Nystroemiaceae, a new family of Permian gymnosperms from China with an unusual combination of features

Jun Wang^{1,*} and Hermann W. Pfefferkorn²

¹LPS, Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China

²Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA

Nystroemiaceae is proposed as a new family of gymnosperms from the Permian of Cathaysia that adds to the diversity of gymnosperms known from this critical time in seed plant evolution. This family is characterized by bifurcating and highly branched pinnate ovuliferous organs bearing bicornute ovules (seeds) and entire leaves with anastomosing veins that are born on complex and modern-looking branching systems with clear axillary branching. The reconstruction is based on numerous large specimens from two localities in North China, in which the different plant parts are attached to each other. The ovulate structures show some apparently plesiomorphic (primitive) character states more typical of early seed plants, whereas the leaves and branches show the clearly apomorphic (derived) character states of broad-leaved gymnosperms.

Keywords: *Nystroemia reniformis* (Kawasaki) Wang; Pfefferkorn; Sun and Liu; *Chiropteris* Kurr; Permian; China

1. INTRODUCTION

The Permian period was a critical time for the evolution of seed plants, when numerous innovations appeared for the first time. There are also several recent reports that plants characteristic of and common in the Mesozoic already occur in the Permian (DiMichele *et al.* 2001; LePage *et al.* 2003; Kerp *et al.* 2006), further emphasizing the significance of this period in the modernization of gymnosperms. We consider here specifically the broad-leaved gymnosperms that today include cycads, *Ginkgo* and Gnetales, and exclude from discussion those that had needle-like leaves that today include conifers. In the Carboniferous period and the early Permian, medullosan, lyginopterid and callistophytalean pteridosperms had a plant habit unlike that of any living plants, while *Cordaites* had strap-shaped leaves with parallel venation. By the mid-Permian time, the situation had changed. For example, glossopterids were trees with laminar entire-margined leaves and anastomosing venation, and by the Mesozoic, with the exception of conifers, broad-leaved gymnosperms were the norm. The Nystroemiaceae introduced here fit into this trend of increasingly modern growth habit and leaves among seed plants, but apparently retain plesiomorphic (primitive) character states in their ovulate organs.

Halle (1927) reported abundant *Nystroemia pectiniformis* Halle and *Chiropteris reniformis* Kawasaki from the Permian

of Taiyuan, as part of his extensive study of the Palaeozoic flora from central Shanxi Province in northern China. Later, he investigated these materials together with fern-like fronds with attached seeds from a botanical point of view (Halle 1929). *Nystroemia pectiniformis* was characterized by Halle (1929) as complex fertile shoots (referred to as megasporophylls by Halle) with a great number of small ovules (seeds). *Chiropteris reniformis* is a reniform leaf with a long petiole. The lamina has numerous fine diverging veins that form long and narrow meshes. Considering the close association of the two genera, Halle speculated that they were from a common parent plant. He noted 'If this should prove to be the case, however, the sporophylls would be highly differentiated from the vegetative leaves, and might be imagined to have formed a kind of primitive inflorescence' (Halle 1929, p. 17). Such a plant would differ from other living or fossil seed plants in its complex, seed-bearing shoot and simple, laminar leaf with reticulate venation.

In the light of the botanical interest in this plant and in view of the close association of *N. pectiniformis* and *C. reniformis*, discovering the organic connection between these two genera has long been an important goal (Wang 1992, 1994; Sun & He 1998; Wang & Zhang 1998). Hilton & Li (2003) performed a very detailed re-investigation of the collection of Halle (1927) and reported new information, as well as insights into the ontogeny of *Nystroemia* ovules, the probable reproductive strategy of the plant and their possible systematic affinity. However, the organic connection between *Nystroemia* and *Chiropteris* remained elusive until Wang *et al.* (2003) demonstrated the connection between these two genera in material from Dengfeng Coalfield in Henan Province. In this publication, we

* Author for correspondence (jun.wang@nigpas.ac.cn).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0913> or via <http://rspb.royalsocietypublishing.org>.

One contribution to a Special Issue 'Recent advances in Chinese palaeontology'.

Figure 1. Maps showing (a,b) the locations where branches of *Nystroemiaceae* Wang and Pfefferkorn fam. nov. with attached ovules and leaves have been found (localities marked by flags) and (c) the position of these sites in the Permian (localities marked by flags) on the North China Plate, a small continent at that time. Palaeogeographical map is based on Ziegler *et al.* (1996).

reinvestigate the Henan material and present it together with new material on *Nystroemia* and *Chiropteris* in an organic connection based on large specimens from another locality approximately 50 km west of Halle's original locality of Eastern Hill Coalfield of Taiyuan, Shanxi Province. Together, these specimens allow a reconstruction of a larger branch of the *Nystroemia*–*Chiropteris* plant as well as consideration of the combination of character states that necessitate the establishment of a new family of gymnosperms.

2. MATERIAL AND METHODS

Specimens were collected from two localities: Sanyuncun Village (approx. 38°1' N; 112°41' E) in Dengfeng, Henan, and Mengjiacun Village (approx. 37°48' N; 112°52' E) in Shouyang, Shanxi, both in northern China (figure 1).

Geotectonically, the two localities are in the centre and southeast corner of the North China Plate, respectively (figure 1c). This plate formed a separate, relatively small continent in the tropical part of the Tethys Ocean throughout Permian time, which later collided with the Tarim and Mongolia plates (Ziegler *et al.* 1996).

In Dengfeng, the bed containing *C. reniformis* Kawasaki and *N. pectiniformis* Halle is a part of the middle Permian (Guadalupian) Xiaofengkou Formation. The taphonomic analysis of this locality indicates that the plant community was preserved autochthonously or parautochthonously (Sun & He 1998). Other members of the fossil plant community include *Lobatannularia*, *Annularia*, *Plagiozamites*, *Fascipteris*, *Gigantonoclea* and *Taeniopteris*. A considerable number of local species are known, and the local macrofossil assemblage has been called the *Gigantonoclea cathaysiana*–*Monogigantopteris clathroreticulatus*–*Lobatannularia ensifolia*–*Fascipteris sinensis* fossil plant assemblage in the Xiaofengkou Formation of western Henan (Yang 2006).

In Shouyang, specimens were collected from the Middle to Late Permian (Capitanian–Wuchiapingian) Upper

Shihhotse Formation. The Upper Shihhotse Formation in Taiyuan Eastern Coalfield generally corresponds to the Middle Permian (Wordian–Capitanian) Xiaofengkou Formation and Late Permian (Wuchiapingian) Yungaishan Formation in Dengfeng Coalfield (Li 1963; He *et al.* 1995; Yang 2006). The taxa associated with *Nystroemia* and *Chiropteris* in Shouyang include *Lobatannularia*, *Annularia*, *Tingia*, *Pecopteris*, *Cladophlebis*, *Sphenopteris*, *Fascipteris*, *Gigantonoclea*, *Gigantopteris*, *Neuropteridium* and *Taeniopteris*. The macrofossil plant assemblage of the Upper Shihhotse Formation in Taiyuan Eastern Hill Coalfield has been called the *Lobatannularia heianensis*–*Gigantonoclea hallei*–*Psygmyphyllum multipartitum* assemblage (He *et al.* 1995).

At both localities, specimens occur as impressions only. Standard maceration techniques have failed to yield any evidence of anatomical detail. In the material from Henan, leaves of *C. reniformis* Kawasaki are generally the same colour as the matrix, although occasionally they may be slightly darker and the petiole may be a dark reddish brown colour. Specimens of *N. pectiniformis* Halle are predominantly reddish brown, but some are greyish black. The main axes are often greyish white. In the material from Shanxi, both leaves and seeds are predominantly reddish brown. X-ray spectrum analysis indicates that the reddish substance is mainly iron oxide.

All specimens are deposited in the palaeobotanical collections of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (catalogue numbers PB19875, PB19877, PB19891, PB21159–21165 and PB21279–21283).

3. SYSTEMATIC PALAEONTOLOGY

Family *Nystroemiaceae* Wang and Pfefferkorn fam. nov.

(a) *Diagnosis of family*

Ovuliferous organ frond-like. The main axis forking with pinnate lateral branches bearing numerous small

Figure 2. Specimen from the Lower Permian Xiaofengkou Formation of Sanyuancun Village in Dengfeng, Henan, China, showing the connection of leaves (*Chiropteris* Kurr) and ovules (*Nystroemia* Halle). Catalogue number PB21159. Scale bar, 20 mm.

bicornute ovules at their tips. Vegetative leaf with a long petiole and a broad lamina with radiate reticulate venation, lamina with entire or undulate margin and cordate or tapering base. Leafy/ovuliferous complex arising from leaf axil. Ovuliferous organs attached in the axil of the petiole of leafy organ, or both organs crowded on a node. Branching system probably woody and with variability in its branching pattern. Long and short shoots differentiated.

Genus *Nystroemia* Halle (1927), emend. Hilton & Li (2003), emend. nov.

Type species *N. pectiniformis* Halle (1927), emend. Hilton & Li (2003).

(b) Emended diagnosis of genus

Seed plant with multi-order branching system. Ovuliferous organ frond-like, with the main axis forking into two or more pinnate branches adaxially bearing numerous small bicornute ovules with zygomorphic symmetry. Vegetative leaf with a long petiole; lamina reniform, basally cordate or tapering, entire or slightly undulate at the margin; veins numerous, finely diverging and reticulate. Leafy/ovuliferous complex arising from leaf axil, forming the last-order branches, which are alternative or opposite on the second-last-order axis. Ovuliferous organs attached in the axil of the petiole of leafy organ, or both organs crowded on a node.

Remarks. On the basis of Halle (1927, 1929) and Hilton & Li (2003), the current emendation of the generic diagnosis includes the features of leaves and their spatial relationship with ovuliferous organs, as the present material demonstrates.

(c) Description of species

Species *Nystroemia reniformis* (Kawasaki) Wang *et al.* (2003) (figures 2–5).

Figure 3. Drawing of specimen shown in figure 2 with numbers in circles indicating the branching points and numbers without circles the axes of both sterile leaves and fertile structures (see text for detailed description of this specimen). The uppermost part of the reconstruction of the *N. reniformis* (Kawasaki) branch (figure 5) is based on this specimen. Scale bar, 20 mm.

There are a number of specimens from Dengfeng showing the configuration of *N. reniformis* (figures 2 and 3; see electronic supplementary material). Among them, a relatively well-preserved representative is selected to demonstrate the key morphological characters (figures 2 and 3).

The specimen in figure 2 very probably represents an apical part of a leafy/ovulate complex of the plant. The main axis is 180 mm long. At the first internode, the axis is 7.8 mm wide; at the second, it is 6 mm; in the lower 1/5 of the third internode, it is 6 mm; but in the upper 4/5 it is 7.4 mm wide. Apically, the axis becomes gradually more slender and is 3.7 mm wide at the apex. In the paragraphs that follow, arrow numbers refer to those in figure 3.

At the first node (arrow 1, circled), a leaf and an axillary second-order axis arise. The leaf petiole is placed at an angle of nearly 90° with the main axis, but immediately curves downwards, which could be a preservational feature. The leaf lamina is not preserved. The preserved length of the petiole is 54 mm. It is 4.5 mm wide basally and slightly thinner towards the leaf lamina. The axillary axis arises at an angle of 60° with the main axis. At approximately 44 mm from the base of the secondary axis, two leaves and three seed-bearing axes arise successively. The first leaf (arrow 1, uncircled) arises from the left side at an angle of approximately 90°, with a 49 mm long petiole that is approximately 3 mm wide at the base. The lamina attached to the apical end of the petiole is wedge-shaped, but incomplete, 35 mm by 25 mm in size. Its axillary seed-bearing axis (arrow 2, uncircled) is 31 mm long and 3 mm wide at the base. It bifurcates at

Figure 4. Specimens from the Lower Permian Xiaofengkou Formation of Sanyuancun Village in Dengfeng, Henan, China, showing branch of *N. reniformis* (Kawasaki) bearing pinnate ovulate structures and entire leaves with anastomosing venation. (a) *Nystroemia* ovule-bearing axis showing two lateral branches arising from the left side of the main axis. The lower branch clearly forks once, producing two subordinate branches that bear numerous small bicornute ovules. The upper branch is not well preserved, with only the basal axis visible. PB21279. (b) Pinna-like *Nystroemia* ovule-bearing axis. PB19877. (c) Magnified part of (b) showing the hydrasperman seeds with two protrusions. (d) A small *Chiropteris* leaf with a cordate lamina base. PB21160. (e) Magnified portion of (d) showing the anastomosing venation. (f) *Chiropteris* leaf with wedge-shaped lamina base and long petiole attached to an axis. PB21280. Scale bars: (a), 5 mm; (b), (d) and (f), 10 mm; (c), 2.5 mm; (e), 2 mm.

the apex and each part is further pinnately divided, bearing numerous seeds with the micropyle pointing upwards. The second leaf (arrow 3, uncircled) and seed-bearing axis (arrow 4, uncircled) are given off from the right side. The leaf petiole is approximately 2.5 mm wide and 31 mm long. The seed-bearing axis is approximately 1.8 mm wide and 25.5 mm long. Most seeds appear to be preserved on the left side owing to a twist of the axis. The third seed-bearing axis (arrow 5, uncircled) branches off in the middle between the former two. It forms an angle of approximately 20° extending approximately 6 mm upwards and then turning left. It is 1.4 mm wide, this width changing minimally up to the apical part, where it bifurcates once. The ultimate branches are approximately 1 mm wide and both bear over 10 seeds. An axis (arrow 6, uncircled) 8.4 mm long and 1.8 mm wide occurs beside the third seed-bearing axis. It could represent a further extension of the second-order axis, but may also be a petiole of a leaf that subtends the third seed-bearing axis.

At the second node (arrow 2, circled), the connection of the second-order axis with the main axis is broken. The secondary axis appears to arise at an angle of

approximately 45° extending forwards 10 mm and turns perpendicular to the main axis. It is 3.5 mm wide and after approximately 2.7 mm starts to give rise to leaves and seed-bearing axes. First, a possible leaf-bearing axis (arrow 7, uncircled) branches off at nearly a right angle, but the lamina is not preserved. A seed-bearing axis (arrow 8, uncircled) extends straight, and its upper part is covered by another seed-bearing organ. A leaf (arrow 9, uncircled) arises afterwards at a distance of 2 mm. The petiole is approximately 2.7 mm wide at the proximal end and 1.5 mm wide at the uppermost part, with a preserved length of approximately 37.7 mm. The seed-bearing axis (arrow 10, uncircled) axillary to the leaf is approximately 1.3 mm wide and 19.5 mm long, with the lower half extending forwards and then forking once and turning upwards. The upper seed-bearing part is pinnately divided. All ultimate branches bear numerous seeds in two lateral rows on the adaxial side.

The third node (arrow 3, circled) is represented by a large leaf and a broken axillary axis (arrow 11, uncircled) with its basal part 3.2 mm wide and a preserved length of only 10 mm. The leaf petiole is given off at an angle of approximately 80° and after approximately 18.4 mm

Figure 5. Reconstruction of larger branch of the gymnospermous *N. reniformis* plant carrying primitive ovules of the hydrasperma type on an advanced branching system with entire leaves that have a modern aspect and reticulate venation. Fertile shoots (third-order axes) all originate in an axillary position and can be interpreted to form a primitive, extremely loose inflorescence. The reconstruction is based on numerous specimens showing the growth habit (see images in electronic supplementary material). Scale bar, 50 mm.

curves downwards. It is 61 mm long, approximately 4 mm wide at the base and 2.5 mm wide where the lamina is attached. The fragmentary leaf lamina is 65 mm by 48 mm in size with typical simple reticulate venation.

At the upper part of the leafy/ovuliferous complex, the main axis gives off a thick secondary axis to the right side as if the axis is bifurcated (arrow 4, circled). The axis on the right side bears a leaf at a distance of 6.7 mm from the base. The lamina is badly broken, but the connection with the petiole and the venation is clearly visible. A seed-bearing axis (arrow 12, uncircled) is given off upwards and bifurcates twice, producing three ultimate branches bearing many seeds, with the micropyle pointing upwards. Another axis (arrow 13, uncircled) arising from the right axis is thicker and may be a leaf petiole.

The axis on the left side is thicker than that on the right and is considered a continuation of the main axis.

The first node (or the fifth node of the main axis; arrow 5, circled) carries only a broken base of an axis that might have been connected with a seed-bearing organ, as indicated by the dashed lines.

After 10 mm, the next node (arrow 6, circled) carries a seed-bearing axis (arrow 14, uncircled) on the right side, and another slender axis (arrow 15, uncircled) occurs just above. It is uncertain whether the latter is a basal part of a leaf petiole or a seed-bearing axis.

Slightly higher on the left side of the main axis, a leaf (arrow 16, uncircled) and an axillary seed-bearing axis (arrow 17, uncircled) are given off. There is another leaf lamina (arrow 18, uncircled) below, but a connection between this leaf and the main axis is not detected.

The distal end of this specimen is not completely preserved and only the broken main axis (arrow 19, uncircled) can be seen.

All specimens from Dengfeng demonstrate essentially the same pattern of arrangement of leafy and ovuliferous organs as in figures 2 and 3. In addition, four specimens of the ovuliferous organ (figure 4a–c) and isolated leaf (figure 4d–f) are illustrated, showing the pinnate ovulate structure (figure 4a,b), the shape of a seed (figure 4c), the leaf with a cordate (figure 4d) or tapering (figure 4f) laminar base and the reticulate venation (figure 4e). In particular, the specimen in figure 4f indicates that a leaf may be independently attached to the axis, unlike other specimens (figures 2 and 3; see electronic supplementary material) where it occurs in a leafy/ovuliferous complex.

Based on materials from Dengfeng, a reconstruction of *N. reniformis* (Kawasaki) is shown in figure 5.

Species *Nystroemia shouyangensis* Wang and Pfefferkorn sp. nov. (figure 6).

Holotype: PB21165 (figure 6a).

Paratype: PB21283 (figure 6d) and PB21282 (figure 6f).

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008.

Type locality: Mengjiacun Village, Shouyang, Shanxi.

Horizon: Middle–Late Permian (Capitanian–Wuchiapingian) Upper Shihhotse Formation.

Etymology: The specific name is given based on the locality in ‘Shouyang’ County.

Diagnosis: Ovuliferous organ with the main axis forking into two or more pinnate-like branches adaxially bearing numerous small bicornute ovules with zygomorphic symmetry. Vegetative leaf with a long petiole; lamina reniform, basally cordate, entire or slightly undulate at the margin; veins numerous, finely diverging and reticulate. Leaves and ovuliferous organs attached to short shoots, forming the last-order branches.

Description: There are over 20 specimens from Shouyang, showing the morphology of the leaves and ovuliferous organs, of which over 10 specimens show leaf and ovuliferous organs attached to a short shoot. Three specimens (figure 6a,d,f) are selected to demonstrate the key morphological characters of the new species. The first specimen (figure 6a) shows that leaf and ovuliferous organ are attached to a short shoot. In this specimen, there are five leaves readily noticeable. They are relatively large, with lamina generally circular and basally cordate, 30–50 mm in diameter. Veins radiate

Figure 6. *Nystroemia shouyangensis* sp. nov. specimens from the Upper Shihhotse Formation in Mengjiacun Village, Shouyang, Shanxi. (a) Several *Chiropteris* leaves and *Nystroemia* pinnate ovulate structures arranged on a short shoot. The right arrow indicates an area that is magnified in (b) and shows a pinnate ovulate structure in which one of the bicornute ovules can be clearly recognized; the left arrow indicates an area that is magnified in (c), which shows the cordate base of a *Chiropteris* leaf with reticulate venation. White arrows labelled 1–5 indicate the position of five small leaves that are less obvious. PB21165. (d) Only *Nystroemia* pinnate ovulate structures arranged on a short shoot. PB21283. (e) A *Chiropteris* leaf with a long petiole. The lamina is fragmental, but the cordate base with reticulate venation is clearly visible. PB21281. (f) At least seven *Chiropteris* leaves and a *Nystroemia* ovulate structure arranged on a short shoot. Arrow indicates the ovulate structure magnified in (g). PB21282. Scale bars: (a), (d), (e) and (f), 20 mm; (b), 2.5 mm; (c) and (g), 5 mm.

and reticulate, slightly thicker in the middle and basal parts of the lamina (figure 6c). Leaf petiole is 20–40 mm long and 2–6 mm wide. There are another five leaves that are not so clearly visible (figure 6a,

arrows 1–5). Their laminae are approximately 20 mm in diameter and petioles are approximately 10 mm long. Five ovuliferous organs are attached to the shoot. The main axes of the ovuliferous organs are 15–20 mm long

and 1–1.5 mm wide. They may distally bifurcate once, resulting in two branches, which are pinnate-like and bear numerous small bicornute ovules with zygomorphic symmetry (figure 6b). The second specimen (figure 6d) shows only a number of ovuliferous organs attached to a short shoot. It is observable that the main axis of an ovuliferous organ bifurcates once at the apex, producing two pinnate subordinate branches bearing numerous seeds. The third specimen (figure 6f) in its original preservation shows that there are several leaves attached to a short shoot without ovuliferous organs. Subsequently, an ovuliferous organ (figure 6f, arrow; figure 6g) is detected through dégagement. The form, dimension and arrangement of leaves are the same as that in the first specimen. The leaf in figure 6e has a petiole more than twice as long as those of leaves attached to a short shoot (figure 6a,d,f). It may suggest that this leaf is attached to a long shoot. The phyllotaxy of the leaves and ovuliferous organs is uncertain owing to preservation.

4. DISCUSSION

The phylogeny of gymnosperms is slowly becoming clearer through new research and syntheses (Crane 1985; Rothwell & Serbet 1994; Crane *et al.* 2004; Doyle 2006; Hilton & Bateman 2006; Rothwell & Dunn 2006). However, many questions remain to be answered. More work is needed to 'reconstruct individual conceptual whole plants from disarticulated fossil organs' (Hilton & Bateman 2006, pp. 119 and 151), and more data are needed for a number of groups (Doyle 2006). We contribute to these efforts by demonstrating organic connection between *Nystroemia* ovules and *Chiropteris* leaves and documenting aspects of its growth form in our reconstruction of *N. reniformis*. This discovery also points to the possible existence of other unrecognized groups. The Cathaysian floral realm in East Asia existed on tropical islands in the Late Palaeozoic Tethys Ocean, a setting that produced floras with a high biodiversity. More discoveries can be expected from this area where fewer studies have focused on evolutionary and phylogenetic questions than in the Euramerican realm.

The reconstruction of *N. reniformis* (figure 5) is based on numerous specimens of *Chiropteris*–*Nystroemia* that show the attachment of *Chiropteris* leaves and *Nystroemia* fertile structures to a multi-order system of branches (figures 2–4; see figures in electronic supplementary material). That *Chiropteris* and *Nystroemia* represent parts of the same plant has been suggested before (Halle 1927, 1929; Hilton & Li 2003) and was demonstrated by Wang *et al.* (2003). The present reconstruction and rendition of the actual growth habit of this plant are based on large specimens, add new information and further clarify the combination of character states that existed in this plant. The plant is characterized by a unique combination of primitive and very advanced features. The numerous small, bicornute ovules have been compared with hydrasperman seeds known since the Late Devonian time (Hilton & Li 2003). Another clearly primitive feature is the fork in the axis of the ovule-bearing structure and the pinnate arrangement of each of the two resulting parts. These three features are reminiscent of early lyginopterid pteridosperms and might well have been inherited from this group (Hilton & Li

2003). The fact that the ovules are not attached in one plane but that the pinnately arranged seed stalks point in a V-shape in one general direction (Hilton & Li 2003) may be a specialized adaptation to facilitate either fertilization or dispersal.

The Dengfeng specimens demonstrate an organic connection between *C. reniformis* Kawasaki and *N. pectiniformis* Halle, so that a new combination *N. reniformis* (Kawasaki) was proposed for the whole plant (Wang *et al.* 2003). We herein assign the Shouyang specimens, which were discovered recently, to a new species because the leaves and ovuliferous organs from the two localities show significant differences. The most critical difference is that the Shouyang species has leaves and ovuliferous organs arranged on a short shoot (figure 6a,d,f), whereas those of the Dengfeng species are arranged on a long shoot (figures 2, 3, 4f and 5). Moreover, the leaf laminae of the Shouyang material have a very distinctly cordate base (figure 6c), whereas those of the Dengfeng material mostly have a wedge-shaped (figure 4f) lamina base, although the lamina base of certain small leaves is cordate to a degree (figure 4d). The ovuliferous organs of the Shouyang material as a rule appear as a main axis that distally bifurcates once, producing two subordinate pinnate branches bearing numerous small bicornute ovules, whereas those of the Dengfeng material are more irregular.

The branching pattern of the shoots includes at least three orders of axes, not counting the rachises of the leaves, apart from the differentiation of long and short shoots. The branching pattern seen in the specimens described and figured here does not support an interpretation that *Nystroemia* was a climbing plant (Hilton & Li 2003). There is no evidence of climbing structures like those of Gigantopterids that occur in the same plant community. Rather, the branching pattern suggests a large shrub, or more probably a tree, of significant size. This combination of characters would not be surprising in a modern plant, or even a late Mesozoic one, but is remarkable in the Late Paleozoic, where most plants had compound leaves with pinnate or open dichotomous venation. There is some similarity in life habit to early Mesozoic ginkgoalean plants (Zhou 1990), and it is also interesting that at least some glossopterids also had distinct short shoots (Pigg & Nishida 2006). The *N. reniformis* plant has a rather advanced appearance, while preserving a few features that appear primitive. The reconstruction demonstrates that gymnosperms bearing simple entire leaves originated by the Middle Permian time, producing plants with essentially modern habits. The genus does not fit into any established family of gymnosperms and thus represents a new family.

In contrast to the ancient pteridosperms, the leaves of *Chiropteris* are entire and have anastomosing venation. They have a long petiole, a reniform shape and appear more like leaves of more modern groups. This leaf form could have been derived from forms similar to those glossopterid plants that do not have a clear mid-vein. There are also similarities to the leaves of the Triassic genus *Batiopteris* Anderson and Anderson (Anderson & Anderson 2003) and the leaves of *Kannaskoppia*.

By Permian time, ovules occur in several forms of attachment. Ovules may be attached singly on vegetative leaves (emphlopterids), in clusters on fertile leaves

(glossopterids) or as loose strobilus-like structures in peltasperms (Anderson *et al.* 2007, p. 77). The form of the fertile compound frond in *Nystroemia* is much more similar to plants known from the Mississippian subperiod, whereas the one-sided attachment apparently represents an advanced feature. However, a similar forking ovulate structure, albeit with recurved ovules, is present in the Triassic genus *Kannaskoppia* (Anderson & Anderson 2003; Anderson *et al.* 2007). Thus, these features are in existence during the Triassic radiation of gymnosperms (Anderson *et al.* 2007).

The configuration of the axillary female fertile shoot of *N. reniformis* is similar in its organization to the seed-scale complex in coniferophytes, such as those of *Cordaites* and *Lebachia*: the leafy and ovuliferous organs could, respectively, correspond to the sterile scale and megasporophyll of *Cordaites* or *Lebachia*. However, the present seed-scale complex is extremely loose compared with these plants, and both the morphology and aggregation of ovules, as well as the arrangement of the leafy and ovuliferous organs, are distinctly different from what is seen in coniferophytes. The situation in *Ginkgo*aleans is more similar. *Ginkgo* has well differentiated long and short shoots. Leaves occasionally develop vein anastomoses, although never to the extent seen in *Chiropteris*. Ovulate shoots are also axillary to a sterile scale or leaf on female fertile shoots. However, the ovulate structures of *Nystroemia* are much more complex than those of *Ginkgo*. Perhaps the strongest similarities, both in the leaves with reticulate venation and the arrangement of the fertile organ, are to glossopterids. However, while glossopterids show a high morphological variation in both leaves and fertile structures (Chandra & Surange 1979; Taylor & Taylor 2009; Taylor *et al.* 2009; Pigg & Nishida 2006), there are none that closely resemble *Nystroemiaceae*. The features of *Nystroemiaceae* lie so far outside those of glossopterids that *Nystroemiaceae* cannot be included in this group. So far, no macroscopic *Glossopteris* floral elements, such as leaves or the glossopterid seeds *Pterygospermum* or *Stephanostoma*, have been documented from northern China or Cathaysia as a whole during the Permian. However, *Glossopteris*-like pollen grains do occur, beginning in the early Permian in North China (oral communication by Ouyang Shu, January 2009). The possibility that *Nystroemiaceae*, or plants like them, might represent a plesiomorphic sister group to glossopterids that existed in Cathaysia deserves further consideration.

From the Permian to mid-Cretaceous, gymnosperms were the dominant plants in most environments. Many of these gymnosperms were broad-leaved plants, of which only few, such as *Ginkgo* and cycads, have survived until today, while most living gymnosperms bear needle-shaped leaves. *N. reniformis* adds to the diversity of broad-leaved gymnosperms known from the Middle Permian and is just one example of such plants that appeared during the Permian radiation of gymnosperms. Some of these plants survived into the Mesozoic time and gave rise to an even higher diversity of broad-leaved gymnosperms, some of which may have themselves given rise to angiosperms. These broad-leaved gymnosperms of the Permian and Mesozoic filled many of the ecological niches in a pre-angiosperm world that angiosperms occupy today.

We would like to acknowledge the Chinese Academy of Sciences (project no. KZCX2-YW-105), Chinese Natural Science Foundation (grant no. 40572008 and 40621062) and the Major Basic Research Project (grant no. 2006CB806400) of the Ministry of Science and Technology of China, for financial support. We are grateful to Professor Zhou Zhiyan and Sir Peter Crane for their kind discussion of the possible systematic position of *Nystroemia*. J.W. would like to thank Professor Else Marie Friis for her kind help in accessing the specimens housed in the Swedish Museum of Natural History. Thanks go to Ren Yugao and Zhang Yi for preparing all reconstruction figures.

REFERENCES

- Anderson, J. M. & Anderson, H. M. 2003 *Heyday of the gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications*. Strelitzia 15. Pretoria, South Africa: National Botanical Institute.
- Anderson, J. M., Anderson, H. M. & Cleal, C. J. 2007 *Brief history of the gymnosperms: classification, biodiversity, phyto-geography and ecology*. Strelitzia 20. Pretoria, South Africa: South African National Biodiversity Institute.
- Chandra, S. & Surange, K. R. 1979 Revision of the Indian species of *Glossopteris*. *Birbal Sahni Inst. Palaeobot. Monogr.* 2, 1–291.
- Crane, P. R. 1985 Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Missouri Bot. Garden* 72, 716–793. (doi:10.2307/2399221)
- Crane, P. R., Herendeen, P. & Friis, E. M. 2004 Fossils and plant phylogeny. *Am. J. Bot.* 91, 1683–1699. (doi:10.3732/ajb.91.10.1683)
- DiMichele, W. A., Mamay, S. H., Chaney, D. S., Hook, R. W. & Nelson, W. J. 2001 An Early Permian flora with Late Permian and Mesozoic affinities from north-central Texas. *J. Paleontol.* 75, 449–460. (doi:10.1666/0022-3360(2001)075<0449:AEPFWL>2.0.CO;2)
- Doyle, J. A. 2006 Seed ferns and the origin of angiosperms. *J. Torrey Bot. Soc.* 133, 169–209. (doi:10.3159/1095-5674(2006)133[169:SFATOO]2.0.CO;2)
- Halle, T. G. 1927 Palaeozoic plants from central Shansi. *Palaeontol. Sin.* A 2, 175–223.
- Halle, T. G. 1929 Some seed-bearing pteridosperms from the Permian of China. *K. Sv. Akad. Handl., Tredje Ser.* 6, 3–24.
- He, X. L., Zhu, M. L., Fan, B. H., Zhuang, S. Q., Ding, H. & Xue, Y. 1995 *The Late Paleozoic stratigraphic classification, correlation and biota from Eastern Hill of Taiyuan City, Shanxi Province*. Changchun, China: Jilin University Press (in Chinese with English summary).
- Hilton, J. & Bateman, R. M. 2006 Pteridosperms are the backbone of seed-plant phylogeny. *J. Torrey Bot. Soc.* 133, 119–168. (doi:10.3159/1095-5674(2006)133[119: PATBOS]2.0.CO;2)
- Hilton, J. & Li, C. S. 2003 Reinvestigation of *Nystroemia pectiniformis* Halle, an enigmatic seed plant from the Late Permian of China. *Palaeontology* 46, 29–51. (doi:10.1111/1475-4983.00285)
- Kerp, H., Hamad, A. A., Vörding, B. & Bandel, K. 2006 Typical Triassic Gondwanan floral elements in the Upper Permian of the paleotropics. *Geology* 34, 265–268. (doi:10.1130/G22187.1)
- LePage, B. A., Beauchamp, B., Pfefferkorn, H. W. & Utting, J. 2003 Late Early Permian plant fossils from the Canadian High Arctic: a rare paleoenvironmental/climatic window in northwest Pangaea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 191, 345–372. (doi:10.1016/S0031-0182(02)00671-5)
- Li, X. X. 1963 *Late Palaeozoic continental formations of China*. Beijing, China: Sciences Press (in Chinese).

- Pigg, K. B. & Nishida, H. 2006 The significance of silicified plant remains to the understanding of Glossopteris-bearing plants: an historical review. *J. Torrey Bot. Soc.* **133**, 46–61. (doi:10.3159/1095-5674(2006)133[46:TSOSPR]2.0.CO;2)
- Rothwell, G. W. & Dunn, M. T. 2006 A century of seed ferns: introduction to the symposium. *J. Torrey Bot. Soc.* **133**, 4–6. (doi:10.3159/1095-5674(2006)133[4:ACOSFI]2.0.CO;2)
- Rothwell, G. W. & Serbet, R. 1994 Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Syst. Bot.* **19**, 443–482. (doi:10.2307/2419767)
- Sun, B. N. & He, X. L. 1998 Study on palaeophytoecology from the Lower Shihhotse Formation in Dengfeng Coal-field, Henan Province. *Geol. J. China Univ.* **4**, 313–317 (in Chinese with English abstract).
- Taylor, E. L. & Taylor, T. N. 2009 Seed ferns from the late Paleozoic and Mesozoic: any angiosperm ancestors lurking there? *Am. J. Bot.* **96**, 237–251. (doi:10.3732/ajb.0800202)
- Taylor, T. N., Taylor, E. L. & Krings, M. 2009 *Paleobotany, the biology and evolution of fossil plants*, 2nd edn. Amsterdam, The Netherlands: Academic Press.
- Wang, Z. Q. 1992 Successional trends of plant community during the Palaeo-mesophytic transition in North China. *Chin. Sci. Bull.* **37**, 1098–1103.
- Wang, Z. Q. 1994 Paleobotanical evidence for the Permian paleowind activities in north China. *Chin. Sci. Bull.* **39**, 62–66.
- Wang, Z. Q. & Zhang, Z. P. 1998 Gymnosperms on the eve of the terminal Permian mass extinction in North China and their survival strategies. *Chin. Sci. Bull.* **43**, 889–897. (doi:10.1007/BF02884606)
- Wang, J., Pfefferkorn, H. W., Sun, B. N. & Liu, L. J. 2003 Discovery of organic connection of *Chiropteris* Kurr and *Nystroemia* Halle from Early Permian of western Henan, China. *Chin. Sci. Bull.* **48**, 2248–2252. (doi:10.1360/02wd0541)
- Yang, G. X. 2006 *The Permian Cathaysian flora in Western Henan Province, China—Yuzhou Flora*. Beijing, China: Geological Society Publishing House (in Chinese with English summary).
- Zhou, Z. Y. 1990 Phylogenetic interrelationships and evolutionary trends of Mesozoic ginkgoaleans. In *Selected papers of theoretical palaeontology* (eds J. Y. Rong, Z. J. Fang & T. J. Wu), pp. 1–19. Nanjing, China: Nanjing University Press (in Chinese).
- Ziegler, A. M., Hulver, M. L. & Rowley, D. B. 1996 Permian world topography and climate. In *Late glacial and postglacial environmental changes: Quaternary, Carboniferous-Permian and Proterozoic* (ed. R. P. Martini), pp. 111–146. New York, NY: Oxford University Press.