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Strobilus organization in the enigmatic gymnosperm *Bernettia inopinata* from the Jurassic of Germany☆

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ABSTRACT

The enigmatic fossil *Bernettia inopinata* from Lower Jurassic strata of Upper Franconia, Germany, has been described as a leaf-like structure a leaf-like structure bearing a proximal cluster of densely spaced, pillow-like objects believed to represent ovules or ovule-containing units. The systematic affinities of *B. inopinata* have remained unresolved. This paper describes five strobili from Pechgraben near Bayreuth that show fertile units composed of *B. inopinata* and the delicate leaf-like structure *Chlamydolepis lautneri* in helical arrangement along a central axis. These fossils provide the first insights into the organization of the *B. inopinata* reproductive structure and demonstrate that *B. inopinata* and *C. lautneri* were produced by the same plant. Moreover, *Desmiophyllum gothanii* leaves closely associated with the strobili, together with specimens showing *C. lautneri* and the enigmatic microsporophyll *Piroconites kuespertii* in organic connection, support the hypothesis that these four taxa represent parts of the same plant. The genus *Piroconites* with its type-species *P. kuespertii* is validated. Although certain structural details of the *B. inopinata* plant are reminiscent of features seen in other gymnosperms, including Bennettitales (i.e. ovule structure, megasporophyll organization, microsporophyll organization), Gnetales (i.e. three-locular synangia, pollen, leaves), Glossopteridales (megasporophylls), and conifers (microsporophyll organization and arrangement), it does not fit well into any of the known groups of gymnosperms.

1. Introduction

The flora from the Rhaetian and Hettangian strata of northeastern Bavaria, more widely known as the "Rhaeto-Liassic" flora or the flora of the "boundary layers" of Upper Franconia (e.g., Schenk, 1867; Jung, 1958, 1960, 1967; Kirchner, 1992), is rich and diverse; approximately 50 species of lycophytes, ferns, seed ferns, Cycadales, Bennettitales, ginkgophytes, and conifers have been reported to date (e.g., Sternberg, 1820–1838; Schenk, 1867; Gothan, 1914; Achilles, 1981; Kirchner, 1992; Van Konijnenburg-van Cittert et al., 1998, 2014; 2016; Bauer et al., 2015 and references therein). However, several characteristic elements in this flora cannot be assigned systematically or remain equivocal with regard to biological function, not because they are scarce as fossils, but rather because the specimens display unusual complements of morphological features and/or have to date exclusively been found dispersed, with no information on the source plants available.

Foremost among the enigmatic fossils are four taxa known exclusively from Upper Franconia, i.e. the putative megasporophyll *Bernettia inopinata* Gothan, 1914, the microsporophyll *Piroconites kuespertii* Gothan, 1914, leaves named *Desmiophyllum gothanii* Florin, 1936, and a delicate, leaf-like structure described as *Chlamydolepis lautneri* Van Konijnenburg-van Cittert, 1992. These taxa are relatively common and in many cases co-occur, and thus have been suggested to belong to the same plant (Van Konijnenburg-van Cittert, 1992). However, a physical connection between any of them has not been documented, with the exception of *C. lautneri* and *P. kuespertii* (Boersma, 1985; Van Konijnenburg-van Cittert, 1992).

Bernettia inopinata is regarded as the most mysterious component of the "Rhaeto-Liassic" flora of Upper Franconia (Gothan, 1914). The taxon is used for detached, cm-sized leaf-like fossils characterized by a cluster of densely spaced, pillow-like structures usually located in the portion of the leaf. Gothan (1914: p. 146–150) suggested that the affinities of *B. inopinata* might lie with the cycadophytes, perhaps representing sheath-leaves tightly surrounding some type of cone. Accordingly, the cluster of pillow-like structures would represent a relief of the outer

☆ Dedicated to the memory of the late Helmut Zapf († 09.12.2014) of Creußen-Ottmannsreuth, Germany, an enthusiastic collector of plant fossils, who readily made his valuable specimens available for this study.

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cone surface that somehow became imprinted into the adaxial side of the leaves. However, most scientists today interpret *B. inopinata* as a megasporophyll. Based on the occurrence of isolated pillow-like structures on the same slabs as *B. inopinata* specimens (Kirchner, 1992), the pillow-like have been regarded as ovules or ovule-bearing structures.

In this paper we present evidence to support the interpretation of *Bernettia inopinata* as a megasporophyll in the form of five compressed strobili from Lower Jurassic strata of the Küfner/Pechgraben locality near Bayreuth, Upper Franconia, that show fertile units composed of *B. inopinata* and *C. lautneri* in helical arrangement along a central axis. These fossils provide the first insights into the overall organization of the *B. inopinata* reproductive structure, and demonstrate that *B. inopinata* and *C. lautneri* were produced by the same plant. This discovery contributes to our understanding of some of the most intriguing Jurassic fossils from Germany.

2. Geological setting, material and methods

The flora from the Upper Triassic and Lower Jurassic beds of north-eastern Bavaria occurs in clay layers and lenses that are (or were in the past) exposed in more than ten outcrops in the area between the cities of Nuremberg, Coburg, Kulmbach, Bayreuth, and Schnaittach. During Late Triassic and Early Jurassic times, this region was situated in the Central European Basin, between 35 and 50° N (Stampfli and Kozur, 2006), at the eastern margin of the Pangea (Seeling and Kellner, 2002). The flora is part of the maritime floristic province of the Euro-Asian Continent (sensu Zhou, 1983, 1995) that extended along the Tethys from Greenland, Scandinavia, Poland, Hungary and Romania to Iran and Afghanistan, and further to China and Japan. Although the flora is often referred to as "Rhaeto-Liassic" in literature, the majority of localities are in fact Hettangian in age; bona fide Rhaetian occurrences are comparatively rare (e.g., Wüstenwelsberg; see Van Konijnenburg-van Cittert et al., 2014; 2016).

The strobili and other specimens described and illustrated here have been collected from finely-laminated, reddish clay lenses ("Pflanzenton" sensu Weber, 1968) in the sand/gravel pit Küfner in the vicinity of the village of Pechgraben near Bayreuth (TK 1:25,000 Nr.5935, Marktschorgast, R ^{44} 67,225, H ^{55} 40,780; Fig. 1). Other specimens included in this study for comparison but not illustrated come from other quarries in the area, including Hohe Warte, Wolfshöhe (Gothan, 1914), and Grossbellhofen (Kirchner, 1992). In all these quarries, fluvial sandstones of Hettangian (earliest Jurassic) age crop out that are occasionally intercalated with up to 3-m-thick clay lenses interpreted as infilled oxbow lakes (Weber, 1968; Schmeißner and Hauptmann, 1998; Van Konijnenburg-van Cittert et al., 2001). The paleoenvironment has been reconstructed based on palynomorphs as terrestrial deltaic plain with occasional floodings (Fechner, 1998).

The specimens were collected by W. Häckel, Sepp and Traute Hauptmann, Stefan Schmeißner, Günter Dütsch, Johanna H.A. van Konijnenburg-van Cittert, and Helmut Zapf, and are housed at the Urweltmuseum Bayreuth (Germany; collection numbers preceded by "BT"), the University of Utrecht (The Netherlands, prefix "UU"), and the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (Germany; prefix "SNSB-BSPG"). Other specimens included in this study come from the private collections of Traute Hauptmann (Hof, Germany; in the process of being transferred to the Urweltmuseum Bayreuth), Stefan Schmeißner (Kulmbach, Germany; prefix "G"), Günter Dütsch (Untersteinach, Germany; prefix "K" in the middle), and the late Helmut Zapf (Creußen, Germany; without numbers). Additional material is stored at the Naturhistorical Museum of Stockholm (Sweden; prefix "S") and Senckenberg Naturmuseum (Frankfurt, Germany; prefix "SM.B."). The fossils are mostly preserved as impressions, a few as compressions. Digital images were captured with a Canon EOS 550D camera.

3. Systematic paleobotany

Gymnosperms.
Genus: *Bernettia* Gothan, 1914.

Type species: *Bernettia inopinata* Gothan, 1914.

Diagnosis (in part based on Gothan, 1914, p. 146–147): Female strobilus with helically arranged fertile units; juvenile strobilus relatively compact, mature ones rather lax in appearance; each fertile unit composed of two superimposed leaf-like elements; one leaf-like element sterile, the other fertile (megasporophyll), bearing a cluster of rhombic, pillow-like structures; each pillow-like structure characterized by a central roundish mark.

Bernettia inopinata Gothan, 1914.
Plates I–III.

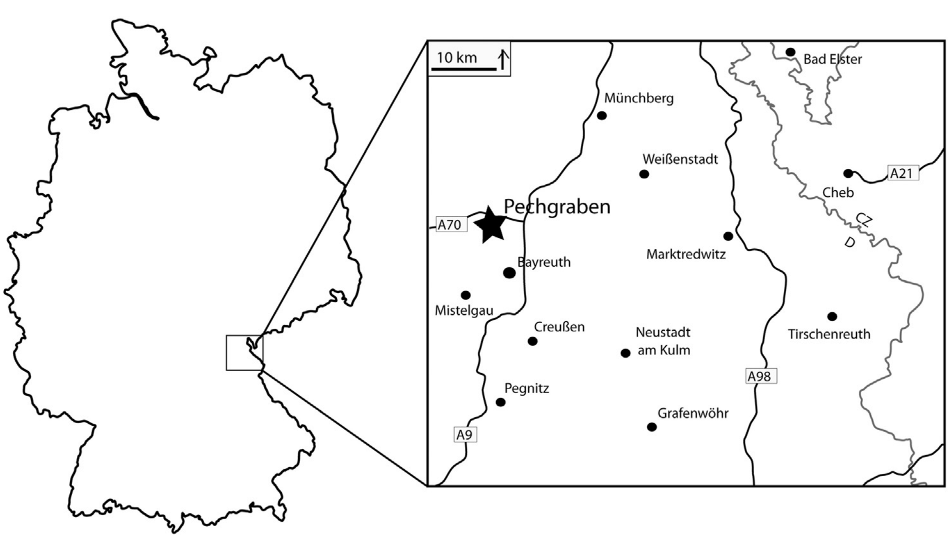


Fig. 1. Map of the Bayreuth area; asterisk indicates the location of the "Pechgraben" quarry.

Selected references:
1914 *Bernettia inopinata* Gothan, p. 146, pl. XXVII, 1–4, pl. XXXIV, 4, text-fig. 5.
1992 *Bernettia inopinata* Gothan, Kirchner, p. 32, pl. VIII, 1–3, text-fig. 5.
1992 *Bernettia inopinata* Gothan, Van Konijnenburg-van Cittert, p. 246.

Neotype (hic designatus) BT012369 (Pl. I, 2, detail in Pl. II, 4), deposited in the collection of the Urweltmuseum Bayreuth, Germany.

Remark The genus *Bernettia* was validly published by Gothan, 1914. However, the holotype cannot be traced, and thus must be regarded as lost. Consequently, designation of a neotype is mandated. The neotype does not come from the same locality as Gothan's specimens because the original locality does no longer exist. The type locality is that of the neotype.

Diagnosis (in part based on Gothan, 1914, p. 146–147): Strobilus > 15 cm long; leaf-like elements of each fertile unit similar in size and shape, lanceolate to rhombic, with pointed to distinctly prolonged apex and wide, crescent-shaped base, vascularized by unforked, parallel veins extending to tip; sterile leaf-like element thinner and more fragile (ephemeral), corresponding to *Chlamydolepis lautneri*; fertile element corresponding to *Bernettia inopinata*; pillow-like structures 20–40, densely spaced (clustered), more or less rhomboidal; epidermis hypostomatic; adaxial cells rectangular, abaxial cells also rectangular but alternating with irregular rows of isodiametric epidermal cells interspaced with haplocheilic stomata; 4–6 subsidiary cells; trophophylls helically arranged, corresponding to *Desmiophyllum gothanii*; microsporophylls known as *Piroconites kuespertii*, containing polyplicate *Ephedripites*-type pollen with straight or tortuous plicae, exine thin and almost smooth (psilate).

Distribution: *Bernettia inopinata* is widespread and locally abundant in the Hettangian of Upper Franconia, Germany. The taxon has not been recorded from outside Germany. *Piroconites*-like fossils have recently been described from the Lower Jurassic of Poland (Barbacka et al., 2010).

Locus typicus (neotype): Küfner/Pechgraben, Upper Franconia, Bavaria, Germany.
Stratum typicum (holotype and neotype): Lower Jurassic "Pflanzenton" sensu Weber, 1968 (=Hettangian).

Material studied: See supplementary file.

Description: Five strobili and strobilus portions, henceforth denoted A (Pl. I, 1), B (Pl. I, 2), C (Pl. I, 3), D (Pl. II, 1), and E (Pl. II, 2), have been discovered from the Küfner/Pechgraben locality (see Fig. 1). Specimens are up to 18 cm long, 10 cm wide, and consist of a stout axis (8–14 mm wide) around which are helically arranged compound structures, henceforth informally termed 'fertile units'. The individual strobili correspond to one another in general organization, but show differences in appearance: Strobilus A (Pl. I, 1) differs from B, C, and D (Pl. I, 1, 2, Pl. II, 1) in the orientation and spacing of the fertile units. The units are relatively closely spaced and more or less adpressed to the axis in strobilus A, whereas they are somewhat more loosely organized and extend from the axis at angles of up to 50° in strobili B, C, and D. Strobilus E (Pl. II, 2) appears to represent an older, partially disarticulated specimen, with only the distal fertile units still attached to the axis. In two of the strobili (i.e. D and E) a portion of the parental axis is preserved ('sa' in Pl. II, 1, 2) that is characterized by faint longitudinal striae and distinct, transversely elongate to crescent-shaped leaf scars in what appears to be a helical arrangement (Pl. II, 3).

Each fertile unit consists of two superimposed leaf-like elements (i.e. a sterile and a fertile one; letters se and fe in Pl. II, 4, 5, 6) enclosing a cluster of pillow-like structures. Strobilus C (Pl. I, 3) suggests that the fertile units were positioned on protrusions (?short branches) of the axis (arrows in Pl. I, 3). The leaf-like elements are 30–50 mm long, 15–30 mm wide, broadly lanceolate to rhombic, and possess a pointed (arrow in Pl. I, 2) to distinctly elongated (arrows in Pl. I, 1) tip. The latter feature, however, is only seen in strobilus A, which probably is an immature specimen (see Discussion section below). The sterile element is thinner and appears to be more fragile (perhaps ephemeral) than the fertile one, which is best recognizable in strobili B and E (compare se with fe in Pl. II, 4–6). In many instances, the presence of the sterile element is only recognizable from imprints of its venation on the more robust fertile element, especially on the pillow-like structures (e.g., Pl. II, 4). Vascularization of both leaf-like elements occurs in the form of several unforked, parallel veins that extend from the base to the tip; anastomoses have not been observed.

Each fertile unit contains a cluster (15–20 × 10–15 mm) of 20–40 densely spaced pillow-like structures. In detached sterile elements (i.e. *Chlamydolepis lautneri* sensu Van Konijnenburg-van Cittert, 1992; see below), these pillow-like structures are still recognizable as (faint) impressions on some specimens (e.g., Pl. III, 4b). The pillow-like structures (Pl. II, 4–6, Pl. III, 1–6) are rhombic in outline, typically slightly wider (4–5.5 mm) than high (3–4 mm high); the surface shows a distinct, more or less circular centre (~1 mm in diameter; Pl. III, 5, 6) surrounded by prominent radial striae extending to the periphery (Pl. III, 5–6). Size and position of the cluster of pillow-like structures may vary; the cluster is usually located in the proximal position of the fertile element, but may also occur more distally.

Remarks: We are currently unable to determine whether *Chlamydolepis lautneri*, *Desmiophyllum gothanii*, and *Piroconites kuespertii* were exclusively produced by the plant that also produced the *Bernettia inopinata* strobili, or represent structures that occurred in several, perhaps not even closely related (groups of) plants. We therefore refrained from formally merging the four taxa into one whole-plant species, although it is very likely that they belong together. Moreover, merging fossil-taxa in this way can lead to all sorts of extensive problems with typification, as well as with using those taxa in other fossil-floras.

4. Discussion

4.1. Morphology and whole-plant reconstruction

The most unusual structural feature of the strobili described in this paper are the fertile units that occur in the form of paired, leaf-like elements enclosing a cluster of rhombic, pillow-like structures. If the classical interpretation of the pillow-like structures as ovules or ovule-containing units (Kirchner, 1992) is correct, then the circular central area seen in many specimens would probably represent the micropylar opening or the upper part of the ovule, that is surrounded by a 'padding'. The latter would either correspond to a part of the ovule itself (e.g., the integument) or some type of protective border or envelope produced by the sporophyll. Unfortunately, section views of the impression fossils do not provide additional insights into the composition of the structures. Accordingly, the leaf-like element producing the ovules would represent a megasporophyll. The fertile element concurs in morphology with a fossil that, if found dispersed is called *Bernettia inopinata* (Pl. III, 1–6), whereas the sterile element, if found separate, would be identified as *Chlamydolepis lautneri*. As to whether the fertile units represent a single leaf that became subdivided and folded, and eventually differentiated into a thicker fertile and thinner sterile part, or two separate leaves cannot be determined. Another problem that cannot presently be solved concerns the position of the alleged ovules or ovule-containing structures. Van Konijnenburg-van Cittert (1992) interpreted the ovules as located on the adaxial side of *B. inopinata* and covered by the sterile *C. lautneri* element. However, the strobilus illustrated in Pl. I, 2, and several of the dissociated fertile units shown in Pl. II, 2, would suggest that the ovules rather occurred on the abaxial side of *B. inopinata* and that the *C. lautneri* element might represent a bract subtending the fertile element.

An alternative, albeit less likely interpretation of the fertile units is based on the fact that the pillow-like structures are generally composed of sediment, while organic material is rarely preserved. It is possible to envisage that the pillow-like structures represent moulds (sediment infillings) of the scars left behind after the shedding of the ovules/seeds, rather than the actual ovules/seeds. If this is accurate, then the pillow-like structures would correspond to the size and shape of the ovule/seed scars. Accordingly, the circular mark in the central part of the pillow-like structures would represent the attachment point of the ovule/seed. If this hypothesis is accurate, then the ovules would be located on the adaxial side of *Bernettia inopinata* and were covered by the sterile *Chlamydolepis lautneri* element. Similar problems have been observed in several impression fossils of glossopterid ovuliferous organs from the Permian of Gondwana (e.g., McLoughlin, 1990, 2011; Prevec et al., 2008; Prevec, 2011, 2014).

Articulated cones composed of *Bernettia inopinata* and *Chlamydolepis lautneri* are rare as fossils. On the other hand, dispersed parts, which usually consist of either the *C. lautneri* or *B. inopinata* element, are quite common (personal observation JHAvK-vC). *Bernettia inopinata* is more common than *C. lautneri*, due probably to the fact that the latter is thinner and more delicate, and thus does not preserve as easily as *B. inopinata*.

The minor differences in overall appearance between the five strobili described and illustrated here probably reflect different stages in development and maturation. Strobilus A appears to be immature, whereas B, C, and D are more or less mature. Several of the fertile units are detached or missing in strobilus E, suggesting that this specimen represents an old, partially disarticulated strobilus. It is also possible, however, that individual fertile units have been lost prior to or during embedding of the strobilus or during fossilization. If our interpretation of the strobili as representing different stages in development and maturation is correct, then the fossils suggest that the fertile units were relatively closely spaced, largely overlapping, and inserted at angles of <40° in immature strobili. During maturation, the central axis then elongated and the insertion angle of the fertile units increased, perhaps in a similar manner as in female cones of certain Paleozoic conifers and modern cycads (e.g., *Cycas revoluta* Thunberg, 1782, *Walchiostrobus*; Florin, 1940; Norstog and Nicholls, 1997). The distinctly elongated tips evident in the immature strobilus (arrows in Pl. I, 1) were probably ephemeral, and wilted or were shed during maturation. *Chlamydolepis lautneri* possibly served as a protective sheath covering the developing ovules. Dispersed *B. inopinata* remains do not normally show evidence of the presence of a *C. lautneri* sheath. Sheath remains are present only in a few specimens, usually along the margins (e.g., see in Pl. II, 4, 5). This suggests that the *C. lautneri* element was either ephemeral and withered during maturation, or was readily destroyed by mechanical forces prior to or during fossilization.

Morphological similarities and frequent co-occurrence on the same bedding planes have been used to suggest that *Bernettia inopinata* was produced by the same plant that also produced the microsporophyll *Piroconites kuespertii*, as well as *Desmiophyllum gothanii* sterile leaves (Van Konijnenburg-van Cittert, 1992; Kirchner, 1992). *Piroconites kuespertii* is represented by large microsporophylls (3–5 × 2–3.5 cm) with a crescent-shaped base, diverging basal margins and an obtuse apex. The abaxial side is characterized by parallel striations and two diverging veins, whereas the adaxial surface is covered by three-locular synangia of about 1 mm in diameter. The pollen are polyplicate with a length of 50–60 μm, and correspond to dispersed examples of *Ephedripites* Bolkhovitina ex Potonié, 1958. *Desmiophyllum gothanii* leaves are linear, 20–25 mm wide, hypostomatic, and characterized by parallel veins at a density of 20/cm. The abaxial epidermis is characterized by irregular rows of haplocheilic stomata surrounded by 4–6 subsidiary cells.

The strobili described here demonstrate that *Bernettia inopinata* and *Chlamydolepis lautneri* were produced by the same plant. Since *Chlamydolepis lautneri* has previously been found physically connected to *Piroconites kuespertii* (e.g., Van Konijnenburg-van Cittert, 1992; Kirchner, 1992; Fig. 2a-c), the physical connection to *B. inopinata* adds support to the hypothesis that *B. inopinata* megasporophylls and *P. kuespertii* microsporophylls were produced by the same plant. Moreover, several fragments of *Desmiophyllum gothanii* leaves occur on the same slabs and in close association with strobili A, B and D (letters 'D' in Pl. I, 1, 2, Pl. II, 1). Although these leaves are not organically connected, their orientation in all three specimens strongly suggests that they were originally attached below the strobilus-bearing axis. Adding further support to the hypothesis that all these fossils were produced by the same plant are small cuticle fragments of *B. inopinata* (Kirchner, 1992: pl. 8, fig. 3) and *Piroconites kuespertii* (Van Konijnenburg-van Cittert, 1992: pl. 2, fig. 4). The epidermal anatomy displayed in these cuticles corresponds well with that of *D. gothanii* as described and illustrated by Florin (1936: p. 49, pl. 6, 8, 9, text-8c). In all three structures, the stomata are haplocheilic and surrounded by 4–6 subsidiary cells. Moreover, they are arranged in irregular longitudinal rows.

4.2. Comparisons

We are not aware of any fossil or modern plant reproductive structure that closely resembles the strobili described here. The cluster of pillow-like structures is somewhat similar in overall appearance to the gynoecial crusts seen in Bennettitales in which the ovules are tightly packed and deeply sunken within a layer of interseminal scales and connected to the surface via a narrow micropyle that appears as a ring-like structure in surface view (e.g., Taylor et al., 2009). The vast majority of bennettitaleans produce female reproductive organs in flower-like arrangements (i.e. surrounded by one to several rings of bracts), rather than clustered on the surface of leaves or leaf-like elements. However, one interesting genus that has been affiliated with the Bennettitales, *Fredlindia* Anderson et Anderson, 2003, from the Carnian of South Africa and Australia (Anderson and Anderson, 2003), produces cones that are composed of bilaterally symmetrical "gynoecia" arranged in superjacent whorls. The "gynoecia" are leaf-like and bear dense clusters of what has been called "ovuliferous cells" on the abaxial side. The "ovuliferous cells" are pentagonal to hexagonal in cross-section view, uni-ovulate with a distinct central micropyle and radial striae on the distal face, which are similar to the pillow-like elements that characterize *Bernettia inopinata*. However, the overall morphology of the cones and individual gynoecia distinguishes *Fredlindia* from *B. inopinata*. Moreover, the shape of the leaves, as well as the epidermal anatomy of *Fredlindia* differ clearly from *Desmiophyllum gothanii*.

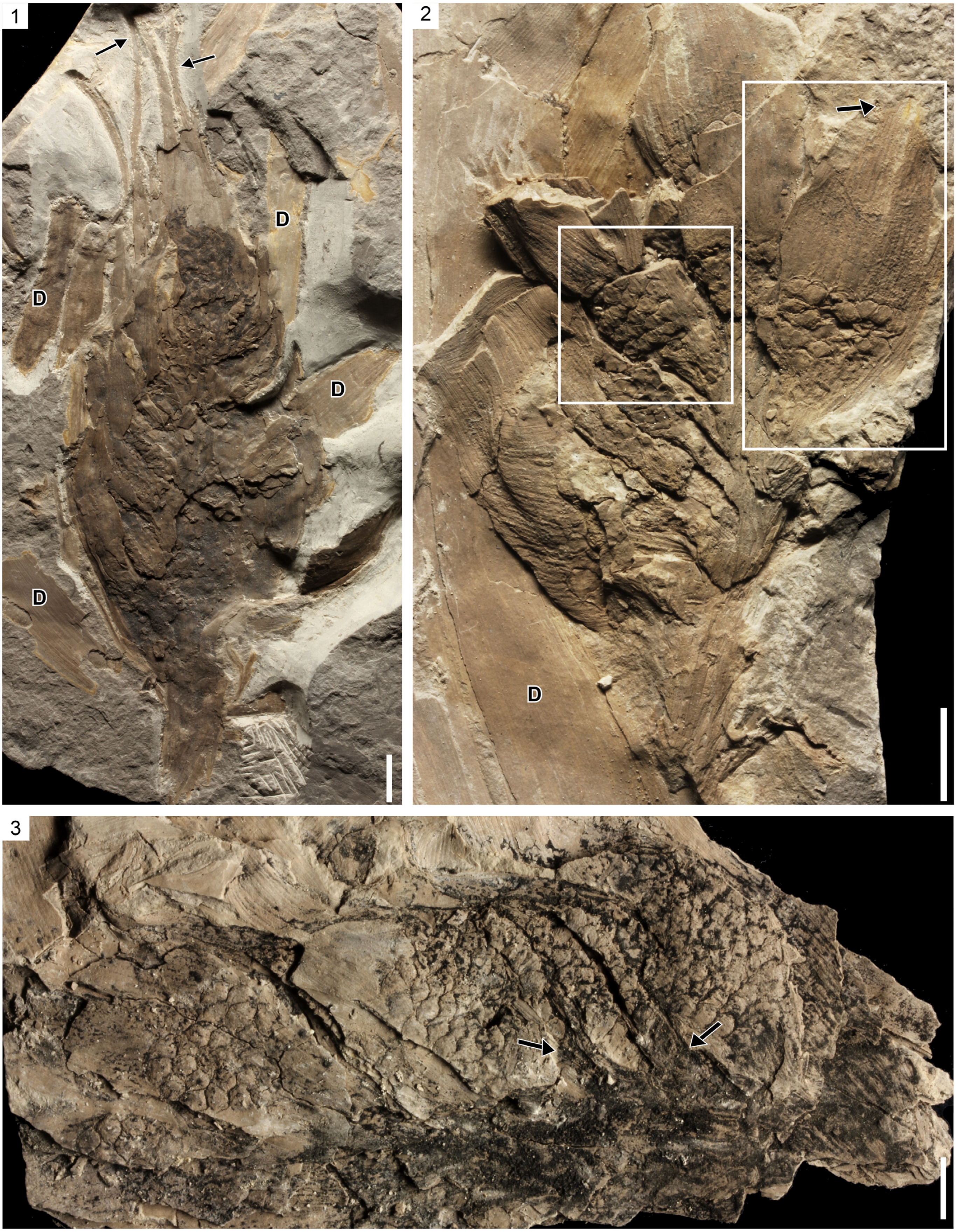
Certain members of the Glossopteridales are also known to produce reproductive organs with clustered ovules located between two leaf-

Plate I. *Bernettia inopinata* strobili from the sandpit Küfner, Pechgraben. All scale bars = 1 cm; D = *Desmiophyllum gothanii*-type leaves

Fig. 1. Strobilus A, immature; note fragments of *Desmiophyllum gothanii* leaves [D] closely associated with strobilius; arrows indicate prolonged tips of sporophylls; specimen BT012371.

Fig. 2. Strobilus B, mature; note closely associated *D. gothanii* leaf [D]; arrow indicates pointed (but no longer prolonged) tip of fertile element; boxed portions of image magnified in Pl. II, 4, 5; specimen BT012369.

Fig. 3. Strobilus C, mature, showing stout cone axis and several fertile units; arrows indicate what appear to be slight elevations giving rise to fertile units; specimen BT 012370.


1
D
D
D
D
2
D
3

like elements (e.g., Taylor et al., 2009; Prevec, 2011). These organs are composed of a dorsi-ventrally flattened, central receptacle with seed-scars on one surface, a protruding reticulate venation on the other, and a variously ornamented and extended marginal wing that in some cases is modified into a double wing (Prevec et al., 2008) or hood (Prevec, 2014). The fructification is subtended by a normal *Glossopteris* leaf (Prevec, 2011), and thus clearly differs from *Bernettia inopinata*. Moreover, megasporophyll arrangement in strobili has not been documented for Glossopteridales.

The ginkgoopsid genus *Hamshawvia* Anderson et Anderson, 2003 from the Carnian of South Africa is characterized by a once-forked axis bearing a pair of megasporophylls, each consisting of a single, erect and fleshy, rounded multi-ovulate lamina (Anderson and Anderson, 2003). The morphology of this structure clearly differs from that of *Bernettia inopinata*, which represents a strobilus comprised of helically arranged fertile unit composed of one sterile and one fertile leaf-like element.

Knezourocarpon narangbaensis Pattemore, 2000, a pteridosperm from the Lower Jurassic of Queensland, is characterized by megasporophylls attached oppositely to sub-oppositely on the axis. The megasporophylls are composed of ovate, leaf-like bracts with a subparallel venation and one single ovule attached on the lower side (Pattemore, 2000). The opposite attachment of the megasporophylls, as well as the fact that each bract bears only a single ovule without protection, distinguishes this taxon from *Bernettia*.

Another fossil that is somewhat similar to *Bernettia* is *Hystricia* Anderson et Anderson, 2003 from the Carnian of the Karoo basin (South Africa). Only a single specimen of this taxon has been discovered to date (Anderson and Anderson, 2003, pl. 128) that shows a gynoecium consisting of a cluster of ovuliferous cells surrounded by a 'perianth' of bracts, each of which extends from a gynoecial cell. The ovuliferous cells are much smaller (c. 0.5 mm in diameter) than those of *Bernettia* and display a central depression which might represent a micropyle. The systematic affinity of *Hystricia* remains unresolved; however, the specimen is reminiscent of certain Bennettitaleans or Glossopteridales such as *Ottokaria* (Anderson and Anderson, 2003; and see below).

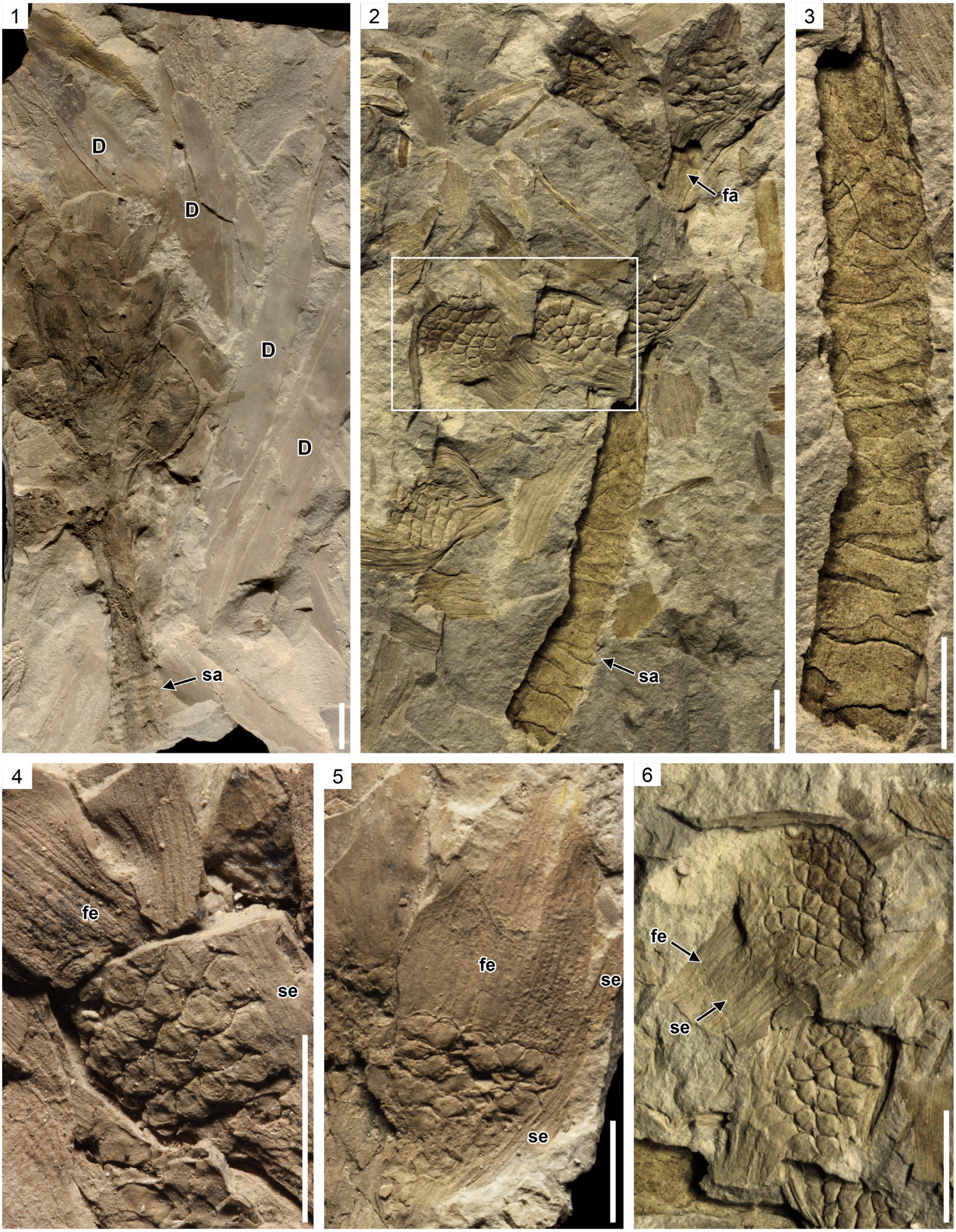
4.3. Affinities

The fact that *Bernettia inopinata* is not readily comparable to any other extant or fossil reproductive structure renders the botanical affinities of this intriguing fossil unresolved. Gothan (1914) initially considered *B. inopinata* as belonging to the cycadophytes, but recognized that the fossil did not correspond to any of the known morphologies within this group of plants. He suggested that *Thinnfeldia* Ettingshausen, 1852 might belong to *B. inopinata*, as this foliage type co-occurs with the latter in all localities. On the other hand, *Piroconites kuespertii* was interpreted as a gnetalean reproductive structure based on the presence of three-locular synangia containing *Ephedripites*-type pollen (Van Konijnenburg-van Cittert, 1992). Crane (1996) and Doyle (1996) concur with this interpretation and view the *B. inopinata*-*P. kuespertii*-*C. lautneri*-*D. gothanii* plant (henceforth simply called '*B. inopinata* plant') as an early member of the Gnetales. Moreover, *Desmiophyllum gothanii* leaves are long, relatively narrow, and possess parallel venation. This leaf type is found in extant Gnetales (*Welwitschia*). An additional feature variously used to suggest gnetalean affinities is the supposedly decussate arrangement of *D. gothanii* leaves (Crane, 1996; Doyle, 1996). However, if our interpretation of the broadly rhombic to crescent-shaped scars seen in the axis portions subtending two of the strobili (Pl. II, 1–3) is correct, then leaves in this plant were arranged helically, rather than opposite and in groups of two per node. On the other hand, Doyle (1996) also noted parallels with the Glossopteridales, and proposed that the *B. inopinata* plant perhaps occupied a phylogenetic position between extant Gnetales and Bennettitales as a sister-group to the extant Gnetales. Dilcher et al. (2005) speculated on possible affinities of *P. kuespertii* to *Welwitschia* J.D. Hooker, 1862, whereas Mundry and Stützel (2004) regarded the similarities to extant Gnetales superficial, and especially the macromorphology of *P. kuespertii* as fundamentally different from that of any living member in this group of plants. These authors also stated that pollen morphology might have been overemphasized in previous considerations on the systematic affinities of *P. kuespertii*. Dispersed *Ephedripites*-type pollen grains have been attributed to various plant groups, including Bennettitales (Schuster, 1911), Gnetales (Schulz, 1967; Balme, 1995), and Peltaspermales [in *Bosea indica* Srivastava, 1974 = *Sobea indica* (Srivastava) Kumaran and Bonde, 1991] some even have been attributed to the fern family Schizaeaceae (e.g., Bolkhovitina, 1961; Schulz, 1967).

As pointed out above, the macromorphology of *Bernettia inopinata* differs from that seen in any other fossil or living plant reproductive structure, but resembles bennettitaleans to a certain extent. If *B. inopinata* belongs to the Bennettitales, then the ovule cluster would represent a gynoecial crust containing ovules embedded in densely spaced interseminal scales. Conversely, microsporangiate reproductive organs in the form of scale-like leaves bearing numerous pollen sacs similar to *Piroconites kuespertii* occur quite frequently among gymnosperms, although in other gymnosperm groups the pollen sacs are usually located on the abaxial side of the microsporophyll (e.g. in cycads and conifers), rather than on the adaxial side as proposed for *P. kuespertii* (Taylor et al., 2009). An exception to this also occurs in certain Bennettitales which have pollen sacs located on the adaxial side of the microsporophylls (e.g., Taylor et al., 2009). However, bennettitalean microsporophylls are usually arranged helically or in whorls to form compound, flower-like structures. One of the few exceptions to this is *Bennettistemon ovatum* Harris, 1932, in which isolated sporangia (not fused to form the typical bennettitalean synangia) cover the adaxial surface of the microsporophylls. Moreover, the microsporophylls are spirally arranged. The spatial arrangement of *Piroconites kuespertii* remains unresolved since this fossil has only been found dispersed. However, the relationship of *P. kuespertii* to *B. inopinata* suggests that the former was also arranged into strobili, perhaps similar to the male cones of certain extant cycads and conifers. The fact that the pollen sacs in *P. kuespertii* are organized in groups of three is more peculiar and rather characteristic of the Gnetales (Van Konijnenburg-van Cittert, 1992). The in situ pollen in *P. kuespertii*, *Ephedripites tortuosus*, has also been recorded in situ in *Bosea indica*, a putative peltaspermalean pollen organ, but otherwise is considered exclusive to the gnetaleans. Alternatively, Dilcher et al. (2005) noted that *Desmiophyllum gothanii* leaves lack the anastomosing venation seen in extant and fossil gnetaleans. However, anastomosing venation does not occur in the extant *Ephedra* Linnaeus, 1753, and is rare in *Welwitschia* (pers. Obs. HvKvC). Finally,

Plate II. *Bernettia inopinata* strobili from the sandpit Küfner, Pechgraben. All scale bars = 1 cm. D = *Desmiophyllum gothanii*-type leaves; fa = strobilus axis; sa = subtending axis; fe = fertile element; se = sterile element.

Fig. 1.	Strobilus D, mature; note several *D. gothanii* leaves [D] surrounding the strobilus; specimen BT010377.00.
Fig. 2.	Strobilus E, old; note relatively long portion of the parental axis [sa] with prominent elongate to crescent-shaped (?leaf) scars; boxed portion of image magnified in Pl. II, 6; specimen K198.
Fig. 3.	Detail of Pl. II, 2, showing axis portion subtending strobilus.
Figs. 4, 5.	Details of Pl. I, 2, showing fertile units constructed of leaf-like elements; scale bar = 5 mm.
Fig. 6.	Detail of Pl. II, 2, showing fertile unit composed of leaf-like elements; scale bar = 5 mm.


1
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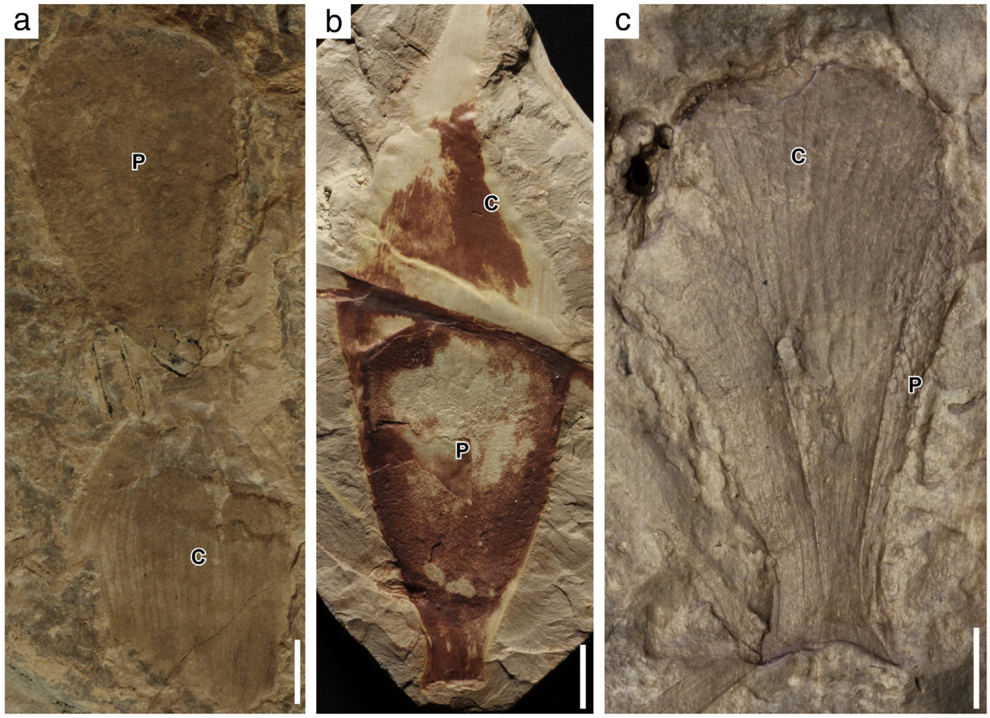


Fig. 2. Specimens from Pechgraben demonstrating physical connection between *Piroconites kuespertii* microsporophylls [P] and *Chlamydolepis lautneri* sterile elements [C]; (a): specimen K97; scale bar = 1 cm; (b): specimen G65–90; scale bar = 1 cm; (c): Specimen 13-2-1991; scale bar = 1 cm.

haplocheilic stomata arranged in irregular rows are not known in either bennettitaleans or gnetaleans.

5. Conclusions

Several of the plants that occurred in Upper Franconia during the Early Jurassic remain enigmatic because they are characterized by unique combinations of structural features. Various aspects of the morphology of the *Bernettia inopinata* plant concur with features seen in other gymnosperms, including Bennettitales (i.e. ovule structure, megasporophyll organization, microsporophyll organization), Gnetales (i.e. three-locular synangia, pollen, leaf shape), Glossopteridales (megasporophyll organization), and conifers (microsporophyll organization and arrangement), but none are of sufficient clarity to determine the systematic affinities of *B. inopinata*. Although the articulated strobili and other remains described in this study provide a wealth of new information on the *B. inopinata* plant, many structural details remain elusive. In spite of these limitations, we believe it is necessary to record these fossils because the reconstruction of whole-plant taxa can provide a valuable template to interpret not only newly discovered isolated parts with regard to morphology, position, and function, but also evaluate certain features with regard to their utility in determining the systematic affinities of a plant. Such information is important as it relates to the identification of disarticulated plant fossils, especially foliage types and reproductive structures, since structural and morphological features are the basis of generic and specific identifications.

6. Addendum: validation of *Piroconites* Gothan and designation of a type specimen

While working on the *Bernettia inopinata* strobili and associated fossils from the Hettangian strata of Upper Franconia, we noted that Gothan (1914) proposed the name *Piroconites* as "*Piroconites* nov. gen. provis" (p. 130) and discussed the provisional status of the taxon later in that paper. However, a provisional genus is not validly published according to the provisions of the ICN (Art. 36.1b). While an emended diagnosis for the only species attributed to *Piroconites*, *Piroconites kuespertii*, was subsequently provided by Van Konijnenburg-van Cittert (1992), the status of *Piroconites* remained unchanged. As a result, the genus *Piroconites* and, consequently, also the species *P. kuespertii*, are not validly published. Although *P. kuespertii* is not in the focus of this paper, it represents an integral part of the whole-plant concept suggested for *B. inopinata*, and thus is formally validated here:

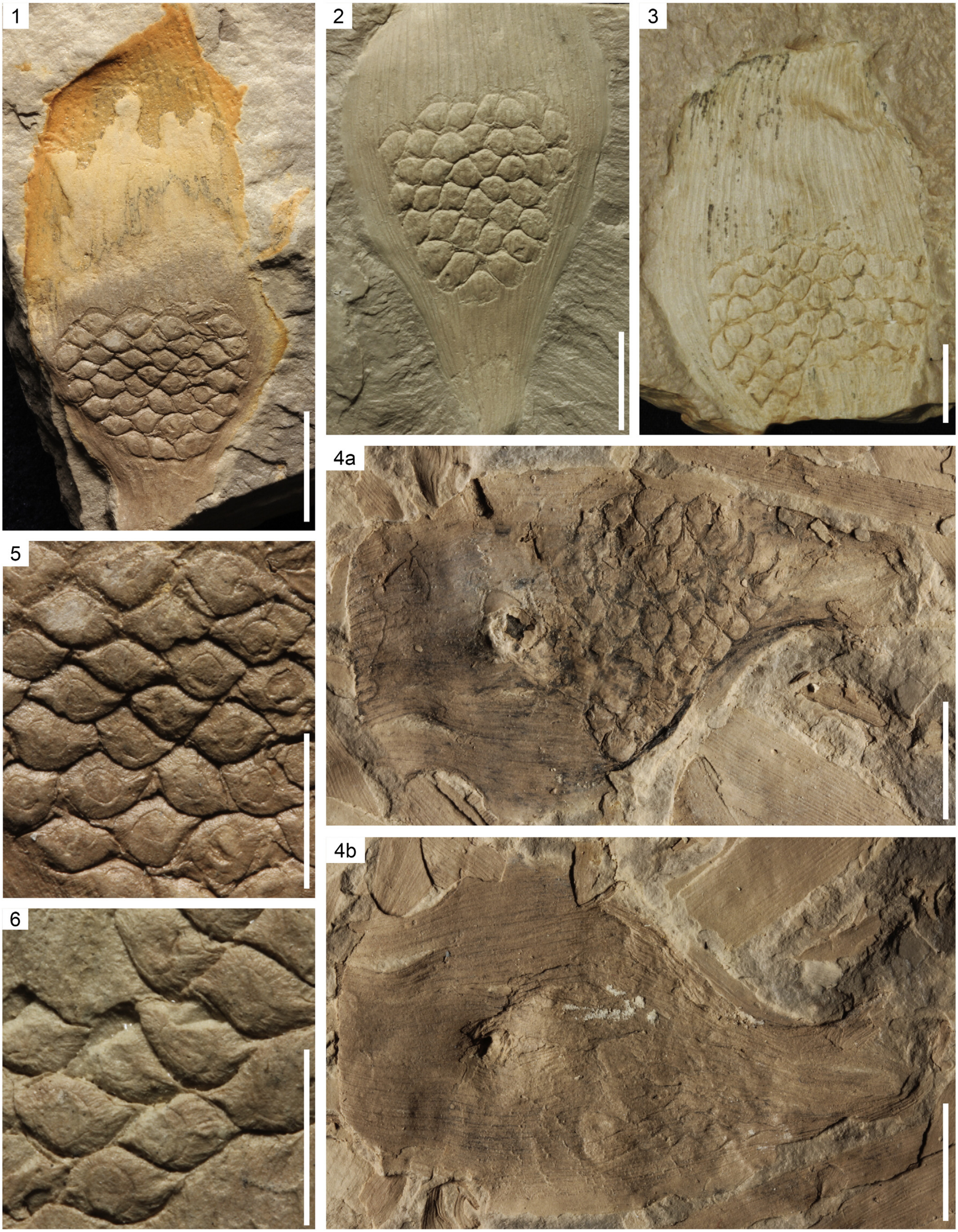
Piroconites Gothan, 1914 ex Kustatscher, Van Konijnenburg-van Cittert, Bauer et Krings.
Figs. 2a-c.

Type species: *Piroconites kuespertii* Gothan, 1914 ex Kustatscher, Van Konijnenburg-van Cittert, Bauer et Krings.

Generic diagnosis: Spatulate microsporophylls with a crescent-shaped base; greatest width in distal portion. One, probably abaxial, surface

Plate III. Detached fertile units and fertile scales of *Bernettia inopinata* from the sandpit Küfner, Pechgraben. All scale bars = 1 cm.

Fig. 1.	Specimen BT 005959.00.
Fig. 2.	Specimens G83–90.
Fig. 3.	Fertile element with ovules showing faint impressions of venation of superjacent sterile element; specimen 12-2-1990.
Fig. 4a,b.	Part and counterpart of fertile unit; (a) fertile element with ovules; (b) sterile element, showing faint impression of the ovule cluster; specimen BT005472.01.
Fig. 5.	Detail of Pl. III, 1, showing ovules; note central, more or less circular areas suggested to represent micropylar openings and radially arranged striae.
Fig. 6.	Several ovules showing central, more or less circular area and radially arranged surface striae; specimen BT005476.01.


1
2
3
4a
4b
5
6

bearing parallel striations and two veins; other surface (except base and margins) covered with three-locular synangia; pollen polyplicate, type *Ephedripites*).

Species: *Piroconites kuespertii* Gothan, 1914 ex Kustatscher, Van Konijnenburg-van Cittert, Bauer et Krings.

Selected references:
1914 *Piroconites kuespertii* Gothan, p. 130–132, pl. XXVIII, 4, text-fig. 4.
1992 *Piroconites kuespertii* Gothan, Kirchner, p. 34–35, pl. VIII, 4–6, text-fig. 5.
1992 *Piroconites kuespertii* Gothan, Van Konijnenburg-van Cittert, p. 241–246, 253, pl. I, 1–3, pls. II–III.
Holotype (hic designatus): Because the genus *Piroconites* was not validly published, designation of a holotype (not neotype) is mandated. Since the repository of the specimen illustrated by Gothan (1914: pl. XXVIII, 4) cannot be traced (probably a private collection), we select specimen UU11085, described and figured by Van Konijnenburg-van Cittert, 1992 (Pl. I, 2 and details of synangia in Pl. II, 2, 3), as the holotype. This specimen is housed in the collections of the Laboratory of Palaeobotany and Palynology, University of Utrecht, The Netherlands.

Specific diagnosis (from Van Konijnenburg-van Cittert, 1992): Spatulate microsporophylls with a crescent-shaped base; greatest width in distal portion. One, probably abaxial, surface having parallel striations and two veins; other surface (except base and margins) covered with three-locular synangia; pollen polyplicate, type *Ephedripites*; pollen length c. 50–60 μm, width c. 25–35 μm; plicae straight or tortuous; exine thin, almost smooth (psilate).

Distribution: *Piroconites kuespertii* is widespread and locally quite abundant in Lower Jurassic strata of Upper Franconia, Germany. *Piroconites*-type fossils have recently also been described from Lower Jurassic strata of Poland (Barbacka et al., 2010).

Locus typicus: Sandpit Lautner, Upper Franconia, Bavaria, Germany.

Stratum typicum: Lower Jurassic "Pflanzenton" sensu Weber, 1968.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.revpalbo.2016.05.003.

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