Chapter 4
Plant Megafossils

SIDNEY R. ASH
Weber State College, Ogden, Utah 84408

INTRODUCTION

This chapter concerns identifiable plant megafossils found mainly in the Ciniza Lake Beds, although it also contains descriptions of plant megafossils encountered in the underlying steeply dipping beds.

The lake beds contain abundant comminuted plant material and many large compressed fragments of plants. These fossils consist of short, leafy conifer shoots and fragmentary leaves and stems of other types of plants. Although the fossils are incomplete, they are usually in remarkably good condition, and their cuticles are often well preserved. Frequently, sheets of almost pure cuticle come free from the shale when it is split, and the leafy conifer shoots can be easily separated from the shale. On the other hand, leaves in the steeply dipping beds are usually preserved as impressions, but some retain a little structureless carbonaceous residue. Uncompressed pith casts of large arthrophytes also occur in the steeply dipping beds.

TECHNIQUES

Most leafy shoots and large leaf fragments encountered in the lake beds were removed from the rock by placing a little water over and around them. After the shale softened, a needle or small knife blade was passed under them, and they were lifted from the rock. Then they were placed in concentrated hydrofluoric acid for about 24 hours to remove any rock material that still adhered to them. At this point some specimens were mounted in glycerine jelly on microscope slides, but most were macerated in the standard manner (Ash 1970b, p. 646) so that their cuticles could be examined. After maceration the cuticles were washed in water, and some were mounted in glycerine jelly on slides. Also, an example of nearly every leafy shoot was embedded in plastic. In addition a leaf or a portion of a leaf of each species was mounted on a stub for photographing with a scanning electron microscope.

PLANT FOSSIL LIST

The following plant fossils are considered in this chapter:

Division Arthrophyta
- Order Calamitales
  - **Neocalamites* sp. A
- Order Equisitales
  - *Equisetites* sp. A

Division Pterophyta
- Family Cynepteridaceae
  - **Cynepteris lasiophora* Ash
- Family Matoniacea
  - *Phlebopteris smithii* (Daugherty) Arnold

Division Cycadophyta
- Order Bennettitales
  - *Nilssoniopteris ciniza* n. sp.
  - **Zamites powelli* Fontaine

Division Coniferophyta
- Order Cordaitales (?)
  - **Pelourdea poleoensis* (Daugherty) Arnold
- Order Coniferales
  - ?Family Araucariaceae
    - *Pagiophyllum readiana* n. sp.
    - *P. zuniana* n. sp.
    - *P. duttonia* n. sp.
    - *P. navajoensis* n. sp.
- Order Uncertain
  - *Dinophyton spinosus* Ash

The lake beds contain the remains of several additional plant fossils, but they are too incompletely known to justify a full description. A few notes about some of them are included here, however, in order to give a more complete picture of plant life around Lake Ciniza. They include the following:

1. The upper part of a leaf with a bifurcate apex reminiscent of the ginkgoalean leaf called *Sphenobaiera*. The base of the leaf is unknown. Only one specimen was found.
2. A narrow linear leaf that has an acute apex and several parallel veins. Fragments of this leaf are about 0.3 cm wide and as much as 4 cm long. The base of the leaf is unknown. About a dozen specimens were found.
3. A wide linear leaf that has parallel veins. The fragments are 1 cm wide and as much as 2 cm long. The base and apex are unknown.
4. The leafy shoots of at least two conifers similar but not identical to those called *P. zuniana* n. sp. Only one short sample of each shoot was found.
5. A structure of unknown function that consists of a hollow eliptical central body from which twenty to thirty linear appendages radiate outward. Three examples of this fossil are known, and one is illustrated in figure 2b.
6. A linear lanceolate leaf about 2 cm long and 2 mm wide. Only one specimen is known.

The almost complete absence of fern megafossils in the lake beds is difficult to understand. Fern megafossils do occur in fairly large numbers at locality FW8 about 21 m east of the lake deposits and at the same approximate stratigraphic level in the main body of the Monitor Butte Member (Ash 1970a). In addition, as shown in chapter 5, several types of fern spores have been isolated from the lake beds. Thus there is no doubt that ferns did grow in the immediate area of the lake. It is probable that they also inhabited the margins of Lake Ciniza and of the streams that entered the lake. Perhaps their almost total absence from the megafossil record is due to the delicate nature of their leaves or to accidents of collecting or to a combination of both factors.

*Occurs only in the steeply dipping beds.

The curled-up fragments of the cuticle of *N. ciniza* and the general fragmental condition of all the plant megafossils in the lake beds seem to indicate that most megascopic plant remains were not immediately carried into Lake Ciniza after they fell from the parent plants. Rather they probably lay on the land surface for some time where they decomposed partially before being transported into the lake and buried.

An alternative explanation for the general fragmentary condition of the plant fossils is that they were mainly broken by waves and currents in the lake. However, the coprolites and conchostracans in the lake beds are not particularly distorted or fragmented, and they would probably show the effects of any movements strong enough to fragment leaves and stems. This is especially true of the coprolites as they must have been just barely coherent when they were deposited in the lake. Thus it does not seem reasonable to suppose that there were currents and waves in Lake Ciniza which could have fragmented the plant remains to any great extent.

The condition of the leaves in three other ancient lake deposits contrasts with that of the leaves in the Ciniza Lake Beds. All three lakes—Pleistocene Lake Rita Blanca, Oligocene Lake Florissant, and Eocene Lake Uintah—were much larger than Lake Ciniza and probably had stronger currents and wave action. Yet according to the authors who studied the plant fossils in those lake deposits (Tucker 1969; Martin 1969; MacGinitie 1953, 1969) the leaves are generally whole and unfragmented, and the strong currents do not appear to have affected them. There is always the possibility, however, that the leaves in these deposits were tougher than those in the Ciniza Lake Beds, but we cannot be sure of this.

I conclude therefore that most of the plant megafossil material in the Ciniza Lake Beds lay on the ground for some time before being carried into the lake. Perhaps it formed a layer of litter on the ground beneath the trees in the area as happens in modern forests, and during the time it lay there some of the leaves were broken up considerably, and others were not.

The plant megafossil material probably was continuously swept into the lake during its existence as the material seems to be fairly evenly distributed throughout the vertical thickness of the lake beds. Some of the leafy shoots, however, were blown or washed in without preliminary decay as they are nearly whole.

SYSTEMATIC DESCRIPTIONS

Division ARTHROPHYTA

Order CALAMITALES

Neocalamites sp. A

(fig. 1)

1941 *Neocalamites virginiensis* auct. non (Fontaine) Berry. Daugherty, p. 58–61, pl. 11, fig. 2. Only the pith casts from Arizona are here removed from the species *virginiensis* and placed in synonymy with the present unnamed species.

1967 *Neocalamites* sp. Ash, p. 125–26, fig. 1.

Description.—This description is based on several dozen pith casts of large *Calamite*-like aerial stems and attached rhizomes that occur in the Upper Triassic rocks in the Fort Wingate area. The stem casts range from 0.3–2.0 m in length and from 10–30 cm in diameter. They show slightly enlarged nodes and many longitudinal ribs separated by narrow grooves. The internodes vary from about 3.2–7.5 cm in length and are consistently wider than long. Generally they differ little in length in the same specimen. The grooves are about 2 mm broad, and the intervening ribs are about 6–14 mm wide. They are straight and cross the nodes without interruption. Branch and leaf scars are rarely seen on the stems. The rhizomes are tapering and are as much as a meter in length (Ash 1967, fig. 1).

Comparisons.—The fossils described here apparently do not represent *Neocalamites virginiensis* (Fontaine) Berry from the Upper Triassic of the eastern United States. Pith casts and compressions attributed to that species by Fontaine (1883, p. 17–18, pl. 1, figs. 4–6) and Bock (1969, p. 59–69, figs. 105–19) indicate that generally it had somewhat shorter internodes (1.5–2.0 cm) and finer ribs (6–10 per cm) than the present species.

The pith casts from the Petrified Forest that Daugherty (1941, p. 58–61, pl. 11, fig. 4) referred to *N. virginiensis* are very similar to the presently unnamed species and are placed in synonymy with it. However, the compressed leaves and stems from the Petrified Forest which also were assigned to *N. virginiensis* are not removed from that species at this time.

Remarks.—It does not seem appropriate at this time to refer the fossils described here to either a previously described species or to a new one. Perhaps when better preserved specimens are collected, it will be possible to determine an appropriate name.

Material.—Holotype: USNM 172328.

Distribution.—This species has been collected from the Monitor Butte Member of the Chinle Formation in the steeply dipping beds that underlie the deposits of Lake Ciniza and from the gently dipping beds on the west side of the spur containing these strata. It also occurs in the lower part of the Petrified Forest Member of the Chinle Formation in Petrified Forest National Park, Arizona.

FIGURE 1.—Uncompressed pith cast of *Neocalamites* sp. A in position of growth in steeply dipping beds on east bank of Eastern Wash near locality FW6.

Order EQUISITALES

Equisetites sp. A

(figs. 2c, 2h)

Description.—Aerial stems (known from fragments only) 12-15 cm in diameter, length unknown. Internodes 6 cm or more long, surface of upper part divided by shallow commissural furrows into decurrent leaf bases about 10 cm wide. Furrows about 2 mm wide near node, tapering to a long narrow point and dying out about 5 cm below node (free part of leaf sheath and leaf teeth not known). Nodes not swollen, showing a slightly constricted band about 1 mm wide at the nodal diaphragm.

Comparisons.—Two other species of *Equisetites* occur in the Chinle Formation. They are *E. bradyi* Daugherty (1941) from Dinnebito Wash, Arizona, and *E.* sp. from Petrified Forest National Park, Arizona, also described by Daugherty. Although the form described in this report and the other two are incompletely characterized, it is apparent that they represent different species. The species from New Mexico is differentiated from the other two by its large size (12-15 cm wide). In *E. bradyi* the stems are only 4 to 14 mm in width; in the other Arizona form they are 3 cm in width.

The fossils described here appear to differ from *Equisetum rogersi* which was described from the Upper Triassic of Virginia by Fontaine (1883, p. 10). That species also has a narrower stem (6-10 cm in diameter), and its commissural furrows are not so long as in the present form.

Equisetites sp. A appears to be differentiated from most other species of *Equisetites* and *Equisetum* described from other parts of the world. For example, *Equisetites* sp. A is larger than the *Equisetites* and *Equiseta* described from the Jurassic of Yorkshire (Harris 1961), Rhaetic and Lias of Greenland (Harris 1931), and the lower Mesozoic of Japan (Oishi 1940), Russia (Genkina 1966), Sweden (Halle 1908), and Queensland (Walkom 1915).

Remarks.—This description is based on 3 compressed stem fragments and 2 uncompressed pith casts. Although *Equisetites* sp. A is not abundant, its presence in the lake beds is of considerable paleoecological significance. The fossils suggest that either the lake margins or margins of a stream entering the lake were swampy. The large size of the fossils indicates that swampy conditions lasted for a considerable time in the area.

Equisetites sp. A has not been referred to the extant genus *Equisetum* because the fossil is not known in enough detail to show that it is indeed close to *Equisetum.* It also has not been referred to either an old or new species for the same reason. It should be possible to go considerably further with these fossils when the wealth of Arthrophytic material in the Chinle can be thoroughly studied.

Material.—USNM 172351, 52.

Distribution.—This species has been collected from the lake beds at locality FW6 (compressions) and from the main body of the Monitor Butte Member on the western escarpment of the Spur (pith casts).

Division PTEROPHYTA

Order FILICALES

Family CYNEPTERIDACEAE

cf. *Cynepteris Lasiophora* Ash, 1969

(fig. 3a)

1970a *Cynepteris lasiophora* Ash, p. D31-D38, pls. 2, 3, figs. 15, 16.

1972a *Cynepteris lasiophora* Ash, p. 30-31, fig. 1E.

Description.—Only one specimen of cf. *C. lasiophora* was found during the course of this study. It is a cast of the apical region of a large pinnate leaf. The pinnules are entire, and the largest is about 13 mm long and 4 mm wide. A straight midrib is visible in most of the pinnules, but the secondary veins are not clearly visible.

Although the fine details are not visible in this fossil, it has the general characteristics of the species, which occurs also at several localities in the area, and it seems reasonable to call this fossil cf. *Cynepteris lasiophora.*

Material.—USNM 172311.

Distribution.—This species occurs in the Monitor Butte Member of the Chinle Formation in the steeply dipping beds just west of locality FW5. It also occurs in the Monitor Butte Member elsewhere in the Fort Wingate area at USGS fossil plant localities 10058 and 10061 and in the lower part of the Petrified Forest Member of the Chinle in Petrified Forest National Park, Arizona, at USGS fossil plant locality 10062. It has also been found in the Dockum Group in eastern New Mexico (Ash 1972b).

Family MATONIACEAE

Phlebopteris smithii (Daugherty) Arnold, 1947

(fig. 2a)

1941 *Laccopteris smithii* Daugherty, p. 53-54, pl. 7, 8, 9, fig. 1.

1947 *Phlebopteris smithii* (Daugherty) Arnold, p. 193-94, figs. 91, 92.

1972a *Phlebopteris smithii* (Daugherty) Arnold. Ash, p. 31, 32, figs. 1d, 1g.

Description.—This species is represented by a single compression of a part of a pinnate leaf. The pinnules are linear with obtusely pointed apices, and they are attached at right angles to the main rachis. They are as much as 2 mm wide and 30 mm long. The margins of the pinnae are entire. A broad straight midrib shows in each pinnule, but the secondary veins are not clear. The substance of the leaf is thick and is irregularly depressed.

Material.—USNM 172349.

Distribution.—This fossil was found in the gray shale in the Ciniza Lake Beds at USGS fossil plant locality 10091. *P. smithii* occurs also in the lower part of the Monitor Butte Member of the Chinle at USGS fossil plant localities 10058 and 10060 in the Fort Wingate area and in the lower part of the Petrified Forest Member of the Chinle at USGS fossil plant locality 10062 in Petrified Forest National Park, Arizona (Ash 1970a, p. D23).

Class BENNETTITALES

Genus *Nilssoniopteris* Nathorst ex Harris

The history of *Nilssoniopteris* was summarized by Harris (1969a). As he shows, it's legal status is somewhat uncertain, and *Taeniozamites* Harris (1932) may be the correct name for this fossil. Florin (1933), however, considered *Taeniozamites* to be a mere synonym of *Nilssoniopteris,* and most authors, including Harris, follow Florin's usage. The problem is further complicated by the fact that a formal diagnosis of *Nilssoniopteris* was not published until a short time ago (Harris 1969a). Although he ascribes the name to Nathorst, Harris probably is the publishing author of the name (see Article 46 and Recommendation 46C, Inter. Code Bot. Nomen., 1972).

Nilssoniopteris ciniza n. sp.

(figs. 2c, 2d, 4, 5, 6)

1941 *Macrotaeniopteris magnifolia* auct. non (Rogers) Schim-

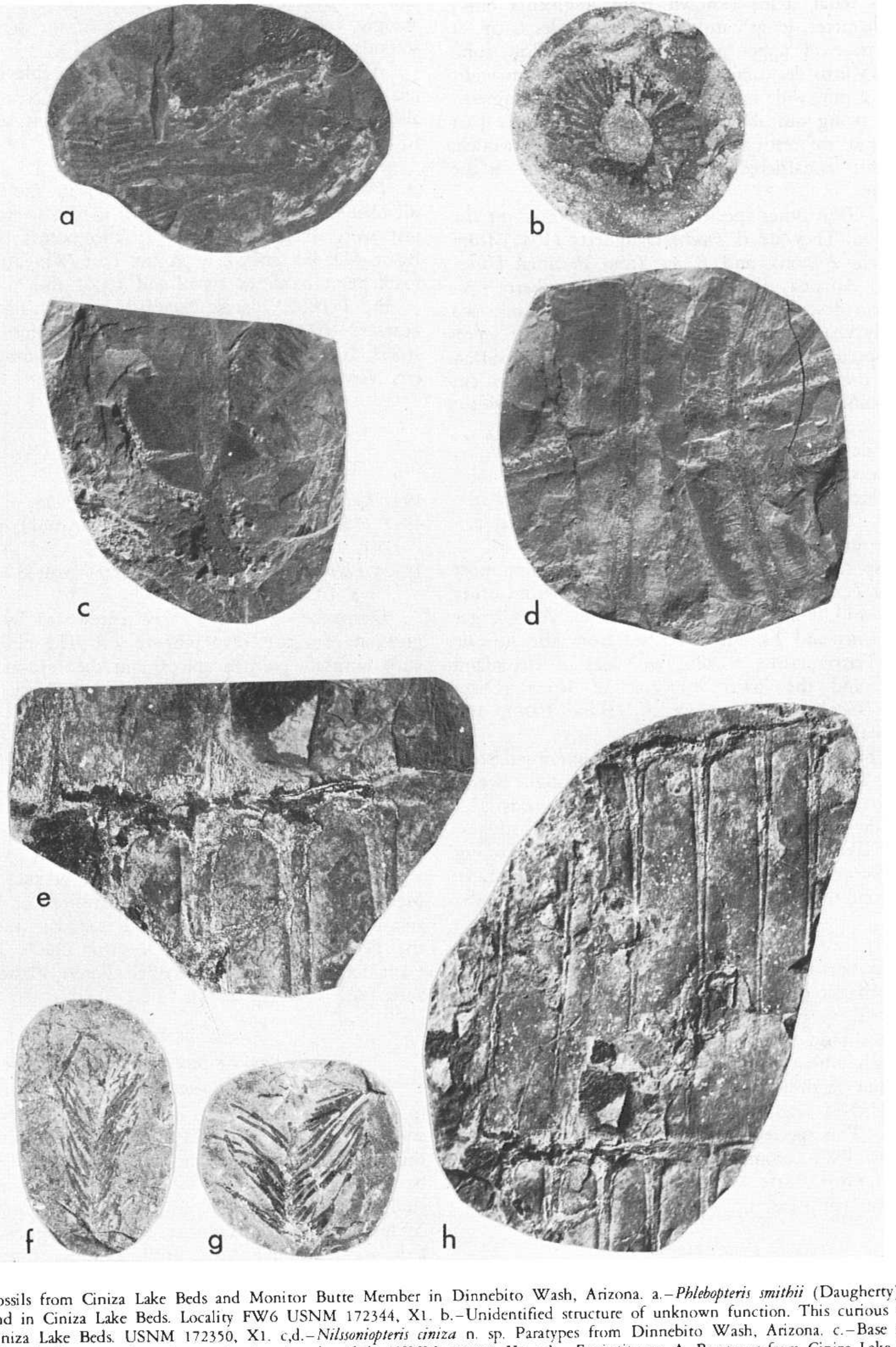

FIGURE 2.–Plant fossils from Ciniza Lake Beds and Monitor Butte Member in Dinnebito Wash, Arizona. a.–*Phlebopteris smithii* (Daugherty) Arnold. Only fern leaf found in Ciniza Lake Beds. Locality FW6 USNM 172344, X1. b.–Unidentified structure of unknown function. This curious fossil is known only from Ciniza Lake Beds. USNM 172350, X1. c,d.–*Nilssoniopteris ciniza* n. sp. Paratypes from Dinnebito Wash, Arizona. c.–Base of leaf, USNM 172340, X1. d.–Middle parts of two leaves showing broad midrib. USNM 172339, X1. e,h.–*Equisetites* sp. A. Paratypes from Ciniza Lake Beds at locality FW6. e.–USNM 172351, X2. h.–USNM 172352, X1. f,g.–*Dinophyton spinosus* Ash. Fragments of two leafy shoots from Ciniza Lake Beds at locality FW6. f.–USNM 172335, X1. g.–USNM 172334, X1.

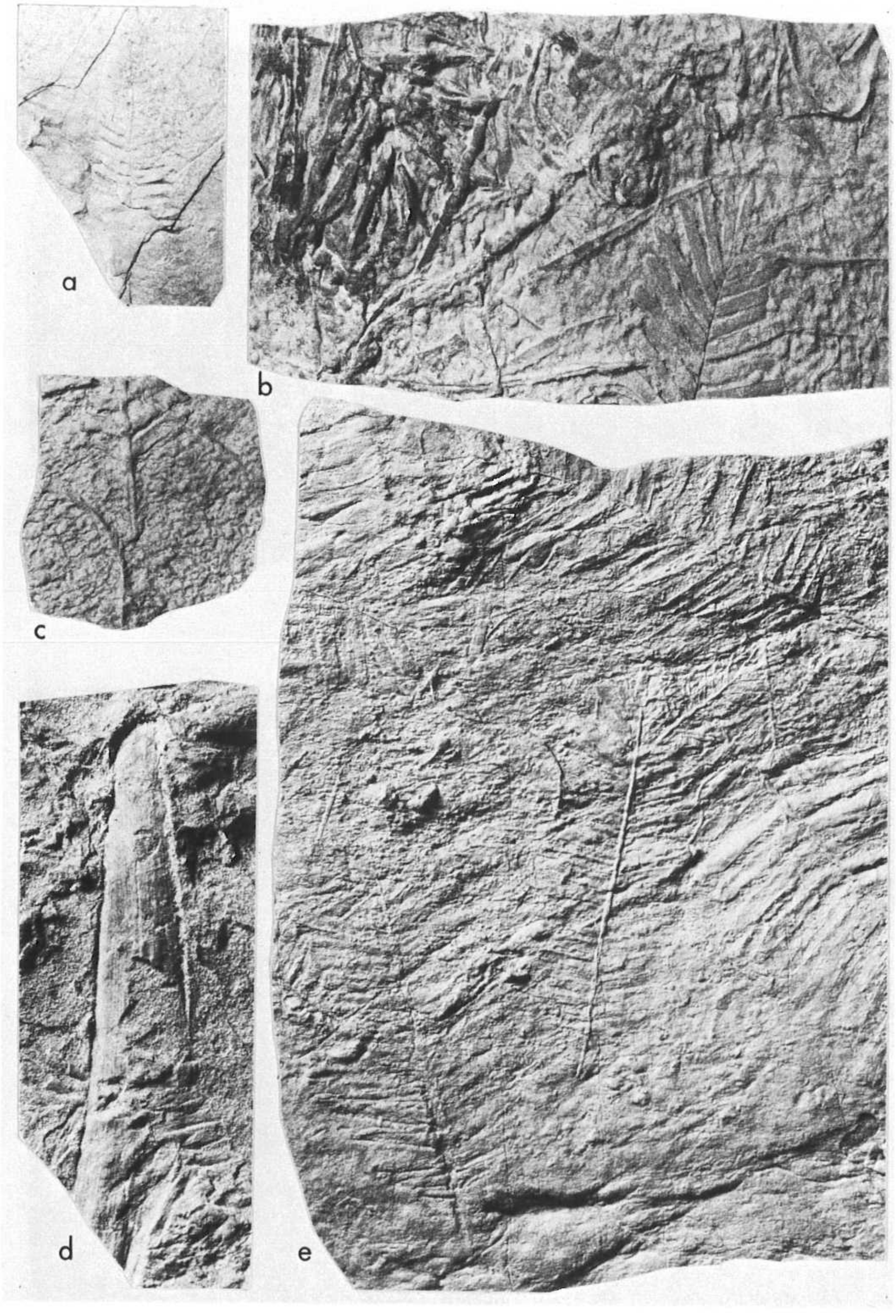

FIGURE 3.–Fossil plants from steeply dipping beds. a.–Cf. *Cynepteris lasiophora* Ash. Cast of upper part of a frond. USNM 172311. b,c,e.–*Zamites powelli*. b, upper part of leaf, miscellaneous plant debris, and raindrop casts, USNM 172328. c, base of a leaf and raindrop casts, USNM 172331. e, several nearly complete leaves and some plant debris, USNM 172332. X.5. d.–*Pelourdea poleoensis* (Daugherty) Arnold. Upper part of a leaf and apex. USNM 172333. All from steeply dipping beds about 3.65 m west of locality FW5. X.5.

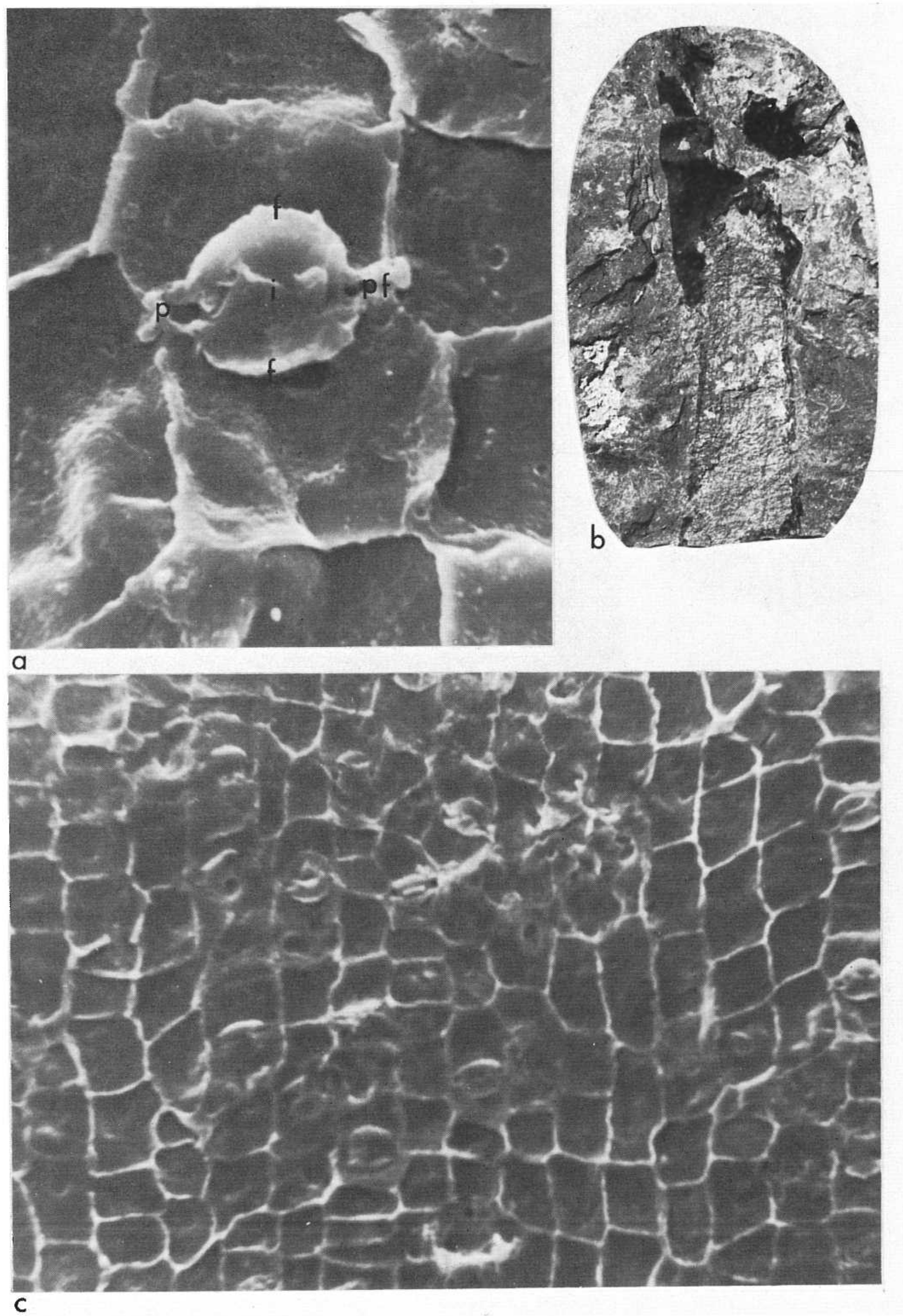

FIGURE 4.—*Nilssoniopteris ciniza* Ash, n. sp. a.—SEM micrograph of the inner surface of a stoma. Free edges of thickenings of both guard cells are at f. One side of inner edge of aperture tube is at i. It obscures other side of aperture tube. Polar regions of the guard cells are at p. About X500. b.—Base of leaf and petiole. Cuticle has fallen away from petiole exposing sediment that infiltrated between cuticles. Some of leaf cuticle was used in the preparation of some of the drawing in figures 5 and 6. Holotype, USNM 172329, X1. c.—SEM micrograph of the inner surface of the cuticle of the leaf. A stomatal file is in the center of the figure, and the edge of another is near the right side. About X150. All material from locality FW6.

per: Daugherty, p. 82–84, pl. 16, figs. 3, 4.
1966 *Nilssoniopteris* n. sp. Ash, p. 130–33, figs. 18D, 18E.
1972a *Nilssoniopteris* sp. A. Ash, p. 37–38, fig. 3d.

Diagnosis.—Leaf of varied size, typically 7–10 cm wide, some as narrow as 1.5 cm, length unknown, possibly as long as 20–30 cm, linear-lanceolate, margins parallel in middle region, apex obtuse, base tapering more or less abruptly, petiole short, about 1–5 mm wide, wrinkled. Midrib prominent, 1–5 mm wide, broad below, narrow above, surface often marked with transverse wrinkles, lamina attached laterally. Lamina thin, margins flat, entire except for tiny rounded bulges. Veins fairly conspicuous, more or less transverse to midrib except near base of leaf, straight, simple, rarely once forked, about 50–70μ broad, ending in a small, elliptical lump about 150 $\times$ 300μ a short distance (0.1–0.2 mm) from leaf margin. Veins about 90–160μ distant, traversing lamina at a concentration of 35–60 per cm, resin bodies often present between veins. Resin bodies up to about 70$\times$150μ, often surrounded by a cuplike structure composed of cutin.

Cuticles thin, upper about 2μ (measured in folds), lower slightly thinner, riblike projections or flanges of cuticle at position of anticlinal walls of epidermal cells, flanges about 3 μ high. Stomata sparse (perhaps 0–5 per mm^2) on upper cuticle of lamina, abundant (about 60–80 per mm^2) on lower cuticle of lamina, frequent (about 40–50 per mm^2) on both surfaces of midrib. Stomata arranged in two or three poorly defined files between and parallel with veins and oriented transverse to veins on lamina, in poorly defined files parallel with sides of midrib on both surfaces of midrib and irregu-

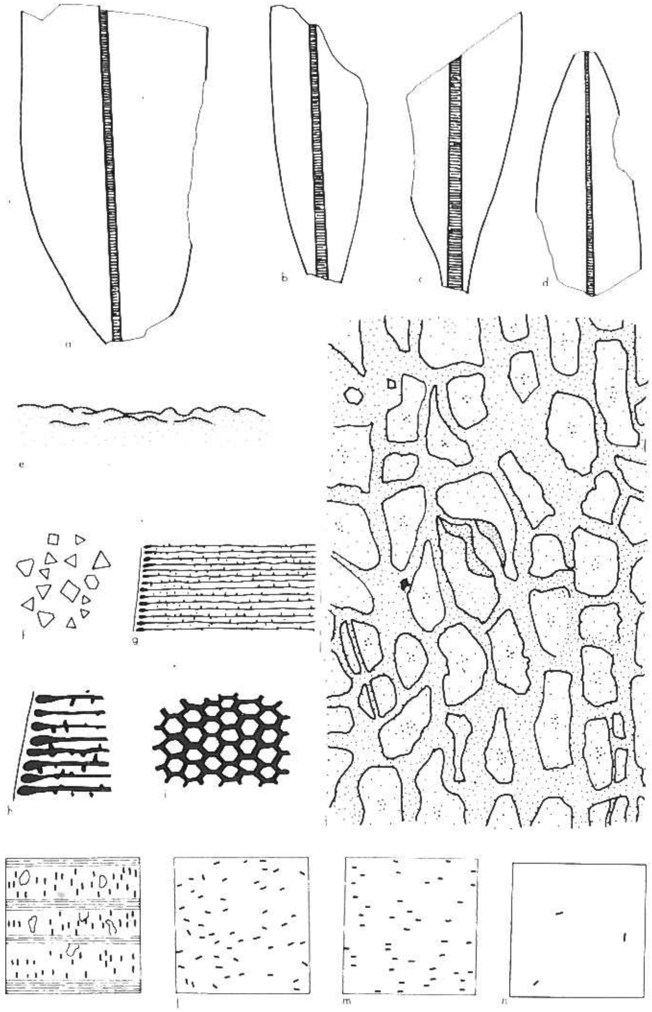

FIGURE 5.—*Nilssoniopteris ciniza* n. sp. a–c.—Basal region of a large leaf and two small leaves. Note that midrib expands downward in these specimens. Transverse wrinkles in midrib are drawn somewhat diagrammatically. Dinnebito Wash locality. a, USNM 172330; b, USNM 172336; c, USNM 172337, all X.7. d.—Apical region of small leaf. Dinnebito Wash locality, USNM 172338, X1. e.—Tiny bulges along margin of leaf. Slide USNM 172341, X140. f.—Selection of pits from lower cuticle of lamina. Slide USNM 172329e, X280. g.—Part of leaf showing veins, club-shaped vein endings, and resin bodies. Leaf margin is to left. Slide USNM 172341, X5. h.—Leaf margin showing club-shaped vein endings and adjacent resin bodies. Slide USNM 172341, X17.5 i.—Thick-walled cells from marginal region of leaf. Compare with cells farther away from the margin shown in figures 6b, 6c. Slide USNM 172342, X70. j.—Upper cuticle from midrib of holotype showing irregular, thick-walled cells characteristic of this part of leaf. A stoma is near center of figure. Slide USNM 172329d, X70. k.—Orientation and distribution of stomata (short lines), resin bodies (irregular figures), and veins (long lines) on 1 square mm of lower cuticle of lamina of species. Leaf margin is to left. Slide USNM 172343, X17.5. l.—Orientation and distribution of stomata on one square mm of transitional zone where lower cuticle of lamina joins midrib of holotype. Leaf margin is to left. Slide USNM 172329b, X17.5. m.—Orientation and distribution of stomata on 1 square mm of lower cuticle of midrib of holotype. Leaf margin is to left. Slide USNM 172329c, X17.5. n.—Orientation and distribution of stomata on 1 square mm of upper cuticle of midrib of holotype. Leaf margin is to left. Slide USNM 172329d, X17.5.

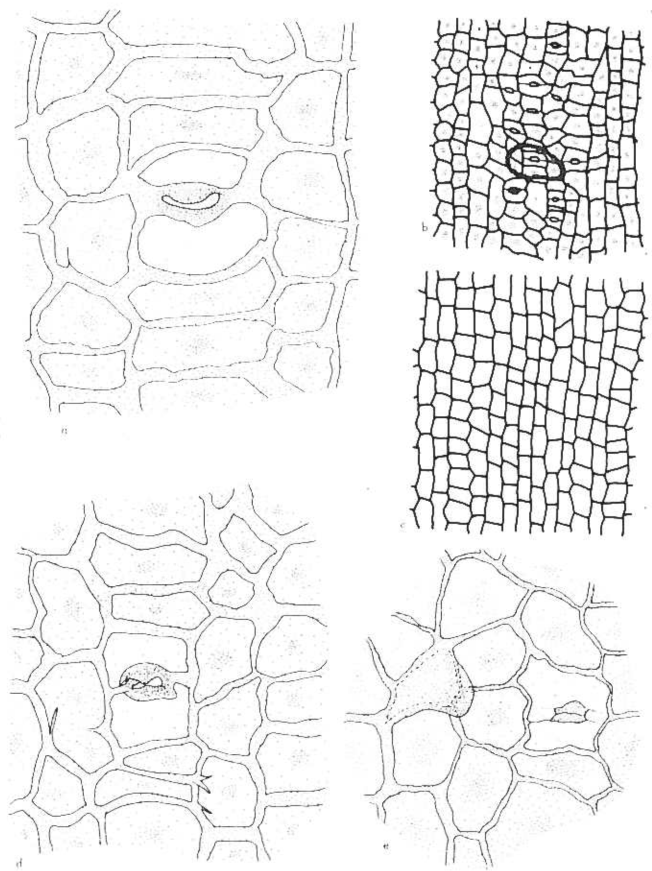

FIGURE 6.—*Nilssoniopteris ciniza* n. sp. a., d., e.—Stomata and ordinary epidermal cells on lower lamina. Medial papillae on epidermal cells shown by heavy stippling. a., d., USNM 172344. e., USNM 172343, all X280. b.—Lower cuticle of lamina showing stomata, ordinary epidermal cells, and "cup" that formerly held a resin body. Slide USNM 172344, X70. c.—Upper cuticle of lamina. Slide USNM 172343, X70.

larly oriented but often transverse to sides of midrib. Stomatal apparatus large, often rectangular, guard cell pair well cutinized (about 6×24μ), slightly sunken, aperture about 18μ long, subsidiary cells roughly rectangular, poorly cutinized, one or both may bear a solid papilla. Papillae arising from inner wall, overarching aperture, ends rounded, up to 8μ long.

Upper cuticle of lamina generally showing nearly uniform ordinary epidermal cells, those along veins often slightly narrower, cells equidimensional to rectangular (range noted 18–54μ wide, 18–80μ long), those near margins typically square, arranged in regular files parallel with veins, anticlinal walls well marked, about 2μ thick except in a narrow zone about 0.5 mm wide along leaf margin where they are much thicker (up to 12μ), straight to slightly curving with small irregular thickenings and thin areas, periclinal walls flat or bearing slightly bulged area near center of each cell, bulges form small pointed papillae (2μ high) along leaf margin. Ordinary epidermal cells of lower cuticle of lamina elongated above veins and more or less equidimensional between veins (range noted 20–46μ wide, 20–100μ long), papillae more prominent than on upper surface, occasional saclike papillae seen, otherwise similar to ordinary cells on upper cuticle. Inner surfaces of both upper and lower cuticle between the veins showing cutinized, irregular, cuplike structures which held resin bodies, structures about 50×70μ in diameter, walls about 1μ thick. Ordinary epidermal cells in basal region of lamina irregularly arranged, files indistinct. Ordinary epidermal cells on both side of midrib similar, equidimensional to rectangular, somewhat smaller and more regular than on lamina (range noted 24–36μ wide, 24–36μ long), arranged in regular files parallel with sides of midrib except in vicinity of stomata where they are irregular in shape, size, and arrangement, anticlinal walls 8–12μ thick, periclinal wall flat to slightly bulging, showing a narrow ridge and occasional small angular cavities (calcium oxylate crystals?).

Discussion.—This description is based mainly on fragments (up to 3 cm square) of cuticle from the Ciniza Lake Beds. Some information was also derived from the compressions from Dinnebito Wash, Arizona, that Daugherty (1941, p. 82–84, pl. 16, figs. 3–4) referred to *Macrotaeniopteris magnifolia* (Rogers) Schimper. Most specimens recovered from the lake beds are the remains of fairly large leaves whereas those from Dinnebito Wash represent both large and small leaves as shown in figures 2c, 2d.

Conventional cuticle preparations could not be made from the Dinnebito Wash specimens as the leaf substance in them is preserved as a thin brownish residue which cannot be removed from the rock by the usual means. Instead, it was necessary to make transfer preparations of the fossils. The transfers often showed the upper epidermis, but none carried any recognizable trace of the lower.

Daugherty (1941) noted that there are irregularities along the midribs of the specimens from Arizona, and there are also such irregularities on the Lake Ciniza specimens. Fontaine (1883) described some similar irregularities on the midribs of *M. magnifolia* from the Upper Triassic of the eastern United States as elliptical sori. That theory was rejected by Daugherty who suggested they were "pustules of a fungus." Cuticle preparations and transfers of the fossils studied here show that the irregularities are neither sori nor pustules. The cuticle in these areas is just the same as the cuticle on the lamina, and no special structures of any sort are present there (see 6b and 6c). It appears at this time that the irregularities on the midribs of the western specimens are merely wrinkles produced by the uneven collapse of thick tissue. Perhaps the irregularities observed on the midrib of the specimens of *M. magnifolia* from the eastern Triassic also have the same origin. The midrib of *N. ajorpokensis* (Harris) Florin from the Jurassic of Greenland shows similar wrinkles (see Harris 1932, p. 38).

Comparisons.—The specimens from Arizona which Daugherty (1941) referred to *Macrotaeniopteris magnifolia* not only have the same megascopic characters as the specimens from the lake beds, but they have some of the same microscopic ones as well. Thus it is apparent that we are probably dealing with the same species in both cases.

The specimens described here can be easily separated from *M. magnifolia* which has been reported from the Upper Triassic rocks in the eastern United States. According to Fontaine (1883, p. 18–22, pl. 3, fig. 3; pl. 4, fig. 1; pl. 5, fig. 4), *M. magnifolia* has 20 lateral veins per cm whereas the new *Nilssoniopteris* has about twice that number. *M. crassinervis,* another rather similar leaf from the Upper Triassic rocks of Virginia, can be distinguished from *N. ciniza* as it has a thickened margin and about 10 lateral veins per mm (Fontaine 1883, p. 22–23, pl. 5, fig. 5; pl. 6, fig. 1).

Nearly all species of *Nilssoniopteris* described elsewhere are considerably smaller than the species described here and have fewer veins per cm. Also the cell walls in these species usually are sinuous rather than straight. *N. jourdyi* (Zeiller) Florin, which has been reported from the Rhaetic of Greenland (Harris 1932) and Tonkin (Zeiller 1903), resembles *N. ciniza* rather closely in certain characteristics. However, it too is distinct as most specimens are slightly smaller and have more veins per cm (about 50) than the new *Nilssoniopteris* (about 40). Also the anticlinal cell walls of the epidermis in *N. jourdyi* are straight to slightly sinuous whereas they are always straight in *N. ciniza.*

The leaves of *N. ajorpokensis* are relatively narrow (2–3 cm) in comparison to those of *N. ciniza* (5–10 cm) although they are about the same length as some of the smaller specimens of the new species. The older species also has fewer veins (11–16) per cm than *N. ciniza* which has 35–60.

Remarks.—This species is named after the Ciniza Lake Beds which contained the type material.

In contrast to the situation in the Ciniza Lake Beds, the species occurs in such large numbers in Dinnebito Wash, Arizona, that they overlap each other and form a dense mat. Only a few other fossils occur with the species in Dinnebito Wash, and one of them is *Equisetites.* Partly as a result of this association Daugherty suggested that the mat represents a marsh or swamp deposit.

Material.—Holotype: USNM 172329.
Paratypes: USNM 172330,172331.
UCMP 1573, 1574.

Distribution.—*N. ciniza* is known from the Ciniza Lake Beds in the upper part of the Monitor Butte Member of the Chinle Formation at USGS fossil plant locality 10091 near Fort Wingate, New Mexico. It is also known from the Petrified Forest Member of the Chinle Formation at MNA fossil locality P.193 and UCMP locality P3904 in Dinnebito Wash, Arizona. The fossils identified as *M. magnifolia* by Brown (in Stewart and others 1972) from a locality in southern Utah and another near St. Johns, Arizona, may well represent *N. ciniza* also.

Zamites powelli Fontaine
(figs. 3b, 3c, 3e, 7)

1890 *Zamites powelli* Fontaine (in Fontaine and Knowlton), p. 284, figs. 5-7.

1927 *Otozamites powelli* (Fontaine) Berry, p. 305-7, figs. 1-3,5.

1941 *Otozamites powelli* (Fontaine) Berry. Daugherty p. 84-85, pl. 17, figs. 1-3,5.

1967 *Otozamites powelli* (Fontaine) Berry. Ash, p. 128, fig. 3h.

1972a *Otozamites powelli* (Fontaine) Berry. Ash, p. 37, figs. 3a, 3b.

1974 *Otozamites powelli* (Fontaine) Berry. Ash, p. 181, fig. 3.

1975 *Zamites powelli* Fontaine. Ash, p. 145-48, text-figs. 3-4, pls. 1-2.

Remarks.—This species has been described in some detail recently (Ash 1975), and the material considered here adds nothing to that description.

Z. powelli is represented in the lake beds by a few bits of cuticle, and large impressions or casts of the entire leaf occur in the steeply dipping beds in Eastern Wash and Western Wash. The species also occurs in abundance at several places in the main body of the Monitor Butte Member in the Fort Wingate area (Ash 1967).

Material.—USNM 172328, 172331, 172332.

Distribution.—*Z. powelli* is one of the most widely distributed leaves in the Upper Triassic rocks of the Southwest as it occurs at 35 known localities there (Ash 1975). It is abundant in the lower part of the Chinle Formation in western New Mexico, Arizona, and Utah (Ash 1972a) and also occurs in the Dockum Group of eastern New Mexico and adjacent areas in Texas.

Division CONIFEROPHYTA
Order CORDAITALES (?)
Pelourdea poleoensis (Daugherty) Arnold, 1964
(fig. 3d)

1941 *Yuccites poleoensis* Daugherty, p. 70-71, pl. 13, fig. 1.

1964 *Pelourdea poleoensis* (Daugherty) Arnold, p. 7, pl. 1, figs. 2, 3.

1972a *Pelourdea poleoensis* (Daugherty) Arnold. Ash, p. 33.

Description.—This species is represented by numerous leaf impressions which lack bases. The fossils show that the leaf is linear with a rounded apex. It varies from 2-3 cm in width. The longest specimen is 26 cm long; the taper suggests that it may have been as long as 30 or 35 cm. The leaves contain many parallel veins (about 2 per mm).

Remarks.—Fossils similar to those described here are known from practically every leaf locality in the Chinle Formation. However, not one that has been studied shows its cuticle or any other fine details. It is possible that these fossils represent more than one species, but, in the absence of data to the contrary, I tentatively refer all large linear leaves in the Chinle to *P. poleoensis.*

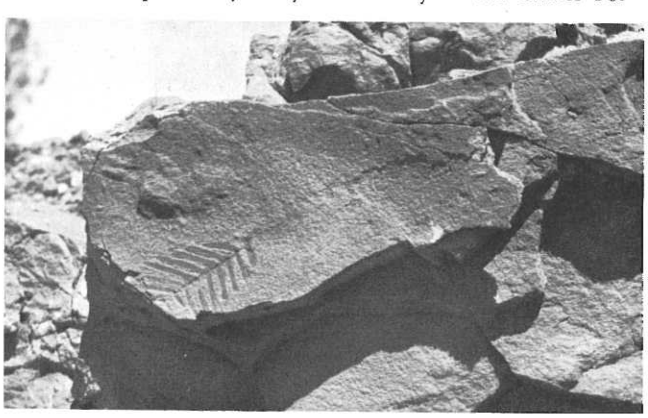

FIGURE 7.—Imprints of bennettitalean leaf *Zamites powelli* Fontaine in place in steeply dipping beds of sandstone about 3.65 m west of locality FW5.

Distribution.—Impressions of this species occur in the steeply dipping beds a short distance west of locality FW5. Similar specimens were also collected elsewhere in the Monitor Butte Member of the Chinle at USGS fossil plant localities 10058-61 (see Ash 1970a). In Petrified Forest National Park, Arizona, it occurs in the lower part of the Petrified Forest Member of the Chinle Formation at USGS fossil plant locality 10062 (see Ash 1970a). Daugherty (1941) originally described the species from the Aqua Zarca Sandstone Member of the Chinle. Later Arnold (1964) reported its occurrence in the Upper Triassic Dolores Formation in western Colorado.

Order CONIFERALES
?Family ARAUCARIACEAE
Pagiophyllum readiana n. sp.
(figs. 8, 9, 10)

1972 *Pagiophyllum* sp. B, Ash, p. 35, fig. 2c.

Diagnosis.—Straight twigs, stem about 0.7 mm in diameter, bearing spirally arranged leaves (phyllotaxis 3/8). Leaves fairly closely set, about 18-24 per cm, sessile, attachment area small, oval to round, typically 400-500μ in diameter, free part not flattened into one plane, directed forward at an angle of about 20-30° from stem, ovate, 1.5-2.5 mm long, about 0.6-0.8 mm wide at broadest place in lower part of leaf, thickness about equal to width. Base of leaf oval as compressed dorsiventrally, sides tapering gradually to apical area, then narrowing abruptly to an acute or acuminate apex, compressed edges entire except for papillae. Laterally compressed leaves having an almost semicircular outer edge, at the base descending vertically to stem, inner edge nearly straight from attachment area to apical acumen. Adaxial (upper) surfaces smaller in area than abaxial and marked off by a distinct lateral angle bearing papillae. No keel present on lower side or median ridge on upper side. Stem surface (apparently) smooth between leaves and without raised cushions.

Cuticle of stem and lower sides of leaf tough, about 2μ thick (in folds), upper slightly thinner and more delicate, about 1μ thick. Stomata present on both sides, many times more abundant on upper (adaxial) than lower cuticle, often missing below. On adaxial side arranged in files a single stomata wide, with many isolated stomata occurring between files. Files not sunken, usually separated by 1-3 files of ordinary epidermal cells, but stomata fewer and scattered below and rare on stem. Stomatal apparatus round to oval, with sunken guard cells, surrounded by a ring of 4-8 (usually 6) subsidiary cells, outer margin of subsidiary cells forming a conspicuous raised ring, surface dipping inward to form a wide pit 10-15μ deep. Each subsidiary cell marked with radial running striations about 0.5μ wide on periclinal surfaces and bearing a solid papilla on its inner surface. Papillae solid, 8μ long, 10μ wide at base, wedge shaped but with rounded apex, directed inward over aperture and slightly upward to reach level of leaf surface. Inner edge of subsidiary cells form a ring at bottom of pit but often concealed by papillae. Guard cell aperture thinly cutinized, orientation unknown. Encircling cells present, probably forming a complete ring but just like ordinary epidermal cells.

Ordinary epidermal cells on lower cuticle typically rectangular (range noted 12-22μ wide, 30-90μ long), longitudi-

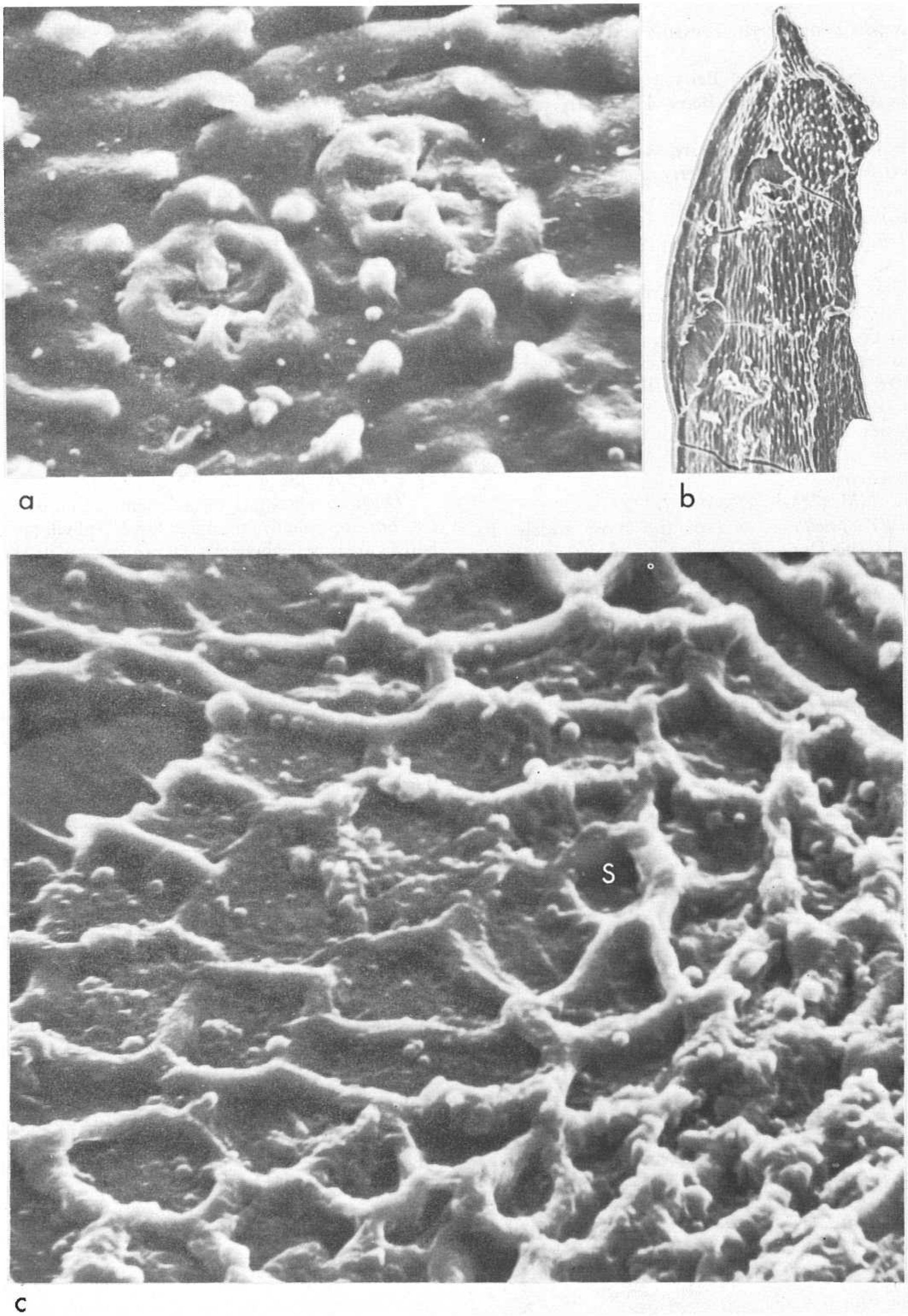

FIGURE 8.–SEM micrographs of *Pagiophyllum readiana* Ash, n. sp. a.–Outer surface of the abaxial cuticle. Two stomata and some small rounded papillae that occur above ordinary epidermal cells on leaves of this species are visible. Compare these papillae with sharply pointed ones on leaves of *P. zuniana* n. sp. (fig. 11a). Note the small papillae that overhang the stomatal apertures. X500. b.–Apical region of dorsiventrally compressed leaf. Outer surface of abaxial side. Note abundant papillae over ordinary epidermal cells and strongly developed apical acumen. Several stomata are visible between papillae. X25. c.–Inner surface of abaxial cuticle. Stoma (S) and narrow ridgelike cuticular flanges that mark positions of epidermal cells are shown. Compare flanges with those of *P. zuniana* (fig. 11c). X500. All materials from locality FW6.

nally oriented, end walls usually perpendicular to lateral walls. Anticlinal walls strongly marked, 3–7μ thick frequently broken by pits. Periclinal walls flat to slightly bulging, occasionally bearing a single rounded, conical, solid papilla near end of cell closest to apex of leaf. Papillae 6–9μ in diameter at base, rarely more than 8μ high, tallest noted 18μ, best developed on cells along lateral angles and near leaf apex. Ordinary epidermal cells on upper cuticle rather shorter and often more irregular in shape and size owing to presence of stomata; walls and surfaces similar but papillae much better developed. Hypodermis not observed.

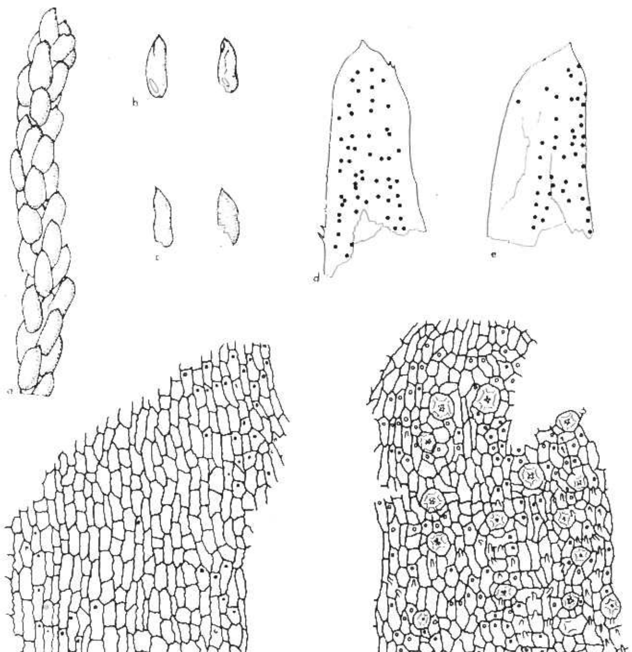

FIGURE 9.–*Pagiophyllum readiana* n. sp. a.–Leafy shoot of the holotype. Slide USNM 43613a, X3.5. b.–Leaves from the holotype. Note attachment scar on each. Leaf on left from slide USNM 43613e, leaf on right from slide USNM 43613b, all X3.5. c.–Laterally compressed leaves from holotype. Slide USNM 43613g, all X3.5. d.–Upper cuticle, each dot represents a stoma. Several large papillae on margins also shown. Slide USNM 43613g, X17.5. e.–Laterally compressed leaf showing abundant stomata on upper cuticle (at right) and their almost total absence on lower cuticle (at left). Slide USNM 43613b, X17.5. f.–Lower cuticle showing the sparse papillae and typical rectangular cells. Slide USNM 43613c, X70. g.–Upper cuticle showing the frequent stomata and papillae. Slide USNM 43613d, X70.

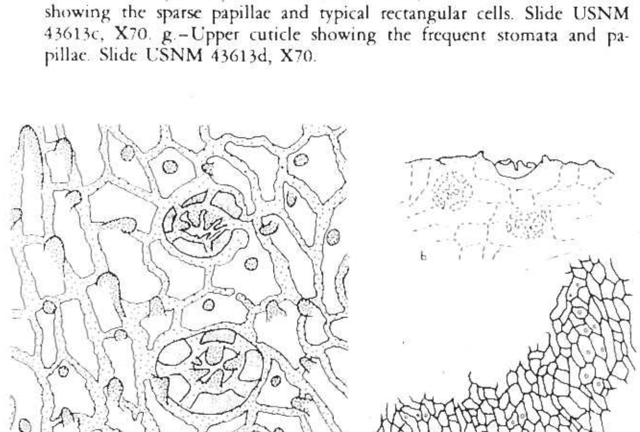

FIGURE 10.–*Pagiophyllum readiana* n. sp. a.–Stomata from upper cuticle. Radiating striations on subsidiary cells shown as well as abundant papillae typically present on upper cuticle. Slide USNM 43613d, X284. b.–Stomata near fold in cuticle. Slide USNM 43613c, X142. c.–Cuticle from stem of twig. Slide USNM 43613f, X71.

Discussion.–*P. readiana* is based on the single fragmentary shoot shown in figure 9 and several isolated leaves. Its correct generic name is a problem. Three form genera as redefined by Harris (1969b) which might accommodate it are *Brachyphyllum, Pagiophyllum,* and *Cyparissidium.* The fossil has least in common with *Brachyphyllum* as its leaves are elongated in comparison to the typical short, broad leaves of that genus. It differs from the other two in having no basal cushion and to some extent also in that the leaf is distinctly dorsiventral and somewhat spreading. *Pagiophyllum* seems to suit it best, but it is by no means an ordinary species. Since it fits none of the genera precisely, it might be placed in a new genus. However, as Harris (1969b) has pointed out, there are so many (about 150) genera available for fossil conifer shoots that no one can remember them all. Thus it simply would be lost to sight if it were placed in a new genus. Under the circumstances it is placed in the old form genus to which it comes closest, *Pagiophyllum.*

Comparisons.–No other species of *Pagiophyllum* is known to me in which the leaves have contracted bases, and the stem is smooth without swollen decurrent cushions. Most species of the genus also have leaves larger than those of *P. readiana.* Two which in several respects are similar are *P. gracillimum* Adams (1951) from the Jurassic of England and *P. magnipapillare* Wesley (1956) from the Jurassic of Italy. The English species, however, differs in that it has falcate to linear leaves compared to the oval ones in the present species. In addition the periclinal walls of its subsidiary cells lack the papillae and radiating striations which occur in *P. readiana.* In the Italian species the stem has swollen leaf cushions. Its subsidiary cells also lack the radiating striations and prominent papillae that occur in *P. readiana.*

Remarks.–The species is named in honor of Mr. Charles B. Read, who first collected fossil leaves from the Chinle Formation near Fort Wingate, New Mexico, during 1941.

Material.–Holotype: USNM 43613a-g.

Distribution.–*P. readiana* is known only from the Ciniza Lake Beds at USGS fossil plant locality 10091 in the Monitor Butte Member of the Chinle Formation near Fort Wingate, New Mexico.

Pagiophyllum zuniana n. sp.

(figs. 11, 12, 13)

1972a *Pagiophyllum* sp. C, Ash, p. 35, fig. 2d.

Diagnosis.–Plant known only from fragments of leafy shoots. Shoots straight, leaves spirally arranged (phyllotaxis probably 3/8). Leaves fairly closely set, about 15–18 per cm, arising from an oval leaf cushion, no boundary present between cushion and free part of leaf. Free part of leaf straight, directed outward, bent into the horizontal plane, projecting at an angle of 60°–70° from axis, typically about 4–6 mm long, 0.7–1.0 mm from top to bottom edge as compressed, probably round in section near middle, possibly having small lateral angles near base, containing a single vascular strand about 0.1 mm in diameter. Basal edge of mature leaf slightly expanded as it joins the cushion, leaf of almost uniform width but narrowing abruptly to a more or less acuminate, forward curving apex, the lower edge bending upward, compressed edges smooth apart from minute projecting papillae.

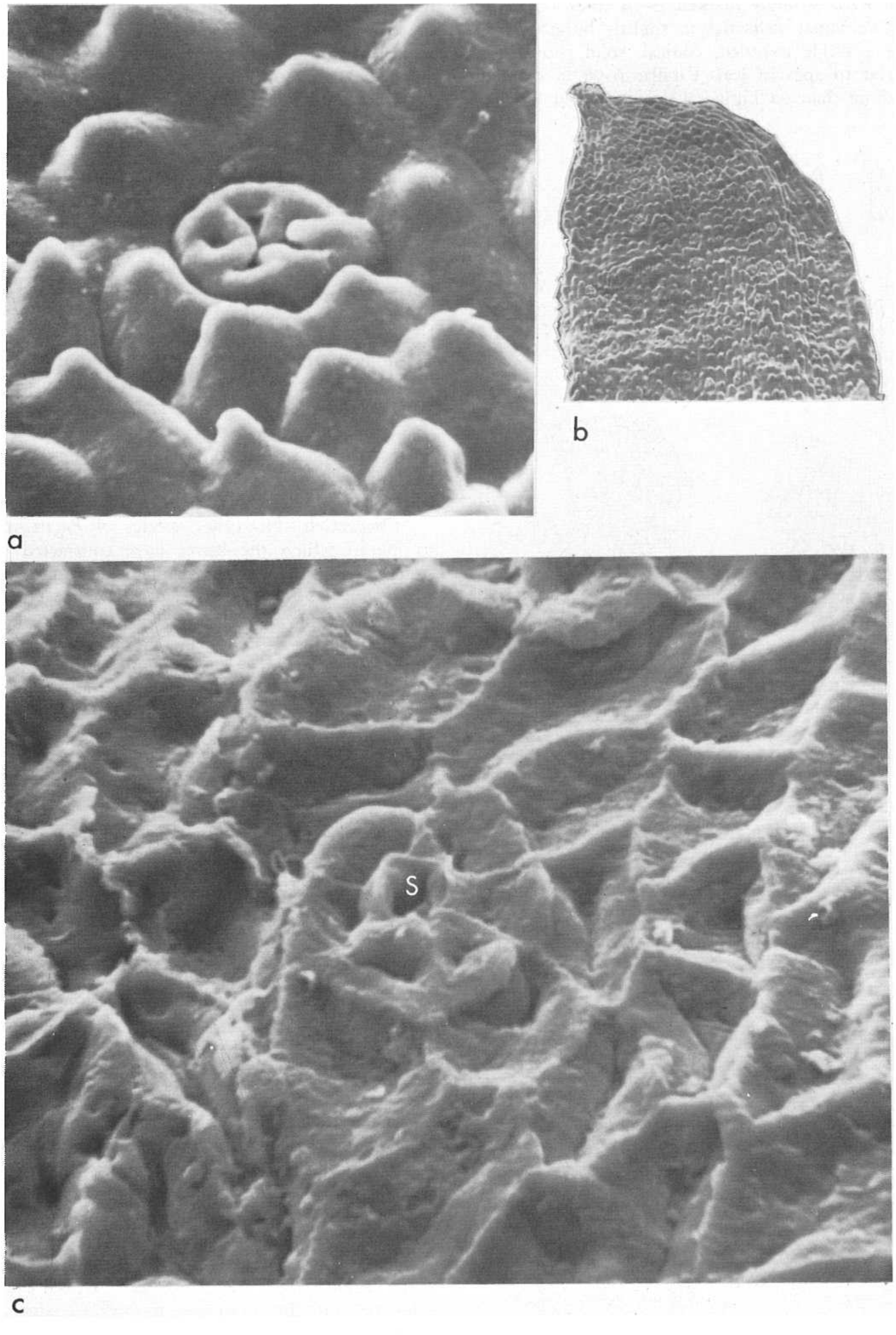

FIGURE 11.–SEM micrographs of *Pagiophyllum zuniana* Ash, n. sp. a.–Outer surface of cuticle. A stoma and small, sharply pointed papillae that occur above ordinary epidermal cells in apical region of leaves of this species are shown. Note small papillae that overhang stoma aperture. X500. b.–Apical region of laterally compressed leaf. Outer surface of side of leaf. Note that papillae that occur above ordinary epidermal cells are more sharply pointed near apex than elsewhere on leaf. X25. c.–Inner surface of cuticle. A stoma (S) and rounded, irregular, cuticular flanges that mark positions of ordinary epidermal cells are visible. Although flanges in this species are narrow at the top, they are rather broad at the base and seem to blend gradually with rest of cuticle. Consequently it is difficult to determine base of flanges at some places. This contrasts with cuticle of *P. readiana* (fig. 8a), in which flanges are narrow at base, usually clearly differentiated from rest of cuticle. X500. All materials from locality FW6.

Apical leaves small, about half as long and wide as lower ones, not spreading in the horizontal plane.

Cuticle of leaf and leaf base on upper edge of leaf tough, about 2μ thick (in folds), on lower edge more delicate about 1μ thick, outer surface frequently showing small wrinkles. Stomata present all over leaf, present also on leaf base, usually absent from a narrow zone near lower edge and lateral angles, irregularly scattered, only occasionally with two in an ill-defined longitudinal file, about 60-80 per square mm. Stomata usually separated by 2-4 ordinary epidermal cells. Stomatal apparatus with sunken guard cells, surrounded by a ring of about six subsidiary cells, outer margins of subsidiary cells forming a conspicuous raised ring, surface dipping inward to form a wide pit $10-15\mu$ deep. Each subsidiary cell bearing on its surface a conspicuous papilla. Papillae pointing upward and inward over the aperture; ends of papillae rounded, up to 9μ long, 6μ wide, inner edge of subsidiary cells forming a ring at the bottom of the pit but usually concealed by papillae. Guard cell aperture slightly cutinized, orientation varied. Encircling cells present, as a rule as a nearly complete ring but just like ordinary epidermal cells.

Ordinary epidermal cells similar all over free part of leaf, square to polygonal, mostly slightly longer than broad (range noted $18-35\mu$ wide, $24-67\mu$ long), trending to form longitudinal files, shorter and more irregularly placed on cushion. Anticlinal cell walls strongly marked on leaf, about $3-7\mu$ thick, more or less straight with some slight waves and interruptions, periclinal cell walls flat over most of leaf, marked with a broad border to the anticlinal wall and leaving a thin strip in middle of cell. Each cell bearing a single conspicuous papilla. Papilla $7-15\mu$ high, $5-8\mu$ in diameter, with a minute basal cavity. Epidermal cells in upper part of leaf with a strongly convex surface which merges into papilla.

Discussion.—*P. zuniana* is based on a small shoot, about 3 cm long, and several isolated leaves. During maceration in the laboratory, the shoot broke into short lengths of which the longest is figured. The leaves are so strikingly regular in their arrangement that I feel sure all were in a horizontal position before compression. The leaf shape was inferred from the dimensions of the apical leaves where the width after compression was equal in leaves compressed at the sides and in ones compressed over the top of the stem. Some leaves show creases and folds near the base. They are similar to those reported in *P. connivens* by Kendall (1948, p. 108)

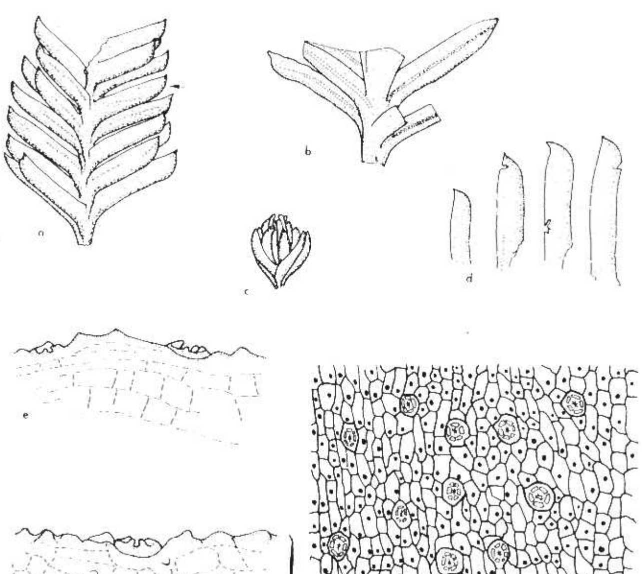

FIGURE 12.—*Pagiophyllum zuniana* n. sp. a.—Fully macerated portion of laterally compressed holotype, folds indicated by heavy stippling. Arrow indicates approximate position of stomata shown in 12f. Slide USNM 43632a, X3.5. b.—Partially macerated portion of leafy shoot of holotype, midveins indicated by heavy stippling. Slide USNM 43632c, X3.5. c.—Apex of a twig, some leaves on exterior removed, and one is shown figure 13a. Specimen broken into two pieces during preparation, and this drawing is slightly reconstructed. Slide USNM 43633a, X3.5. d.—Laterally compressed leaves obtained from holotype. Two middle specimens on slide USNM 43632c, right-hand specimen on slide USNM 43632b, left-hand specimen on slide USNM 43634, all X3.5. e., f.—Stomata near folds in cuticle. e, Slide USNM 43632a; f, Slide USNM 43632c (from the end of the leaf marked by the arrow in a). All X138. g.—Cuticle from the side of a laterally compressed leaf, papillae shown by black dots. Slide USNM 43634, X69.

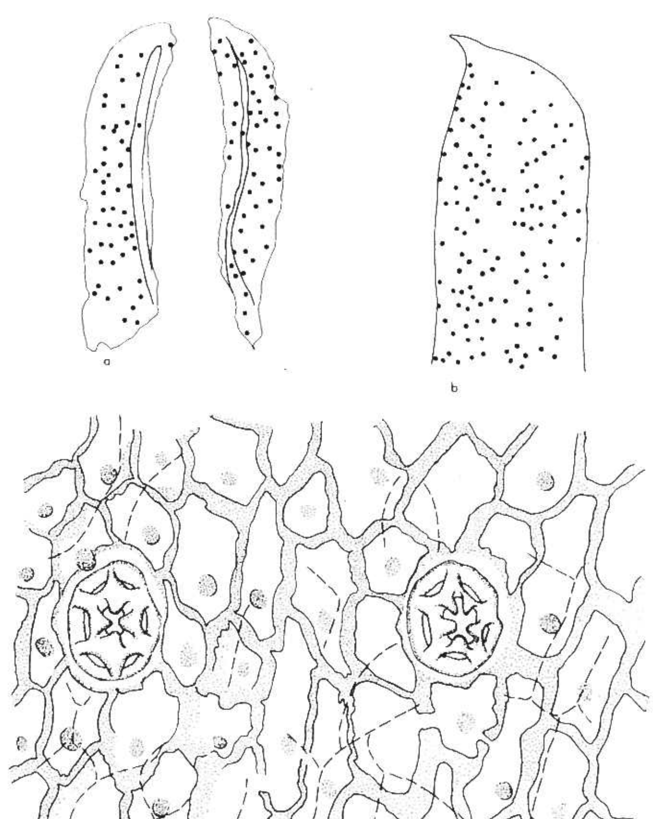

FIGURE 13.—*Pagiophyllum zuniana* n. sp. a.—Cuticles from opposite sides of laterally compressed leaf from shoot apex shown in figure 12c. Each dot represents a stoma; folds are indicated by heavy lines. Slide USNM 43633b, X20. b. Cuticle from one side of apical region of laterally compressed leaf (second one from right in fig. 12d); each dot represents a stoma. Slide USNM 43632c X20. c.—Stomata, papillae on the periclinal cell walls shown by heavy stippling, impressions of anticlinal flanges on opposite cuticle indicated by broken lines. Guard cells not preserved in these stomata. Slide USNM 43634, X320.

which, according to her interpretation, are caused by lateral angles on the leaves. It is possible but not certain that the basal parts of the leaves of *P. zuniana* also had small lateral angles.

The statement that the leaves of this species contain a single vein is based on the dark narrow strand that occurs in many of the unmacerated leaves. At the suggestion of Professor Harris, several of the leaves containing a strand were macerated in HNO_3 for a short time. Much of the coaly matter in and on the leaf disappeared, and the strand was seemingly unaffected and more prominent than previously, as shown in figure 12b. When a leaf treated in such a manner was placed in a weak solution of ammonia, the strand disappeared entirely, strongly suggesting that it was composed of vascular tissue.

Comparisons.—The only Chinle conifer with which *P. zuniana* might possibly be confused is *P. navajoensis.* That species has somewhat similarly shaped leaves and flattened shoots. Although the leaves of that species are about the same diameter as those of the present one, they are twice as long. The two species can be easily distinguished on the microscopic level also as the inner surface of the outer periclinal walls of the epidermal cells in *P. navajoensis* bear many angular pits, whereas they are smooth and bear papillae in the new species. Also the periclinal walls are sinuous in *P. navajoensis,* whereas they are straight to only slightly curving in *P. zuniana.*

Shoots of *P. zuniana* might possibly be mistaken for the shoots of the problematical plant *Dinophyton spinosus* Ash (1970b) which has been described from the Chinle Formation and other Upper Triassic units in the Southwest. The leaves of that species are about the same diameter as the leaves of *P. zuniana,* but they are more than twice as long. They also can be easily differentiated on the microscopic level as the epidermal cells of *D. spinosus* frequently bear long pointed hairs whereas the epidermal cells of *P. zuniana* have relatively low papillae (figs. 11a, 11b). Furthermore, the stomatal pits of *D. spinosus* are rectangular and are not protected by papillae of any sort; in the present species the stomatal pit is oval and protected by several papillae that arise from the subsidiary cells.

Many living conifers have spirally arranged leaves with blades twisted into the horizontal plane, but most have dorsiventrally flattened and petiolate leaves (e.g., *Sequoia sempervirens*). *Araucaria cunninghamia* is similar though with much wider shoots, and so is *Podocarpus dacrydiodides.* The latter species is particularly similar because the apex of the leaf bends forward. The cuticle of *P. zuniana* is not at all like either in detail.

Remarks.—The species is named for the Zuni Mountains, the site of the locality that yielded the type specimen.

Like the previous species, this one is aberrant as a *Pagiophyllum,* although it does fit better there than in one of the other form genera redefined by Harris (1969b).

Material.—Holotype: 43632a-d.

Distribution.—*P. zuniana* is known only from the Ciniza Lake Beds at USGS fossil plant locality 10091 in the Monitor Butte Member of the Chinle Formation near Fort Wingate, New Mexico.

Pagiophyllum duttonia n. sp.
(figs. 14a, 14c, 15)

Diagnosis.—Plant known only from fragments of a leafy shoot. Shoot straight, axis about 1 mm in diameter, bearing small, spirally arranged leaves (phyllotaxis probably 3/8). Leaves fairly closely set, about 16-20 per cm, arising from an oval leaf cushion, no boundary present between cushion and free part of leaf. Free part of leaf straight, outward directed, bent into horizontal plane, projecting at an angle of about 35°-50° from axis, typically about 6-8 mm long, 0.8 mm from top to bottom edge as compressed, possibly having small lateral angles. Base of mature leaf slightly expanded (in compression) as it joins cushion, leaf of almost uniform width but narrowing abruptly to distinctly acuminate outward directed apex, compressed edges entire except for papillae. No keel present on lower side or median ridge on upper side.

Cuticle of lower side of leaf tough, about 3μ thick (in folds), upper slightly thinner and delicate. Stomata present on both sides of leaf and on leaf base, usually absent from narrow zones near lateral angles of leaves, arranged in files a single stoma wide, irregularly distributed stomata occasionally occurring between files. Files not sunken, usually separated by 2 files of ordinary epidermal cells, becoming indistinct and irregular on leaf cushion and stem. Stomatal apparatus round to oval, 28-78μ in diameter, oriented longitudinally on free part of leaf, round and irregularly oriented on cushion and stem. Guard cells sunken, surrounded by ring of 4-6 irregular subsidiary cells, terminal ones usually different from lateral ones, typically polygonal. Outer margins of subsidiary cells forming a conspicuous raised ring, surface dipping inward to form a shallow depression about 4-8μ broad. Each subsidiary cell bearing on its surface a small hollow papilla. Papillae arising from inner wall, pointing upward, converging over aperture, ends rounded, up to 9μ long, 6μ wide at base. Surface of subsidiary cells flat, smooth, showing a thin strip at base of papillae. Inner edge of subsidiary cells forming a ring at bottom of a shallow pit about 8-12 × 10-16μ, ring usually concealed by papillae. Guard cell aperture slightly cutinized. Encircling cells often unrecognizable, if present, unspecialized and forming an incomplete ring.

Ordinary epidermal cells generally similar all over free part of leaf and leaf base, mostly rectangular between stomatal files, somewhat irregular and polygonal in stomatal files, dimensions vary according to position with respect to stomata (range noted 12-14μ wide, 22-155μ long). Cells oriented longitudinally, end walls usually perpendicular to side walls, anticlinal walls strongly marked, straight to slightly curving, frequently broken by pits. Cuticular flanges about 3μ high, approximately 5μ wide at base, narrowing fairly abruptly to a width of about 1μ at top. Periclinal cell walls usually flat, frequently bearing a single rounded, conical, solid papilla near end of cell closest to apex of leaf. Papillae 6-9μ in diameter at base, commonly 2μ or less in height (tallest noted 8μ), best developed on cells near leaf apex. Cells in upper part of leaf with strongly convex surface which merges into the papillae.

Discussion.—This species is based on a single small shoot which originally was about 2 cm long. When it was removed from the rock for maceration, it broke into several fragments, and the three largest are shown in figures 15a-15c. The leaves were probably arranged in a horizontal position before compression as they are now very regular in arrangement. It is impossible to determine the leaf shape of the species because a shoot apex has not been found. The presence of lateral angles in the leaves is suggested by the folds that frequently occur along the lateral margins of the leaves (figs. 15a-15c).

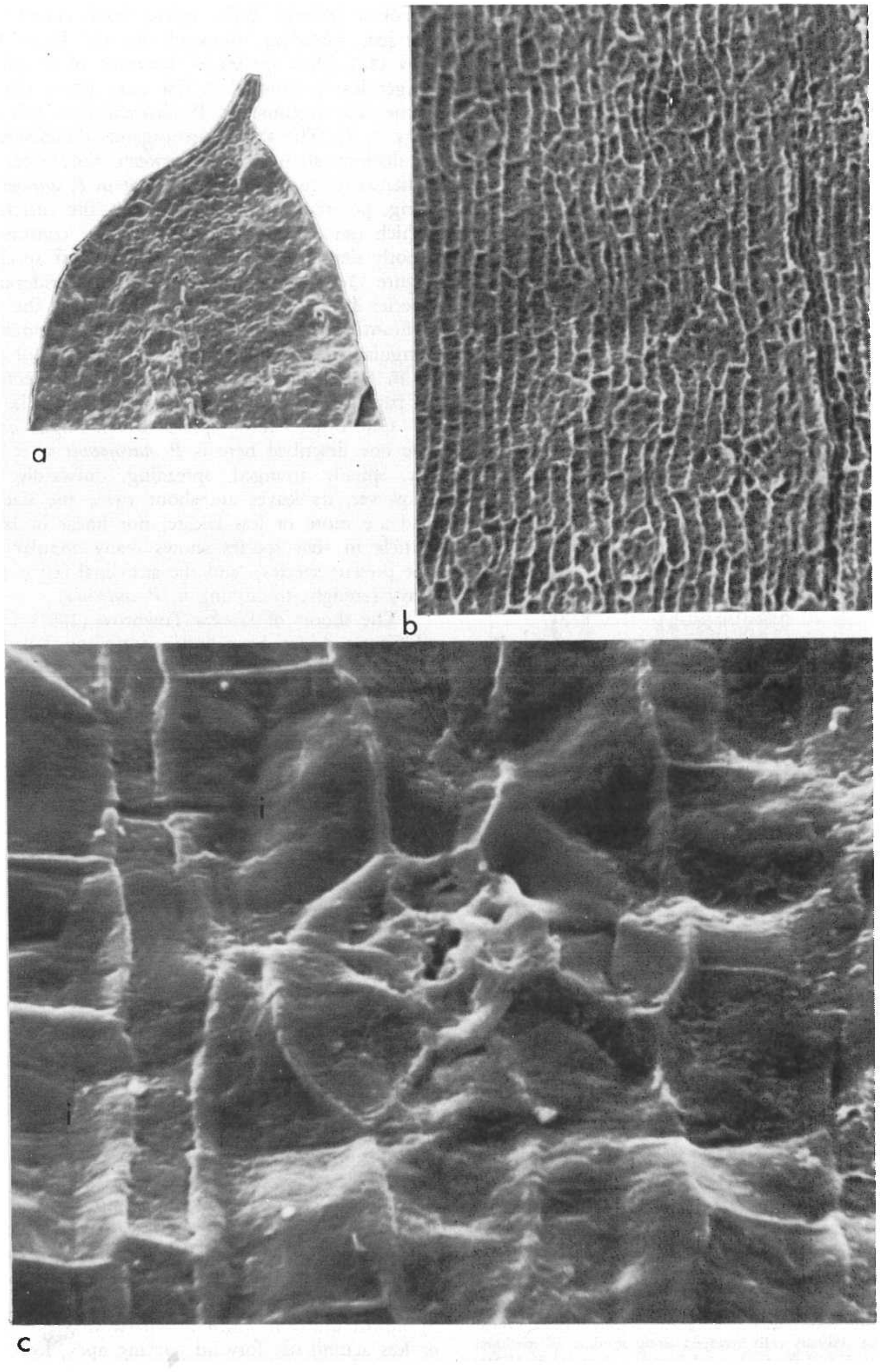

FIGURE 14.–SEM micrographs of *Pagiophyllum duttonia* Ash, n. sp. and of *Pagiophyllum navajoensis* Ash, n. sp. a., c.–*Pagiophyllum duttonia* Ash, n. sp. a.–Outer surface of apical region of laterally compressed leaf. Note elongated apical acumen. Papillae over ordinary epidermal cells in lower part of figure are less prominent than those nearer apex of leaf. About X25. c.–Inner surface of a stoma. Note that anticlinal flanges are rather low and in many places blend smoothly into periclinal surfaces of cuticle. Impressions of anticlinal flanges of opposite cuticle are visible at i. About X500. b.–*Pagiophyllum navajoensis* Ash, n. sp. Inner surface of cuticle showing generally rectangular form of ordinary epidermal cells and oval stomata. Angular pits that occur in cuticle are visible. About X100. All materials from locality FW6.

The anticlinal flanges of the cuticle on each side of the leaf often have left impressions on the opposite cuticle as shown in figure 14c. Presumably this occurred during fossilization when the leaves were compressed. When these marks were first observed, it was thought they might be the anticlinal flanges of a cutinized hypodermis. Eventually, however, it was possible to match the impressions on one cuticle with the anticlinal flanges on the opposite cuticle conclusively proving their true origin.

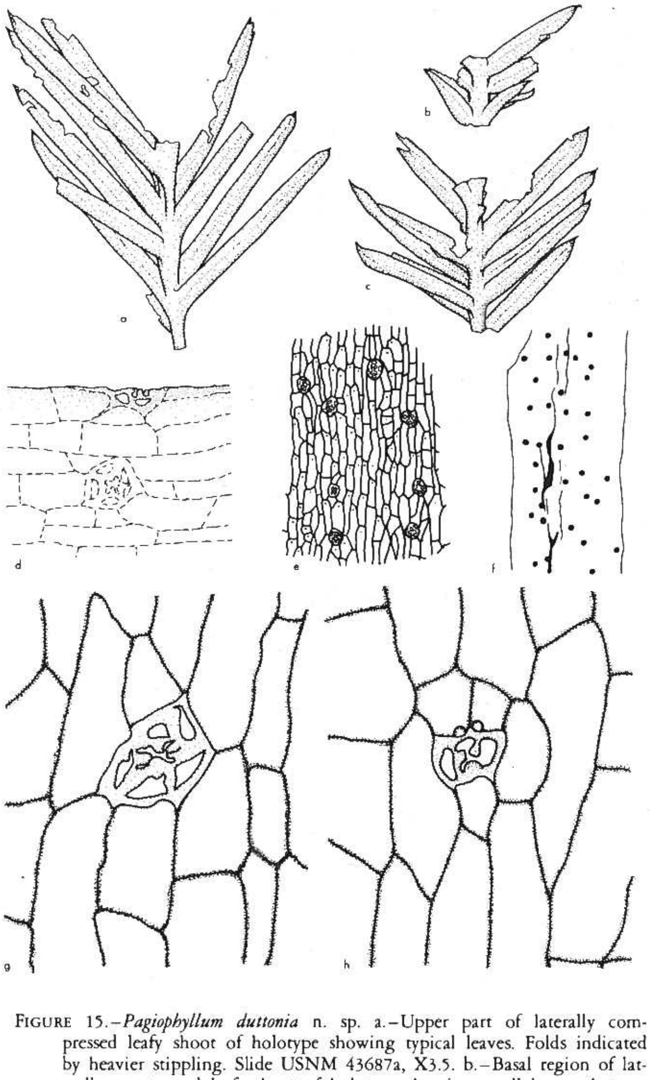

FIGURE 15.—*Pagiophyllum duttonia* n. sp. a.—Upper part of laterally compressed leafy shoot of holotype showing typical leaves. Folds indicated by heavier stippling. Slide USNM 43687a, X3.5. b.—Basal region of laterally compressed leafy shoot of holotype showing small leaves that occur in this part. Folds indicated by heavy stippling. Slide USNM 43687c, X3.5. c.—Upper part of laterally compressed leafy shoot of holotype, folds indicated by heavy stippling. Slide USNM 43687b, X3.5. d.—Stomata near a fold in cuticle. Slide USNM 43687a, X140. e.—Cuticle from side of a laterally compressed leaf showing general form and arrangement of ordinary cells of epidermis and distribution of stomata and papillae (dots). Lateral margin of leaf is marked by two files of rectangular ordinary cells arranged along midline of specimen. Upper part of leaf is to left of files and lower to right. Slide USNM 43687f, X70. f.—Cuticle from side of a laterally compressed leaf showing distribution of stomata (dots). In this specimen lateral margin of leaf is marked by folds (heavy lines). Upper part of leaf is to left of folds and lower to right. Slide USNM 43687d, X17.5. g., h.—Stomata and ordinary epidermal cells. Solid line outlining cells represents top of cuticular flange where it is narrow, and shading on either side of line represents broad base of flange. Slide USNM 43687d, X280.

Comparisons.—*P. duttonia* compares most closely in external form with small shoots of the common Chinle plant *Dinophyton spinosus.* Both species have closely set, spirally arranged, spreading, outward directed linear leaves (cf. figs. 15a–15c). Most specimens, however, of *D. spinosus* have much larger leaves although a few have leaves that are about the same size as those of *P. duttonia* (see Ash 1970b, pl. 122, figs. 5, 8). The shoots are organized somewhat differently as a distinct stem occurs between the leaves in *D. spinosus* whereas no such organ is present in *P. duttonia.* The frequent long, pointed hairs that occur on the cuticle of *D. spinosus,* which can be seen with a hand lens, contrast with the low, poorly developed papillae in the present species as shown in figure 15e. The anticlinal walls of the epidermal cells in both species are fairly straight to curving, but the stomata are significantly different. In *D. spinosus* the stomatal pits are rectangular and are not protected by papillae of any sort, whereas in *P. duttonia* the pits are oval and protected by a number of papillae that arise from the subsidiary cells.

One other Chinle species which might be confused with the one described here is *P. navajoensis* as it also has closely set, spirally arranged, spreading, outwardly directed leaves. However, its leaves are about twice the size of *P. duttonia* and are more or less falcate, not linear in lateral view. The cuticle in that species shows many angular pits (absent in the present species), and the anticlinal cell walls are distinctly wavy (straight to curving in *P. duttonia*).

The shoots of *Rissikia* Townrow (1967) from the Triassic of South Africa bear linear, spreading leaves of about the same proportions as those of the present species. However, they are set farther apart on the axis than in *P. duttonia* and are also about twice as large.

Remarks.—This species is named in honor of Captain C. E. Dutton of the U.S. Army, who was one of the first geologists to describe (1885) the Zuni Mountains where the holotype was collected.

Material.—Holotype: USNM 43687a-f.

Distribution.—*P. duttonia* is known only from USGS fossil plant locality 10091 in the Ciniza Lake Beds of Monitor Butte Member of the Chinle Formation near Fort Wingate, New Mexico.

Pagiophyllum navajoensis n. sp.
(figs. 14b, 16, 17, 18)

1972a *Pagiophyllum* sp. D. Ash, p. 35, fig. 2e

Diagnosis.—Plant known only from fragments of leafy shoots. Shoots straight, axis about 1 mm in diameter, bearing spirally arranged leaves (phyllotaxis probably 3/8). Leaves widely separated, about 8–10 per cm, arising from an oval leaf cushion, no boundary present between cushion and free part of leaf. Free part of leaf falcate, directed outward, bent into the horizontal plane, projecting at an angle of 60°–70° from axis, typically 7–10 mm long, about 1 mm from top to bottom edge at widest near cushion as compressed, probably showing moderate lateral angles in all but lower part. Basal edge of mature leaf slightly expanded as it joins cushion, leaf of almost uniform width but narrowing gradually to a more or less acuminate, forward curving apex, lower edge bending upward, compressed edges smooth.

Cuticle of leaf and leaf base tough, about 4–6μ thick (in folds), covered with conspicuous angular pits. Stomata present all over leaf, present also on leaf base, usually absent from narrow zones near lower edge and lateral angles, arranged in files a single stomata wide, irregularly distributed

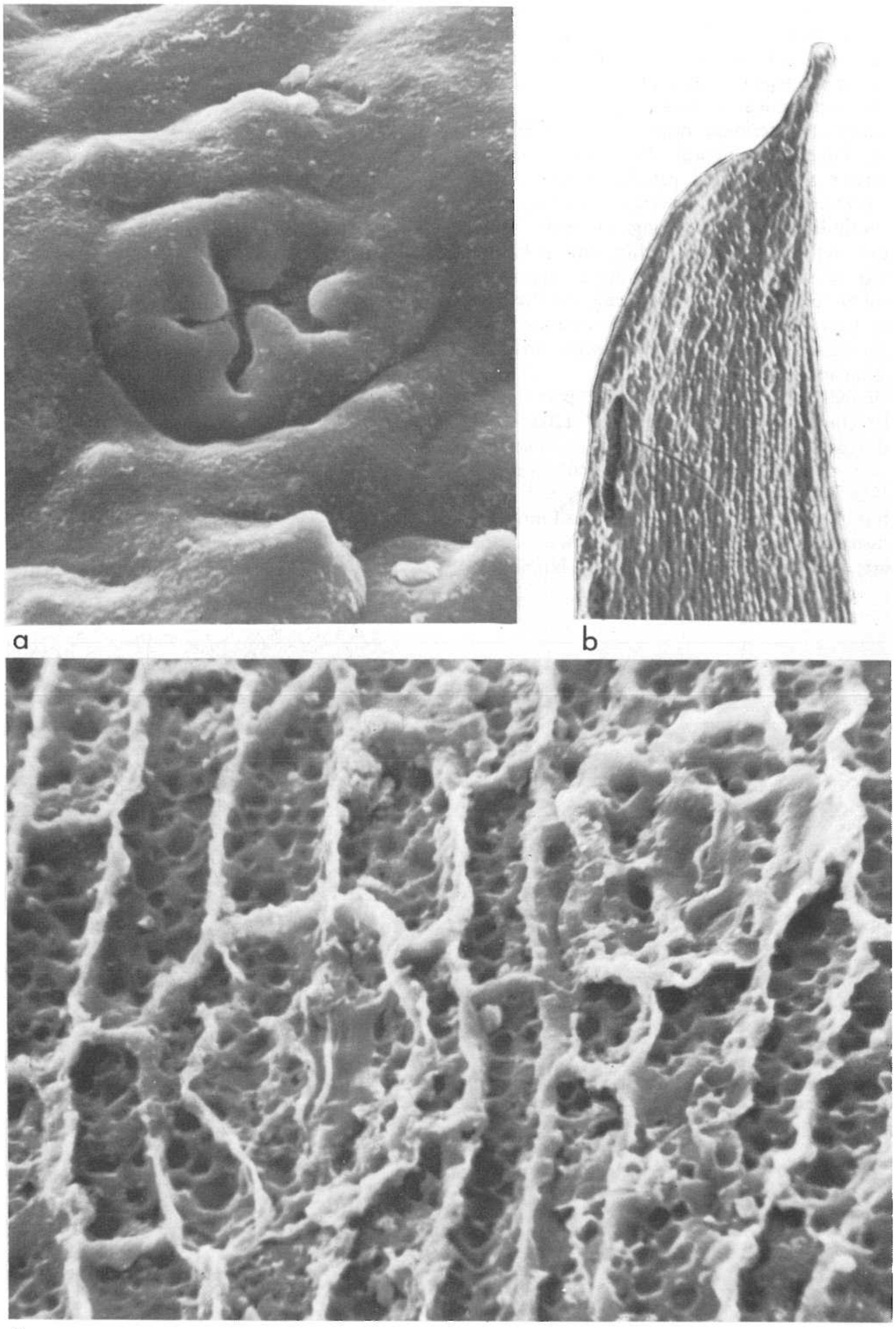

FIGURE 16.–SEM micrographs of *Pagiophyllum navajoensis* Ash, n. sp. a.–Outer surface of a stoma. Note that stoma is not sunken but is surrounded by narrow groove. In this figure five rounded papillae arise from surface of stomatal subsidiary cells and converge over aperture. Two low, rounded papillae that often occur on ordinary epidermal cells of this species are visible near bottom of figure. About X500. b.–Apical region of a laterally compressed leaf. Outer surface. Note long tapering acumen that frequently occurs in this species. Stomata show as small, oval structures between small, rounded papillae of ordinary epidermal cells. About X25. c.–Inner surface of two stomata. Compare relatively tall, narrow anticlinal flanges of this species with low, rounded flanges of *Dinophyton spinosus* in figure 19a. Note many small angular pits in the periclinal surface of cuticle. About X500. All materials from locality FW6.

stomata occurring occasionally between files. Files not sunken, usually separated by 2–4 files of ordinary epidermal cells, becoming indistinct and irregular on leaf cushion. Stomatal apparatus oval and oriented longitudinally on free part of leaf, round and oriented irregularly on cushion, with sunken guard cells, surrounded by oval ring of 4–8 (usually 6) irregular subsidiary cells, terminal ones sometimes different from lateral ones, typically polygonal. Each subsidiary cell bearing on its surface a small, solid papilla. Papillae arising from inner wall, pointing upward, converging over aperture, ends of papillae rounded, up to 10μ long, 6μ wide. Outer surface of subsidiary cells flat showing a thin strip at base of papillae. Inner edge of subsidiary cells forming a ring at the bottom of a shallow pit about $45 \times 75\mu$, ring usually concealed by papillae. Guard cell aperture slightly cutinized. Encircling cells often unrecognizable and, if present, unspecialized and forming an incomplete ring.

Ordinary epidermal cells similar all over free part of leaf, mostly rectangular (range noted 7–30μ wide, 30–120μ long), oriented longitudinally, irregular, often polygonal, sometimes equidimensional on cushion. Anticlinal cell walls strongly marked, about 3–5μ thick, more or less straight, not interrupted by pits but with short, jagged extensions onto surface, end walls usually perpendicular to lateral walls (especially on free part). Periclinal cell walls slightly bulging to flat, inner surface showing many small conspicuous angular cavities. Cavities occasionally occurring in anticlinal flanges and in walls of subsidiary cells.

Discussion.—This species is based on the small fragment shown in figure 17a and several isolated leaves. I believe that all the leaves were in a horizontal position before compression as they are very regular in their arrangement. The suggestion that there are lateral angles in the middle and upper parts of the leaves is based on the folds that consistently occur in these parts. These folds are shown by heavy shading or solid lines along the lateral margins of the leaves in figures 17b and 18c.

The angular pits on the underside of the cuticle of this species are somewhat unusual, but they are not unique. Similar pits have been reported in a few other fossil conifers including *Stabbarpia* Florin (1958) from the Lower Jurassic of Sweden, *Farndalea* Bose (1955) from the Middle Jurassic of Yorkshire, and *Elatocladus perforatus* Harris (1935) from the

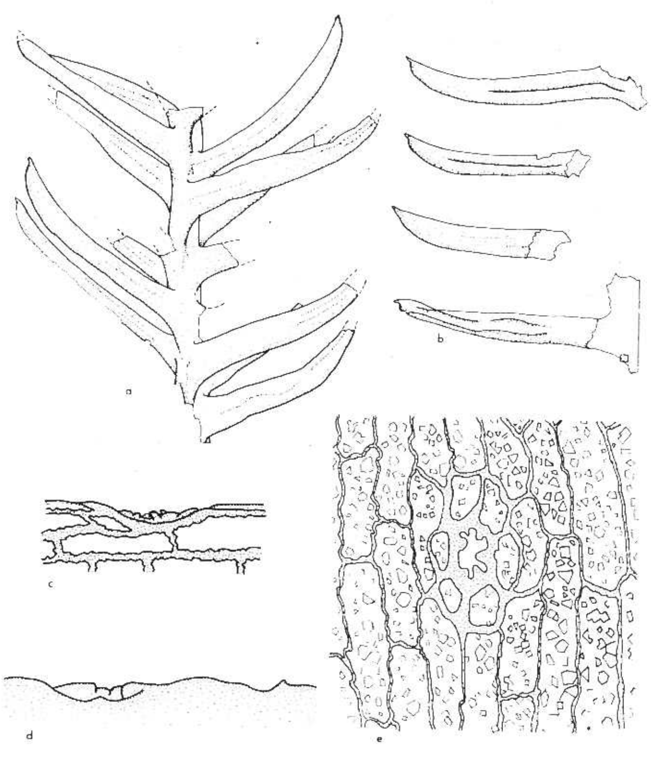

FIGURE 17.—*Pagiophyllum navajoensis* n. sp. a.—Macerated portion of laterally compressed holotype, folds indicated by heavy stippling. Slide USNM 43631a, X3.5. b.—Laterally compressed leaves, folds indicated by heavy stippling. Location of figure 18a shown by small square near base of lowermost leaf. Slides (from top to bottom) USNM 43631e, 43631d, 43631c, all X3.5. c., d.—Stomata near folds in cuticle. Cell walls more clearly visible in 17c than in 17d. Both from slide USNM 43631c, X480. e.—Stoma, pitting indicated by small, angular figures. Guard cells not preserved in this example. Slide USNM 43631b, X480.

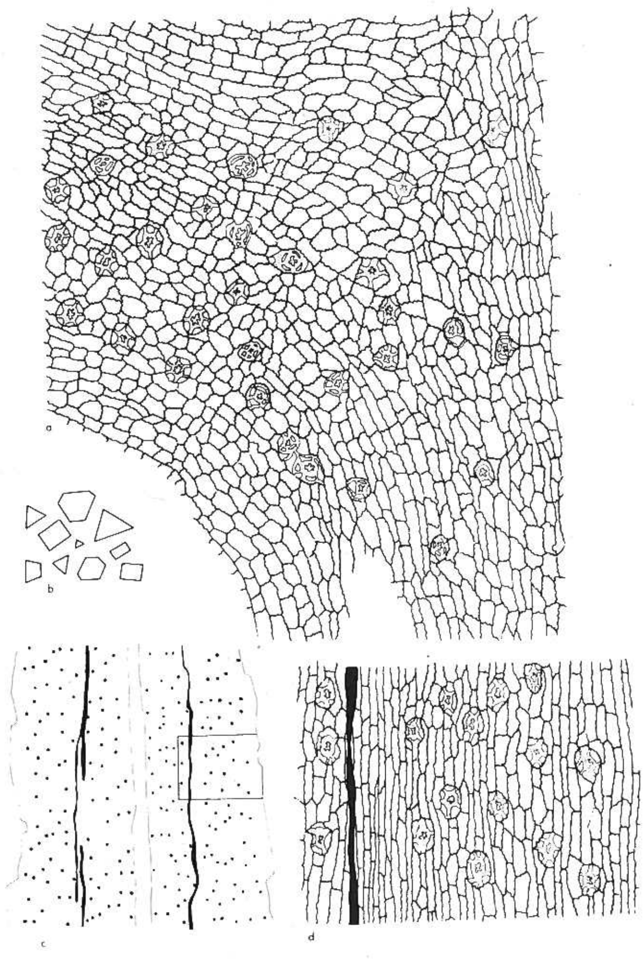

FIGURE 18.—*Pagiophyllum navajoensis* n. sp. a.—Cuticle from base of leaf (to left) and portion of leaf cushion and adjacent axis. From lowermost leaf in figure 17b. Slide USNM 43631c, X70. b.—Selection of pits from one leaf of species. Slide USNM 43631b, X700. c.—Cuticles from adjacent sides of a laterally compressed leaf, each dot represents one stoma, longitudinal folds indicated by broad irregular lines. The location of 14d is shown by rectangle on right side of figure. Slide USNM 43631b, X17.50. d.—Cuticle from free part of leaf shown in 14c, irregularities of anticlinal cell walls shown somewhat diagrammatically. Slide USNM 43631b, X70.

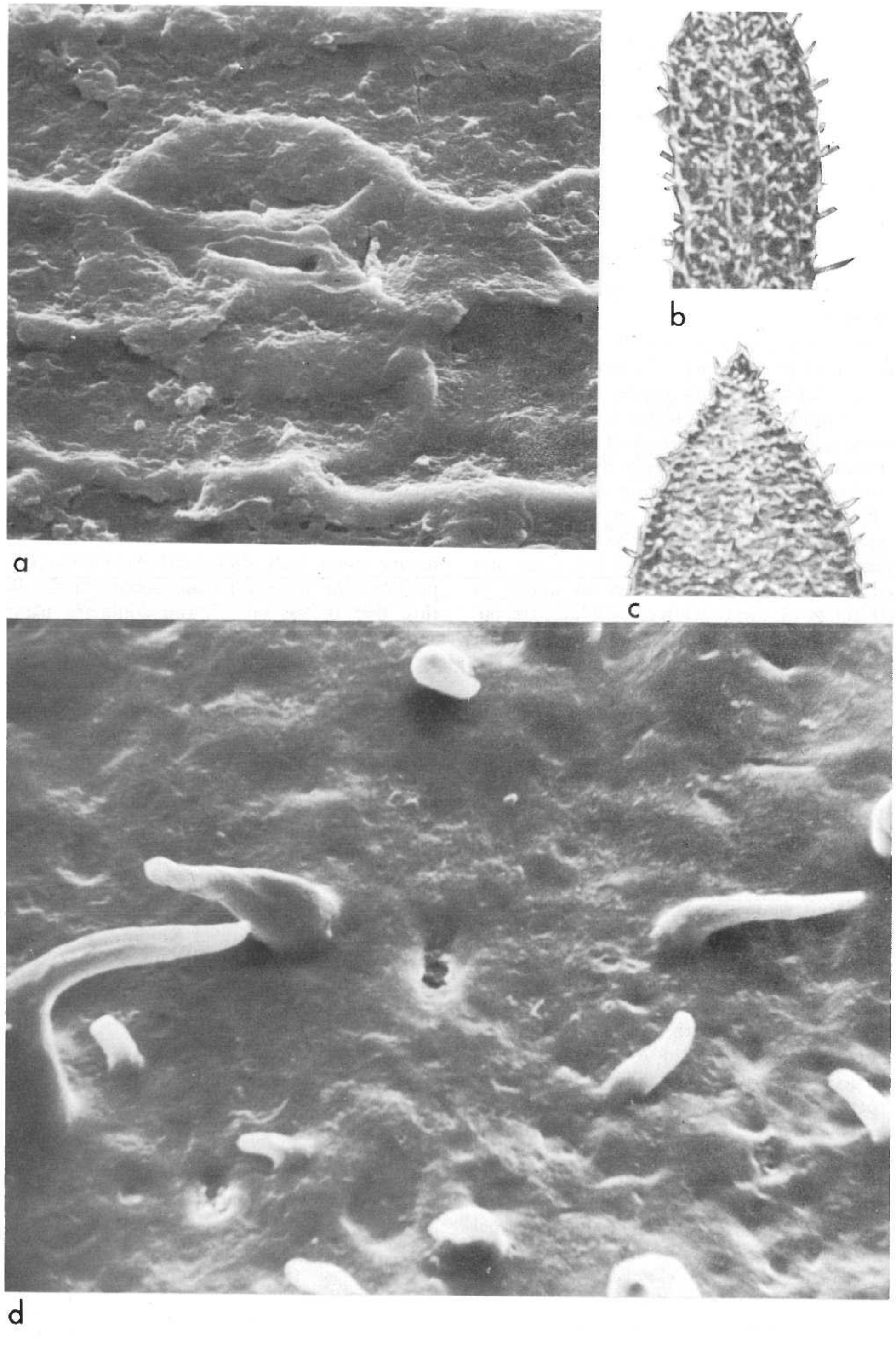

FIGURE 19.–SEM micrographs of *Dinophyton spinosus* Ash. a.–Inner surface of a stoma. Note that aperture is rectangular. Stomatal apertures are also visible in upper left and upper center. Cutinized anticlinal flanges are rounded and somewhat irregularly developed in this species. About X500. b, c–Apices of two leaves. As is typical of species, surfaces of leaves are covered with many unicellular hairs. About X25. d.–Outer surface of cuticle of a leaf. Note rectangular stomatal aperture in center and sharply pointed hairs that occur above ordinary epidermal cells. About X500. All materials from locality FW6.

Uppermost Triassic of Greenland. Angular pits also are known in the leaves of the extant conifers *Sequoiadendron giganteum* (see Florin 1931, pl. 40, fig. 8) and *Dacrydium kirkii* (see Florin 1931, pl. 20, figs. 2-3). In addition one or more living species of *Podocarpus, araucaria* (sect. *Eutaca*), and Tsuga (sect. *Eutsuga*) show such angular pits (Florin 1958). Although angular pits occur in the cuticles of a few other conifers, their distribution is very limited, and Florin (1958, p. 366) believes that they may be of some value in tracing relationships of extinct conifers.

These pits are thought to be due to calcium oxylate crystals embedded in the outer walls of the epidermal cells (Florin 1958, p. 310, 366). I have obtained calcium oxylate crystals by evaporating a solution of powdered calcium oxylate dissolved in dilute hydrochloric acid. The resulting crystals in general resemble at least some of the angular pits observed in the cuticle of *P. navajoensis.*

Comparisons.–The only species in the Chinle flora with which *P. navajoensis* might be confused are *Dinophyton spinosus* and *P. zuniana* n. sp. Leaves of both species are spreading and about the same length, but they are more or less falcate in *P. navajoensis* whereas they are straight in *D. spinosus.* Also the leaves of the present species are generally wider (about 2 mm at base narrowing rapidly to 1 mm a short distance above base) than the leaves of *D. spinosus* (typically slightly less than 1 mm wide at base, narrowing only slightly above base). In *P. navajoensis* leaf apices are more or less acute and unequally narrowed (the lower edge more than the upper) in contrast to the leaf apices of the other species which are obtuse to acuminate and generally equally narrowed. The two species are even more distinct on the microscopic level. For example, in *P. navajoensis* the stomata are amphicyclic and oval (monocyclic and rectangular in *D. spinosus*). Also the periclinal walls of the ordinary and subsidiary cells bear many small angular cavities (totally absent in *D. spinosus*), and the periclinal walls of the ordinary cells do not bear trichomes of any type (sharply pointed hairs often present in *D. spinosus*).

P. zuniana has a smaller shoot but similar leaves. The pitted cuticle of *P. navajoensis* distinguishes it at once, however.

Several conifers have been described that have more or less falcate leaves of about same size as those of the present species. *Pagiophyllum veronense* Wesley (1956) from the Lower Jurassic of Italy is one of these. Its leaves, however, are about twice as wide at the base and are not flattened into the horizontal plane. The two species can be easily differentiated on the microscopic level. In the Italian species the stomata are more or less round (oval in *P. navajoensis*), and the subsidiary cells lack papillae that are present in the new species. Also the periclinal walls of the epidermal cells are smooth in *P. veronense,* not pitted as in *P. navajoensis.* Another Italian species, *P. revoltinum* Wesley (1956), has rather similar leaves except that they have rounded, not acutely pointed, apices. The stomata in that species are round not oval as in the new species. Also the periclinal walls of the epidermal cells are smooth in the Italian species, not pitted.

Shoots of the two species of *Rissikia* Townrow (1967) from the Triassic of South Africa resemble the shoots of *P. navajoensis* in that they all have linear leaves of about the same size and approximate proportions. Also the leaves have spirally arranged, decurrent bases and obtuse apices with acuminate tips. The leaves, however, are much more closely set in *P. navajoensis* than in the two species of *Rissikia.* They are easily distinguished on the microscopic level as the epidermal cells in the South African species have straight side walls (wavy in *P. navajoensis*), and the periclinal walls are smooth (pitted in *P. navajoensis*).

Remarks.–The species is named for the Navajo Indians who have lived for many years in the area where the holotype was collected.

Material.–Holotype: USNM 43632a-e.

Distribution.–*P. navajoensis* is known only from the Ciniza Lake Beds in the Monitor Butte Member of the Chinle Formation at USGS fossil plant locality 10091, Fort Wingate, New Mexico.

Order Uncertain

Dinophyton spinosus Ash, 1970

(figs. 2f, 2g, 19)

1967 Gymnospermous shoot. Ash, p. 128–30, fig. 3.

1970b *Dinophyton spinosus* Ash, p. 651–63, pls. 122–24, text-figs. 1–6.

1972a *Dinophyton spinosus* Ash, p. 39–40, fig. 2f, pl. 1, nos. 2,3.

1972b *Dinophyton spinosus* Ash, p. 127, figs. 2D, E.

Remarks.–This problematical plant was described (Ash 1970b) in considerable detail, and nothing need be added to that description. Some SEM micrographs of the species, however, are included here as none have ever before been published.

D. spinosus is represented in the lake beds by many fragments of the leafy shoot and the pinwheel structure. This is probably the most abundant species in the lake beds, suggesting that it was one of the dominant plants near the lake and elsewhere in the region.

Material.–USNM 172334, 172335.

Distribution.–Since the publication of my 1970 report, *D. spinosus* has been found at a new locality in the Upper Triassic Santa Rosa Sandstone of the Dockum Group near Santa Rosa, New Mexico (Ash 1972b) and at a locality in the Monitor Butte Member of the Chinle Formation in southern Utah. Consequently the species is now known from 12 localities in the Upper Triassic rocks of the Southwest.

Acknowledgments

I am indebted to Professor T. M. Harris and Dr. P. D. W. Barnard, University of Reading, who have read this chapter and made many useful suggestions. Research support by the Earth Sciences Section, National Science Foundation, Grant GA-25620.

REFERENCES CITED

Adams, A. W., 1951, *Pagiophyllum gracillimum* sp. nov., a conifer from the Yorkshire Jurassic: Ann. Mag. Nat. History, v. 12, ser. 4, p. 1132–40.

Arnold, C. A., 1947, An introduction to paleobotany: New York, McGraw-Hill, 433 p.

——, 1956, Fossil ferns of the Matoniaceae from North America: Paleo. Soc. India Jour., v. 1, p. 118–21, pl. 16.

——, 1964, *Cordaites*-type foliage associated with palm-like plants from the Upper Triassic of southwestern Colorado: Indian Bot. Soc. Jour., v. 42A, p. 4–9, pl.1.

Ash, S. R., 1966, The Upper Triassic Chinle flora of the southwestern United States: Ph.D. dissert., Univ. Reading, Reading, England, 212 p.

——, 1967, The Chinle (Upper Triassic) megaflora of the Zuni Mountains, New Mexico: New Mexico Geol. Soc. Guideb., 18th Field Conf., p. 125–31.

——, 1970a, Ferns from the Chinle Formation (Upper Triassic) in the Fort Wingate area, New Mexico: U.S. Geol. Surv., Prof. Paper 613-D, p. D1–D52.

——, 1970b, *Dinophyton,* a problematical new plant genus from the Upper Triassic of the southwestern United States: Palaeontology, v. 13, p. 646–63.

———, 1972a, Plant megafossils of the Chinle Formation: In Breed, C. S., and Breed, W. A., Symposium on the Chinle Formation: Mus. Northern Ariz. Bull. 47, p. 23-43.

———, 1972b, Upper Triassic Dockum flora of eastern New Mexico and Texas: New Mexico Geol. Soc., Guidb., 23rd Field Conf., p. 124-28.

———, 1974, Upper Triassic plants of Cañon del Cobre, New Mexico: New Mexico Geol. Soc. Guideb., 25th Field Conf., p. 179-84.

———, 1975, *Zamites powelli* and its distribution in the Upper Triassic of North America: Palaeontographica, v. 149, pt. B, p. 139-52.

Berry, E. C., 1912, American Triassic *Neocalamites*: Bot. Gaz., v. 53, p. 174-75.

———, 1927, Cycads in the Shinarump Conglomerate of southern Utah: Washington Acad. Sci. Jour., v. 17, p. 303-7.

Bock, W., 1969, The American Triassic flora and global distribution: Geol. Cen. Res. Ser., v. 3 and 4, 406 p.

Bose, M. N., 1955, On two new conifers from the Jurassic of Yorkshire: Annals Mag. Nat. History, 12th ser., v. 8, p. 111-20.

Daugherty, L. H., 1941, The Upper Triassic flora of Arizona: Carnegie Inst. Washington Pub. 526, 108 p.

Dutton, C. E., 1885, Mount Taylor and the Zuni Plateau (New Mexico): U.S. Geol. Survey Ann. Rept. 6, p. 105-98.

Florin, R., 1931, Untersuchungen zur stammesgeschichte der Coniferales und Cordaitales: Kungl. Svenska Veten. Handb., v. 10, no. 1, 588 p.

———, 1933, Uber *Nilssoniopteris glandulosa* n. sp., eine Bennettitaceae aus der Duraformations Bornholms: Ark. Bot., v. 25A. p. 1-19.

———, 1958, On Jurassic taxads and conifers from northwestern Europe and eastern Greenland: Acta Horti Bergiana, v. 17, no. 10, p. 259-402.

Fontaine, W. M., 1883, Contribution to the knowledge of the older Mesozoic flora of Virginia: U.S. Geol. Survey Mon. 6, 144 p.

Fontaine, W. M., and Knowlton, F. H., 1890, Notes on Triassic plants from New Mexico: U.S. Natl. Mus. Proc., v. 13, p. 281-85.

Genkina, R. Z., 1966, Fossil and flora stratigraphy of the lower Mesozoic deposits of the Issyk-Kul basin (northern Kirghizia): HAYKA, Moscow 148 p. In Russian.

Halle, T. G., 1908, Zur Kenntnis Mesozoichen Equisetales Schwendens: Kgl. Svenska vetenskapskad. handlingar, v. 43, p. 1-40.

Harris, T. M., 1931, The fossil flora of Scoresby Sound, east Greenland, part 1: Cryptogams (exclusive of Lycopodiales): Medd. Gronland, v. 85, no. 2, 102 p.

———, 1932, The fossil flora of Scoresby Sound, east Greenland, part 2: Description of seed plants incertae sedis together with a discussion of certain cycadophyte cuticles: Medd. Gronland, v. 85, no. 3, 133 p.

———, 1935, The fossil flora of Scoresby Sound, east Greenland, part 4: Ginkgoales, coniferales, lycopodiales, and isolated fructifications: Medd. Gronland, v. 112, no. 1, 176 p.

———, 1961, The Yorkshire Jurassic flora, I, Thallophyta-Pteridophyta: British Mus. (Nat. Hist.), 212 p.

———, 1969a, Naming a fossil conifer: Bot. Soc. Bengal, Sen. Mem. vol., p. 243-52.

———, 1969b, The Yorkshire Jurassic flora, III, Bennettitales: British Mus. (Nat. Hist.), 186 p.

Kendall, M. W., 1948, On six species of *Pagiophyllum* from the Jurassic of Yorkshire and southern England: Annals Mag. Nat. History, 12th ser., v. 1, p. 73-108.

Martin, W. C., 1969, Fossil flora of the Rita Blanca Lake deposits: In Anderson, R. Y., and Kirkland, D. W. (eds.), Paleoecology of an Early Pleistocene lake on the high plains of Texas: Geol. Soc. America Mem. 113, p. 101-106.

MacGinitie, H. D., 1953, Fossil plants of the Florissant Beds, Colorado: Carnegie Inst. Washington. Pub. 599, 198 p.

———, 1969, The Eocene Green River flora of northwestern Colorado and northeastern Utah: Univ. California Pub. Geol. Sci., v. 83, 140 p.

Oishi, S., 1940, The Mesozoic floras of Japan: Jour. Fac. Sci., Hoddaido Imp. Univ., ser. 4, v. 5, p. 123-480.

Rogers, W. B., 1843, On the age of the coal rocks of eastern Virginia: Trans. Assoc. American Geol. and Nat., 1840-42, p. 298-316.

Schimper, W. P., 1869, Traité de paleontologie végétale, v. 1, p. 610.

Stewart, J. H., Poole, F. G., and Wilson, R. F., 1972, Stratigraphy and origin of the Chinle Formation and related Upper Triassic strata in the Colorado Plateau region: U.S. Geol. Survey Prof. Paper 690, 336 p.

Townrow, J. A., 1967, On *Rissikia* and *Mataia*, podocarpaceous conifers from the lower Mesozoic of southern lands: Pap. Proc. Royal Soc. Tasmania, v. 101, p. 103-36.

Tucker, J. M., 1969, Oak leaves of the Rita Blanca Lake deposits: In Anderson, R. Y., and Kirkland, D. W. (eds.), Paleoecology of an Early Pleistocene lake on the high plains of Texas: Geol. Soc., America Mem. 113, p. 97-99.

Walkom, A. B., 1915, Mesozoic floras of Queensland, part 1: The flora of the Ipswich and Wallon Series, (a) Introduction, (b) Equisetales, with a geological note by Dunstan, B.: Queensland Geol. Survey Pub. 252, 40 p.

Wesley, Alan, 1956, Contributions to the knowledge of the flora of the grey limestones of Veneto, part I: Mems. Inst. Geol. Min. Univ. Padua 19, 68 p.

Zeiller, René, 1903, Études des gîtes mineraux de la France, flore fossile des gîtes de charbon du Tonkin: 320 p.