Life and time of Indian *Williamsonia*

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The *Williamsonia* plant, belonging to the order Bennettitales, consists of stem—*Bucklandia* Presl, leaf—*Ptilophyllum* Morris, male flower—*Weltrichia* Braun and female flower—*Williamsonia* Carruthers. This plant was perhaps a small, much branched woody tree of xerophytic environment. It co-existed alongwith extremely variable and rich flora including highly diversified plant groups from algae to gymnosperms. In India, it appeared during the marine Jurassic, proliferated and widely distributed in the Lower Cretaceous and disappeared from the vegetational scenario of Upper Cretaceous Period with the advent of angiosperms.

Key-words—Bennettitales, *Williamsonia*, Jurassic-Cretaceous (India).

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साराँश

भारतीय विलियमसोनिया का जीवनकाल

जयश्री बैनर्जी

बैन्नेटाइटेलिस क्रम से सम्बद्ध **विलियमसोनिया** पौधे के विभिन्न अवयव अलग-अलग नामों से जाने जाते हैं इसका तना–**बुक्लैंडिया** प्रेस्ल, पत्ती–**टाइलोफ़िल्लम्** मोरिस, नर पुष्प–**वेल्ट्राइकिया** ब्रॉन एवं मादा पुष्प–**विलियमसोनिया** कैरुथर्स से नामाँकित किया जाता है। यह पौधा शुष्क वातावरण में उगने वाला एक छोटा, अधिक शाखाओं से युक्त वृक्ष था। यह विभिन्नता से युक्त वनस्पतिजात, जिसमें शैवालों से लेकर अनावृतबीजी समूह के पौधे विद्यमान थे, का ही एक अवयव है। इसका समुद्री जूराई कल्प में उदय हुआ, अधरि क्रीटेशी कल्प में विकसित एवं दूर-दूर तक फैला तथा उपरि क्रीटेशी कल्प में आवृतबीजी पौधों के उदय होने के साथ-साथ विलुप्त हो गया।

LIFE OF *WILLIAMSONIA* PLANT

In the Upper Mesozoic Era, a new group of plants—the Bennettitales, developed that colonised various habitats of terrestrial areas. This group continued till Early Cretaceous. In India, it is represented by the members of the family Williamsoniaceae and occurs pre-dominantly during Lower Cretaceous Period (Text-figure 1). The *Williamsonia* plant is known through its stem—*Bucklandia* Presl, leaf—*Ptilophyllum* Morris, male flower—*Weltrichia* Braun, and *Williamsonia* Carruthers female flower.

Stem—*Bucklandia* Presl

The *Bucklandia* stem was erect and cylindrical, protected by armour of rhomboidal leaf-bases. Four species of *Bucklandia* described from India are: *B. indica* Seward, *B. sahnii* Bose, *B. guptai* Sharma and *B. dichotoma* Sharma. In *B. indica* Seward, the secondary wood is more compact than recent cycads and cycadeoids. The medullary rays are uniseriate and tracheids have multiseriate bordered pits on their radial walls instead of scalariform pitting in the majority of cycadeoid stems. Secretory canals are abundant in the parenchymatous ground tissue, the cambium and phloem are not preserved. The cross section (Text-figure 2) of *B. sahnii* Bose 1953a shows well-defined growth rings in the secondary wood, 4-9 cell thick cork cambium present outside the cortex. Cortex is fairly wide, parenchymatous with thick-walled cells, singly or in group and leaf traces with a single bundle which finally breaks up into 5-7 strands. Pericycle is with few layers of polygonal cells. The phloem ring is marked by alternate bands of poorly developed rays leaving big

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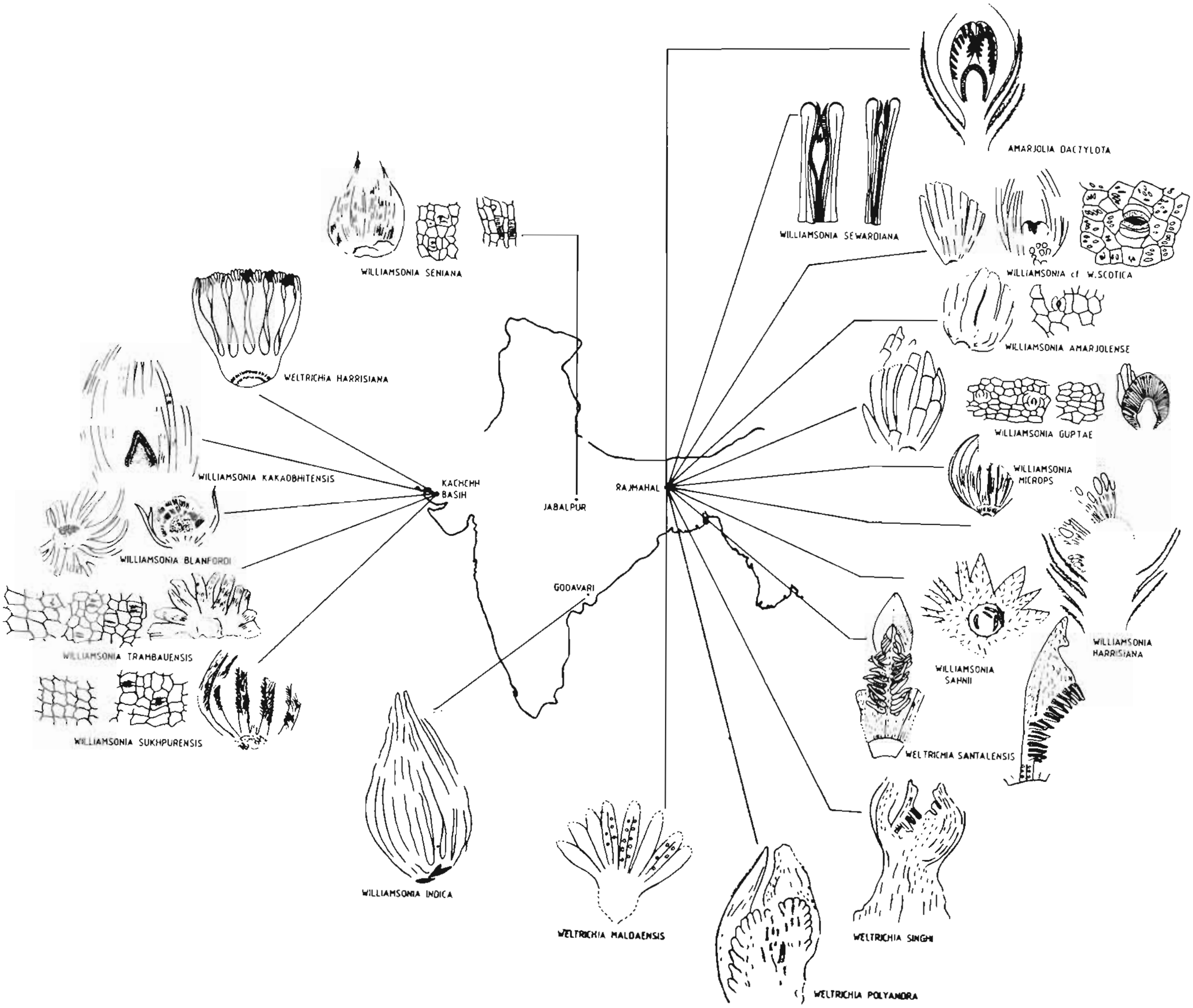
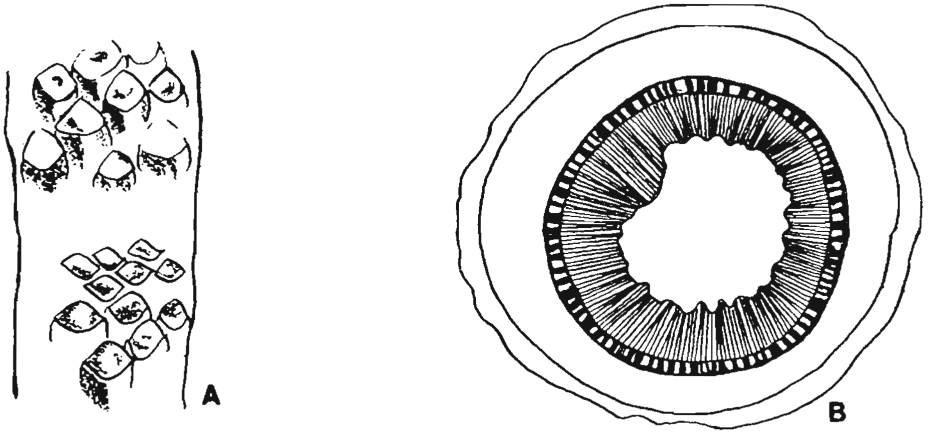


Text-figure 1—Distribution of Indian Williamsonian flowers.

cavities. Phloem consists of alternate thick- and thin-walled elements. Traces of cambium are seen below the phloem. The tracheids of early wood have a large diameter with a thinner wall than those of the late wood. The late wood is remarkably developed and occupies about two-third of the whole growth rings. Radial surface of the late wood tracheids have not so variable pitting but the early wood shows different type of pitting from scalariform to multiseriate. Ray cells in radial view are rectangular and much wider than high. The pits in the field are bordered, usually one to six or more, oval or circular in shape. Longitudinal section shows that the inner-most part of xylem ring consists of 4 to 8 layers of slender tracheids with spiral thickening in their walls. Pith is very wide and consists of parenchymatous cells with numerous scattered thick-walled cells similar to the cortex. In *B. sahnii* the stem had forked branches and the flowers were borne at the point of bifurcation as in *Wielandiella angustifolia* Nathorst. *Bucklandia guptai* Sharma 1967 has sparsely arranged symmetrical leaf basis and anatomically it shows the presence of numerous growth rings and mostly uniseriate medullary rays which are rarely biseriate. *B. dichotoma* Sharma 1969b is characterised by having longer rays, biseriate in nature and bordered pits with narrow elliptical pit pores. According to Bose (1974, p. 196), this species is based on variable characters and these should not be used for specific differentiation. Besides, he considers it perhaps as a young stem.

Mode of branching—Seward (1912), while describing petrified *Williamsonia* from Scotland, suggested the existence of a sympodial branching,



Text-figure 2—A, *Bucklandia*—stem; **B,** T.S. of *Bucklandia*—stem.

while Sahni (1932) suggested monopodial branching in *W. sewardiana.*

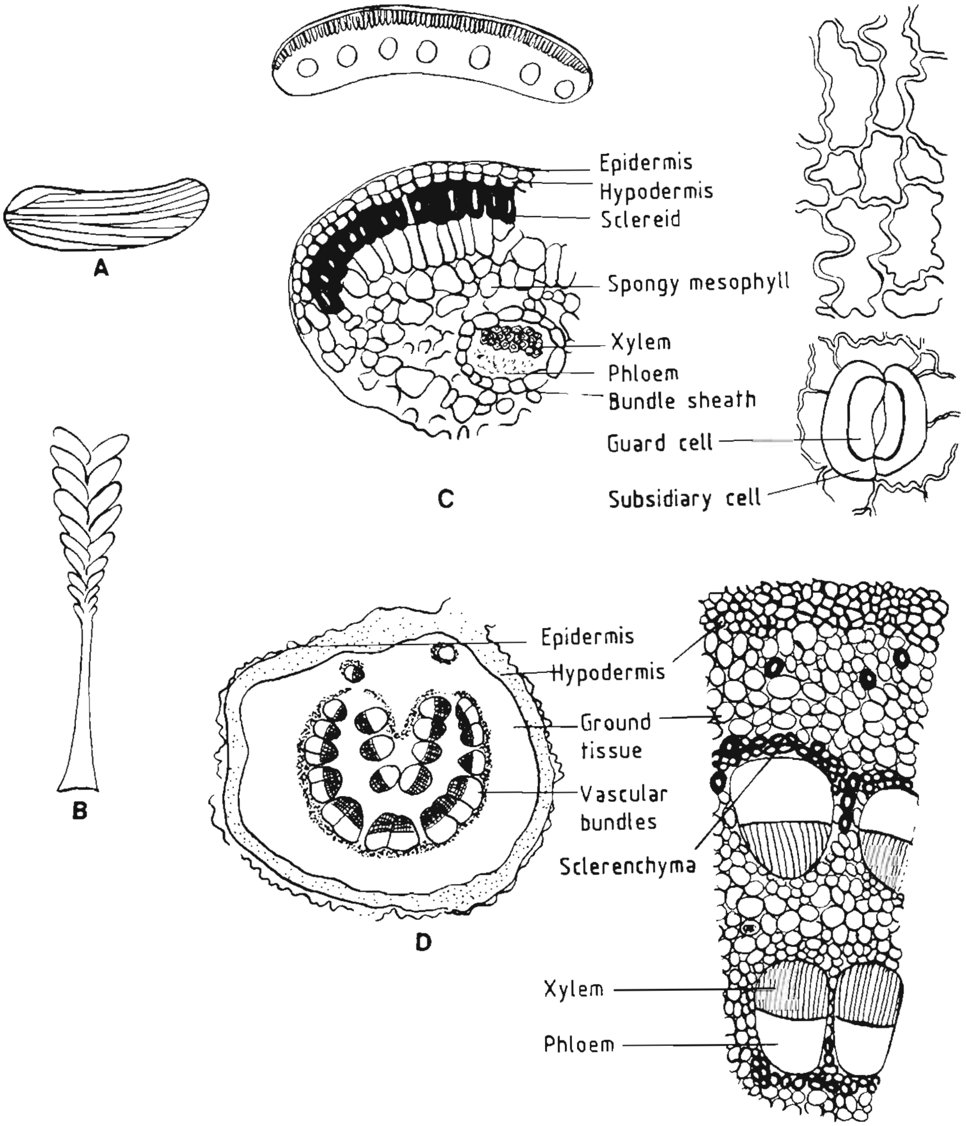
Leaf—*Ptilophyllum* Morris

The genus *Ptilophyllum* Morris in Grant (1840) originally comprised pinnate fronds, pinnae with acute or obtuse apices. The circumscription of the genus was later enlarged to include pinnate frond, pinnae linear-falcate in shape with acute, sub-acute to obtuse apices, basal acroscopic margin round, basal basiscopic margin decurrent and veins sub-parallel to slightly diverging towards the apical margin. The rachis contains a double arc of collateral vascular bundles comparable to the pteridosperms (Text-figure 3). Sclerenchymatous patches and sclereids are found in the cortex. Single bundle arises from the upper corner of the double arc of vascular bundle of rachis which divides into two at the base of the pinna. It is repeatedly forked at different levels to form a more or less parallel venations.

The anatomy of pinna shows collateral, exarch xylem with a parenchymatous bundle sheath. Sclereids occur isolated or in groups in the palisade and spongy mesophyll. The salient features of the cuticle of *Ptilophyllum* leaves are hypostomatic condition with syndetocheilic stomata, but vary in the pattern of distribution of stomata, papillae and its morphological differences, being the main criteria for speciation. *P. acutifolium* Morris has pinnae with acute apices, whereas *P. cutchense* Morris possesses sub-acute to obtuse apices. *P. rarinervis* (Feistmantel) Bose has pinnae with 2-3 veins only. *P. tenerrimum* Feistmantel has narrow, long pinnae. In *P. indicum* Jacob & Jacob 1954, stomata are distributed in stomatal bands. *P. oldhami* Jacob & Jacob 1954 shows irregular distribution of stomata except on the marginal region. In *P. distans* Jacob & Jacob 1954 pinnae have acute apices and the lower cuticle is differentiated into broad stomatiferous and narrow non-stomatiferous bands, cells are devoid of papillae and the outer wall of the subsidiary cells is looped. *P. jabalpurensis* Jacob & Jacob 1954 is characterised in having 1-3 papillate marginal cells and papillae are solid circular or semi-circular, hollow-circular or crescent-shaped. In *P. nipanica* Vishnu-Mittre 1956 lower epidermis has non-papillate cells and stomata are arranged in bands. *P. gladiatum* Bose & Sukh-Dev 1958 is distinct in having gladius-like pinnae and non-papillate epidermal cells of veins and subsidiary cells. *P. institacallum* Bose 1959 is significant in possessing papillae of various shapes. The epidermal cells of lower cuticle and stomata are irregularly scattered in the inner zone. *P. sakrigaliensis* Sah 1958 has elongated pinnae with acute apices. Lower cuticle is studded with stomata arranged in bands. One or two papillae are present on each epidermal cell of the vein band. *P. horridum* Roy 1967 shows lower cuticle with stomata in bands and two or more papillae on each epidermal cell of the vein band but they do not form a frill-like structure over the vein band as in *P. institacallum. P. sahnii* Gupta & Sharma 1968 has small pinnae, oblong or oval in shape with obtuse apices, lower cuticle is differentiated into broader stomatal, narrow non-stomatal band and marginal non-stomatal region, epidermal and subsidiary cells are devoid of papillae. *P. amarjolense* Bose 1953b is distinguished by its broader leaves and stomatal bands are 4-5 stomata broad.

Male flower—*Weltrichia* Braun

The male flower is characterised by having microsporophylls forming a cup-shaped structure at



Text-figure 3—A, *Ptilophyllum*—pinna showing venation; **B,** *Ptilophyllum* leaf; **C,** T.S. of pinna; **D,** T.S. of rachis.

the base. They bear polleniferous appendages adaxially or distally. Each appendage has two rows of pollen chambers. The pollen grains are oval and monocolpate.

From India, male flower was first described as *Williamsonia santalensis* Sitholey & Bose 1953. Later, Bose (1967) suggested that the specimen of *Williamsonia santalensis* be included under the genus *Weltrichia* Braun as it has priority. The male flower consists of a whorl of 20 (?)microsporophylls coalescent towards the base to form a shallow cup. Each microsporophyll bears on its upper surface two rows of finger-like appendages which are presumed to have been the spore-bearing organs. The rows of small chambers are present inside each appendage. The distal sterile portion of the microsporophyll shows an asymmetrical and obliquely twisted expansion of the lamina. Sharma (1969a) suggested that there are two whorls, the outer whorl consists of 20 sterile bracts and the inner whorl has 20 twisted microsporophylls. He also opines that the appendages are in two rows on the adaxial side of the proximal part of the microsporophyll and there is only one row on the distal part of the microsporophyll (Text-figure 4C). Later, Sitholey and Bose (1971) commented that the bracts are spirally arranged and are not in whorls. The receptacle of *Weltrichia* is, in fact, cup-shaped flower formed by the fusion of microsporophylls. The fertile organ consists solely of a tubular thick-walled structure, tapering distally which completely encloses the polleniferous chambers. Revised restoration of microsporophyll given by Sitholey and Bose (1971) shows that the microsporophylls were bilaterally symmetrical structures without any twisting of distal portion. The abaxial surface of the expanded distal portion is raised into a prominent hump-like structure (Text-figure 4A, B).

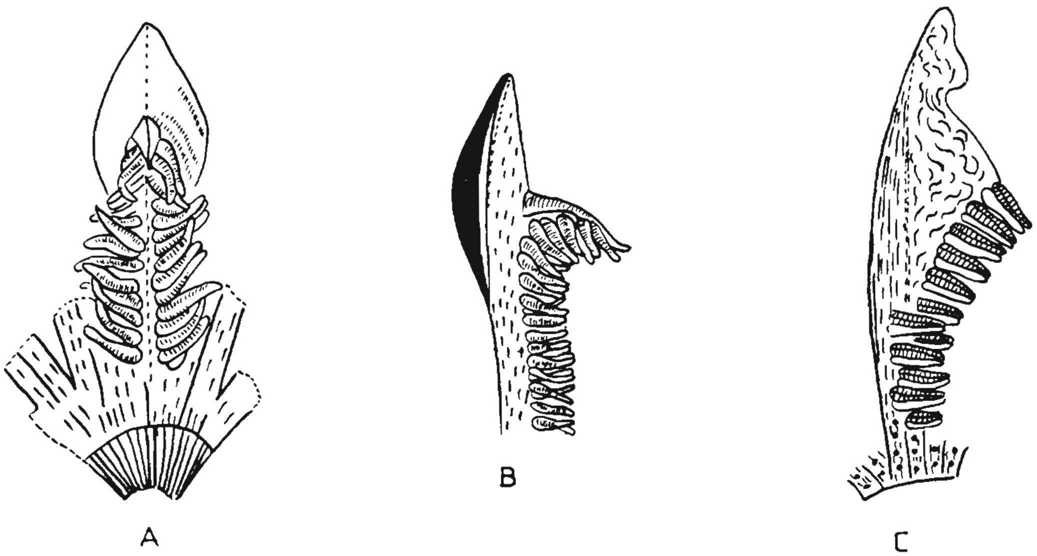
Ontheanthus polyandra Ganju 1947, a unique bennettitalean fructification, was transferred by Sharma (1969a) to *Williamsonia santalensis* Sitholey & Bose 1971 recognised it as a separate taxon under *Weltrichia*. It needs further examination whether it is a part of an unopened flower of *Weltrichia santalensis* or an incomplete preserved part of a bisexual flower—*Amarjolia dactylota*. *Weltrichia singhii* Bose 1967 is supposed to represent bud conditions of *W. santalensis* (Sharma, 1969a). *Williamsonia companulatiformis*, known by an incomplete specimen, is built more or less on the same plan of construction as *Weltrichia santalensis* (Sharma 1969a, p. 102; Sitholey & Bose 1971). *Weltrichia harrisiana* (Bose & Banerji, 1984) is about 12-15 cm in diameter. Microsporophylls 12-14 in number, coalesce towards the base and form a circular depression, about 2 cm in diameter. The microsporophylls are distally expanded, coriaceous and their adaxial surface exhibits prominent ridges. Each microsporophyll terminates into five uniformly broad fertile appendages, each appendage having a double row of polleniferous chambers. *Weltrichia maldaensis* Pal & Ghosh 1985 shows microsporophylls with some small circular lateral projections.

Female flower—*Williamsonia* Carruthers

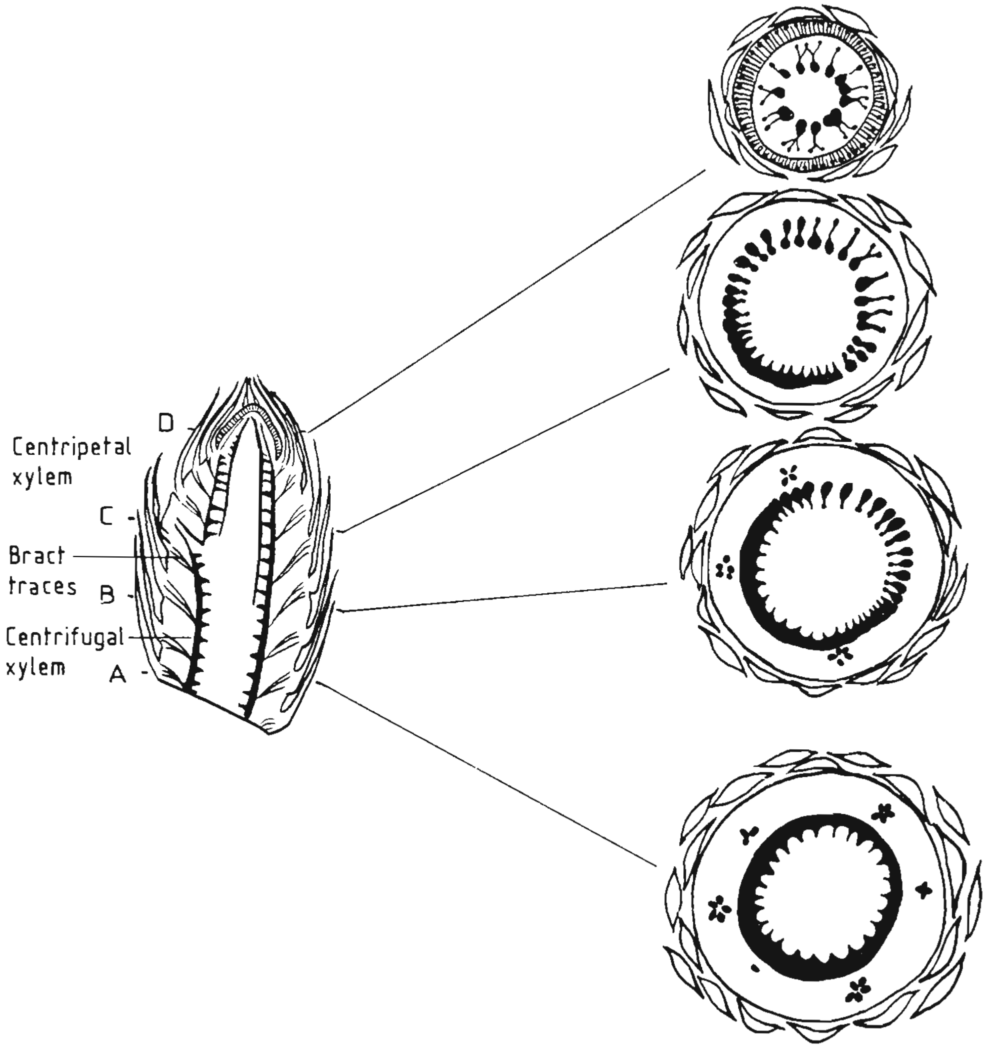
Williamsonia Carruthers, the female flower, has receptacles of various shapes, e.g., rhomboidal, hemispherical-conical with numerous interseminal and seminal scales. The receptacle is surrounded by numerous spirally arranged bracts.

The anatomy of peduncle (Text-figure 5) shows the changes in the vascular organisation at different levels (Sharma, 1973b). The centrifugal xylem is gradually reduced in thickness and broken into segments. Centripetal xylem originates from the endarch protoxylem points of centrifugal xylem and gradually increases in amount towards the upper side of peduncle. In the receptacle centripetal xylem forms the main vascular cylinder and the remnants of the centrifugal xylem are connected with each other by their tangentially elongated protoxylem points.

Anatomy of receptacle shows the main stele consisting of a number of isolated, collateral inverted, exarch vascular bundles which maintain their shape and size from base to apex (Text-figure 6). In the basal position bundles gives off paired traces to the bracts, while in the middle part of the receptacle they are connected with isolated, collateral or concentric, endarch or mesarch vascular bundles present in the peripheral region of cortex. These peripheral bundles are the source of vascular traces to the scales. The tracheids of bract traces have spiral thickening on their lateral walls. Transverse section through the concavity of receptacle shows inverted bundles in the main stele indicating a change from endarch condition of vascular bundle in the peduncle to exarch condition in the receptacle. The main stele gives off traces only at two places in the whole receptale. The first point lies in the pedicel while the second is present in the middle part of receptacle. These two points in the



Text-figure 4—Restoration of microsporophyll—**A, B,** after Sitholey and Bose (1971); **C,** after Sharma (1969a).



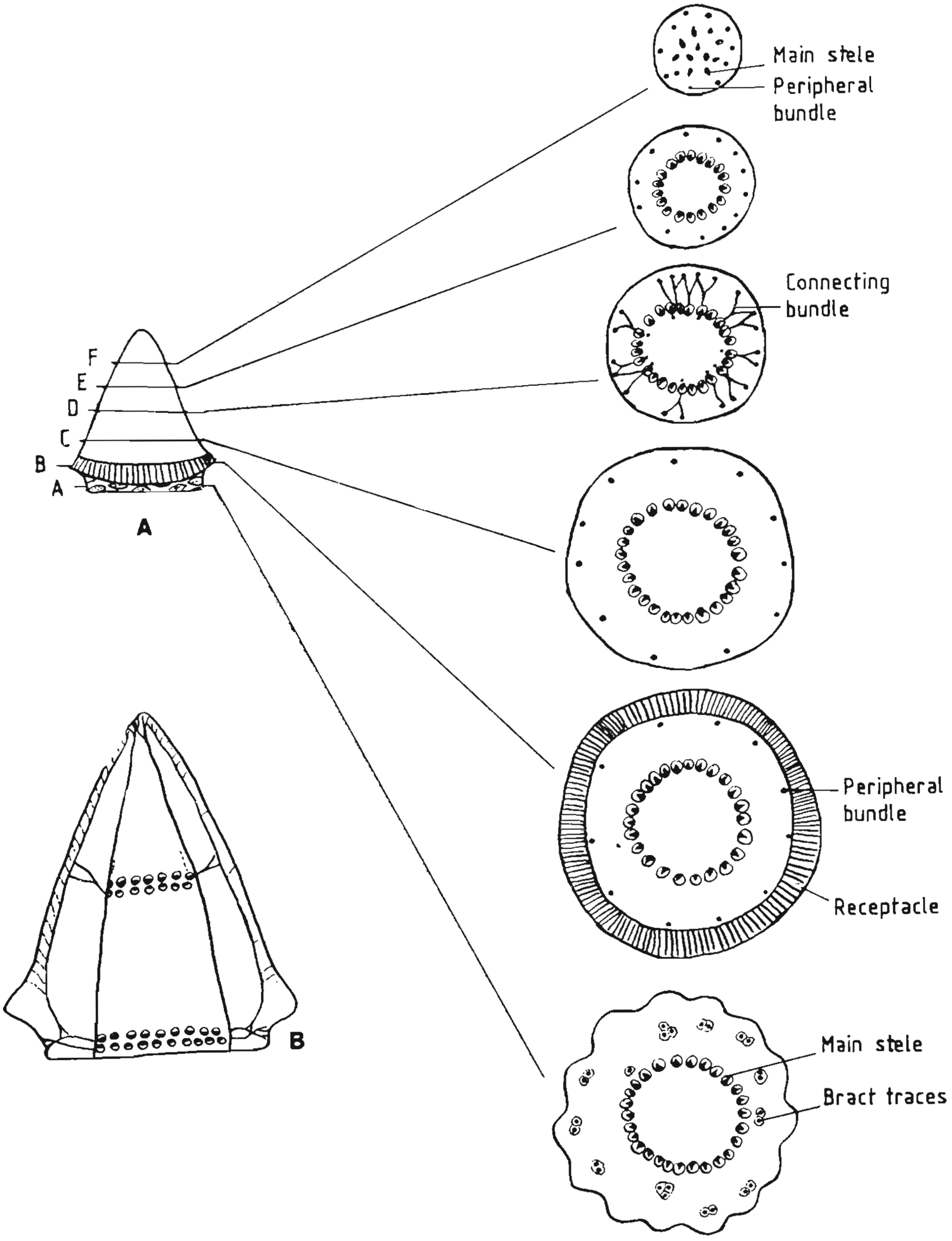
Text-figure 5—Reconstruction of the vascular organisation in transverse and longitudinal section of peduncle.

receptacle may be compared with the two modes of a branch or stem. According to Sharma (1973b) the receptacle of a seed-bearing *Williamsonia* is comparable with a two noded inflorescence axis.

Bract anatomy shows a thick sclerenchymatous hypodermal zone which consists of relatively larger cells on the abaxial side. There are usually 7 collateral, endarch vascular bundles, two above near the middle line and five forming an arc parallel to the lower surface. The xylem of the bundles facing each other in the radial portion of the bract and in the distal flattened part, the number of bundles reaches up to 11 or more. The ground tissue is parenchymatous but without mucilage canals (Sahni, 1932; Sharma, 1975).

The upper surface of the bracts has rectangular or squarish epidermal cells which are arranged in rows, parallel to the long axis of the bracts. The lateral walls of the cells are thin and sinuous. Outer wall of the epidermal cells is provided with circular, scattered simple pits. Stomata are syndetocheilic, non-sunken and transversely oriented.

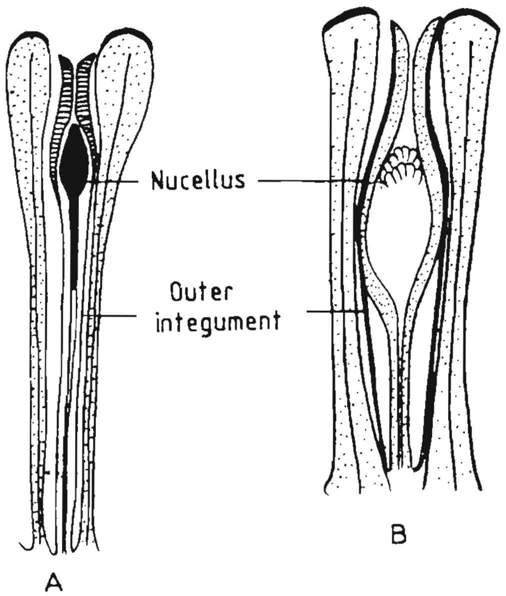
The fertile portion consists of a small, conical receptacle which is produced terminally on a thick peduncle. The receptacle is covered with a thick layer of sterile and fertile scales. The sterile scales consist of hexagonal-rectangular parenchymatous cells with a central vascular strand up to the highly cutinized distal regions. Five or six sterile scales surround a fertile seminiferous scale represented by an orthotropous ovule which consists of a small, thick stalk or funiculus and a long, oblong body. The stalk has a definite concavity at its basal end, representing the abscission point of the scale. From the upper part of funiculus arise a central long, slender nucellar stalk and a thin outer integument. The former consists of two types of cells, central thin-walled parenchymatous and the surrounding



Text-figure 6—A, Transverse section of the receptacle showing vascular organisation; **B,** Longitudinal section of the receptacle showing vascular organisation.

thick-walled, darkish, elongated cells. The nucellar stalk terminates into an oval-shaped nucellus, the apical end of which is made up of a rosette of elongated cells. The nucellus is fused with integument which is made up of rectangular, parenchymatous cells. It is three or four cells thick in the region of micropyle but reduces downward, so that near the basal part of nucellus it is only one cell thick and then merges into the surrounding layer of nucellar stalk.

The distal end of micropyle is more or less a funnel-shaped structure and reaches the level of the terminal end of the surrounding interseminal scales. The outer integument arises from the funiculus remains which are thin, delicate and mostly one cell thick throughout its length. It remains free from the



Text-figure 7—Vertical section of ovule—**A**, after Sahni (1932), and **B**, after Sharma (1975).

nucellar stalk, but fuses with the inner integument near the basal part of the nucellus and then continues upwards as an outermost layer of integument up to the distal end of micropyle (Text-figure 7A, B.

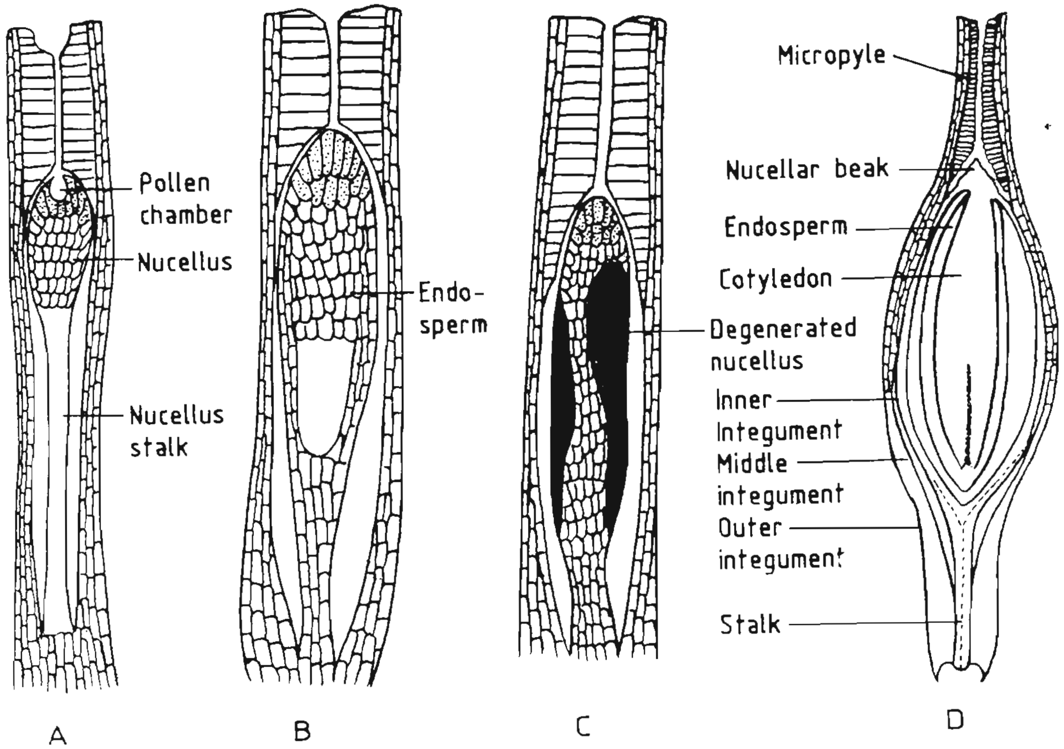
The different developmental stages of an ovule show that the development of fertile layer is basipetal (Sharma, 1974b). In the basal part of receptacle the fertile layer consists of thin-walled polygonal cells without any distinction of scales. The scales are produced as a result of ingrooving of epidermis. Differentiation of fertile scale starts from the micropylar end. The development of integument takes place at an early stage of ovule ontogeny. In a young ovule there is a long cylindrical nucellar stalk which terminates into a conical nucellus; pollen chamber is differentiated in the upper part of nucellus (Text-figure 8A). A megaspore mother cell is produced in the nucellus which divides by free nuclear divisions for the formation of an endosperm. The endosperm wall formation starts from the micropylar side and continues on the descending side (Text-figure 8B). On maturity of endosperm the surrounding cells of nucellus degenerate, except the micropylar side (Text-figure 8C). Pollen chamber formed by the degeneration of nucellar cells shows affinity of *Williamsonia* with the cycads on one hand and *Ephedra* on the other (Sharma, 1974b). Sharma (1979) further observed that the megaspore mother cell is situated not very deep in the nucellus. The female gametophyte covers almost whole nucellus and is made up of thin-walled cells. In the apical part of endosperm two or more archegonia are seen arranged in a ring and distinct from the cells of endosperm. The micropylar canal in young ovule is long, narrow and lined with large cells, while in mature ovules or seeds the canal becomes small, wide and filled by a nucellar plug. The thickness of micropyle reduces from 3-4 cells to one showing relationship with *Cycadeoides* and *Gnetum*. Mature seeds are found in ripe, nacked, bractless fruits. Seeds are oblong or ovate, stalked, dicotyledonous, partially endospermic and have a long micropyle (Sharma, 1970c). Seed coat includes outer tubular cells, middle parenchymatous true integument and inner vascularized tissue formed after fertilization by modification of the peripheral portion of nucellus. The seed of *Williamsonia* differs from cycadeoideas in being partially endospermic and shows more affinities with the seeds of pteridosperms and Gnetales than with the angiosperms.

On maturity, the flower produces abscission layer in between the receptacle and the compact layer of sterile and fertile scales. The sterile scales and ovules are ontogenetically identical. It is related to the extant genus *Ginkgo* in the manner of detachment of flower from the parent plant before fertilization. The inter-locking cells of the micropyle was either absent or the flower was detached before pollination.

ATTACHMENT OF FLOWER

On the basis of their plan of construction the flowers can be divided into two main types, viz., "exposed type" as in *W. guptae* and *W. amarjolense* Sharma and partially "hidden type" as in *W. sewardiana* Sahni. In exposed type, the flower were borne either terminally on the branches or directly on the sides of the stem. They had a definite point of abscission and covered with bracts produced from the base of the receptacle. Moreover, on the basis of number, shape and size of bracts they can be further divided into three main types (Sharma, 1971). In the first type, the bracts are large, incurved and mostly arranged in one row as in *W. amarjolense* (Text-figure 9A). The second type has long, linear bracts arranged in two rows as in *W. guptae* (Text-figure 9B). The third type includes the flower with linear, thin, straight and arranged in several rows of bracts as in *W.* cf. *W. scotica* (Text-figure 9C). The second type of partially embedded flower probably detached itself from the parent plant on maturation leaving a depression on the side of the stem (Text-figure 9D). The variation on the basis of number, shape and size of bracts might be due to seasonal fluctuation.

Feistmantel (1876) described *Williamsonia*



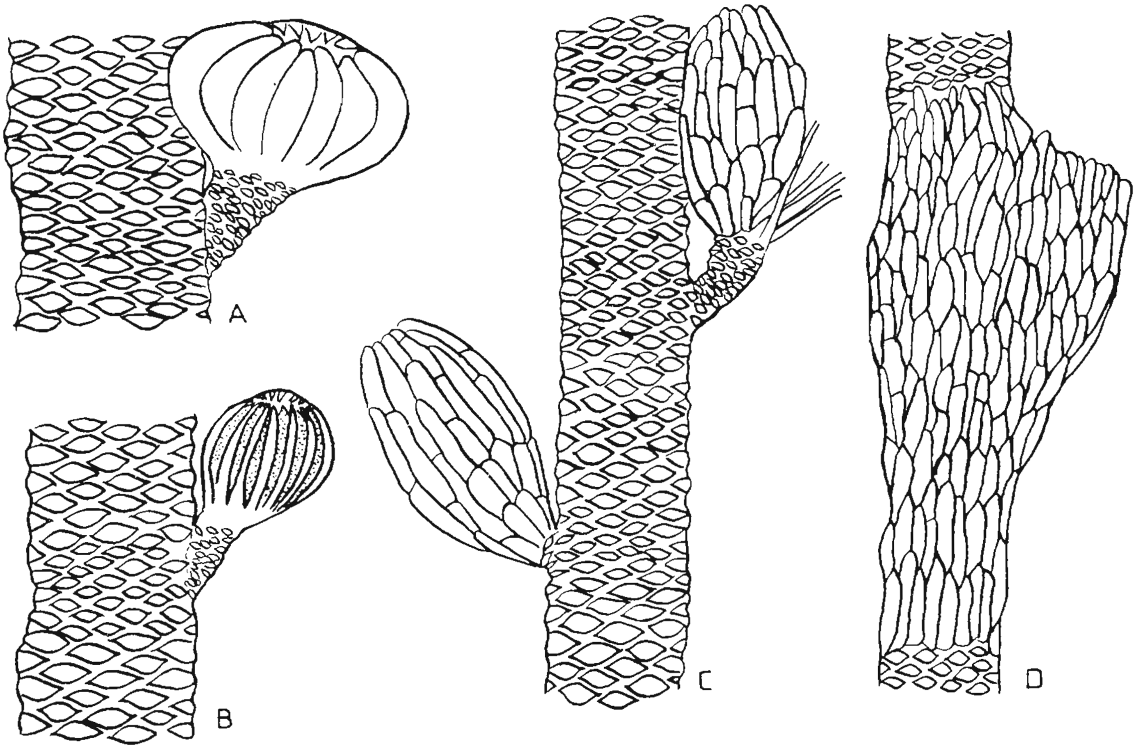
Text-figure 8—A-C, Vertical section of ovules showing different stages of development; **D,** Seed restoration.

blanfordi from Kachchh. *W. gigas* Carruthers recorded by Feistmantel (1877a) has been ultimately placed under *Weltrichia santalensis. W. microps* Feistmantel 1877a is visualized as a small pedicellate bud-like specimen of *W. gigas* or *W. blanfordi* by Seward (1917, p. 445) and Seward and Sahni (1920). *Williamsonia* comb. *W. gigas* Feistmantel 1877b has been placed under a new species—*W. indica*, by Seward (1917) in being larger in size. In *W. sewardiana* (Sahni, 1932) the flower has hemispherical receptacle, seminal and interseminal scales 3 mm in length which gradually reduce up to 1.5 mm. Soft investment around the nucellus continued downwards forming the outer layer of nucellar stalk. Sharma (1975) observed adherence of nucellus and integument throughout its length (Text-figure 7B). *W. sahnii* Gupta 1943 is supposed to be a bisexual flower but as there is no positive evidence of the presence of androecium, the author himself doubts about its bisexuality. *W. harrisiana* Bose 1968 is characterised by dome-shaped receptacle, seminal and interseminal scales up to 1 cm in length and the presence of a sterile disc. Sharma (1977) observed sterile disc in almost all the species.

W. guptae Sharma 1968 has conical receptacle with seminal and interseminal scales up to 1 cm in length, epidermal cells of the bract rectangular and stomata sunken. *W. amarjolense* Sharma 1968 is distinct in having hemispherical receptacle, epidermal cells of bracts are polygonal and stomata non-sunken. Perhaps *W. guptae* is similar to *W. harrisiana* in shape of receptacle, size of seminal and inter-seminal scales and epidermal features of the bracts. *W. seniana* Bose & Kasat 1969 can be distinguished by its epidermal features. In *W.* cf. *W. scotica*, the bracts are considered as reduced pinnate leaves having pinnae in the form of reduced vascularised appendages (Sharma, 1970a). *W. kakadbhitensis* Bose & Banerji 1984 is distinct in having rhomboidal receptacle and hairy bracts. *W. trambauensis* (Bose & Banerji, 1984) is characterized in having ramentum scars and trichome bases. *W. sukhpurensis* (Bose & Banerji, 1984) has jagged-thickening on the lateral walls of epidermal cells.

HABIT OF *WILLIAMSONIA* PLANT

On the basis of morphological and anatomical characters, it is suggested that the plants of *Williamsonia* were perhaps small, much branched woody trees of xerophytic environment. They had adopted various ecological strategies to meet the water stress conditions as shown by different parts of the plants. The columnar stem was branched monopodially or sympodially, bearing large and small slender branches with spirally arranged



Text-figure 9—A, B, Showing attachment of flower on lateral branch; **C,** Reconstruction showing terminal or lateral attachment as shown by *Williamsonia* cf. *W. scotica*; **D,** Partially hidden type of *Williamsonia* flower.

pinnate foliage leaves. The pedunculate flowers were borne terminally/laterally at the point of dichotomy or the sessile flowers were partially embedded into the stem. These woody trees perhaps formed a part of mixed subtropical community of the forest. The palaeolatitudinal position of the Indian subcontinent during the period was between 20°-45° south latitude (Smith & Briden, 1979) and this supports the existence of tropical to subtropical climate. The stem of ***Williamsonia*** possesses persistent armours of leaf-bases which perhaps acted as a protective covering either from predators or to withstand unfavourable conditions. The armours might have provided mechanical strength to the stem also. The variation in size and shape of the leaf scars depends upon the position of abscission layer and is probably environmentally induced variation. The presence of periderm and the stem anatomy show arborescent nature of the plant. The periderm protects the inner tissue from weathering. The presence of sclereids in the peduncle and rachis, sclerenchyma cells outside and in between the vascular bundle of the rachis provides hardness to these parts. Stem has a large pith and less secondary tissue suggesting that the plant could grow in moisture deficit soil. The secondary wood shows large lumened variously pitted tracheids in the growing season (Early wood) indicating that water availability was high. Thick-walled tracheids with less variable pitting (Late wood) show water stress condition. The leaf anatomy shows sheathed vascular bundles. Sclerenchymatous hypodermis acts as a supporting tissue and provides rigidity to the leaves to withstand wilting. The occurrence of sunken stomata on the lower surface (hypostomatic condition) in most of the species and sclerenchymatous hypodermis show xeromorphic characters. Sclerenchyma and sclereids give mechanical strength and protection. Papillae in the epidermal cells as well as subsidiary cells act in two ways, i.e., they reduce the intensity of the incoming radiation and also check the wind action. High stomatal frequency of occurrence in a few species perhaps is due to high rate of transpiration. Growth rings in the secondary wood and abscission of leaf show seasonal fluctuation in light, temperature and water availability. The mechanism of abscission gives protection against desiccation in adverse conditions. Abscission of bracts shows maturity of the flowers. The abscission of the reproductive parts, i.e., seminal, interseminal scales and microsporophylls from the receptacle base helps in dissemination for fertilization and manner of dispersal. Hairs on the bracts perhaps protect the reproductive parts from insect predators and also reduce the transpiration rate. The ovules are further protected by interseminal scales which possibly acted as protective covering but, later attracted the insects for pollination. In *Williamsonia*, flowers were unisexual suggesting out-breeding by anemophilly, whereas *Amarjolia*-flower (another bennettitalean flower) was hermaphrodite. The curved nature of microsporophyll and protandrous nature of *Amarjolia* also indicate out-breeding by entomophily. Whether these major selective characters provide protection from phytophagus insects or from self-incompatibility are questions to be considered squarely.

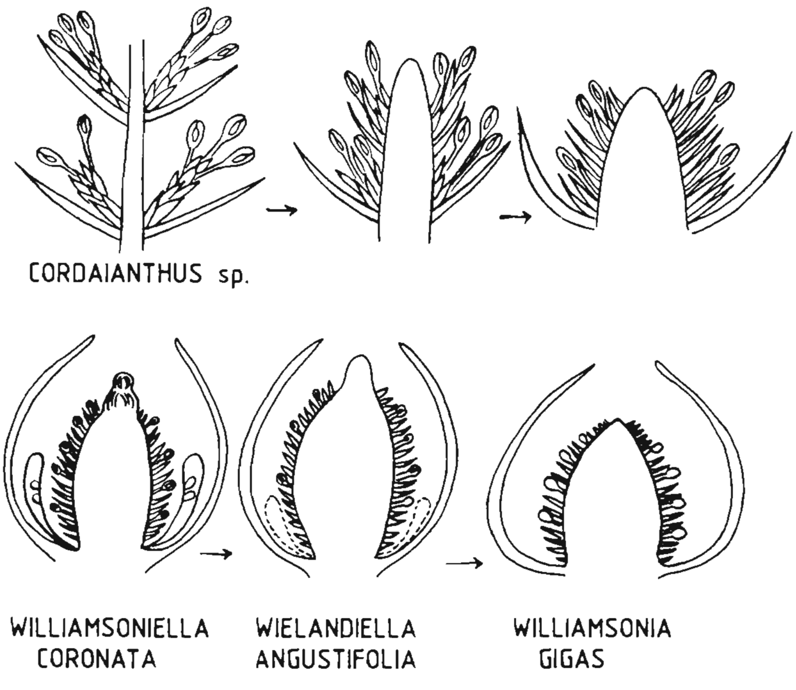
A cycas-like habit for *Williamsonia sewardiana* was proposed by Sahni (1932), plant with columnar stem—*Bucklandia indica* Seward, crown of pinnate foliage leaves—*Ptilophyllum* cf. *cutchense* Morris and female flower borne terminally on short branched laterals—*Williamsonia sewardiana*. Later, the recovery of more species of female flower: *W. guptae* Sharma, *W. amarjolense* Sharma, Stem—*Bucklandia sahnii* Bose, and leaves—*Ptilophyllum amarjolense* Bose and *P. sahnii* Gupta & Sharma from the same locality raised doubts about Sahni's reconstruction of *W. sewardiana, Bucklandia indica* and *Ptilophyllum* cf. *cutchense*. Anatomically the peduncle of *W. sewardiana* is more similar to *Bucklandia sahnii* Bose than with *B. indica* Seward (Bose, 1953a; Sharma 1975). Besides, the discovery of branched stem of *B. sahnii* and *B. dichotoma* suggested that these plants had equal or unequal branched stems and perhaps due to the deciduous nature of small laterals and leaves they were found in large number. Recently, a specimen has been recovered from Rajmahal Hills in which the *Williamsonia*-flower seems to be laterally attached to a narrow branch perhaps by a small peduncle. On the basis of these evidence, the branching in *Williamsonia* was probably more akin to the reconstruction of Harris (1969, fig. 59c) for *Bucklandia pustulosa, Ptilophyllum pecten* and *Williamsonia leckenbyi*. This view has also been supported by Bose (1974, p. 197), but it needs better specimens with branching habit.

RELATIONSHIPS OF *WILLIAMSONIA*

Williamsonia, belonging to Bennettitales, shows primitive as well as advance gymnospermous characters. It shows affinities with the plants of Pteridospermales, Cordaitales, Cycadales, Gnetales, etc.

Affinities with Pteridospermales

Presence of secretory canals in pith and cortex of stem shows affinity with the Pteridospermales. In the petiole the bundles are united at places exhibiting a continuous C-shaped strand as in some pteridosperms, viz., *Rhetinangium arberi* Gorden. The endospermic seed of *Williamsonia* also shows



Text-figure 10—Stages showing derivation of an ovulate cone of *Williamsonia* from a female inflorescence of *Cordaianthus* sp. as a result of condensation and swelling of the axis.

affinity with the seed of pteridosperms. The microsporangiate flower having pinnate microsporophylls shows some similarities with pteridosperms. But, in *Weltrichia*, a cup-shaped receptacle with microsporophylls and microsporangia which are either directly attached or arranged on finger-like appendages are those notable characters not exhibited by an extinct or extant group of plants.

Affinities with Cordaitales

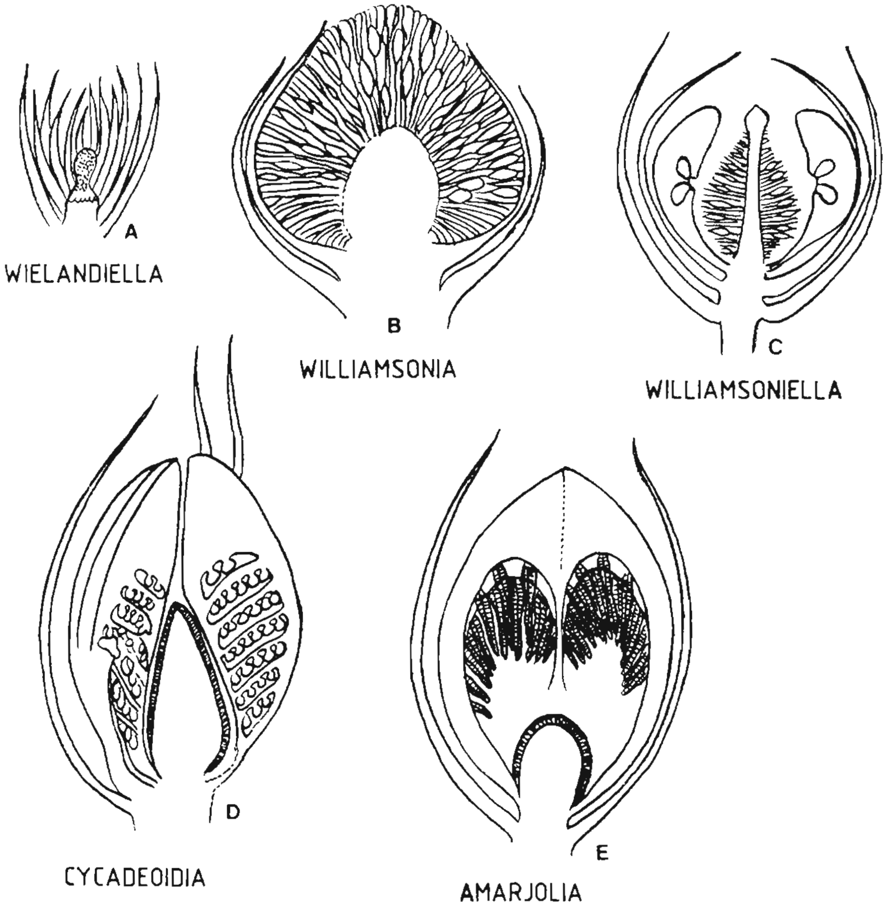
Sharma (1982) derived bennettitalean seed bearing fructification from *Cordaianthus* as a result of reduction and swelling of inflorescence axis producing receptacle and modification of the axillary bud bearing megasporophylls and scales to seminiferous and interseminal scales (Text-figure 10). However, in ovule ontogeny *Cordainthus* and *Williamsonia* are different from each other.

Affinities with Cycadales

Presence of armours of leaf bases on the stem, crown of pinnate leaves and secretory canals in pith and cortex shows similarity with that of *Cycas*. Girdle leaf traces are absent unlike *Cycas*. Cuticle and anatomy of leaf also differ from *Cycas*. In *Williamsonia*, stomata are syndetocheilic and transversely oriented, whereas in Cycadales stomata are haplocheilic. Diploxylic condition in the anatomy of *Cycas* leaf is also unlike Williamsonias. In *Cycas*, petiole shows omega-shaped, collateral endarch bundles, whereas in *Williamsonia* they are arranged in double row. Non-vascularised integument of ovule differs from cycads but the megagametophyte with 3-4 archegonia and pollen chamber formed by the degeneration of nucellar cells are the common features.

Other affinities

Mehra (1988) derived Bennettitales independently from Protoseminales, a plexus which gave rise to Cordaitales and Pteridospermales. Presence of definite abscission point at the base of fructification suggests similarity with the *Ginkgo*. In *Williamsonia*, the integument surrounding each

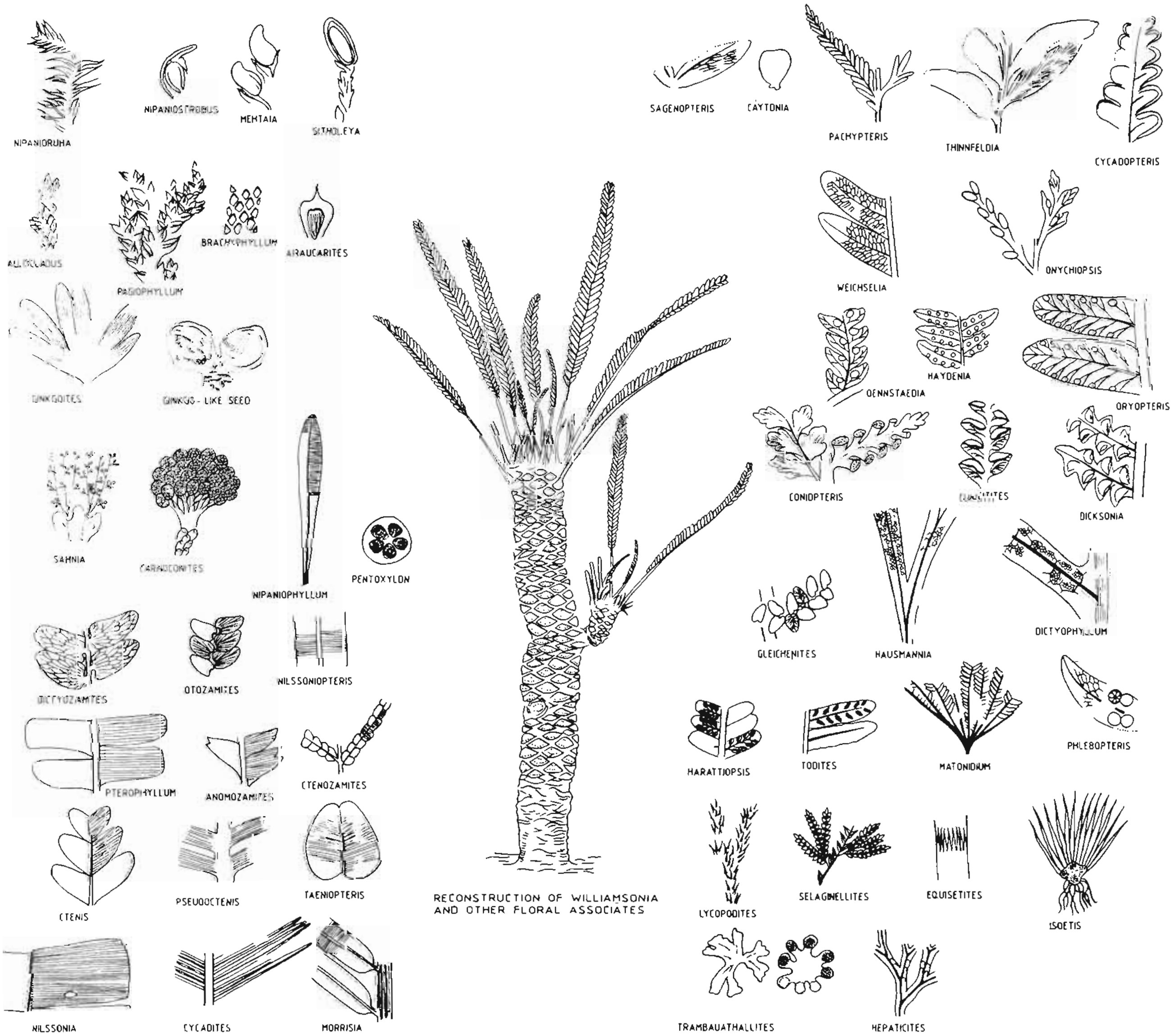


Text-figure 11—Showing gradual sequence of flower from monosporangiate to bisporangiate condition or vice versa; **A,** *Weilandiella*; **B,** *Williamsonia*; **C,** *Williamsoniella*; **D,** *Cycadeoidea*; and **E,** *Amarjolia*.

ovule and extending up to a long micropyle exhibits an advanced feature shown by *Gnetum* and *Welwitschia*. The formation of pollen chamber by the degeneration of nucellar cells shows its relationship with *Ephedra*. Flower-like organisation of *Williamsonia* fructifications led Wieland (1906) and Arber and Parkin (1907) to suggest that Mesozoic Bennettitales are the ancestral group of angiosperms. A gradual sequence can be drawn from monosporangiate to bisporangiate flower, i.e., *Wiellandiella, Williamsonia, Williamsoniella, Amarjolia* to *Cycadeoidea* or vice versa (Text-figure 11), but which one is primitive is difficult to say.

TIME OF WILLIAMSONIAS

The Williamsonias appeared in India during Upper Jurassic Period and flourished well in tropical to subtropical climate of Lower Cretaceous Period. The other floral associates of Williamsonias are represented by extremely variable taxa of highly diversified plant groups (Text-figure 12). They are: *Hepaticites* Walton, *Trambauathallites*' Banerji, *Equisetites* Sternberg, *Lycopodites* Lindley & Hutton, *Isoetes* Linnaeus, *Selaginellites* Zeiller, *Marattiopsis* (Oldham & Morris) Seward & Sahni, *Todites* Seward, *Klukia* Raciborski, *Gleichenites* Goeppert, *Matonidium* Schenk, *Phlebopteris* Brongniart, *Hausmannia* Dunker, *Dictyophyllum* Lindley & Hutton, *Haydenia* Seward, *Dicksonia* L'Heritier, *Culcitites* Appert, *Onychiopsis* Yokoyama, *Coniopteris* Brongniart, *Dennstaedtia* Bernhardi, *Weichselia* Stiehler, *Pachypteris* Brongniart, *Cycadopteris* Zigno, *Thinnfeldia* Ettingshausen, *Sagenopteris* Presl, *Caytonia* Thomas, *Pterophyllum* Brongniart,



Text-figure 12—Reconstruction of *Williamsonia* (after Sahni, 1932) and other floral associates.

Otozamites Braun, *Dictyozamites* Oldham, *Anomozamites* Schimper, *Nilssoniopteris* Nathorst, *Pentoxylon* Srivastava, *Nipaniophyllum* Sahni, *Carnoconites* Srivastava, *Sahnia* Vishnu-Mittre, *Nilssonia* Brongniart, *Morrisia* Bose, *Pseudoctenis* Lindley & Hutton, *Ctenozamites* Nathorst, *Cycadites* Sternberg, *Taeniopteris* Brongniart, *Ginkgoites* Seward, *Araucarites* Presl, *Brachyphyllum* Lindley & Hutton, *Pagiophyllum* Heer, *Nipanioruha* Rao, *Elatocladus* Halle, *Nipaniostrobus* Rao, *Mehtaia* Vishnu-Mittre, *Sitholeya* Vishnu-Mittre, *Podostrobus* Rao & Bose and *Stachyotaxus* Nathorst.

The Williamsonias were one of the dominant plant groups growing in dry open lands alongwith pteridophytes and conifers and perhaps formed a part of tropical semi-evergreen and subtropical broad-leaved type of forest. In India, they appeared and established themselves during the Upper Jurassic (marine), proliferated in the Lower Cretaceous and disappeared in the Upper Cretaceous with the advent of the highest evolved plant group the angiosperms perhaps due to inherent genetic factors. The rapid radiation of angiosperms caused the sudden extinction of Williamsonias due to strong selective pressure. Perhaps they could not compete with the early angiosperms and ultimately perished from the Upper Cretaceous floristic scenario.

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