DINOPHYTON, A PROBLEMATICAL NEW PLANT GENUS FROM THE UPPER TRIASSIC OF THE SOUTH-WESTERN UNITED STATES

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ABSTRACT. *Dinophyton* gen. nov. is based on ultimate and penultimate shoots bearing spirally arranged, outward directed, linear leaves and on some associated, bilaterally symmetrical organs superficially resembling pinwheels. The pinwheels have four arms and bear an empty cup-like structure at the centre. Cuticles of the pinwheels are very similar to those of the shoots and it is concluded that the two organs belonged to the same plant. The function of the pinwheel is uncertain; it may have been seedbearing or possibly had a role in vegetative propagation. *Dinophyton* does not resemble any known plant when all of its characters are considered and for this reason is tentatively assigned to the gymnosperms. The type species, *D. spinosus* sp. nov., has been collected from ten localities in rocks of Late Triassic age in Texas, New Mexico, and Arizona.

TWO of the more common plant fossils found in the Upper Triassic Chinle Formation and Dockum Group of the south-western United States are described in this report. One resembles the shoot of a modern conifer with medium-sized needle-leaves (see text-fig. 2A). The other looks superficially like a pinwheel with four arms or a leaf whorl of *Annularia* (see Pl. 124, figs. 1–6). Close examination shows, however, that the structure is bilaterally, not radially, symmetrical and actually more closely resembles an upside-down Latin cross (see text-fig. 2B). Cuticular study demonstrates that the two fossils probably are parts of the same plant, although the function of the bilaterally symmetrical structure is questionable. Possibly it bore an ovule but since that can not be proven at this time the structure will be referred to as a pinwheel. Neither the shoot nor the pinwheel can be identified with any known plant, fossil or living, so they are both referred to *Dinophyton spinosus* gen. et sp nov.

Although the early Mesozoic gymnosperms of the world are poorly known it is apparent that a number of unusual forms developed during this important time in plant history. Their classification and relationships are uncertain and it is difficult to assign many of them to presently recognized groups. *Dinophyton* is assigned tentatively to the gymnosperms because further classification of the fossil would be premature and must await the results of future research.

Cuticles used in this study were prepared by the standard maceration technique as follows: Compressions and coaly material were placed in concentrated nitric acid and potassium chlorate for a few hours. Then the cuticles were washed with water and cleared with dilute ammonia. Any rock material that still adhered to them after maceration was removed by placing the specimens in concentrated hydrofluoric acid for a day or so. Several of the fairly complete fossils were embedded in plastic but the majority of the material was mounted unstained in glycerine jelly. All slides and specimens have been deposited in the U.S. National Museum (USNM), Washington, D.C.

Previous investigations. Plant fossils of Late Triassic age have been known from the south-western United States for many years. They occur mainly in the Chinle Formation

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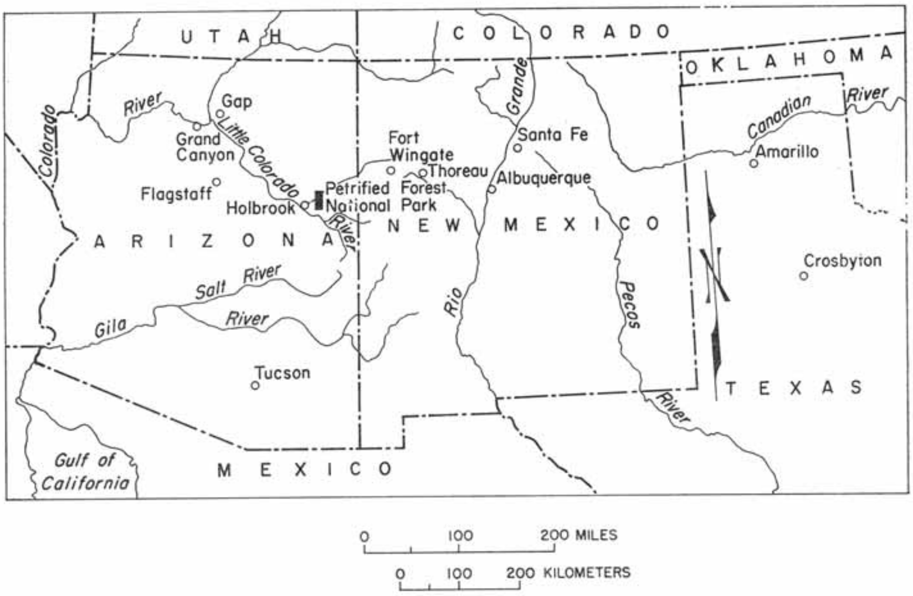
in New Mexico and Arizona although a few have been collected from a generally equivalent unit, the Dockum Group in west Texas. A number of palaeobotanists have worked on this flora but over-all progress has been slow and erratic and it is apparent that there is still much to learn about these plants.



TEXT-FIG. 1. Index map of the south-western United States.

The principal report on the Triassic plants of the Southwest was published by Daugherty (1941). A detailed review of the flora and a history of its investigation were published recently (Ash 1970*a*, *b*, *c*). These reports show that the Chinle Formation contains 51 well-characterized species. The Dockum contains 6 species, 5 of which also are known from the Chinle Formation. Only two species in the Chinle and Dockum floras occur in any other formation and it appears that the floras in the Chinle and Dockum are more closely related to each other than to any other flora.

LOCALITIES

Specimens of the shoot of *D. spinosus* and the pinwheel have been collected from ten different localities in the Upper Triassic rocks of west-central Texas, west-central New Mexico, and east-central and north-central Arizona (text-fig. 1). The distance between the easternmost locality (in Texas) and the westernmost (in north-central Arizona) is about 700 miles. In Texas the fossils occur in the Dockum Group; in New Mexico and Arizona they occur in the Chinle Formation. Both units are considered more or less equivalent (Reeside *et al.* 1957, p. 1464) and a chart showing the currently accepted nomenclature and correlation of the subdivisions of the two units is given in Table 1. The approximate stratigraphic level of the ten localities mentioned in this report are also indicated on the correlation chart.

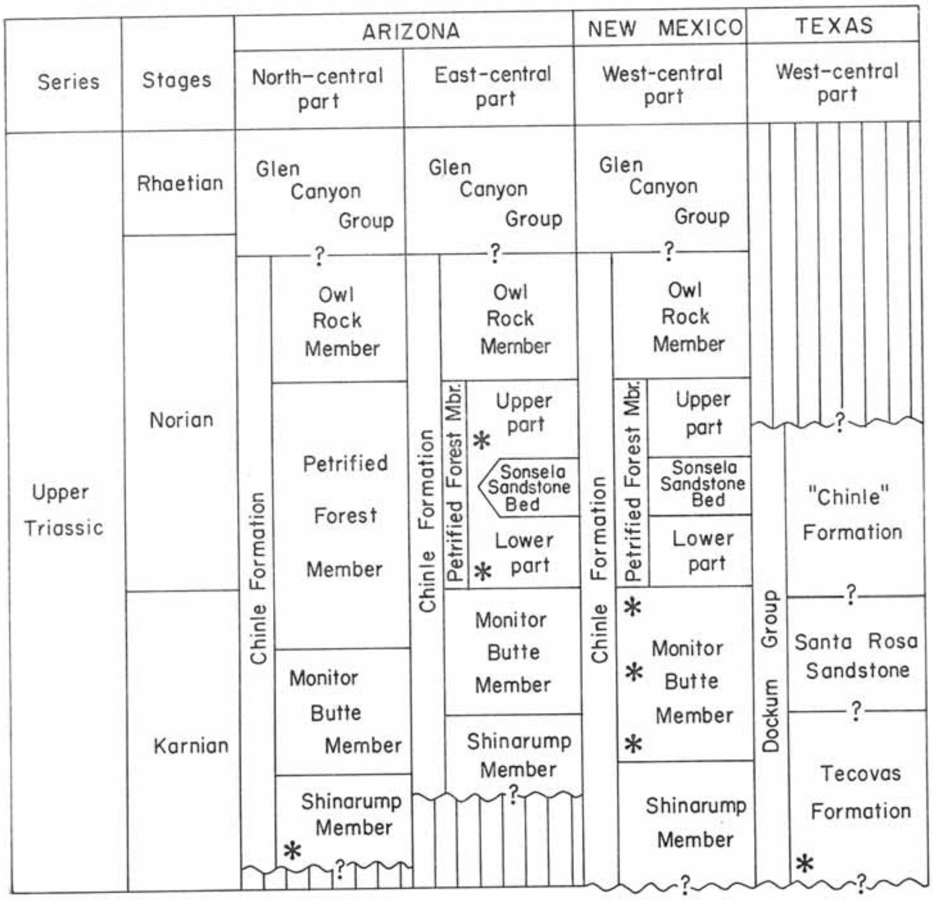
Texas. The remains of both the shoot of *D. spinosus* and the pinwheel have been collected from a locality in west-central Texas about 15 miles south-east of Crosbyton in the drainage of Home Creek. They occur in a discontinuous bed of brownish mudstone in the lower part of the Tecovas Formation of the Dockum Group and about 20 ft. above the Permian rocks in that area. Hand specimens of the mudstone frequently show poorly preserved plant remains including fragments of the new species, the bennettite *Otozamites powelli* and some small, round unidentified seeds. Bulk maceration of the mudstone, however, yields many fragments of the distinctive cuticle of *D. spinosus*. Most of the fragments are large enough to show that both the shoot and the pinwheel are present at the locality. Scale leaves of several unidentified conifers and the cuticles of a number of large and unknown leaves were also noted in the bulk macerations from the locality.

New Mexico. All of the localities in New Mexico which have yielded specimens of *D. spinosus* are in the west-central part of the state and in the Monitor Butte Member of the Chinle Formation. A few well-preserved examples of the shoot and the pinwheel have been collected from a locality approximately 4 miles south-west of Thoreau in sec. 13, T. 13 N., R. 14 W. They occur in a bed of soft, greenish, sandy mudstone in the lower part of the Monitor Butte Member and are associated with several other plant fossils including a fern resembling *Cladophlebis reticulata*, *Otozamites powelli*, and some unidentified leaves and seeds.

Many shoots and pinwheels have been collected from four localities about 1 mile south of the Fort Wingate Trading Post. Two are in beds of soft greenish mudstone and sandstone in the lower part of the Monitor Butte Member where it is exposed in road cuts along the highway from Fort Wingate to McGaffey. They have been assigned USGS fossil plant locality numbers 10058 and 10059 and part of the flora they contain has been described recently (Ash 1967, 1970*a*). It includes the ferns *Todites fragilis Cynepteris lasiophora*, *Phlebopteris smithii*, *Wingatea plumosa*, *Clathropteris walkeri*, and *Cladophlebis daughertyi*, the bennettite *O. powelli* and several unidentified leaves, seeds, and fragmentary cones. Two localities in the upper part of the Member have also yielded specimens of *D. spinosus*. One is in a bed of grey mudstone exposed in the badlands a few thousand feet east of the Fort Wingate–McGaffey highway and the two localities mentioned above. It is referred to as USGS fossil plant locality 10061 and a portion of the flora it contains has also been described (Ash 1967, 1968, 1970*a*). That flora includes *T. fragilis*, *C. lasiophora*, *C. daughertyi*, *O. powelli*, *Williamsonia nizhonia*, and a number of unidentified leaves, seeds, and cone scales. Also the wings of an unidentified insect, apparently related to the modern locusts, has been reported from the same locality (Breed 1970).

One of the most productive localities for *Dinophyton* in the Fort Wingate area is on the dissected plateau between the Fort Wingate–McGaffey highway and the badlands containing the previously mentioned locality (no. 10061). The new locality is about 150 ft. west of that locality and is assigned USGS fossil plant locality number 10088. Here the fossils occur in a bed of dark brown shale which is about 5 ft. thick. These rocks are very fossiliferous and the remains of five new conifers, and several unidentified

TABLE 1. Correlation chart of the Upper Triassic rocks in the southwestern United States. The asterisks (*) mark the approximate stratigraphic position of fossil plant localities containing *Dinophyton*. Chart adapted from Reeside and others (1957, pl. 1).



leaves have been collected from them. Other fossils which have been observed there include phytosaur teeth, coprolites of several sizes, and the remains of the branchiopod *Cyzicus* (*Estheria*) sp. The unit is of limited lateral extent and is exposed at only a few other places on the plateau. It is generally a foot or less in thickness at these localities and contains few plant fossils although abundant coprolites and the shells of *Cyzicus* are usually present.

Arizona. At least two of the several fossil leaf localities in Petrified Forest National Park in east-central Arizona contain the remains of *D. spinosus*. One of them is in a thin layer of paper coal in the lower part of the Petrified Forest Member of the Chinle about 150 ft. below the Sonsela Sandstone Bed and about 20 ft. above the Newspaper Rock Sandstone of Stagner (1941). The locality is in the badlands south of the principal road through the Park in the NE $\frac{1}{4}$, sec. 22, T. 18 N., R. 24 E. (USGS fossil plant locality 10090). Specimens of the pinwheel are particularly abundant at this locality whereas the shoot is uncommon. Remains of many unidentified leaves including those of several conifers are also present in the paper coal. The second locality is in a bed of coaly material and associated sediments in the upper part of the Petrified Forest Member of the Chinle about 90 ft. above the Sonsela Sandstone Bed. It is in a small hill approximately $\frac{1}{2}$ mile west of the principal road through the Park in the NE$\frac{1}{4}$, sec. 29, T. 17 N., R. 24 E. (USGS fossil plant locality number 10089). The coaly material contains abundant plant fossils but most are unidentified. One of the conifers in the flora, however, was recently described as *Pagiophyllum simpsonii* (Ash 1970*d*).

Two localities in the Shinarump Member of the Chinle Formation about 10 miles south-west of the Gap Trading Post at the abandoned A and B uranium mine in north-central Arizona contain large quanities of the foliage of *D. spinosus* but only a relatively few examples of the pinwheel. Several specimens of the penultimate shoots with attached ultimate shoots were collected at both localities but most of the material consists of fragments of just the ultimate shoots. The only other fossils noted at the localities are the shoots of an unidentified scale-leaf conifer and the leaf of *Otozamites powelli*. At these localities fossils are represented typically by limonite encrusted impressions in hard black shale or coarse-grained, tan sandstone. Cuticles are not preserved and identification is based only on the gross morphology of the fossils.

SYSTEMATIC DESCRIPTIONS

Genus DINOPHYTON gen. nov.

Type species. *Dinophyton spinosus* sp. nov.

Diagnosis. Shoots with many spirally arranged, spreading, needle-like, persistent foliage leaves and a few small leaves. Foliage leaves linear, round in section, containing two parallel veins, apices obtuse to more or less acuminate, base broad, petiole absent. Small leaves clasping, less than 2 mm. long, apices acuminate, attached by entire base. Narrow stumps attached to stem of certain ultimate shoots among typical adult leaves. Possible ultimate female reproductive organ consisting of a pinwheel or cross-shaped structure composed of four appendages and containing a cup which may have held an

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EXPLANATION OF PLATE 122

Figs. 1–10. *Dinophyton spinosus* gen. et sp. nov. 1, Apical region of penultimate shoot with portions of five ultimate shoots, USNM 43671, ×1. 2–7, Fragments of ultimate shoots. 2, USNM 43672, ×1. 3, USNM 43673, ×1. 4, USNM 43674, ×1. 5, USNM 43675, ×1. 6, USNM 43676, ×1. 7, USNM 43677, ×2. 8–10, Fragmentary penultimate shoots with one or more attached ultimate shoots. 8, USNM 43678, ×1. 9, USNM 43679, ×2. 10, USNM 43680, ×2. Variation in lengths of leaves is from about 1 cm. in figs. 3 and 5 to about 2 cm. in fig. 2. Specimen in fig. 5 is from USGS fossil plant locality 10060; others from USGS fossil plant locality 10061, and all from Monitor Butte Member, Chinle Formation, Fort Wingate area, New Mexico.

ovule. Stomata occurring on both sides of leaf and pinwheel, mostly monocyclic, stomatal pit rectangular, longitudinally orientated. No other parts of the plant are known.

Derivation of name. The name is derived from *diné* which means 'The People' in the language of the Navajo Indians who have inhabited north-western New Mexico and adjacent areas for several hundred years. *Diné* is what the Navajo call themselves.

Dinophyton spinosus sp. nov.

Plates 122–124; text-figs. 2–6

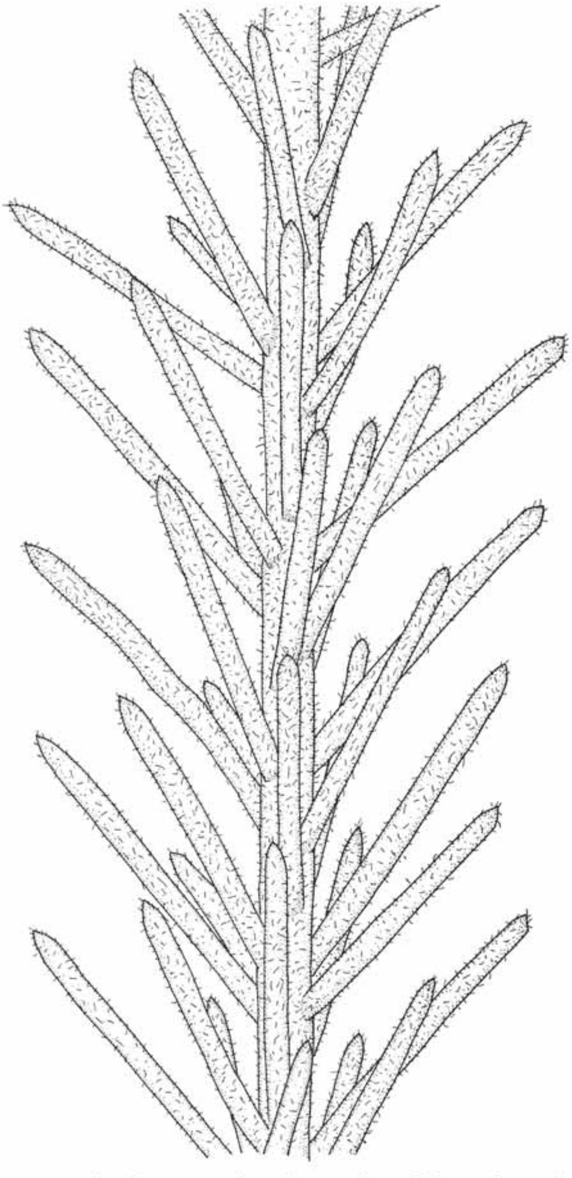
1967 Gymnospermous shoots, Ash, pp. 128–30, fig. 3.
1970*b* Foliage of undescribed conifer, Ash, p. 37, fig. 2F.

Holotype. USNM 43639. Paratypes: USNM 43637, 43638, 43649.

Distribution. The shoot of *D. spinosus* and the pinwheel occur in the Tecovas Member of the Dockum Group near Crosbyton, Texas; in the Monitor Butte Member of the Chinle Formation near Thoreau and Fort Wingate, New Mexico; in the Petrified Forest Member of the Chinle in Petrified Forest National Park, Arizona; and in the Shinarump Member of the Chinle Formation near Gap, Arizona.

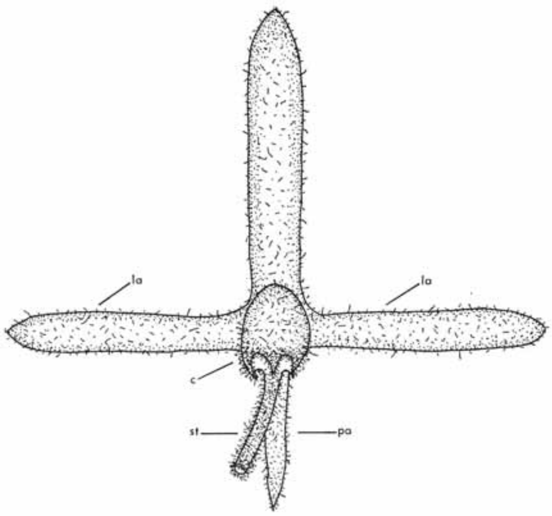
Diagnosis. Axis of penultimate shoots 1–2 mm. wide, straight, bearing leaves similar to foliage leaves of ultimate shoots. Ultimate shoots arising alternately at intervals of 15–20 mm. and at an angle of about 35–45° from penultimate shoots, axis about 0·8 mm. wide, bearing many spirally arranged (phyllotaxis probably 2/5), closely set, spreading, outward directed, long, linear foliage leaves and a few, rather small, clasping leaves. Foliage leaves (text-fig. 3) arising from an inconspicuous oval, decurrent leaf cushion about the same width or slightly smaller than leaf, cushion gradually merging with stem. Free part of leaf straight, round in section, projecting at an angle of about 30–50° to stem, about 10–25 mm. long, about 0·35–0·75 mm. broad, sides parallel except in vicinity of base and apex, occasionally narrowing slightly near base to meet leaf cushion, in upper part narrowing abruptly to an obtuse to more or less accuminate apex. Leaf typically containing two veins about 70–90 μm. wide, arising dichotomously from one vein in base of leaf, unbranched, generally parallel except in leaf base where they diverge and in apical region where they unite, resulting vein appears to continue to within a very short distance of apex. Small leaves inconspicuous, concealed by adult leaves, rare, occurring at base of some adult leaves, usually one to three leaves present at one position, small leaves elongate, obtusely pointed, clasping, size ranges from 170–340 μm. wide near base, 500–1700 μm. in length. Narrow stumps about 300 μm. wide, 3–3·5 mm. long arising from stem at several places between foliage leaves on certain shoots.

Cuticle of leaf (text-fig. 4) tough, about 5 μm. thick; cuticle of stem slightly thinner and more delicate, rib-like projections or flanges of cuticle at position of anticlinal walls of epidermal cells, flanges about 3 μm. high. Stomata present on leaf and on stem in approximately equal numbers (about 100 per mm.^{2}), rather widely spaced in poorly defined rows a single stoma wide on leaf and stem. Stomatal rows not sunken, typically separated by 2–5 rows of ordinary epidermal cells, individual stomata in rows separated by 2–6 ordinary epidermal cells. Stomata mostly monocyclic with 2–4 lateral and two terminal subsidiary cells, rarely amphicyclic, subsidiary cells having thickened inner walls, otherwise unmodified except by position, rarely shared, stomatal pit rectangular,



TEXT-FIG. 2A. Reconstruction of part of an ultimate shoot of *Dinophyton*, approximately $\times 5$. The position, size, and number of trichomes is generalized.

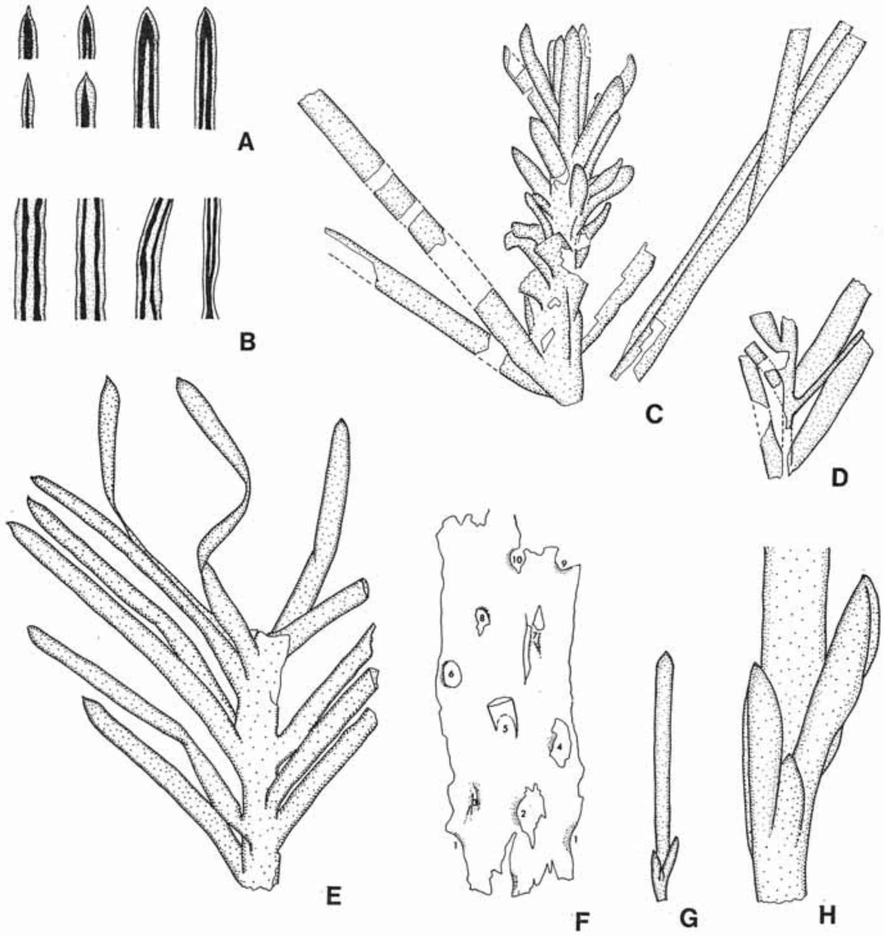
about 10–14 μm. $\times$ 3–6 μm., longitudinally orientated, shallow, guard cells slightly sunken, thinly cutinized. Ordinary epidermal cells similar on leaf and stem, longitudinally oriented, polygonal (range noted 7–21 μm. wide, 24–56 μm. long) in and adjacent to margins. Anticlinal cell walls strongly marked, about 1–2 μm. thick, straight to curving with only slight irregularities. Outer periclinal cell walls containing small irregularly distributed pits (usually less than 0·5 μm. in diameter) and often bearing a single, cutinized, simple, usually unicellular hair or low papillae about 7–24 μm. wide at base,



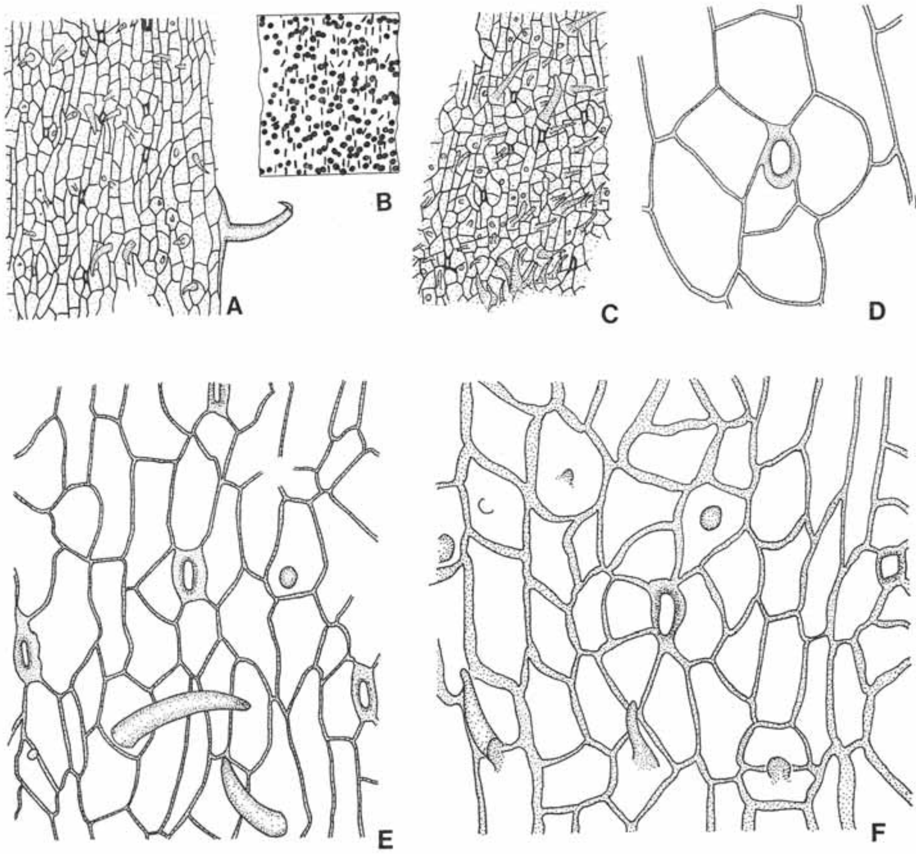
TEXT-FIG. 2B. Reconstruction of the adaxial side of the pinwheel of *Dinophyton* showing the nomenclature used for the several parts of the organ, approximately $\times$ 5. The position, size and number of trichomes is generalized. c, cup; st, stalk; la, lateral appendage; da, distal appendage; pa, proximal appendage.

14–450 μm. long, sides of hair taper gradually from base to acutely pointed apex, base of hair a simple ring on an ordinary epidermal cell. Hypodermal cells having straight to curving walls about 0·5 μm. thick, cells generally rectangular along margins, often about 15 μm. $\times$ 45 μm., elsewhere polygonal, isodiametric to elongate, usual size about 22 μm. $\times$ 30 μm.

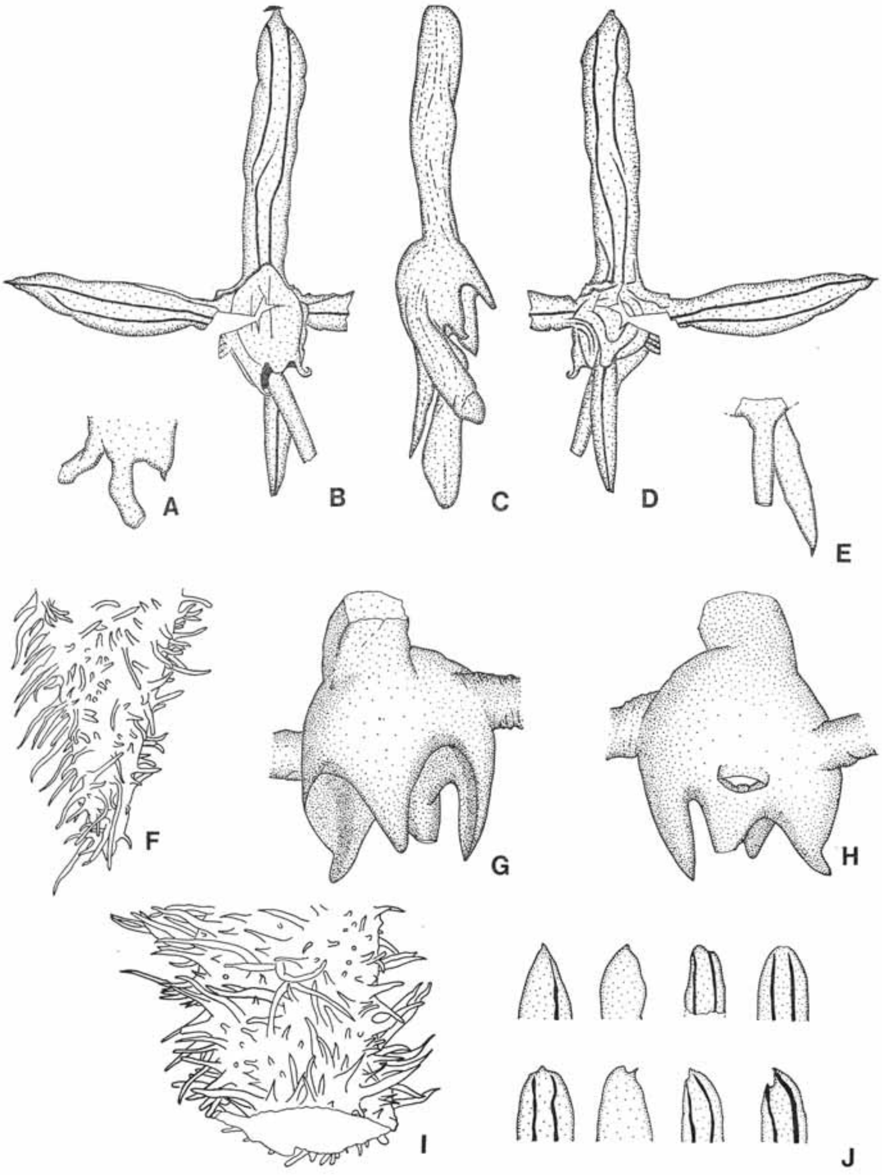
Pinwheel organ (?ovuliferous) dorsiventrally flattened, bilaterally symmetrical, consisting of four appendages forming a structure shaped like a pinwheel (text-fig. 5) or more accurately a Latin cross, a small hollow, elipsoidal structure or cup (which might have contained an ovule) positioned at intersection of appendages and a narrow stalk attached to and near proximal end of cup. Cup 2–3 mm. wide, 3–5 mm. tall, long axis orientated along long axis of cross, proximal end open, free part of wall (?integument) divided into three evenly spaced lobes and an elongated stalk-like structure. Lobes acutely pointed, 1·5–2·0 mm. wide and tall, stalk narrows slightly then drawn out into



TEXT-FIG. 3. Shoot of *Dinophyton spinosus* gen. et sp. nov. A, Upper portions of six isolated and slightly macerated leaves showing characteristic venation and typical obtuse to acuminate apices. Four short specimens on left, slide USNM 43644; two large specimens on right, slide USNM 43645; all ×5. B, Fragments of four leaves showing characteristic venation. Specimen on right from basal region of leaf and shows bifurcating vein; other specimens from areas above the basal region. Two specimens on left, slide USNM 43645; two specimens on right, slide USNM 43644; all ×5. C, Paratype showing apex of shoot surrounded by small leaves with a few fragmentary full-size foliage leaves near base of drawing, slide USNM 43649; ×5. D, Portion of shoot with remains of three narrow stumps among typical foliage leaves; one stump between two leaves on right side of drawing, slide USNM 43647; ×5. E, Holotype, slide USNM 43639; ×5. F, Exterior of shoot cuticle from which all but the base of one leaf has been naturally broken off. Irregular holes indicate position of leaves and darkly stippled areas are folds in cuticle; numbers indicate leaf sequence; slide USNM 43648, ×10, G, H, Typical foliage leaf with three small leaves at base; slide USNM 43646. G, ×5. H, ×25. Specimens in A–E, G, H from Monitor Butte Member of Chinle Formation, Fort Wingate area, New Mexico. Four short specimens in A, and two specimens on right in B from USGS fossil plant locality 10088; two long specimens in A, two specimens on left in B and specimens in C–E, G, H from USGS fossil plant locality 10061. Specimen in F from USGS fossil plant locality 10089, lower part of Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona. For simplification trichomes are not shown in these drawings.



TEXT-FIG. 4. Cuticles of shoot and pinwheel structure of *Dinophyton spinosus* gen. et sp. nov. A, Cuticle of leaf, margin to right; compare with cuticle of pinwheel (text-fig. 6E), epidermal cells generally smaller; slide USNM 43657, ×100. B, Cuticle from typical leaf showing distribution and orientation of stomatal apertures (short lines) and trichomes (large dots); slide USNM 43658, ×25. C, Cuticle from axis of shoot showing stomata and trichomes; cells smaller than on leaf; slide USNM 43655, ×100. D, Stoma on cuticle of pinwheel appendage; slide USNM 43651, ×400. E, Stomata and trichomes on leaf cuticle; slide USNM 43658, ×400. F, Stomata and trichomes on cuticle of pinwheel appendage; slide USNM 43656, ×400. Specimen in A from USGS fossil plant locality 10088, Monitor Butte Member, Chinle Formation, Fort Wingate area, New Mexico. Specimens in B and E from lower part of Tecovas Member, Dockum Group, near Crosbyton, Texas. Specimens in C, D, and F from USGS fossil plant locality 10089, lower part of Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona.



TEXT-FIG. 5.

a long, narrow, linear structure about 0·5–0·7 mm. wide, 2–3 mm. long, broken end not eroded. Appendages linear to oblanceolate, sides generally parallel to subparallel, round in section, apexes usually acute, appendages sometimes slight constricted in basal regions, margins usually entire, occasionally showing low teeth. Lateral appendages of same size (range noted about 1–2 mm. wide, 5–12 mm. long), attached to side of cup, containing two parallel veins. Distal appendage typically slightly longer than lateral appendages (range noted 1–2·5 mm. wide, 9–15 mm. long), attached to distal end of cup, containing two parallel veins about 120 μm. wide; apex sometimes bifurcate for a short distance. Proximal appendage usually shorter and narrower than other appendages, about 1 mm. wide and 4–8 mm. long, attached to back of cup between centre and stalk, containing one vein.

Cuticle of pinwheel (text-fig. 6), except for that lining cup, generally similar to cuticle of leaf. Stomata present on appendages, stalk and exterior of cup in approximate equal numbers (about 50 per mm.^{2}), typically longitudinally orientated, but larger proportion obliquely orientated than on shoot, otherwise identical. Ordinary epidermal cells somewhat larger and more irregular than cells on leaves and stems, epidermal hairs more abundant, especially on cup and stalk, than on shoot. Hypodermal cells present, similar to those on shoot. Upper part of cup and lower part of lobes lined with cuticle, lining extending at least 350 μm. below base of lobes and to within about 100 μm. of the apex of the lobes where it joins typical external cuticle. Internal cuticle delicate, thin, 1 μm. or less in thickness, composed entirely of ordinary epidermal cells, cells mostly polygonal, equidimensional to distinctly elongated, of various sizes, largest noted 30×75 μm. often smaller, elongated cells usually arranged longitudinally in rows, near margins 2–3 rows of rectangular cells (range noted, 7–20 μm. wide, 15–70 μm. long) typically present, anticlinal cell walls about 2–3 μm. thick, straight to curving, smooth, few irregularities, periclinal cell walls smooth, flat. Hypodermal cells present, similar to those on foliage. Female cone as a whole, ovule, male cone, and pollen unknown.

Attribution. Although the shoot of *Dinophyton* and the pinwheel have not been found connected the two structures are attributed to the same plant because of the evidence

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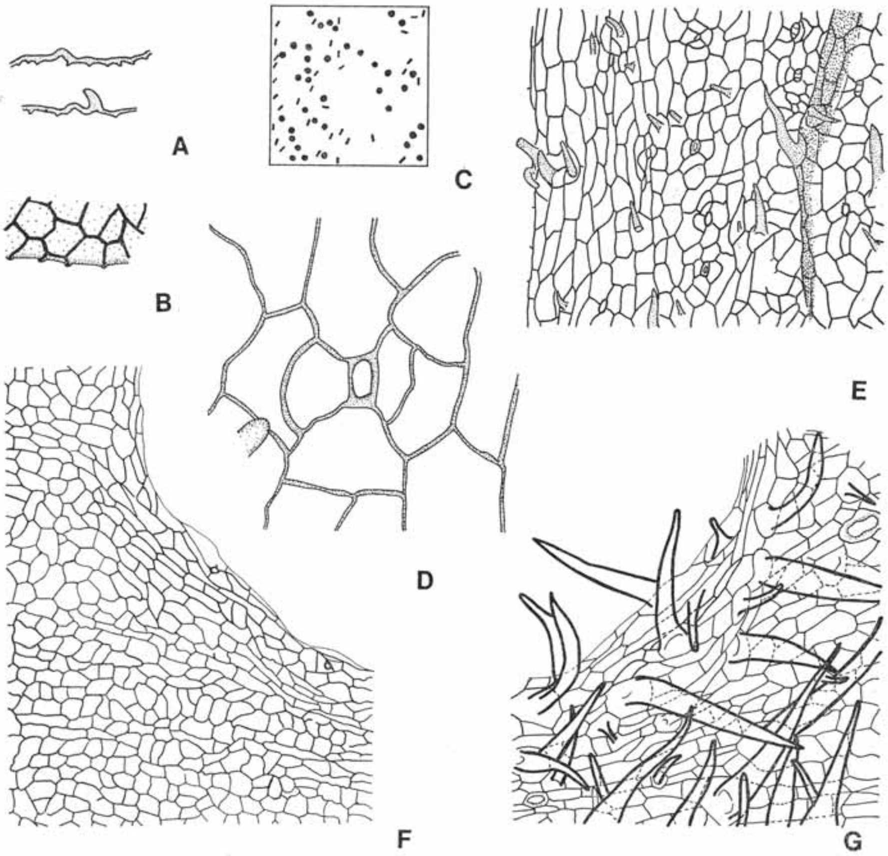
TEXT-FIG. 5. Pinwheel organ of *Dinophyton spinosus* gen. et sp. nov. A, Obliquely flattened fragment of side and back of a cup showing from left to right, the proximal appendage (slightly distorted), the stalk, and a lateral lobe; slide USNM 43640, $\times 10$. B, D, paratype. B, Adaxial side of pinwheel. D, Abaxial side; specimen unmacerated and broad lines in appendages probably represent veins; slide USNM 43637, $\times 5$. C, Paratype specimen compressed laterally, with front of cup to right, showing both lateral lobes and front lobe of cup; left lateral appendage bent downward nearly completely hiding the stalk; slide USNM 43638, $\times 5$. E, Fragment of back of cup showing stalk at front and proximal appendage behind it; slide USNM 43641, $\times 10$. F, Apex of one lateral lobe of a cup showing typical distribution of trichomes; slide USNM 43642, $\times 25$. G, H, Cup viewed from adaxial and abaxial sides; only bases of four appendages and stalk shown; slide USNM 43643, $\times 10$. I, Broken end of stalk showing typical distribution of trichomes; slide USNM 43654, $\times 25$. J, Upper portions of eight isolated, slightly macerated distal appendages showing apical variation and veins; upper left specimen slide USNM 43659, next to right slide USNM 43661, remainder slide USNM 43660, all $\times 5$. Specimens in A, C, G–I, and second specimen from left in top row of J from USGS fossil plant locality 10089, lower part of Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona. Specimens in B, D–F, and all other specimens in J from USGS fossil plant locality 10088, Monitor Butte Member, Chinle Formation, Fort Wingate area, New Mexico. For simplification trichomes not shown in A–E, G, H, J.



TEXT-FIG. 6. Cuticle of pinwheel of *Dinophyton spinosus* gen. et sp. nov. A, Cross-section of cuticle of distal appendage showing cutinized anticlinal flanges; slide USNM 43650, ×200. B, Fold in lower cuticle of appendage viewed from below showing outlines of polygonal epidermal cells with cutinized anticlinal flanges; slide USNM 43651, ×200. C, One square mm of cuticle of distal appendage showing distribution and orientation of stomatal apertures (short lines) and trichomes (large dots); slide USNM 43651, ×25. D, Stoma, slide USNM 43651, ×400. E, Cuticle from proximal appendage; heavily stippled area near right side represents a fold (cf. leaf cuticle in text-fig. 4); slide USNM 43651, ×100. F, Interior cuticle from a cup lobe; margin marked by narrow elongated cells; note total absence of stomata and trichomes; slide USNM 43652, ×100. G, Exterior cuticle from a cup lobe, margin marked by narrow elongated cells; note stomata and abundant trichomes; slide USNM 43653, ×100. Specimens in A–E from USGS fossil plant locality 10090, lower part of Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona. Those in F and G from USGS fossil plant locality 10088 Monitor Butte Member, Chinle Formation, Fort Wingate area, New Mexico.

of association and the evidence of similar cuticle. Careful collecting has shown that when the remains of one structure are found at a locality examples of the other are always present also. Both the shoot and the pinwheel are now known to occur together in rocks of Late Triassic age at ten localities extending from west-central Texas to north-central Arizona, a distance of about 700 miles. No locality is known where only one of the structures occurs.

The distinctive cuticle of the leaf of *Dinophyton* is easily distinguished from all other Chinle cuticles, the stomata and the papillae being highly characteristic. On the other hand, the resemblance between the cuticles of the shoot of *Dinophyton* and the pinwheel is very close as they agree in: (1) the form and size of stomata; (2) the form and size of the papillae and hairs on the ordinary epidermal cells; (3) the general shape and arrangement of the epidermal cells; (4) the form of the anticlinal walls of the epidermal cells; and (5) the form and size of the tiny pits on the outer periclinal walls of the epidermal cells. Accordingly it is concluded that both the shoots and 'pinwheels' described in this report are parts of the same plant.

Some slight differences have been noted in the cuticles but they are considered unimportant. For example, the epidermal cells are somewhat smaller on the shoot than on the lateral appendages of the pinwheel and the anticlinal walls of the epidermal cells are somewhat thinner on the shoot (about 1–2 μm.) than on the lateral appendages of the pinwheel (about 2–3 μm.). In addition the stomata and papillae are about twice as abundant per square millimetre on the shoot as on the lateral appendages of the pinwheel, but papillae are just as abundant on the stalk of the pinwheel as on the leaf of *Dinophyton*. None of these differences are thought to be significant. Thomas (1925, p. 338), in his study of the Caytoniales, showed that the epidermal cells on the petiole of *Sagenopteris phillipsi* were larger than the epidermal cells on the stalk of the fruit *Caytonia nathorsti*. Nevertheless, he attributed them to the same plant because of several similarities. Harris (1964, pp. 12–13, 23) confirmed Thomas's observations and also attributed the two forms to the same plant. Their findings are just the reverse of mine on *Dinophyton* but it suggests the cell size is not of great importance when there are a great number of similarities as in the present situation. As noted elsewhere in this paper the number of stomata on the two organs may be only an indication of the primary role each played in the life of the plant and are not of importance when attribution is concerned.

Discussion. The function of the stumps (text-fig. 3D) on the ultimate shoot axes of some specimens is uncertain. Possibly they are the bases of the pinwheels but there is no definite information to support this except that the stump and the stalk of the pinwheel are about the same diameter. The ends of the stumps and the stalks are not eroded or worn, suggesting that abscission has taken place. The small leaves at the bases of some of the adult leaves are also of uncertain function. They do not appear to have originated with the stumps, as in the best example of a stump there is no evidence of such leaves. Small leaves are present at the bases of some adult leaves on the same specimen and there is no indication that they surround a stump or any other organ. At present, no special function is attributed to these leaves; perhaps they were merely diminutive leaves; in this connection the shoot apex shown in text-fig. 3C is surrounded by many of the same sort of small leaves.

Isolated but complete leaves of *Dinophyton* are rarely found at any locality. They are uncommon even in the dark, highly fossiliferous shale at locality 10088 and in the coaly material at localities 10089 and 10090. Usually the isolated leaves which are found at these localities are fragmentary, consisting of only the apex and the upper portion of the lamina. A number of short lengths of the ultimate shoot have also been isolated from bulk macerations of material from the same localities. In most of these specimens the leaves were still attached to the axis of the shoots even though they had undergone a certain amount of rough treatment during both deposition and more recently in the laboratory when they were recovered from the rock and macerated. Examinations of these specimens shows that the leaves are still fairly firmly attached to the axis. Actually the upper portions of the leaves are usually missing suggesting that the leaves have more of a tendency to break apart at some point above their base rather than to separate from the axis at the base. A few shoot axes which do not bear leaves were found only in bulk macerations from locality 10090; they are exceptional occurrences. The leaves in these cases typically have not separated cleanly from the axes as irregular holes in the cuticles show where the leaves were attached (text-fig. 3F).

At practically all localities the foliage of *Dinophyton* is represented only by fragments of the ultimate shoot about 5–10 cm. long, rarely longer. A few penultimate shoots with attached ultimate shoots have been found in New Mexico at locality 10061 (see Pl. 123, figs. 8–10) and at the two localities near Gap, Arizona. Most of the foliage referable to *Dinophyton* at these localities, however, consists of short lengths of the ultimate shoots. The comparative rarity of complete, isolated leaves and the common occurrence of specimens of the ultimate shoots with attached leaves suggests that the leaves were normally retained and that the ultimate shoots themselves were deciduous as in some modern members of the Taxaceae, Podocarpaceae, Araucariaceae, and Taxodiaceae.

It is possible that the strands in the leaves of *Dinophyton* which are thought to be veins are actually resin ducts such as occur in the leaves of the modern *Abies lasiocarpa*. Resin ducts in modern conifers, however, usually do not rejoin as the strands do in the leaves of *Dinophyton*. A careful but unsuccessful search was made for evidence of vascular elements in the strands. High magnification showed that they consist mainly of dark, generally structureless material and occasional discontinuous lines which could be anticlinal walls of cells. Usually the strands were visible only in leaves which had been either treated with a commercial bleaching solution for a few hours or had been macerated for about half an hour or less. Continued bleaching or maceration caused them to disappear entirely. In a number of leaves only a single wide strand is present; this could be due to two strands drifting together prior to fossilization giving the appearance of a single strand.

Several lines of evidence seem to indicate that the leaves of *Dinophyton* were round

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EXPLANATION OF PLATE 123

Figs. 1–9. *Dinophyton spinosus* gen. et sp. nov.; macerated compressions of pinwheel, all ×5. 1, USNM 43670. 2, USNM 43662. 3, USNM 43663. 4, USNM 43664. 5, USNM 43665. 6, USNM 43666. 7, USNM 43667. 8, USNM 43668. 9, USNM 43669. All specimens collected from USGS fossil plant locality 10090 in bed of paper coal, lower part of Petrified Forest Member, Chinle Formation, Teepee Buttes area, Petrified Forest National Park, Arizona.

in cross-section and were not flattened appreciably, if at all, during life. The leaf cushion is round to oval on the few shoot axes known that have lost their leaves and also on the many leafy shoots which have been macerated. Apices of the leaves often do not appear to be compressed and look very much like tips of cones. During maceration the leaves swell and become round as if returning to their original shape. Swelling also occurs sometimes when the fossil is embedded in plastic. The leaves do not have specialized margins which typically are found on the edges of most flattened conifer leaves. Finally, the frequency of stomata on the leaves seems to be about the same on all parts of the leaf. The difference in frequency of stomata on the foliage (about 100 per mm.^{2}) and the pinwheel (about 50 per mm.^{2}) is puzzling.

Comparisons. The leaves of *Dinophyton* can be easily distinguished in shape and size from the leaves of all plants in the Chinle Formation (Ash 1970*b*). Only one conifer, *Pagiophyllum* sp. D, could conceivably be confused with *Dinophyton* as they both have leaves of about the same size, but the leaves are distinctly falcate and not linear as in *Dinophyton*. The two species can easily be differentiated on the microscopic level even if only a small fragment of cuticle is available. In *Dinophyton* the stomata are mainly monocyclic and possess small (10–14 × 3–6 μm.) rectangular stomatal pits, in contrast to the *Pagiophyllum* stomata which are amphicyclic and have comparatively large (20–5 × 12–15 μm.) oval stomatal pits. In the *Pagiophyllum* the anticlinal walls of the epidermal cells are thicker and more irregular than comparable cell walls on the leaves of *Dinophyton*. Also the outer periclinal walls of the epidermal cells on the leaves contain large angular pits whereas in *Dinophyton* they contain tiny round pits and often bear single, simple papillae. The stomatal pits are overhung by cuticle projections from the subsidiary cells whereas in *Dinophyton* the subsidiary cells do not have any such projections or papillae.

Of plant fossils known to me, *Dinophyton* compares most closely with *Rissika media* Townrow 1967, from the Middle Triassic rocks of South Africa. The gross morphology of the foliage of the two species is remarkably similar (Townrow 1967, pl. 1, fig. E, and Pl. 123, figs. 2–7 of this paper). Both species have leaves of about the same size and with approximately the same proportions. The leaf attachment (spiral with decurrent bases) and the leaf apex (obtuse with an acuminate tip) are very close in certain specimens of the two species. In addition on the microscopic level the anticlinal cell walls of both species are straight and narrow and the cells are usually rectangular to polygonal in shape. In both species the stomata are usually monocyclic with two–four lateral and two terminal subsidiary cells, and the stomatal pits are rectangular.

The two species have dissimilarities which are probably more significant and include round, closely set leaves (1 mm. or less apart) which are not modified by twisting into two lateral rows in *Dinophyton* as against the flat, remotely-set leaves (2–5 mm. apart) which are modified by twisting into two lateral rows in *R. media*. The ultimate shoots of the present species do not seem to bear any small leaves at their base as do the foliar spurs of *R. media*. *Dinophyton* does have small leaves at the base of some adult leaves but they are not present in *R. media*. In *R. media* the stomatal pits are overhung by two to four projections of cutin which extend from the subsidiary cells and walls of the ordinary epidermal cells are smooth; in *Dinophyton* the outer periclinal walls of the ordinary epidermal cells often bear a single, simple cutinized papillae. The apical seed cones and the three-lobed ultimate seed-bearing structures of *R. media* cannot be matched in *Dinophyton* and it is concluded that the two fossils are not very closely related.

Pinus monophylla is the only conifer I know with leaves which are round in section. The way they are borne on the stem, however, is fundamentally that of the other species of *Pinus* and different from *Dinophyton* where they arise directly on the stem. Apart from having stomata with rectangular pits on all surfaces the cuticle of *P. monophylla* is unlike that of *Dinophyton*.

The shoots of the new species resemble those of many other fossil and Recent conifers and taxads but in no case in all characters. Many genera have narrow leaves but most are dorsiventrally flattened and the leaves, though arranged spirally, curve basally to bring them into the horizontal plane. The narrow leaves contain one vein in contrast to the leaves of *Dinophyton* which apparently have two veins. Two separate veins would be unusual in a conifer leaf less than 1 mm. in width but the 'veins' of *Dinophyton* may be merely two woody strands of a single 'mid vein' as it is ordinarily called in a living conifer.

It is the microscopic features which are so anomalous. In conifers with dorsiventrally flattened needle leaves the stomata are limited to a band on each side of the mid-rib and confined to the lower side; occasionally they are on both sides but the upper commonly has fewer. In only *P. monophylla* are there stomata on all sides of the leaf in about equal numbers. The equal frequency of stomata on the leaves and stem is anomalous as conifer stems bearing needles have but few stomata on the stem, for the leaves are the specialized photosynthetic organs. The form of the stoma (in a pit surrounded by 4–6 unspecialized subsidiary cells) and their arrangement in short longitudinal files is easy to match in living and fossil conifers of various families but is not exclusive to conifers. It is for example seen in *Czekanowskia* (?Ginkgoales) and in *Stenopteris* (?Pteridosperms.) In many genera (Taxaceae, *Sciadopitys*, etc.) strong outgrowths occur on the subsidiary cells which might almost be called 'trichomes' but are not so named. In some conifers and taxads small outgrowths from the marginal cells of the leaf are frequent, and they form microscopic teeth; but in none does one see flat subsidiary cells and strong, hollow, conical outgrowths on the ordinary epidermal cells (properly called trichomes). This feature is foreign to conifer and taxad families and gives the cuticle a strange aspect. Very similar trichomes are seen in certain *Stenopteris* species and in a good many Ginkgoales but there, if trichomes occur, the subsidiary cells are usually more or less papillate.

The strange little pinwheel structure is perhaps very incompletely known; I have assumed that it originally bore an ovule, but another possibility is that it is a vegetative reproductive unit, a kind of bulbil (cf. *Lycopodium selago*) in which case it is perhaps of

EXPLANATION OF PLATE 124

Figs. 1–10. *Dinophyton spinosus* gen. et sp. nov. 1–6, Compressions of pinwheel. 1, USNM 43681, ×1. 2, USNM 43682, ×1. 3, USNM 43683, ×2. 4, USNM 43684, ×2. 5, USNM 43681, ×2. 6, USNM 43685, ×2. 7–10, Cuticle of distal appendage of pinwheel, slide USNM 43686, ×250. Specimens in figs. 1–6 from Monitor Butte Member, Chinle Formation, Fort Wingate area, New Mexico; figures 1, 2, 4, 5 from USGS fossil plant locality 10061, 3 from USGS fossil plant locality. 10060, 6 from USGS fossil plant locality 10058. Cuticle in figs. 7–10 from USGS fossil plant locality 10090 in bed of paper coal, lower part of Petrified Forest Member, Chinle Formation, Teepee Buttes area of Petrified Forest National Park, Arizona.

less taxonomic significance. No bulbil occurs in the conifers or taxads, but *Dinophyton* has not yet been proved to be either. It is reasonable to regard the four little outgrowths or appendages as small leaves and these could well have surrounded an ovule. One possibility is that the structures were attached singly on ordinary vegetative shoots but it is only suggested by a few examples of outgrowths or stumps which might be pedicels. Certainly if these organs bore a median ovule it is unlike the ovuliferous part of any known conifer or taxad.

Summary. Dinophyton has more features in common with the conifers and taxads than with any other group, but in detail the shoots are distinct by having: (1) a cuticle uniform over the whole surface of the leaves and stem; (2) many trichomes all over the leaf and the stem; and (3) stomata all over the leaf and the stem. The curiously shaped detached organs here called 'pinwheels' do not at present help at all in placing *Dinophyton*, but it seems reasonable to regard *Dinophyton* as a gymnosperm of unknown affinities.

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ASH, Problematic Triassic plant

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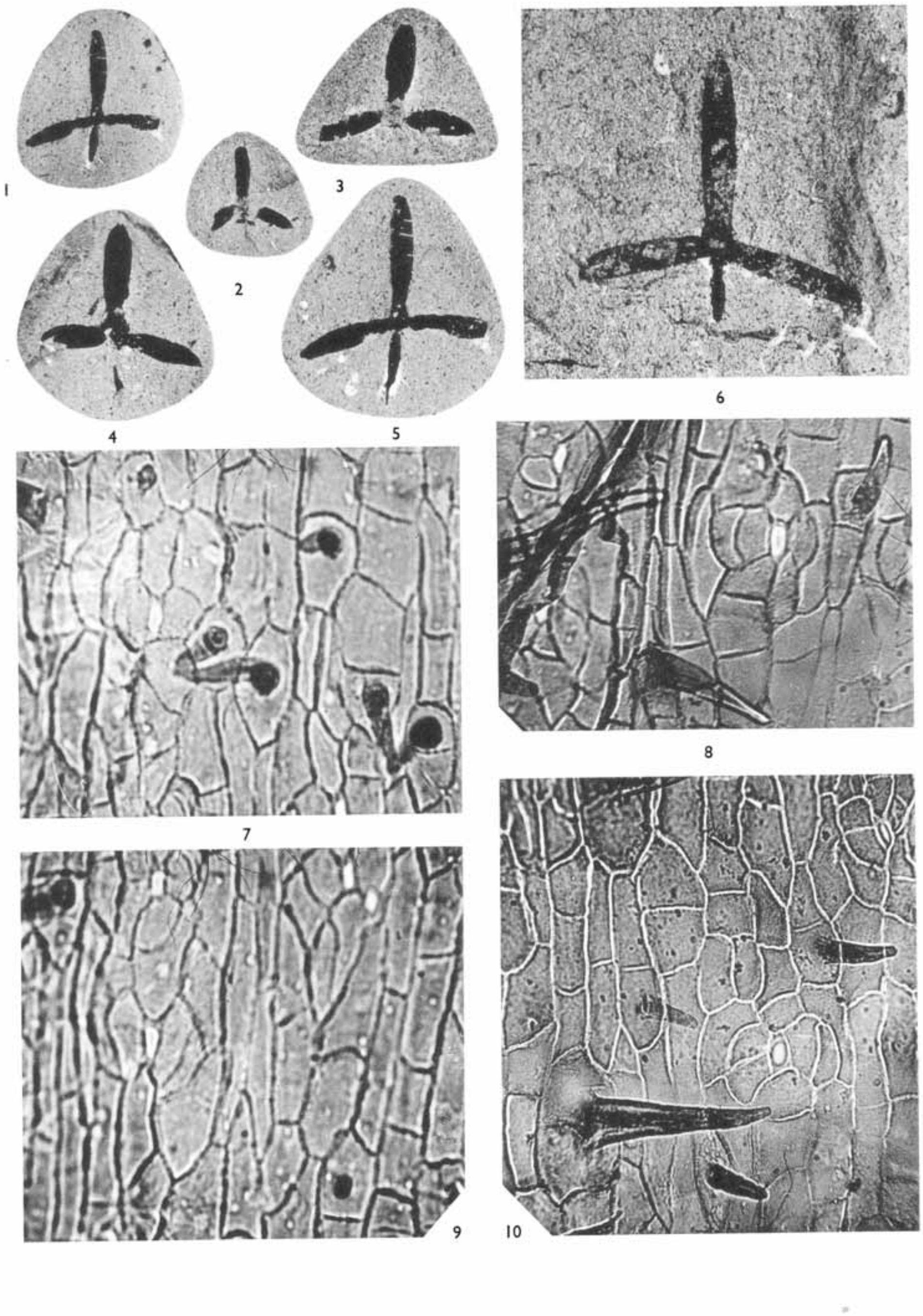

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