Indian Williamsoniaceae—an overview

B. D. Sharma

Sharma BD 1992. Indian Williamsoniaceae—an overview. *Palaeobotanist* **40** : 260-265.

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 syndetocheilic stomata. The stems *Bucklandia* and *Sahnioxylon* show minor variations in structure of tracheary elements and are related with cycadeoideas and homoxylous angiosperms. The male fructification *Weltrichia* is built on very distinct and different plan than the seed-bearing fructification—*Williamsonia*, which has been derived from *Cordaianthus*. The bisexual fructification—*Amarjolia* 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.

B. D. Sharma, Department of Botany, University of Jodhpur, Jodhpur 342 001, India.

सारांश

भारतीय विलियमसोनिएसी—एक समालोचना

बी० डी० शर्मा

भारत से विलियमसोनिएसी कुल के विदित विलुप्त सदस्यों की आकारिकी, शारीर एवं जातिवृत्त की विवेचना की गई है। यह कुल उपरि मध्यजीवी चट्टानों में मिलता है तथा इसके सदस्यों के अश्मित प्रपर्ण, तना तथा नर, मादा एवं उभयलिंगी फलन मिलते हैं। प्रपर्ण हालाँकि आकार तथा शिरान्यास में विभिन्नता प्रदर्शित करते हैं तथापि इनके वातरन्ध्रों में समानता है। **बुक्लैंडिया** एवं **साहनिऑक्सीलॉन** नामक तने में वाहिनिकाओं में थोड़ी सी विभिन्नता है तथा ये साइकेडिऑयडीयों समदारु आवृतबीजीयों से सजातीयता व्यक्त करते हैं। बीज-धारक फलन—**विलियमसोनिया** की अपेक्षा नर फलन—**वेल्ट्राइकिया** बनावट में बिल्कुल भिन्न है। बीज-धारक फलन की उत्पत्ति कोर्डेन्थस से हुई है। उभयलिंगी फलन—**अमरजोलिया** ऊपर स्थित होता है तथा **विलियमसोनिया** की भाँति प्रतीत होता है। विन्यास एवं संरचना में लघुबीजाणुपर्ण **साइकेडिऑइडिया** से सजातीयता व्यक्त करते हैं। विभिन्न अवयवों में पारस्परिक सम्बन्ध प्रदर्शित किये गये हैं तथा **विलियमसोनिया** के जातिवृत्त की विवेचना की गई है।

FAMILY Williamsoniaceae, belonging to the class Bennettitopsida, flourished and dominated the vegetation during the Mesozoic Era (Harris, 1969). Members of this family originated sometimes during Middle Triassic and disappeared by the end of Lower Cretaceous. The family includes extinct plants in which the stem surface has spirally arranged rhomboid leaf bases, parenchymatous pith and cortex well developed with mucilage ducts; vascular zone narrow made up of collateral, conjoint and endarch bundles; secondary wood mano-or picnoxylic; leaf trace is unilacunate. Leaves are pinnate or partly pinnate, with parallel or reticulate venation; stomata transverse to veins and syndetocheilic. Fructifications are terminal, exposed, seed-bearing and bisexual. Microsporophylls are spread with two rows of appendages on which microsynangia are produced. Ovules/seeds are produced intermingled with sterile scales in a compact layer covering the receptacle. In bisexual fructification baloon-shaped microsporophylls encircle the central receptacle with a covering of ovules and sterile scales.

In India, members of this family occur at several Mesozoic localities, e.g., Rajmahal Hills, Bihar; Golapilli near Elore; Madras outliers, Jabalpur, Jaisalmer, Kachchh, etc. (Oldham & Morris, 1963; Feistmantel, 1876, 1877, 1879; Seward & Sahni 1920; Sitholey, 1954; Gupta, 1966; Sharma, 1967a, 1977,

Four Decades of Indian Palaeobotany
Editors : B. S. Venkatachala & H. P. Singh
Publisher : Birbal Sahni Institute of Palaeobotany, Lucknow

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— Weltrichia (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 asymetrical, upper basal angle round, lower decurrent; apex acute, obtuse, truncate or round; veins parallel with forkings. 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. nipanica* Mittre 1956, *P. indicum* Jacob & Jacob 1954, *P. sahnii* 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 forkings. 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 Benerji (1981, 1984) retransferred 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 asymetrical 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 & Zeba-Bano 1981, *O. kachchhensis* 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 asymetrical 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. falcatus* Oldham 1963, *D. indicus* Feistmantel 1877, *D. hallei* Sahni & Rao 1933, *D. sahnii* 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

Frond lobed or pinnate, pinnae unequal, base symmetrical, attached on lateral side of rachis, apex obtuse to truncate, veins parallel with forkings. Epidermal cells sinuous. Stomata hypostomatic, transversely oriented and syndetocheilic. Important species of the genus known from India are: *A. fissa* (Feist.) Sharma 1969b, *A. amarjolense* Sharma *et al.* 1971, and *A. haburensis* Bose & Banerji 1981. Associated stems and fructifications remain unknown.

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

Bucklandia Presl.

Stem simple (*B. indica*), branched (*B. sahnii*) 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 growth rings. The tracheids have spiral, scalariform or bordered pits on radial walls. Rays 1 to many cells high, uni-to-multiseriate, homogeneous. Pits in crossfield 1-4 or more, circular with narrow border. Leaf trace is unilacunate and divides into a number of bundles (5-11) in cortex.

Four species of *Bucklandia*, Viz., *B. indica* Seward 1917, *B. sahnii* Bose 1953, *B. guptai* Sharma 1967b and *B. dichotoma* Sharma 1970d are known from India. Anatomically, *B. dichotoma* resembles cycadeoideas and homoxylous angiosperms in having cross-shaped pit pores and scalariform pittings (Gupta, 1934).

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 cycadeoidea. 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 microsynangia occur. Sharma (1969a) suggested restorations of *W. santalensis* and also described a new species *W. campanulatiformis* preserved as cast and mold. Bose and Banerji (1984) described another species of *Weltrichia, W. harrisiana* from Kachchh. In this fructification the fertile appendages are terminal on 12-14 microsporophylls which are coalescent towards base forming a circular depression. Further investigations are required on *W. campanulatiformis* and *W. harrisiana* 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. sahnii* 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. sahnii*, 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. sahnii* only a seed-bearing fructification. Bose (1968) described *W. harrisiana* 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. kakadbhitensis, 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. kakadbhitensis* and *W. sukhpurensis* the bracts are densely hairy while trichomes/ramenta bases are rare in *W. trambuensis*.

Amarjolia 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 *Amarjolia* was proposed by Bose, Banerji and Pal (1984) and called it *A. dactylota*. The bracts are hairy like in *W. sewardiana* Sahni 1932b. There are nearly 20 baloon-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 *Amarjolia* 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 (*Cycadolepis*) 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 Sakrigalighat 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 tracheary 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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