AN UPDATE ON THE FLORA OF THE KINNEY QUARRY OF CENTRAL NEW MEXICO (UPPER PENNSYLVANIAN), ITS PRESERVATIONAL AND ENVIRONMENTAL SIGNIFICANCE

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Abstract—The flora of the Kinney Brick Pit, Missourian age, central New Mexico, is revised. Total species diversity, estimated conservatively, is about 30. The flora is dominated by conifers and pteridosperms, and shows a preservational bias in favor of robust remains. Its varied composition reflects the various different habitats in the vicinity of the lagoonal (?) depositional environment. The various taxa identified are almost entirely the same as those known from Lower Rotliegend (Autunian) floras in Europe (Annularia spicata megafloral Zone).

INTRODUCTION

The Kinney Quarry site in central New Mexico is one of the few fully described Late Pennsylvanian Missourian-age floras in North America. The macroflora has been described in detail by Mamay and Mapes (1992), and particularly unusual taxonomic elements were singled out for description by Mamay (1981, 1990, 1992). Additional comments on the macroflora were included in the synthesis of Lucas et al. (2011), who determined the age of the deposit to be middle Missourian rather than Virgilian, as had long been asserted. Willard (1992) has described the palynoflora.

The flora appears to have been drawn from a coastal setting and deposited in a quiet, shallow embayment. These are certainly drifted remains preserving a mixture of plants from different habitats. It is emphasized that the collections available were made without record of the degree to which they are quantitatively similar to unbiased field collections, or of the degree to which unidentifiable fragments (comminuted plant debris) were excluded from the collections. Although plant fossils are known to come from at least two levels in the quarry, from an overall plant-bearing interval of less than 20 m thickness, collections were not systematically separated by collecting site or level. Consequently, it has not been possible to determine, from the collections themselves, if there were changes in the plant assemblages through time. Two color-variant lithologies are most common, and their floras do differ to some degree, suggesting variations of possible taphonomic or ecologic origin.

In this review, we re-illustrate the macroflora and provide some notes on the original identifications, updating some of these and adding a few additional taxa. The review is based on the collections made by Charles B. Read, Sergius H. Mamay, and Arthur D. Watt, of the U.S. Geological Survey, presently part of the collections of the National Museum of Natural History (NMNH). We stress that this is not a comprehensive systematic revision of the flora, but is intended as critical notes and an illustrated guide.

FLORA

The flora of the Kinney site is described below, and the various elements of this flora are listed in Table 1.

Lycopsids

**Sigillaria brardii** Brongniart (Fig. 1.1)

Lycopsid remains are exceptionally rare in the collections. Nearly all can be attributed to *Sigillaria brardii* (Figure 1.1) and range from small scraps of leaf cushion to larger pieces of bark with faint leaf-bases visible. This arborescent lycopsid is common throughout the Late Pennsylvanian (Stephanian) wherever originally swampy, particularly organic-accumulating environments are represented. The large amount of variation in this species (and associated nomenclature) is reflected in the exhaustive monograph by Weiss (1893) (see also the discussion and enormous list of synonymy in Crookall, 1966). One of the North American synonyms is *Sigillaria approximata* Fontaine and White (1880).

A fragment with small leaf scars (Fig. 1.2) cannot be attributed confidently to any particular kind of lycopsid, but may represent part of a small ground cover or shrubby plant. Fragments of what may have been small lycopsids appear in many floras; no doubt, given the diversity of this group today, and its apparent long evolutionary history, small lycopsids were part of many floras.

Sphenopsids

The calamitalean sphenopsids are common elements of most late Paleozoic floras, generally in a context of wet environments. Only *Calamites gigas* Brongniart appears to have been adapted to drier conditions (Barthel and Kerp, 1992). Three different kinds of calamitalean remains are encountered in the Kinney floral assemblage, including foliaceae, fertile remains (strobili) and stems/rhizomes (Fig. 2.1), the latter generally as casts. These are not uncommon in the Kinney locality, but are taxonomically insignificant. Strobili are often quite spectacular, but difficult to interpret as adpressions with respect to sporangial attachment. Adpressed leaf whorls are generally easier to interpret, particularly where flattened whorls allow the shape and proportions of the individual leaves to be observed.

Reproductive organs

Calamitalean strobili are rarely preserved in their entirety. Three different kinds are recorded from Kinney, identified by Mamay and Mapes (1992) as *Calamostachys*? cf. *ludwigii*, *Calamostachys? pedunculata* and ?*Asterophyllites* sp. However, considerable doubt was expressed with regard to these identifications, which were considered provisional.

**Palaeostachya?** sp. (Fig. 2.2)

A fairly well preserved succession of small strobili attached to a slender axis was figured by Mamay and Mapes (1992, fig. 21) as *Calamostachys? ludwigii* Weiss. There is, indeed, certain resemblance with this Westphalian taxon, but the bracts in the strobili in Kinney are more curved and not reflexed as in *C. ludwigii*. The pointed bracts largely overlap, extending upward to about two thirds of the next leaf whorl. Sporangia are poorly preserved and relatively small, thus producing a lax aspect. The position of the sporangia appears axillary.
Lycopsids
  Sigillaria brardii (stem)
  Unidentified small lycopd (stem)

Sphenopsids
  Calamites spp. (stem)
  Palaeostachya thuringiaca (reproductive organ)
  Palaeostachya sp. (reproductive organ)
  Calamostachys spicata (reproductive organ)
  Annularia spicata (foliage)
  Annularia spinulosa (foliage)
  Annularia carinata (foliage)
  Annularia sphenophylloides (foliage)

Ferns
  Nemejcopters feminaeformis (foliage)
  Danaeites emersonii (foliage)
  Pecopteris potonieii (foliage)
  Pecopteris cf. oreopteridio (foliage)
  Pecopteris cf. monyi (foliage)
  Pecopteris spp. (foliage)
  Remia pinnatifida (foliage)
  cf. Pecopteris (Discopteris?) hadrophylla (foliage)

Pteridopsperms
  Macroneuropteris scheuchzeri (foliage)
  Neuropteris ovata (foliage)
  Neuropteris cordata (foliage)
  Athropterus schneideri (foliage)
  cf. Blanzyopteris praedenta (foliage)
  Mixoneura subcrenulata (foliage)
  Mixoneura cf. gimmi (foliage)
  Neurodendropteris auriculata (foliage)
  Neurocallipteriis planchardii (foliage)
  Pseudomariopteris cordato-ovata (foliage)
  Sphenopteridium manzitanum (foliage)

Coniferophytes
  Walchia piniformis (stems, foliage)
  ?Hermitia schneideri (stems, foliage)
  Culmitzschia cf. C. speciosa or C. laxifolia (stems, foliage)
  Ernestiodendron filiciforme (stems, foliage)
  Dickranophyllum radiati (foliage)
  Gymnothorbus sp. (reproductive organ)
  Cordaites spp. (foliage)
  Cordaitanthus sp. (reproductive organ)
  cf. Podozamites sp. (stem, foliage)

Noeggerathiales
  Plagiozamites rochei (foliage)
  Charilia manzitanana (foliage)

Cycadopsids?
  Taeniopteris sp. (foliage)

Palaeostachya thuringiaca (Weiss) Barthel (Fig. 2.3)

A single, pedunculate strobilus (figured as Calamostachys? pedunculata Weiss by Mamay and Mapes, 1992, fig. 2J) shows a Calamites stem with longitudinal ribbing, to which are attached several slender "branches" possessing well spaced whorls of tiny upswept leaves or bracts (although sporangia are absent). These thin "branches" are placed in such a manner as to suggest insertion on the stem nodes, and some of them are certainly attached.

The most obvious comparison is with Calamostachys spicata as figured and described by Remy and Remy (1975) as a special variety, which has not been accepted as such by later authors. The most complete specimen figured by Remy and Remy (1975, taf. 12, fig. 1) was partially refuged by Barthel (2012, abb. 2) with a very instructive enlargement (Abb. 2a) showing curved bracts similar to the leaves of Annularia spicata (Guthier) Schimmer.

It may well be that Asterophyllites dumasii Zeiller, with Calamostachys strobili, as figured and described by Zeiller (1892) from Autunian strata at Brive, Massif Central, France, should be regarded as identical to Annularia spicata (even though Zeiller did not seem to consider this possibility). Kerp (1984) pointed out that the remains figured as A. dumasii probably represented strobili from which the sporangia had been removed. In this case, the upswept, sideways flattened foliar elements identified as Asterophyllites would be bracts rather than leaves. The bracts would be less "fleshy" than the leaves (see below under A. spicata), although the broadly curved shape is identical. Although Kerp's interpretation of the "Asterophyllites" as strobili without preserved sporangia is accepted by the present writers, there is some doubt about his identification of "dumasii" for the material he described from Sobernheim, Saar-Nahe Basin, Germany. This material from Sobernheim shows stiffer, straighter bracts, and there is also a suggestion that the positioning of its sporangia might fit Palaeostachya rather than Calamostachys. However, sporangial insertion is not always straightforward, as interpreted from adpressions. It is noted that Gastaldo (1981) referred to Good (1975) for regarding Calamostachys and Palaeostachya as artificial genera; Gastaldo cited Calamostachys spicata as an intermediate case.

Annularia spicata (Guthier) Schimmer (Figs. 3.3, 3.4)

The small, rather "fleshy," pointed and curved leaves of this species are illustrated quite well by Mamay and Mapes (1992, fig. 2E) under the name of Annularia cf. asteris Bell. The latter is another species characterized by small, pointed leaves. However, these are narrower and not quite as "fleshy" as those of Annularia spicata, which are also more distinctly curved.

Annularia spicata has been profusely illustrated from various Lower Rotliegend (Autunian) localities in eastern Germany by Barthel (2012), who also discussed its synonymy and the various records of this species in the general type area (Guthier's types are from the Erzgebirge in Saxony). This species is widespread in Europe and characteristic for the highest Stephanian, i.e. the Autunian Substage (see Wagner and Alvarez-Vazquez, 2010a – an earlier Stephanian record of A. spicata, op. cit., table 8, is due to an error of transcription). In the Appalachian region of North America, it is recorded from the Conemaugh (post-Mahoning), Saar-Nahe Basin, Germany. This material from Sobernheim shows stiffer, straighter bracts, and there is also a suggestion that the positioning of its sporangia might fit Palaeostachya rather than Calamostachys. However, sporangial insertion is not always straightforward, as interpreted from adpressions. It is noted that Gastaldo (1981) referred to Good (1975) for regarding Calamostachys and Palaeostachya as artificial genera; Gastaldo cited Calamostachys spicata as an intermediate case.

Calamostachys spicata (Guthier) Remy and Remy (Figs. 3.1, 3.2)

A single specimen figured as ?Asterophyllites sp. by Mamay and Mapes (1992, fig. 2H) shows a Calamites stem with longitudinal ribbing, to which are attached several slender "branches" possessing well spaced whorls of tiny upswept leaves or bracts (although sporangia are absent). These thin "branches" are placed in such a manner as to suggest insertion on the stem nodes, and some of them are certainly attached.

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may be borne at nearly right-angles to the stem. Some give the impression of being fused in their basalmost parts, though this is uncertain. In addition, Mamay and Read (1956) described whorls of up to 20 leaves. No whorls with that high a leaf count are present in this single specimen from Kinney.

**Annularia spinulosa** Sternberg (Fig. 4.2)

Barthel (2004) has argued that *Annularia spinulosa* should be preferred to the more commonly used name *Annularia stellata* (Schlotheim) Brongniart, not only because the International Code has declared Schlotheim’s names illegitimate, but also because Schlotheim’s type specimen could not be located (and is possibly lost). It also appears that *A. spinulosa* has pointed leaves, whereas specimens identified as *A. stellata* in the literature often show blunt leaf endings. The remains with several leaf whorls as found in the Kinney locality conform to the characters of *A. spinulosa* as figured from its type area in Saxony (Lower Rotliegend of Döhlen Basin).

This specimen was identified as *Annularia cf. pseudostellata* Potonié by Mamay and Mapes (1992, Fig. 2F). The latter, however, has more parallel-sided leaves in laxer whorls than occur in *Annularia spinulosa*.

**Annularia carinata** Gutbier (Fig. 4.3)

Two anisophyllous leaf whorls are shown with closely spaced mucronate leaves showing their maximum width in the upper third of the leaf length.

This is a highly characteristic species figured and described from the Lower Rotliegend (Autunian) of Saxony (e.g. Barthel, 2004, abb. 19, 20). It has been synonymized with *Annularia mucronata* Schenk (op. cit.). This species is regarded as widespread but uncommon with a stratigraphic range from Saberian to Autunian.

**Annularia sphenophylloides** (Zenker) Gutbier (Fig. 4.4)

A single, anisophyllous leaf whorl has been illustrated under this name by Mamay and Mapes (1992, fig. 2G). This long-ranging species (from late Bolsovian upwards throughout the entire Stephanian) is both common and easily recognized by its rather short, spatulate, mucronate leaves, which are normally very closely spaced. The earliest occurrence of *Annularia sphenophylloides* in the Appalachian region is recorded as upper Kanawha by Blake et al. (2002). This would correspond to upper Bolsovian in Europe.

**Ferns**

Identifiable fern remains are rare in the plant assemblage. However, due to various factors, the degree of difference between the abundance of ferns in the original vegetation and that in the fossil assemblage is difficult to quantify. Fern foliage in general is usually thin-limbed and species characterized by more sturdy laminae are relatively uncommon. Combined with prolonged maceration in water, non-robust construction will lead to decay of tissues and disintegration of fern foliage, particularly if there is no thick cuticle to hold pinnules together. Ground cover and low stature ferns, in particular, tend to be undersampled in most fossil floras, particularly when there was a well developed canopy that shielded low-growing plants from the effects of wind (Scheihing, 1980).

Pennsylvanian ferns are preferably classified on sporangial structures. This is particularly relevant for the incised pinnules with fan-shaped venation, which are regarded as sphenopteroid (with reference to *Sphenopteris* Brongniart, a morphogenus). Certain genera with sphenopteroid foliage (e.g. *Discopteris*) have more sturdy laminae and are thus more capable of resisting disintegration. The other large group of fern-like foliage, the pecopteroids (after *Pecopteris* Brongniart, another morphogenus), may also be classified on sporangiate structures. However, the most common synangia, *Scolecopteris* (*Asterotheca*), occur in...
many different forms of pecopteroids, which may be subdivided in more detail on pinnule and venation development.

Pecopteroid fern remains are uncommon in the Kinney plant assemblage. On the whole, these are small fragments with poorly preserved venation, making identification difficult. A notable exception is a quite characteristic species (here identified as *Pecopteris potoniei* Nemejc) that Mamay and Mapes (1992) recorded as *Pecopteris* sp. (their Fig. 3B, G, non A). These specimens are fertile (*Asterotheca*) and it seems that the fairly large specimens may owe their cohesion to the sporangial cover, which lent strength to the pinnules.

It must be emphasized that preservational conditions may have thinned out the total representation of floral elements to the detriment of the ferns.

*Nemejcopteris feminaeformis* (Schlotheim) Barthel (Fig. 5)

Zygopterids, a large group of ferns with habits ranging from small trees to groundcover (Barthel, 1968; Phillips and Galtier, 2005), are represented by small fragments of foliage belonging to *Nemejcopteris feminaeformis*. This foliage is very recognizable, with elongate simple veins that terminate in the marginal teeth; thus, even small debris can be identified. *Nemejcopteris feminaeformis* occurs throughout the Stephanian, from Barruelian upwards.
**Danaeites emersonii** Lesquereux (Fig. 6.1).

Clearly a marattialean fern, fertile examples of *Danaeites* can be identified by the elongate synangia (fused groups of sporangia) on the lower surfaces of pinnules. *Danaeites emersonii* is most easily recognized on fertile remains, but can also be distinguished on the relatively broad, closely spaced pinnules with a rounded apex and at least twice bifurcate vein groups. *Danaeites* is characteristic of mid-Stephanian (Saberian) and younger rocks (Wagner and Álvarez-Vázquez, 2010a).

**Pecopteris (Asterotheca) potoniei** Nemejc (Figs. 6.2, 7)

Among the remains of pecopterid foliage are fairly large specimens, such as that figured by Mamay and Mapes (1992, fig. 3B, re-illustrated here, Fig. 7), which shows the subtriangular shape of widely spaced pinnules and gradually tapering pinnae with a small, poorly individualized apical pinnule. The pinnule lamina is covered by sporangia in a stellate pattern (*Asterotheca, Scolecopteris*). The veins are almost invariably obscured. In the rare cases where they are not (Fig. 6.2), the widely spaced lateral veins regularly fork once, with a second bifurcation occurring in the basal basiscopic part of larger pinnules.

The nearest comparison is with *Pecopteris (Asterotheca) potoniei* Nemejc, from the Rotliegend of Thuringia, Germany. This form, misidentified as *Pecopteris pennaformis* Brongniart by Potonié (1893, taf. IX, figs 1-2), was renamed by Nemejc (1940, p. 14-15). It has the subtriangular, well-spaced pinnules that are partially fused at the base with adjacent pinnules. Lateral veins are generally once forked and rarely
fork once again in the basal part of the longer pinnules. The size and shape of both pinnules and pinnae are the same for the Thuringian species and the material at hand. It is therefore proposed to accept a direct identification.

The relative frequency of these remains at Kinney (about 5% of the specimens in the collection) and their fairly large size probably can be explained as a result of increased cohesion due to the presence of sporangia, which would have made these (invariably fertile) remains more resistant to disintegration on (prolonged) maceration in water.

Pecopteris cf. oreopteridia (Schlotheim) Brongniart (Fig. 8.1)

A penultimate pinna fragment shows gradually fused, rapidly tapering pinna terminals with a poorly individualized, subtriangular apical pinnule. Poorly preserved lateral pinnules are up to twice as long as broad, with rounded apices, and tending toward a subtriangular shape. Veins are barely discernible, but a well developed midrib seems to be present, and there is a suggestion of rather widely spaced laterals.

The size and shape of last order pinnae characterized by rather short, gradually fused terminals allow comparison with Pecopteris...
FIGURE 5. Fern foliage. *Nemjcopteris feminaeformis* foliage. **6.1**, USNM specimen 558134 (Mamay and Mapes, 1992, Fig. 3F). **6.2**, USNM specimen 450779. Scale bars in mm.
FIGURE 6. Fern foliage. **6.1**, *Danaeites emersonii*, fertile, USNM specimen 450776 (Mamay and Mapes, 1992, Fig. 3C). **6.2**, *Pecopteris* cf. *potoniei*, USNM specimen 558263. Scale bars = 1 cm.

FIGURE 7. Fern foliage, *Pecopteris* (*Asterotheca*) *potoniei* Nemejc, fertile. **7.1**, Terminal portion of a pinna, USNM specimen 450780 (Mamay and Mapes, 1992, Fig. 3B), scale bar in mm. **7.2**, Higher magnification view of specimen in 7.1, scale bar = 1 cm.
(Scoleopteris) oreopteridia as figured by Barthel (1980, taf. 1) from its type area. The pinnule shape is also similar. A definite identification is precluded by the lack of detail with regard to venation.

**Pecopteris cf. monyi** Zeiller (Figs. 8.2, 8.3)

A fairly large fragment of a penultimate pinna shows a broad rachis with up to six pinnules inserted on either side. No pinna terminals are preserved. Pinnules are subtriangular, apparently thin-limbed, with a thin, decurrent midrib. Lateral veins are indistinct, but possibly rather widely spaced. The subtriangular shape of pinnules with an apparently thin lamina, and showing a decurrent midrib, suggest *Pecopteris monyi*, as described from the Massif Central, France. This is a reasonably common species in the Stephanian of Europe. In the absence of details about the lateral veins, the specimen in hand can only be identified tentatively. It is noted that *Pecopteris monyi* needs a critical revision in view of the fact that several pecopterids with a sloping midrib have been figured under this name in the literature.

**Pecopteris sp. indet.** (Figs. 8.4)

This is a small fragment, only 2.5 cm long, which shows parallel-sided pinnules with a thin, slightly decurrent midrib and once bifurcate veins. There is a certain resemblance to *Pecopteris oreopteridia* (Schlotheim) Brongniart, but this pinna fragment is too poorly preserved to insist on the determination. There is a suggestion of a small apical pinnule, such as occurs in *Pecopteris densifolia* Göppert, but this seems to be a fortuitous superposition of pinna fragments rather than an organic connection.

**Remia pinnatifida** (Gutbier) Knight emend. Kerp et al. (Fig. 9.1)

A single pinna fragment of the penultimate order shows a sturdy rachis on which short, bluntly terminated last order pinnules are inserted at a high angle. Some pinnules are preserved as small, though well individualized, elements with a vaulted lamina showing deeply immersed veins consisting of a short midrib and oblique, simple and once bifurcate laterals. A portion of this specimen may be fertile, although this is open to interpretation, given the state of preservation.

*Remia pinnatifida* occurs from Saberian (Knight, 1985) to Autunian (e.g. Barthel, 2005; Kerp et al., 1991) in Europe (compare Wagner and Álvarez-Vázquez, 2010a). It does not seem to have been recorded previously from North America. The specimen recorded here has been transported and it not well preserved, but is sufficient to show the salient characters of this species.

**cf. Sphenopteris (Discopteris?) hadrophylla** Knight (Fig. 9.2)

A poorly preserved specimen consisting of two parallel pinnules showing fairly robust pinnules with subrounded, perhaps angular lobes is compared with this species, which was described from Saberian and Stephanian B strata in NW Spain (Knight and Wagner, 2012). Pinnule laminae are too faintly preserved (as a result of maceration) to show the lobate pinnule margins in sharp outline. Only remnants of the venation can be seen, thus allowing limited recognition. As far as can be seen, the veins appear to fork once and are strongly apically directed. Following bifurcation, the resultant veins curve in the same direction, thus forming a rather closed space between them. In the smaller pinnules, the veins are almost concave upward and a midvein is not well developed.

*Sphenopteris hadrophylla* is characterized by its sturdy pinnules with a vaulted lamina. This would have allowed fragments of this species to be preserved where other sphenopterids with a thinner lamina would have fallen apart.

**Pteridosperms**

The pteridosperms, also known as seed ferns, are a common element overall in the Kinney flora. They are represented by several taxa and present an array of variation that is challenging to sort out when dealing with fragmentary specimens.

**Macroneuropteris schuchzeri** (Hoffmann) Cleal, Shute and Zodrow (Figs 10.1, 10.2)

This species is represented by large, elongate, linguoid pinnules with characteristic short, apically directed surface hairs (see Laveine and Behlis, 2007). This plant is typical of wetland habitats (Stull et al., 2012), and in some Virgilian floras, such as that from north-central Texas, the taxon is found in dense, nearly monospecific accumulations in environments transitional between clastic to peat-forming swamps (DiMichele et al., 2005; Tabor et al., 2013). The presence of *M. schuchzeri* in the Kinney flora, as with Sigillaria, suggests that standing water or periodically flooded swamps were present in places on the landscape. *Macroneuropteris schuchzeri* has an appreciably longer range in North America than it has in Europe, where it occurs in strata up to and including the upper Cantabrian (Wagner and Álvarez-Vázquez, 2010a).

**Neuropteris ovata** Hoffmann (Figs 11, 12, 13)

This taxon encompasses a considerable range of variation, some of which has been segregated at the species or subspecies level (see illustrations and discussion in Castro, 2005). In its most characteristic form (Figs. 11 and 12.2), pinnules of *Neuropteris ovata* are short and tongue-shaped, with a distinct basal “auricle” – a small extension of the lamina directed basiscopically. The lateral veins are fine, dense, and arch toward the margin from a thin, often weakly developed midvein. In the terminal portions of pinnae, lateral pinnules may become broadly attached to the rachis and fuse to various degrees (see particularly Fig. 12.2). There is considerable variation in this basic ground plan, expressed in the size and shape of the terminal pinnules, lateral pinnule size and shape, and degree to which pinnules near the termini of pinnae are fused to the rachis or to one another (see, for example, the large size of the *N. ovata*-like pinnules illustrated in Fig. 13, or the specimens illustrated in Fig. 20, the affinities of which could be with *N. ovata* or *Neurodontopteris auriculata* – see below). Given the range of variation encompassed by specimens assigned to this species at different times and places, it might be concluded that *Neuropteris ovata* is in fact a species complex comprising several subtly different species.

The specimens collected from Kinney Quarry show the relatively broad pinnules with a dense venation that is characteristic of *Neuropteris ovata var. grandeaury* of Wagner (1963). This refers to *Neuropteris flexuosa* Grand’Eury (non Sternberg) as figured by Bertrand (1930) from the Cévennes in the French Massif Central. It is a rare element in the classic Stephanian floras of the Massif Central (figured as *Neuropteris ovata* by Doubinger et al., 1995, from Saint Étienne, and misidentified as *Neuropteris heterophylla* Brongniart by Zeiller, 1890, pl. XII, fig. 1 from Épiauc). *Neuropteris ovata* is a common species in the coastal Stephanian basins of NW Spain, up to and including the Saberian substage level (sensu Wagner and Álvarez-Vázquez, 2010a), and occurs less frequently higher up (e.g., Stephanian C of Puertollano, Wagner, 1985). It is shown as ranging throughout the Allegheny, Conemaugh, Monongahela and Dunkard of the Appalachian Basin in North America (Blake et al., 2002). This species appears to have been closely tied to swampy, frequently peat-forming habitats (Stull et al. 2012).

**Neuropteris cordata** Brongniart (Fig. 14)

A poorly preserved fragment of the terminal part of a penultimate pinna shows elongate pinnules, 2.5 to 3 times longer than broad, with subparallel margins and a bluntly pointed apex. Pinnule attachment is neuropteroid. The terminal pinnule is relatively short and more or less individualized, with a rounded apex. In the lower part of this specimen, small, subcircular pinnules are separated off from the basal parts of pinnules in the process of being converted into last order pinnae.

The pinnule lamina seems fairly sturdy, but not vaulted, with a thin midrib marked clearly for about two thirds of the pinnule length. Lateral veins arise at a narrow angle and curve away from the midrib to reach the pinnule margin slightly obliquely.
The nearest comparison is with *Neuropteris cordata* as figured by Barthel (1976, tafn 33-34) from the Lower Rotliegend (Autunian) of Saxony. Barthel’s photographs and drawings illustrate a range of morphological variation into which the specimen from Kinney fits without difficulty.

Cleal and Shute (1995) regarded *Neuropteris cordata* as a poorly known species (Brongniart’s holotype is a single pinnule), which they considered as possibly the same as *Neuropteris pseudoblissii* Potonié. This is not a foregone conclusion however. At least two different species have been recorded in the literature as *Neuropteris cordata*, and Cleal and Shute (1995) are correct that this species is in need of revision. With regard to the specimen from Kinney Brickpit, it suffices that this specimen fits the well illustrated material recorded as *Neuropteris cordata* from Germany.

**Alethopteris schneideri** Sterzel (Fig. 15)

A single specimen in the NMNH collections can be referred to the genus *Alethopteris*. It is only a small fragment (Fig. 15) but it seems fairly characteristic of this later Stephanian or early Rotliegend plant (compare Barthel, 1976), which is regarded as latest Stephanian by Wagner and Álvarez-Vázquez (2010a). As is typical of this species, the pinnules are inserted obliquely, are elongate with obtusely rounded ends, have a fairly deep acroscopic incision, and a relatively dense venation. The specimen also compares to some extent with *Alethopteris zeilleri*, although the latter’s venation is coarser and the pinnule insertion is more nearly perpendicular.

**cf. Blanzyopteris praedentata** (Gothan) Krings and Kerp (Fig. 16)

Several neuropteroid pinnules from the Kinney collections re-
FIGURE 10. Pteridosperm foliage. 10.1-10.2, Macroneuropteris scheuchzeri, USNM specimen 450786 (Mamay and Mapes, 1992, Fig. 5B). 10.3, Neurodontopteris auriculata, USNM specimen 450789 (Mamay and Mapes, 1992, Fig. 5D). Scale bars = 1 cm.

semble Blanzyopteris praedentata (Krings and Kerp, 1999). All are fragmentary, but show the pointed shape and crenulate margin of this rare species. This species was formerly treated as Neuropteris by Gothan (1909). Cleal and Shute (1995) treated it as Sphenoneuropteris; however, Sphenoneuropteris Schegolev, with two species, is a synonym of Ulvopteris crenulata (Brongniart) (unpublished data, RHW). Blanzyopteris has variable pinnule shapes, strongly dependent on position within the frond. Importantly, pinnules may have denticulate margins, particularly in the upper one-third. Veins are sparse, widely spaced, strongly marked and steeply arching. They terminate in marginal crenulae or teeth in those pinnules in which crenulate margins occur. Terminal pinnules are elongate and tongue shaped. Krings and Kerp (1999) noted that the species is only known conclusively from the Massif Central of France, and questioned other reports (from Spain, Portugal and Russia). The taxon was erroneously identified in the Kinney flora as Neuropteris pseudoblissii (listed in Lucas et al., 2011, p. 18). Neuropteris pseudoblissii also is Stephanian in its stratigraphic distribution, the species being typified on material from Commentry in France (Crookall [1959] identified a single Westphalian/Duckmantian specimen from Britain, but that seems to have been in error). Krings and Kerp (1999) make a strong case for a climbing growth habit in B. praedentata.

Mixoneura subcrenulata (Rost) Zeiller (Figs. 17.1, 17.2, 18)

A large number of specimens in the Kinney collection is attributed to the group of species within the genus Mixoneura, originally defined as a subgenus of Odontopteris Brongniart by Weiss (1870). It is quite different from Odontopteris sensu stricto (see discussion in Wagner and Castro, 1998, and Laveine and Dufour, in press). Although a larger number of species are currently attributed to this genus than Weiss originally
envisaged, the most common elements of Mixoneura belong to the subcrenulata-lingulata group and that around Mixoneura schlotheimii (Brongniart) (= osmundaeformis Schlotheim), with Mixoneura pseudoschlotheimii de Maistre as a possible synonym. Essentially, M. subcrenulata and M. lingulata are characterized by largely fused, rather massive terminals, whereas M. schlotheimii shows more gradually tapering, less fused terminals.

Doubinger and Remy (1958) compared Mixoneura subcrenulata with Mixoneura lingulata from upper Stephanian strata (including Lower Rotliegend) in Germany and France. They distinguished M. lingulata primarily on the more largely fused terminals and subdivided M. subcrenulata into three different varieties, which they suggested might be regional varieties. The subtleties of varietal differentiation may be difficult to grasp, but it is clear that the more commonly found M. subcrenulata has a longer recorded range. This range is extended downward into lower Cantabrian by a single find reported by Iwaniw (1985). For a recent figuration and discussion of Mixoneura subcrenulata from France, see Krings et al. (2000). These authors (op. cit., p. 387) regarded Mixoneura lingulata as a successor to Mixoneura subcrenulata, thus suggesting a link between these two taxa.

The taxon represented at Kinney shows an array of morphologies that seem to have been derived from different parts of fronds. One population of specimens consists of pinnae bearing clearly individualized pinnae, each with a rounded shape, a broad basal attachment, and multiple vein entries into the lamina (Fig. 17.1, 17.2; 18.7). Such pinnae typically have large, irregularly triangular, blunt apical pinnae (Fig. 17.1, 17.2). The other population consists of frond segments in which pinnae comprise small pinnules at the base, these fusing into elongate tongue-shaped laminar elements with strong midribs, which terminate the pinnae (Figs. 18.1 – 18.4). In some specimens, this transition is very subdued, and the free pinnae are little more than lobes at the pinna base (Figs. 18.5, 18.6). The more fused pinnae segments probably are from more distal, apical portions of the frond, whereas pinnae with more abundant and better-developed free pinnae at their base are from more proximal parts. The mixoneuroids, as a group, had highly variable frond morphologies (e.g., Odontopteris schlotheimii as figured by Barthel and Amelang, 2011, fig. 3), with an array of pinnule shapes that, if viewed in isolation, could easily be placed into several species, or even different
FIGURE 12. Pteridosperm foliage, *Neuropteris ovata*. 12.1, Large specimen, USNM specimen 422651 (part of left, upper portion of this specimen was illustrated by Mamay and Mapes, 1992, Fig. 4A; specimen edge is a break that has since been repaired). Scale bar = 5 cm. 12.2, USNM specimen 450781 (Mamay and Mapes, fig. 4C). Scale bar = 1 cm.
genera. A large number of specimens is needed in an assemblage to ascertain the range of variability of a single species.

Some of the specimens from Kinney Quarry assigned to Neuropteris ovata by Mamay and Mapes (1992; e.g., their fig. 4D) might belong to Mixoneura subcrenulata. In comparison with typical Neuropteris ovata, these examples show more ovoid pinnules in overall aspect that are not auriculate and are broadly attached to the rachis. A midrib is not developed in all the lateral pinnules of these specimens. They also display rather massive, spoon-shaped terminals.

**Mixoneura cf. gimmii (Remy and Remy) Wagner (Fig. 17.3)**

Within the group of Mixoneura subcrenulata-lingulata, there is a third species, Mixoneura gimmii, which is quite similar to Mixoneura subcrenulata, were it not for a preponderance of neuropteroid pinnules. First described by Remy and Remy (1958), from the Lower Rotliegend of Manebach, Thuringia, it has later been recognized, with abundant material, from the Autunian of Valdeviar, SW Spain (Wagner and Mayoral, 2007, fig. 25). One specimen from Kinney (Fig. 17.3), showing an apparently quite massive pinna terminal (only partially preserved) and partly mixoneuroid and partly neuropteroid ovoid pinnules, is most comparable. This specimen was figured previously by Mamay and Mapes (1992, fig. 4B) as Neuropteris and compared with Neuropteris heterophylla Brongniart. Although the latter does show mixoneuroid pinnules in part of the frond, the shape and proportion of the pinnules are quite different, and the comparison with Neuropteris heterophylla has been rejected (Lucas et al., 2011). A second specimen with ovoid pinnules and a fairly massive terminal (Fig. 30.3) may possibly be ascribed to this species as well.

The problem with the mixoneuroid fragments in the Kinney flora is the great difficulty in determining intraspecific variation. Because this is a transported and mixed assemblage of plant fragments of varied provenance, it is unlikely that similar plant remains might have originated from the same parent plant.
Neurodontopteris auriculata (Brongniart) Potonié (Figs. 10.3, 19.1, 19.2, and possibly Fig. 20)

Among the most common fragmentary pteridosperm remains in the Kinney flora are those of a neuropteroid very similar to that described by Knaus and Lucas (2004) from the Carrizo Arroyo locality in central New Mexico (latest Pennsylvanian to earliest Permian). The plant has highly variable foliage morphology, with pinnule attachment ranging from neuropteroid to mixoneuroid. Knaus and Lucas (2004) recognized the different fragments as belonging to a single species due to the preservation of relatively large frond segments. However, the frond reconstruction of Knaus and Lucas (2004, fig. 1) is likely not justified by the fragmentary remains figured. With regard to the specimens encountered in Kinney Quarry, the pinnules are generally elongate with rounded apices and bases (Fig. 19.1, 19.2). They have dense lateral veins and a variably distinct midrib. Some pinnules are markedly elongate with both basiscopic and acrosopic auriculae (Fig. 10.3, Fig. 20). These auriculate forms enter into the range of variation of Neurodontopteris auriculata (Laveine and Dufour, in press), particularly in their variable pinnule shapes and insertion angles, a dense but often somewhat variable lateral venation, and a midrib that is strong at the base and dissipates in the upper third of the pinnule.

Neurodontopteris auriculata was distinguished as a separate generic entity by Potonié (1893) on the basis of possessing both neuropteroid and odontopteroid pinnule attachment. He compared with Mixoneura Weiss, which was based on “Odontopteris” subcrenulata (Rost) Zeiller, and admitted that small fragments of the latter might be confused with partial remains of Neurodontopteris auriculata. He quite correctly saw Brongniart’s species as more neuropteroid than odontopteroid, while Mixoneura was taken out of Odontopteris (sensu lato). Cleal and Shute (1995) briefly discussed Neurodontopteris auriculata, which they apparently accepted as a monotypic genus, but did not compare it with Mixoneura, presumably because they regarded the latter as an odontopterid and, thus, not immediately comparable. Laveine and Dufour (in press) recently discussed the frond morphology and variation in pinnule shape and attachment of Neurodontopteris auriculata.

Doubinger et al. (1995, p. 199, 202) figured Neurodontopteris auriculata from its type area, the Saint Étienne Basin in central France (Brongniart, 1831, p. 236), and referred it to Neuropteris osmundae (Artis) Kidston, following a synonymy published by Crookall (1959). However, this rare Westphalian species is known too incompletely for a proper identification with Neurodontopteris auriculata.

Neurodontopteris auriculata is also a rare element, although ap-
parently quite widespread. It is commonly reported from high Stephanian strata, but there is a mid-Stephanian (Sabarian) record from NW Spain (Wagner, 1963), albeit on very fragmentary remains. It may be an element of drier habitats, although in a general “coal-measure” context.

Neurocallipteris planchardii (Zeiller) Cleal, Shute and Zodrow
(Fig. 19.3)

A small number of specimens in the collections conform fairly well to the taxon Neurocallipteris planchardii (Figs 19.3) (see Zeiller, 1906; Doubinger et al., 1995; Laveine and Dufour, in press). The specimens have neuropteroid pinnules with a narrow attachment to the rachis, a cordate base, and almost parallel lateral margins that taper toward a rounded apex. The lateral venation is dense and arcs strongly to meet the margin at almost right angles, a strongly marked midrib is present, reaching to near the pinnule apex. Neurocallipteris planchardii is a rare element, occurring throughout the Stephanian, but often recorded from single pinnules, which have not always been identified beyond doubt.

Pseudomariopteris cordato-ovata (Weiss) Gillespie, Clendening and Pfefferkorn (Figs. 21, possibly 30.1)

Pseudomariopteris Danzé-Corsin belongs to the callistophytalean pteridosperms, a group of small, scrambling to climbing forms (Kings and Kerp, 2000). In the Kinney flora, only a few fragmentary specimens could be attributed to this genus, specifically to P. cordato-ovata. The specimens conform to this species, as re-diagnosed by Krings and Kerp (2000), in having small, more or less ovoid pinnules with a constriction above the wide basal attachment and a thick-lamina, which often obscures the venation, leaving only the short midrib well marked (Fig. 21). No pinnae with the characteristic tendril-like terminals have been collected. Elsewhere in the paleoequatorial belt, P. cordato-ovata is a common element (Wagner and Álvarez-Vázquez, 2010a; Tabor et al., 2013). The species has a long stratigraphic range, extending from the upper Middle Pennsylvanian (upper Asturian) into the highest Upper Pennsylvanian (Autunian) (Wagner and Álvarez-Vázquez, 2010a).

Sphenopteridium manzanitanum Mamay (Figs. 22.1, 22.2)

Fairly abundant material of a small bifurcate frond with sphenopteroid foliage has been described by Mamay (1992) as a new species of Sphenopteridium, a generic attribution normally applied to plants of Mississippian age. Mamay’s determination of Sphenopteridium manzanitanum is based on the bifurcate frond morphology, the deeply incised rather thick-limbed pinnules with a fan-shaped venation and, above all, the faint imprint of a fertile structure comparable to that of Diplopteridium teilianum Walton and identified as Telangiopsis. Mamay’s
poorly preserved and that its attachment to the vegetative frond has not
that its attachment to the vegetative frond has not

FIGURE 17. Pteridosperm foliage. 17.1, Mixoneura subcrenulata, USNM specimen 450788, note marginal arthropod feeding damage, especially on large terminal pinnule (Mamay and Mapes, 1992, Fig. 3E). 17.2, Mixoneura subcrenulata, USNM specimen 450782, note marginal arthropod feeding damage, especially on large terminal pinnule (Mamay and Mapes, 1992, Fig. 4D). 17.3, Mixoneura cf. gimmii, USNM specimen 450783 (Mamay and Mapes, 1992, Fig. 4B). Scale bars in mm.

description is impeccable, but it is admitted that the fertile material is poorly preserved and that its attachment to the vegetative frond has not been demonstrated (even though its relative position is suggestive).

Mamay’s attribution of this material to Sphenopteridium was surprising because this genus was regarded as exclusively Mississippian. However, the present writers regard this attribution as worthy of serious consideration, and his suggestion that the Kinney material would represent a “lazarus” taxon is quite reasonable. However, Mamay (1992) did not compare his specimens with Sphenopteris germanica Weiss (1879). This Lower Rotliegend plant shows the same bifurcate frond structure (Remy and Renny, 1977, bild 87c; Rössler and Barthel, 1998, pl. X, fig. 2) and pinnule shape and venation as Sphenopteridium manzanitanum, with a degree of morphological identity that allows considering both species as probably one and the same. Fertile axes with synangia composed of partly coalesced sporangia have been described as Schuetzia anomalala by Geinitz (1863), and assigned to Sphenopteris germanica by Gothan (1937). The latter pointed out that Schuetzia anomalala possesses bifurcate axes with short transverse bars (op. cit., taf. 27, figs 2, 3), which are also seen in the associated remains of Sphenopteris germanica. Gothan (1937) also mentioned the consistent association of Schuetzia with Sphenopteris germanica in several Lower Rotliegend localities in Germany. Remy and Rettschlag (1954) macerated spores from Schuetzia anomalala, which they regarded as a male sporangiate structure. Although the attribution of this presumed male synangiate structure to “Sphenopteris” germanica cannot be regarded as fully secure, the circumstantial evidence points in this direction. It would also suggest that “Sphenopteris” germanica is a pteridosperm.

The fertile specimen associated with Sphenopteridium manzanitanum is too poorly preserved to allow a straightforward identification with Schuetzia anomalala, but there is a vague resemblance. It is clear that the taxa discussed above need more complete material with well-preserved fertile structures in connection with the vegetative frond. The existing information can only be regarded as tentative.

However, there is no reason not to follow Mamay (1992) in using Sphenopteridium as a generic identification for the specimens, which he described as a new species, but which could be identical with “Sphenopteris” germanica. The present writers thus conclude that this plant should be referred to as Sphenopteridium germanicum, a formal synonymy of which will need to be presented elsewhere. It also is reasonable to regard this taxon as a probable pteridosperm.

Coniferophytes

Walchian Conifers (Fig. 23)

At least two, and possibly three, types of “walchian” conifers occur as a conspicuous part of the Kinney flora (Fig. 23). The reader is referred to Looy (2007) for a discussion of various conifer groups, the complexities of conifer taxonomy, and their phylogenetic relationships.

Mamay and Mapes (1992) assigned the Kinney conifer remains to two species, Walchia piniformis (Schlotheim) Sternberg and Hermitia (Walchia) cf. schneideri (Zeiller) Kerp and Clement-Westerhof. We concur with the W. piniformis identification and Figure 23.3 is a re-illustration of their specimen (Mamay and Mapes, 1992, Fig. 8A). Walchia piniformis is a very widely occurring species in the Pennsylvanian and Early Permian throughout the Pangaean tropics. The specimen Mamay and Mapes (1992, Fig. 8D) identified as Hermitia (Walchia) cf. schneideri based on its long, lax leaves is re-illustrated here as Figure 23.1. The long leaves may reflect its position on a lateral branch, perhaps as the principal axis, or as the stem of a small individual of W. piniformis, rather than being representative of a distinct species. Comparable variation can be observed in juvenile specimens of some modern araucarian conifers with plagiotropic branching patterns, such as Araucaria heterophylla, the Norfolk Island Pine. Somewhat more distinctive is a specimen (Fig. 23.2) that we attribute to the genus Culmitzschia (Mamay and Mapes, 1992, Fig. 8B, identified the specimen as W. piniformis). This type of conifer foliage has been reported widely in rocks of Stephanian through Early Permian age in Europe (e.g., Kerp et al., 2007; Bercovici and Broutin, 2008; Simunek and Martinek, 2009; Wagner and Alvarez-Vazquez, 2010a) and in the western USA (e.g., Chaney and DiMichele, 2007; Lucas et al., 2012; Voigt et al., 2013). As with Walchia, Culmitzschia is almost always preserved in sedimentary settings and in floristic associations that suggest seasonally dry climates, though not necessarily without significant moisture availability. The described species most...
FIGURE 18. Pteridosperm foliage, Mixoneura subcrenulata. 18.1-18.2, USNM specimen 558139, Note evidence of marginal damage due to possible arthropod feeding. 18.3-18.4, USNM specimen 558147. 18.5-18.6, USNM specimen 558124, Note evidence of marginal damage due to possible arthropod feeding. 18.7, USNM specimen 558149. Scale bars = 1 cm.
FIGURE 20. Pteridosperm foliage, *Neurodonotopterus* cf. *auriculata*. 20.1-20.2, USNM specimen 450789 (Mamay and Mapes, 1992, Fig. 5E). 20.3-20.4, USNM specimen 558127. Scales in 20.1, 20.2 and 20.3 in mm. Scale bar in 20.4 = 1 cm.

FIGURE 22. Pteridosperm foliage, *Sphenopteridium manzanitanum*. 22.1-22.2, Holotype, USNM specimen 450796 (Mamay and Mapes, 1992, Fig. 6E). 22.2 is an enlargement of a pinnae from 22.1. Scale bars = 1 cm.
similar to those in the Kinney collections are *Culmitschia laxifolia* (Florin) Clement–Westerhof and *Culmitschia speciosa* (Florin) Clement–Westerhof.

**Ernestiodendron filiciforme** (Schlotheim) Florin (Fig. 24)

Also in the Kinney collections are rare specimens that are morphologically similar to *Ernestiodendron filiciforme* (Fig. 24). The fragments bear leaves that are inserted nearly normal to the axis and curve strongly upward over the last third of their length. The dark color of the specimens is typical of *Ernestiodendron* and reflects the thickness of the leaf in life. *Ernestiodendron*, like *Walchia* and *Culmitschia*, occurs widely in both European/North African (in addition to the above citations, see: Kerp et al., 1990; Hmich et al., 2006; Galtier and Broutin, 2008) and American (e.g., Hotton et al., 2002) floral assemblages, generally with other conifers and in association with physical conditions and plant types indicative of seasonally dry climatic conditions. Hernández-Castillo et al. (2003) suggested that *Ernestiodendron* may have been a tree of small stature. The presence of *Ernestiodendron* in the Kinney flora is, to our knowledge, the oldest reported occurrence of this genus in North America.

**Dicranophyllum readii** Mamay (Fig. 25)

The long, repeatedly bifurcate leaves figured and described as *Dicranophyllum readii* by Mamay (1981) (see also Mamay and Mapes, 1992, Figs. 7E, F) have been assigned correctly to *Dicranophyllum*. Whether or not a new species should have been recognized on the basis of isolated leaves, is more debatable. *Dicranophyllum* has been described more completely by Barthel et al. (1998), recording axial remains as well as the characteristic long, repeatedly bifurcate, slender leaves. These authors also described the male and female cones inserted on the axes of this small gymnospermous tree, for which they provided a reconstruction. A long list of *Dicranophyllum* leaf taxa described from North America is quoted by Mamay (1981). Now that this plant is known more comprehensively, it may be regarded less useful to distinguish species of *Dicranophyllum* exclusively on size and bifurcation of the leaves, distinctive though they may be. A large number of species has been described in the past on the basis of leaf remains only (e.g. *D. gallicum* (Dawson) Stopes, *D. lusitanicum* (Heer) Lima). *Dicranophyllum readii* differs from the relatively common species *Dicranophyllum gallicum* Grand’Eury by its very long (up to 50 cm length), at least twice bifurcate leaves. These are also described as very mighty, quite stalked and are inserted on straight, rather sturdy axes. In these taxa the leaves are positioned in two-dimensional, very flat arrays, such that the helical leaf arrangement is not immediately obvious. Differences between these leaf taxa are found in length-breadth ratios, entire as against incised distal margins and the ending of all veins on the distal margin, as against some veins abutting onto the lateral margins. These variables may allow segregation.

**Plagiozamites rochei** (Renault) comb. nov. (Figs. 27.1, 27.2)

A second noeggerathialean element from the Kinney flora was described by Mamay and Mapes (1992) as *Plagiozamites planchardii* (Renault) Zeiller, a taxon described originally from the upper Stephanian of Commeny, south-central France (Renault and Zeiller, 1888-1890), and recorded subsequently from the Rotliegend of Trienbach (Weilerthal) in the Voges (Alsace, France) by Zeiller (1894), who introduced the genus. Zeiller compared it with both *Noeggerathia* and *Zamites*, and considered it to be a cycadopod, on the basis of leaf morphology, but noted the absence of fertile material. In North America, the species has been recorded from the Missourian Conemaugh Formation of the Appalachian Basin, USA (Bassler, 1916), which is approximately same age as the Kinney Quarry deposit, from an unidentified Pennsylvanian location in New Mexico in collections made by Charles B. Read (noted by Ash and Tidwell, 1982), and from the Lower Permian Abo Formation of southern New Mexico (DiMichele et al., 2013).

**Plagiozamites planchardii** is here identified with *Sphenozamites rochei* Renault, a European species recorded from high Stephanian strata in France and Spain (Renault, 1882; Wagner and Mayoral, 2007). *Sphenozamites* is another Mesozoic genus belonging to the cycadopsids. Both Renault (in Renault and Zeiller, 1888) and Zeiller (1894) overlooked *Sphenozamites rochei* Renault 1882, which seems the same species and has priority. The present writers thus suggest that this element should be recorded as *Plagiozamites rochei* (Renault) comb. nov. [Basionym: *Sphenozamites rochei* Renault, 1882, Archives botaniques du Nord de la France, p. 180-184, 1 fig.].

**Charliea manzanitana** Mamay (Figs. 27.3, 27.4)

Mamay (1990) described some of the specimens from Kinney Quarry as *Charliea manzanitana*, which shows oval leaves with more-or-less parallel lateral margins and a distal margin with, characteristically, two incisions, dividing the apex into three lobes. The parallel veins are
FIGURE 23. Conifers. 23.1, *Walchia* sp., USNM specimen 455001 (Mamay and Mapes, 1992, Fig. 8D). 23.2, *Culmitschia* sp., USNM specimen 455002 (Mamay and Mapes, 1992, Fig. 8B). 23.3, *Walchia piniformis*, USNM specimen 450803 (Mamay and Mapes, 1992, Fig. 8A). All same magnification, scale bar in 23.2 = 1 cm.

FIGURE 25. Conifers, *Dicranophyllum readii*. 25.1, Holotype, USNM specimen 267277. 25.2, USNM specimen 267281 (Mamay and Mapes, 1992, Fig. 7E). Both same magnification. Scale bar = 10 cm.
Cycadopsids?

Two fragmentary specimens of *Taeniopteris* were discovered in the NMNH collections from Kinney Quarry (Fig. 28). This is a morphogenus characterized by leaves with a strong central vein and perpendicular to subperpendicular lateral veins, which may bifurcate near the central vein. Apart from *Taeniopteris jejunita* Grand’Eury, which Remy (1953) excluded as a fern with synangia (*Ilfeldia*), the majority of *Taeniopteris* might be cycadopsids (see Cridland and Morris, 1960; Gillespie and Pfefferkorn, 1986; Axsmith et al., 2003). *Taeniopteris* leaves are extremely variable in size. The veins may branch, and often do so relatively close to the midvein. The various species are distinguished on relative leaf width and vein density; they also are distinguished to a lesser extent on shape, since *Taeniopteris* leaves are normally found in fragmentary condition. This is certainly the case for the Kinney material, which is clearly affected by maceration and is highly fragmentary.

Remy and Remy (1975) attempted to tabulate the various characters such as leaf width, constitution of central vein, vein density and presence or absence of vein bifurcation. This useful exercise served to show that quite a number of species were introduced on inadequate material, and that the undoubtedly large amount of intraspecific variation was not taken into account sufficiently.

The two small fragments collected from the Kinney Quarry belong to a relatively broad-leaved form with dense venation (c. 35-40 veins/cm), oriented perpendicular to both the central vein and leaf margin. These characters fall within the range of *Taeniopteris fallax* (Göppert, 1864-65) and *Taeniopteris multinervia* (Weiss, 1869), as tabulated by Remy and Remy (1975). Leaf shape is unknown. *Taeniopteris multinervia* is the most common identification in Europe. However, Barthel (1976) placed *Taeniopteris multinervia* in synonymy with *Taeniopteris abnormis* (Guthier, 1835). This synonymy was accepted by Wagner and Álvarez-Vázquez (2010a), and should probably be respected for the leaf fragments found in the Kinney Quarry. It is further noted that Halle (1927) placed *Taeniopteris smithii* (Lesquereux, 1879-80), from Alabama, USA, in synonymy with *Taeniopteris fallax*. In view of the fragmentary nature of the two specimens from Kinney, it seems most reasonable to record these as *Taeniopteris cf. abnormis*, this being the earlier described species. Whether or not the various species mentioned warrant distinction as separate taxonomic entities (see discussion in Wagner and Martinez-Garcia, 1982), must await the availability of more complete specimens. *Taeniopteris lescuriana* (Fontaine and White, 1880) described from an equally fragmentary specimen in the Dunkard Group of West Virginia, may well be another synonym. Such remains, recorded as *Taeniopteris*
**FIGURE 27.** Noeggerathian foliage. **27.1-27.2,** *Plagiozamites rochei,* USNM specimen 422621 (Mamay and Mapes, 1992, Fig. 9A). **27.3,** *Charliea manzanitana,* Holotype, USNM specimen 422628 (Mamay and Mapes, 1992, Fig. 9B). **27.4,** *Charliea manzanitana,* USNM specimen 422624. Scale bars = 1 cm.

*abnormis* Guthier by Wagner and Álvarez-Vázquez (2010a), range from Stephanian B upward into the Autunian.

**Incertae Sedis**

There are a several specimens of interest from Kinney Quarry that cannot be assigned to a species or genus with confidence.

The specimen illustrated in Figure 29 was described by Mamay (1990, Fig. 11), and Mamay and Mapes (1992, Fig. 9F) as *Podozamites*-like. The single specimen shows parallel-veined, elongate, entire leaves that clearly are helically arranged on the supporting stem. These leaves show distinct flexure, suggesting that they were borne in an orthotropic posture in life, rather than in a bilateral, plagiotropic orientation. In the features of its leaves, the specimen is similar to *Yuania* (*Russellites*) as described by Mamay (1968); however the leaves in *Yuania* (*Russellites*), as Mamay (1992, p. 15) notes, are “arranged in flat planes”, unlike this specimen, which is why he differentiated it. Although the leaf shape and venation are similar to plant remains ascribed to the Noeggerthiales, *Podozamites* is a characteristically Mesozoic genus of conifers. The fragmentary specimen figured as *Podozamites* sp. by DiMichele et al. (2001, Fig. 3.3) from Texas also could well be a conifer, as claimed (op. cit.), but is more poorly preserved than the material from Kinney Quarry and might be a different taxon.

Figure 30.1 was illustrated by Mamay and Mapes (1992, Fig. 5H) as cf. *Neuropteris obliqua.* This identification was proposed tentatively and is certainly not correct. We suggest that it may be a large specimen of *Pseudomariopteris cordato-ovata.*

Figure 30.2 may be a small representative of *Neurodontopteris auriculata.* The veins appear too arched to be a small example of *Odontopteris,* and larger pinnules show a degree of midrib development. We note that the leftmost pinnule appears to have a rounded base.

Figure 30.3 is possibly attributable to *Odontopteris gimmii,* as discussed above.

Figure 30.4 appears to be a small plantlet of indeterminate affinity, and the strands emanating from its base are interpreted as roots.

**KINNEY FLORAL ASSEMBLAGE: PRESERVATIONAL ASPECTS**

The floral remains from the Kinney Quarry have been collected from shales of brackish to marine facies. Several slabs with plant fragments also show the presence of *Dunbarella* shells, which suggest quiet waters of brackish salinity. The depositional environment has been interpreted as corresponding to an embayment in a tidally influenced estuary (Archer and Clark, 1992). This would imply that the plant fragments came down the estuary and drifted into the embayment, becoming waterlogged and settling on the mud floor in this sheltered environment. However, if the embayment could be seen as a more extensive lagoon, it would allow shallow streams draining the adjacent land area to bring in plant fragments of a certain size. Archer and Clark (1992) also mention bands with finely comminuted plant debris, such as one would expect of plant material subject to tidal action in an estuarine setting once entrained in the sediment. Residence time in water is apparent for many specimens from the evidence of frizzling and other damage to foliar remains due to tissue decay and by the apparent attachment of *Dunbarella* shells to many specimens.

The Kinney floral assemblage was collected from an unknown number of bands in a c. 14 m thick shale interval in the lower part of the Kinney Quarry (Willard, 1992, p. 49-50; Mamay and Mapes, 1992, p. 65; Lucas et al., 2011, fig. 6). The macroflora is wholly allochthonous, presenting a mixture of plants that, we presume from many other published analyses of their ecological preferences, are from varied microhabitats on the original landscape. Willard (1992) examined two independently assembled collections, from two portions of the Kinney Quarry and found them to be palynologically distinct. One palynoflora, from the lower portion of the shale (the NMNH collection described in this paper) was a typical seasonally-dry, Late Pennsylvanian assemblage dominated by cordaitalean, conifer and pteridosperm pollen. The second collection was from the upper portions of the plant-bearing shale interval; it was dominated by small fern spores and a problematic palynomorph, the affinities of which are with Gondwana, and had a diversity of palynomorphs from sphenopsids and other lower vascular plants. Such a distinction was not detected in the NMNH Kinney macrofloral collections, and Mamay and Mapes (1992) explicitly state that they recognized no consistent spatial or temporal floristic compositional changes during their collecting activities. Unfortunately, there is no record of the different assemblages that may have been obtained from more than one fossiliferous bedding plane. This means that one can only judge from the total collection, which was brought together by different collectors (Lucas et al., 2011, p. 18). A museum collection may reflect a bias for the better preserved, larger specimens, though this depends strongly on the research objectives of the collector. Even so, the variety of specimens of different kinds shows that different habitats were represented in the area from which the plant remains originated.

The quiet "lagoonal" environment of deposition implies low-lying coastal conditions. The (occasional) presence of relatively large plant fragments capable of being imprinted on the mudrock (in some cases in surprising detail), suggests that their place of growth cannot have been very far away. Even though different habitats are inferred, these were
probably all situated in one and the same general area. Elements possibly brought in from farther away include the conifers, and then only because of their robust construction, not because of some necessary confinement to “uplands”.

The local landscape may have included swamps as well as relatively drier ground, with better drained soils. Since transported plant remains are involved, implying a mixture, there is no direct evidence of different floral associations linked to specific habitats.

FLORAL COMPOSITION

A census of the NMNH collection reveals that there are subtle compositional differences between two facies, separable by color, one gray and one buff, otherwise similar in terms of plant preservation and host-rock characteristics. The facies color difference most likely indicates collection from different beds in the Kinney succession. Willard (1992) noted color differences between the two collections she analyzed palynologically. The most common plant in the gray facies is *Dicranophyllum*, which is much less common in the buff facies. Second most abundant in the gray facies are conifers, followed by neuropterid pteridosperms, and cordaitaleans. The buff facies is dominated by neuropterid pteridosperms and *Sphenopteridium*, with a large element of conifers. Pecopterid ferns, *Mixoneura* and *Sphenopteridium* are found nearly exclusively in the buff facies, and neuropterid foliage is about twice as abundant in the buff facies as in the gray.

Mamay and Mapes (1992) noted the relative frequency of conifer foliage. This is easily understood in terms of durability. Conifers are characterized by leaves with thick cuticles capable of withstanding prolonged immersion in water. Likewise, pteridosperm foliage is more likely to survive prolonged maceration than that of ferns, with generally thinner cuticles. In this respect, it is worthy of note that the relatively common (and comparatively large) pinna fragments of *Pecopteris potoniei* are invariably fertile, the inference being that the *Asterotheca synangia* strengthened the pinnules, thus allowing for increased resistance to disintegration. It is also noted that a few of the other fern remains encountered as relatively large fragments occur as “ghosts”, with only the outline of pinnules preserved. This creates the impression of tissue decay in relatively large pinna fragments, which became waterlogged in very quiet, almost still waters. The absence of currents capable of breaking up weakened plant remains will have been an important factor for preservation.

In conjunction with a varied suite of sphenopsids, these ferns remains may well have corresponded to wet environmental conditions in the source area, i.e. to a wet substrate floral habitat. This habitat is probably underrepresented as a result of the preservational bias. A genuine hygrophyte element is *Sigillaria brardii*, a lycopsid tree that is known to have contributed significantly to Stephanian coal swamps (e.g., Willard et al., 2007; Tabor et al., 2013, and as confirmed by personal observation, RHW/CAV).
Kerp (1984) associated Calamostachys dumasii “Asterophyllites” dumasii with foliage of the Annularia carinata-type and stems referable to Calamites gigas. This is consistent with the stem and foliage assemblage found at Kinney Quarry. This association has important paleoecological implications, as Calamites gigas has been interpreted as a plant typical of Mediterranean-type seasonal climates (Naugolnykh, 2004), perhaps even with specializations for water storage under xeric conditions (Barthel and Rössler, 1994; Rössler and Noll, 2002).

The quite varied pteridosperm foliage (including Sphenopteridium?) could well belong to habitats of various different kinds. These plants are generally classed as mesophiles, not growing directly in swamps but living in close association, as well as including a category that possibly lived on hill slopes.

The species recorded as noeggerathialean (a controversial group of plants regarding their systematic position) belong to a habitat not normally represented in Pennsylvanian floras of the paleoequatorial belt. These noeggerathialeans occur throughout the Pennsylvanian, but are exceedingly rare, since they are apparently linked to higher ground. These are so-called “extrabasinal” elements, a term coined by Havlena (1970) for plants that lived outside the swamp area and directly associated environments. One of the most significant papers with regard to the presence of noeggerathialean remains is that published by Leary and Pfeflkerkorn (1977), who recorded floral remains from the sides of a paleovalley of Early Pennsylvanian (mid-Namurian) age in Illinois, USA. More recently Wang et al. (2009) reported on plants of Early Permian age from China found buried in volcanic ash beds above a coal seam, indicating that they were growing, at the time of burial, in a swampy, peat-forming habitat, and thus indicating an expansion of the group, ecologically, in the Permian of western Pangea. There are many other published reports on this group, and those mentioned here may serve as examples and lead into the more extensive literature.

Conifers are regarded as favoring drier habitats, meaning better drained soils. The pattern of conifer occurrence during the Pennsylvanian is complex, however. In the western equatorial regions, these plants are prominent members of plant communities well back into the Middle Pennsylvanian. And conifer pollen is reported in rocks as old as latest Mississippian. This group was present at tropical latitudes, but rarely preserved in basinal lowlands, long before it rose to prominence in the later Pennsylvanian. Conifers become increasingly common, even in coal basins, during the Missourian across the west-central and western Pennsylvania.
paleoequatorial region (e.g., Cridland and Morris, 1963; Feldmann et al., 2005; Falcon-Lang et al., 2011). This reflects in part what has been described as a “taphonomic megabias”. The Pennsylvanian was a time of strong glacial-interglacial cyclicity with attendant changes in sea-level and climate. The widespread swamp environments that formed during the wetter phases of these cycles supported floral associations from a habitat inimical to the conifers, and also were the most favorable times for the preservation of plant material. In contrast, during the drier parts of cycles water tables were generally much lower, limiting the environments favorable for the preservation of plants (Gastaldo and Demko, 2011). Only when or where the wetter parts of ice/sea-level/climate cycles became drier, did conifers come to the fore. Whereas it is admitted that the presence of conifer remains does not constitute evidence of a late Pennsylvanian age (prime examples being reports of conifers from Moscovian strata in the Illinois coal basin – Falcon-Lang et al., 2009; Plotnick et al., 2009), the widespread occurrence of a varied conifer assemblage does provide a climatic signal. Taken in its proper context, this may have time-stratigraphic significance.

In summary, the composition of the Kinney floral assemblage shows the effect of preferential preservation of elements capable of withstanding prolonged maceration in water. In addition, it reflects a mixture of habitats, which shows that these plants originated from a varied source area, likely from an environmentally heterogenous landscape.

### STRATIGRAPHIC INFERENCEs

The taxonomic diversity of the Kinney floral assemblage, as with virtually any paleobotanical assemblage, must be reported with a caveat making note of the fragmentary nature of the plant fossil record and the difficulty of assembling dispersed organs into whole plants. Thus – what to count is always a major concern. At Kinney, there may be as many as 39 identifiable taxa, that is organs that can be placed into a Linnean stratigraphic range. In view of the probable synonymy between

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range beyond Stephanian C, but last occurrences are traditionally sus-

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Neuropteris ovata is another element of lowland flora, apparently linked to an alluvial plain environment. Originally regarded as characteristic of Westphalian D (Asturian Substage), it has long been recognized as occurring in Stephanian (Upper Pennsylvanian) strata of North America. In the more complete Stephanian record of NW Spain its highest occurrence is in the upper Saberian. However, a more extended range is appar-

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Neuropteris cordata, as identified in the present paper, refers specifically to the plant figured and described by Barthel (1976) from the Lower Rotliegend (Autunian) of Saxony, Germany. The use of this name in the literature is quite varied, making it pointless to attempt establishing a stratigraphic range.

Mixoneura subcrenulata and Mixoneura gymnii are two meso-

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Another Autunian element is Sphenopteris germanica, the pre-

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With reference to the hygrophyte elements, it is not surprising that this is one of the most characteristic elements of the Kinney floral assemblage, with its presence in the Kinney Quarry seeming to coincide with that recorded as var. grandeuryi Wagner from NW Spain. It may also be compared with Neuropteris pseudovata Gothan and Sze as recorded from the Stephanian C of North Portugal.

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ence in the Permian of the Czech Republic (N.B. “Permian” should be interpreted in this case as Autunian, which is currently regarded as highest Carboniferous).

*Pecopteris oreopteridia* is characteristic of Lower Rotliegend (Autunian) strata. However, there is no guarantee that this species does not appear earlier. Records under this name should be subjected to a critical revision.

*Pecopteris monyi* is an oft-quoted species (but not always identified correctly), from the Stephanian of Europe. It is recorded from Asturian upwards into Stephanian C, with a total range that probably reflects the wide sense in which this species has been recorded in the literature. A critical revision of these records will be necessary.

*Taeniopteris* is another case in point. Excluding *Taeniopteris jejunata* Grand’Eury (not part of the Kinney assemblage), which is unique, the densely veined *Taeniopteris abnormis/fallax/multinervia*, of uncertain affinity, is clearly associated with non-wetland (especially peat-forming) environments. This large-leaved *Taeniopteris* occurs most commonly in Autunian strata (and in the Permian), but it has been recorded as far down as Stephanian B (Wagner and Álvarez-Vázquez, 2010a). *Taeniopteris* fragments have been found in Bolsovian marine strata in NW Spain (van Loon, 1971), providing a glimpse of “extrabasinal” plants living beyond the alluvial plain.

The enigmatic gymnosperm, *Dicranophyllum*, may be another “extrabasinal” element. It ranges throughout the Pennsylvanian and into the Permian, including in the New Mexico Abo Formation.

Disputed noeggerathialean remains, such as *Plagiozamites rochei* and *Charlia manzanitana*, are “extrabasinal” elements, so scarce as to be of little stratigraphic significance (even though the published records are from high in the Stephanian).

The conifers are a special case, referred to earlier. Conifers are recorded palynologically as far down as Moscovian in the Paradox Basin of Colorado, USA (Rueger, 1996), and in coal basins of the American

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**FIGURE 31.** Known stratigraphic ranges of specifically identified taxa from the Kinney Quarry flora, set against the substages of the Stephanian Stage (practically equivalent to Upper Pennsylvanian Series in international usage: Kasimovian and Gzhelian stages). *Sphenopteris germanica* is shown as the probable equivalent of *Sphenopteridium manzanitana*.
Reasons have been given by Wagner and Álvarez-Vázquez (2010a, p. 314) to translate this into the higher Gzhelian. It is noted that a fusulinacean assemblage found immediately below the Kinney plant-bearing strata has been dated as early to middle Missourian (Lucas et al., 2011), which is equated to part of the Kasimovian. This apparent contradiction between the marine faunal data and the terrestrial flora in immediately overlying deposits needs further investigation.

CONCLUSIONS

The Kinney floral assemblage, obtained from shallow brackish to marine (lagoonal?) strata, shows transport selection due to the different degrees of resistance to disintegration following upon decay with residence time in water. This has favored the preservation of conifers, pteridosperms, and (putative) noeggerathialeans. Fern foliage may have suffered most of all and is likely underrepresented.

The plant remains record the presence of different habitats in the source area, and this is clearly apparent from the fairly large variety of plant remains collected at Kinney. Mesophile and drier substrate, so-called “extrabasinal” plants are much in evidence. The transported nature of the occurrence limits the extent of any climatic inferences that can be drawn from this assemblage.

The floral assemblage is most similar to Autunian, possibly Stephanian C floras, known principally from Europe, but also widespread in North America. Indeed, the Kinney floral assemblage is almost entirely identical to those of the Lower Rotliegend (Autunian) in Europe.

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The man, the myth, the legend---of “puff baby,” aka William DiMichele, seen here pushing the scientific envelope in 2009 in the Cerros de Amado of Socorro County, New Mexico.