American Journal of Botany 89(9): 1447–1458. 2002.

ANATOMICALLY PRESERVED *CYCADEOIDEA* (CYCADEOIDACEAE), WITH A REEVALUATION OF SYSTEMATIC CHARACTERS FOR THE SEED CONES OF BENNETTITALES[1]

GAR W. ROTHWELL[2,4] AND RUTH A. STOCKEY[3]

[2]Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701 USA; and [3]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Four anatomically preserved ovulate cycadeoid cones have been recovered from three localities in Upper Cretaceous (Turonian/Coniacian-Late Campanian) sediments of Vancouver and Hornby Islands, British Columbia, Canada. All of the specimens are preserved by calcareous cellular permineralization and are quite similar to seed cones described as several species of *Cycadeoidea* and *Bennettites*. These cones, described as *Cycadeoidea maccafferyi* sp. nov., consist of tightly packed interseminal scales and ovulate sporophylls with terminal ovules. Two specimens also preserve remains of a small receptacle. Interseminal scales and ovulate sporophylls are oriented parallel to one another. Ovules are distinctly stellate at the base of the micropylar tube, and the sarcotesta consists of both longitudinally oriented tubular cells and large radially elongated cells attached to the sclerotesta. The vascular strand below each ovule is highly contorted in a pattern that is characteristic of contractile tissue in the roots of living plants. These specimens are the most recent anatomically preserved cycadeoid cones yet discovered, revealing details of the reproductive biology shortly before extinction of the clade. Superb preservation of the British Columbia cones confirms that Bennettitales lack a cupule, have radial seeds, and have a vascularized nucellus (but no integumentary tracheids), and that no pollen chamber is produced. Together with a new species of *Williamsonia* preserved at one of the same localities, these specimens reveal a clear set of contrasting systematic characters for differentiating between isolated seed cones of Williamsoniaceae and Cycadeoidaceae.

Key words: Bennettitales; Cretaceous; *Cycadeoidea*; seed cones; *Williamsonia*.

Cycadeoids are an important extinct clade of Mesozoic seed plants also known as Bennettitales (Watson and Sincock, 1992). For nearly a century numerous characters have implicated cycadeoids in the origin of flowering plants (Arber and Parkin, 1907). Cladistic analyses of morphological characters have consistently supported this hypothesis by placing Bennettitales within the anthophytes, a clade that also includes flowering plants (Crane, 1985; Doyle and Donoghue, 1986, 1992; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996; Pryer et al., 2001). However, results of these analyses are not fully concordant, and the absence of a complete character set for any of the extinct taxa weakens support values for all of the resulting hypotheses of cladistic relationships.

By contrast, several strongly supported but distinctly dissimilar hypotheses of relationships for living seed plants have been developed from analyses of molecular data (discussed by Donoghue and Doyle, 2000; and Sanderson et al., 2000). Unfortunately, the cumulative results of these studies further cloud, rather than clarify, our understanding of spermatophyte phylogeny (Donoghue and Doyle, 2000). Because only five of the major seed plant clades have living representatives, there is a strong probability that the results of the molecular analyses reflect high levels of error and bias (Felsenstein, 1978), and it is becoming increasingly likely that resolving the overall pattern of spermatophyte relationships will not be achieved by a analysis of extant groups alone (Sanderson et al., 2000). Therefore, the discovery and characterization of fossils that provide missing characters for extinct spermatophyte clades are important priorities for systematic studies that focus on the resolution of seed plant phylogeny.

Over the past several years Late Cretaceous deposits of Vancouver and Hornby Islands along the west coast of southern British Columbia, Canada have yielded large numbers of plant fossils (Ludvigsen and Beard, 1997; Smith and Stockey, 2002) with superb anatomical preservation. These include the most recent permineralized cones of the Bennettitales yet discovered. The specimens are assignable to *Cycadeoidea* Buckland and *Williamsonia* Carruthers, and they display several previously unknown or incompletely understood characters (Rothwell and Stockey, 2001).

The current investigation focuses on ovulate cones assignable to *Cycadeoidea* that display features of the sporophylls, seeds, interseminal scales, and receptacle. These cones differ from all previously described species of *Cycadeoidea* in overall size and shape, features of the interseminal scales and seeds, and unique features of the seed integument and sporophyll vascularization. Therefore, they are described as *Cycadeoidea maccafferyi* sp. nov. A new species of *Williamsonia* that displays structural features of the cone, as well as anatomical details of seeds, megagametophytes, pollen tubes, and immature embryos, is being published separately.

Many features of *C. maccafferyi* compare favorably with those that have been described thoroughly for other species of *Cycadeoidea* (including those assigned to *Bennettites* Carruthers by previous authors). Therefore, the description in this paper focuses primarily on specific characters of *C. maccafferyi*

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[1] Manuscript received 3 January 2002; revision accepted 18 April 2002.

The authors thank Graham Beard for collecting assistance and for making specimens from the Vancouver Island Paleontology Museum, Qualicum Beach, BC available for study. Additional specimens were generously provided by Dane McCaffery, Nanaimo, BC, Joe Morin, Courtenay, BC, and Doug Embry, Parksville, BC. Theodore Delevoryas made preparations of one of the specimens. This work was supported in part by the Natural Sciences and Engineering Research Council of Canada (Grant A-6908 to RAS).

[4] Author for reprint requests (Tel: 740-593-1129; FAX: 740-593-1130; e-mail: rothwell@ohio.edu).

and on new information for the genus. This material helps clarify several systematically informative characters of the Bennettitales and allows for the development of a contrasting set of characters to differentiate confidently seed cones of Cycadeoidaceae from those of Williamsoniaceae.

MATERIALS AND METHODS

The current study is based on four Late Cretaceous seed cones found at three collecting localities in southwestern Canada. The cones are preserved either in carbonate concretions or as isolated calcareous permineralizations. Two of the cones (i.e., BO211 and VIPM1884) were recovered from abandoned shale pits at the Brannen Lake fossil locality (49°12′16″ N, 124°06′01″ W; [Universal Transverse Mercator Grid] UTM coordinates 10U DK 198495) about 3 km west of Nanaimo on Vancouver Island, British Columbia (Ludvigsen and Beard, 1997). These are from the Upper Cretaceous Haslam Formation of the Nanaimo Basin, now dated as early Campanian based on the occurrence of the ammonite *Sphenoceramus schmidti* (J. Haggart, Geological Survey of Canada, personal communication, 2001). A third specimen (EMB052) is from Piggot Creek, an abandoned quarry pit along a logging road east of Courtenay (49°46′30″ N, 125°22′30″ W; UTM coordinates 10U CA 162291) on central Vancouver Island, and comes from the Comox Formation believed to be Turonian/Coniacian (J. Haggart, personal communication, 2001). The fourth specimen (VIPM 118) was collected on the beach at Collishaw Point (49°33′04″ N, 124°41′03″ W; UTM coordinates 10U CK 777897) along the north coast of Hornby Island, just west of Vancouver Island (Ludvigsen and Beard, 1997). Specimens at this locality come from the Upper Cretaceous (late Campanian) Lambert Formation of the Comox Basin, the date based on ammonite succession (Ludvigsen and Beard, 1997; J. Haggart, personal communication, 2001).

Specimens were photographed and then serially sectioned by the well-known cellulose acetate peel technique (Joy, Willis, and Lacey, 1956). Peels for microscopic examination and image capture were mounted on microscope slides with Eukitt mounting medium (O. Kindler, Freiburg, Germany). Images were captured with a Microlumina digital scanning camera (Leaf Systems, Bedford, Massachusetts, USA), and processed with Adobe Photoshop (Adobe Systems, Inc., San Jose, California, USA). Specimens, peels, and microscope slides are housed at the Vancouver Island Paleontology Museum (VIPM; 118 and 1884) and the Courtenay and District Museum, Courtenay, British Columbia (EMB 052 and BO 211).

Cycadeoid systematics and nomenclature have a long, confusing history of inconsistent application. Names used in this paper follow the rationale of Seward (1917) and Watson and Sincock (1992). Specifically, we use *Cycadeoidea* Buckland and Cycadeoidaceae Buckland and consider *Bennettitites* Carruthers to be a junior synonym of *Cycadeoidea*. However, we use Bennettitales Engler, because it is the first and most distinctive name proposed for the order.

SYSTEMATICS

Order*—*Bennettitales Engler

Family*—*Cycadeoidaceae Buckland

Genus*—Cycadeoidea *Buckland

Species*—*Cycadeoidea maccafferyi sp. nov.

***Specific diagnosis*—**Ovulate cones, up to 7.8 cm long and 3.7–7.6 cm wide (exclusive of bracts); displaying small dome-shaped receptacle with anastomosing vascular bundles. Receptacle with resinous cells; interseminal scales with 1–2 resin canals; resinous tissues absent from ovulate sporophylls. Sporophylls and interseminal scales 2.0–5.3 cm long. Seeds 12–19 mm long, 2.1–4.1 mm wide, with micropylar canal terminating just below apices of 5–6 encircling interseminal scales; round at apex, becoming distinctly 4–5 winged at base of micropylar tube. Wings produced both by sclerotesta and sarcotesta; greatly accentuated by sarcotesta apically, diminishing basally, absent from chalaza. Sporophyll with highly convoluted vascular strand immediately below seed; straight basally.

***Holotype hic designatus*—**Cone specimen BO 211 from Brannen Lake, showing receptacle, interseminal scales, sporophylls, and seeds with megagametophytes and dicotyledonous embryos is here designated the holotype. This specimen is deposited in the Courtenay and District Museum, Courtenay, British Columbia, Canada.

***Stratigraphy*—**Haslam Formation, Upper Cretaceous, early Campanian.

***Paratypes*—**Specimen VIPM1884 in the Vancouver Island Paleontology Museum, Qualicum Beach, British Columbia, from Brannen Lake, EMB 052 (Courtenay and District Museum) from Piggot Creek, and specimen VIPM118 from Hornby Island are designated paratypes.

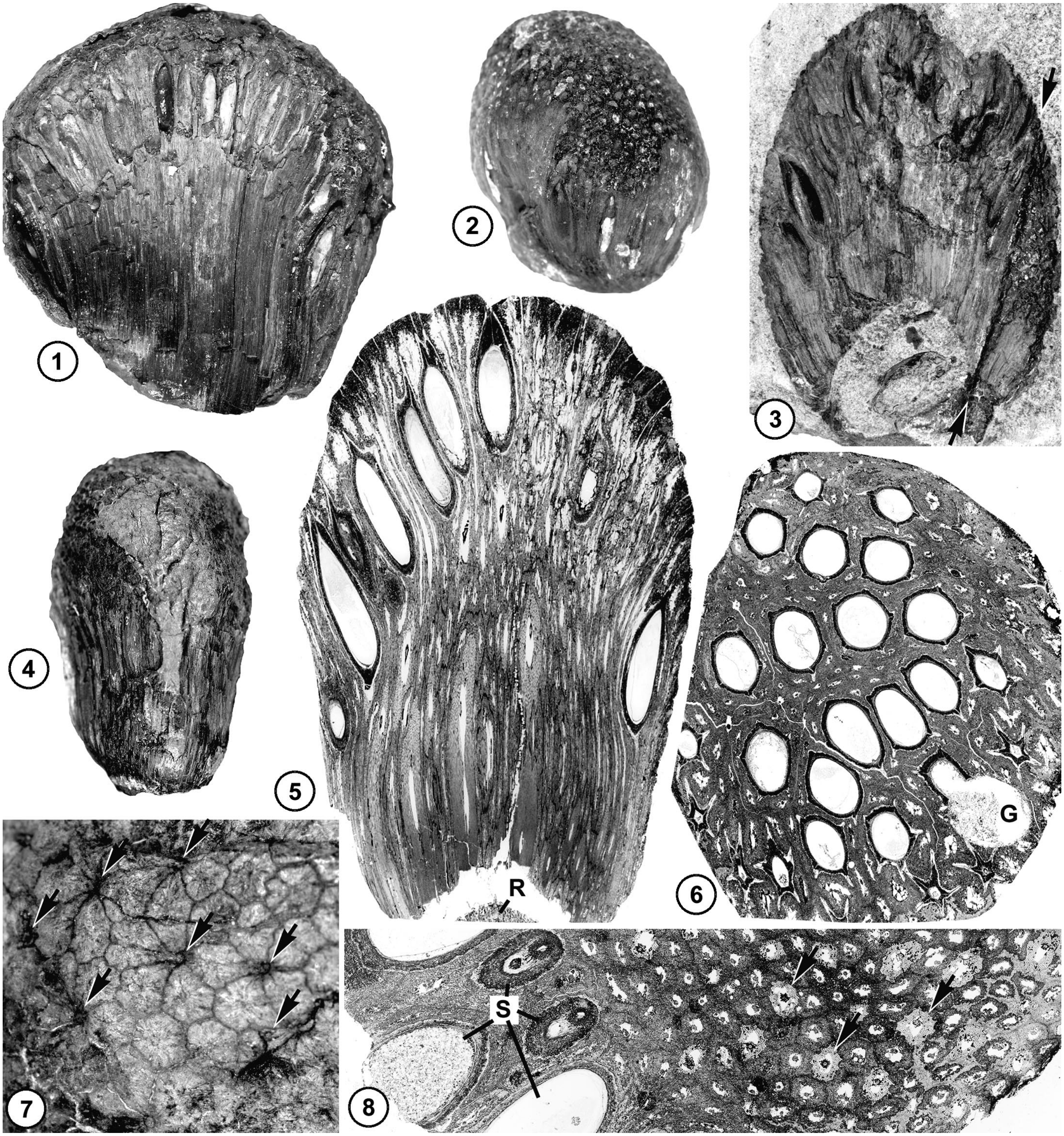
***Etymology*—**The specific epithet *maccafferyi* is proposed for Dane McCaffery, Nanaimo, British Columbia, who generously provided the holotype specimen for study.

DESCRIPTION

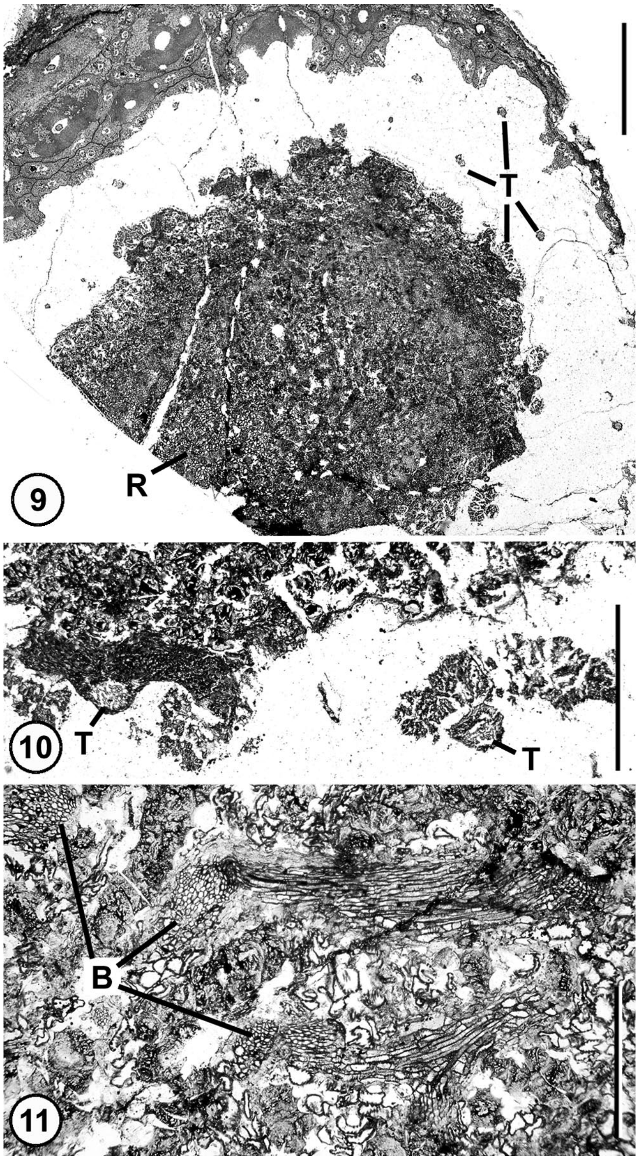
The four specimens of *Cycadeoidea maccafferyi* range up to 7.8 cm long and are 3.7–7.6 cm in diameter at their widest level. All four cones are represented by interseminal scales and interspersed ovulate sporophylls that each bear a terminal ovule (Figs. 1–4). No subtending bracts are present on any of the specimens. Tissues of the receptacle are present in one cone (Figs. 5, 9), and the shape of the receptacle is preserved in another (Fig. 3). The cones are roughly ellipsoidal, with their greatest dimension one-half to two-thirds the distance to the apex (Figs. 1–5), and the cone tip is rounded (Figs. 1–5). The receptacle is dome-shaped (Fig. 3), up to 2.5 mm long, and truncated at the base (Fig. 4) where abscission of the cones apparently occurred as it does in *Williamsonia* (Sharma, 1970).

Sporophylls are produced over the entire distal surface of the receptacle, and each bears a single, apical orthotropous seed (Figs. 1–3, 5). Seeds are elongated (Figs. 1–3, 5), round to stellate in cross sections, and display longitudinal ribs that are most pronounced at the juncture of the seed cavity and micropylar tube (Figs. 6, 12, 13, 15). In one cone (i.e., VIPM 1884) elongated galleries extend inward from the base, are oval to circular in cross section (Fig. 6, lower right), and suggest that either a herbivore fed on the seed cones of *C. maccafferyi* or teredo-like organisms bored the specimen after permineralization. The galleries are 4–7 mm in diameter and are loosely occupied by a combination of inorganic sediment and detrital plant material (Fig. 6). No recognizable fecal pellets are preserved.

Surface views in the apical half of the cones show polygonal tips of tightly packed interseminal scales and the small, round apices of seed micropyles (Fig. 7, arrows). All the interseminal scales and sporophylls extend from the receptacle in the same direction (Figs. 1–5), paralleling each other for most of their length. Centrally located (i.e., most apical) interseminal scales



Figs. 1–8. *Cycadeoidea maccafferyi* n. sp. **1.** Internal view of largest cone showing interseminal scales interspersed with terminal ovules on long sporophylls. VIPM 118 × 1. **2.** Specimen showing features of interseminal scale apices in upper half, and split surface with exposed seeds below. 1884 × 1. **3.** Nodule split through cone in longitudinal view, showing shape of receptacle, seeds at the tips of sporophylls, and interseminal scales. Interseminal scales and seed apices exposed in surface view to right of arrows. EMB 052 × 1. **4.** External surface of isolated specimen showing general features of cones from the outside. Holotype, BO 211 × 1. **5.** Longitudinal section of cone in Fig. 4 showing tip of receptacle (R) from which sterile scales and ovulate sporophylls diverge parallel to one another. Note that central appendages are longest and that progressively more lateral organs are shorter, with seeds that bend toward cone periphery. Holotype, BO 211 Side # 107 × 2. **6.** Cross section of cone near apex, showing interseminal scales and seeds in cross sections. Seeds at center are cut more basally than seeds near cone periphery. Note that seeds display four or five ribs and that ribs increase in length, producing a stellate seed shape below the tip of the micropyle. Also note herbivore gallery or teredo boring (G) at lower right. 1884 A Top # 111 × 3. **7.** Surface view of cone, showing polygonal tips of interseminal scales and round tips of seed micropylar tubes (arrows). Note either five or six interseminal scales surround each seed. Holotype, BO 211 × 4. **8.** Cross section of cone at midregion showing cross sections of interseminal scales (some identified by arrows) and sporophylls at center. Seeds (S) of shorter peripheral sporophylls appear in oblique sections. 1884 A Side # 10 × 5.2.



Figs. 9–11. *Cycadeoidea maccafferyi* n. sp., features of receptacle **9.** Cross section at cone base showing receptacle (R) surrounded by bases of interseminal scales and sporophylls. Note terete traces (T) extending from receptacle to interseminal scales and sporophylls across space filled with calcite. Holotype, BO 211 Bot #24 × 6. Scale = 2.5 mm. **10.** Cross section of cone at margin of receptacle showing divergence of one trace (T) and another trace (T) that will diverge at a slightly more distal level. Note that traces are made up of terete strand of tracheids surrounded by incompletely preserved tissue and that each occurs immediately outside a crescent-shaped patch of incompletely preserved tissue. Holotype, BO 211 Bot #28 × 22. Scale = 1 mm. **11.** Enlargement of receptacular tissue showing histology of ground tissues and anastomosing vascular bundles (B). Holotype, BO 211 Bot #21 × 80. Scale = 0.25 mm.

and sporophylls are longer than the others and are erect to the apex. Successively more lateral appendages are progressively shorter and have tips that bend toward the margin of the cone (Figs. 1, 3, 5, 8).

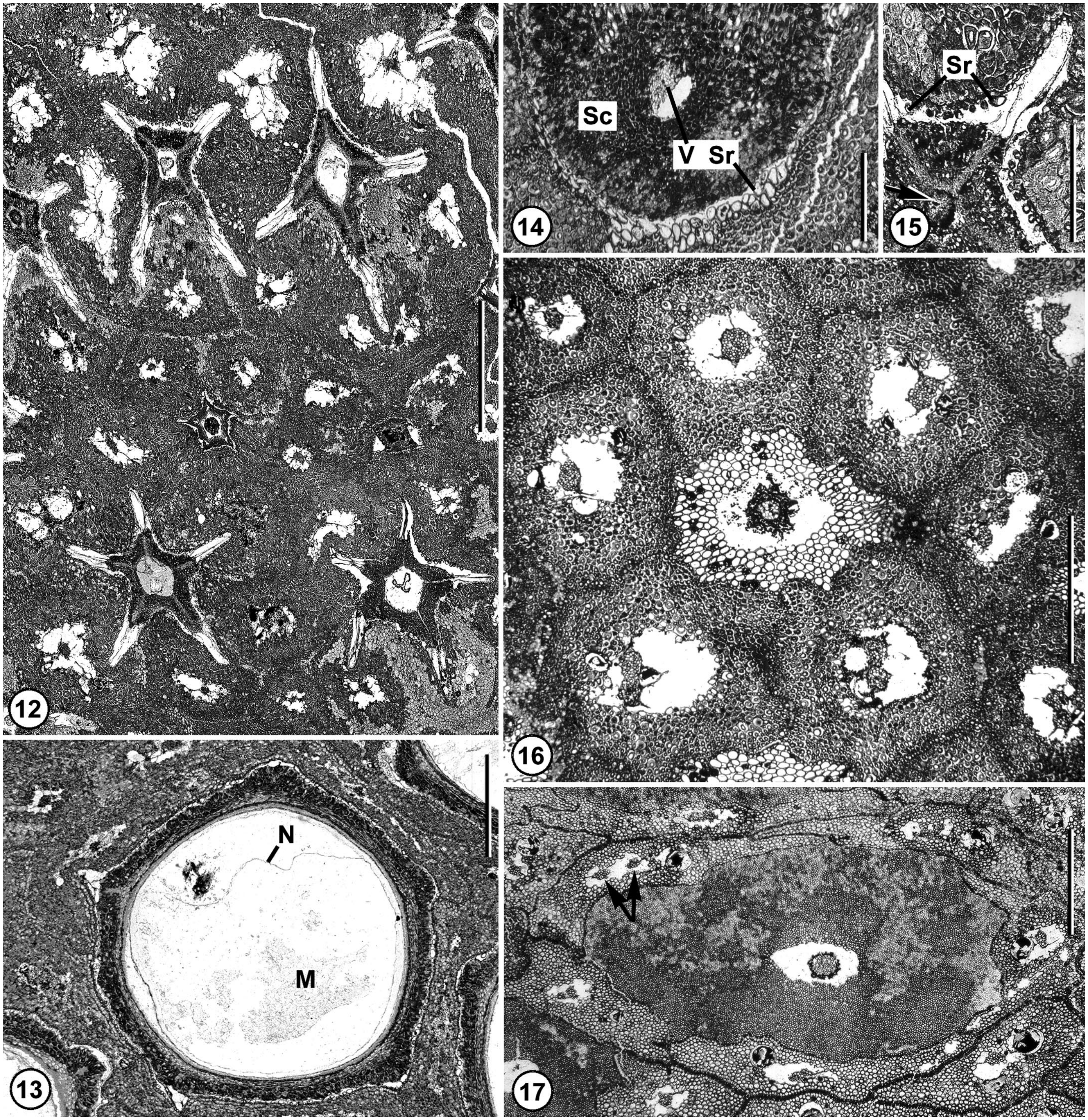
The receptacle is more or less round in cross sections (Fig. 9) and ranges from 1.5 to 2.5 cm in diameter (Figs. 3, 4). Except for traces that extend into the interseminal scales and sporophylls (Fig. 9, at T), the receptacle is separated from these organs by calcite filling (Fig. 9). Ground tissues of the receptacle are compact, consisting of cells that appear resinous and that are interspersed with cells that have prominent walls and no internal contents (Figs. 10, 11). Numerous small, terete vascular bundles are preserved near the periphery of the receptacle (Fig. 10). Although the available material is insufficient to interpret vascular architecture in the receptacle, the bundles anastomose (Fig. 11) in a fashion that appears to be similar to trace divergence described for specimens of *Williamsonia* (Sharma, 1970).

Individual bundles are small and oval, and are represented by tracheids (Fig. 11) with scalariform secondary wall thickenings. In cross sections most of the tracheids are randomly arranged, but there is some indication of radial alignment to one side of some bundles. This suggests that there was limited secondary vascular tissue production in the cones. Interseminal scale traces and sporophyll traces appear to diverge in a common phyllotactic helix (Fig. 9), and each trace consists of a terete xylem strand that is surrounded by a thin zone of dark, incompletely preserved cells (Fig. 10). A crescent-shaped patch of poorly preserved tissue occurs to the inside of each trace at the periphery of the receptacle (Fig. 10). This tissue accompanies the traces as they diverge from the receptacle (Fig. 10, at right), truncates rapidly (Figs. 9, 10), and is absent distally.

Sections in the midregion of the cone reveal cross sections of numerous polygonal interseminal scales (Fig. 8) and interspersed sporophyll stalks (Fig. 8, arrows). Toward the periphery of the cone at these levels, seeds of the shortest sporophylls are cut obliquely (Fig. 8 at S). The latter orientation is the result of peripheral ovules bending toward the cone surface (Figs. 3, 5). More distal levels of the cone reveal cross sections of seeds on the centrally located sporophylls (Fig. 6).

At their base the interseminal scales are arranged around the much larger sporophylls and are flattened with their greatest dimension paralleling the periphery of the sporophyll (Fig. 17). At all levels each interseminal scale displays a terete xylem strand that is surrounded by a narrow cylinder where no cells are preserved (Figs. 8, 16, 17). As is also characteristic of some previously described *Cycadeoidea* species (Lignier, 1894; Stopes, 1918), a small percentage of the interseminal scales display two traces (Fig. 17, at arrows). Cortical cells have prominent walls and no internal contents, and there is a distinct epidermis of darkly stained cells on the surfaces where interseminal scales abut each other (Fig. 17). Epidermis is less prominent on surfaces that are adjacent to a sporophyll (Fig. 17). Interseminal scales typically display one or sometimes two large resin canals. These canals are roughly round in cross sections and have dark contents (Fig. 17).

More distally, the interseminal scales increase in size and become polygonal in cross sections (Figs. 8, 12, 16). Cortical cells consist of thick-walled sclerenchyma (Fig. 16), and both the resin canals and epidermis are much less distinct (Figs. 8, 12, 16) than in basal sections. In longitudinal sections the cortical sclerenchyma cells are elongated (Fig. 26). Many cortical cells show scalariform or oval simple pits, but the dark walls of the epidermal cells are smooth (Fig. 26). At the level of the seeds, the interseminal scales become flattened parallel to the periphery of the seed body (Figs. 6, 13), but at their tips (i.e., at the cone periphery) they are again polygonal and surround the seed micropyles (Fig. 7). At distal levels the cortical sclerenchyma cells become isodiametric (Fig. 20), developing extremely thick, dark walls (Figs. 5, 20, 21) and very small lu-



Figs. 12–17. *Cycadeoidea maccafferyi* n. sp. **12.** Cross section of seeds and interseminal scales near apex of cone, showing stellate form of four- and five-ribbed seeds at and below base of micorpylar tube. Note the loose tissue immediately surrounding the vascular bundle of the interseminal scales. 1884A Top #30 × 6. Scale = 2 mm. **13.** Cross section of seed in midregion, surrounded by interseminal scales and other seeds. Five integumentary ribs are constructed of both sclerotesta and large, thin-walled sarcotestal cells. Note nucellus (N) appearing as a thin line and faint megagametophyte tissue (M). 1884 A Top #138 × 17. Scale = 1 mm. **14.** Oblique cross section of seed chalaza showing vascular bundle (V) surrounded by sclerotic sclerotesta (Sc), tubular cells of the sarcotesta (Sr), and thick-walled cells of encircling interseminal scales (at bottom). 1884 A Side #10 × 30. Scale = 0.5 mm. **15.** Cross section of seed at base of micropylar tube, showing prominent rib, produced primarily by large, radially elongated thin-walled sarcotestal cells that are attached to sclerotesta. At this level tubular sarcotestal cells (Sr) are confined to one incomplete layer between ribs. Note that micropylar canal is sealed by solid tip of elongated nucellar apex (arrow). 1884 A Top #9 × 20. Scale = 1 mm. **16.** Cone in midregion showing interseminal scales and one sporophyll in cross section. Contrast numbers and sizes of tubular cortical cells with more basal level of sporophyll (Fig. 17). Note change in cortical cell walls of interseminal scale from more basal level (Fig. 17). 1884 XS #10 × 25 Scale = 1 mm. **17.** Cross section at base of sporophyll and surrounding interseminal scales. Sporophyll is large with numerous small cortical cells surrounding trace at this level. Note change in numbers and sizes of sporophyll cortical cells from slightly more distal levels (Fig. 16). Most interseminal scales have one trace, but one scale at the upper left has two traces (arrows). Cortical cells of interseminal scales have thinner walls than at more distal levels (Fig. 16); there is a prominent epidermis of dark cells between adjacent interseminal scales, but no differentiated epidermis at the sporophyll periphery. Holotype, BO 211 Bot #28 × 35 Scale = 0.5 mm.

mina (Figs. 12, 15, 20), and producing a highly sclerotic tissue that encloses the seeds.

At basal levels the sporophylls are oval in cross sections and considerably larger than the interseminal scales (Fig. 17). Each has a terete trace that consists of randomly arranged tracheids surrounded by dark, poorly preserved cells that may represent phloem (Fig. 17). As with the interseminal scales, there is a hollow space surrounding the sporophyll trace (Figs. 16, 17). At this level the cortex consists of 35–40 layers of small, tightly packed cells 10–15 μm in diameter, with dark walls and empty lumens (Fig. 17). Longitudinal sections reveal that these cells are extremely elongated, like the cortical cells of the interseminal scales. No resin canals are present in the sporophylls, and a distinct epidermis is not produced.

Somewhat more distally the sporophyll cortex diminishes to four to nine cell layers thick, and the cortical cells increase in size dramatically, measuring 40–50 μm in diameter (Fig. 16). At still more distal levels the thickness of this zone continues to decrease, being only about two cell layers thick at the juncture of the sporophyll apex and seed base (Figs. 14, 23, 24). In the apical-most regions, these cells form a single cell layer of sarcotesta that incompletely surrounds the sclerotesta of the seeds (Figs. 12, 15). From just above the base of the sporophyll to the apex of the seeds there are obvious intercellular spaces that separate and emphasize the tubular nature of these cortical/sarcotestal cells (Figs. 12, 14, 15, 26).

For most of the length of the sporophylls the course of the sporophyll trace is straight, but just below the base of the seed it becomes highly convoluted (Figs. 19, 23, 24). These convolutions extend for a distance of 1–1.5 mm immediately below the base of each seed (Fig. 19) and follow a roughly helical course in three dimensions (Figs. 23, 24). By measuring the length of the vascular strand along the length of the convolutions in a single section and then doubling this length to account for the convolutions occurring in three dimensional space, it is estimated that the trace is approximately 5–7 mm longer than the sporophyll over this small distance. Convolutions are absent from the adjacent tubular cells, which remain straight (Figs. 23, 24) over the entire length of the sporophyll and seed. Vascular trace convolutions of this type are not known for any other species of *Cycadeoidea* and are therefore a diagnostic character of *C. maccafferyi*. Perhaps more importantly, this distinctive structure is characteristic of contractile roots in monocotyledonous flowering plants (Davey, 1946) and is the basis for suggesting that the seeds of this species were initially emergent and then retracted below the tips of the interseminal scales following pollination (Rothwell and Stockey, 2001).

Each sporophyll terminates as a single erect seed (Figs. 1, 3, 5) 12–19 mm long and 2.1–4.1 mm wide. Seeds have a round micropylar tip (Fig. 7) and chalaza (Fig. 8), but there are four or five integumentary ribs in the midregion (Figs. 6, 12, 13, 15). The length of each rib increases distally, giving the seeds a stellate appearance at the base of the micropylar canal (Figs. 6, 12, 15), and then the rib truncates below the tip of the micropyle. Seeds show a multilayered integument (Figs. 12, 13, 15, 20–22) that surrounds a nucellus that is attached only at the chalaza (Fig. 22).

The seed integument is basically similar to that of many other nonangiospermous seed plants, consisting of endotesta, sclerotesta, and outer sarcotesta. However, unlike many major gymnospermous clades, there is no evidence of vascular tissue in the integument of any bennettitalean species. The endotesta and sclerotesta are comparable to those that have been previously recognized and thoroughly characterized for several species of *Cycadeoidea*, particularly species described as *Bennettites gibsonianus* (Carruthers, 1870; Solms-Laubach, 1890), *B. morierei* (Lignier, 1894), and *B. albianus* (Stopes, 1918). Endotestal cells are not always easily recognized, but where preserved they are narrow and longitudinally elongated, thin walled, and often contain dark contents (Fig. 22). Cells at the inner margin of the sclerotesta are also longitudinally elongated, but are wider than the endotestal cells and have thicker cell walls (Figs. 20, 22). Toward the outer margin of the sclerotesta the cells intergrade with progressively darker, thicker walled, and isodiametric stone cells (Figs. 20–22) and commonly display prominent lumina (Figs. 22, 26).

As is elaborated in the discussion section of this paper, cells of the sarcotesta have not always been recognized as such, but their features are more or less similar in all species of *Cycadeoidea* for which this tissue is well known (Lignier, 1894; Stopes, 1918). Most sarcotestal cells are tubular and are an apical continuation of the cortex of the sporophyll (Figs. 21, 22). As in the region of the sporophyll, these tubular cells are usually not in organic attachment to more centrally located tissues (cf. Figs. 16 and 20, at left). Small, isodiametric cells with thin walls connect the tubular sarcotestal cells to the sclerotesta in *B. albianus* (Stopes, 1918), but similar cells are not preserved in *C. maccafferyi*. In *C. maccafferyi*, tubular sarcotestal cells completely surround the sclerotesta at the chalaza (Fig. 14), but are restricted to radii that alternate with ribs at more distal levels (Fig. 15).

Distal to the chalaza, large thin-walled sarcotestal cells are attached to the integumentary ribs (Figs. 13 at left and bottom, 15) and are comparable to tissue described for the best preserved specimens of previously described species (Table 1). These cells extend away from the sclerotesta on the radius of each integumentary rib and produce the stellate outline of the seed below the level of the micropylar tip (Figs. 6, 12, 15). Sarcotestal cells have not been observed at the most distal levels of the micropylar tube.

The nucellus is several cell layers thick at the base, where it separates from the integument (Fig. 22). It contains the only vascular tissue in the seeds. The vascular tissue enters the base of the seed and extends through the sclerotesta into the nucellus, where it forms a shallow cup of tracheids (Fig. 22) with reticulate-scalariform wall thickenings (Fig. 25). In the midregion of the seed the nucellus is usually represented by a thin line made up of one or two layers of crushed, thin-walled cells (Figs. 13, 20). At the apex it narrows to a slender, solid rod of cells that extends into and plugs the base of the micropylar tube (Figs. 20, 21). As in the seeds of *Williamsonia* (Rothwell and Stockey, 2001; Stockey and Rothwell, 2001), no pollen chamber is produced. Rather, the slender tip of the nucellus is made up of tightly packed, thin-walled cells with amber contents (Figs. 20, 21).

The seed cavity in many seeds is occupied by embryos that are surrounded by incompletely preserved tissues of the megagametophyte (Figs. 18, 20, 21). The embryos of *C. maccafferyi* are comparable to those that have been thoroughly described for several other cycadeoid species (Carruthers, 1870; Solms-Laubach, 1890; Lignier, 1894; Wieland, 1906, 1916). They have two straight cotyledons (Fig. 18) in which the provascular strands are prominent. The radicle is tightly pressed into the apical region of the seed cavity (Figs. 20, 21) and

TABLE 1. Permineralized cones of *Cycadeoidea*.

Species	Geographical source	Stratification and age	Borne	Elongated peduncle	Microsporophylls	Cone size (L × W, cm) & shape[a]	Subtending bracts	Peduncle diameter	Receptacle
Cycadeoidea maccafferyi sp. nov.	Vancouver and Hornby Islands, western Canada	Late Cretaceous, (Campanian)	isolated cones	?	absent	49–76 × 38–72, ellipsoidal	not preserved	ca. 15 mm	small, dome-shaped, 15–25 mm.
Bennettites gibsonianus Carruthers, 1870	Isle of Wight	Lower Cretaceous (Aptian)	in axils of leaves on trunk	no	absent	2.0 × 3.0, narrowly conical-ellipsoidal	present	ca. 5 mm	small, dome-shaped, ca. 12 mm
Bennettites morierei (Saporta and Marion) Lignier	Normandy, France	Middle Oxfordian, Jurassic[b]	isolated cone with bracts	?	absent	ca. 35 × 55, ellipsoidal	present	ca. 25 mm	small, low dome
Bennettites albianus Stopes	Folkestone Warren, England	Gault, Cretaceous	isolated cone fragment	?	absent	? (30 × 55 mm frag.)	not preserved	?	?
Cycadeoidea spp. of Wieland[c] (putative seed cones[d])	several, North America	Lower Cretaceous	in axils of leaves on trunk	no	?, absent	>31 × >55, conical-ellipsoidal-cylindrical	present	various	small, dome-shaped-conical
Cycadeoidea spp. of Wieland[c] (bisporangiate)	several, North America	Lower Cretaceous	in axils of leaves on trunk	no	present	>55 × >31, conical-ellipsoidal-cylindrical	present	various	large, conical

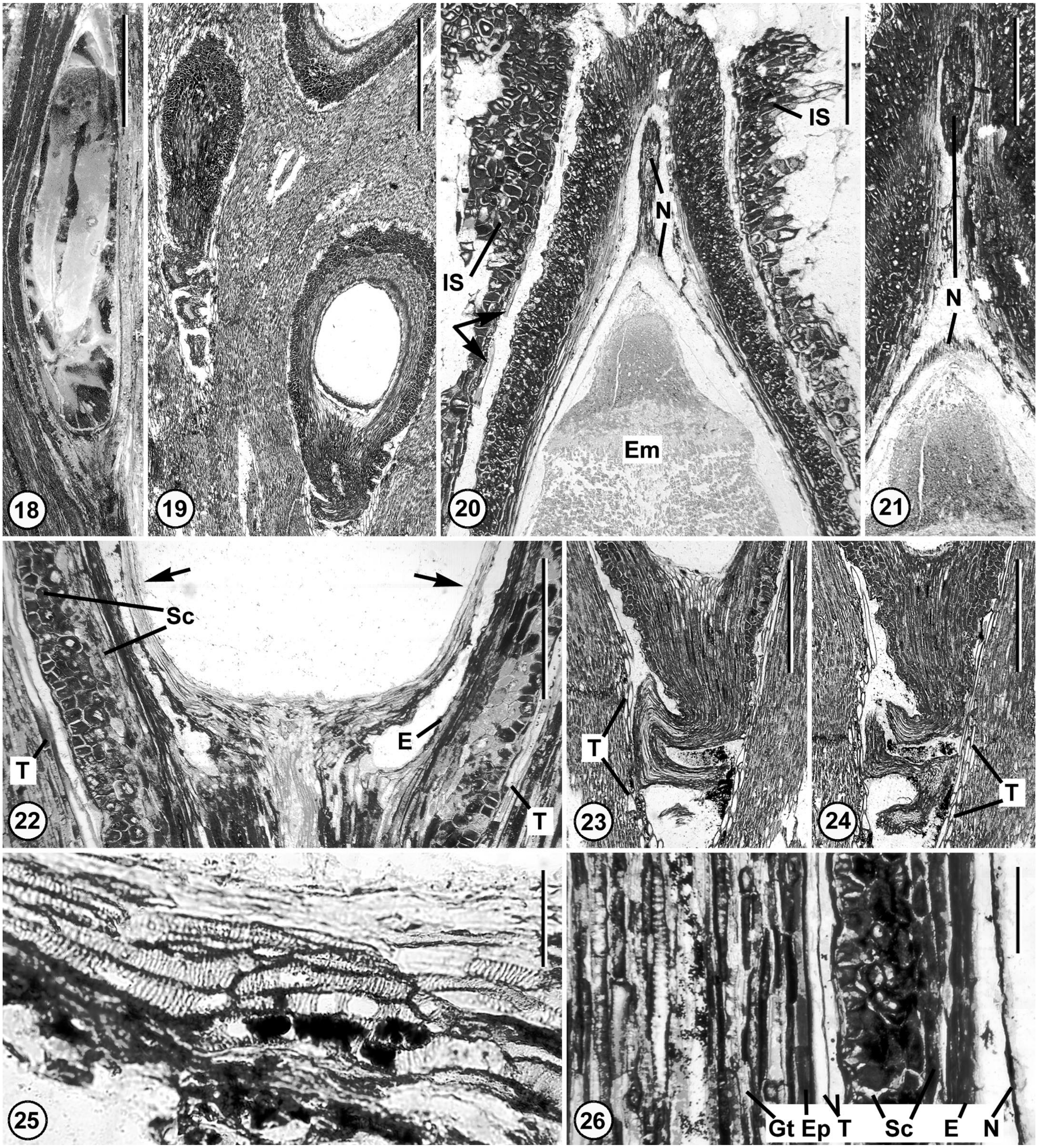
	Intersemial scales						Seed		
Species	L × W (mm)	Fused at apex	Bundle sheath	Resin canals	No. around each seed	Micropyle	XS, near apex	L × W, (mm)	Sarcotestal cells
Cycadeoidea maccafferyi sp. nov.	20–52 × 1.8–2.5	no ?	yes	1 (2)	5–6	slightly sunken	stellate	12–19 × 2.1–4.1	tubular cells and large, attached, thin-walled cells
Bennettites gibsonianus Carruthers	35 × 1.5–1.9	?	yes	no?	5?	flush	?	6 × 2	tubular cells
Bennettites morierei (Saporta et Marion) Lignier	45 × 1.0–1.5	no	no	no?	4 (5)	flush-slightly sunken	stellate	6–7 × 2.5–3	tubular cells and large, attached, thin-walled cells
Bennettites albianus Stopes	32 (incomplete) × 0.2–0.4	yes	no	1–3	5–6	?	stellate	5–6 × 1–1.2	tubular cells
Cycadeoidea spp. of Wieland (putative seed cones)	various	?	no	no?	5–6	flush-slightly protruding?	stellate	6.5–7 × 3	tubular cells
Cycadeoidea spp. of Wieland (bisporangiate)	various	?	yes	no?	5–6	flush-slightly protruding?	stellate	6.5–7 × 3	tubular cells

[a] Cone measurements exclude bracts, microsporophylls when present, and any peduncle that protrudes below attachment of basal-most interseminal scales. L, length; W, width.

[b] See Lignier (1910) for Cretaceous interpretation.

[c] Wieland (1906, 1916) describes numerous species of *Cycadeoidea*. His emphasis is on the overall characters of each species, and the histological preservation of specimens varies considerably, often being less complete than the isolated cones of *C. maccafferyii, B. morierei*, and *B. albianus*. Wieland's description of the cones is taxonomically generalized, focusing on characters that are common to some or all of the species. His measurements typically either are generalized or use one species as an example of all species. No specific set of contrasting characters has been developed or recorded for any of the species described by Wieland (1906, 1916). Characters scored as ''various'' denote that there is variation among specimens, but that the specific ranges are not known for any of the species.

[d] Distinctions between bisporangiate cones with large conical receptacles and putatively ovulate cones with small dome-shaped receptacles have been discussed thoroughly by Delevoryas (1968) and Crepet (1972). Ontogeny of the cones is elaborated by Crepet (1974), who questions whether any are truly monosporangiate.



Figs. 18–26. *Cycadeoidea maccafferyi* n. sp. **18.** Longitudinal section of seed with dicotyledonous embryo at apex of sporophyll. Holotype, BO 211 Side, reflected light image of surface with peel attached, × 20. Scale = 1 mm. **19.** Oblique, longitudinal section of cone showing highly convoluted sporophyll trace immediately below base of three seeds. 1884 A Bot #17 × 10. Scale = 2 mm. **20.** Slightly oblique longitudinal section near seed apex showing radicle of dicotyledonous embryo (Em) in seed cavity and elongated, solid tip of nucellus (N) extending into base of micropyle. Note histology of sclerotesta (Sc), elongated tubular sarcotestal cells (arrows), and prominent sclereids at tip of interseminal scales (IS). Holotype, BO 211 Side #99 × 19. Scale = 1 mm. **21.** Adjacent section of seed in Fig. 20 showing nucellus (N) with oblique (oval) apex constructed of tightly packed thin-walled cells with dark contents and filling micropylar canal. Holotype, BO 211 Side #100 × 19. Scale = 1 mm. **22.** Longitudinal section of seed chalaza, showing histological features of integument at this level, attachment of nucellus (N) only at base, and histological features of nucellus. Endotestal cells (E) are innermost layer of integument, and sclerotesta (Sc) consists of both longitudinally elongated cells to inside and isodiameteric stone cells to outside. Sarcotesta of elongated tubular cells (T). Note shallow

connected to the cotyledons by a short hypocotyl. The epicotyl is quite small and is not evident in most sections (Fig. 18).

DISCUSSION

In contrast to many extinct groups of vascular plants that were originally recognized from isolated organs of a single preservational mode, cycadeoids have been represented by multiorgan specimens preserved by a variety of modes since the earliest studies (e.g., Buckland, 1828; Carruthers, 1870; Ward, 1900; Wieland, 1906). Therefore, many species are characterized by a combination of morphological, cuticular, and internal anatomical features of vegetative and fertile organs. A large number of permineralized specimens of the Cycadeoidaceae have been described either as species of *Cycadeoidea* Buckland or *Bennettites* Carruthers, but all are now widely regarded as belonging to a single genus, wherein *Cycadeoidea* has nomenclatural priority (Seward, 1917; Watson and Sincock, 1992). The majority of *Cycadeoidea* species are described from stems bearing leaf bases and cones (e.g., Wieland, 1906, 1916). A few additional species, including *C. maccafferyi*, are represented by isolated seed cones for which the other organs of the sporophyte are unknown. Nevertheless, these isolated cones display a large enough number of diagnostic characters that they can be confidently identified as either belonging to well-known species of *Cycadeoidea* or to new species (Table 1).

Cycadeoidea maccafferyi is among the geologically youngest species of permineralized Cycadeoidaceae thus far described (Nishida, 1994; Saiki and Yoshida, 1999; Rothwell and Stockey, 2001). Cones are larger and have distinctly larger seeds than any of the previously described species (Table 1). *Cycadeoidea maccafferyi* is also the only species to display distinctive contractile tissue below the seed at the distal end of the sporophyll (Figs. 19, 23, 24; Rothwell and Stockey, 2001). Additional characters that set *C. maccafferyi* apart from previously described species include the combination of (1) monosporangiate seed cones with small dome-shaped receptacles, (2) length of sporophylls and interseminal scales, (3) distribution of tubular and attached sarcotestal cells, and (4) histological features of the various tissues (Table 1).

Sarcotesta or cupule?—In previous studies of Bennettitales, some authors have recognized the presence of a cupule surrounding the seeds, whereas others have not. Bennettitalean cupules have been interpreted from studies of both permineralized specimens and from cuticular studies of compressed remains (Harris, 1932; Pederson, Crane, and Friis, 1989). From permineralized specimens, the extremely elongated tubular cells that surround the vascular bundle in the sporophyll and the sclerotesta of *Cycadeoidea* seeds are interpreted quite differently by different authors. Lignier (1894) provides the first detailed description of this tissue for *B. morierei*. He considers the tissue to be a multilayered epidermis at the level of the sporophyll, an interpretation that is accepted by Stopes for *B. albianus* (Stopes, 1918). More distally, at the level of the seeds, Lignier interprets the tubular cells and the large, thin-walled cells that accentuate the integumentary ridges to be outer fleshy layers of the integument (i.e., ‘‘envelope tubuleuse’’ and ‘‘l’assise plissée,’’ respectively, of Lignier, 1894).

Wieland interprets the tubular cells to be outer cortex at the level of the sporophyll that ‘‘instead of passing over into an outer integumentary layer, forms a cup-shaped supporting basal husk. . . ’’ (Wieland, 1906, p. 120). We concur with Wieland (1906) that the tubular cells of the sporophyll probably represent cortex. Stopes (1918) interprets the tubular cells surrounding the seeds of *B. albianus* to be a multicellular aril-like cup that is an apical extension of the multilayered epidermis (sensu Lignier, 1894) of the seed stalks (= cortex of Wieland [1906] and as interpreted in this study). Interestingly, Stopes (1918) also describes a zone of delicate cells that are in organic continuity with both the seed sclerotesta (to the inside) and the tubular cells (to the outside; e.g., Text-Figs. 7–9 of Stopes, 1918), but considers these delicate cells to represent a ‘‘deliquescent layer of surrounding stalk tissues’’ (Stopes, 1918, p. 404). To our knowledge, this is the only specimen of *Cycadeoidea* in which these delicate cells are preserved.

The interpretation of a cupule surrounding the seeds in the Bennettitales derives from the descriptions by Wieland (1906) and Stopes (1918), whereas the alternative interpretation that the same tissues represent seed integument derives from the studies of Lignier (1894). We agree with Lignier (1894) that both the tubular cells and the large thin-walled cells that accentuate the seed wings in *Cycadeoidea* are parts of the seed sarcotesta. This is for several reasons. First, the tubular cells are an apical extension of the outer tissues of the sporophyll, as is the sarcotesta in other groups of seed plants with seeds placed apically on sporophylls (i.e., cordaites—Rothwell, 1981; walchian conifers—Mapes and Rothwell, 1984; vojnovskyaleans—Rothwell, Mapes, and Mapes, 1996) or on ovulate stalks (i.e., *Ginkgo biloba* L.—Chamberlain, 1935; Bierhorst, 1971). This indicates that the tubular cells are homologous to the mesophyll and epidermis of a leaf, not a separate organ, such as a cupule. Second, the tubular cells of *B. albianus* are in organic continuity with the sclerotesta (through the ‘‘deliquescent layer’’ of Stopes, 1918). Third, a sarcotesta is differentiated in the integument of *Williamsonia* (Rothwell and Stockey, 2001; Stockey and Rothwell, 2001), but a cupule is clearly absent. Fourth, no cuticle has been recognized either to the outside of the tubular cells or between the tubular cells and the sclerotesta in the permineralized specimens, as would be expected if there were a cupule surrounding the seed.

If the tubular cells of *Cycadeoidea* do represent a cupule, then this genus is cupulate but the seeds lack a sarcotesta, whereas *Williamsonia* has sarcotesta but lacks a cupule. We consider the tubular cells of *Cycadeoidea* to be homologous to the peg-like sarcotestal cells of *Williamsonia* (Seward, 1912; Stockey and Rothwell, 2001), and for this to be, by far,

←

cup of tracheids (up to level of arrows). 1884 B Bot #25 × 50. Scale = 0.5 mm. **23** and **24.** Two parallel sections at level of attachment of one seed to sporophyll, showing highly convoluted sporophyll trace that represents contractile tissue. Note tubular cells (T) of cortex/sarcotesta extend straight across contractile region. 1884 A side #15 and #22 × 20 Scale = 1 mm. **25.** Enlargement of vascularized nucellar tissue at base of nucellus, showing reticulate/scalariform wall thickenings. Holotype, BO 211 Side #17 × 170. Scale = 1 mm. **26.** Longitudinal section of interseminal scale and adjacent seed near chalaza, showing histological features. Ground tissue of interseminal scale (Gt) has pitted elements but epidermal cells (E) have uniformly dark walls. Seed shows features of tubular sarcotestal cells (T), sclerotestal cells (Sc), endotestal cells (E), and nucellus (N). Holotype, BO 211 Side #107 × 75. Scale = 2 mm.

TABLE 2. Seed cone characters of Cycadeoidaceae and Williamsoniaceae.

Character	Family Cycadeoidaceae	Family Williamsoniaceae
Position of attachment	sessile, among leaf bases	at branch tips
Cones	bisporangiate and monosporangiate?	monosporangiate only
Divergence of interseminal scales and sporophylls	nearly parallel to one another	diverging around an arc of ≤300°
Seed shape in cross sections	ribbed and distinctly winged toward apex	nearly round
Sarcotesta	longitudinally elongated tubular cells	horizontally oriented, short, multicellular pegs

the more parsimonious explanation of homology for this tissue. Interpreting the outer tubular cells of *Cycadeoidea* as part of the integument also establishes the existence of sarcotesta in this genus, as is characteristic of ovules and seeds in nearly all other gymnospermous spermatophyte clades (Chamberlain, 1935; Rothwell and Serbet, 1994). If this reasoning is correct, then seed cones of both *Cycadeoidea* and *Williamsonia* lack a cupule.

Compression remains from which a bennettitalean cupule has been interpreted are assignable to the Triassic genus *Vardekloeftia* Harris. In his original study of *Vardekloeftia* (Harris, 1932), and in a more recent investigation using both light and scanning electron microscopy, Pedersen, Crane, and Friis (1989) interpret the cuticles of *V. sulcata* Harris as being derived from the inside of the integument, from the outside of the integument, and from a cupule. However, the much more complete and easily interpreted permineralized cycadeoid specimens now allow us to explain the cuticular envelopes of *Vardekloeftia* in terms of what is preserved in *Cycadeoidea* and *Williamsonia*. Although some authors interpret bennettitalean seeds to have a pollen chamber (i.e., Sharma, 1976; Ohana, Kimura, and Chitaley, 1998), figures of permineralized specimens of *Bennettites*, *Cycadeoidea*, *Williamsonia* and *Bennetticarpus* all show nucellar plugs like those that we have found in *Cycadeoidea maccafferyi* and the new species of *Williamsonia* from Vancouver Island (Lignier, 1894; Stopes, 1918; Wieland, 1906, 1916; Sharma, 1970, 1976; Delevoryas and Gould, 1973; Ohana, Kimura, and Chitaley, 1998). Seeds in these reproductive structures all lack a pollen chamber. Lignier (1894) and Stopes (1918) originally showed that *Cycadeoidea* (= *Bennettites* of these authors) has a plug of nucellar tissue in the micropyle and a nucellus that is free to the base of the integument. Despite some interpretations to the contrary, figures of all subsequently described, permineralized bennettitalean cones support Lignier and Stopes. With this improved understanding of bennettitalean seed anatomy, the elongated structure with a thick cuticle at the apex of *Vardekloeftia* (e.g., Plate V, Fig. 3 of Pedersen, Crane, and Friis, 1989) is much more reasonably interpreted to be a nucellar plug like that of the other bennettitaleans. If this interpretation is correct, then the two cuticles surrounding the plug probably represent the inner and outer cuticles of the integument, rather than a cupule. It therefore follows that there is no evidence from fossils to support the conclusion that a cupule was produced by any bennettitalean.

Familial characters of cycadeoid seed cones—Bennettitalean species with massive, sparsely branched trunks traditionally have been assigned to the Cycadeoidaceae Buckland (i.e., *Cycadeoidea* Buckland and *Monanthesia* Wieland ex Delevoryas), whereas those with more slender, highly branched trunks are most often grouped within the Williamsoniaceae (e.g., *Williamsonia* Carruthers; Alvin et al., 1967; Watson and Sincock, 1992). Cones of the Cycadeoidaceae traditionally have been regarded as both monosporangiate and bisporangiate and are borne among the leaf bases on stout trunks (Delevoryas, 1968). However, there is some evidence that the monosporangiate cones of some species may actually represent bisporangiate cones for which the microsporangiate structures simply have not been recognized (Crepet, 1972). In contrast, cones of the *Williamsonia* are apparently all monosporangiate and are borne at the tips of lateral branches (e.g., Sahni, 1932). While some other genera of the Williamsoniaceae appear to bear bisporangiate cones (Watson and Sincock, 1992), cones of the family all appear to be borne at the tip of either main or axillary branches.

As now confirmed by the excellently preserved specimens from western Canada and elsewhere (Rothwell and Stockey, 2001; Stockey and Rothwell, 2001), seed cones of the two families display several other contrasting characters that allow for their familial assignment (Table 2). Whereas the interseminal scales and sporophylls of seed cones in the Cycadeoidaceae nearly parallel one another, those of the Williamsoniaceae do not. Instead, they radiate from the receptacle around an arc of up to 300°. Some bisporangiate cones of *Cycadeoidea* also have interseminal scales and sporophylls that radiate in many directions (e.g., Wieland, 1906, 1916; Delevoryas, 1968; Crepet, 1974), but those of the putative seed cones do not. Seeds of the Cycadeoidaceae have distinct longitudinal ribs below the apex of the micropylar canal, while those of the Williamsoniaceae are round or oval in cross sections at all levels (Seward, 1912; Rothwell and Stockey, 2001; Stockey and Rothwell, 2001). The sarcotesta is also distinctly different in seeds of the two families. Sarcotestal cells of Williamsoniaceae form small, radially protruding pegs (Stockey and Rothwell, 2001), whereas those of the Cycadeoidaceae are of two distinct types. Large, loosely arranged tubular cells extend from the base of the seeds to near the apex. Other large, thin-walled sarcotestal cells are attached to the sclerotesta and extend radially to accentuate the longitudinal ribs of the integument.

Systematic significance and conclusions—Although fossils play a crucial role in resolving deep branches in the polysporangiophyte tree (Kenrick and Crane, 1997), all too often the systematic importance of these data are not widely appreciated because of the combination of relatively low support values for many nodes, and the much more easily developed data used in molecular analyses. For seed plants, the anthophyte hypothesis was first developed using morphological data from both living and extinct taxa (Crane, 1985), and it has been supported by virtually every subsequent broad-based analysis of morphological characters (Doyle and Donoghue, 1986, 1992; Loconte and Stevenson, 1990; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996; Pryer et al., 2001).

Even as the homologies, definitions, and scorings of some characters have remained in dispute (cf. Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996), there is a concordance of results with respect to the existence of an anthophyte clade. We consider it to be unlikely that the results of all of these studies would include an anthophyte clade, unless they were detecting a true phylogenetic signal.

If this rationale is correct, then the degree of concordance among the results of analyses using different data sets and methodologies (not merely support values for the results of a given analysis) is the more valid test for hypotheses of phylogenetic relationships. Most current attempts to achieve congruence among cladistic studies of seed plants begin with the premise that the framework for spermatophyte relationships can be developed using molecular characters of living taxa, to which extinct taxa can be added later (e.g., Frohlich and Parker, 2000). Given the small number of extant seed plant groups (i.e., only five), the probability of ever achieving success using this approach may be extremely low (Felsenstein, 1978; Sanderson et al., 2000). As a result, the alternative approach of developing the framework for seed plant relationships from morphological characters of living and extinct taxa, and then using this framework to test which results of the more restricted analyses (i.e., of living taxa only) reflect a true phylogenetic signal, may prove more fruitful. Although the latter approach necessitates the extremely time-consuming tasks associated with developing and scoring morphological characters (particularly for extinct clades), it may be our current best option for resolving the overall pattern of land plant phylogeny. In this regard, the continued focus on identifying, developing, and clarifying cladistically informative morphological characters for extinct clades is an important priority for systematic paleontology.

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