A NEW GENUS OF GIGANTOPTERID FROM THE MIDDLE PERMIAN OF THE UNITED STATES AND CHINA AND ITS RELEVANCE TO THE GIGANTOPTERID CONCEPT

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The gigantopterids are a poorly understood group of plants defined primarily on the basis of a particular type of reticulate leaf venation in combination with stratigraphic distribution. It is generally agreed that many, if not all, are seed plants. A new genus of gigantopterid, *Euparyphoselis* gen. nov., is described from foliage only, derived from the Middle Permian of the southwestern United States and eastern China. One species occurs in each area: *Euparyphoselis gibsonii* sp. nov. in the United States and *Euparyphoselis marginervum* (Yao and Liu) comb. nov. in China. The most significant characteristic of the new genus is a marginal vein. The foliage displays three and occasionally four orders of venation, with a variably distinct suture vein between second-order veins, formed by the fusion of tertiary veins from adjacent secondaries. The leaves are obovate in shape and unforked, tapering toward the base. Leaf margins are smooth or bluntly toothed with broad, shallow sinuses between the teeth. Secondary veins end or dissipate into the teeth, where present. Leaves are amphistomatic; stomatal complexes are haplocheilic and monocyclic. The two species differ mainly in the characteristics of the epidermal surfaces, including the shape and size of the epidermal and subsidiary cells, stomatal complexes, number of subsidiary cells, orientation of the stomatal complexes, and secretory structures. *Euparyphoselis marginervum* was originally described as a species of *Gigantopteridium*, with which it shares certain characteristics of venation. However, it clearly differs from *Gigantopteridium* in the details of venation and in leaf architecture. It is argued that leaf venation should not be given primacy over all other characteristics when assessing gigantopterid relationships and therefore as a basis for taxonomy. As previously suggested, the gigantopterids, as presently construed, may not be a monophyletic group.

Keywords: gigantopterid, Permian, *Gigantopteridium*, *Euparyphoselis*, cuticle.

Introduction

Investigation of Permian-age floras from the southwestern United States has revealed several assemblages of unusual taxonomic composition, hinting at the existence of major biomes rarely preserved in the terrestrial fossil record (DiMichele et al. 2000, 2001, 2004; Looy 2007). One of these floras, in particular, that from the Middle Permian South Ash Pasture locality in King County, Texas, is composed entirely of plants with uncertain affinities (DiMichele et al. 2004). One of those plants is a gigantopterid, an enigmatic group of probable seed plants with uncertain higher-order relationships (Mamay et al. 1988; Glasspool et al. 2004; DiMichele et al. 2005; Taylor et al. 2006), although a new taxonomic name was not assigned to the material at the time the original article was published. At about the same time as publication of the South Ash Pasture flora, an extremely similar leaf was described from the Middle Permian of China, under the name *Gigantopteridium marginervum* Yao and Liu (2004).

A detailed comparison of the South Ash Pasture gigantopterid and the material from China described as *G. marginervum* indicates many similarities between these two forms,

which are likely different species of the same genus. That genus is not *Gigantopteridium* Koidzumi (1936), despite some similarities, but rather a new genus, formally described herein. In each case, the leaves are characteristically unforked, with variably developed marginal teeth, three to four orders of venation, irregular suture veins, and a marginal vein, the latter a most unusual feature within the gigantopterids.

The connection between Permian floras from the southwestern United States and China has been a subject of discussion for many years, beginning with the initial discovery of gigantopterid plants in North America (White 1912). Detailed study of American gigantopterids has shown most of them to differ from the Chinese forms in a variety of ways, from the details of venation to gross leaf architecture. Although some points of morphological and taxonomic similarity remain (e.g., possible *Gigantonoclea* Koidzumi in both places; Mamay 1988; Li et al. 1994; Wang 1999), the concept of a coherent phylogenetic group remains in question (Mamay 1989; Glasspool et al. 2004). The new genus described herein bears resemblance to other North American gigantopterids with simple unforked leaves, such as *Evolsonia* Mamay (1989) and *Delnortea* Mamay, Miller, Rohr and Stein (1988), and its occurrence in both China and the southwestern United States supports previous suggestions of biogeographic links between these two widely separated areas.

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Location and Specimens

The American specimens that form the basis of this taxonomic revision come from King County, Texas, on the Bob Creek 7 1/2′ USGS Quadrangle map. The South Ash Pasture locality (see DiMichele et al. 2004) is located on the eastern shelf of the Midland Basin. The plant-bearing deposit is within the Blaine Formation and is likely of Middle Permian age. The age of these rocks is difficult to define with certainty because the sequence contains few marine invertebrate–fossil-

bearing rock units and the plant fossils themselves are not diagnostic of a particular time interval. On the basis of a suite of long-ranging marine macroinvertebrates, the deposit appears to be early Middle Permian (Guadalupian), close to the Early-Middle Permian boundary.

Plant fossils were found in a deposit of gray mudstone containing thin layers of dolomite throughout and siltstone at the base. The unit is enclosed by red mudstones that contain thin beds of gypsum, part of a thicker sequence of bedded gypsum, oolitic dolomite, and reddish mudstones, variously
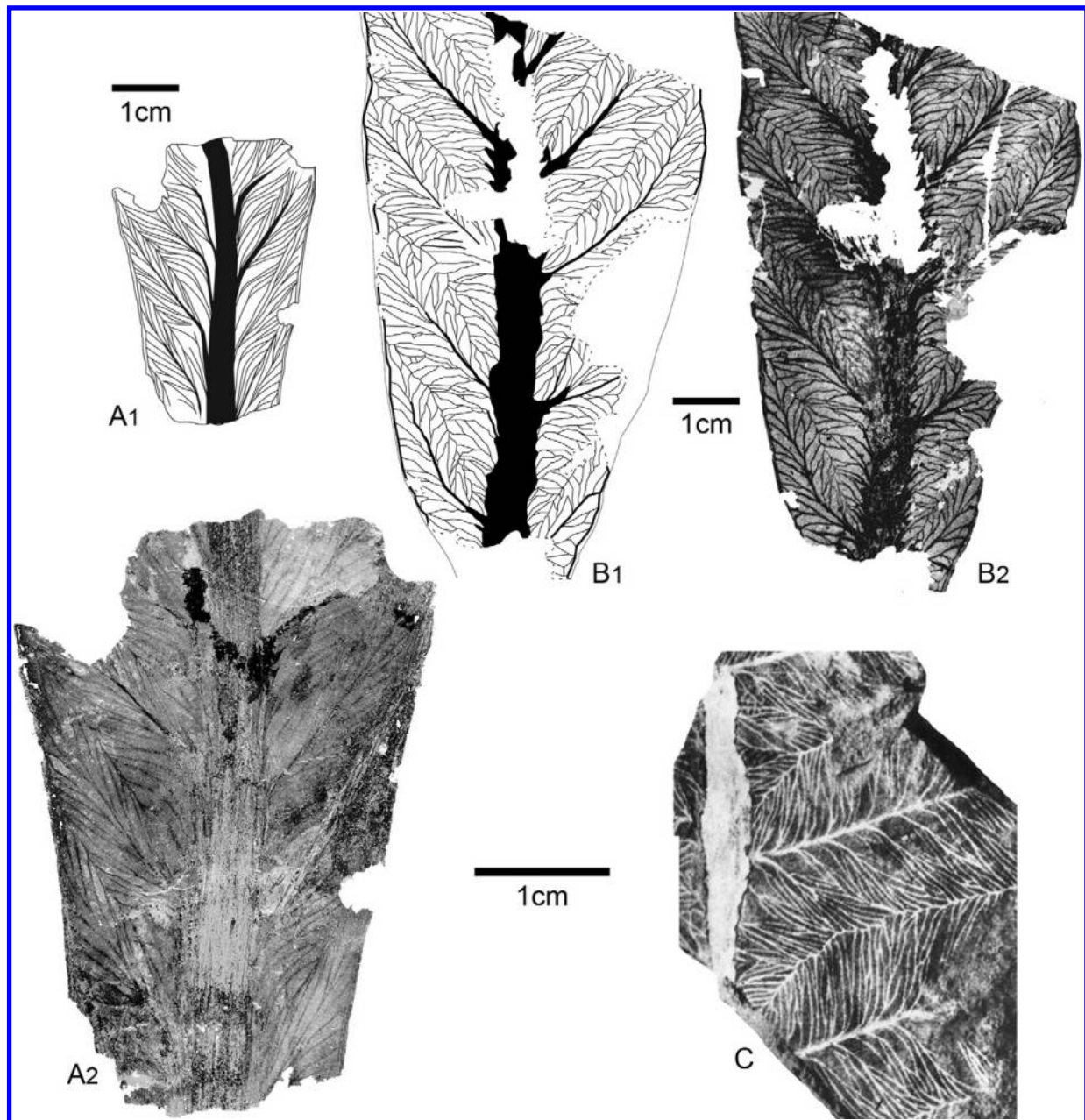
Fig. 1   Comparison of gigantopterids mentioned in this article. Scale bars = 1 cm. *A, Euparyphoselis gibsonii* n. gen. et sp., USNM 520383; holotype from loc. 41017, South Ash Pasture. *A1,* Line drawing of *A2* at ×1. *A2,* Photograph of holotype at ×2. *B, Euparyphoselis marginervum* (Yao et Liu) comb. nov. DiMichele et al.; paratype PB9157 (after Yao and Liu 2004). *B1,* Line drawing of *B2* at ×1. *B2,* Photograph of paratype ×1. *C,* Venation of *Gigantopteridium americanum* (White) ×2 (after White 1912, pl. 46, fig. 2).

pedogenically overprinted. A cross section through this deposit (fig. 3 of DiMichele et al. 2004) reveals an asymmetrical channel-form shape. The channel base lies in erosional contact with the surrounding lithologies and was likely cut into them, possibly as a tidal channel on a flat coastal plain. The mudstone and dolomite fill appears to have accumulated in standing or only sluggishly moving water, as if the channel had been abandoned. The flora is most likely parautochthonous and represents the plants that grew immediately around the margins of the water body.

The American specimens described herein reside in the Paleobotanical Collections of the U.S. National Museum of Natural History (NMNH). All specimens bear unique NMNH identification numbers. The gigantopterids were represented by approximately a dozen specimens; more than 600 specimens were collected from 12 separate 1-m^2 × 0.5-m-deep excavations in the fossiliferous deposit, the exposure of which was 76 m long and 18 m wide. The described fossil leaves are preserved as carbonaceous compressions. Cuticle was not preserved on the leaf surfaces; epidermal features could be observed in some parts of leaves, where surfaces were preserved as limonite petrifactions.

The Chinese material originally described as *Gigantopteridium marginervum* was collected in the Funiushan coal mine, which lies at the eastern extension of the Nanjing Hills (see fig. 1 of Yao and Liu 2004) in Jiangsu Province on the central eastern margin of China. They are from the uppermost beds of the Kuhfeng Formation, which is of mid-Middle Permian, latest Wordian age (see fig. 3 of Yao and Liu 2004). According to Yao and Liu (2004), the fossils occurred in a black mudstone at the top of the Kuhfeng Formation, which formed the transitional bed to the overlying Lungtan Formation.

Systematics

Genus—Euparyphoselis *DiMichele, Looy and Chaney, gen. nov.*

Type Species—Euparyphoselis gibsonii *DiMichele, Looy and Chaney, spec. nov. (Figs. 1–6)*

Genoholotype. USNM 520383 (fig. 1*A1*, 1*A2*).
Description. Gigantopterid (figs. 9–12 in DiMichele et al. 2001).

Generic diagnosis. Broad leaf with entire lamina (unforked, nonpinnate, nonpalmate), tapering at base, with bluntly rounded apex. Base not known. Leaf margin smooth, entire to toothed. Three orders of venation, on occasion four orders. Ultimate venation coarse, veins widespread. First-order vein (midvein) a vein bundle composed of many separate veins that diverge to form secondary veins. Secondary veins subopposite to alternate, end at leaf margin and in teeth. Tertiary veins herringbone in form, with limited lateral reticulation. Tertiary veins from adjacent secondaries variably fused, forming a suture vein between adjacent secondary veins; suture veins formed by fusion of fourth-order veins where present. Strength of suture vein variable. Suture vein base is at variable distance from midvein. Tertiary veins forming acute angle with secondary vein. Distinct marginal vein occasionally present, formed by a vascular bundle that arches between secondary veins, below leaf margin. Leaves amphistomatic. Stomata distributed irregularly between veins, sparse to absent above veins. Stomatal complexes haplocheilic and monocyclic, round to elliptical in shape, with two to seven subsidiary cells. Epidermal cells square to polygonal between veins and elongated above veins.
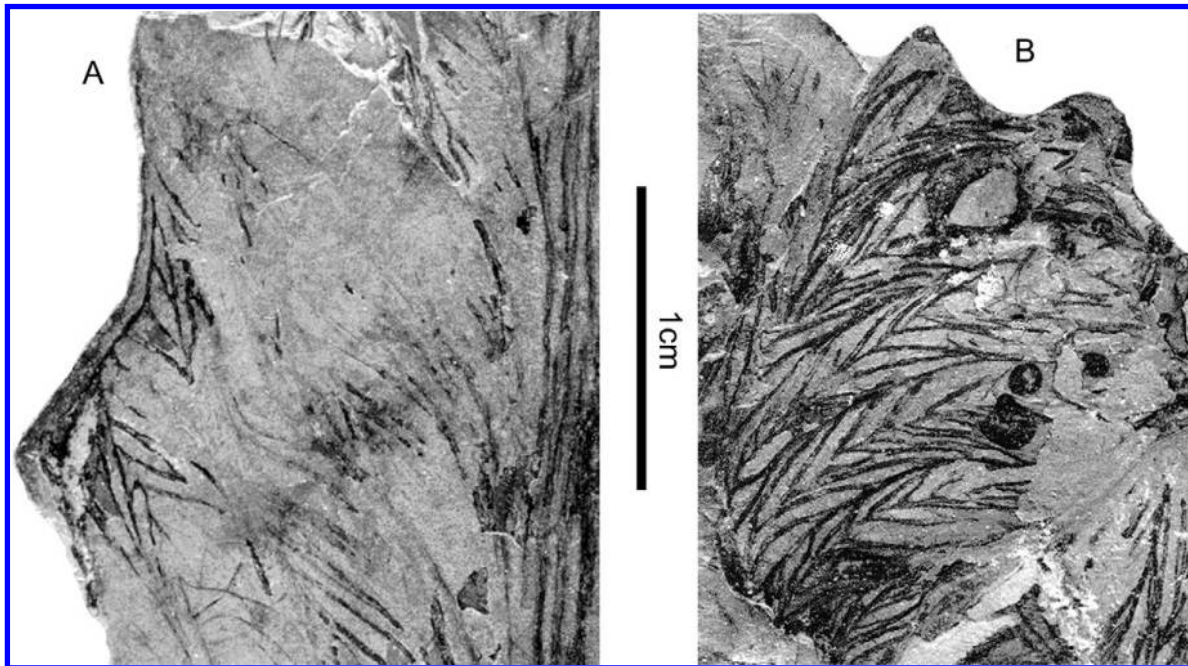
Fig. 2 Enlargement of laminar sections of the leaf illustrating the venation of *Euparyphoselis gibsonii* n. gen. et sp. Scale bar = 1 cm. *A*, Partial lamina near apex. Possible toothed margin. Note submarginal vein, suggesting that the scalloped edge is not the result of damage. USNM 520384; loc. 40968, South Ash Pasture ×4. *B, Euparyphoselis gibsonii* n. gen. et sp. Lamina fragment with well-marked secondary and tertiary veins. Note suture vein where tertiary veins fuse. USNM 520384; loc. 40968, South Ash Pasture ×4.
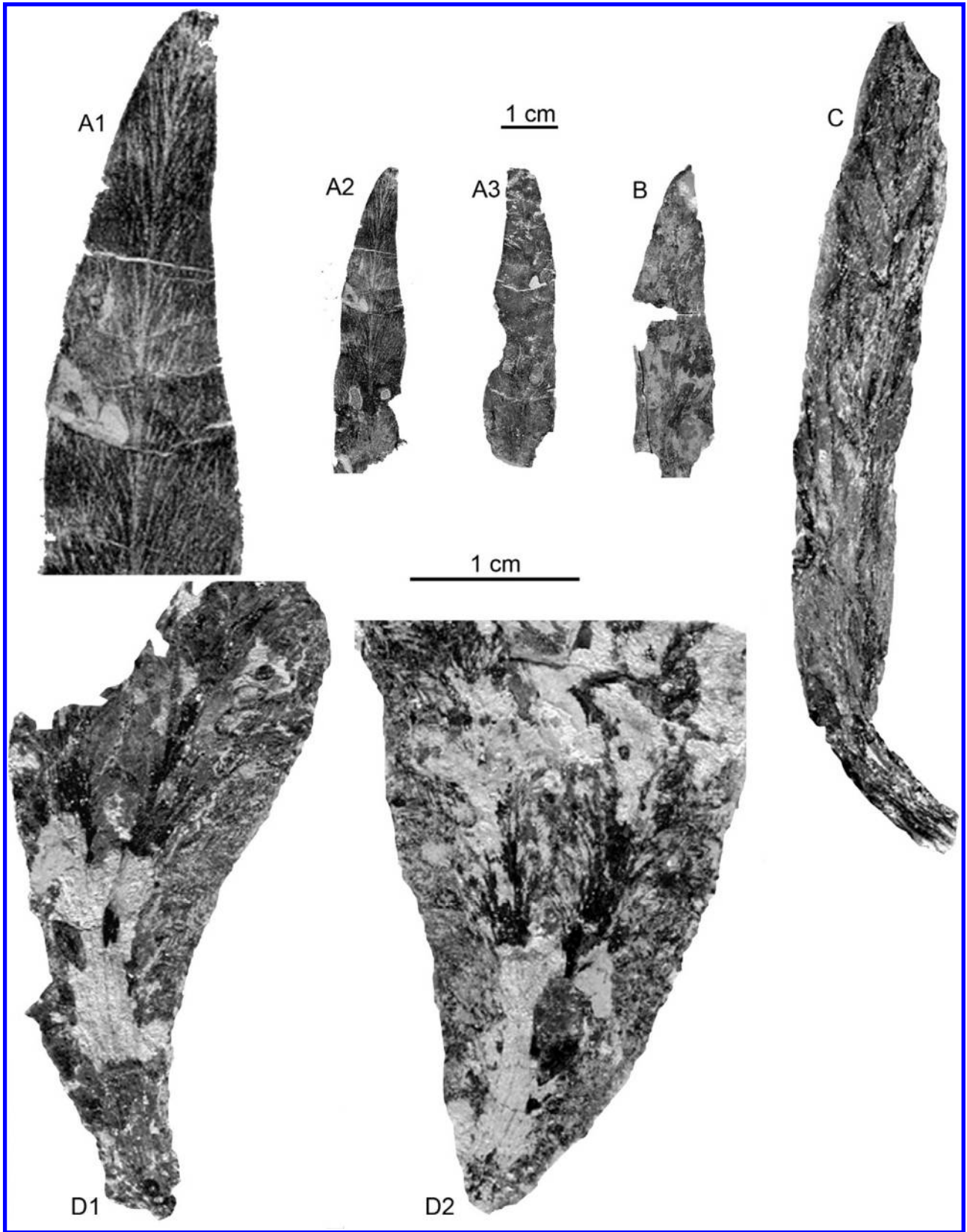
Fig. 3 *Euparyphoselis gibsonii* n. gen. et sp. Features of smaller leaves. Scale bars = 1 cm. Small scale bar applies to *A2*, *A3*, and *B*; large scale bar applies to *A1*, *C*, and *D*. *A*, Tip of small narrow leaf (*A2*, ×1; *A1*, ×3) and counterpart (*A3*, ×1). USNM 520387; loc. 41017, South Ash Pasture. *B*, Tip of small narrow leaf (×1). USNM 520389; loc. 41017, South Ash Pasture. *C*, Narrow lamina with well-marked primary and

Etymology. Greek, *Euparyphos* ("with a fine border") + *selis* ("leaf"), reflecting the fine marginal vein characteristic of this genus.

Type locality. South Ash Pasture, King County, Texas, Bob Creek 7 1/2′ Quadrangle map.

Euparyphoselis gibsonii *sp. nov.*

Holotype. USNM 520383.

Paratypes. USNM 520384, 520386, 520387, 520389, 520390, 520391.

Additional material. SEM stubs USNM 520376 and 520382.

Specific diagnosis. Leaf with three orders of venation. Secondary vein bundles may become progressively less distinct as they approach margin and split into several veins near terminus. Secondary veins of different weight, some very strong throughout their length, others less well defined; pattern not consistent between specimens. Tertiary veins form relatively narrow angles with the secondary veins. Suture veins vary in strength between different pairs of secondary veins. Leaves amphistomatic. Stomata distributed irregularly between veins and sparse to absent above veins. Stomatal complexes haplocheilic and monocyclic, round to elliptical in shape, with four to six subsidiary cells. Epidermal cells square to polygonal between veins, elongated above veins.

Etymology. Named for Mike Gibson, of Guthrie, Texas, general manager of the 6666 Ranch.

Type locality. South Ash Pasture, USNM locality numbers 41017, 40968; King County, Texas, Bob Creek 7 1/2′ Quadrangle map.

Type specimen. USNM 520383. Housed in the Paleobotanical Type and Illustrated Collections, U.S. National Museum of Natural History, Washington, DC, U.S.A. *Euparyphoselis gibsonii* is here designated as the type species of the genus.

Description. *Euparyphoselis gibsonii* leaves vary from broad and reticulate veined to relatively small and narrow but still preserving the distinctive pattern of venation (figs. 1–3). Such variation in size and shape is typical of American gigantopterid species. The size spectrum preserved in the population is, however, smaller than that known for any other American gigantopterid sample. Widths vary in the sampled population from >1 to ~4 cm. The maximum observed lengths, reaching as much as 7 cm, occur in some of the more narrow specimens. Leaves taper toward the base, though no specimens preserve the point of attachment to the stem. Leaf apices are known but only from the more narrow specimens (fig. 3). They appear to taper gradually to an acutely rounded tip. One of the narrow specimens tapers from 1.2 to 0.2 cm in width over a length of 5.5 cm. Most known specimens have smooth leaf margins. Several have what appear to be blunt teeth, apically oriented and separated by broad, shallow sinuses. These teeth may have re-

sulted from insect damage to leaves during the early phases of development; however, the marginal veins appear to follow the marginal shape, as if the teeth are indeed representative of the unmolested original marginal shape.

Leaves of all sizes have three orders of venation (fig. 1). The first-order vein, which is the midvein, and the secondary veins comprise bundles of numerous small-diameter vascular strands. The midvein is up to 5 mm wide in the middle of the lamina. The secondary veins diverge from the midvein bundle at an angle of ~45°. Approaching the margin, the secondary veins may become less distinct as tertiaries diverge from the secondary vein bundle; at their terminus, secondary veins splay out, and the coherence of the vein may disappear as it dissipates or terminates at the leaf margin and in the teeth, if present. Secondary veins can be of different weight or thickness. Some secondary veins are very strong throughout their length, whereas others may be less well defined; this pattern is inconsistent between specimens. Tertiary veins diverge steeply from and form an acute angle with the secondary veins. The tertiaries show limited lateral reticulation with veins derived from the same secondary. However, some of the tertiaries from adjacent secondaries come into contact and fuse, forming a variably strong suture vein between adjacent secondary veins. This gives the venation a herringbone appearance.

Perhaps the most distinctive attribute of the venation of *Euparyphoselis* is the marginal vein (fig. 1A1, 1A2), which is quite distinct in some specimens, though not as well developed or perhaps simply not as visible (due to preservational factors?) in others. The marginal vein, which led Yao and Liu (2004) to apply the specific epithet "marginervum" to the Chinese species (fig. 1B1, 1B2), arches between secondary veins, just below the leaf margin. This feature is unique among the gigantopterids.

The leaves of *E. gibsonii* are amphistomatic (fig. 4D1, 4D2). The stomata are distributed irregularly between veins in short ordered rows along the margin of the veins (fig. 5A) and are sparse to absent above the veins. The adaxial and abaxial epidermal surfaces cannot be positively identified. The stomatal complexes are usually separated by one to two epidermal cells (figs. 4D1, 5B). Adjacent stomatal complexes are present, but shared subsidiary cells have not been observed (fig. 4D1, center). Stomatal complexes are haplocheilic and monocyclic (fig. 6). The complexes are round to elliptical in shape, on average 85 μm long and 73 μm wide (min–max: $67–130 \times 52–105$ μm, $n = 32$). Most commonly, there are four to five polygonal to elongated trapezoidal subsidiary cells per stomatal complex (four : five : six-cell ratio of 5 : 4 : 1), with an average cell size of 40 μm × 29 μm (min–max: $22–67 \times 13–53$ μm, $n = 145$). The subsidiary cells in four-cell complexes are generally more elongated (mean L : W ratio = 1.55; see fig. 7) than their five-celled counterparts (mean L : W ratio = 1.38; see fig. 7). The anticlinal wall flanges of the subsidiary cells are straight to slightly curved and not strongly thickened. Because the cuticle is not preserved, it is not possible to establish whether the subsidiary
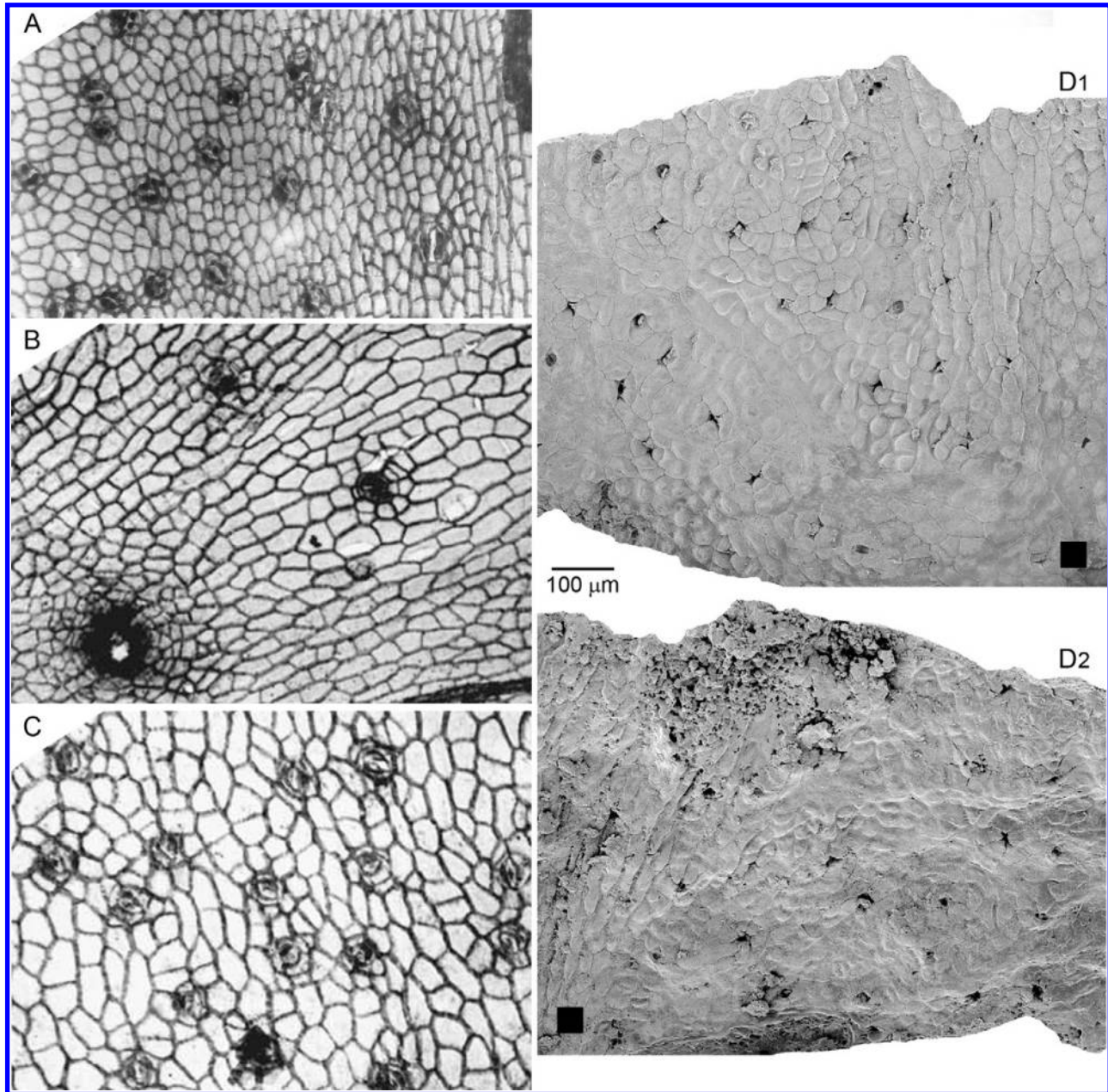
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secondary veins and blunt tip (×3). USNM 20390; loc. 40968, South Ash Pasture. *D*, *D1* (part), *D2* (counterpart), leaf base with tapering and venation (×3). USNM 520391; loc. 40968, South Ash Pasture.

Fig. 4 Comparison of the cuticle of *Euparyphoselis marginervum* (Yao et Liu) comb. nov., with epidermal features of *Euparyphoselis gibsonii* n. gen. et sp. Scale bar = 100 μm, all $\times$100. *A, Euparyphoselis marginervum.* Cuticle of the abaxial surface near leaf margin, showing transition of the stomata with papillate subsidiary cells to nonpapillate subsidiary cells; leaf margin to right. PB9156, slide 12 (after Yao and Liu 2004). *B, Euparyphoselis marginervum.* Abaxial cuticle, showing stomata with papillae and a secretory opening. PB9156, slide 02 (after Yao and Liu 2004). *C, Euparyphoselis marginervum.* Adaxial cuticle. PB9156, slide 03 (after Yao and Liu 2004). *D, Euparyphoselis gibsonii.* D1 and D2 are opposite sides of same leaf fragment. It is not known which is the adaxial or abaxial surface, as stomatal density is similar on both sides and epidermal cells are elongated on both surfaces in the costal areas. The black squares are in approximately the same relative position but on opposite sides of the specimen.

cells bore papillae. The stomatal pores are, on average, 27 μm long and 14 μm wide ($n = 25$), many of them orientated in the same general direction (fig. 7). The guard cells are sunken and reniform in shape (fig. 6A). The dimensions of the intercostal epidermal cells are about a quarter larger than the subsidiary cells. The epidermal cells are square to polygonal in the laminar portions of the leaf, with an average inter-

costal cell size of 50×36 μm (min–max: 27–79×19–58 μm, $n = 82$) and are distinctly elongated above the veins (100×26 μm; min–max: 27–166×14–34 μm, $n = 50$). The length:width ratio of the epidermal cells above veins varies but can be as high as 8 (figs. 5C, 7). Epidermal cell patterns are more regular above the veins and their margins (fig. 5A). Trichome bases or secretory structures are absent.

Euparyphoselis marginervum (Yao and Liu) comb. nov.

Basionym. *Gigantopteridium marginervum* Yao and Liu (2004).

Type specimen. PB9156 and slides 01–15, Palaeobotany Collection, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu Province, P. R. China. Type illustrated in plate I, figures 2–6, plate II, plate III, and plate IV, figures 1–4, of Yao and Liu (2004).

Diagnosis. The following is the original diagnosis given by Yao and Liu (2004, p. 34):

Leaf narrowly elliptic, not forked. Margin entire to slightly undulate. Veins pinnate, in three orders. Primary vein (midvein) distinct proximally, composed of numerous individual vascular strands, becoming indistinct distally, not persisting to the leaf apex. Midvein with up to about 10 pairs of opposite to alternate secondary veins. Secondary veins rather distinct, branching and becoming less distinct distally, sometimes branching dichotomously and forming a forked secondary vein. Tertiary veins arising from secondary veins and also directly from the midrib. Tertiary veins typically branching once or twice, sporadically anastomosing with neighboring tertiaries. Tertiaries from adjacent secondary veins fusing to form a sutural vein, in some cases a sutural vein also formed between two more developed tertiary veins joining to form a thin marginal vein that is present around the edge of the leaf. Resin bodies ("black dots") present but extremely sparse. Leaf amphistomatic. Adaxial cuticle rather thin, not much thicker than abaxial one, and with a little differentiation between costal and intercostal areas. Cell outlines in intercostal areas irregularly arranged, polygonal, usually three- to six-sided, ranging from isodiametric to elongated: 70 μm long and 45 μm wide in average. Cell outlines over veins rectangular to square, usually arranged in rows. Stomata scattered at random, with stomatal density about 25 mm^2 on an average. Stomata cyclocytic, with five to six subsidiary cells, forming a thick cutinized ring around stomatal pore, but a little thinner cutinized in polar positions. Guard cells D-shaped to reniform, level. Abaxial cuticle slightly thinner than adaxial one. Anticlinal flanges straight to slightly curved. Outer periclinal walls of ordinary cells lacking obvious ornamentation. Cells in intercostal areas being about 60 μm long and 35 μm wide in average. Secretory openings scattered on lower epidermis. Stomata scattered at random, and mainly in intercostal areas. Stomatal density about 16 per mm^2. Stomata cyclocytic, with five to six, rarely two subsidiary cells. Each stomatal pore overarched by two to seven papillae, except for stomata close to the leaf margin, which are similar to those on the adaxial epidermis. Cell outlines near leaf edge narrowly rectangular, arranged parallel to leaf margin. Inner side of periclinal cell walls of both adaxial and abaxial cuticles with granular ornamentation. In costal area, especially over midvein, periclinal ornamentation is tuberculate-granulate, while in the intercostal zone it is mainly granulate.

Description and comparisons. *Euparyphoselis marginervum* as described by Yao and Liu (2004) conforms to the new genus in its possession of a marginal vein, tertiary vein suture zones between secondary veins, limited tertiary vein reticulations, widely spaced veins that do not form distinct fascicles, unforked lamina, and generally small to medium size. The leaf margins are smooth to shallowly toothed, and tooth development is irregular, as in *Euparyphoselis*. Although not mentioned in the diagnosis, *E. marginervum* occasionally may have a fourth order of venation (see Yao and Liu 2004, pl. 1, fig. 1, bottom), the architecture of which is essentially the same as that of typically terminal third-order veins.

Euparyphoselis marginervum differs from *E. gibsonii* in several ways, mostly with regard to size and the features of the epidermal surface. On the basis of the lamina width of known leaves, *E. marginervum* is about twice the size of *E. gibsonii*. However, it must be understood that the number of known specimens of *E. gibsonii* is small, and there is no reason to believe that the leaves of the two species could not have a similar size range. Our personal observations of American specimens indicate great variability of leaf size in some gigantopterid taxa. Leaves of other taxa, when a large sample is available, show great variability not only in leaf dimensions but also in the general morphology of the lamina (Chaney et al. 2009).

The differences in epidermal surface characters between the two species of *Euparyphoselis* include epidermal cell shape and size, epidermal and subsidiary cell size ratio, number of subsidiary cells, and orientation of the stomatal pore (fig. 7). On average, the stomatal complexes of *E. gibsonii* have four to five but no more than six polygonal to trapezoidal subsidiary cells that are about half the surface area of the epidermal cells. For *E. marginervum*, five to six subsidiary cells per stomatal complex are typical, but the number varies between two and seven. The subsidiaries of *E. marginervum* are more elongated than those of *E. gibsonii* and are about a quarter of the epidermal cell surface area. Stomatal complexes of *E. gibsonii* show a distinct orientation, whereas those of *E. marginervum* are nonorientated. In addition, *E. marginervum* has distinct secretory structures on the abaxial surface; these are absent in *E. gibsonii*.

Whereas venation is similar in the two species, that of *E. marginervum* includes somewhat more reticulations among the tertiary veins than does that seen in *E. gibsonii*, and, in some instances, a tertiary vein of *E. marginervum* is unusually strong and straight and gives rise to what may be considered a fourth order of vein branching. These features of venation possibly are attributable to the greater size of the study specimens in *E. marginervum*. The suture vein of *E. marginervum* is approximately the same thickness as the tertiary veins from which it is formed, whereas that of *Gigantopteridium* is more consistently developed and thus obviously a suture vein.

Discussion

Euparyphoselis has gross morphology that conforms to the traditional phenetic concept of gigantopterid foliage: megaphyllous leaves with complex, reticulate venation. It may, however, fall outside of a more restricted concept recently
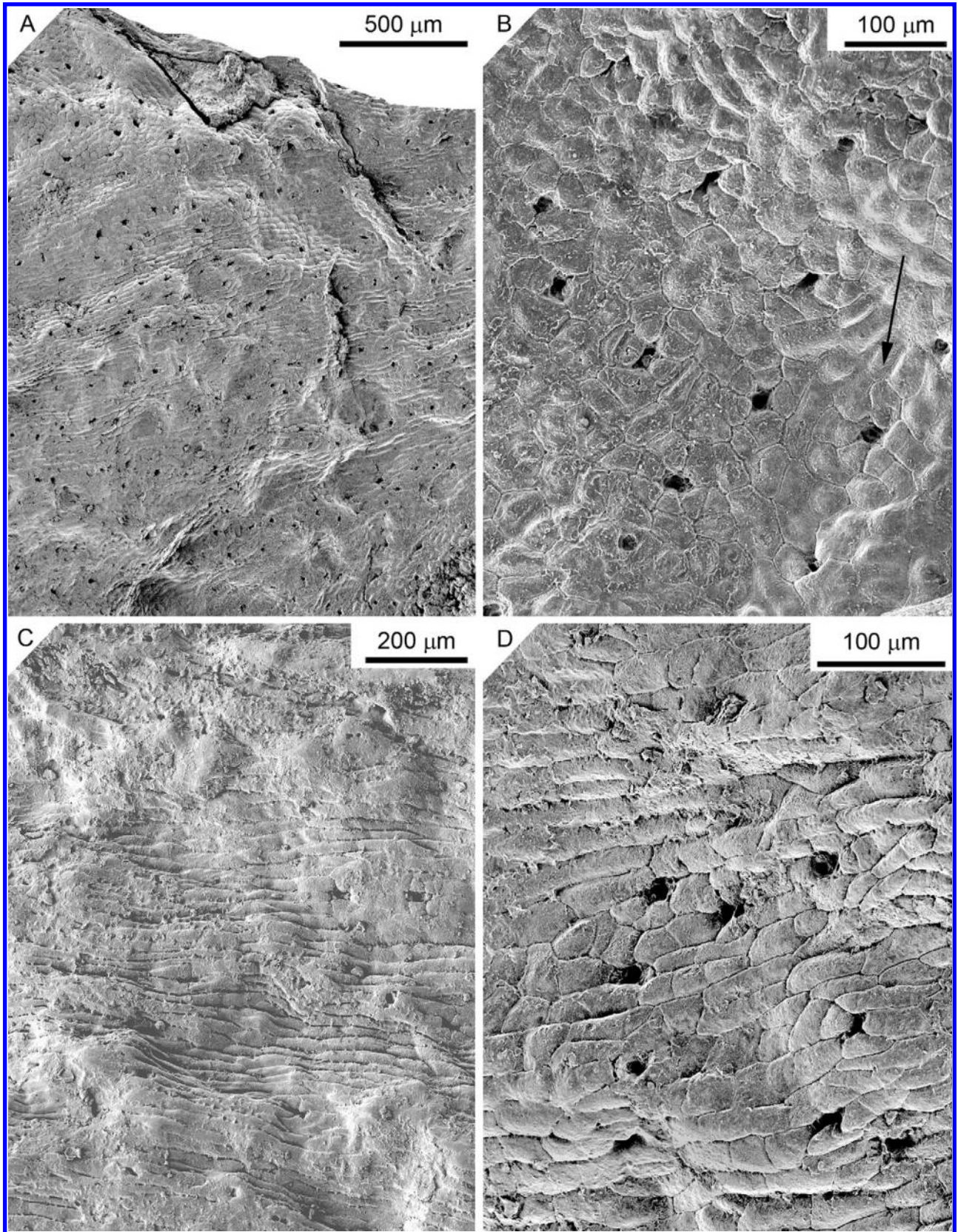
Fig. 5 *Euparyphoselis gibsonii* n. gen. et sp. Epidermal features. USNM 520376; loc. 40968, South Ash Pasture. Scanning electron microscopic images. Scale bars as shown. Adaxial and abaxial surfaces cannot be positively identified. *A*, Elongate cells grade to more isodiametric
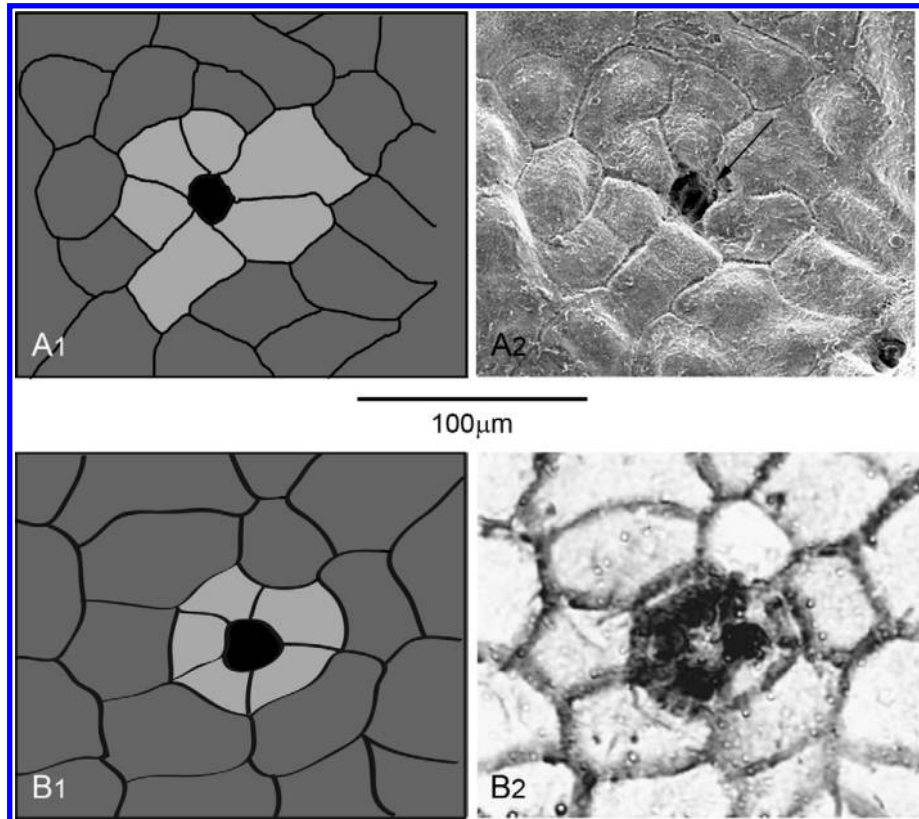
Fig. 6 Comparison of single stomata of *Euparyphoselis gibsonii* n. gen. et sp. and *Euparyphoselis marginervum* (Yao et Liu) comb. nov. DiMichele et al. All ×300. *A*, Stomatal complex of *E. gibsonii*; *A1*, line drawing of *A2*. USNM 520376; loc. 40968, South Ash Pasture. Detail of stomatal complex indicated by arrow in fig. *5B*. Six polygonal subsidiary cells (light gray) surrounding the elliptic stomatal pore. Guard cells sunken. Note the relatively small size difference in subsidiary and epidermal cells (dark gray). *B*, Stomatal complex on abaxial cuticle surface of *E. marginervum*; *B1*, line drawing of B2. PB9156, slide 02 (after Yao et Liu 2004); loc. Funiushan coal mine. Five trapezium to polygonal subsidiary cells (light gray) surrounding the elliptic stomatal pore (black). Note solid papillae on the subsidiary cells and the size difference in subsidiary and epidermal cells (dark gray).

proposed by Glasspool et al. (2004). The range of leaf morphologies included in the traditionally used concept is considerable and, when examined in detail, appears to lack a suite of well-understood derived characters that holds it together as a monophyletic group. Glasspool et al. (2004) examined the morphologies of the taxa included within this original concept of the Gigantopteridales and reanalyzed the earliest described forms, now placed in the genus *Gigantopteris* Schenk ex. Potonié emend Glasspool et al. They suggested that the gigantopterids sensu stricto should be restricted to the genera *Gigantopteris* and *Gigantonoclea*, characterized by the presence of megaphylls with continuous laminae, eucamptodromous venation (Hickey 1979), and higher-order veins, third order or above, that anastomose to form complex meshes while lacking suture veins. In addition, the anatomy of these two genera is partially known, indicating the presence of vessels and vinelike habit (Li and Taylor 1998, 1999). Few other gigantopterids, sensu lato, are known anatomically, so ability to compare this suite of characters is lim-

ited. This restriction of the gigantopterid concept is a step forward in understanding the phylogenetic relationships of these plants.

Glasspool et al.'s (2004) gigantopterid concept excludes most of the other genera of plants with traditional gigantopterid leaf form, including *Cathaysiopteris* Koidzumi; *Cathaysiopteridium* Li; *Delnortea* Mamay, Miller, Rohr & Stein; *Evolsonia* Mamay; *Gigantopteridium* Koidzumi; *Gothanopteris* Koidzumi; *Lonesomia* Weber; *Neogigantopteridium* Yang; *Palaeogoniopteris* Koidzumi; *Zeilleropteris* Koidzumi; and the new genus *Euparyphoselis*. Most of these genera have entire leaves, forked or unforked, and all have some degree of reticulate venation and suture veins. These features could be construed, in the lack of more complete understanding of the plants (none of which is understood in terms of anatomy or growth habit), to be features uniting them in a common evolutionary lineage. The relationships of these taxa within this lineage are not determinable, however, due to the lack of a larger suite of characters, continuing to cast

cells near the margin. *B*, Surface area between veins. Stomata surrounded by four to six subsidiary cells. Arrow indicates stomatal complex enlarged in fig. 6*A*. *C*, Costal area with elongate cells and few stomata. *D*, Transitional area between costal and intercostal regions.
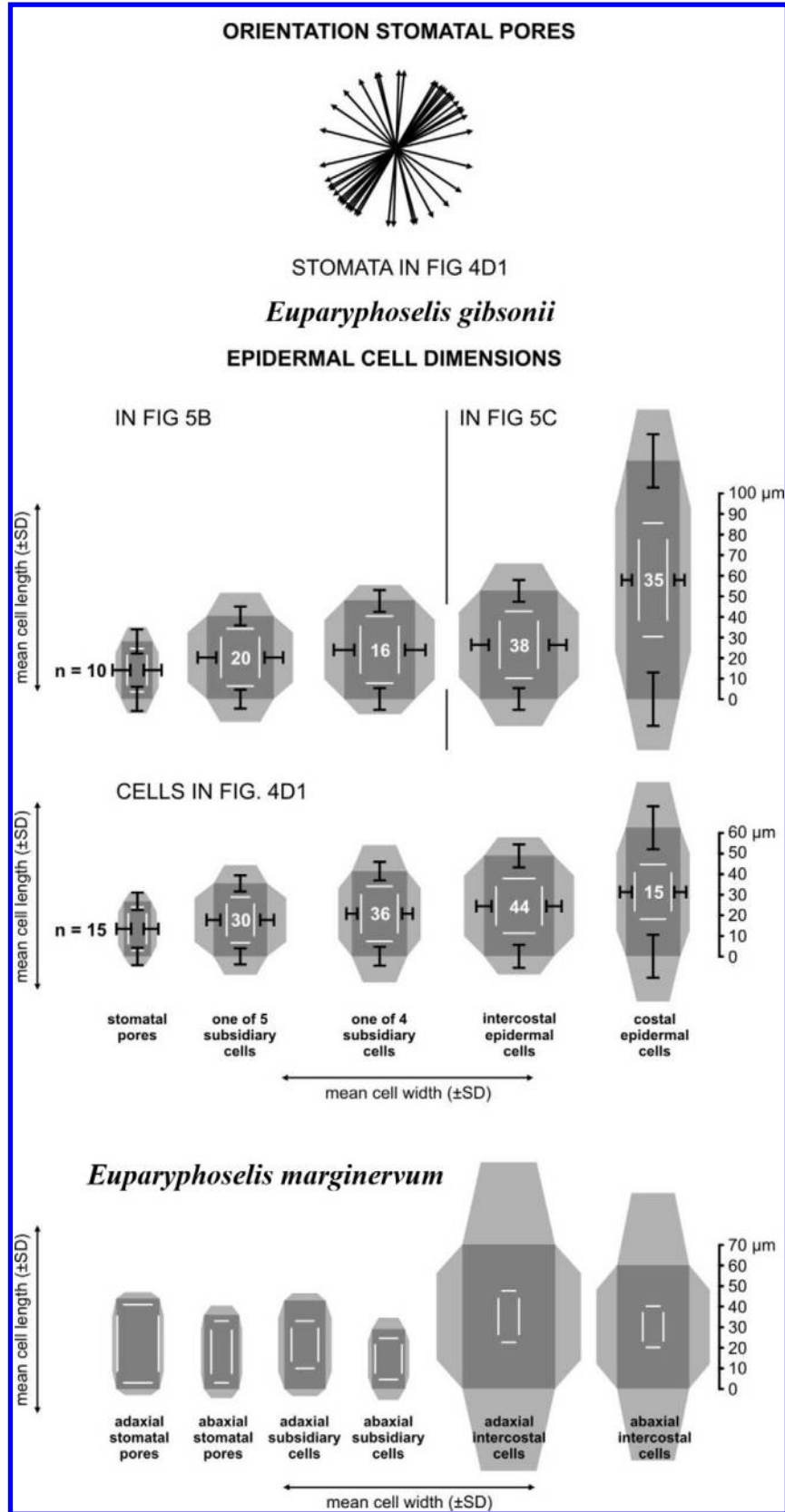
Fig. 7 Orientation and dimensions of stomatal pores and epidermal cells of *Euparyphoselis gibsonii* n. gen. et sp. and *Euparyphoselis marginervum* (Yao et Liu) comb. nov. For *E. gibsonii*, data are derived from measurements of specimens shown in figs. 4D1, 5B, and 5C; those for

some doubt on the certainty of monophyly. Furthermore, the relationships of this possible clade to other seed plant groups remains uncertain. Most of the genera occur either exclusively in North America–South America or in China–Southeast Asia, with *Cathaysiopteris*, *Euparyphoselis*, *Gigantopteridium*, and *Zeilleropteris* reported from both areas. *Gigantonoclea* also has been reported from North America (Mamay 1988). As we discuss below, the supposed Chinese occurrences of *Gigantopteridium* are questionable, and the American occurrences of *Cathaysiopteris* and *Gigantonoclea* are uncertain. This greatly reduces the likelihood of overlap of American and Asian gigantopterids at the generic level but leaves open the possibility of some degree of overlap at the more inclusive clade level. At the same time, it points to the need for a much more detailed analysis of the morphologies of these plants and reassessment of the homologies among them.

In light of what is presently known, the most confident paleogeographic overlaps of gigantopterids in the Americas and Asia are *Zeilleropteris*, *Euparyphoselis*, and possibly *Gigantonoclea*. For each genus, the stratigraphically earliest occurrence is in North America. They encompass a range from the middle of the Early Permian through the middle of the Middle Permian.

The most diagnostic characteristics of *Euparyphoselis* are the presence of at least three orders of venation with reticulations and a suture zone between the secondaries formed by the fusion of the tertiary veins. The closest similarities morphologically are with the American taxa *Delnortea* Mamay et al. (1988) and *Evolsonia* Mamay (1989). Most of the stratigraphically older gigantopterids known from North America, *Gigantopteridium*, *Cathaysiopteris* Koidzumi (1936), and *Zeilleropteris* Koidzumi (1936), are typically smooth margined without lobes or teeth and have a fork in the lamina near the base of the leaf. In contrast, both *Evolsonia* and *Delnortea* have unforked leaves. In addition, *Delnortea* has rounded marginal teeth. Its secondary veins end in the sinuses between the teeth. It also has strongly herringbone venation of four orders (Mamay et al. 1988). The leaf margins of *Evolsonia* vary from smooth to shallowly toothed. Secondary veins end in the teeth, where teeth are present. The four-order venation is herringbone in form (Mamay 1989).

There also are a few similarities between *Gigantonoclea* Koidzumi (1936) and *Euparyphoselis*, though primarily in certain aspects of leaf shape, particularly marginal characteristics that vary from smooth to acutely toothed. The venation, however, is quite different from that of *Euparyphoselis*, forming a fine reticulate mesh (Li et al. 1994) rather than a coarse herringbone pattern with relatively widely spaced veins. *Gigantonoclea* is reported in Texas—however, only from four small laminar fragments, lacking the margin. It may have venation similar to that of the Chinese material, four orders of venation, strong secondary veins, and the absence of suture veins, though the known specimens represent such a small sample size that it is difficult to ascertain these features se-

curely. It also is not possible to determine whether the American material was part of a compound or an entire leaf.

Yao and Liu (2004) assigned *Euparyphoselis marginervum* to *Gigantopteridium* on the basis of the herringbone venation, the presence of a suture vein between the true secondary veins, and the lateral reticulations of the tertiary veins. Whereas these features are, indeed, superficially similar to those of *Gigantopteridium*, they also differ in detail. First of all, the venation is considerably coarser than that typical of *Gigantopteridium* and, consequently, is less dense, with both secondary and tertiary veins of greater weight than is typical of *Gigantopteridium*. The suture vein between secondaries, formed by the juncture of tertiary veins, is more variable in character in *Euparyphoselis* than in *Gigantopteridium*, where it is quite regular in weight and disposition. Finally, the tertiaries do not form the internally reticulate and irregular fascicles typical of *Gigantopteridium*.

There is little published on the epidermal characteristics of other gigantopterids, with the exception of some members of the genus *Gigantonoclea* and *Gigantopteris* (Guo et al. 1989; Li et al. 1994; Yao and Liu 2004). The two *Euparyphoselis* species can be distinguished easily from *Gigantonoclea guizhouensis* Gu and Zhi (1974), and *Gigantonoclea hallei* Gu and Zhi, and *Gigantopteris dictyophylloides* Gu and Zhi on the basis of a combination of cuticular characters, including the position and structure of the stomatal complexes and their undulating anticlinal cell walls (Yao and Liu 2004).

The new genus is considerably younger than the American occurrences of *Gigantopteridium americanum* (White) Koidzumi, although this is not sufficient reason in and of itself to reject generic identity. Another species of *Gigantopteridium* has been reported from the Middle Permian of China, *Gigantopteridium huapingense* (Feng) Shen emend. Liu and Yao (2002), which indeed has fasciculate venation similar to that of *G. americanum*, though it differs in detail, such as the presence of blind vein endings. This leaf, however, is not like *Gigantopteridium* in a number of other aspects of form; it has a serrate, toothed leaf margin and acute apices and is unforked. We do not believe it to be a species of *Euparyphoselis*, nor does it conform to the circumscription of the genus *Gigantopteridium*. As such, the stratigraphic differences between *Gigantopteridium* and *Euparyphoselis* loom somewhat larger in importance and are consistent with the morphological differentiation.

Ecologically, *Euparyphoselis gibsonii* occurs in rocks with signatures of strongly seasonally dry, semiarid to arid landscapes. The channel-like plant-bearing deposit occurs in a section of strata otherwise dominated by bedded gypsum, shales, and dolomitic limestones (including oolitic dolomites). Perhaps the plant grew only along water courses but still reflects water stress in such features as small leaves. On the other hand, the channel may represent a period of somewhat wetter conditions. In either case, the environment contrasts sharply with the inferred habitat of *E. marginervum*,

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E. marginervum are taken from Yao and Liu (2004). Average cell or pore size is indicated by the dark gray area; the minimum dimensions measured are shown by white lines and the maximum dimensions by light gray areas. Where known, the standard deviations are shown as bars, and the number of cells included here is given.

which was found in dark organic shales, associated with coal beds, and presumed to represent humid climates (Yao and Liu 2004). Yao and Liu (2004, pp. 31–32) note the plant "only in the topmost portion, in the transitional beds, [where] there is a thin layer with plant remains (including *Gigantopteridium marginervum* sp. nov.) intercalated among beds with marine animal fossils." Thus, in China this new genus is associated with indicators of wet climate and probably lived close to the shoreline.

Architecturally, *Euparyphoselis* is much smaller than *Gigantopteridium* and shows no evidence of lamina or midvein forking. Study of large populations of other American gigantopterids, such as *Gigantopteridium* or those that have been assigned to *Cathaysiopteris* (but see below), shows that typically forked leaves may, on occasion, be unforked. However, in the similarly large populations of unforked leaves, such as *Evolsonia* or *Delnortea*, there are no known examples of the occasional forked lamina. Even though the bases of *Euparyphoselis* have not been found, clear tapering to the base has been identified, and no evidence of a fork has been seen. In *Gigantopteridium* and other forked gigantopterids, the forking occurs near the base of the leaf but nonetheless well within the laminar portion.

Mamay et al. (1988), later followed by Liu and Yao (2002) and Yao and Liu (2004), opined that gigantopterid leaf architecture is not a taxonomically significant diagnostic feature. Rather, they argued, leaf venation is the preeminent indicator of gigantopterid generic affinity. Most of these plants are too poorly known, however, either anatomically or in terms of their growth habits, to understand the relative importance of various characters and their distributions among described taxa. It is extremely difficult to identify static mature-state characters or character suites that are more diagnostic of evolutionary history than others, especially without a clear understanding of the developmental basis of the characters in question and in the absence of a phylogenetic framework. Understanding of the significance of variation in architecture, epidermal features, and venation among the many described forms of gigantopterids awaits an explicitly character-neutral, evolutionarily based phylogenetic analysis. If, however, one presumes that venation alone is the key to gigantopterid evolutionary affinity, leaves that are quite different architecturally can be placed in the same genus if the details of venation are similar. A possible example of this, and the taxonomic confusion that can result when dealing with incompletely known plants, is the genus *Cathaysiopteris*, segregated by Koidzumi (1936) from *Gigantopteris*. The type species, *Cathaysiopteris whitei* (Halle 1927), has venation similar to but less fasciculate than that of *G. americanum*, with forked but nonanastomosing tertiary veins and strong suture veins. Halle (1927) described the new species with some reservation because he felt it to be very similar to North American *G. (Gigantopteris) americanum* of White

(1912). However, the lamina, unlike that of *Gigantopteridium*, shows no clear indications of forking and has a constricted cordate base and a narrow, ribbonlike shape. Later, Asama (1959, pl. XX, fig. 2) described pinnate architecture in an Asian specimen. What has been described as *Cathaysiopteris* in North America, *Cathaysiopteris yochelsonii* of Mamay (1986), has simple herringbone tertiary venation, without tertiary vein forks or anastomoses and with strong suture veins. North American specimens are once basally forked or occasionally unforked. In addition, intermediates in venation are known between North American *Gigantopteridium* and *Cathaysiopteris*, all of which have similar basally forked architectures (Beck and Labandeira 1998). The venation of these intermediates is similar to that of the *Cathaysiopteris* type species, *C. whitei* of Halle (1927), although leaf architecture is like that of *G. americanum*. The existence of these intermediates might be taken to indicate that American *C. yochelsoni* Mamay (1986) is part of a complex of related species with similar leaf architecture and a range of tertiary venation types ranging from fasciculate to simple. This suggests that the American forms all should be considered part of the same genus, *Gigantopteridium*. It leaves unclear the relationship of Asian *Cathaysiopteris* to the American forms because of the ambiguity regarding the leaf architecture of the Asian forms. Of course, if one decides in advance that venation is to be the basis for taxonomic determination, then architectural patterns can be consigned to insignificance.

The higher-level affinities of this genus, and all gigantopterids sensu lato, are uncertain. Affinities with angiosperms have been suggested (Taylor et al. 2006), though this has been disputed by other authors (Glasspool et al. 2004). DiMichele et al. (2005) suggested a peltaspermous affinity for American gigantopterids on the basis of associations between leaves and peltaspermous reproductive organs and the similarity of venation to that of other plants more clearly related to peltasperms.

Acknowledgments

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