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A New Permian Gnetalean Cone as Fossil Evidence for Supporting Current Molecular Phylogeny

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• *Background and aims* The order Gnetales has been the central focus of controversy in seed plant phylogeny. Traditional treatment of morphology supports the anthophyte hypothesis with Gnetales sister to angiosperms but current molecular data reject this hypothesis. A new fossil gnetalean cone, ***Palaeognetaleana auspicia*** **gen. et sp. nov.**, is reported from the Upper Permian in North China, and its phylogenic implications are considered.
• *Methods* Samples of cones from the upper part of the Upper Permian redbeds of Baode section, northwestern Shanxi Province, China, were examined.
• *Key results* The cone is characterized by its unusual nature of reproduction that combines features of post-Triassic gnetaleans and some of the Palaeozoic conifers. It is made up of a number of imbricate axillary units, each simply formed by an ovule and a subtending bract, which may be comparable with the axillary seed-scale complex of some of the Palaeozoic conifer cones. The cone exhibits at least a partially bisexual character that appears to have pollen sacs with monosulcate ribbed pollen grains and sessile, asymmetric, and radiospermic ovules. The ovule has an integument of three envelopes: an outer one of pointed scales; a middle sclerified one; and an inner cuticle that extends upward into a micropyle with an oblique tip.
• *Conclusions* The new Permian cone has unequivocal affinity with the Gnetales. The fossil has considerably extended the divergence time of the Gnetales from 140 (210?) back to 270 myr ago and, therefore, provides the first significant fossil evidence to support the current conclusion based on molecular data of seed plants, i.e. monophyletic gymnosperms, comprising the Gnetales are closely related to conifers.

Key words: *Palaeognetaleana auspicia* (gen. et sp. nov.), Gnetales, bisexual fossil cone, phylogeny of seed plants, radiation of gymnosperms, molecular data, Late Permian, North China.

INTRODUCTION

The Gnetales is a small group of seed plants that has generated diverse controversies on phylogeny over many years. The order has attracted much attention from traditional botanists (Arber and Parkin, 1908; Crane, 1996; Endress, 2001), palaeobotanists (Cornet, 1996; Doyle, 1996; Krassilov, 1997) and molecular systematists (Frohlich, 1999; Hansen *et al*., 1999; Winter *et al*., 1999; Chaw *et al*., 2000; Rydin *et al*., 2002), because of its potential significance for understanding the phylogeny of seed plants. In past literature, the Gnetales was widely considered to be the closest sister group to the angiosperms (Arber and Parkin, 1908; Crane, 1985) as being a central concept of the anthophyte hypothesis (Doyle and Donoghue, 1986). Around the late 1990s, almost all results from multiple gene sequences claimed the anthophyte hypothesis to be incorrect (Bowe *et al*., 2000; Chaw *et al*., 1997, 2000; Hansen *et al*., 1999; Qiu *et al*., 1999; Winter *et al*., 1999). Meanwhile, many authors also recognized that most estimates of when extant seed plants diverged, based on molecular data, showed conflict either with each other or with fossil evidence (Axsmith *et al*., 1998; Donogue and Doyle, 2000; Sanderson *et al*., 2000; Sanderson and Doyle, 2001; Soltis *et al*., 2002*b*). Our understanding of the relationship among the main seed plant groups would be put into perspective by more attention to fossil taxa (Soltis *et al*., 2002*a*).

A total of five or six gnetalean megafossil genera have been described but these provide only limited information, mainly due to poor preservation of the fossils (Crane, 1996). The timing of divergence of the Gnetales from other seed plants has generally been estimated as Triassic and Jurassic (Crane *et al*., 1995; Doyle, 1996; Krassilov, 1997). Earlier than this, there was no record on fossil gnetalean plants but similar palynomorphs were reported in the Permian deposits (Wilson, 1959; Osborn *et al*., 1993).

MATERIALS

During the 1990s, the author collected about 30 what were thought to be 'conifer' cones from the upper part of the Upper Permian redbeds of Baode section, northwestern Shanxi (Fig. 1). The plant-bearing bed is a small yellow-greyish sandy or silty lens, 10 m long and no thicker than 0.4 m. Other associated fossil plants are mostly characteristic of the Late Permian flora in north China such as *Lobatannularia ensifolia* (Halle) Halle., *L. heianensis* (Kodaira) Kawasaki, *Pecopteris hemitelioides* Brongniart, *Sphenopteris gothanii* Halle, *Emplectopteris triangularis* Halle, *Gigantonoclea crenata* Wang, *Ginkgophytopsis* sp.,

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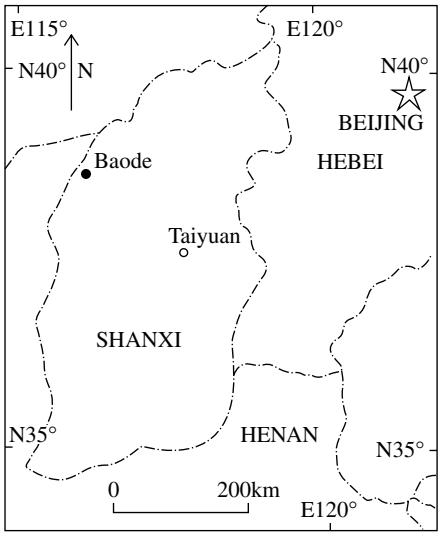

FIG. 1. Map of the fossil locality.

Psygmophyllum sp., *Nystroemia pectiniformis* Halle, *Chiropteris reniformis* Kawasaki, *Pterophyllum erratum* Gu et Zhi, *Taeniopteris densissima* Halle and *T. tingii* Halle, among others. The stratigraphical horizon of the fossil-bearing bed corresponds to the uppermost plant-assemblage zone of the Tianlongsi Formation (=Upper Shihhotze Fr.) near Taiyuan, central Shanxi (Halle, in Norin, 1924). The new cone species, because of its superficial resemblance to Palaeozoic and Mesozoic conifer cones, was initially misidentified as Podocarpaceae (Wang and Zhang, 1998). The cone specimens are mostly compressed or adpressed in preservation but their carbonized remains contain ribbed pollen (or pollen masses) typical of the Gnetales, ovules and fragments of bract. Over a half of the cones have been investigated and seven of them were treated by bulk maceration. All have produced residues on the basis of which a new Permian cone with gnetalean affinity has been described.

SYSTEMATICS

Order *Gnetales Engler 1892*

Genus **Palaeognetaleana *gen. nov***.

Diagnosis: Cone at least partially bisexual, consisting of simple axillary units in imbricate and helical arrangement, each comprising a subtending bract, an asymmetric ovule, a number of fibres or scales surrounding the ovule, and pollen sacs appearing to be concealed beneath the ovule. Ovule enclosed by integument of three envelopes: an outer scale one, a middle sclerified one and an inner cuticle one. Pollen grains exhibiting slightly twisted ribs with monosulcate aperture.

Type species. **Palaeognetaleana auspicia *gen. et sp. nov***.

Etymology: The generic name refers to a Palaeozoic gnetalean plant.

Horizon and location: Lower Upper Permian *Gigantonoclea*-dominant assemblage (f10) from the Baode section in northwestern Shanxi, China (Wang, 2000).

Species Palaeognetaleana auspicia *sp.nov. (Figs 2–6)*

Diagnosis: Cones at least partially bisexual, asymmetrically ellipsoidal or ovoid in shape, 35–60 mm long and 25–45 mm wide, closely arranged by imbricate axillary units. Each unit simple, consisting of a single ovule lying on a subtending bract, fibres or pointed scales surrounding the ovule, and pollen sacs seemingly concealed beneath the ovule. Ovules sessile, radiospermic more or less asymmetric in outline, rounded, ovoid or ellipsoidal in shape, 0·6–7 mm long and 2–5 mm in diameter. The integument of the ovule comprises three envelopes: an outer pointed scales (or fibre); a middle sclerified envelope; and an inner cuticle that extends upward into a micropyle with an oblique tip. Bract lanceolate or wing-like with bilaterally asymmetric margins, 15–25 mm long and 2–5 mm wide at base, having acute apex and expanded base with denticles or spines developing along its anterior margin. Megaspore walls tough and thick. Pubescence of the tapetal tissue occurring either in wall of the ovule or in that of the pollen sac. Pollen grain *Ephedripites*-type, 40–50 μm long with monosulcate aperture and more or less twisted ribs.

Description: Figures 2 and 3A show the elliptical or obovate cones in longitudinal outline. The cone consists of a number of axillary fertile units in imbricate helical arrangement, and is terminally borne on a short or long peduncle that probably extends from a thick primary axis (Fig. 3A, lower right). The axis is possibly prostrate, about 10 mm thick, covered with fine longitudinal striae but no leaves. Bracts, asymmetrically lanceolate, 15–25 mm long and 3–5 mm wide at expanding base where the dentate and spinate anterior margin develops (Fig. 3D, arrow b), accompanied by numerous delicate fibres (Fig. 3D, arrow a). Each bract bears an ovule adnate to its expanding base (Fig. 3C). Part of a degraded pollen sac with pubescence of the tapetum tissue is seen in Fig. 4A and an *in situ* ribbed pollen mass was extracted from the sac (Fig. 4B). Another pollen mass (Fig. 4C and D) shows details of pollen grains with monosulcate aperture. Figure 5A (upper left) exhibits a small ovule enclosed by an outer envelope made up of fine fibres, and a much larger ovule surrounded by pointed scales (lower right). Figure 5B is another ovule or seed showing the rough surface of the solid middle envelope which is exposed after detachment of the scales and fibres. An ovule after strong maceration exhibits an inner cuticular envelope that extends upwards into the prominent micropyle (Fig. 5C) and there is a rare relict of pubescent tapetum tissue at the base. A long but unbifid micropylar tube can be sometimes visible (Fig. 6A) and some micropyles show an askew tip (Fig. 6B). All the ovules are generally 1–5 mm in diameter, sessile and more or less asymmetric in outline.

Holotype: Specimen No. 9107–1 (Figs 2–3)

Etymology: Specific name prefers to this auspicious discovery of the so far earliest record of this group.

Specimen deposition: All specimens described here are deposited in Tianjin Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences.

Comparisons: For *Palaeognetaleana auspicia* gen. et sp. nov., the most impressive feature is its reproductive nature that combines gnetalean and conifer-like features.

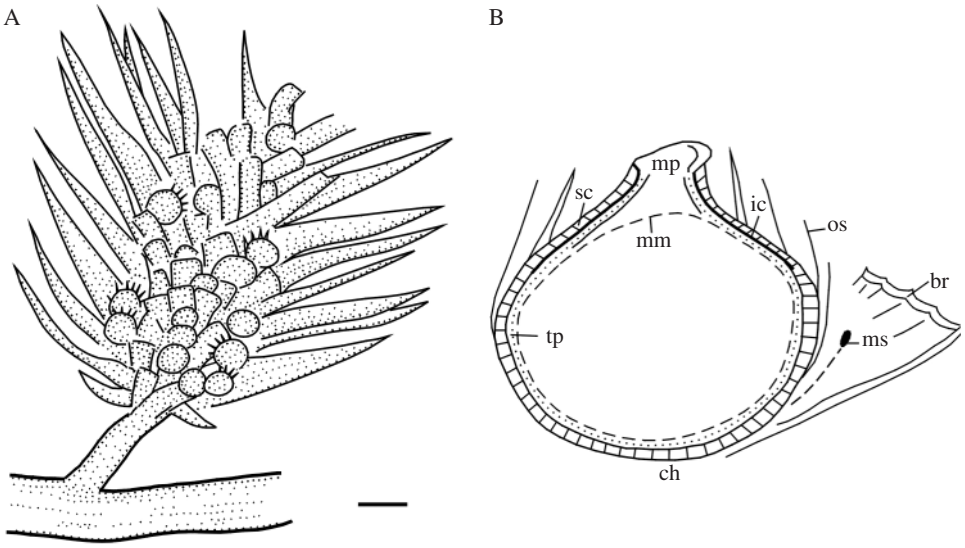

FIG. 2. Drawings of ***Palaeognetaleana auspicia*** **gen. and sp. nov.**: (A) reconstruction of a *Palaeognetaleana auspicia* cone (holotype); (B) diagram of an axillary unit, showing structures of ovular integument: mm (dashed line), megaspore membrane (see Fig. 6A); tp, tapetal tissue (see Fig. 6A); ic, cuticle of inner envelope (see Fig. 5C, only developing at micropyle end); sc, sclerotic envelope (see Fig. 5B); os, outer scales or fibres (see Fig. 5A); ms, a presumed pollen sac; br, bract; ch, chalazal end (see suture of the ovule in Fig. 5B).

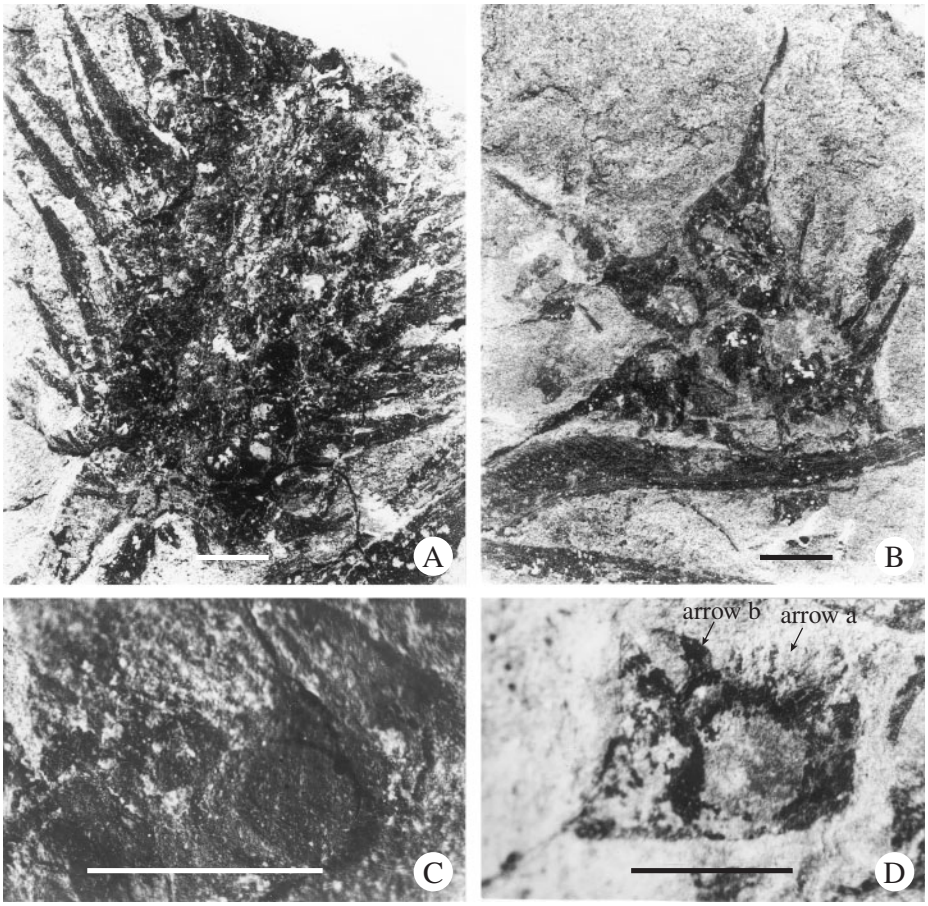

FIG. 3. ***Palaeognetaleana auspicia*** **gen. and sp. nov.** cone and its bracts. (A) A cone borne terminally on a short peduncle that possibly extends from the primary axis (lower right), showing attached rounded ovules near to the cone axis and dentate margin of the bract (lower left), 9107–1, ×2. (B) Some isolated bracts preserved in a transverse plan, each showing a long lateral ridge and an expansive base on which one ovule overlies, 9705–45, ×2. (C) Basal part of a bract showing one ovule lying on it, 9705–41, ×8. (D) An isolated bract showing the long lateral ridge of its margin and dentate anterior margin (arrow b) at expansive base. Note the ovule having become detached but having left delicate fibres (arrow a), 9805–048, ×5. All scale bars = 5 mm.

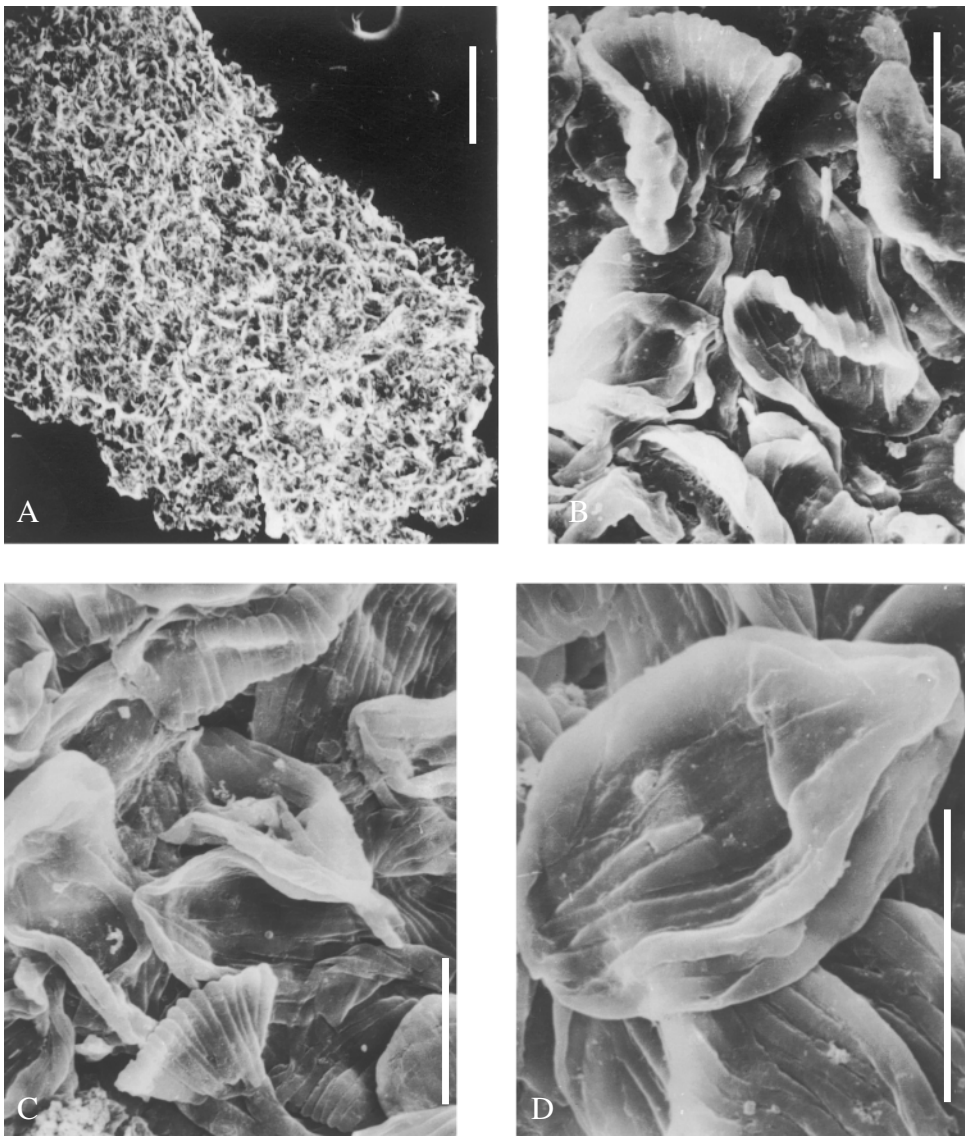

FIG. 4. Pollen sacs and *in situ* pollen grains. (A) Part of a degraded pollen sac enclosed by pubescence of tapetal tissue, 9705–37, ×42; scale bar = 240 μm. (B) Local magnification of A showing ribbed pollen mass, ×600. (C) Another pollen mass, 9705–39, ×600. (D) Showing an entire ribbed grain of C, ×1200. Scale bars in B and C = 25 μm.

In terms of current male theory (Frohlich and Parker, 2000), a critical feature for determining affinity of the *Palaeognetaleana* cone is the ribbed pollen with monosulcate aperture and slightly twisted ribs, which is so far known only from living *Welwitschia* of the Gnetales (Crane, 1996; Osborn, 2000). *Vitattina* polynomorph, which was partially attributed to some of the upper Permian peltasperms in Angara (Meyen, 1984), shows little superficial similarity to the ribbed grain of the Gnetales but is different from the latter in a faint area longitudinally across the distal surface of the pollen without sulcate aperture.

In the ovulate structure, on the other hand, a significant correlation for *Palaeognetaleana* with living Gnetales is the presence of a micropylar tube of ovule that has an askew tip (Endress, 1996). The three envelopes of the *Palaeognetaleana* integument also correspond to those of living Gnetales (Rodin and Kapil, 1969) or 'initiate (bitegmic) integument' interpreted by Endress (2001: 107). The sex distribution of the new gnetalean cone has been cautiously interpreted as at least partially bisexual because more than half the cones collected produce both ovulate and polleniferous organs. This is the main character of a clade referred to as anthophyte group (Crane *et al*., 1995; Doyle, 1996).

On the whole, there seems to be little doubt about the gnetalean affinity of the new fossil cone.

The most remarkable distinction of *Palaeognetaleana* from living Gnetales is the imbricate cone with upward and outward bracts extending in a helical arrangement. This is clearly different from the opposite-decussate arrangement of paired bracts in all extant Gnetales and most known fossil ones (Crane and Upchurch, 1987; Krassilov, 1997). Another critical feature in which the new cone

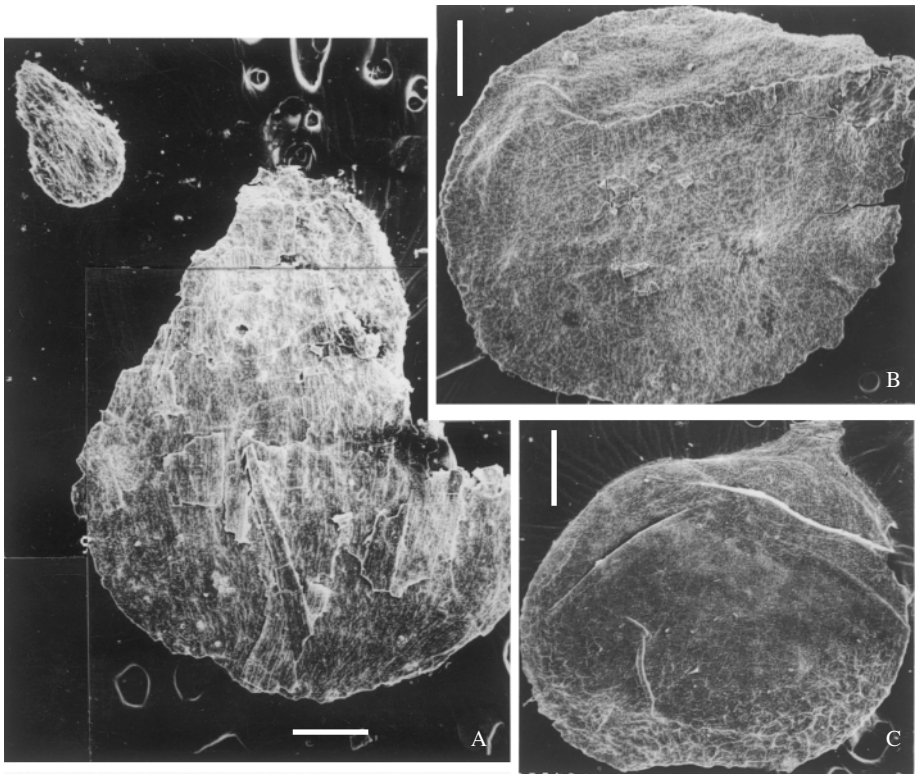

FIG. 5. Ovules without or with little maceration. (A) A small ovule (upper left) enclosed by fine fibres, and a large ovule (lower right) enclosed by narrow and pointed scales, both from same cone, 9805–045, ×20. (B) An ovule after incomplete maceration, showing the solid middle layer of the integument and a suture ridge, 9705–39a, ×20. (C) An ovule after complete maceration, exhibiting the thin cuticle of the inner integument that extends upwards into an asymmetric micropyle and rare remnants of fibres at the base, 9107–8 (counterpart of 9107–1), ×8. All scale bars = 0·5 mm.

differs from extant Gnetales is in its reproductive organization: the *Palaeognetaleana* cone has a number of axillary fertile units, each consisting of one subtending bract, one ovule plus pollen sacs that appear to be concealed beneath the ovule, and fibres or scales filling the gap between the two. This is much simpler than those reproductive organs of living Gnetales with a cone-like inflorescence that is organized by paired or decussate bracts (collar), each containing two or more ovuliferous organs plus pollen sacs (Endress, 1996). In these features, the *Palaeognetaleana* cone exhibits obvious similarities to those of some Palaeozoic conifers with an axillary dwarf-shoot system (Florin, 1951). This is an old issue argued by many authors who paid special attention to the anthophyte hypothesis (Crane, 1985; Doyle and Donogue, 1986, 1992; Taylor and Taylor, 1993; Rothwell and Serbert, 1994; Doyle, 1996, 1998). The wing-like bract and subtended ovule of the *Palaeognetaleana* cone could be correlated with the axillary fertile system borne in the axils of scales in most Paleozoic conifer female cones (Rothwell and Mapes, 2001), if considering those pointed scales surrounding the ovule as being homologous to the axillary dwarf shoot of the conifer. The dentate or spinate margin at the bract base may also be observed in some of the Palaeozoic conifers (Hernandez-Castillo *et al*., 2001). However, the specific ovule of *Palaeognetaleana* is characterized by its sessile base, radiospermic–asymmetric shape, and prominent but unbifid apex of the micropyle. These can all exclude the possibility for *Palaeognetaleana* to be attributed to Coniferophytes that have stalked, platyspermic and flattened, bilaterally symmetric ovules with a bifid micropyle at the apex such as that of the Permian *Otovicia hypnoides* (Brongniart) in West Europe (Kerp *et al*., 1990).

DISCUSSION

The *Palaeognetaleana* cone is important for its unusual nature that links it to the Palaeozoic conifers in some critical aspects, implying that a certain relationship between gnetaleans and conifers existed early in the Permian. This is congruent with current conclusion drawn by molecular analyses to extant main seed plants. Therefore, *Palaeognetaleana* provides the first fossil evidence to support the gnetaleans–conifers relationship of current molecular data.

Among those molecular analyses during 1999–2000, however, an agreed phylogenetic tree for seed plants has not yet been produced, except for one consistent point that the Gnetales is sister to conifers rather than to angiosperms, as previously thought (Donogue and Doyle, 2000). Nevertheless, through calibration to bias or error in age estimates by using molecular clock (Sanderson *et al*., 2000; Sanderson and Doyle, 2001) and analyses of more gene sets (Bowe *et al*., 2000; Soltis *et al*., 2002*b*), a congruent conclusion has been reached to the effect that extant gymnosperms are monophyletic and extant Gnetales are closely related to

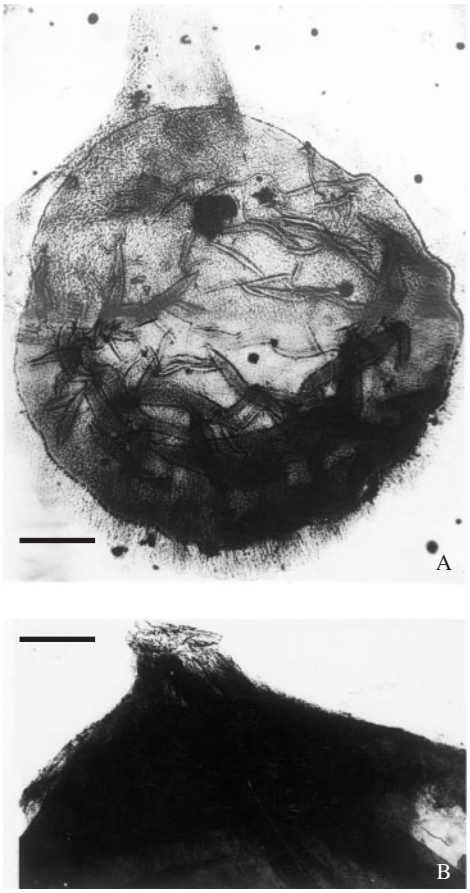

FIG. 6. Ovules through maceration: (A) an ovule showing a long, unbifid micropylar tube at apex, 9705–0; ×40; (B) upper part of an ovule showing a prominent micropyle with an oblique tip, 9107–8, ×40. Both scale bars = 0·25 mm.

conifers, although the precise relationship of the Gnetales to conifers is unclear (Soltis *et al*., 2002*a*).

The discovery of *Palaeognetaleana* is an important contribution to our understanding of the Permian radiation of gymnosperms. In macroevolution, the great radiation of the angiosperms in the Cretaceous has attracted much attention, as has the faunal radiation in the Cambrian (Stanley, 1990); but the Permian gymnosperm radiation has been the subject of less interest (DiMichele *et al*., 1987; Kerp *et al*., 2001). The radiation of gymnosperms in the Permian floras took place somewhat diachronously in the Northern Hemisphere, including the conifers (Kerp *et al*., 1990; Kerp, 1996; Rothwell and Mapes, 2001), ginkgophytes (Yao, 1989; DiMichele *et al*., 2001), cycads (Mamay, 1976; Zhu and Du, 1981; Wang, 2000) and peltasperms (Poort and Kerp, 1990; Wang and Zhang, 1998; Kerp *et al*., 2001).

The appearance of the Permian *Palaeognetaleana auspicia* (gen. et sp. nov.), so far the earliest known fossil record of the Gnetales, demonstrates that the divergent time of the group from other seed plants was in the Late Palaeozoic, much earlier than the previously known Late Triassic (Ash, 1972) or even Late Jurassic–Cretaceous (Hughes, 1994; Krassilov, 1997). It may represent an archetype of the crown lineage of Gnetales. It is now clear that all four extant gymnosperm orders (Cycadales, Ginkgoales, Coniferales and Gnetales) have their own ancestors, which roughly simultaneously appeared during the Late Paleozoic, and became dominant members of the Latest Permian and Mesozoic floras. This means that extant gymnosperms all have their own crown clades evolved early in the Permian (Soltis *et al*., 2002*b*), and therefore has satisfied a precondition for establishing monophyletic gymnosperms that could have diverged about 274·5 myr ago based on molecular data by using the calibration point approach (Soltis *et al*., 2002*b*). Recently, a significant magnetostratigraphic marker, the late Permian Illawarra Reversal, was identified in the typical Late Palaeozoic Section near Taiyuan, Shanxi (Embleton *et al*., 1996) and is delimited a little above the bottom of the Tianlongsi Formation spanning 268 myr or so in the geological timescale. This has ascertained the age of the Late Permian floras containing *Palaeognetaleana* in Shanxi to about 270–250 myr ago, which may be near to the divergent time of gymnosperms based on the molecular estimate (Soltis *et al*., 2002*b*), or about 300 myr ago based on the estimation from MADS-box genes (Becker *et al*., 2000).

It is notable that some of the current results of molecular data have not entirely ruled out the possibility of an anthophyte clade sister to angiosperms (Sanderson and Doyle, 2001; Rydin *et al*., 2002; Soltis *et al*., 2002*a*). This opens up the potential to look deep within the phylogeny of seed plants to examine the sources of other characters such as sex distribution (bisexual), seed structure and others.

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