REPRODUCTIVE BIOLOGY OF THE CERRO CUADRADO (JURASSIC) FOSSIL CONIFERS: PARARAUCARIA PATAGONICA

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ABSTRACT

Seventy-two silicified cone specimens of *Pararaucaria patagonica* Wieland from the Cerro Cuadrado (Jurassic) petrified forest in Patagonia were studied by use of thin sections and reflected light. Traces from the cone axis stele to the bract and ovuliferous scale are separate at their origins. In cross section the abaxially concave ovuliferous scale trace and massive circular bract trace branch half-way out into the cone-scale complex. Two triangular-shaped bundles of fibers follow the scale trace into the laminar part of the ovuliferous scale. Both surfaces of the ovuliferous scale possess hairs which may have assisted in cone closure. Cones typically contain one flattened, winged seed per ovuliferous scale. Multi-layered seed integuments are represented by an inner fleshy layer of large cells filled with a black amorphous material, a sclerotesta consisting of wedges or fan-shaped groups of sclereids oriented at right angles to the seed surface, and a thin, often crushed fleshy layer. Seed wings consist of anastomosing, branched cells resembling glandular hairs and containing many intercellular spaces. Well-preserved polycotyledonous embryos containing up to eight cotyledons are present in several cones. Tissues of the embryo including the shoot apex, calyptroperiblem, hypocotyl, and cotyledons are described. On the basis of anatomical and morphological features, specimens of *P. patagonica* are compared to members of both extant and extinct families of conifers including the Araucariaceae, Taxodiaceae, Pinaceae, Cupressaceae, and Cheirolepidaceae.
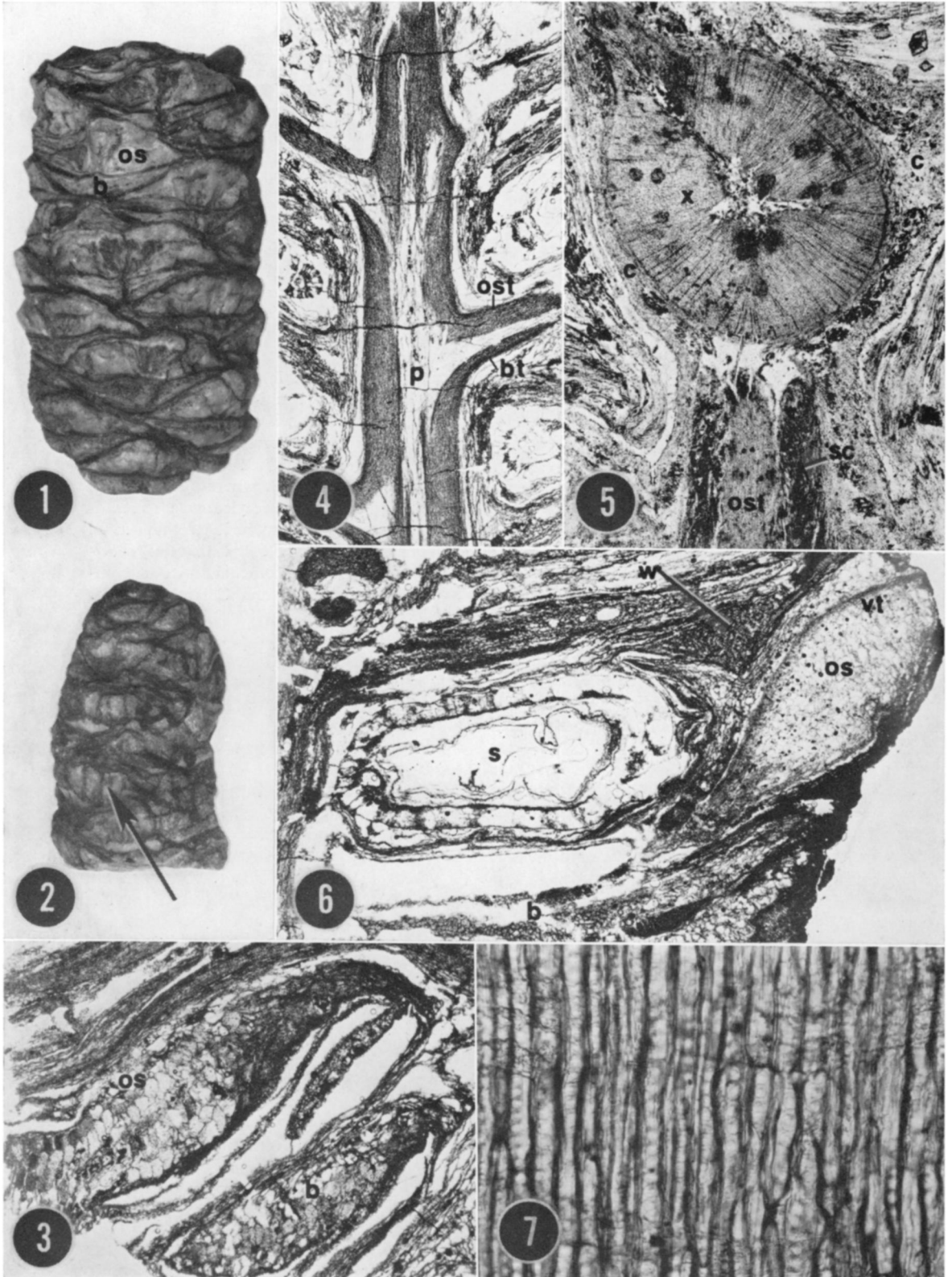
THE CERRO CUADRADO petrified forest in Patagonia (Santa Cruz, Argentina) was initially described by Windhausen (1924). Among the silicified remains found there are twigs with leaf scars, wood, supposed seedlings, and three genera of coniferous cones that were deposited in place by a volcanic ash (Wieland, 1935; Menendez, 1960). Many specimens, principally collected from the three volcanic peaks of the region (Cerro Cuadrado, Cerro Alto, and Cerro Madre e Hija) ultimately became the property of American and European museums. Among these remains is the silicified ovuliferous cone *Pararaucaria patagonica*, first described by Wieland (1929) in a preliminary treatment of the Field Museum of Natural History (Chicago) collection. This cone is the smaller of the two ovulate cones

known from the petrified forest and at first was thought to represent two distinct species, *P. patagonica* and *P. elongata*. In 1935 Wieland demonstrated that the range of characters in specimens of *Pararaucaria* did not warrant the recognition of two species, since the variation within the cones was no more than that occurring in cones of extant *Pinus* species. This initial description was based on 20 cone specimens of the Field Museum collection through the use of polished surfaces (Wieland, 1935). Wieland believed the cone represented a transition form between the Araucariaceae and the Pinaceae based on seed and cone-scale features, and cone vascularization. He placed it in the Cheirolepidaceae, a family of Mesozoic conifers erected by Hirmer and Hörhammer (1934) and emended by Jung (1968).

Calder (1953) emended the generic diagnosis of *Pararaucaria* to fit the range of variation seen in the British Museum collection and employed thin sectioning in addition to studies of polished faces. Structure of the xylem in the cone axis was compared to extant conifer families. In addition, the presence of many cotyledons in the embryo and the winged nature of the seed were reported. Calder placed *Pararaucaria* in the Taxodiaceae because of the great diversity within the family (*sensu* Pilger, 1926) stating that it resembled no one living genus in the combination of characters.

The excellent silica permineralization of these cones offers a rare opportunity to study delicate seed and embryo tissues some of which appear to have cellular contents. The purpose of this paper is to provide a detailed analysis of the cones of *Pararaucaria* with particular emphasis directed at seeds and embryos and to compare these cones with those of several extant as well as extinct conifer families.

MATERIALS AND METHODS—The present study utilizes 72 cone specimens assignable to the fossil taxon *Pararaucaria patagonica* on the basis of external morphology and previously cut surfaces. Thirty-five cones were selected for sectioning based on examination of previous cuts made by earlier workers. Material includes specimens from four collections: The Field Museum of Natural History (Chicago), the British Museum (Natural History) London, Naturhistoriska Riksmuseet (Stockholm), and Orton Museum of Geology (The Ohio State University, Columbus).

The cones are completely silicified and apparently contain little or no organic material. Darrow (1936) pointed out the tendency of cones from these localities to display different colors of quartz replacing different seed tissues. Embryos appear to be replaced by chalcedony, and the space once occupied by the nucellus is filled with a transparent quartz. Some cone specimens appear to be more porous than others, especially between the ovuliferous scale and bract, between sclereids of the stoney layer of the seed, and in the cavity once occupied by nucellus. Most cones are composed of dense α-quartz (Stockey, 1975a). None of the specimens thus far observed are known from a volcanic ash matrix, as is the case for some specimens of *Araucaria mirabilis* (Calder, 1953).

TRA-Bond 2114 Water White Transparent Epoxy Adhesive (TRA-CON, Inc., Medford, Massachusetts) was used for mounting specimens to the glass slides. This epoxy has a refractive index (1.565) close to that of quartz thus giving excellent optical properties. Few cones showed little contrast with most tissues appearing clear-buff in color. Thin sections of these were stained in a 5% aqueous Malachite Green solution (Bartholomew, Matten, and Wheeler, 1970) for 1½ minutes. Details of pitting on the tracheids showed a greater contrast with this technique. Most slides, however, were left unstained and mounted in HSR (Harleco Synthetic Resin).

A number of taxa of conifer seed wings were studied for comparison with those of *Pararaucaria*. These included seed wings of several genera of the Pinaceae, Cupressaceae, Taxodiaceae, and *Agathis australis* (D. Don) Salisbury in the Araucariaceae.

STRATIGRAPHY—The age of the petrified forest is still not accurately determined; however, most workers today follow the interpretations of Feruglio (1949, 1951) who believes that the Cerro Cuadrado sediments have a Middle to Late Jurassic age (Calder, 1953; Menendez, 1960; Stockey, 1975a).

DESCRIPTION—*General features*—Cones vary in shape from conical to cylindrical, sometimes ovoid, and are 5.1–2.3 cm long and 2.6–1.3 cm in diam (Fig. 1). Numerous helically arranged cone-scale complexes are arranged in a ⅗ phyllotaxy around a slender cone axis. Each cone-scale complex is composed of a large, woody ovuliferous scale which is subtended by a smaller woody, flattened bract (Fig. 1, 2). Externally cone-scales resemble those of certain members of the Taxodiaceae, e.g., *Sciadopitys* Siebald and Zuccarini and *Sequoiadendron* Buchholz; however, the bract and ovuliferous scale of *Pararaucaria* are not fused but free for almost their entire length (Fig. 3, 6).

In less weathered specimens (Fig. 2), the outer surface of the ovuliferous scale appears striated. No laminar tip, umbo, or extension of the ovuliferous scale into distinct lobes has been observed. Some cones show evidence of scorched areas or pitting of the ovuliferous scales and distortion due to crushing, suggesting evidence of burial by volcanic ash. In a few weathered cones, seeds with visible internal tissues are exposed. Only four specimens of those examined show pieces of cone peduncle, and all of these appear to have poorly preserved leaves surrounding the axis of the type described by Calder (1953). She figured one British Museum specimen with spirally arranged, broad, lanceolate leaves with striated surfaces that show a sharp transition to fertile scales. No cuticle remains are present.

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Fig. 1–7. *Pararaucaria patagonica.* **1.** External surface of ovulate cone. 031218. × 2. **2.** External surface of less weathered cone. Arrow indicates striation of ovuliferous scale external surface P13988. × 2. **3.** Outermost portions of the cone-scale complex showing large cells with amorphous contents. P139-- I #1. × 25. **4.** Longitudinal section of the cone axis at a level of trace divergence. P13978 A #1. × 7. **5.** Transverse section of cone axis. P13961 #2. × 14. **6.** Longitudinal section of cone-scale complex showing position of seed. P13978 A #2. × 10. **7.** Radial longitudinal section of cone axis with uniseriate circular bordered pits of tracheids. P139-- I #1. × 250. b, bract; bt, bract trace; c, cortex; os, ovuliferous scale; ost, ovuliferous scale trace; p, pith; s, seed; sc, sclerenchyma; w, wing; x, xylem.
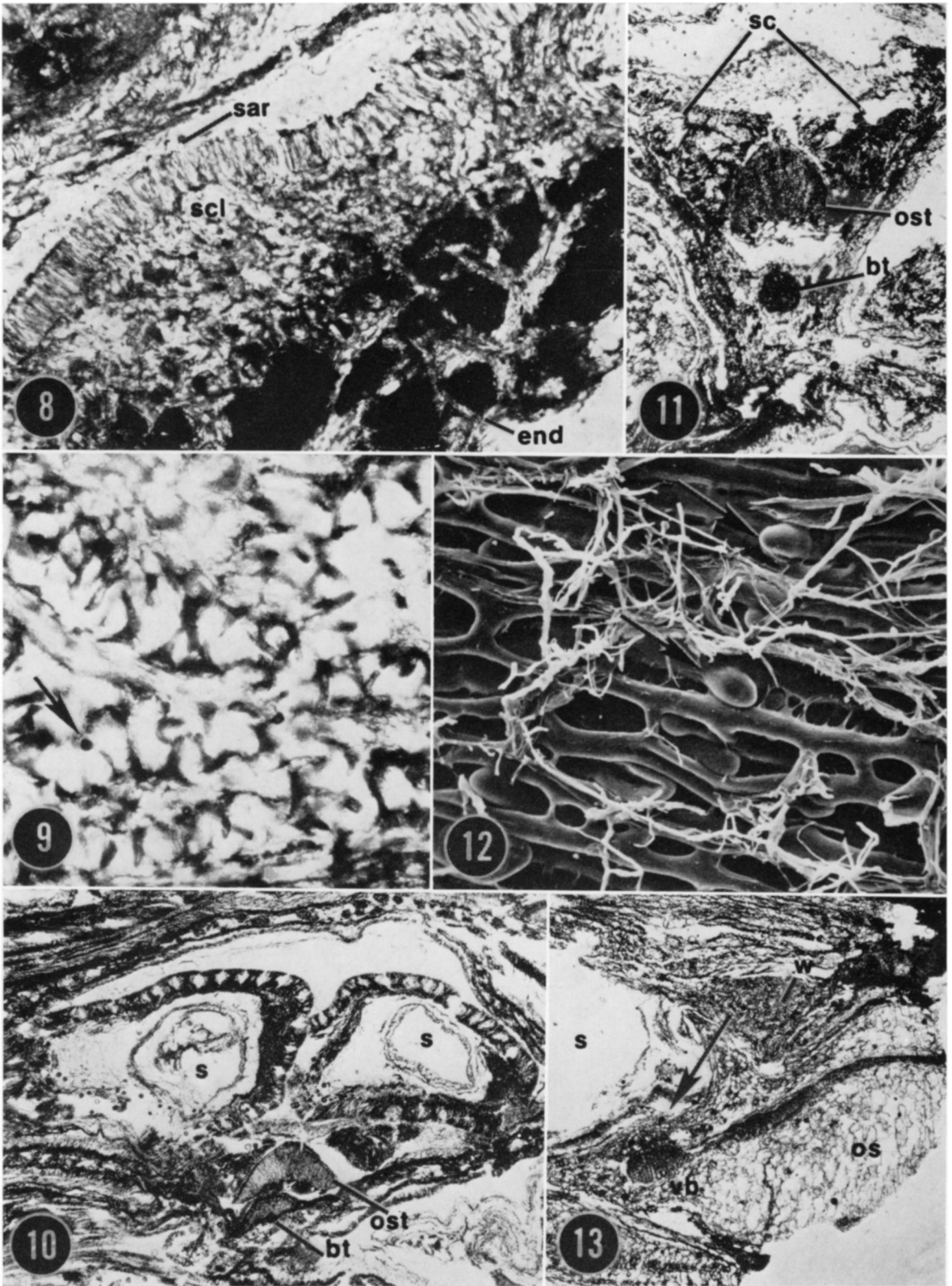
Cone axis—The pith of the cone axis is small (0.5–0.8 mm) and often not well preserved (Fig. 5). Cells appear small, thin-walled, isodiametric (45 μm diam). Some apparent cellular contents and small spherical (5–6 μm diam) structures are common inside the best preserved cones. Larger cells about 65 μm in diam with dark brown contents are scattered throughout the pith. In longitudinal sections small, scattered, square-rectangular sclereids up to 80 μm in diam can be seen. This type of pith structure is similar to that in *Taiwania cryptomerioides* Hayata (Doyle and Doyle, 1948).

Maturation of the primary xylem is endarch. There are helical wall thickenings on the innermost tracheids and these are succeeded by reticulate pitting. Some tracheids show biseriate, circular-bordered pits between the helical bands.

The wide zone of secondary xylem is relatively undissected and composed of small diametered (20–30 μm) tracheids (Fig. 7). Pitting on the radial walls is uniseriate and circular-bordered. Vascular rays range from 1–5 cells high; no ray tracheids were observed. Resin canals and growth rings are absent. Crushed cells, often appearing in radial rows to the outside of the xylem, may constitute a zone of cambium, secondary phloem, and cortex (Fig. 5). In the outer cortical region are groups of thick-walled fibers that follow the vascularization of the cone-scale complex out into the ovuliferous scale (Fig. 5, 11).

Cone-scale complex—Traces to the bract and its associated ovuliferous scale are separate at their origins from the axis stele (Fig. 4). Thick woody bracts each with one large vascular trace are characteristic of *Pararaucaria*. The bract is free from the associated ovuliferous scale for most of its length and is fused near the cone axis. Each bract trace is circular to oval in cross section for about half the length of the bract. Farther out in the bract and ovuliferous scale are numerous isodiametric tracheids with circular-bordered pits linking the vascular strands, making up what Calder (1953) refers to as a bulky transfusion tissue. The outer tissues of the bract and scale contain large cells 120–180 μm in diam that are filled with brown amorphous contents (Fig. 3). Both surfaces of the bract appear to be smooth.

The abaxially concave ovuliferous scale trace is formed by the fusion of two separate strands that bend 180° and results in the protoxylem directed toward the bract trace on the abaxial surface of the bundle. As the ovuliferous scale trace departs from the axis stele it is accompanied on the adaxial side by two massive, triangular-shaped sclerenchyma strands that follow the trace out into the ovuliferous scale (Fig. 5, 11). These sclerenchyma strands originate from the dissection of one mass of sclerenchyma in the cortex of the cone axis. They remain in a triangular configuration about half-way out into the scale, spread out laterally, and eventually disappear distally. These sclerenchyma strands contain extremely thick-walled fibers 45 μm in diam.

The upper and lower surfaces of the ovuliferous scale are covered with what appear to have been glandular trichomes. They are short cells that occasionally branch. Similar hairs have been reported by Chowdhury (1961) on the surfaces of scales of *Cedrus*, and it is believed that they function in cone closure after pollination by the production of a resinous substance that hardens to seal the cone closed. No actual resin canals have been found in the bracts or ovuliferous scales of *Pararaucaria*.

Seeds—Tissues of the seeds are well preserved in several specimens. One flattened, winged seed is embedded in the upper surface of each ovuliferous scale (Fig. 6). Seeds are roughly heart-shaped in outline and about 6 mm long.

One seed per cone-scale complex is characteristic of araucarians, hence, the name *Pararaucaria* (Wieland, 1935). Seed integuments are usually represented by wedges or fan-shaped bundles of cells in transverse section (Fig. 10, 17–20). The integument of the seed is multi-layered (Fig. 8) as is common in the Taxodiaceae and the Cupressaceae at later stages of development (Konar and Banerjee, 1963). The innermost cells compose an inner fleshly layer of large cells filled with a black amorphous material which may have been a mucilage or resinous substance in the living seed (Fig. 8).

The stony layer of the seed is composed of many layers of cells (Fig. 8). The inner layer consists of small, rounded sclereids in transverse section that measure 35 μm in diam. They are overlain by a layer of tightly packed radially

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Fig. 8–13. Seed and cone-scale features. **8.** *Pararaucaria patagonica*, seed integument. P13979 #4. × 36. **9.** *P. patagonica*, seed wing. Arrow indicates trichome tip. Note branching of individual trichomes. P13958 #1. × 170. **10.** *P. patagonica*, transverse section of two-seeded cone-scale complex. P13979 side #3. × 12. **11.** *P. patagonica*, tangential section of cone showing vasculature of cone-scale complex. P139-- III A #2. × 22. **12.** *Abies grandis*, seed wing surface. Arrows indicate bulbous tips of cells. × 200. **13.** *P. patagonica*. Arrow indicates seed abscission layer. P13978 B #1. × 12.5. bt, bract trace; end, endotesta; ost, ovuliferous scale trace; s, seed; sar, sarcotesta; sc, sclerenchyma; sc, sclerotesta; vb, vascular bundle; w, wing.
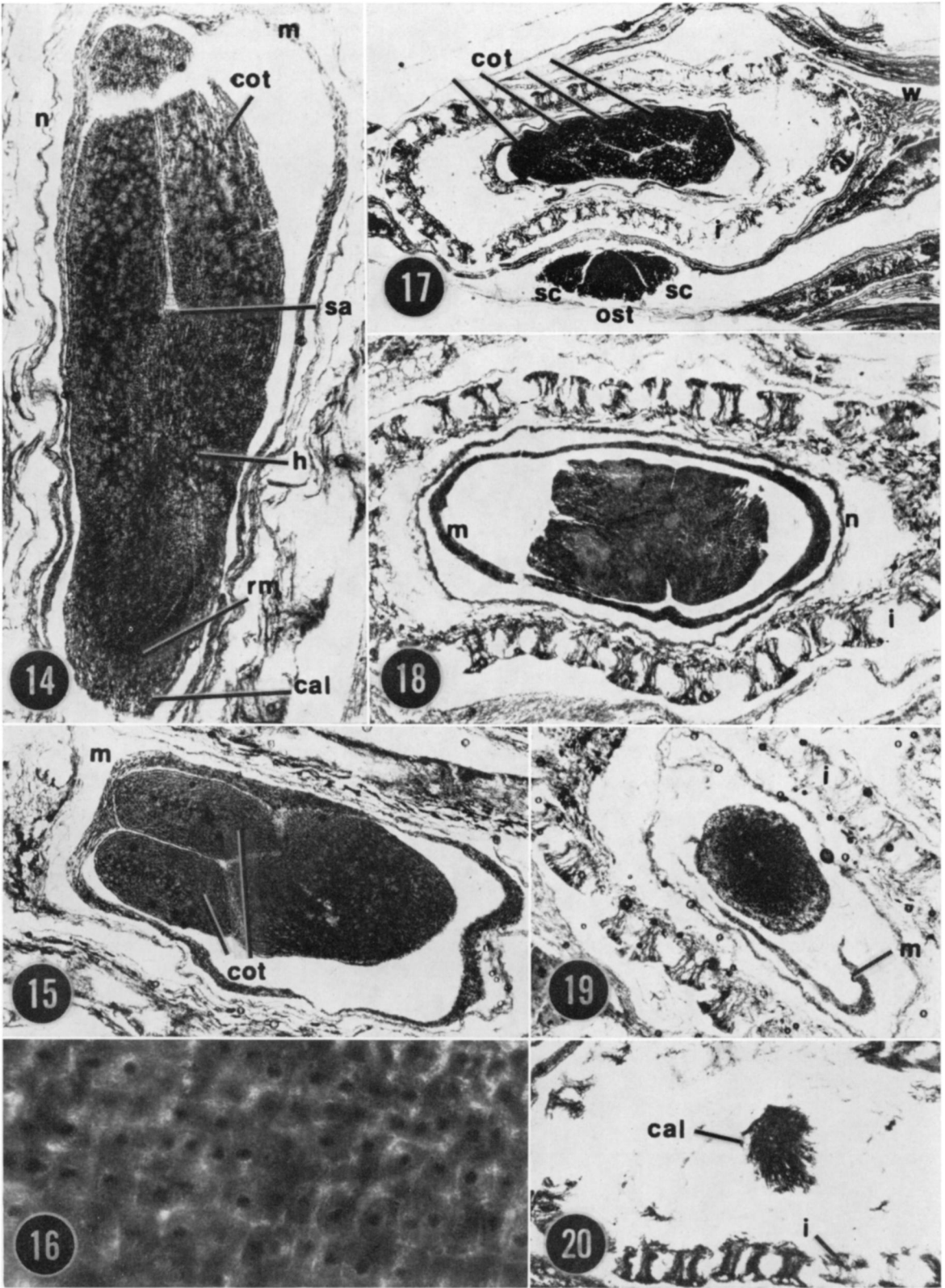
elongate sclereids (65 μm long) which is usually one cell thick. Some seeds show two layers of radially elongate cells in this region. Konar and Banerjee (1963) have reported a similar type of seed integument in the extant *Cupressus funebris* in which sclerotestal cells are rounded sclereids at early stages of seed development and become radially elongate with time. The formation of an additional layer of elongate sclereids in *Cupressus funebris* marks the seed integument at maturity. A surface view of the seed of *Pararaucaria* shows that the sclereids are oriented in longitudinal rows over most of the seed surface and not in isolated groups or bundles. If preserved as a compression fossil, the seed of *Pararaucaria* would probably appear to have a striated surface similar to that reported for seeds of *Elatides williamsoni* by Harris (1943) from the Jurassic of Yorkshire, and *Elatocladus ramonensis* by Lorch (1967) from the Jurassic of Israel.

External to the stony layer are the possible remains of a fleshy layer of cells which appear crushed in most cases (Fig. 8). Cells in this region when they are preserved are 20 μm in diam and relatively thin-walled.

Seed wings are small and measure a maximum of 2 mm in length. They are composed of anastomosing rows of glandular hairs with patches of thin-walled cells and many intercellular spaces (Fig. 9). These hairs are continuous with those on the upper surface of the ovuliferous scale. A similar type of seed wing to that of *Pararaucaria* was found only in *Abies grandis* (Fig. 12) whose surface reveals a series of anastomosing cells, some that end in rounded tips such as those seen in *Pararaucaria* seed wings and on ovuliferous scale surfaces. Most of the other taxa examined have wings composed of 1–3 layers of elongate straight walled cells, or cells with slightly wavy margins with no intercellular spaces or anastomoses. Seeds of *Araucaria* are typically wingless.

The nucellus is preserved in most seeds as a thin layer of crushed cells that attaches only at the seed chalaza. This tissue appears wavy in outline in most seeds.

The megaspore membrane is thin and appears crushed when present. Remains of megagametophyte cells are often present as a few rows of slightly compressed cells (Fig. 14, 15, 18, 19). Cells are 60–90 μm in diam, contain granular appearing cell contents, and often spherical cellular

inclusions up to 5 μm in diam. Cells do not show any evidence of alveoli as in *Taxus* megagametophyte types (Chamberlain, 1935), but do show a regular arrangement of isodiametric thin-walled cells. This type of cell structure would indicate the presence of a *Pinus* type of megagametophyte (Chamberlain, 1935). None of the seeds thus far examined contains solid megagametophyte tissue in which there is no embryo preserved; therefore, the innermost cells of this tissue are unknown. No archegonia have been observed in any of the seeds.

The elongate, slender micropylar tube is oriented toward the cone axis and tangent to it. One vascular strand enters the seed from the distal portion of the ovuliferous scale (Fig. 6, 13). There is a thinning of the stony layer in the region of attachment and a pad of thin-walled parenchyma cells just outside the integuments which Calder (1953) referred to as a possible abscission zone (Fig. 13, arrow). Outside this zone is a group of small diameter tracheids which usually have a lobed, rectangular configuration in cone longitudinal sections (Fig. 13).

Wieland (1935) described a cone of *Pararaucaria patagonica* (*P13939*) that contained two seeds per ovuliferous scale, and in this study another specimen (*P13979*) has also yielded two seeds per scale (Fig. 10). Externally these cones appear identical with some of the larger *Pararaucaria* specimens. Seed integuments, cone vascularization and other features of these cones are indistinguishable from other cones of this taxon, suggesting that such variation occurred within the genus in low frequency. Mitra (1927) and Wilde and Eames (1955) point out variations in seed number in the genus *Araucaria* which has one seed per scale in most cases but in rare instances may have two to three seeds per scale. In cones of *Pararaucaria* with two seeds per scale, there is no massive interseminal ridge as occurs in *Pseudoaraucaria* (Fliche, 1896; Alvin, 1953, 1957a, b).

Embryos—The majority of seeds are sterile; however, where embryos are present, they are exceptionally well-preserved. The embryos of *Pararaucaria patagonica* are well-developed (Fig. 14–20). The shoot apex, cotyledons, hypocotyl, root meristem, and calyptroperiblem are all present indicating that embryos may have been in the

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Fig. 14–20. *Pararaucaria patagonica* embryos. **14.** Longitudinal section of telo-stage embryo. 031217 #1. × 28. **15.** Oblique embryo section with cellular megagametophyte. 031217 #1. × 30. **16.** Embryo tissue with spherical cellular inclusions. 031218 #2. × 300. **17.** Transverse section of embryo with 8 cotyledons. 031218 #4. × 20. **18.** Transverse section of embryo at cotyledonary node. 031218 #2. × 22. **19.** Transverse section of embryo in hypocotyl region. 031217 #2. × 22. **20.** Transverse section of embryo in calyptroperiblem or "root cap" region. 031218 #2. × 25. cal, calyptroperiblem; cot, cotyledon; h, hypocotyl; i, integument; m, megagametophyte; n, nucellus; ost, ovuliferous scale trace; rm, root meristem; sa, shoot apex; sc, sclerenchyma; w, wing.

dormant state when fossilized (Fig. 14). Some cellular remains of the megagametophyte occur around the embryo proper with crushed nucellar tissue surrounding them. There is no provascular tissue apparent in this section, but it does appear to be present in transverse sections of some cotyledons. Cellular detail of the embryo tissue is well preserved. Delicate cell walls as well as cellular contents and small spherical structures (5–6 μm diam) like those in pith cells are present (Fig. 16). The protoderm especially, covering hypocotyl and cotyledons, shows excellent preservation of cell walls and the small spherical structures (Fig. 16). These structures might have represented a number of things in the living state: protein bodies, starch grains, oil globules, other stored food material, condensed cytoplasm, or most probably nuclear material. Their size range and position within the cells would seem to favor the latter view. Additional support for this interpretation is their similarity and presence in a number of different tissues—megagametophyte, embryo, and pith parenchyma cells.

The shoot apex is about 200 μm in diameter at the point of attachment of the cotyledons and has one prominent surface layer of cells also with cellular contents. The hypocotyl extends for a length of 1.8 mm below the shoot apex and cotyledonary node. The generative meristem of the root can be distinguished in the fossil by the change in orientation of the cells from hypocotyl to calyptroperiblem (Fig. 14). The calyptroperiblem or "root cap" (Buchholz and Old, 1933) extends beneath the root meristem for a length of 0.9 mm (Fig. 14, 20). Also apparent in the fossil embryos is the column or columellar region that in living conifer embryos adds cells to the "root cap" by periclinal divisions (Allen, 1947).

Figures 17–20 represent a series of transverse sections taken through the embryo of *Pararaucaria*. Figure 20 represents a transverse section through the tip of the calyptroperiblem in which the cells can be seen converging toward a central point, the column or columellar region. Figure 19 is a section through the embryo hypocotyl, and at a higher level (Fig. 18) through the cotyledonary node. The indication of a three-parted symmetry and the presence of three distinct lobes or cotyledonary primordia are seen in Fig. 18, an embryo which had six cotyledons. Figure 17 shows an embryo with eight cotyledons, probably the result of the dissection of each of four cotyledonary primordia. There are 6–8 cotyledons per embryo, eight being the common number. This cotyledon number corresponds to embryos in the Pinaceae (2–15) and the Taxodiaceae (2–9) (Butts and Buchholz, 1940; Bierhorst, 1971). Araucarians commonly have 2–4 cotyledons per embryo (Burlingame, 1915). No resin canals have been seen in embryo transverse sections as

have been described in the hypocotyl of *Araucaria mirabilis* from this locality (Stockey, 1975a).

DISCUSSION—With the advent of more recent investigations of living and fossil conifers, and in particular cone vascularization and resin canal distribution (Miller, 1969, 1970, 1972, 1973, 1974a, b, 1976; Miller and Robison, 1975), it is possible to compare more thoroughly this fossil genus with those of both extant and extinct conifer families. Historically, *Pararaucaria patagonica* has been placed in a number of conifer families by different authors. Wieland (1935) believed it to be intermediate between the Pinaceae and the Araucariaceae on the basis of seed number, large expanded cone-scale complexes, and cone vascularization. Calder (1953) placed it in the Taxodiaceae based on a combination of characters including the large conspicuous bract and ovuliferous scale, lateral seed attachment, winged nature of the seed, and cotyledon number. Archangelsky (1968) placed *Pararaucaria* in the Cheirolepidaceae (Hirmer and Hörhammer, 1934) a family of Mesozoic conifers containing about six genera. Wieland (1935) suggested the Cheirolepidaceae for *Pararaucaria* due to the peculiar combination of characters of the cone. *Hirmerella münsteri* (Schenk) Jung comb. nov. (= *Cheirolepidium muensteri* (Schimper) Takhtajan) and *Tomaxellia* Archangelsky contain two seeds per scale. *Pararaucaria* has one or two seeds per scale, the usual number being one. Members of the Cheirolepidaceae, however, are characterized by having prominently lobed cone-scale complexes. Since most of the specimens of *Pararaucaria* studied thus far have undergone some weathering, the tips of the ovuliferous scales or cuticle are not present for comparison. In cones where there is a large portion of the ovuliferous scale present the scale appears striated and unlobed (Fig. 2). Compressed cones of *Tomaxellia* have the same general dimensions as those of *Pararaucaria*, but shed their scales and retained their seeds at maturity like extant araucarians (Archangelsky, 1968).

Calder (1953) in a table of positive correlation with some families and genera of Coniferales, compared *Pararaucaria* to the extant Araucariaceae, Pinaceae, Taxodiaceae, and Cheirolepidaceae. Many characters were difficult to correlate to any degree because of the types of information available due to differences in preservation type among the fossils and the current state of knowledge of living conifers. Members of the Cheirolepidaceae, for example, are preserved as compressions with cuticular remains and are difficult to compare in many cases with the petrified remains of *Pararaucaria*.

Externally, the cone resembles genera of the Taxodiaceae, in particular *Sciadopitys* and *Se-*

quoiadendron. The degree of fusion of the bract and ovuliferous scale is more pronounced in these genera which show prominent bracts (Hirmer, 1936). The Pinaceae, on the other hand, are usually characterized by an inconspicuous bract (Hirmer, 1936; Miller, 1976). The ovuliferous scale of *Pararaucaria* is the dominant structure within the cone-scale complex. This feature, unlike the situation seen in araucarians, is similar to that in the Pinaceae and the Taxodiaceae. Eames (1913) points out that bract or scale dominance is a character that varies in the Taxodiaceae, in particular in the genus *Athrotaxis* Don. Within this genus, *A. cupressoides* Don shows an ovuliferous scale larger than the bract, *A. laxifolia* Hooker has a scale equal in size to the bract, and *A. selaginoides* Don has a bract larger than the ovuliferous scale. Miller (1976) also points out that in the Pinaceae superficial appearances of fossil cones are of limited value and can be highly misleading.

Romeroites, a genus of taxodiaceous cones from the Neuquen province of Argentina (Spegazzini, 1924), is a structurally preserved cone described from a single cone specimen and some fragments. The dimensions and external appearance are very similar to those of *Pararaucaria* which prompted Florin (1940, 1944) to suggest that the two might be identical. Internal structure reveals, however, many-seeded ovuliferous scales, orthotropous seeds, and a bract and scale that are reportedly fused for a greater part of their length.

Cone vascularization interpreted by Wieland as being like *Pinus,* and by Calder (1953) as being like the Pinaceae, *Araucaria* (section *Bunya*), and some Taxodiaceae was never really studied in detail. In *Pararaucaria,* the ovuliferous scale and bract traces are separate at their origins from the axis stele. The general configuration is unlike that of *Pinus* and certain *Pityostrobus* but is similar to *Pseudoaraucaria* and other genera of the Pinaceae. The ovuliferous scale trace has the abaxially concave configuration like that of a pinaceous cone (Miller, 1976, Fig. 1) and unlike that of taxodiaceous or araucarian forms (Radais, 1894; Worsdell, 1899; Aase, 1915; Hirmer, 1936). The bract trace is stout unlike most pinaceous genera, except *Pseudoaraucaria* and some *Pinus* species (Miller, 1976). It splits and becomes extensive as in many cones of the Taxodiaceae (Eames, 1913; Radais, 1894).

Seed numbers are similar to the Araucariaceae. The Taxodiaceae usually have 3–5 seeds per scale, although as few as two and as many as nine seeds per scale have been reported (Bierhorst, 1971). The extant genera of the Pinaceae are characterized by two seeds per scale.

Many-layered seed integuments are known to occur in the Taxodiaceae and Cupressaceae. *Pararaucaria* shows some resemblance to *Cupres-*

sus funebris described by Konar and Banerjee (1963) in numbers and appearance of sclerotestal layers. The fossil *Cunninghamiostrobus hueberi* (Taxodiaceae) was also described as having a multi-layered seed integument (Miller, 1975). The holotype (*USNM #31639*) was reexamined in this study and revealed a similar structure to the integuments of *Pararaucaria* in longitudinal section. The sclerotesta contains a layer of radially elongate sclereids surrounding a region of isodiametric sclereids. The presence of two radially elongate rows of sclereids, a feature which indicates a later developmental stage in *Cupressus* and other genera, was observed in one seed. *Cunninghamiostrobus* seeds do not, however, show a ribbed integument or prominent sclereid groupings.

The general shape of the seed itself is similar to pinaceous types. The distal extent of the wing is not known for certain because many cones of *Pararaucaria* have undergone some weathering; however, the maximum seed wing length appears to have been approximately 2 mm. The one character which Calder believed might indicate affinities for *Pararaucaria* outside the Taxodiaceae is seed development. Taxodiaceous seeds are free throughout their development from the fertile scale except in the basal region (Pilger, 1926). Pinaceous seeds are not free during development, their wings being derived from ovuliferous scale tissue. Most *Pararaucaria* seeds studied by Calder (1953) and in this investigation are separated from the scale except at the chalaza. The similarity of the seed wings to the upper scale surface, however, and the attachment of the wings in some cones to the ovuliferous scale would indicate that developmentally the wing probably arose from the ovuliferous scale tissue. Calder (1953) believed that if *Pararaucaria* could be shown to have pinaceous seed-wing development that it should be placed within a new family intermediate between the Pinaceae and the Taxodiaceae.

Structure of the seed wings is similar to that of pinaceous genera such as *Abies.* The anatomosing stellate sclereids which Calder (1953) compares to the "cellules étoilées" of *Abies nordmanniana* described by Radais (1894) are here interpreted as glandular, hair-like trichomes similar to those found in *Cedrus* by Chowdhury (1961), which also occur on the surfaces of the ovuliferous scale and from which the wings are derived. They may have functioned in cone closure after pollination by the production of resinous substances as they do in *Cedrus.* Of the 20 taxa of pinaceous seed wings figured by Tubeuf (1892), only *Pinus wallachiana* A. B. Jackson (= *P. excelsa* Wallich) and *Cedrus libani* A. Richard showed cells of the seed wing that appear to anastomose and to contain some intercellular spaces. A similar structure occurs in

Abies grandis seed wings (Fig. 12). Seed wings of other species have cells with straight or wavy margins and no intercellular spaces.

The structure of the embryo is similar to that of other living conifers at the telo-stage period of development (Schopf, 1943). No leaf primordia have been observed in shoot apices as occur in *Cedrus* (Buchholz and Old, 1933). All the typical features of a conifer embryo at this developmental stage are present: shoot apex, cotyledons, root meristem, hypocotyl, and calyptroperiblem or "root cap." Cotyledon number is similar to that in the Pinaceae and Taxodiaceae. The most common number of cotyledons is eight in *Pararaucaria*; although, six cotyledons are present in some embryos. The transverse section in Fig. 18 is the cotyledonary node of an embryo with six cotyledons. The three segments or lobes of embryo tissue represent the number of cotyledonary primordia in *Pararaucaria*. Lobing at the cotyledonary node is known to indicate the numbers of cotyledonary primordia, for example in *Larix* (Schopf, 1943, Fig. 73, 77). Three or four lobes are common in *Pararaucaria*. In Buchholz's (1919) studies of pinaceous embryos he found that several genera show a fusion of cotyledonary primordia to give the numbers of cotyledons seen in the mature state. Many showed no cotyledonary fusion and none showed the splitting of cotyledonary primordia to give the numbers of cotyledons seen in the mature embryo. In *Pararaucaria*, however, the three cotyledonary lobes probably represent the number of cotyledonary primordia that, upon dichotomizing, resulted in the six cotyledons seen in such embryos. Thus *Pararaucaria* is different than Buchholz's pinaceous genera in this feature. Cotyledon asymmetry observed at the cotyledonary node in *Pararaucaria* (Fig. 18) is the common case in embryos of the Pinaceae (Buchholz, 1919).

Polycotyledony in *Pararaucaria* is noteworthy, since this condition for conifer embryos existed concomitant with the dicotyledonous condition in *Araucaria mirabilis* (Stockey, 1975a). The suggestion that polycotyledony in conifers gave rise to the dicotyledonous condition (Buchholz, 1919) will have to be re-examined in fossils from sediments older than the Jurassic Cerro Cuadrado deposits.

Of some interest are the two triangular shaped strands of sclerenchyma arising in the cortex of the cone axis of *Pararaucaria* that accompany the ovuliferous scale trace on its adaxial face into the distal part of the scale. Miller (1970) reports a dense tissue of sclereids, filling the gap between the traces of the bract and scale and following the traces out into the cone-scale complex of *Picea diettertiana*. Extending through this sclerenchyma are two resin canals. The number varies from 2–13 in the genus *Picea*. There are no resin canals associated with the sclerenchyma of *Pararaucaria*. Their peculiar triangular configuration and persistence in the scale is unknown in other conifer genera. Calder (1953) suggests that these sclerenchyma strands may have been associated with the separation of the scales at maturity and the liberation of seeds. Thus in *Pararaucaria* we not only see evidence of a mechanism for cone closure after pollination by the glandular hairs of the scale surface but also a possible mechanism of cone opening after maturation to effect seed release. *Pararaucaria* probably retained its scales and shed its seeds at maturity like members of the Pinaceae and Taxodiaceae. Evidence that the seeds were in fact released from the scale can be seen directly in the presence of thick, woody bract and scale traces without abscission layers and an abscission layer at the seed chalaza, and indirectly by the absence of isolated cone scales at the Cerro Cuadrado localities.

Fossil ovulate cones of *Pararaucaria patagonica* do not conform to any extinct or extant conifer genus but instead combine a number of features from four or five families of conifers. The one-seeded condition of araucarians is almost the only feature linking it with that group; *Pararaucaria* represents a misnomer suggesting a relationship that probably does not exist (Gothan, 1950).

The systematic position of *Pararaucaria* would also appear to be more Pinaceae centered than has been thought by previous workers. This idea corresponds partially to what Wieland (1935) originally suggested. Pinaceous characters include vascularization of the cone-scale complex, seed wing features, cotyledon numbers, and secondary xylem pitting. Seed integuments are taxodiaceous and cupressaceous. Taxodiaceous characters also include the conspicuous, woody bract and strongly developed bract trace, cotyledon numbers, pith structure, and secondary xylem lacking resin canals. *Pararaucaria* is a petrifaction genus; therefore, comparisons with the Mesozoic Cheirolepidaceae (*Hirmerella* and *Tomaxellia*) are limited.

This study supports Calder's idea that seed number in fossil cones appears to have a limited diagnostic value and that of Miller (1976) that external resemblances of fossil cones are often misleading. Takhtajan (1953) suggests that the Taxodiaceae may have arisen from the earliest primitive Pinaceae. The intermediate position of *Pararaucaria* between the Taxodiaceae and the Pinaceae may lend support to this interpretation. It may, however, suggest the opposite, i.e., the Pinaceae may have arisen from primitive taxodiaceous stock. It is the opinion of this writer that the genus *Pararaucaria* is sufficiently different in the combination of characters to warrant family status, and that further investigations of

Jurassic age conifers will provide the opportunity of placing *Pararaucaria* in the proper perspective with reference to other conifer families.

The excellent silica permineralization of *Pararaucaria* which has allowed developmental interpretations of *A. mirabilis* cone structures from the Cerro Cuadrado localities (Stockey, 1975b), and the large numbers of specimens available, have provided us with information about the reproductive strategies of the plant: the retention of scale, shedding of seeds, possible mechanism for seed dispersal, and mechanism for cone closure after pollination. The polycotyledonous condition is seen to have existed in *Pararaucaria* during the Jurassic and probably came about by the dissection of cotyledonary primordia. Preservation of the delicate embryo tissues, so rare in the fossil record, has allowed direct comparison of the telo-stage embryo of *Pararaucaria* to those of living conifers at a comparable developmental stage.

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