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INDIAN WILLIAMSONIAS — AN ILLUSTRATED REVIEW

Williamsonie z Indii — ilustrowany przegląd

ABSTRACT. Bennettitalean plants occur frequently in India in exposures of Upper Gondwana rocks. A list of the species of the female fructification *Williamsonia* described by different authors is given and the structure and interpretation of some of them is discussed, in particular that of *W. santalensis*. The conclusion is reached that although certain species of *Williamsonia* from India added much to our knowledge of this fructification, others still need further studies.

The Upper Gondwana rocks are exposed at a number of places in India e. g. the Rajmahal Hills, Golapili, Kota, Madras, Jabalpur, Jaisalmer and Cutch (Sitholey 1954). And in all these places bennettitalean plants are occurring frequently (Gupta 1966). Oldham and Morris (1863) illustrated a specimen (Pl. 32, fig. 12) and described it as an "inflorescence or development of young fronds of *Palaeozamia*". This specimen was later described as a Williamsonian fructification by Feistmantel (1877). He also described a number of species of this genus from the Mesozoic rocks of India e. g. *Williamsonia blanfordi* Fst. (1876, Pl. 12, figs. 5—7) from Cutch, *W. microps* Fst. (1877, Pl. 42, figs. 4,5), *W. gigas* Carr. (Fst. 1877, Pl. 44, figs. 2—4) from the Rajmahal Hills and a *Williamsonia* cf. *W. gigas* (Fst. 1877a, Pl. 7, figs. 1—4) from Golapili. However, his descriptions were based on the study of only the external morphological features like the shape and size of the fructifications and the surrounding bracts. *Williamsonia blanfordi* Fst. is a small, crushed strobilus provided with numerous, linear and curved bracts (Text-fig. 1,1, redrawn from Fst. 1876, Pl. 12, fig. 6). Fertile parts are unknown. Similarly, *W. microps* Fst. is a small, poorly preserved fructification (Text-fig. 1, 2, redrawn from Fst. 1877, Pl. 41, fig. 4). Size is not an important characteristic in the identification

of different species of *Williamsonia* (Sharma 1971) and so, more material is needed for establishing the validity of *W. microps*.

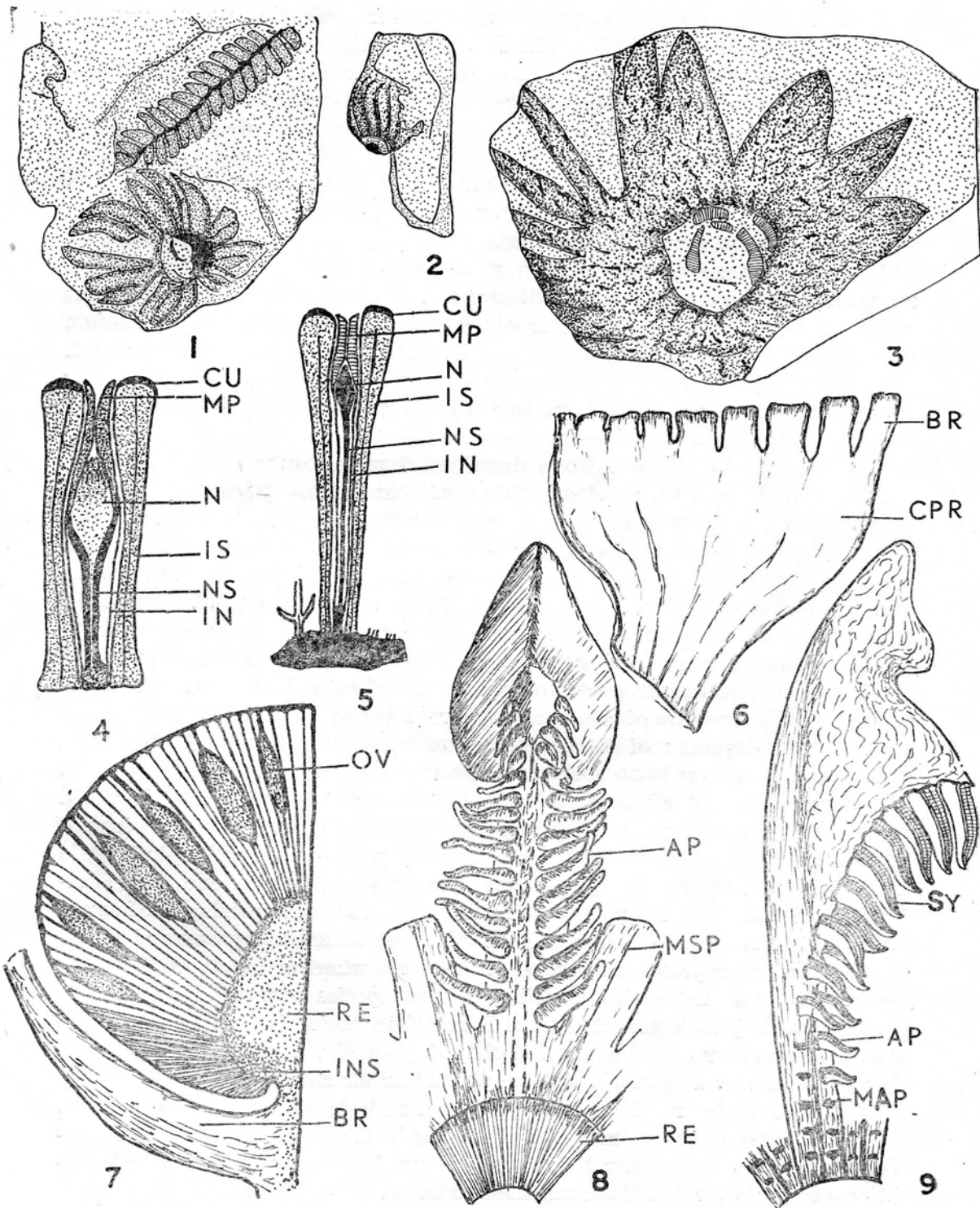
Feistmantel (1877b) compared the Indian material of the Williamsonian fructifications with those described from the Secondary rocks of Britain by Carruthers (1870). Seward (1917) and Seward & Sahni (1920) also found similarities between the Indian Williamsonsias and those collected from Britain and Mexico (Wieland 1916).

Seward (1917) and Seward & Sahni (1920) recognised the presence of four species of *Williamsonia*, *W. blanfordi* Fst., *W. microps* Fst., *W. indica* Sew. and *Williamsonia* cf. *W. setosa* Nath. from India. Seward (1917) established the new species *Williamsonia indica* for the larger but poorly preserved specimens of *Williamsonia* cf. *W. gigas* described by Feistmantel from Golapili (1877a, Pl. 7, figs. 1—4). However, Seward gave neither the diagnoses nor the figure and number of the type specimen. So a reconsideration of the validity of this species is necessary.

Sahni (1932) for the first time studied the internal structure of an Indian material of the genus *Williamsonia* which he described as *Williamsonia seawardiana* Sahni. Surrounding the central receptacle there was a compact but thin layer of seminiferous and interseminal scales. The former had an orthotropous ovule with a long micropylar canal (Text-fig. 1,5, redrawn from Sahni 1932, fig. 4). The nucellar stalk terminates in a conical nucellus which was free from the integument. Recently, the present author (Sharma 1975, in press) collected some very well preserved specimens of *W. seawardiana* Sahni from Amarjola in the Rajmahal Hills and found that the nucellus closely adhered to the integument (Text-fig. 1,4). In addition to the anatomical details of the fertile parts, epidermal structures of the bracts are also described. Sahni (1932) also suggested a reconstruction of the plant *Williamsonia seawardiana* in which he associated *Bucklandia indica* as the stem bearing *Ptilophyllum* cf. *P. cutchense* like leaves.

Text-fig. 1. 1 — *Williamsonia blanfordi* Fst., $\times 1$; 2 — *W. microps* Fst., $\times 1$; 3 — *W. sahni* Gupta spread bracts with hairs, $\times 1$; 4 — *W. seawardiana* Sahni. A reconstruction of an ovule and the surrounding interseminal scale. Nucellus is adhered with integument, $\times 24$ (after Sharma 1975); 5 — Same. Nucellus is free from integument, $\times 27$ (after Sahni 1932); 6 — *Weltrichia campanulatiformis* (Sharma) Sith. & Bose. Bell-shaped receptacle with bracts at the brim, $\times 1.5$ (after Sharma 1969); 7 — *Williamsonia harrisiana* Bose. Receptacle with a group of interseminal scales at the base, $\times 7$ (after Bose 1968); 8 — *Weltrichia santalensis* (Sith. & Bose). A microsporophyll with two rows of appendages on the adaxial side, $\times 1$ (after Sith. & Bose 1971); 9 — Same. A twisted microsporophyll with two rows of appendages on the abaxial side in the proximal part but in one row in the distal flat part, $\times 1$ (after Sharma 1969)

Abbreviations used: CU — cuticle, MP — micropylar canal, N — nucellus, IS — interseminal scale, NS — nucellar stalk, IN — integument, OV — ovule, RE — receptacle, INS — ring of interseminal scales, BR — bract, AP — appendage, MSP — microsporophyll, CPR — cup shaped receptacle, SY — synangium, MAP — marking of appendage



In 1943, Gupta described a probably bisexual fructification of *Williamsonia*, *W. sahnii* Gupta from the Rajmahal Hills. Surrounding the central seed bearing receptacle there were present nearly 20 elongated markings which were thought to be the remnants of the fallen microsporophylls (Text-fig. 1,3, redrawn from Gupta 1943, fig. 1). Bose (1968) however, considers *W. sahnii* only a seed bearing fructification.

In 1958, Gupta suggested a division of the Williamsonian fructifications into two types i. e. "close type" and "open type". In the former fertile parts were hidden by the numerous surrounding bracts e. g. *Williamsonia seawardiana*; while in the latter type the bracts were fewer in number and the fertile parts remained exposed e. g. *W. sahnii*. Sharma (1973) has expressed his agreement with this scheme and gave further observations on the plan of construction of Indian Williamsonsias. Gupta (1958) also made an attempt to distinguish the different species of seed bearing Williamsonsias on the basis of the number of ovules per unit area on the surface of the receptacles; but this characteristic did not prove fruitful.

In 1953, Sitholey and Bose described a male flower of *Williamsonia*, *W. santalensis* Sith. & Bose from Sakarigalighat in the Rajmahal Hills. It was described to possess a single whorl of 20 twisted microsporophylls. Each was provided with two rows of finger like appendages on their adaxial surfaces. On either side of an appendage two rows of synangia were produced. Sitholey and Bose also suggested that *Ontheanthus polyandra* Ganju (1947) is not different from *W. santalensis* and merged the former and the latter. Sharma (1969) collected a large number of beautifully preserved specimens of *W. santalensis* with their counter parts from Sakarigalighat and gave further observations on the structure of the flower. Several reconstructions showing different stages of development of the fructification were also attempted. According to Sharma there were two whorls surrounding the central cup-shaped receptacle. The outer one was sterile and made up of 20 linear bracts, while the inner had the same number of twisted microsporophylls. The appendages were in two rows and on the adaxial side in the proximal part of microsporophyll while in the distal flat part, the appendages were arranged only in one row (Text-fig. 1, 9). Synangia were produced on the adaxial side of appendages. Sharma (1969) considered that *Williamsonia* cf. *W. setosa* described by Seward (1917, fig. 557 A P. 444) represents a portion of the sterile whorl of bracts of *W. santalensis*. Sharma (1969) also described a new species of male *Williamsonia*, *W. campanulatiformis* collected from Dhokuti in the Rajmahal Hills. In this fructification the receptacle was bell-shaped (Text-fig. 1,6) and different from that of *W. santalensis* in size, shape and other characteristics.

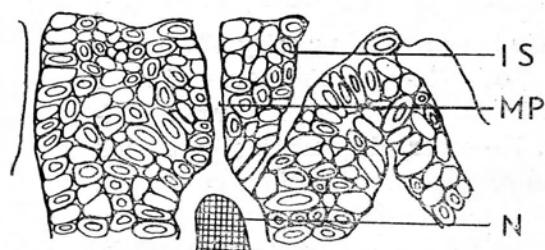
Bose (1967) described a poorly preserved male fructification of *Weltrichia*, *W. singhii* Bose collected from Sakarigalighat in the Rajmahal Hills. It resembles *W. santalensis* in general structure and probably represents the bud condition of the latter (cf. Sharma 1969, Fig. 8).

Harris (1969) suggested that the microsporangiate Williamsonian fructifications should be named *Weltrichia* Braun on the basis of priority of nomenclature. So in the year 1971, Sitholey and Bose changed the name of their species *Williamsonia santalensis* to *Weltrichia santalensis* and merged *Williamsonia campanulatiformis* Sharma with it. However, they neither examined the type specimen nor had they any material of the latter in their collection. In addition to *Weltrichia santalensis* they also included in this paper the descriptions of *Weltrichia singhii* Bose and *Weltrichia polyandra* (Ganju) comb. nov. Sitholey and Bose (1971) did not agree with the reconstructions of *Williamsonia santalensis* given by Sharma (1969) and suggested that there were no bracts outside the whorl of microsporophylls. There was neither twisting of microsporophylls (contrary to their description 1953, P. 32) nor were there appendages on the abaxial side in the proximal parts of the sporophylls. In their reconstruction (Sitholey & Bose 1971) they have shown two rows of appendages on the adaxial side of microsporophyll (Text-fig. 1, 8, redrawn from Sith. & Bose 1971).

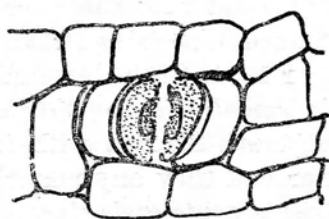
In 1968, on the basis of epidermal characteristics of the bracts, two new species of *Williamsonia*, *W. guptai* Sharma (Text-fig. 2,12) and *W. amarjolense* Sharma were described (Sharma 1968) collected from Amarjola in the Rajmahal Hills. Epidermal cells were rectangular, nonsinuous, without or with few papillae. Stomata were syndetocheilic, transversely oriented and present on the outer surface of bracts. In *W. guptai* cellular details of the interseminal scales were also present (Text-fig. 2,10). Surrounding each ovule or the seminiferous scale there were 5—8 sterile scales (Text-fig. 2,13). From the same locality another new species of *Williamsonia*, *W. harrisiana* was described by Bose (1968) which closely resembles *W. guptai* in size, shape and other characteristics. Bose distinguished the new species from others by the presence of a sterile zone of interseminal scales surrounding the basal part of the receptacle (Text-fig. 1,7), redrawn from Bose 1968, Pl. 2, fig. 4). But this kind of ring is found in almost all the seed bearing Williamsonsias known from India. This ring is not made up of only interseminal scales but a tissue of undifferentiated scales.

In 1969, Bose and Kasat established a new species of seed bearing *Williamsonia*, *W. seniana* collected from the carbonaceous shales of Jabalpur Series. Only the epidermal structures of the bracts were described (Text-fig. 2,11, redrawn from Bose & Kasat 1969, Pl. 1, fig. 8). This specimen does not differ much from *W. guptai* Sharma in size, shape and nature of fructification. Epidermal characteristics are also not different from that of the latter.

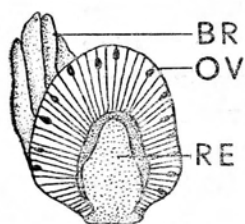
The fossiliferous locality of Amarjola in the Rajmahal Hills is very rich in seed bearing Williamsonsias. These are found as petrifications and preserve all the anatomical details. In 1970, a specimen of *Williamsonia* cf. *W. scotica* (Sharma 1970) was collected from this locality in which the cells of the micropylar canal were very well preserved. The canal was lined internally by transversely elongated cells similar to those found in the micropylar canal of *Gnetum*



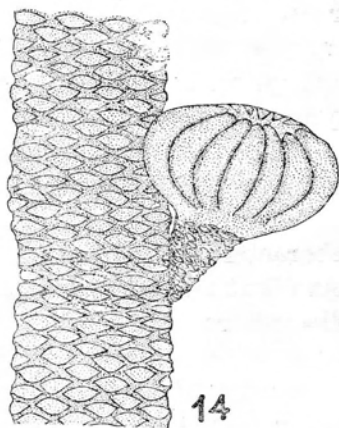
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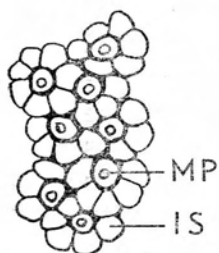
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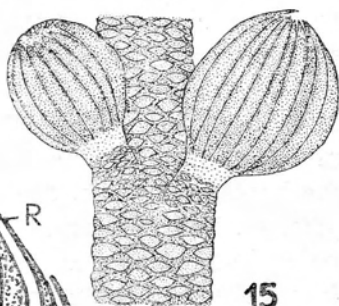
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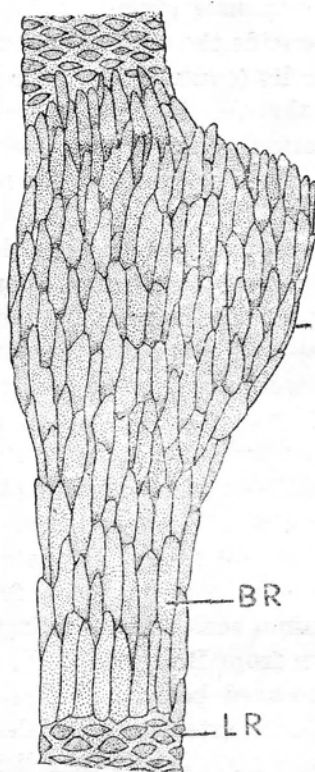
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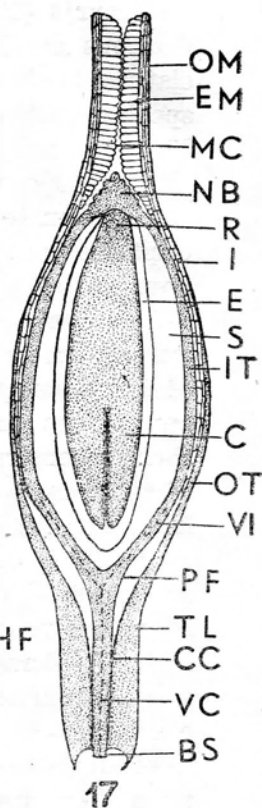
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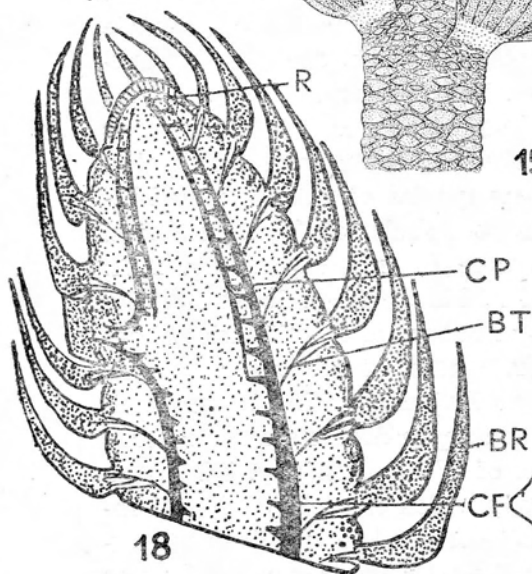
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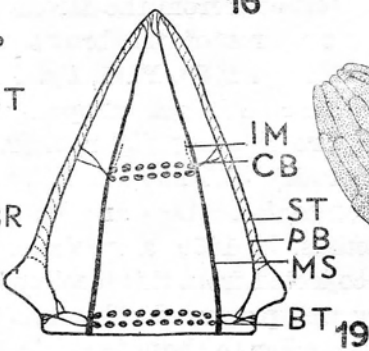
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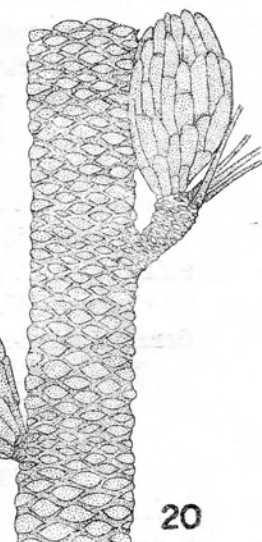
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(Maheshwari & Vasil 1961). In a mature seed the embryo is dicotyledonous and the inner layer of testa is formed by the peripheral portion of nucellus. (Text-fig. 2,17, Sharma 1970b).

In *Amarjola*, seed bearing *Williamsonias* occur in different forms i. e. as complete fructifications, bractless fruits and naked receptacles (Sharma 1974a). The complete fructifications are either of the „exposed type” (Text-fig. 2,14, 15) e. g. *W. guptai*, *W. amarjolense*, *W. harrisiana* or “partially hidden type” (Text-fig. 2, 16) e. g. *Williamsonia* sp. (Sharma 1971). The former are produced on small lateral branches and have a definite number of well developed bracts which surround the receptacle; while in the two latter types, the bracts are numerous and indistinct from those found on the peduncle part of fructification.

The anatomy of the receptacle was studied for the first time by Sharma (1970a) and found peculiar in being provided with numerous, inverted and exarch bundles in the vascular zone. In addition to the main bundles there are small, concentric peripheral bundles from which traces were supplied to the seminiferous and interseminal scales. The receptacle was considered to be a two noded structure as the traces from the main bundles to the peripheral ones were given off at two points i. e. near the basal and middle part of the receptacle (Text-fig. 2, 19).

The vascular cylinder in the stem of *Williamsonia* i. e. *Bucklandia* consisted of a single ring of numerous, endarch bundles with well developed and compact secondary xylem (Sharma 1967). Whereas, in the receptacle part of the fructification the bundles are inverted, exarch and without secondary xylem.

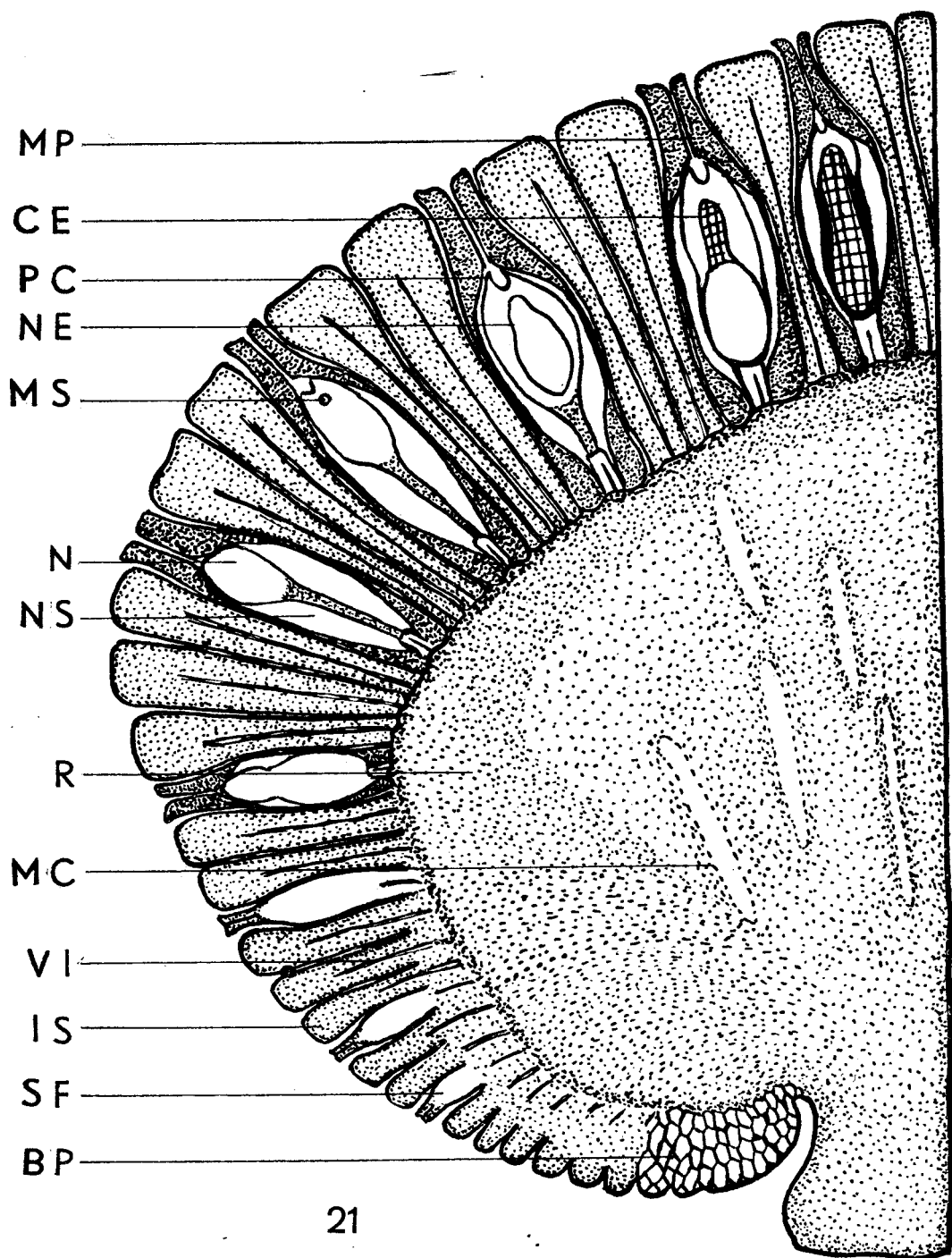
Text-fig. 2. 10 — *Williamsonia guptai* Sharma. Cellular structure of interseminal scales, $\times 300$ (after Sharma 1968); 11 — *W. seniana* Bose & Kasat. Epidermal cells and a stoma on the outer surface of bract, $\times 360$ (after Bose & Kasat 1969); 12 — *W. guptai* Sharma. Receptacle and the surrounding layer of fertile and sterile scales, $\times 1$; 13 — Same. Surface view of fertile and sterile scales, $\times 100$ (after Sharma 1968); 14 — *W. amarjolense* Sharma. “Exposed type” of fructification and attachment with the stem, $\times 1$ (after Sharma 1971); 15 — *W. guptai* Sharma. Same, $\times 1$ (after Sharma 1971); 16 — *Williamsonia* sp. A “completely hidden type” of fructification, $\times 1$ (after Sharma 1971); 17 — A reconstruction of the seed of *Williamsonia*, $\times 24$ (after Sharma 1970b); 18 — *W. seawardiana* Sahni. Anatomy of peduncle, $\times 1.5$ (after Sharma 1973 a); 19 — *Williamsonia* sp. receptacle showing vascular organisation, $\times 2$ (after Sharma 1970a); 20 — *W. seawardiana* Sahni. A “partially hidden type” of fructification, $\times 1$ (after Sharma 1971)

Abbreviations used: IS — interseminal scale, MP — micropylar canal, N — nucellus, BR — bract, OV — ovule, RE — receptacle, CP — centripetal xylem, BT — bract trace, CF — centrifugal xylem, IM — inner mesarch bundle, CB — connecting bundle, ST — scale trace, PB — peripheral bundle, MS — main stele, HF — hidden fructification, LR — leaf base, OM — outer layer of micropyle, EM — inner layer of micropyle, MC — micropylar canal, NB — nucellar beak, R — radicle, I — integument, E — endosperm, S — space, IT — inner layer of integument, C — cotyledon, OT — outer layer of integument, VI — vascular supply, PF — bifurcation of nucellus, TL — tubular layer, CC — central cylinder of stalk, VC — vascular bundle of stalk, BS — base of stalk

Thus interest was aroused as to how and where the disappearance of secondary xylem and inversion of bundles took place. The anatomy of the peduncle was studied and it was found that the amount of secondary xylem of the centrifugal side gradually decreases towards the distal end of the peduncles, so much so, that it is absent in the receptacle. The protoxylem points of the vascular bundles elongate and start cutting off metaxylem cells on the centripetal side resulting in the formation of inverted and exarch bundles of the receptacle (Text-fig. 2, 18), (Sharma 1973).

Interseminal and seminiferous scales are produced in a compact layer surrounding the entire surface of the receptacle. The thickness of this layer varies from 1.2 mm e. g. in *W. seawardiana* Sahni to 1.5 cm e. g. in *W. guptai*, *W. harrisiana*; but the fundamental structures and arrangement are similar in all the species of seed bearing *Williamsonias* described from India. Surrounding a seminiferous scale there are 5—8 interseminal scales. In the basal part of the receptacle there are immature and undifferentiated scales (Sharma 1974b). They are arranged basipetally, so those present at the top of the receptacle are larger and provided with mature seeds while the lower ones are comparatively smaller and have immature ovules. Interseminal scales are made up of parenchyma, having a narrow, central strand of xylem. Tracheids are provided with spiral and scalariform thickenings on their lateral walls. The distal ends of sterile scales are covered with thick deposition of cuticle e. g. in *W. seawardiana* (Sahni 1932; Sharma 1975). Recently, Sharma has described the ontogeny of ovule in *Williamsonia* (Sharma 1974b) and suggested that the differentiation of integument started as a result of ingrowing of the outer surface into the fertile scale. The nucellus is made up of large, elongated cells. The pollen chamber is produced as a result of degeneration of the upper cells of the nucellus (Sharma 1974a). The megaspore mother cell is comparatively larger in size than the surrounding cells of the nucellus and it is not deeply situated unlike that of *Cycadeoidea* (Crepet & Delevoryas 1973). The endosperm is produced by free nuclear divisions and wall formation starting from the micropylar end (Text-fig. 2, 21) (Sharma 1974b). Archegonia are yet to be found.

From the above description it is clear that the determination of the majority of the Indian species of *Williamsonia* is based on insufficient material and knowledge and that further studies are required to establish their taxonomic status e. g. *Williamsonia blanfordi* Fst., *W. microps* Fst., *W. indica* Sew. The others are morphologically so alike that they cannot be separated easily on external features e. g. *W. guptai* Sharma, *W. amarjolense* Sharma, *W. harrisiana* Bose and *W. seniana* Bose & Kasat. On the other hand some of the species have been elaborated in such detail e. g. *W. seawardiana* Sahni and *W. guptai* Sharma that they have added much to our knowledge about the seed bearing *Williamsonias* as a whole. Especially the petrified material collected from the fossiliferous locality of Amarjola is very well preserved and shows all the cellular details.



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Text-fig. 3. *Williamsonia* sp. A reconstruction showing different stages of ovule ontogeny, $\times 8$ (after Sharma 1975)

Abbreviations used: MP — micropyle, CE — cellular part of endosperm, PC — pollen chamber, NE — noncellular part of endosperm, MS — megaspore mother cell, N — nucellus, NS — nucellar stalk, R — receptacle, MC — mucilage canal, VI — vascular strand of interseminal scale, IS — interseminal scale, SF — seminiferous scale, BP — basal polygonal cells

The male fructifications are comparatively rare in occurrence. They are known only from the Rajmahal Hills and also from some of the Northern localities like Sakarigalighat, Onthea and Dhokuti. The flowers are much larger than seed bearing fructifications. Microsporophylls spread out on maturation and each had two rows of finger like appendages which in turn produced the paired rows of synangia. However, the details of synangia and spores are yet to be studied.

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STRESZCZENIE

WILLIAMSONIE Z INDII — ILUSTROWANY PRZEGLĄD

Autor wymienia gatunki *Williamsonia* występujące w skałach górnej Gondwany oraz omawia krytycznie znane dotychczas opisy ich żeńskich owocowań, ze szczególnym uwzględnieniem *W. santalensis*. Wypowiada pogląd, że jakkolwiek niektóre gatunki *Williamsonia* z Indii przyczyniły się w znacznym stopniu do naszej wiedzy o ich owocowaniu, to jednak inne wymagają dalszych badań.