LATE TRIASSIC PLANTS FROM THE CHINLE FORMATION IN NORTH-EASTERN ARIZONA

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ABSTRACT. Three plants based on megafossils are described from the Late Triassic Chinle Formation at a new locality in north-eastern Arizona. They are the leafy shoot and cone of *Selaginella anasazia* sp. nov., the leafy and fertile branches of *Dechellyia gormani* gen. et sp. nov., a conifer of uncertain affinities, and *Masculostrobus clathratus* sp. nov., a male coniferous cone. The cone is noteworthy because it contains pollen closely resembling the Late Triassic grains called *Equisetosporites chinleana* by Daugherty (1941) and later referred to the genus *Ephedra* by Scott (1960).

THIS paper contains the results of a study of the recognizable species of plant megafossils recently obtained from the Late Triassic Chinle Formation at a locality near the mouth of Canyon de Chelly (locally pronounced de-shay) in north-eastern Arizona. Prior to this investigation little was known about the Late Triassic plants in the area.

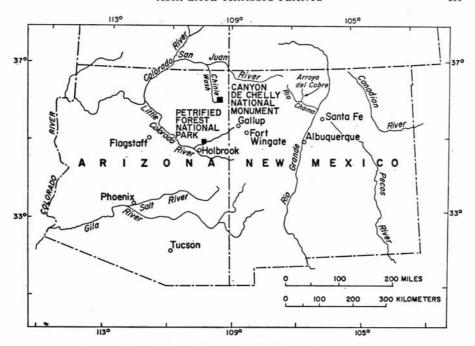
The first Late Triassic plant fossil to be reported from north-eastern Arizona and the entire south-west as well, was discovered on 4 September 1849 by Lieutenant J. H. Simpson (1850) of the U.S. Army. The fossil was a piece of petrified wood which Simpson found in a bed of conglomerate (now called the Shinarump Member of the Chinle Formation) exposed in the wall of a tributary canyon of Canyon de Chelly. Although the specimen was taken back to Washington, D.C. for study, it was never described and its present whereabouts is unknown. The only other reference to Late Triassic plant fossils in the immediate area is contained in a recent review of the Chinle flora (Ash 1972a). In that report a sketch was given of the fertile branch shown in Plate 118, figure 7 and a few remarks were made about it.

Fossil plants have been found at many localities in the Chinle Formation since 1849 and a history of the search for them has been given recently (Ash 1972b). As shown elsewhere (Ash 1972a), most of the localities have yielded only a few specimens of just a small number of species. Until now, the largest and most significant collections have been described from three localities—Arroyo del Cobre, New Mexico (Newberry 1876), Fort Wingate, New Mexico (Ash 1970a) and Petrified Forest National Park, Arizona (Daugherty 1941, Ash 1970a, 1970b). Publication of this report increases the number of significant localities to four; their locations are shown on the index map (text-fig. 1).

LOCALITY

The fossils described in this report were collected from the Monitor Butte Member of the Chinle Formation on the north bank of Chinle Wash at the mouth of Canyon de Chelly in north-eastern Arizona (see text-fig. 2). They occur in beds of mudstone and sandstone exposed near the west boundary of Canyon de Chelly National Monument in the N ½, SW ½, sec. 15, T. 32, R. 10 W. and about 70 meters west of the bridge over Chinle Wash. The fossil-bearing beds have been assigned U.S. Geological Survey (USGS) fossil plant locality number 10093 and Museum of Northern Arizona (MNA) locality number 200,

[Palaeontology, Vol. 15, Part 4, 1972, pp. 598-618, pls. 114-119.]



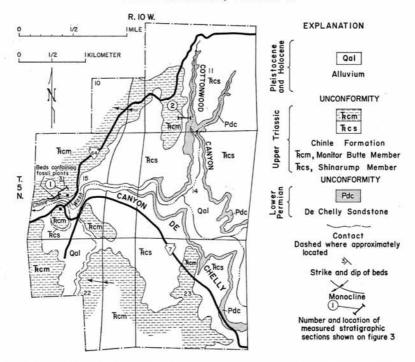
TEXT-FIG. 1. Index map of part of the south-western United States showing the location of Canyon de Chelly National Monument in north-eastern Arizona where the plant fossils described in this report were collected. Also shown on the map are the other three places in the southwest where the Chinle Formation has yielded large numbers of leaf fossils which have been described in the past.

The fossils described here include the leafy shoot and cone of Selaginella anasazia sp. nov., the leafy and fertile branches of Dechellyia gormani gen. et sp. nov., a conifer of uncertain affinities, and Masculostrobus clathratus sp. nov., a male cone of possible coniferous affinities. The cone is of particular interest because it contains pollen grains which are very similar to the Late Triassic grains that were first called Equisetosporites chinleana by L. H. Daugherty (1941) and then transferred to the genus Ephedra by R. A. Scott (1960). The beds also contain the remains of several other plants, but they are too poorly preserved and fragmentary to describe. One may be the pinwheel structure of Dinophyton spinosus which commonly occurs in the Chinle Formation (see Ash 1970c). Others are fragments of large, linear, single- and multi-veined leaves. Portions of stems of several sizes are also present.

The fossils described in this report have been deposited in the U.S. National Museum (USNM), Washington, D.C. Duplicates have also been deposited in the Museum of Northern Arizona, Flagstaff, Arizona.

STRATIGRAPHY

The Chinle Formation is about 400 meters thick in most of north-eastern Arizona (Repenning and others, 1969, fig. 6). In the vicinity of the fossil locality, however, erosion has removed much of the formation and only the lower 60 m have been preserved. It consists of the Shinarump Member (at the base) and the Monitor Butte Member at the top (text-figs. 2 and 3). The Chinle Formation is

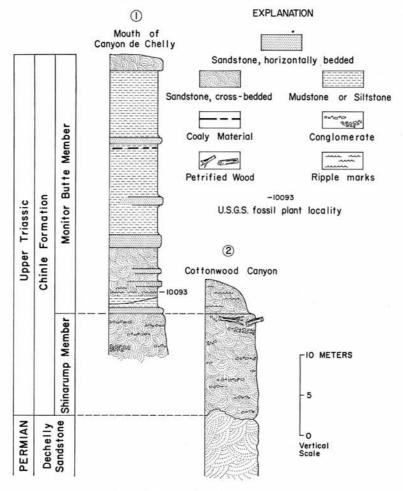


TEXT-FIG. 2. Geologic map of the extreme western end of Canyon de Chelly National Monument, Arizona, showing the location, near the mouth of Canyon de Chelly, of the beds containing the fossil plants described here. The base map was adapted from the U.S. Geological Survey Chinle 4 NE topographic quadrangle and the geology is modified from Cooley and others (1969, pl. 1, sheet 5).

underlain unconformably by the Dechelly Sandstone of Early Permian age and locally both formations are overlain unconformably by Quaternary alluvium.

The Shinarump Member of the Chinle is about 16 m thick near the locality and usually forms rounded ledges and cliffs. It is composed mainly of reddish-brown, coarse-grained, crossbedded conglomeratic sandstone (see text-fig. 3) and is thought to have been deposited by ancient streams and rivers. In places, such as in nearby Cottonwood Canyon, the Shinarump contains petrified logs as much as a meter in diameter. Elsewhere the Shinarump also contains fossil leaves (Ash 1972a).

In the vicinity of the fossil locality the Monitor Butte Member is about 40 m thick. It consists mainly of dark red mudstone and several discontinuous beds of ripple-marked, fine to medium grained, sandstone that are often dark-red to light-grey in colour. The sandstone beds generally form prominent ledges while the mudstone usually weathers into steep, irregular slopes. Plant fossils occur in the lower part of this member in a unit that is approximately 2–3 m above the Shinarump and 20 m above the Dechelly Sandstone (see text-fig. 3). The plant-bearing unit is about 2 m thick and is composed of grey, fine-grained, flaggy sandstone and an underlying bed of massive grey mudstone. Rocks in the fossil bearing unit are relatively soft and usually form a slope below a prominent ledge of hard, brown sandstone. Fossils seem to occur throughout the unit wherever it is exposed over a horizontal distance of at least 50 m.



TEXT-FIG. 3. Stratigraphic sections of the pre-Cenozoic rocks exposed near the mouth of Canyon de Chelly, Arizona. The localities where the sections were measured are indicated on text-fig. 2.

SYSTEMATIC DESCRIPTIONS

PTERIDOPHYTA
Class LYCOPSIDA
Family SELAGINELLACEAE
Selaginella anasazia sp. nov.
Plate 114; text-fig. 4

Holotype. USNM 168945. Paratypes. USNM 168903, 168909.

Distribution. This species occurs in the lower part of the Monitor Butte Member of the Chinle Formation at the mouth of Canyon de Chelly, Arizona at USGS fossil plant locality 10093 and MNA locality 200.

Derivation of name. The name is derived from the Navajo word 'anasazi', old or ancient people.

Diagnosis. Shoots all (as far as known) leafy, axis dichotomous, but one branch often stronger and tending to continue in nearly the same direction, lateral branches continue to fork but axis becoming thinner and leaves smaller and more crowded. Angle of dichotomy 50°–80°. Larger stems 1 mm thick, substance dense, smaller ones less dense. Stems showing two closely placed steles. Each stele having 4–8 tracheids. Tracheids 8–18 μ m wide and up to 450 μ m long, walls scalariform, spiral tracheids also present. Ordinary epidermal cells of stem rectangular to wedge-shaped, about 8–16 μ m wide, up to 60 μ m long, anticlinal walls usually straight, about 1 μ m thick. Stomata not noted on stems.

Leaves in four ranks, two ventral ranks of large spreading leaves, two dorsal ranks of small leaves on top of stem, one dorsal leaf being at the same node as a ventral leaf. Large leaves ovate, 0.6–1.0 mm wide, 1.5–2.3 mm long, apices acute to mucronate, arising alternately at interval of about 1.7–2.0 mm and at an angle of about 45°, spreading, a similar leaf also occurring in fork of each dichotomy. Leaf slightly asymmetrical with the midrib nearer the lower margin. Small leaves lanceolate, 0.4–0.6 mm wide, 1.0–1.2 mm long, apices acute to mucronate, arranged in two ranks along dorsal side of stem, arising alternately at intervals of 1.7–2.0 mm and at an angle of about 30°, somewhat adpressed to stem, apices often overlapping large leaves. Shape slightly bent with the midrib curving to be parallel to the stem.

Leaves of both sizes containing a conspicuous midrib up to 35 μ m wide. Midrib containing a vascular bundle composed of 1–5 rows of tracheids with scalariform thickenings. Vascular bundle departing from stele of stem without forming a leaf gap, extending to within 30–50 μ m of leaf apex, narrow and inconspicuous in leaf base, containing 1–2 rows of tracheids, becoming broad above leaf base, containing as many as 5 rows of tracheids. Margins of leaves flat entire, bordered with 4–10 rows of narrow, rectangular cells in a single layer, anticlinal cell walls thick (3–5 μ m), cells about 10 μ m wide, up to 50 μ m long. In apical region ordinary epidermal cells of one side nearly rectangular, about 4–25 μ m wide, 25–60 μ m long, anticlinal walls about

EXPLANATION OF PLATE 114

Figs. 1–10. Selaginella anasazia sp. nov. 1–3, transfer, USNM 168945, apical regions of three large lower leaves. The several rows of thick-walled cells along the margins and the midveins show as dark zones in the photographs. Note that the epidermal cells generally are rectangular and occur in longitudinal rows. All × 30. 4, transfer, USNM 168946, basal portion of a large lower leaf showing the spindle-shaped ordinary epidermal cells that prevail in this region. Compare the straight side walls of these cells with the sinuous side walls shown by the ordinary cells in the apical regions of the leaves in figures 1–3, × 30. 5–7, leafy shoots showing the growth habit of this plant, all × 1. 5, USNM 168910. 6, USNM 168909. 7, USNM 168908. 8–10, Stomata. The stomata in figures 8–9 are beside the midvein in the central part of a leaf whereas the stomata in figure 10 is near the upper end of a midvein in the apical region of a leaf. Note that the guard cells clearly overlap the ordinary epidermal cells in these examples. Compare the thick anticlinal walls of the marginal cells to the left in figure 10 which the thin anticlinal walls of the other cells elsewhere in the figure and in figures 8–9. Tracheids of the midveins are visible in places in figures 8–9. All × 400. 8–9, transfer, USNM 168947; 10, transfer, USNM 168945.

 $1-2~\mu m$ thick, side walls markedly sinuous (maximum sinus amplitude about $3~\mu m$) end walls straight to slightly sinuous, anticlinal walls becoming progressively less sinuous towards leaf base. Ordinary cells of the other side of leaf elongated with straight to wavy (rarely sinuous) walls. Ordinary epidermal cells of both sides gradually become spindle-shaped with more or less straight anticlinal walls in basal part of leaf, remaining about the same size as those in apical part. Periclinal walls of all epidermal cells flat, smooth. All epidermal cells arranged in distinct longitudinal rows, leaf widening by addition of rows of ordinary cells interior to marginal cell rows. Stomata few, occurring in rows a single stoma wide on either side of midrib, or directly under midrib, stomatal rows not sunken, individual stoma separated by 2–6 ordinary epidermal cells, about 6–10 per leaf. Guard cell pair oval, usually longitudinally oriented, 140–160 μ m long, 80–100 μ m wide, aperture elliptical about 70 μ m long, guard cells overlapping epidermal cells to a small extent. Mesophyll probably represented by darker strips beside the midrib. Ligule forming a dark area at leaf base about 0·3 by 0·2 mm broad (outline and cells not observed clearly), base of ligule dense.

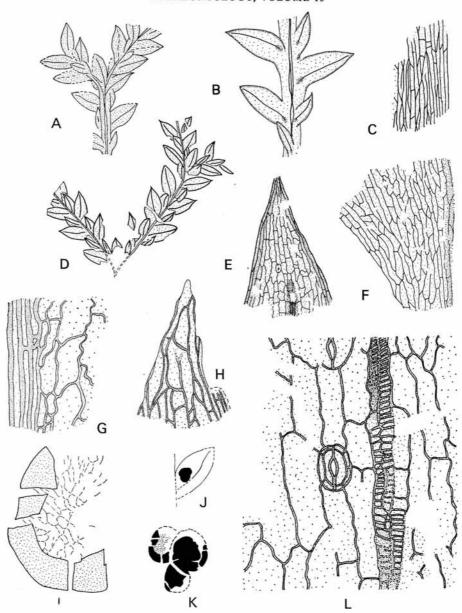
Cone known to be at least 3 mm long, 1.5 mm wide, sporophylls not forming an enlarged ventral set but all alike, megasporophylls at base, ovate, about 1 mm wide, 2 mm long, pointed, texture resembling a leaf. Megasporangia not preserved but still containing at least 3 of the spore tetrad. Megaspores about 200 μ m in diameter, wall thick apparently pitted but details not clear. Microsporophylls not observed.

Discussion. S. anasazia is not very common and occurs only in the lower part of the fossiliferous zone at locality 10093. It is preserved in a fine grained slightly calcareous mudstone and the plant substance is rather dark. Although the fossil shows the epidermal cells rather indistinctly to direct observation, transfers show them very clearly in both the leaves and the stems. Remains of four cones were recognized; all are poorly preserved but clearly are attached to the ends of leafy shoots.

Some leaves in transfer show one set of cells (with coarsely sinuous walls) clearly and the other set of the opposite epidermis (with straight to wavy walls) only obscurely or scarcely at all. Other leaves, however, show both sets clearly. I am not sure which is the upper epidermis in any of the specimens. However, in certain living species of Selaginella, such as S. martensii and S. producta, the upper sides of the leaves have straight to wavy walled epidermal cells and lack stomata, whereas the lower sides have sinuously walled epidermal cells and bear a few sparse stomata over the midrib. Thus, I think that the side of the leaf in the fossil that bears stomata and shows sinuously walled epidermal cells is the lower. I cannot explain why only one epidermis is preserved on some of these leaves but a similar type of preservation was shown by some specimens of the fern Cladophlebis daughertyi (Ash 1970a, p. D43) which was also described from the Chinle Formation at other localities in the south-western United States.

If S. anasazia has a cuticle at all it must be exceedingly delicate, and this is ordinarily taken as there being none. Although the epidermis is beautifully preserved and excellent acetate transfers were obtained and gently macerated in HNO₃+KClO₃ for half an hour, all organic matter dissolved when the transfer was placed in NH₄OH.

The broad, spreading leaves of the species described here are similar to the leaves of many living selaginellas, such as *S. krausiana* and *S. abyssinica*, which typically live in a fairly moist, and shady habitat. On the other hand, they contrast with the tiny,



TEXT-FIG. 4. (See opposite).

strongly appressed leaves of several species, such as *S. pilifera* and *S. mutica* which inhabit a much more arid environment. This suggests that *S. anasazia* lived in a moist environment.

In most places the stems show two steles clearly but below a dichotomy there seems to be three and at some places only one was seen. The vascular bundles in a few leaves clearly appear separate from stem vascular bundles in transfers (see text-fig. 4A, 4B) but the gap is rather small (perhaps 0·1 mm). In others, however, it is continuous. In these the veins are quite narrow and delicate in the leaf base and expand upward as commonly occurs in many living species of *Selaginella* (Harvey-Gibson 1897, p. 152).

New features for a fossil *Selaginella* presented by *S. anasazia* are firstly the cellular details of the leaf and stem, and secondly the ligule, although this is seen imperfectly. The details of the cone are not very good. We have, however, apart from the missing cone details, remarkably close agreement with many living species.

This species raises the question of the separation of Selaginellites from Selaginella acutely. If all fossil plants or at any rate all Mesozoic and Paleozoic ones are to be separated (on age) as a convention, there is no problem. But if a genus is only held to be valid if it has clear morphological distinctions from other genera then the fossil described here would be placed in Selaginella. It is not differentiated by any known character and agrees in a large number with Recent species. Admittedly the cone is only poorly known, but so far as it goes, it is typical and a better specimen may well remove any doubt and also provide good spores. We do not have its rhizophore (a part which is likely to be missing from the detached fragments found as fossils) and of course we have no information about gametophytes and other soft parts and this we may never have.

Certain authors, however, have held that knowledge of a fossil can never be complete and this, in effect, is a difference. Thus Seward (1910), has used *Selaginellites* in preference to *Selaginella*, *Lycopodites* instead of *Lycopodium*, etc. More recently Chaloner (1967) followed this principle and transferred several fossil species from *Selaginella* to *Selaginellites* in volume two of the Traité de Paléobotanique.

Florin (1936) considered the problem when he was working with fossil ginkgos. He took the position that while *Ginkgo* was suitable for fossil leaves which in his

TEXT-FIG. 4. Selaginella anasazia sp. nov. A, Portion of a leafy shoot showing a leaf in the fork of the bifurcated axis. Transfer, USNM 168947, \times 5. B, Portion of a leafy shoot showing three large lower leaves, three small upper leaves, and the distribution of vascular tissue in the leaves and shoot axis. The remains of the ligules are indicated by the dark oval areas in the leaf bases, transfer, USNM 168948, ×20. C, Epidermal cells on the shoot axis, transfer, USNM 168947, ×100. D, Leafy shoot, transfer (holotype), USNM 168945, ×5. E, Epidermal cells in the apical region of a leaf. The dense stippling along the margin shows the distribution of thick-walled cells in this part of the leaf. The end of the mid-vein and a stoma is also shown. Transfer, USNM 168945, ×100. F, Irregular epidermal cells between the midrib (to the left) and the margin (to the right) in the basal portion of a leaf, transfer, USNM 168946, ×100. G. Epidermal cells near the edge of leaf. The rectangular, thick-walled cells at the left are along the margin and contrast with the irregular, thin-walled cells elsewhere on the lamina of the leaf, transfer, USNM 168947, ×400. H, Apex of a leaf, transfer preparation, USNM 168945, ×400. I, One of the spores in K showing some of the pitting on the walls. Transfer, USNM 172282, ×200. J, Reconstruction of a leaf bearing three spores. Based on a transfer, USNM 172283, ×10. K. The remains of three spores. The stippled area shows pitting on the spore wall. Transfer, USNM 172282, ×10. L, Two stomata on the epidermis of a leaf. The midrib is to the right, transfer, USNM 168947, ×400.

personal opinion showed morphological points of agreement with the leaves of *G. biloba*³ he used *Ginkgoites* for species where the form, or the fine structure, were different enough to leave him (again personally) in doubt. He also used it where he had doubt of another kind, that is where some sort of the necessary evidence, such as the fine structure, was not available. He attempted no definition of how great a difference should be or what sort to cause him to doubt generic identity.

At one time Harris (1941, 1945) followed Seward and used *Equisetites* for Jurassic fossils he considered to be like *Equisetum*. Recently (1961), however, he has changed his opinion and reassigned some of the fossils he had called *Equisetites* to *Equisetum* because he could not show a real morphological difference between them and the Recent genus.

Since I cannot show any real morphological differences between the fossils described here and the Recent *Selaginella*, I refer them to that genus.

Comparisons. A considerable number of Paleozoic and Mesozoic fossils have been described as species of Lycopodites, Selaginella, and Selaginellites. Many are probably twigs of conifers and are not considered further, but others show important points of resemblance to Selaginella. Not one of these shows a full set of characters—form of shoot, leaf, cone, mega- and microspores, cellular details of leaf and stem, the ligule and rhizophore (the two last organs are not clearly shown in any description of a fossil species known to me). The better known species are not satisfactorily comparable, for in some the shoot, cone, and spores are well known but there is little if any information on the fine structure of stem or leaves. S. anasazia on the other hand has a poorly known cone but the fine structure of the stem and leaves is exceptionally well known.

One species that resembles S. anasazia in general form is L. macrophyllous Goldenberg, 1855 (see also Halle 1908). It, however, can be easily distinguished by its large leaves (twice the size of those of S. anasazia). L. falcatus Lindley and Hutton from the Middle Jurassic of Yorkshire (see Harris 1961) agrees in size of the foliage and in its anisophylly, but the small leaves are not arranged as in Selaginella and there also are differences in the leaf epidermis. For example, the stomata are wide spread on the leaves of L. falcatus, whereas they are highly localized in S. anasazia (just over and near the midrib). Selaginellites nosikovii Kryshtofovich and Prinada (1932) from the Jurassic of Siberia also agrees in some features but it has lower leaves that are much longer than in S. anasazia and that point at right angles to the stem, not at a much lower angle as in the Arizona fossil.

The most similar species known to me are *L. scanicus* Halle (see Lundblad 1950) from the Rhaetic of Sweden. The shoot and leaves, however, are more crowded and their margins are microscopically denticulate instead of entire.

Three species of what are believed to be Lycopods are already known from the Chinle Formation, namely Lycostrobus chinleana Daugherty, Chinlea campii Daugherty em. Miller (1968), and Lycopodites (?) sp. Daugherty. All of these represent far larger plants with nothing in common with the delicate little fossil described here. Spores named Lycospora sp. by Peabody and Kremp (1964) have been described from the Chinle Formation but there is no reason to identify them with S. anasazia.

Full comparison with the species of the huge living genus *Selaginella* would be a formidable task as a large number of the species growing in the dark and shade have shoots looking much like *S. anasazia*. The familiar *S. krausiana* for instance agrees in

the appearance of its shoots in the general form of the leaves and even in several of the microscopic characters of the leaves, but there are also small differences. For example, the dorsal leaves are of slightly different shape and *S. anasazia* leaves lack the marginal teeth of the leaf of *S. krausiana*.

GYMNOSPERMOPHYTA Class CONIFEROPSIDA Order CONIFERALES, Family?

Genus Dechellyia Ash, gen. nov.

Type species-Dechellyia gormani Ash, sp. nov.

Diagnosis. Leafy shoot and foliage shed in one piece, main axis bearing opposite branches. Branches bearing linear foliage leaves and small clasping scale leaves. Foliage leaves persistent, opposite, arising in two decussating pairs but flattened into the horizontal plane, confined to upper two-thirds of axis, bases evenly contracted but not forming distinct petioles, lamina containing a broad midrib and several narrow parallel strands. Scale leaves persistent, apparently opposite, abruptly giving place to foliage at end of lower third of branch axis. Fertile branches borne on same shoot as foliage. Fertile axis often elongated, other forms with one or more elongated lateral branches or with several very short lateral branches. Fertile axis covered with small outgrowths (presumed to be reduced leaves) along its margins (and surface?), at its end bearing a pair or two pairs of sporophylls. Each sporophyll comprising a single basal seed surmounted by a lanceolate lamina. Lamina containing two broad parallel ribs and two narrow strands, all apparently ending separately at apex. Sporophylls with their seeds readily detached.

Derivation of name. The name is derived from Canyon de Chelly, Arizona, at whose mouth the type species was collected.

Dechellyia gormani Ash, sp. nov.

Plates 115-118; text-figs. 5, 6 A-C

1967 Samara, Ash, p. 130, fig. 3a. 1972a New genus A, Ash, p. 19, fig. 4.

Holotype. USNM 168919. Paratypes: USNM 168915, 168907.

Distribution. Dechellyia gormani occurs in the lower part of the Monitor Butte Member of the Chinle Formation at the mouth of Canyon de Chelly, Arizona at USGS fossil plant locality 10093 (also MNA locality 200) and in the Fort Wingate area, New Mexico at USGS fossil plant locality 10060.

Derivation of name. The species is named in honour of Mr. David Gorman of Canyon de Chelly National Park who told me about the presence of fossil plants at the mouth of the canyon.

Diagnosis. Main axis 2–5 mm wide, repeatedly branching. Leafy branches 9–25 cm long, foliage 2–10 cm wide, axis 1–2 mm wide, straight, furrowed, bearing many spreading, outward directed, typically straight to curving, linear persistent foliage leaves above and small clasping leaves below. Foliage leaves projecting at an angle of $40^{\circ}-70^{\circ}$ to the stem, often at a lower angle near apex and a higher angle near base, 1-2–4 mm wide, 1–7.5 cm long, margins nearly parallel except near base and apex, apex acutely pointed,

basal 2–4 mm evenly contracted to a width of 0·5–1 mm. Midrib about 200–300 μ m wide. Strands four (rarely five), about 50 μ m wide, typically two on either side of midrib, more or less parallel except in leaf base where they originate. One member (midrib marginal strand) of each pair is very close to vein, the other (marginal strand) is about 100 μ m from the margin. Each pair arising by the forking of a single basal strand which enters the leaf base beside the midrib, each strand apparently ending separately near leaf apex. Occasionally marginal strands bifurcate once near leaf base, outer member of the pair running parallel to other veins for a short distance and then disappearing near leaf margin. Scale leaves acutely pointed, about 4 mm long, 1 mm wide at base, extending parallel to axis and situated close to it.

Fertile axis bearing along its length spine-like reduced leaves about 1 mm long. Sporophyll consisting of seed attached to axis at its base and continued above into a symmetrical lanceolate lamina. Seed oval, about 7 mm long, 3 mm wide, firmly attached to lamina, made up of a (hollow) interior about 2.5×1.5 mm, enclosed in a shell nearly 0.5 mm thick and surrounded by a delicate flange 0.2-0.3 mm wide which continues the lamina downwards. Lamina 3-4.2 cm long, 7-10 mm wide, apex obtusely rounded, lower part narrowed gradually to the seed, containing two broad ribs and two narrow marginal strands. Ribs about 300 μ m wide, more or less parallel except in base where they are close and in apical region where they converge slightly, ending separately in apical region, generally about 1.5-2.0 mm apart. One narrow strand about 50μ m wide arising from the basal area of the lamina on either side of the pair of ribs, running parallel and close to lateral margins of lamina, apparently ending separately in apical region.

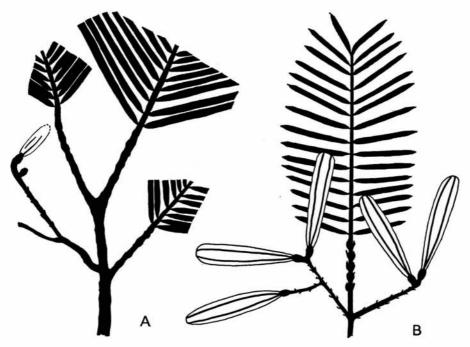
EXPLANATION OF PLATE 115

Figs. 1–5. Dechellyia gormani gen. et sp. nov. illustrating the variation in the size of the leafy branches and the foliage leaves. All ×1. 1, USNM 168948, portion of a large leafy branch bearing very large foliage leaves. The two midrib marginal strands are clearly visible as narrow dark lines in many of the leaves. The midrib itself is represented by a wider clear band between the two strands. 2, USNM 168926, the upper portion of a leafy branch bearing foliage leaves of typical size. Here the midribs and associated strands are often represented by a clear band where the carbonaceous material has fallen off. 3, USNM 168949, the central portion of a leafy branch bearing several foliage leaves that show swellings. The portion of the leaves above the swellings is broken off in most of these cases. Exceptions are the two near the top of the branch and to the right which are bent downward at the swellings. Compare figs. 1, 2, 5, Plate 116. 4, USNM 168921, lower part of a leafy branch showing typical foliage leaves and several scale leaves on the lower part of the axis. 5, USNM 168941, the upper portion of a leafy branch. Here once again the midrib and associated strands are represented by a broad clear band.

EXPLANATION OF PLATE 116

Figs. 1–5. Dechellyia gormani gen. et sp. nov. All ×1. 1, USNM 168942, the base of a specimen showing unusually small foliage leaves. Scale leaves are visible along the axis below the foliage leaves. 2, USNM 168950, a leafy branch bearing a number of foliage leaves that show swellings. Note that only about half of the leaves show this feature and that the swellings all occur about 1 cm from the branch axis. 3, USNM 168951, portion of another leafy shoot that bears many leaves showing swellings. Note that several of the leaves on the right side of the stem are bent at the swellings whereas the others are broken off. 4, USNM 168952, bifurcated shoot axis. Scale leaves are visible along the axes of several of the leafy branches. 5, USNM 168953, a specimen in which about half the leaves have swellings. Note that the sixth leaf from the top on the right side of the axis has two swellings. Typically the swellings occur about 1 cm from the axis.

Preservation. To the naked eye Dechellyia looks well preserved but unfortunately destruction has occurred at some stage. The leaves are black to dark brown and the fossil substance has often adhered to both sides of the rock (usually with more on one than the other) causing numerous gaps. Then the plant substance has often contracted into little polygonal blocks about $10~\mu m$ broad and they are separated by narrow gaps.



TEXT-FIG. 5. Dechellyia gormani gen. et sp. nov. A, penultimate shoot. An axis bearing the remains of two sporophylls is to the left, the naked branch below the axis may be either another fertile axis or the base of an ultimate leafy branch. Drawn from USNM 168915, $\times 1$. B, reconstruction of a fertile branch, $\times 1$.

This, of course, precludes making a typical cuticle preparation. Even where this has not happened the substance adheres firmly to the rock and needs transfer treatment to remove large areas. The transfers give little additional information even when they are macerated or bleached. Thus practically all that is known about *Dechellyia* is what the specimens show to the naked eye or at a low magnification. We have no knowledge at all of the fine structure beyond what is shown by surface observation. It is particularly regrettable that we have no fine structure of the body here regarded as a seed.

Discussion. The organization of the foliage and the fertile organ is by no means certain. For the purpose of description the following assumptions which seem to be the simplest possible have been made. I call the simple spreading organs of the foliage 'leaves' or

'foliage leaves' and the smaller ones below 'clasping' or 'scale leaves'. They are borne on what I term a 'leafy shoot'. Admittedly, the spreading organs might have been described as 'pinnae' or 'reduced pinnae' on the rachis of a pinnate leaf. Whether leaf or leafy shoot it clearly is of strictly limited growth. It seems likely that the part which bears the leafy shoots is itself a stem.

For purpose of this description I have assumed that we are dealing with deciduous leafy shoots because isolated leaves are rarely found. If this is so, then the shoots are rather like those of such conifers as *Taxodium* and *Metasequoia* although the fructifications are quite different. On the other hand if they are simply pinnate leaves borne on rather slender stems then they would be like the Triassic Pteridosperms *Stenopteris* and *Xylopteris*. No little clasping scale leaves, however, are seen in those plants.

Several forking stems are known (see Pl. 117, figs. 13–15). The branches in most are short and do not bear foliage leaves. One large specimen, however, has branches bearing typical foliage leaves (Pl. 117, figs. 13–14). Most of the forking stems also show a short stump in the angle of the fork. Probably they represent the uppermost portion of a main stem and the stump is the apex of the main axis as in many modern trees and shrubs.

A small percentage (perhaps 5%) of the leafy shoots have leaves showing conspicuous swellings (see Pl. 116, figs. 2, 5) and some show them on nearly all leaves (see Pl. 115, fig. 3, pl. 116, fig. 3). Most leaves have only one swelling but a few have two (Pl. 116, fig. 5). Very often the leaf is broken off or at least its direction changes at the swelling. Most swellings occur about 1 cm from the leaf base and maybe on the side of the leaf facing the stem apex or the side facing the stem base or in about the middle of the leaf. Many are oval and broader (about 3 mm) than the leaves on which they occur, but smaller and round ones are also known. All of the swellings bulge strongly and are composed of a good deal of brittle coaly matter. On one specimen there appears to be a series of

EXPLANATION OF PLATE 117

Figs. 1-15. Dechellyia gormani gen. et sp. nov. All ×1.

1–11. Detached sporophylls. 1, USNM 168918, the largest specimen. 2, USNM 168943, the lamina and seed in this rather large specimen are not connected because the rock was broken in collecting. The two ribs in the lamina are clearly visible as dark lines in some places. 3, USNM 168917, a fairly complete example of a detached sporophyll in which the ribs, strands, and lamina apex are fairly well preserved. 4, USNM 168920, the remains of a sporophyll which has an unusually broad lamina. 5, USNM 168923, a typical specimen. 6, USNM 168939, a complete example of a small sporophyll with a narrow lamina and the basal portion of another sporophyll. 7, USNM 168911, lower part of a specimen in which the seed has not been compressed and stands about 0.5 mm above the level of the lamina. 8, USNM 168940, the apical constriction of the lamina in this very small example is probably due to an accident of preservation. 9, USNM 168912A, basal part of a specimen in which the hollow interior of the seed is filled with sediment. The shell is preserved as a small ridge around the interior filling and a narrow band of lamina appears to enclose the seed. 10, USNM 168913, the remains of a fairly large megasporophyll. 11, USNM 168944, the marginal strands show fairly clearly as dark lines in this specimen. In places strands are preserved near the margins of the lamina.

12, USNM 168922, a fairly complete shoot.

13, USNM 168927A, the fork of a large shoot axis. There is a slight indication of the stump between the two leafy branches. 14, USNM 168927B, counterpart of the lower part of the specimen in 13. The stump is clearly visible between the branches.

15, USNM 168914, the fork of a small shoot axis. A low stump is visible between the two branches.

radiating ridges and grooves. Maceration of the coaly matter and of transfers of the swellings yielded no useful information. The swellings are here described as galls caused by some parasite rather than as reproductive structures.

I have used the following terminology in referring to the several linear structures shown in the foliage leaves and the lamina of the structures I call sporophylls. The broad (about 200–300 μm) central structure in the foliage leaves is termed a midrib whereas the narrow (about 50 μm) structures are called strands with the ones that are close to the midrib being designated midrib marginal strands and those near the lamina margins, marginal strands. The two broad structures in the laminae of the sporophylls are called ribs and the two narrow structures near the margins of the lamina are called marginal strands.

The marginal strands in both the foliage leaves and the sporophyll laminae look just like the midrib marginal strands but may be slightly narrower. They are composed of a somewhat coherent brown material which occasionally can be detached, bleached and mounted on a glass slide. They are then seen to be made up of rectangular parenchyma cells in longitudinal files. Neither tracheid thickenings or elongated thick-walled cells such as fibres were seen.

Frequently the midribs of the leaves and the ribs in the laminae of the sporophylls are almost black although in other cases they are only slightly darker than the lamina. Its substance has decomposed into little blocks separated by narrow gaps. These blocks tend to form longitudinal files which probably represent elongated thick-walled cells. Nothing like tracheid thickenings could be recognized in these structures.

The lamina is the palest part and again its substance has disintegrated into separate little blocks. For the most part these are uniformly scattered but at some points they are broader than long and tend to form transverse files. These blocks are more visible under low magnification than high.

A possibility is that:

- The midrib in the leaves and the ribs in the sporophyll laminae are the only vascular strands.
- (2) The midrib marginal strands and the marginal strands are resin ducts, the resin forming the coherent brown matter. Or they may be supporting tissue but if so it is strange that nothing like a fibre was seen. It is even possible they represent air canals in a water plant but though the cells seen do seem to be of reasonable shape, they are unlikely to be preserved as a dark, coherent strand.

Again, I cannot be sure that the exposed oval bodies looking like seeds are indeed seeds because they have not been shown to have the fine structure of gymnosperm seeds. Also, I cannot be sure of their exact relation to the sporophylls as I have not yet found a specimen showing the relations clearly. Nevertheless, the gross characteristics of the bodies suggests they are seeds. For example, the shell of the body is substantially thicker than the carbonaceous film of the sporophyll lamina indicating that it originally was much bulkier and thicker than the lamina. Several specimens show an oval gap in the carbonaceous material where the shell has fallen off (see Pl. 118, fig. 9). In some there is either a depression or mound showing as much as 0.5 mm relief at the site of the body (see Pl. 117, fig. 7). All of this evidence is consistent with the view that the body is truly a seed.

Comparisons. I know of no plant, fossil or living, that exhibits the combination of characteristics shown by Dechellyia. Probably the most outstanding are the winged structures thought to be sporophylls. Some fossil plants and many living trees have some sort of a wing attached to a seed or fruit that aids wind dispersed. For instance, Fraxinus, Acer, and Tilia have such an appendage although its morphology is entirely different. Among fossils there are Dioonitocarpidium, Cycadocarpidium, Fraxinopsis, and Dinophyton.

Dioonitocarpidium Lilienstern (1928) is from the Late Triassic of Bavaria. It has a narrow rachis bearing four rows of sickle-shaped pinnae and two basal bodies thought to be seeds. The fossil described here has no pinnae and a single seed. Cycadocarpidium Nathorst (1886) from the Late Triassic of Sweden, Russia, and Greenland is more similar. It has a broad lamina containing several (4–10) parallel veins and two seed-like bodies which are borne on a small separate, basal, ovuliferous scale. Evidently it is distinct from the sporophyll of Dechellyia which has only two ribs and a single seed-like body imbedded in the base of the lamina. Fraxinopsis Wieland (1929) from the Middle Triassic of Argentina and Australia is still more similar. Here again the lamina is broad but it contains several (7 or more) parallel veins. There are, however, two bodies thought to be seeds imbedded in the base of the lamina not one as in Dechellyia. The fructification of Dinophyton, Ash 1970c (from the same flora as Dechellyia) differs greatly in having four wings but in view of a certain similarity in its shoot, is referred to again.

It is possible to make some comparison between *Dechellyia* and the conifer *Podozamites* because the shoots of *Podozamites* often bear basal scale leaves and the foliage leaves may be in two lateral ranks but normally they are not opposite in decussate pairs. In all species of *Podozamites*, however, even ones with very narrow leaves, there are several veins and these converge towards the apex, as they do in other conifers with several veins.

In an earlier report (Ash 1972a) *Dechellyia* (though not named) was tentatively compared with *Podozamites arizonicus* Daugherty because the leafy shoots are superficially similar. A recent study of the cotypes of *P. arizonicus* shows, however, that they actually

EXPLANATION OF PLATE 118

Figs. 1-8. Dechellyia gormani gen. et sp. nov. All ×1. 1, USNM 168928, pedicel bearing the bases of several sporophylls. Two of the organs are attached to the end while the others are attached alternately to the sides of the structure. 2, USNM 168907A, sporophyllus organ composed of four sporophylls attached to an unbranched spiny pedicle. 3, USNM 168907B, counterpart of the specimen in 2. 4, USNM 168929, lower part of a fertile branch bearing two empty pedicels. 5, USNM 168916, upper portion of a leafy branch axis and the detached end of a fertile branch bearing the bases of two sporophylls which are attached to the end of a pedicel. 6, USNM 168924A, lower part of a fertile branch bearing a fragmentary pedicel on the left and the right. Excavation on the counterpart has shown that the central linear structure is connected to the left pedicel near the fork. That structure may be another pedicel or the axis of a leafy branch. 7, USNM 168919, holotype, a leafy branch bearing two pedicels. The pedicel on the right bears the seedlike body of a sporophyll; the other pedicel bears two complete sporophylls. One of these sporophylls (on the right) is flattened in the same plane as the leafy axis whereas the other is more or less perpendicular to the plane and shows as a dark line in the photograph. The line actually is the edge of a sporophyll as excavation on the specimen has shown. Scale leaves are fairly obvious on the branch axis between the foliage leaves and the pedicels. 8, USNM 168925A, sporophyllus organ consisting of a branched pedicel bearing one sporophyll on one branch and two on the other.

are distinct. One of the outstanding differences involves the venation. In *P. arizonicus* the leaves contain 10 or more veins, as is characteristic of the genus, and thus contrast with the leaves of *Dechellyia*.

No firm classification for *Dechellyia* is offered but since the shoots do recall those of several conifers I think it may be a conifer. The fructification is plainly not like that of any conifer family yet described.

Genus MASCULOSTROBUS Seward 1911, em. Barnard 1968

Masculostrobus clathratus sp. nov.

Plate 119; text-fig. 6 D-K

Holotype. USNM 168984. Paratypes. USNM 168956, 168955, 168954.

Derivation of the name. The specific name is derived from the Latin, 'clathratus', latticed, and refers to the lattice-like appearance of the ektexine of the pollen that occur in these cones.

Diagnosis. Cone cylindrical, shortly stalked; length about twice the diameter, length 9-18 mm, diameter 4-8 mm; stalk smooth, 2 mm long by about 1 mm wide. Cone axis bearing spirally arranged fertile appendages; axis containing 4-6 narrow strands of parenchyma (c. 50 μ m wide) and associated tracheids. Appendage consisting of a broad head and a slender stalk. Stalk 0.5 mm wide by about 2-3 mm long, attached at 90° to the cone axis in the mid region of the cone; containing two narrow parenchyma strands. Head a depressed oval in outline, width exceeding the height, about 2-2.5 mm wide by 1.7-2.0 mm high; apex acuminate, pointing upwards; outer surface of head normally convex, inner surface concave, rounded into the expanded end of the stalk; stalk attached to the lower part of the inner surface of the head. Heads occasionally inverted with outer surface concave. Parenchyma strands in appendage arising from those of the cone axis by forking, disappearing in upper part of head. Head bearing 5 pollen sacs. Pollen sacs elliptical, attached to the lower edge and inner surface of the head, fused above, distal ends hanging free; walls poorly preserved. Pollen masses ellipsoidal, about 400–550 μ m long, 200-300 µm wide, containing numerous pollen grains. Epidermal cells of head (outer surface?) isodiametric, irregularly rectangular, anticlinal walls thick, average with 8 μ m (range noted 6–10 μ m).

Pollen grains round to elliptical in distal view, about $48-60~\mu\text{m} \times 24-60~\mu\text{m}$, consisting of a sulcate endexine and a ridged ektexine. Endexine thin (about $1~\mu\text{m}$ thick), smooth, sulcus extending full length of grain, greatest width near middle, narrowing at ends, lips narrowing at ends, lips narrow. Ektexinous ridges 12-25, alternating with narrow furrows, extending longitudinally, often with a slight spiral. Ridges about $2-5~\mu\text{m}$ wide, $1~\mu\text{m}$ thick, semicircular in cross section, converging near the ends of the major equatorial axis, usually forming four distinct areas of convergence. Areas of convergence opposite to sub-opposite at the ends of the equatorial axes, separated by 1-3 ridges that extend with a slight spiral almost around the grains in the direction of the equatorial axis. Ridges sometimes joined near the ends of the major equatorial axis, in some grains partially reflexed by extensions of sub-opposite convergence points past the midline of the grain. Ridges marked on their inner side by granules called 'columellae'. Rarely all bands fuse at the ends of the major equatorial axis to form a single small area.

Discussion. M. clathratus is fairly common at locality 10093 being represented by 40 more or less good specimens. As far as can be seen, they are all very much alike. The heads of the appendages usually are preserved as a coaly structure showing no surface details of interest and no remains of any coherent surface membrane or cuticle. In these, the substance has cracked into tiny pieces and on maceration it gives no useful result. Transfers do give a little additional information and a dozen or so were made. Epidermal cells were observed on two heads in one cone that had been transferred. Some of these cells are shown in text-fig. 6K, but I do not know whether they come from the outer or inner surface of the heads. Other transfers showed masses of pollen and some of the internal structure of the cone axes and appendage stalks (see text-fig. 6H).

Pollen sacs are preserved at or near the lower edges of several of the heads (see text-figs. 6D–6H) and these show many pollen grains but no definite details of the wall tissue. Pollen is fairly numerous in some of the sacs but does not form a dense mass. It looks as though the sac had opened but many grains had stuck to the wall. Although they often look well preserved in the transfers, the pollen grains contained in the cones were entirely destroyed by maceration. The cone axes contain several narrow coherent strands composed of parenchyma cells. The strands fork occasionally and a pair of branches from adjacent strands enters each appendage stalk (text-fig. 6H) and then passes into the appendage head where they disappear some distance below the upper margin (see text-figs. 6E, 6F). These strands closely resemble the strands that occur in the leaves and sporophylls of *Dechellyia* and as in that plant their function is uncertain. In contrast to *Dechellyia*, however, tracheids are preserved in the cone axes and appendage stalks in association with the strands.

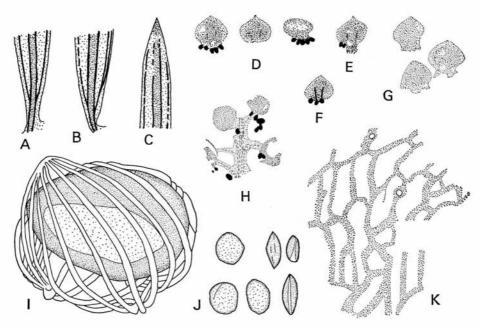
Comparisons. I find it difficult to compare this cone because I know so little about its gross organization. However, what little is known suggests that it does not compare very closely with any of the fossil cones which have been described in detail during the past. This is emphasized when the sacs on the appendage heads of *M. clathratus* and the pollen grains they contain are considered.

The pollen grains contained in these cones agree with the microfossil that was described from the Chinle Formation as *Equistoporites chinleana* by Daugherty in 1941. It was originally interpreted as being a round spore wrapped in two elaters resembling the spores of the living *Equisetum*. I have examined Daugherty's specimen and it seems to me that the supposed elaters are merely ektexine ridges somewhat similar to those of the present grains and of the pollen of some living species of *Ephedra*, as Scott noted

EXPLANATION OF PLATE 119

Figs. 1–22. Masculostrobus clathratus sp. nov. 1–8, pollen grains. The dark area in each specimen is the endexine of the grain and the narrow indistinct, light coloured bands are the ektexinous ridges. In figure 1 the ektexinous ridges are some distance from the endexine and a convergence area is clearly shown. In the other grains the convergence areas are not as prominent and the ektexinous ridges frequently cross each other. Note the prominent sulcus in the elliptical grains in figures 6 and 8 and the apparent absence of this feature in the oval grains in figures 2–5. All ×400. 1, 5–8, transfer, USNM 168957. 2–4, transfer, USNM 168954.

^{9–22,} cones. 9, USNM 168932, ×2. 10, USNM 168955, ×1. 11, USNM 168955, ×2. 12, USNM 168956, ×2. 13, USNM 168931, ×2. 14, USNM 168930, ×2. 15, USNM 168933, ×2. 16, USNM 168936, ×2. 17, USNM 168938, ×2. 18, USNM 168937, ×1. 19, USNM 168935, ×2. 20, USNM 168937, ×2. 21, USNM 168936, ×2. 22, USNM 168934, ×2.



TEXT-FIG. 6. Dechellyia gormani gen. et sp. nov., (A-C), and Masculostrobus clathratus sp. nov., (D-K). A-B, bases of two leaves showing the midrib (heavy stippling) and several strands (broad solid or broken lines). Note that two strands enter the bases of the leaves on either side of the midrib and that each strand bifurcates a short distance above the leaf base. The branch which becomes the marginal strand on the right in B is exceptional as it bifurcates once a short distance above its base so that there are five strands in the lower part of this leaf. A dashed line is used where the strands are poorly preserved. A, transfer, USNM 172286, ×5. B, transfer, USNM 172285, ×5. C, the apical region of a leaf showing the midrib and four strands. The apex is very dark and it is impossible to determine whether the strands join or are free at the margins. Transfer, USNM 172287, ×5. D-G, dorsiventrally compressed heads of the appendages of M. clathratus. The black oval structures below several of the heads are sacs containing pollen grains. In some specimens (such as E) the sacs are covered by the appendage stalk or are not preserved (the centre specimen in D). The two strands that frequently occur in the heads are fairly prominent in E and F. The three heads in G are from the same cone and are shown in the position in which they were fossilized. D, transfer, USNM 172288, \times 5. E, transfer, USNM 172289, \times 5. F, transfer, USNM 172290, \times 5. G, transfer, USNM 172291, ×5. H, portion of the cone axis and the remains of five appendages. Dashed lines represent the strands in the axis and appendages. Each of the black, oval structures consists of a mass of pollen, the contents of one sac. Holotype. Transfer, USNM 168954, ×5. I, pollen grain showing extexine bands and a slightly shrunken endexine which is clearly sulcate. Note that the bands converge near the ends of the equatorial axis where they fuse. Holotype. Transfer, USNM 172284, \times 1000. J, a series of drawings showing variations in the form of the endexine of the pollen grains in a single cone. The ektexine bands are preserved on each grain but for simplification they are not shown here. Holotype. Transfer, USNM 172284, ×200. K, epidermal cells and possible trichome bases (small circles) from the head of an appendage. Transfer, USNM 172284, ×400.

(1960). The fossil called Eq. chinleana resembles the pollen described here in most characters. It falls within the size range shown by them and all have a smooth, thinwalled endexine and a ridged ektexine. The ridges and furrows of the ektexine are about the same size and have the same arrangement and converge at the ends of the major equatorial axes of the grains where they are typically united.

In 1960 Scott reported the discovery in the Chinle Formation of pollen grains that fairly closely resemble the grains of the living *Ephedra*. He demonstrated that his fossils were also very close to *Eq. chinleana* and concluded (1960, p. 276) they were conspecific. Scott proposed, therefore, a new combination of names for both Daugherty's fossil and the grains he had discovered, calling them *Ephedra chinleana* (Daugherty) Scott. I have examined several examples of the grains Scott described and agree that they are indeed similar to the fossil Daugherty called *Eq. chinleana* and are probably conspecific.

The pollen grains described here are also similar to those described by Scott in 1960. They are about the same size and have a smooth endexine and a ridged ektexine. The ridges have conspicuous granules or columellae on their inner faces and converge to two points near the ends of the major equatorial axis (called polar areas by Scott) where they typically are united. The only noticeable difference is that in the grains found in the cones of *M. clathratus*, the endexine occasionally is elliptical with pointed ends and has a sulcus extending the entire length of the grain. Scott figured some grains which show only the endexine and none of these are sulcate. Only one of Scott's grains consists of both the endexine and ektexine and although it is elliptical, it is not sulcate. All the other grains figured by him have lost their endexine.

M. clathratus shows no resemblance to either the cones of Equisetum, or to the male cones of Ephedra. So although Daugherty had referred the grains now known to be from these cones to the first genus and Scott to the second, this is not supported by the morphology of the cones. Although I see no resemblance to Ephedra, I admit that further knowledge might disclose some. If the cone should prove to belong to the same plant as Dechellyia, with which it is so closely associated, then the number of differences from Ephedra would be considerably increased.

Some of the grains of *M. clathratus* also resemble certain of the microfossils described by Wilson (1962) from the Upper Permian rocks of Oklahoma. The ones described by him under the names *Vittatina lata*, *V. costabilis*, *V.* sp. and *Ephedripites corrugatus* are all somewhat similar in size, shape and in their external ribs. The ribs, however, differ in being united to the endexine and not separate as here. Furthermore, none of these Permian grains have been shown to have a sulcus.

The pollen grains in the cones described here should be referred to *Equisetosporites chinleana* Daugherty if found dispersed. Although the holotype of that genus is difficult to photograph as Scott (1960) indicated, it is identifiable contrary to the opinion of Balme (1970). Thus, *Equisetosporites* has priority over *Ephedripites* Bolkhovitina (1953) ex Potonie (1958), if they are congeneric as some suspect.

Acknowledgements. I am grateful to Mr. David Gorman of Chinle, Arizona, for telling me about the locality that yielded the fossils described here. The co-operation of Mr. Leslie Cammack, Superintendent of Canyon de Chelly National Monument, who authorized me to collect fossils from the area under his supervision is appreciated. I am also indebted to Mr. Victor Means, Bureau of Indian Affairs of the Chinle Agency for his comments about the geology of the fossil locality, to Professor T. M.

Harris, University of Reading, for his many helpful suggestions about this report, to Mr. Howard Schorn, University of California Museum of Palaeontology for loaning me the type specimen of Equisetosporites chinleana and to Dr. Richard A. Scott, U.S. Geological Survey for loaning me specimens of the pollen he called Ephedra chinleana and for interesting discussions about these grains. This work was supported by National Science Foundation Grant GA-25620.

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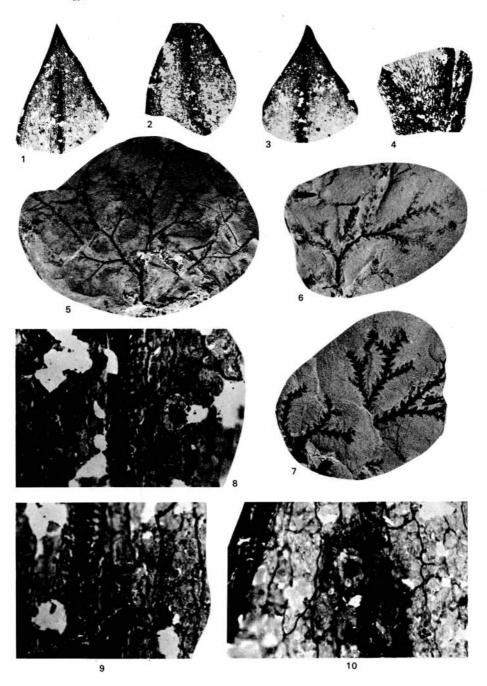
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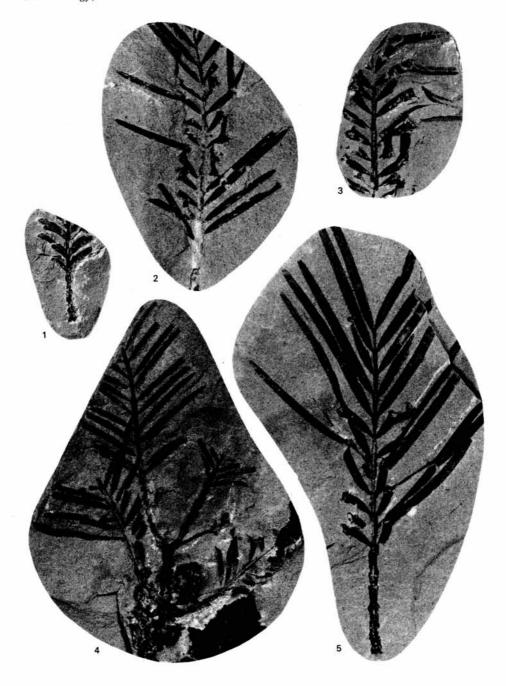
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ASH, Selaginella



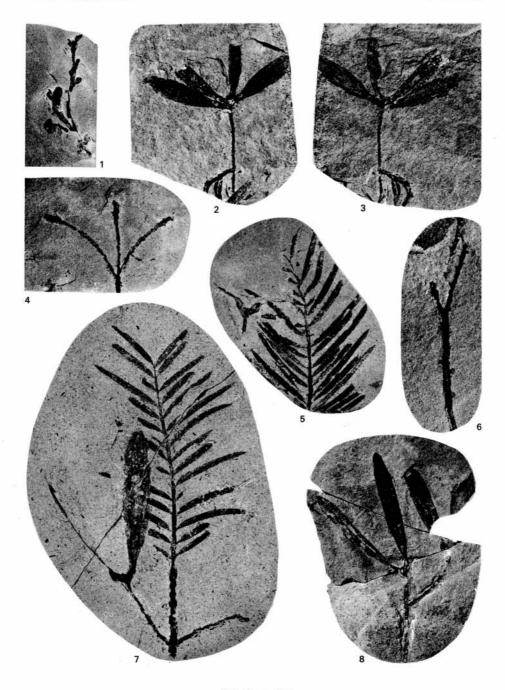
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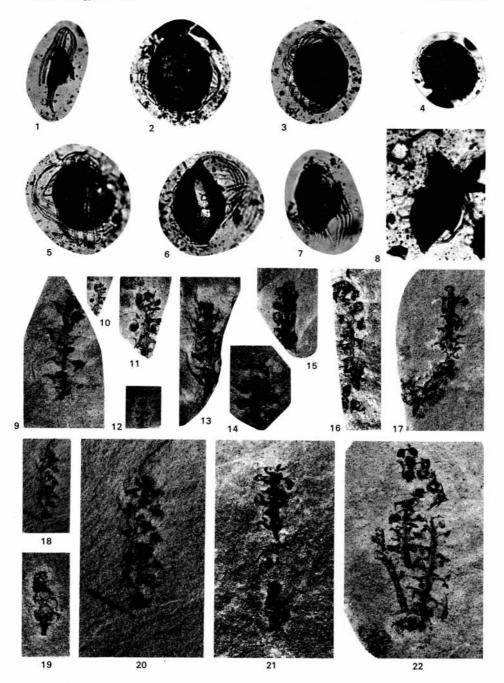
ASH, Dechellyia



ASH, Dechellyia



ASH, Dechellyia



ASH, Masculostrobus