Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia

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Plant communities of the geologic past can be reconstructed with high fidelity only if they were preserved in place in an instant in time. Here we report such a flora from an early Permian (ca. 298 Ma) ash-fall tuff in Inner Mongolia, a time interval and area where such information is filling a large gap of knowledge. About 1,000 m^2 of forest growing on peat could be reconstructed based on the actual location of individual plants. Tree ferns formed a lower canopy and either *Cordaites*, a coniferophyte, or *Sigillaria*, a lycopsid, were present as taller trees. Noeggerathiales, an enigmatic and extinct spore-bearing plant group of small trees, is represented by three species that have been found as nearly complete specimens and are presented in reconstructions in their plant community. Landscape heterogenity is apparent, including one site where Noeggerathiales are dominant. This peat-forming flora is also taxonomically distinct from those growing on clastic soils in the same area and during the same time interval. This Permian flora demonstrates both similarities and differences to floras of the same age in Europe and North America and confirms the distinct character of the Cathaysian floral realm. Therefore, this flora will serve as a baseline for the study of other fossil floras in East Asia and the early Permian globally that will be needed for a better understanding of paleoclimate evolution through time.

coal-swamp plant community | plant paleoecology | volcanic ash-fall tuff | Wuda

The understanding of paleoecosystems in Earth's deep past ideally requires the reconstruction of actual sites of ancient plant communities. Only vegetation buried in growth position in a geological instant can offer such an unbiased window into the composition and ecology of ancient vegetation, which in turn enhances larger scale paleoecological and paleoclimatic interpretations (1, 2). Early Permian floras are of particular importance because they represent a time of oscillating climatic changes during transitions between icehouse and greenhouse times that might serve as an analog for modern global vegetational change (3). These catastrophically preserved floras, which capture the composition of vegetation in a specific area and at a moment in time, can be generated by various types of volcanic action or flooding, of which volcanic air-fall tuffs produce the most reliable representation of the existing vegetation (1). Such occurrences have not been described frequently from Paleozoic rocks, but those that have been reconstructed have been Carboniferous in age (2, 4–7) (i.e., older than the one described here). Other published reconstructions of fossil vegetation have been mostly conceptual approximations because they were based on different types of depositional systems in which preservational biases had to be taken into consideration (8).

Our identification (9) and quantitative analysis and characterization of a peat-forming forest preserved in an air-fall tuff in Inner Mongolia (Fig. 1) enables us to reconstruct the actual vegetation for an area of more than 1,000 m^2. The complexity the reconstruction reveals contributes significantly to a more complete understanding of paleoecology and paleophytogeography of tropical vegetation of the earliest Permian. This quantitative spatial reconstruction represents the only Carboniferous or Permian flora reconstructed so far in East Asia and is a unique example of peat-forming flora from the Permian that allows for such a detailed analysis. This flora records heterogeneity of vegetation on the landscape scale and demonstrates similarities and differences between the Cathaysian and Euramerican floral realms of the Early Permian. Three additional reconstructions of noeggerathialean plants emerge from the analysis of this flora and add significantly to our understanding of the ecological role played by this enigmatic group.

The Wuda coal field is located on the northwest margin of the Helanshan mountain chain. The volcanic-tuff bed lies between coal seams No. 6 and No. 7, which occur in a syncline (N39°28′48′′ to N39°33′36′′, E106°36′36′′ to E106°39′36′′) of about 20 km^2 (Fig. 1). The vegetation preserved in the tuff grew on the peat that later formed coal No. 7 (9). The tuff is of early Permian age, based on the floral composition and its uppermost position in the Taiyuan Formation (10), which is assigned a late Carboniferous through early Permian age in North China based on marine invertebrates and regional correlations (11). During Permian times, Wuda was located on the northwest part of the North China Block, which appeared as a large island/microcontinent in the tropical zone in the paleo-Tethys Ocean (9, 12).

The peat-forming forest was preserved in a manner similar to the towns of Pompeii and Herculaneum (13) by a smothering volcanic ash-fall. This ash-fall buried and killed the plants, broke off twigs and leaves, toppled trees, and preserved the forest remains in place within the ash layer. The layer is now 66-cm thick after compaction and lithification. The original thickness can only be estimated at this point but would have been about 100 cm, based on compaction features visible in the fossil plants. The thickness of the ash layer is relatively consistent over the area of current exposure, which has a north-south extension of over 10 km. From these data it appears that the volcanic eruption was quite large and the area covered with tuff was quite extensive.

Systematical excavation of the volcanic tuff in quadrats at three different sites (see *Materials and Methods* for procedures used) allowed reconstruction of the actual spatial distribution of stems and other plant parts.

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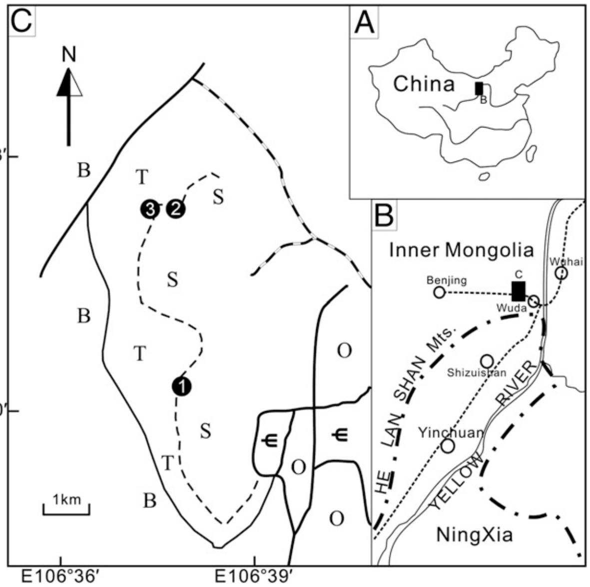

Fig. 1. Location of study area in China (*A*) and the northern Helanshan Mountains (*B*) in Inner Mongolia 8 km west of Wuda. Geologic sketch map (*C*) of syncline, based on satellite image, geologic map 1:50 000, and field observations, showing sites 1–3 where quantitative macrofloral data were collected. B, Benxi Formation and lower units; O, Ordovician; S, Shanxi Formation and higher units; T, Taiyuan Formation; dashed line, approximate outcrop of volcanic tuff between No. 6 and No. 7 coals before extensive open cast mining; thin line, boundary between Benxi and Taiyuan Fms.; thick lines, faults; ∈, Cambrian; railroad (thick dashed line) is shown for orientation.

Results

Six groups of plants make up this peat-forming vegetation (Fig. 2 and Figs. S1–S6). Most abundant were the marattialean tree ferns represented by eight species. Herbaceous ferns include *Nemejcopteris feminaeformis*, *Cladophlebis*, and *Sphenopteris*. Lycopsids are represented by *Sigillaria* cf. *ichthyolepis* (14, 15), the tall pole-like trees in the reconstruction. Two sphenopsids were encountered, *Sphenophyllum*, a dwarf shrub, and a small *Calamites.* Noeggerathiales, an extinct spore-bearing group of uncertain systematic position, are represented by species of *Tingia* (16) and *Paratingia* (17). Gymnosperms include possible early representatives of the cycads, *Taeniopteris* and *Pterophyllum*, and *Cordaites*, trees that were early coniferophytes with a generally modern growth habit, except for the large strap-shaped leaves with parallel venation. *Pecopteris lativenosa* Halle 1927 is also present in this flora. Known only from Asia and normally considered to be a marattialean tree fern, the reproductive structures of this species are not known and the pinnules appear to be thick and show a notably high degree of variability in shape and size. The foliage variation is more typical of Carboniferous and Permian pteridosperms than tree ferns. Thus, there is a chance that future finds of reproductive structures might show that it is a pteridosperm. Such a discovery would not change the reconstruction of the forest because the leaves of *P. lativenosa* are quite large and have been found attached to a stem, confirming that the plant was a tree very similar in overall habit and size to tree ferns.

Sigillaria and *Cordaites* were tall trees that grew to mature heights exceeding the general canopy, many attaining heights of up to 25 m or more. Marattialean tree ferns reached heights of up to 10–15 m and formed an actual canopy. Noeggerathiales and early cycads were smaller trees. Vines were rare but were probably represented by one species of *Sphenopteris*. The groundcover, composed of the fern *N. feminaeformis* and the sphenopsids *Sphenophyllum* and *Asterophyllites*, developed only in small patches as is typical in tropical swamp forests (18).

At the three excavation sites (Figs. 1*C* and 2*A*), counts of entombed macroflora were performed in 3, 4, or 18 subareas, respectively (Dataset S1). The distance between sites or subareas is shortened on the map but indicated numerically. The location and size of the counting areas was dictated by accessibility during the mining process and access to machinery.

As shown in Fig. 2*A*, tree ferns (green) are dominant in most areas. *Sigillaria* (blue) and Noeggerathiales (red) are subdominant or can become locally dominant or codominant. Early cycads and *Cordaites* are patchy in distribution, as is the herbaceous layer composed of sphenopsids and herbaceous ferns. The reconstruction (Fig. 2*B*) is based directly on the mapped distribution of taxa (Fig. 2*A*) and represents only the areas that were counted. It is likely that the same type of vegetation would have covered the very extensive mire in all directions and to the horizon.

Combined data indicate that tree ferns were most commonly dominant, with lycopsids and Noeggerathiales as the other common groups (Fig. 3*A*). In contrast, sphenopsids, early cycads, and *Cordaites* were rare. In terms of vegetational architecture (Fig. 3*B*), trees of the lower story predominate numerically, whereas the upper-story trees are subdominant. Vines are very rare and the herbaceous layer is not continuous. These overall patterns characterize the vegetation. However, there is local variation, leading to the kind of patchyness that one expects in any natural landscape.

Tree ferns and *Cordaites* are codominant in the subarea of 50 m^2, designated C-D in site 1 (Figs. 2*A*, 3 *C* and *D*, and 4), but Noeggerathiales are present in small numbers. This site represents a two-story forest without groundcover or vines. This forest structure appears to have been common in the area south of site 1, where one commonly finds *Cordaites* branches and leaves but no *Sigillaria* parts.

Another pattern occurs in the subarea E-F of a 125 m^2 in site 2 (Figs. 2*A* and 3 *E* and *F*). Noeggerathiales are dominant but tree ferns and lycopsids are represented only in smaller numbers. This site also was a two-story forest in which plants of the lower story, composed mostly of Noeggerathiales, were most abundant.

A common pattern is exhibited by the subarea of 50 m^2, designated G-H in site 3 (Figs. 2*A*, 3 *G* and *H*, and 5). Ferns dominate, and Noeggerathiales and *Sigillaria* are subdominant, whereas sphenopsids and cycads are rare. In terms of life habit this site represents a tree fern and Noeggerathialean forest with a number of taller *Sigillaria* trees. Small trees with *Tingia*, *Pterophyllum*, and *Taeniopteris* foliage were present, beneath which the groundcover consisted of *Sphenophyllum* and *N. feminaeformis*.

Discussion

Plant preservation in situ in air-fall tuffs is well known and has been reported (for a summary see refs. 1 and 8, p. 51–55). However, there are few places where excavations have been possible, which allowed a quantitative floral census (19). In other cases, only small excavations form the basis of a floral reconstruction (5–7). The early Permian vegetational Pompeii at Wuda was made accessible by coal mining and later by the intensive work and rapid mining in connection with a coal-fire extinction program. Excavation was necessary to secure the stunning specimens of this flora because weathering occurs rapidly and destroys the fossils. The quantitative collecting and recording of data became possible only with the use of heavy machinery because the fresh volcanic tuff is exceedingly hard. Thus, the discovery happened at an opportune time, when circumstances permitted access and the present study could be performed. (See *SI Text* and Table S1 for a brief comparison with similarly preserved floras.)

In modern plant ecology, the minimum area to obtain statistically meaningful data to characterize forest phytocoenoses

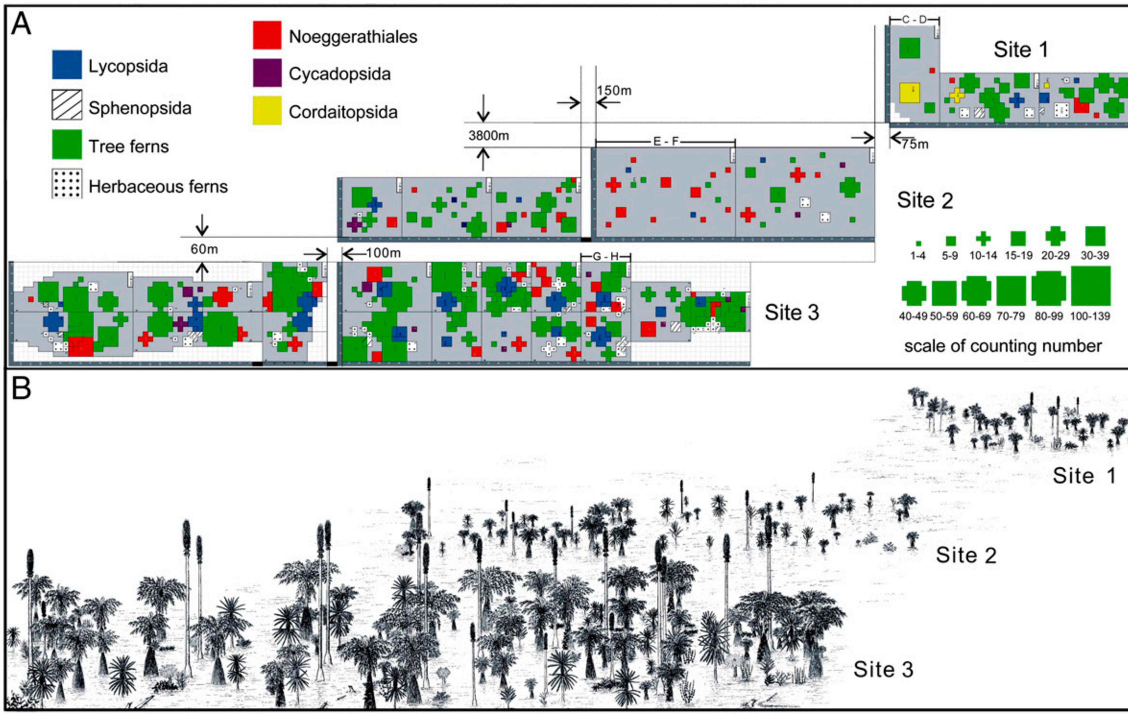

Fig. 2. Spatial data for peat-forming swamp forest buried in volcanic tuff near Wuda, Inner Mongolia, China, showing (*A*) graphic representation of results and (*B*) reconstruction of the forest only in these areas. (*A*) Mapping and counts could be performed in three sites that were subdivided into several subareas each. The distances between the three areas and subareas are indicated and are not drawn to scale. Tree ferns (green) are dominant; lycopsids (blue) and noeggerathialeans (red) are other common groups. Sphenopsids (white with black lines), *Cordaites* (yellow), and early cycads (purple) were rare or occurred only in certain areas. Herbaceous plants (white with black dots) are found only in isolated spots. The reconstruction (*B*) of the flora on these sites is based on the actual position of trees. The areas between the studied areas were also forested but have not been reconstructed in this drawing and are shown as much narrower than in reality. Site 1, 155 m^2; site 2, 390 m^2; site 3, 592 m^2. Total 1,137 m^2. C-D, E-F, and G-H indicate specific sample areas referred to in Fig. 3.

ranges from 200 to 500 m^2 (5, 6, 20). The counted area at Wuda is over 1,000 m^2 in entirety (Fig. 2), and therefore large enough to characterize the forest ecology. In addition, our collections from other outcrops of the tuff bed in the syncline yielded very few additional taxa from those recorded in our counting area.

The community heterogeneity and ecological gradients are clearly noticeable in our reconstructions (Figs. 2*B*, 4, and 5) based on the "Pompeii" maps. Local differences become apparent (Figs. 2–5 for comparison of the two reconstructions), showing the heterogeneous structure of the flora that existed in this actual landscape. In particular, Noeggerathiales exist throughout the forest, and locally can be the dominant group as shown in the subarea E-F in site 2 (Figs. 2*A* and 3 *E* and *F*). This finding represents the unique recording of a site of Noeggerathiales as the major group in a late Paleozoic peat-forming community, and thus distinct from those species of the group living in extrabasinal settings in Euramerica (21). The canopy trees *Cordaites* and *Sigillaria* occur together in site 1, but do not co-occur in other parts of the excavated areas (14). These two taxa, one a seed plant and the other as a spore-producing plant, show spatial differentiation and a pattern of co-occurrence only in an ecotone. Previously, based on investigation of coal balls, they were both known as major taxa in Early Permian coal-swamp forests in northern China, without any information on their spatial distributions relative to one another (22–25).

Other fossil floras from the area of Wuda and the northern Helanshan mountain chain, and also from the same time interval as the flora studied here, have in part a distinctly different taxonomic composition because they grew on different substrates (9). However, certain trends are the same. For example, Noeggerathiales and early possible cycadophytes are also common in floras growing on clastic substrates, although the species are different from those growing on peat substrates (9). In contrast to the absence of pteridosperms in the peat-forming community, the floras growing on clastic alluvial soils contain numerous species of pteridosperms. Thus, there is a distinct partitioning of this Permian landscape as seen in modern environments. Such a pattern, in which the taxa are sharply separated by substrate affinity (no co-occurrence), represents a change from Carboniferous tropical lowland landscapes in Euramerica, where all taxa co-occur over different substrates and where the change in substrate is marked by a change in dominance and diversity (26).

Reconstructions of Carboniferous coal swamps are some of the most common images of Late Paleozoic terrestrial ecosystems in Euramerica (2, 4, 27). Similarly, reconstructions of Permian swamp vegetation represent the common images of Late Paleozoic terrestrial ecosystems in China and East Asia (28), where previous investigations are all based on palynological data or coal-ball collections (23–25, 29, 30). All of these reconstructions are conceptional and are time-averaged because of preservational bias. Our present study confirms the composition of the Permian coal-swamp community as known from palynology and coal-ball studies, but resulted in a unique documentation of spatial heterogeneity and ecological gradients. The reconstructions (Figs. 4 and 5) present actual sites with detailed quantitative data for the Permian and Carboniferous in East Asia and are globally unique for presenting a Permian peat-forming habitat.

In previous studies of Permian coal-swamp communities from the Taiyuan Formation of northern China species of *Sigillaria* proved very common in coal balls (permineralized peat-stages of the coal), but the genus had never been recorded from compression floras of swamp communities (22). The occurrence of

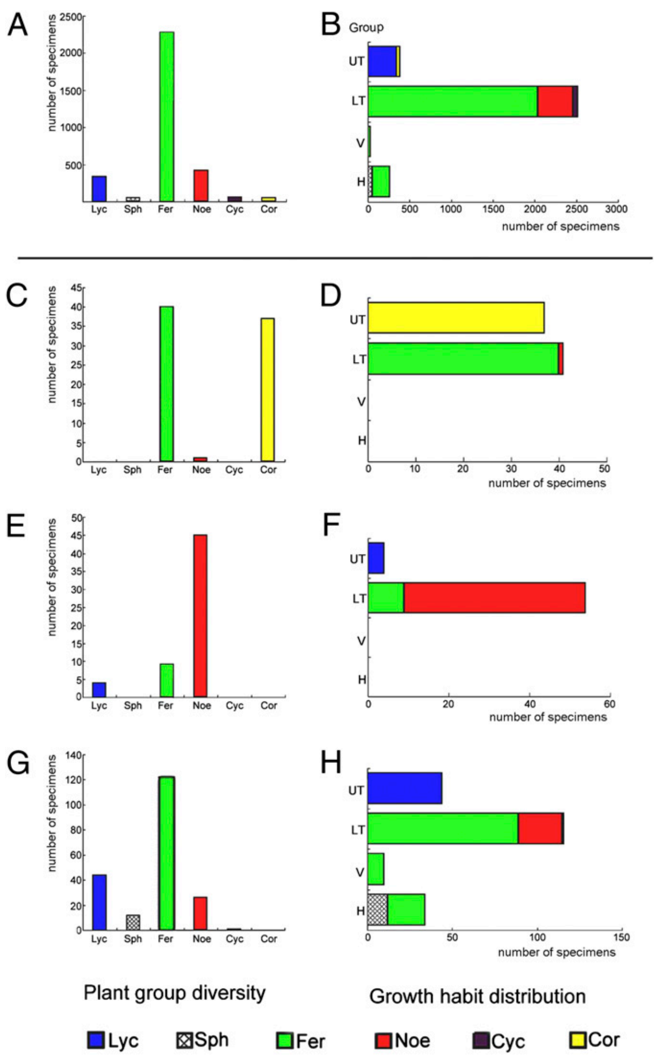

Fig. 3. Dominance patterns of plant groups (*Left*) and growth habits (*Right*) for the entire surveyed area (*A* and *B*) and three specific subareas (*C–H*) of the peat-forming flora preserved in a volcanic tuff layer between the No. 6 and No. 7 coals of the lowermost Permian of the Wuda mining district, Inner Mongolia, China. (*Left*: *A*, *C*, *E*, *G*) Plant group frequency. Cor, cordaitaleans; Cyc, possible early cycads; Fer, tree ferns; Lyc, tree lycopsids; Noe, Noeggerathiales; Sph, sphenopsids . (*Right*: *B*, *D*, *F*, and *H*) Growth habit distribution. H, herbaceous layer including dwarf shrubs and scramblers; LT, lower-story trees; UT, upper-story trees; V, vines. *A* and *B* show data for entire area; *C* and *D* are subarea of site 1 (marked C-D in Fig. 2*A*) tree fern and Cordaites-dominated area; E and F are subarea of site 2 (marked E-F in Fig. 2*A*) Noeggerathiales-dominated area; *G* and *H* are subarea of site 3 (marked G-H in Fig. 2*A*) tree fern-dominated area with lycopsids and Noeggerathiales.

Fig. 4. Reconstruction of the peat-forming forest of earliest Permian age preserved by a volcanic ash-fall that buried stems, broke off twigs, toppled trees, and preserved the forest at site 1 (of Figs. 1 and 2) near Wuda, Inner Mongolia, China, based on actual location of trees. The rare upper-canopy trees are *Sigillaria* (an extinct tree lycopsid) on the right and *Cordaites* (an early coniferophyte) on the left. The lower-story canopy is made up of several species of Marattialean tree ferns and Noeggerathiales (an extinct group of spore bearing plants of uncertain systematic position). The appearance of Noeggerathialean plants is based on nearly complete specimens that have been or will be described elsewhere (17). A species of *Sphenopteris* appears to have been a vine but was present only in small numbers. A sporadic herbaceous layer was made up of ferns (mostly *N. feminaeformis*, a representative of the extinct family Zygopteridaceae) and *Sphenophyllum* (belonging to an extinct group of sphenopsids). The peat was covered most of the year by a few centimeters of standing water protecting it from oxidation as shown in the reconstruction.

this genus in the Wuda tuff flora confirms *Sigillaria* as a coal-forming plant based on compression fossils (14). However, other lycopsids, such as *Lepidodendron* (*sensu lato*), which usually dominate coal-ball floras (22–25, 30), are absent in the Wuda tuff flora. At the same time, Noeggerathiales are very common in the peat-forming vegetation at Wuda but have never been documented in coal-ball floras.

The peat-forming flora at Wuda is surprisingly dissimilar to the well-known plant macrofossil assemblages of the Taiyuan Formation (11, 22, 31, 32). The characteristic species of this formation, *Neuropteris pseudovata* and *Lepidodendron* (*sensu lato*) *posthumii*, as well as many other typical floral elements, are missing at Wuda, whereas taxa such as *Paratingia*, *Taeniopteris*, and *Pterophyllum*, which elsewhere are known in much younger beds, occur in the Wuda tuff flora. This finding suggests that the known assemblages of the Taiyuan Formation in northern China probably only include floral elements from clastic lowland non-peat-forming environments. Few detailed taphonomic studies of the Late Paleozoic floras in China have been done, so that the ecological settings of the Cathaysian floras are not well constrained. As a consequence, comparisons of iso-taphonomic or iso-ecological floral assemblages are not yet possible.

Comparing tropical wetland floras of early Permian age from different parts of the globe, one can see as a common phenomenon the dominance of tree ferns both in diversity and biomass. The *Sigillaria brardii-ichthyolepis* group, *Sphenophyllum oblongifolium*, *N. feminaeformis*, and *Cordaites* are species groups, species, or genera, respectively, which occur in the flora described here and throughout the Cathaysian and Euramerican floral realms. Moreover, there are significant numbers of genera in common among China, Europe, and North America based on coal-ball floras of the late Paleozoic (33, 34). However, distinct differences exist at the specific level between tree ferns in China and those in Europe/North America. Furthermore, Noeggerathiales are an important part of the Cathaysian flora, but occur

Fig. 5. Reconstruction of actual site 3 (of Figs. 1 and 2) of a peat-forming forest of earliest Permian age that was preserved by a volcanic ash-fall near Wuda, Inner Mongolia, China. The upper-story trees are *Sigillaria* (an extinct tree lycopsid) that are carrying bundles of cones below their tuft of narrow leaves. The lower-story forest is made up of several species of Marattialean tree ferns that are characterized by a brown root mantle in the lower part of the stem and dead leaves hanging down. The other component of the lower-story forest is a species of *Paratingia*, a representative of the Noeggerathiales, present here in five individuals. Other smaller trees shown from left to right carry *Tingia*, *Pterophyllum*, and *Taeniopteris* foliage. A *Sphenopteris* species appears as a vine on two tree-fern root mantles. An herb layer existed only in some areas and is shown in the right foreground with *Sphenophyllum*, belonging to an extinct group of sphenopsids, and *N. feminaeformis*, a representative of the extinct fern family Zygopteridaceae. The peat was covered most of the time by a few centimeters of standing water protecting it from oxidation.

mostly in extrabasinal settings in Euramerica and are taxonomically distinct from those reported here.

In Euramerica, lycopsid-dominated forests in peat-forming environments were replaced by tree-fern forests during the Middle-Late Pennsylvanian transition (35, 36). This transition is not the case in Cathaysia. Compared with particularly well-analyzed Pennsylvanian coal-swamp communities before (4–6, 27) or after (2) the transition, the Wuda flora described here is remarkably short of pteridosperms, and has a lower diversity of lycopsids and a greater diversity of tree ferns, apart from abovementioned common occurrence of Noeggerathiales and possible early cycads.

Terrestrial vegetation presents a progressive increase in provinciality in the Late Paleozoic, resulting in four floral realms: Gondwanan and Angaran in the southern and northern middle-to-high paleolatitudes, and Euramerican and Cathaysian in the subtropical to tropical paleolatitudes (37). The Gondwanan and Angaran floras are quite distinct and easily recognizable, but the Euramerican (in present day Europe and North America) and Cathaysian (in present day China and east Asia) floras are similar in many respects, and their relationship has been discussed as a concern in Late Paleozoic paleophytogeography (33, 34, 38, 39). In our opinion, Permo-Carboniferous taxa shared by China, Europe, and North America (33) are expected because in the Carboniferous and Permian both areas shared elements of a global tropical rain forest biome (i.e., the same large-scale ecosystem) (40). However, there are distinct differences at the specific level among the common genera from China/East Asia and those from Europe/North America. Additionally, such genera as are held in common (33) come from different time intervals, respectively the Pennsylvanian of Euramerica and the Early Permian of China. Furthermore, as the present study shows, significant differences in the distribution and ecology of some groups (e.g., Noeggerathiales) exist between Cathaysia and Euramerica. Thus, there are clear paleophytogeographic differences that justify the separation into Euramerican and Cathaysian floral realms. It is important to maintain the distinction between large-scale climate ecology (i.e., biomes) versus regional taxonomic differences (i.e., biogeography).

Materials and Methods

The tuff is exposed in exploratory cuts or near mine-tunnel openings. To reach the tuff over an area large enough to carry out quantitative sampling, substantial amounts of overburden have to be removed, which requires the use of heavy machinery. Mining in connection with a coal fire-extinguishing project (41) systematically removed all near-surface coal seams, providing access to the volcanic tuff over hundreds of square meters at a time. The 66-cm thick tuff layer was then broken up by a power shovel but the blocks left in place. A grid was established and the blocks in each grid section investigated in turn. The blocks of tuff were split and the plant fossils recorded together with the size of the specimen (= quadrat) according to established methods (42) that were modified slightly in the present study.

The actual size of each quadrat was recorded. At the same time, the size of quadrats was kept more or less equal based on the general pattern of rock fracture. The average quadrat size in the first site (Fig. 1 *C*, 1) is about 10.5 cm × 13.0 cm; that of the second site (Fig. 1*C*, 2) is 9.4 cm × 13.6 cm; that of the third site (Fig. 1*C*, 3) is 7.6 cm × 13.0 cm. The average quadrat size in all three sites is about 8.2 cm × 13.2 cm. For any of a specific area or the whole area of a specific site, the analyses were done twice, once with the actual size of the counting quadrats and another time assuming that all quadrats were equal. The two results were so similar that the simpler method was used for all other areas. In other words, the coverage can be calculated assuming that all quadrats were of equal size, and the frequency of occurrence generally reflected the coverage (Figs. S1–S6 and Dataset S1).

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