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A new and diverse plant fossil assemblage from the upper Westphalian Benxi Formation, Shanxi, China, and its palaeofloristic significance

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Abstract – A diverse assemblage of Carboniferous plant fossils occurs in the upper Benxi Formation at the Kaihuagou Section near Taiyuan, Shanxi, China. It consists of impressions and fusain fragments, the latter revealing anatomical details. Unlike previously published assemblages from the Benxi Formation, there are no pteridosperms, but a predominance of noeggerathioids and fern fragments. There are three new species: *Achlamydocarpon taiyuanensis*, *Conchophyllum suboblongifolium*, and the first reported example of a *Selaginella* from the Carboniferous System of China, *S. benxiensis*. The arborescent lycophytes do not to belong to *Lepidodendron*, as previously claimed, but to *Synchysidendron*, and three new combinations are therefore proposed for species from the Benxi Formation: *S. galeatum*, *S. subrhombicum* and *S. tripunctatum*. The Benxi Formation flora represents a transition between the tropical swamp vegetation represented in the Westphalian floras of Europe and North America, and the Stephanian and Permian Cathaysian floras of China. It is evidence of an essential continuity between the Late Palaeozoic vegetation of the western and eastern tropics, which should be united as a single phytochorion, the Amerosinian Realm.

1. Introduction

The Benxi Formation consists of Pennsylvanian ('Late Carboniferous') shallow marine and lagoonal deposits formed on the Sino-Korean Craton (the North China Region *sensu* Yang, Li & Gao, 1983). It unconformably overlies Ordovician basement, and is conformably overlain by coal-bearing Taiyuan Formation (Yang, Li & Gao, 1983; Zhang, 1987; Xu *et al.* 1987; Liu, 1990). It is up to 350 m thick in Liaoning Province, but thins to the south and west and is a mere 20–30 m thick in Shanxi. The lower beds (Iron Minerals Member) are mainly argillaceous with iron ores and bauxite. The rest of the formation (Bangou Member) consists of alternating marine limestones and coal-bearing strata. The coals are not associated with palaeosols and may be allochthonous. Fusilinids from limestones in the Bangou Member belong to the *Fusulina-Fusulinella* Biozone (Sheng, 1958; Zhang *et al.* 1987; Rui & Hou, 1987) and correlate with Myachkovsky 'Horizon' (upper Moscovian) faunas of the Ukraine. They thus correlate with upper Westphalian D to lower Cantabrian sequences in Western Europe (Wagner & Winkler Prins, 1985).

Benxi Formation plant fossils were first reported by Schenk (1883). However, they tend to be more fragmentary than the Cathaysian floras from the overlying Taiyuan Formation (e.g. Halle, 1927; Stockmans & Mathieu, 1939, 1957; Li, 1963) and have subsequently attracted less attention. Stockmans & Mathieu (1939, 1957) described some Benxi Formation fossils from the Kaiping Coalfield (Hebei Province), and Li (1957) described an impoverished assemblage from the Zibo Coalfield (Shandong Province). There is also an unillustrated record of *Annularia* from the Bangou Member (Liu, Dog & Yin, 1957). Otherwise, however, little attention was paid to the palaeobotany of these beds until the late 1980s, probably triggered by the 11th International Congress on Carboniferous Stratigraphy, held in Beijing in 1987. In that year, a series of Benxi Formation plant fossil assemblages were described from Inner Mongolia (Huang, 1987*a*), Liaoning Province (Huang, 1987*b*), Henan Province (Wu, Xi & Yan, 1987) and Shanxi Province (Zhao, Liu & Hou, 1987; Zhang *et al.* 1987). A second assemblage from Inner Mongolia was later documented by He *et al.* (1990), and Wu (1988) published a general review of the Benxi Formation palaeobotany that included a number of unillustrated records from Shaanxi and Ningxia provinces. The palaeobotany of the Benxi Formation has also been briefly reviewed by Liu, Wang & Zhao (2000), which includes the description of a new *Calamites* species.

What we shall hereafter refer to as the Benxi Flora is of interest for several reasons. From a Chinese perspective, it is the oldest direct evidence of land vegeta-

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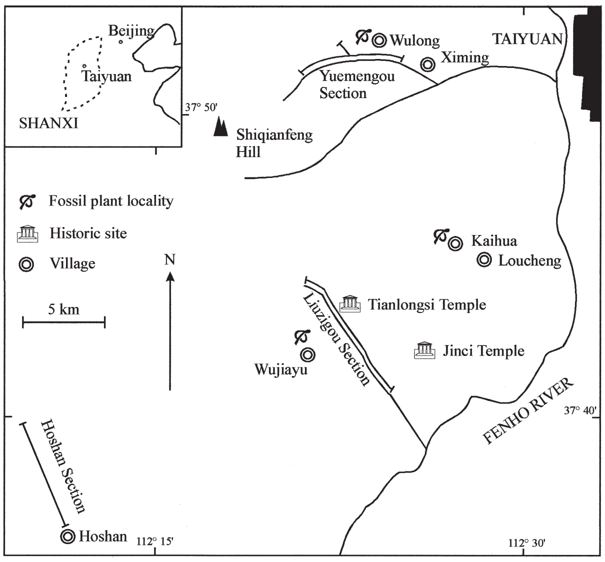

Figure 1. Main sections and plant fossil locations of the Benxi Formation, Western Hill, Taiyuan, Shanxi.

tion in the North China Region. It is the precursor of the well-known Cathaysian floras from the Taiyuan Formation and higher strata, whose associated coal deposits are of great economic importance. From a broader perspective, it is the only Chinese flora that was contemporary with the Westphalian coal floras of Europe and North America (Euramerica). Improving our understanding of the relationship between the Euramerican and Chinese coal forests will be vital if we are to interpret correctly Late Palaeozoic tropical ecosystems and their possible relationship to contemporary climate (Phillips, Peppers & DiMichele, 1985; Cleal & Thomas, 1999).

In this paper, we describe a new and diverse fossil plant assemblage from the Benxi Formation, which provides a new insight into the vegetation of the eastern coal forests and includes some evidence of the epidermal structure of the plants. We use the opportunity to compare the Benxi Flora with contemporary floras from Euramerica. We use the currently accepted spelling of the formation name (Benxi) rather than the old spelling (Penchi) which occasionally still finds its way into the literature.

2. Locality details

The fossils were collected by the second author from the Benxi Formation of Western Hill, Taiyuan (Fig. 1) while accompanying the 212 Geological Survey Team of Shanxi Province during a stratigraphical survey of the area between 1987 and 1990. Most came from the Kaihuagou Section near Kaihua Village, Loucheng, *c.* 7 km northeast of Jinci Temple, a famous historic spot in Taiyuan. Plant fossils were collected from a 10 m thick shale bed high in the Bangou Member, between the Bangou Limestone (below) and the Jinci Sandstone (Fig. 2). The shales are black, weathering to a dark brown, and are in an estuarine lagoonal facies (Chen & Niu, 1993). The fossils are mostly preserved as fusain (*sensu* Scott, 1989, 2000) fragments revealing anatomical detail. The fossils are now in the collections of the Tianjin Institute of Geology and Mineral Resources (TIGMR) under the prefix BK90.

Also described in this paper are lycopsids collected by WZ from the lower Bangou Member of the Liuzigou Section, *c.* 5 km southwest of Kaihua (Fig. 1). These are stored in the TIGMR collections, under the prefix BL90. These came from the roof-shale of a thin coal and fragmented on collection. Attempts at preparing cuticles from these specimens were unsuccessful and they may be partly preserved as fusain.

3. Systematic palaeontology

Class LYCOPSIDA
Order LEPIDOCARPALES
Family DIAPHORODENDRACEAE

Remarks. Associated with the stems and sporophylls of arborescent lycophytes described below are numerous isolated leaves and leafy shoots (Fig. 3i) and rooting structures (Fig. 3m). However, they are specifically indeterminate and so are not discussed further in this paper.

Genus *Synchysidendron* DiMichele & Bateman, 1992

Remarks. Most stems from China that have been assigned to *Lepidodendron* lack an infrafoliar parichnos (Li, 1980), a characteristic of *Lepidodendron sensu stricto* (DiMichele, 1983; Bateman, DiMichele, & Willard, 1992). The Benxi Formation stems are more compatible with the Diaphorodendraceae (DiMichele & Bateman, 1992). There are two stem morphogenera in that family, *Diaphorodendron* DiMichele, 1985 and *Synchysidendron* DiMichele & Bateman, 1992, both originally erected on anatomically preserved fossils. However, these genera can also be recognized on morphology alone (DiMichele, pers. comm.; see Table 1) and based on these characters, the Kaihuagou and Liuzigou stems clearly belong to two species of *Synchysidendron*.

A third well-documented species of lycophyte stem in the Benxi Flora is *Lepidodendron tripunctatum* Stockmans & Mathieu, 1939, which has distinctive, 'trowel-shaped' (trullate) leaf scars. The holotype is from the Taiyuan Formation, but it is also known from the Benxi Formation (Stockmans & Mathieu, 1957; Huang, 1987*a*). It has all of the characteristic morphological features of *Synchysidendron* stems (protruding large leaf cushions, large leaf scars, prominent foliar parichnos, no infrafoliar parichnos) and so we formally propose here the new combination *Synchysidendron tripunctatum* (Stockmans & Mathieu).

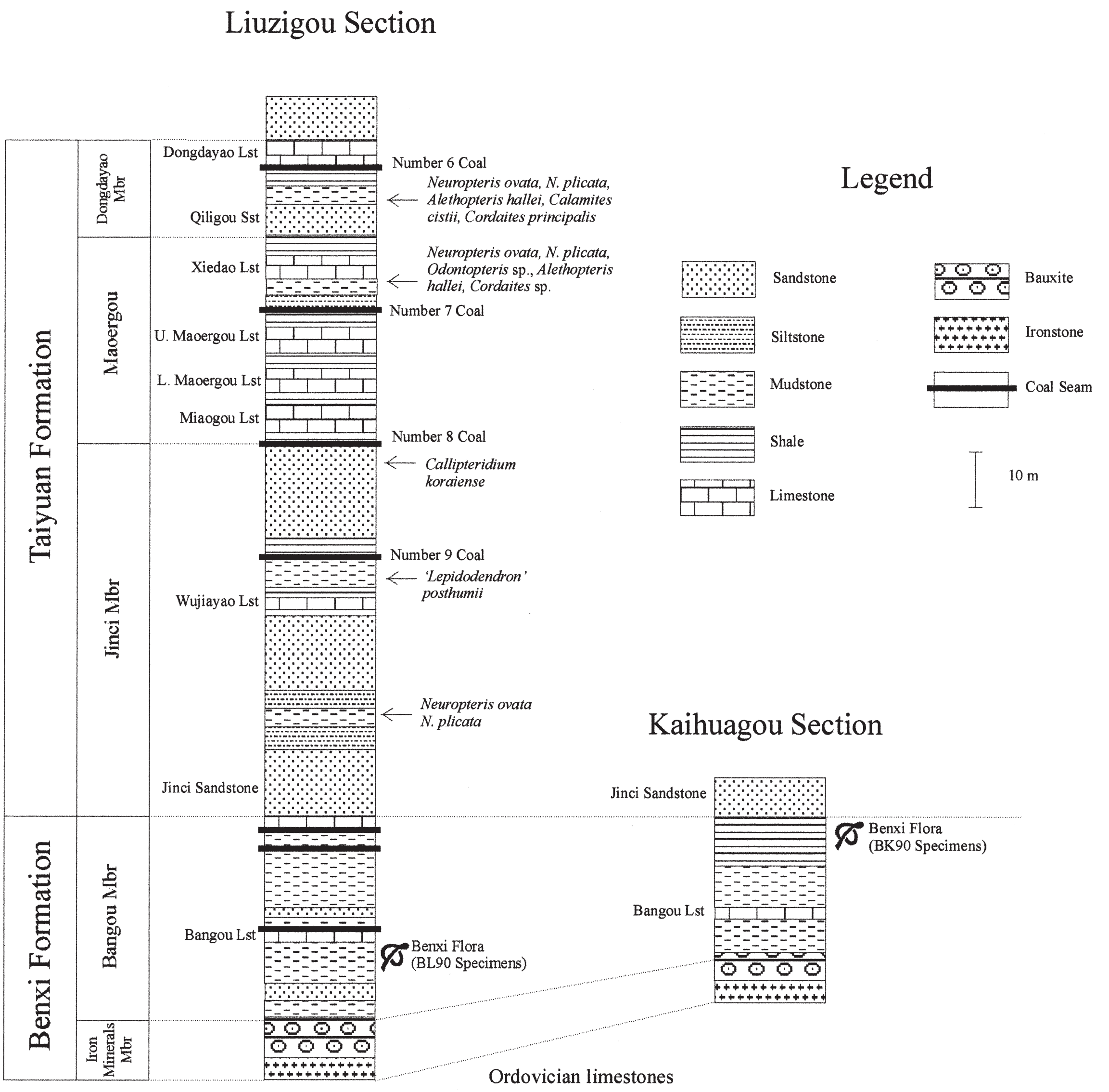

Figure 2. Late Carboniferous sections in Western Hill, Taiyuan, Shanxi.

Table 1. Distinguishing morphological characters for the two morphogenera of stems of the Diaphorodendraceae

Diaphorodendron	*Synchysidendron*
Leaf cushions flattened against stem	Leaf cushions protrude from stem
Leaf cushions always much longer than broad	Leaf cushions on smaller stems tend to be nearly equi-dimensional
Leaf cushions small, even on larger stems	Leaf cushions large on larger stems, approaching those of *Lepidodendron*
Leaf scars tend to be small relative to the cushions	Leaf scars tend to be large relative to the cushions, especially on the smaller stems
Foliar parichnos almost invisible	Foliar parichnos large
No interareas between cushions	Some cushions have interareas

Based on DiMichele & Bateman (1992), Bateman, DiMichele & Willard (1992) and W. A. DiMichele (pers. comm., 1999).

The types of *'Lepidodendron' huixianense* Xi *in* Wu, Xi & Yan, 1987 from the Benxi Formation of north-west Henan are slender stems with 'trowel-shaped' leaf scars. The leaf cushions do not protrude so much as in typical *S. tripunctatum*, but this is probably due to poor preservation and the twigs being from the distal part of the plant. In our opinion, they are merely distal branches of *S. tripunctatum*. Another stem from that assemblage with 'trowel-shaped' scars was described by Wu, Xi & Yan (1987) as *Lepidodendron aolungpylukense*. This is intermediate in size between the more typical *S. tripunctatum* and the slender stems described as *'L.' huixianense*. The specimens from the Eastern Hills of Taiyuan described by Zhang *et al.* (1987) as *Lepidodendron worthenii* Lesquereux are also like this.

Slender *Cathaysiodendron*-like stems from the Benxi Formation have been described by Zhang *et al.* (1987)

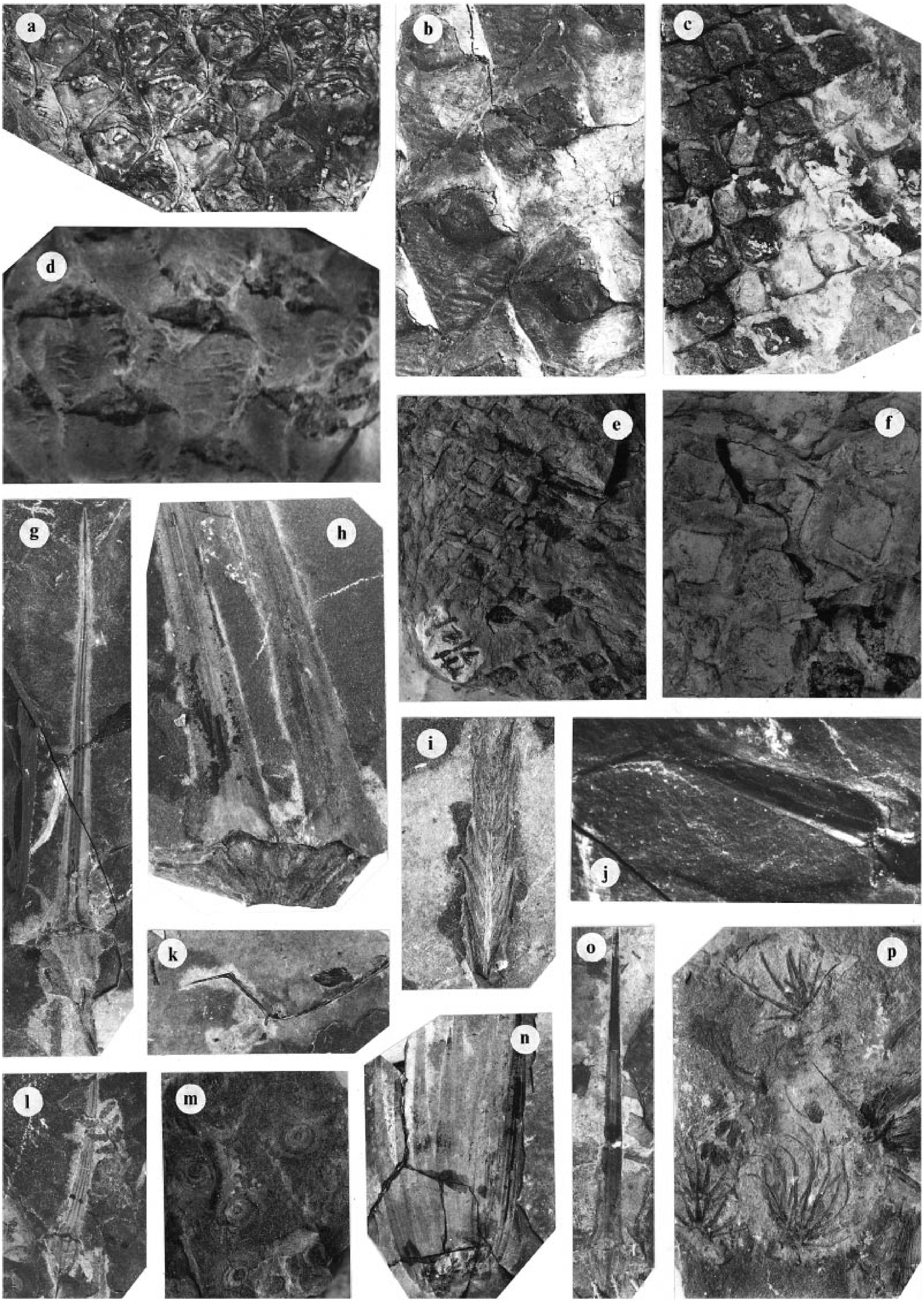

Figure 3. For legend see facing page.

as *Lepidodendron nanpiaoense* (Li) Li *et al.* and an example is figured here in Figure 3e,f. A very similar stem was figured by Wu, Xi & Yan (1987) as *Archaeosigillaria* sp. Wu, Xi & Yan state that the leaf cushions are fusiform-hexagonal, but some are rhomboidal, similar to *Cathaysiodendron*. They also state that there is a single, large vascular trace in the middle of the leaf scar. However, in poorly preserved examples of *Cathaysiodendron*, the vascular and parichnos traces can become merged into a large structure, resembling that seen in the Wu, Xi & Yan specimen. *Cathaysiodendron* stems have small, rhombic to quadrangular leaf cushions with no infrafoliar parichnos, and leaf scars that are almost as large as the cushions (Li, 1963). The Benxi Formation specimens probably represent the distal parts of *Synchysidendron* but whether this is true for the original *Cathaysiodendron* will require further work on the types of the latter.

In the following descriptions, the leaf cushions are orientated in the traditional way when dealing with such lycopsids, with the ligule above the leaf scar.

Synchysidendron galeatum (Li *et al.*) comb. nov., emend.

Figures 3a–c, 6d

?1939 *Lepidodendron* aff. *oculus-felis* (Abbado); Stockmans & Mathieu (*non* Abbado), p. 110, pl. 3, fig. 3.
1957 *Lepidodendron* sp. Li, p. 5, pl. 2 figs 3, 3a.
1974*a* *Lepidodendron galeatum* Li *et al.*, p. 27, pl. 8, figs 3, 4.
?1988 *Lepidodendron oculus-felis* (Abbado); Wu (*non* Abbado), p. 148.

Material. There are two specimens from the Liuzigou assemblage (BL90-1, BL90-2) and one from the Kaihuagou assemblage (BK90-1).

Emended diagnosis. Stems with helically arranged, protruding leaf cushions. Cushion length : breadth ratio 2.0–0.6. Lateral angles of cushions rounded. Upper and lower angles acute in more elongate cushions, becoming more obtuse in squatter cushions. Leaf scars rhomboidal, subtriangular or ‘eye-shaped’. In more elongate cushions, scars lie in upper part of cushion and cover only a small area of cushion; in squatter cushions, scars in middle of cushion and cover over half of cushion area. Prominent lateral lines extend from scars in elongate cushions, but not in squatter cushions. Elongate cushions have keel with transverse plications below the scar. In squatter cushions, the steep and narrow area surrounding the scar shows no ornamentation.

Description. The specimens of stem bark show helically arranged contiguous leaf cushions, which clearly protrude from the stem, and have a prominent leaf scar. The cushions are mostly 12–14 mm wide but vary considerably in shape and length. The more elongate cushions (15–25 mm long) have rounded lateral angles, and acute upper and lower angles (Fig. 3a). These grade morphologically into cushions (12–15 mm long) that are one-and-a-half times as long as wide to nearly isodiametric, and have more obtuse upper and lower angles. These in turn grade into isodiametric or slightly squat cushions (9–12 mm long) (Fig. 3c).

The cushions have a prominent rhomboidal, subtriangular or ‘eye-shaped’ leaf scar, mostly 4–7 mm wide (Fig. 3b). In the more elongate cushions, the scar is only 3–4 mm long and occurs just above the middle of the cushion. In the smaller cushions, the scars become longer, 4–6 mm long in the smallest cushions, and occur nearer the middle of the cushion.

A large vascular trace 1–2 mm in diameter occurs in the upper to middle part of the scar. Traces of the foliar parichnos are often difficult to see but are sometimes represented by two round marks just below the centreline of the scar. There is no evidence of infrafoliar parichnos.

In the more elongate cushions, lines extend from the lateral angles of the scars, clearly dividing the cushions into upper and lower fields, but these are absent in the less elongate cushions. The upper field shows no ornamentation, but there is a prominent ligule mark just above the upper angle of the scar. The lower field has transverse plications that become thickened along the keel. These transverse plications are most obvious on the more elongate cushions, but rare plications may also be present on the narrow lower field of the less elongate cushions.

Figure 3. Clubmosses and horsetails from the Benxi Formation of Western Hill near Taiyuan. All are from the Kaihuagou Flora except (a, b, e, f, m), which are from the Liuzigou Flora. (a–c). *Synchysidendron galeatum* (Li *et al.*) comb. nov.; (a) BL90-1, elongate leaf cushions, × 1; (b) BL90-2, close-up of ‘eye-shaped’ leaf scars, × 2; (c) BK90-1, squatter form of leaf cushions, × 1. (d) *S. subrhombicum* (Li *et al.*) comb. nov., BK90-2, showing leaf scars in upper part of cushions, × 5. (e, f) *Synchysidendron* sp. twig with *Cathaysiodendron*-like leaf scars and cushions, BL90-3; (e) × 1; (f) × 3. (g, h, j–l, n, o) *Achlamydocarpon taiyuanensis* sp. nov. (g) BK90-3 (holotype), typical elongate lamina, × 1; (h) BK90-4, pair of sporophylls joined near base, each showing a prominent midvein, × 2; (j) BK90-5, close-up of pedicel alation, × 5; (k) BK90-6, sporophyll in lateral view, with blade directed towards right of picture, and showing small heel at the base of the blade, × 1; (l) BK90-7, shorter sporophyll, × 1; (n) BK90-8, part of broken cone showing several sporophylls joined near base, × 2; (o) BK90-9, sporophyll showing tear-shaped scar on pedicel, × 1. (i) Leafy shoot probably of a diaphorodendracean, BK90-10, × 2. (m) Stigmarian rooting structure, probably of a *Synchysidendron*, showing root-scars, BL90-4, × 1. (p) *Asterophyllites* cf. *grandis* (Sternberg) Geinitz, BK90-11, several whorls of leaves, × 2.

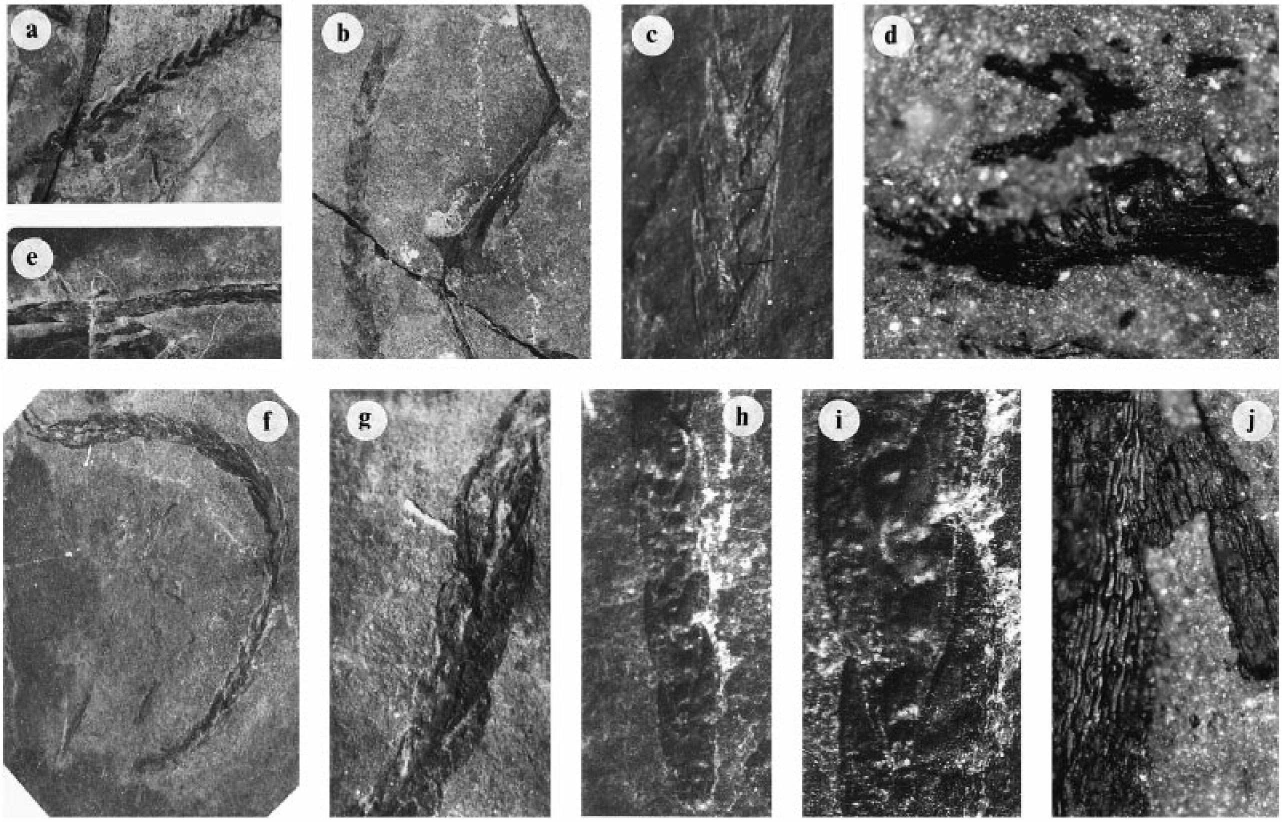

Figure 4. *Selaginella benxiensis* sp. nov., Benxi Formation, Kaihuagou, Western Hill near Taiyuan. (a) BK90-12 (holotype), typical leafy shoot, × 2. (b) BK90-13, shoot showing helically arranged leaves, × 2; (c) BK90-14, close-up of leaves showing acute apices, × 5; (d) BK90-15, leaf-margin photographed using darkfield illumination, showing delicate hairs, × 100; (e) BK90-16, shoot showing closely adpressed leaves, × 2; (f) BK90-17, long leafy shoot, × 2; (g) close-up of previous specimen, showing curved leaves, × 5; (h) BK90-18, possible megasporangiate cone, × 5; (i) close-up of previous specimen, showing circular bodies possibly representing megaspores, × 10; (j) same specimen as in (d), showing epidermal cells including possible stomata in upper part of picture, photographed using darkfield illumination, × 100.

Associated with the Liuzigou stem fragments were numerous fragments of leaf, probably originating from the same plant. One fragment from the distal end of a leaf was examined under SEM (Fig. 6d). It is 0.35 mm wide, tapered and rather curved. It has elongate epidermal cells, up to 140 µm long and 15–30 µm wide, with slightly sinuous walls. No sign of stomata could be seen.

Remarks. The above description is based mainly on specimens from Liuzigou, which show the gradation between the elongate and squat leaf cushions. The width of the cushions does not vary significantly, the change in shape being due to elongation of the cushion (at least in the specimens dealt with here). If anything, the leaf scars become larger in the smaller cushions, and consequently take up more of the cushion area.

The more elongate cushions are similar in shape to those on the type of *Lepidodendron galeatum* Li, 1957, which came from the basal Benxi Formation of Shandong. The cushions are much smaller in Li's specimen, but this is probably due to the stem fragment being from a more distal part of the branching system. The size difference might explain why the Shandong specimen has no ornamentation on the lower field of the cushion, and the lateral extensions of the leaf scars do not reach the margins of the cushion. Li's species has been transferred to *Synchysidendron* because the smaller cushions tend to be squat and protrude from the stem, the leaf scars are well-developed and there is no infrafoliar parichnos.

If considered in isolation, the single specimen from Kaihuagou is rather different from the holotype of *S. galeatum*, having squatter leaf cushions, most of which are taken up by the leaf scars. However, if we look at the morphological range in the Liuzigou material, we see that this type of cushion grades into the more typical form of *S. galeatum* and evidently reflects variation in different parts of the plant. This has allowed us to emend the diagnosis of the species.

There is some similarity to *'Lepidodendron' oculusfelis* (Abbado) Zeiller from the Taiyuan Formation. Typical stems of that species have squat and sigillarioid leaf cushions (e.g. Li, 1963, pl. 8, figs 1, 3; pl. 9, fig. 2) but others have more isodiametric or even slightly elongate cushions (e.g. Li, 1963, pl. 8, fig. 2; pl. 9, fig. 1; pl. 20, fig. 3). The most notable difference is the absence of a lower keel in the more elongate cushions of *'L.' oculusfelis*. The latter species also has more consistently developed lateral lines on either side of scars, even on the squatter cushions (in *S. galeatum*, they are only present on the more elongate cushions). *S. galeatum* tends to have more elongate cushions but there is, nevertheless, a considerable overlap in the range of morphological variation. *S. galeatum* may have been ancestral to *'L.' oculusfelis*. There has been no illustrated documentation of undoubted *'L.' oculusfelis* from the Benxi Formation.

The specimen from the Benxi Formation figured by Stockmans & Mathieu (1939) as *Lepidodendron* aff. *oculusfelis* has far more elongate cushions than Abbado's species. Although there is no keel in the lower part of the cushion, in other characters it compares closely with *S. galeatum* (shape of scar, development of foliar cicatrices, prominent transverse plications).

Synchysidendron tripunctatum (Stockmans & Mathieu) comb. nov. has a similar range of cushion shapes, from somewhat elongate to almost isodiametric, with the leaf scar remaining relatively constant in size (Li *et al.* 1974*a*; Huang, 1987*a*). The more elongate cushions also have a distinct lower keel as in *S. galeatum*, although there are not the same marked plications in the lower field. However, *S. tripunctatum* has much smaller cushions (mostly 3–4 mm wide) and distinctive elongate, 'trowel-shaped' leaf scars with a large, vertically elongate vascular trace.

Synchysidendron subrhombicum (Li *et al.*) comb. nov., emend.
Figure 3d

1974*a* *Lepidodendron subrhombicum* Li *et al.*, p. 26, pl. 9, figs 2, 3.

1987 *Lepidodendron* cf. *canobianum* Crookall; Wu, Xi & Yan (*non* Crookall), p. 423, pl. 1, fig. 4; pl. 2, figs 1–7.

1987 *Lepidodendron subrhombicum* 'Gu & Zhi'; Zhang *et al.*, p. 8, pl. 1, figs 3, 3a.

1995 *Lepidodendron subrhombicum* 'Gu & Zhi'; Li, pl. 35, fig. 3 (copy of photograph in Zhang *et al.* 1987).

Material. A single specimen (BK90-2).

Emended diagnosis. Stems with helically arranged, protruding leaf cushions. Cushion length : breadth ratio 1.3–0.7. Lateral angles of cushions rounded. Lower angle acute in more elongate cushions, becoming obtuse in squatter cushions. Upper angle obtuse to rounded. Lower field of cushion with no ornamentation, or with a weakly developed keel and transverse plications. Leaf scars rhomboidal, 2–3 mm wide and 1 mm high, occurring in uppermost part of cushion. In the squatter cushions, the scars cover over half of the cushion area, in the more elongate cushions they cover about a quarter of the area. In the centre of the scar is a prominent vascular cicatrix, and two smaller foliar parichnos cicatrices.

Description. A small stem fragment showing helically arranged, contiguous leaf cushions, 4–6 mm long and 4–5 mm wide, with a more or less round upper margin and a bluntly acuminate lower margin. The leaf scar is in the uppermost part of the cushion, which has very little upper field. The scar is laterally elongate and extends for over a half of the cushion width. A large vascular trace, 0.5 mm in diameter, is in the upper part of the scar, and two prominent parichnos marks of about the same size occur below it. No evidence of a ligule is visible. Several prominent transverse wrinkles occur on the lower part of the cushion but there is no distinct keel. There is no evidence of infrafoliar parichnos.

Remarks. Wu, Xi & Yan (1987, pl. 1, fig. 4; pl. 2, figs 1–7) figured a series of specimens from the Benxi Formation of Henan as *Lepidodendron* cf. *canobianum* Crookall. They have cushions that vary from short and squat, to more elongate and obovate. They have little in common with *L. canobianum* Crookall *sensu* stricto, which has very slender leaf cushions (except in the smallest stems) with a centrally placed leaf scar. Some of the Henan specimens (e.g. Wu, Xi & Yan, 1987, pl. 2, figs 5, 6) are indistinguishable from the holotype of *Lepidodendron subrhombicum*, which also originated from the Benxi Formation (Li *et al.* 1974*a*). We have emended the diagnosis of that species to take into account the morphological variation shown by the Wu, Xi & Yan (1987) specimens. We have also transferred the species to *Synchysidendron* because of the well-developed foliar parichnos and leaf scars, the cushions tending to be squat and protruding from the stem, and the absence of infrafoliar parichnos.

The Kaihuagou specimen has more elongate, obovate cushions than the holotype of *S. subrhombicum*, but is indistinguishable from the stems with more elongate cushions figured by Wu, Xi & Yan (1987, pl. 2, figs 2, 3). Also very similar is a specimen from the Eastern Hills near Taiyuan figured as *Lepidodendron subrhombicum* by Zhang *et al.* (1987) and Li (1995).

Genus *Achlamydocarpon* Schumacker-Lambrey, 1966

Remarks. This morphogenus was erected for *Lepidocarpon*-like sporophylls, in which the sporangium is not surrounded by wing-like projections of the pedicel ('integuments'). Based on association they are assigned to the Diaphorodendraceae (DiMichele & Bateman, 1992) and were probably shed from the cone with their single megaspore still attached, acting as an aid to its dispersal (Thomas, 1981; Habgood,

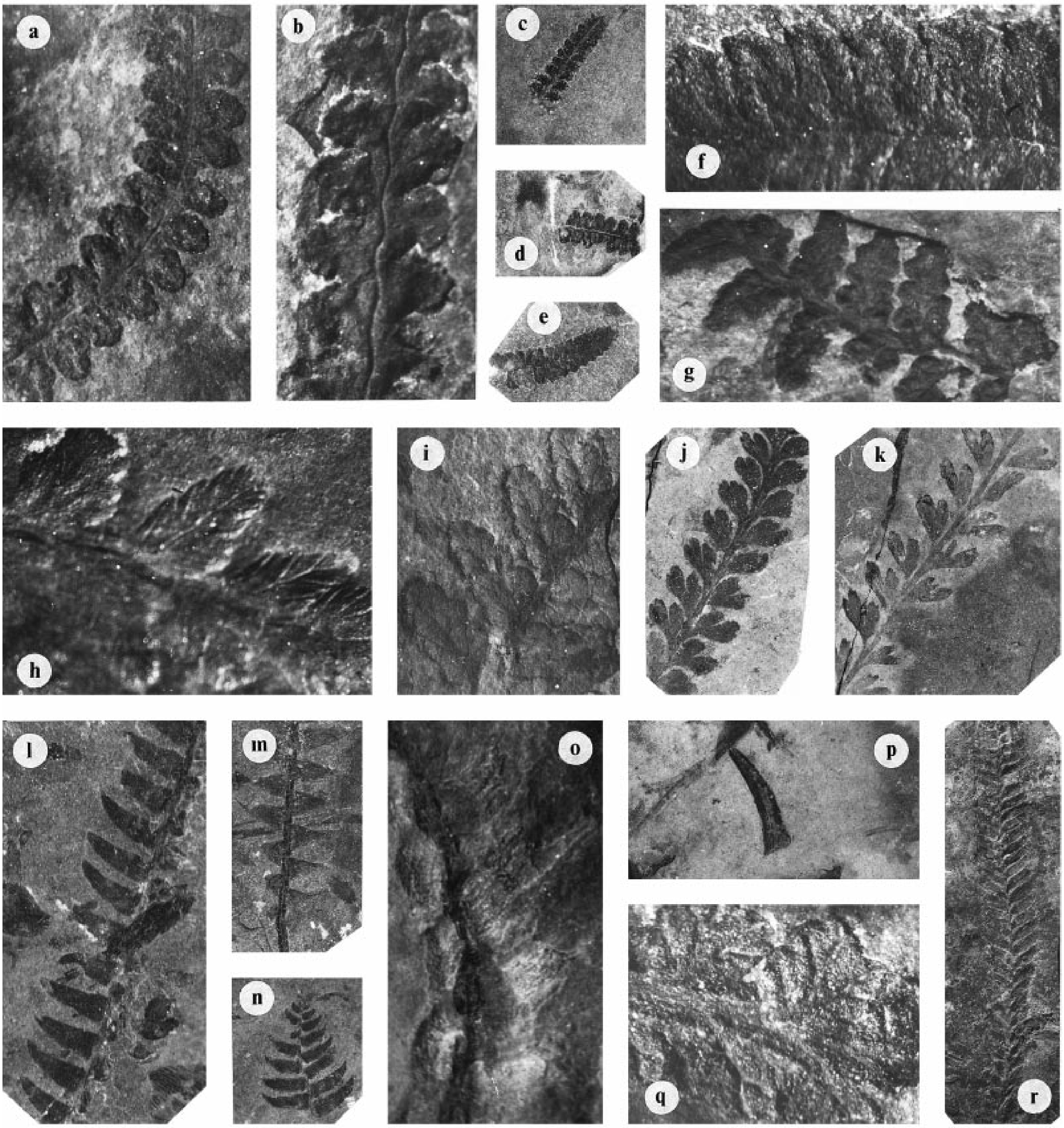

Figure 5. Pteridophyll and other foliage from the Benxi Formation of Kaihuagou, Western Hill near Taiyuan. (a–d, q) ?*Boweria* sp. (a) BK90–19, pinna fragment, × 5; (b) BK90–20, pinna fragment showing *Boweria*–like 'sporangia', × 8; (c) BK90–21, × 2; (d) BK90–20, × 2; (q) BK90–22, close–up of pinnules showing widely–forked veins, × 14. (e–f) ?*Alloiopteris* sp., BK90–23; (e) longest preserved pinna fragment, × 2; (f) close–up of pinnules, × 14. (g–i) Pecopteroid fragments, (g) BK90–24, pinnules with undulate margin, × 5; (h) BK90–25, pinnules with more triangular shape and incised margin, × 8; (i) BK90–27, × 5. (j–k) Sphenopteroid fragments, both × 2. (j) BK90–28; (k) BK90–29. (l–p) Specimens of uncertain affinities. (l) BK90–30, medial part of foliar shoot with subtriangular pinnules, × 2; (m) BK90–31, proximal part of leafy shoot showing leaves decreasing in size towards base, × 2; (n) BK90–32, tapering apex of leafy shoot, × 2; (o) BK90–33, shoot showing leaves in helical arrangement, × 5; (p) BK90–34, isolated leaf, × 5. (r) Cf. *Tingia* sp., BK90–35, leafy shoot, × 1.

Hemsley, & Thomas, 1998). It can sometimes be difficult to tell in non-anatomically preserved fossils whether or not there are integument-like structures, and such fossils may be assigned to the more generalized morphogenus *Lepidocarpon* (e.g. see Thomas, 1978). However, as these Benxi Flora specimens clearly show narrow, non-surrounding alations, and the only associated arborescent lycophyte stems belong to the Diaphorodendraceae, we believe that they can be assigned with confidence to *Achlamydocarpon*.

Achlamydocarpon taiyuanensis sp. nov.
Figures 3g,h,j–l,n,o, 4b

Diagnosis. Sporophylls with slender, elongate lamina, 30–80 mm long. Lamina tapers gently to an acuminate apex but flares proximally near its base. Strongly tapered pedicel 11–22 mm long and 3–7 mm wide, with two 3 mm wide lateral alations and a small distal heel on the lower side. Pedicel lies at 115° to lamina.

Holotype. Specimen TIGMR BK90-3, collected from the upper Bangou Member, Kaihuagou Section, Western Hill, Taiyuan (Fig. 3g).

Paratypes. Isolated sporophylls and two fragmented cones on six hand-specimens (nos BK90-4–BK90-9).

Description. The sporophylls have a slender, elongate lamina, 30–80 mm long (Fig. 3g,l,o). A prominent midvein lies along the length of the lamina, usually represented as three parallel lines (Fig. 3h). For most of its length, the lamina tapers gently to an acuminate apex, but at the base flares to where it joins the pedicel. The pedicel is strongly tapered towards where it was narrowly attached to the cone axis. The pedicel is 22 mm long and 7 mm wide in the largest preserved sporophyll (Fig. 3g), and 11 mm long and 3 mm wide in the smallest. In some specimens (e.g. Fig. 3o) there is a tear-drop shaped scar along most of the pedicel, which is assumed to be the attachment scar of the megasporangium. The pedicel has prominent *c*. 3 mm wide alations on either side of the scar. Each alation has a longitudinal ridge midway between the scar and the lateral margin.

Two specimens (Fig. 3k, 4b) show sporophylls in lateral view. In the most complete specimen (Fig. 3k) the lamina is preserved for a length of 48 mm and is gently curved. It lies at 115° to the pedicel, which is 15 mm long. In both cases there is a small heel on the lower side of the pedicel, near its attachment with the lamina. Attached at the proximal end of the pedicel is a slender piece of tissue, which probably represents part of the cone axis.

No isolated megaspores were found associated with the sporophylls. Some sporophylls have ovate bodies apparently attached to the pedicel. However, when the carbon film was macerated from one of these bodies (Fig. 3j) it merely dissolved away suggesting that it was part of the pedicel alation.

The broken cones are represented by fragments showing groups of sporophylls attached (or nearly attached) to each other at the pedicels (Fig. 3h,n). The most complete example has eight sporophylls arranged in what appears to be a very shallow helix.

Remarks. The sporophyll lamina is more slender than any other *Lepidostrobophyllum*-like sporophylls reported from the Benxi Formation (Huang, 1987*a*, pl. 3, figs 2–7; Huang, 1987*b*, pl. 10, figs 6, 9–14; Wu, Xi & Yan, 1987, pl. 1, figs 6–8). The nearest comparison is with the holotype of *Lepidophyllum minus* Schenk, 1883 whose sporophyll lamina narrows markedly above its attachment to the pedicel. However, as most of the lamina is lost, we do not know if it had the same distinctive slender shape as the Kaihuagou specimens. The specimen figured by Stockmans & Mathieu (1939, pl. 5, fig. 4) as *L. minus* has a much broader lamina than our specimens.

The alations appear to have extended laterally from the pedicel, as in *Achlamydocarpon*. The longitudinal ridge on either side of the megasporangium attachment scar suggests the alations may have been slightly inflexed, but they did not completely envelop the megasporangium, as in *Lepidocarpon*.

Order SELAGINELLALES
Family SELGINELLACEAE
Genus *Selaginella* Beauvoir, 1805

Remarks. We have followed Thomas (1997) in using *Selaginella* rather than *Selaginellites* Zeiller, 1906 for fossils of this type of herbaceous lycopsid.

Selaginella benxiensis sp. nov.
Figure 4

Diagnosis. Slender shoots, 1–3 mm wide, bearing leaves arranged in tight helix and closely adpressed to stem. Leaves slender, 3 mm long and 1 mm wide, tapering along entire length to an acute apex, often slightly incurved towards stem. Leaf margin with fine hairs. Megaspores 0.3 mm in diameter.

Holotype. Specimen TIGMR BK90-12, collected from the upper Bangou Member, Kaihuagou Section, Western Hill, Taiyuan (Fig. 4a).

Paratypes. TIGMR specimens BK90-13–BK90-18 (Fig. 4b–j). All were collected from the upper Bangou Member, Kaihuagou Section.

Description. There are ten specimens of slender, leafy shoot that are 1–3 mm wide, the longest (Fig. 4f) being 30 mm long. The leaves appear to be arranged in a tight helix around the stem. The leaf arrangement is difficult to see due to compression of the shoot but is not decussate (Fig. 4b,c,g). Each leaf overlaps the leaf immediately above it by up to half its length.

The leaves are consistently about 3 mm long, and are broadly attached to the stem at about 15–35° with an amplexicaul or slightly constricted base (Fig. 4c). The leaves are slightly bulbous in their lower one-third, but for the rest of their length they taper gradually to a very acute apex. The leaves are often straight and relatively rigid (Fig. 4a–c), although some are slightly incurved, so that the leaf becomes tightly

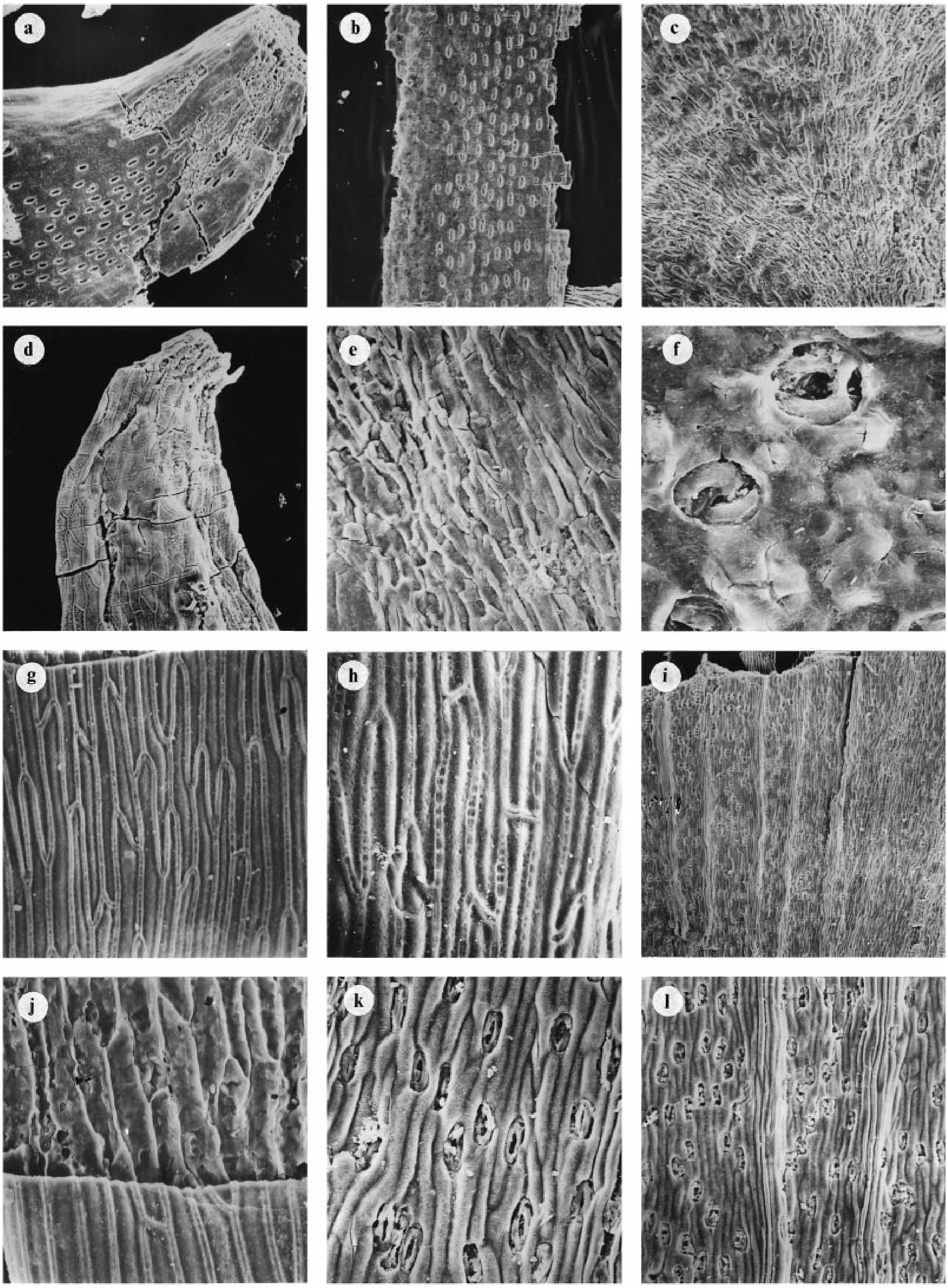

Figure 6. For legend see facing page.

adpressed to the stem (Fig. 4e). Due to poor preservation, details of the leaf margin are difficult to make out. However, one specimen (Fig. 4d) shows a leaf margin with numerous delicate hairs, *c*. 75 µm long.

When viewed using darkfield microscopy (Fig. 4j), elongate epidermal cells can be seen, up to 60 µm long and 10 µm wide, with tapered ends. A number of stomata were also seen, consisting of pairs of guard cells, 40 µm long. There are no subsidiary cells, and the guard cells appear level with the rest of the epidermis. The distribution of the stomata could not be determined, but their polar axis lies along the length of the leaf.

One specimen (Fig. 4h,i) shows clear impressions of circular bodies, 300 µm in diameter, distributed among the 'leaves'. These are interpreted as megaspores and so we regard this specimen as being part of a megasporangiate cone. The leaf-like bracts on this cone are almost indistinguishable from the normal vegetative leaves, except they are more curved towards the stem.

Remarks. Although only small, these specimens show a number of characteristic features of *Selaginella*. The stomata with no subsidiary cells are very similar to those of living lycopsids (Thomas & Masarati, 1982) and clearly not coniferoid. The megasporangiate cone on one of the shoots, with bracts that are essentially similar to the vegetative leaves also suggests *Selaginella*. Although most *Selaginella* species are anisophyllous, Thomas (1997) has shown that some species can be isophyllous.

Palaeozoic *Selaginella* usually produced megaspores of the *Triangulatisporites*-type (Thomas, 1997). These tend to be larger (> 400 µm diameter) than the circular bodies seen on the Kaihuagou shoot and have a more subtriangular outline. However, the central body of such megaspores is similar in size and shape (e.g. Spinner, 1965) and it is possible that this is all that is preserved on the Chinese specimen.

This is the first reported *Selaginella* from the Benxi Formation or similar aged floras in China. The only other Palaeozoic species from China is *'Selaginellites' tibeticus* Li & Zhu *in* Li *et al.* 1982 from the Upper Permian Rejuechaka Flora of northern Xizang. This clearly differs from the Kaihuagou species in being anisophyllous, with leaves that are more ovoid and attached to the stem at a wider angle.

Most Pennsylvanian *Selaginella* species from Euramerica are also anisophyllous and have broader leaves attached to the stem at a wider angle (Thomas, 1997). The only similar species is *'Selaginellites' elongatus* (Goldenberg) Halle, 1907, which is isophyllous with leaves of similar shape and angle of attachment. However, its leaves are significantly larger (up to 11 mm long) and do not have a ciliate margin.

Class EQUISETOPSIDA

Remarks. Horsetails are generally rare in the Benxi Formation, the best examples (including reproductive structures) being from Inner Mongolia (Huang, 1987*a*). In the present assemblage, the only possible horsetail remains are some leaf whorls.

Genus *Asterophyllites* Brongniart, 1822

Asterophyllites cf. *grandis* (Sternberg) Geinitz, 1855

Figures 3p, 6a,b

1987*a* *Asterophyllites tenuifolius* (Sternberg) Stockmans & Willière; Huang (*non* Sternberg), p. 11, pl. 1, figs 5–10.

Material. Nine specimens, including BK90-11 (Fig. 3p).

Description. The most complete specimen (Fig. 3p) shows three or possibly four incomplete leaf whorls. The leaves are slender, essentially linear, up to 12 mm long and 0.2–0.5 mm wide, and appear to be fused to a basal sheath. There are 7–12 leaves in the largest whorl. A number of other specimens show similar shoots but with distorted leaves.

Two specimens show fragments of similar-sized, curved leaves, partly preserved as fusain. One (Fig. 6b) is from the proximal part of the leaf near to where it was attached to a basal sheath, while the other (Fig. 6a) is from near the leaf apex. They indicate that the leaves were fleshy, with a featureless surface except for distinct stomatiferous bands, 220 µm wide. Any one specimen shows only a single band. However, this may be due to the leaf being preserved side-on (note the curvature shown in Fig. 6a) and there may have been two stomatiferous bands, one on either side of the vein. The stomata are sunken below the surface of the epidermis and are regularly aligned with their polar axis parallel to the length of the leaf. The elliptical openings are 55–80 µm long and 15 µm wide. The stomatal density within the bands is 50–55 per mm^2.

Figure 6. SEMs of fusainized plant fossils from the Benxi Formation of Western Hill near Taiyuan. (d) from Liuzigou section, rest from Kaihuagou section. (a, b) *Asterophyllites* cf. *grandis* (Sternberg) Geinitz, × 75. (a) BK90–36, part of leaf from near its apex, showing marked stomatiferous band; (b) BK90–37, basal part of leaf, showing continuation of stomatiferous band. (c, e, f) ?*Boweria* sp. (c) BK90–38, adaxial surface showing division into costal and intercostal fields, × 78; (e) close–up of adaxial surface from same specimen, showing elongate veins, × 220; (f) BK90–39, stomata on abaxial surface, × 800. (d) Leaf probably of *Synchysidendron galeatum* (Li *et al.*) comb. nov., BL90–5, showing elongate epidermal cells, × 116. (g–l) *Conchophyllum subboblongifolius* sp. nov. (g) BK90–40, adaxial surface showing elongate cells, × 217; (h) close–up of same specimen showing anticlinal walls with cross–bars, × 357. (i) BK90–41, general view of abaxial surface showing division between costal and intercostal fields, × 35. (j) BK90–40, adaxial surface showing area where the cuticle has been lost but which still shows evidence of epidermal cells, × 350; (k) BK90–40, stomata on abaxial surface, × 217; (l) wider view of costal and intercostal fields on previous specimen, × 112.

Remarks. These fossils have been assigned to *Asterophyllites* because of the linear shape of the leaves; they are not lanceolate, obovate or spathulate as in *Annularia* (Abbott, 1958). Huang (1987*a*) described some very similar leaves from the Shangshetai Formation of Inner Mongolia. He identified them as *A. tenuifolius* (Sternberg) Stockmans & Willière but that species has much longer leaves and more leaves per whorl, and is generally regarded as a synonym of *Asterophyllites longifolius* (Sternberg) Brongniart, 1828, (e.g. Crookall, 1969). *Asterophyllites equisetiformis* Brongniart, 1828 has leaves of more comparable size and shape to Huang's material but tends to have more leaves per whorl (Abbott, 1958). Among the well-documented Euramerican species, the best comparison is with *A. grandis*, although the latter has somewhat smaller leaves.

The stomata in the Kaihuagou specimens are similar in size and shape to those of *A. equisetiformis*, except the latter are not sunken below the epidermal surface (Abbott, 1958). However, the Chinese leaves have a much higher stomatal density and more sharply defined stomatiferous bands. Unfortunately, the epidermal structure of *A. grandis* is unknown. Thomas (1911) described petrified leaves under that name from lower Westphalian coal balls but these have smaller leaves and fewer leaves per whorl, and are more likely from the larger axes of *Asterophyllites charaeformis* (Sternberg) Unger, 1845.

The Kaihuagou specimens and Huang's well-preserved material from Inner Mongolia probably represent a new species. However, our material is too fragmentary to form the basis of a new species description and Huang's material needs to be re-described. Provisionally, therefore, we have named the specimens *Asterophyllites* cf. *grandis*.

Class PTEROPSIDA

Remarks. Fern fragments are abundant in the Kaihuagou assemblage but, as is normal with the Benxi Flora, they are preserved as small fragments of frond that are difficult to identify. Where details of reproductive structures are present, preservation is too poor to determine details of the sporangia. The only fern species to have been established on fossils from the Benxi Formation is *Sphenopteris neimongolensis* Huang, 1987*a*, but the illustrations show neither detailed foliar morphology nor reproductive structures.

Genus *Boweria* Kidston, 1911

?*Boweria* sp.

Figures 5a–d,q, 6c,e,f

?1883 *Sphenopteris* sp. Schenk, p. 216, pl. 42, figs 2–6, 8; pl. 43, fig. 28.
?1939 *Sphenopteris* sp. Stockmans & Mathieu, p. 54, pl. 2, fig. 2.

Material. Fourteen fragments of pinnae, including BK90-19–BK90-22 (Fig. 5a–d,q).

Description. These are short fragments of pinnae with very small pinnules (e.g. Fig. 5c,d). The rachis is straight or slightly arched, with a fine undulate furrow on the adaxial surface (Fig. 5a,b). Small pinnules, 1–2 mm long and *c*. 1 mm wide, are attached to the rachis at 70–90° (Fig. 5a). The pinnules are rounded with gently undulate margins. Adjacent pinnules are narrowly confluent at the base, or in some cases somewhat constricted in the lower part. There is a decurrent midvein with secondary veins emitted at *c.* 45°; the secondary veins fork once at wide angle (Fig. 5q). Attached near the margin of some pinnules are round objects, *c.* 0.3 mm in diameter, which may be sporangia (Fig. 5b).

Fusainized specimens show the adaxial surface is covered by mainly elongate cells with tapered ends, aligned approximately with the venation (Fig. 6c). Along the veins, the cells are elongate, up to *c*. 100 µm long and 20 µm wide. Between the veins, the cells are less elongate, sometimes isodiametrically polygonal, *c.* 20 µm in size (Fig. 6e). On the abaxial surface, the veins and inter-vein areas are clearly demarcated. Along the veins are elongate cells with tapered ends, similar in size and shape to those on the adaxial surface. Between the veins, cell structure is difficult to discern, except for small stomata, *c.* 15–18 µm long and 13–15 µm wide, lying approximately parallel to the veins. The stomata are not significantly sunken below the epidermal surface and have a pair of guard cells, each *c.* 5 µm wide (Fig. 6f). The stomatal density in the inter-vein areas is *c*. 530 per mm^2. No evidence of epidermal hairs or papillae could be seen.

Remarks. This fern is abundant in the Kaihuagou assemblage and very similar remains have been described by Schenk (1883) and Stockmans & Mathieu (1939) from elsewhere in the Benxi Formation. However, all the fossils are fragmentary and difficult to classify. *'Alloiopteris' gansuensis* Li *et al.* 1993 also has very small pinnules that are often basally constricted. The only figured specimen of that species (Li, 1995, pl. 33, figs 1–2) is clearly not an *Alloiopteris*, as the ultimate pinnae are too oblique to the penultimate rachis and the pinnules are insufficiently asymmetrical. If the Li *et al.* species had been described from the Benxi Formation, we might have been tempted to use the species epithet for the Kaihuagou specimens. However, the type is from the Tsingyuan Formation in Gansu, which has been independently dated as early Namurian on goniatite evidence, and so significantly older than the Kaihuagou assemblage.

The fossils have been tentatively assigned to *Boweria* based on the presence of what may be single sporangia around the margins of the pinnules (see Kidston, 1923 for the most detailed account of this genus). However, if the round objects are in fact groups of sporangia or sori, they may belong to *Renaultia* or *Oligocarpia*. None of these three genera have hitherto been reported from the Benxi Flora.

Little is known of the epidermal structure of Pennsylvanian ferns as they tend to be weakly cutinized. However, similar small, anomocytic stomata are known from most families of living fern (van Cotthem, 1973).

Genus *Alloiopteris* Potonié, 1896

Remarks. We follow Brousmiche (1983) and use this morphogenus for sterile foliage resembling that of the Corynepteridaceae (see also Galtier & Scott, 1979).

?*Alloiopteris* sp.
Figure 5e,f

?1987 *Alloiopteris*? sp.; Wu, Xi & Yan, p. 427, pl. 4, figs 17, 17a.
?1996 *Alloiopteris* sp.; Laveine *et al.*, p. 784, pl. 2, fig. 1.

Material. Three pinna fragments including BK90-23.

Description. These are short fragments of slender pinnae, the longest preserved for a length of 12 mm (Fig. 5e). The rachises are *c*. 0.5 mm wide, more or less straight or slightly curved. Tiny pinnules, *c.* 2 mm long and 1 mm wide, are inserted at 60–80° to the rachis (Fig. 5f). Pinnules are sub-rhomboidal, with between one and three short, blunt teeth on the distal margin. Adjacent pinnules appear fused for over half the length of the pinnules. A decurrent midvein extends for most of pinnule length. Lateral veins are difficult to see but appear to branch once or twice at a wide angle.

Remarks. There have been previous records of *Alloiopteris*-like fronds from the Benxi Formation (see synonymy) but none are complete enough to identify to species. No fertile foliage has been found to confirm the presence of the Corynepteridaceae in these assemblages.

Although both have widely forking lateral veins, we do not believe these sterile fragments to be conspecific with the fertile ?*Boweria* sp. There is a clear-cut morphological difference between the pinnule-types: in ?*Alloiopteris* sp., adjacent pinnules are fused to one another by more than half their length, and the pinnules have distal teeth; in ?*Boweria* sp., adjacent pinnules are fused to one another by only a quarter or less of their length, and the pinnules have no distal teeth.

Sphenopteroid fragments
Figure 5j,k

Material. Seven pinna segments including BK90-28 and BK90-29.

Description. The fragments of pinnae are 6–7 mm wide and preserved for lengths of 35–60 mm. They are parallel-sided for most of their length, becoming slightly tapered towards the end. Small pinnules are alternately arranged along the rachis, attached at *c.* 45°. The pinnules are obovate, 3–4 mm long and *c*. 2 mm wide. In the terminal part of the pinna, the pinnules are narrowly cuneate, with a rounded, shallowly dentate distal margin. Pinnules in a more proximal position are lobed. There are usually two main lobes, the anadromic one being significantly less developed. The main lobe often has one or more shallower incisions on the distal margin. In the smaller pinnules, the veins radiate from the base. In the larger, more lobed pinnules there is a midvein from which lateral veins are produced.

Remarks. These small sphenopteroid fragments are highly distinctive but, as there are so few of them, we have decided not to erect a new species. Their small size suggests they were probably from a fern but no reproductive organs are preserved. A search through the literature has not revealed any comparable foliage from the Benxi Formation or the overlying Taiyuan Formation.

Pecopteroid fragments
Figure 5g–i

1987 *Pecopteris aspera* Brongniart; Wu, Xi & Yan (*non* Brongniart), p. 430, pl. 5, figs 9, 10.

Material. Seven fragments including BK90-24–BK90-27 (Fig. 5g–i).

Description. Short fragments of pinnae with a relatively robust rachis (*c.* 0.5–1.0 mm wide rachis) bear pinnules attached at 70–80°. The pinnae are mainly parallel-sided, although they taper near the pinna-apex. Shorter pinnules are 2.0 mm long and 1.5 mm wide, with slightly undulate margins and rounded apex. Larger pinnules are up to 6 mm long and 2 mm wide, parallel-sided or slightly tapered, with very undulate margins. The sinuses between the lobes extend for nearly halfway between the pinnule margin and the midvein. The lobes are mainly rounded or occasionally slightly angular. A thick midvein extends for most of the length of the pinnule. Lateral veins extend from the midvein at *c.* 60° and are not curved; the lateral veins fork once or in the larger pinnules twice at a wide angle.

Remarks. Wu, Xi & Yan (1987) figured very similar specimens from the Benxi Formation as *Pecopters aspera*. Wu (1988) also records *P. aspera* from a similar horizon in Ningxia. However, true *P. aspera* (e.g. Dalinval, 1960, pls 1–4) has significantly more tapered ultimate segments with a better-individualized apical

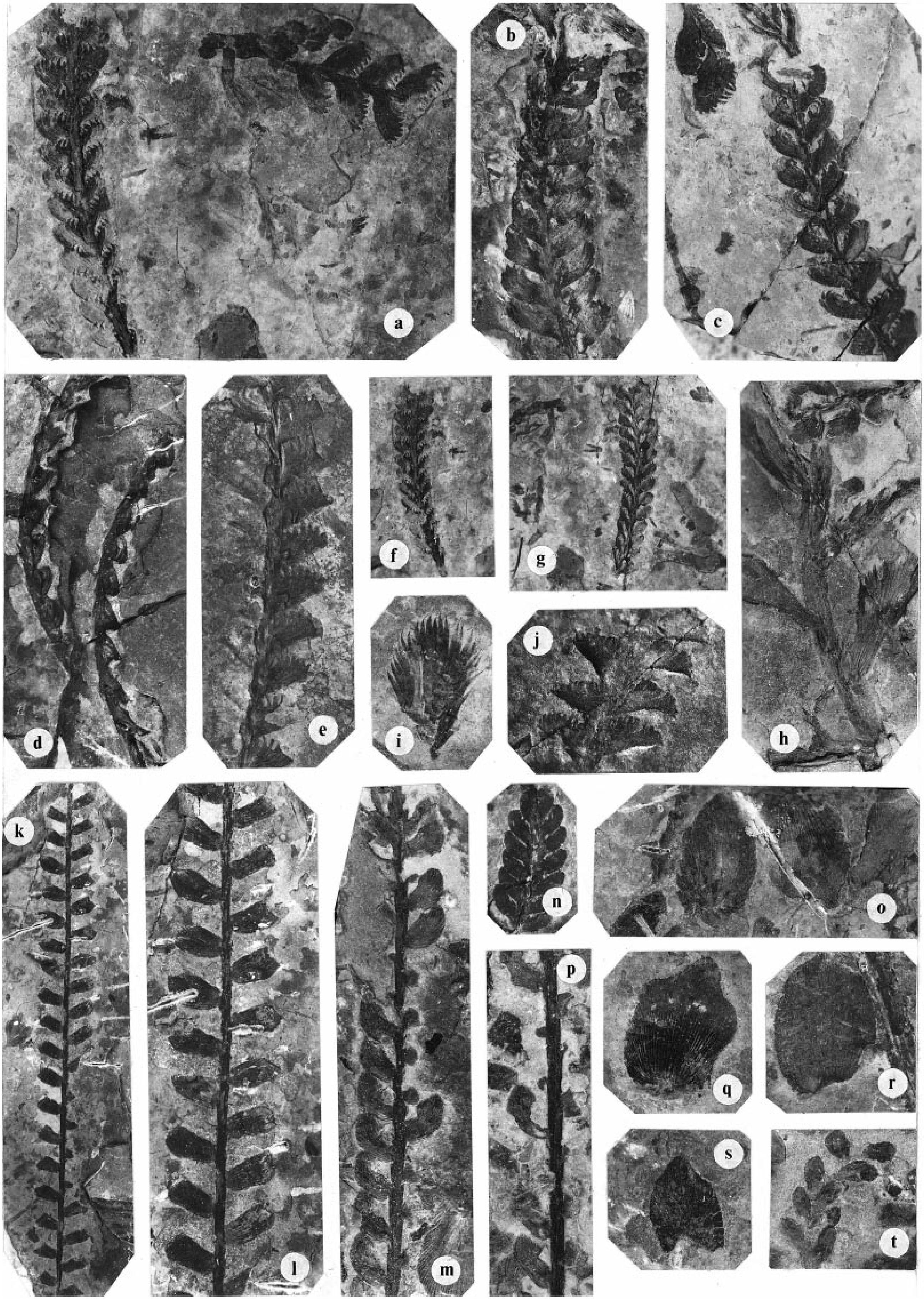

Figure 7. For legend see facing page.

lobe than the Benxi Formation specimens. Huang (1987*a*) reported *P. aspera* from similar-aged strata (the Shangshetai Formation) of Inner Mongolia but did not state if his figured specimens came from those beds or the underlying late Namurian Xiashetai Formation. All other verifiable records of *P. aspera* from China come from strata independently dated as Namurian (Li *et al.* 1974*a*, pl. 53, figs 5–12; Li *et al.* 1974*b*, pl. 2, fig. 6; Zhang *et al.* 1993, pl. 5, figs 3–9).

Class *incertae sedis*
Genus *Conchophyllum* Schenk, 1883, nov. emend.

Emended diagnosis. Rigid stems bearing small, amplexicaul leaves in an alternate arrangement. Leaves heteromorphic, usually with dentate or digitate margin. Leaves usually asymmetrical with more pronounced teeth on the distal margin. Veins fine, dichotomous, radiating from base of leaf. Leaves hypostomatic with anomocytic stomata restricted to intercostal zones.

Remarks. *Conchophyllum* was originally interpreted as fragments of conifer cone with helically arranged bracts (Schenk, 1883; Sze *in* Gothan & Sze, 1930), but Stockmans & Mathieu (1939) showed the 'bracts' to be alternately arranged leaves. As there has been no formal redefinition of the genus since the publication of the protologue, we propose the above emended diagnosis, which also incorporates the epidermal evidence described by Bohlin (1971) and in the present paper.

Bohlin (1971) regarded *Conchophyllum* as similar or possibly identical to *Noeggerathia* but Němejc (*in* Bohlin, 1971) regarded them as distinct. Both genera have amplexicaul leaves, often with a dentate or digitate distal margin. *Noeggerathia* leaves tend to be larger and more symmetrical, but the degree of asymmetry can be variable. Epidermal structure is of little help, as it is poorly known for *Noeggerathia*; the cuticle fragments described by Němejc (1935) only show cellular details along the veins. Fructifications are similarly of little help; although they are well-known for *Noeggerathia* (e.g. Hirmer, 1941) they are unknown for *Conchophyllum*.

Another morphogenus of Chinese noeggerathioid foliage is *Plagiozamites*. The basal leaves of a *Plagiozamites* shoot (e.g. Halle, 1927, pl. 63, fig. 6) are very similar to those of *Conchophyllum* but the more distal leaves tend to be more symmetrical. Again, however, there is not a sharp demarcation between the morphogenera.

Tingia is a morphogenus of possible noeggerathioid foliage that occurs commonly in China (Halle, 1927; Gao & Thomas, 1987). It is readily distinguishable from *Conchophyllum*, *Plagiozamites* and *Noeggerathia* by having anisophyllous shoots with leaves arranged in four rows along the stem. Some *Tingia* shoots have associated cones with bowl-shaped sporophylls completely or partly embracing the cone-axis (Stockmans & Mathieu, 1939; Li *et al.* 1974*a*; Zhang *et al.* 1993), very similar to *Discinites* found associated with *Noeggerathia* in Europe. However, Gao & Thomas (1987) reported a quite different cone associated with *Tingia*, in which there are helically-arranged leafy-sporophylls.

Conchophyllum richthofenii Schenk
Figure 7a–g,j; h–i(?)

1883	*Conchophyllum Richthofeni* Schenk, p. 223, pl. 42, figs 21–26.
1939	*Conchophyllum Richthofeni* Schenk; Stockmans & Mathieu, p. 90, pl. 3, figs 6, 7.
1974*a*	*Conchophyllum richthofenii* Schenk; Li *et al.*, p. 65, pl. 41, figs 2–5 (copy of specimen in Stockmans & Mathieu).
?1975	*Conchophyllum tsaidamense* Bohlin, p. 89, pl. 20, figs 1–6; pl. 22, figs 1–5; pl. 32, figs 5, 6.
?1993	*Conchophyllum* cf. *richthofenii* Schenk; Zhang *et al.*, p. 17, pl. 10, fig. 11–13 (*non* fig. 10).
1995	*Conchophyllum richthofenii* Schenk; Li, pl. 34, figs 6, 7 (copy of specimen in Stockmans & Mathieu).
1996	*Conchophyllum richthofenii* Schenk; Laveine *et al.*, p. 784, pl. 1, figs 11, 11a.

Material. Twenty specimens showing leafy shoots including BK90-42–BK90-48 (Fig. 7a–g,j). There are also specimens with larger leaves (BK90-49, BK90-50) which are provisionally assigned to the species.

Description. This species is preserved as fragments of straight or slightly curved leafy shoot, the longest example being 32 mm long (Fig. 7a). Stems are *c.* 1 mm wide. Leaves alternately or suboppositely arranged on either side of the stem, with adjacent leaves just touching or (in what are probably terminal parts of the shoot) showing some degree of overlap. Leaves attached to the stem at 40–60°, being more oblique in the proximal and distal parts of the shoot, less so in the medial parts. The leaves are asymmetrically

Figure 7. *Conchophyllum* from the Benxi Formation of Kaihuagou, Western Hill near Taiyuan. (a–g, j) *Conchophyllum richthofenii* Schenk, leafy shoots showing characteristic dentate distal margin of the leaves; all × 2 except f–g, which is × 1. (a, f) BK90–42; (b) BK90–43; (c) BK90–44; (d) BK90–45; (e) BK90–46; (g) BK90–47; (j) BK90–48. (h–i) Cf. *Conchophyllum richthofenii* Schenk, large, fimbriate leaves, possibly from the lower part of a leafy shoot, both × 2. (h) BK90–49; (i) BK90–50. (k–t) *Conchophyllum suboblongifolium* sp. nov. All × 2, except (k) which is × 1. (k–l) BK90–51 (holotype), proximal part of shoot with widely spaced leaves. (m, p) medial parts of shoots with slightly overlapping leaves; (m) BK90–52; (p) BK90–53. (n, t) distal parts of shoots with overlapping leaves; (n) BK90–54; (t) BK90–55. (o, q–s) large isolated leaves; (o) BK90–56; (q) BK90–57; (r) BK90–58; (s) BK90–59.

subcuneate (Fig. 7e, j) or obovate (Fig. 7c), and clasp the stem at their base (amplexicaul). The distal margin of each leaf has pronounced teeth up to 1.5 mm long and 0.5 mm wide. Each leaf has 4–12 veins more or less radiating from a narrow base. The veins branch 2–4 times, with a vein-terminal entering each marginal denticle of the leaf. Both veins and stems show fine longitudinal striae, probably representing the lignified vascular fibres.

One fragment (Fig. 7h) probably represents the proximal part of a shoot, 30 mm long, with a stem 2 mm wide. Four laciniate leaves are attached at *c.* 45° to the stem, all apparently to the side facing the viewer. An isolated laciniate leaf (Fig. 7i) also probably comes from the proximal part of a shoot. In both cases, the leaves are cuneate, with their venation radiating from the base and a vein terminal entering each of the distal teeth.

Remarks. Although widely regarded as a characteristic species of the late Westphalian floras of China, it has been only poorly documented. The syntypes (Schenk, 1883) were fragments illustrated as line drawings and have never been re-figured. Stockmans & Mathieu (1939) and Li *et al.* (1974*a*) illustrate photographs of fragments but they give only a limited impression of the species. The Kaihuagou material is far more complete, consisting of several shoots showing the variation in the leaves.

Most recorded specimens of this species are from the Benxi Formation. Zhang *et al.* (1993) figured some fragments as *C.* cf. *richthofenii* from the upper Tsingyuan Formation of Ningxia, which they regarded as late Namurian. However, the only control on the age is an Early Namurian goniatite fauna some 1000 metres lower in the sequence. There are other discrepancies in the upper Tsingyuan Formation flora, such as the presence of *Sphenophyllum emarginatum* Brongniart, which normally occurs in late Westphalian and younger floras. We do not, therefore, regard it as evidence that *C. richthofenii* ranges below the upper Westphalian Stage.

Zhang *et al.* (1993) figured another specimen as *C.* cf. *richthofenii*, from the underlying Zhongwei Formation in the same area of Ningxia, which is stratigraphically nearer the Pendleian goniatite fauna. However, this isolated fragment is too small for a reliable identification.

Bohlin (1971) illustrated numerous *Conchophyllum* fragments from Gansu Province, showing very variable leaves. However, the specimens were very fragmentary and Bohlin was unsure if he had one highly polymorphic species or several related species. The more complete shoots from Kaihuagou do not show such leaf polymorphism along the shoot or between shoots, and suggest that Bohlin was in fact dealing with several species.

Conchophyllum parvifolium Bohlin, 1971 differs from *C. richthofenii* by its rounder leaves with only poorly developed distal teeth. *C. tsaidamense* Bohlin, 1975, from the lower Keluke Group of Oulongbuluke, southern Qilian Mountains, has the same type of dentate, cuneiform to ovoid leaves as *C. richthofenii*, and is probably conspecific.

Conchophyllum suboblongifolius sp. nov.

Figures 6g–l, 7k–t

Diagnosis. Small, weakly amplexicaul leaves, alternately attached to stem. Leaves mostly ovoid to subrectangular, 2–12 mm long and 1–10 mm wide, typically about 5 mm long and 2 mm wide. Leaf margin smooth or slightly dentate. Leaves widely spaced along stem except in distal part of shoot where they overlap with each other. Veins dense and radiating from base of leaf; venation density *c.* 40 veins per centimetre along leaf margin.

Holotype. TIGMR Specimen BK90-51 (Fig. 7k,l), in the collections of the Tianjin Institute of Geology and Mineral Resources. Originated from the upper Westphalian Benxi Formation, Kaihua Village, Loucheng, Shanxi.

Paratypes. TIGMR Specimens BK90-52–BK90-59.

Derivation of name. The name reflects the possibility that this species was ancestral to the Permian *Plagiozamites oblongifolius* Halle, 1927.

Material. In addition to the types, there are four other shoots and ten isolated leaves.

Description. The most complete specimens show straight, apparently rigid stems, with small leaves attached laterally in two rows along the stem. The longest (Fig. 7k) has a stem that is 1 mm wide and 95 mm long. Along most of the shoot, alternately arranged and widely spaced leaves are attached at 60°. In the terminal part of shoots (e.g. Fig. 7n,t) the leaves are similar in shape, but are smaller, more closely spaced and attached at *c.* 45°.

The leaves are mostly ovoid (Fig. 7m,p) to subrectangular (Fig. 7l), up to 5 mm long and 2 mm wide, but as little as 2 mm long and 1 mm wide near the shoot apex (Fig. 7n). There are also some larger leaves, 9–12 mm long and 8–10 mm wide (Fig. 7o,q–s). These are not found attached to a stem, but are similar in shape to the smaller leaves and we believe they are conspecific. The leaves are usually symmetrical about their long axis, but some of the larger leaves are slightly asymmetrical. The margin of most leaves is smooth or slightly dentate, but in the proximal part of the shoot they are more laciniate. The venation is dense, with fine veins radiating from base of leaf, producing a venation density of *c.* 40 veins per centimetre along the leaf margin.

Table 2. Comparison of the main plant fossil assemblages from the Benxi Formation and equivalent strata in North China

Assemblage	Dashetai[1]	Northwest Henan[2]	Zibo[3]	Southeast Shanxi[4]	Benxi District[5]	Taiyuan[6]	Taiyuan[7]	Kaiping[8]
Synchysidendron galeatum (Li *et al.*) comb. nov.			X				X	?
S. subrhombicum (Li *et al.*) comb. nov.						X	X	
S. tripunctatum (Stockmans & Mathieu) comb. nov.	?	X				?		X
Lepidodendron ophiurus Brongniart		?						
'L.' posthumii Jongmans & Gothan						X		
Cathaysiodendron nanpiaoense Lee		X				X		
Bothrodendron sp.			X					
Kaipingia sinica Stockmans & Mathieu								X
Lepidostrobophyllum hastatum (Lesquereux) Chaloner		X			X			
L. ovatifolium (Lesquereux) Chaloner	X	X			?			
Achlamydocarpon taiyuanensis sp. nov.							X	
Selaginella benxiensis sp. nov.							X	
Sphenophyllum tenerrimum Stur		X						
S. oblongifolium (Germar & Kaulfuss) Unger						X		X
Calamites taiyuanensis Zhao & Chang						X		
C. cf. *cistii* Brongniart						X		
C. cf. *suckowii* Brongniart								X
Asterophyllites cf. *grandis* (Sternberg) Geinitz	X						X	
Calamostachys sp.	X							
Pecopteroid spp.	?	X				X	X	X
Lobatopteris sp.						X		
Rhodeopteridium sp.								X
Alloiopteris sp.		X					X	
?*Boweria* sp.							X	X
Sphenopteroid sp.	X						X	
Sphenopteris taiyuanensis Halle								X
Conchophyllum richthofenii Schenk						X	X	X
C. parvifolium Bohlin		X						
C. suboblongifolius sp. nov.							X	
Cf. *Tingia* sp.	X				X	X	X	X
Paripteris spp.	X	X	X	X	X	X		X
Linopteris spp.	X	X	X	X	X	X		X
Eusphenopteris eurasiatica (Stockmans & Mathieu)								X
E. marchalii (Stockmans & Mathieu)								X
E. neuropteroides (Boulay) Novik								X
Dicranophyllum latum Schenk								X
Cordaites principalis (Germar) Geinitz								X
Poacordaites linearis Grand'Eury								X

[1]Huang (1987*a*); [2]Wu, Xi & Yan (1987); [3]Li (1957); [4]Zhao, Liu & Hou (1987); [5]Huang (1987*b*); [6]Zhang *et al.* (1987); Liu, Wang & Zhao (2000); [7]this paper; [8]Stockmans & Mathieu (1939, 1957).

The leaflets are hypostomatic. The epidermis of the presumed upper surface shows elongate, irregularly polygonal cells, up to 300 µm long and 15–30 µm wide, with pointed or blunt ends, and straight or slightly waved lateral margins (Fig. 6g). There is no differentiation in epidermal cell structure between the veins and the intercostal areas. There is a thick cuticle over the upper epidermis. The inner surface of the cuticle is flat except for the wide thickenings along the anticlinal walls of the epidermal cells. The outer surface of the cuticle is vaulted over the epidermal cells. The anticlinal walls are clearly marked by wide cuticular ridges. In some places, these ridges have lost their outer surface, to reveal cross-bars of cuticle below (Fig. 6h). Where the cuticle has been lost, evidence of the epidermal cells may still sometimes be preserved (Fig. 6j).

The lower cuticle is also covered by elongate irregularly polygonal cells, which are clearly differentiated between the costal and intercostal fields (Fig. 6i). The costal cells are slender, up to at least 250 µm long and 10–15 µm wide. The intercostal cells are 15–20 µm wide and rarely more than 150 µm long (Fig. 6l). Slightly sunken stomata occur in the intercostal fields of the lower cuticle, and are consistently parallel to the venation (Fig. 6k,l). They are 30–40 µm long and *c.* 12 µm wide, with two prominent guard-cells. There are *c.* 280 stomata per mm^2 over the intercostal fields, and a Stomatal Index of *c.* 36.

Remarks. This species is so far unique to the Kaihuagou assemblage. It is not a typical *Conchophyllum*, as the leaves are only slightly asymmetrical, and have a smooth or only very shallowly dentate distal margin. However, the epidermal structure compares closely with that described by Bohlin (1971) from his unnamed species of *Conchophyllum*. The anomocytic stomata with prominent guard cells in Bohlin's specimens are more sunken below the epidermal surface, but are otherwise very similar. The distribution of the stomata in Bohlin's material is more variable, but this may be partly due to there being more than one species present.

The leaves of *Plagiozamites oblongifolius* Halle, 1927 from the Permian floras of of Shanxi are larger but otherwise very similar in shape. We have included this new species in *Conchophyllum* because of its epidermal structure, the size of the leaves and their tendency to be asymmetrical and dentate, but we regard it as possibly ancestral to *Plagiozamites*.

Genus *Tingia* Halle, 1925

Type. Holotype of *Tingia carbonica* (Schenk) Halle.

Remarks. This morphogenus was established by Halle (1925) for leafy anisophyllous shoots with two ranks of larger leaves on one side of the stem and two ranks of smaller leaves on the other side (see also Halle, 1927; Gao & Thomas, 1987).

Cf. *Tingia* sp.

Figure 5r

Material. A single specimen (BK90-35).

Description. This poorly preserved fragment of a shoot is 75 mm long and 9 mm wide, with two rows of leaves attached at *c.* 60°. The leaves are closely spaced, with adjacent leaves touching or slightly overlapping. The leaves are 6 mm long and 1.5 mm wide, subfalcate with a tapered apex and decurrent base that seems to partly clasp the stem. The distal margin of each leaf has 1–2 small denticles. The venation is not well preserved, but 3–4 veins appear to run along the length of the leaf.

Remarks. This is one of a number of specimens reported from the Benxi Formation that superficially resemble *Tingia* in the general shape of the leaves (see also Stockmans & Mathieu, 1939; Huang, 1987*a*,*b*; Zhang *et al.* 1987). None show the four rows of leaves that are diagnostic of *Tingia*, although the two rows of smaller leaves can be difficult to see (Gao & Thomas, 1987). In the absence of a well-established morphogenus for the reception of such shoots, they have been provisionally referred to as Cf. *Tingia* sp.

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Figure 5l–p

Material. Twelve specimens including BK90-30–BK90-34 (Fig. 5l–p).

Description. These fossils are fragments of foliar shoots, the most complete being 38 mm long (Fig. 5l). The stems are 0.5–1.0 mm wide, and straight or slightly curved. The shoots are parallel-sided for most of their length, but tapered at 45° in their most distal part (Fig. 5n). The shoot was also probably tapered in its proximal part (Fig. 5m). Compressed leaves occur on both sides of the stem, in an apparently pinnate arrangement (Fig. 5l–n). Occasionally, however, the leaves can be seen to be helically arranged (Fig. 5o) and the apparent pinnate arrangement is due to leaves being lost when the rock was split. The leaf arrangement was clearly helical but not decussate, although there are not enough leaves preserved to identify the exact phyllotaxy.

The leaves are inserted at about right-angles to the rachis, except in the very distal part of the shoot, where they become slightly oblique. They are subtriangular, usually acroscopically curved except near the base of the shoot where they are straighter and more symmetrical; they are up to 6 mm long and 2 mm wide. The limb of the leaves appears to have been fleshy, and compression of the tissue has tended to mask any surface features. In a few cases, however, there appear to be up to five parallel lines running along the length of the leaf.

Remarks. Shoots such as these from the Pennsylvanian, with helically arranged leaves, could be from either a coniferophyte or a lycophyte. For instance, they bear some resemblance to the type variety of *Ernestodendron filiciforme* (Sternberg) Florin, as documented by Florin (1939, pls 111–124, pl. 125/125, figs 1–6). However, there is also comparison with the leafy lycophyte shoots *Selaginellites resimus* Rowe, 1988, from the Mississippian (‘Lower Carboniferous’) Drybrook Sandstone flora. In the absence of any anatomical detail, it is impossible to be certain.

4. Comparison with other Benxi Formation assemblages

A comparative analysis of assemblages from the Benxi Flora is hindered by the poor locality details given in much of the published literature. Zhang *et al.* (1987) detail the composition of the three separate assemblages they studied, but most other published accounts are clearly syntheses of information from several different localities. Table 2 shows the composition of the principal assemblages from the Benxi Flora, which is adapted from a table given by Wu (1988), checked against the original literature, and including the taxonomic changes discussed in the present paper. However, the columns mostly do not refer to individual assemblages but are syntheses of several assemblages from a particular region.

The assemblages all have a broadly similar composition. Most have one or more of the *Synchysidendron* species discussed earlier in this paper (*S. galeatum*, *S. subrhombicum*, *S. tripunctatum*) together with abundant *Lepidostrobophyllum* sporophylls. There are other taxa present, such as *Bothrodendron* sp., *Kaipingia sinica* Stockmans & Mathieu and *‘Lepidodendron’ posthumii* Jongmans & Gothan, but they are rare and have only each been reported from one region. Calamites and sphenophylls are also generally rare, except for the Dashetai assemblage (Huang, 1987*a*).

Ferns are usually abundant and diverse, but mostly preserved as small indeterminate fragments.

The most obvious difference between the Kaihuagou assemblage and the others from the Benxi Flora is the total absence of parispermaceaens. The fronds *Paripteris* and *Linopteris* appear to have shed their leaflets very readily, and so detached examples are common in most Benxi Flora assemblages. Even relatively small and poorly preserved assemblages, such as those from Zibo (Li, 1957) and southeast Shanxi (Zhao, Liu & Hou, 1987), have detached pinnules. Their absence from the Kaihuagou assemblage must therefore be regarded as significant. The taxonomy of the parispermacean foliage of the Benxi Flora is problematic, as they are only known from isolated pinnules. They show less morphological variation than the Visean parispermaceans (Zhang *et al.* 1993), but it is still sufficient to make the identification of isolated pinnules difficult, and the Benxi Formation fossils are probably best referred to simply as *Paripteris* sp. and *Linopteris* sp. We do not agree with Zhang *et al.* (1993) who assign all paripterids to *P. gigantea*, and the variations in pinnule morphology are reflected by the use of morphological forma. This would imply that the same species was in existence for some 30 million years, which we think unlikely.

Pteridosperms are otherwise absent from the Benxi Flora, except at Kaiping where three species of the lagenostomalean *Eusphenopteris* were described by Stockmans & Mathieu (1939). The record of *Eusphenopteris obtusiloba* (Brongniart) from Liaoning by Huang (1987*b*) is based on a specimen that is too small to identify.

Noeggerathioids are common at Kaihuagou. Elsewhere in the Benxui Formation they are rarer, although only at Zibo and the localities in southeast Shanxi has no noeggerthioid been reported. Poorly preserved *Tingia*-like foliage is the most commonly found. *Conchophyllum*, widely claimed as a characteristic endemic of the Benxi Flora, is in fact much less common except at Kaihuagou.

There is no obvious geographical pattern to the observed variations in the Benxi Flora. The diverse Kaiping assemblage and the impoverished asemblages from the Benxi District all occur in the northeast part of the North China Region, where the Benxi Formation is most thickly developed. Similarly, there are both relatively diverse assemblages (northwest Henan) and impoverished assemblages (southeast Shanxi) in the more thinly developed Benxi Formation in the southwestern part of the Province. The low diversity of the Zibo assemblage is probably due to it coming from the Iron Minerals Member, which was formed before the swamp vegetation was firmly established. The other assemblages originated from the coal-bearing strata within the Bangou Member. However, the fossils have almost certainly been transported some distance from where the plants grew, which hinders the interpretation of the variations in the fossil assemblages in terms of variations in the original vegetation.

5. Palaeoecology

Most of the fossils in the Kaihuagou assemblage are very small, but this is not because they represent small organs of plants. Most of the lycophytes were arborescent plants, and yet we only see detached leaves and sporophylls, and relatively small pieces of bark. The fern fronds must have been significantly larger than the small fragments that we find preserved. This size range suggests the fossils are allochthonous plant fragments and not the remains of the local vegetation. This is also indicated by associated coals of the Benxi Formation not having palaeosols.

There has been insufficient sedimentological research on the Benxi Formation to enable us to detail the biostratinomic history of these fossils, and thus to identify the source vegetation. One possible origin for such plant remains would be coastal marsh, mangrove-like vegetation. This was favoured by Li (1995, p. 255) because (1) the plant- and coal-bearing beds are associated with limestones, (2) the coals have a high sulphur content, and (3) the arborescent lycophytes were hydrophilous with shallow rooting structures. However, the presence of limestones reflects where these beds were deposited rather than the origin of the plant debris. If the coals were autochthonous, then their high sulphur content might have been significant, but the evidence suggests they were allochthonous. The lycophytes were undoubtedly hydrophilous but were probably adapted to freshwater rather then saline swamps. The Pennsylvanian mangrove-like vegetation of North America was dominated by cordaitanthaleans rather than lycophytes (Raymond & Phillips, 1983; Raymond, 1988). The dominant gymnosperms of the Benxi Flora are parispermaceans, which have large seeds but not as an adaptation to dispersal by marine currents (Laveine, Lemoigne & Zhang, 1993). Finally, the fact that the fossils are preserved as fusain, indicating the presence of extensive wildfire in the area, goes against a mangrove interpretation.

Fusain fragments can travel a considerable distance in water (e.g. Falcon-Lang & Scott, 2000; Scott, 2000) and the possible coniferophyte specimens in the assemblage could have originated from relatively dry, upland habitats. However, the bulk of the assemblage represents vegetation that probably favoured lowland habitats, associated with freshwater conditions (parispermaceans, lycophytes). It is likely, therefore, that most of the Benxi Flora came from the vegetation growing alongside rivers flowing into the area. There is no evidence of extensive coal-forming swamp vegetation growing between the rivers, as occurred during Taiyuan Formation times, but this may simply be because plant debris from here did not find its way into the fossil record.

6. Comparison with late Westphalian floras of Euramerica

Traditionally (e.g. Li, 1963; Yang, Li & Gao, 1983) the Benxi Flora has been regarded as essentially similar to the contemporaneous floras of Euramerica. If the Benxi Formation is of late Westphalian D age, comparative floras in Europe include those of the upper Pennant and Suprapennant Formation of southern Britain (Cleal, 1997), the post-Leonian strata of the Guardo Coalfield, northern Spain (Wagner, Fernandez Garcia & Eagar, 1983), and the upper Heiligenwalder Schichten of Saar-Lorraine (Laveine, 1989). In North America, comparable floras are found in the Canadian Maritime Provinces, such as the Sydney Coalfield (Zodrow & McCandlish, 1980), and Mazon Creek (Darrah, 1969). Some genera occur in both floras, such as *Linopteris*, which probably migrated into Euramerica from China in early Westphalian times (Laveine, Lemoigne & Zhang, 1993). *Paripteris* also occurs in the Euramerican coal forests but had become extinct before the Westphalian D Age. *Asterophyllites*/*Calamostachys*, *Sphenophyllum* and *Eusphenopteris* occur in both regions, but tend to be much rarer in China than in the west. *Synchysidendron* also occurs in both regions, but in the Euramerican forests was mainly restricted to the backswamp vegetation preserved in the coal seams. The noeggerathioid *Conchophyllum* has no obvious counterpart in the Euramerican floras, other than the much larger-leafed and relatively rare *Noeggerathia*.

There were many taxa in the western coal forests that were rare or absent in the Benxi Flora. By late Westphalian times, the western adpression assemblages are dominated by marattialean ferns (*Lobatopteris*, *Polymorphopteris*, *Cyathocarpus*) and non-parispermacean medullosalean pteridosperms (*Alethopteris*, *Neuropteris*), none of which occur in the Benxi Formation. Huang (1987*b*) records *Neuropteris ovata* Hoffmann from the Benxi Formation of Liaoning, but all his figured specimens are from the Taiyuan Formation. The only possible marattialean from the Benxi Formation is a *Lobatopteris*-like frond figured by Zhang *et al*. (1987, pl. 3, figs 4–6) from the Xishan Coalfield. The lagenostomalean liana-like plants *Mariopteris* and *Karinopteris*, and the scrambling callistophyte shrub *Dicksonites*, were all absent from the Benxi Flora. Among the lycophytes found in the Westphalian adpression record of Euramerica, by far the dominant species belong to *Lepidodendron* and *Sigillaria*, both of which appear to be absent from the Benxi Flora.

Palaeomagnetic evidence suggests that Euramerica and North China occupied similar palaeoequatorial latitudes during late Westphalian times (e.g. Lin, Fuller & Zhang, 1985). Many palaeogeographic reconstructions (e.g. Rowley *et al.* 1985; Nie, Rowley & Ziegler, 1990) show North China and South China as separate 'microcontinents' with no 'land bridge' with Euramerica or Angara. However, this is based largely on equivocal palaeomagnetism evidence (see comments by Nie, Rowley & Ziegler, 1990, p. 404) and an interpretation of the timing of the collision of these plates that is still far from confirmed (Enos, 1995, table 1). It also ignores the floristic evidence, which indicates that there must have been a land connection between these areas to allow the migration of seed plants, whose disseminules were probably incapable of dispersal by sea (Laveine, Lemoigne & Zhang, 1992; Laveine, Zhang & Lemoigne, 2000). For instance, Zhang *et al.* (1987) have clearly demonstrated a westwards spread of *Paripteris* from China to Europe during the Namurian, and Zhang *et al.* (1993) have suggested a reverse migration of *Alethopteris* and *Lonchopteris* from Europe to China. Despite this, most assemblages described from the Benxi Flora appear rather different from typical late Westphalian floras of Euramerica. However, the more diverse Kaiping assemblage reveals closer similarities with the Euramerican floras, suggesting that the observed differences in the other Benxi Flora assemblages reflect taphonomic rather than vegetational differences.

7. Comparison with Cathaysian floras

Some Chinese authors have recently argued that the Benxi Flora is essentially Cathaysian in aspect (Wu, 1988; Liu, Wang & Zhao, 2000). The Cathaysian Realm was originally taken to correspond to the *Gigantopteris* Flora of Halle (1927) found in the Shihhotze Group (Huaketou and Tianlongsi formations) and Shihchienfeng Formation of Shanxi. Most authors now take a somewhat wider view and include the floras of the underlying Shanxi and Taiyuan formations. The Shanxi Formation lacks true gigantopteroids, but includes *Lobatannularia*, *Tingia*, *Emplectopteris*, *Emplectopteridium* and various lycophytes including *'Lepidodendron' oculusfelis* and *'L.' posthumii* (e.g. Shen *in* Li, 1995). The upper Taiyuan Formation (lower part of Lower Permian Series) has very similar floras to the Shanxi Formation except for the absence of *Lobatannularia*, but *Emplectopteris* and *Emplectopteridium* are absent from the lower part of the formation (Stephanian). The Taiyuan Formation also includes a number of medullosalean and marattialean species, giving it a distinctly Euramerican aspect.

The Taiyuan Formation with these early Cathaysian Floras conformably overlies the Benxi Formation in Shaanxi, Shanxi and Hebei provinces (Yang, Li & Gao, 1983; Zhang, 1987). Although there is no significant time-gap between the two formations (Yang, Li & Gao, 1983), there are marked differences between their fossil floras. The parispermaceans and *Conchophyllum* do not range above the Benxi Formation. Two of the three *Synchysidendron* species of the Benxi Formation also do not range into the Taiyuan Formation. Horsetails, sphenophylls, ferns and medullosalean-like pteridosperms are all abundant and diverse in the Taiyuan Formation (e.g. Halle, 1927; Stockmans & Mathieu, 1939, 1957; Li, 1963) but are absent or rare in the Benxi Formation. However, these differences may just be due to the Benxi Flora representing the drifted remains of riparian vegetation, whereas the Taiyuan Formation floras represent more fully developed swamp vegetation. Both vegetation types were growing in essentially freshwater habitats, which explains why some taxa occur in both (e.g. *Synchysidendron*).

Certain elements of the Benxi Flora may be ancestral to species found in the Taiyuan Formation: *Synchysidendron galeatum* may be closely related to '*Lepidodendron*' *oculusfelis*, and *Conchophyllum suboblongifolius* to *Plagiozamites oblongifolius*. There are also in the Benxi Flora early occurrences of typical Cathaysian species, such as *Synchysidendron tripunctatum* and '*Lepidodendron*' *posthumii*. There is no obvious evidence, however, of taxa that might have been closely related to many of the key Cathaysian forms, such as the *Gigantopteris*/*Emplectopteris*/*Emplectopteridium* complex and *Lobatannularia*.

8. The Benxi Flora – a link between the Euramerican and Cathaysian floras

The evidence presented in this paper indicates that the Benxi Flora represents a link between the typical Westphalian Euramerican floras of Europe and North America, and the Stephanian and Permian Cathaysian floras of East Asia. It supports the hypothesis of Cleal & Thomas (1991) who, whilst retaining the Benxi Flora within what they called the Europe Palaeofloristic Realm (that is, the Euramerican Floras of previous authors), distinguished it as a lower-ranked palaeofloristic area. However, it also supports the view of Chaloner & Meyen (1973) and Li *et al.* (1993) that the Benxi Flora was ancestral to the fully-fledged Cathaysian Realm floras found in Stephanian and Permian deposits (Li *et al.* 1993 referred to them as 'Protocathaysian').

It seems that the Cathaysian Realm evolved out of a subset of the Europe Realm growing in China during Westphalian times (the Benxi Flora). The two realms thus have an ancestor–descendant relationship rather than representing two discrete floristic zones growing at any one time in different parts of the world. In the Stephanian Epoch, when the earliest true Cathaysian floras were growing in the eastern tropics, only remnant Europe Realm vegetation was present in the western tropics. This remnant western vegetation, such as seen in the intramontane basins of central and southern Europe, and in the northern Appalachians, was of quite different character from the classic Europe Realm floras of the Westphalian Age. Genera such as *Laveineopteris*, *Reticulopteris*, *Lonchopteris*, *Mariopteris*, and *Karinopteris* ceased to be dominant elements of the clastic substrate vegetation, and were replaced by genera such as *Callipteridium*, *Odontopteris* and *Nemejcopteris*, together with the marattialean ferns. The peat-forming vegetation is even more strikingly different, with the arborescent lycophytes having been replaced as the dominant plants by marattialean ferns and medullosaleans. It is in fact arguable that Westphalian floras of the western tropics have more in common with the Stephanian floras of China than with the Stephanian floras of Europe, especially in the context of the dominant peat-forming vegetation. During the Permian Period, when the classic Cathaysian floras were growing in the eastern tropics, aridification all but eliminated the swamp forests in the western tropics.

We therefore agree with Havlena (1970) that there were not separate Cathaysia and Europe realms (the latter including North America), but a single pantropical phytochorion, which he called the Amerosinian Realm. The Chinese Stephanian and Permian floras are, essentially, what would have grown in the western tropics, if aridification there had not destroyed the swamp habitats. It is even possible that some of the so-called 'characteristic' Cathaysian elements were able to grow in the Permian Period in a few parts of the western tropics, especially from North America (e.g. Read & Mamay, 1964; Mamay, 1986, 1988, 1995). This idea is based mainly on the presence of leaf fossils in North America that resemble Chinese species. It is possible that such similarities in leaf morphology are due to convergence in unrelated groups. However, the similarities are in several different leaf-types, as well as just the well-documented gigantopteroids, and so it may reflect a real relationship between the floras. There was undoubted provincialism within the Amerosinian Realm, such as between the Stephanian vegetations of Europe and China. However, these differences are nowhere near as marked as from the higher latitude Angara and Gondwana realms, and should consequently be recognized at lower phytochorial ranks (probably areas or provinces).

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