Sinocarpus decussatus gen. et sp. nov., a new angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China

Q. Leng[1] and **E. M. Friis**[2]

[1]Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing,
The People's Republic of China
[2]Department of Palaeobotany, Swedish Museum of Natural History, Stockholm, Sweden

Abstract. An Early Cretaceous angiosperm, *Sinocarpus decussatus* gen. et sp. nov., is described from the Yixian Formation in Liaoning, China, based on an infructescence fragment. It is probably ebracteate, consisting of one terminal fruit and two pairs of pedicellate lateral fruits arranged decussately. Carpels are probably borne on a small convex receptacle. There are no distinct remnants of a perianth although fragments observed at the base of immature fruits may represent perianth parts. No remnants of androecial parts have been observed, and it is unknown whether the flowers were unisexual or bisexual. The basally syncarpous ovary is superior and composed of 3 or 4 carpels. Each carpel contains about 10 anatropous ovules/ seeds borne along the linear placentae. Seeds are flattened and embedded in a thick amorphous material. The character combination of *Sinocarpus* indicates a systematic position among the basal grade of eudicots or the basal core eudicots, and particularly shows similarities to extant Ranunculaceae, Buxaceae, and Myrothamnaceae, but based on the available data the fossil cannot unambiguously be placed in any modern family.

Key words: *Sinocarpus decussatus*, fossil, infructescence, angiosperms, eudicots, Yixian Formation, Cretaceous.

The Mesozoic Jehol Group from North and Northeast China is well known for its rich and exquisitely preserved fauna including numerous birds and dinosaurs as well as a wealth of other vertebrate and invertebrate fossils unique to this assemblage (Chang 2001, Chen and Jin 1999). It also yields many plant fossils but they are generally of poorer preservation than the animal fossils and for most of the fossil plants only gross morphology is known while details of reproductive organs and anatomical structures are rarely preserved (Cao 2001, Chen et al. 1980, Ding 2000, Guo and Wu 2000, Sun et al. 2000, Sun et al. 2001, Wu 1999, Zhang and Shang 1996). The flora is, however, of considerable interest in providing information on the vegetational and environmental basis for the faunal elements. Further, it is also of interest as a potential source for understanding early angiosperm diversification. Since the work of Yabe and Endo (1935) a number of Jehol plant fossils were described as angiosperms but with a few exceptions the angiospermous affinity of these fossils has convincingly been rejected. Among these fossils is a diversity of small shoots with opposite branching and reproductive struc-

tures in small spikes described as *Potamogeton jeholensis* Yabe et Endo (1935), *Chaoyangia liangii* Duan (1998), *Liaoxia chenii* Cao and Wu (Cao et al. 1998), and *Eragrosites changii* Cao and Wu (Cao et al. 1998). They all show close similarity to extant *Ephedra* of the gymnosperm order Gnetales and were transferred to the extinct genus *Ephedrites* by Guo and Wu (2000). Other putative angiosperms, mainly based on vegetative remains, such as *Potamogeton*? sp. described by Yabe and Endo (1935) and *Typhaera fusiformis* Krassilov, *Lilites reheensis* Wu, *Orchidites linearifolius* Wu, and *O. lancifolius* Wu reported by Wu (1999) have not been investigated in detail and the systematic position of these fossils is as yet unresolved. Of all previously described angiosperm fossils from the Jehol Group two taxa, *Archaefructus liaoningensis* Sun, Dilcher, Zheng et Zhou (Sun et al. 1998) and *A. sinensis* Sun, Dilcher, Ji et Nixon (Sun et al. 2002), show the most complete preservation. The fossils were assigned to a new family Archaefructaceae that according to Sun et al. (2002) is the sister clade to all living angiosperms. The original interpretation and systematic position of *Archaefructus* is, however, problematic (Friis et al. 2003).

In this study we describe a new taxon, *Sinocarpus decussatus* gen. et sp. nov., with unambiguous angiospermous features based on an infructescence fragment from the Yixian Formation of western Liaoning, Northeast China. The characters of the new angiosperm, particularly the basally syncarpous gynoecium, indicate that angiosperms of the Yixian Formation had already developed some advanced characters. The new fossil is most comparable to extant members of the basal grade of eudicots such as the Ranunculaceae and Buxaceae and the basal core eudicots such as the Myrothamnaceae (for phylogenetic framework see APG II 2003 and Soltis et al. 2000). This information is also in accordance with our current understanding of the timing of early angiosperm radiation that displays the first appearance of tricolpate pollen characteristic of eudicot angiosperms

in the Barremian (e.g. Hughes and McDougall 1990, Friis et al. 1999, Friis et al. 2000), probably contemporaneous with the new Jehol fossil.

Material and methods

The fossil material studied here was collected from a stratum belonging to the Dawangzhangzi (Daxinfangzi) Bed (for circumscription see Wang et al. 1998 and Wang et al. 2000a) of the Yixian Formation in the Dawangzhangzi Village, Songzhangzi Town, Lingyuan County of Liaoning Province, China (41°15′N, 119°15′E, Fig. 1).

The Yixian Formation is a lithostratigraphic unit of the Jehol Group. It consists mainly of volcanic deposits with subordinate sedimentary interbeddings that are rich in fossils. As a result of strong tectonic and volcanic activities the strata of Yixian Formation occur in many small depositional basins and may be further discontinued within the basins by faulting (Fig. 1 in Wang et al. 2000a). Correlations from basin to basin or from locality to locality are therefore not always straightforward. The Dawangzhangzi Village is situated in the Lingyuan-Sanshijiazi Basin in the westernmost part of Liaoning, and the sedimentary sequence here consists of lacustrine sediments of shales and tuffs (Wang et al. 2000b). Wang and co-workers (2000b) designated the Dawangzhangzi Bed to the middle part of the Yixian
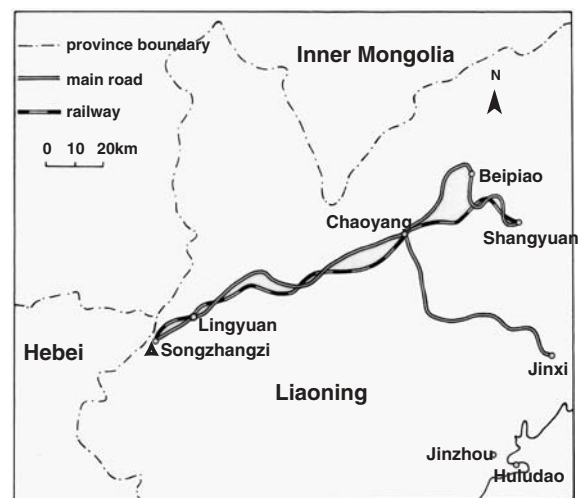

Fig. 1. Map showing the fossil locality (black triangle) in western Liaoning, close to the boundary between Hebei Province and Liaoning Province

Formation between the basal Jianshangou Bed and the upper Jingangshan Bed recognized in Beipiao County (Beipiao-Chaoyang Basin) about 125 km (direct line) northeast of Dawangzhangzi (Fig. 1), while Ren et al. (1995) and Sun et al. (2001) considered the Dawangzhangzi Bed as a lateral equivalent to the basal Jianshangou Bed.

Currently there is no consensus regarding the age of the Yixian Formation. Based on different chronological approaches the deposits have been assigned to the Late Jurassic, the Late Jurassic-Early Cretaceous, or the Early Cretaceous (see discussion in Barrett 2000). Recent assignment to a middle or late Early Cretaceous age has been supported by radiometric dating of volcanic tuffs sampled from the Beipiao-Chaoyang Basin using ^{40}Ar/^{39}Ar analyses of sanidine and biotite (Swisher III et al. 2002, Swisher III et al. 1999) as well as U-Pb analyses of zircon (Wang et al. 2001). According to these analyses the age estimates are about 139 Ma for the upper part of the Tuchengzi Formation (underlying the Yixian Formation) and about 125 Ma for the Jianshangou Bed (Swisher III et al. 2002). A mid-Early Cretaceous age is also supported by radiometric dating obtained from tuffs in the Lingyuan area that gave an estimated age of about 122 Ma for the Dawangzhangzi Bed (Smith et al. 1995, Wang et al. 2000b). If these age estimates are correct the fossil plant studied here from the Dawangzhangzi Bed is of Aptian (if stratigraphic position above the Jianshangou Bed) or Barremian (if equal to Jianshangou Bed) using the timescale of Harland et al. (1989), or Barremian using the International Stratigraphic Chart (Remane 2000).

The fossil plant is preserved as compressed part and counterpart on a slab of light grey to yellowish finely laminated siltstone. Organic material is partly preserved but strongly compressed and affected by post-depositional pyritisation. The pyrite was formed as microcrystallines and framboids precipitated on and within most part of the plant tissue (Leng and Yang 2003).

Gross morphology of the fossil material was observed under a dissecting microscope. Further morphological and anatomical details were studied using a Hitachi S-4300 Field Emission Scanning Electron Microscope. Small pieces of organic remains from different parts of the fossil were removed by fine tools and isolated pieces were mounted directly on aluminium stubs using nail-polish, or they were cleaned chemically in hydrofluoric and hydrochloric acid and rinsed in water before mounting. No essential difference was observed from these two treatments. The mounted stubs were sputter-coated with gold and studied with the Scanning Electron Microscope (SEM).

The type specimen B0162 (part and counterpart) and SEM stubs with pieces from the specimen are deposited in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences (Beijing).

Systematic description

Class: Angiospermae
Order and Family: Incertae sedis
Genus: *Sinocarpus* Leng et Friis gen. nov.

Derivation of generic name – from the country (Sino-, referring to China) where the fossil was collected, and fruit (-carpus, Greek).

Generic diagnosis. Infructescence with a main axis bearing one terminal fruit and pairs of lateral fruits in a decussate arrangement. Main axis slender with dilated nodes and long internodes. Pedicels of lateral fruits slender and long. Receptacle convex. Nature of perianth unclear due to incomplete preservation. Androecium not observed. Gynoecium superior and basally syncarpous, composed of 3 or 4 carpels in a whorled arrangement and united for about half their length. Each carpel containing about 10 anatropous ovules/seeds borne along linear placentae. Seeds flattened and embedded in a thick amorphous material. Surface cells of the seeds in the hilar and raphal regions rectangular, with protruding anticlinal walls and concave periclinal walls.

Type species. *Sinocarpus decussatus* Leng et Friis gen. et sp. nov.

Sinocarpus decussatus Leng et Friis sp. nov.
(Figs. 2–22)

Derivation of specific name – from the decussate arrangement of the fruits.

Specific diagnosis – as for the genus *Sinocarpus*.

Holotype – B0162.

Type locality – Dawangzhangzi Village, Songzhangzi Town, Lingyuan County, Chaoyang District, Liaoning Province, the People's Republic of China.

Type stratum – Dawangzhangzi Bed, middle Yixian Formation (Wang et al. 1998, Wang et al. 2000b) or lower Yixian Formation (Ren et al. 1995; Sun et al. 2001).

Age – Early Cretaceous (Barremian or Aptian), about 125 or 122 Ma.

Occurrence – Known only from the type locality.

Lithology – Light grey to yellowish finely laminated siltstone.

Description and remarks: The fossil is preserved on the part (B0162A) and counterpart (B0162B) of a single rock sample and consists of an infructescence fragment with several fruits attached to the axis as well as two isolated fruits that are probably
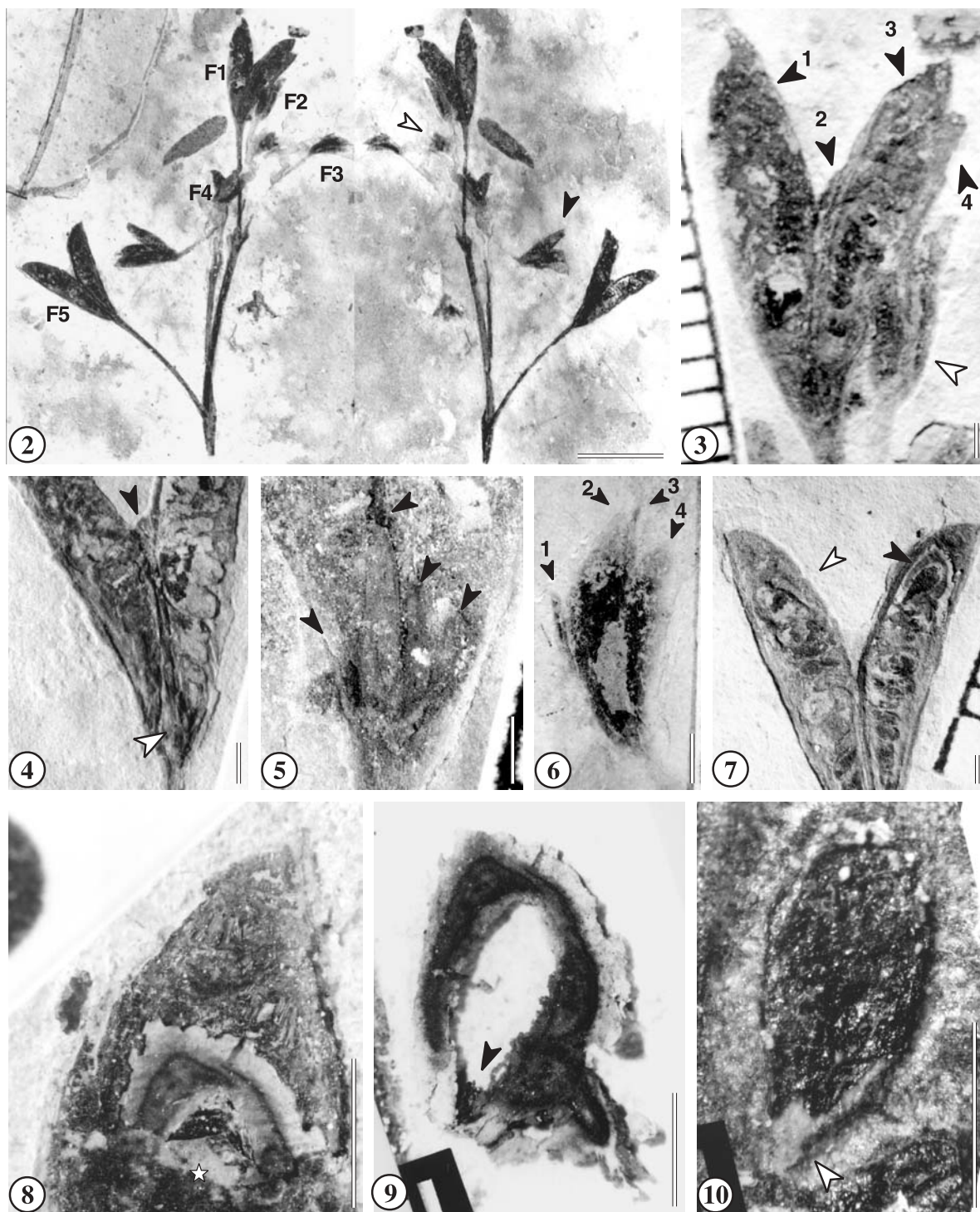
detached from the same plant as the larger specimen (Fig. 2). The infructescence is preserved as a compression fossil with morphological features well preserved. The original tissues are, however, strongly pyritised leaving only sparse information on cell structures and anatomy of fruit and seed walls (Leng and Yang 2003).

The infructescence fragment is either the terminal part of a simple infructescence, the terminal part of a compound infructescence, or the terminal part of a partial infructescence of a compound structure. It consists of a terminal fruit and two decussate pairs of fruits with long pedicels (Fig. 2). For convenience, the terminal fruit is numbered as "F1", whereas the upper pair is labelled as "F2" and "F3", and the lower pair "F4" and "F5" respectively (Fig. 2).

The main axis is slender, about 1 mm wide, with distinctly dilated nodes. The basal node is about 1.6 mm in diameter, the upper 1.3 mm. The only completely preserved internode is about 21 mm long. The pedicels of the fruits are slender, 0.4–0.5 mm wide, and 12–15 mm long. No bracts or scars from bracts have been observed, and the excellent preservation of the axis indicates that bracts were probably not present and the inflorescence was ebracteate.

The plant was fossilised in the fruiting stage and the organisation and structure of floral organs other than carpels is unknown. However, the terminal fruit ("F1"), which is less mature than the lower pair of the lateral fruits ("F4" and "F5") but more mature and better preserved than the upper pair ("F2" and "F3") has remnants of three or four structures of unequal size at the base of the ovary that may be remnants of a perianth (Figs. 5, 23), but the nature of these structures is uncertain.

No stamens or scars from stamens have been observed and it is unknown whether the flowers were originally unisexual or bisexual.

The gynoecium is superior, formed from three or four carpels borne in a whorl on a convex receptacle (Fig. 4). In several of the fruits three carpels are clearly visible (Fig. 2, black arrowhead), and in two of the fruits remnants that probably represent a forth carpel are also observed (Figs. 3, 6, numbered arrowheads). The decussate phyllotaxis of the infructescence suggests that the number of carpels was four for all fruits, but due to the strongly compressed nature of the fossil with carpels overlapping each other this cannot be established with certainty. Carpels are closely adherent basally for about half or less of their length (Figs. 4, 7). Due to the compressed nature of the fossil it is not possible to establish with certainty whether the carpels are free, but closely pressed together or truly fused. However, the shape of the carpels and the slightly thickened carpellary tissue along the contact area indicate that the carpels are fused, with a syncarpous region restricted to a narrow zone along the ventral side.

No trace of a stigma has been found. However, the morphology of the carpels, especially as

◄──

Figs. 2–10. *Sinocarpus decussatus* gen. et sp. nov. (Holotype). Scale bar = 1 mm except in Fig. 2 where it is 1 cm. **Fig. 2.** Part (B0162A, left) and counterpart (B0162B, right) of the specimen. "F1"–"F5" are the terminal fruit and two pairs of lateral fruits of the infructescence. White and black arrowheads indicate two detached fruits. **Fig. 3.** "F1" (larger) and "F2" (white arrowhead) (B0162A). Numbers together with their accompanying black arrowheads indicate four carpels of "F1". **Fig. 4.** United part of "F5" (B0162B), showing two carpels united basally. Black arrowhead indicates the remnant of the third carpel; white arrowhead indicates the inflated and elongated receptacle exposed by the probable removal of a fourth carpel. **Fig. 5.** Enlarged base of "F1" (B0162B), showing remnants of three (or four, left arrowhead) perianth like structures. **Fig. 6.** "F3" (B0162A), numbers together with their accompanying black arrowheads indicate four carpels of "F3". **Fig. 7.** Part of "F5" (B0162A), showing the apical free part and basal united part of the carpels and the ovules/seeds inserted along the linear placentae. White arrowhead indicates the possible decurrent stigmatic area along the free part of the ventral suture. Black arrowhead indicates an exposed seed surrounded by amorphous material (circular). Fruit wall (enlarged in Fig. 8) is removed for SEM observation (see Fig. 11). **Fig. 8.** Enlargement of Fig. 7 before the removal of the fruit wall (star). **Fig. 9.** Amorphous infilling removed for SEM observation (see Fig. 12). Arrowhead indicates the hilar region of the seed. **Fig. 10.** Seed exposed by the removal of fruit wall and amorphous tissue, with its hilar region removed for SEM observation (white arrowhead, see black arrowhead in Fig. 9)
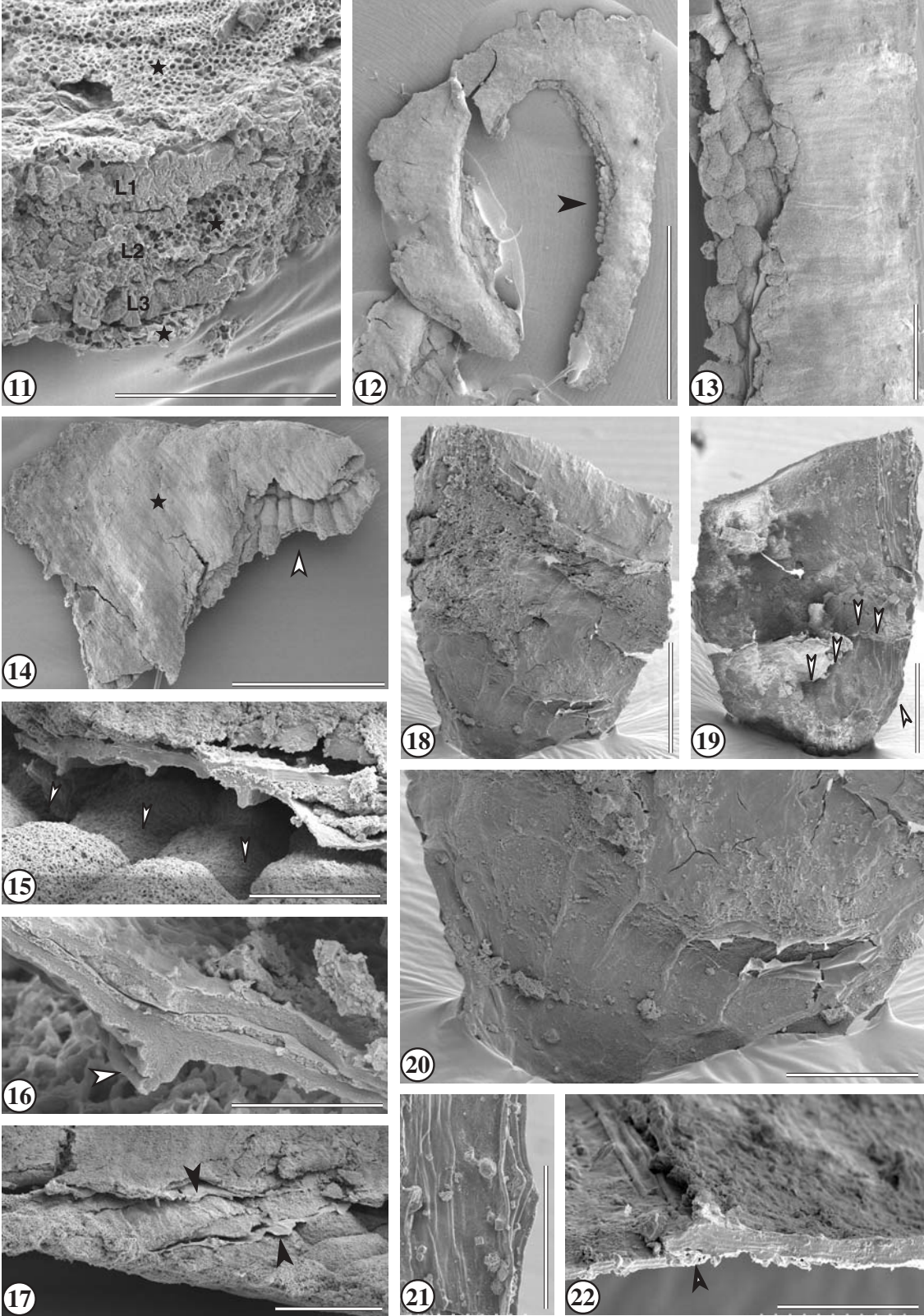
observed in less mature ones indicates that the stigma was probably decurrent along the free part of the ventral suture of the carpel (Fig. 7).

The mature carpels are elongate elliptic (slightly asymmetric), with mucronate apices, up to 12.5 mm long and 3 mm wide, each containing about 10 ovules/seeds borne along the linear placentae (Figs. 3, 4, 7, 23).

No shrinkage due to dehydration during the fossilisation has been observed, which apparently implies that the fruits were originally dry. None of the fruits has dehisced and there is no indication of dehiscence lines. Fragments of the fruit wall (pericarp, Fig. 8) observed under SEM show that the wall is composed of an outer, a middle, and an inner layer (Fig. 11). The locules are filled by an amorphous material that separates the seeds from each other. The original organic substance of this material is completely replaced by pyrite and there is no cell structure preserved (Figs. 12–15. For details see Leng and Yang 2003). An oblique dense striation on the outer surface of this locule infilling (Figs. 12–14) is imprinted from the fruit wall, probably from elongated sclerenchyma cells of the inner epidermis of the fruit wall.

Seeds are densely packed in the carpels with their margins sometimes overlapping but the seeds are separated from each other and from the fruit wall by the amorphous infilling (Fig. 17). The seeds are up to about 2 mm long and 1 mm wide, laterally flattened and ovate with slightly asymmetric outline, slightly pointed hilar region and rounded antihilar region (Figs. 7, 10). The shape of the seeds strongly suggests that they are anatropous with the micropyle adjacent to the hilum and the chalaza in the rounded antihilar position. Details of the seed wall are poorly preserved and distinct surface cell outlines were only observed in the hilar region and on the raphe. They sometimes leave distinct imprints on the surrounding amorphous material (Figs. 12–15). These surface cells are rather large, with protruding, straight to slightly sinuous anticlinal walls and slightly concave periclinal walls (Figs. 13, 14, 16, 18, 20). Cells in the hilar region are about 49–78 μm x 24–45 μm, more or less rectangular in outline (Figs. 14, 18, 20); while cells on the raphe are irregular in shape with an average size of about 44 μm × 35 μm (Fig. 13). Other areas of the seed sometimes show indistinct longitudinal protruding flanges that perhaps imply the presence of elongate epidermal cells (Fig. 19). At the seed margin (antiraphal side) the flanges are very densely aligned (Figs. 19, 21). In cross sections of the seeds several layers have been observed, varying from two to many in different positions (Figs. 16, 22), but the detailed anatomy of the seed is not preserved.

Figs. 11–22. SEM micrographs of *Sinocarpus decussatus* gen. et sp. nov. (Holotype). **Fig. 11.** Cross section of a piece of fruit wall. "L1", "L2", "L3" indicate three layers of the wall. Pyrite microcrystallines (star) are deposited on the surface and within the wall (The crystals were dissolved with only the frame left). Scale bar = 30 μm. **Fig. 12.** Amorphous material surrounding a seed (see Fig. 9). Arrowhead indicates the area enlarged in Fig. 13. Scale bar = 1.2 mm. **Fig. 13.** Close up view, showing distinct cell imprints left on the amorphous material by the seed raphe (left), and the imprint of the striation of the internal surface of the fruit wall (right). Scale bar = 120 μm. **Fig. 14.** Amorphous material. Star indicates the imprint of the striation of the internal surface of the fruit wall. Arrowhead shows the area enlarged in Figs. 15–16, where the hilar region of the seed is embedded. Cell outlines in the hilar region left strong imprints. Scale bar = 300 μm. **Fig. 15.** Cross view of the seed at the hilar region, showing the surface cell structure and their imprints left on the amorphous material (arrowheads). Scale bar = 30 μm. **Fig. 16.** An enlarged cross view of the anticlinal cell wall (arrowhead), also showing the layers of the seed. Scale bar = 6 μm. **Fig. 17.** Cross view of the margins of two seeds (arrowheads) overlapped but separated by amorphous material. Scale bar = 60 μm. **Fig. 18.** Part of seed, showing cell structures in the hilar region (lower part of the sample, enlarged in Fig. 20). Scale bar = 120 μm. **Fig. 19.** Back side of Fig. 18, showing sparsely aligned longitudinal flanges (arrowheads) on the main body and densely aligned flanges at the antiraphal margin (right). Scale bar = 120 μm. **Fig. 20.** Enlargement of Fig. 18, showing cell structures in the hilar region. Scale bar = 60 μm. **Fig. 21.** Enlargement of Fig. 19, showing densely aligned longitudinal flanges at the antiraphal margin. Scale bar = 60 μm. **Fig. 22.** Cross section of a seed, showing different layers of the seed (arrowhead). Scale bar = 30 μm

Discussion

Systematic position of *Sinocarpus*. The general features of the fossil plant described here are shown in a schematic drawing (Fig. 23). Although only fragmentarily preserved, characters of the infructescence together with the basally united carpels, the whorled arrangement of the carpels, and the arrangement of the ovules/seeds along linear placentae, firmly place this ancient plant within the angiosperms. The decussate branching of the inflorescence and the possibly tetramerous flower further provide evidence for a systematic position among the dicotyledonous angiosperms. In monocots decussately arranged flowers with long pedicels are not reported.

The decussate phyllotaxis of *Sinocarpus* together with the possible syncarpous gynoecium and also the apparently fixed number of carpels indicate that the fossil should be placed among the eudicots. Although many families among magnoliid dicotyledons contain taxa with decussate phyllotaxis, e.g. Chloranthaceae and Calycanthaceae, they all differ from *Sinocarpus* in having either unicarpellate or multicarpellate, apocarpous gynoecia and carpels containing only a single or few ovules. The incomplete fusion of the carpels in *Sinocarpus* with only the basal part of carpels fused, the superior ovary, the three or four carpels, and the possible long decurrent stigmatic region further indicate that this fossil does not belong to the advanced eudicots, but rather represents a basal lineage. Comparison with modern angiosperms shows that features comparable to those of *Sinocarpus* occur dispersed among members of early-diverging eudicots and basal core eudicots.

Of particular interest for discussing the systematic position of *Sinocarpus* is the family Myrothamnaceae. The family comprises a single genus, *Myrothamnus*, with two species of small xerophytic shrubs distributed in dry, tropical parts of southern Africa and Madagascar (Kubitzki 1993). Flowers in *Myrothamnus* are unisexual without remnants of the other sex. *Myrothamnus* is similar to *Sinocarpus* in its decussate phyllotaxis and in most features of the gynoecium. Its pistillate flowers have a superior ovary composed of three or four carpels that are syncarpous at the base and apically free. The free parts of the carpels have a ventrally decurrent and crested stigma and the syncarpous region is restricted to a narrow zone along the ventral side. Placentation is linear and each carpel includes about 10–50 ovules/seeds. Seeds are small, simple and anatropous with reticulate testa (Endress and Igersheim 1999, Jäger-Zürn 1966, Takhtajan 1969). Another feature that may be homologous in *Myrothamnus* and *Sinocarpus* is the separation of the ovules/seed in the carpels by an infilling of the locules. In *Myrothamnus* this infilling is by a secretion (Endress and Igersheim 1999). For *Sinocarpus* the origin of the infilling is unknown. It may resemble the seed cushion of some legumes formed from parenchymatic carpellary tissue (Reeve and Brown 1968a, 1968b), but its amorphous structure and spongy appearance perhaps more likely indicate that it was originally a secretion similar to that of extant *Myrothamnus* rather than a tissue. However, the preservation of the fossil does not allow a more detailed analysis of this structure.

Despite the above similarities, *Sinocarpus* differs from *Myrothamnus* in some features impeding an inclusion of the fossil into this modern family. In *Myrothamnus* ovules/seeds do not occur above the syncarpous zone and the free parts of the carpels are expressed as a style. In contrast, in *Sinocarpus* seeds occur from base to apex in the carpels. In *Myrothamnus* flowers are sessile and aggregated in dense spikes while in *Sinocarpus* the inflorescence/infructescence is loose and the flowers are pedicellate.

Myrothamnaceae are generally included in the core eudicots, but their systematic position therein is not fully resolved. Molecular analyses, however, indicate that the family, together with the Gunneraceae, should be placed as sister to all other core eudicots (e.g. APG II 2003, Soltis et al. 2003, Soltis et al. 2000). Apart from Myrothamnaceae, several extant families among the basal grade of eudicots show also similarities with *Sinocarpus*; among

Fig. 23. Schematic reconstruction of the type specimen

them Buxaceae and Ranunculaceae deserve more attention.

Buxaceae resemble *Sinocarpus* in having decussate phyllotaxis and a superior gynoecium that is syncarpous at the base (von Balthazar and Endress 2002). Its long decurrent stigma is probably also possessed by *Sinocarpus*. Members of the Buxaceae differ, however, from *Sinocarpus* in having 2–3 carpels, each carpel always with 2 ovules (Endress and Igersheim 1999, von Balthazar and Endress 2002). In extant Buxaceae the carpels are typically fused for half of their length or more, while the mid-Cretaceous fossil *Spanomera* (Drinnan et al. 1991) described as a putative buxaceous plant shows carpels that are very similar to *Sinocarpus* with the basal part of the carpels fused and a considerably free apical part. This fossil, however, differs from *Sinocarpus* in being bicarpellate and also in having a substantially different inflorescence structure.

Many of the features in *Sinocarpus* also occur in extant members of the Ranunculaceae, but the characters observed in *Sinocarpus* are scattered within this family and no single taxon of Ranunculaceae combines the characters known for *Sinocarpus*, and thus a close affinity of the fossil to Ranunculaceae cannot be established based on the information available. Multiovular and connate carpels with ovules borne along linear placentae occur in the subfamilies Helleboroideae and Isopyroideae including such genera as *Aquilegia* L., *Garidella* L., *Helleborus* L., and *Nigella* L. (Rohweder 1967, Tamura 1995) Decussate phyllotaxis is present in *Clematis* L. of the subfamily Ranunculoideae, but carpels in members of Ranunculoideae are uniovular (Rohweder 1967, Tamura 1995).

Significance of *Sinocarpus*. Terrestrial deposits of Early Cretaceous age are widespread in China (Li 1995, Sze et al. 1963) but only a few megafossils of angiosperm reproductive organs have been reported from these strata (e.g. Sun and Dilcher 1997, Tao and Zhang 1992), and their contribution to the understanding of angiosperm evolution is limited. The new discovery from the Yixian Formation of an angiosperm with relatively advanced features shows that angiosperms in East Asia had already attained some diversity at this time, and also indicates that eudicots were established in Asia by the mid-Early Cretaceous. Although *Sinocarpus* cannot be included with certainty in any existing family its character combination strongly indicates a systematic placement among the basal grade of eudicots or perhaps the basal core eudicots. The presence of eudicots in Asia at this time is in line with information from Europe, Africa, and North America where the first radiation of eudicot angiosperms was initiated around the Barremian-Aptian border (Crane and Lidgard 1990, Crane et al. 1995, Hughes and McDougall 1990).

Sinocarpus is significant in showing a gynoecium of basally united carpels, which probably did not have a compitum. Syncarpy is very rare among other early angiosperm

structures described from Europe and from North and South America. From the Crato Formation of Aptian or Albian age one syncarpous fruiting structure was reported (Mohr and Friis 2000) and from the Barremian or Aptian floras of Portugal where more than 100 different angiosperm reproductive organs have been observed the vast majority has gynoecia with free carpels and only a few possible syncarpous forms were discovered (Friis et al. 1999). It is also interesting that the carpels have considerably free apical part which are follicle-like and the fruits may have originated by the fusion of three or four follicles. *Sinocarpus* thus appear to combine some advanced features (for the early Cretaceous) with more basal features.

References

APG II (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Barrett P. M. (2000) Evolutionary consequences of dating the Yixian Formation. TREE 15: 99–103.

Cao Z.-Y. (2001) Occurrence of *Ruffordia* and *Nageiopsis* from the Early Cretaceous Yixian Formation of western Liaoning and its stratigraphic significance. Acta Palaeontol. Sin. 40: 214–218.

Cao Z.-Y., Wu S.-Q., Zhang P.-A., Li J.-R. (1998) Discovery of fossil monocotyledons from Yixian Formation, western Liaoning. Chin. Sci. Bull. (English Version) 43: 230–233.

Chang M.-M. (ed.) (2001) Jehol Biota. Shanghai Science & Technology Press, Shanghai.

Chen P.-J., Jin F. (eds.) (1999) Jehol Biota. Press of University of Science and Technology of China, Hefei.

Chen P.-J., Wen S.-X., Zhou Z.-Y., Li B.-X., Lin Q.-B., Zhang L.-J., Li W.-B., Liu Z.-S., Li Z.-P. (1980) Studies on the Late Mesozoic continental formation of western Liaoning. Bull. Nanjing Inst. Geol. Palaeont., Acad. Sin. 1: 22–55.

Crane P. R., Friis E. M., Pedersen K. R. (1995) The origin and early diversification of angiosperms. Nature 374: 27–33.

Crane P. R., Lidgard S. (1990) Angiosperm radiation and patterns of Cretaceous palynological diversity. In: Taylor P. D., Larwood G. P. (eds.) Major evolutionary radiations. Systematics Association Special Volume No. 42. Clarendon Press, Oxford, pp. 377–407.

Ding Q.-H. (2000) Research on fossil wood from the Yixian Formation in western Liaoning Province, China. Acta Palaeontol. Sin. 29 (Suppl.): 209–219.

Drinnan A. N., Crane P. R., Friis E. M., Pedersen K. R. (1991) Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. Amer. J. Bot. 78: 153–176.

Duan S.-Y. (1998) The oldest angiosperm – a tricarpous female reproductive fossil from western Liaoning Province, NE China. Science in China (Series D, English Version) 41: 14–20.

Endress P. K., Igersheim A. (1999) Gynoecium diversity and systematics of the basal eudicots. Bot. J. Linn. Soc. 130: 305–393.

Friis E. M., Doyle J. A., Endress P. K., Leng Q. (2003) *Archaefructus* – angiosperm precursor or specialized early angiosperm? Trends in Plant Science 8(8): 369–373.

Friis E. M., Pedersen K. R., Crane P. R. (1999) Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. Ann. Missouri Bot. Gard. 86: 259–296.

Friis E. M., Pedersen K. R., Crane P. R. (2000) Reproductive structure and organization of basal angiosperms from the Early Cretaceous

(Barremian or Aptian) of western Portugal. Int. J. Plant Sci. 161 (6 Suppl.): S169–S182.

Guo S.-X., Wu X.-W. (2000) *Ephedrites* from latest Jurassic Yixian Formation in western Liaoning, Northeast China. Acta Palaeontol. Sin. 39: 81–91.

Harland W. B., Armstrong R. L., Cox A. V., Craig L. E., Smith A. G., Smith D. G. (1989) A geological time scale. Cambridge University Press, Cambridge.

Hughes N. F., McDougall A. B. (1990) Barremian-Aptian angiospermid pollen records from southern England. Rev. Palaeobot. Palynol. 65: 145–151.

Jäger-Zürn I. (1966) Infloreszenz- und blütenmorphologische, sowie embryologische Untersuchungen an *Myrothamnus* Welw. Beitr. Biol. Pfl. 42: 241–271.

Kubitzki K. (1993) Myrothamnaceae. In: Kubitzki K., Rohwer J. G., Bittrich V. (eds.) The families and genera of vascular plant, II, flowering plants, dicotyledons, magnoliid, hamamelid and caryophyllid families. Springer, Berlin, pp. 468–469.

Leng Q., Yang H. (2003) Pyrite framboids associated with the Mesozoic Jehol Biota in northeastern China: Implications for microenvironment during early fossilization. Progr. Nat. Sci. 13: 206–212.

Li X.-X.(ed.) (1995) Fossil floras of China through the geological ages. Guangdong Science and Technology Press, Guangzhou.

Mohr B., Friis E. M. (2000) Early angiosperms from the Aptian Crato Formation (Brazil), a preliminary report. Int. J. Plant Sci. 161 (6 Suppl.): S155–S167.

Reeve R. M., Brown M. S. (1968a) Histological development of the green bean pod as related to culinary texture. 1. Early stages of pod development. J. Food Sci. 33: 321–326.

Reeve R. M., Brown M. S. (1968b) Histological development of the green bean pod as related to culinary texture. 2. Structure and composition at edible maturity. J. Food Sci. 33: 326–331.

Remane J. (2000) International stratigraphic chart. Division of Earth Sciences, UNESCO and International Union of Geological Sciences, Geneva.

Ren D., Lu L.-W., Guo Z.-G., Ji S.-A. (1995) Faunas and stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas. Earthquake Publishing House, Beijing.

Rohweder O. (1967) Karpellbau und Synkarpie bei Ranunculaceen. Ber. Schweiz Bot. Ges. 77: 376–432.

Smith P. E., Evensen N. M., York D., Chang M.-M., Jin F., Li J.-L., Cumbaa S., Russell D. A. (1995) Dates and rates in ancient lakes: (40)Ar-(39)Ar evidence for an Early Cretaceous age for the Jehol Group, northeast China. Can. J. Earth Sci. 32: 1426–1431.

Soltis D. E., Senters A. E., Zanis M. J., Kim S., Thompson J. D., Soltis P. S., Ronse Decraene L.-P., Endress P. K., Farris J. S. (2003) Gunnerales are sister to other core eudicots: implications for the evolution of pentamery. Amer. J. Bot. 90: 461–470.

Soltis D. E., Soltis P. S., Chase M. W., Mort M. E., Albach D. C., Zanis M., Savolainen V., Hahn W. H., Hoot S. B., Fay M. F., Axtell M., Swensen S. M., Prince L. M., Kress W. J., Nixon K. C., Farris J. S. (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Sun G., Dilcher D. L. (1997) Discovery of the oldest known angiosperm inflorescence in the world from Lower Cretaceous of Jixi, China. Acta Palaeontol. Sin. 36: 135–142.

Sun G., Dilcher D. L., Zheng S.-L., Zhou Z.-K. (1998) In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from Northeast China. Science 282: 1692–1695.

Sun G., Ji Q., Dilcher D. L., Zheng S.-L., Nixon K. C., Wang X.-F. (2002) Archaefructaceae, a new basal angiosperm family. Science 296: 899–904.

Sun G., Zheng S.-L., Dilcher D. L., Wang Y.-D., Mei S.-W. (2001) Early angiosperms and their associated plants from western Liaoning, China. Shanghai Scientific and Technological Education Publishing House, Shanghai.

Sun G., Zheng S.-L., Mei S.-W. (2000) Discovery of *Liaoningocladus* gen. nov. from the lower part of Yixian Formation (Upper Jurassic) in western Liaoning, China. Acta Palaeontol. Sin. 39 (Suppl.): 220–208.

Swisher III C. C., Wang X.-L., Zhou Z.-H., Wang Y.-Q., Jin F., Zhang J.-Y., Xu X., Wang Y. (2002) Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: New ^{40}Ar/^{39}Ar dating of the Yixian and Tuchengzi Formations. Chin. Sci. Bull. (English Version) 47: 135–138.

Swisher III C. C., Wang Y.-Q., Wang X.-L., Xu X., Wang Y. (1999) Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400: 58–61.

Sze H.-C., Li X.-X., Li P.-J., Zhou Z.-Y., Wu S.-Q., Ye M.-N., Shen G.-L. (eds.) (1963) Mesozoic plants from China. Fossil plants of China, 2. Science Press, Peking (Beijing).

Takhtajan A. (1969) Flowering plants, origin and dispersal. Oliver & Boyd, Edinburgh.

Tamura M. (1995) Ranunculaceae. Reproductive structures. In: Engler A., Prantl K. (eds.) Die natürlichen Pflanzenfamilien, Vol. 17a IV. Duncker & Humblot, Berlin, pp. 41–76.

Tao J.-R., Zhang C.-B. (1992) Two angiosperm reproductive organs from the Early Cretaceous of China. Acta Phytotax. Sin. 30: 423–426.

von Balthazar M., Endress P. K. (2002) Reproductive structures and systematics of Buxaceae. Bot. J. Linn. Soc. 140: 193–228.

Wang S.-S., Wang Y.-Q., Hu H.-G., Li H.-M. (2001) The existing time of Sihetun vertebrate in western Liaoning – evidence from U-Pb dating of zircon. Chin. Sci. Bull. (English Version) 46: 779–781.

Wang W.-T., Liou L., Wang S.-H., Chang M.-C., Ting C.-T., Ling P.-P., Fang M.-Y. (1980) Ranunculaceae (2). In Flora Reipublicae Popularis Sinicae, Tomus 28, Science Press, Beijing, pp. 1–390.

Wang X.-L., Wang Y.-Q., Wang Y., Xu X., Tang Z.-L., Zhang F.-C., Hu Y.-M., Gu G., Hao Z.-L. (1998) Stratigraphic sequence and vertebrate-bearing beds of the lower part of the Yixian Formation, in Sihetun and neighboring area, western Liaoning, China. Vertebrata PalAsiatica 36: 81–99.

Wang X.-L., Wang Y.-Q., Zhang F.-C., Zhang J.-Y., Zhou Z.-H., Jin F., Hu Y.-M., Gu G., Zhang H.-C. (2000a) Vertebrate biostratigraphy of the Lower Cretaceous Yixian Formation in Lingyuan, western Liaoning and its neighboring southern Nei Mongol (Inner Mongolia), China. Vertebrata PalAsiatica 38: 81–99.

Wang X.-L., Wang Y.-Q., Zhou Z.-H., Jin F., Zhang J.-Y., Zhang F.-C. (2000b) Vertebrate faunas and biostratigraphy of the Jehol Group in western Liaoning, China. Vertebrata PalAsiatica 38 (Suppl.): 40–63.

Wu S.-Q. (1999) A preliminary study of the Jehol Flora from western Liaoning. Palaeoworld 11: 7–57.

Yabe H., Endo S. (1935) *Potamogeton* remains from the Lower Cretaceous? *Lycoptera* bed of Jehol. Proc. Imp. Acad. Tokyo 11: 274–276.

Zhang W., Shang P. (1996) *Xenoxylon yixianense* sp. nov. from Lower Cretaceous of Yixian, western Liaoning, China. Palaeobotanist 45: 389–392.

Addresses of the authors: Qin Leng (e-mail: qin.leng@nigpas.ac.cn), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, The People's Republic of China. Else Marie Friis (e-mail: else.marie.friis@nrm.se), Department of Palaeobotany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.