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Studies on the bennettitalean fructification *Williamsonia* Carruthers

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ABSTRACT

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The genus *Williamsonia* was instituted on the basis of study of the specimens collected from the Secondary rocks of Yorkshire (Britain). More than 80 species of this genus are known from the world and over a dozen from the Indian sub-continent. This seed bearing cone has a conical/hemispherical receptacle covered by a compact layer of seminiferous and interseminal scales. In some species (*W. gigas*), the apical portion of the receptacle is naked and without scales. Each fertile scale has an orthotropus ovule with a long micropylar canal. 5-8 sterile scales surround an ovule which has an uneven, non-vascularised integument and free nucellus with a long nucellar stalk. Seed is endospermic with a dicot embryo. Linear, little curved bracts protect the compact layer of scales. Relationship of *Williamsonia* with allied taxa of Bennettitales (*Cycadeoidea, Williamsoniella* and *Amarjolia*) is discussed and made use in tracing the phylogeny of *Williamsonia* and origin of angiosperms.

Key-words: Bennettitalean fructification, *Williamsonia*, phylogeny, Mesozoic, India.

INTRODUCTION

The class Bennettitopsida is divided into two orders, i.e. Cycadeoidales and Williamsoniales (Taylor et al. 2009). In the former, the fructifications are bisexual, lateral and embedded in the cortex of tuberous stem whereas in the latter, the fructifications, in majority, are unisexual and terminal on columnar stems or branches. Bisexual fructifications also exist in the order Williamsoniales, e.g. in *Williamsoniella* Thomas (1915) and *Amarjolia* Bose et al. (1984). In old literature, the term *Williamsonia* was also used for the male fructifications, e.g. *Williamsonia santalensis* Sitholey & Bose (1953), *W. campanulatiformis* Sharma (1969), but now *Williamsonia* is used only for the seed bearing fructifications (Bose 1967, Harris 1969) and the male ones are described under the genus *Weltrichia* Braun.

Feistmantel (1876), for the first time, reported *Williamsonia* (*W. blanfordii*) from the Mesozoic rocks of Kutch. Feistmantel (1877) also described *W. microps* and *Williamsonia* cf. *W. gigas* from the Rajmahal Hills, Bihar (now Jharkhand). Since then, a number of species of the genus *Williamsonia* have been described from the Indian sub-continent (Sharma 1977, Banerji 1992, Pandya & Sukh-Dev 1990). These are: *W. indica* Seward (1917), *W. sewardiana* Sahni (1932), *W. sahnii* Gupta (1943), *W. harrisiana* Bose (1968), *W. guptae* Sharma (1968), *W. amarjolense* Sharma (1968), *W. seniana* Bose & Kasat (1969), *Williamsonia* cf. *W. scotica* Sharma (1970a), *W. kakadbhitensis* Bose & Banerji (1984), *W. trambauensis* Bose & Banerji (1984) and *W. sukhpurensis* Bose & Banerji (1984).

Phylogeny of the bennettitalean plants has long been a controversial topic. Wieland (1906, 1916), Arber and Parkin (1907), Lignier (1909), Nathorst (1909), Seward (1911, 1917), Thomas (1915), Arber (1919), Scott (1923), etc. correlated them with Magnoliales (angiosperm). Doyle and Doneghue (1986, 1987) and Doyle (2006), on the basis of cladistic studies, showed a common ancestor of Cycadeoidales and early angiosperms. Crane (1985, 1986, 1988) discussed the evolution of gymnosperms using cladistic technique and suggested a common clade of Bennettitales and early angiosperms. But, the Bennettitales differ fundamentally from angiosperms in morphology, anatomy and reproductive biology (Eames 1961, Sharma 1984a, b). Sharma (1982) suggested derivation of williamsonian fructification from Cordaitales as a result of modification of scales into interseminal scales and megasporophylls into fertile scales (Florin 1951).

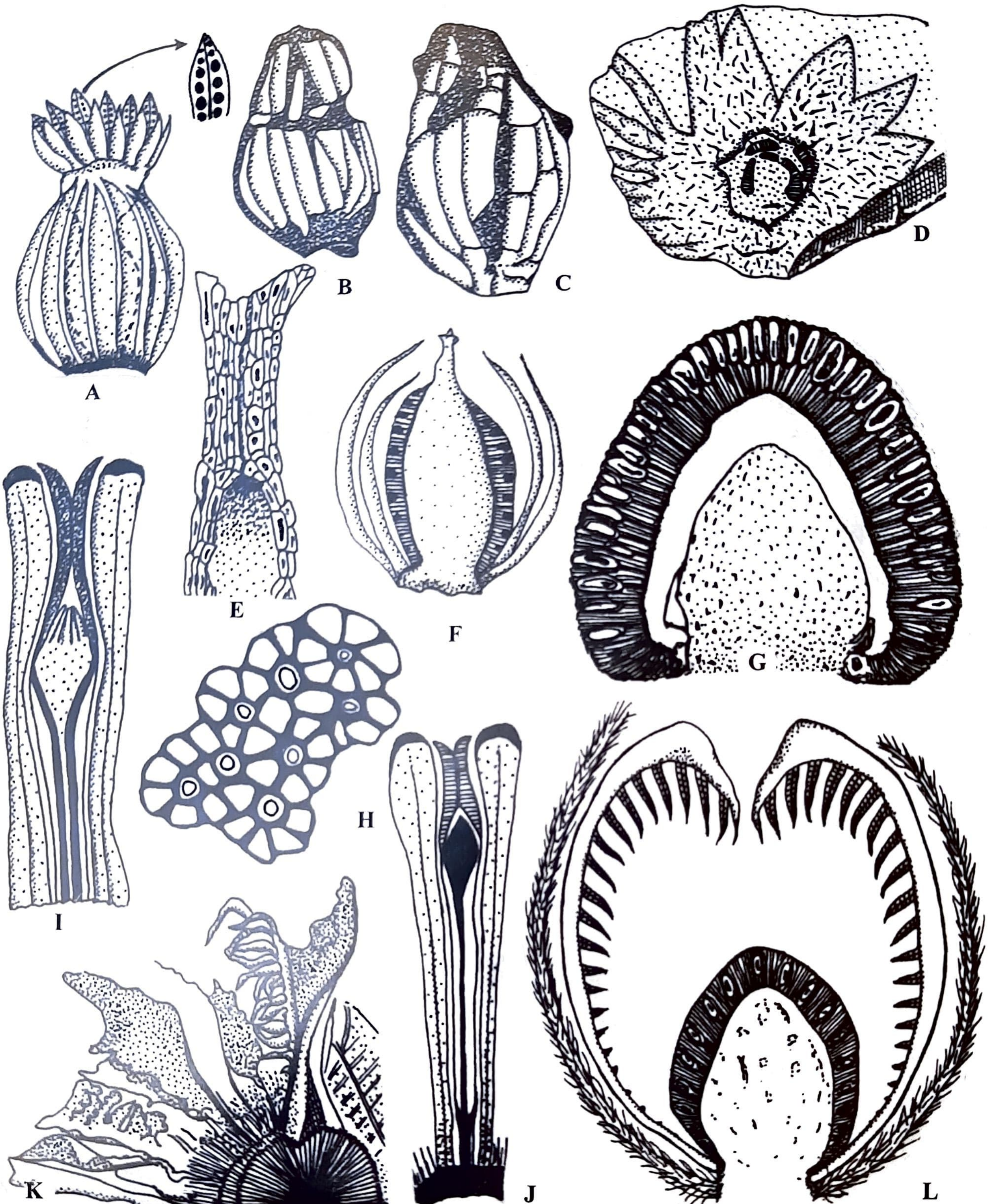
MATERIAL AND METHOD

The material of the seed bearing fructifications of *Williamsonia* has been collected from the Mesozoic rocks of many countries of the world (Trutunowa-Ketova 1963, Harris 1969, Taylor et al. 2009) but the permineralized/petrified specimens are available only at few places, viz. Scotland, Rajmahal Hills, India, U.S.A., etc. (Seward 1911, Sahni 1932, Bose 1968, Sharma 1968, 1977, Delevoryas & Gould 1973, Banerji 1992, Stockey & Rothwell 2003). In the Rajmahal Hills, Amarjola is the treasury of petrified specimens of *Williamsonia* (Sharma 1974b, 1977, Bose 1974, Bose et al. 1990). At Amarjola, the fossil specimens of *Williamsonia* are taken out from the hard, sandy, dark brown rock by digging with an axe. Being soft and fragile, specimens need cooking in canada balsam prior to sectioning with a wire bandsaw. Slides were prepared by the usual technique of cutting, grinding and polishing methods and mounted in dilute canada balsam (Sharma 1970a, 1974c).

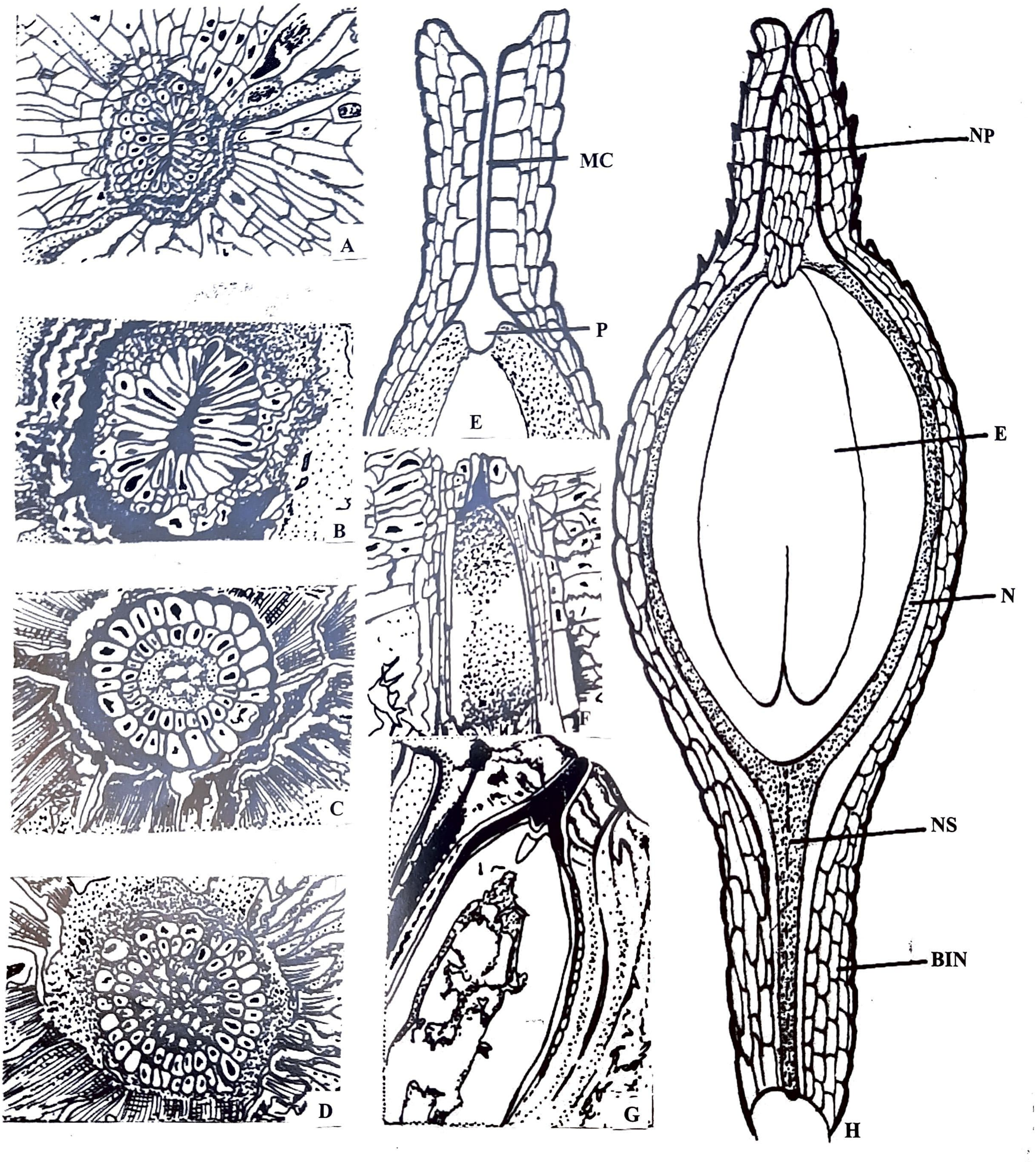
DESCRIPTION

Gupta (1958) divided the williamsonian fructifications into 'close type' (*W. sewardiana, W. harrisiana, W. guptae*, Text-figure 1-B, C) and 'open type' (*W. sahnii*, Text-figure 1-D). In the former, the fertile portion is covered by linear, little curved bracts while in the latter, the bracts get spread and the fertile portion exposed. In both the types, there is a central conical to hemispherical receptacle (Text-figure 1-G), which is covered with a compact layer of fertile and sterile scales. In *W. gigas* Carruthers, the compact layer of scales is present only on the lateral sides of the receptacle and its terminal portion is naked (Harris 1967, Text-figure 1-F). Arber (1919) showed the presence of an urn of microsporophylls at the terminal portion of the conical receptacle of *W. gigas* (Text-figure 1-A). Each microsporophyll had two adaxial rows of microsynangia. Arber (1919) aimed to correlate *Williamsonia* fructification with a bisexual flower of an angiosperm. But, Harris (1967) did not approve Arber's concept and called *W. gigas* only a seed bearing fructification.

Sahni (1932) described the structure of a petrified specimen of *Williamsonia sewardiana* and suggested its association with the stem *Bucklandia indica* Seward and leaves of *Ptilophyllum cutchense* Morris. Sahni (1932) also suggested the structure of its seed (Text-figure 1-J). At the terminal end of the long nucellar stalk, there is an oval nucellus which is free from integument. Sharma (1975) studied a nicely preserved specimen of *W. sewardiana* and noticed the adherence of nucellus with the uneven, non-vascularized integument (Text-figure 1-I). Sharma (1970a) studied the structure and arrangement of fertile and sterile scales in a specimen of *Williamsonia* cf. *W. scotica*. Sharma (1970b) described the anatomy of the receptacles of *Williamsonia* collected from Amarjola and reported the presence of inverted bundles. Sharma (1970c) also described the structure of the seed of *Williamsonia* (Text-figure 1-I). The basal portion of the fertile scale is like an inverted cup and



Text-figure 1. A. *Williamsonia gigas* with an urn of microsporophylls at the top. One microsporophyll enlarged for showing two adaxial rows of microsynangia (as suggested by Arber 1919), x1. B, C. *Williamsonia guptae*, two different sized fructifications, x0.75. D. *Williamsonia sahnii*, spread bracts and the central seed bearing receptacle, x1. E. Micropylar canal in *Williamsonia* ovule, x80. F. *Williamsonia gigas,* showing bracts, lateral compact layers of fertile and sterile scales and naked terminal portion of receptacle (from Harris 1967), x1. G. *Williamsonia*, L.S. with a compact layer of fertile and sterile scales covering the central receptacle, x2. H. *Williamsonia*, tangential section through compact layer of fertile and sterile scales. An ovule is surrounded by 5-8 scales, x30. I. L.S. of an ovule with two sterile scales, x30. J. *Williamsonia sewardiana*, L.S. of ovule and two interseminal scales. Nucellar stalk long, integument uneven in thickness, x30 (from Sahni 1932). K. *Weltrichia santalensis*, male fructification with twisted microsporophylls surrounding a cup shaped receptacle, x1. L. *Amarjolia dactylota*, L.S. of bisexual fructification showing hairy bracts, large microsporophylls with adaxial appendages, compact layer of fertile and sterile scales surrounding the central conical receptacle, x3.



Text-figure 2. A-H. *Williamsonia* sp. A-D. Tangential cross sections through micropylar portion from outside to inside. Note interlocking cells and wall cells, x200. E. L.S. of ovule showing long micropylar canal and a pollen chamber in nucellus, x200. F. An ovule in L.S. showing free nuclear female gametophyte, x200. G. L.S. of seed with a distinct nucellar plug in micropyle, thin integument and poorly preserved embryo, x80. H. L.S. of a seed with an uneven, non-vascularized integument, long nucellar stalk, dicotyledonous embryo in megagametophyte and a nucellar plug in micropyle, x200. (MC: Micropylar canal, P: Pollen chamber, NP: Nucellar plug, E: Embryo, N: Nucellus, NS: Nucellar Stalk, BIN: Basal portion of integument).

nucellar stalk is divided into two parts. In a mature seed, a distinct nucellar plug is present in the micropylar canal (Text-figure 2-G, H). An ovule has a long micropylar canal (Text-figure 1-E). Its wall is 3-4 cells thick with interlocking cells lining the canal (Text-figure 2-E) identical to that of *Gnetum* (Maheshwari & Vasil 1961). Serial cross sections through the long micropylar canal (Text-figure 2-A to D) show all details. Sharma (1974a) could also report the presence of pollen chamber in an ovule of *W. guptae* (Text-figure 2-E). 5-8 interseminal scales surround an ovule (Text-figure 1-H). Sharma (1974c) studied a large number of sections cut through the fertile and sterile scales. Fertile and sterile scales develop in basipetal succession (Text-figure 1-G). Mature ovules/seeds are present at the top of the receptacle (Sharma 1976). Megagametophyte was produced by free nuclear divisions of the functional megaspore. A number of ovules could be seen with many free nuclei (Text-figure 2-F). Generally, a distinct detachment point is present at the basal portion of the williamsonian fructification (Sharma et al. 2013). That is why none of the fructification could be collected attached to the parent stem, probably a condition identical to that of *Ginkgo* (Chamberlein 1935, Sharma 1976, Gifford & Foster 1989). That is, development of embryo took place on the ground and not on the parent plant. Sharma (1979) could also figure a group of archegonia in an ovule of *Williamsonia* collected from Amarjola, Rajmahal Hills, India.

The bisexual fructification *Amarjolia* Bose et al. (1984) resembles *Williamsonia* in external morphology but inside the bracts it has large fleshy microsporophylls covering the receptacle bearing a compact layer of fertile and sterile scales (Text-figure 1-L).

The male fructification *Weltrichia* has large spreading microsporophylls surrounding a cup-shaped receptacle (Text-figure 1-K). Microsporophylls have finger like appendages which bear microsynangia in rows (Sharma 1969, Sitholey & Bose 1971).

PHYLOGENY

Despite of a long history of investigations (Carruthers 1870) and study of beautifully preserved specimens of *Williamsonia,* our knowledge about its relationship and origin remains incomplete and controversial because of the theoretical interpretations given without making proper studies on the fructification. Secondly, majority of workers have related it to angiosperms. Arguments given in support and against are discussed below:

1. **Bisexual nature:** Presence of bisexual nature of fructifications (*Cycadeoidea, Williamsoniella, Amarjolia*, Text-figure 1-L) favours angiospermy. Similarly, the arrangement of male and seed bearing organs also favours relationship with angiosperms. But neither the structure of microsporophylls, i.e. the spread one (*Weltrichia*, Text-figure 1-K) nor the fleshy ones (*Cycadeoidea, Amarjolia*, Text-figure 1-L) are comparable to that of the androecium of an angiosperm flower. No group of plants is known to have a structure identical to that of stamen of an angiosperm.
2. *Williamsonia* is a unisexual seed bearing fructification. An ovule bearing scale (seminiferous scale) is surrounded by 5-8 interseminal (sterile) scales (Text-figure 1-H). Stockey and Rothwell (2003) correlated the sterile scales with the reduced megasporophyll. Ontogeny of scales (Sharma 1974c) suggests the origin of both sterile and fertile scales from a common, undifferentiated tissue. But their structures are not identical. Many botanists considered the surrounding sterile scales with the 'contents' of carpellary wall (Arber & Parkin 1907, Lignier 1907, 1909, Nathorst 1909). How one will explain the occurrence of common sterile scales (Text-figure 1-H) for two or more ovules?
3. **Bitegmic seed coat:** Crane (1986) pleaded for the presence of bitegmic ovules in *Cycadeoidea*. Bitegmic seed coat is a feature of angiospermous plants (Eames 1961). The

structure of ovule/seed and the surrounding interseminal scales both in *Cycadeoidea* and *Williamsonia* are identical (Wieland 1906, 1916, Seward 1917, Delevoryas 1962, Taylor et al. 2009). There is only a single uneven and non-vascularized integument (Text-figure 1-I, J, Text-figure 2-G, H) in the bennettitalean plants unlike the bitegmic seed coat of angiosperms (Sahni 1932, Sharma 1970c, 1977).

4. In a mature bennettitalean seed, a distinct nucellar plug is present (Text-figure 2-G, H), a condition that exists in some of the pteridosperms as a central column (Doyle 2006, Taylor et al. 2009) but not known in angiosperms.
5. The long nucellar stalk of *Williamsonia* (Text-figure 1-I, J, Text-figure 2-H) is not comparable to any structure of an angiosperm seed.
6. **Relationship with the cordaitalean plants:** Sharma (1982) associated the interseminal scales of *Williamsonia* with the vegetative scales of *Cordaianthus*. But, this needs more evidence and further investigations.

On the basis of present investigation it is believed that making relationship between the bennettitalean plants and early angiosperms is an arbitrary exercise and further investigations are needed.

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