns. Usually less than 10 % of taxa pertain to the sphenophytes (Table 4).

There are no common taxa between the Bintan and Krusin, east Malaysia floras, while leaves determined as *Anomozamites minor* occur at both Bintan and Khorat, Thailand (Table 3). The Khorat *A. minor* appears to be similar to some of the examples of *Pterophyllum* (*Anomozamites*) *inconstans* figured by Zeiller (1903, pl. 43, figs. 7, 8, pl. 44, fig. 3), although, like the Bintan examples of this species, it falls at the lowest end of the size range of the Tonkin leaves, around 100 mm long and 15 mm wide (Zeiller, 1903, p. 178). Still, it may not be sensible to look for similarities among these floras. New evidence from fossil wood provides evidence that the Khorat Group formations overlaying the Huai Hin Lat Formation are Middle Jurassic to Early Cretaceous (Philippe *et al*., 2004), which lends doubt to the Late Triassic age suggested for the Khorat flora.

Because of the major differences between the Bintan flora versus the Khorat and Krusin floras, Kon'no (1972) and Kon'no & Asama (1973) wrote that the Bintan flora was much the younger. These authors suggested that the Bintan flora was allied with the

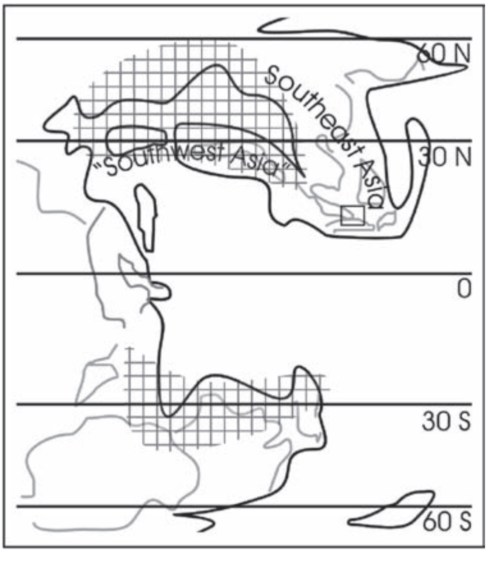

Fig. 2. Palaeogeographical reconstruction for 210 Ma. Reconstructed coastlines indicated by black lines; light grey coastlines delineate modern landmasses for reference. The area labeled southeast Asia includes most of modern southeast Asia. Southwest Asia includes parts of Iran, Afghanistan and Tajikistan. The small box indicates the presumed location of Bintan Island at that time. Palaeogeography after Scotese (2006).

Table 4. The percentage of leaf taxa pertaining to the stated taxonomic group in the Bintan and other southeast Asian floras. Total leaf taxa indicates the number included in the percent calculation. Data sources: Zhou (1978), Norian-Rhaetian taxa in the figures list; Xu *et al*. (1979), in-house compilation list at the LPP; Lee (1964), summary; Ye *et al*. (1986, table 2); Zeiller (1903, table, p. 251); Kon'no (1972, table 1.8); Kon'no & Asama (1973, list 1, p. 150); Kon'no (1966, table 1); Kon'no (1968, p. 139). Lycophytes form 0 % of leaf taxa at all these localities.

	RIAU ARCHIPELAGO	**CHINA**	**CHINA**	**CHINA**	**CHINA**	**VIETNAM**	**OTHER SE ASIA**	**OTHER SE ASIA**	**OTHER SE ASIA**
	Bintan	Fujian	Baoding	Hsuchiaho	Hsuchiaho	Tonkin	Krusin	Khorat	Gagua
	Present study	Zhou (1978)	Xu *et al*. (1979)	Lee (1964)	Ye *et al*. (1986)	Zeiller (1903)	Kon'no (1972)	Kon'no & Asama (1973)	Kon'no (1966, 1968)
Leaf taxa	"Upper Triassic"	Norian-Rhaetian	Upper Triassic	Upper Triassic	Upper Triassic	Rhaetian	Carnian-Norian	"Norian"	"Lower" Cretaceous
Bennettitales	79 %	21 %	30 %	17 %	17 %	23 %	12 %	13 %	14 %
bryophytes	0 %	0 %	0 %	2 %	0 %	0 %	0 %	0 %	0 %
coniferophytes	14 %	4 %	3 %	13 %	16 %	4 %	0 %	13 %	50 %
Cycadales	7 %	21 %	23 %	17 %	14 %	19 %	0 %	13 %	0 %
ferns	0 %	34 %	32 %	28 %	26 %	36 %	53 %	25 %	29 %
ginkgophytes	0 %	9 %	0 %	15 %	6 %	2 %	0 %	0 %	0 %
Pteridospermae	0 %	6 %	8 %	0 %	5 %	4 %	0 %	0 %	0 %
sphenophytes	0 %	4 %	4 %	7 %	13 %	6 %	29 %	38 %	7 %
unknown	0 %	0 %	0 %	0 %	5 %	4 %	6 %	0 %	0 %
Total leaf taxa	**14**	**47**	**115**	**46**	**88**	**47**	**17**	**8**	**14**

Gagau florula of west Malaysia, which was attributed to the Lower Cretaceous (Kon'no, 1966, 1968). However, Kon'no's (1972) likening of *Pterophyllum* cf. *contiguum* (here redetermined as *P. inconstans*) to *Otozamites gagauensis* from the Gagau florula is not supported in light of the additional specimens of *P. inconstans* from Bintan examined herein. While the fossils of Bintan are not really stratigraphically diagnostic, they can be reconciled with a Rhaeto-Liassic age, which is consistent with some publications on the geology of the Malayan peninsula (e.g., Hutchison, 1993). Despite the lack of typical Upper Triassic Dipteridaceae, and the Sphenophyte genera *Neocalamites* and *Equisetum*, the Bintan flora does not contain indicators of a much younger age. The one exception could be *Ptilophyllum* sp. A, reported herein (Pl. 2, fig. 4), which is quite similar to the Gagau florula leaves called *Ptilophyllum* cf. *pterophylloides* by Kon'no (1966, pl. 27, figs. 6-9). However, more types of evidence for the age of the localities of the Gagau florula are desirable before using its fossil remains as a reliable indicator of the Early Cretaceous.

Afghanistan, Iran and Tajikistan – The configuration of the continents during the Late Triassic (Scotese, 2006) provides the impetus to compare the Bintan flora with fossil floras outside modern southeast Asia (Fig. 2). During the Permian, parts of the continental masses that today underlie Iran, Afghanistan and Tajikistan were joined to what is now the Malayan peninsula, likely including what is today Bintan Island (Hutchison, 1993). As these pieces of the modern southwestern Asian countries drifted northwards during the Triassic, they continued to form a band of islands and/or peninsulas stretching from modern Iran, at around 30° N, to the southern tip of the Malayan peninsula (Scotese, 2006) (Fig. 2). For that reason, the Bintan flora was compared with the Upper Triassic floras of Pamir (Tajikistan), Alborz (Iran), Kerman (Iran) and the Saighan Series (Afghanistan).

As in the Bintan flora, in the southwestern Asian floras there are more species of bennettitaleans than of any other group and a few of these taxa are comparable to the Bintan plants (Schweitzer & Kirchner, 2003; Prynada, 1934). *Pterophyllum bavieri* (Pl. 1, fig. 7) occurs in the Bintan flora, in the Upper Triassic floras of the Pamirs (Prynada, 1934), and in Alborz and Kerman in Iran (Schweitzer & Kirchner, 2003) (Table 5). *Anomozamites minor* (Pl. 1, fig. 3) can be compared to *A.* cf. *minor* in the Rhaetian at Alborz (Schweitzer & Kirchner, 2003, pl. 8, figs. 6-8). *Ptilophyllum* cf. *vasekgahense* (Pl. 2, fig. 5) is a third taxon from Bintan that is similar to *P. vasekgahense* from the younger Iranian and Afghani sedimentary rocks. *Ptilophyllum vasekgahense* occurs in the lower Middle Jurassic of Alborz, Kerman and the Saighan-Series, and possibly the Lower Jurassic of Alborz (Schweitzer & Kirchner, 2003).

The other fossil plant groups that occur in the Upper Triassic southwest Asian floras include elements that are familiar in the previously discussed southeast Asian floras. Indeed, the Iranian floras, which have been examined exhaustively, are in many respects similar to the well studied Tonkin flora from Vietnam. There are examples of *Equisetites* and *Neocalamites* from most of the southwest Asian localities, as well as ferns of the Dipteridaceae and Osmundales (Prynada, 1934; Schweitzer *et al*., 1997). Although those taxa do not appear in the Bintan flora, the coniferophytes and cycads of the southwest Asian floras do have similarities to the plants of Bintan. Many of the cycads from the Upper Triassic of southwest Asia pertain to the genus *Nilssonia* (Prynada, 1934; Schweitzer *et al*., 2000). Among the cycadophyte leaf genera from Bintan, the one that does not appear to belong to the Bennettitales has characteristics of the Nilssoniales (*Nilssonia* sp.; Pl. 1, fig. 1).

With respect to the coniferophytes, leaves of the morphogenus *Podozamites* are found commonly in the Upper Triassic or slightly younger southwest Asian collections (Prynada, 1934; Schweitzer & Kirchner, 1996) (Table 5) as with the floras from China and Vietnam (Table 3). Also, shoots from the morphogenus *Brachyphyllum* occur among the Upper Triassic plants of Pamir (Tajikistan) and Kerman (Iran) (Prynada, 1934; Schweitzer & Kirchner, 1996), as they do in the Bintan flora (Table 5). However, *Brachyphyllum* is not reported anywhere else in the Upper Triassic of southeast Asia except for once in the Rhaetian of Guizhou, China (Bureau of Geology & Mineral Resources of Guizhou, 1987). The shared presence of *Brachyphyllum* and the similarity among the cycadophytes seems to suggest that the Bintan flora has stronger affinities with the Upper Triassic plants of southwest Asia than with those of southeast Asia.

A second explanation for the differences between the Bintan flora and the Upper Triassic floras of southeast Asia could be the age. Some plants from Bintan seem more related to Lower Jurassic than Triassic species. For example, *Brachyphyllum* is found in the Jurassic sedimentary rocks from Khorat, Thailand (Kon'no & Asama, 1973). Also, *Ptilophyllum* cf. *vasekgahense* is similar to a Lower to lower Middle Jurassic species from southwest Asia (Schweitzer & Kirchner, 2003). Perhaps the Bintan flora is younger than currently believed, but this is contradicted by the existing geological data (Hutchison, 1993; Jongmans, 1951).

Taphonomy – Before asserting any conclusions about the age or other affinities of the fossil plants from Bintan Island, it is necessary to consider the taphonomy of the flora. The total absence of ferns and sphenophytes from the Bintan flora could be a case of

Table 5. Co-occurring bennettitalean and coniferophyte taxa between the Bintan flora and southwest Asian floras of approximately the same age. The co-occurrences are indicated by the published age of the occurrence. Co-occurrence ages in parenthesis indicate the co-occurrence of a similar, but not identical, taxon, as assessed by the authors. . The following abbreviations are used in the table: Nor. = Norian; Rhaet. = Rhaetian; LM Jurassic = Lower Middle Jurassic.

Riau Archipelago	**Tajikistan**	**Iran**	**Iran**	**Afghanistan**
Bintan Taxa	**Pamir**	**Alborz**	**Kerman**	**Saighan-Series**
	Prynada, 1934	Schweitzer & Kirchner, 1996, 2003		
Bennettites				
Anomozamites minor		Rhaet.		
cf. *Anomozamites* sp.				
Pterophyllum bavieri	Upper Triassic	Nor-Rhaet.	Rhaet.	
Pterophyllum/Anomozamites inconstans	(Rhaet.)			
Pterophyllum bintanense				
Pterophyllum sp. A				
Pterophyllum sp. B				
Ptilophyllum cf. *vasekgahense*		(LM Jurassic)	(LM Jurassic)	(LM Jurassic)
Ptilophyllum sp. A				
cf. *Otozamites* sp.				
cf. *Zamites* sp.				
Coniferophyte genera				
Podozamites	Upper Triassic	Upper Triassic	Rhaet.	LM Jurassic
Brachyphyllum	Upper Triassic	LM Jurassic	Rhaet.	LM Jurassic

selective fossilization and not an indication that the plants were absent from the regional floral assemblage of Bintan during the Late Triassic. Indeed, there is evidence that the components of the Bintan assemblages were transported some distance before fossilization, which could lead to taphonomic biases.

For example, at the localities West Pulu Penjengat and South Pulu Penjengat (Fig. 1), large, albeit dissimilar seeds were found (Pl. 3, figs. 9, 10). Bennettitalean seeds from the Upper Triassic of East Greenland are about 10 mm long (Pedersen *et al*., 1989), whereas the seeds found at Bintan are about 20 and 50 mm long. Since such seeds occur alongside diminutive cycadophyte leaves at these two localities, the assemblages probably show inputs of fossil plant remains from different environments and distances with respect to the site of fossilization. At all four localities the leaf fossils are very fragmented. This also provides evidence that the material was transported, perhaps in a high energy environment, rather than being deposited directly into the site of fossilization.

The components that are missing from the Bintan flora might be considered typical lowland or riparian plants; both sphenophytes and ferns require ample water and they often grow very near to a water source that also could serve as a site of fossilization. The Bintan fossil assemblage, with small-leaved bennettitaleans and *Brachyphyllum*, may represent the remains of an upland flora composed of plants more tolerant of periodic dryness. After significant transport, these leaves could still be fossilized, whereas more delicate leaves from ferns might have been destroyed (e.g., differential degradation observed for angiosperm leaves; Ferguson, 1985). The Bintan flora contrasts sharply with the southeast Asian floras of Thailand and east Malaysia, which consist primarily of sphenophytes and ferns. Rather than representing a different climate or age, those fossil assemblages may have captured the riparian, but not the upland, portions of the regional vegetation. The Chinese, Tonkin and Iranian floras, on the other hand, are diverse. These may provide a more complete picture of all the vegetation elements that populated southern Asia during the Late Triassic.

The contrasts among the Bintan, southeast Asian and other Asian floras might be comparable to the effects of taphonomy on the Upper Triassic floras of the Chinle Formation (Colorado Plateau, U.S.A.). In the case of the Chinle Formation, the fossil plants of the lower part of the formation include ferns, sphenophytes, cycadophytes and conifers, and indicate a wet environment (Demko *et al*. 1998). However, the upper part of the formation has scarce plant remains, including one species of *Pagiophyllum*, a conifer morphogenus similar to *Brachyphyllum*, which indicate drier conditions (Ash, 1987). Demko *et al.* (1998) argued that the fossils of the lower part of the formation represented riparian plants growing near a fluvial channel, but that the sedimentology indicates an overall drier climate for the Chinle Formation region during the Late Triassic.

Geologists have not interpreted the climatic conditions and sedimentary environments that contributed to the Bintan Formation (Jongmans, 1951; van Bemmelen, 1949). However, the difference between the fossils of the Bintan formation, and those of east Malaysia and Thailand can be likened to the difference between the fossils from the top and base of the Chinle Formation. The Bintan flora may give a glimpse of the assemblage of plants that populated areas away from the banks of rivers and lakes during the Late Triassic in southeast Asia. This assemblage could have been captured as fossils due to periodic flooding of the areas slightly more distant from bodies of water (Ferguson, 1985).

Conclusions

This study of the entire plant fossil collection from the Bintan Formation showed that bennettitaleans were the most common plants at the time of sedimentation. The leaf remains are more similar to the cycadophytes and conifers of the southwest Asian floras of Iran, Afghanistan and Tajikistan than they are to those of the southeast Asian and south Chinese floras. The occurrence of *Brachyphyllum* sp. is especially diagnostic for the southwest Asian affinity of the Bintan flora.

It is not likely that the Bintan flora is significantly younger than the southeast Asian floras, as previously suggested by Kon'no (1972) and Kon'no & Asama (1973). There are no strong indications that the flora is much younger than Late Triassic, which was the age suggested by Jongmans (1951) after his original description of a small part of the entire collection gathered by the Billiton Mining Company from Bintan Island. Furthermore, recent publications on the geology of Malaysia show that the Riau Archipelago is characterized by Upper Triassic sedimentary rocks (Hutchison, 1993), although these ages are not always very well supported (Philippe *et al*., 2004).

The differences between the Bintan and southeast Asian floras may hinge upon taphonomic effects on preservation. Comparisons with the Chinle Formation floras (Demko *et al*., 1998) suggest that the Bintan flora reflects a drier, non-riparian environment, while the other floras of southeast Asia primarily capture the signal of plants living near to the water's edge, to a varying degree (Table 4).

A fuller understanding of the conditions that led to the unusual fossil plant assemblage of Bintan will require multidisciplinary information. Above all, interpretation of the Bintan flora could be improved by studies of the sedimentary environment of the Bintan Formation, and of the tectonic history of Bintan Island and the Riau Archipelago.

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Plate 1

Fig. 1. *Nilssonia* sp., JMS 52207.
Fig. 2. cf. *Anomozamites* sp., JMS 52190.
Fig. 3. *Anomozamites minor*, JMS 52189.
Figs. 4-6. *Pterophyllum bintanense*,. (4) JMS 52179, arrow indicates apical pinna. (5) JMS 52185. (6) JMS 52184.
Figs. 7, 8. *Pterophyllum bavieri*. (7) JMS 52177. (8) JMS 52173, leaf apex.
Fig. 9. *Pterophyllum* sp. A, JMS 52205.
Fig. 10. *Pterophyllum inconstans*, JMS 52175, leaf apex.

All scale bars represent 10 mm.

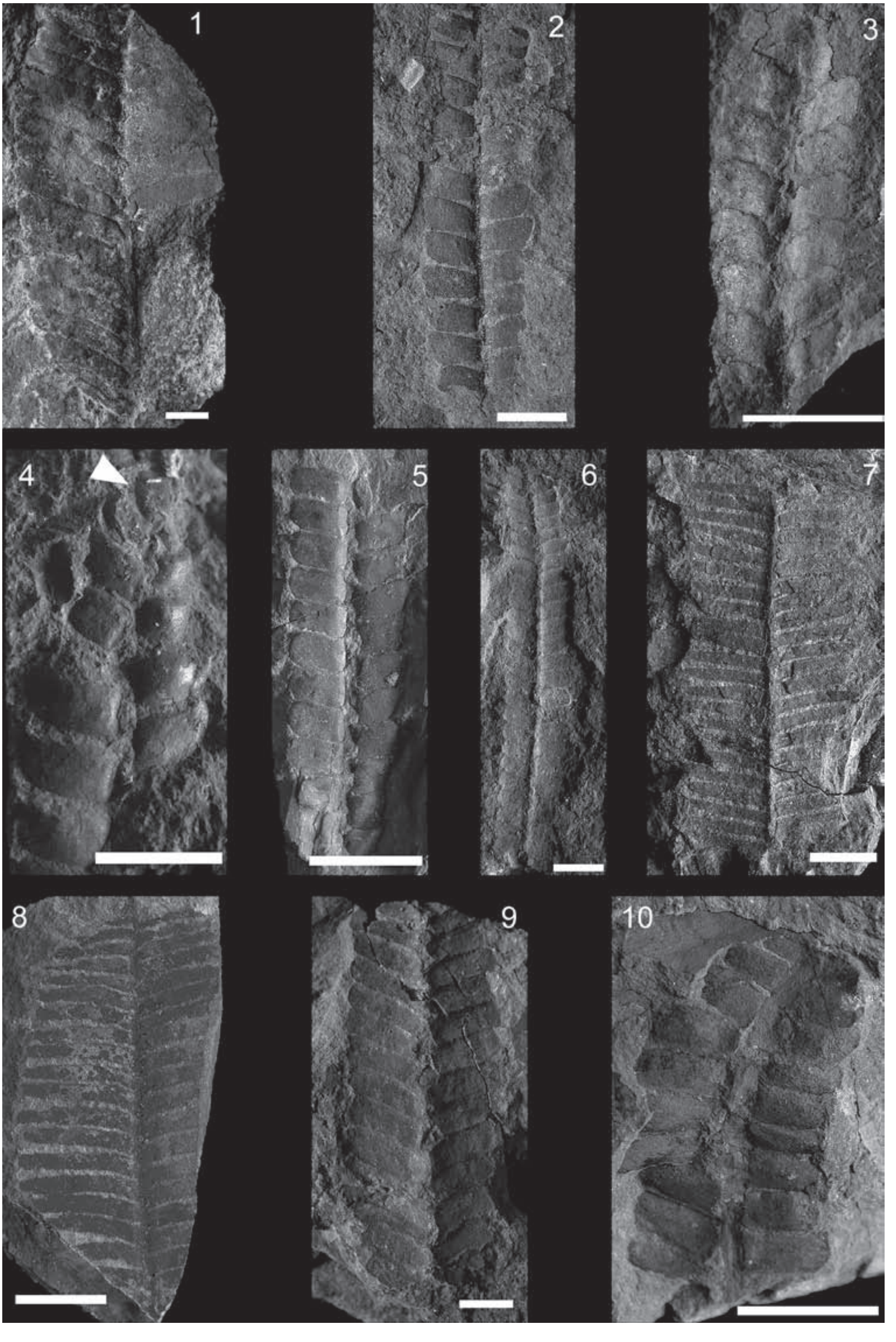
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Plate 2

Fig. 1 *Pterophyllum inconstans*, JMS 52171.
Fig. 2. *Pterophyllum* sp. B, JMS 52198.
Figs. 3, 4. *Ptilophyllum* sp. A. (1) JMS 52200, leaf apex. (2) JMS 52203.
Fig. 5. *Ptilophyllum* cf. *vasekgahense*, JMS 52206, arrow indicates leaf base.
Fig. 6. *Williamsonia* sp., JMS 52170.
Fig. 7. cf. *Bennetticarpus* sp., JMS 52175. Arrow a indicates one edge of the cup-shaped gynoecium; arrow b points to the peduncle.
Fig. 8. cf. *Zamites* sp., JMS 52188.
Fig. 9. *Bucklandia* sp., JMS 52186, arrow indicates one of several leaf scars.

All scale bars represent 10 mm.

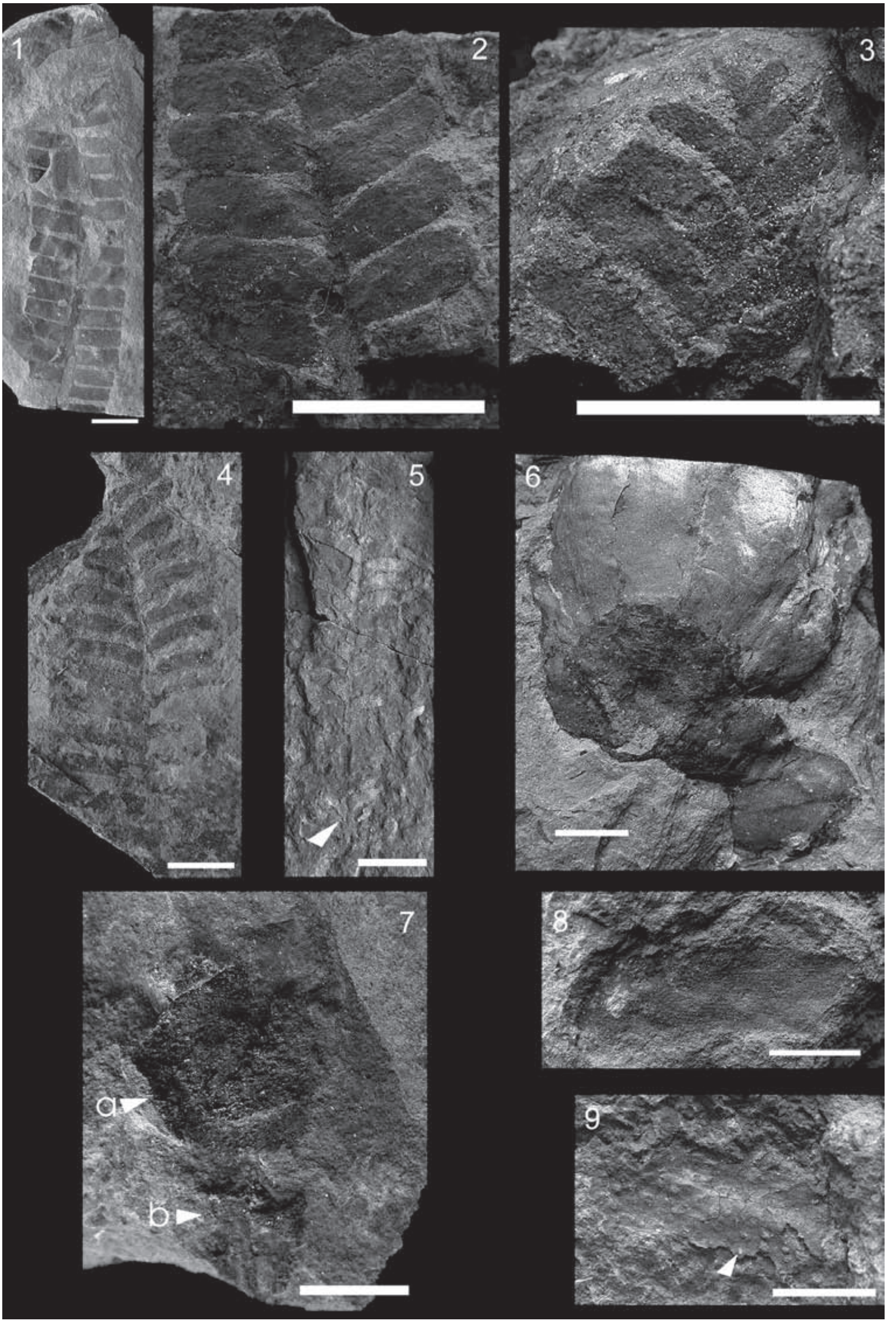
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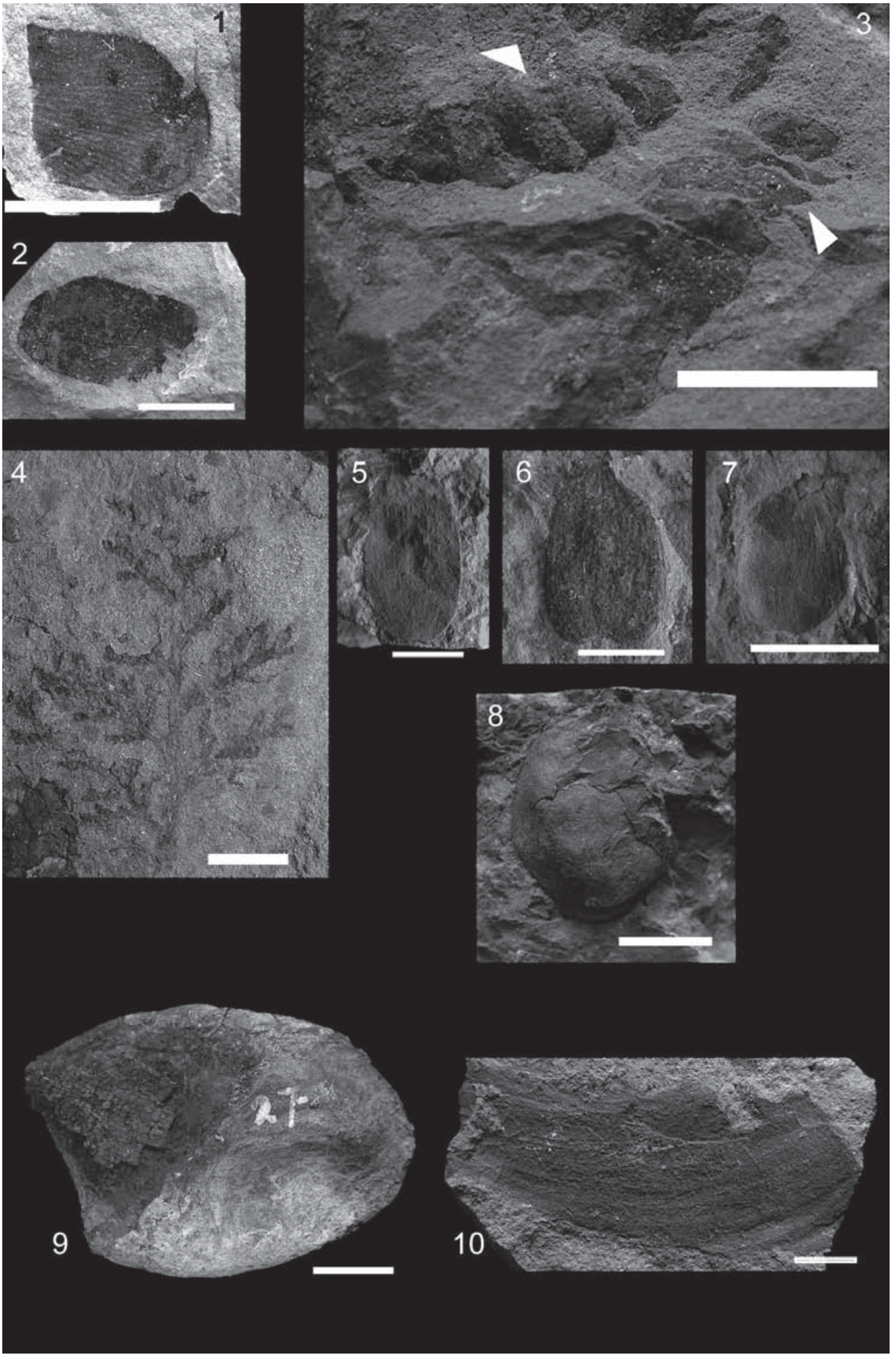
Plate 3

Figs. 1, 2. cf. *Otozamites* sp., JMS 52209. (1) Part, showing venation, but much of pinna is missing. (2) Counterpart; note auricle-like feature at upper right of image.
Fig. 3. Two *Brachyphyllum* sp. cones, JMS 52176. Each arrow indicates the centre of a lengthwise cone.
Fig. 4. *Brachyphyllum* sp., JMS 52191, branch fragment.
Fig. 5. *Podozamites* sp., JMS 52199.
Fig. 6. *Cardiocarpus* sp., JMS 52214.
Fig. 7. Seed A, JMS 52181.
Fig. 8. Seed B, JMS 52216.
Fig. 9. Seed C, JMS 52215.
Fig. 10. Problematicum, JMS 52204.

All scale bars represent 10 mm.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