

PAST GLOBAL FLORISTIC CHANGES: THE PERMIAN GREAT EURASIAN FLORAL INTERCHANGE

by WANG ZI-QIANG

ABSTRACT. It is widely held that during the Permian, especially the Late Permian, the Subangara flora spread southwards into China, where it mingled with the 'Cathaysian flora'. However, the reputedly Angaran or Subangaran elements found in North China, which are common in, or even characteristic of the *Psugmophyllum* Zone of that region, include gymnosperms such as callipterids, peltasperms and psugmophylloids, which are in fact Euramerican in origin. The evidence rather suggests that many Eurasian gymnosperms moved into Angara in the Late Permian, and were part of a large scale biotic exchange that may be termed the Great Eurasian Floral Interchange. It can be recognized as having occurred from two directions: from western Europe, via the Russian Platform into Angaran Pechora; and from the northern border of South China, via North China into Angaran Mongolia and eventually to the Kuznetsk. There was also some migration of Angaran elements into the neighbouring areas, but to a much lesser extent, and the floral interchange was thus clearly asymmetrical. The functional mechanisms driving the interchange were palaeomonsoons in the northern Palaeotethys, and the expansion of the Eurasian Arid Province.

MAJOR palaeobiotic invasion and interchange were first recognized over a century ago, but it has only been over the last two decades that the processes involved have been properly understood, following their incorporation into the continental drift model. The collision of plates, previously occupying different latitudes, provided routes for the migration and interchange of faunas and floras that had long-separated evolutionary histories. The subject is currently an important part of the Past Global Changes project (Ricklefs *et al.* 1990). Well documented examples include the Great American Biotic Interchange that occurred in the Late Pliocene, after the development of the Panama Isthmus between North and South America (Marshall 1981; Webb 1991), and the Trans-Arctic molluscan interchange in the Early Pliocene, after the opening of the Bering Strait between the North Pacific and the Arctic Atlantic (Vermeij 1991).

During the Permian, one of the major significant palaeogeographical changes was the collision between the Siberian and Laurasian plates (Sengör *et al.* 1993). This provided the opportunity for the migration of land vegetation that had previously developed along quite independent evolutionary paths. Important for understanding this problem is the relationship between the plant fossils from Angara, and those of the so-called 'Northern Cathaysian Subprovince' (Li and Yao 1979). Since Norin (1924) referred to the Permian of central Shanxi as the 'Angara Series', the relationship between its fossils and those of Siberia has been a topic of considerable debate. Of central importance to this debate was the report of Angaran-like plant fossils from the C-Bed in Bexell's Nanshan Section in western China by Halle (1937). The potential significance of this discovery was immediately realized (Jongmans and Gothan 1937), and it has now become generally accepted that there are Angaran plant fossils in the Permian of North China (Sze 1953, 1954; Lee 1963; Chaloner and Meyen 1973; Chaloner and Creber 1988; Lemoigne 1988; Scotese and McKerrow 1990; Cleal and Thomas 1991; Durante 1992). Meyen (1981, 1982, 1987) incorporated the area within what he called the Subangara Palaeoarea—a transitional zone (ecotone) surrounding the Angara Palaeokingdom proper, extending from the Russian Platform, through Ural-Kazakhstan, Junggar and south Mongolia. According to Meyen, the northernmost part of

China was on the southern extension of this Subangara Palaeoarea, linking the Ural-Kazakhstan deposits to the west with those of the Far East.

Although on the face of it this model appears very reasonable, there have been widely diverging views as to the floristic composition and thereby the affinities of the Nanshan plant fossil assemblage, expressed variously by Russian and Chinese palaeobotanists. The present author has published a number of studies on the Permian and Triassic palaeophytogeography of North China, including extensive comparisons with the Russian literature (Wang 1985, 1989, 1991; Wang and Wang 1986). The present paper is an attempt to provide a comprehensive analysis of the problem, with special reference to certain key groups of gymnosperm foliage which are thought to have particular palaeophytogeographical significance. Chaloner and Creber (1988) have pointed out the problems of trying to establish the relationships between floristic provinces based on isolated plant leaves usually lacking reproductive features. However, the original recognition of the four main Late Palaeozoic phytochoria (Gondwana, Euramerica, Angara, Cathaysia) was based on the distribution of isolated leaves, and so it does not seem unreasonable to try to extend the database of such fossils. Furthermore, recent discoveries of reproductive structures attached or associated with some of the gymnosperm foliage have helped clarify their taxonomy and thus their palaeophytogeographical standing.

THE 'ANGARAN PLANTS' FROM NANSHAN

Halle's (1937) announcement of the presence of 'Angaran plants' at Nanshan appears to have been accepted by most palaeobotanists, despite the fact that he did not illustrate any of the material. The first illustrations of specimens from Nanshan were not until Chao (1963) and Gu and Zhi (1974) published examples of *Zamiopteris glossopteroides* Schmalhausen and *Iniopteris siberica* Zalesky, which had been returned to China from Sweden.

More detailed studies began in the late 1970s, by both Russian and Chinese palaeobotanists. Durante (1980, 1992) re-examined the Bexell collection of Nanshan specimens, stored at the Swedish Natural History Museum, and which included material identified by Halle. Her paper includes illustrations of about 30 species, albeit in many cases based on indeterminate specimens. Durante (1992, p. 36) argued that the assemblage was directly comparable with the Late Permian (Tatarian) assemblages of Subangara, and that characteristically Cathaysian elements are very rare ('with a small admixture of Cathaysian plants').

At about the same time, a Chinese professional working-group re-investigated Bexell's Nanshan section and collected a number of plant fossils. A series of stratigraphical and palaeontological reports were produced (Liang *et al.* 1979; Liu *et al.* 1981; Shi and Liu 1981; Zhang and Shen 1987a, 1987b). These Chinese palaeobotanists argued that one-third of the species are commonly found in the lower Upper Permian 'Upper Shihhotze Formation' in North China, and that neither Angaran nor Cathaysian taxa are typical in the mixed assemblage. According to Zhang and Shen (1987a, 1987b), *Paracalamites tenuicostata* Neuburg, *Zamiopteris*, *Comia* and *Pursongia* are the only Angaran immigrants at Nanshan.

Wang *et al.* (1984) illustrated plant fossils from areas adjacent to Nanshan and their taxonomic list included genera of apparently Angaran affinities. Judging from the photographs, however, many of their identifications are doubtful.

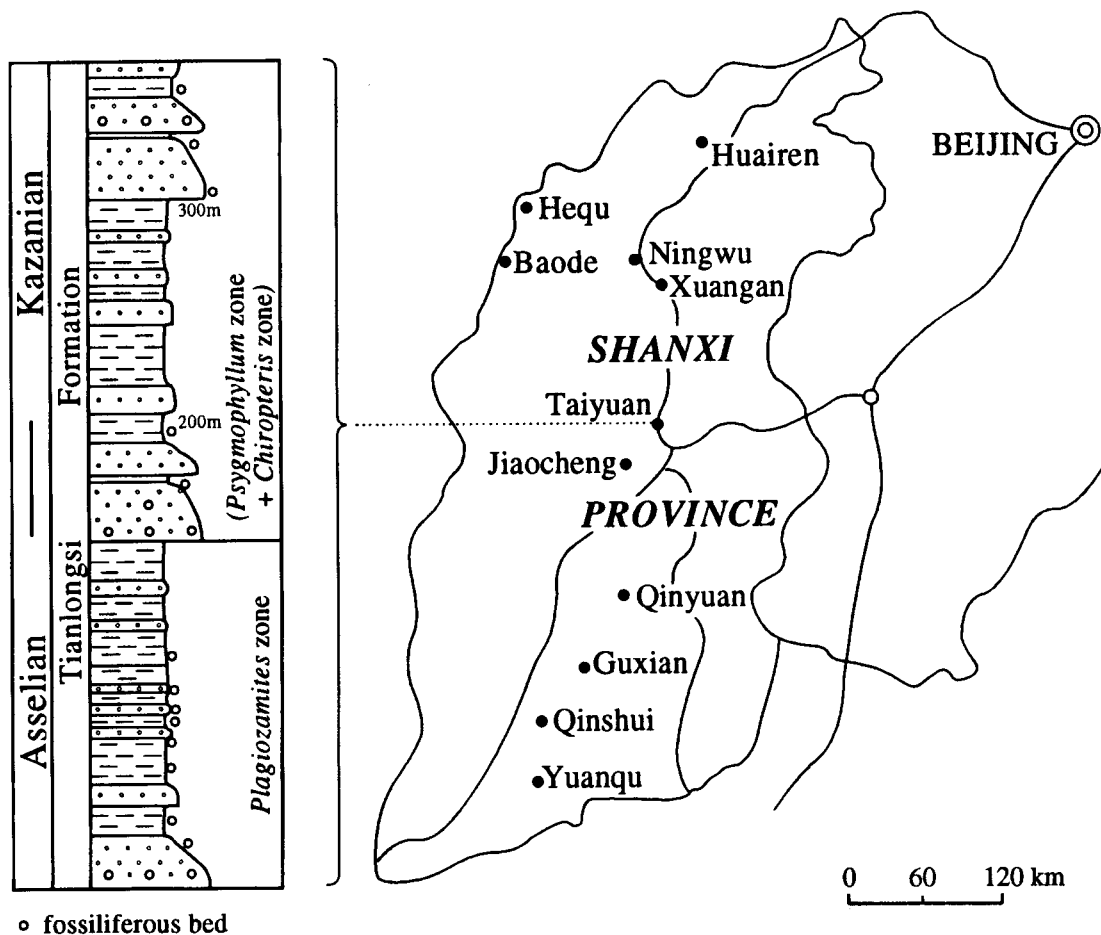
The species lists provided by these two schools of workers have upwards of two-thirds of the genera in common, e.g. *Psymphyllum*, *Peltaspermum*, *Callipteris* and *Protoblechnum-Compsopteris*. From a palaeophytogeographical point of view, the most significant difference is the presence in Durante's list of rare Tatarian taxa (e.g. *Pursongia*, cf. *Sashinia* and questionable *Phylladoderma* and *Comia*). It is important to point out, however, that the Nanshan specimens do not yield cuticles, and epidermal structure is needed to identify these taxa reliably. On the other hand, judging from the illustrations, there are no obvious mistakes in the identifications by either Durante or the Chinese palaeobotanists; it would be expected, after all, that Russian palaeobotanists

should be able to recognize typically Angaran taxa, while Chinese palaeobotanists should be able to identify Cathaysian forms. The differences between the lists may thus reflect hitherto unrecognized relationships between the Late Permian floras of North China and Siberia. To try to understand this better, it is therefore necessary to re-examine the relevant Chinese plant fossils, i.e. those from the 'Upper Shihhotze Formation'.

A NEW ASSEMBLAGE OF PERMIAN PLANT FOSSILS

In Halle's (1927) memoir, most of the documented Permian plant fossils originated from the 'Upper Shihhotze Formation' in central Shanxi. However, they were mainly from the lower part of that formation; plant fossils from the middle and upper parts of the formation are rare and so the biostratigraphical position of these higher strata was problematical.

For the past five years, the geology of the classic Upper Paleozoic sections at West Hill of Taiyuan, Shanxi (Text-fig. 1), has been extensively re-investigated. As a result, the 'Upper



TEXT-FIG. 1. Generalized stratigraphical log of the Tianlongsi Formation in Shanxi. Also locality map showing sites mentioned in text.

Shihhotze Formation' has been renamed the Tianlongsi Formation, to avoid a duplication of names with the Shihhotze Group (Chen and Niu 1993). At the same time, the present author has undertaken a comprehensive revision of the plant biostratigraphy, palaeoecology and systematics of the red beds of the Tianlongsi Formation, and has recognized two more-or-less stable biozones (Wang 1993a, fig. 1).

1. *Plagiozamites* Zone (early Early Permian). The base of this zone is placed at the first occurrence of *Gigantonoclea*, and coincides with the first occurrence of red beds in the Shihhotze Group.
2. *Psymophyllum* Zone (late Early Permian). This occurs in the middle and upper parts of the Tianlongsi Formation, and is identified by the first occurrence of *Psymophyllum*.

The present paper concentrates on the plant fossils from the *Psymophyllum* Zone, most of which have hitherto not been studied in detail.

So far, 45 species belonging to 35 genera have been identified from this new zone. They include a number of relic Carboniferous genera, such as *Lepidodendron*, *Sphenophyllum*, *Annularia*, *Cordaites*, *Pecopteris* and *Sphenopteris*. Also present are abundant Mesophytic gymnosperms, these being the oldest assemblages with such gymnosperms known from North China; psymophylloids are unique to this zone. Also important are peltasperms, including callipterid fronds, *Autunia* and *Peltaspermum* fructifications, and other allied genera (*Supaia*, *Protoblechnum-Compsopteris*, *Neuropteridium*, *Comia*, etc.). Cycad leaves and megasporophylls, although known from the basal Permian of China (Gao and Thomas 1989), increase significantly in diversity in the *Psymophyllum* Zone. They include a series of *Taeniopteris* leaves varying from small, narrow, linear forms, to large, broad or elliptical ones. Cycad ovuliferous scales range from the fan-like *Norinia* to the pinnate *Tianbaolinia* Gao and Thomas, 1989 (similar to *Chulakia* Salmenova, 1984). Ancestors of ginkgos (*Sphenobaiera*, *Ginkgophyton? spirata* Sze, *Ginkgophytopsis*) and conifers (*Walchia*, *Majonica*) also appear here and sometimes are dominant.

The rest of this paper will concentrate on the psymophylloids and peltasperms, these being the taxa regarded by Meyen (1988, pp. 344–357) as endemic to the Subangara Palaeoarea. The main difficulty is trying to compare species described by Russian palaeobotanists from Angaran floras with species described by Chinese palaeobotanists from North China. To avoid exaggerating the palaeobiogeographical differences that such subjective difference could introduce at the rank of form-species, the discussion and comparison will be kept at the rank of genus, following the practice of earlier studies (e.g. Chaloner and Creber 1988; Cleal and Thomas 1991). The descriptive style of the form-genera follows that of Zoderow and Cleal (1993).

SYSTEMATIC PALAEOLOGY

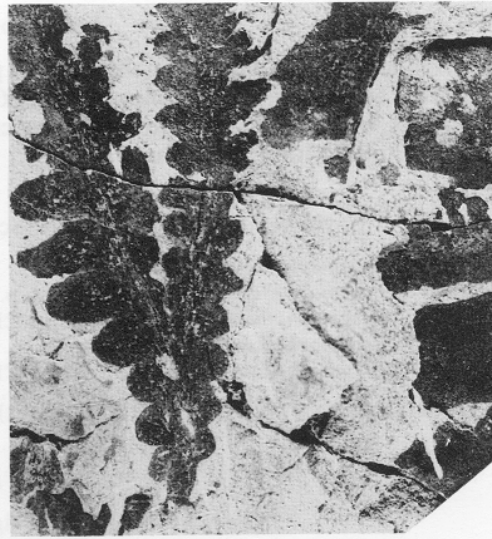
The synonymy lists of each taxon are not complete, those entries prefixed by an asterisk include cuticular evidence. All figured specimens are stored in the Tianjin Institute of Geology and Palaeontology (TIGP).

EXPLANATION OF PLATE 1

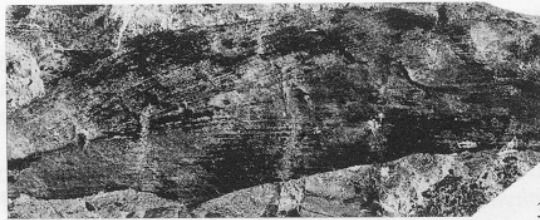
- Figs 1–2, 6 *Supaia* sp. A. Forked fronds; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 1, TIGP 9306-1. 2, TIGP 9306-2. 6, TIGP 9306-4.
- Fig. 3. *Psymophyllum multipartitum* Halle. K-1-6; narrow segment similar to *Zamiopteris*-type leaf; Kuantou village, Taiyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.
- Fig. 4. Cf. *Zamiopteris*-type leaf. TIGP Th7126-061; Hoshan village, Jiaocheng district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.
- Fig. 5. *Autunia*-type fructification. TIGP 930-33; numerous megasporophylls attached to rachis, with seeds on inner side; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 2.



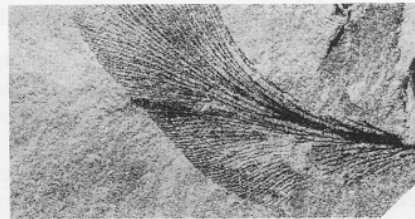
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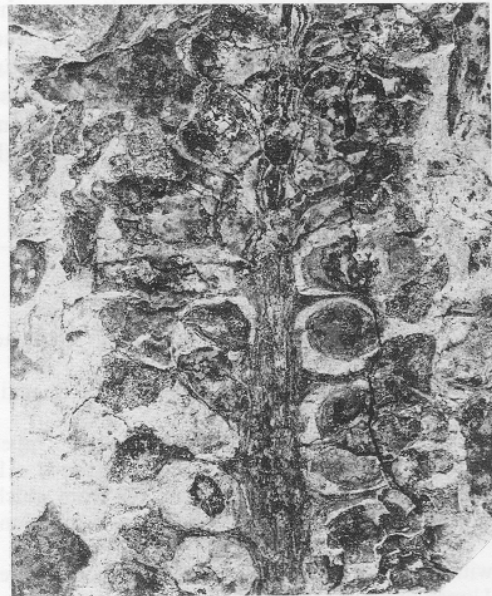
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PSYGMOPHYLLOIDS

Yao (1989) used this name for certain Permian palmate leaves, including *Psygmophyllum* Schimper *sensu stricto* and several allied genera such as *Ginkgophytopsis* Høeg and *Ginkgophyllum* Saporta. In this paper, other palmate gymnosperm leaves, including *Chiropteris*, *Rhipidopsis* and *Saportana* are also included within this group.

Form-genus PSYGMOPHYLLUM Schimper, 1870 emend. Saporta, 1878

- *1870 *Psygmophyllum* Schimper, p. 192.
- 1878 *Psygmophyllum* Schimper; Saporta, p. 869.
- 1927 *Psygmophyllum* Schimper; Halle, p. 214.
- 1982 *Psygmophyllum* Schimper; Burago, p. 133.
- 1989 *Psygmophyllum* Schimper; Yao, p. 171.

Type species. Psygmophyllum expansum (Brongniart) Schimper, 1870.

Psygmophyllum multipartitum Halle

Plate 1, figure 3; Plate 4, figures 1–2; Plate 5, figures 1–3;
Plate 6, figures 5–8

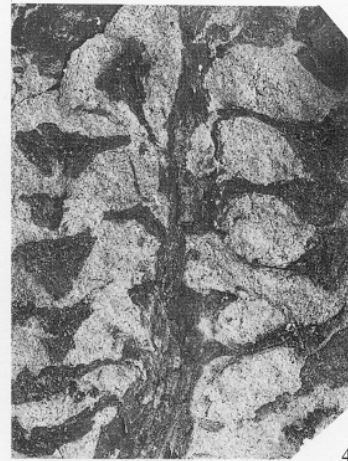
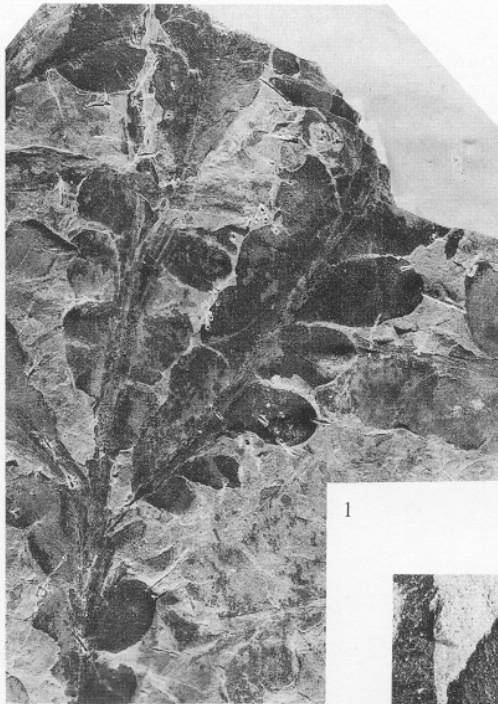
- *1927 *Psygmophyllum multipartitum* Halle, p. 214, pls 57–58.
- 1989 *Psygmophyllum multipartitum* Halle; Yao, p. 174, pl. 1, figs 1–7; pl. 2, figs 1–11; text-fig. 1.

Remarks. From their mode of preservation, foliage physiognomy, cuticles, and petiole anatomy, this species is interpreted as an aquatic or seasonally emergent plant with a rosette-like habit (Wang 1993b). The long, thick petioles extend from their base and then dissolve into a large, dissected lamina.

Halle (1927, p. 221) compared the general mode of division in these Chinese leaves with that of two Permian species from the Urals (*Psygmophyllum cuneifolius* (Kutorga) Schimper and *P. expansum* Brongniart). However, he suggested that they may be more closely related to *Odontopteris siberica* Zalesky from Kuznetsk, a species subsequently transferred first to *Iniopteris* (Zalesky 1934) and eventually to *Psygmophyllum* (Burago 1982). Burago's study was important because she demonstrated the great diversity of *Psygmophyllum* leaves from Angara and Subangara, and reclassified numerous genera from those floras as later synonyms of *Psygmophyllum* (*Syniopteris*, *Idelopteris*, *Iniopteris*, *Comipteridium*, *Biarmella*, *Uralopteris* and *Zalesskyella*). The Chinese specimens from the *Psygmophyllum* Zone illustrated in the present paper, which originate from various locations in Shanxi, show a similar diversity in gross morphology and are consistent with the generic diagnosis re-written by Meyen (1987, p. 221).

EXPLANATION OF PLATE 2

- Fig. 1. *Callipteris changii* Sze. TIGP 8837-1; apical part of frond showing overtopped branching; Gaomao village, Hequ district, Shanxi; middle Tianlongsi Formation, Upper Permian; $\times 1$.
- Fig. 2. *Chiropteris reniformis* Kawasaki. TIGP 8851-1; small leaf; Wangtao village, Qingyuan district, Shanxi; middle Tianlongsi Formation, Upper Permian; $\times 1$.
- Figs 3, 5. *Supaia* sp. A. Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian. 3, TIGP 9306-28; single pinnule; $\times 2$. 5, TIGP 9306-5; basal part of a large, forked frond; $\times 1$.
- Fig. 4. *Autunia*-type fructification. TIGP 9306-36; many megasporophylls attached to rachis, but from which seeds have become detached; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 2$.
- Fig. 6. *Supaia* sp. B. TIGP 8915-1; part of forked frond, with pinnules constricted at base; Hekou village, Xuangan district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 1$.



WANG, Permian plant fossils

There is relatively little known of the cuticles of the Subangara *Psygmophyllum* species. However, Meyen (1982, p. 60) claimed that they had petalocyclic stomata randomly arranged over the lamina. This is very similar to the stomata described from Chinese material by Yao (1989, p. 186). In fact, the specimens figured in the present paper (Pl. 6, figs 5–8) show that *P. multipartitum* exhibits considerable variability in its cuticular features.

Distinguishing *P. multipartitum* from the Angaran and Subangaran species is clearly difficult, although the former appears to have larger leaves which have a thicker limb, more rugose surface, less dissected lobes, and occasional vein anastomoses. There is also the possible phytogeographical difference, with *P. multipartitum* being considered as a Cathaysian endemic (Yao 1989), while the Uralian species were regarded by Meyen (1982) as endemic to Subangara. Durante's (1992, p. 29) proposal to establish *Psygmophyllopsis* for the Chinese specimens is unconvincing.

The floristic significance of *Psygmophyllum* has tended to be ignored by most palaeobotanists, due to its reputedly wide distribution in Angara, Cathaysia and Euramerica. In fact, the genus may be regarded as a distinctive group of Middle–Late Permian foliage from eastern Laurasia.

Form-genus NYSTROEMIA Halle, 1927

Type species. Nystroemia pectiniformis Halle.

Nystroemia pectiniformis Halle

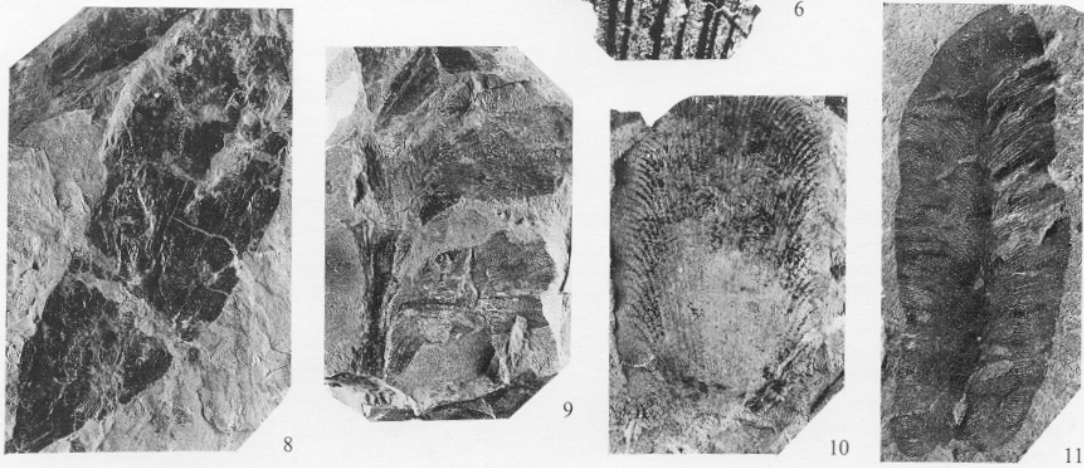
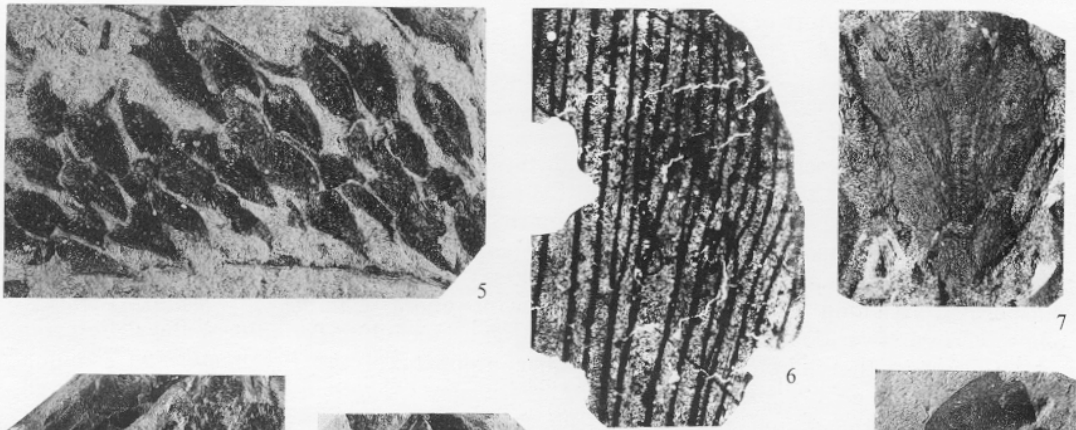
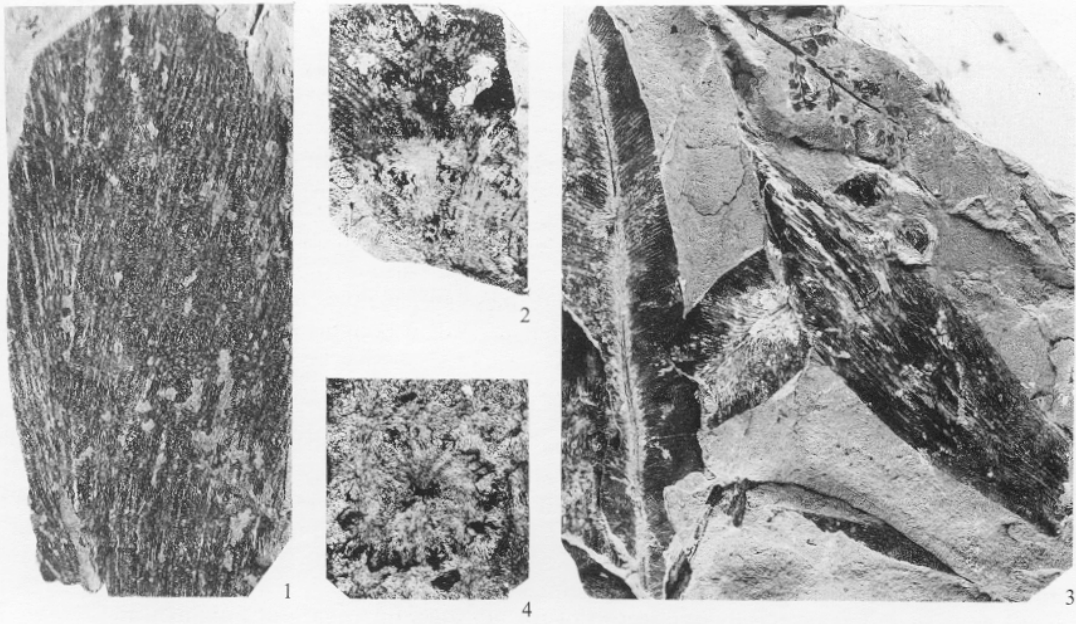
Plate 3, figure 5

*1927 *Nystroemia pectiniformis* Halle, p. 221, pl. 59.

Remarks. This type of inflorescence, bearing numerous possible ovules or seeds, is associated in Shanxi with *Psygmophyllum* foliage. Although not found in attachment, the constant association

EXPLANATION OF PLATE 3

- Figs 1–2. Aff. *Comia* sp. Large pinnae showing lateral veins clustered in fascicle. 1, TIGP 87Y5-28; Yaotou village, Yuanqu district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 2$. 2, TIGP 8833-6; Maliankou village, Hequ district, Shanxi; lower Tianlongsi Formation, Lower Permian; $\times 1$.
- Fig. 3. *Cordaites* sp. (right) and *Taeniopteris* aff. *tingii* Halle (left). TIGP 8833-5; reduced cordaitan leaf with denser venation in central part, more or less similar to *Zamiopteris*; Maliankou village, Hequ district, Shanxi; lower Tianlongsi Formation, Lower Permian; $\times 1$.
- Fig. 4. *Peltaspermum* sp. TIGP 9494-p; isolated peltate disc; Hekou village, Xuangan district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 2$.
- Fig. 5. *Nystroemia pectiniformis* Halle. TIGP 8851-8; fructification with many possible seeds, with two filiform hairs extending from the micropylar end of each seed; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 2$.
- Fig. 6. *Lesleya* sp. TIGP 8908-O; cuticles of apical part of leaf, showing rare anastomosing veins; Nanhegou village, Baode district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 2$.
- Figs 7–8. *Cordaites* sp. Upper Tianlongsi Formation, Upper Permian; $\times 1$. 7, TIGP TH1210-32; short leaf similar to *Petscheria*-type scales; Tianlongsi temple, Taiyuan district, Shanxi. 8, TIGP 9106-1; small leaf similar in outline to *Zamiopteris*; Nanhegou village, Baode district, Shanxi.
- Fig. 9. *Supaia* sp. A. TIGP 87Y5-19; partial frond showing its decurrent base; Yaotou village, Yuanqu district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 1$.
- Fig. 10. *Wattia* sp. TIGP K-1-18; aplebia-type scale; Kuantou village, Taiyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 1$.
- Fig. 11. *Supaia* sp. B. TIGP TH7126-21; isolated pinna, showing constricted base and fine, fascicular veins; Hoshan village, Jiaocheng district, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 1$.



WANG, Permian plant fossils

suggests that they may have belonged to the same plant. Two apical hairs extend from the top of each of the ovules, possibly indicating wind dispersal (Wang 1994). Although this type of inflorescence is so far unknown from Angara, Neuburg (1948) has reported *Samaropsis*-type seeds from Kuznetsk, with two apical, spine-like projections similar to those of *Nystroemia*.

Form-genus CHIROPTERIS Kurr in Bronn, 1858

Type species. Chiropteris digitata Kurr in Bronn, 1858, p. 143.

Chiropteris reniformis Kawasaki

Plate 2, figure 2

- *1925 *Chiropteris reniformis* Kawasaki, p. 27, pl. 17, fig. 56; pl. 18, figs 57–58.
1927 *Chiropteris reniformis* Kawasaki; Halle, p. 175, pl. 55, figs 5–8.

Remarks. This genus is another distinctive type of foliage found in the mid–upper parts of the Tianlongsi Formation, although it ranges down a little lower than *Psymphyllum*. The genus shows great diversity in gross morphology. It is generally smaller than *Psymphyllum*, with a more or less dissected limb, and the veins are anastomosing. *C. reniformis* has no midvein, but the other species, *C. kawasakii* Kon'no, sometimes shows a weakly developed midvein. The distinction of the latter from *Psymphyllum multipartitum* can sometimes be very difficult.

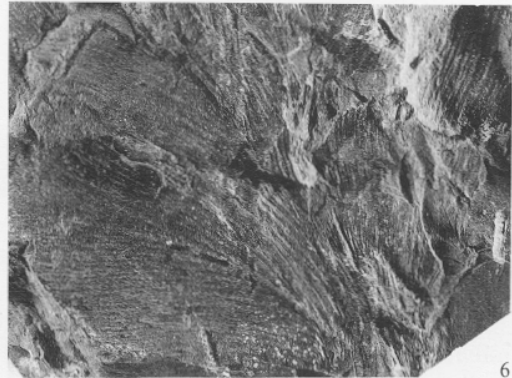
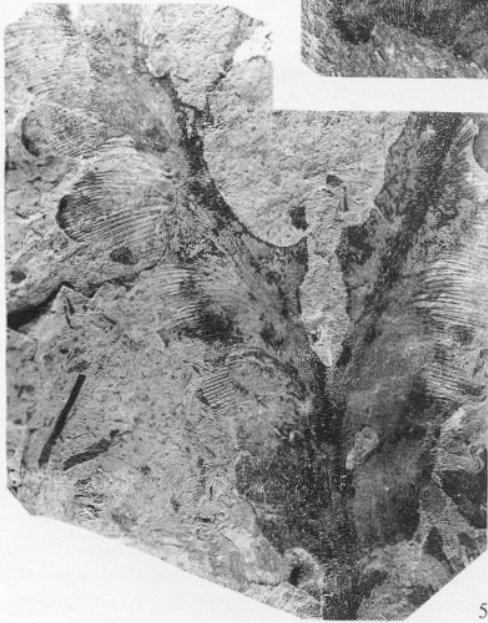
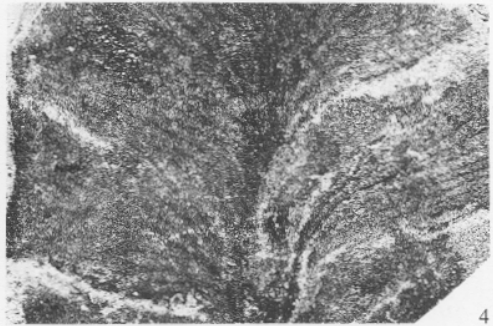
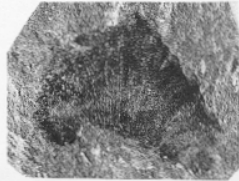
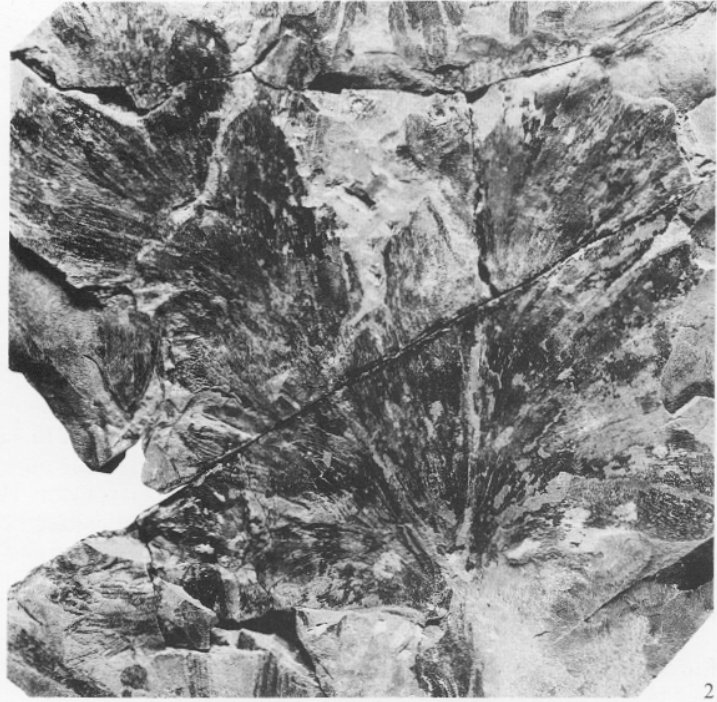
Until now, there has been only one record of the genus from Angara or Subangara: *Chiropteris palmilobata* Zalesky from the Upper Permian of Kuznetsk (Neuburg 1948, text-figs 25–26). This Angaran species has a more or less dissected lamina, rarely anastomosing veins and no midvein, and is thus very similar to *C. reniformis* from China.

PELTASPERMS

In this paper, the peltasperms are taken to include the callipterids and their associated fructifications, from the Permian, and the lepidopterids and their fructifications, from the Permo-Triassic. Kerp and Haubold (1988) revised much of the European material, and assigned it to a natural genus *Autunia*, and five foliage form-genera: *Dichyphyllum*, *Rhachiphyllum*, *Lodevia*, *Gracilopteris* and *Arnhardtia*. At the same time Meyen (1982, 1988) reviewed the Angaran and Subangaran peltasperms, assigning them to the foliage form-genera *Callipteris* (*Foenia*), *Comia* and *Compsopteris*, and various genera of reproductive organs, including *Permotheca* and *Peltaspermum*. In North China, the callipterids are the main component of the *Psymphyllum* assemblage, including the foliage *Callipteris*, *Supaia*, *Protoblechnum-Compsopteris* and *Comia*, as well as probably *Neuropteridium* and *Autunia*-like fructifications.

EXPLANATION OF PLATE 4

- Figs 1–2. *Psymphyllum multipartitum* Halle. Upper Tianlongsi Formation, Upper Permian; × 1. 1, TIGP TH1209-9; linear segment; Tianlongsi temple, Taiyuan district, Shanxi. 2, TIGP 87Y5-24; small leaf similar to that seen in Angaran species; Taotou village, Yuanqu district, Shanxi.
Fig. 3. *Cordaites* sp. TIGP 9010-1; leaf similar to the Angaran *Crassinervia*; Jiuxian village, Guxian district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.
Figs 4–6. Aff. *Comia* sp. 4, TIGP 9406-c4; partial pinna; Hekou village, Xuangan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 5, TIGP 8837-6; forked frond with fascicular veins; Gaomao village, Hequ district, Shanxi; middle Tianlongsi Formation, Upper Permian; × 1. 6, TIGP 87y5-29; large pinna showing venation; Yaotou village, Yuanqu district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.



WANG, Permian plant fossils

Form-genus *CALLIPTERIS* Brongniart, 1849 (*non* Bory, 1804)

- *1849 *Callipteris* Brongniart, pp. 66, 73.
- 1970 *Callipteris* Brongniart; Meyen, p. 525.
- 1980 *Callipteris* Brongniart; Barthel and Haubold, p. 49.
- 1981 *Callipteris* Brongniart (*non* Bory, 1804); Kerp, p. 660.

Type species. *Callipteris conferta* (Sternberg) Brongniart, 1849, p. 73.

Callipteris changii Sze

Plate 2, figure 1; Plate 6, figures 1–4

- *1954 *Callipteris changii* Sze, p. 83, pl. 1, fig. 1; pl. 3, fig. 2.
- 1989 *Callipteris changii* Sze; Si, p. 47, pl. 57, figs 1–3.

Remarks. Sze (1954) compared the leaf-size and venation of this species to those of the Angaran *C. zeilleri* Zalesky. However, its basic frond architecture, including features such as the presence of a pseudo-dichotomy in the distal part of the primary rachis (Barthel and Haubold 1980; Kerp 1988), appears to be identical to that of the European callipterids. The same architecture has also been demonstrated in a specimen of the Angaran *C. adzvensis* Zalesky from the Upper Permian of Pechora (Meyen 1983, pl. 10, fig. 1). The cuticles of *C. changii* (Pl. 6, figs 1–4) have clear papillae similar to the Angaran material (Meyen 1970). Meyen proposed that the Angaran callipterids with papillate, amphistomatic cuticles should be assigned to a separate sub-genus, *Foenia*, but the European callipterids were subsequently shown to have the same cuticular characteristics (Barthel and Haubold 1980) and so the distinction breaks down.

Callipteris? *laceratifolia* Halle

- *1927 *Odontopteris?* (*Callipteris?*) *laceratifolia* Halle, p. 118, pl. 32, figs 1–2 (*non* pl. 20, figs 15–17).
- 1974 *Callipteris?* *laceratifolia* Halle; Gu et Zhi, p. 123, pl. 93, figs 1–2.

Remarks. This type of callipterid is characterized by large fronds with more or less dissected pinnules, and its generic position is still in question. The species is restricted to the mid-upper part of the Tianlongsi Formation, where it forms a distinctive member of the assemblage. Interestingly, Neuburg (1948, p. 182) compared the Shanxi fronds to the Angara plant *Comia(?) primitiva* Neuburg from the Permian of Kuznetsk.

Form-genus *SUPAIA* White, 1929

Type species. *Supaia thinnfeldioides* White, 1929, p. 54.

Supaia spp.

Plate 1, figures 1–2, 6; Plate 2, figures 3, 5–6; Plate 3, figures 9, 11

Remarks. Two forms of *Supaia* have been recognized in North China. They will be formally described elsewhere, and will be referred to here simply as *Supaia* sp. A and sp. B. The genus is characterized by a dichotomous primary rachis producing two monopinnate branches. The individual pinnules of sp. A are broadly attached to the rachis and decurrent at the base, whilst in sp. B they are constricted at the base.

For a long time, the genus was regarded as characteristic of the Upper Permian of the western United States (Read and Mamay 1964; Chaloner and Meyen 1973). However, the fronds also occur widely in coeval strata in North China, forming one of the main components of the *Psygmodphyllum* Zone. In earlier Chinese studies, such bipartite fronds with monopinnate branches were mistaken for *Protoblechnum wongii*; examples include the specimen figured by Si (1989, pl. 65, fig. 2) from the Permian Shihhotze Group, and that designated *Compsopteris wongii* (Halle) Gu and Zhi (1974, pl. 130, fig. 6).

Rare evidence of *Supaia* has also been seen in the Upper Permian of Subangara and Angara. For instance, *S. tomiensis* Tschirkova from the Late Permian of Kuznetsk (Neuburg 1948, p. 131) and the specimens figured as *Callipteris bella* and *Comia biarmica* by Vladimovich (1986, pl. 140, fig. 6; pl. 149, fig. 4), from the Kungarian-Ufimian of the Urals, clearly have bipartite fronds. In addition, *Supaia tieliensis* Huang (1977), from the Upper Permian Hongshan Formation of north-east China, is from an Angaran terrane.

Form-genus PROTOBLECHNUM Lesquereux, 1880

Type species. Protoblechnum holdeni (Andrews) Lesquereux, 1880, p. 188.

Protoblechnum wongii Halle

- *1927 *Protoblechnum wongii* Halle, p. 135, pls 35–36; pl. 64, fig. 12.
1989 *Protoblechnum wongii* Halle; Liu, p. 447, pls 1–5 (*non* pl. 4, fig. 1).

Remarks. The superficial similarity between this species and the Angaran *Compsopteris adzvensis* Zalesky has been noted by many authors (e.g. Halle 1927; Sze 1954; Lee 1963; Meyen 1970) and Gu and Zhi (1974) went as far as to transfer Halle's species to *Compsopteris*. However, *P. wongii* has been revised recently by Liu (1989), based on numerous good specimens from the lower part of the Shihhotze Group, and it has been shown that the fronds were bipartite, with bipinnatifid branches. They thus clearly differ from the unforked, monopinnate fronds of *Compsopteris*. *P. wongii* is most abundant at levels below where *Supaia* occurs in North China, although its occurrence at higher levels cannot be ruled out. Using Asama's (1960) 'growth retardation' hypothesis, it is possible to interpret *Supaia* as a retarded form of a *Protoblechnum* frond, reflecting an increase in climatic aridity.

Form-genus COMIA Zalesky, 1934

- *1934 *Comia* Zalesky, p. 268.
1973 *Comia* Zalesky; Fefilova, p. 118.

Type species. Comia pereborensis Zalesky.

Aff. *Comia* spp.

Plate 3, figures 1–2; Plate 4, figures 4–6

Remarks. *Comia* is a monopinnate form-genus characterized by fascicled veins, found in Subangaran and Angaran assemblages. There has been a number of earlier records of similar specimens from the Permian of North China. For instance, the types of *Fascipteris hallei* Gu and Zhi (1974) have

a very similar venation, and Zhang *in* Zhang and Mo (1979) erected a new genus, *Fascipteridium*, for specimens from the 'Upper Shihhotze Formation' of Henan with fasciled veins. Xiao (1985, pl. 187, figs 2–3) described specimens as *Comia* sp. from the lower Upper Permian of Shanxi, while very similar specimens from higher stratigraphical levels were described as *Scytophyllum sunjiagouense* Wang and Wang (1986, pl. 16, figs 4–8). Illustrated here are isolated pinnae from the Tianlongsi Formation of North China, again with fasciled veins very similar to those of *Comia*.

Meyen (1970) argued that the specimen illustrated by Read and Mamay (1964, pl. 19, fig. 5) as *Callipteris* cf. *adzvensis* Zalessky from the Permian of North America, which also has fasciled veins, probably belongs to *Comia*.

Genus AUTUNIA Krasser, 1919

- *1919 *Autunia* Krasser, p. 20.
- 1982 *Autunia* Krasser; Kerp, p. 423.

Type species. *Autunia milleryensis* (Renault) Krasser, 1919, p. 20.

Autunia-type fructification

Plate 1, figure 5; Plate 2, figure 4

Remarks. The ovule-bearing reproductive structures figured in the present paper consist of small, spirally arranged, peltate megasporophylls, which are bilaterally symmetrical, and are very similar to *Autunia* as re-defined by Kerp (1982). They are closely associated with the foliage *Supaia* sp. A in one biostrome. They are quite different from the seed-bearing pteridosperm frond described by Mamay and Watt (1971), which resembles both *Callipteris* and *Supaia* of the Hermit Shale. On the other hand, they compare well with the specimens illustrated by Meyen (1982, text-fig. 18) as *Peltaspermum?* sp. A from the Upper Permian of Pechora, which were associated with *Compsopteris adzvensis* Zalessky foliage. There is clearly a possibility of a close relationship between *Supaia* and *Protoblechnum/Compsopteris* in Asia.

Genus PELTASPERMUM Harris, 1937

Type species. *Peltaspermum rotula* Harris, 1937, p. 34.

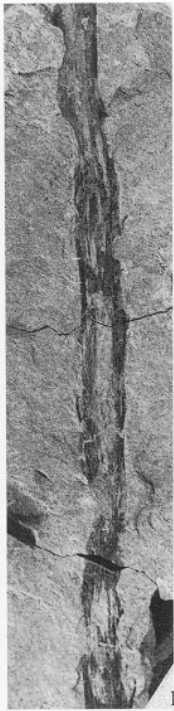
Peltaspermum sp.

Plate 3, figure 4

Remarks. A peltate disc, showing clear 'rib-lobelets', is indeed similar to *P. multicostratum* Zhang and Shen (1987a) from the C-bed of the Nanshan section.

EXPLANATION OF PLATE 5

Figs 1–3. *Psymphyllum multipartitum* Halle. Xinyu village, Qingshui district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 1, TIGP 8802-14; long petiole. 2, TIGP 8802-15; basal part of leaf with thick petiole. 3, TIGP 8802-11; average-sized leaf.



WANG, *Psymphyllum*

CORDAITEAN FOLIAGE

Besides the above mentioned pteridosperms, there are other plant fossils which give an Angaran feel to the assemblages, in particular the cordaite-like leaves. These leaves in the Permian of North China are mainly of the short, scale-like forms, probably reflecting the relatively arid climate. Some can be compared quite closely with Angaran cordaitean scales. For instance, one figured on Plate 3, figure 7 is very similar to the Upper Permian *Petscheria tomiensis* Zalesky of Kuznetsk (Neuburg 1948, p. 198, pl. 45, fig. 8) and another, on Plate 4, figure 3, hardly differs from a coeval specimen assigned by Durante (1976, pl. 70, fig. 5) to *Crassinervia* sp. nov. 1 from Mongolia. The specimen illustrated as Plate 3, figure 3 can be compared with *Zamiopteris*, as it has a denser venation in the central part of the leaf than near the margins (e.g. Meyen 1970, p. 530, pl. 77, fig. 1). The aphlebia-like scale shown in Plate 3, figure 10 appears identical to *Wattia*, a Permian genus of uncertain affinities, originally described from North America, but which was also recorded from the Kazanian of Subangara by Meyen (1982, pl. 16, fig. 128).

It should finally be pointed out that all specimens from Nanshan previously recorded as *Zamiopteris*, by both Russian and Chinese palaeobotanists, are almost certainly misidentified. They all show a rather pronounced midvein, and some of them compare more closely with the Euramerican leaves *Lesleya* and *Taeniopteris*.

PALAEOPHYTOGEOGRAPHY

During the Permian, the pteridosperms described above had an extensive distribution throughout the Northern Hemisphere, including Euramerica (western Europe, south-west USA), Angara, Subangara, Cathaysia and North China. I cannot therefore agree with Meyen (1982, 1987, 1988) that these plants were endemic to Subangara.

Western Europe

The callipterids have been traditionally used as an important index for the Lower Permian Rotliegend, in which they are very diverse, with one natural genus and five foliage form-genera (Kerp 1988). Broutin (1986) has also reported psygmyphylloid foliage from the Lower Permian of Spain. In the Upper Permian Zechstein flora, lepidopterids are common (Schweitzer 1986; Poort and Kerp 1990).

South-west USA

This area has yielded well documented pteridospermous assemblages. The Lower Permian Hermit Shales assemblages are dominated by *Callipteris*, *Supaia*, '*Brongniartites*', *Protoblechnum* and what Meyen (1970, p. 530) referred to as *Comia*. In addition, White (1929) described a questionable

EXPLANATION OF PLATE 6

Figs 1–4. *Callipteris changii* Sze. TIGP 8908-0; Nanhegou village, Baode district, Shanxi; upper Tianlongsi Formation, Upper Permian. 1, lower and upper cuticles; $\times 4$, 2, fragment of lower cuticle; $\times 100$. 3, lower cuticle from pinnule apex; $\times 60$. 4, upper cuticle from pinnule apex; $\times 60$.

Fig. 5. *Psygmyphyllum multipartitum* Halle. TIGP 9016-2; thin cuticle; Jiuxian village, Guxian, Shanxi; upper Tianlongsi Formation, Upper Permian; $\times 60$.

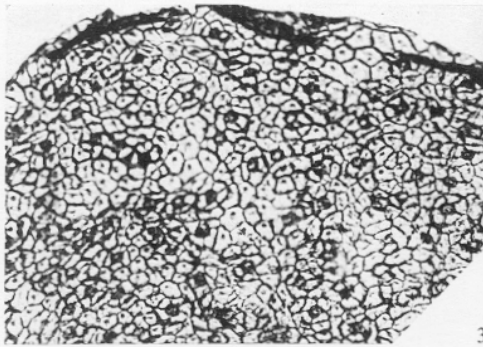
Figs 6–8. *Psygmyphyllum multipartitum* Halle. Thick cuticles showing stomata varying from randomly distributed (6) to arranged in regular files (7–8); upper Tianlongsi Formation, Upper Permian; $\times 60$. 6, TIGP 9016-2; Jiuxian village, Guxian, Shanxi. 7, TIGP 8912-1; Hekou village, Xuangan district, North Shanxi. 8, TIGP 8822-25; Shandaogou village, Pingliang district, East Gansu.



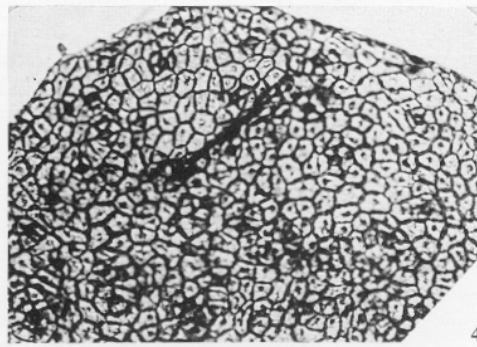
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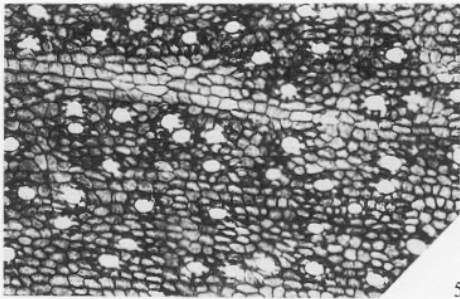
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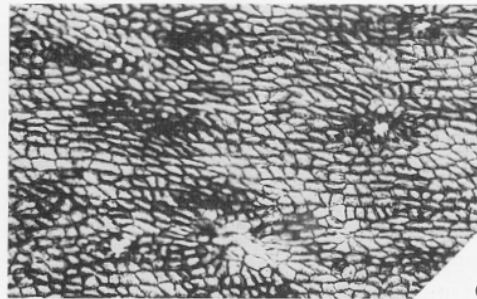
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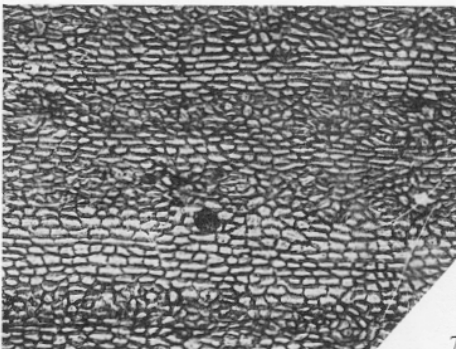
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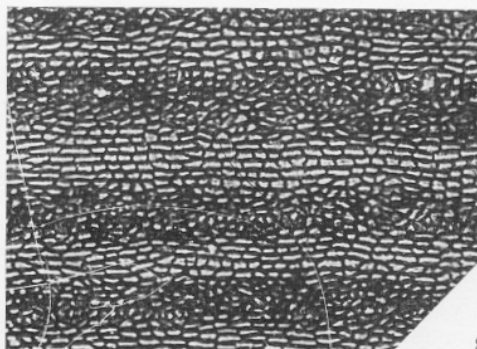
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6



7



8

Psygomophyllum from these strata. The Upper Permian (Leonardian) is, in contrast, characterized by unusual giantopterids and taeniopterids (e.g. Mamay *et al.* 1984).

Subangara

Meyen (1981) proposed the name Subangara for the western periphery of Angara proper during the Permian, including most of what was previously called West Angaraland (Meyen 1978a), i.e. the Russian Platform, the Urals, west and south Kazakhstan, etc. In the Late Permian, 'the Subangara flora spread out to the south and east from areas proximal to the Urals' (Meyen 1987, p. 309). He regarded it as an intermediate zone (ecotone) between the Angara and adjacent areas; it yielded typical Angaran elements (*Rufloia*, *Protosphagnum*, *Paracalamites*) associated with elements characteristic of the other areas: the Euramerican *Quadrocladus*, *Pseudovoltzia* and *Callipteris*; the North American *Wattia* and *Pseudovoltzia*-like conifers; the Cathaysian *Lobatannularia* and *Taeniopteris*, amongst others (Meyen 1982, p. 73; 1987, p. 308). Significantly, most of the elements regarded by Meyen as endemic to the Subangara belt are peltasperms (*Callipteris*, *Compsopteris*, *Peltaspermum*, etc.) and psygomophylloids (*Syniopteris*, *Psygomophyllum*), which are found in strata of Artinskian to Tatarian age.

Vladimirovich (1986) illustrated most of the c. 160 species that have been described by Russian palaeobotanists from the Asselian to Tatarian floras of the Urals and Russian Platform. In the Artinskian to Ufimian interval, 15 per cent. of the reported genera are peltasperms (*Callipteris*, *Comia*, *Permotheca*, 'Odontopteris') and psygomophylloids (*Syniopteris*/*Psygomophyllum*). The total assemblage comprises 69 species belonging to 38 genera, and includes some Angaran elements (*Rufloia*, *Viatcheslavia*, *Zamiopteris*, *Paracalamites*) together with some common Euramerican form-taxa (*Pecopteris*, *Sphenopteris*, *Walchia*, *Calamites*, *Cordaites*, etc.). The Kazanian to Tatarian has yielded 21 plant form-genera. Many of the Lower Permian callipterids were replaced by *Phylladoderma*, *Tatarina* and *Peltaspermum*, amongst others, although rare *Comia*, *Brongniartites*, 'Odontopteris' and *Syniopteris* persisted; together, the callipterids make up 40 per cent. of the genera. Only a few Angaran elements, such as *Paracalamites*, persisted into these later assemblages. It is noteworthy that, in the Asselian to Sakmarian, assemblages listed by Vladimirovich with only Euramerican elements are rare. On the other hand, Angaran taxa are not dominant in any part of the Permian of western Subangara, and only in the Kungurian do they achieve any sort of diversity, reaching a maximum of 17 per cent. of the assemblage (e.g. *Rufloia*, *Paracalamites*, *Crassinervia*, *Zamiopteris*, *Nephropsis*).

In south-western Kazakhstan, Salmenova (1979) recognized four successive plant assemblages in the Upper Carboniferous and Permian. All four included characteristic Euramerican form-taxa (*Calamites*, *Walchia*, *Lebachia*, *Dicranophyllum*, etc.). Only in the uppermost assemblage do rare and questionable Subangaran elements occur (*Paracalamites*, *Noeggerathiopsis?*, *Koretrophyllites?*), associated with Euramerican elements (e.g. *Dzungariella*, *Chulakia*, *Peltaspermum*, *Ullmannia*, *Voltzia*). *Chulakia* may be a type of cycad cone scale similar to *Tianbaolinia* from the Permian of Shanxi (Gao and Thomas 1989), while *Peltaspermum dzungariense* Salmenova has been transferred to *Autuniopsis* by Poort and Kerp (1990). The palaeophytogeographical position of this area has been discussed by several authors (Meyen 1982; Chaloner and Creber 1988; Cleal and Thomas 1991). Superficially, the assemblage appears to be most similar to the Zechstein flora of western Europe. However, Cleal and Thomas (1991, p. 164) have argued that it in fact represents an ecotonal assemblage between Angara and Cathaysia, and that its apparent Euramerican aspect is the result of errors of biostratigraphical and taxonomic interpretation.

Southern periphery of Angara

This belt, which Meyen claimed to be the extension of Subangara to the south and east in the Late Permian, is situated to the south of the suture between the Siberian Platform and the Sino-Korean Block, and extends from the Junggar (Dzungar) Basin of North Xinjiang (China) in the west, via

southern Mongolia and the northern Da Khinggan Range of north-east China, to the South Primorye.

In the Junggar Basin, the Upper Permian *Callipteris-Comia* assemblage consists of 19 genera, including *Callipteris*, *Comia*, *Compsopteris*, *Supaia?* and *Iniopteris* (= *Psygmo-phyllum*) (Dou and Sun 1985a, 1985b). The assemblage overlies the *Angaropteridium-Zamiopteris* assemblage, and includes a mixture of Angaran (*Zamiopteris*, 'Noeggerathiopsis', *Crassinervia*), Euramerican (*Walchia*, *Ullmannia*, *Taeniopteris*, *Schizoneura*) and rare Mesophytic (*Pterophyllum*, *Sphenobaiera*) elements.

Durante (1976, tables 1–2, p. 80) described five plant assemblages in the Carboniferous and Lower Permian of Mongolia, and two assemblages from the Upper Permian. In south Mongolia, the Upper Carboniferous to Lower Permian assemblages are typically Angaran, with *Angaropteridium*, *Angaridium*, *Zamiopteris*, *Gaussia*, *Vojnovskya*, *Ruflo-ria*, *Crassinervia*, *Nephropsis*, *Cardioneura*, *Tomiodendron* and *Angarophloios*. The Upper Permian assemblages, as well as including *Callipteris*, *Comia*, *Iniopteris* and *Compsopteris*, together with Angaran elements such as *Zamiopteris*, *Ruflo-ria*, *Lepeophyllum*, *Crassinervia* and *Paracalamites*, contain elements also found in the Permian of North China (*Taeniopteris*, *Cladophlebis*, *Sphenopteris*, *Pecopteris*, *Rhipidopsis*, etc.). The psygmo-phylloids and peltasperms comprise about 16 per cent. of the 25 genera in both assemblages.

A synthesis of the Carboniferous and Permian plant fossils from the northern Da Khinggan Range has been presented by Huang (1993). The assemblages from the Carboniferous (referred to as the Baolige flora) are typically Angaran and include 'Noeggerathiopsis', *Lepeophyllum* and *Nephropsis*. The Upper Permian contains some of these Angaran elements, together with *Callipteris*, *Comia*, *Supaia*, *Compsopteris*, *Rhipidopsis*, *Crassinervia* and *Paracalamites* amongst others, but also includes taxa characteristic of the Permian of North China, such as *Schizoneura*, *Pecopteris*, *Taeniopteris*, *Nilsson-ia* and *Pterophyllum*. Huang thus suggested that this reflected a northwards migration of the North China vegetation during the Late Permian.

In the South Primorye, Zimina (1977) has described the plant fossils from three Permian Formations as being typically Angaran, with *Zamiopteris*, *Vojnovskya*, *Ruflo-ria*, *Gaussia*, *Angaropteridium*, *Paracalamites*, *Crassinervia* and *Annulina*, amongst others. The Upper Permian also included the callipterids *Callipteris*, *Compsopteris* and *Comia*. She also described leaves with a midvein and anastomosing lateral veins as *Glossopteris*, although they are more likely to be fragments of *Psygmo-phyllum* leaves.

More recently, Burago (1986, 1989) reported a 'Cathaysian flora' from the Kazanian–Tatarian of the South Primorye, consisting of some 200 species. They included species of *Bico-emp-lectopteridium* (= *Gigantonoclea*), *Annularia*, *Protoblechnum*, *Lobatannularia*, *Pecopteris*, *Callipteris*, *Comia*, *Neuropteridium*, *Syniopteris* and *Taeniopteris*, which are all undoubtedly common plants of what is referred to in the present paper as the *Psygmo-phyllum* assemblage of North China. They were associated with a number of typically Angaran elements (e.g. *Zamiopteris* and *Ruflo-ria*-like leaves). Among the approximately 50 genera in this Sizinskaya flora, 14 per cent. were either peltasperms (*Callipteris*, *Comia*, *Protoblechnum*, *Peltaspermum*), *Phylladoderma* or psygmo-phylloids (*Psygmo-phyllum*, *Ginkgo-phytopsis*).

From the above, it is clear that the fossil record reflects significantly different vegetational histories between Subangara and its extension. In the west, psygmo-phylloids and peltasperms occurred throughout the Permian, sometimes in association with Angaran plants; in the south and east, these pteridosperms did not appear until the Late Permian, the Early Permian vegetation being typically Angaran in character.

Angara proper

The most typical Angaran assemblages are found in the Kuznetsk Basin, where the Lower and Upper Permian are known respectively as the Upper Balakhonskaya and Kolchuginskaya 'subseries'. Meyen (1982) assigned the former to the *Ruflo-ria* Cordaitan 2 Assemblage, dominated

by the typical Angaran taxa *Ruffloria*, *Vojnovskya*, *Gaussia*, *Zamiopteris*, *Crassinervia*, *Nephropsis* and *Lepeophyllum*. In contrast, the Kolchuginskaya 'Subseries' was placed in his *Ruffloria-cordaitean* 3(–4) Assemblage, containing *Callipteris*, *Comia*, *Compsopteris*, *Supaia* and psymgophylloids (*Iniopteris*). The photographic illustrations of the Kuznetsk Upper Permian plant fossils by Neuburg (1948) show that, in addition to the callipterids listed above, there are also present in the Kuznetsk taxa very similar to those found in similar aged strata in North China, e.g. *Pecopteris anthriscifolia* (Göppert) Zalessky (as pointed out by Halle 1927) and *Taeniopteris norinii* Halle. *Annularia lanceolata* var. *tenuinervis* Radchenko (Neuburg 1948, pl. 3, fig. 2) has bi-lobed leaf whorls similar to *Lobatannularia*. Also, *Zamiopteris glossopteroides* Schmalhausen (Neuburg 1948, pl. 45, figs 1–2) is very similar to *Lesleya* in North China. These taxa form only a small portion of the overall flora, but may be of considerable palaeophytogeographical significance.

The palaeobotany of the famous Pechora area of north-west Angara has been reviewed by Meyen (1982). A few plant fossils occur in the Artinskian, but are too poorly preserved to identify. The higher horizons were divided into the Vorkutskaya (Kungurian–Ufimian) and Pechorskaya (Kazanian–Tatarian) 'series'. The Vorkutskaya plant assemblages are dominated by *Ruffloria-cordaitean* elements (*Ruffloria*, *Vojnovskaya*, *Zamiopteris*, *Crassinervia*, *Nephropsis*), associated with mosses (*Protosphagnum*, *Intia*), articulates (*Sphenophyllum*, *Annularia*, *Annulina*, *Phyllothea*), ferns (*Sphenopteris*, *Pecopteris*, *Danaeites*), conifers (*Walchia*) and *Psymgophyllum expansum*. In the uppermost part of the 'Series', rare callipterids (*Callipteris*, *Compsopteris*) appear, and become increasingly diverse at higher levels. In the upper Pechorskaya, these groups, including *Callipteris*, *Peltaspermum*, *Comia*, *Compsopteris*, *Permothea* and *Psymgophyllum*, form about one-sixth of the 43 genera found. Meyen (1982, p. 71) reported that the Pechora Palaeoarea grades into the Subangara Palaeoarea to the south, indicating a close relationship between the two regions in the Late Permian.

In the north-eastern part of Kazakhstan (e.g. Balkhash) which belongs to Angara proper, Salmenova and Koshkin (1990, pp. 40–51) recognized three plant-bearing horizons in the Permian. Mostly, they are dominated by typically Angaran elements (*Ruffloria*, *Zamiopteris*, *Paracalamites*, *Angaropteridium*). However, the highest one also contains a few peltasperms (*Peltaspermum*?) and psymgophylloids (*Rhipidopsis* and *Psymgophyllum*, assigned by Meyen).

To summarize, the peltasperms and psymgophylloids did not appear in Angara proper until the Late Permian, which is significantly later than in Subangara. They are also much less diverse than in Subangara.

THE GREAT EURASIAN FLORAL INTERCHANGE

The collision of the Siberian plate with Laurasia was the most important tectonic event in the Northern Hemisphere during the Permian. Initially, the European (Baltic) Platform collided with Siberia in the Early Permian, while the Sino-Korean Block did not fuse with the rest until the Late Permian (Nie *et al.* 1990, p. 406; Scotese and McKerrow 1990, p. 17). This difference in timing is in full agreement with variations in the vegetational histories in the western and southern parts of Subangara, as discussed above. It would appear to be contradicted by the palaeomagnetic data (Opdyke *et al.* 1986; Zhao and Coe 1987) which suggests that there was a considerable latitudinal difference between Siberia and the Sino-Korean Block at the end of the Permian, hindering floral interchange between the blocks. However, Scotese and McKerrow (1990, p. 17) have proposed that the western part of the Sino-Korean Block (Tarim) collided with Siberia in the Early Permian, while the north-eastern part of China (Manchuria) did not fuse with Siberia until the Late Permian. This would explain the apparent latitudinal separation between the two blocks, while still allowing floral interchange.

The relative positions of the North and South China blocks in the Permian is also not certain, due to the superimposition of post-Palaeozoic tectonic movement (Sengör 1985).

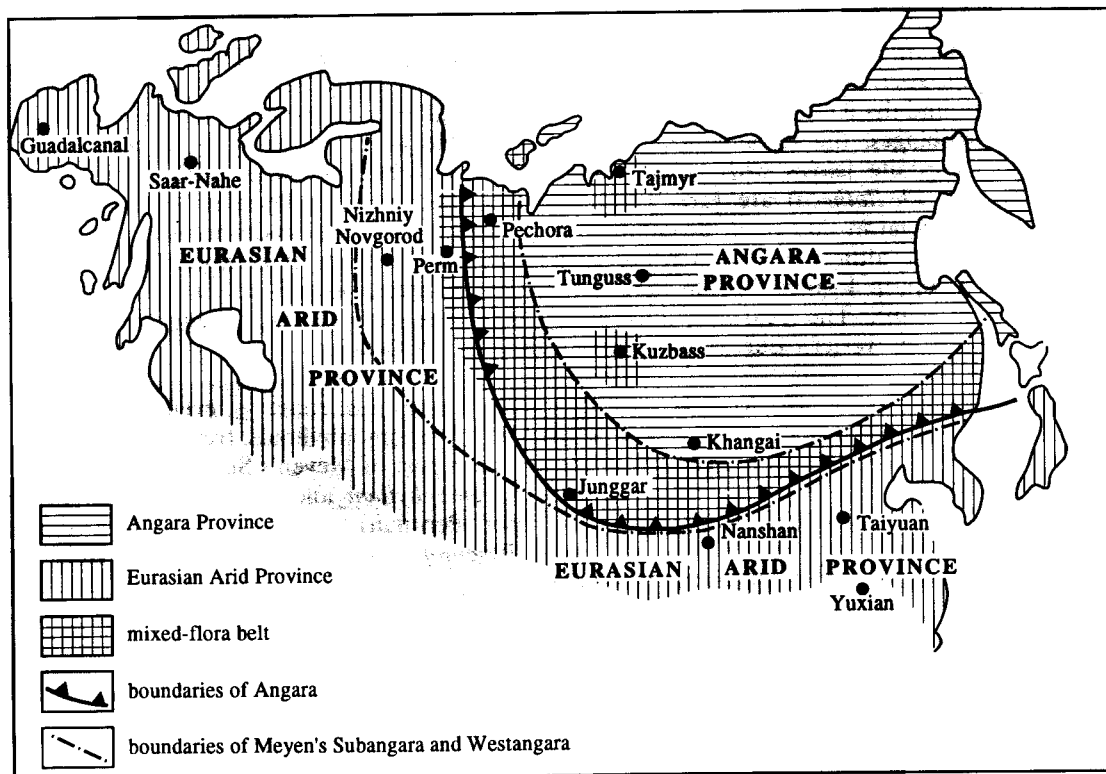
Based on palaeobotanical evidence, Wang (1985, p. 39) proposed that, during the Permian and Triassic, the North China Block was much closer to western Europe than at present, adjacent to the

Urals. This has been further supported by a map showing the expansion of the Isoetaceae during the Triassic (Wang 1991, text-fig. 11).

Floral migrations

Biotic migration or invasion is a topic of current interest in both palaeontology (e.g. Chaloner and Lacey 1973; Vermeij 1991; Webb 1991) and biology (e.g. Sauer 1988; Hengeveld 1989). However, establishing the details of such large-scale biotic movements in such distant times as the Permian is difficult, due to lack of reliable data and a feasible mechanism.

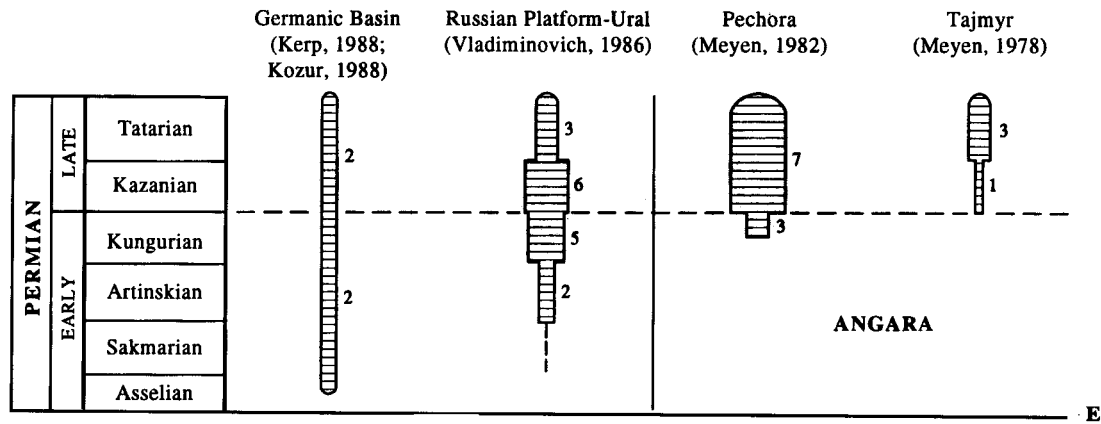
I recently proposed that there had been a northwards migration of the Permian vegetation in North China (Wang 1994). This was based on an ascending trend of the first occurrences of *Psymophyllum* in a series of ten sections of the Tianlongsi Formation from the south to the north of Shanxi. A similar method can also be used to estimate larger-scale vegetational migrations, such as that being considered in this paper. Using this approach, the data suggests that there had been two discrete routes by which low-latitude vegetation migrated into the Angara region (Text-fig. 2):



TEXT-FIG. 2. Upper Permian palaeophytogeography of Eurasia.

a western route, from western Europe, via the Russian Platform, into Pechora and Tajmyr; and a southern route from North China, via south Mongolia to the Kuznetsk.

Western route (Text-fig. 3). Vegetational migration along this route is indicated by the first occurrences of the callipterids. In western Europe, they first appear in the Lower Permian



TEXT-FIG. 3. Ranges and diversity of peltasperm and psygmyphyloids genera (combined) in the Permian, from west Europe to Siberia.

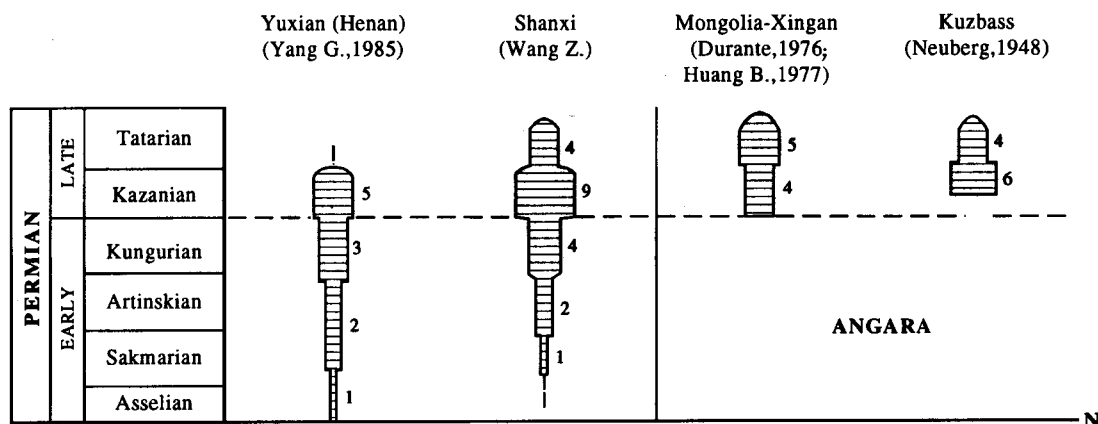
Rotliegend with *Autunia*, and are replaced by lepidopterids with ovuliferous *Peltaspermum* in the Upper Permian Zechsteins.

In the Urals and the Russian Platform (Subangara), the callipterids first appear in the Artinskian. In these assemblages, the Euramerican gymnosperms tend to be dominant, and the Angaran *Ruffloria*-like cordaite leaves with narrow dorsal furrows, and articulates with narrow stems (*Paracalamites*, *Phyllothea*) are rare. Farther east in Pechora, the Permian assemblages are dominated by Angaran taxa, and the callipterids (and psygmyphyloids) do not appear until the Lower Kungurian, although they then persist right up to the topmost Permian (Meyen 1982). Further east again, in Tajmyr (Meyen 1982, p. 70), the callipterids do not appear until the Upper Permian (Kazanian). The evidence thus clearly indicates an eastwards migration of these pteridosperms from western Europe to Angara during the Permian.

Southern route (Text-fig. 4). Vegetational migration along this route is even more clearly demonstrated by the ascending trend of first occurrences of psygmyphyloids, from northern South China, via North China (Henan, Shanxi) and the southern part of Meyen's Subangara, to Angara proper. In Jiangsu and Fujian of South China, *Psygmyphyllum* and *Compsopteris* (= *Protoblechnum*) occur in the Longtanic (Lower-Upper Permian), in association with typical Cathaysian elements (Yao 1989). In Central Henan, *Psygmyphyllum* first occurs in the middle part of the 'Upper Shihhotze' Formation, becoming progressively more diverse until it reaches a maximum in the upper part (Yang 1985). In North Shanxi, the first occurrence of the psygmyphyloids is rather higher, in the upper Tianlongsi Formation (Wang 1992).

Farther north, in the northern Khinggan Range and in south Mongolia, the Kazanian peltasperm-bearing strata immediately overlie upper Carboniferous-Lower Permian deposits with typical Angaran assemblages including *Angaropteridium*, *Zamiopteris* and *Ruffloria*, corresponding to the Balakhongskaya assemblages of the Kuznetsk (Huang 1993; Durante 1976). Finally, a few callipterids and peltasperms appear in Angara proper in the upper Kazanian, where they persist through to the end of the Permian in association with the declining Angaran taxa. In comparison with the western migration route, the southern migration was on a much larger scale, and was also more complex, involving both Permian components from North China and Cathaysian elements from South China (Wang 1989).

It is noticeable that there was little reverse migration of plants from Angara into the adjacent areas. Some of the few exceptions include the rare presence of the Angaran taxa *Ruffloria* and *Paracalamites* in the Kungurian of western Subangara, associated with the previously mentioned



TEXT-FIG. 4. Ranges and diversity of peltasperm and psygmophylloid genera (combined) in the Permian, from North China to Siberia.

pteridosperms (Meyen 1982, p. 74). However, it never occurred to the same extent as the migration in the other direction.

In summary, after the collision of the Laurasia and Siberia plates in the Permian, there was a marked floral interchange, predominantly of Euramerican and Chinese elements into Angara, although also to a lesser extent in the opposite direction. The former was by far the more marked, representing the movement of plants over hundreds or thousands of kilometres, from either Euramerica or South China into Siberia. The reverse migration, in contrast, merely represents the outwards diffusion of a few Angaran taxa into the areas marginal to Siberia, such as the Urals and the Russian Platform.

Meyen's (1982, p. 77) comments on the position of the Subangaran assemblages are confusing. On the one hand he stated that 'since the Early Permian, the Angara Kingdom was divided into the Angara and Subangara areas', which implies that the Angara Kingdom contracted due to floral invasion from adjacent areas. On the other hand, he clearly suggested that the Subangara flora with its endemic pteridosperms was expanding from areas proximal to the Urals, eventually arriving in Nanshan in North China. This can make it difficult to distinguish between what are Subangaran and what are Angaran taxa, and may give the misleading impression of an expanding Angara.

An asymmetrical interchange

Marked asymmetry in the pattern of migration is a characteristic of almost all well known biotic interchanges, usually reflecting an imbalance in the ecosystems. Such an asymmetry is clearly observable in the Permian floral interchange between Angara and Laurasia. Among the taxa discussed in this paper, most are Eurasian genera that migrated towards Angara: pteridosperms *Callipteris*, *Comia*, *Compsopteris*, *Rhaphidopteris*, *Supaia*, *Peltaspermum*, *Phylladoderma*, *Tatarina*, *Psygmophyllum*, *Rhipidopsis*, *Chiropteris*, *Neuropteridium*, *Gigantonoclea*; conifers *Walchia*, *Ullmannia*; cyads *Nilssonia*, *Taeniopteris*, *Pterophyllum*; ginkgos *Sphenobaiera*, *Dicranophyllum*; and articulates *Calamites*, *Schizoneura*, *Lobatannularia* and *Annularia*. In contrast, only five Angara genera migrated into the adjacent areas (*Rufloia*, *Zamiopteris*, *Crassinervia*, *Nephropsis* and *Paracalamites*). Although the data presented in this paper are still far from complete, it is already evident that the appearance of exotics in Angara, either via the western or southern route, is roughly coincident with when those taxa achieved their greatest diversity.

The invasion of exotics can result in the extinction of endemic taxa. An outstanding example is the Great American Biotic Interchange (Marshall 1981), which resulted in a mass extinction of the endemic vertebrates in both North and South America during the Cenozoic. The floral interchange

that is the subject of this paper has been interpreted as one of the three major palaeobotanical events during the Permian of North China (Wang 1989), and may have resulted in increased extinction rates. This in turn may have resulted in an acceleration of the transition from Palaeophytic to Mesophytic vegetation towards the end of the Permian. When interpreting the Palaeophytic–Mesophytic transition in North China, I previously suggested (Wang 1992) that the unidirectional migration of the *Psymphyllum* assemblage might be linked with the end-Permian mass extinction, that caused the disappearance of many Palaeozoic dominants, such as cordaitaeans, lepidodendroids, calamites and sphenophylls. Meyen (1982, p. 79) also pointed out that the invasion of Mesophytic elements from Subangara may have reduced the areal extent of Angara and eventually caused its end.

Mechanism

Seed dispersal is obviously one of the main means of seed-plant migration and can be strongly influenced by environmental selection (Sauer 1988); high-speed winds can provide an effective means of dispersing seeds over large distances (Hengeveld 1989). Many of the Permian gymnosperms of North China were particularly well adapted to wind dispersal, such as the platyspermic *Samaropsis*-like seeds of callipterids, the winged *Pityospermum* and the plumed *Nystroemia* (Wang 1994).

In general, plant migration is the result of two types of dispersal: short- and long-distance. According to Hengeveld (1989), short-distance dispersal was the result of neighbourhood diffusion between adjacent areas, while long-distance reflects discontinuous jumps between non-adjacent areas and consequently progressed patchily.

A vast semi-arid area, known as the Eurasian Arid Province (Wang 1985) had developed and expanded after the collision between the Siberian Platform and Laurasia. In western Europe, aeolian sandstones and evaporites began to be deposited in the Early Permian (Glennie 1972; Turner 1980). Such deposits extended into North China in the Late Permian (Norin 1924; Wang 1993a), where there is evidence of alternating arid and wet climates with seasonal rainfall. This resulted in the vegetation being restricted and subdivided into small niches, where it would have been subjected to strong selective pressure, and where long-distance, 'jump' dispersal would have had to play a significant role.

As stated above, the migration of gymnosperms into Angara may have been by long-distance, 'jump' dispersal. In contrast, the much weaker migration of Angaran plants into Subangara may reflect short-distance dispersal by neighbourhood diffusion. The mechanism behind these migrations was probably influenced most strongly by palaeowind activity and moisture-limitation.

Monsoon activity. I have argued earlier (Wang 1993a) that the northwards migration of the *Psymphyllum* assemblage was linked with the palaeomonsoon prevailing in North China in the Permian. The existence of the Palaeomonsoon is indicated by several phenomena, such as the deposition of biotic silica indicating coastal upwelling, and the taphonomy of *Psymphyllum* indicating deposition in ephemeral channel deposits resulting from rainstorms in an alternating wet–arid climatic setting. In the Permian palaeogeography of Nie *et al.* (1990), North China is located on the north-eastern margins of Palaeotethys, at latitudes of 20°–30° and thus within the range of the monsoonal circulation. The existence of a strong monsoonal system having developed in West Pangaea during the Sakmarian (Early Permian) is supported by Patzkowsky *et al.* (1991) using the Fujita–Ziegler palaeoclimatic model. The patchy dispersal of the vegetation in North China in the Middle–Late Permian (Wang 1992) also supports its movement by long-distance wind dispersal.

Moisture-limitation. Such stress can be a major factor promoting plant migration, especially in vast arid and semi-arid areas. For example, the steppe of the Sahel zone, along the southern margins of the Sahara desert, moved up to over 100 km per annum between 1984–1985 (estimated from satellite observation; Tucker *et al.* 1991). In the Great American Interchange, increasing aridity of the subtropical regions also resulted in an asymmetrical interchange, i.e. the southwards movement of the Savanna-adapted biota through the American tropical zone during the Cenozoic (Webb 1991).

After the collision between Siberia and Laurasia, an imbalance of ecological pressure occurred on the two sides of the plate suture. On the Laurasian side, there was the Eurasian Arid Province, where moisture-limitation must have imposed a major stress on the vegetation. On the other side of the suture, such stress was far less marked and an archaic flora with low levels of innovation had developed there (Meyen 1982, p. 78). This strong asymmetry would clearly favour the migration of the newly evolved and more innovative plants from Eurasia, where they would have a competitive advantage over the more primitive Angaran vegetation.

Much of the above evidence for the Great Eurasian Floral Interchange in the Permian is based on the relationship between Angara and North China. However, it almost certainly involved other regions, such as South China and Euramerica. There is clearly much potential for future work in establishing the detailed patterns of vegetational migration during this key time in the evolution of terrestrial vegetation.

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WANG ZI-QIANG

Tianjin Institute of Geology and Mineral Resources
Chinese Academy of Geological Sciences
No. 4, 8th Road, Dazhigu, 300170
Tianjin, People's Republic of China

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