

REVIEW

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Review of the bennettitalean genus *Weltrichia*

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Abstract

The bennettitalean male reproductive structure *Weltrichia* Braun 1849 emend. Harris 1969 (Family Williamoniaceae) is discussed from several points of view, including anatomy and morphology, species diversity and validity, phytogeographical and stratigraphical distribution, and reproduction strategy. A very rare fossil, genus *Weltrichia* includes 25 valid species distributed in both hemispheres during Triassic and Jurassic times. This contribution critically reviews the systematics of the entire genus, together with its stratigraphical and palaeophytogeographical significance.

Keywords: Bennettitales, *Weltrichia*, Male reproductive structure, Triassic, Jurassic

1 Introduction

The Order Bennettitales Engler 1892 represents a highly interesting group of extinct gymnosperms in terms of anatomy, high biodiversity and widespread phytogeographical distribution during the whole Mesozoic (Stewart 1983; Taylor et al. 2009; Friis et al. 2011). In the same time, their evolutionary significance is related to the origin of angiosperms, as the Bennettitales innovated radial, complex, unisexual or bisexual reproductive structures resembling the angiosperm flowers. Such reproductive structures are true gymnospermous cones and they represent a convergent evolutionary trend with true flowers, an experiment which the Bennettitales undertook before the first flowering plants originated (Friis et al. 2011; Pott 2014). The reproductive structures resembling flowers were not the only peculiar characters of Bennettitales, they also possessed syndetocheilic stomata in their epidermal tissues. These types of stomata separate them from morphologically similar vegetative organs of plants belonging to the Order Cycadales, among other characters. Bennettitales are related to Gnetales and angiosperms in cladistic studies (Doyle 2006; Hilton and Bateman 2006). They are divided into two separate families, based on vegetative and reproductive anatomy: Family Williamoniaceae, dominantly with Late Triassic and Jurassic representatives, and Family Cycadeoidaceae (Bennettitaceae), with mainly

Cretaceous representatives. The Williamoniaceae includes plants with a slender stem and unisexual and bisexual reproductive structures, such as the unisexual, male *Weltrichia* Braun 1849 emend Harris 1969, the female *Williamsonia* Carruthers 1870 or the bisexual *Williamsoniella* Thomas 1915.

Weltrichia consists basically of a central cup to which radially equal, centrifugal rays are attached, bearing bivalve pollen sacs (also called synangia) with elliptical, monocolpate pollen, the whole structure having a radial symmetry. The substance of the cup and rays is usually thick, and the rays occur in a single whorl. Variations to this basic morphology include equal centripetal rays over the central cup, attractants or resin (resinous) bodies within the cup, unipinnate (pedicellate) pollen sacs, trichomes, appendages, striae and ridges over the centrifugal rays. *Weltrichia* is associated with *Williamsonia* female reproductive structures, with foliage belonging to the genera *Zamites*, *Otozamites* and *Ptilophyllum* and with other vegetative parts such as *Bucklandia* cortical fragments (Harris 1969).

Genus *Weltrichia* was defined by Braun (1849), with the type species *Weltrichia mirabilis* from Lower Jurassic sediments of Franconia, Germany. He also defined two more species of *Weltrichia* in the same paper, synonyms of *W. mirabilis*. The new taxon was dedicated to Johann P. A. Weltrich, who collected the material, and it was considered as belonging to the Family Rafflesiaceae (Braun 1849). Initially, the *Weltrichia* denomination did not reach a wide use, as such

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structures were often referred as “male *Williamsonias*”, in relation with and resembling the female bennettitalean reproductive structures *Williamsonia* Carruthers 1870. Krasser (1912, 1913, 1915, 1919, 1922), Nathorst (1909, 1911a, 1912) and Sharma (1969) used the term “male *Williamsonia*” for various *Weltrichia* species, while Schuster (1911) and Nathorst (1911b) used *Weltrichia*. Saporta (1891) used *Weltrichia* in his contribution on Jurassic plants of France, erecting two new species, *W. fabrei* from France and *W. oolithica* from Italy. Discussion over the relationship between *Weltrichia* and *Williamsonia* and on their nomenclature was continued by Harris (1969), Sitholey and Bose (1971), Schweitzer and Kirchner (2003) and Popa (2014), next to emendations of previous species or with definitions of new species. As *Weltrichia* has priority over *Williamsonia*, it was kept by Harris (1969) as a legitimate denomination for male, unisexual structures, keeping *Williamsonia* only for female, unisexual structures. Harris (1969) emended the diagnosis of the genus, supplementing it with microscopical characters, noting the high variation in attaching the pollen sacs to the centrifugal rays, directly or on supplementary, sterile appendages. Harris refrained from splitting the genus and erecting new genera based on this variation of characters, for practical reasons. Popa (2014) briefly reviewed the valid species of *Weltrichia* and their ranges when introducing new species of this genus, stressing the most important characters in *Weltrichia*: shape and number of centrifugal rays, ornamentation and shape of centripetal rays, distribution and types of pollen sacs, ornamentation of the central cup, and occurrence of resin bodies.

Since Braun (1849), *Weltrichia* species were described from Franconia, Germany (Schuster 1911), Banat, Romania (Krasser 1915, 1922; Humml 1969; Givulescu 1990, 2001, 2014), Yorkshire, United Kingdom (Nathorst 1909, 1911a, 1911b, 1912, 1913; Florin 1933; Harris 1969), Tirol, Germany (Krasser 1919), Veneto and Sardinia, Italy (Saporta 1891; Krasser 1912), France (Saporta 1891), Alborz Mountains, Iran (Schweitzer and Kirchner 2003), Rajmahal, Malda and Katchchh, India (Sharma 1969, 1971, 1977; Sitholey and Bose 1971; Bose and Banerji 1984; Pal and Ghosh 1985; Banerji 1992), Malaysia (Asama 1974), Nepal (Kimura et al. 1985), China (Sun et al. 2001; Li et al. 2004), Japan (Kimura and Ohana 1989) and Oaxaca, Mexico (Delevoryas and Gould 1973; Delevoryas 1991; Silva Pineda et al. 2011; Velasco de Leon et al. 2012). The distribution of *Weltrichia* species in the world is illustrated in Fig. 1.

The stratigraphic ranges of *Weltrichia* species vary from Late Triassic to Late Jurassic, from the earliest representative *Weltrichia alpina*, Late Triassic in age, to its latest representatives, *W. maldaensis* and *W. huangbanjigouensis*, Late Jurassic in age.

2 Material and methods

The Romanian material belonging to genus *Weltrichia* has been surveyed and described in a previous work (Popa 2014), curated at the University of Bucharest and at University of Petroşani. Previous palaeobotanical literature was carefully surveyed and large sized differential tables were synthesized. I have produced the reconstructions

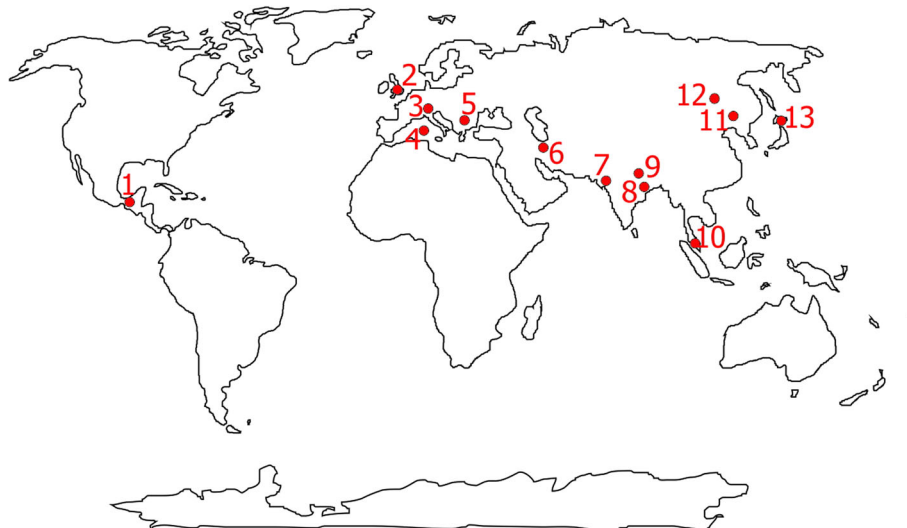


Fig. 1 Geographical distribution of genus *Weltrichia*. 1. Oaxaca State (Mexico); 2. Yorkshire (United Kingdom); 3. Tirol, Franconia (Germany), Veneto (Italy), Lozère (France); 4. Sardinia (Italy); 5. Anina (Romania); 6. Alborz (Iran); 7. Kachchh (India); 8. Rajmahal and Malda (India); 9. Palpa (Nepal); 10. Ulu Endau (Malaysia); 11. Liaoning (China); 12. Chifeng (Inner Mongolia Autonomous Region, China); 13. Samenoura (Japan)

manually, using a protractor, a ruler, a pair of compasses and soft lead 0.5 mm mechanical pencils (2B), as well as normal and semi-transparent paper for continuously refining the drawings. The numbers of centrifugal and centripetal rays were considered, in order to divide angles and circles accordingly, while ray lengths, widths and diameters of central cups were reflected in reconstructions, for correct dimensional ratios in drawings. All dimensions and preserved anatomical and morphological characters were considered in order to produce accurate reconstructions. Drawings with adaxial and abaxial perspectives were produced, depending on the preservation of the original fossil material. Some reconstructions are more detailed, such as the reconstructions of *Weltrichia givulescui* (Fig. 8), *W. pecten* (Fig. 15), *W. setosa* (Fig. 16), *W. sol* (Fig. 17), and *W. spectabilis* (Fig. 19), as they possess better preserved fossil material than other species. Other species have less detailed reconstructions, such as those belonging to *Weltrichia alpina* (Fig. 4), *W. antonii* (Fig. 5), *W. sp.* (Fig. 18), and *W. steierdorfensis* (Fig. 20), as their fossil material is less preserved. Vectorial images (Figs. 1, 2) were generated using CorelDRAW ver. X7 software.

3 Terminology

The terminology used in *Weltrichia* parts is very variable and sometimes confusing. Harris (1969) used the terms central cup, rays or microsporophylls and pollen sacs for the main parts of *Weltrichia*, as well as resin or resinous bodies (sometimes also called resinous sacs), sterile scales, and fertile appendages (Fig. 2). The preference for pollen sacs instead of synangia was explained for the gymnospermous nature of *Weltrichia* (Harris 1969, p. 159), in contrast with the more pteridophytic synangia. Although the term synangia is also correctly used for these structures (Pott et al. 2017), pollen sacs being basically synonym to synangia, I also use here the term pollen sacs (Fig. 2). The terms centrifugal rays, instead of just rays or microsporophylls (another perfectly correct synonym for centrifugal rays) and centripetal rays instead of sterile scales describe better the form and function of these *Weltrichia* parts (Fig. 2). The term median ridge is preferred in this paper to synonym terms such as midrib, middle ridge or central rib.

4 Systematics

Harris (1969) emended the diagnosis of genus *Weltrichia*: “Bennettitalean male flower consisting of a massive

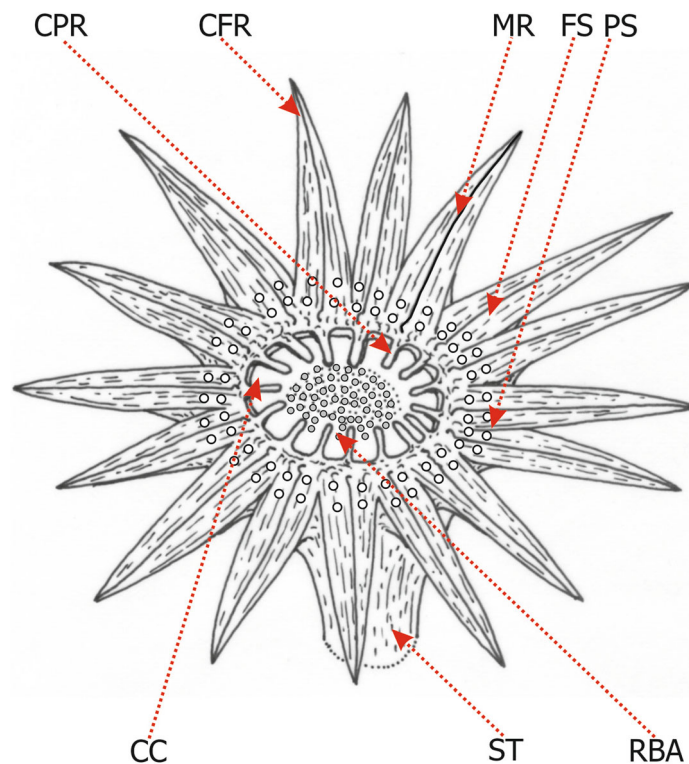


Fig. 2 Terminology of genus *Weltrichia*, illustrated on the reconstruction of *Weltrichia givulescui*, modified from Popa (2001). CFR Centrifugal ray; CPR Centripetal ray; MR Median ridge; FS Fibrous strand; PS Pollen sac position (in this case, pollen sac attachment); CC Central cup; RBA Resin (resinous) body or attractant; ST Stalk

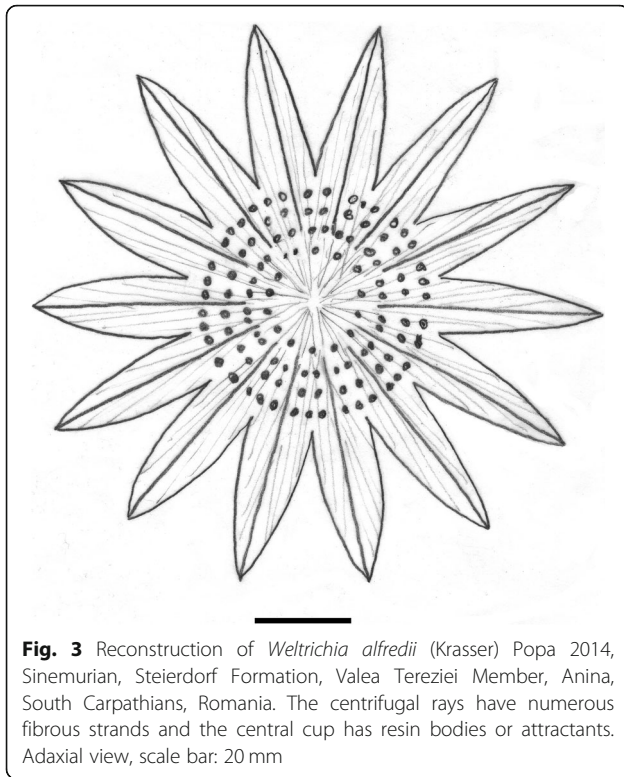


Fig. 3 Reconstruction of *Weltrichia alfredii* (Krasser) Popa 2014, Sinemurian, Steierdorf Formation, Valea Tereziei Member, Anina, South Carpathians, Romania. The centrifugal rays have numerous fibrous strands and the central cup has resin bodies or attractants. Adaxial view, scale bar: 20 mm

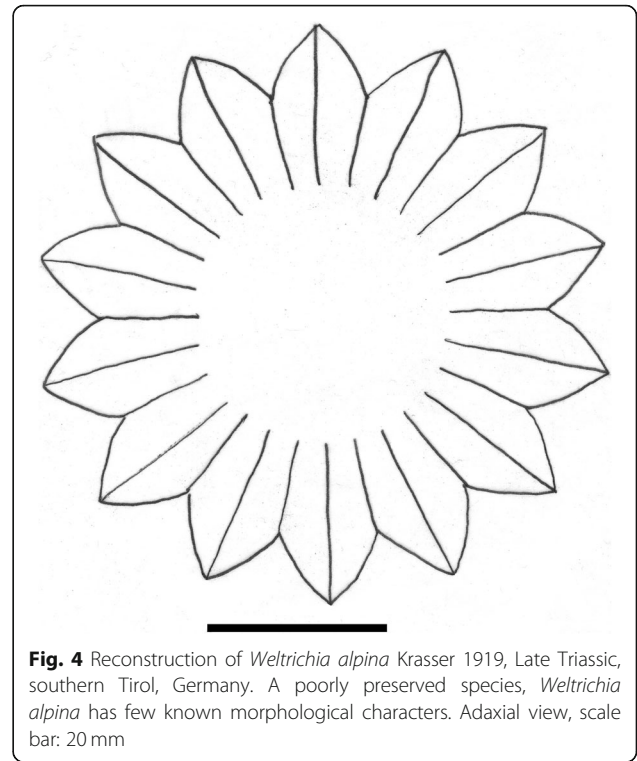


Fig. 4 Reconstruction of *Weltrichia alpina* Krasser 1919, Late Triassic, southern Tirol, Germany. A poorly preserved species, *Weltrichia alpina* has few known morphological characters. Adaxial view, scale bar: 20 mm

cup dividing above into numerous equal lobes or rays; rays of thick substance, tapering to a point. Outer surface of cup and rays without appendages. Cuticles (where known) showing syndetocheilic stomata with single subsidiary cell opposite each guard cell. Inner side of cup and of rays bearing pollen sacs, either directly, or on appendages. Pollen sacs (synangia) where known consisting of two equal valves, each valve with a single row of microsporangia opening on to inner face. Pollen grains oval, monocolpate". Twenty five valid species of *Weltrichia* were described from the Triassic and Jurassic formations of the world.

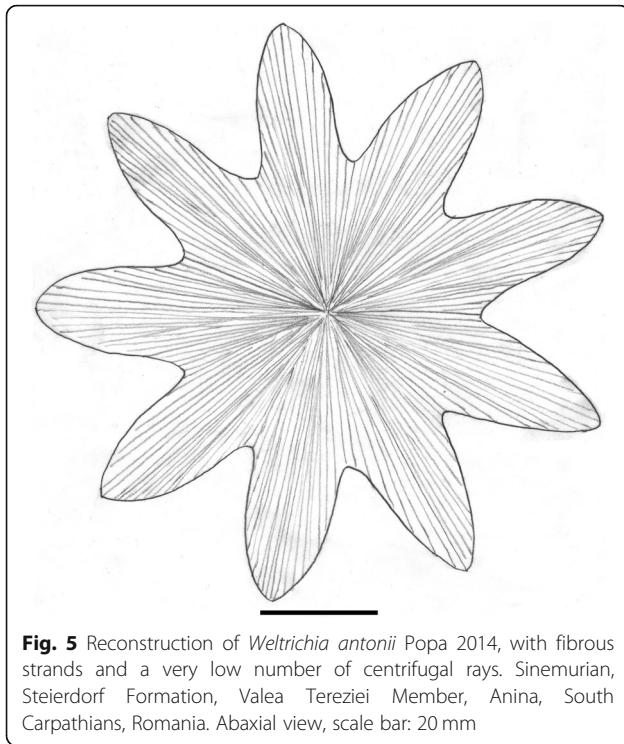
4.1 *Weltrichia alfredii* (Krasser) Popa 2014 (Fig. 3)

Weltrichia alfredii is 120 mm in external outline diameter, with a central cup about 54–55 mm in diameter, 10 mm deep, with a thick substance, ornamented with fine radial striae and prominent adaxial ridges continued along each centrifugal ray. Abaxial surfaces of the centrifugal rays are smooth and planar, while the adaxial surfaces have a strong median ridge. The central cup has regularly-arranged tubercles along its adaxial surface, which acted probably as attractants or as resin bodies, as they look thick and dense. The species has 13–14 thick centrifugal rays, triangular-elongated in shape, with slightly-curved margins; they are 30–32 mm long and 10–12 mm wide at the base, next to the central cup. Both cup and rays have radial fibers embedded in their thick substance. No

centripetal rays and pollen sacs are known (Fig. 3). Although it lacks pollen sacs, this species is better understood after new findings in the South Carpathians (Popa 2014). Its systematic affinities lay with *Weltrichia pecten* and *W. whitbiensis* (Harris 1969; Popa 2014). *Weltrichia alfredii* is associated with *Ptilophyllum* sp. foliage. It has been defined and described by Krasser (1922) and emended by Popa (2014) from Anina, South Carpathians, Romania, within the Steierdorf Formation, Valea Tereziei Member, where it is Sinemurian in age. Anina, formerly known as Steierdorf, is a fossil-Lagerstätte locality for both preservation and biodiversity (Popa 1997, 2014). The holotype was lost (Popa 2014). The repository of the neotype and of the rest of the type series, including one paratype, is at the Laboratory of Palaeontology, Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania.

4.2 *Weltrichia alpina* Krasser 1919 (Fig. 4)

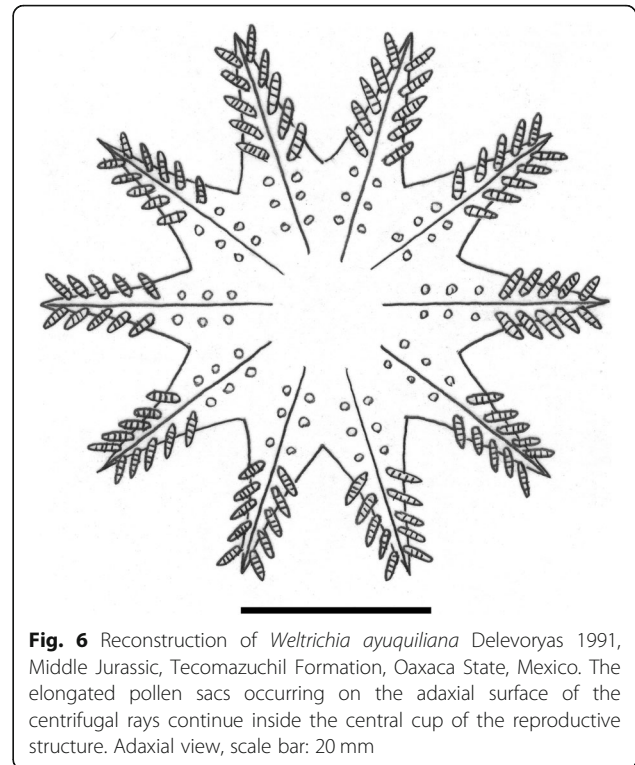
A small sized *Weltrichia* species, *W. alpina* is about 54 mm in diameter, with a wide central cup and 14 short centrifugal rays with rounded margins and sharp apices. Excepting a low median ridge along the rays, the ornamentation of the cup or of the rays is unclear, with no pollen sacs recorded. Krasser (1919) gave a sketch drawing of this species, and its outline is here shown (Fig. 4). Knowledge on this species is rather poor, as the degree of preservation of the holotype is rather poor as



well. *Weltrichia alpina* is rather unique, with its size and short centrifugal rays. It is not associated with any other organs. Krasser (1919) published it as a male *Williamsonia* species and Popa (2014) assigned it to *Weltrichia*. It was collected from the Cassian Beds, southern Tirol, Germany, and it is Late Triassic in age, therefore it is the oldest species of *Weltrichia*. The repository of the holotype is unknown.

4.3 *Weltrichia antonii* Popa 2014 (Fig. 5)

Weltrichia antonii is 100 mm in diameter, with a central cup diameter of 52 mm. The central cup is smooth, with a moderately thick substance, with fine, radial fibrous strands, a cup height of 5–7 mm. It has 9–10 centrifugal rays which are short triangular, with rather smooth surfaces, with slightly rounded apices, decurrent and wide bases, 25 mm long and 13 mm wide at their base, and with no known centripetal rays and pollen sacs. The substance of the rays is moderately thick, and it has fine fibrous strands (Fig. 5). The main peculiarity of *Weltrichia antonii* is the reduced number of centrifugal rays (9–10), the lowest number of rays recorded in the genus. It has no apparent affinities with other *Weltrichia* species. Schweitzer and Kirchner (2003) published a *Weltrichia* sp. A from Nessen, Alborz Mountains, Iran, Middle Jurassic in age, resembling superficially *W. antonii*. *Weltrichia antonii* is associated with a single *Ptilophyllum* sp. leaf fragment, and it was collected from Anina, Banat region, South Carpathians, Romania, within



the Steierdorf Formation, where it is Sinemurian in age (Popa 2014). The holotype is the only known fragment and it is stored at the Laboratory of Palaeontology, Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania.

4.4 *Weltrichia ayuquiliiana* Delevoryas 1991 (Fig. 6)

This species is rather small, about 60 mm in outer diameter, with a stalked central cup, 30 mm in diameter, and with a stalk diameter of 15 mm. To the central cup are attached ten short centrifugal rays, 15 mm long, triangular, with entire margins and acute apices. The rays have a strong median ridge reaching the apex, expressed on both their sides. The pollen sacs are attached on the adaxial surface, in two rows per ray, on both sides of the median ridge, occurring continuously also into the central cup. The pollen sacs are elliptical, elongated, 6 mm long and 2 mm wide, bearing sporangia (Fig. 6). No pollen grains were recorded. *Weltrichia ayuquiliiana* is quite peculiar in size and in the low number of centrifugal rays. In number of rays it resembles only *Weltrichia antonii*, which has only nine rays, but the latter is much larger in size, with narrower centrifugal rays. *Weltrichia ayuquiliiana* is not associated with other bennettitalean organs. Delevoryas (1991) argued that the bodies inside the central cup must be pollen sacs, as they are too substantial, but the occurrence of resin bodies or attractant bodies is quite possible too. Silva Pineda et al. (2011) and Velasco de Leon et al. (2012) discussed the

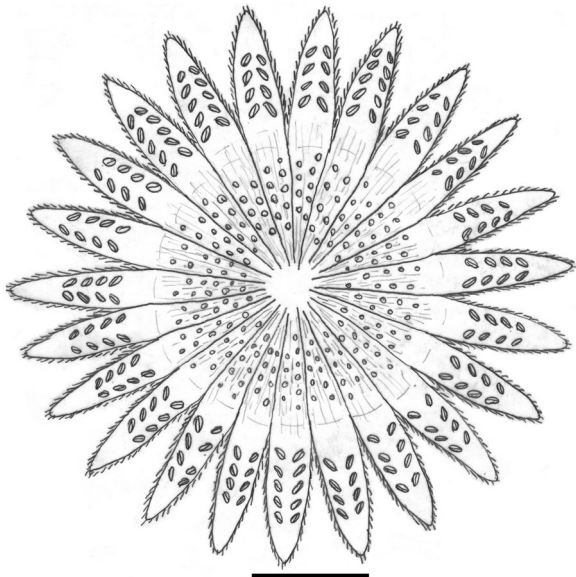


Fig. 7 Reconstruction of *Weltrichia daohugouensis* Li et al. 2004, Middle Jurassic, Daohugou, Inner Mongolia Autonomous Region, China. The centrifugal rays are hairy, with elliptical, bivalve pollen sacs while the central cup shows fibrous strands and resin bodies or pollen sacs. Adaxial view, scale bar: 20 mm

occurrence of this species. This structure was collected from the Tecmazuchil Formation, near Pena de Ayuquila, 15 km northwest from Huajuapán de León, Oaxaca State, Mexico. It is Middle Jurassic in age. The holotype is stored at University of Texas, Austin, Texas, United States of America.

4.5 *Weltrichia daohugouensis* Li et al. 2004 (Fig. 7)

Weltrichia daohugouensis has a 48–50 mm in diameter central cup which is finely striated radially, fibrous, with resin bodies or incompletely-developed pollen sacs. The diameter of the structure is 98–100 mm. To the central cup are connected about 22–23 centrifugal rays with striations and fibers which continue from the central cup, as the cup seems generated by the fusion of the basal parts of the centrifugal rays, therefore creating circular sectors. The centrifugal rays are 20–25 mm long and 4–5 mm wide to their middle part, with slightly acute apices. The abaxial surface of the centrifugal rays is hairy, while the adaxial surface is rather smooth, yielding two parallel rows of pollen sacs grouped in the second, apical part of the rays (Fig. 7). The pollen sacs are elliptic, flattened, made of two valves, occurring obliquely to the centrifugal ray axis, 2 mm long and 1–1.5 mm wide in their middle part. Each valve has about 7–8 sporangia with elliptical, monosulcate pollen grains, 40 µm long and 20 µm wide (Li et al. 2004). No centripetal rays were recorded. The peculiarities of *Weltrichia daohugouensis* include the short, abaxially hairy

centrifugal rays in high numbers and the pollen sacs. It is a well understood and defined species, based on well preserved material. However, the number of centrifugal rays may be higher than 22–23, as the holotype shows 11 rays which cover less than half of the central cup. It is associated with *Cycadolepis* sp. This species was collected from Daohugou village, Shantou town, Ningcheng county, Chifeng City, Inner Mongolia Autonomous Region, China, from the Middle Jurassic Haifanggou Formation. The material includes only the holotype, probably stored in Shenyang, Liaoning Province, China.

4.6 *Weltrichia fabrei* Saporta 1891

The central cup is probably not preserved in the material. The centrifugal rays are 50–60 mm long in fragmented state. 8–10 mm wide in the lower part of the fragments, they are striated longitudinally along their abaxial surface, with entire margins, with a tendency of curving inwards. Pollen sacs are elongated, narrow, 3–4 mm long and 1 mm wide, inserted along two parallel rows on the adaxial surface of the centrifugal rays (Saporta 1891). Due to the poor state of preservation and to the scarcity of the material, this species is less understood, and the total number of centrifugal rays cannot be deduced or reconstructed. I refrain from proposing a reconstruction. It has strong similarities with *Weltrichia mirabilis* in shape of the centrifugal rays and of the pollen sacs. No other bennettitalean organs were

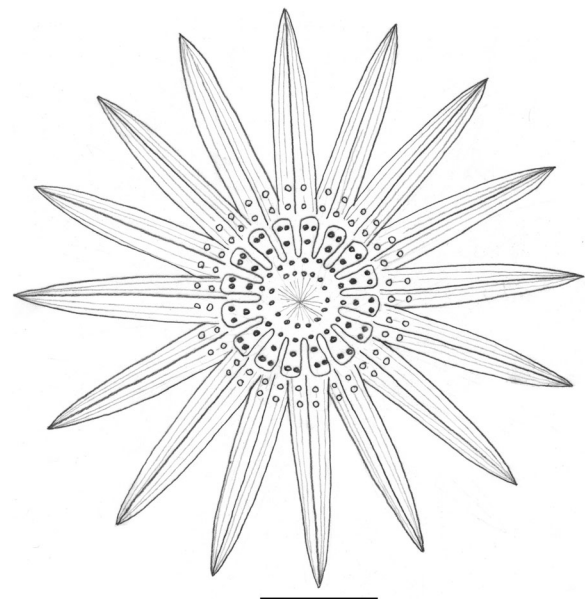


Fig. 8 Reconstruction of *Weltrichia givulescui* Popa 2001, Sinemurian, Steierdorf Formation, Valea Tereziei Member, Anina, South Carpathians, Romania. Black dots indicate resin bodies or attractants within the central cup, while white circles indicate pollen sacs insertions to the centrifugal rays. Adaxial view, scale bar: 20 mm

found in association with it. It was discussed by Nathorst (1911b) and Schuster (1911) and referred to by Harris (1969). It was collected from Mende, in Lozère area, France by M. Fabre, to whom this species was dedicated, from ambivalent “infraliassic sandstones of the Rhaetian stage”. The material is probably Early Jurassic in age. The type series has only a single fragment, the holotype, and its repository is however unknown.

4.7 *Weltrichia givulescui* Popa 2001 (Fig. 8)

A moderately sized *Weltrichia* species, *W. givulescui* is 80–90 mm, maximum 100 mm in diameter, with a central cup 30–40 mm in diameter. The cup height is large, of 15–20 mm, with a base of 10 mm in diameter. The cup has a thick substance and it also has irregularly distributed tubercles which represented attractant or resin bodies. It has 16 triangular, elongated, centrifugal rays, 40–50 mm long and 7–10 mm wide at the base, which are rhombic in cross section, smooth, with median ridges on both adaxial and abaxial surfaces of the rays. The centrifugal rays tend to overlap superficially at their bases, still forming a single whorl. On the adaxial surface of rays occur circular to elliptic scars, possible pollen sacs badly preserved. *Weltrichia givulescui* has 16 centripetal rays, which are elongated, rather narrow and clearly smooth, 7–10 mm long and 2 mm wide (Fig. 8). No well-preserved pollen sacs were recorded (Popa 2001, 2014), but some scars on the centrifugal rays suggest that the pollen sacs were connected

directly to the rays, possibly without fertile appendages. This species is peculiar through its elongated centrifugal rays, centripetal rays and tubercles (attractants or resin bodies) on the adaxial surface of the central cup. The resin bodies or attractants are figured as black dots, while the pollen sacs insertions are figured as white circles (Fig. 8). Its affinities are related to *Weltrichia johannae*, also from Anina. *Weltrichia givulescui* is associated with *Zamites aninaensis* foliage (2001, 2014). Popa (2001) reconstructed this species three-dimensionally; the present reconstruction does not change it with anything, but only adds circular scars to the base of the centrifugal rays (Fig. 8). *Weltrichia givulescui* has been collected from Anina, Romania, from the Steierdorf Formation, Valea Tereziei Member. It is Sinemurian in age. The type series includes besides the holotype several paratypes preserved both transversally and longitudinally, curated at the Laboratory of Palaeontology, Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, Romania (Popa 2001).

4.8 *Weltrichia harrisiana* Bose et Banerji 1984 (Fig. 9)

This species is about 120–150 mm in diameter, with a 20 mm diameter central cup. The central cup is striated radially and yields 12–14 centrifugal rays. The rays are 25–35 mm long and 5–8 mm wide to their middle part. They are strongly striated longitudinally, with a thick substance, and with a prominent median ridge which is thicker towards the cup and less prominent to the apex of rays. The rays yield to their apex five pollen sacs, elongated in shape, 7–9 mm long and 1.5 mm wide, each pollen sac yielding two rows of sporangia (Fig. 9). No centripetal rays were recorded, and the pollen grains are not known (Bose and Banerji 1984). The peculiarities of *Weltrichia harrisiana* lay with the apical pollen sacs and with the median-inflated centrifugal rays. It has affinities with *Weltrichia hirsuta* from Iran, but its hair bases are very rare, and the pollen sacs are simpler, different of the apical appendages of the Iranian species. The degree of knowledge of this species is rather good, although its pollen has not been described and the number of centrifugal rays is not precisely established. The type series includes five fragments, collected from Kurbi and Kakadbhit, Kachchh region, Middle to Late Jurassic in age. The type series is stored in Birbal Sahni Institute of Palaeosciences, Lucknow, India.

4.9 *Weltrichia hirsuta* Schweitzer 1977

Weltrichia hirsuta is a peculiar and flamboyant species with centrifugal rays well developed since their basal most part, in the center of the central cup. It has an outer diameter of about 130–140 mm. The central cup itself seems generated by the lateral fusion of the

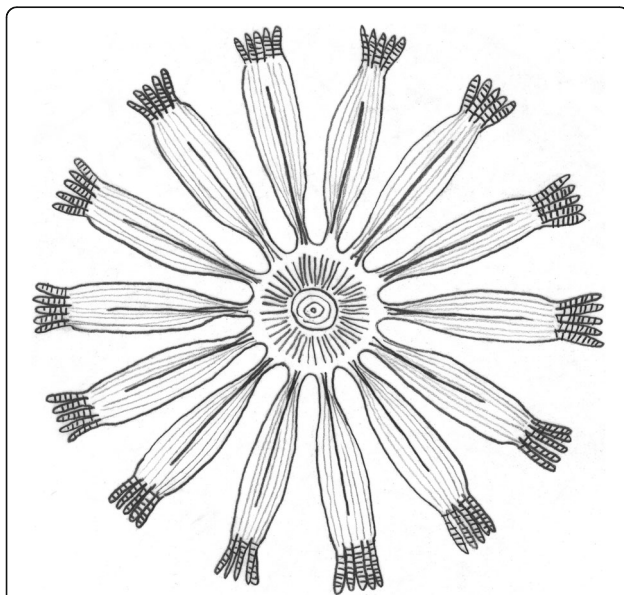


Fig. 9 Reconstruction of *Weltrichia harrisiana* Bose and Banerji 1984, Middle Jurassic, Kachchh, western India. *Weltrichia harrisiana* has five, elongated pollen sacs with apical position on the centrifugal rays. Adaxial view, scale bar: 20 mm

centrifugal rays and has a wide stalk. It has about 46 centrifugal, narrow and hairy centrifugal rays. These rays are usually fused laterally in numbers between two and six, which are very hairy along their abaxial surface and smooth or finely striated longitudinally along their adaxial surface. To the apex of each centrifugal ray occurs a pair of fertile appendages, to which elongated-elliptical pollen sacs are attached adaxially and in pairs, with a centripetal orientation of their apices. Neither centripetal rays, nor attractant or resin bodies were recorded. The typical characters of *Weltrichia hirsuta* are represented by its centrifugal, hairy rays which are basally fused to form the central cup, and their double fertile appendages with an apical position in each ray. It resembles superficially *Weltrichia harrisiana*, but in *W. harrisiana* the central cup is clearly defined, whose centrifugal rays are much less numerous, and the apical fertile appendages are more numerous and digitate. It is associated with *Anomozamites* sp. foliage. It was briefly defined and illustrated by Schweitzer (1977) and discussed later by Schweitzer and Kirchner (2003). Schweitzer (1977) gave the first reconstruction, reproduced by Schweitzer and Kirchner (2003), so a new reconstruction is not necessary here. *Weltrichia hirsuta* has been collected from Zangerud, Alborz Mountains, Iran, from the Shemshak Group, Upper Liassic (Sinemurian–Toarcian in age). The material is curated in the Swedish Museum of Natural History in Stockholm, Sweden.

4.10 *Weltrichia huangbanjingouensis* Sun et al. 2001

This species has a long stalk of 20 mm long and 4 mm wide, and a small central cup lacking visible centrifugal rays which probably were not preserved. The central cup is 35 mm in diameter and 20 mm in height. Pollen sacs occur irregularly on the adaxial surface of the central cup (Sun et al. 2001). The degree of knowledge on this species is rather poor, as the material is not preserving centrifugal rays, although it is preserving pollen sacs in its central cup. Its peculiarities lay with the long stalk and with the pollen sacs preserved inside the central cup. It is associated with *Williamsonia jianshangouensis* female structure. Li et al. (2004) also observed that the material is incompletely preserved. Proposing now a reconstruction is impossible. It was collected from Huangbanjingou, Liaoning Province, China, within the lower sequence of the Yixian Formation, Late Jurassic–Early Cretaceous in age. Only the holotype was recorded, which is curated in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu Province, China.

4.11 *Weltrichia johannae* Popa 2014 (Fig. 10)

A rather small, slender *Weltrichia* species, *W. johannae* is 70 mm in diameter, with a central cup diameter of 15 mm. The cup has a smooth surface, and a thick substance. The species has 12 elongated, slender and flattened dorsi-ventrally centrifugal rays, with thick

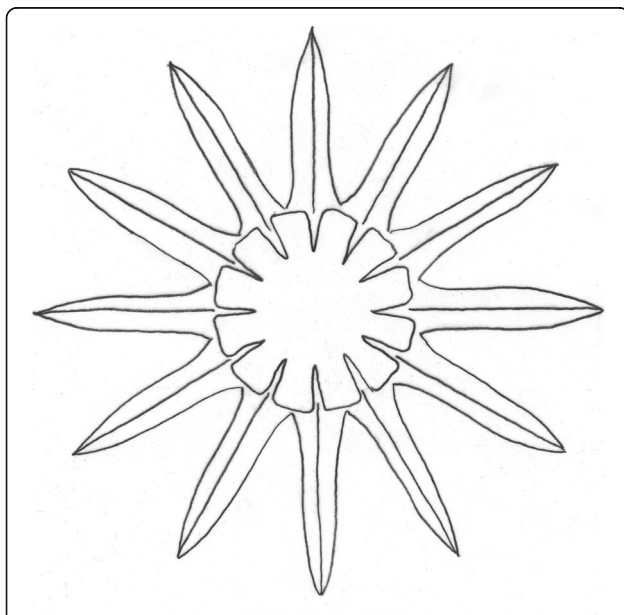


Fig. 10 Reconstruction of *Weltrichia johannae* Popa 2014, with gracile centrifugal and centripetal rays. Sinemurian, Steierdorf Formation, Valea Tereziei Member, Anina, South Carpathians, Romania. Adaxial view, scale bar: 20 mm

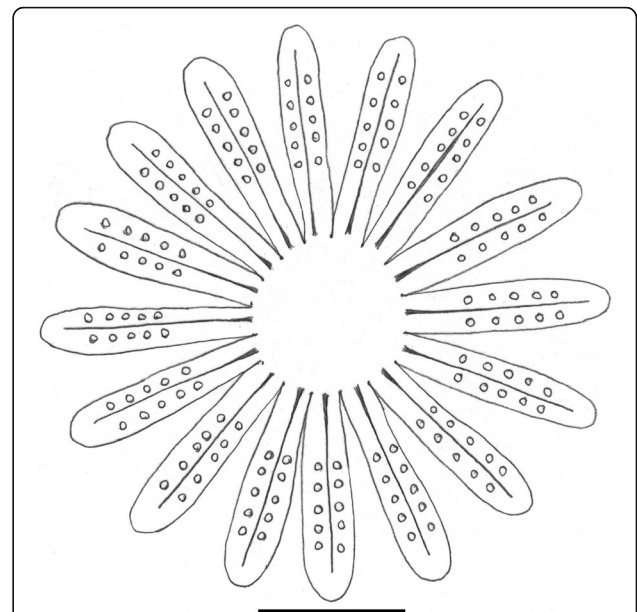


Fig. 11 Reconstruction of *Weltrichia maldensis* Pal and Ghosh 1985, with spatulate centrifugal rays. Late Jurassic, Milky, West Bengal, India. Adaxial view, scale bar: 20 mm

substance, smooth surfaces and with a median ridge, 25–27 mm long and 5–6 mm wide at the base. It has at least 12 centripetal rays, which are smooth, elongated, and narrow, with a sharp apex, 4–5 mm long and 1 mm wide at their base (Fig. 10). Neither pollen sacs, nor resin bodies or attractants were recorded (Popa 2014). The systematic affinities of *Weltrichia johannae* lay with *W. givulescui*, but *W. johannae* is smaller than the latter and has less centrifugal and centripetal rays. It is associated with *Zamites schmiedelii* foliage and with *Williamsonia banatica* ovulate structures. This species was collected in Anina, South Carpathians, Banat region, Romania, from the Steierdorf Formation, Valea Tereziei Member, Sinemurian in age. The type series has a holotype and a paratype, curated at the University of Bucharest, Romania.

4.12 *Weltrichia maldaensis* Pal et Ghosh 1985 (Fig. 11)

This species has a central cup with only eight centrifugal rays preserved, out of probably 16. The central cup is 20 mm in diameter and about 12–15 mm in height. The rays are slightly concave, 25 mm long and 5 mm wide in their median part, with a median ridge on both sides and with attenuate apex. No ornamentation of the rays is visible. The pollen sacs are circular in outline, and they are arranged in two parallel rows, along each side of the median ridge (Pal and Ghosh 1985). The peculiarities of this species lay with the circular shape of the pollen sacs and with the attenuated apices of the

centrifugal rays (Fig. 11). The shape of the pollen sacs may be difficult to assess, if they seem to be expressed as bulges through the substance of the centrifugal rays, visible from the abaxial (outer) sides of rays. *Weltrichia maldaensis* is associated with *Taeniopteris spatulata* and *Ptilophyllum* sp. Pal and Ghosh (1985) considered that the structure has only half of the rays preserved. The holotype shows a *Weltrichia* preserved longitudinally and symmetrically, so such a conclusion makes sense. This species needs revision, as the original description is too short, and the photographic illustration is unclear. The material includes only the holotype. It was recorded from borehole samples from Milki, Malda region, West Bengal, India. The stratigraphic level of the collected material is within the intertrappean beds, between volcanic flows IV and V, Upper Jurassic, correlated with the Rajmahal Basin. The repository of the material is unknown.

4.13 *Weltrichia microdigitata* Delevoryas 1991 (Fig. 12)

Weltrichia microdigitata is the smallest species of *Weltrichia*, with a diameter of only 30 mm. The shallow central cup is 15 mm in diameter, supporting 14 centrifugal rays. The rays are about 7–8 mm long, with a median ridge visible on their adaxial sides, and with rounded apices. The pollen sacs occur on the adaxial surface of centrifugal rays, along two parallel rows, at least three of them on each ray (Fig. 12). They are elongated and each of them includes 15 microsporangia

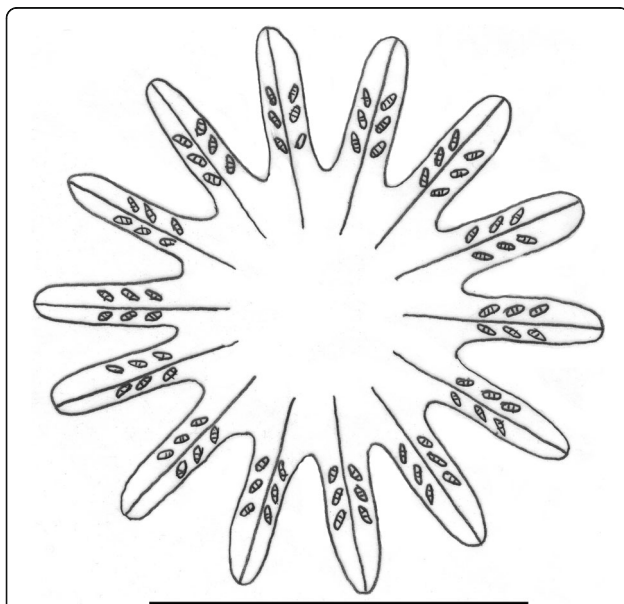


Fig. 12 Reconstruction of *Weltrichia microdigitata* Delevoryas 1991, with short centrifugal rays. Middle Jurassic, Tecomazuchil Formation, Oaxaca State, Mexico. Adaxial view, scale bar: 20 mm

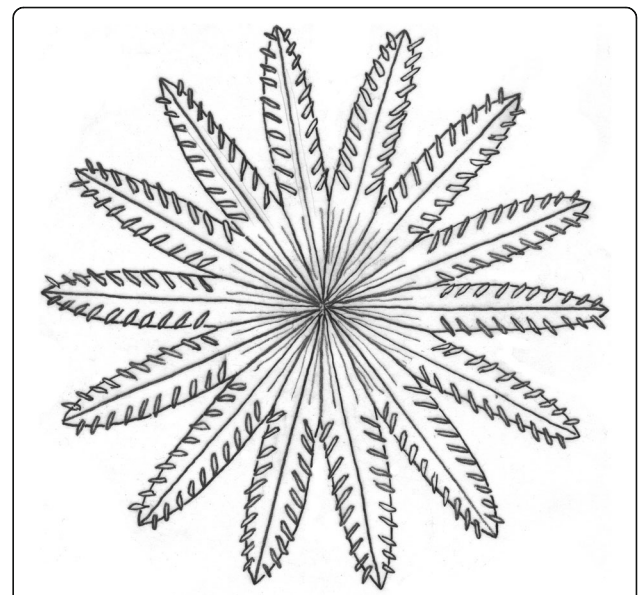


Fig. 13 Reconstruction of *Weltrichia mirabilis* Braun 1849, with elongated pollen sacs, and per centrifugal ray with a median ridge on both adaxial and abaxial sides. Early Jurassic, near Veitlahm, Franconia, Germany. Adaxial view, scale bar: 20 mm

(Delevoryas 1991). The particular characters of this species are represented by size, and by the shape and number of centrifugal rays. It has no systematic affinities, resembling distantly only *Weltrichia ayuquiliiana* from the same region. It has no other bennettitalean organs associated with it. Delevoryas (1991) did not insist on too many character descriptions, such as the tips of the centrifugal rays and the number of pollen sacs per row, still visible in his illustrations. Silva Pineda et al. (2011) and Velasco de Leon et al. (2012) discussed its stratigraphy and occurrence. It was collected from Oaxaca State, near Pena de Ayuquila, Mexico, from the Tecmazuchil Formation, Middle Jurassic in age. Only the holotype was recorded, curated at the University of Texas, Austin, United States of America.

4.14 *Weltrichia mirabilis* Braun 1849 (Fig. 13)

The type species of genus *Weltrichia*, *W. mirabilis* has a central cup to which are attached at least 10–11 centrifugal rays, with an external diameter of the structure of about 100 mm. The central cup seems rather smooth, with radial ridges which continue as median ridges for each centrifugal ray. The cup is about 50 mm in diameter and 20 mm in height, considering the published illustrations. The centrifugal rays are triangular-elongated in shape, which seem finely striated longitudinally, at least along the abaxial surface, with the median ridge expressed on both of their sides. The rays are 30–40 mm long, and tend to curve inwards. Pollen sacs are attached to the adaxial side of the centrifugal rays. They are

elliptical and elongated, almost perpendicular to the adaxial surface, 3–5 mm in length. They seem to be inserted symmetrically along two parallel rows, on both sides of each ray median ridge. Each row may have up to 20 pollen sacs, arranged in two rows of 10 pollen sacs each (Fig. 13). Rays tend to curve inwards, as the details illustrated by Braun (1849) and Nathorst (1911b) show. Next to *Weltrichia mirabilis* were introduced *W. ovalis* and *W. campanulata*, which are synonyms to *W. mirabilis*, considered as different ontogenetic stages by their author. No cuticles were preserved. The affinities of *Weltrichia mirabilis* are with *W. fabrei* defined by Saporta (1891), in terms of centrifugal rays and of pollen sacs. It is not associated with any other bennettitalean organs. It was defined and described by Braun (1849) from the Lower Jurassic of Veitlahm, near Bayreuth, Franconia, Germany. Later, Saporta (1891), Nathorst (1880, 1909, 1911b), and Schuster (1911) discussed and illustrated in detail the species. The total number of centrifugal rays is unknown. It is unclear that the rays' margins are entire or lobed, because of different interpretations of pollen sacs. The original illustrations of Braun (1849) seem without lobes, while those of Saporta (1891) are clearly lobed (his plate 37, Figs. 1, 2; plate 38, Fig. 1). The photographs made by Nathorst (1911b) show pollen sacs and centrifugal rays with entire margins. Braun's fragment illustrated in his Fig. 3 is illustrated by Nathorst (1911b) and it is curated in the Swedish Museum of Natural History in Stockholm, Sweden (Nathorst 1911b). The location of rest of the type series is unknown, probably in Uppsala, Sweden.

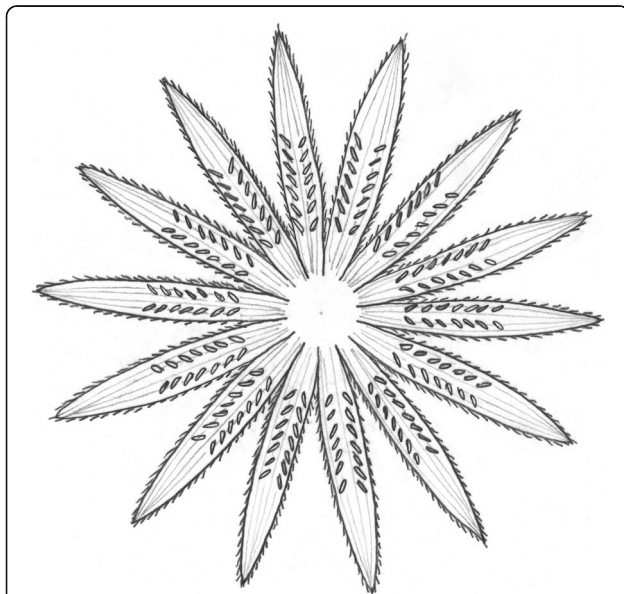
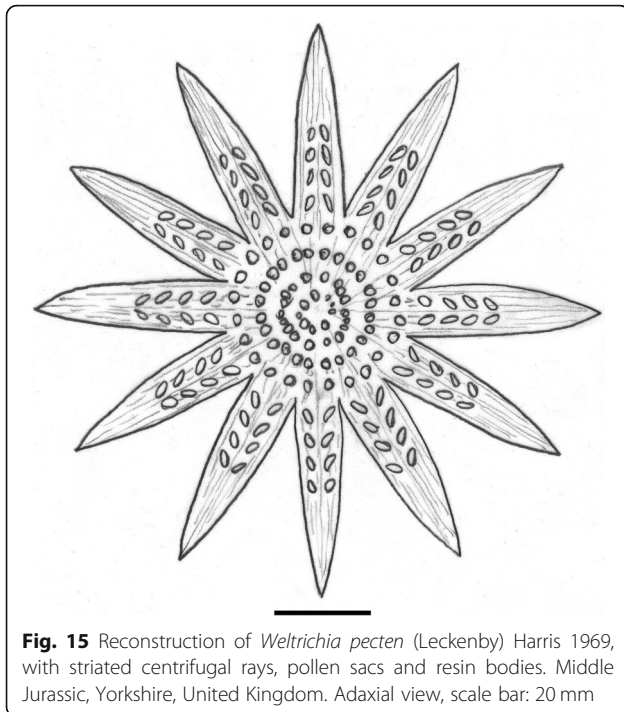


Fig. 14 Reconstruction of *Weltrichia mixtequensis* Silva Pineda et al. 2011, with striated and hairy centrifugal rays, elliptical pollen sacs, and a small sized central cup. Middle Jurassic, Tecmazuchil Formation, Oaxaca State, Mexico. Adaxial view, scale bar: 20 mm

4.15 *Weltrichia mixtequensis* Silva Pineda et al. 2011 (Fig. 14)

This species has a small central cup, 10–20 mm in diameter, and about 14 centrifugal rays. The diameter of the entire structure is 160 mm, the authors who defined this taxon correctly referring to a diameter of 80 mm with folded centrifugal rays. The centrifugal rays are large, 75–80 mm long and 7–9 mm wide towards their median part, with entire margins and acute apices, longitudinally striated and fibrous, without a clear median ridge, and with hairs towards the margins of the rays. The pollen sacs are arranged in rows on the adaxial side of the rays, probably in two parallel rows per ray. The pollen sacs are elongated, 1.65–5.54 mm long and 0.39–1.37 mm wide, with sporangia arranged transversally inside them (Silva Pineda et al. 2011). The visible centrifugal rays are seven, as the cone is preserved longitudinally; and the structure may not be able to accommodate 14 rays, therefore it may have had less than 14 rays (Fig. 14). The peculiar characters of *Weltrichia mixtequensis* lay with the shape and size of the centrifugal rays, next to the very small size of the central cup. This material of this



species is not associated with vegetative organs of Bennettitales. It was collected from the Tecomazuchil Formation, Middle Jurassic in age. The type series has ten specimens, curated at Facultad de Estudios Superiores Zaragoza, Mexico.

4.16 *Weltrichia oolithica* Saporta 1891

Weltrichia oolithica has a central cup about 40 mm in diameter, with an undetermined number of centrifugal rays which are 30–40 mm long. The illustration of the holotype (Saporta 1891: pl. 38, Fig. 2) shows at least 9 rays, as the structure is preserved longitudinally. The rays are finely striated longitudinally along their abaxial surface with entire margins, and they seem to bear fertile appendages yielding pollen sacs. Saporta (1891) refers to this structure as fluffy, emphasizing the scarcity of preserved characters. It is a less understood species of *Weltrichia*, mainly due to the unclear characters of the material. It resembles *Weltrichia mirabilis* and *W. fabrei*, although if the fertile appendages yield double rows of pollen sacs, it may share similar characters with *W. spectabilis* or *W. sol.* It was discussed by Nathorst (1911b) and Schuster (1911) and referred to by Harris (1969). It is difficult to propose a reconstruction, at least without revising the original material. The holotype was collected by Achille de Zigno from the Venetian Alps, reported as being Late Jurassic (Oxfordian) in age. Saporta (1891) worked on a photograph sent by de Zigno, and the storage location of the holotype is unknown.

4.17 *Weltrichia pecten* (Leckenby) Harris 1969 (Fig. 15)

Weltrichia pecten is usually 100–120 mm in diameter, having a central cup of diameter between 30 and 50 mm (usually 40 mm), a thick substance, fibrous radial strands, and an adaxial surface covered with resin sacs. It has 10–12 centrifugal rays and no centripetal ones. The centrifugal rays are triangular, elongated, 30 mm long and 5–10 mm wide, strongly striated longitudinally because of fibrous strands, having a thick substance and without transversal wrinkles, with incurved apices. The pollen sacs are semicircular, arranged along two parallel rows per ray, with short peduncles, 3 mm long and 1 mm wide (Fig. 15). The number of pollen sacs pairs per centrifugal ray is unknown. The pollen sacs are grading into short-stalked resin bodies in the central cup which decrease in size towards the center (Harris 1969). The strongest affinities of *Weltrichia pecten* lay with *W. whitbiensis*. *Weltrichia pecten* is slightly smaller and less woody than *W. whitbiensis*, and Harris (1969) also noted that *W. pecten* probably had a tendency of opening more. Some affinities lay also with *Weltrichia alfredii*. The degree of knowledge over this species is rather good, considering the frequency of the fossil material, its preservation and the literature it produced. It has been discussed and illustrated by Nathorst (1909, 1911a, 1913) as *Williamsonia pecten*. *Weltrichia pecten* is associated with *Ptilophyllum pecten* foliage, *Williamsonia leckenbyi* female structures and with *Cycadolepis nitens* scales. It has been recorded from Cloughton Wyke and Gristhorpe, in Yorkshire, United Kingdom, from the Lower–Middle Deltaic Series, Middle Jurassic in age (Harris 1969) and from Sardinia, also Middle Jurassic (Krasser 1912). The Yorkshire material is stored in the Natural History Museum in London, United Kingdom.

4.18 *Weltrichia primaeva* Schweitzer et Kirchner 2003

This species is known only as fragments of centrifugal, complex and very large rays. The ray fragments are 60 mm long and 9 mm wide. The rays have a strong adaxial median ridge, having inserted laterally, oppositely and symmetrically leaf-like, flattened, elliptical fertile appendages with acute apices, at intervals of 7–8 mm. The authors use the term microsporophylls for these appendages. The appendages have also a strong median ridge expressed both adaxially and abaxially, to which are laterally inserted short pedunculate, elliptical pollen sacs, arranged symmetrically in 4–5 pairs along both sides of the appendage median ridge. The peculiarity of *Weltrichia primaeva* is represented by the leaf-like, flattened fertile appendages, unique until now in genus *Weltrichia*. *Weltrichia spectabilis* resembles somehow *W. primaeva*, but *W. spectabilis* has filiform fertile appendages. Schweitzer and Kirchner (2003) considered this species as having a basal position in genus *Weltrichia*, interpreting the flattened fertile appendages

(microsporophylls) as simple flattened leaves. They consider the lineage *Weltrichia primaeva*, *W. spectabilis*, *W. sol* and *W. whitbiensis* as a continuous evolutionary line based on the continuously reducing morphology of the fertile appendages of these species, from large and leaf-like in *W. primaeva* to no fertile appendages in *W. whitbiensis*. *Weltrichia primaeva* is associated with *Anomozamites majus* foliage. The knowledge about this species is limited by the preservation of the fossil material, as the central cup is missing, as well as the base and apices of the centrifugal rays. I refrain from proposing a reconstruction of this species. It has been collected from Alborz Mountains in Zirab, Iran, from the Shemshak Group, upper Liassic in age (Pliensbachian–Toarcian). The material is curated in the Swedish Museum of Natural History in Stockholm, Sweden.

4.19 *Weltrichia santalensis* (Sitholey et Bose) Harris 1969

This is one of the largest *Weltrichia* species, with an outer diameter of 220–230 mm. The central cup is striated radially along both sides, lacking attractants or resin bodies, 28–45 mm in diameter, 10–25 mm in height, and with a narrow stalk and a curved rim. It has 20 centrifugal rays, narrow and long, flattened towards the cup and strongly thickened and widened towards the apex. Pollen sacs are elongated, arranged adaxially in two parallel rows per ray. No pollen was recorded from this structure. In size, *Weltrichia santalensis* is similar to *Weltrichia sol* and *W. primaeva*, as the largest sized species of *Weltrichia*. The species was introduced by Sitholey and Bose (1953) as *Williamsonia santalensis*, and later Bose (1967) defined as *Weltrichia singhii* (now a synonym of *Weltrichia santalensis*). Harris (1969) correctly assigned *Williamsonia santalensis* to genus *Weltrichia*. There has been a series of discussion regarding the morphology of *Weltrichia santalensis*. First, it was considered that the cup and the centrifugal rays have beneath them a lower whorl of 20 sterile bracts (Sharma 1969). Secondly, it was proposed that the parallel rows of pollen sacs of each ray converge to the apical part of the centrifugal rays, and that the apical part of rays are thickened and waved adaxially, while all rays are twisted laterally (Sharma 1969, 1971, 1977). A first reconstruction of *Weltrichia santalensis* was proposed by Sharma (1969). Sitholey and Bose (1971) reviewed the structure and suggested that the rows of pollen sacs remain parallel, the apical parts of the rays are thickened only abaxially into a hump-like thickening and that the rays are spirally arranged and not in whorls. Banerji (1992) reviewed the genus *Weltrichia* in India, with a history of researches and of opinions on this species too. *Weltrichia santalensis* includes *Ontheanthus polyantra* Ganju 1947, and *Williamsonia campanulatiformis* Sharma 1969, while *Weltrichia singhii* Bose 1967 is

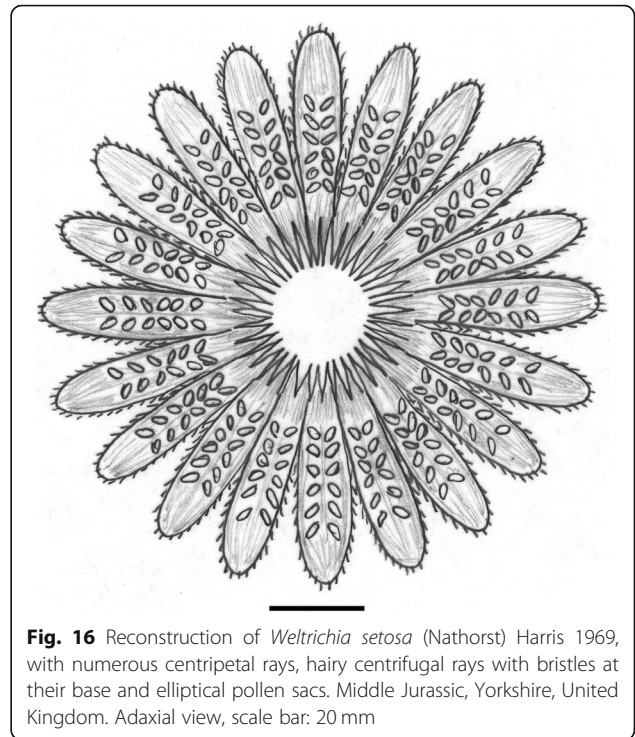


Fig. 16 Reconstruction of *Weltrichia setosa* (Nathorst) Harris 1969, with numerous centripetal rays, hairy centrifugal rays with bristles at their base and elliptical pollen sacs. Middle Jurassic, Yorkshire, United Kingdom. Adaxial view, scale bar: 20 mm

interpreted as a bud of *W. santalensis* (Sitholey and Bose 1953, 1971; Bose 1967; Sharma 1969, 1971, 1977; Banerji 1992). This species needs a revision of its material, mainly because the geometry of all its reconstructions does not fit the ripening and opening geometry of the initial, ellipsoidal bud, especially because of the apical widening and thickening of the rays. Realizing this geometry of accommodation of rays to an initial bud is possible when trying to draw a reconstruction of this species, which I did, only to realize that the geometry of the centrifugal rays does not fit properly. I think it was a problem which Sharma (1969) encountered too, when proposing the twisting of the rays and their adaxial thickening. It is difficult to propose a reconstruction without revising the type series. *Weltrichia santalensis* has been collected from Rajmahal Hills, Bihar, India, where it is Middle to Late Jurassic in age (Banerji 1992), after some interpretations even Early Cretaceous in age. The material is stored at the Birbal Sahni Institute of Palaeosciences in Lucknow, India.

4.20 *Weltrichia setosa* (Nathorst) Harris 1969 (Fig. 16)

Weltrichia setosa is about 120 mm in diameter, with a central cup 40 mm wide, and with a thick substance. To the central cup are attached 20 centrifugal rays with slightly incurved and rounded apices. The centrifugal rays are 40–60 mm long and 10–16 mm at their middle part where their maximal width occurs, 5 mm wide at the base, spatulate in shape, ornamented with bristles (rigid, sometimes toothed and bearing spines) and hairs (shorter, less rigid and thinner). The bristles, 3 mm long,

occur to the base of the centrifugal rays, and interlock with those of the neighbor rays. The substance of the centrifugal rays is rather thick. This species has 40 elongated, linear delicate centripetal rays (about two centripetal rays per base of each centrifugal ray), 10 mm long and 1 mm wide, also covered with bristles and hairs. The margins of the centripetal rays are covered with 2-mm-long hairs. The pollen sacs are flattened, 3–7 mm long, arranged in two parallel rows along each centrifugal

ray (Fig. 16). They have two valves and a thick cuticle, which yield pollen masses. The pollen grains are ellipsoidal, 37 μm long, with a slightly granular ornamentation (Harris 1969). It is associated with *Otozamites beaniei* foliage. It was recorded only from Whitby, Yorkshire, United Kingdom, from the Middle Deltaic Series, Middle Jurassic in age. Harris (1969) considered it a rare species. The type series includes three samples, a neotype and two paratypes, curated in the Natural History Museum in London,

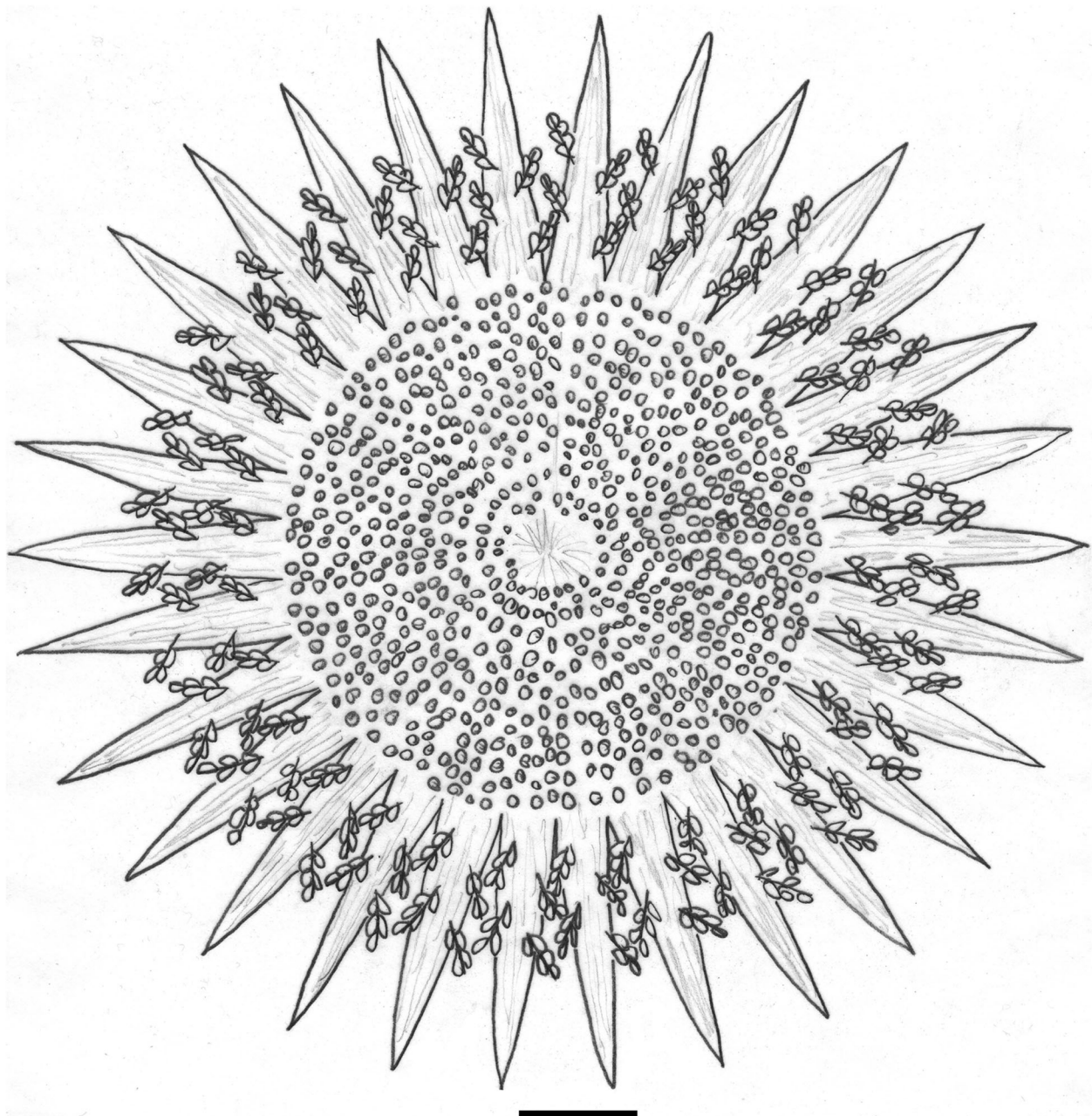


Fig. 17 Reconstruction of *Weltrichia sol* Harris 1969, one of the largest species of genus *Weltrichia*, a flamboyant reproductive structure with a high number of centrifugal rays (30), fibrous centrifugal rays with pollen sacs occurring adaxially on appendages (peduncles) and a large central cup with resin bodies. Middle Jurassic, Yorkshire, United Kingdom. Adaxial view, scale bar: 20 mm

United Kingdom and in the Swedish Museum of Natural History in Stockholm, Sweden.

4.21 *Weltrichia sol* Harris 1969 (Fig. 17)

This is one of the largest species of *Weltrichia*, with a diameter of 170–200 mm. The central cup is 100 mm in diameter, fibrous, covered with resinous, hairy sacs, with a rather thick substance, and with a height of 70–80 mm. It has 30 centrifugal rays which are triangular and elongated, 50–60 mm long and about 10 mm wide. They are almost smooth adaxially, with longitudinal ridges (caused probably by fibers) and sometimes transverse wrinkles, and with a thick substance. It has no centripetal rays, or these were not preserved. The cuticle of the central cup and of the centrifugal rays is about 1 μ m thick, with syndetocheilic stomata irregularly distributed, and with thickened guard cells, small subsidiary cells and no trichome bases. The pollen sacs are pedunculate, with two pollen sacs rows associated with a long fertile appendage; each appendage is 10 mm long and 1 mm wide; and each pollen sac is 4 mm long and 2.5 mm wide. The fertile appendages are inserted more or less alternately to the adaxial side of the centrifugal rays, each appendage having four to five sacs (Fig. 17). Each pollen sac has two valves, with the outer cuticles lacking stomata. The sporangia inside the pollen sacs are about 2 mm long and 0.3 mm wide. The pollen grains are elliptical and monosulcate, 45–50 μ m long (Harris 1969). This is a peculiar *Weltrichia* species as it is of one largest structure, with the highest number of centrifugal rays, with lots of resin bodies along the adaxial surface of the central cup and with pedunculate pollen sacs. This flamboyant species was studied in detail by Harris (1969) who provided one of the most detailed accounts on a *Weltrichia* species, both macroscopically and microscopically (cuticles and pollen). It has been also described by Seward (1900) as a part of *Williamsonia gigas* structure and by Thomas (1915) as a male flower. The preservation degree of the fossil material is very good. It is associated with *Zamites gigas* foliage and *Williamsonia gigas* female structures. It has been described from Whitby and Haiburn Wyke in Yorkshire, United Kingdom, within the Middle Deltaic Series, Middle Jurassic in age. Fossil material belonging to this species is curated in the Natural History Museum in London, United Kingdom and in the National Museum of Natural History in Paris, France.

4.22 *Weltrichia* sp. (sp. nov.? Figure 18)

This Japanese species has a central cup to which are attached 15–16 centrifugal rays, about 100 mm in outline diameter of the structure. The cup is 27 mm in diameter, and is striated radially along its abaxial side, with a thick substance. The centrifugal rays are 37 mm long and 10 mm wide at the base, fibrous and striated

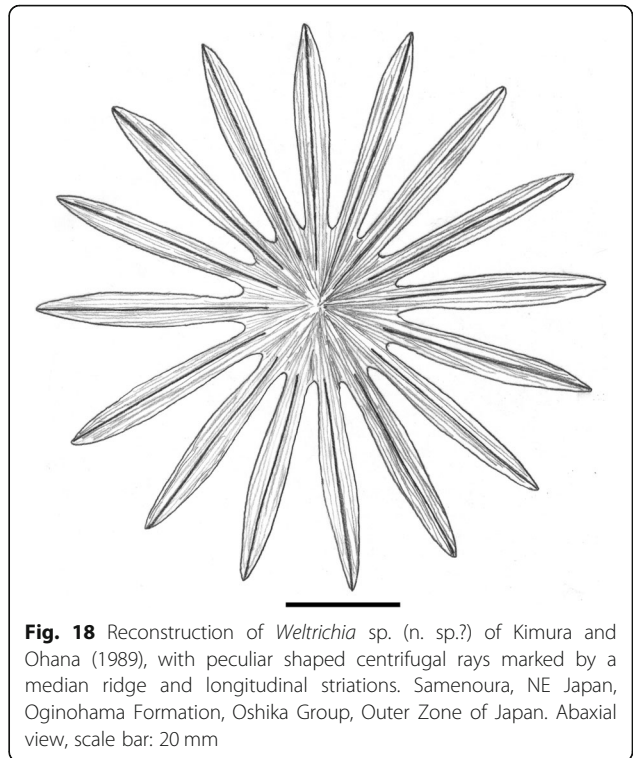


Fig. 18 Reconstruction of *Weltrichia* sp. (n. sp.?) of Kimura and Ohana (1989), with peculiar shaped centrifugal rays marked by a median ridge and longitudinal striations. Samenoura, NE Japan, Oginohama Formation, Oshika Group, Outer Zone of Japan. Abaxial view, scale bar: 20 mm

longitudinally, with a strong median ridge, entire margins and slightly sharp apices, and with a thick substance (Kimura and Ohana 1989). No filiform whiskers at the tips of the rays were recorded, neither were pollen sacs or fertile appendages (Fig. 18). The peculiarities of the material are represented by the shape of the centrifugal rays which are marked by a prominent, median ridge and lacking apical whiskers, which could define quite easily a new species of *Weltrichia*. The affinities of this species lay mainly with *Weltrichia spectabilis* (Kimura and Ohana 1989), but the Japanese material is missing apical whiskers as well as any adaxial, fertile appendages. The latter, if they existed, could have been lost too due to taphonomy or to the maturity of the structure. It is associated with *Zamites densipinnatus* (Kimura and Ohana 1989). The structure is showing abaxial surface, which is rather well preserved, and can represent quite well a new species. It was collected from Samenoura, from the Oginohama Formation, Oshika Group, in the Outer Zone of NE Japan, Late Jurassic in age. The material includes only a single fragment, curated in the Institute of Natural History, Tokyo, Japan.

4.23 *Weltrichia spectabilis* (Nathorst) Harris 1969 (Fig. 19)

Weltrichia spectabilis has a central cup usually 40 mm in diameter and 30 mm in height, with a short stalk. To the cup are attached 13 centrifugal rays with apical filiform extensions (or “whiskers”) which are curved inwards. The rays are 30–50 mm long and about 10 mm wide at

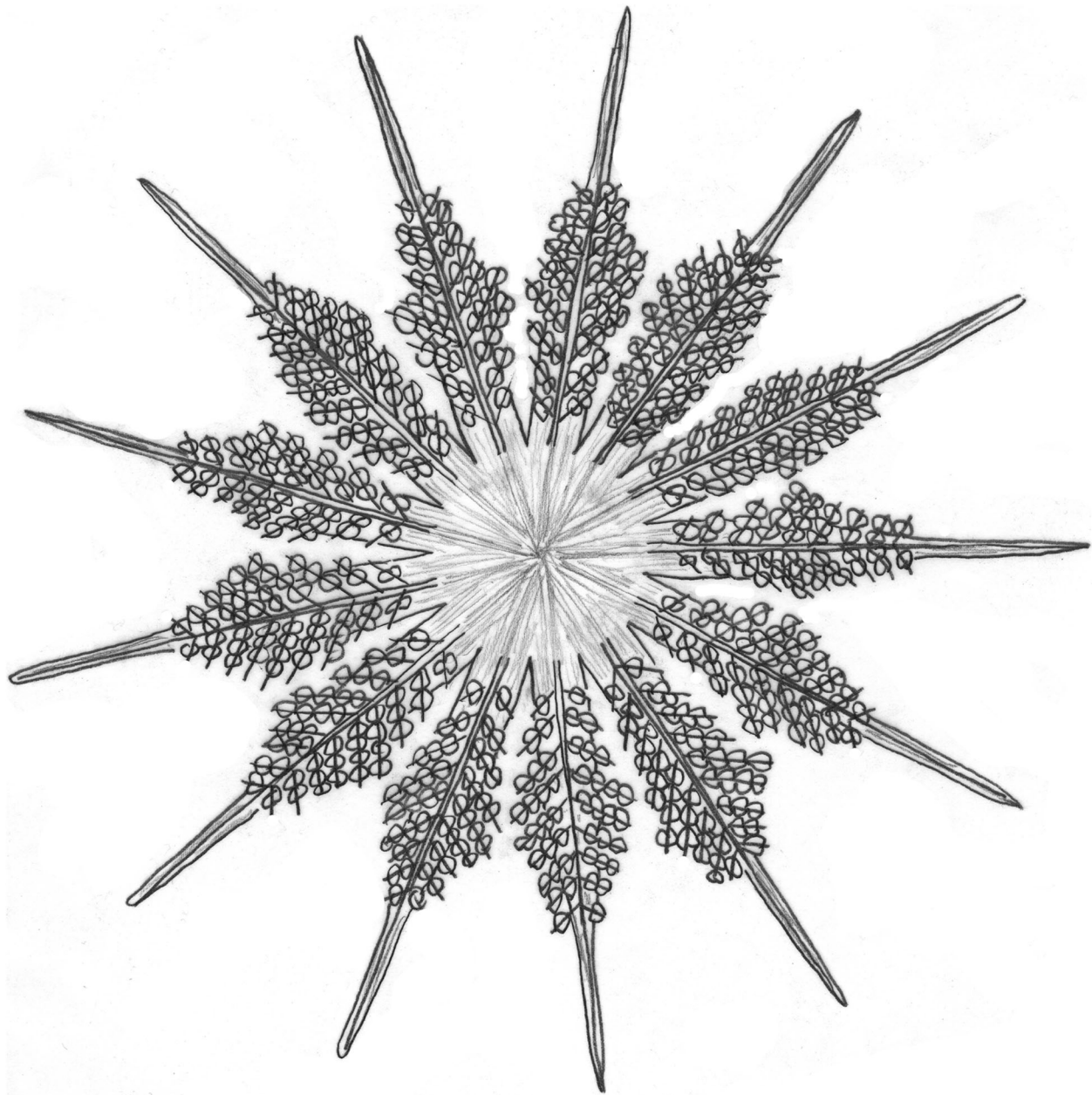


Fig. 19 Reconstruction of *Weltrichia spectabilis* (Nathorst) Harris 1969, a large, flamboyant species with centrifugal rays with adaxial appendages bearing pollen sacs and apical filiform extensions ("whiskers"). Middle Jurassic, Yorkshire, United Kingdom. Adaxial view, scale bar: 20 mm

their base, while the filiform whiskers can reach 30 mm, sometimes even 60 mm in length in the largest structures. The rays are strongly striated longitudinally, with transverse wrinkles and sometimes having a median ridge, mainly on their abaxial (external) surface. Along the adaxial surface of the centrifugal rays, along both sides of the median ridge, occur two rows of fertile appendages (or branches), each appendage yielding laterally and symmetrically pollen sacs. The appendages

vary between 15 and 20 mm in length, bearing laterally 1–3 pairs of semicircular or elongated pollen sacs on each side of the appendage (Fig. 19). The pollen sacs are presumed as having two equal valves (Harris 1969), which are 1–1.5 mm long and include about 14 microsporangia. The pollen grains are ellipsoidal, monocolpate, psilate, and about 60 µm long. The rays and cup have cuticles of moderate thickness, without hair bases, with stomata rather randomly distributed, and with

thickened guard cells. No centripetal rays and resin bodies inside the central cup were recorded. This species is quite particular, even flamboyant in size and morphology, with its dimensions, centrifugal rays with filiform extensions, and characteristic fertile appendages with pollen sacs. The systematic affinities of *Weltrichia spectabilis* lay superficially only with *W. primaeva* Schweitzer and Kirchner 2003 from Iran, but *W. spectabilis* has simple fertile appendages. These fertile appendages also remind those of *Weltrichia sol*, but in *W. spectabilis* they are much more developed and with more pollen sacs. *Weltrichia spectabilis* is associated with *Otozamites gramineus* leaves. The degree of knowledge over this species is quite good and the works covering it are detailed, making it one of the best known *Weltrichia* species, next to *W. pecten* and *W. whitbiensis*. The species was defined by Nathorst (1909) as *Williamsonia spectabilis*, and subsequently described, illustrated and discussed by Nathorst (1911a, 1912), Thomas and Bancroft (1913), Florin (1933), Harris (1969), Schweitzer (1977) and Van Konijnenburg-van Cittert (2008). Harris (1969) emended its diagnosis and assigned it to genus *Weltrichia*. It has been collected from Whitby and Marske Quarry in Yorkshire, United Kingdom, from the Lower Deltaic Series, Middle Jurassic in age. Material belonging to this species is curated in the Swedish Museum of Natural History in Stockholm, Sweden, and in the Natural History Museum in London, United Kingdom.

4.24 *Weltrichia steierdorfensis* Popa 2014 (Fig. 20)

This Romanian species has a diameter of about 105–120 mm and a central cup diameter of 40–45 mm. The central cup has smooth abaxial surface and a thick substance, with a base 10 mm in diameter and about 5 mm in height. *Weltrichia steierdorfensis* has 12 centrifugal rays, 25 mm long, which are short triangular, with curved margins, acute apices, with a median ridge reaching the apex of each ray, and with a smooth abaxial surface. Centrifugal rays sometimes overlap as a result of taphonomy (flattening) and they tend to curve inwards (Fig. 20). No pollen sacs or cuticles were recorded. Its peculiarities are given by its large size, and by its short, centrifugal rays in a low number. It is associated with *Ptilophyllum* sp. leaves (Popa 2014). It was collected in Anina, Romania, within the Steierdorf Formation, Valea Tereziei Member, Sinemurian in age. The type series has only a fragment, the holotype, curated at the Faculty of Biology and Geology, Babeş-Bolyai University, Cluj-Napoca, Romania.

4.25 *Weltrichia whitbiensis* (Nathorst) Harris 1969 (Fig. 21)

This species is large, woody in appearance, 120–130 mm in diameter, with a central, almost hemispherical cup of 40–50 mm in diameter and at least 25 mm in height, with a thick substance, and with resin sacs over the adaxial surface. It has 13–16 centrifugal rays which are

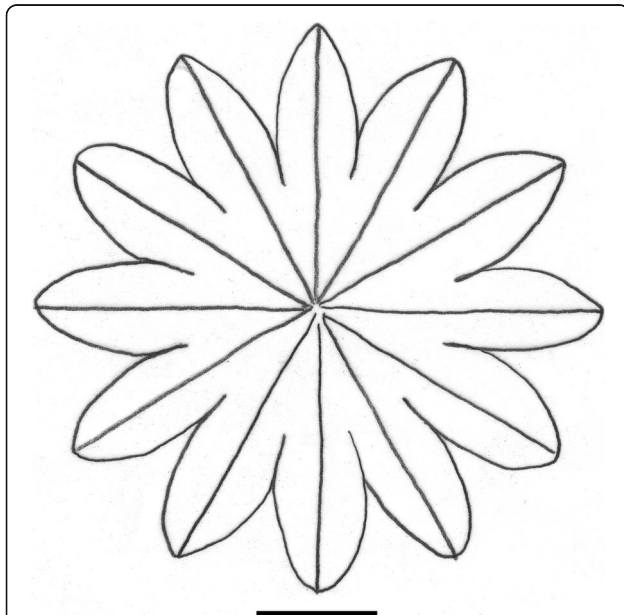


Fig. 20 Reconstruction of *Weltrichia steierdorfensis* Popa 2014, with short and wide centrifugal rays which sometimes overlap to their base, having abaxial, prominent median ridges. Sinemurian, Steierdorf Formation, Valea Tereziei Member, Anina, South Carpathians, Romania. Abaxial view, scale bar: 20 mm

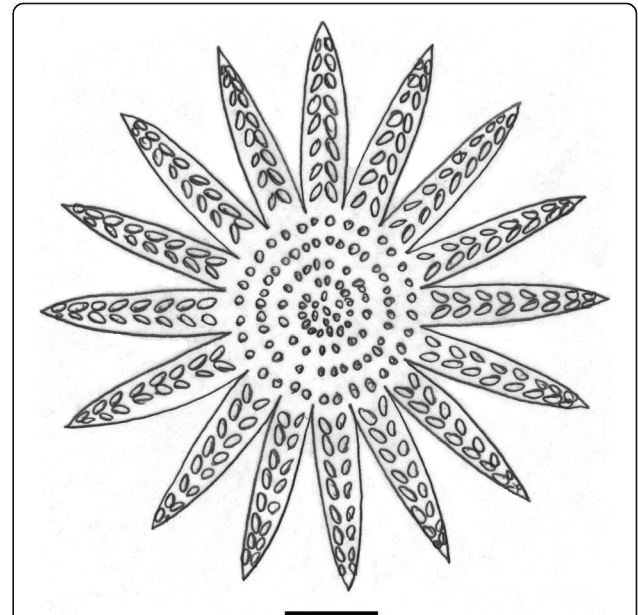


Fig. 21 Reconstruction of *Weltrichia whitbiensis* (Nathorst) Harris 1969, a large-sized species, with centrifugal rays yielding elliptical pollen sacs which grade into resin bodies inside the central cup. Middle Jurassic, Yorkshire, United Kingdom. Adaxial view, scale bar: 20 mm

elongated, triangular, 40 mm long and 10 mm wide at their base, with a thick substance, longitudinal striations but hairless and inward-curved apices and recurved entire margins. *Weltrichia whitbiensis* has no centripetal rays. The pollen sacs are elliptic, 2–3 mm long, and are arranged in two rows along the adaxial surface of each centrifugal ray; these rows continue inside the central cup as resinous bodies. Each row has seven to eight pollen sacs, densely inserted to the centrifugal rays (Fig. 21). Pollen grains are elliptical, monosulcate, 48 µm long. Harris (1969) observed the vascular bundles of this structure, distributed radially, dividing repeatedly along the central cup, six of such bundles entering each ray base, continuing parallelly and ending in the ray margins. Different bundles were feeding the pollen sacs. The morphological peculiarities of *Weltrichia whitbiensis* are represented by the size of the structure, and the double rows of pollen sacs grading into resinous sacs inside the central cup. Material of this species offered a glimpse into the vascular bundles of *Weltrichia* (Harris 1969). Discussions on *Weltrichia whitbiensis* were undertaken in detail by Nathorst (1911a, 1912). *Weltrichia whitbiensis* includes *W. bituberculata* Nathorst 1909 (Nathorst 1911a). It has been often confused with *Weltrichia pecten*, with which it has the most systematic affinities, having almost the same size, although *W. pecten* has a slightly lower number of centrifugal rays and is less woody (Harris 1969). Nathorst (1911a) and Schweitzer (1977) provided beautiful reconstructions of this species, although Schweitzer (1977) shows 12 pairs of pollen sacs per centrifugal ray, instead of seven to eight. *Weltrichia whitbiensis* is associated with *Ptilophyllum pectinoides* foliage, *Williamsonia hildae* female structures, *Cycadolepis hypene* scales and *Bucklandia pustulosa* barks (Harris 1969). It has been described from Yorkshire, United Kingdom, mainly from Whitby (Long Bright Plant Bed), but also from Roseberry, Ravenscar, Hasty Bank, Hawsker, and Beast Cliff (Harris 1969), from the Lower Deltaic Series, Middle Jurassic in age. *Weltrichia whitbiensis* has been described also from Sardinia (Krasser 1912), where it is also Middle Jurassic in age, but the modern revision of the historical collection of Domenico Lovisato could not confirm this species (Scanu et al. 2012). Asama (1974) referred to this species (*Weltrichia* sp., cf. *Weltrichia whitbiensis*) on fragmentary material collected from Ulu Endau, Pahang, West Malaysia, with an unknown modern repository of the published material. The Yorkshire material is curated in the Natural History Museum in London, United Kingdom.

5 Discussion

5.1 Affinities

As a unisexual, male reproductive structure, *Weltrichia* has a few affinities. One of the closest structures of *Weltrichia* is *Lunzia* Krasser 1917 emend. Pott et al. 2017, with the type species *Lunzia austriaca* (Krasser) Pott et al. 2017 from the Upper Triassic (Carnian) of Lunz, Austria. This structure has a cup shape with fused lobes bearing adaxially supplementary microsporophylls with pollen sacs yielding elliptic, monosulcate and psilate pollen grains. It is usually associated with *Pterophyllum filicoides* foliage and *Westersheimia pramelreuthensis* ovulate structure (Pott et al. 2017). As Pott et al. (2017) observed, *Lunzia* even fits the generic diagnosis of *Weltrichia* given by Harris (1969) but in the same time it is different of *Weltrichia* as the pollen sacs (synangia) of *Lunzia* occur on supplementary microsporophylls with the pollen sacs dehiscent on all sides and not made of two valves like in *Weltrichia*, and the syndetocheilic stomata of *Lunzia* have four subsidiary cells instead of the typical two in *Weltrichia*. Also, although the pollen grains of both genera are similar in shape and ornamentation, their sizes are very different, two to three times larger in *Weltrichia* (Pott et al. 2017).

Genus *Welsbergia* Pott et al. 2016, a segregate from genus *Bennettistemon*, from the Upper Triassic of Franconia and of Jameson Land, Greenland, also has affinities with *Weltrichia*. In *Welsbergia*, the centrifugal rays are transformed into narrow appendages yielding bivalve pollen sacs (Pott et al. 2016). *Welsbergia bursigera* (Harris) Pott et al. 2016, the only species of genus *Welsbergia*, is associated with *Pterophyllum aequale* (Brongniart) Pott et McLoughlin 2009.

Genus *Bennettistemon* Harris 1932 is a form-genus defined by Harris (1932) for imperfectly known male fertile fragments belonging to Bennettitales, fragments which cannot be surely attributed to *Weltrichia* due to various reasons, such as the poor degree of preservation. *Bennettistemon* is a related genus to *Weltrichia*, as often centrifugal rays or central cups can be easily fragmented and separated of the whole *Weltrichia* structure. Radial bracts surrounding an ovulate cone with ovules and interseminal scales occur in genus *Williamsonia*, superficially resembling *Weltrichia*.

An example of taxonomical difficulty related to the scarcity of the fossil material, *Weltrichia mexicana* (Wieland) Harris 1969 was a frequently used taxon when dealing with the Mexican Bennettitales. Wieland (1914–1916) defined the species on a single specimen collected from Diquiyu, Oaxaca State, Mexico, Lower or Middle Jurassic in age. Later Delevoryas and Gould (1973) and Person and Delevoryas (1982) rejected the

species. They considered that this material is not a *Weltrichia* as it lacks the necessary characters, and it is impossible to assign the material to a plant taxon due to its poor preservation.

Under *Weltrichia* sp., Kimura et al. (1985) described and illustrated a possible *Weltrichia* species from the Taltung Formation of the Tansen Group in Amile, Palpa District, Lesser Himalaya, Nepal. It ranges in age between Late Jurassic and Early Cretaceous. The structure shows a deep central cup, very similar in shape with *Weltrichia mexicana*, with a wrinkled external surface to which possible centrifugal rays seem to be attached, possibly showing pollen sacs. It is a small sized structure and the preservation of the material is poor. The revision of the material, as in the case of *Weltrichia mexicana*, is necessary.

5.2 Anatomy

The structural variation in *Weltrichia* species is high, especially related to the morphology of the central cup and to number and shape of the centrifugal rays, occurrence of centripetal rays or of fertile appendages yielding pollen sacs, pollen sac contents and structure and even in the pollen itself. Original colors of *Weltrichia* species are difficult to identify but these colors could be related to their pollination strategy, related to insect or to wind pollination. The monoecious or dioecious nature of the bennettitaleans yielding *Weltrichia* and *Williamsonia* unisexual reproductive structures is also difficult to demonstrate due to the scarcity of the fossil record.

The substance of the central cup and of the centrifugal rays can be thin, as in *Weltrichia ayuquilianana*, moderately thick as in *W. antonii*, or it can be thick, as in *W. alfredii*, *W. givulescui* or *W. spectabilis*. These parts, when thick and woody, can be strongly striated longitudinally or radially, fibrous and rather rigid, versus un-ornamented when thin and flexible. Median ridges can occur in various species along both sides of the rays (*Weltrichia givulescui*, *W. maldaensis*) or they can be missing abaxially (*W. alfredii*) or along both surfaces. The cup itself looks like the result of lateral fusion of centrifugal rays, as in *Weltrichia hirsuta*, or the cup looks entire, with the rays resembling centrifugal lobes of the cup, as in *W. sol* or in *W. steierdorfensis*.

Centrifugal rays can be short (as in *Weltrichia ayuquilianana*) or strongly elongated with filiform apices (as in *W. spectabilis*), flattened (as in *W. whitbiensis*) or rhombic in cross section (as in *W. givulescui*), even spatulate (as in *W. setosa*). The tendency of curving of the centrifugal ray apices is also variable, higher in *W. spectabilis*, *W. fabrei* or *W. mirabilis* and missing in *W. givulescui* or *W. alfredii*. The general shape of the

centrifugal rays can be triangular-elongated (*W. alfredii*), extremely elongated with whiskers (*W. spectabilis*), or reaching their maximal width towards their median part (*W. harrisiana*, *W. maldaensis*). A peculiar thickening along the abaxial, apical surface of the centrifugal rays occurs in *W. santalensis*, probably related to its ontogeny, marked by a peculiar flexed deploying (unfurling) of centrifugal rays. A bud of *Weltrichia* was described as *Weltrichia* sp. A by Popa (2014) from Anina, Romania, with centrifugal rays still connected laterally. Maturation of such a structure meant the simple deploying of centrifugal rays, without unfurling as in *Cycadeoidea* structures (Wieland 1906). Therefore, generating adaxial, longitudinal ridges along the centrifugal rays of *Weltrichia* was possible.

Due to the scarcity of the fossil record of *Weltrichia* species, considering that some species are represented only by their holotype, it is difficult to assess the intra-specific variability in terms of numbers of centrifugal and centripetal rays. Considering the studied material and the previous reports, the number of centrifugal and centripetal rays in *Weltrichia* species is rather constant.

Hairs and bristles are highly variable, occurring mainly along abaxial surfaces of cups and centrifugal rays. Extreme cases with dense trichomes belong to *Weltrichia hirsuta*, and with dense bristles, equipped with spike-like apices, belong to *W. setosa*.

Centripetal rays can occur in a few species (*Weltrichia setosa*, *W. johannae*, *W. givulescui*) or can simply miss, as a preservation effect or because those species themselves did not possess them when alive. Resin bodies or attractants (*W. givulescui*) and immature pollen sacs (*W. sol*) can occur in the central cup. The difference between these types of adaxial bodies was explained by Harris (1969) in relation to their resistance to acids: delicate, easy to macerate when being pollen sacs and difficult to macerate when being resin bodies. Pollen sacs occurring on the adaxial surface of centrifugal rays can grade into immature pollen sacs or possibly even into resin bodies, both types occurring also adaxially in the central cup. This transition can be related to the ontogeny of pollen sacs in *Weltrichia*, the first to mature being the pollen sacs occurring distally (apically) on the centrifugal rays.

Pollen sacs (synangia) can be elliptical as in *Weltrichia pecten* to strongly-elongated in shape, as in *W. santalensis*, *W. mirabilis* and *W. fabrei*. They can occur directly on the adaxial surface of the centrifugal rays, as in *Weltrichia whitbiensis*, or can occur on simple fertile appendages, as in *W. spectabilis*, *W. sol* and *W. santalensis*, or on complex, leaf-like appendages, as in *W. primaeva*. Fertile appendages can occur also apically, to the apex of the centrifugal rays, as in *Weltrichia hirsuta* or *W. harrisiana*, with digitate shapes. The pollen sacs always consist of two valves, but the number of

microsporangia inside each valve can vary, although their microsporangia orientation inside the pollen sacs is usually parallel. The pollen grains are always elliptical, monocolpate and usually psilate or slightly granulate.

5.3 Taphonomy

Taphonomy and the degree of preservation are highly responsible with character occurrence in *Weltrichia* material, mainly because these complex structures could have been easily destroyed and dismembered by mechanical and biotic factors. Centripetal rays, which are always slender, thin and gracile, are preserved very rarely. Structures with centripetal rays such as *Weltrichia setosa*, *W. givulescui* and *W. johannae* barely preserve them. Popa (2014) showed that a part of the holotype of *Weltrichia johannae* shows no evidence at all of centripetal rays, while only the counterpart preserved them, acting like a lid to the central cup. Therefore, species which are reported as having no centripetal rays simply may have had lost them due to preservation and taphonomy. The same with pollen sacs, which are fragile and easily removable from the adaxial surfaces of the centrifugal rays, especially when they occurred on simple or complicated fertile appendages. Many species, such as *Weltrichia givulescui*, *W. alfredii*, etc. do not have pollen sacs recorded.

When the structures are preserved longitudinally, the total number of centrifugal rays is difficult to estimate, such as in *Weltrichia mixtequensis*, *W. mirabilis* or *W. fabrei*. Centripetal rays and ornamentation of the central cup is also difficult or impossible to identify, but stalks may be visible only this way. When preserved transversally, centripetal rays can be visible, as well as pollen sacs and resin bodies inside the central cups, but stalks are very difficult to observe.

Associations of organs in Bennettitales may provide a hint for the whole bennettitalean plant yielding reproductive and vegetative organs, but it cannot be a proof to it (Harris 1969; Popa 2014). Conspecificity of these organs can be only demonstrated through anatomical connections or with cuticular analysis.

5.4 Pollination

Form and function in *Weltrichia* structures are intimately controlled by the pollination strategy of these species. Two main types of pollination strategies can be invoked in relation to both unisexual and bisexual Bennettitales: wind/water pollination and insect pollination.

The wind pollination has been invoked in the case of the bennettitalean male structure *Lunzia austriaca* (Krasser 1917; Pott et al. 2017), based on the robust nature of the structure, on the psilate exine of the pollen grains and on the upward bending shape of its microsporophylls. *Weltrichia* includes similar characters,

therefore wind pollination seems very plausible to many of its species. Thickness of substance, fibrous strands and strong, prominent ridges in cup and centrifugal rays in *Weltrichia* can be correlated with mechanical robustness and with the woody character, very well visible in *W. spectabilis*, *W. alfredii*, *W. givulescui*, *W. whitbiensis* and in many other *Weltrichia* species. The woody types may have been rather rigid in structural construction. Also, many species have inward curved tips of the centrifugal rays, as in *Weltrichia spectabilis* and *W. whitbiensis*. And all *Weltrichia* species have psilate, monosulcate pollen, all these characters pointing to a wind pollination reproductive strategy. Moreover, species with fertile appendages yielding pollen sacs on the adaxial surface of centrifugal rays (*W. spectabilis*, *W. sol*) or to their apices would have been in a better position to disperse their pollen using air streams.

However, there is strong and growing evidence of interactions between Bennettitales and insects, ranging from herbivory (Pott et al. 2012), leaf mining, oviposition (Pott et al. 2008; Popa and Zaharia 2011) and larvae growth inside fertile structures. In the same time, cupedid beetles began diversifying since the Late Triassic, providing candidates for insect pollination of Williamsoniaceae.

Resin bodies or attractant bodies in the central cup of *Weltrichia*, as occur in *W. alfredii*, *W. givulescui* and *W. whitbiensis*, may represent a character evolved in connection with insect pollination, particularly for cupedid pollination. Attracting insects to the center of the structure looks like a convenient strategy for dispersal of pollen. Attractants in female unisexual bennettitalean structures, such as in *Wielandiella* and *Williamsonia*, were also identified (Pott et al. 2008, 2010; Pott 2014). The thick substance of the *Weltrichia* structures as a whole or of their parts, such as cups and both types of rays, their mechanical robustness and their woody nature in some *Weltrichia* species, can be interpreted also as an adaptation against beetle biting and chewing, as beetles generally and cupedids particularly have strong masticatory parts.

Insect repellent means are more clearly expressed in *Weltrichia*. Centripetal rays were covering the central cup, and in one species (*Weltrichia givulescui*) they occur also over resin bodies or attractants. These centripetal rays in *Weltrichia givulescui* were rigid, considering their thickness. Covering resin bodies or attractants meant still attracting beetles but also preserving these bodies against insect damages, a strategy towards beetles outlined as “visit but do not damage”. In *Weltrichia johannae*, the centripetal rays were rigid and sharp. Also, dense and strong hairs and complicated, sharp and spike-like bristles along the abaxial surfaces of centrifugal rays and central cups, as those of *Weltrichia setosa*, functioned as some types of repellents for insects.

Moreover, *Weltrichia setosa* has centripetal rays covered with forward pointing hairs, although these hairs were not so rigid and sharp as those from the centrifugal rays. Interlocking abaxial bristles and hairs between centrifugal rays in *Weltrichia setosa* meant also a supplementary protection against insect access and damage from below.

6 Conclusions

Genus *Weltrichia* is a rare male bennettitalean reproductive structure with a peculiar anatomy, highly diverse in morphology, with its form and function controlled by the pollination strategy of the bennettitalean plant. Wind pollination seems to be the dominant strategy in *Weltrichia*, but hints for insect pollination, particularly for cupedid beetle pollination, occur as well in the anatomy of this genus, related to resin or attractant bodies inside the central cup and to centripetal rays of various species. The high morphological variability represents a highly interesting aspect in bennettitalean systematics and reproductive strategies. Co-evolution with insects, especially with the cupedid group, may well explain such variability of the genus *Weltrichia*, related to dedicated species of pollinators and pointing to specialized collaborations between bennettitaleans and insect species already occurring in the Late Triassic and the Early Jurassic. Far from being well understood in form and function, genus *Weltrichia* still raises a series of unanswered questions regarding various characters of some of its species, such as the architecture and colors of centrifugal and centripetal rays, resin bodies and attractants, pollen sacs and microsporangia structures, and pollen morphology and dispersal. The monoecious or dioecious nature of such Williamsoniaceae plants having unisexual reproductive structures of *Weltrichia* and *Williamsonia* types remains also a matter of debate. Whole plant reconstructions are still difficult to demonstrate, but organ associations together with cuticle analysis provide the necessary means for reaching this goal.

Abbreviations

CC: Central cup; CFR: Centrifugal ray; CPR: Centripetal ray; FS: Fibrous strand; MR: Median ridge; PS: Pollen sac position (pollen sac attachment); RBA: Resin (resinous) body or attractant; ST: Stalk

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Authors' contributions

This paper is a contribution of one author. The author read and approved the final manuscript.

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