

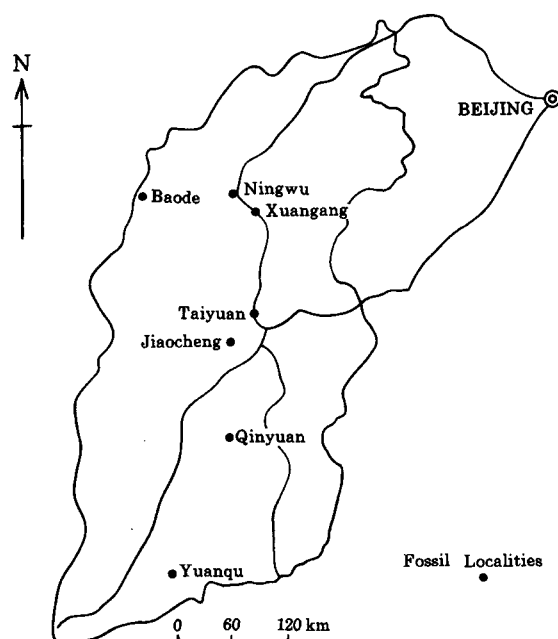
# PERMIAN *SUPAIA* FRONDS AND AN ASSOCIATED *AUTUNIA* FRUCTIFICATION FROM SHANXI, CHINA

by WANG ZI-QIANG

**ABSTRACT.** Three new species of bipartite *Supaia* frond, one associated with an *Autunia* ovuliferous organ, have been identified. *S. shanxiensis* sp. nov. from Central Shanxi is roughly similar in gross morphology to *Supaia* species from the Permian Hermit Shale of North America, but differs in the size, shape and other features of the frond. It can also be distinguished by the pinnules having an entire margin, a faintly decurrent base and being more closely spaced, and the venation consisting of a weak mid-vein. *S. contracta* sp. nov., from North Shanxi, is characterized by pinnules with a markedly constricted base and distinctive cuticles, and compares closely with some of the Upper Permian *Tatarina* species from the Urals. The Southern Shanxi species, *S. yuanquensis* sp. nov., is distinguishable from both the above in its smaller frond with a delicate primary rachis, its strongly decurrent and elongate pinnules, and its thin lamina texture. *Autunia shanxiensis* sp. nov. shows individual cones consisting of bilaterally symmetrical megasporophylls in spiral attachment, in contrast to the lax, modified, fertile pinnae of *A. milleryensis*. Although not found in attachment, the close association of *S. shanxiensis* fronds and *A. shanxiensis* ovuliferous organs suggests that, at least in North China, the *Supaia*-type frond may have belonged to the Peltaspermaeae. It is argued that the names *Autunia* and *Peltaspermum*, originally proposed as 'organ'-genera, should not be used for natural genera based on partly reconstructed fossil plants. Abundant fungal-spots on or within *Supaia* fronds in North China are evidence of the increasing deterioration of the environment during the Permian.

*SUPAIA* White, 1929 has been regarded as endemic to the Permian Hermit Shale of the southwestern United States (Read and Mamay 1964; Chaloner and Meyen 1973; Meyen 1987; Lemoigne 1988; Cleal and Thomas 1991; DiMichele and Hook 1992). However, there is some evidence that it also occurs elsewhere in the Northern Hemisphere, such as Lodève in southern France (Doubinger and Heyler 1975), Moravia in the Czech Republic (Němejc and Augusta 1937; Dijkstra 1965), the Kuznetsk Basin of Siberia (Zalessky and Tchirkova 1935; Neuburg 1948), and the northern periphery of China (Huang 1977; Zhou and Zhou 1986). Significantly, all previously reported Chinese specimens came from north of the Tianshan-Xinggan Suture, and are thus from the Angaran terrane.

Hitherto, our knowledge of the genus has been restricted to its gross morphology, with nothing known of the fructification or cuticles. Thus, its affinities have been uncertain. Between 1987 and 1991, when studying the phytostratigraphy of the Permian red-beds in North China, I recognized that most specimens previously assigned to *Protoblechnum* or *Compsopteris* from the Tianlongsi Formation had bipartite fronds with two monopinnate branches, like *Supaia*. Later professional collections made at a locality in the Qingyuan District of Shanxi (Wang-tao village) eventually yielded many entire bipartite *Supaia*-type fronds, associated with *Autunia*-type ovuliferous organs. This previously unknown obligate association suggests that both belong to one plant. Fronds of another type of *Supaia* from Xuangan Coal-Mine have yielded well-preserved cuticles and particularly exhibit many fungal-spots. Although some of these specimens have been illustrated previously (Wang 1996) the present paper provides the first full documentation.



TEXT-FIG. 1. Localities in Shanxi yielding *Supaia* from the upper Tianlongsi Formation.

#### STRATIGRAPHICAL SETTING

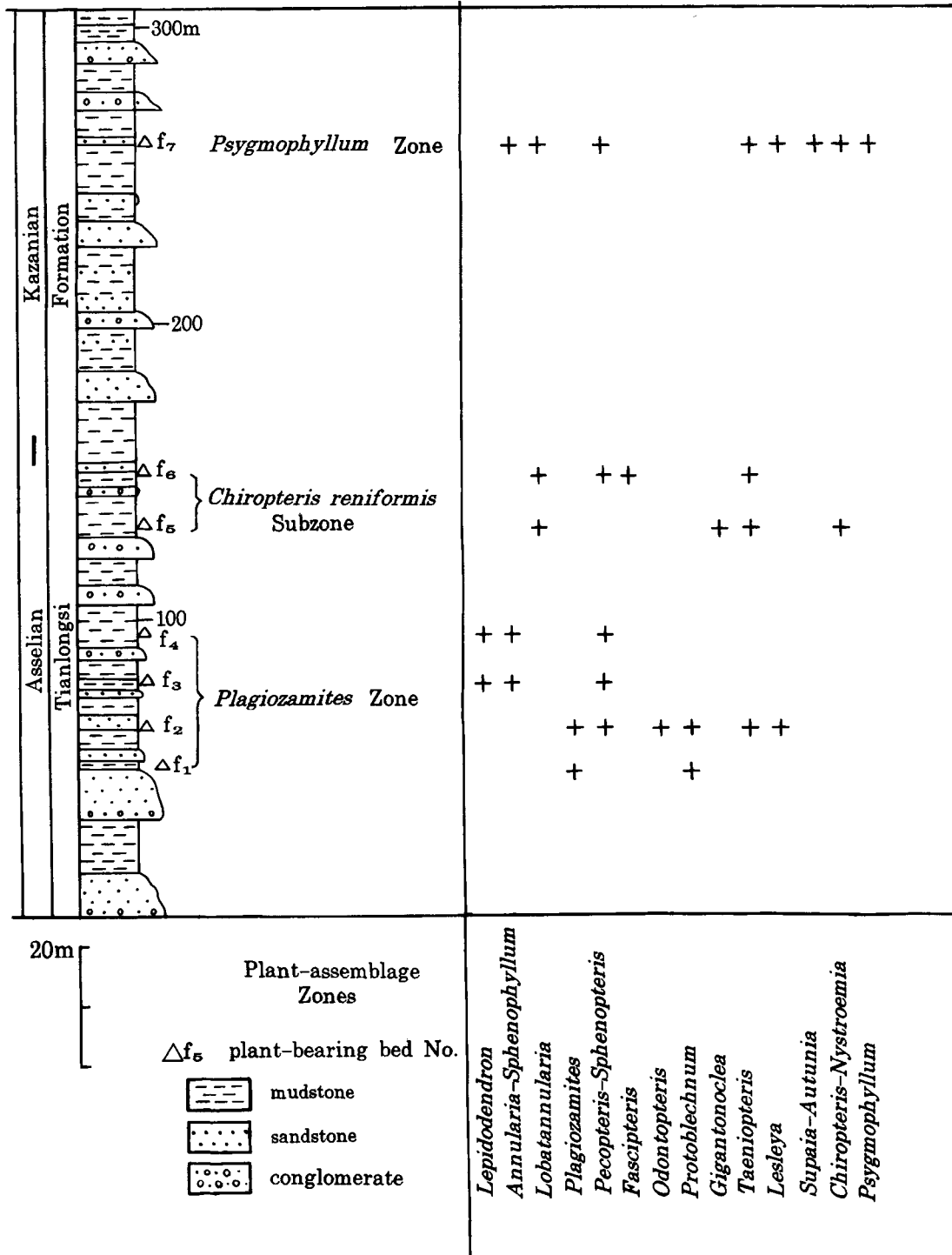
The plant-bearing strata belong to what until recently was known as the 'Upper Shihhotze Formation', but which was renamed the Tianlongsi Formation to avoid a nomenclatural duplication with the Shihhotze Group. This lithostratigraphical unit was re-defined by the 212 Geological Survey Team of Shanxi Province (Chen and Niu 1993). I have recognized three plant-assemblage zones within the Tianlongsi Formation in its type section in the Western Hill of Taiyuan, Shanxi in ascending order: the *Plagiozamites* Zone, the *Chiropteris* Zone (or subzone) and the *Psymophyllum* Zone. In the north of Taiyuan, the *Chiropteris* Zone is absent. Of these zones, the *Psymophyllum* Zone has hitherto not been studied in detail, although Halle (*in* Norin 1924, p. 23) had referred to it as 'the uppermost plant-bearing zone of the Upper Shihhotze Series with *Psymophyllum* and *Taeniopteris*'. A summary of the *Psymophyllum* Zone floras is given in Appendix 1.

All plant-bearing biostromes in the *Psymophyllum* Zone are small lenses of grey-greenish muddy or silty sandstone about 10–50 mm thick and 1–2 m in lateral extent. The lenses are within or under the two to three sets of white-greyish channel sandstones or sandy conglomerates (1–20 m thick), which in turn form large intercalations within thick red mudstones and represent ephemeral channel deposits in a seasonally alternating arid-wet climate.

The fossils only rarely represent autochthonous or parautochthonous burials, in which the plants can easily be identified at the species level. Most are allochthonous or even fragmentary burials, where the plants can be barely assigned at the generic level based on their gross morphology.

In all the sections (Text-fig. 1), the *Supaia*-bearing biostromes are restricted to the uppermost part of the Tianlongsi Formation. Among them, only those at the Qinyuan (= Wangtao), Xuangan and Yuanqu sections are parautochthonous burials, the rest being fragmentary ones. In general, the total plants in each biostrome are of rather low diversity, not exceeding ten species belonging to five to seven genera.

*Wangtao section* (Text-fig. 2). The *Supaia*-bearing lens is a thin grey mudstone or siltstone, lying below a 2 m thick white-yellowish sandstone, and is about 40 m from the top of the formation



TEXT-FIG. 2. Distribution of main plant fossil form-genera in the Tianlongsi Formation at the Wangtao section, Qinyuan, Shanxi.

(Text-fig. 2, plant-bearing bed No. 7). The lens comprises two biostromes: the upper one with abundant *Psymphyllum multipartitum* Halle and occasional *Sphenopteris* cf. *gothanii* Halle; the lower one containing rich *Supaia*, and rare '*Chiropteris kawasaki*' Kon'no, *Rhipidopsis* sp., *Nystroemia pectiniformis* Halle, *Lobatannularia heianensis* (Kodaira) Kawasaki, *Annularia shirakii* Kawasaki, *Lesleya* sp. (= *Taeniopteris* cf. *schenki* Sterzel). *Supaia shanxiensis* sp. nov. and associated *Autunia shanxiensis* sp. nov. are well preserved but unfortunately lack cuticle.

*Xuangan section.* The biostrome here is a thin, monocyclic, silty shale, 0.1–0.2 m thick. It occurs in the second from top set of grey-greenish sandstone, which is about 15 m thick, and is about 80 m from the top of the formation. The fossils are an parautochthonous burial, representing plant foliage that was transported for short distance. The main identifiable plants are *Supaia contracta* sp. nov., *Psymphyllum multipartitum* Halle, *Fascipteridium ellipticum* Zhang and Mo, *Lobatannularia multifolia* Kon'no and Asama, *Pecopteris* cf. *feminaeformis* (Schlotheim) Sterzel, *P. arcuata* Halle, *Taeniopteris densissima* Halle, *T. szeiana* Chow, *Lesleya* sp. and *Peltaspermum* sp. Among these, *Supaia contracta* is significant in having well-preserved cuticles, which hitherto have not been known from this genus.

*Yuanqu section.* The *Supaia*-bearing biostrome here is in the middle-upper part of the formation, probably at a lower level than those in the previous sections. The main plant fossils are parautochthonously buried pteridosperms, including *Psymphyllum multipartitum* Halle, *Chiropteris reniformis* Kawasaki, *Callipteris changii* Sze, *Supaia yuanquensis* sp. nov., *Neuropteridium coreanicum* Koiwai and *Gigantonoclea* sp. There are also rare allochthonous *Lobatannularia multifolia* Kon'no and *Taeniopteris densissima* Halle, amongst others.

*Institutional abbreviation.* TIGM, Tianjin Institute of Geology and Mineral Resources.

## SYSTEMATIC PALAEOLOGY

Order PELTASPERMALES Němejc, 1968

Satellite form-genus SUPAIA White, 1929

*Type species.* *Supaia thimfeldioides* White, 1929, p. 62.

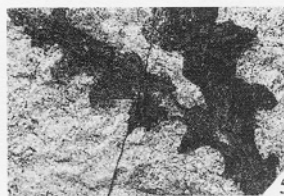
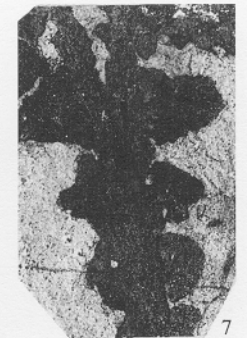
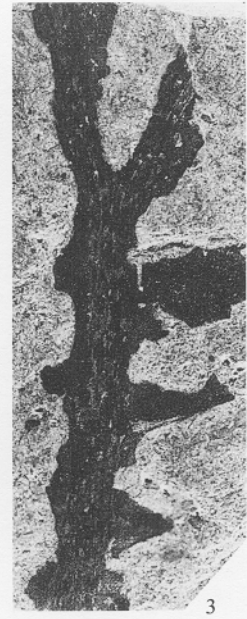
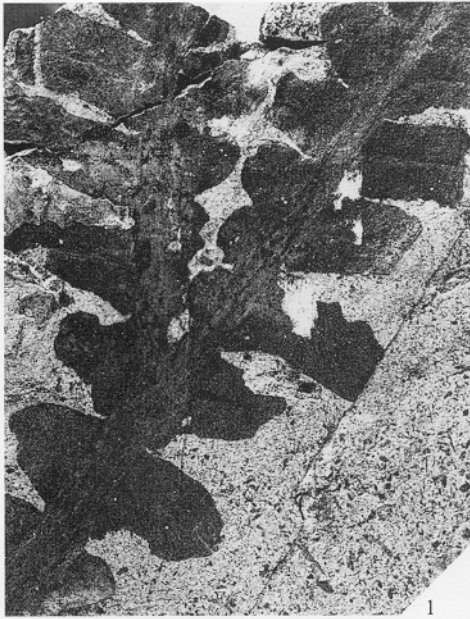
*Diagnosis.* Bipartite frond with two branches or pinnae, each of which is asymmetrical, with larger outer pinnules and smaller inner ones. Primary rachis forked near the stout base, producing two rigid, long branches. Pinnules vary from alethopteroid-like to neuropteroid-like in shape, either broadly attached to the rachis with decurrent base, or fairly constricted at the base prior to

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### EXPLANATION OF PLATE 1

Figs 1–8. *Supaia shanxiensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 1, 9306-1 (holotype); bipartite frond with medianly forked primary rachis. 2, 6, partial frond with normal pinnules attaching to a slender rachis; 2, 9306-8; 6, 9306-4. 3, 9306-16; part of forked primary rachis covered with longitudinally vascular striation and with several remnants of pinnules attached. 4, 9306-2; small whole frond. 5, 9306-7; small frond with thickened base of the primary rachis to which a few reduced pinnules are attached. 7, 9306-9; part of bipartite frond, showing the thickened base of its primary rachis. 8, 9306-12; smaller frond, with a well-developed pinna on the right and a reduced one on the left, and the shortened base of its primary rachis.

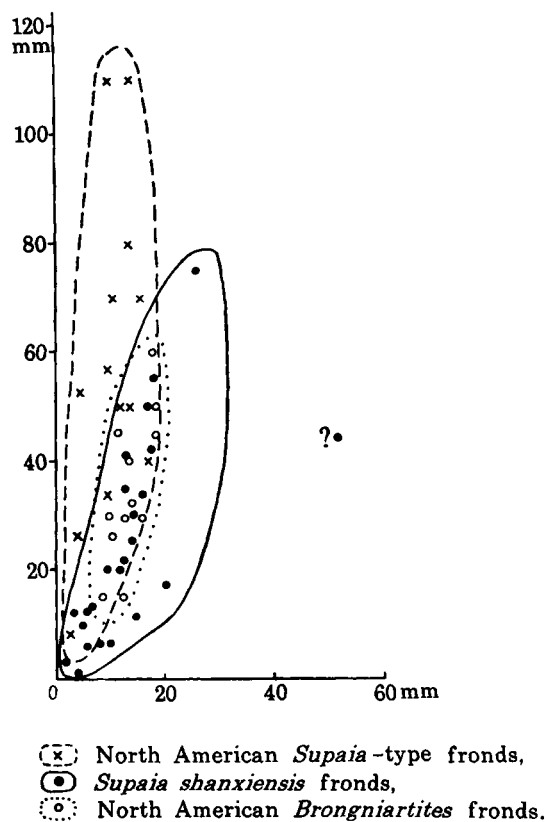






TEXT-FIG. 3. The lower parts of various *Supaia shanxiensis* sp. nov. fronds; Tianjin Institute of Geology and Mineral Resources. A, 9306-2; B, 9306-12; C, 9306-7; D, 9306-9; E, 9306-1 (holotype); F, 9306-4; G, 9306-3; H, 9306-31; I, 9306-5; J, 9306-16. All  $\times 0.92$

TEXT-FIG. 4. Variation in ranges of pinnule size between: A, North American *Supaia*-type fronds; B, *Supaia shanxiensis* sp. nov. fronds; C, North American *Brongniartites* fronds. Sizes of the American fronds are estimated from the photographs illustrated in White (1929).



attachment. The near-terminal pinnules are connate, lobed or pinnatifid. Below the main fork of the frond are three to five pairs of more or less reduced, triangular or semicircular pinnules. Laminae thick, coriaceous in texture. Midvein well-developed. Lateral veins generally extend from midvein at 45°, fork one or twice, and are often hidden in the pinnule lamina.

*Supaia shanxiensis* sp. nov.

Plates 1–3; Plate 6, figures 6–9; Text-figures 3, 5

1989 *Protoblechnum wongii* Halle; Si (*non* Halle), p. 56, pl. 65, fig. 2.

1996 *Supaia* sp. a Wang, pl. 1, figs 1–2, 6; pl. 2, figs 3, 5.

*Derivation of name.* From Shanxi province, where the main locality for the plant occurs.

*Holotype.* TIGM 9306-1 (Pl. 1, fig. 1); upper Tianlongsi Formation, Wangtao village, Qinyuan, Shanxi.

*Diagnosis.* Frond of medium size, about 100 mm long and 70 mm wide, bipartite with two equal or unequal branches, each one lanceolate-oblong, asymmetrical, with its outer side wider than the inner one. Primary rachis forked into two rigid branches at acute (20–40°) angle. A few pairs of reduced or undeveloped pinnules attached to both sides of the basal part of frond, below the forked

point. Pinnules alternate or subopposite, closely spaced. Pinnules callipteroid-alethopteroid in shape, about  $5-75 \times 6-26$  mm in size, with obtuse apex and slightly decurrent base, and entire or sometimes undulate margins. Outer pinnules of a branch markedly larger than inner ones, especially near the fork of the primary rachis. Pinnules near terminal connate, forming a rather large, obtuse apex. Midvein well-developed, nearly reaching to the apex in larger pinnules but faint in smaller ones. Lateral veins generally obscure, concealed within the thick lamina; they extend obliquely from the midvein at about  $45^\circ$  and then bifurcate once or twice. Several veins extend immediately from the rachis.

*Description (gross morphology).* The whole frond has an obovate or elongatedly triangular form, varying from 80 mm long by 40 mm wide, to 150 mm long by 100 mm wide. The primary rachis is forked, with two equal or unequal branches arching away from one another at  $15-40^\circ$ . Below the fork, the primary rachis is 10-70 mm long and 2-7 mm thick, strong and woody, covered with fine striations, and slightly widens towards its proximal end. The fronds illustrated on Text-figure 3E-G have two roughly equal branches, but those on Text-figure 3A-C clearly show two unequal branches, especially that shown on Text-figure 3B, which has a normal pinna on the right and an undeveloped (or abortive) pinna on the left. As shown in Text-figure 3, most fronds are not strictly speaking bisymmetrical.

The branches (or pinnae) are monopinnate, lanceolate or oblong-obovate, usually 60-100 mm long and 15-65 mm wide, but with a maximum length of over 120 mm and width of 65 mm. The branches are asymmetrical, with pinnules larger on the outer side than on the inner side. The broadest portion of the branch is in its upper part.

The pinnules vary from 5 mm long by 6 mm wide to 75 mm long by 26 mm wide (Text-fig. 4). They are mostly of an alethopteroid-type, oblong or obtusely triangular, with a rounded apex and fully expanded or decurrent base; only rarely are slightly constricted pinnules present. Nine to 12 pairs of pinnules occur on each branch, alternately or suboppositely arranged, closely spaced or a little overlapping, and vertically or obliquely attached to the rachis. Pinnule margins are entire or sometimes slightly undulate. Towards the distal end of the branches, adjacent pinnules gradually become connected to each other to form an obovate or broad fan-like terminal pinnule (Pl. 2, fig. 1). Near the base of the frond, three to five pairs of pinnules are attached to the primary rachis, sparsely spaced, and more or less reduced or scarious. The pinnule lamina is rather thick and rugose; it appears uneven or may have been scabrous prior to being buried. Table 1 shows the main measurements from some selected specimens of the new species.

Venation is alethopteroid or callipteroid, with a moderately thick but (on the surface) faint midvein, which dissolves about two-thirds of the way along the pinnule. Ten to 15 pairs of lateral veins are produced obliquely by the midvein at an acute angle, and are always concealed within the lamina. Some veins in the basal portion of a pinnule arise immediately from the rachis. Many striped rusts occur along the lateral veins (Pl. 3, figs 5-6) as result of fungal infection.

*Description (microscopic features).* Unfortunately, virtually no cuticles can be extracted from the type specimens from Wangtao section, to show the epidermal characters of the new species. However, some minute fragments of residue left on the specimens can provide some limited information. For example, a fragment of cuticle illustrated on Plate 6, figure 6 shows the skeleton of an epidermal cell with spines extending from the

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#### EXPLANATION OF PLATE 2

Figs 1-7. *Supaia shanxiensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian. 1, 9306-24; apex of pinna showing widening terminal pinnule;  $\times 1$ . 2-5, variation in pinnule morphology;  $\times 2$ . 2, 9306-28; normal pinnule showing clear venation and attachment to rachis along its entire decurrent base. 3, 9306-30; two pinnules attached vertically to the rachis, showing many splits along the veins, which had developed prior to burial. 4, 9306-45; semi-round pinnule attached to the basal part of primary rachis. 5, 9306-27; lanceolate pinnule attached to rachis with slightly constricted base. 6, 9306-60; part of large pinna;  $\times 1$ . 7, 9306-3; smaller bipartite frond, with asymmetrical branches;  $\times 1$ .

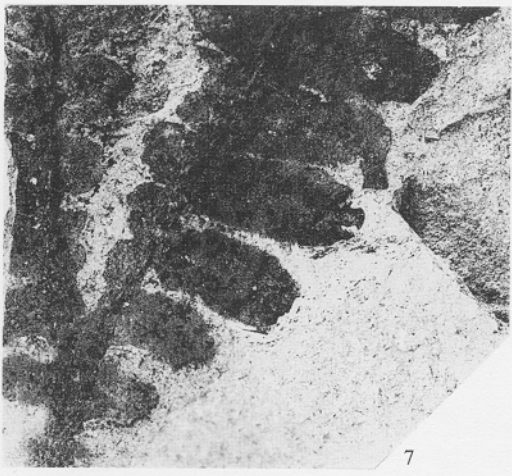
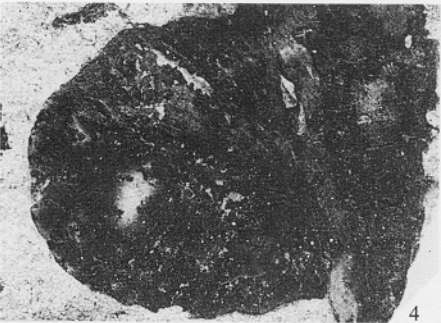
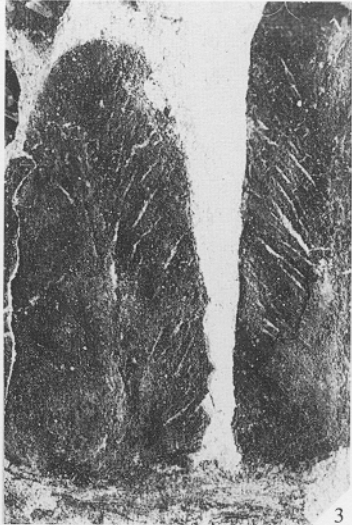


TABLE 1. Dimensions of main specimens used in the description of *Supaia shanxiensis* sp. nov.

Specimen number	Size of frond (mm)	Primary rachis length × width (mm)	Angle of primary rachis dichotomy	Length × width (mm) of branches produced by dichotomy	Size of largest pinnules (mm)
9306-1 (a)	110 × 100	60 × 7	35°	60 × 30	30 × 12
-1 (b)	100 × 90	40 × 5	30°	60 × 40	12 × 15
-2	80 × 40	20 × 3	20°	60 × 19	12 × 6
-3	100 × 80	25 × 7	40°	80 × 45	25 × 15
-4	120 × 60	75 × 5	15°	—	30 × 15
-5	—	20 × 6	20°	—	22 × 13
-6	80 × 90	—	35°	100 × 60	35 × 13
-7	—	—	30°	—	5 × 6
-8	100 × 70	20 × 2	40°	80 × 40	20 × 10
-9	—	40 × 6	25°	—	20 × 12
-10	—	10 × 6	—	—	5 × 8
-12	70 × 60	—	—	50 × 27	12 × 6
-17	—	—	40°	100 × 80	50 × 18
-22	—	—	—	110 × 60	34 × 16
-25	—	—	—	50 × 30	55 × 19
-26	—	—	—	—	75 × 26
-45	—	20 × 2	30°	—	17 × 20

corner of the cell wall in the inner view. More importantly, the SEM photograph on Plate 6, figure 5 shows clearly one of the small, dark spots along both sides of veins that represent fungal bodies. These spots are also visible in most hand specimens (Pl. 3, fig. 5).

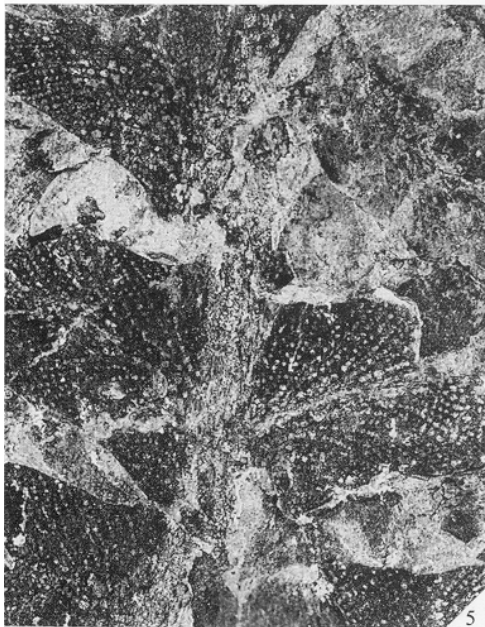
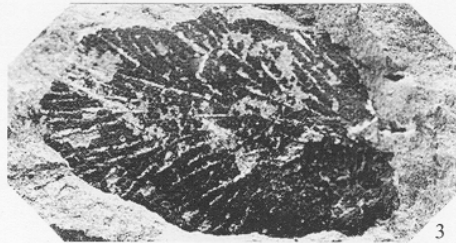
*Comparison with North American species.* There is no fundamental difference at the generic level between the present specimens and material from the Hermit Shale in America. They both have (1) a distinctive bipartite frond architecture with two monopinnate branches; (2) alethopteroid-type pinnules with a thick coriaceous texture; (3) pinnules of similar appearance on both sides of the branches and below the fork of the primary rachis; and (4) oblique lateral veins concealed within the laminae.

Within this genus, White (1929, pp. 54–86) described 12 species (three of which are indeterminable) from the Hermit Shale in Grand Canyon, Colorado. He also attributed some other bipartite fronds from there to *Brongniartites* Zalessky, including *B. ? aliena* White (pl. 27, fig. 2) and *B. ? yakiensis* White (pl. 28, fig. 3). In my opinion, all of these species may belong to one genus and even one species. Most are not strictly delimited on the basis of a constant feature and those which are separated on more clear-cut features (e.g. size, shape, base and apex of a pinnule) are rare (e.g. *Supaia rigida* White, *S. anomala* White, *S. linearifolia* White).

#### EXPLANATION OF PLATE 3

Figs 1–6. *Supaia shanxiensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian. 1, 9306-61; part of forked-primary rachis from which pinnules had been shed, showing longitudinal vascular striation; × 2. 2, 9306-47; isolated pinnule with fine veins, showing extensive base; × 2. 3, 9306-29; similar pinnule but with slightly contracted base; × 2. 4, 9306-5; lower part of bipartite frond, showing the thickened base of primary rachis below the fork; × 1. 5–6, parts of pinnae infected by fungi, showing many small fungal spots along both sides of lateral veins; × 2; 5, 9306-44; 6, 9306-22.





Among White's species, only *Supaia thinnfeldioides* (White 1929, pl. 14) shows a close comparison with *S. shanxiensis*, having similarly closely spaced pinnules with a coriaceous lamina concealing the venation, and a similar overall architecture of the frond. However, the former differs in having much longer pinnules with a stronger midvein that reaches to the pinnule apex, and a marked expansion of the base of the pinnule with a decurrent distal margin.

*S. shanxiensis* differs consistently from most of the other of White's species. For example, the Chinese species have a much lower pinnule length:width ratio than the American ones (Text-fig. 4). The Chinese species also has a much less variable pinnule shape than the American ones, which vary from slender-linear to lanceolate. A few American fronds have markedly lobed pinnules, in contrast with the Chinese frond which has consistently entire margined (though sometimes a little uneven) pinnules. The base of the pinnules in these American species also tends to show more variation, from broadly decurrent to constricted, while the pinnules of *S. shanxiensis* are consistently fused to the rachis along their entire base, except below the fork of the main rachis where they may have a reduced or slightly constricted (on acroscopic side) base. The Chinese species consistently presents closely spaced pinnules, while a marked separation tends to occur between adjacent pinnules in the American fronds, although a few more closely spaced pinnules may also occur in the latter; the latter also clearly show an upper 'puckered corner' at the base of the pinnule, resulting from the base buckling or twisting prior to attachment. Finally, the midvein of the Chinese species is weakly developed and clearly differs from the strong, prominent midvein reaching the apex of the pinnule in the American species.

*Comparison with Asian species.* A few records of *Supaia*-type fronds occur in the literature on the Permian floras of East Asia, especially from the Angaran Kingdom. In North China, several specimens assigned to *Protoblechnum wongii* Halle from the Tianlongsi Formation show the same type of distinctive bipartite frond with two branches bearing alethopteroid pinnules and a *Supaia*-like venation (Chow *et al.* 1955, pl. 1; Si 1989, pl. 65, fig. 2).

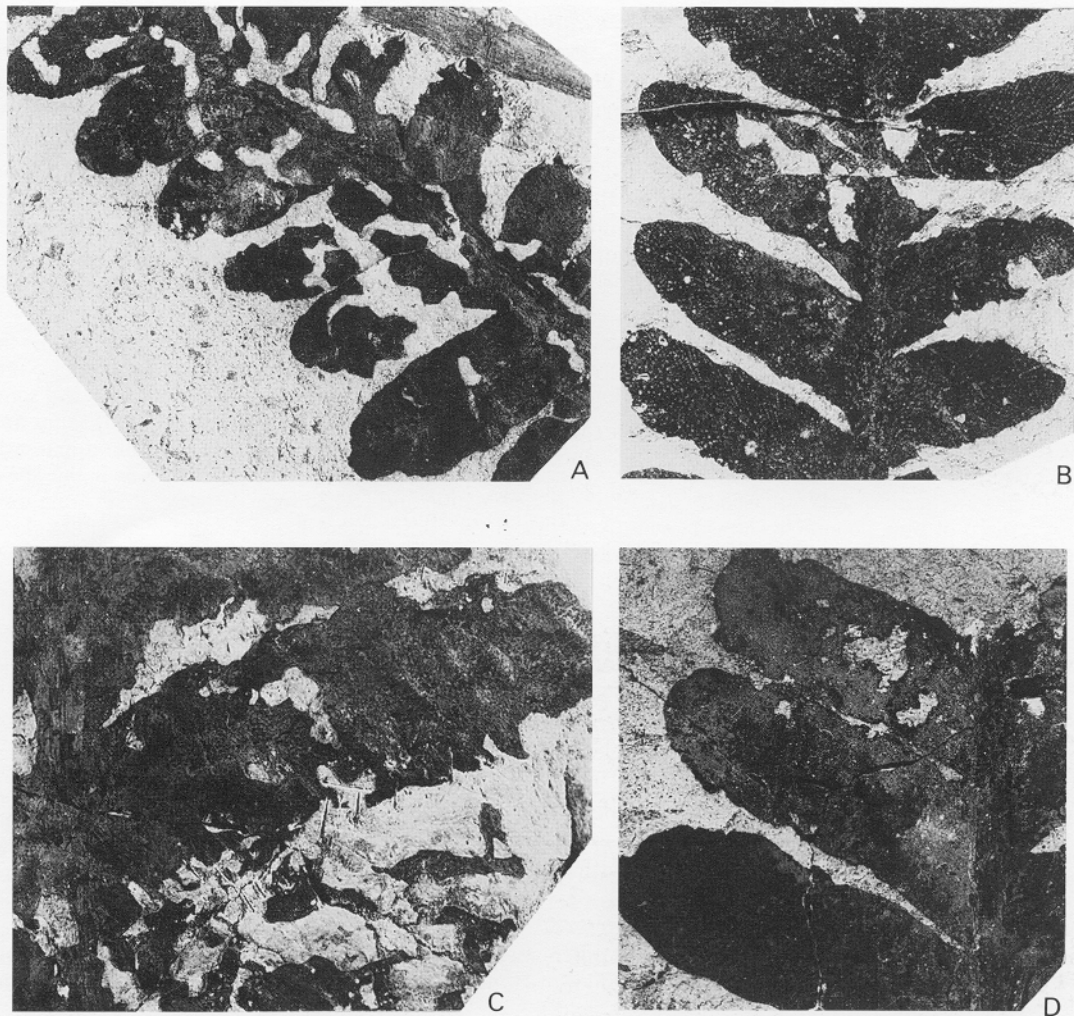
Tchirkova (*in* Zalesky and Tchirkova 1935, p. 1108, fig. 6) described a new species, *Supaia tomiensis* Tchirkova, from the Upper Permian of the Kuznetsk Basin, Siberia (see also Neuburg 1948, pl. 42, fig. 4). It was based only on a small bipartite frond with a slender primary rachis but lacking the part below the fork. Compared with the *S. shanxiensis*, its pinnules are much smaller and seemingly, have a thinner lamina with a less developed midvein.

Huang (1977) described two species of *Supaia* frond from the so-called 'Permian Angaran floras' in the Xiao Hinggan Range of North-east China. *S. shenshuensis* Huang shows a large frond but does not appear to have any pinnules below the fork of the main rachis. Its terminal pinnules are elongate, and more or less dichotomously formed, clearly differing from those of *S. shanxiensis*. The other species, *S. tieliensis* Huang, has a frond more similar to *S. shanxiensis*, having closely spaced pinnules with an obtuse apex (Huang 1977, p. 46, pl. 36, figs 1-3; pl. 37, figs 1-2; pl. 38, figs 1-5; text-fig. 14). However, it differs from the latter in each branch bearing fewer pinnules (six to seven pairs), which are more oblique (50-60°) to the slender rachis and which have much denser lateral veins (9-10 veins per 10 mm). Also, its terminal pinnule is single, rather than connate as in other *Supaia* species.

Zhou and Zhou (1986, p. 56, pl. 9, fig. 3) assign a specimen from the Upper Permian of Xingjian, China, to *Supaia* sp.

In addition, the following specimens from the Kazanian of the Urals, probably belong to *Supaia* due to the bipartite architecture of the frond: *Callipteris adzvensis* Zalesky (Fefilova 1973, pl. 30, fig. 4), *Callipteris bella* Zalesky (Vladimirovich 1986, pl. 140, fig. 6), and *Comia biarmica* Zalesky (Vladimirovich 1986, pl. 149, fig. 4). However, these specimens are too fragmentary or poorly preserved to be identified accurately.





TEXT-FIG. 5. *Supaia shanxiensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian. Parts of pinnae showing several blanks or gaps on the uneven surface, indicating that the lamina was desiccated prior to burial;  $\times 1$ . A-B, upper parts of median pinnae; A, 9306-23; B, 9306-22; C-D, parts of large pinnae; C, 9306-26; D, 9306-25.

*Supaia contracta* sp. nov.

Plate 5; Plate 6, figures 1-5, 10; Text-figures 6-7

1996 *Supaia* sp. b Wang, pl. 2, fig. 5; pl. 3, fig. 9.

*Derivation of name.* From the constricted nature of the pinnule base.

*Holotype.* TIGM 8915-7; upper Tianlongsi Formation, Xuangan Coal Mine, Yuanping, Shanxi. The gross morphology of the main part of the bipartite frond is shown in Text-figure 6A, C; Plate 5, figures 1, 3-6 and Text-figure 7 show the cuticles.

*Diagnosis.* Frond moderate in size, bipartite into two monopinnate asymmetrical branches, on which are developed strong outer pinnules and reduced inner ones. Primary rachis thick and strong,

and covered with dense woody striations. Pinnules neuropteroid-like, with a round apex and a considerably constricted base. Midvein well-developed and reaching to the apex of pinnule. Lateral veins fine, arching outwards, bifurcated once or twice, more or less fascicled. Cuticles amphistomatic, enclosing the thick hypodermis or mesophyll which tends to be infected by fungi bodies. Both epidermises are alike, but with minor differences in the shape of cell and stomatal index (i.e. about 8–9 in the upper cuticle and 11–12 in the lower one). Stomatal apparatus round, surrounded by a prominent rim formed by the elevated anticlinal wall of each subsidiary cell. Each stoma generally with more than five subsidiary cells, which are not so specialized that a distinctive area of subsidiary cells can not be recognized around each stoma. Guard cells sunken below a deep stomatal cavity. Papillae generally weakly developed, except locally.

*Description (gross morphology).* Of all the present specimens, only one (Text-fig. 6A) shows the main part of the bipartite frond. The primary rachis is thick and strong, and forked at about 40°, 3 mm wide above and 5 mm wide below the fork. This rachis is covered with longitudinal striations representing vascular strands, and some strumolose projections. Pinnules are general large, over 50 mm long and 15 mm wide, with an obtuse apex and a distinctively constricted base. Pinnule margins are entire and the lamina is thick, coriaceous but apparently easily infected by fungi. Venation is of a neuropteroid-type, but with the midvein dissolving near the apex; lateral veins are more or less fascicled, fine, costally arched, dense, and forked once or twice. Plate 6, figure 5 shows a piece of pinnule cuticle showing vein-like stripe-rusts, consisting of many small fungal spots along both sides of the lateral veins. The stripe-rust clearly illustrates the traces of the fascicled-style of venation, which is a characteristic of this new species.

*Description (microscopic features).* Cuticles are moderately thick, the upper one being slightly thicker than the lower one. The epidermis is amphistomatic, but the upper epidermis consists of more regularly rectangular cells with a lower stomatal index. The upper epidermis consists of isodiametric cells with even or smooth periclinal walls and poorly developed papillae, and does not show a marked differentiation between the costal and intercostal areas, nor between the ordinary and subsidiary cells. Stomata are random in arrangement, round to oblong-elliptical in view from the outer surface of the cuticle. In general, a stomatal apparatus is 20–30  $\mu\text{m}$  in diameter. A highly elevated, thickened rim surrounds the aperture, formed by a raised part of the anticlinal wall of each subsidiary cell adjacent to the aperture. Guard cells are strongly cutinized, reniform especially along their dorsal portion, and sunken at the bottom of a deep cavity (Text-fig. 7G–I). Four to six subsidiary cells surround the guard cells, and are weakly distinguishable from the ordinary cells, so that a subsidiary cell ring or area is either invisible or only poorly visible (Pl. 5, fig. 1; Text-fig. 7D). The stomatal index is normally constant at 8–10, but is sometimes much lower.

The lower epidermis (Pl. 5, fig. 3; Pl. 6, fig. 1) differs mainly from the upper one in the ordinary cells being more or less elongate, in the occurrence of rare files of elongate cell along the veins (Pl. 5, fig. 6) and in the occasional appearance of hollow papillae (Pl. 6, fig. 1).

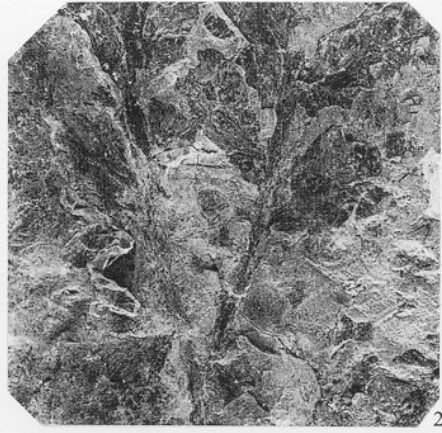
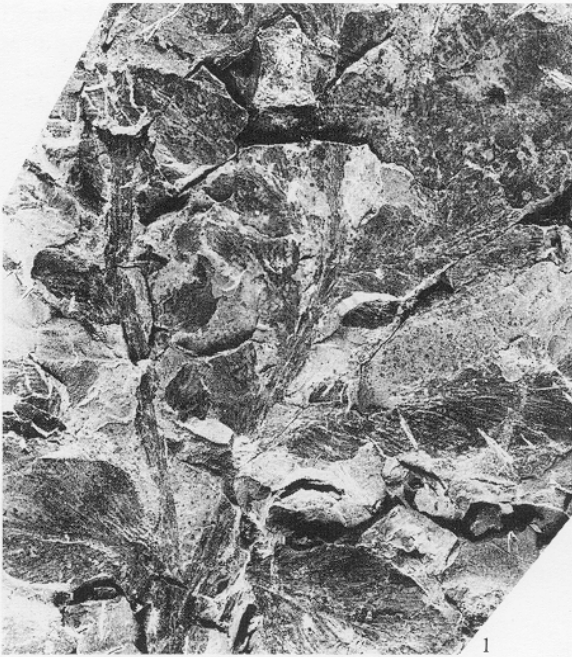
The epidermis of the rachis (Pl. 5, fig. 5) consists of elongate cell with rare stomata. Papillae are poorly developed.

*Fungal remains.* Almost all the known fronds of this species were infected by fungi and bacteria prior to burial, and show fungal-stripe rusts. These are in the form of small strumolose dark-spots

#### EXPLANATION OF PLATE 4

Figs 1–2, 4–9. *Supaia yuanquensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Yaotou village, Yuanqu, Shanxi; upper-middle Tianlongsi Formation, Upper Permian. 1–2, bipartite fronds showing pinnules and forked primary rachis. 1, 8806-1 (holotype);  $\times 1$ . 2, 87Y5-1;  $\times 1$ . 4, 7–9. various pinnules from adult fronds, showing obliquely extending lateral veins and strongly decurrent base;  $\times 1$ . 4, 87Y5-19. 7, 87Y5-e. 8, 87Y5-9. 9, 87Y5-11. 5–6, 87Y5-S1; part of young bipartite frond showing rare oblique veins; 5,  $\times 1$ ; 6,  $\times 2$ .

Fig. 3. *Supaia yuanquensis* sp. nov.? Tianjin Institute of Geology and Mineral Resources; 87Y5-12; a questionable specimen, showing larger pinnules and denser lateral veins; Yaotou village, Yuanqu, Shanxi; upper-middle Tianlongsi Formation, Upper Permian;  $\times 1$ .



occurring along both sides of the veins (Pl. 6, fig. 5). They are mostly multicellular, spherical, fungal bodies (Pl. 5, fig. 2; Text-fig. 7B, right) but rarely are slender, monocellular mycelia adhering to a cell wall (Text-fig. 7A). A detailed description of these bodies will be published elsewhere.

*Comparison.* *Supaia contracta* is characterized by pinnules with a markedly constricted base and a more or less fascicled venation. Significantly, this is the only species of *Supaia* known to date in which cuticular evidence is available. In the northern hemisphere, cuticular characters are known for many Permian peltaspermous genera, e.g. *Callipteris* Brongniart *non* Bory (Barthel 1962; Barthel and Haubold 1980; Wang and Wang 1986; Kerp 1988, Kerp and Barthel 1993), *Lepidopteris* Schimper (Townrow 1960), *Compsopteris* Zalesky (Meyen and Migdissova 1969); *Rhaphidopteris* Barale (Meyen 1979; Gomankov and Meyen 1986), *Tatarina* Meyen (Meyen and Gomankov 1980; Gomankov and Meyen 1986; Wang and Wang 1986), and *Comia* Zalesky (Fefilova 1973). These cuticles are mainly characterized by a poor differentiation between the costal and intracostal zones.

In general, *Callipteris* fronds have amphistomatic epidermises, where the intercostal zones consist of irregularly arranged ordinary cells with randomly distributed stomata, and which are separated by narrow and faint costal zones. Hollow and solid papillae and hairs are locally developed. The stomatal apertures are surrounded by a ring of thickened subsidiary cells, which are clearly distinguishable from the ordinary cells, and strong papillae overhang the aperture. Significantly, there are marked differences between the west European *Callipteris* and the Angaran or so-called 'Subangaran' ones, in cell ornamentation: the European Rotliegend species have many elongately hollowed mono- and multicellular papillae (Kerp and Barthel 1993), particularly many multicellular trichomes (Barthel and Haubold 1980, pl. 1, figs 3–5); the Angaran species, in contrast, have numerous solid papillae or thickenings of the periclinal walls (Meyen 1970, pl. 75). This distinction could reflect differences in climate. On the other hand, the Angaran *Callipteris* are seemingly close to the European *Lepidopteris* species such as *L. martinsii* (Kurtze) Townrow, 1960 although their stratigraphical horizons are mostly equivalent to the Kungurian-Kazanian (i.e. so-called 'Middle Permian') and are thus higher than the European Rotliegend.

Meyen and Migdissova (1969) described poorly preserved cuticles of *Compsopteris adzvensis* Zalesky from the Upper Permian of the Pechora Basin in West Angara, and this is the only available evidence of the stomatal structure of this genus. The stomata have a monocyclic ring consisting of four to seven subsidiary cells, each of which has a strongly thickened anticlinal wall around the pit as in most callipteroid fronds. In addition, Fefilova (1973) presented some fragments of *Comia* cuticle, but these are too poorly preserved to identify.

The cuticular characters that *S. contracta* shares with most other peltasperms are its moderate thickness, the less regularly aligned ordinary cells, and the more or less specialized stomatal apparatuses with a prominently thickened rim around the pit, consisting of the raised neighbouring wall of each subsidiary cell. However, the main distinguishing character is the poorly developed ring of subsidiary cells, i.e. most stomata are anomocytic or only partially monocyclic.

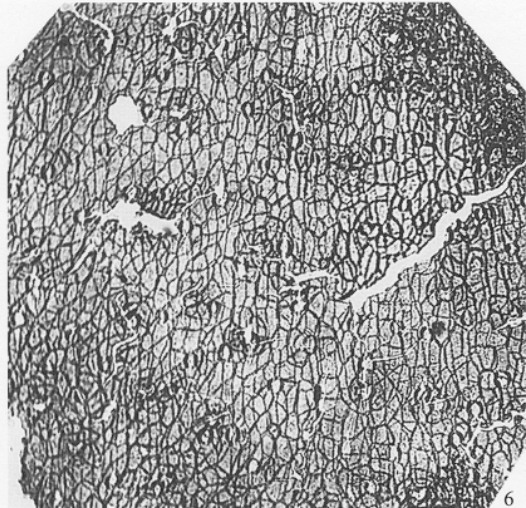
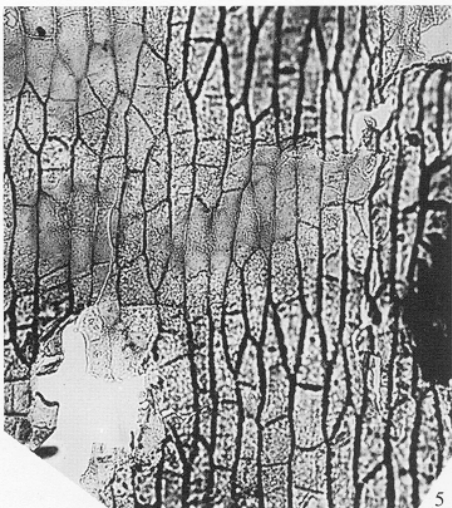
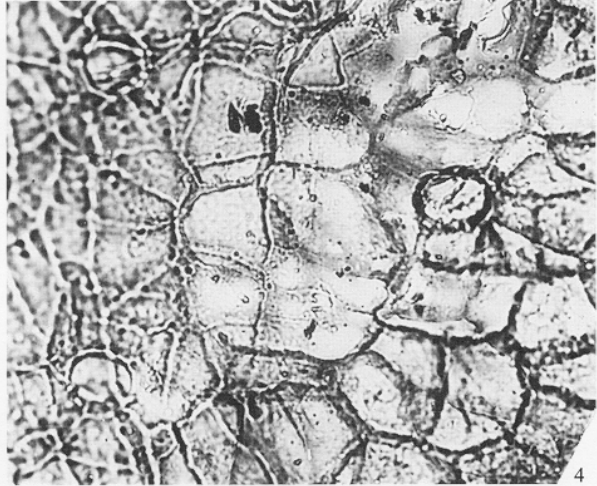
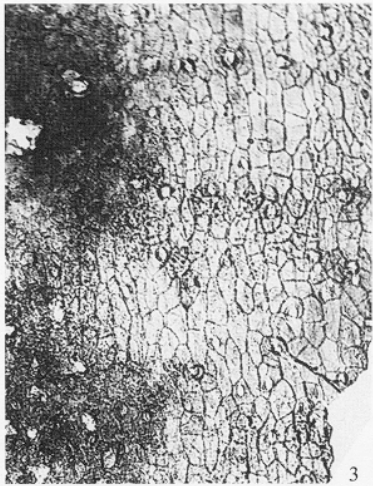
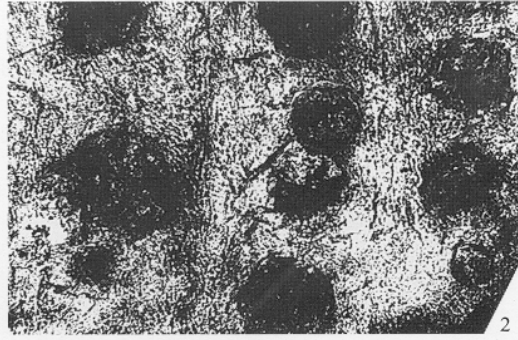
Among the peltasperms for which cuticular evidence is known, only some *Tatarina* species have cuticles similar to those of *S. contracta*. These include species considered to be endemic to the Upper Permian of the so-called 'Subangara', such as *T. conspicua* Meyen (Meyen and Gomankov 1980;

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#### EXPLANATION OF PLATE 5

Figs 1–6. *Supaia contracta* sp. nov. Tianjin Institute of Geology and Mineral Resources; cuticles; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian. 1, 8915-7 (holotype); stoma on lower cuticle;  $\times 400$ . 2, 9406-s1; unseparated upper and lower cuticles showing dark-spots caused by fungi;  $\times 40$ . 3–5, 8915-7 (holotype); lower cuticle;  $\times 40$ . 4, upper cuticle, showing two or three stomata;  $\times 400$ . 5, upper cuticle on the rachis;  $\times 200$ . 6, 8915-11a; lower cuticle showing rare files of ellongate cell;  $\times 40$ .





Gomankov and Meyen 1986). As in *S. contracta*, they have stomatal apparatuses that are mostly faintly monocyclic and subsidiary cells that are not clearly differentiated from the ordinary ones in size or shape. In addition, a projecting rim surrounding the stomatal aperture is sometimes visible (Gomankov and Meyen 1979, text-figs 7–9) like that of the present new species.

*Supaia yuanquensis* sp. nov.

Plate 4, figures 1–2, 73, 4–9

- 1955 *Protoblechnum wongii* Chow *et al.*, p. 167, pl. 1 [refigured in Gu and Zhi 1974, p. 115, pl. 130, fig. 6 and Liu 1989, p. 449, pl. 6, fig. 1].  
 1996 *Autunia* sp. A Wang, pl. 3, fig. 9.

*Derivation of name.* From Yuanqu district where the type specimens were found.

*Holotype.* TIGM 8860-1 (Pl. 4, fig. 1); upper-middle Tianlongsi Formation, Yaotou village, Yuanqu, Shanxi.

*Diagnosis.* Small frond, not exceeding 150 mm long and 100 mm wide. Primary rachis delicate, 1–3 mm thick, forked at acute angle into two equal branches, each one bearing four to six pairs of alternating pinnules. Pinnules narrowly elongate to lanceolate, with a gradually acuminate base and a subacute apex, measuring up to 60 mm long and 20 mm wide. Pinnules acropically contracted to form a clear ‘puckering’, and basiscopically decurrent to form a narrow wing along the rachis. Midvein only faint in the decurrent base of the pinnule and then rapidly vanishing. Lateral veins normally sparse but occasionally dense, extending strongly and obliquely from midvein at acute angle (no more than 40°), and bifurcating once or twice. Laminae thinner and weaker in texture than both the above two species.

*Comparison and remarks.* This new species is a form-type with the following features that distinguish it from the other species of the genus: a delicate primary rachis, a smaller frond, narrowly lanceolate pinnules with a decurrent base, a thin pinnule lamina, and sparse, obliquely extending lateral veins.

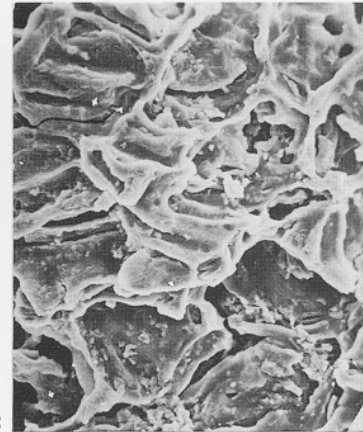
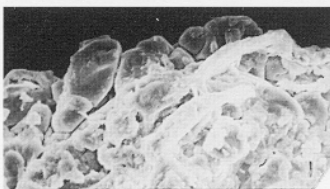
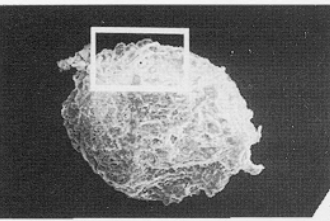
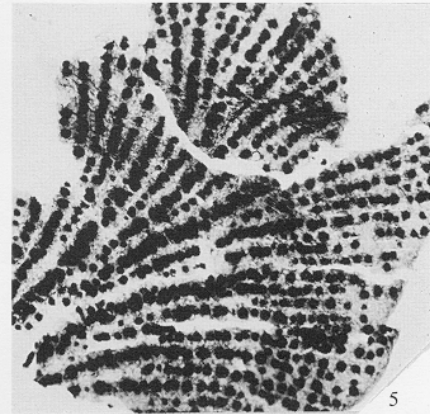
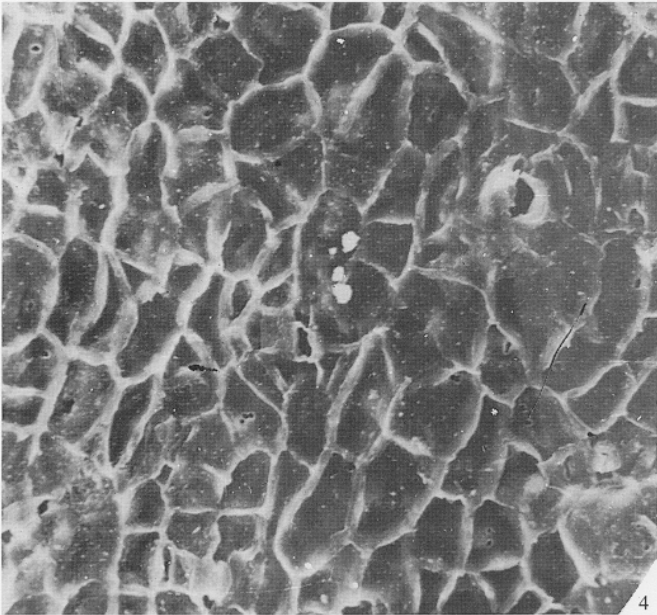
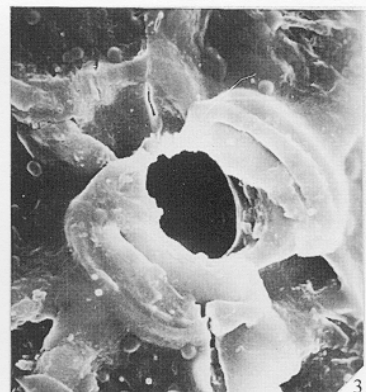
A specimen assigned to *Protoblechnum wongii* by Chow *et al.* (1955) from the ‘Upper Shihhotze Formation’ in south-eastern Shanxi shows a forked primary rachis, pinnules with a constricted and decurrent base, and obliquely extending veins. On these features, it is clearly attributable to *S. yuanquensis*.

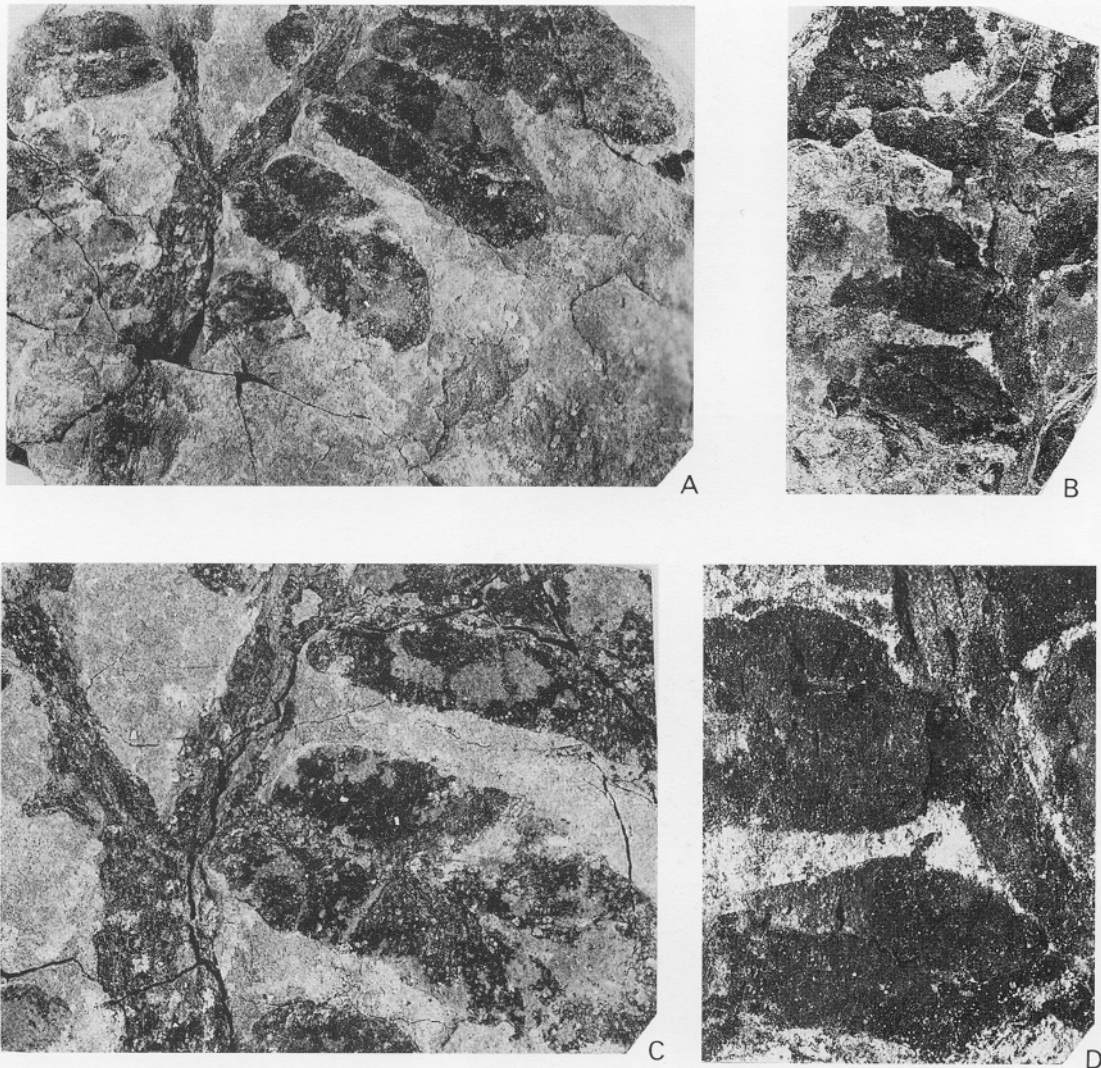
*S. yuanquensis* appears to be endemic to south-eastern Shanxi.

EXPLANATION OF PLATE 6

Figs 1–5, 10. *Supaia contracta* sp. nov. Tianjin Institute of Geology and Mineral Resources 9406-S1; Xuangan Coal Mine, Yuanping, Shanxi; upper Tianlongsi Formation, Upper Permian. 1–4, 10, cuticles viewed under SEM. 1, outer side of lower cuticle, showing locally developed papillae; × 180. 2, stoma viewed from inner side; × 900. 3, same; × 1800. 4, inner side of the upper cuticle; × 360. 5, piece of cuticle torn from hand specimen showing slightly fascicled venation with spherical fungal spots along both sides of the veins; × 4. 10, fungal filament attached to cell wall; × 1800.

Figs 6–9. *Supaia shanxiensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian. 6, 9306-37; minute piece of cuticle showing small spines extending from the corner of cell walls; × 200. 7–8, isolated fungal body. SEM photographs, both from specimen 9306-27 (shown in Pl. 2, fig. 5). 7, × 60; 8, details of fig. 7; × 300. 9, details of minute residue of mesophyll; × 180.





TEXT-FIG. 6. *Supaia contracta* sp. nov. Tianjin Institute of Geology and Mineral Resources; Xuangan Coal Mine, Yuanping, Shanxi; upper Tianlongsi Formation, Upper Permian. A, C, 8915-7 (holotype); main part of bipartite fronds. B, D, 9406-S1; parts of branch. A-B,  $\times 1$ ; C-D,  $\times 2$ .

Family PELTASPERMACEAE Thomas ex Harris, 1937

Form-genus AUTUNIA Krasser, 1919

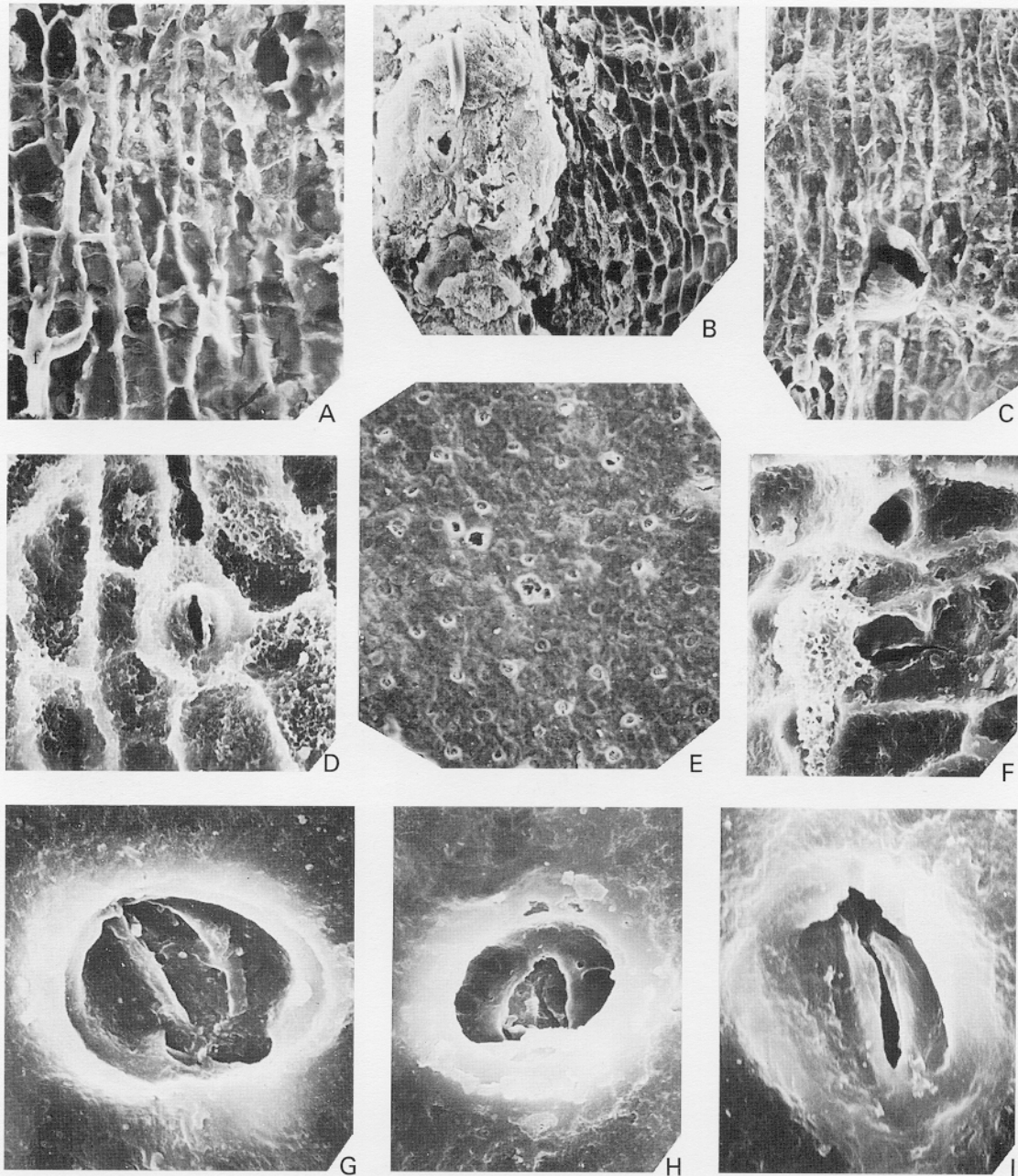
*Autunia shanxiensis* sp. nov.

Text-figs 8, 9A-D

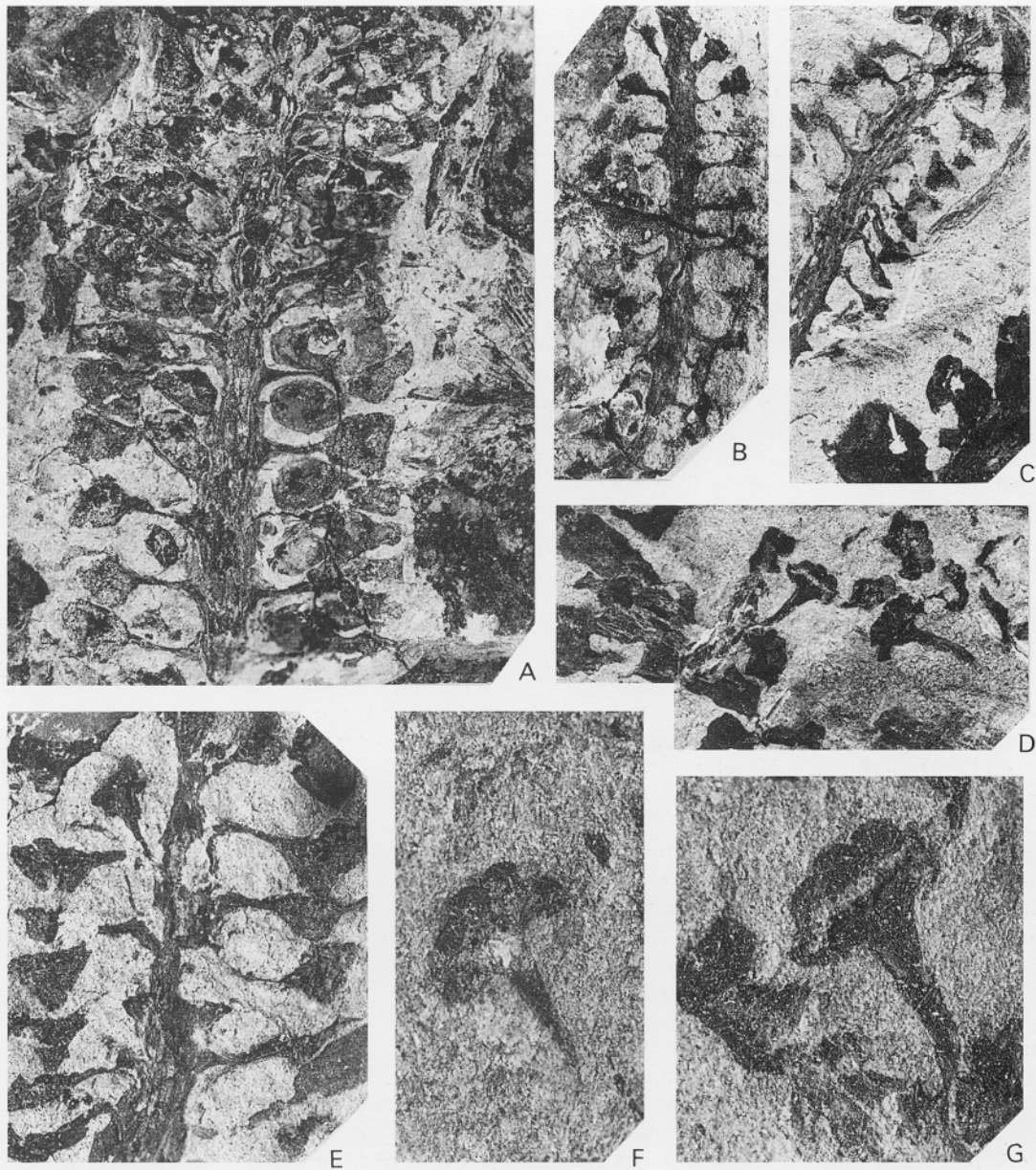
1996 Aff. *Autunia* sp. Wang, pl. 1, fig. 5; pl. 2, fig. 4.

*Derivation of name.* From Shanxi province where the type specimens were found.





TEXT-FIG. 7. *Supaia contracta* sp. nov. Tianjin Institute of Geology and Mineral Resources; all SEM photographs from specimen 8915-7 (holotype, see Text-fig. 8A); Xuangan Coal Mine, Yuanping, Shanxi; upper Tianlongsi Formation, Upper Permian. A, piece of cuticle from near rachis, showing fungal filament (f);  $\times 300$ . B, inner side of lower cuticle, showing remains of large fungal body (right);  $\times 180$ . C, showing a covering membrane of a fungal body;  $\times 180$ . D, inner side of stoma, showing guard cells infected by fungi;  $\times 900$ . E, outer side of upper cuticle, showing the raised circular rim of subsidiary cells;  $\times 90$ . F, showing the degraded cell walls;  $\times 900$ . G-I, stomata viewed from outer side, showing sunken guard cells and raised rim surrounding the aperture;  $\times 1800$ .



TEXT-FIG. 8. *Autunia shanxiensis* sp. nov. Tianjin Institute of Geology and Mineral Resources; Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian. A, 9306-33 (holotype); ovuliferous cone with ovules; many megasporophylls spirally and vertically attached to rachis, probably each one with two reversed ovules;  $\times 2$ . B-C, E, ovuliferous cones having shed ovules. B, 9306-39;  $\times 1$ . C, 9306-31;  $\times 1$ . E, 9306-36,  $\times 2$ . D, F-G, isolated megasporophylls. D, 9306-32;  $\times 2$ . F, 9306-32;  $\times 5$ . G, 9306-58;  $\times 5$ .

*Holotype.* TIGM 9306-33; upper Tianlongsi Formation, Wangtao village, Qinyuan, Shanxi. The specimen is illustrated in Text-figure 8A, and is closely associated with many *Supaia shanxiensis* fronds.

*Diagnosis.* Detached ovuliferous cone, 20–25 mm in diameter and probably over 100 mm long. The cone is cylindrical, abruptly constricted at both ends. Cone axis rather thick, 3–5 mm wide, bearing spirally arranged megasporophylls attached at a large angle or at right-angles. Megasporophyll has a peltate or semi-round head and is bilaterally symmetrical, with five or six lobes on the border and has a funnel-form in the central portion passing immediately into a slender petiole which attaches to the rachis with its prominently expanding base. On the adaxial side of the peltate head, two or probably more flattened seeds or ovules are fixed. Seeds elliptical, *Carpolithus*-type, 3–5 mm in length, with a narrow border around the nucellus, slightly concave at its bottom and obtusely acute at the apex.

*Remarks and comparison.* Three species were originally attributed by Kerp (1982) to the *Autunia* ovuliferous genus: *A. milleryensis* (Renault) Krasser, *A. thomasi* (Thomas) Kerp and *A. dzungarica* (Salymenova) Kerp. In addition, he regarded *Sandrewia texana* Mamay, 1975, from the Lower Permian of Texas and Kansas, as a synonym of *A. milleryensis*, though its associated callipterid frond had not been accurately identified. Kerp (1988) later successfully documented the direct connection between the *Callipteris conferta* frond and the ovuliferous *A. milleryensis*, both having the same type of epidermal structure, and both being consistently associated in most localities in Europe. Significantly, he utilized *Autunia* as the name of a natural genus, in which he included two species: *A. conferta* (Sternberg) Kerp and *A. naumannii* (Gutbier) Kerp. According to the diagnosis emended by Kerp (1988, p. 305), *A. naumannii* differs substantially from *A. milleryensis*, mainly in the sterile frond having wedge-lobed, acroscopically constricted and strongly basiscopically decurrent pinnules, and in the fertile fronds having modified pinnules, but not in the architecture of the ovuliferous organs themselves. Furthermore, when emending the organ-genus (*sensu* pre-1978 editions of ICBN) *Peltaspermum* Harris, to form another peltaspermous natural genus, Poort and Kerp (1990) established *Meyenopteris* as a natural genus for replacing *Autunia thomasi* and the form-genus *Autuniopsis* for *Autunia dzungarica*.

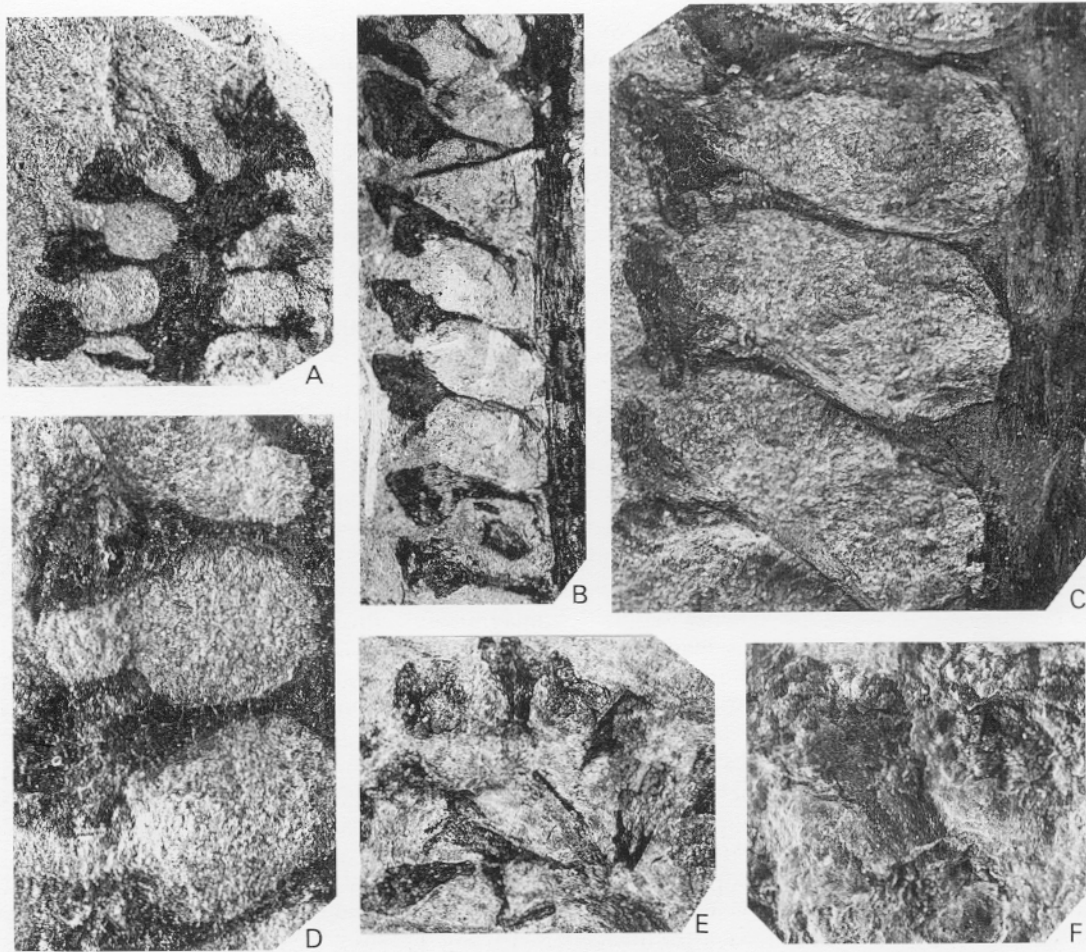
As to the nature of the ovules in *Autunia*, Kerp (1982, 1988) and Meyen (1984) presumed that they were abaxially attached to the megasporophyll, but none of the illustrated photographs clearly indicate their actual attachment. The specimens of *A. shanxiensis* show no prominent traces or scars where ovules could have been attached to both sides of the petiole, but instead two or probably more scars are clearly visible on the adaxial surface of the petiole head (Text-fig. 8G), as in *Peltaspermum*.

*A. shanxiensis* exhibits the following characters that distinguish it from the above mentioned Euramerican types: all the ovuliferous megasporophylls were closely imbricated into an independent cone rather than forming a laxly fertile dwarf cone as in *A. milleryensis*; its peltate head shows obscured or weak ribs, and has a markedly constricted or cordate base, which contrasts with the gradually acuminate, wedge-formed base of the petiole and the prominent radial ribs on the head seen in the European species. Among previous records, only a fructification assigned by Meyen (1982, text-fig. 18) to *Peltaspermum?* sp. A from the Upper Permian of the Pechora Basin can be compared to *A. shanxiensis*. This is also a discrete cone like *A. shanxiensis*, especially in lateral view, but the more or less bilateral head of its megasporophyll shows clear radial ribs. Significantly, Meyen's fructification is associated with a *Compsopteris* rather than a *Callipteris* frond.

#### (?)Pollen-bearing cone

Text-figure 9E–F

*Description.* Only one specimen shows a cone about 20 mm in diameter, with a strong, 3 mm wide rachis to which many oboval scales are spirally attached. Each scale divides distally into two or three small lobes, on which many spherical bodies are adhered as microsporangia.



TEXT-FIG. 9. A-D, *Autunia shanxiensis* sp. nov.; parts of cone having shed ovules. A, 9306-57; B-C, 9306-56; D, 9306-40. E-F, apical part of (?)pollen-bearing cone; 9306-55. All from Wangtao village, Qinyuan, Shanxi; upper Tianlongsi Formation, Upper Permian; Tianjin Institute of Geology and Mineral Resources A, C,  $\times 5$ ; B, D-E,  $\times 2$ ; F,  $\times 6$ .

*Remarks.* This cone is closely associated with the foregoing *Supaia* frond and *Autunia* ovuliferous cone, but unfortunately no details of its microscopic structures are visible, to establish its nature and affinities.

## DISCUSSION

### *Systematics and nomenclature*

When establishing the genus *Supaia*, White (1929, p. 55) interpreted it to be a product of 'a frond reduction in the direction of simplicity as a result of environmental adaptation to a semi-arid climate, from bipinnate *Callipteris* to monopinnate *Supaia*', although he also cited some comparison of *Supaia* with several Permian alethopteroid fronds, such as *Protoblechnum* from China, *Glenopteris* Sellards from America, '*Odontopteris rossica*' Zalessky from Angara, and even some Mesozoic forked pteridosperm fronds, including *Dicroidium* Gothan, *Thinnfeldia* Ettingshausen and '*Danaeopsis*' *hughsii* Feistmantel. Many palaeobotanists have accepted this view (Neuburg 1948; Asama



1960, 1985; Boureau and Doubinger 1975; Haubold 1980) and it has become generally accepted that the characteristics of *Supaia* are its bipartite frond with two monopinnate branches, and the occurrence of several pairs of pinnules on both sides of the basal rachis below the fork. Due to the limited knowledge of its fructifications (White 1934; Mamay and Watt 1971), palaeobotanists have tended not to be concerned with its systematic position, but with the significance of its limited distribution in the USA and to its correlation with allied fronds (Neuburg 1948; Sze 1955a, 1955b; Read and Mamay 1964; Chaloner and Meyen 1973; Huang 1977; Lemoigne 1988; Liu 1989).

The late Serge Meyen (1984, p. 47, text-fig. 16-3) was the first to classify *Supaia* in the Peltaspermales, based on a report of pinnate ovuliferous organs associated with *Callipteris* and *Supaia* fronds in America (Mamay and Watt 1971), although no detailed information on these fructifications was then available. The obligate association reported in this paper of *Supaia* fronds and an *Autunia* ovuliferous cone strongly supports Meyen's classification. Furthermore, special attention should be paid to the similarity in cuticular structure between *Supaia contracta* from North China and some *Tatarina* species from the Upper Permian of the Urals, as the latter was also classified by Meyen in the Peltaspermales. In gross morphology, *Tatarina* foliage (i.e. the form-genus *Pursongia* Zalesky) shows considerable variation from simple, undissected and bifurcate, to pinnate or pinnatifid fronds like callipterids. This is thus very similar to the trend of reduction of fronds from *Callipteris* to *Supaia* recognized by White (1929) in the areas of semi-arid climate, although its associated ovuliferous scales are radially symmetrical similar to those of *Peltaspermopsis*, and differ markedly from the *Autunia*-type scales. Significantly, *Tatarina* has been identified from dispersed cuticles from the uppermost Permian Sunjiagou Formation in Shanxi (Wang and Wang 1986), overlying the present *Supaia*-bearing bed. It thus seems that an evolutionary series could have occurred in the bipartite fronds in eastern Laurasia during the middle to late Permian, from the bipinnatifid *Protoblechnum wongii* (Liu 1989) via the monopinnate *Supaia* to the undissected or monopinnate *Tatarina*, and is similar to what Asama (1960) referred to as growth retardation.

The main difficulty that faces me in the identification of *Supaia* comes from the complicated and confused nomenclature for pteridosperms generally. The establishment of a fossil natural taxon is a long-term goal sought by current palaeobotanists. Where many of the plant's organs are preserved in isolation, whole-plant reconstructions should be a prerequisite before establishing such a natural taxon. At present, however, the opportunity for establishing such reconstructions for the fossil gymnosperms of the Permian-Triassic red-beds has not yet arisen, because their fructifications are mostly separated from the parent plants during preservation. Although Kerp (1988) has successfully demonstrated the direct relationship between an *Autunia* ovuliferous organ and the frond known as *Callipteris conferta*, it is much more difficult to ascertain exactly how this fructification was attached to the parent plant, and so the organizational architecture of the whole plant is still obscure. We do not know if the ovuliferous organ was an imbricate strobilus or only an axis with laxly attached megasporophylls; nor can we ascertain whether the organ should correspond in architecture to an entire frond or only to a pinna or modified pinnule. Of special importance, because of the lack of evidence of the anatomy of the ovuliferous organ, the exact number of ovules in each megasporophyll is not yet even confirmed, although two ovules tend to be reported in most investigations on the gross morphology. The attachment of the ovules is also in question – were they abaxially fixed on both sides of the petiole, or only on the adaxial surface of the disk-like head, as in *Peltaspermum*? Such differences would be important enough to distinguish generic or even suprageneric taxa. A natural genus should not be a potentially compound taxon that may have to be divided in the future.

Another, purely nomenclatural question arises from the change in usage of a name, initially defined as a form-genus, to being a newly erected natural genus. The emendation or expansion of its original definition will result in a number of specimens that were assigned to the form-genus having to be transferred elsewhere, causing considerable confusion. Based on the obligate association of the ovuliferous *Autunia milleryensis* and the *Callipteris conferta* frond in coeval strata at many localities in west-central Europe, Kerp (1988) established a natural genus which he referred to as *Autunia*. However, he then had to erect a new form-genus, *Autuniopsis* Poort and

Kerp, 1990, to replace the old organ-genus (in the sense of the pre-1978 editions of ICBN) concept, although the type specimen (Salymenova 1979) had not then been described in detail.

Far more difficulties have arisen in the nomenclature of *Peltaspermum*. The genus was introduced by Harris (1937) for a type of Late Triassic, pteridospermous ovuliferous organ, closely associated with the frond *Lepidopteris ottonis* (Göppert) Schimper. Many other similar organs from the Permian–Triassic of Laurasia were later attributed to it (Townrow 1960; Dobruskina 1980; Wang and Wang 1986). Poort and Kerp (1990) changed the essence of the genus from that of a form-genus to that of a natural genus. Following Gomankov and Meyen (1986), they used the name *Lopadangium* Zhao, which was originally based on an isolated organ of uncertain nature, as a form-genus to receive almost all of the specimens from outside of Europe, that had previously been assigned to *Peltaspermum*. In fact, most of these specimens had been demonstrated to be peltasperms, either because of the nature of their cuticles or through obligate association; for example, *P. usense* Dobruskina is associated with *Lepidopteris/Scytophyllum* fronds in the middle to upper Triassic of the Pechora Basin (Dobruskina 1980, p. 101; 1994, p. 307) and *P. dafengshanse* Wang and Wang is associated with *Callipteris* and *Tatarina* fronds in the Upper Permian of Shanxi, China (Wang and Wang 1986). *Lopadangium* is only a disc-like organ found in the purely Cathaysian floras of South China (Zhao *et al.* 1980), whose relationship with the peltasperms or even the pteridosperms has not been established. If the exact affinities of the type specimens of *Lopadangium* can be established in the future, all of those specimens transferred there by Poort and Kerp (1990) will have to be moved again.

In practice, there are great difficulties with using natural genera for Permian peltasperms. On the one hand, very similar callipterid foliage is thought to have borne different types of fructification, such as *Autunia* and *Peltaspermum* (Naugolnykh and Kerp 1996); on the other, the same type of fructification (*Autunia*) can be found in close association with different frond-types (*Supaia*, *Callipteris*). It is clear that neither *Autunia* nor *Peltaspermum* are correlated with a particular type of foliage and so cannot be the bases of natural genera.

The Permian–Triassic red-bed floras contain most of the earliest-known gymnosperms that occurred in dry and drier terrains. These gymnosperms are characterized by great species diversity and marked polymorphism in plant ontogeny, which may have been the result of adaptation to a semi-arid or arid climate. They are thus mostly endemic to certain restricted areas. They are also of uncertain affinities due to their isolated distribution and poor preservation, resulting in a lack of knowledge of their fructifications. In nomenclature, the concepts of satellite taxa hierarchy (Thomas and Brack-Hanes, 1984) and operational taxonomic units (Bateman *et al.* 1992) should be encouraged in such cases as this, i.e. it is better to retain *Autunia* and *Peltaspermum* as form-generic names.

#### *Palaeophytogeography*

During the Permian, great changes occurred in the ecosystem, resulting in the development of global biotic provincialism and, in particular, the four main palaeophytogeographical provinces. In the plant kingdom, the considerable development of xeromorphic elements, especially among the seed plants, resulted in these plants dominating the Permian red-bed floras, as they were better adapted to seasonally dry climates. These plants were susceptible to edaphic variation and endemic representatives therefore reflect the range of regional physical habitats.

As stated above, *Supaia* is famous for being reputedly restricted to certain areas in western North America and has sometimes been regarded as a characteristic endemic genus of that area (Read and Mamay 1964; Chaloner and Meyen 1973; Meyen in Vakhrameev *et al.* 1978; Lemoigne 1988; DiMichele and Hook 1992). Although occasionally mentioned in the earlier literature, its abundant occurrence in the Permian of Shanxi reported in the present paper will bring this genus more attention in palaeobotany and especially in palaeophytogeography.

Some superficial similarities of the Permian floral components in East Asia to those of the south-western United States produced some discussion and argument in the 1930s (Darrach 1937;

Jongmans and Gothan 1937). These comparisons were largely based on the distribution of enigmatic groups (Sze 1955a, 1955b; Lemoigne 1988) but more detailed studies in both areas have shown that the similarities are often at suprageneric rank, such as between the taeniopterids, callipterids, gigantopterids, noeggerathiopterids and conifers. There is in fact no strong support for a close relationship between the Permian floras of China and North America, in spite of the apparent presence of many common elements, such as *Taeniopteris*, *Callipteris*, *Prototoblechnum* (= *Glenopteris*), *Sphenopteridium*, *Discinities*, *Russellites*, *Lesleya* and *Walchia* (Mamay 1966, 1968, 1989, 1990, 1992; Mamay *et al.* 1984, 1988). Regrettably, little attention has been paid to this in recent papers on Permian biogeography (Wagner 1993; Wnuk 1996). The similarity between these floras remains open to question.

The *Supaia* flora of south-western North America is characterized by low diversity: the total number of whole-plant species may be as low as 15 to 20. The *Supaia* plant was also highly xeromorphic, with leathery laminae covered with heavy hairs, spines and sunken veins (DiMichele and Hook 1992).

Ziegler (1990) applied the concept of extant biomes to illustrate climatically the Permian phytogeographical world. Western North America (together with Europe) was assigned to the low diversity, summer-wet Biome 2, characterized by the occurrence of *Callipteris*. On the basis of outdated information, North China was mistakenly placed in the tropical, ever-wet Biome 1 (i.e. the typical Cathaysian Realm, which also included South China), though the area had been regarded as part of Laurasia during the Permian and Triassic (Wang 1985) based on the uniform phytostratigraphical sequence. In fact, most of the Permian floral elements of North China are of Eurasian type, except for the gigantopterids, rather than Cathaysian. The *Psygmoephyllum* Zone assemblages bearing *Supaia*, which can be at least dated to Kungurian–Kazanian (Wang 1996), is typical of a seasonally alternating humid-arid biome, similar to that of the Hermit Shale flora in Texas. Significantly, the Permian floras in south-western North America, including that of the Hermit Shale, are in some aspects very similar to the *Psygmoephyllum* Zone assemblages in North China: all fossil taphocoenoses occur in red-beds; the main components of both are common either at the suprageneric or generic rank; and much of the ecophysiological evidence is the same (this latter issue will be discussed elsewhere).

At least in North China, the three species of *Supaia* show considerable ecomorphic changes from south to north, representing variation in regional physical environments such as habitat heterogeneity and increasing climatic aridity. *S. yuanquensis* from south Shanxi has relatively small fronds with a slender or delicate primary rachis and more elongate pinnules; its veins extend obliquely from the midrib or rachis; the pinnule lamina is thinner and apparently weakly cutinized. This contrasts with *S. contracta* from north Shanxi, which has large fronds and pinnules with a thick and leathery lamina and concealed veins; the pinnules have a strongly constricted base and are covered with heavy hairs, papillae and sunken stomata. *S. shanxiensis* can be regarded as a transitional ecomorph between the other two. The emergence of these three regional ecomorphological types clearly reflects vegetational endemism and isolation, and a regressive succession of *Supaia*-bearing communities within North China during the Permian (Wang 1993).

#### *Ecophysiology*

Initially, White (1929) presumed *Supaia* to have belonged to a plant inhabiting areas with a semi-arid or alternating arid-humid climate, with long intervals of desiccation. This was based on a combination of the sedimentary phases of its red-bed matrix, and of the greater simplicity of its compound, pinnate frond. He also noticed that the pinnule lamina was rigid and coriaceous, had concealed veins and was covered with dense scales, and thus probably belonged to an amphibious plant. Particularly, fronds with apparently chewed margins were stated to be the result of the activities of larvae, insects and microbes (nematodes) (White 1929, p. 66). In addition, he mentioned a drainage system in the apical part of the *Brongniartites* pinnae, explaining it as a

physiological adaptation for the capture of rain. In this aspect, more important information can be extracted from the present material.

*Xeromorphic habit.* The regressive simplification of the fronds, from the bipinnate *Protoblechnum* to the monopinnate *Supaia*, was the result of long-term adaptation to a semi-arid climate. Another indicator of preburial desiccative laminae is the many blanks or gaps left in the laminae when splitting the matrix embedding the frond (Text-fig. 5). Partially rolled or wilted mature fronds reflect air-drying during the growing period of the plant, as in many modern desert plants, i.e. the so-called poikilohydric xerophytes (Brown 1974). In addition, primary rachises with a wilted base and reduced or enrolled pinnules indicate that the plant could have naturally disarticulated due to wilt in the dormant season. A similar case of wilt occurred in some Triassic *Isoetes*, in which various isolated organs of the same plant are found preserved in parautochthonous burials (Wang 1991).

On the other hand, the cuticles show sunken guard-cells below a deep pit with a constricted aperture, which was probably an adaptation to reduce excessive evapo-transpiration (Spicer 1989, p. 324).

*Taphonomic setting.* Most plants of the Permian red-beds in North China were buried in ephemeral water-bodies in an arid-humid alternating terrestrial ecosystem, rather than in a uniform wet-temperate ecosystem with persistent drainage (Wang 1993). As stated above, the *Supaia*-bearing biostromes are typically parautochthonous burials, representing an association of shore-inhabiting bushes, limited to the terraces surrounding small, seasonal ponds and playas. The size of the pond or playa was roughly equal to the dimensions of the biostrome. I have previously suggested that the gradual regressive fragmentation of the vegetation in North China during the Permian and Triassic is an indicator that the vegetation would gradually disappear (Wang 1993).

*Stomatal index.* Traditionally, cuticular features have tended to be regarded as important evidence for classifying plant taxa and only rarely to be of ecological or ecophysiological significance. However, recent botanical (Murray 1995) and palaeobotanical (Visscher 1993) studies have demonstrated the potential significance of the Stomatal Index and of stomatal aperture size for evaluating the CO<sub>2</sub> content of palaeoatmospheres and ecophysiological responses to photosynthesis. Such studies started with angiosperms from Recent European mountains and some herbarium specimens from leaves collected over the last 200 years (Woodward 1987). Using fossil leaves, the evidence was then extended back to the Late Tertiary (van der Burgh *et al.* 1993; Masterson 1994).

In the remote past such as the Permian, however, estimation is very difficult, and can only be based on the relative values of absolute stomatal indices. There exists no model to compare effectively the CO<sub>2</sub> levels of Permian palaeoatmospheres with that of today. An attempt must be made to accumulate more relevant data, although what the results will yield is far from certain.

The stomatal density of *Supaia contracta* varies from 100–360 mm<sup>-2</sup> (mean value 250 mm<sup>-2</sup>), which is comparable to the values estimated from several xerophytic plants growing today near the margins of the Tungeli Desert in north-western China (Zhao and Huang 1981). The Stomatal Index values from the upper cuticles are mostly 9–11, and those of the lower cuticle 13–14 (this is excluding extreme values obtained from cuticles on or near the rachis or margins of the pinnule). Such low values again are indicative of xerophytic plants.

#### *Plant-fungal interaction*

A number of dark spots in or on fossil leaves have been interpreted as various fungal remains since early in the nineteenth century but most were recorded from post-Cretaceous specimens. Knowledge of Palaeozoic epiphyllous fungi, especially the parasitic ones, is very limited. Of the 145 records listed by Dilcher (1965), only 11 are of pre-Cretaceous examples, and most of these are unreliable nineteenth century identifications made prior to the development of microscopic techniques for fungal identification. Thus, Sherwood-Pike (1988) claimed that in the Late



Cretaceous such fungi had not developed to the level that they could be reliably identified, and that the oldest records were from the Palaeocene. However, some fungi had in fact been previously microscopically documented, in Jurassic–Cretaceous cycad leaves (Krassilov 1967; Zheng and Zhang 1986) and even in Late Carboniferous plants (Hutchison 1955; Stubblefield *et al.* 1983).

The epiphyllous fungi found within these Permian *Supaia* fronds are clearly of considerable significance, even though they have yet to be identified in detail. They are the first examples of Palaeozoic leaf-inhabiting fungi with a reliably parasitic relationship, other than the isolated parasitic hyphae recorded in a Late Carboniferous gymnospermous cone (Stubblefield *et al.* 1984). More importantly, these fungal-spots on the laminae occur regularly along both sides of the veins (Pl. 6, fig. 5) all over both the lamina and primary rachis of the frond. This contrasts with the locally isolated or random distribution of such spots in previous records. Numerous fungal colonies growing within the mesophyll would produce little or no damage to the cuticles and the occurrence of small rounded bodies, termed wall appositions or callosities, which are attached to the wall of cell also supports the inference of a parasitic relationship, as argued by Stubblefield *et al.* (1984) and Taylor and Osborn (1996) based on Devonian–Carboniferous material.

In addition, the specialization of the fungal infection unique to this kind of frond can be affirmed at two locations yielding *Supaia* in Shanxi. These localities are more than 45 km apart and it can therefore be assumed that both represented an ecologic niche where the vegetation was suffering from a geographically widespread infectious disease. Of course, expansion and reduction of an ecotonal vegetation could have been directedly related to the decreasing survival of vegetation towards the end of the Permian. Desert conditions were then starting to develop in North China, as it became part of the vast barren terrain in the Northern Hemisphere, where there were many factors militating severely against vegetation survival (e.g. severe water limitation, strong winds, rainstorms, wild-fire) and which effectively destroyed most of the continental vegetation (Wang 1993). The infectious fungal disease may therefore be seen as part of a general ecological crisis that developed towards the end of the Permian (Eshet *et al.* 1995; Visscher *et al.* 1996).

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## APPENDIX 1: PSYGMOPHYLLUM ZONE FLORAS OF SHANXI

A total of 46 species belonging to 36 genera has been identified from the *Psymophyllum* Zone in a north–south series of ten sections in Shanxi. The following species are unique for the zone: *Psymophyllum multipartitum* Halle, *Nystroemia pectiniformis* Hall, *Rhipidopsis* sp., *Supaia shanxiensis* sp. nov., *S. contracta* sp. nov., *S. yuanquensis* sp. nov., *Callipteris? laceratifolia* Halle, *Autunia shanxiensis* sp. nov., *Peltaspermum* sp., *Fascipteridium ellipticum* Zhang and Mo, *Pelourdea reflexa* Halle, *Lesleya* sp., *Ginkgophytopsis* sp., *Sphenobaiera tenuistriata* (Halle) Florin and *Lixotheca (Cladophlebis) permica* (Lee and Wang) Yao and Liu.

The following already occur in the underlying *Plagiozamites* and *Chiropteris* Zones but may persist into the *Psymophyllum* Zone: *Lobatannularia ensifolia* (Halle) Halle, *L. heianensis* (Kodaira) Kawasaki, *L. lingulata* (Halle) Halle, *Discinites orientalis* Gu and Zhi, *Yuania chinensis* Du and Zhu (= *Russellites chinensis* Mamay, 1995), *Giantonoclea hallei* (Asama) Gu and Zhi, *G. lagrelii* (Halle) Koidzumi, *Callipteris changii* Sze, *Fascipteris hallei* (Kawasaki) Gu and Zhi, *F. sinensis* (Stockmans and Mathieu) Gu and Zhi, *Rhomboidopteris yongwolensis* (Kawasaki) Sze, *Neuropteridium coreanicum* Koiwai, *Chiropteris reniformis* Kawasaki, *Protoblechnum wongii* Halle, *Taeniopteris taiyuanensis* Halle, *T. tingii* Halle, *T. densissima* Halle, *Norinia* sp. and *Walchia* sp.

In addition, there are some relicts of the Carboniferous genera such as *Calamites*, *Annularia*, *Asterophyllites*, *Sphenophyllum*, *Lepidodendron*, *Cordaites* and fern-like plants attributed to form-genera *Pecopteris*, *Sphenopteris* and *Odontopteris*, among others.

The most remarkable character of the zone is the predominance of Mesophytic gymnosperms, and the zone is referred to as the oldest gymnospermous assemblage in North China (Wang 1993). In particular, psymophyloids (*Psymophyllum*, *Rhipidopsis*, *Chiropteris*) are unique to this zone. Also important are peltasperms (callipterid fronds, *Autunia*- and *Peltaspermum*-type ovuliferous organs) and other allied genera (*Supaia*, *Protoblechnum-Compsopteris*, *Neuropteridium*, *Fascipteridium* (similar to *Comia*-type fronds)). Cycad leaves and megasporophylls, although known from the basal Permian of China, significantly increase 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*. In Shanxi Province, ancestors of ginkgos (*Sphenobaiera* and *Ginkgophytopsis*) and conifers (*Walchia*) rarely appear in this zone, but are abundant in other areas such as Inner Mongolia (*Ginkgophyton? spirata* Shi) and Gansu (conifer *Majonica*).