

JURASSIC ARAUCARIAN CONE FROM SOUTHERN ENGLAND

by RUTH A. STOCKEY

ABSTRACT. A well-preserved araucarian cone measuring 4.5 × 5.0 cm is described from Jurassic age limestone from near Osmington Mills, Dorset. Four pieces of cone material representing a single specimen are somewhat flattened and lignitic, with intact seed and cone-scale tissues. The cone axis and bract apophyses are replaced with a calcitic matrix. Helically arranged cone-scale complexes with a prominent ligular sulcus surround a wide pith. One recurved wingless ovule 0.8 cm long is deeply sunken into the cone-scale tissue. Seed integuments are relatively mature and contain three distinct layers the most prominent of which is the sclerotesta constructed of interlocking zig-zag sclereids. The nucellus, in some cases still cellular, is free from the integuments except at the chalaza and has the characteristic wavy apex common to extant araucarians at a comparable developmental stage. A well-developed vascular system like that in *Araucaria bidwillii* Hooker is present near the seed chalaza. Cellular megagametophyte and embryos are present within some seeds. The specimen is described as a new species, *A. brownii* sp. nov. in which the cone structure most closely resembles that of the section *Bunya* of the genus *Araucaria*. This discovery extends the range of this section to the Northern Hemisphere during the Mesozoic.

THE Araucariaceae, an extant conifer family with a very restricted distribution, has often been considered primitive among conifer families. Two genera, *Agathis* and *Araucaria*, grow as natives in South America, Australia, New Caledonia, New Guinea, and a few South Pacific islands. Although the group has only a few relict species today, it was at one time widespread and included numerous species in the Northern Hemisphere during the Mesozoic Era. Araucarian cones display what have been suggested as primitive characters that readily distinguish them from those of other conifer groups (Wieland 1935; Thomson 1905a, 1907, 1913; Eames 1913; Wilde and Eames 1948, 1952; Burlingame 1913, 1914, 1915; Chamberlain 1935; Hirmer 1936; Seward and Ford 1906). The genus *Araucaria*, usually believed to be the more primitive of the two genera, has ovulate cones with large bracts and partially fused ovuliferous scales. *Agathis* exhibits cone-scales composed of completely fused bracts and scales, believed to be a derived condition (Eames 1913). Well-preserved fossil conifer cones of any type are rare; however, a few well-preserved araucarian fossils have been found, and these have revealed important information about the geologic history of this family, its distribution, and reproductive biology (Kendall 1949; Wieland 1935; Darrow 1936; Calder 1953; Stockey 1975, 1977, 1978; Vishnu-Mittre 1954). The uniquely preserved fossil conifer cone reported here is closely compared with other fossil and living araucarians. The information obtained has proved useful in elucidating phylogenetic trends within the family, and in particular, within the genus *Araucaria*.

MATERIALS AND METHODS

The cone was found in 1973 by Mr. P. A. Brown of Dorset in a block of limestone lying on the beach under Black Head, west of Osmington Mills. Specimens are lignitic, in a matrix best described as a compacted bio-pel-micrite with pelecypod shells, fecal pellets, tests of foraminifera, and corals which have all undergone a considerable amount of diagenesis. The recrystallized calcite composing these fragments is held together with a CaCO₃ cement that has infiltrated many of the preserved cone parts including the seeds. Specimens were prepared for study by a modified coal ball peel technique (Joy, Willis, and Lacey 1956) using 76 μm cellulose acetate sheets and by thin sections after epoxy

infiltration of the cut face. Some cone parts were examined after gold sputter coating using an AMR 1000 scanning electron microscope at 20 kV. A few whole seeds and cone fragments were demineralized in 2% HCl overnight and washed in distilled water. These parts were then embedded in glycol methacrylate and sectioned with a rotary microtome after a technique by Robison and Miller (1975).

Since the cone was not found in place its exact age needs some discussion. The area west of Osmington Mills, Dorset, to Black Head where the cone was found consists of cliffs composed of Corallian and Kimmeridge Clay sediments. These correspond to the Oxfordian and Kimmeridgian Stages respectively of the Upper Jurassic (Arkell 1947). The cone most likely comes from the Osmington Oolite Series which is exposed along the shore west to Shortlake. The beds within this series contain several clay layers with nodules, in addition to the oolites and marlstones (Arkell 1947). The matrix surrounding the specimen closely resembles these beds. Its age is therefore certainly Upper Jurassic, and probably Upper Oxfordian.

SYSTEMATIC DESCRIPTION

Order CONIFERALES

Family ARAUCARIACEAE

Genus ARAUCARIA de Jussieu, 1789

Section BUNYA Wilde and Eames, 1952

Araucaria brownii sp. nov.

Plates 83–86

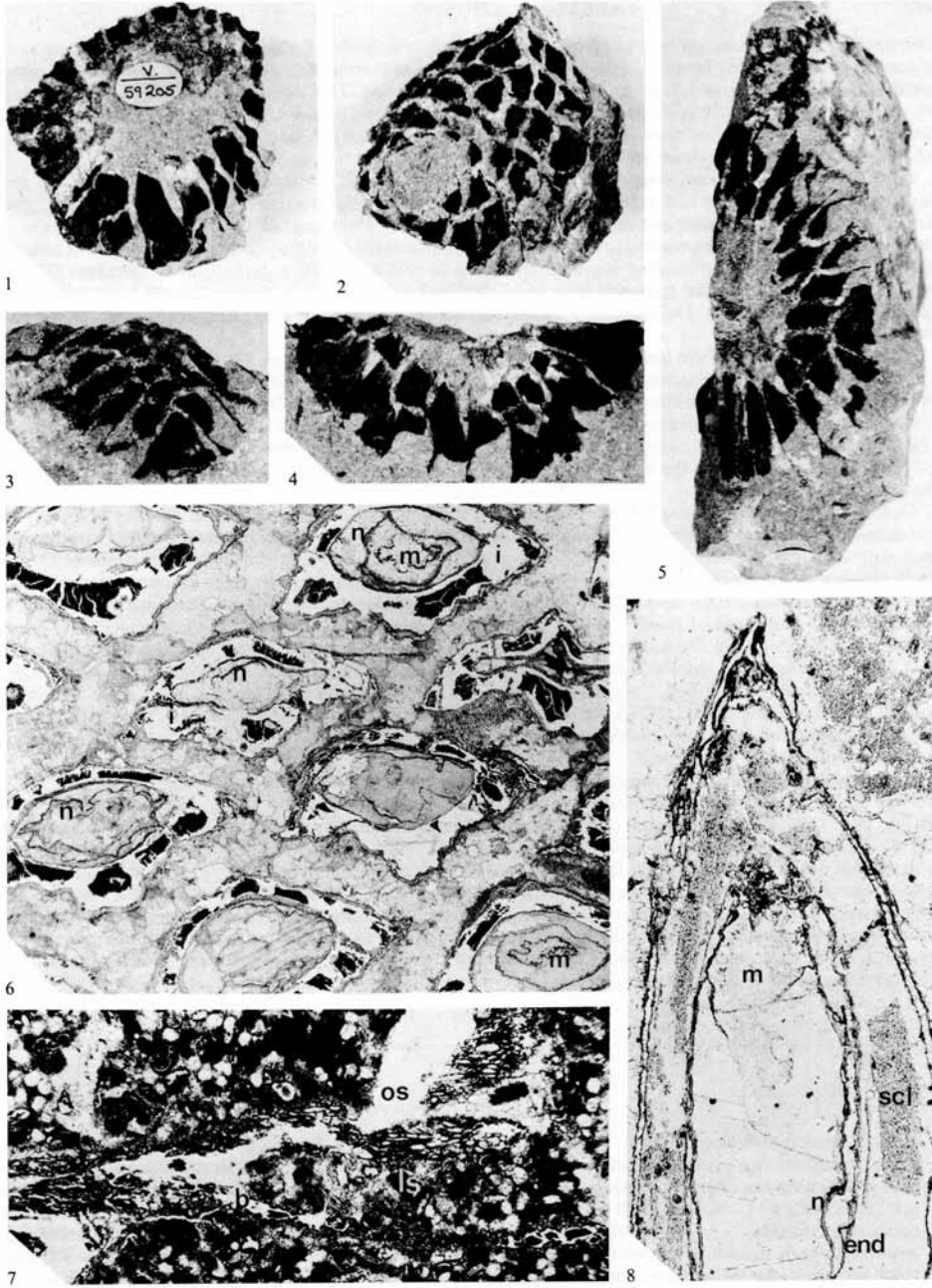
Diagnosis. Ovulate cone, 4.5 × 5.0 cm diameter, pith 1.4 cm diameter near point of attachment to peduncle, expanding to 3.2 cm wide near centre of cone. Cortical resin canals present. Winged cone-scales 1.7 cm long × 1.1 cm wide. Bract and ovuliferous scale free for two-thirds of length, both with a system of resin canals. Ovules 0.8 cm long × 0.3 cm wide, wingless, embedded in ovuliferous scale tissue with micropyle oriented towards cone axis; one seed per cone-scale complex. Seed integuments with prominent branched sclereids of sclerotesta arranged in a zig-zag pattern. Complex system of vasculature at ovule chalaza. Nucellus with wavy apex free from integuments except at base, 0.2 mm thick. Megaspore membrane thin (7 μm) and discontinuous. Megagametophyte composed of polygonal cells 30–50 μm in diameter.

Holotype. British Museum (Natural History) London, V59205, and one fragment housed at Corfe Castle Museum, Dorset.

Etymology. This cone is named after Mr. P. Anthony Brown of Corfe Castle, Dorset who discovered the specimen and made it available for study.

EXPLANATION OF PLATE 83

Figs. 1–8. *Araucaria brownii* sp. nov. Holotype, BMNH V59205 from Osmington Mills, Dorset. *b*, bract; *end*, endotesta; *i*, integument; *ls*, ligular sulcus; *m*, megagametophyte; *n*, nucellus; *os*, ovuliferous scale; *scl*, sclerotesta. 1, cone axis region showing position of ovules, and arrangement of cone-scale complexes, × 1. 2, reverse side of cone in fig. 1, showing cone axis region, rhomboidal cone-scale complexes, and flattened nature of cone, × 1. 3, tangential portion showing seed transverse sections, × 1. 4, cone portion with part of axis and many closely spaced cone-scale complexes, × 1. 5, reverse side of portion in fig. 4, showing limestone nodule matrix and numerous cone-scale complexes with ovules, × 1. 6, V59205 B 25. Cone tangential section with ovule transverse sections. Note large calcite crystals replacing most bract tissue, × 7. 7, V59205 B 21, longitudinal section of cone-scale showing the separation of bract and scale resulting in a wide ligular sulcus, × 23. 8, peel of V59205 B 6, ovule micropylar end showing well-developed seed integuments, megagametophyte tissue and wavy nucellar apex, × 15.



STOCKEY, Araucarian cone

Description. Cone represented by four pieces which are slightly flattened. Plate 83, figs. 1 and 2 show both sides of central portion of cone revealing position of cone axis and numerous helically arranged, seed-bearing cone-scales. Plate 83, figs. 4 and 5 show an external portion of the cone. This piece was attached to that shown in Pl. 83, fig. 1 with an epoxy before sectioning. Plate 83, fig. 3 shows a third cone fragment, a tangential cone piece belonging to the same cone. The remaining part of this specimen was retained by Mr. Brown and is housed at Corfe Castle Museum in Dorset.

Cone measures 4.5 × 5.0 cm in diameter and was probably spherical in shape before burial. Pith of cone axis reaches a width of 3.2 cm and approaches 1.4 cm in the most basal portions. Little organic material preserved in central part of cone, and no peduncle is present in available material. Organic remains are found in some cases in a region corresponding to the cortex of the cone axis (Pl. 86, fig. 6). Small parenchymatous cells are often found in groups surrounding resin canals, some of which contain a dark opaque substance (Pl. 86, fig. 6, arrows). A few isolated tracheids have been identified in the cone axis region; these exhibit scalariform secondary wall thickenings. Unfortunately these tracheids are isolated and their exact position within the axis stele is questionable.

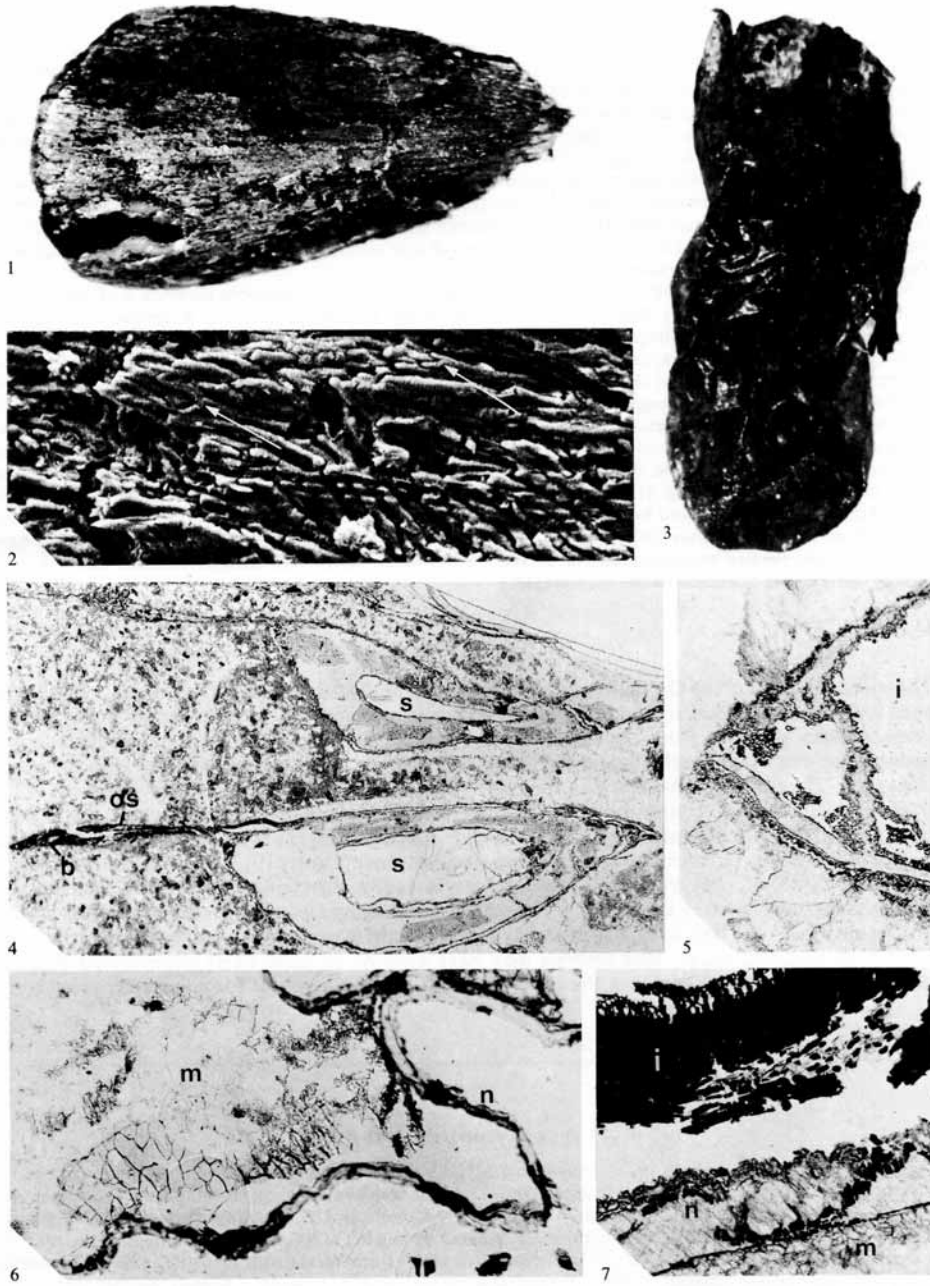
Cone-scales measure 1.7 cm long and 1.1 cm wide, and are distinctly winged. On first examination the cone appears similar in size, shape, and appearance to those of the genus *Agathis* Salisbury. The bract and scale, however, are free for most of their length, a character typical of species of *Araucaria* (Pl. 83, fig. 7). Vascular system of the ovuliferous scales consists of at least four bundles (Pl. 84, fig. 5). Bract apophyses are replaced by coarsely crystalline calcite making vascular bundles generally difficult to observe. There is a system of resin canals in the scale as well as the bract, although their number and placement is difficult to determine because the cone-scales are flattened.

Ovules of *A. brownii* measure 0.8 cm in length by 0.3 cm in diameter (Pl. 84, figs. 1, 4). One wingless seed per cone-scale complex deeply embedded in ovuliferous scale tissue with its micropyle oriented towards the cone axis. Although both *Agathis* and *Araucaria* have one seed per scale, only seeds of *Araucaria* are wingless. Ovules show an advanced state of integumentary development. The sarcotesta, or outer layer, is represented by a thin layer of crushed cells 20 μm thick (Pl. 85, fig. 1). The middle sclerotesta or stony layer is quite thick (up to 0.2 cm) and is composed of thick-walled branched sclereids, each about 30 μm in diameter (Pl. 83, fig. 8; Pl. 84, fig. 2; Pl. 85, fig. 5). These cells are hexagonal in transverse section (Pl. 85, fig. 3) with very small lumens and thick walls. In many cases the walls are no longer distinguishable, but the entire cell, or layer, has been replaced by calcite (Pl. 85, figs. 1, 3). The endotesta, or inner integumentary layer, is thin, up to three cells in thickness and often crushed (Pl. 85, fig. 1). In places where it is present, the cells are short and often barrel-shaped with relatively thin walls (Pl. 85, fig. 2). Integumentary differentiation within the ovules indicates a nearly mature developmental stage.

The non-adnate nature of the nucellus and integument is shown in all of the ovules examined (Pl. 83, fig. 8; Pl. 84, fig. 7). Where well preserved the nucellus has a thick cuticle (Pl. 83, figs. 6, 8; Pl. 84, figs. 3, 6; Pl. 86, figs. 1, 2). It is basally attached to the inner integumentary layer and appears somewhat shrunken (Pl. 86, fig. 2). The nucellar apex appears convoluted as in living araucarians (Pl. 83, fig. 8). In extant plants it protrudes out of the micropyle at the time of pollination and later may retract by drying or by subsequent integumentary growth (Eames 1913). Some authors (Darrow 1936; Eames 1913) have suggested that the convoluted apex was the result of pollen tube damage; however, on examining some living araucarian ovules, a disruption of the apex by pollen tube damage seems unlikely. Plate 85, fig. 4 shows the wavy nucellar apex of the extant *A. montana* Brongn. et Gris. and is typical of most known araucarians at this stage of development. The configuration of the apex appears to represent a drying phenomenon rather than the result of extensive pollen

EXPLANATION OF PLATE 84

Figs. 1-7. *Araucaria brownii* sp. nov. Holotype, BMNH V59205. *b*, bract; *i*, integument; *m*, megagametophyte; *n*, nucellus; *os*, ovuliferous scale; *s*, seed. 1, isolated seed, × 10. 2, paradermal section of sclerotesta cells showing zig-zag cell arrangement. Arrows indicate branched sclereids, × 380. 3, isolated nucellus with apex removed, × 17. 4, V59205 B 6, cone longitudinal section showing sunken nature of seeds within the cone-scale complex, × 7. 5, V59205 B 25 transverse section of ovule showing lateral vascular bundle of ovuliferous scale outside of the seed integuments, × 37. 6, V59205 A 40, ovule transverse section showing thick wavy nucellus and cellular megagametophyte tissue, × 90. 7, V59205 B 26, ovule transverse section showing the relationship of integument, nucellus, and cellular megagametophyte, × 85.



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tube damage. The ease with which the nucellus is removed from isolated ovules is due to its narrow attachment as well as its thick cuticle (Pl. 84, fig. 3). External surface shows little cellular detail while internally outlines of elongate, rectangular cells are visible (Pl. 85, fig. 7).

Ovule attachment and vascularization are difficult to determine with peels. However, thin sections of the chalaza of some ovules where preservation of the bract and ovuliferous scale is partial show a well-developed system of conducting cells (Pl. 86, fig. 5). Using scanning electron microscopy, the chalazal end of each ovule exhibits a series of small holes penetrating the sclerotesta (Pl. 84, fig. 6, arrows), as in the living *A. bidwillii* Hooker. There appears to be what Wilde and Eames (1948, p. 326) term a vascular 'plexus', a complex system of vascularization near the ovule base. Holes in the mature seed integuments correspond to points of entry of numerous vascular bundles. The same type of attachment also occurs in *A. mirabilis* from the Jurassic Cerro Cuadrado Petrified Forest (Stockey 1975).

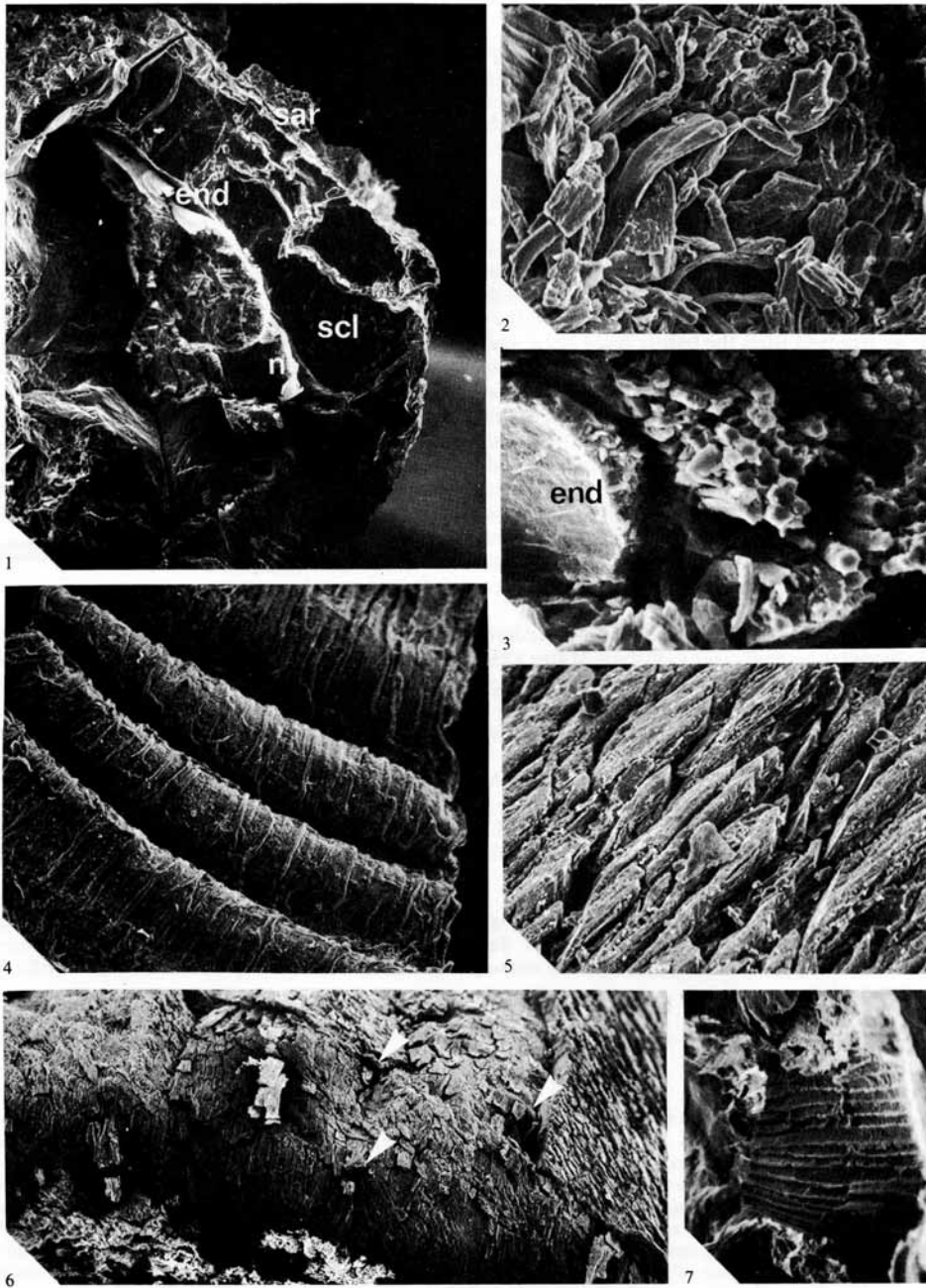
Most ovules show some tissue remains inside the nucellar cavity. The megaspore membrane of some ovules is thin (7 μm) (Pl. 84, fig. 7), and similar to that in living araucarian cones at a comparable stage of development (Eames 1913; Burlingame 1915; Thomson 1905b). Many of the ovules reveal preservation of tissues within this membrane. In most, megagametophyte tissue is either poorly preserved or represented by a free nuclear stage of development at the time of preservation (Pl. 84, fig. 8; Pl. 86, figs. 2, 7). Other ovules show cellular preservation of the megagametophyte (Pl. 84, fig. 6; Pl. 86, fig. 4). These polygonal cells (30–50 μm in diameter) occur in the outer portions of the megagametophyte proper. No ovules have been found with solid megagametophyte tissue preserved within the seed cavity. However, some ovules do show two distinct regions of poorly preserved tissue (Pl. 86, fig. 2). The boundary between the two regions appears to be a discontinuous layer. In other ovules (Pl. 86, fig. 4) the cellular megagametophyte and a centrally located region probably representing the embryo are replaced by calcite. Other specimens contain a four-parted cellular structure that may represent an embryo with four cotyledons (Pl. 86, fig. 3, arrows). An alternate possibility is that this may have been a partially formed megagametophyte at the time of preservation. The seed itself is not crushed, even though parts of the integuments are very crumbly.

DISCUSSION

The spherical shape of the Osmington Mills cone with helically arranged cone-scales, large pith in the cone axis region, cortical resin canals, and presence of one seed per ovuliferous scale are general characteristics of cones from the family Araucariaceae. The presence of a ligular sulcus (space between the ovuliferous scale tip and the bract) and wingless seeds suggest affinities with the genus *Araucaria*. The cone of *A. brownii* was apparently in a relatively mature state of development at the time of fossilization. The appearance of the three-layered integument with a thin sarcotesta, thick sclerotesta composed of elongate branched sclereids, and a thin layer of endotesta composed of thin-walled cells is characteristic of araucarian cones near maturity (Eames 1913; Burlingame 1915; Wilde and Eames 1948; Stockey 1978). The seed contents including the configuration of the nucellus and thin megaspore membrane support this view. A cellular megagametophyte is present with a hollow central cavity (Pl. 86, figs. 2, 4) that probably represents the remains of an embryo rather than free nuclear megagametophyte. This embryo may have aborted or more likely deteriorated prior to preservation since it is likely that the cone remained floating in water for some time prior to its

EXPLANATION OF PLATE 85

Figs. 1–7. *Araucaria brownii* sp. nov. Holotype, BMNH V59205, scanning electron micrographs. *end*, endotesta; *n*, nucellus; *sar*, sarcotesta; *scl*, sclerotesta. 1, ovule transverse section showing three integumentary layers at a late developmental stage, $\times 90$. 2, cells of the endotesta, $\times 425$. 3, transverse section of integument showing hexagonal sclerotesta cells completely replaced by calcite, $\times 400$. 4, *A. montana* Brongn. et Gris., nucellar apex from a mature seed, $\times 100$. 5, surface view of sclerotesta with sarcotesta removed showing elongate interlocking sclereids, $\times 425$. 6, seed chalaza, surface of sclerotesta. Arrows indicate holes of the ovular vascular bundles in the plexus, $\times 90$. 7, elongate nucellar cells, $\times 450$.



STOCKEY, Araucarian cone

burial. Plate 86, fig. 3 may show the cellular remains of such an embryo. Extant araucarian cones, at the time when free nuclear megagametophyte is present (about the time of pollination), show ovules with the integumentary layers of approximately equal thickness with little if any expansion and thickening of the sclerotesta (Wilde and Eames 1948; Stockey 1978).

According to Wilde and Eames (1952) the living genus *Araucaria* may be divided into four sections: *Columbea*, *Bunya*, *Eutacta*, and *Intermedia* based on seedling morphology, foliage type, and cone morphology. The differences in cone structure between the section *Columbea* and the other three sections is distinct, while the differences between the other three are more subtle. The *Columbea* species found only in South America have wingless cone-scales, the bract and scale are nearly completely fused and never separate after the scales are shed from the cone axis. Sections *Eutacta*, *Intermedia*, and *Bunya* have winged cone-scales, those of *Intermedia* being widest, up to 10 cm in *A. klinkii* Lauterb. (White 1947). Seeds in the closely related *Eutacta* and *Intermedia* sections are never removed from the tightly fused bract and scale. The winged cone-scale complex is the unit of dispersal for these species. Seeds from *A. bidwillii*, the only living member of the section *Bunya*, are easily removed from the cone-scales which are more fleshy than those of the *Eutacta* and *Intermedia* sections. These seeds are often dispersed by birds and small animals in Queensland but are easily removed from the cone-scale complex even though the cone disaggregates as in the other species.

A. mirabilis from the Jurassic Cerro Cuadrado Petrified Forest is also included within the Section *Bunya* (Calder 1953; Stockey 1975, 1978). These ovulate cones are only one-third as large as those of *A. bidwillii* at maturity and have winged cone-scales, a zig-zag pattern of sclereids in the sclerotesta of the seed integument, a complex system of vasculature at the seed chalaza, and a dicotyledonous embryo characteristic of *A. bidwillii* (Wilde and Eames 1948; Stockey 1975, 1978). There is some evidence to suggest that these cones shed their seeds and not their scales at maturity (Stockey 1978).

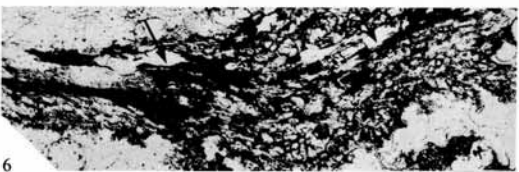
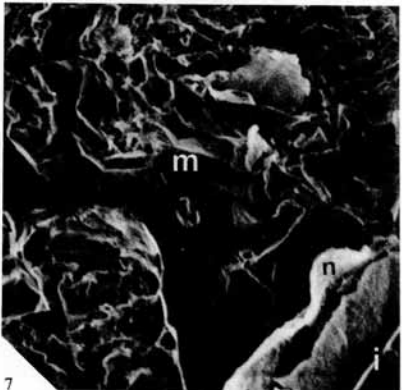
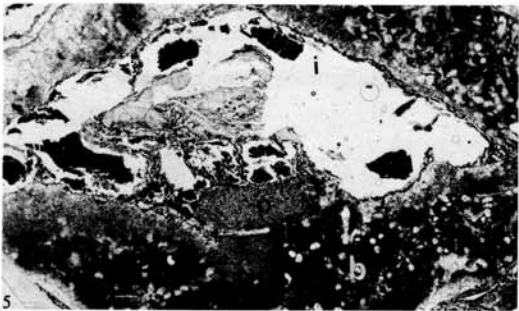
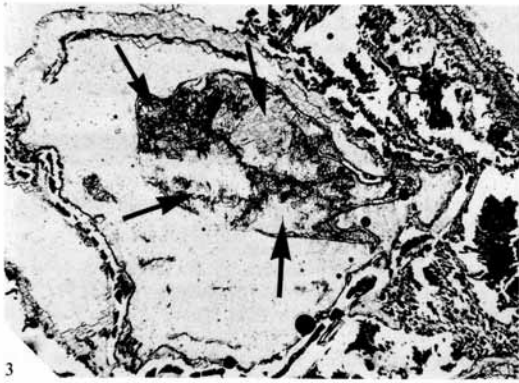
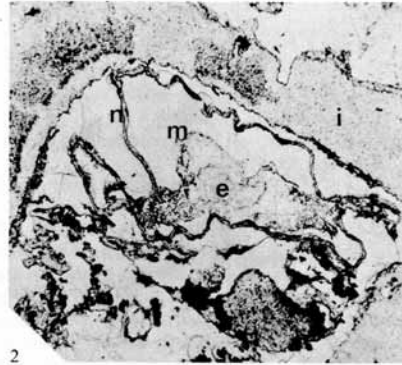
Another ovulate cone which can be considered to be closely related to these three *Bunya* species is *Araucarites bindrabunensis* (Vishnu-Mittre 1954) from the Jurassic of India which shows a slightly larger size than most *Araucaria mirabilis* cones, and is also larger than the cone from Osmington Mills. The origin of the cone-scale complex vascular supply, nature of the winged cone-scales, presence of a ligular sulcus, and vascularization of the ovuliferous scale tip (ligule) place it in the section *Bunya*.

The cone described here from Osmington Mills in Dorset should also be considered under the section *Bunya* of the genus *Araucaria*. The winged cone-scales, zig-zag sclereid pattern and vascular plexus, and deep ligular sulcus are similar to *A. mirabilis* and *A. bidwillii*. These comparisons extend the range of the section *Bunya* into the Northern Hemisphere where it was probably widespread during the Jurassic and Cretaceous.

Acknowledgements. I thank Dr. C. R. Hill, British Museum (Natural History), and Mr. P. A. Brown for making the material available for study; and Dr. T. N. Taylor for review of the manuscript and use of laboratory facilities. This publication is dedicated to the memory of the late James M. Schopf. I acknowledge NSERCC Grant A-6908.

EXPLANATION OF PLATE 86

Figs. 1-7. *Araucaria brownii* sp. nov. Holotype, BMNH V59205. *e*, embryo; *i*, integument; *m*, megagametophyte; *n*, nucellus; *p*, plexus. 1, V59205 B 24, ovule transverse section showing lateral extensions of the seed integuments and well-preserved endotesta cells, $\times 9$. 2, V59205 A 40, seed transverse section with well-preserved nucellus, megagametophyte, and a possible embryo, $\times 25$. 3, V59205 B 23, transverse section of seed showing possible embryo with four cotyledons, $\times 35$. 4, V59205 B 25, transverse section of seed with cellular megagametophyte and crystalline central area, possibly representing an embryo, $\times 50$. 5, V59205 B 26, transverse section near seed chalaza showing vascular plexus leading into ovule, $\times 15$. 6, V59205 C 8, longitudinal section of resin canal (arrows) in cortex of cone axis, $\times 30$. 7, transverse section of ovule showing disorganized megagametophyte tissue, $\times 925$.



STOCKEY, Araucarian cone

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DR. R. A. STOCKEY

Department of Botany
The University of Alberta
Edmonton, Alberta

Typescript received 24 June 1979

Revised typescript received 20 November 1979