Morphology of Bennettitalean fructifications

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The Bennettitales dominated the vegetation throughout the world during Mesozoic Era. In external morphology they were cycad-like, but had distinct type of fertile parts. Fructifications were monosporangiate or bisporangiate. In seed-bearing fructifications a compact layer of fertile and sterile scales surrounded the conical/hemispherical receptacle. On the basis of ontogeny and anatomy, both types of scales are described as appendicular structures and derived the fructification from *Cordaianthus*. Bisexual fructifications resemble cycadeoideas. Male fructifications are unique and can be correlated neither with any known extinct nor extant plant. Bennettitales originated independently from protoseminales, a plexus which also gave rise to cordaitales and pteridosperms. Bennettitales ended abruptly.

Key-words—Morphology, Bennettitales, Fructifications, Mesozoic (India)

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सारांश

बैन्नेटाइटेली फलनों की आकारिकी

बी० डी० शर्मा

मध्यजीवी महाकल्प में समस्त विश्व में बैन्नेटाइटेली पौधों की बाहुल्यता थी। बाह्य आकार में ये साइकेडों की भाँति थे, परन्तु अबन्ध्य अंगों में द्विबीजाणुधानीय थे। बीज़-धारक फलनों में अबन्ध्य एवं बन्ध्य शल्क-पत्रों की एक सघन तह से शंक्वाकार/अर्धगोलाकार धानी चारों ओर से घिरी है। पादपवृत्त एवं शारीर के आधार पर दोनों ही प्रकार के शल्क पत्रों को उपांगीय संरचनाओं के रूप में वर्णित किया गया है। उभयलिंगी फलन साइकेडिऑइडियों से अनुरूपता प्रदर्शित करते हैं। नर फलन विशिष्ट प्रकार के हैं तथा इन्हें किसी भी वर्तमान अथवा अश्मित पौधे से सम्बद्ध नहीं किया जा सकता। बैन्नेटाइटेल्स प्रोटोसेमीनेल्स से विकसित हुए हैं और इन्हीं से ही कोर्डेटेल्स एवं टेरिडोस्पर्मी पौधों का विकास हुआ है। बैन्नेटाइटेली पौधे अचानक ही विलुप्त हो गये।

THE bennettitalean plants dominating the vegetation during the Mesozoic were cycad-like in external appearance and anatomy, but their fertile parts had a distinct morphology from the latter. Some of the bennettitalean fructifications were bisexual, e.g., *Wielandiella* Nathorst 1880, *Williamsoniella* Thomas 1915, *Sturianthus* (*Sturiella*) Kräusel 1948 and *Amarjolea* Bose *et al.* 1984, while others had either seed-bearing fertile parts, e.g., *Williamsonia* Carruthers 1870 and *Bennettiticarpus* Harris 1932, or the fructification was microsporangiate, e.g., *Weltrichia* Braun 1849. The Cycadeoidales had the fructifications quite similar to those of the Bennettitales except that they were lateral, bisexual and embedded in the cortex of the trunk (Wieland, 1906, 1916), whereas in Bennettitales the fructifications were terminal and of exposed type. In the present paper the morphology of the bennettitalean fructifications is discussed.

Since the publication of Williamson (1868) on *Zamites gigas* Lindley & Hutton, a number of interpretations have been published on the morphology of fructifications of bennettitalean plants (Carruthers, 1870; Lignier, 1907; Arber & Parkin, 1907; Nathorst, 1909; Arber, 1919; Krässer, 1919; Sahni, 1932; Delevoryas, 1968; Harris, 1969; Sitholey & Bose, 1971; Sharma, 1969, 1982). On the basis of recent investigations, the interpretations suggested by earlier authors are rediscussed in this paper.

A typical bennettitalean seed-bearing fructification consists of a small pedicel provided with spirally arranged, linear, flat bracts which protect the conical/hemispherical receptacle. The

receptacle is either completely covered with a compact layer of seminiferous (fertile) and interseminal (sterile) scales, e.g., *W sewardiana* Sahni 1932, *Williamsonia guptai* Sharma 1968, *W. harrisiana* Bose 1968, or the apical portion of receptacle is naked, e.g., *Williamsonia gigas* Carruther (Harris, 1967), *Williamsoniella coronata* Thomas 1911. The fertile scales bear orthotropus ovules, while the distal ends of sterile scales are swollen and fleshy, 5-8 sterile scales surround a fertile scale. In bisexual fructifications, a whorl of approximately 20 microsporophylls is present surrounding the central receptacle, e.g., *Amarjolea dactylota* and *Williamsoniella coronata*. Bose (1968) and Harris (1969) suggested that the microsporangiate fructifications be included under the genus *Weltrichia* Braun 1843. In a male fructification there are approximately 20 pinnate microsporophylls in a whorl. Microsynangia are produced on pinnae or on finger-like appendages. The presence of a whorl of bracts surrounding the whorl of microsporophylls (Sharma, 1969), or its absence (Sitholey & Bose, 1971) in *Weltrichia santalensis* Sitholey & Bose 1971 is a controversial problem and has been discussed in the present paper in the light of new collections and recent observations.

MATERIAL AND METHODS

The material for the present paper was collected from different places throughout the Rajmahal Hills. Impressions of *Weltrichia* occur frequently at Sakrigalighat and Dhokuti, while petrified materials of seed-bearing Williamsonias occur in the fossiliferous localities of Amarjola, Chilgujari and Hiranduba. Epidermal structures of bracts were studied by using an adhesive 'Quickfix'; for anatomical details slides were prepared by the usual method of cutting, grinding and polishing. Because of the fragile nature of Amarjola material, it was boiled in Canada balsam prior to sectioning with the help of a wire band saw. Slides were mounted in Canada balsam.

DESCRIPTION

Seed-bearing Williamsonias—They are of two types, i.e., 'Open type' and 'Close type' (Gupta 1958). In open type the bracts are large and spread, while the central conical receptacle is comparatively smaller and possesses a narrow layer of fertile and sterile scales (*Williamsonia sahnii* Gupta 1943). Gupta (1943) suspected the presence of a whorl of microsporophylls surrounding the central receptacle, but no such structure could be seen in the specimens present in his collection.

At the fossiliferous locality of Amarjola, the petrified seed-bearing Williamsonias of close type occur in three forms, i.e., complete fructifications covered with bracts (Pl. 1, figs 1-7, 9-12, 14-23), bractless fruits (Pl. 1, fig. 13) and the naked receptacles (Pl. 2, fig. 1). These are bulbous, oval, globose in shape and ranging in size from 2.5 × 2 to 12 × 10 cm (Pl. 1, figs 1-23). However, at the bases of all these forms, a circular depression is present (Pl. 1, figs 2, 4, 6, 7, 13) representing the point of detachment of the fructification from the peduncle (parent plant). The bracts are linear, curved structures (Pl. 1, figs 3, 4, 6) bearing stomata on their outer surfaces. Epidermal cells are squarish to rectangular and nonsinuous; stomata are typical syndetocheilic (Sharma, 1968; Bose & Kasat, 1969). Anatomy of the receptacle shows a large number of inverted vascular bundles arranged in a ring surrounding a wide pith. Loss of secondary wood and invertion of bundles take place in the peduncle of the fructification (Sharma, 1973). Sharma (1970a) described a receptacle to be the two-noded structure. Vascular supply in scales (fertile & sterile scales) originates indirectly from vascular bundles of the receptacle.

Leaving aside a few exceptions (*Williamsonia gigas, Williamsoniella coronata*), in majority of bennettitalean fructifications the scales are arranged in basipetal manner and cover the entire surface of the receptacle. In the basal portion of the receptacle there is no differentiation of fertile and sterile scales, and all the scales are identical. Sharma (1974a) described the ontogeny of scales and ovules. The body of a mature ovule may be divided into three portions, i.e., stalk, swollen body and long micropyle (Pl. 2, fig. 4). The stalk has a distinct cordate base. A narrow nucellar stalk (Pl. 2, fig. 9) is surrounded by 4-5 cell-thick layer of integument which gradually becomes narrower towards the distal side so much so that in the body portion it remains only 1-2 cell-thick layer (Pl. 2, fig. 10). A

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PLATE 1

1-23. Petrified seed-bearing Williamsonias from Amarjola, Rajmahal Hills. Note variations in shape and sizes. All possess a definite circular detachment point at the basal end, × 3/4.

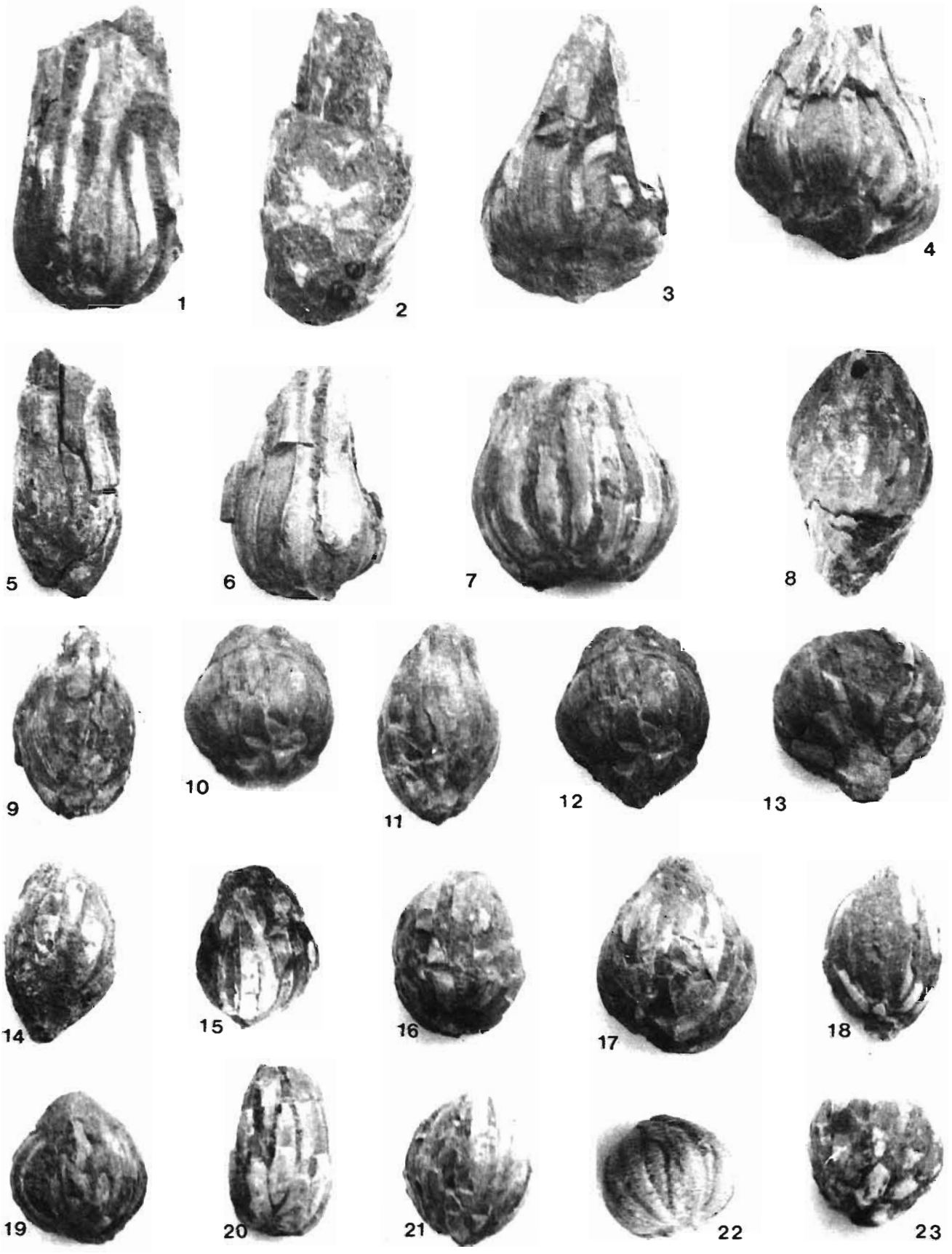

PLATE 1

poorly developed vascular strand enters the base of nucellar stalk and travels up to its distal end. In the body region of ovule the nucellar stalk expands into an oval/globose nucellus. It is closely adhered with the integument and bears a deep pollen chamber (Pl. 2, fig. 5) in its distal end (Sharma, 1974b). Micropyle is long and lined by a 3-5 cell-thick layer of integument (Pl. 2, figs 2-4). The innermost layer of cells are modified and look similar to the interlocking cells of *Gnetum* (Sharma, 1970, 1980). In a seed, the micropylar canal is blocked (Pl. 2, figs 8, 10) by the nucellar plug (Sharma, 1976).

The distal portion of nucellus is made up of elongated cells (Pl. 2, fig. 7). A megaspore mother cell is differentiated in the nucellus which divides by meiosis and forms 4 cells in a linear tetrad. The lowermost cell acts as functional megaspore. Endosperm is produced by free nuclear divisions of the functional megaspore. Wall formation begins from the micropylar end (Sharma, 1974a). Three or four archegonia (Pl. 2, fig. 6) are produced in the upper portion of endosperm (Sharma, 1979). The seed (Pl. 2, fig. 10) is dicotyledonous (Sharma, 1970b). With the formation of seeds, the compact layer of scales also gets detached from the receptacle. However, individual seed could never be collected as it remains encircled by the surrounding interseminal scales. The seed-bearing fertile parts are identical in all the bennettitalean fructifications, viz., *Williamsonia, Williamsoniella, Wielandiella, Sturianthus* and *Amarjolea*. In bisexual fructifications the microsporophylls show wide variations in their structures. In *Amarjolea* the microsporophylls are well-developed and have been compared with that of the *Cycadeoidea* (Delevoryas, 1968; Bose *et al.*, 1984). In *Williamsoniella* (Thomas, 1915; Harris, 1969), the microsporophylls are comparatively lesser developed than *Amarjolea*, while in *Wielandiella* the microsporophylls are much reduced and do not possess the pollen-bearing structures. Pollination mechanism is yet to be understood in these fructifications.

The microsporangiate bennettitalean fructifications were comparatively larger and open type of flowers. *Weltrichia santalensis* Sitholey & Bose 1971 is one of the best known male fructification. They suggested the presence of a single whorl of microsporophylls surrounding a cup-shaped receptacle. Sharma (1969) described two whorls, the outer of sterile bracts (Pl. 3, fig. 2) and inner of microsporophylls (Pl. 3, fig. 1). The microsporophylls were twisted, bearing two rows of appendages on abaxial side in the proximal portion (Pl. 3, figs 3, 4) and one row on adaxial side in the distal portion. Two parallel rows of microsporangia were produced adaxially on the midrib of each appendage (Pl. 3, figs 5, 6). Sitholey and Bose (1971) did not agree with the interpretations of Sharma (1969). On the basis of the study of additional collections from Sakrigalighat earlier interpretations of the author get confirmed. A specimen collected from Dhokuti possesses a whorl of only bracts, and microsporophylls are absent in it.

Weltrichia (Williamsonia) companulatiformis Sharma 1969 is another species of microsporangiate bennettitalean flower. Sitholey and Bose (1971) treated it to be a junior synonym of *W. santalensis*. The author, however, disagrees with them and considers it a distinct species.

DISCUSSION

Bennettitales were peculiar plants which resemble primitive gymnosperms in vegetative features (Cycads) while their fertile parts had the characters of advanced gymnosperms (Gnetales) and angiosperms (Wieland, 1906, 1916; Arber & Parkin, 1907; Pearson, 1929; Seward, 1917; Arber, 1919). The presence of a definite abscission point at the base of young fructification suggests its detachment from the parent plant, a condition identical to the ovule of the extant genus *Ginkgo* (Chamberlain, 1935). Probably similar to *Ginkgo*, in bennettitalean plants too the fertilization and formation of embryo took

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PLATE 2

1-10. Seed-bearing Williamsonias.
1. Naked receptacles from Amarjola, × 1/4.
2, 3. Cross section—Compact layer showing circular micropyles and surrounding interseminal scales.
4. Longitudinal section—Compact layer showing an ovule with long micropylar canal and interseminal scale. × 40.
5. Same, pollen chamber in upper portion of nucellus, × 150.
6. Archegonia chamber with 3-4 archegonia in upper portion of endosperm, × 200.
7. Nucellus with elongated cells, × 200.
8. Mature ovule with nucellar plug in micropyle, × 50.
9. Distal portion of nucellar stalk is seen dividing into two and the surrounding integument, × 50.
10. Upper portion of seed, × 30.

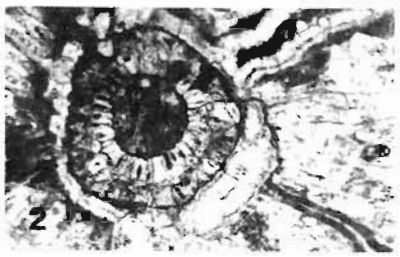
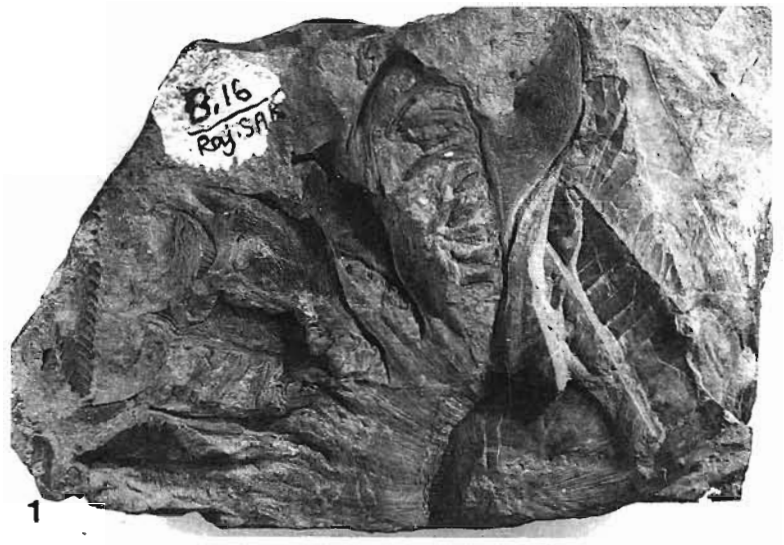


PLATE 2



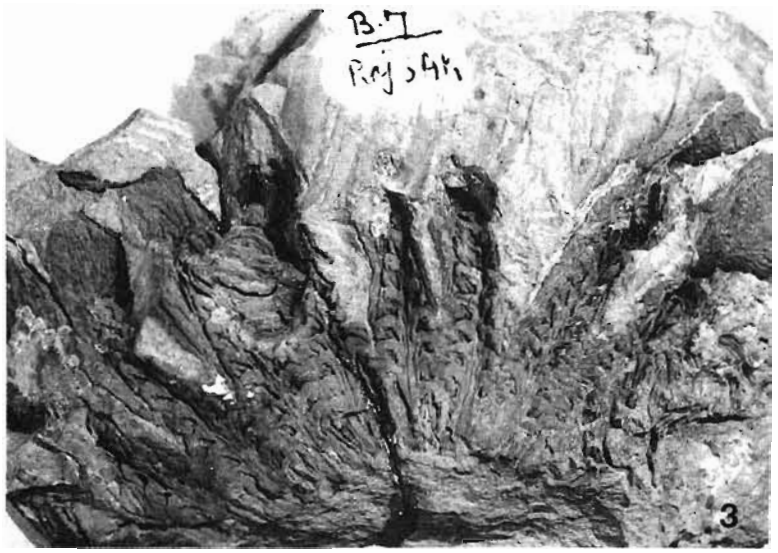


PLATE 3

place on the ground and not on the parent plant. However, in morphology, *Ginkgo* ovule is distinct from the bennettitalean fructification.

The anatomy of receptacle suggests a mixture of primitive and advanced features. Though, there are large number of vascular bundles in the vascular cylinder, they are inverted with exarch protoxylem points; secondary growth is absent. There is no direct vascular supply to the scales from bundles of the vascular cylinder. Seminiferous and interseminal scales get independent vascular supply from the peripheral vascular strands of receptacle (Sharma, 1970) suggesting appendicular nature of scales, a view contrary to that of Lignier (1908) who believed seminiferous scales axillary to interseminal scales.

In seed-bearing Williamsonias there is no distinction of fertile and sterile scales at the basal portion of receptacle, i.e., in ontogeny both kinds of scales are identical (Sharma, 1974a). Formation of ovule begins from periphery to inner side, i.e., the micropyle is differentiated first and the funiculus develops quite late. Integument originates as a circular unit, unlike that of pteridosperms (Lyginopteridales & Medullosales; Meyen, 1987).

Sharma (1982) derived bennettitalean seed-bearing fructification from *Cordaianthus* as a result of reduction and swelling of inflorescence axis to receptacle and modification of the axillary buds-bearing megasporophylls and scales to seminiferous and interseminal scales. However, in ovule ontogeny *Cordaianthus* and bennettitalean fructifications are different from each other.

The bisporangiate bennettitalean fructifications show similarities with that of the Cycadeoidales. However, in the former the microsporophylls are comparatively less developed. A gradual sequence may be drawn from monosporangiate to bisporangiate, i.e., *Williamsonia, Wielandiella, Williamsoniella, Amarjolea* to *Cycadeoidea*, or vice versa. It is difficult to say which of the two conditions—monosporangiate or bisporangiate, is primitive. However, in geological time, unisexual Williamsonias appeared earlier than bisexual Cycadeoideas. The microsporangiate bennettitalean fructifications show similarities with pteridosperms in the presence of pollen-bearing organs as microsporangia and their direct association with the microsporophylls. The microsporophylls were pinnate structures in which the pinnae modified into finger-like appendages. In gross morphology, the microsporangiate bennettitalean fructifications can neither be related with any extinct nor extant group of plants.

Mehra (1988) derived Bennettitales independently from Protoseminales, a plexus which gave rise to Cordaitales and Pteridosperms. Bennettitales achieved maximum evolutionary development in a short geological span from Upper Triassic to Lower Cretaceous and then ended abruptly.

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PLATE 3

1-6. Male fructification *Weltrichia santalensis*

1. A portion of fructification with microsporophylls and bracts surrounding a circular receptacle, × 3/4.
2. A whorl of sterile bracts, × 3/4.
3. A whorl of twisted microsporophylls, × 3/4.
4. Twisted microsporophylls with two rows of markings of appendages, × 2.

5 6. Finger-like appendages, each with two rows of microsporangia, × 2.

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