Bennettitales

Meaning of Bennettitales:

This group of fossil plants flourished well during the Triassic to Lower Cretaceous periods of Mesozoic era. As the Carboniferous period is called the **"Ages of Ferns ",** the Mesozoic era is called the 'Ages of Cycads'. It is due to the fact that Cycadeoideales co-existed with Cycadales during Mesozoic era from Jurassic up to Cretaceous period, and hence this period is called Age of Cycads.

Bennettitales are found either in the form of compressions or petrifactions. Due to Cycad-like form of their fronds and the presence of short stems covered with an armour of presistent leaf bases Bennettitales (Cycadeoideales) have been treated under Cycadophyta by some workers. However, the two groups are quite distinct from each other and maintain their independent identity.

Origin of Bennettitales

- Palaeobotanists believe that Bennettitales originated from Pteridospermales. But presence of stalked ovules in Bennettitalean members is a strong evidence against such a theory.
- Some workers have, however, shown resemblance between the fronds of Pteridospermales and the stalked ovules and inter-seminal scales of Bennettitales. But it is hard to imagine that stalked ovules and inter-seminal scales are homologous with the fronds.
- Discovery of a fossil plant, Westersheimia, from the Triassic of Austria, is again a step towards the possible Pteridospermean ancestry of Bennettitales. This genus occurs along with Bennetticarpus, the seed-bearing organs of Bennettitales.

characteristics

Some peculiar characteristics present in Bennettitales and not in any other group of gymnosperms, include:

- (i) Bisporangiate strobili,
- (ii) Synangium-bearing fused microsporophyll's,
- (iii) Close occurrence of ovules and inter-seminal scales, and
- (iv) Production of stalked ovules.
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Nomenclature, History and Distribution of Bennettitales

- The name **“Bennettitales”** has been given to honour J.J. Bennett, an English botanist. The fossilized trunk of genus Bucklandia was the first specimen of Bennettitales, collected from Great Britain in 1825. A silicified trunk of Cycadeoidea etrusca was discovered in 1867 in an Etruscan tomb.
- Williamson (1870) coined the name Williamsonia for a combination of foliage and reproductive organs of Williamsonia gigas. Professor Birbal Sahni (1932) discovered Widiamsonia sewardiana from the Upper Gondwana beds of India.
- A rich fossil flora of Bennettitales has been reported from Rajmahal Hills of Bihar (India). Some of the reported members include Bucklandia sahnii, B. indica, Dictyzamites, Otozamites benghalensis, Cycadinocarpus rajmahalensis, Sahnioxylon rajmahalensis, Williamsonia indica, W. sahnii and W. sewardiana.

classified

Arnold (1948) classified Bennettitales into two families viz. Williamsoniaceae and Cycadeoideaceae while Sporne (1965) divided it into following three families

- 1. Williamsoniaceae, e.g. Williamsonia, Pterophyllum.
- 2. Wielandiellaceae, e.g. Wielandiella, Williamsoniella.
- 3. Cycadeoideaceae, e.g. Cycadeoidea (=Bennettites)

Distinguishing Features of Bennettitales

- **:**
- 1. These extinct Mesozoic plants were present were present on the earth from Triassic to Cretaceous.
- 2. Bennettitales were so abundant during Mesozoic era that this period is known as 'Age of Cycads'.
- 3. The members of this group are found either as compressions or petrifactions.
- 4. The stems were stout or slender and had a wide pith.
- 5. The stem grew very slowly and had manoxylic wood.
- 6. Resembling living Cycads, the Bennettitalean leaves were mostly pinnately compound, and only occasionally simple.
- 7. Venation was open, and only rarely closed.
- 8. Syndetocheilic type of stomata were present.
- 9. The wall of the epidermal cells was sinuous.
- 10. The reproductive organs were organised in the form of hermaphrodite (e.g. Cycadeoidea) or unisexual (e.g. Wielandiella) "flowers", which in turn were protected by many bracts.
- 11. The 'flowers' developed in the axil of leaves.
- 12. Male reproductive organs were borne in a whorl. They were free or fused, entire or pinnately compound.
- 13. Microsporangia were present abaxially in the form of synangia.
- 14. Microsporophyll's sometimes surrounded megasporophylls forming hermaphrodite "flowers".
- 15. Ovules were numerous and stalked and borne on a conical, cylindrical or dome-shaped receptacle.
- 16. Many inter-seminal bracts were present on the ovule containing receptacle.
- 17. The scales or bracts were united at end to form shield through which micropyle protrudes.
- 18. Seeds were dicotyledonous.

Affinities of Bennettitales:

- **Resemblances of Bennettitales with Ferns:**
- Bennettitalean plants had multicellular ramenta on their entire body, a characteristic also seen in ferns.
- **Some other features suggesting the filicean affinity of Bennettitales include the presence of:**
- (i) Direct leaf traces,
- (ii) Scalariform tracheids, and
- (iii) Large pith.
- **Resemblances of Bennettitales and Cycads:**
- **Bennettitales resemble cycads in the:**
- (i) structure of their fronds,
- (ii) presence of short stems covered with an armour of persistent leaf bases,
- (iii) presence of barrel-shaped trunk,
- (iv) presence of very thick cortex, relatively thin wood and large pith in the stem,
- (v) manoxylic wood,
- (vi) monocolpate pollen grains,
- (vii) orthotropous ovules, and
- (viii) dicotyledonous embryo.

- On the basis of several such affinities, Chamberlain (1935) opined that both Bennettitales and Cycadales arose by parallel evolution from some common ancestor. The ancestral type must have had a foliar megasporophyll having the ovules at the apex as well as on both the sides.
- During course of evolution, the lateral ovules must have suppressed and the megasporophyll must have reduced to a stalk-like structure, and thus the Bennettitales must have come into existence. On the other hand there exist several fundamental differences between Bennettitales and Cycadales, already listed in Table 6.1.
- Due to so many dissimilarities it will not be possible to visualize any phylogenetic connection between two groups. Andrews (1961) concluded on the basis of such differences that both the groups have evolved along with two different and independent lines.

Resemblances and Difference between Bennettitales with Pteridospermales

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- **Characters common in both Bennettitales and Pteridospermales include:**
- (i) Presence of ramenta] hairs,
- (ii) Syndetocheilic stomata,
- (iii) Direct leaf traces,
- (iv) Similar anatomical details,
- (v) Leafy microsporophyll's, and
- (vi) Presence of cupule.
- The so-called bisporangiate 'flower' of Bennettitales could be compared with the bisporangiate fronds of Ptendospermales. Scientists are of the opinion that there exist two lines of evolution from Pteridospermales. Of these, one line gave rise to Bennettitales possessing both uni- and bisporangiate forms, and the other gave rise to mono-sporangiate forms of cycads.

Among the major differences include the:

- (i) Presence of smaller and stalked ovules in Bennettitales, which are absent in Bennettitales, and
- (ii) Prominent vascular supply to the nucellar tissue in Bennettitales which is not seen in Pteridospermales.
- **Resemblances of Bennettitales with Gnetales:**
- The two groups resemble each other in their seed structure but differ completely in several aspects. According to Rodin and Kapil (1969), **"the complex and highly specialised inflorescence of the Bennettitales, the presence of inter-seminal scales and some vegetative features fail to show homologies with Gnetum".**

Resemblances of Bennettitales with Angiosperms:

- Endarch siphonostelic vasculature of Bennettitales resemble very closely with sympetalous angiosperms. Frequent occurrence of scalariform tracheids in both the groups also brings them close together. Flowers of several primitive angiosperms (e.g. Magnoliaceae) also resemble closely with the strobili of Bennettitales, and on this basis Arber and Parkin (1907) opined that Bennettitales are the ancestors of flowering plants.
- Contrary to this, the Bennettitalean stamen is large, front -like and compound structure, and cannot be compared with that of the stamen of Magnoliaceae. Moreover, there is no point of comparison between typical carpel of Magnolia and ovule of Cycadeoidea which is strictly gymnospermous.
- Ovules are naked in Bennettitales while it is not so in angiosperms. The wood rays of Bennettitales lack marginal cells which are present in angiosperms. The two groups also differ in their general habit and floral morphology.

Features of Cycadeoideales

(A) Morphological features:

- In Cycadeoidea the stem was un-branched with a single crown of pinnate leaves at the tops, but some species had branched stem with a multiple crown. In some the stem was tuberous. In all cases the stem was covered up by persistent leaf bases as we find in Cycas.

(B) Anatomical Features:

- In structure the stem usually had large pith and thin vascular cylinder in which the protoxylem was endarch, thick cortex with a number of gum canals in it. There was small amount of secondary growth. Growth rings were only in few cases where the cambium persisted and was more active, so on the whole the stem anatomy was like those of present day cycads i.e., with large pith, broad cortex and narrow vascular cylinder.
- In some few cases, however, the vascular cylinder was sufficiently broad. In the stem there were no traces of mesarch vascular bundles which is a common feature of leaf traces of present day cycads.
- Another distinction from cycads was that the leaf traces were direct and no girdles while in present day cycads the girdling of leaf traces is quite common. The xylem had scalariform thickenings; pitted thickenings rather rare. This is an unusual feature because in the xylem of Cycadofilicales pitted thickening was very common and the group is much older than Cycadeoideales (Bennettitales).
- The feature can only be explained that it was case of reversion.

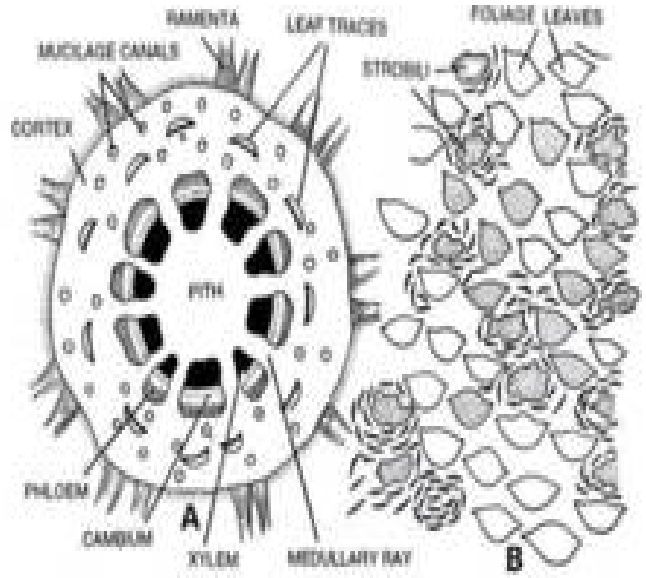
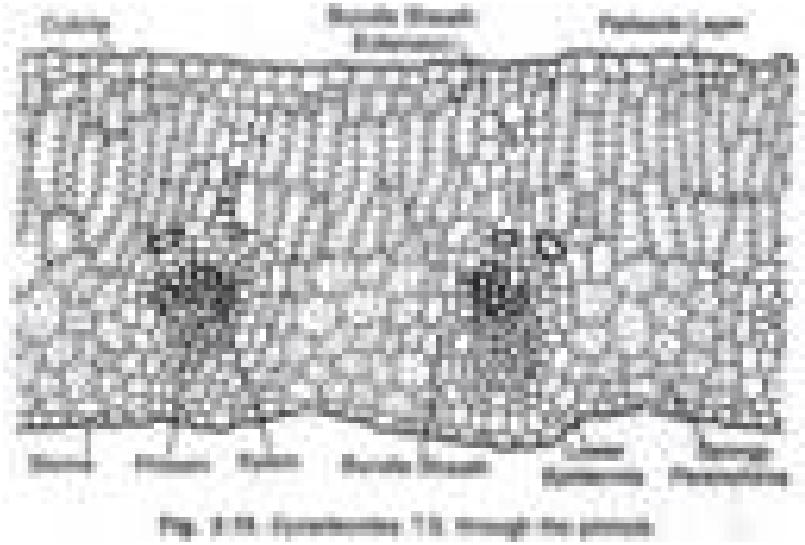


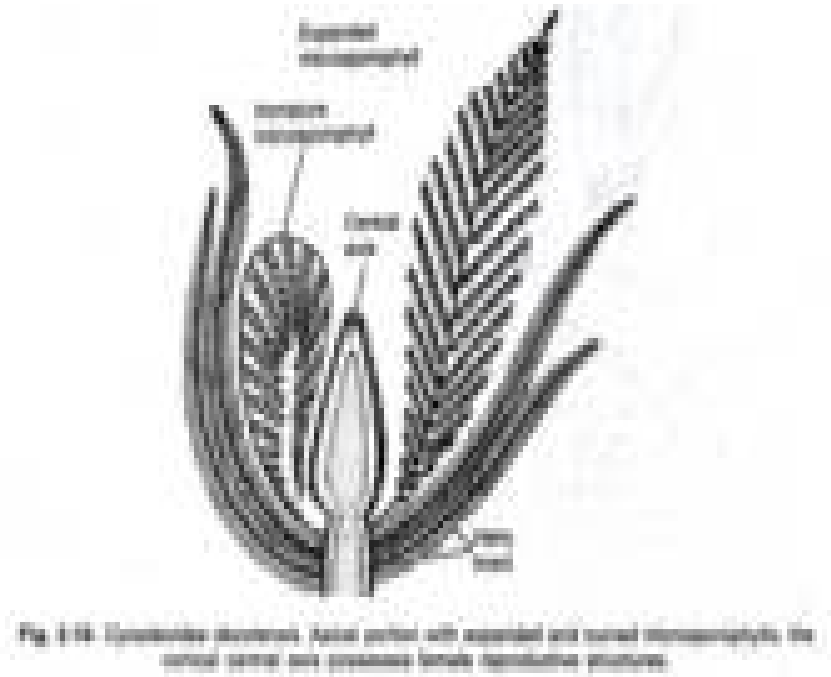
Fig. 2.13. Cycadeoidea. A, T.S. of stem showing primary structure; B, tangential section of a trunk.

Leaves of Cycadeoideales

- The leaves in Cycadeoidea (Bennettites) were large pinnate and showed xerophytic features. The vascular bundles in petiole and leaflets were mesarch with a strong sheath of sclerenchyma around it. Bipinnate leaves were rarely found in Cycadeoidea so the form and structure of leaf is practically like that of living cycads.



Fructification in Cycadeoideales



The fructification in Cycadeoidea was bisporangiate. The strobili were developed in the upper part of the plant in large numbers. In some cases each leaf seems to have an axillary strobilus.

The whole of the strobilus and the bases of leaves were covered up by large sized scales which were several cells in breadth and sometimes more than one cell in thickness; strobili so were axillary and borne at the tip of axillary stalk or peduncle and therefore, these strobili can be described as dwarf branches.

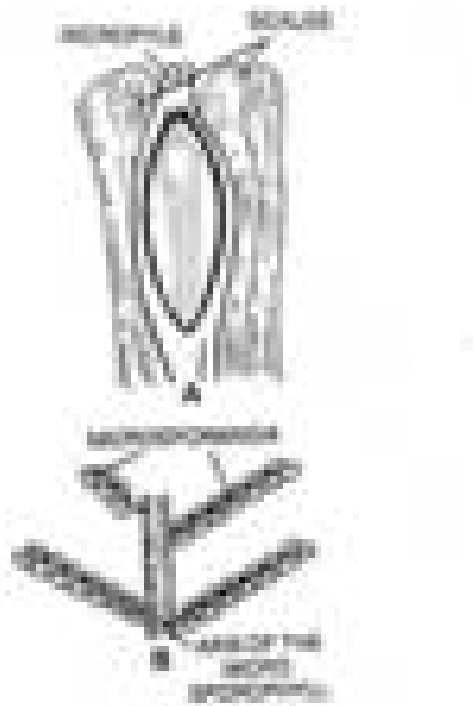


Fig. 3.17. *Cycadeoidea dacotensis*. A, longitudinal section of the seed; B, portion of a male reproductive organ with microsporangia

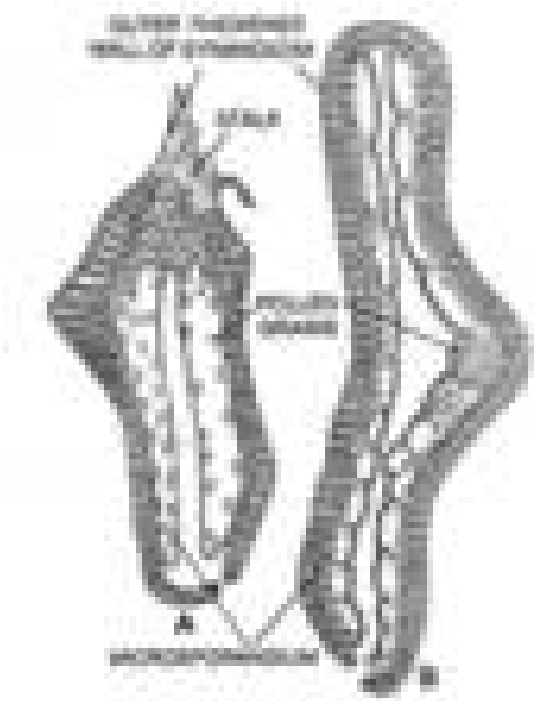


Fig. 3.18. *Cycadeoidea dacotensis*. A, lateral aspect of a synangium showing stalk and two microsporangia in longitudinal section; B, T.S. of the synangium showing thickened outer wall and inner parenchymatous layer

- Each strobilus was made up of a number of heavy imbricate reduced leaves or bracts. These bracts completely surrounded the strobilus when it was the earliest stage of development where the strobilus developed these imbricate bracts separated and the inner part of the strobilus exposed.
- The second whorl was made up of a number of leaf like microsporophylls, all of which were united at the base to form a cup-shaped structure round the central part of strobilus. The third central portion was hemispherical or dome-shaped in appearance. The central part was made up of a number of ovulate sporophylls. These megasporophylls were simply stalked.
- At the tip of the stalk was developed an ovule. Some stalks were sterile and the tips of sterile stalks were flattened. The central stalks stood up vertically upward and they were longer in length.
- The lateral ones continue to decrease in size from above downwards and stood projecting from lateral side, so the ripe female portion of strobilus hemispherical or dome-shaped in appearance. It is clear that in this bisporangiate strobilus the stamens or microsporophyll's ripe first at which time the ovules were immature.
- When the ovules matured the stamens were shed, so in the strobilus in which the ovules were ripe the microsporophyll's were absent but in young strobilus both were present.
- The microsporophyll's or the stamens were 10 or 20 in number. These microsporophyll's or stamens were all united at the base and each stamen was pinnate in form and on each stamen there were about twenty slender pinnae on either side, under the pinnae were developed two rows of fused sporangia or synangium had a short stalk and two pollen sacs in it; so each stamen was pinnate in form and was very much like the Marattious ferns in which we know the sporangia fuse to form synangia.
- When stamens were very young they rolled downwards; so on the whole we can say that the stamens of Cycadeoidea (Bennettites) were very much like those of ferns, while in living gymnosperms they have lost their resemblance with the ordinary ferns.
- The central portion was dome-shaped in form and this part was made up of a number of slender stalks, the central ones were long and stood vertically upwards, the lateral ones short and they diverged outwards. On the whole the female part was oblong in shape. Some of the stalks bore ovules while the others were sterile and their tips were expanded.
- The male and female parts of strobilus were separated by the presence of some sterile bracts or scales. The ovule was orthrotropous and terminal. It was small in size and was surrounded by three-layered testa like that of Cycas. The nucellus was spearate from integuments only in the upper part the integument projects forward to form a long micropyle.
- At the base of the micropyle the nucellus projected to form nucellus beak and round the base of nucellus beak there was a depression, the pollen chamber.
- On the outside of the ovule there was a small basal cup which suggests the cupule of Lagenostoma, but it was much reduced in size and never surrounded the whole of ovule or seed at any time.

- The ovule seems to fertilize by swimming sperms. After fertilization the ovule developed into a dicotyledonous embryo which was non-endospermic. When the seeds were developed the whole of the female part of strobilus became fleshy and formed a fruit.
- In ripe fruit holes were present on the surface and at the base of these holes was dicot embryo while the fleshy portion of fruit was formed by stalk and interspersed sterile scales.
- During the development of seed it appears that there was no suspensor developed. It might have been developed in the earlier stages of development of seed, but it is doubtful, so Cycadeoideales (Bennettitales) differ from other gymnosperms in these two important respects- 1. The non-formation of suspensor and 2. The presence of a non-albuminous dicot embryo.

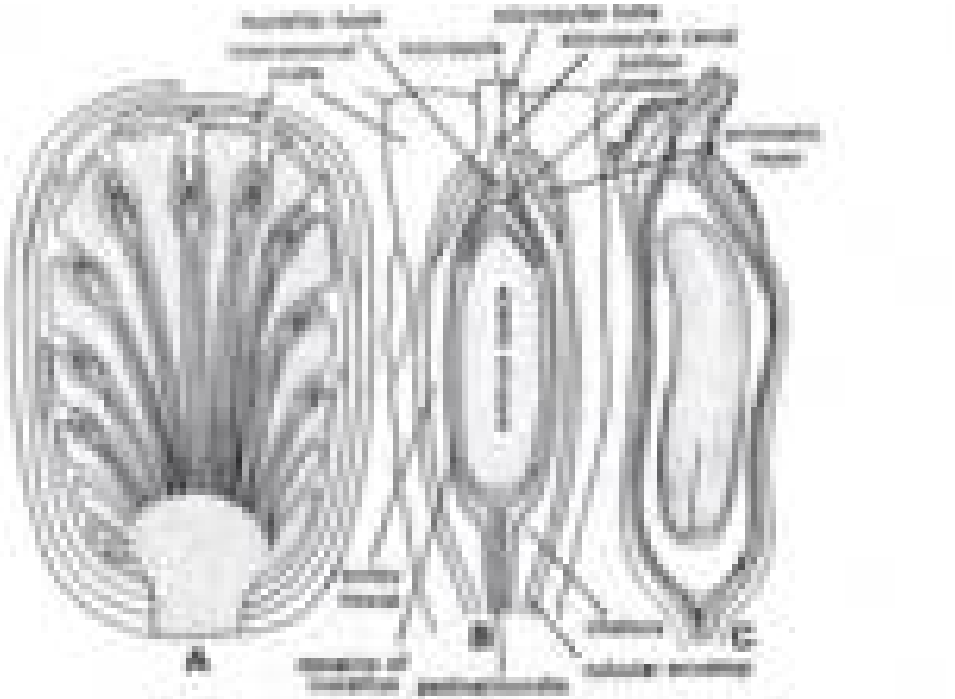


Fig. 3.35. Dyctiosomes: A, V.S. of gymnosperm showing convex trans face; B, V.S. of cells; C, V.S. of stem