The morphology, anatomy and phylogeny of the known extinct representatives of the family Williamsoniaceae from India have been overviewed. The family occurs in the Upper Mesozoic rocks and is represented by fronds, stems, male, female and bisexual fructifications. Though the fronds vary in shape, size and venation, all possess identical sydetocheilic stomata. The stems Bucklandia and Sahnoxyylon show minor variations in structure of tracheary elements and are related with cycadeoideas and homoxylous angiosperms. The male fructification Welrichia is built on very distinct and different plan than the seed-bearing fructification—Williamsonia, which has been derived from Cordaitanthus. The bisexual fructification—Amargolica is terminal and exposed like Williamsonia, while in structure and arrangement of microsporophyll resembles Cycadeoidea. Relationship among different organs is suggested and phylogeny of Williamsoniaceae is discussed.

**Key-words**—Williamsoniaceae, Morphology, Phylogeny, India.

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1990; Bose, 1953a, 1953b, 1968; Bose & Kasat, 1972a; Bose & Banerji, 1981, 1984). The Williamsonian fossil plants described from the Indian rocks are:

**Fronds**—*Ptilophyllum* (18 sp.), *Pterophyllum* (10 sp.), *Otozamites* (7 sp.), *Anomozamites* (3 sp.) and *Dictyozamites* (7 sp.).

**Stems**—*Bucklandia* (4 sp.) and *Sahnioxylon* (2 sp.).

**Male fructification**—*Weitrichia* (3 sp.).

**Seed-bearing fructification**—*Williamsonia* (12 sp.).

**Bisexual fructification**—*Amarjolia* (1 sp.).

Plant remains of Williamsoniaceae occur as impressions, incrustations and petrifactions. The impressions show external morphology. In incrustations the epidermal characters are studied through maceration and peel techniques using nitric acid as etching acid (Jacob & Jacob, 1954; Bose & Kasat, 1972a; Bose & Banerji, 1981, 1984; Sukh-Dev & Rajnikanth, 1988a, 1988b). The petrifactions have been studied by the usual method of cutting, grinding and polishing techniques. At Amarjola, the material being soft and fragile needs cooking in Canada balsam prior to sectioning. Canada balsam is used as mounting medium. Sometimes, the polished surface is examined with a water film under reflected light.

**DESCRIPTION**

A systematic account of the extinct plants of Williamsoniaceae known from India is given as under:

**Fronds**

*Ptilophyllum* Morris

Frond pinnate, pinnae linear to round, base asymmetrical, upper basal angle round, lower decurrent; apex acute, obtuse, truncate or round; veins parallel with forking. Epidermal cells mostly sinuous, stomata hypostomatic, transversely oriented and syndetocheilic. Rachis with a number of bundles arranged in double U-manner.

Sharma (1967a), Bose and Kasat (1972a) and Bose and Banerji (1981, 1984) published reviews on the Indian species of the genus *Ptilophyllum* and identified 18 species. Some of these fronds are morphologically alike but separated on epidermal characters, e.g., *P. niponica* Mittre 1956, *P. indicum* Jacob & Jacob 1954, *P. sabnii* Gupta & Sharma 1968. Minor variations in morphological and epidermal characters may be due to environmental differences and age of the frond. A re-investigation is likely to reduce the number of species of *Ptilophyllum* in India. Search should also be made to find out their associated stems and fructifications.

**Pterophyllum Brongniart**

Frond pinnate, pinnae linear, base symmetrical attached on lateral side of rachis, apex acute, obtuse or truncate, veins parallel with few forking. Epidermal and anatomical characters of Indian species are not known. Oldham and Morris (1863) and Feistmantel (1877) identified a number of species of this genus from India, but Seward and Sahni (1920) merged many of these species into the genus *Nilssonia* Brong. Sharma (1969b) also transferred two species of *Pterophyllum* into *Nilssonia*. On the other hand Bose and Banerji (1981, 1984) transferred all known *Nilssonia* species from India into *Pterophyllum* species without studying the epidermal and anatomical characters.

**Otozamites Braun**

Frond pinnate, pinnae small to linear to triangular or round; base asymmetrical and auriculate, apex acute, obtuse or round; veins diverging and dichotomised. Epidermal cells sinuous, stomata hypostomatic, syndetocheilic and restricted to stomatal bands.

Oldham and Morris (1963) and Feistmantel (1876, 1877, 1879) described a number of species of this frond genus from India. Seward and Sahni (1920) merged many of the species into the genus *Ptilophyllum*. Roy (1963) described *Otozamites bellus* from Kachchh. Bose and Banerji (1981, 1984) described the morphology and epidermal characters of *O. imbricatus* Feistmantel 1876, *O. Walkamotaensis* Bose & Zaba-Bano 1981, *O. kachcbbensis* Bose & Banerji 1984. *Otozamites* occurs more frequently in the Mesozoic rocks of Kachchh than any other exposure in India.

**Dictyozamites Oldham**

Frond pinnate, pinnae linear, falcate or round, base asymmetrical and auriculate, apex acute, obtuse or round, venation reticulate, stomata hypostomatic, syndetocheilic and restricted to stomatal bands. Rachis has vascular bundles arranged in double U-manner similar to that of *Ptilophyllum* (Bose & Kasat, 1972a). In *Dictyozamites*, the number of areoles present in the middle of pinna is used in the identification of species. Seven species, viz., *D. falcatu* Oldham 1963, *D. indicus* Feistmantel 1877, *D. ballei* Sahni & Rao 1933, *D. sabnii* Gupta & Sharma 1964, *D. feistmantelii* Bose & Zaba-Bano 1978 and *D. gondwanensis* Sukh-Dev & Rajnikanth
1988a are known from India. Associated stems and fructifications are yet to be discovered.

**Anomozamites Schimper**


**Stems**—Bennettitalean stems are simple or branched and possess spirally arranged rhomboid leaf bases on the surface. Two stem genera, viz., *Bucklandia* Prest. 1825 and *Sahnioxylon* Bose & Sah 1954 are known from the Indian rocks.

**Bucklandia Presl.**

Stem simple (*B. indica*), branched (*B. sabnii*) or dichotomised (*B. dichotoma*). Stem surface has close or sparse leaf bases. Pith and cortex are parenchymatous with mucilage ducts. Vascular zone is made up of a large number of collateral, conjoint, open and endarch bundles. Secondary wood is compact and differentiated into cortical rings. The tracheids have spiral, scalariform or bordered pits on radial walls. Rays 1 to many cells high, uniserial to multiseriate, homogeneous. It is suggested that the pith and cortex of *B. indica* are conjoined, and the term *conjoint* is used to denote this condition. Secondary wood is compact and differentiated into cortical rings. The tracheids have spiral, scalariform or bordered pits on radial walls. Rays 1 to many cells high, uniserial to multiseriate, homogeneous. This is a characteristic feature of *B. indica*.


**Sahnioxylon Bose & Sah**

Originally the wood was described as *Homoxylon rajmahalense* by Sahni (1932a) who believed that it was an angiospermous wood. But Gupta (1934) related it with cycadeoideas. Hsü and Bose (1952) made further observations on this wood. Bose and Sah (1954) transferred the *Homoxylon* to *Sahnioxylon* as the earlier name had already been used for a fossil conifer wood, so they called it *Sahnioxylon rajmahalense* (Sahni) Bose & Sah and also described a new species—*S. andrewsii* Bose & Sah 1954. In the former only wood is known, while in the latter partly preserved ground tissues are also seen. Whether *Sahnioxylon* had leaf bases on surface and what kind of leaf traces were present, is yet to be discovered.

**Fructifications**

**Weltrichia Braun**

This male fructification was described earlier under the generic name *Williamsonia*. Sitholey and Bose (1953) instituted *Williamsonia santalensis* which was later on transferred to *Weltrichia santalensis* by Sitholey and Bose (1971). Sitholey and Bose (1953) described a single whorl of microsporophylls surrounding a cup-shaped receptacle, while Sharma (1969a) on the basis of study of more than 50 specimens, some of which are nicely preserved counter parts, suggested two whorls, i.e., the abaxial of sterile bracts and adaxial of microsporophylls. Sitholey and Bose (1971) did not agree to it. Each microsporophyll has two rows of appendages on which parallel rows of microscoliophrayls which are coalescent towards base forming a circular depression. Further investigations are required on *W. campanulatiformis* and *W. barrassiana* as these are established on insufficient and poorly preserved materials.

**Williamsonia Carruthers**

Feistmantel (1876) described *W. blanfordii* from Kachchh and *W. microps* from the Rajmahal Hills (Feistmantel, 1877). Sahni (1932b) described *W. sewardiana* from the Rajmahal Hills and suggested its restoration and showed its association with the stem *Bucklandia indica* and fronds of *Ptilophyllum cf. cutchense*. Gupta (1943) described a probable bisexual fructification—*W. sabnii* in which the bracts are spread and in the basal portion of receptacle 20 markings are seen, which may be of fallen microsporophylls. Gupta (1958) divided williamsonian fructification into open type and close type. In the former, bracts spread out as in *W. sabnii*, while in the latter the bracts did not open out as in *W. guptai*. This hypothesis is applicable to all the known species of *Williamsonia* throughout the world. Bose (1966a) called *W. sabnii* only a seed-bearing fructification. Bose (1968) described *W. barrassiana* from Amarjola in the Rajmahal Hills which is identical to *W. guptai* Sharma 1968.
collected from the same locality. Sharma (1968) also established *W. amarjolense* and separated it from *W. guptai* on the basis of different epidermal characters of bracts. Bose and Kasat (1969) instituted *W. seniana* in honour of Dr J. Sen (Calcutta) from Jabalpur. It is an incrustation and preserves the epidermal structures.

Sharma (1970a, 1970b, 1970c, 1974, 1975, 1976, 1980) studied petrified specimens of *Williamsonia* collected from Amarjola and described the anatomy of peduncle and receptacle, structure of seed, ovule ontogeny and development of fruit. Sharma (1977) published an illustrated review as Indian *Williamsonias*. Sharma (1982a) interprets the morphology of interseminal scales and derives *Williamsonia* from *Cordaianthus* as a result of modification and condensation of cone axis. Bose and Banerji (1984) described three new species of *Williamsonia*, viz., *W. kakadbitensis*, *W. trambuensis* and *W. sukhpurensis* from Kachchh. All these are incrustations and fertile structures remain unknown. Identification is based mainly on epidermal characters of bracts. In *W. kakadbitensis* and *W. sukhpurensis* the bracts are densely hairy while trichomes/ramenta bases are rare in *W. trambuensis*.

**Amarjola Bose et al.**

This bisexual fructification was originally described as *Cycadeoidea dactylota* by Bose (1966b). Sitholey and Bose (1971) amplified the description. The fructification is terminal and exposed, and the microsporophylls differ in structure from *Cycadeoidea* so the new genus *Amarjola* was proposed by Bose, Banerji and Pal (1984) and called it *A. dactylota*. The bracts are hairy like in *W.ewardiana* Sahni 1932b. There are nearly 20 balloon-shaped microsporophylls, surrounding the central conical receptacle which bears a compact layer of seminiferous and interseminal scales. Each microsporophyll bears appendages on which rows of microsynangia are produced. Our present knowledge on *Amarjola* is based only on two specimens and more collection is required for further investigations.

In addition to the above described fructifications, a number of incomplete (Sharma, 1982b) or poorly preserved (Sharma, 1990) bennettitalean organs and scales (*Cycadeolepis*) are also known from the Mesozoic rocks of India (Bose & Banerji, 1984).

**DISCUSSION**

The extinct representatives of the family Williamsoniaceae dominated the vegetation during the Mesozoic Era in India, especially the frond genus *Ptilophyllum* which occurs in all the Upper Mesozoic exposures and is represented by nearly half the total number of species known throughout the world. This frond is associated with the stem *Bucklandia* and the seed-bearing fructification *Williamsonia* (Feistmantel, 1877; Sahni, 1932b). The male fructification *Weltrichia* is also found in close association with the fronds of *Ptilophyllum* (Sharma, 1969a) both at Sakrighat and Dhokuti in the Rajmahal Hills. The association of other fronds—*Otozamites, Pterophyllum, Anomozamites* and *Dictyozamites* with allied stems and fructifications are yet to be discovered. Similarly, the phylogeny of reticulate venation of *Dictyozamites* needs investigation.

*Sahnioxylon* though resembles in the structure of trachceal elements with the stem *Bucklandia*, specially *B. dichotoma*, its affinities remain doubtful for want of complete and better preserved material to study the origin and nature of leaf traces and structure of pith and cortex. Associated leaves and fertile parts of *Sahnioxylon* are yet to be discovered. The stem genus *Bucklandia* also needs further investigations as wide variations occur in the morphology and distribution of leaf bases on stem surfaces.

In all the species of *Weltrichia* known from India the microsporophylls originate from the brim of a cup-like receptacle. The abaxial whorl of sterile bracts is present in *W. santalensis*, while in others it is yet to be seen. *W. companulatiformis* and *W. harrisiana* are based on the study of 1-3 incomplete specimens.

Though the seed-bearing *Williamsonia* is represented by several species (12 sp.), the basic structure, i.e., presence of a compact layer of sterile and fertile scales surrounding a receptacle, and the linear, simple, curved bracts which protect the fertile parts are identical. Despite the study of all internal details including anatomy, ontogeny and structure of seeds/ovules, and fruit development, the phylogeny of the fructification remains doubtful. Though Sharma (1982a) derives *Williamsonia* from *Cordaianthus*, the intermediate presumptions are hypothetical and need proof. Further investigations of the petrified fructifications are likely to provide solution to the problem.

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