

Diverse sexual strategies in fossil gymnosperms: pollination in the *Bennettitales* revisited

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with 3 figures and 1 table

Key words: *Bennettitales*, *Williamsonia*, *Williamsoniella*, *Cycadeoidea*, sexual system, pollination, protandry, beetles.

Summary

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Literature, images and anatomical slides of bennettitalean fossils were studied to gain insights into pollination biology. Our review grounded in modern concepts of floral biology and plant-animal interactions leads to new interpretations of existing data. Focusing on bisexual bennettitaleans, especially *Cycadeoidea*, we propose a novel explanation of how pollination occurred. Pollination was similar to an angiosperm cantharophilous syndrome, complete with pollination chamber, except that bisexual bennettitalean flowers were *protandrous* rather than *protogynous*. Small-bodied beetle pollinators arrived at the protandrous flowers just prior to or at the time of pollen release. Beetles in the pollination chamber mated and females oviposited in the androecium and larvae developed there, maturing on the ground after androecium shedding; adults later emerged from the ground litter. At the time of androecium shedding and shortly after, adult beetles carrying pollen fly to other flowers, if attracted to female-stage flowers, briefly visit and pollinate.

1. Introduction

Considered iconic Mesozoic plants, the *Bennettitales* is an enigmatic group of extinct gymnosperms that flourished from the Upper Triassic until the Middle – Late Cretaceous (BLOMENKEMPER & al. 2021, McLOUGHLIN & al. 2018); there is evidence that certain taxa survived until the Oligocene in refugia (McLOUGHLIN & al. 2011). The earliest reliably bennettitalean leaf dates from the lower Permian of Shanxi, China; this, together with findings of leaves from the upper Permian in Jordan, indicate that although never common, the *Bennettitales* were a wide-spread element of the paleoequatorial flora by the end of the Permian (BLOMENKEMPER & al. 2021). Superficially resembling cycads in their vegetative form, they were originally considered closely related, but it has long been established that these two major lineages bear little in common (THOMAS & BANCROFT 1913). This said, *Cycadales* and *Bennettitales* appear to have evolved about the same time “... and first appeared in seasonally dry environments in paleoequatorial regions” (BLOMENKEMPER & al. 2021). The *Bennettitales* early attracted interest

because of their “flowers”, and NEWELL ARBER & PARKIN (1907) proposed that angiosperms and *Bennettitales* were derived from a common ancestor. Modern phylogenetic analyses regularly exchange the position of *Bennettitales* with respect to *Gnetales*, *Pentoxylales*, angiosperms, conifers, *Caytonia* and glossopterids (see DOYLE 1996); among more recent analyses *Bennettitales* are placed nearer to *Gnetales* and angiosperms (FRIIS & al. 2009). In a pilot study using a novel approach based on infrared spectroscopy of extant and fossil gymnosperm cuticles, *Bennettitales* were found to be close to the extinct *Nilssoniales*, and as long recognized, but distantly related to cycads (VAJDA & al. 2017).

Two families are generally recognized on the basis of growth habit (WATSON & SINCOCK 1992), *Williamsoniaceae* (slender branched shoots having flowers exposed on branch axils) and *Cycadeoideaceae* (massive, tall or short in stature, sparsely branched trunks bearing flowers on short stalks embedded among persistent leaf bases). Many researchers think that *Williamsoniaceae* may be paraphyletic (POTT & AXSMITH 2015, McLOUGHLIN & al.

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Table 1. Summary of sexual systems in selected *Bennettitales*.

Family	Genus	Sexual system
<i>Williamsoniaceae</i>	<i>Williamsonia</i> (female flowers)	Diclinous; dioecious and/or monoecious
	<i>Weltrichia</i> (male flowers)	
	<i>Williamsoniella</i>	Bisexual; dichogamous
<i>Cycadeoideaceae</i>	<i>Cycadeoidea</i>	Bisexual; strongly dichogamous
	<i>Monanthesia</i>	Bisexual; strongly dichogamous, monocarpic

2018, and see ANDERSON & al. 2007). It is traditional to refer to bennettitalean reproductive structures as “flowers”, and this accords well with the broad morphological definition of a flower as a shoot bearing fertile and associated sterile appendages used by FRAME (2003); there is no implied direct homology of bennettitalean floral appendages to those of angiospermous flowers. *Williamsoniaceae* is considered geologically older in origin (STEWART 1983, POPA 2019); the oldest known bennettitalean reproductive structure is *Williamsonia eskensis* from the Middle Triassic (McLOUGHLIN & al. 2018) whereas *Cycadeoidea* reproductive structures date from the Upper Jurassic. While *Williamsoniaceae* was widespread it is thought that *Cycadeoideaceae* was more restricted in distribution, essentially to western Laurasia and into the Tethyan margin of northern Gondwana (McLOUGHLIN & al. 2018). For much of the Cretaceous both families were common floristic elements, but *Bennettitales* petered out towards the end of the Cretaceous (WATSON & SINCOCK 1992). *Williamsoniaceae* comprises at least three genera, the best known being *Williamsonia* (female flowers)/*Weltrichia* (male flowers), *Williamsoniella* and *Vardekloeftia*; *Cycadeoideaceae* is made up of at least two genera, the most studied being *Cycadeoidea* and *Monanthesia*. Many fossils attributable to *Bennettitales*, readily distinguished by their brachyparacytic (syndetocheilic) stomata and female receptacles consisting of ovules and interseminal scales, are too poorly characterized to allow assignment to genus.

Fossil evidence relating to sexual system evolution is sometimes ignored, and even though whole plants are rarely available, if researchers are cautious much can be deduced from available remains. *Bennettitales* is the fossil group par excellence for this endeavor: there is sufficient fossil evidence and it exhibits a range of reproductive strategies.

2. Materials and methods

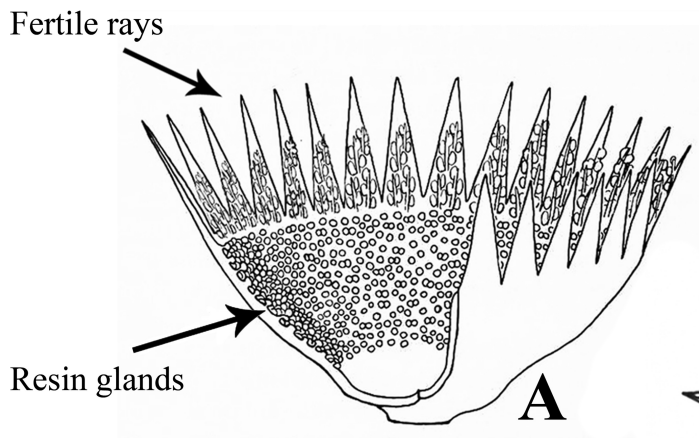
Literature pertaining to *Bennettitales* was reviewed. Additionally, bennettitalean specimens (photographs of whole trunks and anatomical slides of sectioned fossils) at BM and images on-line through the Yale Peabody Museum paleobotany collections website (<https://peabody.yale.edu/explore/collections/paleobotany>) were examined.

3. Review of literature and specimens

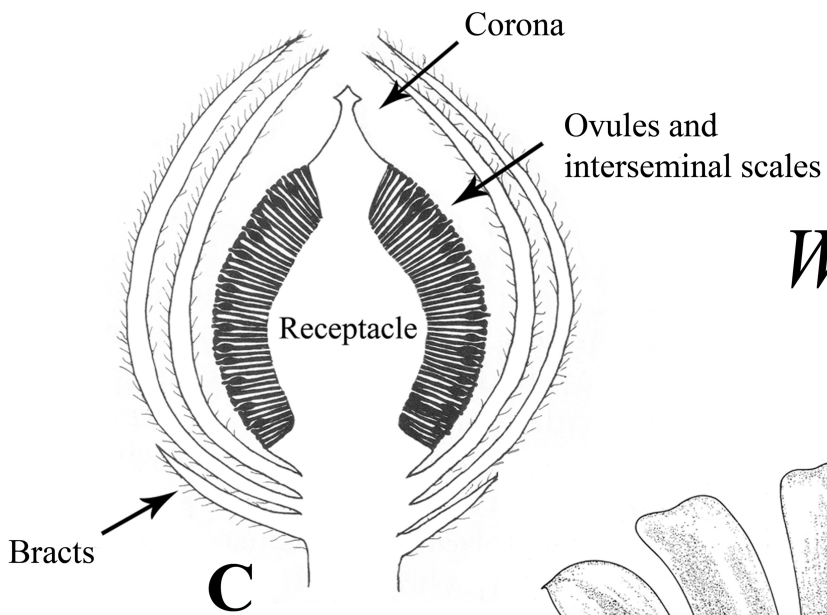
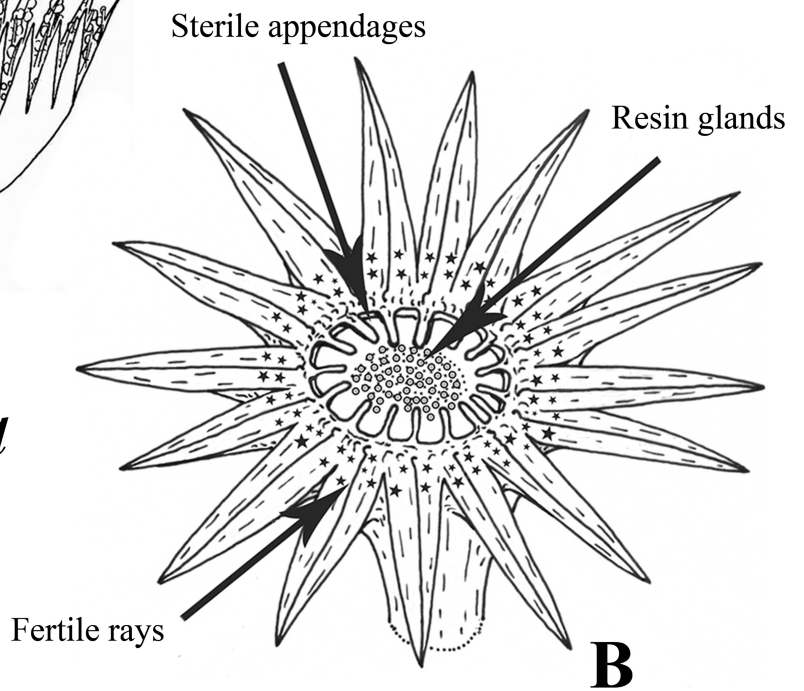
Table 1 summarizes what is known respecting sexual system in selected *Bennettitales*. Well-characterized members of the *Williamsoniaceae* exhibit at least two sexual systems.

Williamsonia/*Weltrichia* are unisexual flowers, female and male, respectively (Fig. 1). Frequently assumed to be strictly dioecious, *Williamsonias* are known from scattered fossils of whole and partial flowers and although leaves have been associated with the unisexual flowers (NAHORST 1902, THOMAS 1916, HARRIS 1969), it cannot be determined if the two sexes of flowers were on one and the same plant or on separate plants or both, hence the plants were diclinous and possibly monoecious or dioecious or both. *Williamsonia*, *Williamsoniella* and *Cycadeoideaceae* female reproductive organs (gynoecia) are similar and consist of a conical or dome-shaped receptacle bearing ovules and interseminal scales, often having sterile appendages distally (“corona”, Fig. 1C), and sometimes proximally; gynoecia are subtended by a whorl of free or basally laterally fused male reproductive organs, i.e. androecium, (*Cycadeoideaceae*, Fig. 2; *Williamsoniella*, Fig. 3) or not (*Williamsonia*, Fig. 1C, 1D), followed by helically arranged sterile bracts inserted on a peduncle (Fig. 1C, 1D, Fig. 2, Fig. 3). In a recent review of *Weltrichia* (the male flowers of *Williamsonia*) a bewildering array of radial symmetrical, frequently ro-

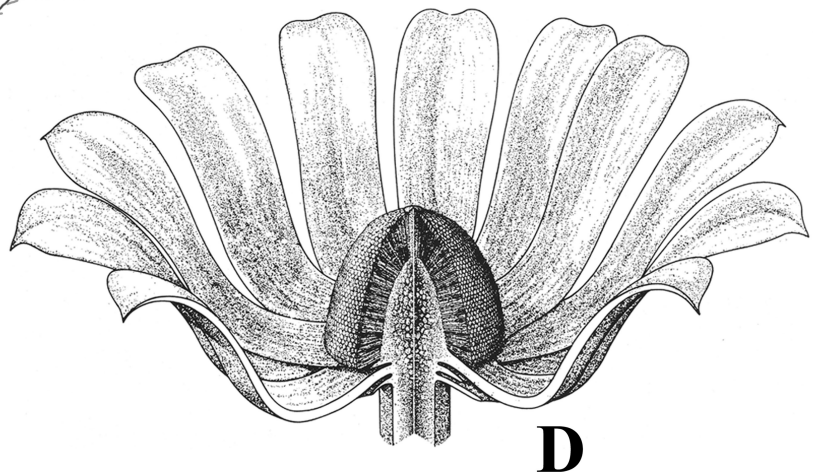
Fig. 1. Reconstructions of *Weltrichia* and *Williamsonia* flowers. (A) *Weltrichia sol*, cut-away view of whole flower, ca. one-third natural size; modified from HARRIS (1969). – (B) *Weltrichia givulescui*, illustrating features of *Weltrichia* flowers; depending on species resin glands and/or sterile appendages may be lacking; ca. natural size; modified from POPA (2019). – (C) Diagrammatic representation of *Williamsonia* flower; modified from WATSON & SINCOCK (1992). – (D) *Williamsonia margotiana*, almost fully opened flower; cut-away to show inferred gynoecium form, ca. one-half natural size; © Joan WATSON 1991.

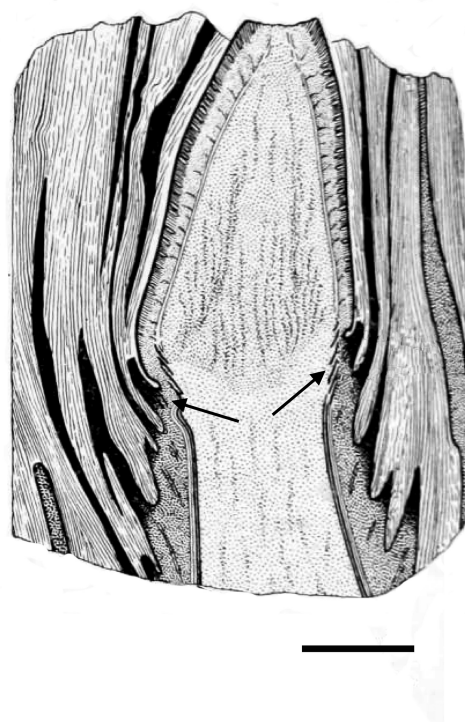
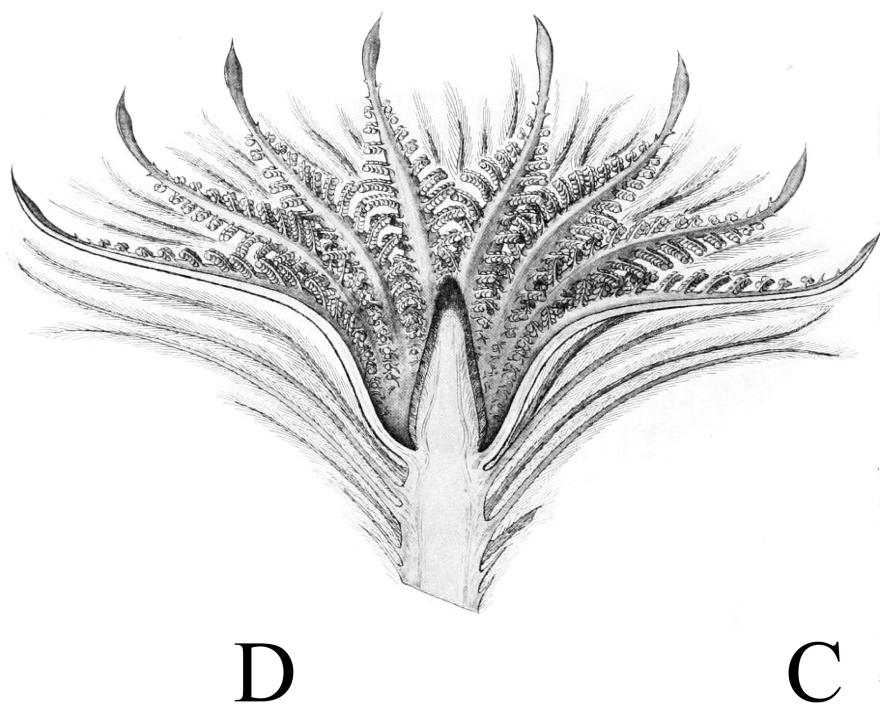
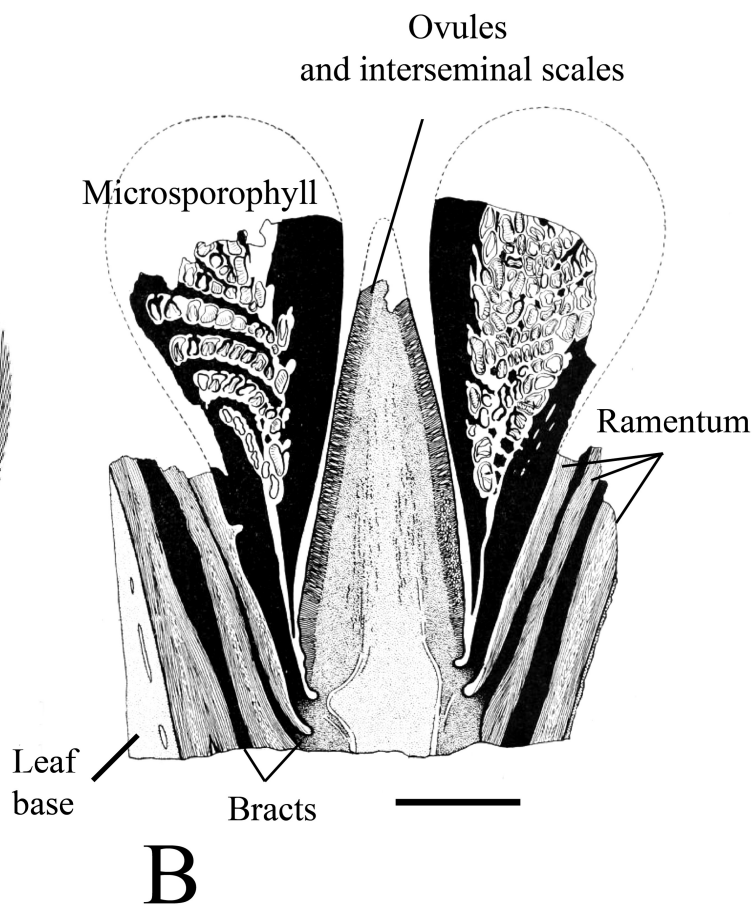
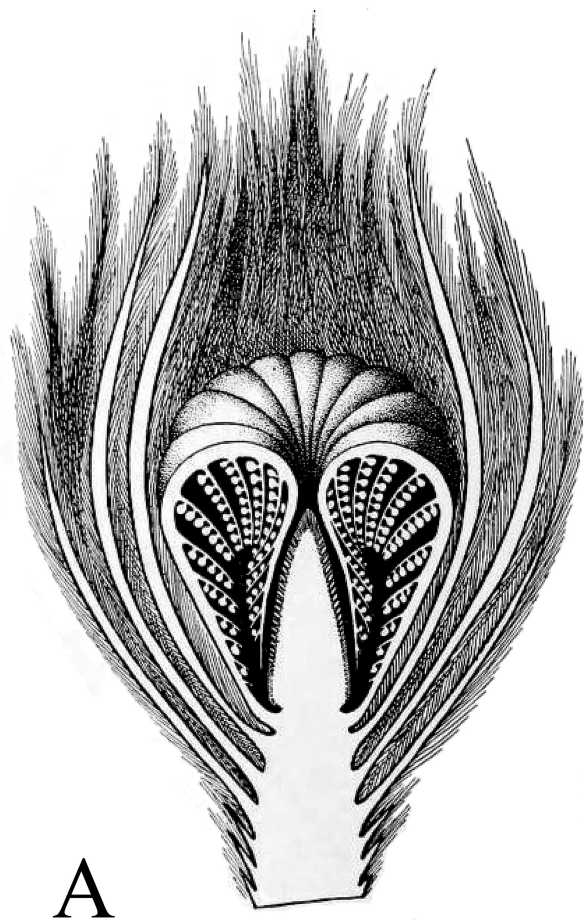


Weltrichia
♂



Williamsonia
♀





bust flowers bearing numerous pollen sacs were reconstructed (POPA 2019). *Weltrichia* species were distinguished by a central cup and radiating rays that bore pollen sacs (fertile rays); pollen sacs might be sessile or attached to appendages (Fig. 1A, 1B). Sometimes sterile appendages were present decorating the adaxial rim of the cup (Fig. 1B). In some species, e.g. *Weltrichia sol* (male flower of *Williamsonia gigas*, Fig. 1A), the interior of the cup was covered by resinous glands (HARRIS 1969, POPA 2019).

Williamsoniella was bisexual (Fig. 3); recent studies suggest that this condition is rare in *Williamsoniaceae* and that unisexual flowers predominate (POTT 2014). *Williamsoniella coronata* had a central axis bearing ovules terminated apically by a “corona” of sterile appendages and bore a perianth of sterile bracts below the androecium (Fig. 3). Flowers were dichogamous, and the androecium abscised prior to ovule maturity (HARRIS 1944), thus, flowers were protandrous. This syndrome of characters reoccurs in *Cycadeoideaceae*, and HARRIS (1944), though he considered the male reproductive organs of *Williamsoniella coronata* “... simpler than those of any other species, and only slightly reduced from the pinnate type seen in *Cycadeoidea* [sic] *colossalis* WIELAND.”, thought that “*Williamsoniella* in flower structure, though not in stem or leaf, is perhaps nearest *Cycadeoidea* ...”. Some of the diclinous species were remarkable for the size of their flowers (*Weltrichia sol*, 17–20 cm in diameter [POPA 2019]; corresponding female flower *Williamsonia gigas* 5–6 cm long and 2–3 cm at widest place [HARRIS 1944]), and were both larger and produced considerably more pollen per flower than their bisexual confamilial *Williamsoniella coronata*, which had flowers on the order of 2 cm long and 3 cm wide (THOMAS 1915).

All members of *Cycadeoideaceae* were bisexual. Fossilized flowers are consistently found either having nearly or possibly mature androecia and undeveloped ovules (Fig. 2B), or well-developed to mature ovules and no or remnants of male reproductive structures (Fig. 2C), similar to what HARRIS (1944) found in *Williamsoniella coronata*. Several reconstructions of nearly mature male-stage *Cycadeoidea* flowers by WIELAND (1906) depicted them

as unexpanded, wherein “microsporophylls” are united in a ring and folded inwardly around the ovulate receptacle (Fig. 2A); at this stage, the flowers projected little “... not more than several centimeters, beyond the surrounding armor of leaf bases and ramentum” (WIELAND 1906: 168). WIELAND (1906) envisaged that when mature, the microsporophylls expanded above the enclosing bracts and spread (Fig. 2D), then later wilted and fell. These stages have never been recovered. This said, WIELAND was cognizant that his reconstructions of expanded mature male-stage flowers were not entirely realistic because “... the surrounding armor of old leaf bases is imagined as arbitrarily removed, contrary to the fact that since the peduncles did not elongate, only the distal half of the fronds could emerge when shedding their pollen.” (WIELAND 1906: 155); he attributed the lack of fossilized expanded androecia to the difficulty of preservation of such delicate exposed structures, “Even had the large and feathery staminate fronds of the disks been silicified in an uncurving or an expanded position instead of a closely folded one, they would have been subject to crushing and breaking, with more or less comminution while yet embedded; or they would have been broken away and destroyed during the process of weathering out, as the tips of the bracts often are.” (WIELAND 1906: 165). Slides and figures redrawn from slides of nearly mature to mature female-stage flowers or even young fruit, at which stages an androecium is lacking, frequently show a structure broken off just a bit above its site of insertion immediately below the gynoecium (Fig. 2C). This structure WIELAND (1906) identified as the remains of the abscised androecium, and termed it the “staminate disk”. It bears mentioning that WIELAND (1906: 149) considered the bisexual flowers of *Cycadeoidea* to be dichogamous: “The structures preserved show well the immature condition of the central cones, and indicate that it could not have been close-fertilized [self-pollinated], unless the pollen of the accompanying fronds retained its vitality for months after being shed ... The considerable time gap between the maturation of pollen and ovules may have made cross-fertilization the rule in these bisexual flowers.”

Fig. 2. *Cycadeoidea* flowers. (A) Restoration of unexpanded bisexual flower with part of enveloping bracts removed; slightly reduced from natural size, from WIELAND (1906: 165; fig. 88). – (B) *C. dacotensis*. Composite drawing based on two parallel longitudinal sections of bisexual flower; upper part of nearly mature microsporophylls and top of immature ovulate cone missing, but general shape indicated by light tracing. Scale bar = 10 mm. Modified from WIELAND (1906: 145; fig. 72. Plate XXVI, S360 & S361) (<https://collections.peabody.yale.edu/search/Record/YPM-PB-005061>; image of S361 unavailable). – (C) *C. dacotensis*. Longitudinal section of immature female-stage flower (ovulate cone) showing remains of abscised staminate disk indicated by arrows. Scale bar = 10 mm. Modified from WIELAND (1906: 181; fig. 97. Plate XLII, S540) (<https://collections.peabody.yale.edu/search/Record/YPM-PB-005153>). – (D) Idealized restoration of *C. ingens* flower in nearly longitudinal section showing hypothetical expansion of mature microsporophylls; surrounding armor of old leaf bases arbitrarily removed; ca. half natural size, from WIELAND (1906: 106; fig. 54).

A later reconstruction by DELEVORYAS (1968), depicted the microsporophylls as distally free but that synangia were inserted on “rods” that connected the distal to the proximal adaxial face of the folded microsporophyll, such a configuration would have precluded further expansion of the androecium, so that in mature male-stage flowers the androecium must have remained folded. Ruminating upon how pollen dispersal and transfer could have occurred in such a flower, among several hypotheses, DELEVORYAS postulated that self-pollination could have occurred when ovules became mature, or that the androecium abscised “... as a unit from the base of the ovulate receptacle.”. DELEVORYAS explains, if this latter were the case then “... it is possible that the entire structure could have dropped from the trunk and been blown about by the wind when it dried.” Lastly, recognizing that some flowers had been eaten by “perhaps beetles” he mentioned that possibly insects were involved in pollination (DELEVORYAS 1968).

Following in the footsteps of DELEVORYAS, CREPET (1974) found that the microsporophylls were in an analogous configuration to a “...pinnate frond bent so that the distal tip is adjacent to the base with the pinnae folded into the plane of the rachis”. In a departure from DELEVORYAS, CREPET did not recognize “rods” connecting the distal and proximal parts of the folded microsporophylls; but nonetheless, he interpreted his anatomical sections of fossil *Cycadeoidea* flowers to have fusions between parts of the microsporophylls in such a fashion that, again, the androecium would have been prevented from opening outward and would have remained folded. CREPET considered that the material he studied for his reconstruction to be just prior to and *at* microsporophyll maturity. At one time, some members of the family (species having small ovulate receptacles) were believed to produce only unisexual flowers (DELEVORYAS 1968); CREPET discovered that they were in fact bisexual, but microsporophylls disintegrated so completely and well before the development of ovules, that no traces of the two were coincident (CREPET 1972, 1974). In fact, all known members of *Cycadeoideaceae* were strongly dichogamous, and published reconstructions are misleading in that they show seemingly mature male and female structures coincident in time. This has had considerable implications for the interpretation of breeding system in these plants.

4. Discussion

Several characters of the robust, often inward curving flowers of *Weltrichia* have long been thought to be indicative of wind-pollination, however, there is a growing consensus that insects like-

ly played a role in pollination (CROWSON 1981, POTT 2014, POPA 2019). Certain features of *Weltrichia* such as overall outline of the flowers, sterile appendages edging, and resin glands in, the cup, strongly suggest an attractive function (POPA 2019). In *Williamsonia* and *Williamsoniella coronata*, papillate cells adorn the interseminal scale heads, and these lie adjacent to the micropyles. These papillate patches closely resemble nectariferous tissue found in extant plants and it is thought they may act as attractants to female reproductive organs (POTT 2014). The precise nature of attraction is unknown but could be in the form of nectar and/or scent (POTT 2014). *Bennettitales* are known to have interactions with insects ranging from herbivory, leaf mining, oviposition and larval development in reproductive structures (cf. POPA 2019). Among potential pollinators, cupedid beetles, which are known to have diversified in the Late Triassic, are often evoked (e.g. POTT & al. 2008, POPA 2019). This said, if the earliest representatives of *Williamsoniaceae*, for which we do not know the reproductive structures, were insect pollinated then it is clear that other beetle or insect groups must have filled this role given that these plants are now known to date to the lower Permian. Yet, just as the earliest *Williamsonias* are now recognized as having already evolved by the lower Permian, the most recent studies on beetle evolution place the origin of *Coleoptera* in the Late Carboniferous (McKENNA & al. 2019, CAI & al. 2022) and a late Palaeozoic origin for all modern beetle suborders has even been suggested (CAI & al. 2022).

CREPET (1972, 1974) hypothesized that as *Cycadeoidea* species were bisexual, but with flowers that seemingly did not open, plants must have experienced “a high degree of self-pollination”. According to CREPET, wind-pollination, although infrequent, must have been important as a source of heterozygosity; the frequent presence of borings (22 % of cones) suggested the presence of insects, and an analogy to the at that time poorly known system of cycad pollination by beetles was evoked. CREPET considered insect pollination to be “supplemental” to self-pollination, and in fact, insufficient over the long-term to prevent the *Cycadeoideaceae* from succumbing to the deleterious effects of homozygosity given the context of Upper Cretaceous climatic changes and competition from the rapidly radiating new comers, the angiosperms. Besides the facts that (1) this does not explain the extinction of the *Williamsoniaceae*; and (2) a wide-spread, speciose and abundant group is not a candidate for inbreeding depression, the theory is flawed because as the *Cycadeoidea* were strongly dichogamous, they could not have been autogamous (and we cannot know their degree of self-compatibility). Even in

the “large-domed” receptacle species, where traces of the androecium are discernable at the time of megasporogenesis, hence prior to ovule maturity, the dissolution of the microsporophylls is so complete that pollen has never been found in flowers at this stage (CREPET 1974).

The most recent treatment of *Cycadeoideaceae* by WATSON & SINCOCK (1992) recognizes three basic flowering patterns: (1) small-domed receptacled flowers occurring in nearly every leaf axil and having synchronous maturation; (2) sparse, large-domed receptacled flowers having successive maturation from base of trunk; (3) small diameter flowers occurring sparsely or densely, or in combination and having maturation of more than one pattern. The first group (*Cycadeoidea saxbyana*/*Monanthesia* type), was allogamous, and believed to be monocarpic (WATSON & SINCOCK 1992). The second group (*C. gibsoniana*/*wielandii* type) could have been somewhat geitonogamous, that is, some flowers may have received pollen from others on the same plant, in addition to allogamous. The third group (*C. reichenbachiana*/*dacotensis* type) was likely both geitonogamous and allogamous.

The bisexual flowers of *Cycadeoidea* were noted as having been visited by beetles, which may have acted as primary or secondary pollinators (DELEVORYAS 1968, CREPET 1972, 1974, TAYLOR & TAYLOR 1993). Several other authors believe that the visiting beetles might even have visited both *Bennettitales* and cycads (e.g. CROWSON 1981). It is relevant that a piece of amber dated to the mid-Cretaceous has been discovered containing a fossilized oedemerid beetle, *Darwinylus marcosi*, surrounded by and carrying *Monosulcites* pollen (PERIS & al. 2017). As a pollen form-genus, *Monosulcites* regroups *Ginkgoales*, *Cycadales* and *Bennettitales*. And although PERIS & al. (2017) favor a cycadophyte source for this pollen (without explanation), the possibility exists that it is bennettitalean. LABANDEIRA & al. (2007) described insect-mediated damage of *Cycadeoidea dacotensis*, the best-documented species, from the Upper Lower Cretaceous of South Dakota, and presented evidence of similar damage from several other taxa of the *Cycadeoideaceae* and *Williamsoniaceae*. Based on the notion that the “strobilus” in *Cycadeoidea* is a closed structure, these authors proposed a pollination syndrome based on the life-history of insect larvae, starting with oviposition externally by adults into the microsporophylls or possibly other exposed appendages, larval penetration of flower tissue, their consumption of internal vegetative and reproductive tissues, to eventual emergence from the host plant and subsequent transformation to the adult phase. Floral damage type was consistent with small robust beetles of the suborder *Polyphaga*, including

cerambycids (long-horned beetles), chrysomelids (leaf beetles), and curculionoids (weevils).

In summary, in what was a composite reconstruction of insect activity based on evidence of different sorts of boring from several different strobili, LABANDEIRA & al. (2007) envisioned that adult beetles oviposited into exposed tissue and initial larval boring was through vegetative tissues; later, larvae formed tunnels at the intersection of the ovular/interseminal scale layer and the microsporophyll layer, the enticement to these places likely being micropylar secretions and pollen. There are also exit holes associated with pupation of the beetles. Such endophytic insect damage, according to the authors, has been found in the U.S.A., Canada, Japan, Poland, and India, and the “highly stereotyped damage of this association collectively suggest a distinctive pollination strategy by beetles similar to that of extant cycads.” To test the likelihood of LABANDEIRA & al.’s (2007) hypothetical pollination syndrome in *Cycadeoidea*, OSBORN & TAYLOR (2010) studied coprolites and frass pellets extracted from presumably insect-made tunnels in *Cycadeoidea* flowers. OSBORN & TAYLOR (2010) reasoned that frass generated from beetle feeding on microsporophylls would naturally leave traces of whole or portions of pollen grains in tunnels; these authors found no pollen, and on this basis reasserted the notion that *Cycadeoidea* were largely self-pollinated. We interpret the results to indicate that the frass and coprolites are simply the product of insect (likely beetle) predation on flowers, which is a common enough occurrence, and that these remnants of insect activity are spurious to the question of pollination in *Bennettitales*.

It is important to recognize that although flowers of *Cycadeoidea* barely protruded beyond the trunks and were surrounded by bracts, they were not closed structures. If we accept that at maturity the androecium was folded and enclosed within the flower as CREPET (1974) suggests, and this is not definitively proven, then entry was restricted to narrow openings and possibly crevices produced upon maturity of the pollen-bearing organs. From the fossil evidence, it is apparent that mature androecia were ephemeral in comparison to the ovulate receptacle (gynoecium) and ovules must have matured comparatively slowly and quite a bit later after disappearance of the androecium (cf. WIELAND 1906: 149, 184). Flowers evinced spatial and temporal segregation of reproductive function in such a way that insect visitors were attracted to different parts of the flower at specific times.

We propose a possible explanation for how pollination occurred in bisexual *Bennettitales*. In our view, the androecium abscised at maturity and fell from the flower. This is what is known to happen in

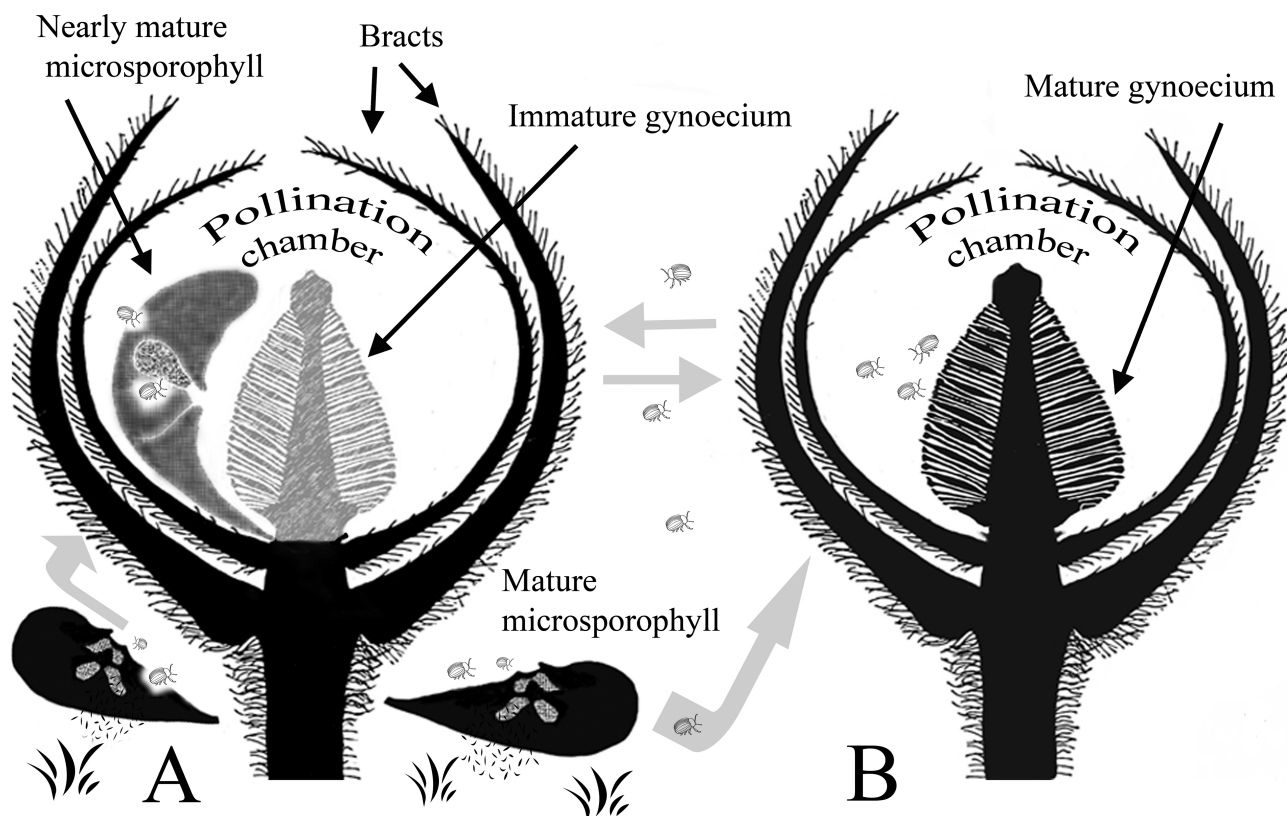


Fig. 3. Hypothetical schema of pollination by insects (beetles) in bisexual *Bennettitales*, flower based on diagrammatic restoration of *Williamsoniella* in longitudinal section. (A) Pollination chamber formed by bracts enclosing immature gynoecium and nearly mature androecium (shading denotes degree of maturity). Nearly mature androecium attracts beetles; beetles meet, mate, feed on pollen and oviposit as microsporophylls mature (male-stage flower). Soon after, mature microsporophylls abscise and fall to the ground along with beetles and developing larvae (shown at bottom, not to scale). Adult beetles carrying pollen can return to male-stage flowers or enter female-stage flowers, thereby effectuating pollination. Larvae in fallen microsporophylls mature into adults in decaying microsporophylls and adjacent ground litter. – (B) Pollination chamber formed by bracts enclosing mature gynoecium (female-stage flower) shown with some attracted beetles. Bract movement not shown but implied. Restored flower ca. 3.5 times natural size; modified from HARRIS (1969).

the bisexual, more or less open-flowered *Williamsoniella coronata* (HARRIS 1944). Here the free, presumably fleshy, concave club-like sporophylls bearing recessed pollen “capsules”, fell at maturity; this took place before ovules were mature (Fig. 3). The specialized apical corona may have been involved in pollinator attraction, by scent, temperature and/or color. No longer exposed openly on slender branches, as in *Williamsonia*, in *Cycadeoidea*, the flower was retained, embedded in the evolving robust trunks. Given the megafauna of the time, this is an understandable adaptation. Moreover, the insect pollinators, or a subset thereof, of the *Williamsoniella*-like flower may have adapted to the increasingly compact flower that became typical of *Cycadeoidea*.

Analogies are often drawn between cycads and *Bennettitales*. With respect to pollination, we think that more pertinent analogies exist between bisexual flowers of beetle-pollinated angiosperms and bennettitalean ones. When studying the cantharophilous family *Annonaceae*, GOTTSBERGER found

that the open flowers had thick, fleshy petals, which, surprisingly, retracted inwards during anthesis, creating what he later termed a “pollination chamber” enclosing the androecium and gynoecium (GOTTSBERGER 1970). A pollination chamber is a disposition of perianth members to form a more or less closed flower; the chamber is attractive to pollinating beetles. There is often a movement of petals involved in pollination chamber formation and dissolution, and dissolution may be achieved by abscission of perianth members. It is not to be confused with a pollen chamber of certain gymnosperms, which is a space created towards the micropylar end of the ovule by cell death of apical nucellar cells. Pollination chambers have been found in several other cantharophilous species of the ANITA group, the *Magnoliales*, *Laurales*, basal monocots and others. Thick petals or tepals provide food for the beetles and are occasionally responsible for warming of the flowers by metabolism of stored starch or lipids; the pollination chamber keeps the beetles together and pro-

protects them against predators. Additionally, pollination chambers have been recognized as promoting beetle activities, such as feeding, digesting and mating. Pollination chambers are nearly omnipresent features of cantharophilous angiosperm flowers, and are functionally important to maintain beetle pollinators inside host flowers for many hours until pollen is shed (GOTTSBERGER 2016).

We construe the particular morphology and temporal integrity of bisexual bennettitalean flowers to be indicative of pollination chambers, similar to those that characterize much of present-day basal angiosperms but with this caveat, that cantharophilous angiosperms are nearly exclusively *protogynous*, while the *Bennettitales* were *protandrous*. In protogynous cantharophilous angiosperms, attracted adult beetles usually remain inside the closed pollination chamber until pollen is shed, however, these pollinating beetles only rarely oviposit in flowers. Bennettitalean bisexual flowers had external bracts and scales, which provided a semi-closed to barely open pollination chamber. Beetles attracted by floral characters such as scent, color, or heat, landed on the flower and made their way by various openings, apically or laterally, to the interior of the flower (Fig. 3A). Here they could deposit their eggs in the androecium. Larvae of the beetles fed on fleshy androecial tissue. Not long after, the bisexual flowers shed the fleshy androecium, which may have contained several beetle larval stages; these continued their development until emerging as adults from the ground litter. It is because flowers were protandrous and the fleshy androecium shed, that the decaying androecium and surrounding litter layer could act as a nursery for the developing beetle larvae, similar to a brood-site pollination mutualism as found in e.g. the protogynous *Eupomatia* (*Eupomatiaceae*) (HAMILTON 1897, ARMSTRONG & IRVING 1990, SAKAI 2002). Pollen-covered adult beetles left the pollen-bearing organs borne either on the flower or in the abscised androecium, and either visited other male-stage flowers or mature ovulate (female-stage) flowers (Fig. 3B), the latter visit leading to pollination. It is not possible to determine if flower bracts opened and closed in a manner similar to cantharophilous angiosperms but it is likely there was some movement of appendages. Loss of the androecium after abscission and dropping was followed by inward closure of bracts and/or scales to cover the young ovulate receptacle in otherwise comparatively open flowers such as those of *Williamsoniella*. A mechanism analogous to that found in cycad pollination systems, whereby female cones open briefly along sites often distally or proximally when ovules are receptive, to allow beetles entry, then close tightly, might be envisioned for trunk-embedded *Cycadeoidea* flowers. In either

case, a new (second) pollination chamber was formed. Mature ovulate flowers possibly attracted their beetle pollinators by scent or heat; CREPET (1974) suggests that “atypical” interseminal scales apically and basally may have fulfilled this role, but here, again, analogous to cycads, it is likely they did not remain for long (TANG 1987) as this could lead to damaging of the ovules, something that flowers have devised many strategies to prevent (FRAME 2003). In situ *Cycadeoidea dacotensis* and *Williamsoniella coronata* pollen grains are on the small side, on the order of 22–28 μm in length (ZAVIALOVA & al. 2009), and compatible with what would be expected for pollination by small beetles. In *Weltrichia*, which often has larger flowers than *Williamsoniella*, pollen grains can reach 60 μm in length (POPA 2019). Given the available fossil evidence, in *Cycadeoidea*, it is not possible to determine if the distal ends of the ephemeral androecium unfolded and protruded beyond the ramentum and subtending leaf-bases, as WIELAND suggests (see above), but in our view, it was shed. With respect to our here described hypothesis of beetle pollination, it does not matter either way because the lower part of the androecium would be sheltered, that is, form a pollination chamber. Moreover, it is not possible to rule out the participation of other insects such as thrips, in pollination. Although our discussion has concentrated on bisexual bennettitalean flowers, we concur with POPA (2019) that insect pollination by beetles in unisexual-flowered taxa was likely quite common and a driving force for male flower divergence. We would interpret the central cup in *Weltrichia*, which is often protected by hairs or ornamented by appendages to possibly function as part of the pollination chamber. The distal portions of *Weltrichia* fertile rays are thought to have been variously somewhat upright to distally spreading and we wonder if they may have undergone movement to form pollination chambers. Another point of interest in *Weltrichia* are the frequent resin bodies always found proximal to the pollen sacs on floral rays (POPA 2019). Several authors (e.g. POTT 2014, POPA 2019) consider them pollinator attractants, their attraction may be as food bodies, sites of odor and/or color, and/or confer guides to the overall flower form, possibly by reflection of light, to the central cup – another probable site of pollinator “rewards”. It is also worthy of mention that resin is produced in certain *Araceae* blossoms, and among other things, serves to “glue” the pollen onto the pollinating beetles (GOTTSBERGER & AMARAL JR. 1984, and many others). From our hypothetical reconstruction of events based on fossil evidence and modern understanding of floral biology and plant-animal interactions, it is evident that cross-pollination was a normal and common process in *Bennettitales*.

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