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Late Palaeozoic foliage from China displays affinities to Cycadales rather than to Bennettitales necessitating a re-evaluation of the Palaeozoic *Pterophyllum* species

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The epidermal anatomy of *Pseudoctenis samchokense* is described revealing non-bennettitalean characters of these leaves from the Permo-Carboniferous of China (and Korea). The specimens were originally described as *Pterophyllum samchokense* suggesting a bennettitalean affinity. They can no longer be considered bennettitalean since their cuticles lack the distinctive brachyparacytic stomata of that clade. *Pterophyllum* was originally erected as a morphogenus for segmented leaves from the Mesozoic and has subsequently been clearly assigned to the Bennettitales. The segmented leaves from the Permo-Carboniferous of Shanxi and Hebei, China described herein require a new ordinal and generic assignment since the non-bennettitalean cuticular characters documented reinforce the uncertainties in attribution of any foliage older than Late Triassic to the Bennettitales. Based on leaf-architecture and epidermal anatomical characters, the specimens are at best assigned to the cycadalean genus *Pseudoctenis*. This genus was formerly known only from Mesozoic rocks. Consequently, the specimens are highly significant, as they are among the oldest known vegetative remains of cycads. Re-evaluation of the affinities of all specimens assigned to *Pterophyllum* from Palaeozoic rocks is thus essential. Based on a review of other Permian–Carboniferous fossil leaves assigned to *Pterophyllum*, we conclude that none yet reveals definitive bennettitalean characters.

Key words: Cycadales, Bennettitales, *Pseudoctenis*, *Pterophyllum*, cuticle analysis, epidermal anatomy, Carboniferous, Permian, China.

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Introduction

The earliest persuasive records of bennettitaleans come from the Late Triassic (Leuthardt 1903; Kräusel and Schaarschmidt 1966; Anderson and Anderson 1989, 2003; Pott et al. 2007c, d). Examples from the Molteno Formation in South Africa are considered to be early to middle Carnian (Anderson and Anderson 2003), whereas those from Lunz, Austria, and Neuewelt, Switzerland, are slightly younger (late Carnian; Cleal 1993; Taylor et al. 2009). Bennettitaleans were widespread and abundant in the Late Triassic–Middle Jurassic, remained locally common in the Late Jurassic and Early Cretaceous, and apparently became extinct in the Late Cretaceous (Mägdefrau 1968; Willis and McElwain 2002). Bennettitaleans reported from older deposits (i.e., pre-Carnian assemblages) need to be considered with caution, since most of those species lack studied or preserved cuticles. The accommodation of species such as *Pterophyllum cultelliforme* Sze, 1936, *Pt. cottaeanum* Gutbier, 1835, *Pt. blechnoides* Sandberger, 1864, *Pt. daihoense* Kawasaki, 1934, *Pt. pruvostii* Stockmans and Mathieu, 1939, *Pt. fayolii* Renault and Zeiller, 1890, *Pt. grandeuryi* Saporta and Marion, 1885 (taxa names in caption of fig. 58 on p. 109 erroneously swapped) or *Pt. eratum* Gu and Zhi, 1974 from the Pennsylvanian and Permian of China, Korea, Germany and France in the genus *Pterophyllum* and thus, in the Bennettitales, remains equivocal.

Although the oldest compelling cycad foliage fossils (i.e., *Pseudoctenis*) in the Northern Hemisphere derive from the late Carnian (Pott et al. 2007b) , the earliest evidence for this genus in the Southern Hemisphere is from the early Carnian (e.g., from the Molteno Formation, cf. Anderson and Anderson 1989). Reports of *Pseudoctenis* from other early Late Triassic floras (e.g., from the Santa Juan Formation, cf. Leppe and Moisan 2003; Nielsen 2005) are questionable because the macromorphology of the fossils closely corresponds to that of certain *Pterophyllum* species rather than to *Pseudoctenis*, and data on the epidermal anatomy are missing. The earliest unequivocal reproductive organs of the true cycads come from the Permian of China (i.e., *Primocycas chinensis* Zhu and Du, 1981; but compare *Norinia cucullata* Halle, 1927) and cycad-like foliage was reported from closely related deposits. Gao and Thomas (1989) assumed that foliage assigned to

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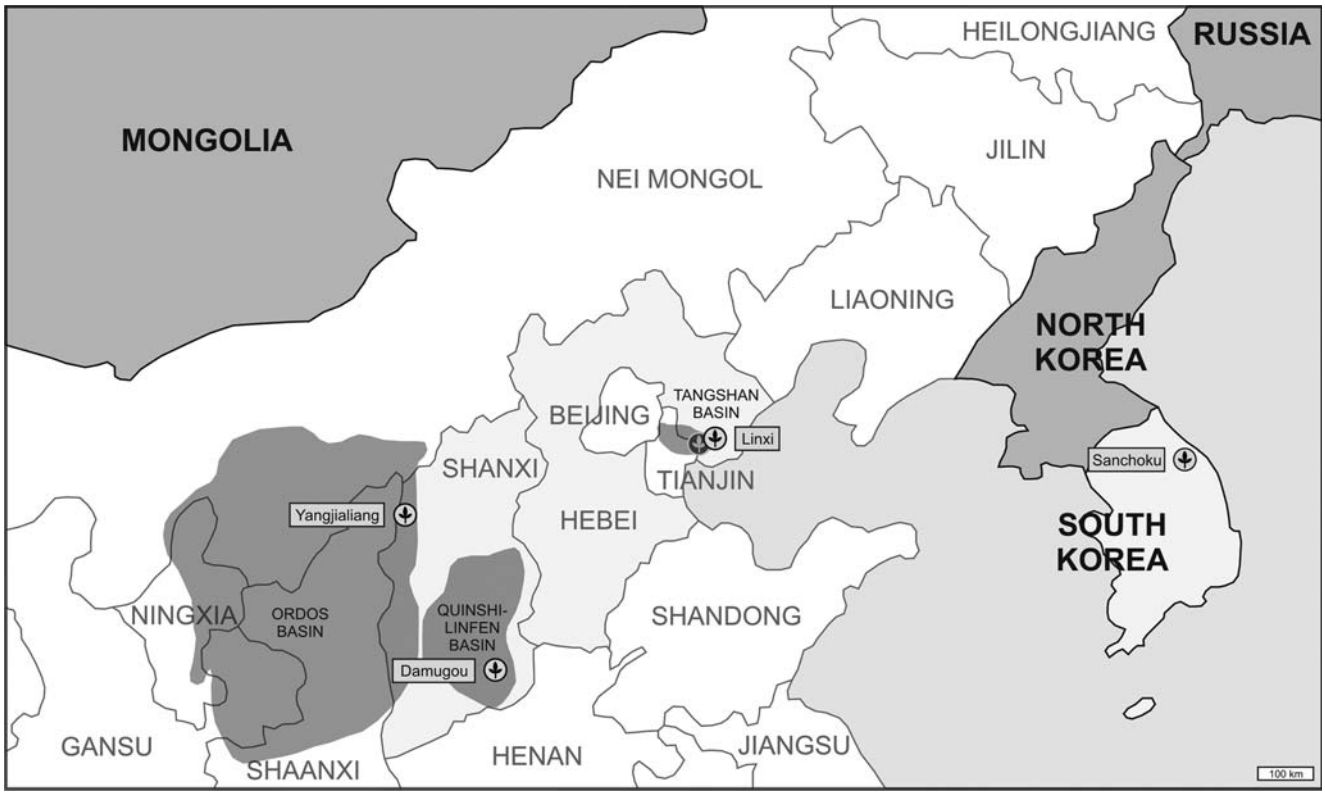


Fig. 1. Map of NE China and Korea showing the localities from which *Pseudoctenis samchokense* fossils have been collected (grey symbols) and the locality from which *Primocycas chinensis* fossils have been described (black symbol).

Yuania might be linked to *Primocycas* megasporophylls due to their occurrence in equivalent beds but since *Yuania* is now considered to be a noeggerathian, a search for other foliage belonging to the *Primocycas* plant is needed.

Many cycadalean and bennettitalean leaves are macromorphologically similar, and can usually be distinguished only on epidermal anatomy following the pioneering work of Thomas and Bancroft (1913). Stomatal morphology is especially significant in the discrimination of the two foliage types (Florin 1933; Martens 1971). Bennettitalean leaves are characterised by syndetocheilic stomata, whereas cycadalean leaves possess haplocheilic stomata. These terms were introduced by Florin (1933), and refer to the development (cellular division) and the resulting morphotype of the stomatal apparatus. However, today the term "brachyparacytic" is the preferred term for bennettitalean stomatal architecture (Martens 1971; Crane 1988; LAWG 1999), rather than the ontogenetic term "syndetocheilic" (Thomas and Bancroft 1913; Florin 1933). Within the gymnosperms, the stomatal type of the Bennettitales is regarded as an autapomorphy with the exception of its occurrence (probably via homoplasy) in two enigmatic groups (i.e., the Welwitschiaceae and the Gnetaceae).

Since the record of possible *Pterophyllum* species (and other potential bennettitaleans) from Permian and Carboniferous deposits, mainly from south-eastern and eastern Asia, has increased in recent decades (up to 20 species known to us; see references below), critical evaluation of the morphology and relationships of these fossils is necessary. Here, we describe fossils from the Permo-Carboniferous of China held in the collections of the NRM that were originally assigned to the Bennettitales but yield cuticles with non-bennettitalean stomata. Although the cuticles are very brittle and poorly preserved, they provide useful information to clearly separate these leaves from the bennettitaleans, thus calling into question the identifications of other reported Palaeozoic *Pterophyllum* species.

Institutional abbreviations.—NRM, Swedish Museum of Natural History, Stockholm, Sweden; specimen numbers are preceded by the letter S (i.e., S141652).

Material and methods

The twenty-six studied specimens (specimen numbers given below) housed in the NRM were collected almost 90 years ago at three localities in northern China (Fig. 1). The specimen from Linxi (also spelt Linsi or Linshi), Tangshan area, Hebei, was collected in 1920 by Yao. Eight specimens from Yangjialiang (also spelt Yang-chia-liang), approximately 45 km to the south and 1.5 km to the west of Baode in the valley of Paloukou, north-western Shanxi, were collected in 1921 by T.C. Wang. Seventeen specimens from Damugou (also spelt Ta-mu-kou) near Hua-pi-chuang, Gaoping district, south-eastern Shanxi, were obtained by an anonymous collector (accessioned in 1929).

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Hand specimens were photographed with a high-resolution Nikon D80 digital camera using polarised light to increase contrast (Schaarschmidt 1973; Crabb 2001). The use of polarised light and high resolution imaging revealed several details (venation, raised surface structures) that are indiscernible to the naked eye. To make the cuticular features visible before destroying the specimens for cuticular analysis, a Leica Diaplan epifluorescence microscope was used. Cuticles were prepared according to procedures outlined by Kerp (1990) and Kerp and Krings (1999). Rock samples with plant remains were dissolved in hydrofluoric acid (40% HF) in order to remove the sediment. Cuticles were macerated according to the standard procedure using Schulze's reagent (35% HNO_3 with a few crystals of $KClO_3$) and 5–10% potassium hydroxide (KOH). Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and finally mounted in permanent glycerine-jelly microscope slides.

Geological setting

Shallow marine and continental coal-bearing strata were deposited extensively across the North China Platform through the Pennsylvanian and Permian. These deposits can be broadly subdivided on lithological criteria into several formations, each unit being generally greater than 100 m in thickness, as summarised by Yang (1986a, b). These formations can be correlated between several basins and structural outliers across northern China on the basis of their macrofloral, palynofloral and invertebrate fossil content (Shen 1995; Wu 1995; Shen et al. 2006; Liu et al. 2008). However, precise stratigraphic placement of assemblages from historical collections, such as the material described herein, remains difficult where precise locality details are lacking and where local mapping of lithostratigraphic units is inadequate. Given these limitations, we tentatively ascribe stratigraphic positions and ages for the studied material on the basis of associated macrofossils as outlined below. All studied assemblages derive from the North China–Cathaysian palaeofloristic subprovince of Li and Wu (1996).

Linxi (Tangshan area).—Fossiliferous coal-bearing strata of the Linxi area, Hebei, were assigned to the Kaiping Series/Formation by Stockmans and Mathieu (1939) and are considered to be broadly correlative with the Taiyuan Formation (Wu 1995). Most of the fossils from this site in the NRM collections provide poor age constraints being only identifiable to generic level (e.g., *Neuropteris*, *Annularia*, *Sphenophyllum*, *Cordaites*, *Pecopteris*, and *Samaropsis* spp.). However, the absence of typical Permian taxa (e.g., *Taeniopteris*, *Callipteridium*, *Emplecopteridium* or *Emplecopteris*) favours a Pennsylvanian (Stephanian or Gzhelian) age for this assemblage, and correlation with the lower part of the Taiyuan Formation (Wu 1995).

Yangjialiang (south of Baode).—This site is located in exposures of late Palaeozoic strata on the northeastern margin of the Ordos Basin. The coal-rich strata of the Shanxi Formation (palynologically dated as Artinskian–Kungurian; Liu et al. 2008) are the most likely source of the fossils from this site based on the presence of taxa such as *Taeniopteris*, *Protoblechnum*, and *Neuropteris* spp. and the absence of *Lobatannularia*, *Gigantonoclea*, and *Gigantopteris*, which mostly characterize Upper Permian strata in this region (Shen 1995).

Damugou (Gaoping area).—This site is near the margin of the Quinshi-Linfen Basin, in which the main coal-bearing units are the Taiyuan and Shanxi formations (Shao et al. 2007). The fossil assemblage includes *Alethopteris ascendens*, *Sphenophyllum thonii*, *Pecopteris orientalis*, *Emplecopteridium alatum*, *Odontopteris subcrenulata,* and *Aphlebia* sp. On the basis of the stratigraphic ranges of taxa outlined by Shen (1995) and the absence of *Lobatannularia* and gigantopterids, the assemblage most likely derives from the Shanxi Formation (Artinskian–Kungurian). However, a younger age (from the Guadalupian Lower Shihezi Formation) can not be excluded.

Systematic palaeobotany

Class Cycadopsida Brongniart, 1843

Order Cycadales Dumortier, 1829

Family unknown

Genus *Pseudoctenis* Seward, 1911 emend. Harris, 1964

Type species: *Zamites eathiensis* Richards, 1884; from the Jurassic of Scotland.

Remarks.—The cycadalean foliage genus *Pseudoctenis* is a common element of several Mesozoic (Rhaetian–Jurassic) floras in Europe (Seward 1911, 1917; Harris 1932, 1950, 1964; Pott et al. 2007b). Seward (1911) introduced the genus for *Zamites*-type leaves from the Jurassic of Sutherland, Great Britain. Although *Ctenis* and *Pseudoctenis* are similar in macromorphology, Seward (1911) noted that they are easily distinguishable based on the occurrence of anastomoses in the venation of *Ctenis*, an interpretation with which Harris (1950) concurred. Nevertheless, historically, *Pseudoctenis* has often been used in an arbitrary manner because no valid generic diagnosis existed. Furthermore, numerous foliage specimens have been accommodated in genera such as *Pterophyllum*, *Ctenophyllum*, and *Zamites* over many years, although they better matched the characters of *Pseudoctenis*. This changed when Harris (1932) described the epidermal features of several *Pseudoctenis* species from the Rhaetian of Greenland. The epidermal anatomy established the cycadalean affinities of *Pseudoctenis* based on the presence of cyclocytic ("haplocheilic") stomata. Harris (1932, 1964) provided a diagnosis for *Pseudoctenis* that included both macromorphological and epidermal characters. The earliest confirmed representatives of the genus occur in the Carnian of Lunz, Austria (Pott et al. 2007b).

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Pseudoctenis samchokense (Kawasaki, 1934) nov. comb.

Figs. 2–4.

1931 *Pterophyllum samchokense* nom. nud.; Kawasaki 1931: pl. 86: 260.

1934 *Pterophyllum samchokense* sp. nov.; Kawasaki 1934: 197, no illustration.

1939 *Pterophyllum pruvostii* sp. nov.; Stockmans and Mathieu 1939: 93, pl. 21: 2, 2a, 3.

1974 *Pterophyllum pruvostii* Stockmans and Mathieu, 1939; Gu and Zhi 1974: 144, pl. 114: 1, 2.

2006 *Pterophyllum pruvostii* Stockmans and Mathieu, 1939; Sun 2006: 385, no illustration.

Basionym: *Pterophyllum samchokense* Kawasaki, 1934.

Type material: Holotype: specimen figured by Kawasaki (1931) on pl. 86: 260 (repository and accession number not recorded). Epitypes: specimens NRM S141652 and NRM S141653 (Fig. 3C, 3F).

Type locality: Sanchoku (Samchok) district, South Korea (Chosen).

Type horizon: Jido Series, Heian Group.

Remarks.—The species was originally established on a single specimen and compared to *Pterophyllum daihoense* by Kawasaki (1934). However, another comment by the author in the same paragraph, later supported by Sze (1936), illustrates that these taxa can not be regarded as conspecific because *Pt. daihoense* includes leaves with laminae that are partly not divided into segments, especially in the distal portion of the leaf. Specimen NRM S141652 is chosen as an epitype, because it provided the cuticular details on which the new combination of the species is based.

Material/repository.—26 specimens from the palaeobotanical collections in the NRM. From Yangjialiang: S141640, S141648, S141650–S141655; from Damugou: S143500-02, S143501, S143502, S143503a, S143503b, S143504, S143505, S143506-01, S143506-02, S143507, S143508-01, S143509, S143510, S143511-01, S143511-02, S143512, S143513-01; from Linxi: S146368.

Emended diagnosis.—Frond pinnate, rachis roughly striate, leaflets attached laterally and almost perpendicularly to the rachis, distinctly separated, never confluent, slender and unequal in width, gradually narrowing into the bluntly pointed apices, slightly narrowing near the base and a little dilated at the attachment to the rachis, basipetal margin slightly decurrent; veins forked at the base and commonly just distal to the base; the marginal veins arching parallel to the margins of the leaflets and the middle ones being straight; leaves hypostomatic, epidermal cells isodiametric polygonal to broadly elongate, cell walls straight, stomata surrounded by 5–7 subsidiary cells (emended after Kawasaki 1934).

Description.—Leaves are petiolate, impari-segmented, regular, oblong to broadly oval in outline (Fig. 2A–C), obtusely rounded at apex, up to 24 cm long and 22 cm wide (incomplete leaves). The petiole is prominent, but incomplete on all specimens (Fig. 2B; arrow). Besides these large leaves, some very small leaves occur (Fig. 3D) that reach only 5 cm long but display identical leaf architecture apart from narrower rachides. The lamina is subdivided into numerous long and narrow, parallel-sided to ensiform leaflets, which are oppositely to sub-oppositely positioned (Fig. 2A–E). The length of the individual leaflets varies depending on the position in the leaf; leaflets are up to 92 mm long and 5–11 mm wide. Leaflet length seems to increase slightly toward the middle of the leaf, and then gradually decrease toward the leaf tip (Fig. 2C). The leaflets are only slightly constricted basally; the basipetal margin is slightly decurrent (Fig. 3B; arrows). Leaflet apices are obtusely to acutely rounded (Fig. 3E). The distance between the individual leaflets is regular within a single leaf but may vary between leaves of this species.

The leaflets are inserted laterally on the prominent and longitudinally striate rachis (Fig. 3B, E, F). The distal leaflets are arched towards the apex and form a rounded leaf apex (Figs. 2B, 3A). Numerous parallel veins enter each leaflet and usually bifurcate once close to the leaflet base (Fig. 3B, C). In some cases, additional bifurcations occur in the proximal portion of the leaflet. Veins positioned close to the lateral leaflet margins do not fork. Cuticles are very thin, brittle and poorly preserved. The leaves are probably hypostomatic; costal and intercostal fields are distinguishable on the abaxial side of the leaf. Stomata are restricted to the intercostal fields (Fig. $4C_1$, C_2). The adaxial cuticle is slightly thicker than the abaxial cuticle (Fig. 4A, C_1).

Few details are available for the adaxial cuticle: epidermal cells are polygonal, elongate to isodiametric in outline, 40–100 μm long and 30–45 μm wide. Anticlinal and periclinal cell walls are smooth. Stomata, papillae and/or hair bases are absent (Fig. 4A).

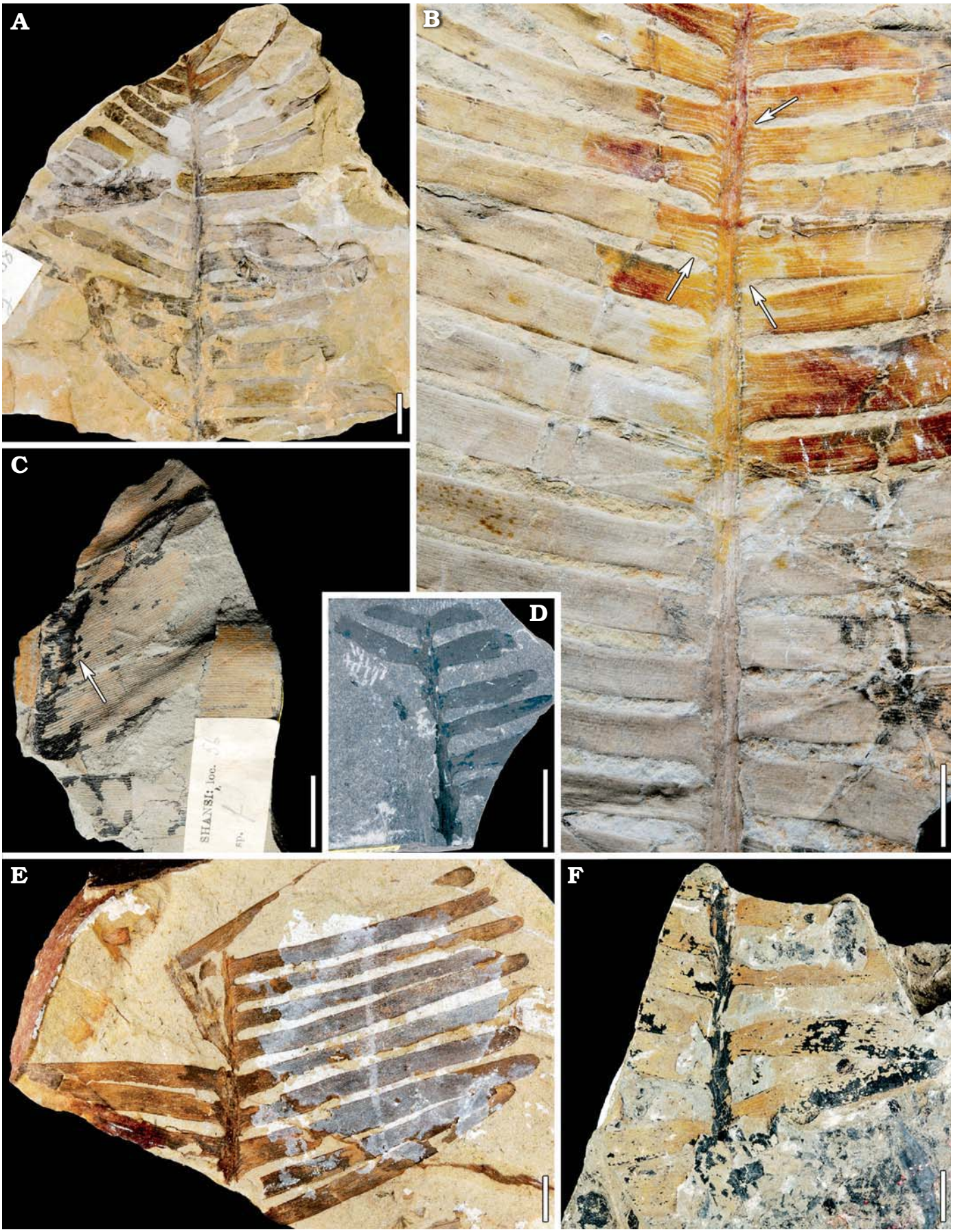
In the abaxial cuticle, costal fields are composed of 6–8 rows of epidermal cells. The cells above the veins are polygonal, elongate to isodiametric, 30–110 μm long, 30–40 μm wide, and possess delicate walls. Anticlinal cell walls are usually straight and periclinal walls are smooth; papillae are absent. Intercostal fields are 200–380 μm wide, with isodiametric polygonal to broadly rectangular cells. Epidermal cells are 30–80 μm long and 30–55 μm wide (Fig. $4C_1$, C_2). Anticlinal cell walls are straight. Stomata (Fig. $4B_1$–B_3, C_3) are cyclocytic ("haplocheilic"), probably slightly sunken, and up to 110 μm in diameter. Pores are orientated almost perpendicularly to the veins (Fig. $4C_1$, C_2; arrows). Stomatal complexes incorporate 5–7 rectangular subsidiary cells that are arranged in a circle around the pit (Fig. $4B_1$, B_2); some stomata appear to be surrounded by a weakly defined second ring of subsidiary cells. The guard cells possess heavily cutinised central portions of the dorsal walls, whereas the polar ends are weakly cutinised (Fig. $4B_1$, B_2, C_3).

Discussion.—This foliage type is assigned to *Pseudoctenis* because essential macromorphological features (e.g., the segmented architecture of the leaf, the lateral and perpendicular insertion of the almost parallel-sided leaflets, and the striate rachis) correspond well to those evident in typical representa-

← Fig. 2. Leaves of cycadalean *Pseudoctenis samchokense* (Kawasaki, 1934) from Damugou, Gaoping, Shanxi, China. **A**. NRM S143500-02. **B**. NRM S143504. **C**. NRM S143503a. **D**. NRM S143505. **E**. NRM S143510. Scale bars 10 mm; arrows indicating prominent petiole and rachis.

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tives of the genus (Harris 1964; Pott et al. 2007b). In addition, the venation is similar, especially with respect to the parallel lateral veins that fork near their base. Furthermore, the epidermal anatomy, characterised by cyclocytic ("haplocheilic") stomata, justifies accommodation of this species in *Pseudoctenis* (Harris 1964; Pott et al. 2007b) and, therefore, in the Cycadales.

Cycadales range from the Permo-Carboniferous to present. Cleal (1993) gave a short overview of their temporal distribution and stated that the first unequivocal cycads derive from the Early Permian of Taiyuan (Shanxi series) in China (Gao and Thomas 1989). We agree with Cleal (1993) who suggested treating several doubtful Carboniferous and Early Permian fossils (for details see Cleal 1993) as precursors of the Cycadales rather than regarding them as true cycads. The fossils described here also come from the latest Carboniferous–Early Permian of China, some of them from close to the source of the early cycads described by Gao and Thomas (1989; see Fig. 1) and thus rank amongst the earliest cycads. The early cycadalean record of Gao and Thomas (1989) is now supported by unequivocal cycadalean foliage from coeval deposits of this region.

Stratigraphic and geographic range.—Latest Carboniferous to Early Permian of China (Hebei, Shanxi) and South Korea (Sanchoku).

Discussion

Permian cycads.—None of the Permian–Carboniferous species assigned to *Pterophyllum* (see below), except *Pt. grandeuryi* and *Pt. pruvostii*, is similar to *Pseudoctenis samchokense* in gross macromorphology. Although cuticle details are lacking, we regard *Pt. pruvostii* from Tangshan (Hebei, China; Stockmans and Mathieu 1939; Gu and Zhi 1974) as most likely conspecific with *Ps. samchokense* based on macromorphological features and dimensions. Although *Pt. pruvostii* has wider interspaces between the leaflets and the material figured by Stockmans and Mathieu (1939) is somewhat incomplete, the wider spacing of the leaflets can be caused by growth conditions as demonstrated for *Pt. filicoides* (Schlotheim, 1822) Zeiller, 1906 from the Upper Triassic of Austria (Pott et al. 2007d). *Pterophyllum grandeuryi* from the Permian of Blanzy, France (Saporta and Marion 1885) is also very similar to *Ps. samchokense* in overall morphology, dimensions and epidermal cell pattern. Zeiller (1906) figured some schematic drawings of cuticular remains he obtained from the original specimens of *Pt. grandeuryi* and Thomas (1930) described the epidermal anatomy of this species in more detail although he mainly referred to the schematic illustrations by Zeiller (1906). Thomas (1930) interpreted the stomata in the drawings and in his own preparations as sunken with up to five thickened subsidiary cells arranged in a circle around the pit. This is not the architecture of a brachyparacytic (syndetocheilic) stoma, hence, Thomas (1930) correctly compared *Pt. grandeuryi* with *Nilssonia mediana* (Leckenby, 1864) Nathorst, 1878 from the Jurassic of Scarborough, UK. The stomatal architecture described by Thomas (1930) assigns *Pt. grandeuryi* clearly to a non-bennettitalean genus. We refrain from regarding *Pt. grandeuryi* as conspecific with *Ps. samchokense* due to differences in the architecture of the stomata (i.e., sunken stomata and thickened subsidiary cells in the former). Moreover, *Pt. grandeuryi* has epidermal anatomy more similar to *Pseudoctenis cornelii* Pott, Kerp, and Krings, 2007, described from the Carnian of Austria (Pott et al. 2007b).

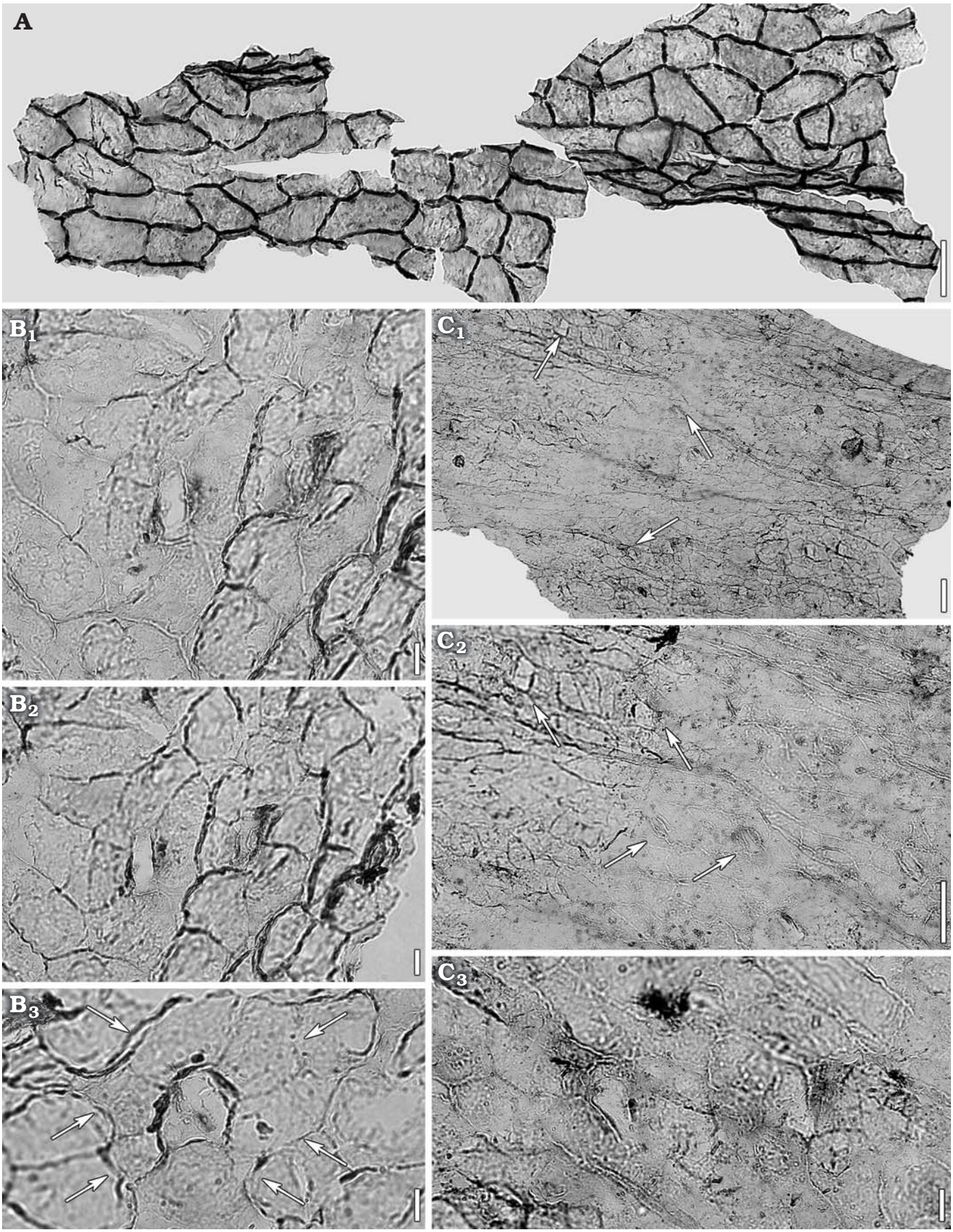
Dioonites densinervis Halle, 1927 from the Permian of the Taiyuan-Fu area in the Shanxi district of China (Halle 1927) is also broadly similar to *Pseudoctenis samchokense*. However, leaves of *D. densinervis* are distinctly smaller (about one-third of the size) than those of the latter and also differ in having leaflet bases that are decurrent on both the acropetal and basipetal margins. This species was erroneously transferred to *Nilssonia densinervis* by Stockmans and Mathieu (1939) and later illegitimately named *N. huabeiensis* by Gu and Zhi (1974). Indeed, both views can not be accepted, since *Nilssonia* is characterised by leaflet insertion on the upper side of the rachis (Pott et al. 2007a), which is not visible in the original specimens, and a cycadalean nature of the epidermis/cuticle is unproven since the specimens do not yield cuticles. Hence, retention of this species in *Dioonites* is recommended.

Cycad or cycad-like remains from Permian deposits are rare; there are only a few species of cycadophyte foliage formally described. Species broadly similar to *Pseudoctenis samchokense* include *Ps. middridgensis* Stoneley, 1958, from the UK, several *Zamites* species from Commentry, France, described by Renault and Zeiller (1890), and some species from China assigned to *Nilssonia, Yuania*, *Tingia*, and *Plagiozamites* (Halle 1927; Ghu and Zhi 1974; see Wang and Shen 2000; Taylor et al. 2009). *Pseudoctenis middridgensis* from the Upper Permian (Thuringian) of England is based on a single specimen that yielded only small, ill-preserved cuticle fragments from the rachis, and Stoneley (1958) noted that, in the absence of adequate knowledge of the epidermal anatomy, assignment of this fossil to *Pseudoctenis* must be considered provisional. The identities of most of the Chinese *Nilssonia* species are questionable since the figures do not provide sufficient details for confident generic or specific assignment. Moreover, *N. huabeiensis* is illegitimate (see above). The *Zamites* remains from France are in almost all cases preserved only as single leaflets and appropriate assignment remains equivocal. The genera *Yuania*, *Tingia*, and *Plagiozamites*, historically included by some researchers in the Cycadales, are better assigned to the Noeggerathiales, an order recently placed in the progymnosperms based on the organisation of their sporophylls

← Fig. 3. Different leaves of cycadalean *Pseudoctenis samchokense* (Kawasaki, 1934); from Damugou, Gaoping (**A**, **B**, **E**), Yangjialiang, Baode, Shanxi (**C**, **F**), and Linxi (Tangshan area), Hebei (**D**), China. **A**. NRM S143507. **B**. Enlargement of NRM S143500-02; cf. Fig. 2A. **C**. NRM S141652 (epitype). **D**. NRM S146368; **E**. NRM S143502; **F**. NRM S141653 (epitype). Scale bars 10 mm; arrows indicating venation details and lateral insertion of decurrent leaflets.

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and other reproductive organs (Taylor et al. 2009). Historically, the poorly understood Noeggerathiales have been included within the cycads by some workers (cf. Taylor et al. 2009). However, none of the mentioned genera includes foliage that is rudimentarily comparable to the leaves described herein apart from their basic segmented (pinnate) plan.

Several studies have reported rare examples of pinnate, cycad-like foliage from the Permian of Gondwana (e.g., McLoughlin 1992). The best preserved of these fossils is *Pteronilssonia gopalii* Pant and Mehra, 1963 from the Late Permian of India. That species is broadly similar to *Pseudoctenis samchokense* in its leaflet dimensions and venation style but differs in having leaflet bases that are decurrent on both the acropetal and basipetal margins. It also has strongly sinuous epidermal cell walls and prominent papillae on the subsidiary cells. On this basis it is considered to represent an atypical compound glossopterid leaf rather than a cycad (Pant 1982).

Since the generic attribution of *Pseudoctenis middridgensis* is equivocal, the next most similar species to *Ps. samchokense* is *Ps. cornelii* from the Carnian of Austria, which to date is the earliest record of a *Pseudoctenis* species in the Northern Hemisphere (Pott et al. 2007b). Both species agree in several characters (i.e., leaflet size, outline, insertion, gross architecture and size) but differ mainly in the details of their epidermal anatomy (e.g., architecture and position of the stomata, cell wall shape) and the great disparity in their ages. Therefore, a close relationship is not assumed.

If *Primocycas chinensis* is accepted as the oldest cycad reproductive structure to date, *Pseudoctenis samchokense* may be regarded as the oldest cycad foliage species. Bennettitaleans appeared, based on our survey of published data, not before the Middle to Late Triassic and were completely absent during the Palaeozoic even if the sudden mass abundance of bennettitaleans in the floras from Lunz and Neuewelt (Kräusel and Schaarschmidt 1966; Pott et al. 2007c, d, 2008) requires that bennettitaleans had originated earlier than the Carnian.

Alleged Permian bennettitaleans.—Since several fossils from Carboniferous or Permian deposits, including the leaves described here, have been described as possible bennettitalean remains, we re-evaluated reports of the oldest pre-Carnian bennettitaleans. Bennettitaleans first arose in noteworthy abundance during the Carnian (e.g., Anderson and Anderson 1989; Pott et al. 2007c, d). Almost all of the reports of bennettitaleans from older floras are unconvincing since, in most cases, cuticles are lacking or were not described. As the epidermal details identified in this study reveal, reports of bennettitalean foliage from older deposits should be considered equivocal if based on macromorphology alone.

At least 27 species of *Pterophyllum* have been formally described from Upper Carboniferous and Permian deposits (see also Table 1). Most of these derive from Western Europe, eastern Russia, East Asia and Laos (Table 1). In the Late Palaeozoic, these regions belonged to the Euramerican, Angaran (Siberian and Far East), and Cathaysian (N and S China) phytogeographic provinces (Chaloner and Meyen 1973; Wang and Shen 1996). Assignment of any of these species to *Pterophyllum* and thereby to the Bennettitales is doubtful. On the basis of the available macromorphological characters and their incompletely known or unknown epidermal anatomies, all species ought to be assigned to *Dioonites* (Halle 1927; Johanna H.A. van Konijnenburg-van Cittert, personal communication 2008) whose higher level taxonomic affinities are unclear. We finally compare these species to *Pseudoctenis samchokense* because of their similar age and original assignment to *Pterophyllum*. Of these, *Pt. pruvostii* is considered conspecific with *Ps. samchokense* (see above).

Six species have been described from Permian–Carboniferous deposits of central Europe. The simple descriptions and schematic illustrations of *Pterophyllum cottaeanum* (Geinitz 1862, 1873) and *Pterophyllum blechnoides* (Geinitz 1873) together with Barthel's (1976) figure are inadequate to allow assignment to *Pterophyllum* or support a combination with *Pseudoctenis samchokense*. *Pterophyllum cottaeanum* differs in gross lamina shape from *Ps. samchokense*. *Pterophyllum blechnoides* from the Carboniferous of southern Germany as figured by Sandberger (1864) is more similar to *Dioonites densinervis* than *Ps. samchokense* in leaf shape, leaflet bases and venation pattern, but differs from both in its dimensions. One of the specimens figured by Sandberger (1864: pl. 2: 1) must have had an impressive length of more than 120 cm. *Pterophyllum fayolii* from the Commentry Basin (France) differs from *Ps. samchokense* mainly in having acutely pointed leaflets (Renault 1890; Zeiller 1906; Thomas 1930) that are more similar to those of *Pt. cultelliforme*. Renault (1896) noted that several additional species of *Pterophyllum* were described from other Carboniferous and Permian localities of France such as Saint Étienne, Montmaillot (Blanzy; i.e., *Pt. grandeuryi*), Commentry (i.e., *Pt. fayolii*) and Autun (i.e., *Pt. cambrayi* Renault, 1894). Some of these lack cuticles, despite Renault's (1890) description of a thin coaly layer partly covering the *Pt. fayolii* specimen. Later, Zeiller (1906) figured a small piece of cuticle of *Pt. fayolii* and provided several schematic drawings of cuticles of *Pt. grandeuryi* but figuring stomata only schematically since he was only able to obtain fragments of the adaxial and abaxial cuticle. The epidermal anatomy of *Pt. grandeuryi* was later discussed by Thomas (1930) who revealed that it distinctly differs from Mesozoic forms in having non-brachyparacytic stomata.

From East Asia, five species assigned to *Pterophyllum* have been reported. *Pterophyllum cultelliforme* differs from

← Fig. 4. Cuticle details of cycadalean *Pseudoctenis samchokense* (Kawasaki, 1934); from Yangjialiang, Baode, Shanxi, China. **A**. NRM S141652-001, adaxial cuticle overview. **B**. NRM S141652-002, two adjacent stomata in the abaxial cuticle (B_1); different focus (B_2), stomata on the abaxial cuticle (B_3), arrows point to subsidiary cells in B_3. **C**. NRM S141652-003, abaxial cuticle overview (C_1), arrows pointing to stomata; enlargement on abaxial cuticle (C_2), arrows pointing to stomata; two adjacent stomata in the abaxial cuticle (C_3). Scale bars 10 μm in B_1–B_3, C_3, and 50 μm in A, C_1, C_2.

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Table 1. Synopsis of the *Pterophyllum* species reported from Permo-Carboniferous deposits.

Species	Authority	Figured by	Also referenced by	Age	Occurrence
Pterophyllum cottaeanum	Gutbier, 1835	Geinitz 1862, 1873; Barthel 1976	Göppert 1844; Sandberger 1864; Renault 1890; Sze 1936	Rotliegend/Zechstein (Permian)	Saxony, Germany
Pterophyllum gonorrhachis	Göppert, 1844		Sandberger 1864	Carboniferous	Upper Silesia, Poland
Pterophyllum blechnoides	Sandberger, 1864	Geinitz 1873	Sze 1936; Zimina and Zimina 2005	Rotliegend/Zechstein (Permian)	Saxony, Baden-Württemberg, Germany
Pterophyllum grandeuryi	Saporta and Marion, 1885	Zeiller 1906	Renault 1890, 1896; Zeiller 1906; Thomas 1930; Kawasaki 1934; Sze 1936; Schwedov 1961; Zimina and Zimina 2005	Permo-Carboniferous	Commentry, France
Pterophyllum fayolii	Renault, 1890	Zeiller 1906	Renault 1896; Thomas 1930; Sze 1936	Permo-Carboniferous	Commentry, France
Pterophyllum crambrayi	Renault, 1894	Renault 1896	Sze 1936	Permo-Carboniferous	Autun, France
Pterophyllum bipartitium	nomen nudum	Kawasaki 1931	Sze 1936	Permo-Carboniferous	South Korea, China
Pterophyllum nilssonioides	nomen nudum	Kawasaki 1931	Sze 1936	Permo-Carboniferous	South Korea, China
Pterophyllum daihoense	Kawasaki, 1934	Gu and Zhi 1974	Sze 1936; Zimina and Zimina 2005; Shen 1995; Sun 2006	Permo-Carboniferous	South Korea, China
Pterophyllum samchokense	Kawasaki, 1934	Kawasaki 1931	Sze 1936; Schwedov 1961	Permo-Carboniferous	South Korea, China
Pterophyllum cultelliforme	Sze, 1936	Gu and Zhi 1974	Shen 1995; Sun 2006	Permo-Carboniferous	South Korea, China
Pterophyllum pruvostii	Stockmans and Mathieu, 1939	Gu and Zhi 1974	Shen 1995; Sun 2006	Permo-Carboniferous	South Korea, China
Pterophyllum kotschetkovii	Schwedov, 1961			Permian	Yenisey-Lena Region, Russia
Pterophyllum slobodskiense	Schwedov, 1961			Permian	Yenisey-Lena Region, Russia
Pterophyllum eratum	Gu and Zhi, 1974	Huang 1987	Zimina and Zimina 2005; Shen 1995; Sun 2006	Permo-Carboniferous	South Korea, China, Mongolia
Pterophyllum fromagetii	Vozenin-Serra, 1979			Permian	Laos
Pterophyllum striatum	Hu and Du, 1982		Shen 1995	Permian	Shanxi, China
Pterophyllum klyuchense	Zimina and Zimina, 2005			Late Permian	Southern Primorye, Russia
Pterophyllum? *ratnoense*	Zimina and Zimina, 2005			Late Permian	Southern Primorye, Russia
Pterophyllum shevelevskiense	Zimina and Zimina, 2005			Late Permian	Southern Primorye, Russia
Pterophyllum? *sitsense*	Zimina and Zimina, 2005			Late Permian	Southern Primorye, Russia

Shen (1995) provided in his synoptic species list six further species that could not be traced completely due to incomplete referencing: *Pterophyllum bifidum* Xiao, *Pt. huabeiense* Fang, *Pt. maxum* Shen, *Pt. nanshanense* Durante, *Pt. shangdonense* Sun, and *Pt. shanxiense* Zhao.

Pseudoctenis samchokense in having leaflets resembling a small knife (Sze 1936). *Pterophyllum daihoense* from the Heian System of South Korea was described by Kawasaki (1931, 1934) as having a segmented proximal region and an entire-margined lamina in the distal part of the leaf; it also differs from *Ps. samchokense* in size and insertion angles of the leaflets. A few illustrations of *Pt. eratum* were provided with the Chinese descriptions of this species by Gu and Zhi (1974) and Huang (1987). Based on the figures, *Pt. eratum* is similar to *Ps. samchokense*, especially to specimens NRM S141652 and NRM S141653 in arrangement, size and shape of the leaflets, but it lacks cuticle and the overall architecture of the leaf is not evident in the figured specimens. *Pterophyllum bipartitium* nom. nud. and *Pt. nilssonioides* nom. nud. (figured by Kawasaki 1931) were discussed by Sze (1936), who doubted their affinity to *Pterophyllum*. In fact, they were not included in *Pterophyllum* later in the text by Kawasaki (1934) accompanying the preceding atlas volume (Kawasaki 1931). Sze (1936) proposed that both species be better included in *Taeniopteris* or *Nilssonia*. Based on exam-

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ination of Kawasaki's (1931) figures, we agree with a preliminary assignment of those specimens to *Nilssonia* due to agreements in macromorphology (i.e., entire-margined lamina parts and leaflets inserted on the upper side of the rachis). Shen (1995) provided in his synoptic species list seven further species: *Pterophyllum bifidum* Xiao, *Pt. huabeiense* Fang, *Pt. maxum* Shen, *Pt. nanshanense* Durante, *Pt. shangdonense* Sun, *Pt. shanxiense* Zhao, and *Pt. striatum* Hu and Du, 1982. All species except the last could not be traced completely due to incomplete referencing and thus comparison was not possible. *Pteropyhllum striatum* from the Permian of Shanxi has distinctly slender leaflets (up to 3 mm in width) than *Ps. samchokense* (Zhu et al. 1982). We assume that the remainder are better referred to *Dioonites* due to their similar lack of epidermal details.

Central Asian assemblages include seven *Pterophyllum* species, of which some were already described as questionably assigned to the genus. The material of Schwedov (1961) and Vozenin-Serra (1979) assigned to *Pt. slobodskiensis* Schwedov, 1961, *Pt. kotschetkovii* Schwedov, 1961, and *Pt. fromagetii* Vozenin-Serra, 1979 is sparse and not convincingly described; hence comparisons can only be superficial. The figured specimens of Schwedov (1961) differ from *Pseudoctenis samchokense* in having relatively wider and shorter leaflets and coarser venation. The descriptions of these taxa lack cuticle details although cuticle possibly exists (at least in *Pt. slobodskiensis* and *Pt. kotschetkovii*, thus accommodation in *Pterophyllum* remains equivocal). Vozenin-Serra (1979) argued that "the cuticle, when preserved, shows the genus *Pterophyllum* to undeniably approach extant *Dioon* in its xerophytic characters". If this view is taken into account, the Laotian material assigned to *Pt. fromagetii* is hard to compare either to *Dioon* or any other cycadophyte, since cuticular details are lacking. Consequently, the systematic position of *Pt. fromagetii* remains equivocal. Zimina and Zimina (2005) described four taxa from the Upper Permian of Southern Primorye but the assignment of *Pt.*? *sitsense* Zimina and Zimina, 2005, *Pt.*? *ratnoense* Zimina and Zimina, 2005, *Pt. klyuchense* Zimina and Zimina, 2005 and *Pt. shevelevskiense* Zimina and Zimina, 2005 to that genus is questionable. The specimens lack cuticular information, which would require assignment of the leaves to *Dioonites* rather than *Pterophyllum*. In addition, the separation of the four species is based mainly on small differences in vein density and leaflet width; hence these forms may represent intraspecific variants (Stearns and Hoekstra 2005).

Conclusion.—Cuticular studies of Permian cycad-like leaves from China revealed that generic and higher taxonomic assignments of foliage from Palaeozoic deposits must be undertaken with great care. No evidence could be found that any Palaeozoic leaves are assignable to bennettitaleans; moreover, the cycadalelan nature of these leaves was demonstrated. Such foliage may not be assigned to *Pterophyllum* due to the clear bennettitalean nature of that genus. Assignment to the typical cycadalean genus *Pseudoctenis* is recommended for *Ps. samchokense*.

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