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Morphology, anatomy and phylogenetic studies on the Indian Mesozoic bennettitalean stems

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ABSTRACT

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The present paper deals with morphology and anatomy of the extinct Mesozoic bennettitalean stems. In most of the cases, the stem surface is covered with rhomboid leaf bases arranged in spiral rows. The stems are branched or unbranched. The branching may be monopodial, sympodial or dichotomous. Vascular cylinder is either monoxylic or polyxylic with the wood manoxylic or pycnoxylic. Wood rays are long and uni- to triseriate. Tracheids have scalariform to multiseriate bordered pits on radial walls with circular or elliptical pit pores resembling those of cycadophytes and homoxylous angiosperms (Magnoliales). In phloem, sieve areas are circular, uniseriate and each with many sieve pores. Fructifications like *Williamsonia, Wielandiella, Williamsoniella, Weltrichia* and *Amarjolia* were associated with the bennettitalean stems. Phylogenetic relationship is suggested with cycadeoideas, cycads and vessel-less angiosperms.

Key-words: Morphology, anatomy, phylogenetic relationship, bennettitalean stem, Mesozoic, India.

INTRODUCTION

Bennettitales is an extinct group of plants which survived from Middle Triassic to Early Cretaceous. The plants were either small sized trees (*Sahnioxylon*) or shrubs with simple or branched columnar stems (*Bucklandia*). In most of the cases, they had pinnate leaves, e.g. *Ptilophyllum, Otozamites, Dictyozamites*, etc. (Seward 1917, Harris 1969, Bose & Zeba-Bano 1978, Taylor et al. 2009). Stem surface was mostly covered with closely placed leaf bases in spiral rows, e.g. *Bucklandia indica, B. sahnii, B. guptae* (Sahni 1932a, Bose 1953, Sharma 1967a, 1970a, 1974), more or less resembling to *Cycas* (Pant 2002). Presl (1825) instituted the genus *Bucklandia* for an extinct cycadean stem. Mantell (1822, 1827) collected identical material from the Wealden of Tilgate and suggested its relationship with the members of angiospermic families Euphorbiaceae and Liliaceae. Brongniart (1822) also agreed with Mantell's view, but in 1828 he modified his opinion and called them cycadean stems and instituted a new genus *Mantellia* for them. Buckland (1828) established the genus *Cycadeoidea* which had the anatomy of typical cycadean stem, i.e. pith and cortex large, parenchymatous with mucilage ducts; wood manoxylic in majority of species (Wieland 1906, 1916). Goeppert (1844) discovered cycadean woods from the Jurassic of Silesia and named it *Reumaria*. Mantell (1851) restudied his earlier collected material from Tilgate and insisted their relationship with Euphorbiaceae or some arborescent ferns. Oldham and Morris (1863) reported occurrence of cycadean stems (Bucklandias?) in the Rajmahal Hills, India. Carruthers (1870) added much to our knowledge about British Mesozoic cycadean stems and established two new genera *Fittonia* and *Yetasia*. He also compared *Bucklandia* Presl with the extant genus *Cycas* L. and defined it as follows: "Trunk cylindrical and sometimes bifurcating, with small scars of the bases of leaves which were arranged in an alternating series of large and small scars of the bases of leaves, the large being placed on swellings and small on constrictions of the stems. Androecium a cone (?). Gynoecium terminal of crown of leaves bearing seeds in somewhat altered margins". Carruthers (1870) described two new species of *Bucklandia*, viz. *B. mantellii* and *B. milleriana*, from the secondary rocks of England. Feistmantel (1877) reported casts and impressions of cycadean trunks from the Rajmahal Hills and suggested associations with *Ptilophyllum* leaves and *Williamsonia* type of fructifications. Nathorst (1886) instituted a new species of *Bucklandia*, *B. saportiana*, from the Jurassic of Stockholm. Wieland (1906, 1916) published two volumes on American fossil cycads and described the anatomy of cycadeoideas and other bennettitalean stems. Seward (1900, 1904) published two volumes on the Jurassic Flora (I & II) and described bennettitalean stems. Bancroft (1913) studied the anatomy of Indian Jurassic gymnosperms including *Bucklandia* stem and observed pycnoxylic wood in this taxon and presence of growth rings. Stopes (1915) prepared a catalogue of Cretaceous flora. Stopes (1920) described a new species of *Bennettites*, viz. *B. scottii*, with foliage attached (Scott 1923, p. 327). Seward (1917) published the 3rd volume of 'Fossil Plants' in which he described many new species of *Bucklandia*, e.g. *B. indica* Seward, *B. ruffordii* Seward, *B. yatesii* (Carruthers) Seward, *B. buzzardensis* (Stopes) Seward, *B. anomala* (Stockes & Webb) Seward, *B. milleriana* (Carruthers) Seward and *B. squamata* (Carruthers) Seward. *Bucklandia indica* was peculiar in having pycnoxylic wood and only uniseriate wood rays and also in absence of scalariform pits.

Sahni (1932a) described a new species of *Williamsonia*, *W. sewardiana*, which was associated with the stem *B. indica* Seward. Sahni (1932b) published a paper on the material (a block of silicified chert) passed on to him by the Geological Survey of India, but without mentioning the exact place of collection and horizon (probably from the Jurassic of the Rajmahal Hills, Jharkhand). Sahni (1932b) noticed interesting features in anatomy, i.e. similarities with the vessel-less (homoxylous) angiosperms, and therefore named it as *Homoxylon rajmahalense*. Gupta (1933, 1934) studied the anatomy of four taxa of homoxylous angiosperms, i.e. *Trochodendron, Tetracentron, Drimys* and *Zygogonium*, and concluded that *H. rajmahalense* had resemblances both with vessel-less angiosperms as well as with Cycadeoidales, e.g. *Cycadeoidea dartonii, C. micromyela*, etc. Hsu and Bose (1952) published further observations on *H. rajmahalense* Sahni and compared its anatomy with that of *Bucklandia* sp. In their material, pith was well developed, wide and had mucilage ducts, i.e. the characters of the bennettitalean stems (Sharma et al. 2006a). Bose (1953) described a new species of *Bucklandia*, viz. *B. sahnii*, collected from Amarjola in the Rajmahal Hills, Jharkhand. The specimens were mostly branched unlike *B. indica* Seward. Bose and Sah (1954) published further observations on *H. rajmahalense* on the basis of study of two more blocks of secondary woods with sharp differentiation of growth rings. They suggested a change in name of *Homoxylon rajmahalense* to *Sahnioxylon rajmahalense* because the term *Homoxylon* had already been used by Hartig (1848) for a conifer wood. They also established a new species of *Sahnioxylon*, *S. andrewsii*, based on the study of a stem piece collected from Kulkipara, near Amarapara, Rajmahal Hills. In this piece, pith was extremely small and poorly preserved. However, the wood characters were more or less like *S. rajmahalense*. Jain (1964) described a cycadean stem with variable amount of secondary wood and presence of pith bundles, i.e. *Fascisvarioxylon mehtae* Jain. In size, it was like *B. sahnii* but did not have leaf bases on stem surface. Sharma (1967a) instituted a new species of *Bucklandia*, *B. guptae*, from the Rajmahal Hills. It was an elliptically compressed, hard, silicified piece with sharply marked leaf bases on the surface. Secondary wood was compact and differentiated into growth rings. Sharma (1967a) also gave further observations on *B. sahnii* Bose.

Nishida (1969) described the anatomy of a badly weathered specimen from the Cretaceous of Japan and named it *Bucklandia chousiensis*. Pith was large and had mucilage ducts. The tracheids were provided with multiseriate, hexagonal, contiguous bordered pits on radial walls resembling an araucarian stem. Greguss (1969) described the presence of transfusion cells in the stems of extant taxa of cycads, but such cells have not been seen in any bennettitalean stems. Harris (1969) suggested an association of *B. pustulosa* with the leaves *Ptilophyllum pecten* and *Williamsonia leckenbyi* fructification (Taylor et al. 2009, figure 17.77). Sharma (1970a) described a new species of *Bucklandia, B. dichotoma*, from the Rajmahal Hills. The surface had faint markings of leaf bases. Secondary wood was compact but without growth rings. Rays were long and mostly biseriate. Radial walls of tracheids bear scalariform to multiseriate bordered pits identical to that of homoxylous angiosperms. Gupta (1971) described the anatomy of a cycadean stem *Sewardioxylon sahnii* Gupta collected from Amarjola, a treasury of Bucklandias. In size, *S. sahnii* resembles *B. sahnii* but is different in anatomy (Sharma 1971b). Sharma (1971b) showed variations in morphology of leaf bases and attachment of *Williamsonia* fructifications on *Bucklandia* stems. Sharma (1973) described the anatomy of the peduncle of *Williamsonia* or a branch of *Bucklandia* which terminated into fructification from endarch to exarch in the receptacle (Sharma 1970a) and lose of the secondary wood. Sharma (1974) published a paper on external morphology and anatomical variations in *Bucklandia* stems collected from Amarjola. In some of the cross sections, he noticed the presence of tracheary cells in the pith. Sharma (1975) studied the apical portion of *Bucklandia* stem enclosed by young, hairy leaves. Watson and Sincock (1992) attempted a reconstruction of *Bucklandia* plant (Taylor et al. 2009, figure 17.77) on the bases of specimens from the Wealden of England. According to them, *Bucklandia* was a big tree with monopodial branching. Lateral branches divided further and had terminal fructifications. Leaf bases were small scars, distantly placed. No Indian *Bucklandia* coincides with the reconstruction of Watson and Sincock (1992). Sharma et al. (2006a) studied distribution of mucilage canals in the stems of the Bennettitales and noticed their presence in the ground tissue, leaf bases and the secondary phloem. Sharma et al. (2006b) described 3 new taxa of cycadean plants, i.e. stem, petiole and leaflet, from the Rajmahal Hills.

The present paper is an attempt to provide information based on the study of large number of specimens and slides of *Bucklandia* and *Sahnioxylon* stems. Phylogenetic relationship is also discussed.

DESCRIPTION AND DISCUSSION

Majority of the known bennettitalean stems have been collected either as casts or impressions/incrustations and permineralized material could be collected only from few localities of India, England, Japan and North America. As such, anatomical investigations are partially complete. Similarly, many specimens of the bennettitalean stems have been collected in badly weathered conditions and surface morphology, i.e. presence and absence of leaf bases remained unknown, e.g. *Bucklandia chousiensis* Nishida (1969), *Sahnioxylon andrewsii* Bose & Sah (1954), etc. In the present paper, morphological and anatomical descriptions are given of Indian petrified specimens of *Bucklandia* Presl and *Sahnioxylon* Bose & Sah. All the known species of these two genera were collected from the Mesozoic rocks of Rajmahal Hills, Jharkhand. These are taken out by digging a dark brown sandy rock. The material, being soft and fragile, needed cooking in canada balsam prior to sectioning with a wire bandsaw. The hard silicified material of *S. rajmahalense*, collected from Onthea, Mundro and Kulkipara, were cut by using diamond edge wheel. Slides were prepared by the usual technique of cutting grinding and polishing methods and mounted in dilute canada balsam (Sahni 1932a, Bose & Sah 1954, Sharma 1967a, 1970a, 1974).

Bucklandia Presl 1825

Altogether, the following 16 species of *Bucklandia* are known: *B. anomala* Presl (1825), *B. squomosa*

Brongniart (1828), *B. mantellii* Carruthers (1870), *B. milleriana* Carruthers (1870), *B. saportiana* Nathorst (1886), *B. ruffordii* Seward (1917), *B. yatesii* Seward (1917), *B. squamata* Seward (1917), *B. gracilis* (Carruthers) Seward (1917), *B. buzzardensis* Seward (1917), *B. indica* Seward (1917), *B. sahnii* Bose (1953), *B. guptae* Sharma (1967a), *B. dichotoma* Sharma (1970a), *B. chousiensis* Nishida (1969), *B. pustulosa* Harris (1969). The stems range in thickness from 14 cm (Harris 1969, Taylor et al. 2009) to 1.5 cm-3.5 cm (Bose 1953). This suggests that the plant was either a shrub of approximately 2 m height (Sahni 1932a) or a tree (Watson & Sincock 1992). The thinner ones were either juvenile plants or lateral twigs of moderate sized shrubs. Bucklandias collected from Amarjola (Plate 1, figures 1-8) range in thickness from 1.5 cm to 6.2 cm (Sharma 1974). *B. chousiensis* from Japan had the diameter 1.5 cm to 3.7 cm (Nishida 1969). *Bucklandia* species known as casts and impressions also show wide variations in thickness (Seward 1917).

Morphology

Branching: A *Bucklandia* stem either shows no branching (Plate 1, figure 1) or little branching as in *B. indica* Seward or the stem is frequently branched, e.g. *B. sahnii* (Plate 1, figures 2-3, 5, 7). The branching may be monopodial or sympodial or dichotomous, e.g. *B. dichotoma* (Plate 1, figure 9). Sometimes, three branches originate from a point, i.e. one is continuation of the main stem and the other two terminate into the fructifications. Bose (1953) also figured branched specimens of *B. sahnii* and suggested presence of dichotomous branching more or less identical to that of *Williamsoniella* Thomas (not clear from any figure of Bose 1953). A true dichotomy is visible in *B. dichotoma* Sharma (1970a) (Plate 1, figure 9). Watson and Sincock (1992) showed a monopodial branching in their reconstruction of *Bucklandia* plant (Taylor et al. 2009, fig. 17.77).

Leaf bases: There are many Bucklandias which do not have distinct marking of leaf bases on the surface either due to bad preservation, e.g. *B. chousiensis* or their absence, e.g. *B. pustulosa* Harris (1969). In Indian species of *Bucklandia,* leaf bases are well developed, distinct and rhomboid (Plate 1, figures 1-3, 5) or elliptical in shape and are arranged in spiral rows (Plate 1, figure 1). In some specimens, there are bands of smaller and larger leaf bases depending on swelling and constriction of the stem. There are many variations in shape, size and arrangement of leaf bases in Indian material of Bucklandias. In *B. guptae* Sharma (Plate 2, figure 4), leaf bases are non-decurrent, rhomboid and each has 5 bundle cavities in upper portion of leaf base. In *B. sahnii* Bose, there are large sized, decurrent, distinctly placed leaf bases (Plate 1, figure 1). In some specimens (Plate 1, figure 3), one side has rhomboid leaf bases while the other side has long, thick linear, flat bracts representing the vegetative and fertile portions. Sometimes, the leaf bases are overlapping, i.e. imbricate. In another specimen, the decurrent leaf bases have circular heads (Sharma 1974). Many specimens have linear, thin, flat bracts covering the entire surface (Plate 1, figure 4) of the stem. These variations in leaf bases are associated with the branching pattern of the stem and origin of the fructifications (Plate 1, figures 1, 7-8). The fructification originates on a small branch hardly coming out of the mantel of foliage armour. This is unlike the reconstruction of *Williamsonia sewardiana* Sahni (1932a) in which the lateral branches are shown comparatively larger and bear terminal fructifications. The description of *W. sewardiana* given by Sahni is perfectly correct. Similarly, the reconstructions suggested by Sharma (1971a) about the attachment of Williamsonias on *Bucklandia* stems are challengeable

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Plate 1

1-9. *Bucklandia* specimens from Amarjola. 1. *B. sahnii*, an unbranched stem with distinct rhomboid decurrent leaf bases in spiral rows. 2. A branched specimen with smaller and bigger sized leaf bases, thicker branch is continuation of stem while the thinner one terminates into a fructification. 3. A branched stem with rhomboid leaf bases on one side and thick linear bracts on the other side. 4. A branched stem covered with thin, linear bracts in close spirals. 5. A branched stem with thick linear bracts and rhomboid leaf bases. 6. C.S. of continuing stem. 7. A branched stem with main branch and the fructification base. 8. A fructification base on the smaller shoot. 9. *B. dichotoma* with faint markings of leaf bases (magnifications: 1-8: x1.25; 9: x0.75).

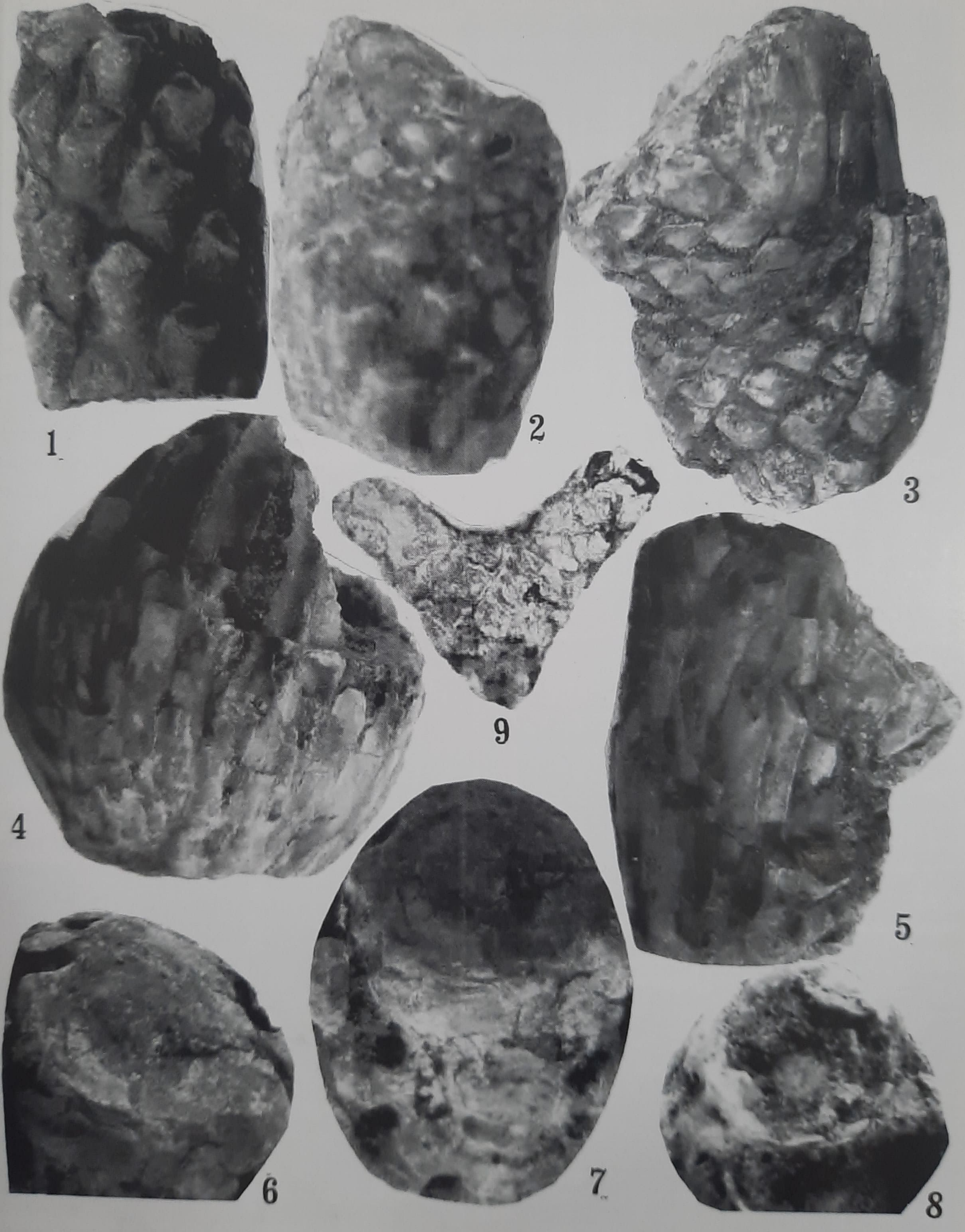

Plate 1

and need modifications. In *B. dichotoma* Sharma, the surface is covered by poorly marked rhomboid leaf bases (Plate 1, figure 9). This is because of weathering effect.

Anatomy

Cross-section: It is generally said that anatomy of bennettitalean stems is identical to that of cycads. But this is only partially true. In *Bucklandia*, pith and cortex are wide and have mucilage ducts similar to the cycadean stems. Vascular bundles are many, conjoint, collateral and endarch (Plate 2, figure 6), either in one ring (*B. sahnii, B. guptae*) or multirings (*B. buzzardensis* Seward). In some of the specimens of *Bucklandia* sp. from Amarjola, a close association of mucilage canals has been seen with the primary xylem. The ducts may be solitary or in groups of 2-5 (Plate 2, figure 10). These ducts are also common in the periphery of the pith (Sharma et al. 2006a). The ducts also occur in tangential lines (Plate 2, figure 11) in the secondary phloem in this species of *Bucklandia*. Secondary xylem may be manoxylic (Seward 1917) or pycnoxylic (Plate 2, figures 9, 12) (Indian and Japanese material). Majority of *Bucklandia* stems are circular in outline, i.e. cylindrical but *B. guptae* Sharma is oval/elliptical (Plate 2, figure 5) due to compression during fossilization. However, the tracheids and their arrangement in secondary wood remained undisturbed (Plate 2, figure 9) and distinction of spring and autumn woods is clear. In some *Bucklandia* specimens from Amarjola, there are present tracheary elements in the pith (Sharma 1974) of unknown functions. In bennettitalean stems, the leaf trace origin is unilacunate while in cycads it is multilacunate (Pant 2002). The trace passes through the secondary wood undisturbed and in cortex it divides into 5 to 7 collateral bundles arranged in a ring (Sharma 1974). These bundles rearrange in the base of the leaf and group into 2 and 3 or 2 and 5 (Plate 2, figure 4). In the petioles, the bundles increase in number and are arranged in double U shaped structure (Sharma 1967a). The foliage bases make an armour to protect the cortex from injury etc. In some of the specimen from Amarjola, 1 or 2 layers of periderm have been seen in cortex suggesting the continuation of meristematic activities for long time.

Tangential longi-section: In majority of Bucklandias, the tracheids are long and tapering without pittings on the tangential face except *B. chousiensis*. The wood rays are one-many cells long and uni to multiseriate (Plate 2, figure 2) and their tangential faces rarely have pits (Bose 1953, Text figure 4).

Radial longi-section: In *B. chousiensis*, tracheids have scalariform thickenings only in primary xylem while the secondary wood tracheids have hexagonal, multiseriate contiguous bordered pits (Plate 3, figure 17) similar to those of araucarian plants. In Indian Bucklandias, the tracheids have scalariform to circular, uniseriate to multiseriate (1 to 4 rows) bordered pits in secondary xylem (Plate 3, figures 15-16). In some tracheids, transitional stages of change from scalariform to circular pits (*B. sahnii* Bose 1953) are also visible. Pits in cross-field 1-6 (Plate 3, figure 16) with a narrow border (Bose 1953). *B. dichotoma* is little different from other Indian species. It has scalariform to multiseriate (1-3 rows) bordered pits which are either elliptical or circular with elliptic (Plate 3, figure 18) or cross shaped pit pores, a condition known in *Sahnioxylon* and homoxylous angiosperms (Gupta 1934, Bailey 1954). In *B. dichotoma,* secondary phloem is well preserved and sieve cells have distinct, circular (Plate 2, figure 8) sieve areas, a feature of

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Plate 2

1. *Sahnioxylon rajmahalense* Bose & Sah collected from Mundro, growth rings distinct, x0.5. 2. *Bucklandia sahnii*, T.L.S. of stem with long, 1-2 seriate rays, x75. 3. *S. rajmahalense* (from Hsu & Bose 1952), C.S. of wood with differentiation of spring and autumn tracheids, x75. 4. *B. guptae*, sparsely placed regular leaf bases, each has 5 bundle cavities, x2. 5. Same, C.S. of stem, compact elliptical wood with growth rings, x3. 6. *B. dichotoma*, primary xylem endarch, poorly preserved, x60. 7. Same, T.L.S. with uni and biseriate rays, x60. 8. Same, a sieve cell with distinct circular sieve areas and sieve pores, x300. 9. Same, C.S. of stem, wood pycnoxylic with differentiation of spring and autumn tracheids, x80. 10. *B. sahnii*, C.S. of stem with many mucilage ducts in pith and primary xylem region, x36. 11. Same, C.S. of stem mucilage cavities in tangential rows in secondary phloem, x36. 12. Same, C.S. of stem, compact secondary xylem, x75.

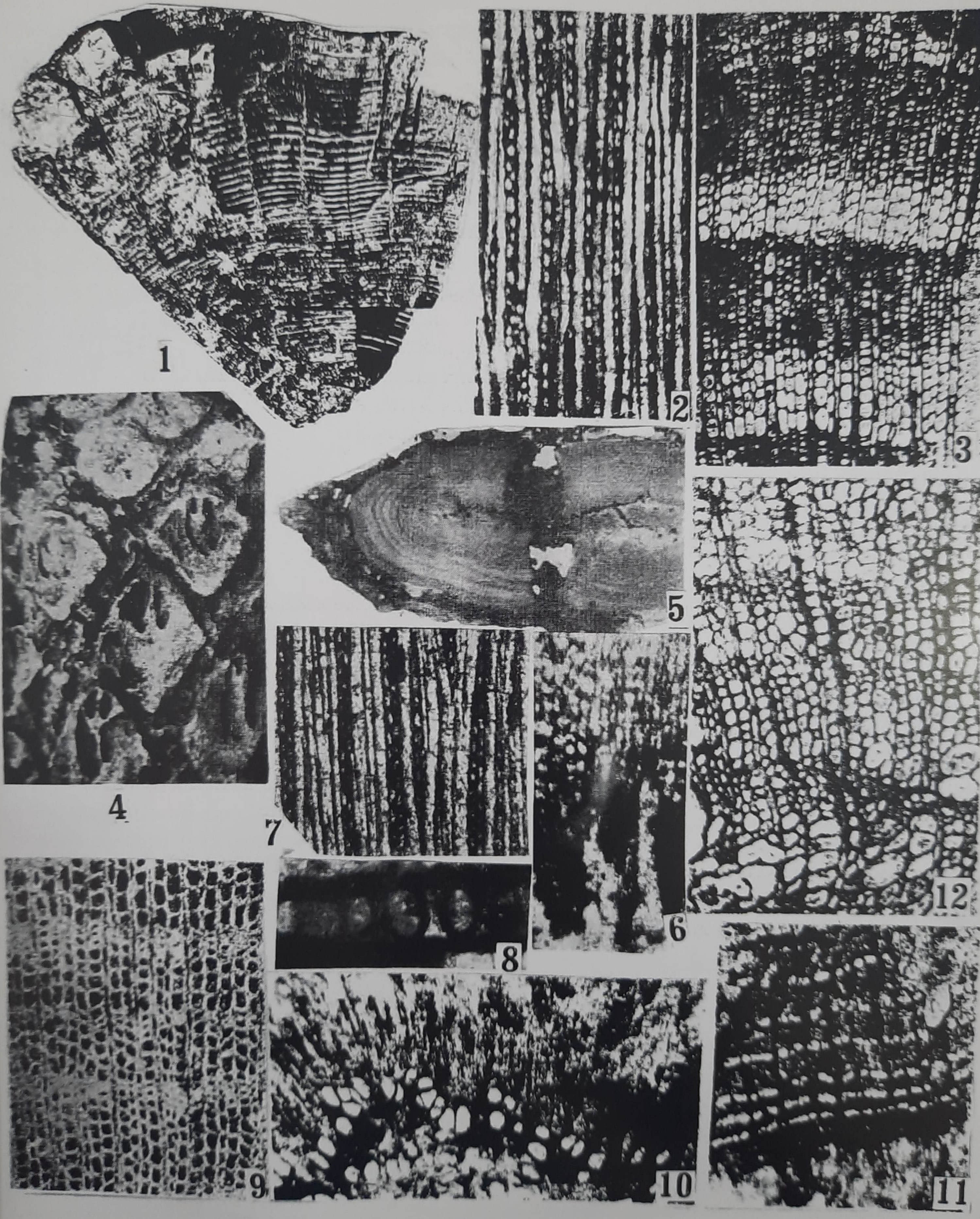

Plate 2

angiosperms (Esau 1965). Each sieve area has many sieve pores.

Sahnioxylon Bose & Sah 1954 (_Homoxylon_ Sahni 1932b)

Sahni (1932b) studied the anatomy of the fossil block given to him by the Geological Survey of India and came to the conclusion that the wood was related to homoxylous angiosperms and named it *Homoxylon rajmahalense*. The wood had distinct growth rings (Plate 3, figure 1) and differentiation of spring and autumn woods. Wood rays were long and uni to triseriate (Plate 3, figure 6). Radial walls of tracheids had scalariform (Plate 3, figure 2) and multiseriate bordered pits (Plate 3, figure 3). Pit pores were elliptical (Plate 3, figure 5). In some tracheids, scalariform and elliptical pits were present intermingled (Plate 3, figure 4). The ray cells had pittings on tangential as well as radial walls - a feature of vessel-less angiosperms of Magnoliales (Bailey 1954). Hsu and Bose (1952) published further observations on *H. rajmahalense* on the basis of study of a specimen collected from Amarjola which measured 4.6 cm in length and 1.8 cm in diameter. Pith was large, parenchymatous with sclerotic nests. Protoxylem many, endarch; secondary wood pycnoxylic and differentiated into growth rings (Plate 2, figure 3). Wood rays long and uni- to triseriate. Only few ray cells had pittings on tangential walls like *B. sahnii*. On radial walls of tracheids were present scalariform and bordered pits with circular and elliptical pit pores. Pits in cross field 2-6, circular and bordered. In size and anatomy, the material of Hsu and Bose was closer to *Bucklandia* than *Homoxylon*. Bose and Sah (1954) not only suggested a new name *Sahnioxylon rajmahalense* but also collected two new blocks of secondary wood and studied them in detail. The material from Mundro measured 21.2 cm x 13 cm (Plate 2, figure 1) while that of Onthea was 16.2 cm x 13 cm. These blocks support the earlier presumption that *Sahnioxylon rajmahalense* was a tree. These blocks had clear distinction of growth rings. Wood rays were long and 1-3 seriate. Radial walls of tracheids had scalariform (Plate 3, figure 7) and multiseriate bordered pits (Plate 3, figure 8). Pit pores were elliptical. Pits in cross field 8-9 with elliptical pits pores. These blocks were quite similar to the one described by Sahni (1932b) as *H. rajmahalense*.

Sahnioxylon andrewsii Bose & Sah 1954

The material was collected from Kulkipara near Amarapara in the Rajmahal Hills. The specimen measured 6 cm x 6.5 cm with a poorly preserved ground tissue (Plate 3, figure 9). Pith was very small about 3 mm in size, a non-bennettitalean character. Neither mucilage ducts nor sclerotic nests could be seen in the ground tissue. Secondary wood had 24 growth rings, i.e. at least a 12 years old twig. Wood rays 1-46 cells high and mostly biseriate (Plate 3, figure 11). Pittings could not be seen on tangential walls of the ray cells. Radial walls of tracheids had scalariform (Plate 3, figure 12) and multiseriate bordered pits with circular pit pores (Plate 3, figure 13). Pits in cross field 1-6, rounded with narrow border and circular pit pore (Plate 3, figure 14), an anatomical character of *S. andrewsii* which neither resembles to those of *S. rajmahalense* nor of homoxylous angiosperms. It is a distinct species but not *Sahnioxylon* of Sahni. Bose and Sah (1954) compared *S. andrewsii* with Bucklandias in anatomy, i.e. *B. sahnii* and *B. indica*. *B. sahnii* differs in nature of ground tissue and leaf bases on the surface which are absent in *S. andrewsii*. *B. indica* does not have scalariform pits on radial walls of tracheids and the rays are only uniseriate (Seward 1917), whereas in *S. andrewsii* scalariform pits are present and the rays are →

Plate 3

1-8. *Sahnioxylon rajmahalense* (from Sahni). 1. C.S. of wood with differentiation of autumn and spring xylem, x8. 2, 3. R.L.S. of wood, tracheids with scalariform and multiseriate bordered pits, pit pores elliptical, x200. 4. A portion of tracheid with scalariform pits, x500. 5. A portion of tracheid with multiseriate bordered pits, pit pores elliptical, x500. 6. T.L.S., rays long, 1-2 seriate, x60. 7-8. Same (from Bose & Sah), R.L.S. of tracheids with scalariform and multiseriate bordered pits, pit pores elliptical, x260. 9-14. *S. andrewsii*. 9. C.S. of stem, wood compact, pith and cortex narrow and poorly preserved, x1. 10. C.S. of stem, tracheids in rows, rays distinct, x80. 11. T.L.S., long 1-2 seriate wood rays, x80. 12-13. R.L.S. of tracheids with scalariform and multiseriate bordered pits, pit pores circular, x400. 14. Pits in cross field circular bordered, x400. 15-16. *B. sahnii*. 15. R.L.S., tracheids with scalariform pits, x500. 16. Pits in cross field many, x500. 17. *B. chousiensis*, R.L.S., tracheids with hexagonal, araucarian contiguous bordered pits, x150. 18. *B. dichotoma*, R.L.S., tracheids with scalariform pits, x225.

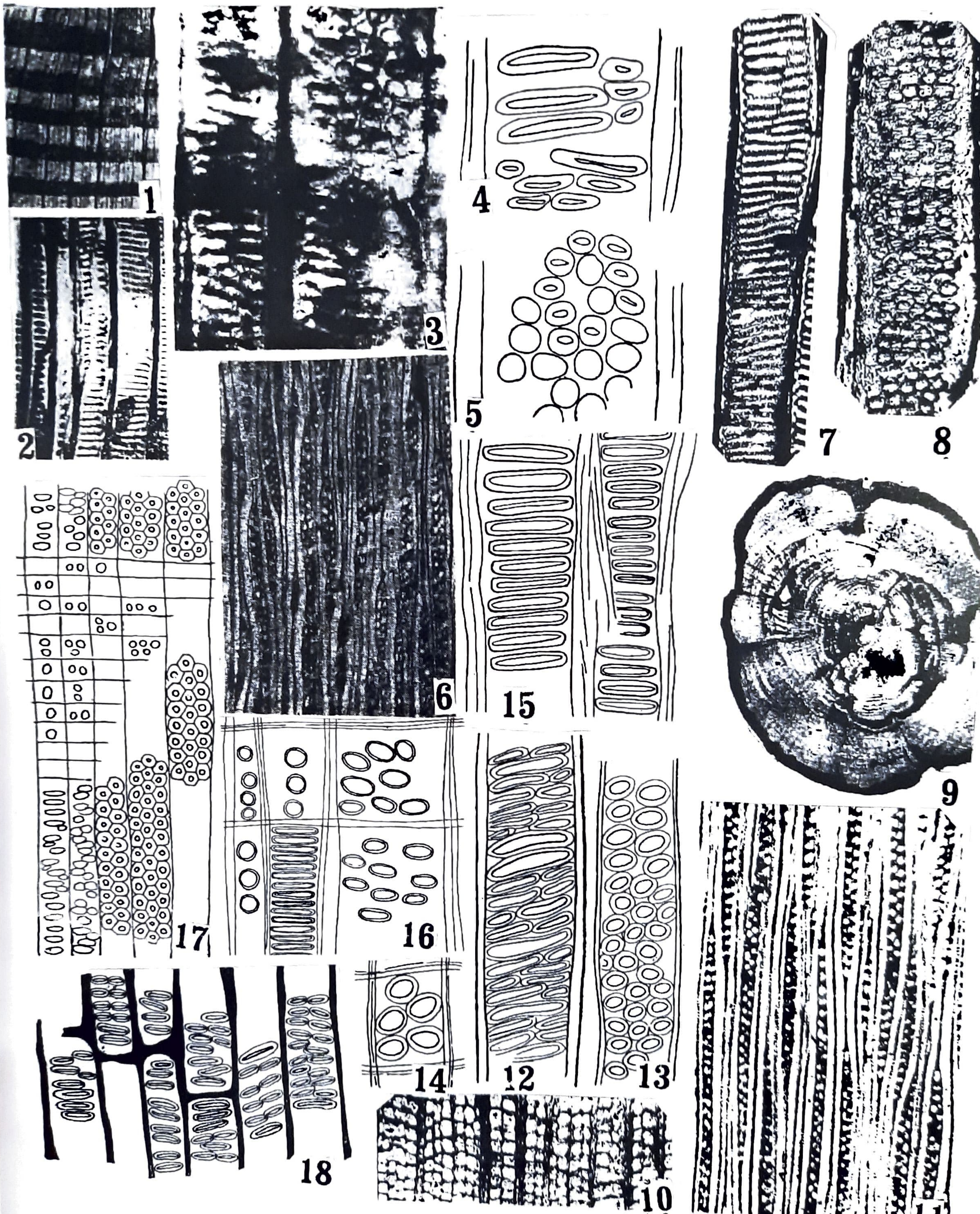

Plate 3

mostly bi- to triseriate. All bennettitalean stems have scalariform pits and rays are 1-3 seriate. A search for better preserved material and careful examination of *B. indica* Seward (1917) is needed.

Sahni's (1932b) interpretation about the affinities of *Sahnioxylon* (*Homoxylon*) with the vessel-less members of Magnoliales, e.g. *Trochodendronmagnolia* Zender and *Pataloxylon* Sahni, was based on comparison of structure of wood rays and pitting on radial walls of tracheids. Gupta (1934) suspected its complete relationship with the Magnoliales and correlated also with the cycadeoideas having pycnoxylic woods, e.g. *Cycadeoidea wielandii, C. painei, C. dortonii* and *C. micromyela*. Gupta (1933, 1934) believed that the vessel-less Magnoliales and Cycadeoidales (Bennettitales) had parallel development and evolution. Neither homoxylous angiosperms originated from Bennettitales nor vice-versa.

Hsu and Bose (1952) published further observations on *Homoxylon rajmahalense* Sahni (1932b) on the basis of study of a poorly preserved specimen of *Bucklandia* sp. and their opinion about the correlation of Sahni's material with the bennettitalean stems was not based on facts. However, their material was very close to a *Bucklandia* sp. and not to *H. rajmahalense* Sahni. Similarly, there is doubt on the correct identification of *Sahnioxylon andrewsii* Bose & Sah (1954). The specimen had neither leaf bases nor wide pith with mucilage ducts. Cortex was also narrow and poorly preserved and therefore nature of leaf traces remained unknown. The wood is pycnoxylic with 24 growth rings, a character shared by conifers also. The round bordered pits with circular pit pores create doubt about the affinities with the *Sahnioxylon* and vessel-less angiosperms. Fossil blocks from Mundro and Onthea, described by Bose and Sah (1954), are very close to the material of *Homoxylon rajmahalense* instituted by Sahni (1932b). The material of Sahni (one block) and two blocks of Bose and Sah (1954) were probably closely related to homoxylous Magnoliales. Further search and investigations are required for finalizing the anatomical relationships of *S. rajmahalense*. Presently, we agree with Gupta (1934) that the bennettitalean stems had parallel development and evolution with the homoxylous Magnoliales.

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