MARCOUIA, GEN. NOV., A PROBLEMATICAL PLANT FROM THE LATE TRIASSIC OF THE SOUTHWESTERN U.S.A.

by SIDNEY R. ASH

ABSTRACT. Marcouia, gen. nov. has large palmately compound leaves in which the pinnae are deeply divided into linear, lateral segments. The segments (pinnules?) contain broad midribs and parallel veins that often divide and anastomose one or more times before reaching the margins. Leaves from the Chinle Formation that were formerly referred to as Ctenis are here assigned to Marcouia. Marcouia is not classified and is known only from the lower part of the Upper Triassic Chinle Formation in eastern Arizona and western New Mexico.

THE purpose of this report is to redescribe some unusual pinnate leaves that occur in the Upper Triassic Chinle Formation in the southwestern United States. Previously the leaves were known only from Arizona, but recently I collected many additional specimens in western New Mexico. The new specimens give us so much information about this unusual leaf that a redescription is thought necessary.

When these leaves were first described they were called *Ctenis neuropteroides* Daugherty (1941, p. 80). Their assignment to the genus *Ctenis* Lindley and Hutton (1834, p. 63, pl. 103), however, is untenable (Ash 1966, p. 146). In *Ctenis* the ultimate segments (pinnae) do not contain a midrib and the veins more or less parallel the pinnae margins (see Florin 1933, p. 81, and Harris 1964, p. 102 for recent treatments of the genus). On the other hand, the ultimate segments (pinnules) of the fossils from the southwestern United States contain broad midribs that extend to within a short distance of the pinnule apices and secondary (lateral) veins lie at a high angle and may parallel the margins for only a very short distance just before they disappear close to the margins (see text-fig. 1c). Since these fossils do not compare very closely with *Ctenis* or any other plant known to me, they are referred to a new genus which I will call *Marcouia*.

The new material considered in this report has been deposited in the U.S. National Museum (USNM) in Washington, D.C. and the Museum of Northern Arizona (MNA) in Flagstaff. The specimens described earlier by Daugherty are in the University of California Museum of Paleontology (UCMP) at Berkeley.

SYSTEMATIC DESCRIPTION

Genus MARCOUIA gen. nov.

Type species. Marcouia neuropteroides (Daugherty) Ash, comb. nov.

Diagnosis. Known portion of plant consisting of a palmately compound leaf composed of several segments (pinnae). Pinnae linear lanceolate, lamina divided into lateral segments (pinnules). Pinnules arising at a high angle from sides of main rachis of pinna, oval to linear, margins wavy to lobed, apex obtusely pointed, upper margin strongly contracted, lower margin strongly decurrent on the rachis, a narrow flange of tissue [Palaeontology, Vol. 15, Part 3, 1972, pp. 423–429, pl. 80.]

running decurrently from one pinnule to the next below. Pinnule midrib broad, well-defined, disappearing a short distance below apex by dissolving into veins. Lateral veins numerous, arising mainly from pinnule midrib at a high angle, several arising from main rachis of pinna and entering decurrent portion of pinnule lamina, typically dividing and anastomosing one or more times with adjacent veins, usually united at margins.

Derivation of name. The name commemorates Jules Marcou, the French-Swiss geologist who accompanied the Whipple expedition through the southwestern United States in 1853–1854. He observed the petrified wood-bearing rocks (which also contain the fossils described here) in what is now Petrified Forest National Park, Arizona, and correlated them with the Keuper stage of the Upper Triassic in Europe, a correlation that is still generally accepted (Ash 1970, pp. D5–D6).

Comparisons. Some of the features shown by Marcouia gen. nov. can be matched in certain other fossils that have linear pinnules. For example, in Glenopteris Sellards (1900), Pachypteris Brongniart (1829) em. Harris (1964), and Protoblechnum Lesquereux (1880) em. Halle (1927) the pinnules have decurrent lower margins and contracted upper margins at the rachis as in Marcouia gen. nov. In the three older genera, however, the lateral veins are simple to forked and do not anastomose as they do in the present genus.

The venation in the pinnules of *Marcouia* gen. nov. compares fairly closely with that in the pinnae of *Scoresbya* Harris 1932 (also see Krausel and Schaarschmidt 1968). The lateral margins of the pinnae of *Scoresbya* are only strongly dentate and the pinnae are not divided into distinct pinnules as in *Marcouia*.

Recently Bock (1969, p. 231) referred to *Strangerites* (sometimes called *Stangerites*) Bornemann (1856), the fossils which Daugherty (1941) assigned to *Ctenis*. Although somewhat similar, those fossils and the new ones described here are distinguished from *Strangerites* by having anastomosing venation while the older genus has free dichotomous venation. Bock (1969, p. 231) also considered *Pseudodanaeopsis* Fontaine (1883) to be a synonym of *Strangerites* but *Marcouia* is distinguished from *Pseudodanaeopsis* by having strongly contracted upper margins of the pinnules at the pinna rachis while the pinnules of the older genus are attached by the whole base.

Marcouia neuropteroides (Daugherty) Ash, comb. nov.

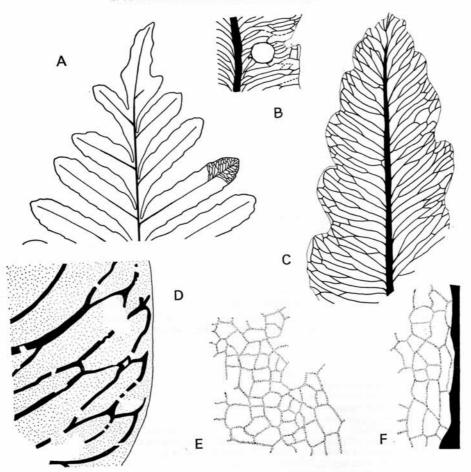
Plate 80; text-fig. 1

1941 Ctenis neuropteroides Daugherty, pp. 80-81, pl. 13, fig. 3, pl. 14, fig. 2 (non 3).

Holotype. UCMP 1571. Paratypes UCMP 1572, MNA P4. 102, USNM 172271, 172273.

Distribution. This species has been collected from the Monitor Butte Member of the Chinle Formation at U.S. Geological Survey (USGS) paleobotany localities 10059 and 10060 in the Fort Wingate area and from the lower part of the Petrified Forest Member of the Chinle Formation at USGS paleobotany locality 10062 in Petrified Forest National Park, Arizona. Detailed data on these localities has been presented elsewhere (Ash 1970, p. D25).

Emended diagnosis. Known portion of plant consisting of a palmately compound leaf, composed of several pinnae united at their bases. Pinnae linear lanceolate as a whole, large, estimated to have been 30 cm or more in length, 15 cm or more in width, lamina divided into lateral segments (here termed pinnules). Pinnules oval to linear more or less opposite, arising at a high angle (typically 60°-75°) from lateral margins of pinna rachis, linear, typically 1.5-2.0 cm wide, 3.5-8.5 cm long (range noted 0.6-4 cm wide, 1-10 cm



TEXT-FIG. 1. Marcouia neuropteroides (Daugherty) Ash, comb. nov. A, Reconstruction of the upper part of a pinna, approximately $\times \frac{1}{2}$. B, Seed-like structure on the lamina of the pinnule shown on the left in Pl. 80, fig. 6. MNA P4. 102, $\times 2$. C, Apical region of a pinnule showing the venation. Note that the vein-meshes occur mainly near the margins and that the veins commonly do not divide or anastomose near the midrib. Drawn from a photograph of USNM 172281a, $\times 5$. D, Venation near the margin (on the right) of a pinnule. Note the irregularly shaped vein meshes and that the free veins frequently follow the margin for a short distance, transfer preparation USNM 172281b, $\times 10$. E, Epidermal cells on the lamina between veins, transfer preparation USNM 172280, $\times 100$. F, Epidermal cells near a vein (at the right), transfer preparation USNM 172279, $\times 100$. Specimens in B and F from USGS fossil plant locality 10062, lower part of the Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona. Those in C-E from USGS fossil plant locality 10061, Monitor Butte Member, Chinle Formation, Fort Wingate area, New Mexico.

long). Margins wavy to lobed, sometimes toothed, apex obtusely pointed, upper margin strongly contracted at the rachis, lower margin strongly decurrent, narrow flange of lamina running decurrently from each pinnule along the lateral margins of pinna rachis, joining lamina of next pinna below. Near pinna apex, division of lamina into separate pinnules incomplete and a series of short rounded segments decreasing in size toward tip is usually present.

Pinnule midrib well defined, 1–3 mm broad, arising at an angle of 30° – 40° to the pinna rachis, typically bending outward near the base to an angle of about 60° – 75° , then following a more or less straight course disappearing 1–2 cm below apex by dissolving into lateral veins. Lateral veins numerous, slender, about 0·1 mm wide, arising mainly from pinna midrib at a high angle (70° – 80°), 1–5 veins arising from pinna rachis and entering decurrent portion of lamina, often dividing near base, typically anastomosing one or more times with adjacent veins in marginal area forming elongated, irregular meshes. Lateral veins usually united at margins, rarely free, free vein endings occasionally following margin for a short distance. Tracheids of lateral veins showing annular, helical, and scalariform thickenings. Epidermal cells rectangular to square, rarely polygonal, 35–80 μ m wide, 46–120 μ m long, rectangular cells usually adjacent to veins with long axis oriented parallel to veins, elsewhere cells more nearly square and irregularly oriented, anticlinal cell walls fairly straight, about 2 μ m thick. Stomata oval, scattered sparse, guard cell pair about 45–60 μ m in diameter.

Discussion. A complete or even nearly complete leaf of *M. neuropteroides* is not known. Most examples consist of just fragments of the pinna rachis with a few attached pinnules. Only one shows the base of the leaf (see Pl. 80, fig. 7) and it is poorly preserved. The fossil consists of the remains of four or five pinnae which are clearly joined at their

EXPLANATION OF PLATE 80

Figs. 1-9. Marcouia neuropteroides (Daugherty) Ash, comb. nov. All × 1. 1, A nearly complete pinnule that bears a large oval structure below the midrib which may be the remains of a seed. This structure, however, is almost twice as large as those in figure 6 and also is below, not above, the midrib. Note the wavy to lobed margins in this specimen. USNM 172271. 2, Main rachis of a pinna bearing several fragmentary pinnules showing contracted upper margins and decurrent lower margins at the rachis, USNM 172272. 3, 4, Apical region of two pinnae showing characteristic lobing of the lamina. Note that in figure 3 the uppermost pinnule is broadly fused with the apical lamina. In contrast the next lower pinnule is nearly free except for a narrow band of tissue that runs decurrently along the rachis to the apical lamina, USNM 172273 and 172274. 5, Apex of a sterile pinnule in which the venation is particularly clear, USNM 172275. 6, Two pinnules bearing the remains of oval seed-like structure on the lamina. Compare with tf. IB. MNA P4. 102. 7, Two nearly complete and unusually small pinnae. Note that the rachises and midveins are nearly the same size as those in the larger examples shown on the plate but the lamina is much smaller. Here again the decurrent lower margins and contracted upper margins of the pinnules are clearly visible. USNM 172276A. 8. Portion of the main rachis of a pinnae bearing the remains of several pinnules, one of which is compound. The contracted upper margin at the rachis is evident in the uppermost pinnule on the left, USNM 172277. 9, The base of a palmately compound leaf composed of five pinnae, USNM 172278. Specimens in figures 1-5, 7, 8 from USGS fossil plant locality 10060 in the Monitor Butte Member of the Chinle Formation near Fort Wingate, New Mexico. The specimen in figure 9 is from USGS fossil plant locality 10059 in the Monitor Butte Member of the Chinle Formation in the Fort Wingate, New Mexico area. The specimen in figure 6 is from USGS fossil plant locality 10062 in the lower part of the Petrified Forest Member of the Chinle Formation in Petrified Forest National Park, Arizona.

bases, demonstrating that the leaf is palmately compound. It shows a remarkable resemblance to the base of *Scoresbya dentata* Harris (1932, pl. 2, fig. 9).

The small pinna to the left in Pl. 80, fig. 7 is probably nearly complete. It is about 2 cm wide and originally may have been 6 cm or more in length. The rachis bears 5 pairs of unusually small lateral pinnules and an apical lamina. A larger (7 cm×13 cm) but very poorly preserved and less complete pinna (USNM 172282) shows 4 pairs of average-size pinnules together with the remains of an apical lamina.

About 40 fairly complete pinnules of M. neuropteroides are now known. They vary somewhat in outline and show a wide range in size. Pinnules from the Petrified Forest are often 3.5 to 4.0 cm wide and 6 to 8 cm long, although some are as much as 5 cm wide and 11 cm long. Usually they are twice as long as wide and are somewhat oval in outline (see Daugherty 1941, pl. 14, fig. 2). In comparison, the pinnules from Fort Wingate typically are 2 to 2.5 cm wide and 7 to 9 cm long. Exceptionally small pinnules $(5 \text{ mm} \times 18 \text{ mm})$ are preserved in one example (see Pl. 80, fig. 7). Most of the pinnules from the Fort Wingate area are three times (or more) as long as wide and are distinctly linear in outline (see Pl. 80, fig. 1).

Small, round to oval structures which may be the remains of seeds occur on the laminae of three pinnules of M. neuropteroides. Two of the pinnules bearing such structures are attached opposite each other on a short length of the main rachis of a pinna (Pl. 80, fig. 6). The structures show as small (about $2 \text{ mm} \times 3 \text{ mm}$) oval gaps surrounded by narrow bands of carbonaceous material. Both structures occur above the pinnule midribs. One is located about half-way between the base and apex of the pinnules while the other is somewhat closer to the base than to the apex of the other pinnule. Both more or less parallel adjacent veins (see text-fig. 1B and Pl. 80, fig. 6).

A third pinnule bears a similar but longer (2 mm×4 mm) structure. It also seems to be surrounded in places by a carbonaceous band within which there is an oval gap. However, in contrast to the other oval structures this one occurs below, not above, the midrib and lies practically transverse to the surrounding veins with one end nearly touching the midrib (Pl. 80, fig. 1).

Although there is always the possibility that these structures are merely accidents of preservation or are pathologic, their regularity and definite outline suggests not. In addition, the gaps on the lamina clearly suggest the sedimentary filling of hollow structures and the surrounding bands of carbonaceous material could be the compressed walls or shells of seeds. Nevertheless, since so few of these structures have been seen and none clearly shows definite seed features, such as a micropyle, stony layer, etc., they are regarded as only problematical structures which could be seeds.

Although the veins are clear in most specimens, the substance of the laminae has almost completely disappeared and it is impossible to make a typical cuticle preparation from them. A few acetate film transfers, however, do show anticlinal walls of the epidermal cells rather faintly. The stomata are not preserved on the transfers, but there are oval spaces scattered among the epidermal cells. It is thought that they mark the position of the guard cells which have totally disappeared. Vascular tissue is preserved in many of the veins on the transfers and the thickenings on the side walls of the tracheids are clearly visible in some.

Comparisons. M. neuropteroides can be distinguished from Strangerites obliquus Emmons

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(1857, pp. 121–122, fig. 89) from the Newark series of the eastern United States by having anastomosing venation whereas the venation in the older species is free dichotomous. The pinnules of *M. neuropteroides* can be differentiated from *Pseudodanaeopsis nervosa* Fontaine (1883, pp. 61–63, pl. 31, figs. 1–2) by having wavy to toothed lateral margins and contracted upper margins at the rachis while the pinnules of *P. nervosa* have smooth lateral margins and the upper margin is not contracted at the rachis. Furthermore, the venation in *M. neuropteroides* is anastomosing, not free dichotomous, as in *P. nervosa*.

The fossils described in this paper can be easily distinguished from the specimen described from the Newark series by Bock (1969, pp. 236–239, fig. 392) as *Stangerites obliqua*. According to Bock the lateral veins in his fossil frequently divide very near the midrib and anastomose fairly regularly in the vicinity of the margins forming a 'W' or 'X' pattern. Also, the lateral margins are straight to curving and are slightly constricted at the rachis. In *M. neuropteroides* the lateral veins rarely divide near the midrib and anastomose very irregularly near the lateral margins which are wavy to lobed. Also, the upper margin is strongly contracted at the rachis and the lower is decurrent.

M. neuropteroides can be distinguished from the fossil (USNM 8208) called Strangerites planus Emmons (1857, p. 122) and the fossil (USNM 30958) referred to Pseudodanaeopteris reticulata Fontaine (1883, pp. 59–60, pl. 30) by having short pinnules with wavy to lobed or toothed margins and strongly contracted upper margins at the rachises. In the two older fossils the pinnules are comparatively long with smooth margins and

have slightly constricted upper margins at the rachises.

The specimens described here can also be differentiated from the fossils Bock (1969, figs. 385–387) called *Stangerites planus* by having wavy to lobed or toothed margins, strongly contracted upper margins, and strongly decurrent margins at the rachis. The pinnules of Bock's fossils have smooth margins, slightly contracted upper margins, and slightly decurrent margins at the rachis. Additionally, the veins in *M. neuropteroides* do not anastomose as regularly as they do in the fossils Bock calls *Stangerites planus*.

Classification. Daugherty (1941, p. 80) considered this plant to be a bennettite. However, the anticlinal walls of its epidermal cells are not sinuous as they usually are in the bennettitales.

Marcouia is not classified at this time because we have no clear evidence of its true affinities.

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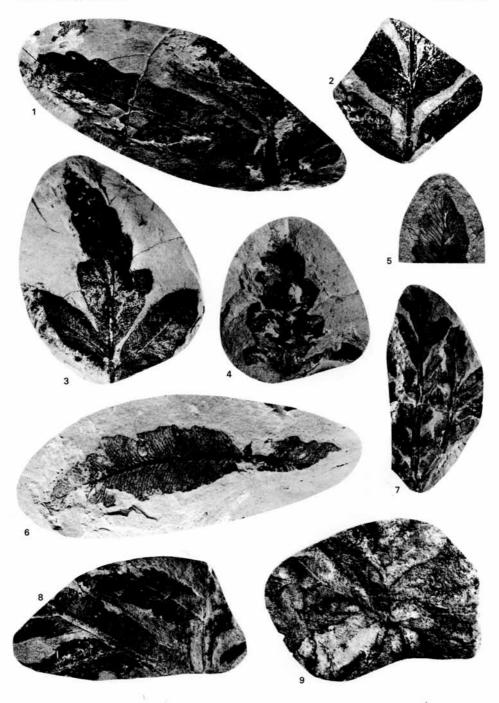
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SIDNEY R. ASH Weber State College Ogden, Utah, U.S.A.

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