THE PERMIAN PELTASPERM RADIATION: EVIDENCE FROM THE SOUTHWESTERN UNITED STATES

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Abstract—The Peltaspermales are a group of pteridosperms or "seed ferns," plants with fern-like, compound leaves (fronds) that also bear seeds. Historically thought to be one of several groups of exclusively Mesozoic seed-ferns, the peltasperms have proven more recently to be widespread and abundant in the Permian tropics, appearing at least as early as latest Carboniferous. The group includes a number of genera, most of which occur in the southwestern United States, which is the focus of this report. The ancestral subgroup appears to be the callipterids, represented by the genera *Autunia* and *Rhachiphyllum*. Derived foliage taxa include the comioids (*Comia* and an undescribed genus), the supaioids (*Supaia*, *Glenopteris*, cf. *Brongniartities*, and perhaps several undescribed genera; this group is taxonomically "difficult"). Several genera of North American gigantopterids also most likely are assignable to the Peltaspermales (*Gigantopteridium*, *Lonesomia*, *Evolsonia*, *Delnortea*, and three genera equated with Chinese taxa on the basis of venation but that, in fact, may be distinct, *Cathaysiopteris*, *Zeilleropteris*, and *Gigantonoclea*, and at least one new genus certainly occurring in China where it was described as "*Gigantopteridium*" *marginervum*). All of these foliage forms are associated with the reproductive organs *Autunia* (= *Sandrewia*) or *Peltaspermum*. The abundance and diversity of this group in southwestern North America indicates an extensive and early radiation of the peltasperms, during which they became ecological dominants in the Permian lowland tropics.

INTRODUCTION

Based on European material, the well known foliage type *Callipteris conferta* and the reproductive organ *Autunia*, a genus originally introduced for strobili with fan-shaped suboppositely-alternately arranged megasporophylls (Figs. 1A-B), were tentatively correlated based on repeated co-occurrences (Kerp, 1982). The reproductive organ *Autunia* was interpreted to belong to the "seed-fern" group Peltaspermales, plants hitherto considered strictly Mesozoic. This correlation established the taxonomic and phylogenetic affinities of the callipterids and pushed the peltasperm lineage back into the latest Carboniferous. The earliest unequivocal records of *A. conferta* are from the Upper Stephanian St. Étienne Basin of central France (Doubinger et al., 1995).

Some time earlier, Mamay (1975) had described the enigmatic reproductive organ *Sandrewia* from Early Permian rocks of north-central Texas, arguing for Vojnovskyalean affinities. The morphology of *Sandrewia* is essentially the same as that of *Autunia*. However, Mamay documented that the fan-shaped lateral, sporangium/ovule-bearing structures were upwardly directed on their stalks, whereas Kerp (1982) had shown the opposite positioning of the lateral structures in *Autunia*. This conflict has yet to be reconciled completely, although new material from Texas with attached lateral organs shows that the concave surfaces can be both upwardly and downwardly directed on the same specimen, suggesting that orientation may be an ontogenetic phenomenon, dependent on the stage of development of the organ. *Sandrewia* and *Autunia* seem to be closely related, if not identical, and indicate that peltasperms were important elements of Early Permian floras throughout Euramerica.

Sandrewia (using the North American name for these specimens until the taxonomic matters are resolved) occurs sparsely throughout much of the Permian section in Texas, New Mexico, and Oklahoma, often in association with callipterids, but also in association with a number of other plant groups. These *Sandrewia* specimens are bimodal in size; a larger and a smaller form occur through the same part of the Texas geological section. In addition, rare occurrences of radially symmetrical peltate structures also have been noted, though these organs
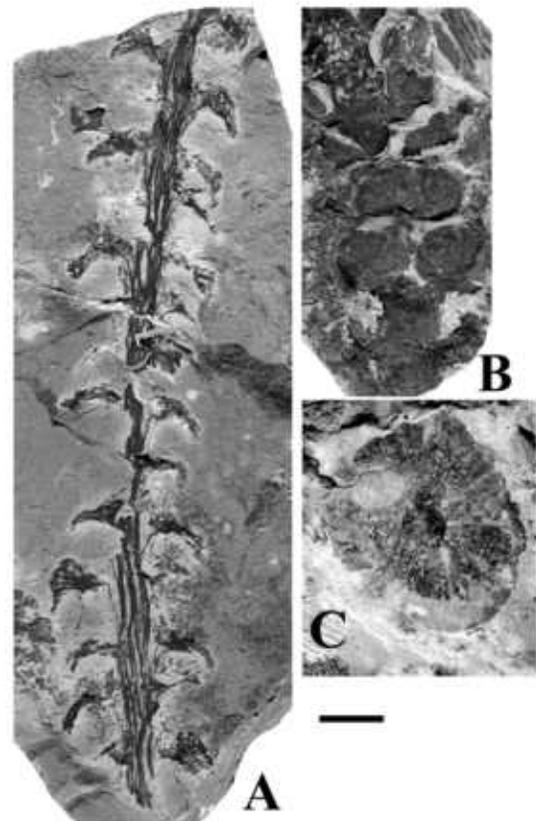

FIGURE 1. A) *Autunia/Sandrewia* sp., Mixing Bowl locality, Texas, USNM 528491; B) *Sandrewia* sp. , Mixing Bowl locality, Texas, USNM 528516; E) *Peltaspermum* sp., Harmel Tank locality, USNM 528490. Bar Scale = 1cm.

occur in isolation, lack presumed stalks, and are not attached to axes; thus, they are not aggregated in the manner of *Sandrewia/Autunia*. Similar, radially symmetrical structures occur in Late Permian floras from

Europe and have been attributed to the Peltaspermales (Gomankov and Meyen, 1979), or even to the genus *Peltaspermum* itself (Poort and Kerp, 1990; Naugolnykh and Kerp, 1996), and lately have been recorded for the Early Permian (Liu and Yao, 2000) and as early as the latest Carboniferous (Kerp et al., 2001).

From this body of work on peltasperms and peltasperm-like plants it can be concluded that the concept of early peltasperms should be expanded (Naugolnykh, 1999). There are several groups with venation patterns and frond architecture that for many years have been noted to be callipterid-like (Asama, 1960). These include a large complex of plants that can be described broadly as "supaioids", including the genera *Supaia*, *Glenopteris*, cf. *Protoblechnum*, cf. *Brongniartites*, and *Compsopteris*. *Supaia* from the Upper Permian of China already has been correlated with the peltasperms through its association with *Autunia* reproductive structures in those deposits (Wang, 1997). In addition are other genera, such as *Comia*, abundant in Texas and frequently associated with large *Sandrewia*-type organs, the American gigantopterids (distinct from the Chinese forms), also co-occurring with *Sandrewia*, and potentially some other undescribed foliage types.

CO-OCCURRENCES OF PRESUMED PELTASPERMS WITH *SANDREWIA*

In the north-central Texas section, *Sandrewia/Autunia* has been identified only in rocks of the Clear Fork Group, which is of middle Leonardian/Artinskian age. The reproductive organ occurs at 8 localities. There are no Asselian-Sakmarian/Wolfcampian occurrences of *Sandrewia/Autunia* in Texas. However, all the occurrences of *Autunia* from Europe are from the Rotliegend, which is an approximate equivalent in age to the Asselian-Artinskian (= lower Leonardian). Two occurrences of *Peltaspermum* have been noted from the basal most Clear Fork Group, still Artinskian in age.

Sandrewia/Autunia and *Peltaspermum*-like organs occur in all cases with mixed assemblages of the presumed members of the Peltaspermales discussed below.

VEGETATIVE CHARACTER OF THE PRESUMED PELTASPERMS

Callipterids of the *Autunia* and *Rhachiphyllum* type

Numerous studies of callipterids have documented the basic architecture of the frond and predominant patterns of pinnule shape, distribution, and venation, but these are best known for the genera *Autunia* and *Rhachiphyllum*, the characteristics of which are reported here. Where known, fronds of these callipterids are relatively compact, up to 80 cm in length in species from the Rotliegend, and unforked (Barthel and Haubold, 1980; Kerp, 1988). *Peltaspermum martinsii* from the Upper Permian has much smaller fronds, rarely reaching a length of 30 cm, a likely adaptation to the more arid climate of that time, as are also the very thick cuticles, the deeply sunken stomata, and the fleshy nature of the leaves (Poort and Kerp, 1990). Callipterid fronds have two orders of branching, the main rachial axis and primary pinnae, on which are borne pinnules. Pinnules also may occur in "intercalary" position, i.e. directly attached to the primary rachis. Fronds are imparipinnate (single terminal pinnules on pinnae and main rachises). Pinnules vary in shape, from profoundly lobed to entire-margined. They are decurrent with rachial veins at the base. The midvein typically is "offset" meaning that the pinnule lamina is not symmetrical around the midvein. Rather, the lamina is wider to the acroscopic side of the pinnule at the base and is wider to the basiscopic side near the apex, so that the midvein appears to cross the lamina obliquely from base to below the apex of a pinnule. Midveins are relatively well defined and persist for about ¾ of the pinnule length. Lateral veins depart the midvein at a high angle. They typically are slightly sinuous, the angle decreasing slightly immediately after departure from the midvein and inflecting upward again near the pinnule margin. This gives the lateral veins a somewhat
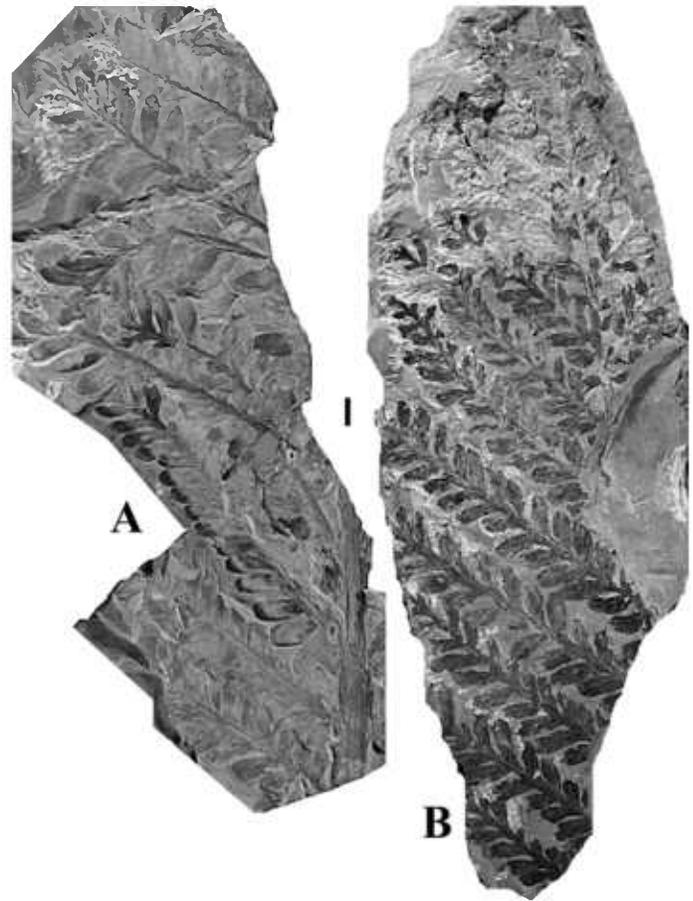

FIGURE 2. Callipterids. A) Mouth Brushy Creek locality, Texas, USNM 528513; B) Mouth of Brushy Creek locality, Texas, USNM 528515. Bar scale = 1 cm.

stretched out 'S' shape. Lateral veins may fork between the midvein and margin.

Kerp and Haubold (1988) divided the genus *Callipteris* into a number of different genera based on pinnule morphology and epidermal anatomy. Only one of these genera and two species, *Autunia conferta* and *A. naumannii*, clearly have been associated with *Autunia/Sandrewia* reproductive organs. In addition, *Rhachiphyllum* has been shown to have certain morphological attributes (i.e., resinous bodies) in common with co-occurring *Peltaspermum* reproductive organs at a site in Morrocco (Kerp et al., 2001). From these and various additional co-occurrences, it is likely that the entire group shares this association with peltaspermalean reproductive organs. *Autunia conferta* is both the best known and earliest member of the callipterid clade; *A. conferta* had been used as an index species for the base of the Permian but has unquestionably been shown to occur in rocks of the uppermost Pennsylvanian of North America and the uppermost Stephanian of Europe (Remy, 1975; Doubinger et al., 1995).

In North America, the diversity of callipterids appears to be high. Most forms have pinnule morphologies that suggest close similarities to *Autunia* or *Rhachiphyllum* (Figs. 2, 3A, 4, 5D-E). Some specimens have been found that appear to lack intercalary pinnules but otherwise display the typically callipterid frond architecture and pinnule morphology. Other forms seem to belong to new species and have yet to be described (Figs. 4B, 5A-C).

Cuticular studies (Barthel & Haubold, 1980; Kerp, 1988; Kerp and Barthel, 1993) have found that pinnules of *Autunia conferta* possess a thick upper (adaxial) and thin lower (abaxial) cuticle. The pinnules of *A. conferta* are amphistomatic (stomata on both leaf surfaces); however, stomata are much more common on the lower leaf surface.
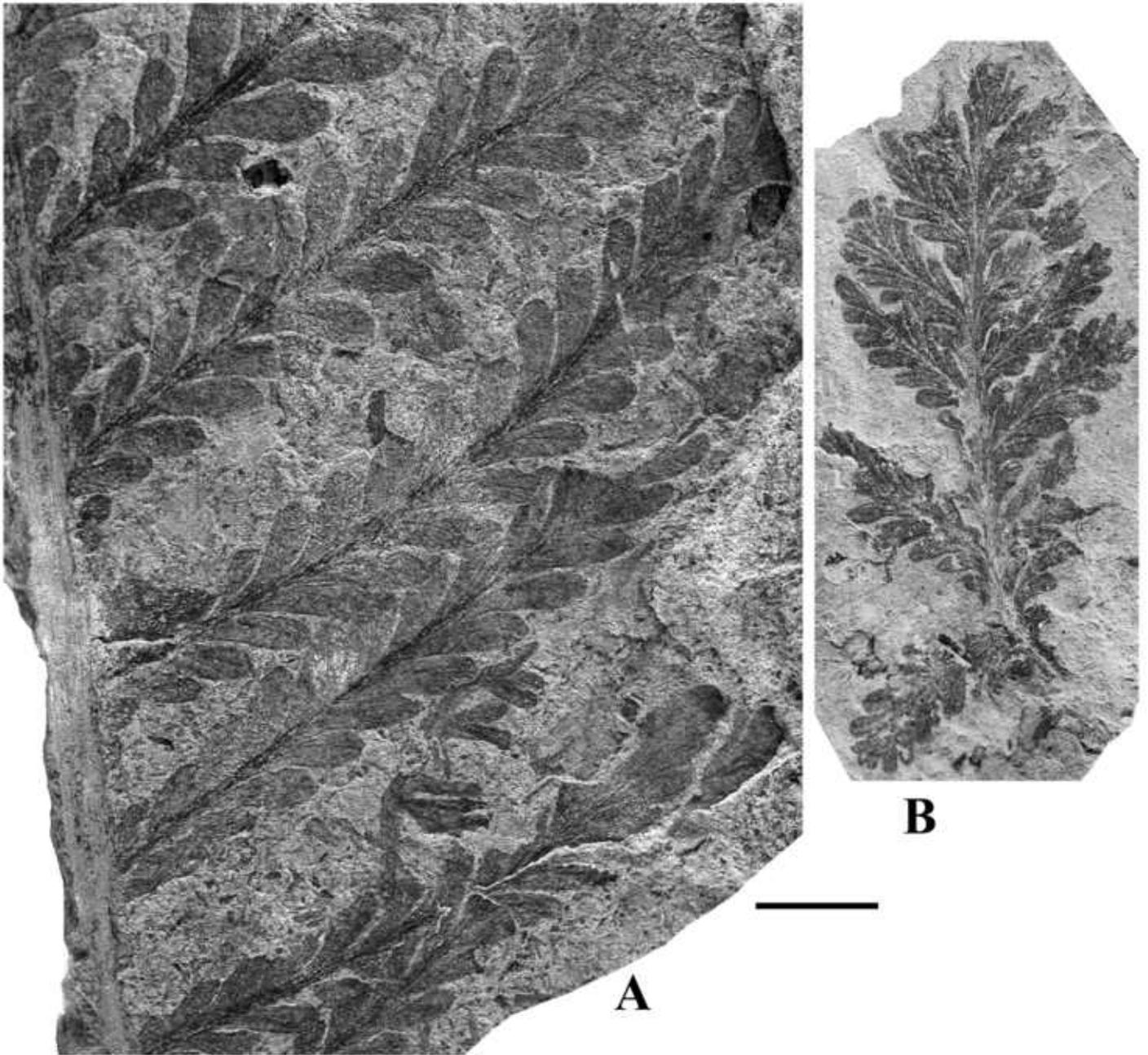
FIGURE 3. Calipterids from Abo and Cutler formations, New Mexico. A) Unidentified callipterid, aff. *Rhachiphyllum schenkii* from Spanish Queen Mine locality, New Mexico (specimen illustrated in Read and Mamay 1964 Pl 13 – 5 as *Callipteris conferta,*), USNM 41224; B) Unidentified callipterid, aff. *Rhachiphyllum schenkii,*possibly a small specimen of the same species illustrated in (3A) from Coyote Post Office locality, New Mexico (illustrated in Read and Mamay 1964 Pl 13 – 4 as *Callipteris lyratifolia*), USNM 41225. Bar scales = 1 cm.

Guard cells of the lower surface have papillae that extend from the subsidiary cells to overarch the stomatal pore. Moreover, characteristic large multiseriate glandular trichomes (or emergences) occur on the rachial parts of many fronds.

Supaioids

The taxonomically most refractory group of putative peltasperms found in the midwestern and southwestern United States can be conveniently labeled the "supaioids." Based on similarities in gross morphology, this group might be considered to include the following described genera: *Supaia* (White, 1929), *Glenopteris* (Sellards, 1900), cf. *Protoblechnum* (Lesquereux, 1879; Halle, 1927), cf. *Brongniartites* (Zalessky, 1927) and *Compsopteris* (Zalessky emend. Naugolnykh,

1999). *Supaia* has been referred to the peltasperms by Wang (1997) due to its association with peltaspermous reproductive organs in Later Permian rocks of China, and such an association may extend across this group of species in light of the similarities in gross morphology and on the basis of association of some genera with *Sandrewia* in the Texas section.

Based on American specimens the following observations might be offered of this group. First, generic descriptions do not appear to circumscribe gross morphologies uniquely, so that generic concepts overlap substantially. Second, there are undescribed forms that belong to none of the currently recognized genera but that may have been included in them as species. Third, it is not clear that all the names are legitimate or that names have been extended properly from the type
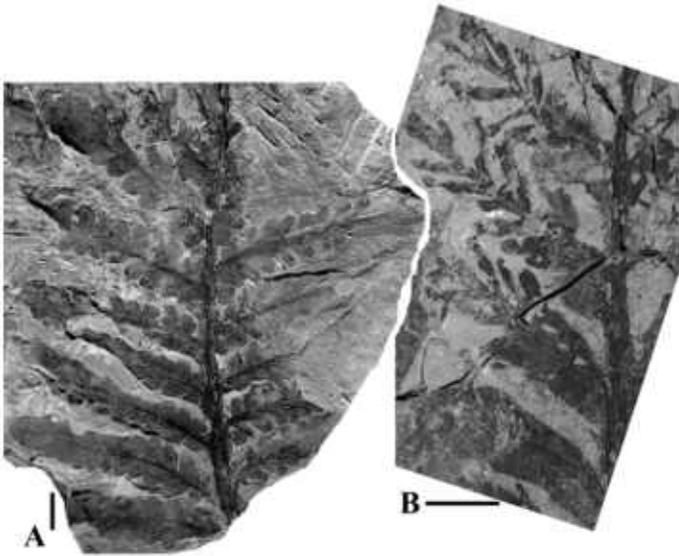
FIGURE 4. Callipterids. A) Harmel Tank locality, Texas, USNM 528519. B) Specimen showing subdivision of terminal area of pinnules near apex of frond, *Wattia* 1 locality, Texas, USNM 528129. Bar scales = 1 cm.

materials to the specimens upon which the currently used concepts are based. Fourth, names have been used across wide expanses of time and between different biogeographic regions. This is not necessarily a problem but does potentially lead investigators to overlook significant, consistent, but minor differences that might indicate distinct affinities, given the time-space separations. And, finally, cuticular and epidermal features, which might help sort out some of these taxonomic differences, are very poorly known for the group.

Naugolnykh (1999) has provided the most recent review of this problem. Looking specifically at *Compsopteris*, he argues that this genus is unique to the Russian Late Permian and has been improperly used for specimens of Early Permian age from Europe and North America. He also presents evidence that *Brongniartites* is an invalid name, even if it circumscribes a unique morphology as currently used for Permian foliage.

Halle (1927) used the name *Protoblechnum wongii* to describe plants from the Lower Permian of China. This generic name originated with Lesquereux (1879) for a plant from the Middle Pennsylvanian of Illinois, which Halle felt was sufficiently similar to his Early Permian specimens to warrant use of the name there. Halle also was convinced that his specimens forked near the base, which White (1929) disputed, leading him (White) to describe a new genus, *Supaia*, with leaf form similar to Halle's *Protoblechnum wongii*, but with clear basal forking of the petiole. Since that time, what Halle called *P. wongii* from China has been shown clearly to demonstrate basal forking (Sze, 1955; Sun et al., 1999).

White (1929) significantly oversplit his new genus, *Supaia*, segregating probable continuous variation into a number of distinct species. The most common of these, *Supaia thinnfeldioides* (Fig. 6B) is also the type species of the genus and bears close similarity to *P. wongii*. However, White also included in *Supaia* the peculiar *S. anomala* (Figure 6A), which may be a composite of two distinct taxa, one of which, with a ribbon-like forking lamina, appears to be outside of the generic concept of *Supaia*.

Complicating this picture still further is the genus *Glenopteris*, described by Sellards (1900) from Kansas (Fig. 8). *Glenopteris* fronds have been demonstrated clearly to be unforked. In gross pinnule form, they are similar to *S. thinnfeldioides* and *S. merriami* of White and *P. wongii* of Halle, however, the plants are covered by a thick cuticle and venation is quite obscure. Based on studies of the epidermal anatomy

and frond morphology, Krings, et al. (submitted) have reconsidered *Glenopteris* and determined that the genus is indeed distinct. However, in fragmentary preservation it could well be confused for one of the other supaioids with similar pinnule shape.

As a consequence, it may be impossible at present to attribute isolated specimens, especially if they are fragmentary, to a particular supaioid genus, at least within the Euramerican tropical realm. The most notable exception to this assertion may be *Glenopteris*, which, although recognizable as currently circumscribed, may be difficult to assign new species to unless they are nearly complete or well preserved cuticles can be obtained.

In the American Southwest, the following forms tentatively have been recognized. Specimens similar in gross morphology to *Supaia thinnfeldioides* (Fig. 7) occur in Texas, New Mexico, and the type area of Arizona, extending from the Wolfcampian (Assellian-Sakmarian in New Mexico and Arizona) well into the Leonardian (Artinskian) in Texas. These specimens appear to be forked with pinnules borne directly on the primary rachides of each fork. They have linear, lanceolate pinnules with acute to rounded apices, well developed midveins extending to near the apex, and high-angle lateral veins that are 'S' shaped. Pinnules are decurrent with rachial veins and tend to be acroscopically constricted. Pinnule width varies from narrow (much like that classically described for *Protoblechnum wongii* – see for example, Broutin, 1986) to wider, in which cases the pinnules look more like some other species of *Supaia*.

Glenopteris recently has been confidently recognized and emended (Krings et al., submitted) based on a reexamination of the type material originally collected in Kansas by Sellards (1900) and on previously unstudied specimens (Fig. 8A-B) from a second locality in Kansas collected by David White in 1909. The plants occur in Cimmarronian (equivalent to Leonardian) Stage rocks in Kansas. These kinds of fronds are unforked with flaring bases. Pinnules are attached directly to the rachis and increase in length from the base of the frond to the center, from which point length decreases. Pinnules are relatively wide and have midveins that persist to near the apex, with high-angle, lateral venation that is not 'S'-shaped. A few rachial veins enter the pinnule in a basal, basicopic auricle. Venation is generally difficult to recognize because the specimens have a thick cuticle and because the laminae appear to have been pachymorphous (succulent) and xeromorphic. The fronds are amphistomatic and no papillae have been reported in association with the stomata (Krings et al., submitted). Specimens similar to *Glenopteris* have been collected from several localities in a restricted stratigraphic zone of Leonardian age in Texas (Fig. 8C-D). These specimens are unforked with pinnules attached directly to the primary rachis, small at the base of the frond, increasing in length to the center and decreasing again to the apex, giving the frond an overall ovoid outline. The venation is obscure and the pinnules heavily carbonized, as if they were quite thick in life. However, the pinnule shape is narrow and lanceolate more like pinnules that might be attributed to *S. thinnfeldioides*. Pinnule attachment, however, is low angled, unlike that in the *Supaia-Protoblechnum* group.

A third suite of specimens falls into a group tentatively designated as *Brongniartities* (Fig. 9). Fronds within this group appear to be unforked. Basal pinnules are short and increase in size upward from the base of the frond and decrease in length again as the apex is neared. A complete frond is not in hand, so overall shape is not known. Pinnules are relatively wide with undulatory, but not really lobed margins, although some pinnules near the base could be described as lobed. Venation is 'S'-shaped and high-angle. Some specimens appear to have concave venation. Much about the pinnule morphology of these plants makes them appear to grade into the more narrowly circumscribed *S. thinnfeldioides* group.

Rare specimens have been found in New Mexico that possibly conform in gross morphology to part of the suite of specimens that White (1929) attributed to *Supaia anomala*. White's original concep-
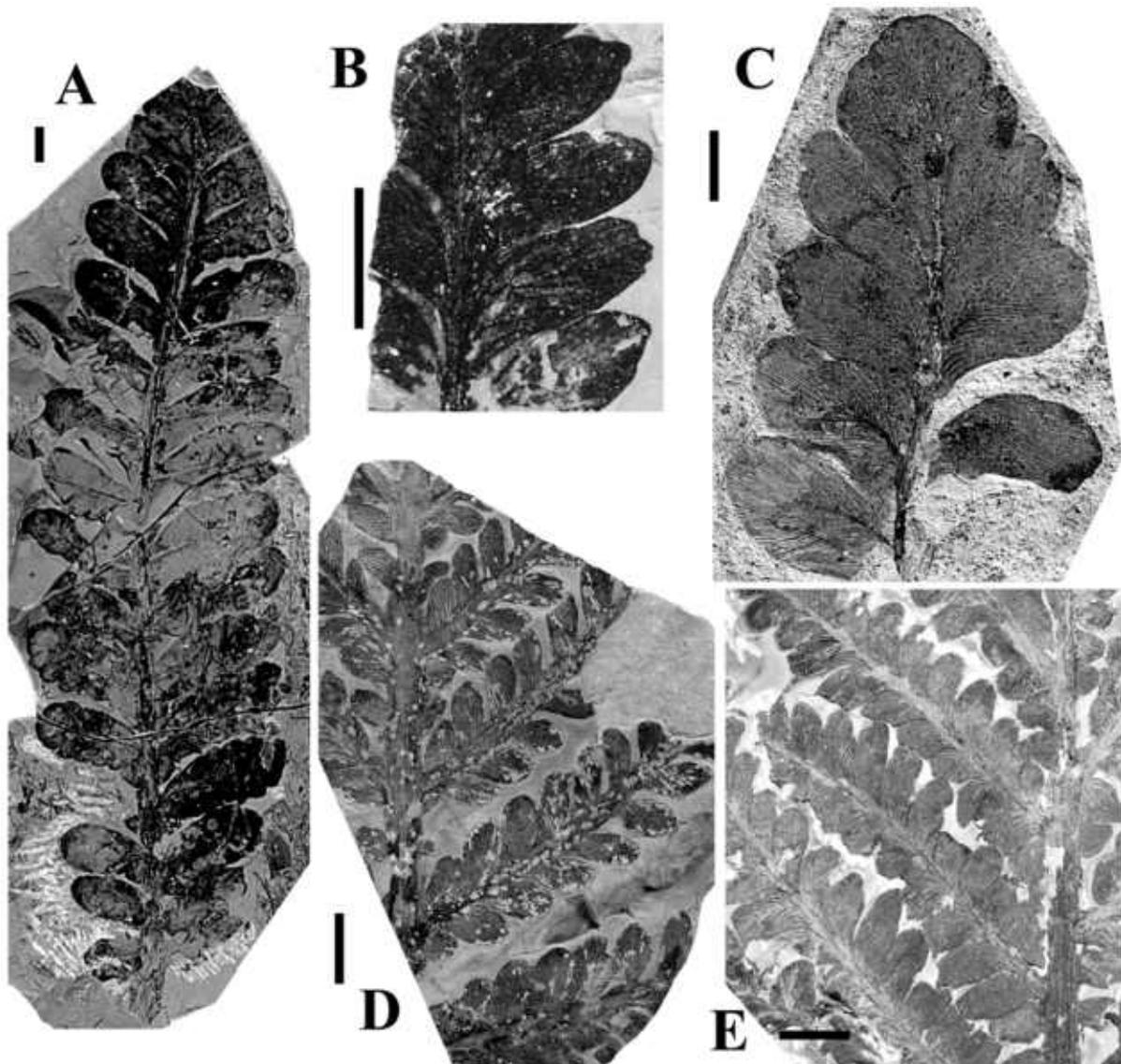
FIGURE 5. Callipterids. A) Form 1 from Mitchell Creek Flats locality, Texas, USNM 528158; B) Form 2 from Mitchell Creek Flats locality, Texas, USNM 528160; C) Harmel Tank locality, Texas, USNM 528511; D) Mouth of Brushy Creek locality, Texas, USNM 528510; E) Brushy Creek#2 locality, Texas, USNM 526035. Bar scales =1 cm.

tion of this species was as a pinnate frond with wide pinnules that, near the apex, become ribbon-like. However, he had, in fact, no apical sections attached to specimens with clearly pinnate morphology. These represent two distinct plants. The specimens from New Mexico (DiMichele et al., submitted) appear to represent a forked frond with a continuous ribbon-like lamina extending downward at least to just below the point of the fork. On the outer sides of each limb of the fork, the frond bears wide pinnules that begin short, increase in length and then again shorten. The terminal pinnule is basally fused to the immediately subjacent laterals, but a continuous lamina covers all. It is uncertain if pinnules are produced to the interior parts of the rachis forks – they appear not to be on the few nearly complete specimens that have been found. Venation is high-angle but widely spaced, generally 'S'-shaped. The frond lamina appears to have been relatively thin. These specimens likely constitute a distinct and new genus.

Finally, there are other specimens that appear related to this group given their overall aspect, but that do not fit clearly into any of the above described taxa (e.g., Fig. 10).

Comioids

The genus *Comia* was first described by Zalessky (1934) from the Upper Permian of Russia. Numerous species of the genus have been described from the Russian platform, but most are illegitimate for lack of description (named only in illustration) or have been inadequately characterized. Nonetheless, the morphological construction of *Comia* is quite well established. The leaves consist of unforked fronds with pinnately arranged pinnules borne directly on the main rachis. The distinguishing characteristic of *Comia* is its distinct venation pattern. Pinnules are decurrent with rachial veins basiscopically. The midvein is strongly marked and extends nearly the length of a pinnule. Lateral veins are grouped into fascicles, originating as a single vein. The originating vein bifurcates and all derivative veins, which may branch further, sweep upward concavely, relative to the pinnule midvein, and reach the pinnule margin. Between successive fascicles are several veins that depart directly from the midvein and that either branch sparsely or remain unbranched, also reaching the pinnule margin.

Two forms of *Comia* have been identified in Leonardian (Artinskian) rocks in north-central Texas (Mamay et al., 1996), thus appearing much earlier in North America than the specimens known from Russia. In the oldest form, the architecture of the leaf is not known,
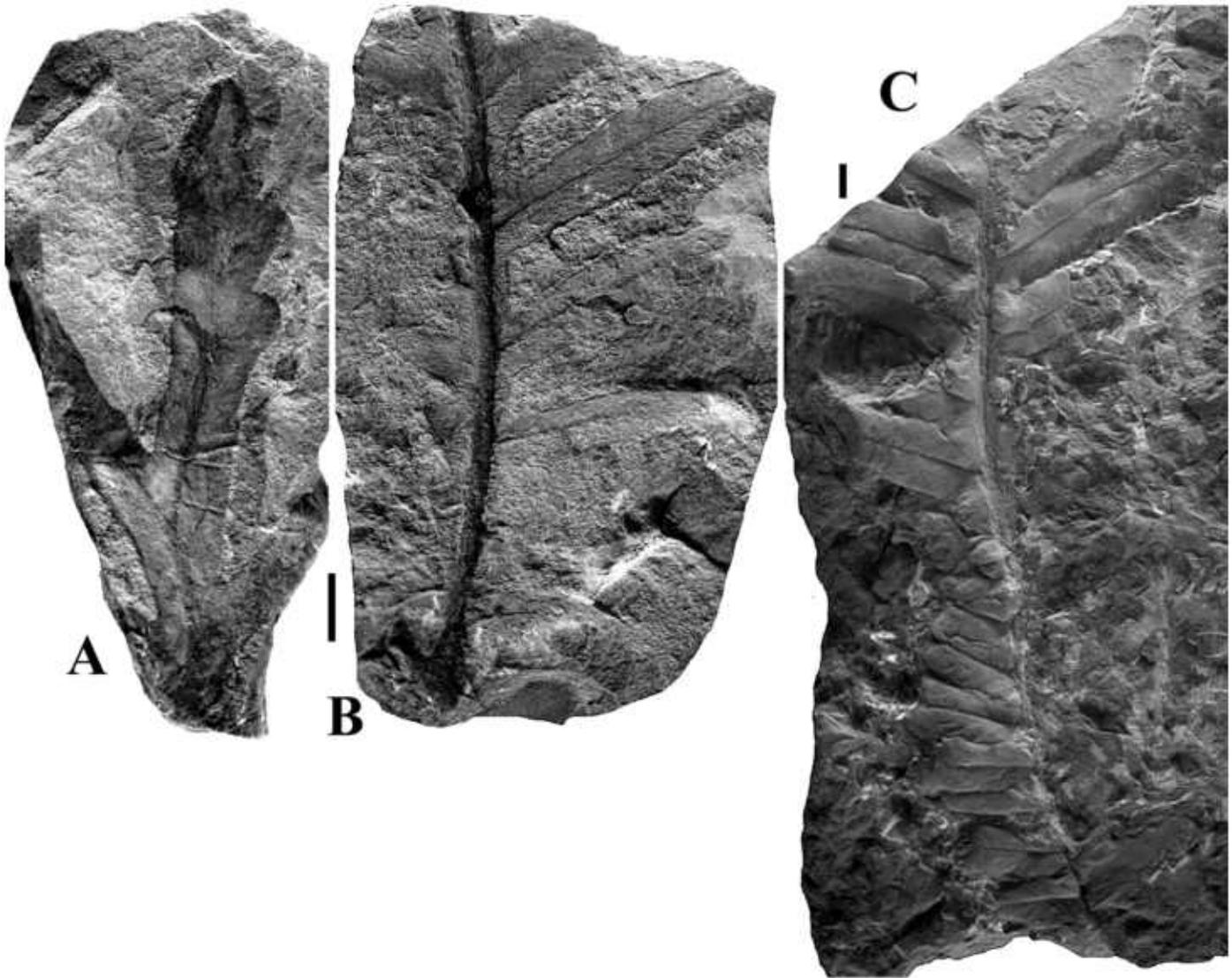
FIGURE 6. *Supaia* from the Hermit Shale, Arizona. A) *S. anomala* USNM 324584; B) *S. thinnfeldioides* USNM 324599; C) *S. merriamii* [illustrated in Read and Mamay, 1964 Pl. 15 – 1] USNM 38033. Bar Scales = 1cm.

but the basic pattern of comioid venation is well developed (Fig. 11A). Lateral veins are long, very fine, and, although closely spaced, extend without anastomoses to the margin of the pinnule. The other form (Fig. 11B) is unquestionably unforked and distinctly pinnate, with pinnules increasing in length from the base to the midsection of the frond and decreasing to the frond apex, which is terminated by a single, rounded pinnule, fused laterally to the near-terminal laterals. Venation is typically comioid, with alternating fasciculate and rachial veins, all of which reach the margin Fig. 11B$_2$).

A third, *Comia*-like form has been identified in Texas and occurs prominently in the middle Early Permian (Leonardian/Artinskian) (Fig. 12). Fronds in this plant are unforked basally. Pinnules are bulbous with rounded apices. At the frond base these pinnules are short, but their length and overall size increase upward, reaching a maximum at the tip of the frond where the main rachis forks, terminating in two long pinnules, the largest of the entire frond, elongated in the direction of the long axis of the frond. Thus, the frond rachis is straight in the lower portion but may start to overtop in the upper part. The morphology of this frond departs from that of known *Comia* species. In addition, the venation differs from that of *Comia* in two distinct, but subtle ways. Although organized in the typically fasciculate-interfasciculate manner of this genus, a small number of the veins in the fascicules do

not reach the margin (Fig. 13B). Consequently they either have blind endings, fuse with the intervening interfasciculate veins, or fuse with one other, forming local anastomoses in the marginal areas of each fascicule. Given the unique aspects of frond architecture and venation, this form is likely a new genus, but one with close affinities to *Comia*.

As with the gigantopterids, the basic venation of these comioids is similar to that of the older callipterids, especially those with *Autunia/Rhachiphyllum* leaf form. Veins are 'S'-shaped in their courses through the lamina. Pinnules are decurrent with rachial veins, and the individual fascicles closely resemble the vein patterns in individual callipterid pinnules. Once again, it appears as if *Comia* may have emerged from callipterid ancestors by lateral fusion of pinnules. In this instance, the fascicles may correspond to the ancestral pinnules, rendering a *Comia* pinnule the homologue to an ultimate pinna of a callipterid frond.

The comioids are more closely associated in the Texas section with *Sandrewia*-type reproductive organs than any other members of this putative peltasperm group, including the callipterids themselves.

Epidermal anatomy of these plants has not been reported.

Gigantopterids

The American gigantopterids presently are assigned to seven

FIGURE 7. *Supaia.* A) Know Where to Park #1 locality, Texas, USNM 526032; B) Venation detail, Know Where to Park #1 locality, Texas, USNM 528125. Bar Scales = 1cm.
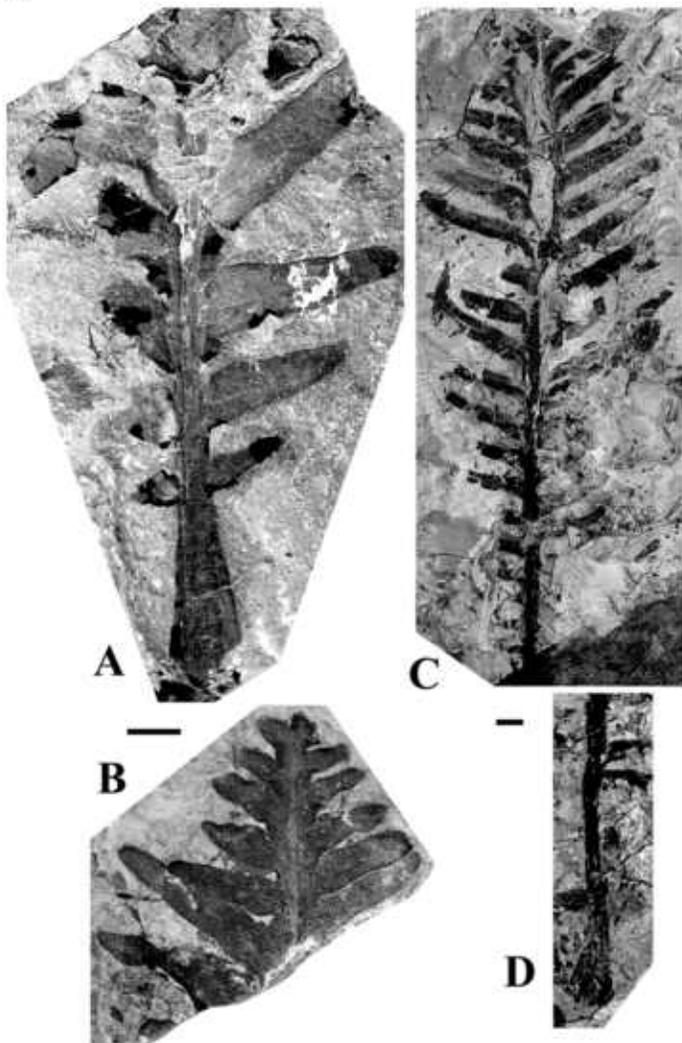
FIGURE 8. *Glenopteris* and similar forms. A) *Glenopteris,* Wellington Formation, Kansas, USGS locality number 8868, USNM 528148; B) *Glenopteris* ?*G. lineata,* Wellington Formation, Kansas, USGS locality number 8868, USNM 8084; C) cf. *Glenopteris,* Eurypterid Locality, Mitchell Creek, Texas, USNM 528127; D) cf. *Glenopteris,* Eurypterid Locality, Mitchell Creek, Texas, USNM 528128. Bar Scales = 1cm.

FIGURE 9. cf. *Brongniartites.* A) Brushy Creek West locality, Texas, USNM 528116, A1 – base of leaf; A2 – venation detail. B) Brushy Creek #2 locality, Texas, USNM 528121, B1 – Near leaf apex, B2 – Venation detail. Bar Scales = 1cm.

monospecific genera. In addition, there is at least one undescribed, monospecific genus, and several inadequately understood morphotypes, representing potentially new taxa, that have yet to be circumscribed taxonomically. The geologically oldest American gigantopterid is *Gigantopteridium* (White, 1912), followed in order of appearance by *Cathaysiopteris* (Mamay, 1986), *Zeilleropteris* (Mamay, 1986), *Evolsonia* (Mamay, 1989), and *Delnortea* (Mamay et al., 1988). These genera overlap variously in stratigraphic distribution and occur from the very latest Wolfcampian (uppermost Sakmarian, Early Permian) to the earliest Guadalupian (Middle Permian). An undescribed genus, essentially identical to a contemporaneous species from China, described as *Gigantopteridium marginervum* (Yao and Liu, 2004), occurs in the earliest Middle Permian (DiMichele et al., 2004); we cannot agree with the generic assignment to *Gigantopteridium,* but agree that this is a new taxon. *Gigantonoclea,* a common Chinese form (Li et al., 1994) also has been identified based solely on the venation of a single, small, fragmentary specimen (Mamay, 1988). Another genus, *Lonesomia,* has been described from Lower Permian rocks of Mexico (Weber, 1997), but has not been identified in the southwestern United States.

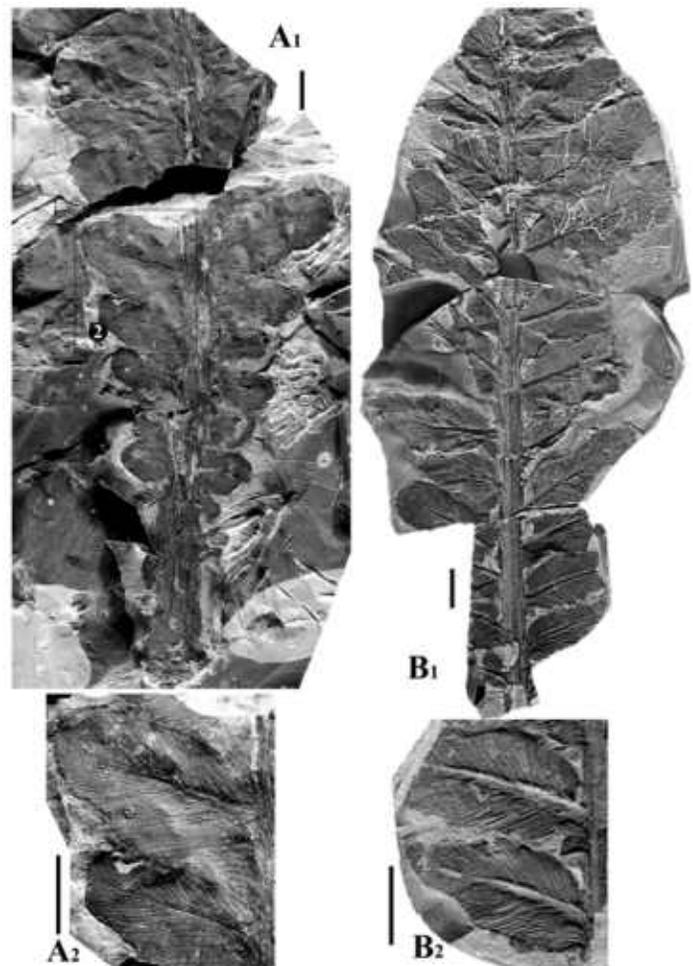The North American gigantopterids fall into two broad groups,

those with herringbone venation and those with reticulate venation. The herringbone-veined forms can be subdivided into two distinct groups, those with three orders of venation (*Gigantopteridium* and *Cathaysiopteris*) and those with four orders of venation (*Evolsonia, Delnortea, Lonesomia,* and an undescribed form).

In *Gigantopteridium* (Fig. 13A-B) the final order of venation dichotomizes, whereas in *Cathaysiopteris* (Fig. 13C) the ultimate order of venation is unforked. Forms "intermediate" between these two genera are known from many locations, raising the possibility that they perhaps should be considered part of a single taxon (assignable to the uniquely American genus *Gigantopteridium,* see Koidzumi, 1936). In this case, the "intermediate" forms would represent a third species thereof. Because *Cathaysiopteris* was described from Chinese material, and it is not certain that the American specimens belong therein, we do not mean to imply here that *Cathaysiopteris,* as originally described based on Chinese specimens, should be considered congeneric with *Gigantopteridium.* Rather, only that the North American material assigned to *Cathaysiopteris* may belong in *Gigantopteridium.* In both *Gigantopteridium* and *Cathaysiopteris* (as presently used for American specimens) the lamina is generally forked with a lobate margin, the secondary veins ending in the sinuses of the lobes. Another new form, as yet undescribed, has been found at a single locality in the middle Leonardian (Artinskian) of Texas. This form has 3 orders of venation, a lobate margin and veins ending in the lobes rather than the sinuses; with the exception of this final trait, it is identical to
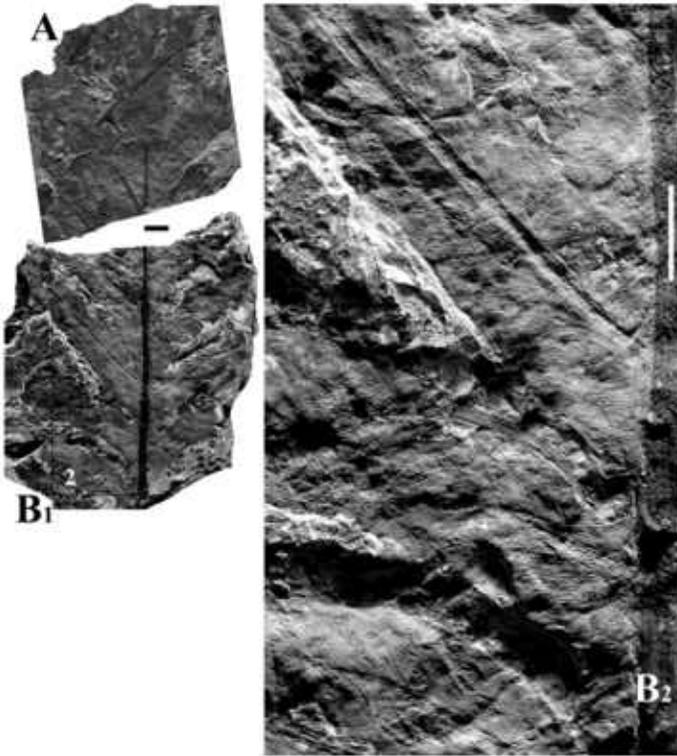
FIGURE 10. Undetermined supaioid. A) Know Where to Park #1 locality, Texas, USNM 520426; B) Know Where to Park #1 locality, Texas, USNM 520428, B1, B2 – detail. Specimens illustrated in A and B1 are juxtaposed to show likely configuration of the upper portion of the leaf. Bar Scales = 1cm.

Cathaysiopteris, as used for North American material, although forked specimens have not been identified.

Of those genera with four orders of herringbone venation, *Evolsonia* (Fig. 14A) has second-order veins that end in the sinuses of the undulate margins. In contrast, *Delnortea* (Fig. 14B) has second-order veins that end in the lobes of the undulate margins. The undescribed genus from Texas and China (Yao and Liu, 2004; DiMichele et al. 2004), "*Gigantopteridium*" *marginervum* (Fig. 15A, B), also has three orders of venation, but the secondaries curve as they approach the margin and fuse with the next acroscopic secondary, thus forming an undulate, marginally circumferential vein.

Among the reticulate-veined forms, *Zeilleropteris* (Fig. 15C) has four orders of veins, the final order forming a network and a true reticulate pattern. The specimen attributed to *Gigantonoclea* also has reticulate venation. Unlike angiosperm venation, however, there are no blind vein endings in these reticulate-veined gigantopterids.

Generally, the leaves of the North American gigantopterid species fork near the base, although the broad lamina extends below the fork to the base of the leaf, so that there is no distinct petiole. However, *Evolsonia*, *Delnortea*, and "*Gigantopteridium*" *marginervum* have been described as unforked in their entirety, and unforked specimens have been found with venation patterns similar to all the other "forked" genera as well. Unforked specimens of otherwise forked species are generally small. They do demonstrate that forking of the primary rachis is a developmentally labile characteristic in the taxa of this group that generally show forking. Such patterns would constitute heterophylly in the form of programmed ontogenetic changes in frond architecture (i.e. heteroblastic development). In such cases, unforked fronds were most likely produced by juvenile plants. The occurrence of heteroblastic development in seed ferns has previously been documented by Kerp (1988) for *Autunia conferta* and *Rhachiphyllum schenkii* from the Rotliegend of central Europe.

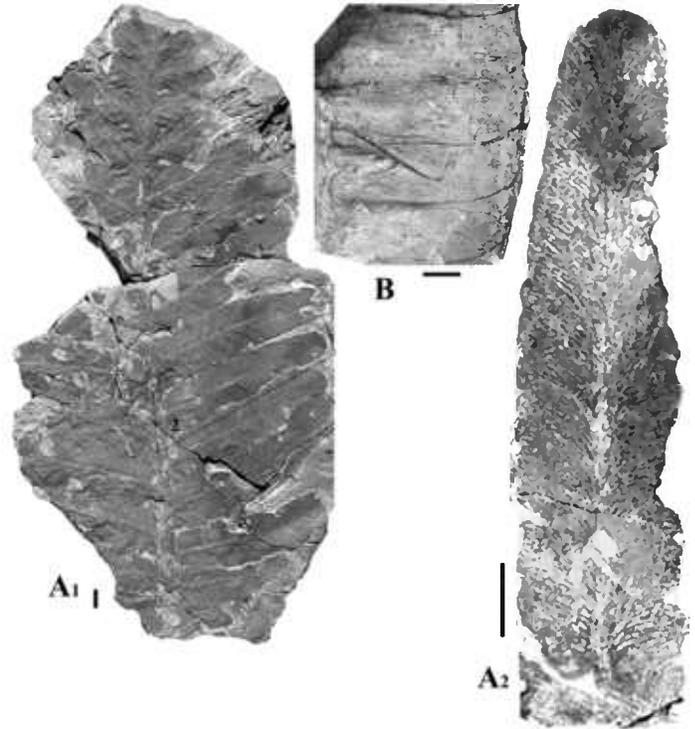In the more "primitive" members of this clade, *Gigantopteridium*

FIGURE 11. *Comia*. A) *Comia* n sp. 1, Stout Ranch locality, Texas, USNM 528459; B) *Comia* n sp. 2, Brushy Creek locality, Texas, USNM 508138. A1 – nearly complete leaf, A2 – venation detail. Bar scales = 1 cm.

and *Cathaysiopteris*, the simplicity of the venation and the size and forking of the fronds can conspire to make it difficult to distinguish small fragments from callipterids of the *Autunia* or *Rhachiphyllum* types. The overall venation pattern is distinctly callipterid in morphology and it could be argued (though, at present, in the absence of a phylogeny of this group) that gigantopterids evolved from callipterid ancestors via the lateral fusion of pinnules (Asama, 1960, 1982).

The relationships between the North American and Chinese gigantopterids remain largely uncertain. The cross-over names *Zeilleropteris*, *Cathaysiopteris*, and *Gigantonoclea* reflect similarity only in venation patterns (Mamay, 1986, 1988). In general, the American forms appear to form a distinct clade that is morphologically quite different from the Chinese forms and may have evolved similarities in venation independently, though perhaps in both instances from similar peltaspermous ancestors. The exception to this regional differentiation is "*Gigantopteridium*" *marginervum*, which appears to be identical in both regions, raising the likelihood of pathways for plant migration between eastern Cathaysia and western Euramerica during the earliest parts of the Middle Permian.

The epidermal anatomy of these plants still remains generally unknown, although it has been reported for "*Gigantopteridium*" *marginervum* (DiMichele et al., 2004).

DISCUSSION

The place of origin and pattern of dispersal of the various Permo-Carboniferous pteridosperm clades is a subject of some discussion. Through detailed examination of the biogeographic occurrences of individual fossil pteridosperm species and genera, Laveine and his colleagues (see Laveine et al., 1993, 1997) have determined that the primarily tropical, medullosan pteridosperms, particularly the neuropterids, had two centers of origination. The paripterids originated in China during the latest Mississippian or earliest Pennsylvanian and spread westward. The neurodontopterids and the neuralethopterids appear to have originated in Europe and spread out from that central part of the
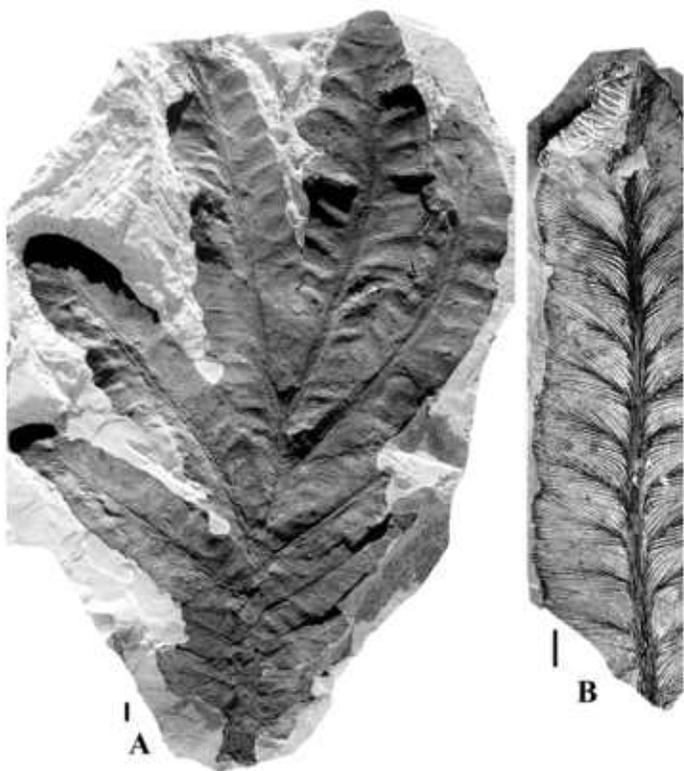
FIGURE 12. Comioid new genus. A) Colwell Creek Pond locality, Texas, USNM 508136; B) Venation detail, Colwell Creek Pond locality, Texas, USNM 528206; Bar scale = 1 cm.
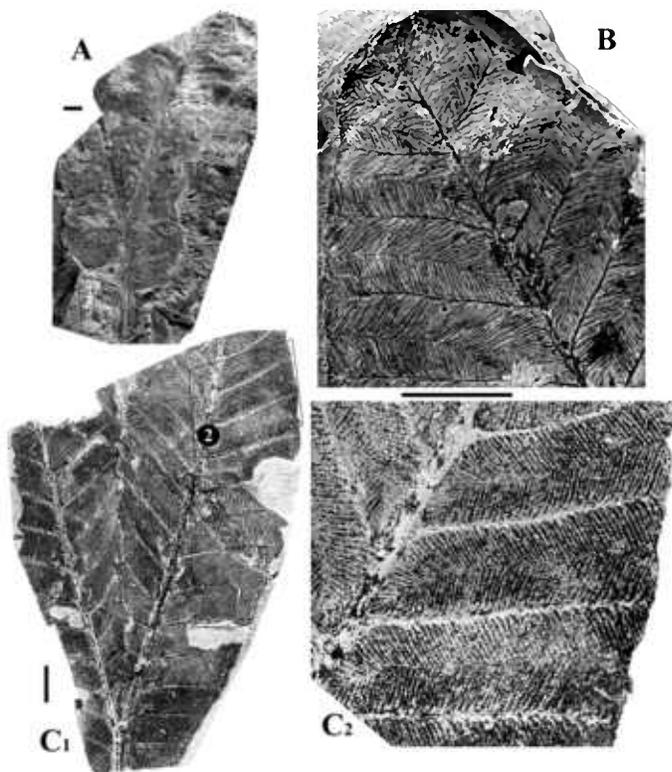

FIGURE 13. A) *Gigantopteridium americanum*, Emily Irish locality, Texas, [illustrated in Read and Mamay 1964 Pl 17-1], USNM 41768; B) *Gigantopteridium americanum*, Fulda locality, Texas, [illustrated in Read and Mamay 1964 Pl 18-1], USNM 41768; C) *Cathaysiopteris yochelsonii*, Lake Kemp Spillway locality, Texas, USNM 41776 [illustrated in Read and Mamay 1964 Pl 19-2], C1 – frond; C2 – venation detail. Bar scale = 1cm.

Euramerican-Cathaysian paleotropical floristic realm. Laveine et al. (2000) argue that an understanding of biogeography, as it relates to evolution, must be done at the level of species and genera rather than the whole-flora approach that has characterized plant paleobiogeographic studies in the past. This would mean that the so-called floral provincialism is a kind of climatic (and hence geographical) and temporal differentiation reflected in the floras rather than a strict separation in terms of isolated floral provinces. In this, global vegetational distribution is better understood in terms of regional "biomes" along the lines of those outlined by Ziegler (1990), although considerable refinement of that outline is needed. Data are still very scarce but in the Late Permian typical Cathaysian elements are found as far west as Unayzah (Saudi Arabia) (El-Khayal and Wagner, 1985), Ga'ara (Iraq) (Ctyroký, 1973), Hazro (Turkey) (Wagner, 1962; Archangelsky and Wagner, 1983), the Dead Sea region (Jordan) (Mustafa, 2003) and in the Early Permian even in as far as southern Spain (Broutin, 1986). These sphenopsid-pecopterid-dominated floras could well represent the everwet tropical vegetation in the Palaeotethys region. It is plate movements though time, interacting with the climatic effects of changing atmospheric circulation that affect the distribution of climatic conditions and vegetation, as has been suggested for the Arabian Plate by Fluteau et al. (2001). The peltasperms, based on the distributional patterns of individual taxa as far as we currently know them, appear to have followed a generally similar pattern to those medullosan clades that originated in Europe and spread from that central area. The oldest elements of the peltasperm clade appear to be the callipterids, represented by the genus *Autunia*, in particular the species *A. conferta*. This species is reported widely, if generally in low abundances, from the latest Pennsylvanian both in Europe (Barthel and Kozur, 1981; Doubinger et al., 1995; Kerp et al., 2001) and the United States (Remy, 1975).

Similarly, the first occurrences of the supaioid clade appear to be *Supaia/Protoblechnum* from the Carboniferous-Permian boundary floras in Spain (Broutin, 1986). Later occurrences of this group in the

mid-Early Permian (Artinskian/Leonardian), in the form of *Supaia* and *Glenopteris*, are in the western and west-central parts of North America (Sellards, 1900; White, 1929; DiMichele et al., submitted), slightly later in the Artinskian (Leonardian) of Texas, and also in the latest Early Permian (Kungurian) of northern Spain (Gand et al., 1996) and southern France (Doubinger and Heyler, 1975). Finally, during the Late Permian, supaioids appear in the form of *Compsopteris* in Russia (Naugolnykh, 1999) and *Supaia* in China (Wang, 1997).

The earliest reports of *Comia* are from the mid-Early Permian (Leonardian) of Texas (Mamay et al., 1996), occurring later in Middle Permian (Wordian) rocks in transition floras from the Middle East (Berthelin, 2002; Berthelin et al., 2003), and finally in Russia (Zalessky, 1934) and China (Huang, 1966) in the Late Permian.

The patterns of origin and expansion among the gigantopterids are problematic because of the uncertain connections between "American" forms and those typical of "China". The American genera mentioned in this paper all appear to originate in the southwestern United States (first reported occurrences in Texas). The earliest occurrence is very near the boundary between the Sakmarian and Artinskian (Wolfcampian-Leonardian boundary), a specimen probably assignable to the *Gigantopteridium-Cathaysiopteris* complex, preserved in a dark organic shale. These plants are rarely reported outside of the western United States. A more direct American-Chinese linkage has been asserted based on the identification of *Zeilleropteris*, *Cathaysiopteris*, and *Gigantonoclea* in Texas (Mamay, 1986, 1988), well before their first appearances in China (Li et al., 1994). However examination of the leaf architectures in these forms suggests caution in the assertion of generic identity. The leaf architecture of the American material is unknown in the case of *Gigantonoclea*, given its preservation as a single,
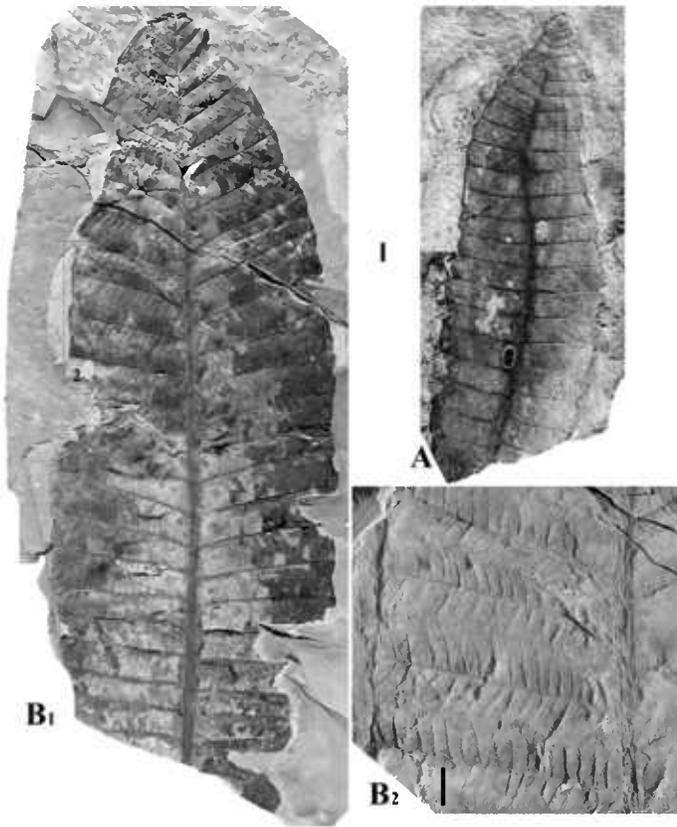
FIGURE 14. A) *Delnortea abbottiae*, Del Norte Mountains, Texas, USNM 387473; A1 – nearly complete leaf, A2 – venation detail; B) *Evolsonia texana*, Colwell Creek Pond locality, Texas, USNM 528205, A1 – nearly complete leaf, A2 – venation detail. Bar scales =1 cm.

FIGURE 15. A) *"Gigantopteridium"marginervosum*, South Ash Pasture locality, Texas, USNM 520383, B1 – base of leaf, B2 – venation detail; B) *"Gigantopteridium"marginervosum*, South Ash Pasture locality, Texas, USNM 520384; C) *Zeilleropteris* sp., Hog Creek Pond locality, Texas, USNM 528208, C1 – lamina, C2 – venation detail. Bar scales = 1 cm.

small, fragmentary specimen. The other two namesakes have either simple or forked leaves, whereas the Chinese forms of have more complex, pinnately compound fronds. A more secure linkage is indicated by the joint occurrence of *"Gigantopteridium" marginervum* in the early Middle Permian of both China (Yao and Liu, 2004) and west Texas (DiMichele et al., 2004). This latter occurrence sheds no light on biogeographic patterns because the appearances are, within the limits of long-distance correlation, contemporaneous and are on opposite ends of the Pangean tropics, which suggests long-distance, non-oceanic, overland routes for migration.

In all of these evolutionary lineages, the pattern is generally one of first appearances at tropical latitudes, but in conditions that appear to be seasonally dry or well drained, the kinds of settings Pfefferkorn (1980) termed "extrabasinal" lowlands. The data here are quite sparse, and should be considered with appropriate caution, especially given that a true "origin" of a group is going to be effectively impossible to determine exactly. Patterns of evolutionary innovation in extrabasinal areas have been identified for primitive conifers (Lyons and Darrah, 1989; Kerp et al., 1990), for some of the more derived conifer groups and some cycadophytic groups (Kerp, 1996; DiMichele et al., 2001), and as characteristic for the general floristic change from the Carboniferous to the Permian (Cridland and Morris, 1963; Broutin et al., 1990; DiMichele and Aronson, 1992; Kerp, 2000; DiMichele et al., 2004). The general phenomenon is suggested by the rare intercalation of transported specimens or floras containing these xeromorphic plants within coal-bearing sequences, otherwise characterized by hygromorphic plant associations. The xeromorphic plants and floras do not occur in direct association with the coals, but in rocks between them, and occur in such coal measure sequences long before they become prominent elements of low-elevation, basinal floras. Such a pattern is typified by the
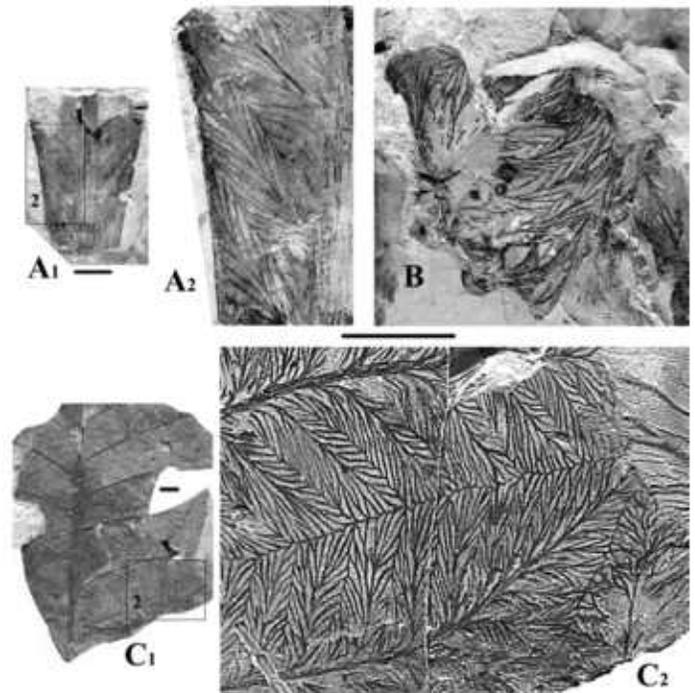
callipterids. In other instances, such as the supaioids and the comioids, earliest occurrences are in association with floras rich in conifers or other xeromorphic plants, often in channel-fill deposits cut into paleosols that have definite indications of climatic seasonality (e.g. Tabor and Montañez, 2002, in Texas). The early occurrences are followed by range expansion within the tropics, presumably as tropical climates became drier and more seasonal during the Carboniferous to Permian transition. Lastly, all groups evidence a latitudinal range expansion from tropical to north temperate latitudes during the Late Permian, as elements begin to appear in the Angaran floristic province. If these groups originated in extrabasinal areas, then tracking their migrational patterns confidently will be difficult. This is especially so early on, when the basinal tropics were wet during times of sediment deposition and tropical seasonally dry to xeric habitats are largely unrepresented in the fossil record. It is not until seasonality spread more widely in the basinal lowlands that preservation of this xeromorphic flora became the rule rather than the exception.

The persistence of the peltasperms well into the Mesozoic makes this one of the longest existing of the pteridosperm lineages originating in the Paleozoic (Kerp et al., 2001).

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