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Article

Friedsellowia gracilifolia gen. nov. et sp. nov., a new gnetophyte from the Lower Cretaceous Crato Formation (Brazil)

by

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With 12 plates and 4 text-figures

Abstract

A new fossil gnetophyte, *Friedsellowia gracilifolia* gen. nov. et sp. nov. from the Crato Formation (northeast Brazil) is described. Several, nearly complete specimens, including seedlings, young and more mature plants are preserved with roots, axes, leaves and reproductive organs. A fully grown plant probably reached more than one metre in height, displaying an articulated gnetalean habit with slender long-jointed stems and leaves usually attached as whorls of four at lower side branches, terminal reproductive organs consist of cones. Ovulate cones bear generally about 8–16 or more ovulate organs in an arrangement in whorls of four or when in pairs of two, in an opposite-decussate arrangement. Small terminal microsporangiate cones sit on long thin axes which subtend the ovulate cones. Based on its anatomy and morphology, the new taxon nests within the Gnetales. Various characters, such as the chevron bearing venation of the cotyledons, the possible presence of a feeder and the cone structures with many reproductive units per cone point to a close relationship to *Welwitschia*. The plant grew most likely in open sunny habitats, possibly in a reed like manner close to the Crato lake.

Key words: fossil Gnetales, Welwitschiaceae, early Cretaceous, Aptian, Gondwana.

Contents

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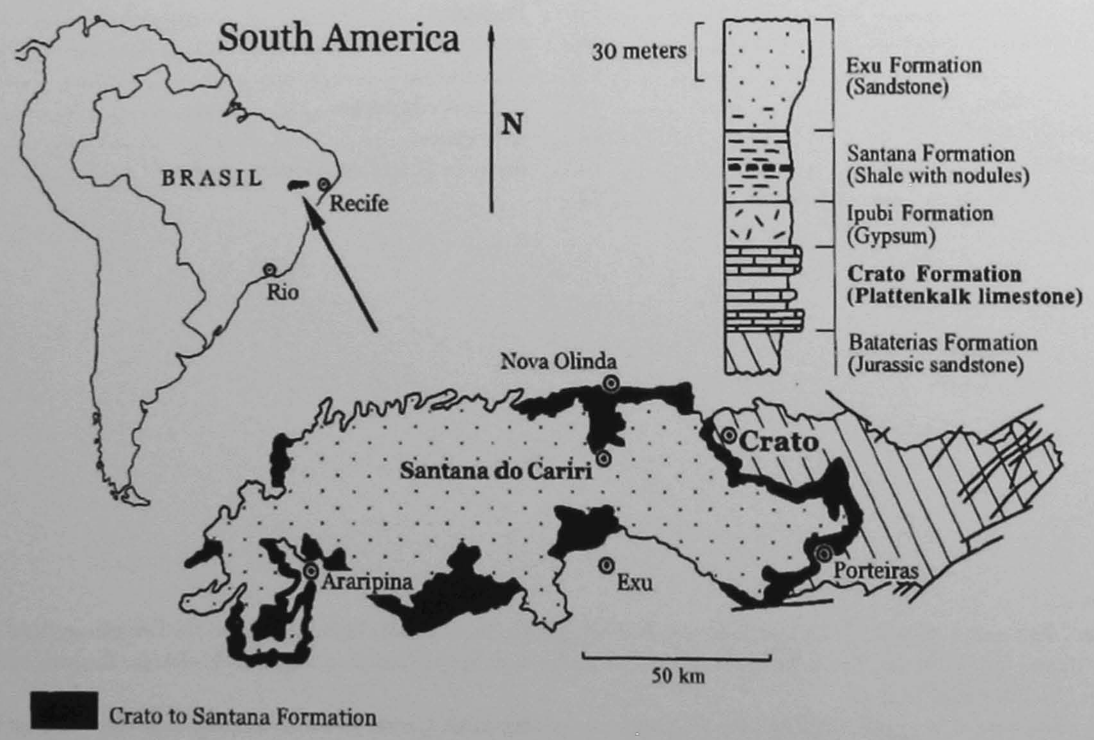
Introduction

Gnetophytes, an ancient group of gymnosperms, were present from the Late Permian in China (Wang 2004). The main diversification of gnetophytes took place in the Mesozoic, with a first radiation possibly during the Triassic (Crane 1988, Krassilov 2009). Vegetative, reproductive structures and pollen are known from the South African Molteno and the North American Chinle Formations (Krassilov & Ash 1988, Cornet 1996, Anderson & Anderson 2003). During the early Cretaceous, concurrent with the appearance of early angiosperms, species richness of Gnetophyta was much higher than today (Crane 1988, Crane 1996). These fossil remains are described from the Baikal area (Krassilov 1986, Krassilov & Bugdaeva 1999, Krassilov & Bugdaeva 2000), North America (Crane & Upchurch 1987, Rydin et al. 2006, Friis et al. 2009), southern Australia (Krassilov et al. 1998), China (Yang et al. 2005), Portugal (Rydin et al. 2006, Friis et al. 2009) and Brazil (Maisey 1991, Martill 1993, Osborn et al. 1993, Rydin et al. 2003, Mohr et al. 2004, Mohr et al. 2007, Dilcher et al. 2005a,b, Kunzmann et al. 2009).

The Crato Formation is known for its diversity of fossil gnetophytes. Due to the excellent preservation of some of these fossils, anatomical details are preserved that are rarely seen in fossil material. In this article a new taxon *Friedsellowia* gen. nov. is described, including young plants with cotyledons plus specimens with microsporangiate and ovulate cones. This new taxon is analyzed in comparison with the three relic extant taxa, *Ephedra*, *Welwitschia* and *Gnetum*, and several fossil gnetalean taxa. Several specimens of seedlings with cotyledons and a first set of leaves belong also to *Friedsellowia* gen. nov. specimens that exhibit only vegetative parts (axes with attached leaves) are here described under the same genus and species name. This procedure is justified under the most recent International Code of Nomenclature for Algae, Fungi and Plants (Miller et al. 2011) since the leaves of *Friedsellowia* gen. nov. are very characteristic. Furthermore one young plant with roots and leaves bears also cones that are identical with the ones of adult *Friedsellowia* gen. nov. plants.

This new genus of gnetophytes *sensu stricto* most likely represents a new family. However, since only this one taxon is formally described, the circumscription of the family is unclear, and therefore we refrain from erecting a new family.



Text-fig. 1. Geography and geology of the Araripe Basin in northeastern Brazil, modified from Maisey (1991).

Geological setting

The described fossils are found mainly in open-air pits that are mined for calcareous limestone, commonly in use as building material. The plant fossils come from quarries south of the town of Nova Olinda near Santana do Cariri in the Araripe Basin in the northeast of Brazil (see Text-fig. 1). The basin is filled with Upper Jurassic to Cretaceous sediments during the opening of the Atlantic and the breakup of western Gondwana (Berthou 1990, Beurlen 1962). The Rio da Batateira Formation, Crato Formation, Ipubi Formation, Romualdo Formation and the Arajara Formation belong to the Araripe Group of Early Cretaceous age (Heimhofer et al. 2010). Stratigraphic index fossils and other geological markers are missing. Palynological studies reveal a late Aptian age (about 112–115 Ma) (Arai et al. 2001, Doyle 1992, Lima 1978, Neumann & Cabrera 1999, Pons et al. 1996, Batten 2007, Heimhofer & Hochuli 2010). According to sedimentological studies of these formations a change from freshwater to marine environments with a transgression, regression and the alternation of drought and flooding events has been postulated. This assumption is based on detailed analyses of the sediment components, structures and fossils (Martill & Heimhofer 2007).

The Crato Formation consists of thinly laminated limestone (Plattenkalk), with embedded thin layers of clay, silt and sandstone. Fine-grained sediments and non-oriented fossils suggest only very weak flows, occasionally even none at all. Marine environments can be excluded because of records of freshwater fish fossils; thus the Crato limestone was deposited in a freshwater lake. Wind and flooding events blew and washed animals and plants from the surrounding areas into the lake, so that a rich flora and fauna were preserved, including invertebrates and vertebrates (Maisey 1991, Martill 1993, Martill & Heimhofer 2007).

Crato flora

The Crato flora is one of the rare Early Cretaceaous floras of the low (palaeo)latitudes. About 80 taxa of plant megafossils are known from the Crato Formation. Ferns are common, but not diverse. Approximately 40 or more are gymnosperm taxa that include conifers, bennettitaleans, seed ferns and gnetophytes have been reported. About 30 angiosperm taxa (Batten 2007, Mohr et al. 2007) include Nymphaeales (Coiffard et al. 2013), magnolians, monocotyledons and eudicotyledons. Not only macrofossils but also spores and pollen are highly diverse (Lima 1978, Lima 1980, Lima 1989, Pons et al. 1990, Pons et al. 1996, Arai et al. 2001, Arai & Machado-Coelho 2001, Osborn et al. 1993).

Many gnetophyte fossils from the Crato Formation appear to be closely related to Ephedraceae or to Welwitschiaceae, but gnetophytes belonging to additional groups have been described as well (Mohr et al. 2007). *Cearania heterophylla* (Kunzmann et al. 2009) and *Cariria orbiculiconiformis*. (Kunzmann et al. 2011) are both taxa with gnetalean characters. *Welwitschiostrobus* (Dilcher et al. 2005a,b) and *Cratonia cotyledon* (Rydin et al. 2003), a seedling with broad cotyledons, belong most likely to a welwitschioid taxon. Taxa with clearly ephedroid characters are published informally under "unnamed group" (Mohr et al. 2007).

Material and methods

The fossil specimens described in this article are preserved as reddish brown impressions or petrifications (mostly iron oxide) on light yellow-brown to grey limestone slabs. The iron oxide that replaced the organic matter is very brittle and crumbly, so that epidermal cell structures are preserved only in rare cases.

Most fossils described in this study are housed in the palaeobotanical collections of the Museum of Natural History, Berlin (Germany). One of the specimens (FCr-78) is located at the palaeontological collection of the Geological Institute of the Free University Berlin, and one specimen is in private ownership (P1). Following UN recommendations the paratype is deposited in the country of origin (Brazil) and will be stored at the Geosciences Institute of the University of São Paulo (MB. Pb.1997/1292).

The fossils consist of four completely preserved specimens: the holotype MB.Pb.1999/544 (Plate 1, Fig. 1), the paratype MB.Pb.1997/1292 (Plate 1, Fig. 2), MB.Pb.1997/1294 (Plate 2, Figs 1, 2), two seedlings MB.Pb.1997/1226 and MB.Pb. 1998/690 (Plate 1, Figs 3, 4), and several incomplete specimens with terminal ovulate and microsporangiate cones, such as MB. Pb.1997/1283a, MB.Pb.1997/1210a, MB.Pb.1999/616, MB. Pb.1997/1288 and FCr-78 (Plate 3, Figs 1–5), MB.Pb.1999/506, MB.Pb.1999/2298a, MB.Pb.1999/515, MB.Pb.1999/2295 (Plate 4, Figs 1, 2, 5, 6), MB.Pb.1997/1293 (Plate 11), two dispersed microsporangiate cones MB.Pb.1999/530 and MB. Pb.2000/76 (Plate 4, Figs 3, 4) that belong with great certainty to *Friedsellowia* gen. nov. A single non-fertile branch with attached leaves is represented by specimen MB.Pb.2001/1466 (Plate 5, Fig. 1), another specimen P1 is figured only for details in leave structures (Plate 6, Fig. 7). In addition, two unfigured specimens aided our description.

All technical work was carried out at the Museum of Natural History Berlin. The macroscopic images were taken with Nikon D700 and Nikon D200 cameras, the microscopic images with a Leica DFC 425 camera at the Leica Wild M10 microscope and with a Leica DFC 495 camera at the Leica multifocus microscope Z16 APOA.

Specimens were directly mounted on stubs and sputtered for 100 seconds with Au/Pd on a BAL-TEC SCD 050 Sputter Coater. The SEM images are taken with a Jeol JSM-6300 and with a Jeol JSM-6610 at 15 kV. The images are edited with Adobe Photoshop 6.0.

Systematic description

Division Spermatophyta
Class Gnetophyta
Order Gnetales
Family unassigned

Genus *Friedsellowia* Löwe, Mohr, Coiffard,
Bernardes-de-Oliveira gen. nov.

Generic diagnosis: Branching plant, slender articulated axes, monoecious with microsporangiate and ovulate reproductive organs. In the juvenile state bearing two broad cotyledons. Adult plant with long, narrow lanceolate leaves, attached in whorls of usually four (or more?), but sometimes with two oppositely arranged leaves. Venation of cotyledons and leaves parallel with typical chevron type veins of higher order. Ovulate cone comprising several ovulate reproductive units, subtended by more than one set of scales. Ovulate structures in a whorled arrangement of two or four in the proximate part of the cone, or in an opposite-decussate arrangement (two units) in the distal part. Ovulate cones sessile with ca. 8–16 (or more) ovules/seeds. Microsporangiate cones small, sitting terminally on thin axes, similarly structured as ovulate cones with more and smaller scales.

Etymology: Named after the German botanist and explorer of southern Brazil Friedrich Sellow (1789–1831)

Type species: *Friedsellowia gracilifolia* Löwe, Mohr, Coiffard & Bernardes-de-Oliveira gen. nov. et sp. nov.

Friedsellowia gracifolia Löwe, Mohr, Coiffard &
Bernardes-de-Oliveira gen. nov. et sp. nov.

Specific diagnosis: Erect, branching plant. Habit dominated by long slender articulated axes. Adult leaves, attached usually as whorls of four or sometimes two at closely spaced nodes of side axes. Cotyledons more or less oval in shape, entire, with linear veins and obtuse tip and chevron type venation of higher order. Adult leaves entire, linear in shape with five to six parallel primary veins, between them three to four parallel secondary veins, sometimes with several chevrons and "braided" third order veins. Shape characteristically longer than wide with a length-width ratio of about 25:1. Cotyledons shorter and wider than the adult leaves with a length-width ratio of about 5:1. Ovulate cones sessile, subtended by four side axes, highly variable in size with few (4–6) to several (12–16) or more ovulate units, arranged proximally in whorls of four, distally in an opposite-decussate arrangement. Ovulate cones with several subtending leave-like bracts. Small microsporangiate cones terminally attached at side axes. Microsporangiate cones consisting of many microsporangiate units with several microsporangia, each producing polyplicate pollen.

Holotype: hic designatus. Specimen MB.Pb.1999/544

Paratype: hic designatus. Specimen MB.Pb.1997/1292

Repository: Museum of Natural History, Palaeobotanical Collections, Berlin, Germany and the Institute of Geoscience, University of Sao Paulo, Brazil.

Type locality: Open air pit south of Nova Olinda near Santana do Cariri, State of Ceará, Brazil.

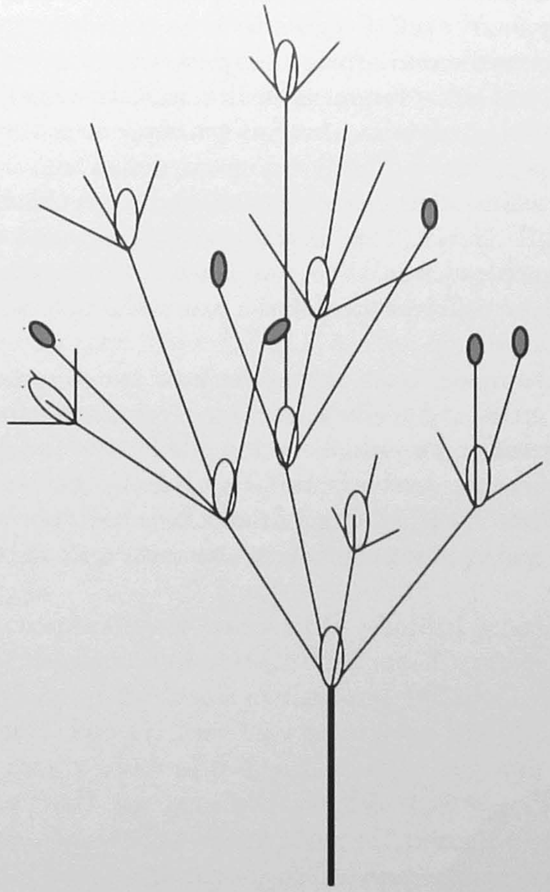
Type stratum: Crato Formation, Araripe Basin,

Etymology: Translated from Latin, meaning "thin leaves".

General description

Axes and roots: The main axis of *Friedsellowia* gen. nov. grew straight upright and reached more than 1 m in height. The conclusion is based on the size of a specimen (MB.Pb.1997/1293; Plate 11) that represents approximately the upper third of a plant, that reaches already more than 40 cm in high. In nearly complete, but not fully-grown plants, the main axis is about 23–25 cm long. The width remains roughly constant over the entire length, in the lower part the maximum width is about 2.8 mm and to the top the axis narrows to 1.5 mm.

The plants branch after a short phase of growth and four side branches are produced that bear leaves. The main axis displays then a very elongated growth pattern. Usually four side branches subtend a central ovulate cone, arising from nodes directly beneath the base of the cone. These side branches may develop a second set of side branches and so on. Small microsporangiate cones sit at the terminal positions. So *Friedsellowia* gen. nov. shows clearly a sympodial growth pattern (see Text-fig. 2).



Text-fig. 2. Habit of the reproductive parts of *Friedsellowia* gen. nov. and arrangement of ovulate and microsporangiate cones; the thick black line represents the main axis, thin lines side branches, white ellipsoids the ovulate cones, grey ellipsoids the microsporangiate cones; constructed with LibreOffice Draw.

The axis seems to be strengthened by a thick outer wall (Plate 5, Fig. 3). The axis is clearly thickened at the nodes where side axes branch off. Sometimes nodes are thickened without side axes, but show a scar of a branch (Plate 5, Fig. 4). Below a terminal cone, the axis appears to grow "barrel shaped" (Plate 5, Figs 5, 7). Usually more than two, generally four secondary axes that subtend a (terminal) ovulate cone (Plate 5, Figs 6, 7), may bear microsporangiate cones (holotype Plate 1, Fig. 1; Plate 3, Figs 1, 2).

Anatomical observations (SEM) on the axes of the specimens MB.Pb.1997/1292 and MB. Pb.1999/2295 show tracheids with slightly sunken circular bordered pits that do not touch each other. They are arranged in single and double rows and have round to slightly oval small openings (Plate 6, Figs 1–3).

Two seedlings and a young plant are preserved with roots and seeds (Plate 1, Figs 3, 4; Plate 2, Figs 1, 2; Plate 5, Fig. 2). The roots are about 5–12 cm long, about 2–3 mm in diameter without branching. The primary root may be nearly straight, sometimes also slightly twisted.

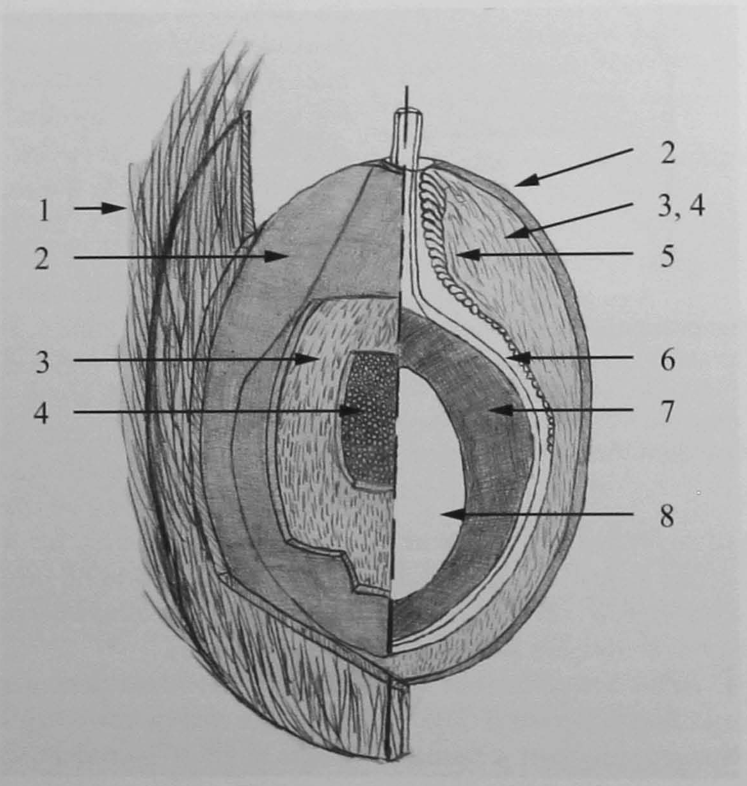
Seedlings: The seedlings that comprise the seed from which the young plant started, the primary root, the hypocotyl, the cotyledons and (three) whorls of four regular leaves are visible in MB.Pb.1998/690 and MB.Pb.1997/1226 (Plate 1, Figs 3, 4), in this case 14 leaves. The overall size of these young plants is approximately 16–20 cm. The seed (three-dimensionally preserved) from which the plant originates, is approximately 5–6 mm in length and 3–4 mm in width, and thus comparable with the ovules in the mature ovulate cones. The hypocotyl is approx. 3–6(?) cm in length, in one very well preserved specimen (MB. Pb.1998/690), 4 cm in length. At the base the cotyledons are united to create a cotyledonary tube. The primary root is slightly twisting and seems to have just a few very thin lateral rootlets. Near the spot where the root and the hypocotyledon grew out of the seed, an extended leafy(?) area is seen, but poorly preserved so that it is not clear, if a "feeder" was originally present (Plate 5, Fig. 2). Each of the two seedlings shows two entire and slightly ovate to linear-spatulate cotyledons with an obtuse tip (Plate 6, Fig. 4). They have an average length of 24–33 mm and a width of 0.3–6.3 mm, resulting in a length-width ratio of about 5:1. Thus they are much wider than the normal (adult) leaves (Plate 6, Fig. 5). The venation of 10–12 veins extends from the cuneate base of the leaf, running parallel to the tip after the leaf reaches its full width (Plate 6, Fig. 4). The parallel running (first order) veins are closely spaced. They are connected by short chevron like veins (Plate 6, Fig. 8).

Leaves: The linear lanceolate and entire margined leaves are narrow and long. On average, they reach a length of 25–67 mm and a width of 2.7 mm, resulting in a length-width ratio of about 25:1. They have a cuneate base and an obtuse tip (Plate 6, Fig. 5). The leaves are attached at nodes usually more than two per node, generally 4 or even more(?) (Plate 1, Figs 1, 2; Plate 2, Figs 1, 2; Plate 5, Fig. 1). The nodes are closely spaced on foliage shoots, so that these lateral axes appear to be densely leafy (Plate 6, Fig. 6). In the juvenile stage, the leaves sit directly below the growing point at the top of the main axis (Plate 1, Figs 3, 4). All leaves show a distinct parallel venation of five to six primary veins, in between them three to four parallel secondary veins, sometimes with chevrons, partly in a "braided" arrangement (Plate 6, Fig. 7). Stomata are poorly preserved, and seem to be arranged in single, not well defined rows between the primary veins; however, details of size and shape of the stomata cannot be determined.

Reproductive structures

Ovulate cones sit terminally attached on axes (Plate 7, 8; Plate 12, Figs 2–4) with lengths of about 16–20 (25) mm and widths of 5–8 mm. The cone size varies with maturity and with life stage of the plant – older plants seem to produce bigger cones. They are elongated oval in shape, more rounded at the base, tapering at the top. The whole cone-complex seems to be subtended by more than one sets (of four?) elongated leaf-like bracts (Plate, 7 Fig. 6). Each cone bears commonly 8–16 ovulate reproductive units (ovules), arranged in three to four or more whorls. Each whorl consists of either four or in small cones two ovules (at the distal part) in an alternating arrangement. Only one specimen (FCr-78) has more ovules and 1–2 more whorls than all the other studied cones (Plate 8, Figs 1, 2). But the cone structure and arrangement are in principle identical. It is possible that this specimen is either a different species or a plant in a more adult stage.

The ovules seem to bear at least two whorls of outer scales, and possibly a set of inner scales that form (?together) an envelope covering the inner ovulate structure completely (Plate 7, Figs 1, 2; Plate 8, Figs 3, 4, 6; Plate 9, Fig. 2). One of the outer whorls of these scales is very fibrous and the scales create a near complete cover of the cone with a dense bundle of fibers at the top of the cone (Plate 9, Fig. 1; Plate 12, Figs 2, 3). When the cones are split open, the outer fibrous scales are well visible, as well as the inner set of scales (see Text-fig. 3). These scales have a smooth shiny surface under the light microscope (e. g. Plate 8, Figs 3, 6) and differ in the original arrangement of the cells and in the fossilized stage in color (Plate 9, Fig. 3). The seed envelope is visible as a layer with inner papillae (Plate 9, Figs 5, 6). This seed envelope covers the straight micropylar tube (Plate 9, Figs 2, 4). The micropylar tube formed by the integument that covers the nucellus is also visible.



Text-fig. 3. Reconstruction of scales (bracts) and envelopes of an ovulate reproductive unit of *Friedsellowia* gen. nov. (without dimensions). Drawing based on fossil material of *Friedsellowia* gen. nov. and extant material of *E. distachya* and *Ephedra foeminea* (Rydin et al. 2010), using photographs and drawings. Left side: drawing based on fossil material/photographs (Plate. 5, Fig. 2, and Plate 9, Figs 1–3). Right side: reconstruction of an ovule.
Explanations: **1.** Scale (bract), consisting of long fibers covering the complete cone, obscuring individual ovules (see Plate 7, Figs 1–3). **2.** Outer scale (bract) of the ovule with smooth (black shiny) surface (see Plate 8, Figs 3 and 6). **3.** Seed envelope consisting of short (reddish-brown) fibers, and papillate cell structures near the micropylar tube. **4.** (Black) Isometric cells most likely belonging to the inner epidermis of the seed envelope (Plate 9, Figs 3, 5, 6). **5.** Area with elongated densely packed papillae **6.** Integument covering the complete nucellus and forming the micropylar tube. **7.** Nucellus, best seen in the seed of one seedling (MB.Pb.1997/1226; Plate 1, Fig. 3 and Plate 5, Fig. 2). **8.** Gametophyte.

Seed: In one of the two seedlings and in one young plant fragments of the actual seed are preserved (Plate 5, Fig. 2). The seed is about 6 mm long and 3 mm wide, oval in shape, rounded at the base and tapering at the top.

Microsporangiate cones sit in terminal position on narrow side axes that arise from nodes directly beneath the base of the sessile ovulate cones (Plate 1, Fig. 3; Plate 3, Fig. 1). They have an average length of 15–20 mm, a width of 6–8 mm, and (mostly very badly preserved) are generally smaller than the ovulate cones. Somewhat better preserved microsporangiate cones have an elongated oval shape, with a rounded base and top (Plate 10, Figs 1, 2).

These cones exhibit more and smaller scales than those of the ovulate cones. At the base a set of outer scales may be visible. The individual cone scales that sit in 6–8 whorls are about 4 mm long and 1.5–1.7 mm broad. There may be up to eight scales per whorl, overall 48–64 individual scales per cone are visible. Microsporangia growing behind these scales show bilobed microsporangia (Plate 10, Figs 1–6), bearing inside two pollen sacs with *in situ* pollen. The number of microsporangia per scale and also their arrangement are not clear, but the microsporangia seem to be not fused to form an antherophore. When mature, the pollen sacs open slit-like with a single dehiscence zone.

By studying samples of these microsporangiate cones under the SEM, cell structures from several tissues of the microsporophylls (Plate 10, Figs 7–9) were identified. Elongated oval shaped pollen grains (Plate 10, Figs 10–12) *in situ* are 40–50 µm in length and 15–25 µm in width, with slightly pointed tips. They are polyplicate and seem to be inaperturate, the psilate surface of the pollen exhibits a zigzag course of the grooves between the plications.

Comparisons with extant and extinct Gnetales

Comparison with extant Gnetales

Today there exist only three families of Gnetales: Gnetaceae, Ephedraceae and Welwitschiaceae. They differ significantly in their morphology (Kubitzki 1990), their reproductive strategy (Friedman & Carmichael 1996) and chloroplast genomes (Wu et al. 2009). But they have also some important similarities in their articulate growth mode, opposite decussate arrangement of (partly) reduced leaves and separated microsporangiate and ovulate cones. They share common features in their wood anatomy, for example, the arrangement and development of gymnosperm bordered pits in the vascular bundles that are arranged in single or double longitudinal rows and characteristic perforation plates (Carlquist 1996).

Gnetum appears as a shrub or liana, as well as a tree. Long axes are articulated. Minor axes branch at nodes, where the leaves are also attached in opposite-decussate mode. The leaves are broad oval in shape and share with flowering plants a reticulate venation. The ovulate reproductive organs are elongated structures without a cone-like habit. The ovules are radially symmetrical and the seeds are enclosed in a fleshy, brightly coloured envelope (Kubitzki 1990).

Welwitschia consists of a large taproot and a short stem from which only two large and long strap-shaped leaves grow above the ground. The leaves have parallel veins; the cotyledons show a typical chevron shaped secondary venation. *Welwitschia* is dioecious. Male and female cones bear many reproductive units (Kubitzki 1990).

Ephedra is a branched, shrub-like plant, rarely a clambering vine or small tree, with long articulated longitudinally grooved axes. Additional axes branch off at nodes. Reduced scale-like leaves are opposite or whorled and fused basally into a sheath. Small cones with opposite decussately arranged bracts in two to ten whorls sit on smaller and much shorter axes. The (reduced) leaves have only a set of two (or three), in one species (*Ephedra foliata*) up to three parallel primary veins. The cones are composed of whorled strobili. The primary root is considered to be a tap-root (Martens 1971, Kubitzki 1990).

Gnetum differs clearly from *Friedsellowia* gen. nov. in growth form, leaf shape and venation pattern as well as in the organization of the reproductive organs, and the pollen type does not match the characters of *Friedsellowia* gen. nov.

Welwitschia differs in various aspects from *Friedsellowia* gen. nov. The latter does not have the extremely specialized set of two very large leaves as seen in *Welwitschia*, but shares the general parallel venation and the "braided" pattern of *Welwitschia's* cotyledons and in its leaves, cones with several reproductive units and possibly a feeder at the germinating stage (Pearson 1929) and possibly sulcate pollen. The reproductive structures of *Welwitschia* are in a dichasial arrangement, cones are usually in groups of two or more, but *Friedsellowia* gen. nov. has terminal single cones. The flowering structure of *Welwitschia* includes staminate and ovulate parts that are combined in a strobilus (though only one sex is functional) which is not the case in *Friedsellowia* gen. nov. Also the wing-like fused bracts seen in *Welwitschia's* ovulate units seem to be not present. Generally spoken, *Friedsellowia* gen. nov. and *Welwitschia* share cone structures with many reproductive units per cone, a character that had been hypothesized by Mundry & Stützel (2009) as being basal for gnetophytes.

Ephedra and *Friedsellowia* gen. nov. differ in several aspects but share also many features. Most species of *Ephedra* have highly reduced leaves, but in *Ephedra foliata* Boiss. leaves are not as reduced and grow in whorls of two, three or four (Deshpande & Keswani 1963). The leaves may also differ in shape on a single plant. In the lower parts of the plant the leaves are longer. In general, both *Ephedra* and *Friedsellowia* gen. nov. share the parallel primary venation, even though it is highly reduced in *Ephedra*. Interesting is also the fact that the cotyledons in *Ephedra foliata* Boiss. remain intact for several months and are sturdy, even when the plant has grown already normal leaves (Deshpande & Keswani 1963). This growth pattern is seen also in *Friedsellowia* gen. nov.

Ephedra and *Friedsellowia* gen. nov. share also the principal cone structures. Both have microsporangiate and ovulate cones that grow on one plant in *Friedsellowia* gen. nov. The number of ovulate reproductive units per cone is relatively high in *Friedsellowia* gen. nov., in *Ephedra* the number is only two to four. However, the general morphology of the ovulate strobilus is very similar. The microsporangiate cones of *Friedsellowia* gen. nov. most likely do not have antherophores, as developed in *Ephedra*. In any case the pollen sacs in *Friedsellowia* gen. nov. are free, but share the bilobed pollen sacs and the horizontal slit-like opening with *Ephedra*. The pollen in *Friedsellowia* gen. nov. is similar in shape, size and surface to the pollen of several *Ephedra* species with its zigzag course of the grooves between the plications, a sulcus might have been present, as seen in *Welwitschia* but this feature is not really visible.

Detailed anatomical studies of microsporangiate and ovulate cones from extant *Ephedra distachya* show clearly some similarities with the microsporangiate and ovulate cones of *Friedsellowia* gen. nov. (Yang 2004, Rydin et al. 2010). A schematic reconstruction (see Text-fig. 3) of a median longitudinal section of an ovulate unit of *Friedsellowia* gen. nov. is very well comparable with the median longitudinal section of a female cone of *Ephedra foeminea*, depicted by Rydin et al. (2010).

Comparison with extinct gnetophytes

Many gnetalean fossil remains, such as ephedroid seeds, sterile parts of ephedroids and obscure reproductive structures have been described in the literature, and are not discussed here because of their incomplete nature (e.g. Rydin et al. 2006). Only two of these fossils are mentioned here, *Cratonia*, a seedling with welwitschioid features (Rydin et al. 2003) and *Eoanthus*. *Cratonia* shares the basic broad oval form of the cotyledons and the general venation pattern with those of the seedlings of *Friedsellowia* gen. nov. that have several parallel first order veins, and chevron shaped secondary veins (Plate 6, Fig. 8). There might have been also a feeder in *Friedsellowia* gen. nov. Even though both are in principle very similar, the difference between the two taxa is obvious; the overall size of *Cratonia* is bigger than the seedling of *Friedsellowia* gen. nov., and the overall shape of *Cratonia's* cotyledons is much broader than the shape of the cotyledons of *Friedsellowia* gen. nov.

Eoanthus specimens consist of four ovule–bearing structures in whorls around a central axis that is subtended by a whorl of sterile bracts (Krassilov 1986). However, *Eoanthus* is very poorly preserved so that a comparison between *Friedsellowia* gen. nov. and *Eoanthus* is not really possible, except for the shared character of whorls of four ovule bearing units.

Among the more complete extinct gnetalean plants are those that share many general characters with extant Gnetales, but do not belong to the gnetophyte families as defined by the character sets of the three extant members *Ephedra*, *Welwitschia* and *Gnetum*. A second group shares many characters with extant Ephedraceae and/or with Welwitschiaceae. So far only a single taxon has been described that may also

have similarities with *Gnetum* based on its reproductive ovulate structure (Rydin & Friis 2010).

The Early Cretaceous *Siphonospermum simplex* (Rydin & Friis 2010) from China shares some characters with extant *Gnetum*. *Siphonospermum* has ovulate reproductive organs that are arranged in units of three. This is in clear contrast to *Friedsellowia* gen. nov. with its well-developed cones with several whorls of two or four reproductive units. Therefore *Siphonospermum* and *Friedsellowia* gen. nov. may not belong to the same subclade of gnetophytes.

Cearania shares several characters with gnetophytes, including the oppositely arranged parallel veined leaves with paracytic stomata arranged in rows (Kunzmann et al. 2009), but may be not part of the crown group Gnetales. Also the single terminally attached ovulate and microsporangiate reproductive structures do have some similarity with gnetalean cones/strobili.

Cariria orbiculiconiformis (Kunzmann et al. 2011) exhibits an overall growth form that is clearly gnetalean. It has an articulated habit, longitudinally grooved axes, terminal, stipitate ovulate and microsporangiate reproductive organs arranged in a dichasium, a growth form that is not unique in the fossil record of gnetophytes (e. g. *Drewria*, see below). The plant is branching profusely. Leaves sit oppositely arranged. The leaves show parallel primary venation possibly several veins of higher order. The microsporangiate organs are unusual for gnetalean plants. They are basket like with upright standing pollen-bearing organs. In principle, the slender long-jointed stems, the oppositely arranged leaves and parallel leaf veins are comparable with *Friedsellowia* gen. nov. However, the microsporangiate and ovulate organs are quite different, even though both share some features such as clearly developed micropylar tubes.

Gurvanella (Krassilov 1982, Krassilov et al. 2004) and/or the related taxon *Chaoyangia liangii* (Sun et al. 1998), an early Cretaceous plant fossil from China and Mongolia, is generally interpreted as a gnetophyte except by Duan (1998) and Wang (2010). This taxon shows some remarkable similarities with other fossil gnetophytes in its general habit, but especially with respect to the morphology of microsporangiate and ovulate reproductive structures. The plant exhibits striate stems, nodal architecture and small narrow leaves in an opposite-decussate arrangement. The latter are only fragmentarily preserved, but have clearly visible parallel primary and less obvious "braided" secondary venation with partially chevrons (see Wang 2010). The reproductive structures consist of terminally attached well developed ovulate cones (Krassilov 1982, Duan 1998, Wang 2010) and microsporangiate structures that possibly belong to this plant (Wang 2010), but are not directly attached. Nearly ball-shaped ovulate reproductive organs consist of three to four seeds enclosed by two sets of scales: the inner one is a thick envelope, the outer one consists of probably two scales forming a thin fibrous envelope, which decomposed in the mature state leaving behind a hairy/fuzzy outer envelope of the seeds plus thick seed coats. Poorly preserved nearly "bowl-shaped" microsporangiate structures are subtended by scales. These structures include pillar-like components with most likely two pollen sacs. These contain boat-shaped monocolpate possibly smooth pollen grains. The connection between ovulate and microsporangiate cones is not clear and thus the arrangement of the reproductive structures in a dichasium is not certain, but possible. Overall the reproductive structures, especially the microsporangiate ones, are similar to the reproductive structures of *Cariria*. In contrast to *Chaoyangia* the cones of *Friedsellowia* gen. nov. have longer axes and several whorls and/or pairs of scales plus ovules. Especially the microsporangiate organs of *Chaoyangia* differ fundamentally from *Friedsellowia* gen. nov. The latter have a general appearance comparable to recent *Ephedra* and/or *Welwitschia*, while the "bowl-shaped" structure in *Chaoyangia* is not found in recent gnetophytes, but perhaps occurs in fossil *Cariria*. Also the pollen of *Chaoyangia* is clearly not ephedroid or welwitschioid, but smooth.

Fossil ephedroid taxa comprise several genera from Russia/Siberia, Mongolia, China and Portugal. The Chinese taxa include *Liaoxia*/*Ephedra cheniae* (Rydin et al. 2006), *Ephedra archaeorhytidosperma* (Yang et al. 2005), and *Alloephedra*/*Ephedra* (Tao & Yang 2003); see also Liu et al. (2008) for taxonomic discussion.

Liaoxia (*Ephedra*) *cheniae* is articulate with slender striate stems. Lateral branches are axillary, the leaves are thin and membranous, linear to lanceolate with an acute apex and two veins, and borne in an opposite arrangement. A pair of small scales arises between leaves and branches at stem nodes. Cones are sessile or stipitate, either terminally attached on stems and branches or sitting in the axils of leaves. Ovules plus bracts are arranged decussately. *Friedsellowia* gen. nov. shares with *Liaoxia* the articulated growth form, but has far less reduced leaves. Cones of *Friedsellowia* gen. nov. are always sessile and the scales (bracts) surround the ovulate organs more or less completely, thus creating a more or less closed cone like structure.

The stems of *Ephedra archaeorhytidosperma* (Yang et al. 2005) are articulated. Two reduced narrow leaves with parallel first order veins sit in an opposite arrangement at the nodes. In addition, minor axes branch off from these nodes. Cones with one or two seeds are attached terminally, surrounded by two pairs of incomplete bracts. The ovulate organ exhibits a micropylar tube.

Alloephedra/Ephedra xingxuei is described as an erect herbaceous plant with articulate finely striated stems, leaves inserted at nodes, triangular to ovate in shape and highly reduced. Only ovulate cones are preserved. Ovulate organs are stipitate, possibly with two pairs of decussate and opposite, connate scales (at the lower half), and with one to two ovules per cone. *Alloephedra/Ephedra xingxuei* is overall poorly preserved, but possibly very closely related to the Chinese taxon *Ephedra archaeorhytidosperma*. Unfortunately no differential diagnosis has been given.

Ephedra archaeorhytidosperma shares with *Friedsellowia* gen. nov. the overall habit, narrow parallel veined leaves and the terminal arrangement of the cones. *Friedsellowia* gen. nov. has well developed leaves with three orders of veins plus cones with several sets of ovules and is thus quite different from *E. archaeorhytidosperma*.

Drewria potomacensis (Crane & Upchurch 1987), from North America, represents a welwitschioid taxon. The articulated, narrow axes branch off at nodes, subtended by opposite and decussately arranged leaves. The leaves are long, narrow, and oval with a round tip and have about two primary veins with chevron shaped secondary/tertiary venation. A triplet (dichasium) of cone(-like) reproductive organs sits terminally on the axes. The cones consist of several whorls of bracts creating a seed cone. About eight to twelve reproductive units, containing seeds with visible micropylar tubes, are present. Consistent with *Friedsellowia* gen. nov. are the articulate construction of the plant, the venation pattern of leaves with primary, secondary and chevron like third order venation and the dichasial arrangement and sympodial growth pattern of the reproductive structures. The basic construction of the individual sessile terminal cones of *Drewria* also shows similarity with *Friedsellowia* gen. nov. in which the seeds are surrounded by several pairs of bracts.

To conclude: in terms of gross morphology several fossil taxa share characters with *Friedsellowia* gen. nov., *Drewria* matches the characters of *Friedsellowia* gen. nov. best, but is distinct in overall gross morphology of the reproductive units.

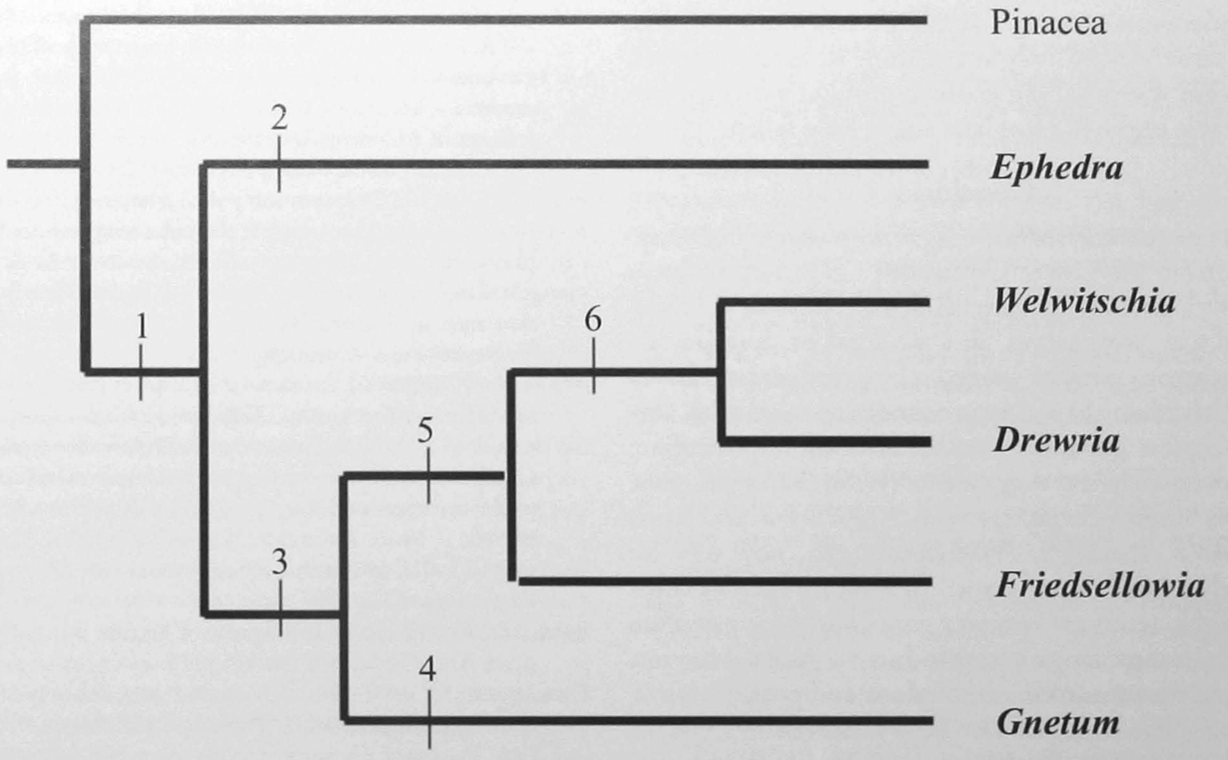
Phylogeny

A phylogenetic analysis was performed by adding the characters of the fossil taxa to a phylogenetic data set of Gnetales based on vegetative and reproductive characteristics. The original analysis included the three living taxa and several fossil taxa plus *Friedsellowia* gen. nov. Maximum parsimony analyses were conducted using PAUP* version 4.0b10 (Swofford 1999). However, after several runs the trees obtained, turned out to be too unstable and ultimately unresolved. Therefore we did not use these trees in this paper. However, when using character optimization on a hypothesized topology *Friedsellowia* gen. nov. shows a sister relationship with a clade comprising *Welwitschia* and *Drewria* (see Text-fig. 4). The topology is based on the molecular studies of Zhong et al. (2010). The diagram shows a sister relationship between *Ephedra* and all the other gnetalean taxa. *Gnetum* is sister to a clade which includes *Friedsellowia* gen. nov. and *Welwitschia* plus *Drewria*.

Ecological considerations

Friedsellowia gen. nov. was a shrub-like plant, most likely more than a meter in height, with robust axes and elongated internodes. Considering the size of the plant, it had overall only a few narrow leaves attached at lower side axes; the upper parts of the main axis was apparently without leaves. A strongly developed main root anchored the plant in the ground. Several cone scales cover the seeds in a relatively thick envelope-like manner. These characters may be interpreted as adaptations to open sunny habitats and possibly (seasonal) low precipitation. The sparse foliage and the leaf shape are interpreted as protections against overheating and water loss by reducing the leaf surface. Also the multilayered seed envelopes may be considered to represent a protection against dehydration. The strong primary root held the plant in the soil, and was especially well suited to supply seedlings and young plants quickly with the much–needed water.

Possibly *Friedsellowia* gen. nov. grew in sunny open environments not far from the shore, since remains of *Friedsellowia* gen. nov. are relatively common in the Crato sediments. Plants in such shore environments may produce grass-like leaves. Thus *Friedsellowia* gen. nov. may be ecologically comparable to modern reed, growing close to the lake shore.



Text-fig. 4. Character optimization on the hypothesized topology. Characters: **1.** Gnetalean articulated habit, cones with many ovulate and microsporangiate units, polyplicate pollen. **2.** Reduction of leaves and number of (ovulate) reproductive units per cone. **3.** Presence of a feeder. **4.** Globular pollen, leaves with reticulate venation. **5.** Leaves with chevron shaped secondary venation. **6.** Polyplicate pollen with sulcus.

Two additional ecological interpretations should be also discussed. *Friedsellowia* gen. nov. may have been a (partly) submerged aquatic plant (hydrophyte) growing in shallow water. The latter idea may stem from the fact that remains are rather common in the sediments of the former Crato Lake. In addition, the cone bearing axes are clearly elevated compared to the lower leaf bearing axes and the latter might have grown below the water surface. However, the interpretation of *Friedsellowia* gen. nov. as a hydrophyte is not convincing, since aquatic plants have normally creeping rhizomes and either large floating lamina or submerged dissected leaves. The axes of hydrophytes were usually not stiff (woody??); in any case they do not break in a brittle manner as *Friedsellowia* gen. nov. did. Furthermore, the nature of the leaves (thick and coriaceous versus thin and floating) is not clear and also the stomatal distribution cannot be determined. Floating leaves would be clearly epistomatic, but this character has not been convincingly demonstrated in *Friedsellowia* gen. nov. Furthermore the strong downward growing root of *Friedsellowia's* is not well suited to fixate the plant in a waterlogged substrate. In this case young plants may have been easily swept away under rainy, stormy conditions and/or flooding events. A third possibility, to interpret *Friedsellowia* gen. nov. as a liana-like climbing plant or a spreading climber/crambler can be ruled out. In the first case, the plant would grow specific organs for an attachment. In the second case *Friedsellowia* gen. nov. would be certainly not as stiff in its appearance but would have developed pliable stems resulting in an arching habit and would have used bristles and spines for clinging on other plants. Geological data from the Crato Formation and paleo-geographical data of the early Cretaceous confirm a warm and seasonally dry climate in the lower latitudes (Doyle et al. 1982, Chumakov et al. 1995, Ziegler et al. 2003) (the Araripe Basin being about 15 degrees south). Today extant Gnetales, especially *Ephedra* (and *Welwitschia* in a desert environment) live in habitats with similar climatic conditions and *Friedsellowia*'s characters may be best interpreted in the same way, namely adaptations to sunny habitats, possibly withstanding seasonal drought when the water table of the (Crato) lake might have fallen.

Conclusions

The new taxon *Friedsellowia gracilifolia* gen. nov. et sp. nov. from the Lower Cretaceous Crato Formation is clearly a gnetophyte. Several characters, such as articulated axes with leaves, in a whorled or opposite arrangement, parallel veined elongated entire leaves with chevron shaped interconnections and with several typical gnetalean ovulate and microsporangiate cones confirm the assignment. *Friedsellowia* gen. nov. shares several characters with *Welwitschia* and fossil *Drewria.* Therefore, *Friedsellowia* gen. nov. may be closely related (sister taxon) to *Welwitschia*, the common characters are complex cones with many ovulate and microsporangiate reproductive units, chevron shaped venation of the cotyledons and possibly also a feeder. (The latter has not been observed in *Drewria* because seedlings were not preserved.) The overall habit with its sparce narrow leaves and the development of pronounced primary roots of *Friedsellowia* gen. nov. are best interpreted as adaptations for warm and seasonally dry climate and/or in sunny environments close to the lake shore, possibly comparable with modern reed.

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Plates 1–12 and explanation of plates

Plate 1

Four nearly complete specimens of *Friedsellowia gracilifolia* gen. nov. et sp. nov.

Fig. 1. Young plant with root, leaves, axes and terminal ovulate and poorly preserved putative young microsporangiate cones (mc, see arrows) (holotype MB.Pb.1999/544).
Fig. 2. Young plant with leaves, articulated axes and terminal ovulate cones (paratype MB.Pb.1997/1292).
Fig. 3. Seedling with seed, root, two cotyledons and first sets of young leaves (MB.Pb.1997/1226).
Fig. 4. Seedling with root, two cotyledons and first sets of young leaves (MB.Pb.1998/690).

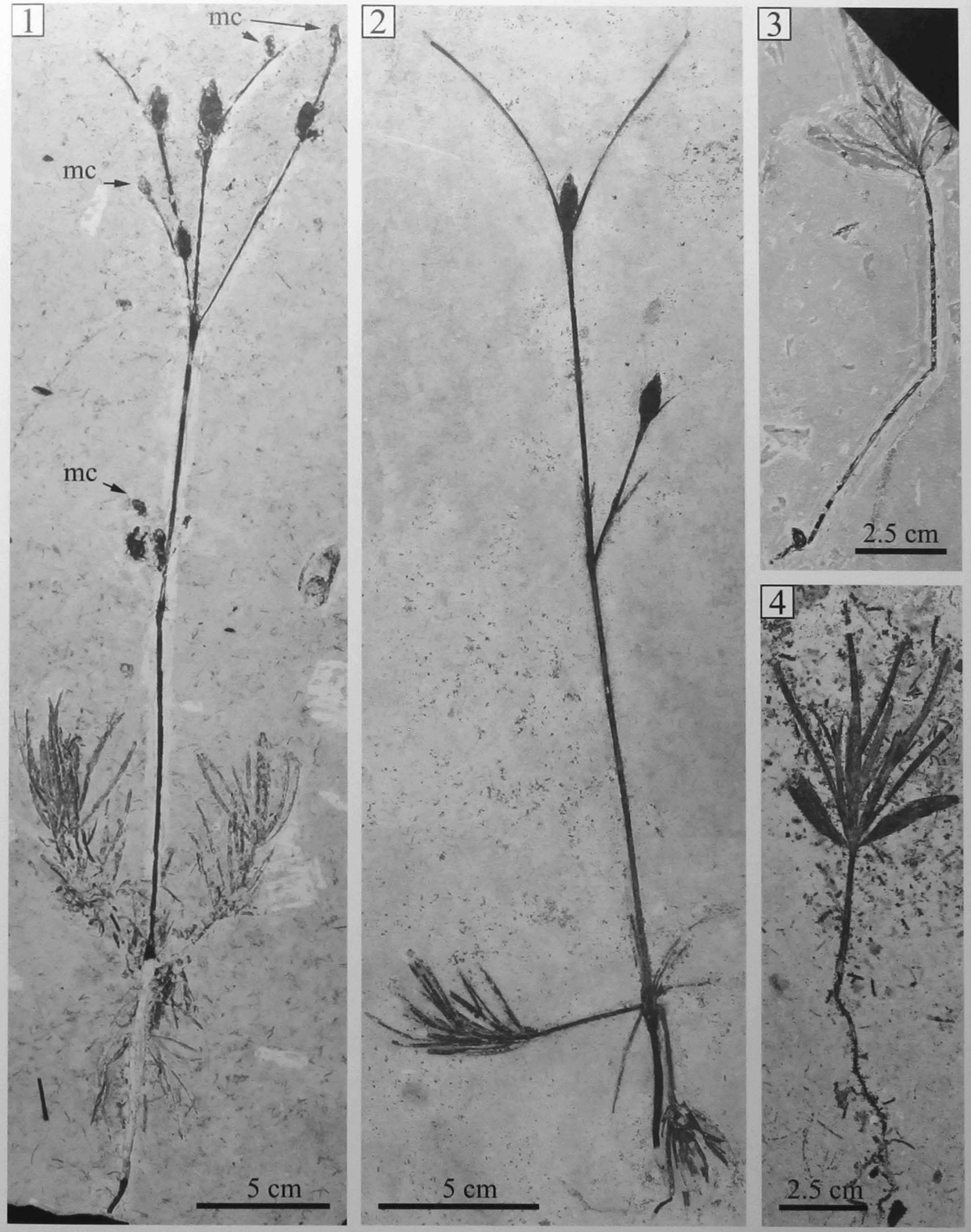

Plate 1. Löwe et al.: *Friedsellowia gracilifolia*, a new gnetophyte from Brazil.

Plate 2

Nearly complete specimen of *Friedsellowia gracilifolia* gen. nov. et sp. nov.

Fig. 1. Young plant with seed, root, leaves, axes and terminal ovulate cones (MB.Pb.1997/1294a).
Fig. 2. MB.Pb.1997/1294b counterpart.

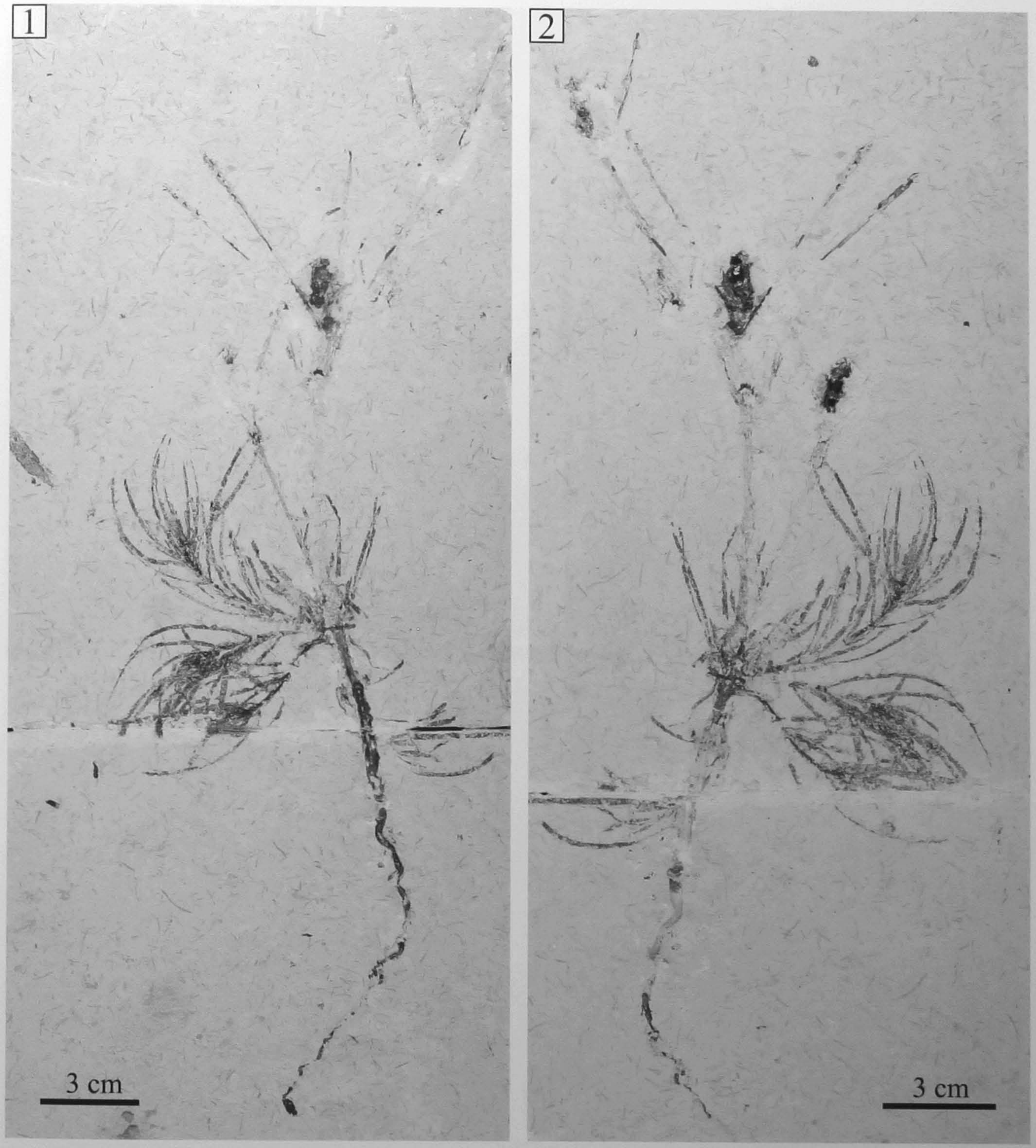

Plate 2. Löwe et al.: *Friedsellowia gracilifolia*, a new gnetophyte from Brazil.

Plate 3

Incomplete specimens of *Friedsellowia gracilifolia* gen. nov. et sp. nov.

Fig. 1. Main axis and side axes with terminal ovulate and microsporangiate cones (mc), see arrows (MB.Pb.1997/1283a).
Fig. 2. Branching axes from the main axis, bearing axillary ovulate and microsporangiate cones (mc), see arrows (MB. Pb.1997/1210a).
Fig. 3. Branching main axis with two terminal cones (MB.Pb.1999/616).
Fig. 4. Articulate main axis, side branches and terminally attached ovulate cones (MB.Pb.1997/1288).
Fig. 5. Specimen with three elongated ovulate cones (FCr-78).

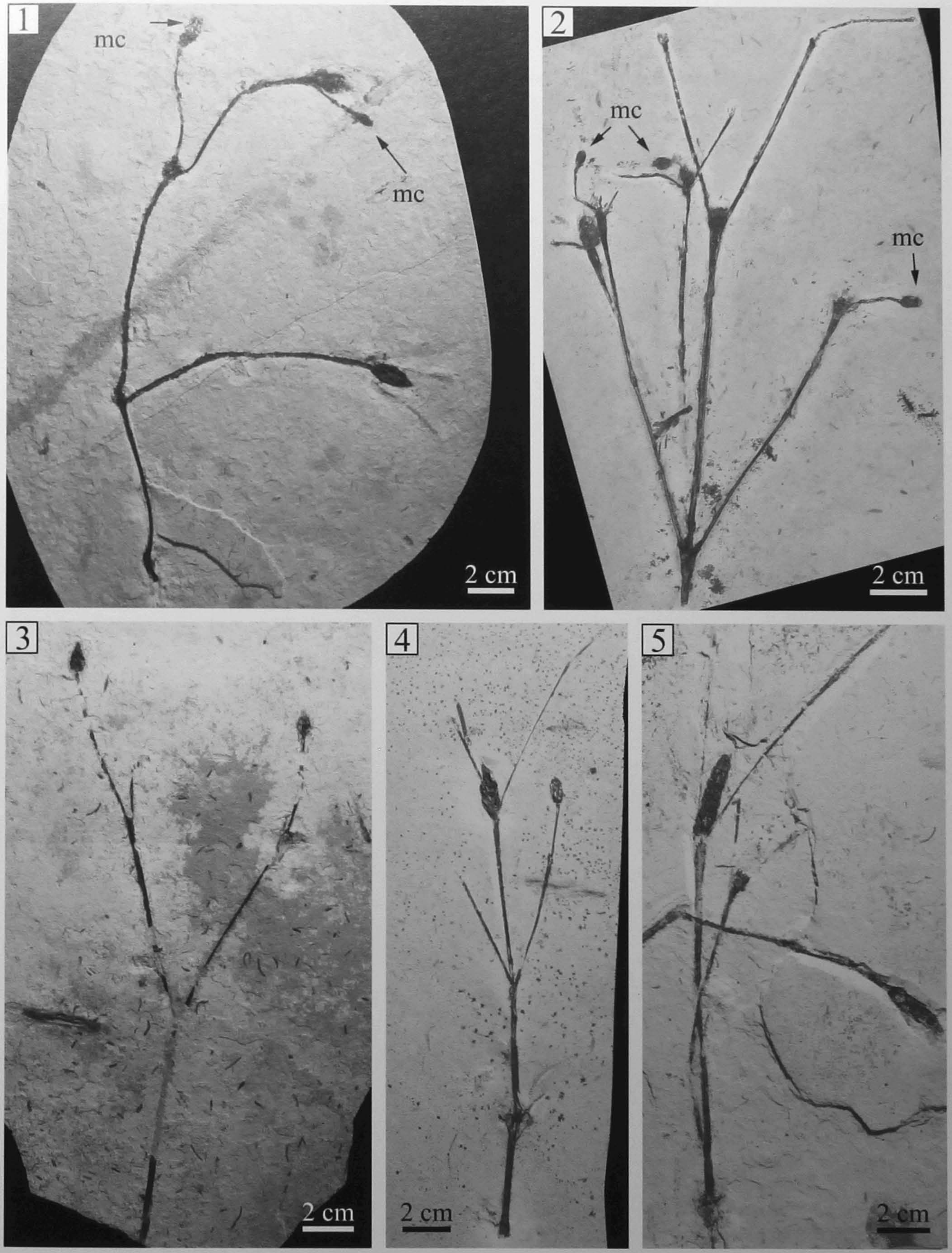

Plate 3. Löwe et al.: *Friedsellowia gracilifolia*, a new gnetophyte from Brazil.

Plate 4

Incomplete specimens of *Friedsellowia gracilifolia* gen. nov. et sp. nov.

Fig. 1.	Terminal ovulate cone with scales and two poorly preserved ?microsporangiate cones (MB.Pb.1999/506).
Fig. 2.	Two terminal cones, one ovulate cone with visible scales and two thin branching axes (MB.Pb.1999/2298a).
Fig. 3.	Dispersed microsporangiate cone with relatively small outer scales and microsporangia (MB.Pb.1999/530).
Fig. 4.	Dispersed microsporangiate cone with very well preserved microsporangia (MB.Pb.2000/76).
Fig. 5.	Terminal ovulate cone with two side axes (MB.Pb.1999/515).
Fig. 6.	Terminal ovulate cone with well developed first set of scales (MB.Pb.1999/2295).

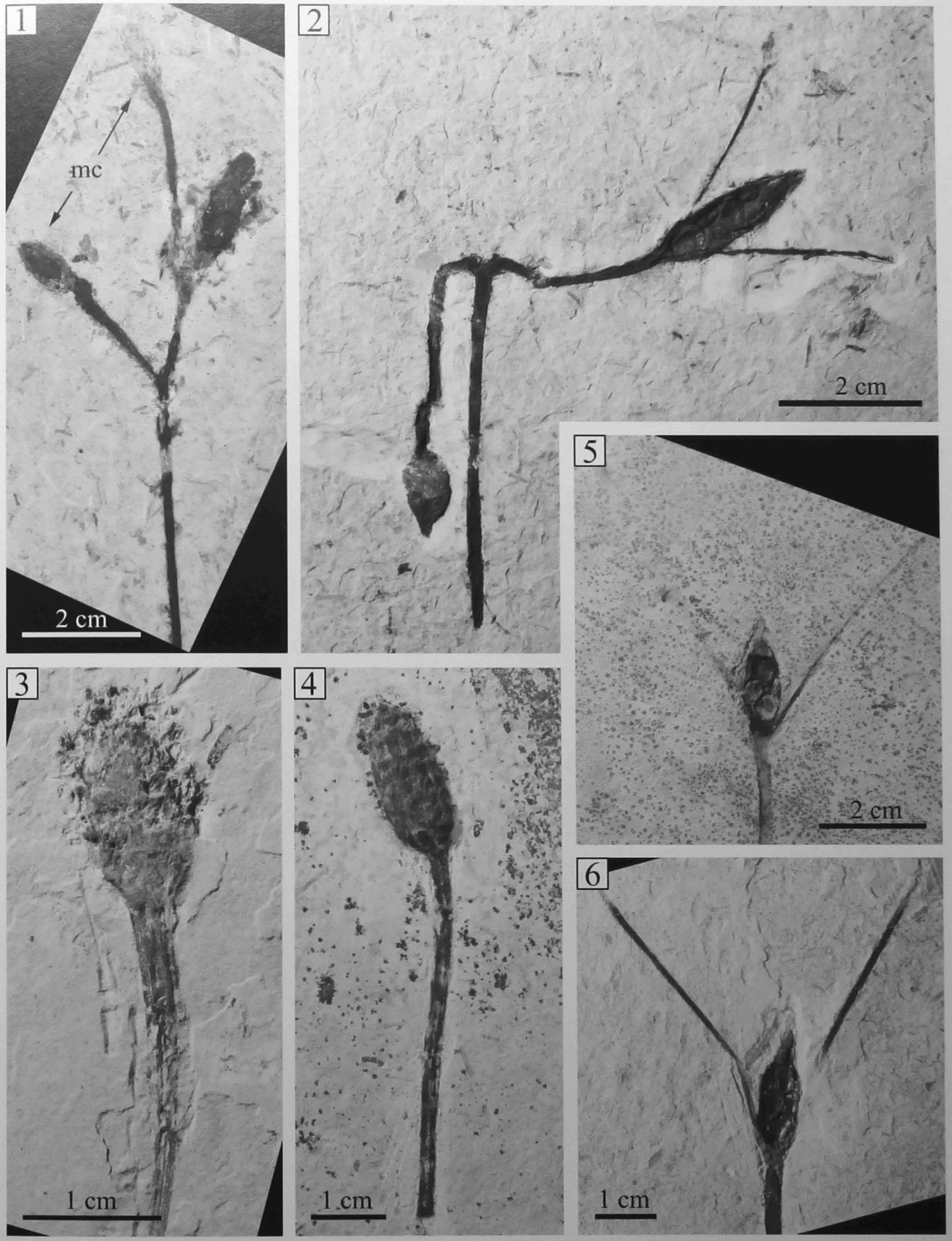

Plate 4. Löwe et al.: *Friedsellowia gracilifolia*, a new gnetophyte from Brazil.

Plate 5

Details of *Friedsellowia gracilifolia* gen. nov. et sp. nov.

Fig. 1. Twig with leaves attached as whorls of four at closely spaced nodes (MB.Pb.2001/1466).
Fig. 2. Oval shaped seed with fragments of a dark-colored smooth envelope; root, main axis and possibly a feeder (see dotted white line) grow out of the seed (MB.Pb.1997/1226).
Fig. 3. Axis with well developed cortex (MB.Pb.1997/1210a).
Fig. 4. A thickened "barrel shaped" node (MB.Pb.1997/1210a).
Fig. 5. "Barrel shaped" axis below a cone (MB.Pb.1997/1210a).
Fig. 6. Remnants of an ovulate cone, with three side axes subtending the cone (MB.Pb.1997/1210a).
Fig. 7. "Barrel shaped" axis below a not preserved cone, plus a small ovulate cone (MB.Pb.1997/1210a).

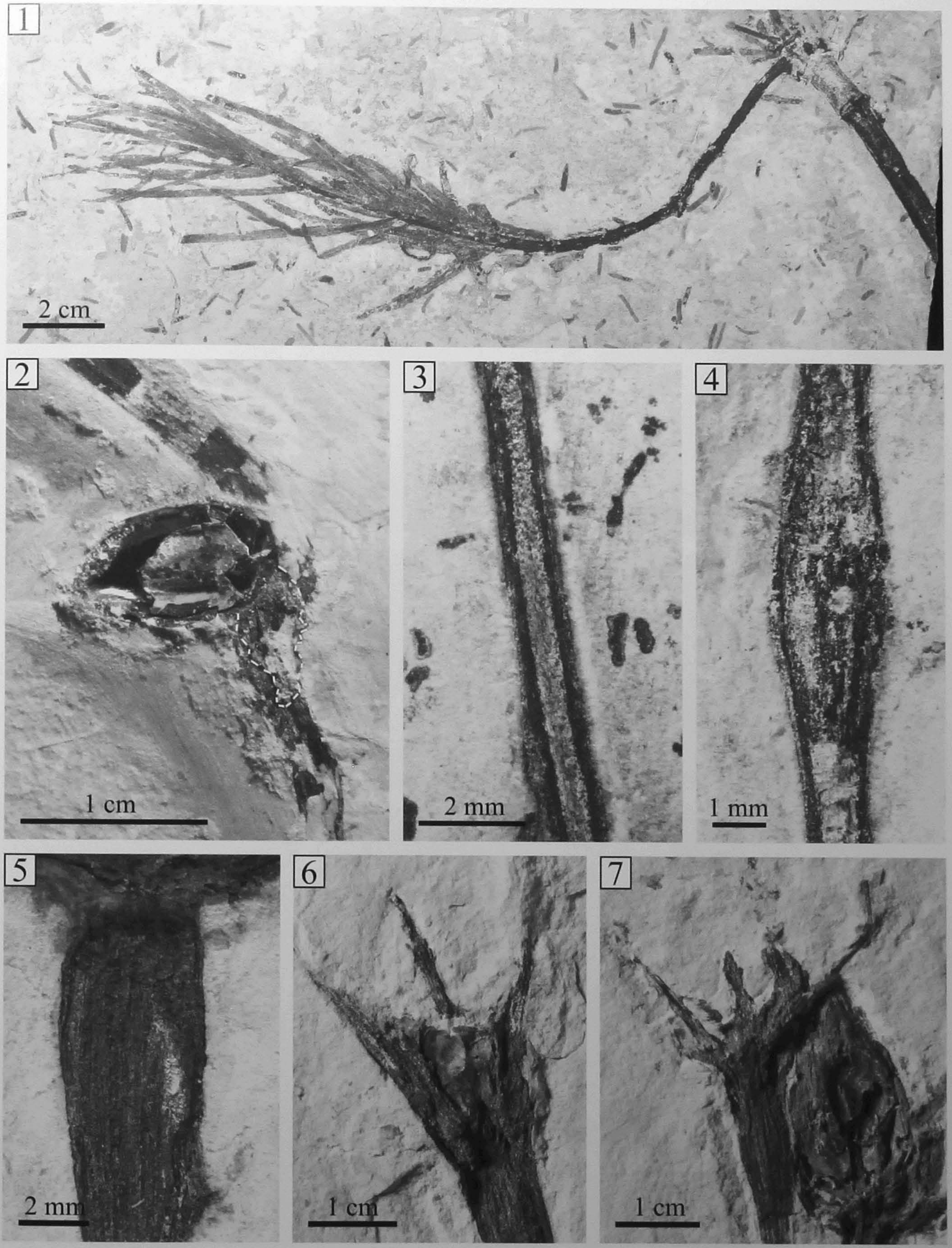

Plate 5. Löwe et al.: *Friedsellowia gracilifolia*, a new gnetophyte from Brazil.