Schozachia donaea n. gen., n. sp., a new cycad megasporophyll from the Middle Triassic (Ladinian) of Southern Germany

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Abstract

A new cycad megasporophyll, *Schozachia donaea* n. gen., n. sp. from the Lower Keuper-Hauptsandstein (Ladinian, Middle Triassic) of Baden-Württemberg (Germany) is described. The fertile completely preserved leaf resembles megasporophylls of the extant cycad genus *Cycas* (Cycadales). Ovules are arranged in two longitudinal rows in the proximal region. The distal part is formed by a pinnate sterile lamina. The specimen is exceptionally well preserved as a compression and impression fossil. It provides information on outer and inner morphology which is documented in detail. *Schozachia donaea* n. gen., n. sp. is compared with fertile Triassic leaves, and also with Palaeozoic leaves which are considered important for the origin and evolution of cycad megasporophylls.

Keywords: Middle Triassic, Ladinian, Lower Keuper, megasporophyll, Cycadales, *Dioonitocarpidium*, *Archaeocycas*, Germany.

Zusammenfassung

Mit *Schozachia donaea* n. gen., n. sp. wird ein neues Cycadeen-Megasporophyll aus dem Unterkeuper-Hauptsandstein (Ladinium, Mittlere Trias) von Baden-Württemberg (Deutschland) beschrieben. Das fertile vollständig erhaltene Blatt erinnert morphologisch an Megasporophylle der rezenten Gattung *Cycas* (Cycadales). Der fertile proximale Abschnitt trägt die in zwei Längsreihen angeordneten Samen bzw. Samenanlagen. Der distale Abschnitt wird von einer gefiederten sterilen Blattlamina gebildet. Das als Positiv und Negativ vorliegende Fossil ist von außergewöhnlich guter Erhaltung und erlaubt einen einzigartigen Blick auf seine innere und äußere Struktur. *Schozachia donaea* n. gen., n. sp. wird detailliert dokumentiert und mit triassischen und paläozoischen Funden fertiler Blätter verglichen, die mit Ursprung und Evolution der Cycadeen-Megasporophylle in Beziehung gebracht wurden.

Contents

1. Introduction

1.1. Records of fossil cycad megasporophylls

The first fossil cycad-like megasporophylls were described by Pomel (1849), who presented the two Jurassic morphospecies *Crossozamia moreana* Pomel and *C. hennocquei* Pomel from Saint-Mihiel, France. In 1897, Nathorst described a megasporophyll with undivided lamina from the Upper Triassic (Rhaetian) of Southern Sweden. Florin (1933) recognised its affiliation to cycads and named it *Palaeocycas integer* (Nathorst) Florin based on epidermal structures (Gao & Thomas 1989; Norstog & Nicholls 1997). Rühle von Lilienstern (1928) recorded *Dioonitocarpidium pennaeforme* (Schenk) Rühle von L. from the Middle Triassic (Ladinian) of Germany and described it as an oblong pinnately compound leaf with two ovules at base. Kräusel (1949, 1953) described the two morphospecies *Dioonitocarpidium keuperianum* (Krasser) Kräusel and *D. liliensterni* Kräusel from the Upper Triassic (Carnian) of Lunz (Austria), bearing more than two ovules. The fourth morphospecies of *Dioonitocarpidium*, *D. moroderi* (Leonardi) Kustatscher et al., is known from the Middle Triassic (Ladinian) of the Dolomites (Northern Italy).

Megasporophylls of the cycad type were also recorded from the Paleozoic, when GAO & THOMAS (1989) described some morphospecies of *Crossozamia* from the Lower Perm (Lower Shihhotse Formation) of Taiyuan (Province Shanxi, China). With their divided lamina, the leaves resemble the megasporophylls of the extant Genus *Cycas*.

1.2. Origin and evolution of cycad megasporophylls

Morphological and recent molecular studies revealed that cycads are monophyletic within the gymnosperms (CHAW et al. 2005; HILL et al. 2003; GRIMM 1999; STEVENSON 1990). The direct ancestor is suspected among the extinct plant group of the pteridosperms. Some authors (CHAMBERLAIN 1919; DELEVORYAS & HOPE 1971; DELEVORYAS 1982) presumed that cycad megasporophylls evolved from a pinnate pteridospermous leaf, while others (MAMAY 1969, 1976; LEARY 1990; GILLESPIE & PFEFFERKORN 1986) proposed that they derived from an entire taeniopterid pteridospermous ancestor.

CRIDLAND & MORRIS (1960) described a fertile taeniopterid leaf from the Upper Pennsylvanian (Virgilian, Carbon; Lawrence Shale, Ireland Sandstone) of Kansas (USA) and established the morphogenus *Spermopteris* with *S. coriacea* (GÖPPERT) CRIDLAND & MORRIS as the single species. The slender elongate leaf is characterized by two longitudinal rows of ovules which are confined to the terminal region, it was supposed to be a pteridospermous leaf bearing ovules attached to the abaxial surface of the lamina. In the bilateral arrangement of ovules, *Spermopteris* was considered as a possible precursor of cycad megasporophylls by MAMAY (1969, 1976). He supposed that cycad megasporophylls evolved from a *Spermopteris*-like ancestor and presented *Phasmatocycas kansana* MAMAY and *Archaeocycas whitei* MAMAY from the Lower Perm of Texas and Kansas (USA) as early stages of cycad megasporophylls (MAMAY 1969, 1973). He reconstructed both morphospecies as bilateral symmetrical leaves with a distal broadened, taeniopterid lamina, and a proximal part bearing two longitudinal rows of ovules. In *A. whitei*, the ovules should be inserted to the lamina, but in *P. kansana* to the elaminar midrib.

MAMAY (1976) proposed an evolutionary transition series with the ovules of the *Spermopteris*-like ancestor getting restricted to the proximal region, and a change in the ovule attachment from the lamina surface to the leaf midrib. The elimination of the lamina from the proximal, fertile portion should result in a *Phasmatocycas*-like structure, the division of the distal lamina in a *Cycas*-like megasporophyll. KERP (1983) proposed a more gradual and more overall reduction of the megasporophyll, and described *Sobernheimia jonkeri* KERP from the Lower Permian (Autunian) of Bad Sobernheim (Rheinland-Pfalz, Germany) as a possible intermediate form between the pteridospermous morphogenus *Spermopteris* and the cycadalean morphogenus *Phasmatocycas*. And LEARY (1990) presented *Lesleya cheimarosa* LEARY & PFEFFERKORN from Lower Pennsylvanian (Naumurian B or C, Carbon) of Illinois (USA) as the stratigraphically oldest ancestor of modern cycads, and proposed the origin of cycads at a minimum of 320 million years ago.

1.3. Present state

Nevertheless, more than 150 years after the first description of a fossil cycad megasporophyll, the origin and evolution of cycads is still unresolved.

Based on more completely preserved specimens, GILLESPIE & PFEFFERKORN (1986) reconstructed *Phasmatocycas kansana* as a linear leaf with the ovule-bearing region neither elaminar nor restricted to the proximal area. And a subsequent reinvestigation of the original specimens of *Spermopteris coriacea* by AXSMITH et al. (2003) revealed that the ovules were attached to the leaf midrib in both morphospecies. Consequently, they transferred *S. coriacea* into the morphogenus *Phasmatocycas* and renamed it *Phasmatocycas bridwellii* AXSMITH et al.

So far, there are but a few fossil remains of fertile leaves associated to cycads or to a possible ancestor. Complete specimens are very rare; usually they are only fragmentarily preserved. The morphotaxa are often represented by only few or even single incomplete specimens. These circumstances hamper the realistic reconstruction of even a single complete fertile leaf. The lack of exact and detailed description and documentation in some publications complicates the subject. In their review of previously described *Cycas*-like megasporophylls, GAO & THOMAS (1989) gave an overview of the confusion resulting from improper and mistaken investigation or documentation. Additional materials and their detailed documentation are needed to build up a sound basis for the reconstruction of the origin and evolution of cycad megasporophylls.

In the present paper, a new genus and species of cycad megasporophylls from the Middle Triassic (Ladinian) of Southern Germany are described and compared with other Triassic species and with Paleozoic fertile leafs, which were previously discussed in context with the origin and the evolution of cycad megasporophylls.

Acknowledgements

I am grateful to the private collector HUBERT DONÀ (Eberdingen-Hochdorf, Germany) for allowing to examine and describe the specimen. He also donated the plate with the compression fossil and specimen P2097 (Fig. 6) to the SMNS. I would like to thank ANNETTE SCHULTHEISS and THOMAS RATHGEBER for taking the photographs and ACHIM LEHMKUHL for preparing the holotype of *Schozachia donaea* n. gen., n. sp. (all SMNS). For their critical review of the manuscript, valuable comments and helpful hints I would also like to thank RONALD BÖTTCHER, RONALD

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2. Material

The here described fossil was discovered in 2005 by the private collector Hubert Donà (Eberdingen-Hochdorf, Germany). The fertile leaf is undistorted and well preserved as a compression and impression fossil, respectively. The two counterparts show the specimen in a longitudinal section. The compression part is complete preserved, with only a small fragment ($10\,mm^2$) of the symmetric sterile lamina being lost, but information content is not reduced. Two-thirds of the impression part are preserved, while the apical end of the sterile lamina is lacking; however, the impression fossil provides additional information on morphological structure of the new morphospecies.

The cleavage plane between the two counterparts runs at a slight angle to the longitudinal axis of the megasporophyll. The fertile area is partially represented as a longitudinal section, but is three-dimensional at its base. The compression fossil (P1994) is deposited in the Staatliches Museum für Naturkunde Stuttgart (SMNS). Its counterpart is housed in the private collection of Hubert Donà.

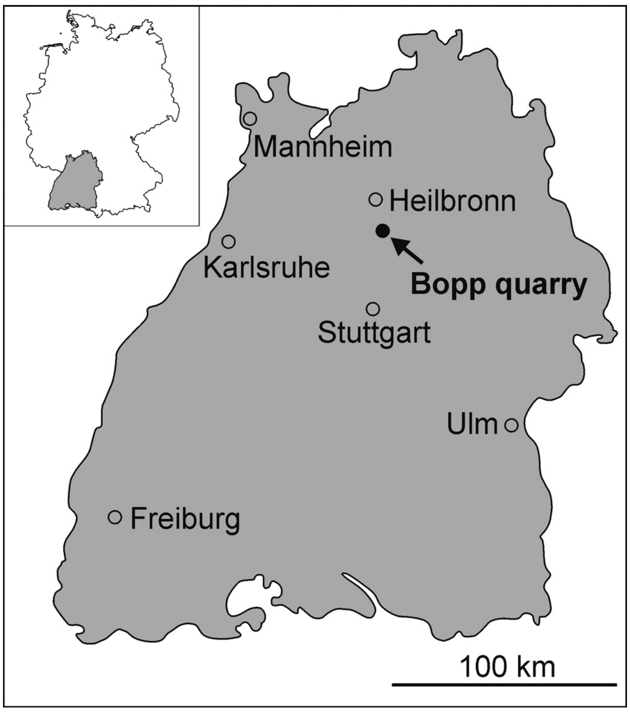

Fig. 1. Map of Baden-Württemberg (Southern Germany) with the type locality of *Schozachia donaea* n. gen., n. sp. ('Bopp quarry' in the Schozachtal near Ilsfeld).

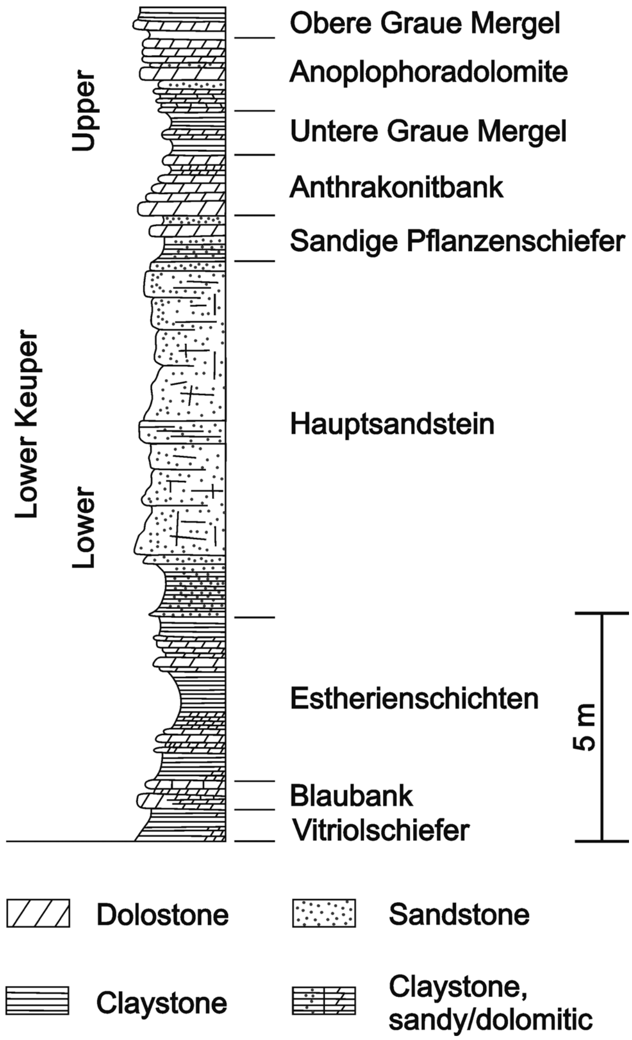

Fig. 2. Stratigraphical column of the Bopp quarry (modified after Brunner 1984) near Ilsfeld (Germany) with the type horizon 'Hauptsandstein' of *Schozachia donaea* n. gen., n. sp. Exact finding level unknown.

The type locality (Bopp quarry, bmk Steinbruchbetriebe) in the Schozachtal at Ilsfeld (Baden-Württemberg, Germany) is an active Muschelkalk quarry (Fig. 1). The Lower Keuper deposits overlaying the Muschelkalk are not commercially used.

The type horizon, the Hauptsandstein of the Lower Keuper (Ladinian, Erfurt Formation, Middle Triassic), is a finely grained clay-bound sandstone, with a thickness in the Ilsfeld area of up to 10 m (Fig. 2; Brunner 1984). The Hauptsandstein is developed as 'Flutfazies' or 'Normalfazies'. The 'Flutfazies' is characterized by broad-layered cross-laminated fluvial sandstones. The 'Normalfazies' consists of thin-layered beds of parallel-laminated sandstone. *Schozachia donaea* n. gen., n. sp. was imbedded in the parallel-laminated sandstone.

Tab. 1. Fossil plant remains of the Lower Keuper-Hauptsandstein (Ladinian, Middle Triassic; Erfurt Formation) of Baden-Württemberg (Germany) (CSAKI & URLICHS 1985).

Lycopodiopsida
Annalepis zeilleri FLICHE, 1910
Equisetopsida
Equisetites arenaceus (JAEGER) SCHENK, 1864
Equisetites latecostatus (MUENSTER) FRENTZEN, 1933
Equisetites sp.
Neocalamites merianii (BRONGNIART) HALLE, 1908
Schizoneura paradoxa SCHIMPER & MOUGEOT, 1844
Phyllotheca sp.
Filicopsida
Anotopteris distans (PRESL) SCHIMPER, 1869
Chiropteris lacerata (QUENSTEDT) RÜHLE VON LILIENSTERN, 1931
Danaeopsis arenacea (JAEGER) CSAKI & URLICHS, 1985
Neuropteris remota PRESL, 1838
Pecopteris schoenleiniana BRONGNIART, 1835–36
Chelepteris sp.
Cycadopsida
Dioonitocarpidium pennaeforme (SCHENK) RÜHLE VON LILIENSTERN, 1928
Bennettitopsida
Pterophyllum sp.
Ginkgopsida
Glossophyllum sp.
Coniferopsida
Willsiostrobus sp.
Swedenborgia sp.
Pagiophyllum foetterlei (STUR) SCHÜTZE, 1901
Incertae sedis
Cladophlebis sp.
Cycadites rumpfii SCHENK, 1864
Sphenopteris sp.
Taeniopteris sp.

Several fossil plant species are known from the Hauptsandstein of Germany. Fossil remains of horsetails, ferns and fernlike leaves, cycads, bennettitals and conifers were found in Baden-Württemberg (Tab. 1), as well as in Bavaria and Thuringia (KELBER 1990; KELBER & HANSCH 1995). From the Hauptsandstein of the BOPP quarry, remains of *Equisetites arenaceus*, *E. latecostatus*, *Neocalamites merianii*, *Taeniopteris* sp. and *Danaeopsis arenaceus* are known.

3. Systematics

Class Cycadopsida BRONGNIARD, 1843
Order Cycadales DUMORTIER, 1829
Family indet.

Genus *Schozachia* ROZYNEK, n. gen.

Etymology: The genus is named after the Schozachtal (valley of the river Schozach), situated in southern Landkreis Heilbronn (Baden-Württemberg, Germany), where the type species has been found.

Type species: *Schozachia donaea* ROZYNEK, n. sp.

Diagnosis. – Megasporophyll consisting of a basal short petiole, a proximal fertile part and distal sterile part. Fertile and sterile parts are divided by a distinct constriction. Fertile part oblong, narrow. Ovules arranged in two longitudinal rows, one on each side of the middle axis. Ovules obliquely attached to the middle axis. Fertile part surrounded by an envelope layer. Sterile part planar; pinnate lamina with a terminal leaflet; leaflets with a single vein.

Schozachia donaea ROZYNEK, n. sp.
Figs. 3–5; Pl. 1, Figs. 1–2

Holotype: Specimen in two plates. Main plate (compression fossil) is deposited in the SMNS under number P1994 (Pl. 1, Fig. 1), the counterpart (impression fossil) in private collection H. DONÀ (Pl. 1, Fig. 2).

Type locality: BOPP quarry (bmk-Steinbruchbetriebe) near Ilsfeld in the Schozachtal, Landkreis Heilbronn, Baden-Württemberg, Germany; 49°03'30"N 9°10'E.

Stratum typicum: Hauptsandstein, Lower Keuper (Erfurt Formation).

Age: Middle Triassic, Ladinian.

Etymology: *Schozachia donaea* n. sp. is named after the private collector HUBERT DONÀ (Eberdingen-Hochdorf, Germany), who found the holotype in 2005 and donated the plate with the compression to the SMNS.

Diagnosis. – Megasporophyll about 100 mm long, length ratio ca. 1 : 4 : 5 (petiole : fertile part : sterile part), bald. Fertile part widened at distal end, ovules very close to each other; ovules numerous, at least 16 per row. Ovules paired in alternate positions. Remains of envelope layer with parallel striation and with gland-like dots. Sterile part of oblong to ovate pinnate lamina, with 35 leaflets at each side; leaflets about 10–15 mm long and 2–3 mm wide, with acute apices; leaflets positioned at a distance of 1–2 mm, in an angle of about 45° to the rachis; basal parts of leaflets partly overlapping.

Description. – *Schozachia donaea* n. gen., n. sp. is a cycad megasporophyll, with a morphological resemblance to megasporophylls of the recent family Cycadaceae PERSOON. The fossil is preserved as a compression (Pl. 1, Fig. 1) and an impression (Pl. 1, Fig. 2). It has a total length of 100 mm. Three distinct parts are clearly recognisable: a short petiole at the base, a fertile in the middle and a distal infertile part.

Petiole ('C' in Figs. 3, 4a): The basal petiole is 7 mm long and 4–6 mm wide. Both the proximal and distal ends of the petiole are expanded.

Fertile part ('B' in Figs. 3, 4a–e): The short petiole is followed by a 38 mm long fertile region. The width of about 7 mm is nearly the same over the whole length, but it is distally widened to 10 mm. The transition to the sterile

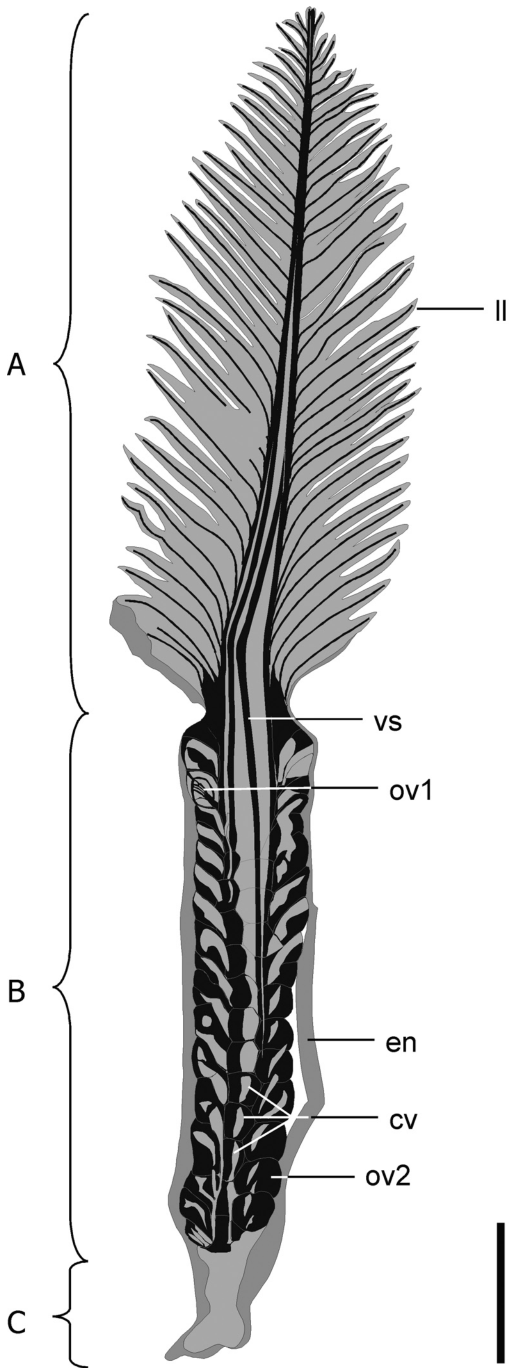

Fig. 3. Semi-schematic figure of *Schozachia donaea* n. gen., n. sp. The megasporophyll is divided in three distinct parts: A: sterile, pinnately compound lamina; B: fertile, ovule bearing part; C: petiole. cv: convex structures on mid-axis, between the ovules; en: remains of layer, presumably enveloped the fertile part; ll: leaflet with single vein; ov1: ovule in longitudinal section; ov2: ovule three-dimensional; vs: remains of vascular system. – Scale: 10 mm.

section is marked by an abrupt 6 mm narrow constriction. The fertile part appears as a longitudinal section (Fig. 4a). Beside the middle axis two longitudinal rows of at least 16 tightly appressed ovules are recognizable in each row. Ovules are in a close series without space in between. The two rows of ovules are arranged alternatingly. Ovules are 3–4 mm long, 2–3 mm wide. The Middle axis of the megasporophyll and the long axis of ovules are forming an acute angle. Longitudinal sectioned ovules resembling scars of female cones ('ov1' in Figs. 3, 4b–c). Only the proximal ovules on the right side are three-dimensional ('ov2' in Figs. 3, 4e). More than half of the proximal part of the area between the rows is not flat but bearing slightly convex structures ('cv' in Figs. 3, 4c, e). Distally, the fertile section is followed by the sterile part of the megasporophyll.

Sterile part ('A' in Figs. 3, 5a–c): Sterile leaf oblong to ovate, approximately 55 mm long, maximum width 21 mm. Lamina pinnate, with 35 leaflets on either side, and one terminal leaflet at the distal end. In the proximal region, the leaflets are approximately 10 mm long, but then rapidly increase to 15 mm, and evenly decrease in the distal one-fourth to 2–3 mm. The leaflets are directed obliquely upwards, occasionally just slightly curved. They mostly overlap at base. The basalmost leaflets are fused. Leaflet width up to 1 mm; leaflets with acute apices, and a single undivided vein (Fig. 5b) consisting of a few bundles arising from the lateral strand in an angle of 45°. Veins arising in regular distances of 1–2 mm. The main axis is gradually decreasing in width from 4 mm at the base to less than 1 mm at the distal end.

Vascular system (Figs. 3, 4, 5c): The megasporophyll is traversed by coalified strands in longitudinal direction, consisting of numerous parallel running veins. The system begins with two strands of approximately 0.8 mm width at base of the fertile part. The right strand dichotomized between the fifth and sixth ovule, and the left strand between the eleventh and twelfth ovule. The resulting four strands pass through the constriction which separates the fertile and sterile parts (Fig. 5c). From the outer longitudinal strans smaller strands branche off ('vb2' in Fig. 4b) and spread out in numerous small veins traversing the ovules ('vb3' in Fig. 4b). In the sterile part, both inner strands approaching the left outer strand, but the right outer strand traverse in nearly straight direction. The outer strands have their maximum distance of 2 mm at base of sterile part. Then the four strands are approaching each other, and in the basal one-third of the sterile lamina both strands of each side fusing together. Apically, the remaining two strands approaching each other while running parallel, closely set.

Envelope layer: Margins of fertile section and petiole of the megasporophyll are surrounded by remains of a thin layer. At both sides an approximately 1 mm wide fringe is recognisable ('en' in Figs. 3, 4d). A similar structure is present on the impression plate as a small 23 mm long and

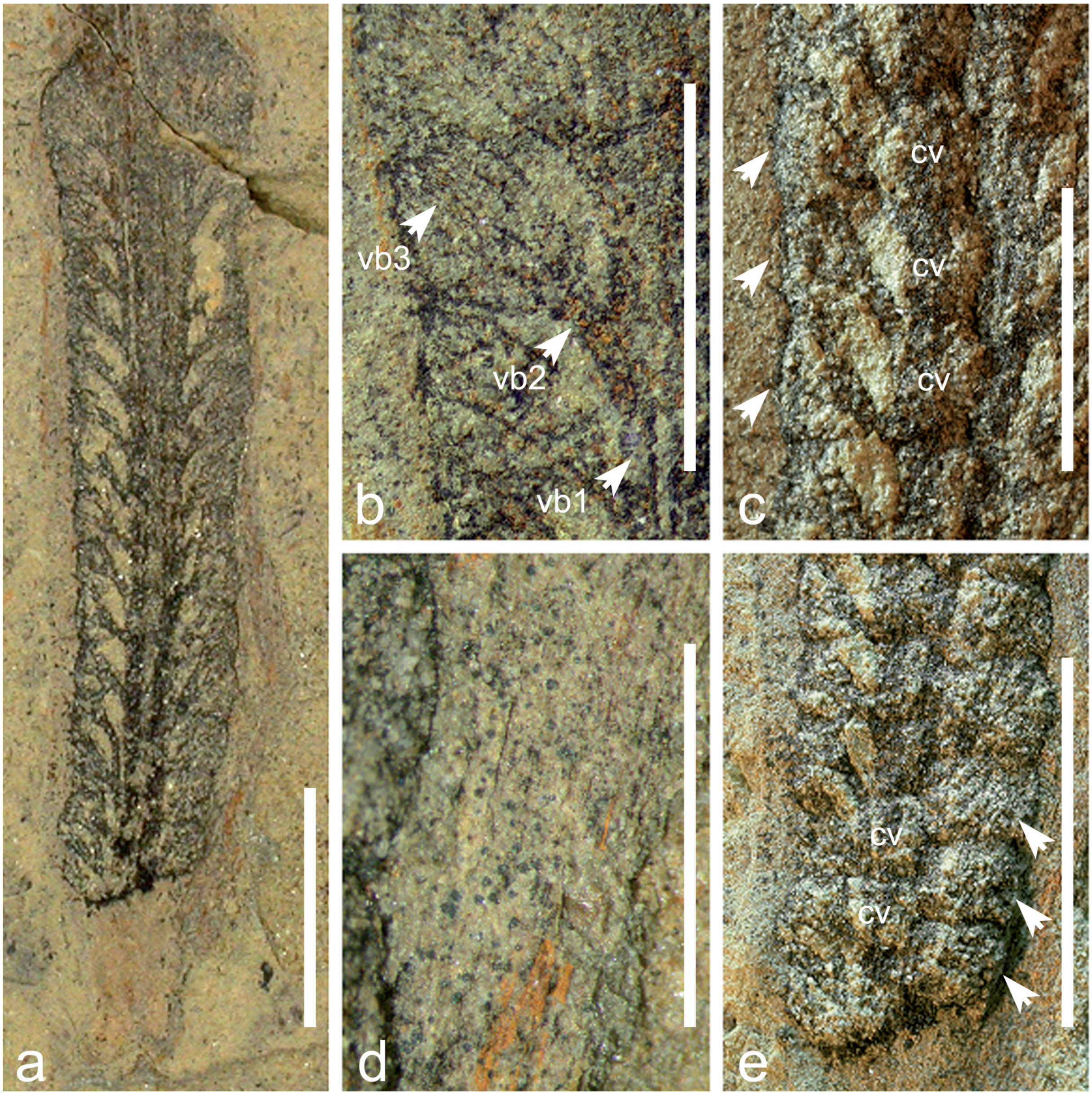

Fig. 4. *Schozachia donaea* n. gen., n. sp**.**, fertile part of megasporophyll, holotype (SMNS P1994); Lower Keuper, Hauptsandstein (Ladinian, Middle Triassic), Bopp quarry near Ilsfeld (Baden-Württemberg, Germany). – **a**. Petiole and fertile part containing two longitudinal rows of ovules. **b**. Vascular system; at left side of the longitudinal vascular strand (vb1) smaller strands branched off (vb2), and spread out in numerous small veins traversing ovule (vb3). **c**. Detail of the fertile part, with ovules in longitudinal section (arrows) and convex structures between the ovule rows (cv). **d**. Remains of layer presumably enveloped the fertile part, showing parallel striation and gland-like dots. **e**. Ovules on the right side in three-dimensional preservation (arrows) and convex structures between the ovule rows (cv). – Scales: a, e: 10 mm; b–c: 5 mm; d: 2.5: mm.

2–3 mm wide stripe (Pl. 1, Fig. 2). These remains of a possible envelope layer show parallel striation and coalified gland-like dots (Fig. 4d). They are observed up to the constriction between fertile and sterile parts.

Surface: The surface of the megasporophyll is completely bald. Neither in the fertile nor in the infertile section or in the remaining envelope layer, hairs or hair-like structures have been observed.

4. Comparisons and discussion

4.1. Comparison of *Schozachia donaea* n. gen., n. sp. with other Triassic fertile leaves

Fossil leaves from the Triassic of Europe which were interpreted as cycad megasporophylls are assigned to the genus *Dioonitocarpidium*, which was introduced by Rüh-

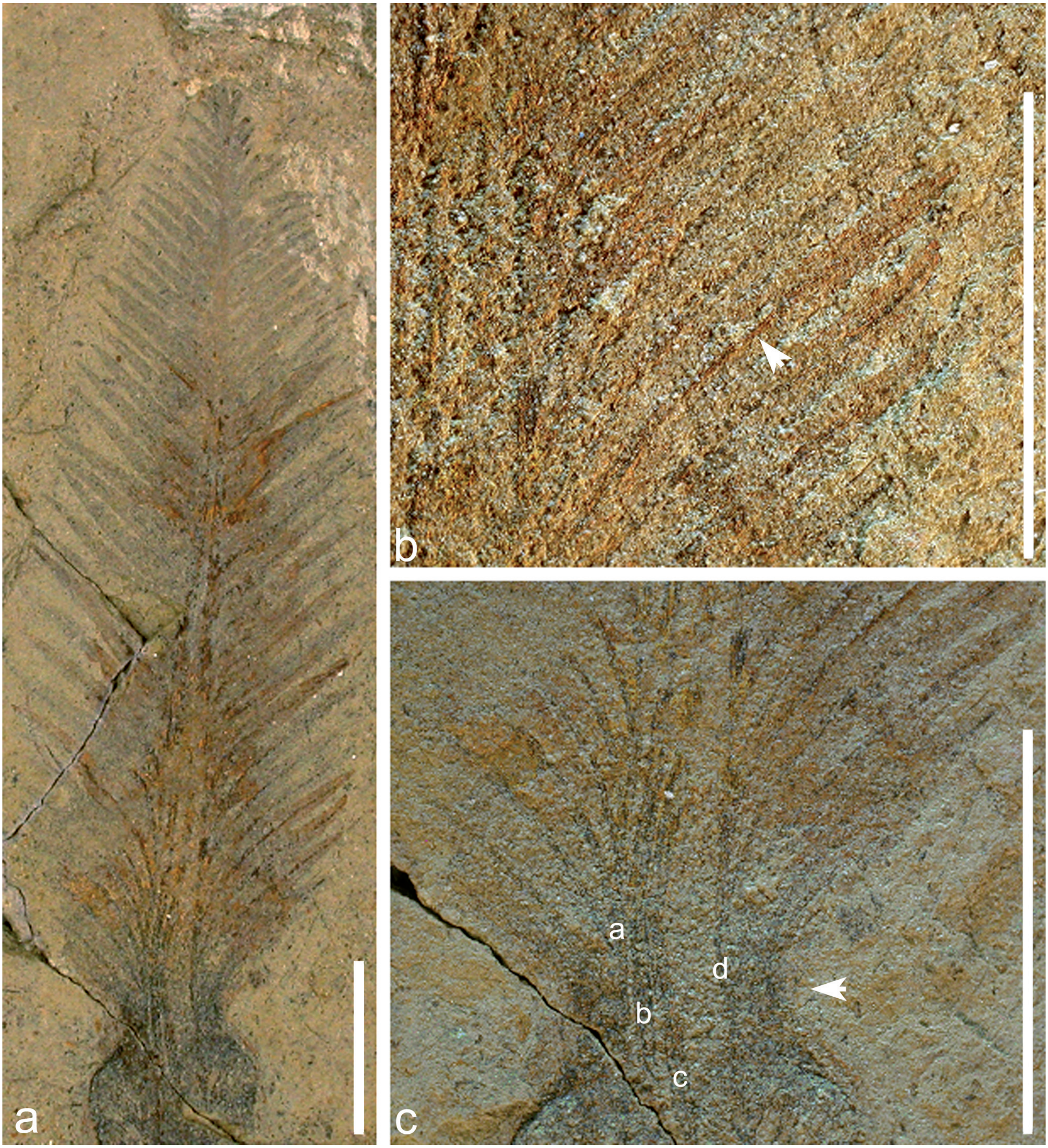

Fig. 5. *Schozachia donaea* n. gen., n. sp., stertile part of megasporophyll, holotype (SMNS P1994); Lower Keuper, Hauptsandstein (Ladinian, Middle Triassic), BOPP quarry near Ilsfeld (Baden-Württemberg, Germany). – **a**. Pinnately compound lamina. **b**. Single veined (arrow) leaflets. **c**. Constriction (arrow) separating the fertile and the sterile part, traversed by four main vascular strands (a, b, c, d). Off the outer strands (a, d) single veins arise and traverse the leaflets. – Scales: 10 mm.

LE VON LILIENSTERN (1928) for cycad-megasporophylls. Today it contains four morphospecies: *D. pennaeforme*, *D. keuperianum*, *D. liliensterni* und *D. moroderi* (RÜHLE VON LILIENSTERN 1928; KRÄUSEL 1949, 1953; KUSTATSCHER et al. 2004; WACHTLER & VAN KONIJNENBURG-VAN CITTERT 2000).

Dioonitocarpidium keuperianum (Krasser) Kräusel, 1949 (Pl. 2, Fig. 1)

Upper Triassic (Carnian), Lunz, Austria

Specimens of *Dioonitocarpidium keuperianum* are slender megasporophylls which are up to 150 mm long. The rachis is bald, but the short pinnae are densely covered with hairs. Length of pinnae only slightly decreasing in apical direction. The basal fertile part is short, extending continuously without a constriction into the sterile part. Several small (< 2 mm) seeds have been recognised, and Kräusel (1953) reported five seeds on a distance of only 8 mm. The surface of the seeds is granulated.

D. keuperianum distinctly differs from *Schozachia donaea* n. gen., n. sp. in lacking a constriction between fertile and sterile parts, and in the surface structure of seeds and pinnae.

Dioonitocarpidium liliensterni Kräusel, 1953 (Pl. 2, Fig. 2)

Upper Triassic (Carnian), Lunz, Austria

The only known specimen of *Dioonitocarpidium liliensterni* consists of a fertile part which is 40 mm long, and a fragmentarily preserved pinnate sterile part of 53 mm; the apex is missing. The fertile and sterile parts are divided by a constriction. The rachis and the 6 to 9 mm long pinnae are distinctly curved. Both rachis and pinnae are covered with fine hairs. The space between pinnae is emarginate. The fertile part is elliptical, widest (7 mm) in the middle. The seeds are ovoid, about 5 mm long, arranged in two longitudinal rows. Kräusel (1953) mentioned a total of four preserved seeds, with three of them arranged in a single row at distances of 12 and 14 mm.

Schozachia donaea n. gen., n. sp. is distinguished in having a straight and bald mid-axis. The leaflets are hairless, straight or only slightly curved, directed towards the apex of the megasporophyll and overlapping each other at the base. The oblong fertile part is equally wide, with the exception of a broadened distal end, and bears much more ovules than *D. liliensterni*.

Dioonitocarpidium moroderi (Leonardi) Kustatscher et. al., 2004

Middle Triassic (Ladinian, La Valle (Wengen) Formation), Dolomites (Italy)

The specimens of *Dioonitocarpidium moroderi* are longer than 180 mm. The fertile and sterile parts are nearly of the same length. The pinnate sterile lamina is up to 30 mm wide, with a very broad (10 mm; almost one-third of the lamina width), longitudinally grooved rachis. The angle between the lamina segments and rachis is ca. 70° (Kustatscher et al. 2004; Wachtler & Van Konijnenburg-Van Cittert 2000).

Schozachia donaea n. gen., n. sp. has a narrower rachis, and an angle of 45° between leaflets and rachis. The preservation state of the proximal section of *D. moroderi* is poor, so the presence of ovules or seeds is uncertain. Therefore a direct comparison of this part between *D. moroderi* and *S. donaea* n. gen., n. sp. is impossible.

Dioonitocarpidium pennaeforme (Schenk) Rühle von Lilienstern, 1928 (Pl. 2, Fig. 3)

Middle Triassic (Ladinian, Lower Keuper, Hauptsandstein), Bavaria and Thuringia (Germany)

Dioonitocarpidium pennaeforme was interpreted as a cycad megasporophyll (Rühle von Lilienstern 1928) with a continuous lamina and two ovoid seeds at its base. The surface of the seeds is granulate or covered with small pits. The rachis is characterized by two longitudinal grooves. The single veined pinnae are covered with fine hairs and arranged in alternate position.

Schozachia donaea n. gen., n. sp. differs from *D. pennaeforme* in the distinct constriction between the sterile and fertile parts of the megasporophyll, in the number and surface structure of seeds and ovules, and the total absence of hairs.

Cycadales gen. et sp. indet. (Pl. 2, Fig. 4)

Middle Triassic (Ladinian, Keuper), Bavaria (Germany)

Additional cycad megasporophylls were mentioned by Kelber (1990) and Kelber & Hansch (1995). The sterile and fertile parts are separated by a constriction. The pinnae are set in short distances, and covered by fine hairs. The ovules are arranged in two longitudinal rows and enclosed by a lamina.

The specimens resemble *S. donaea* n. gen., n. sp. in their overall appearance but contrary to the new species they are not bald.

Cycadales gen. et sp. indet. (Fig. 6)

Middle Triassic (Ladinian, Lower Keuper), Baden-Württemberg (Germany)

Another cycad megasporophyll was collected by H. Donà from Rielingshausen (SMNS P2097). This specimen is also covered by fine hairs.

In contrast to *S. donaea* n. gen., n. sp., the leaflets of this specimen are curved and bent downwards. Also, the mid-axis of the leaflets is broader, and the distances between the leaflets are notably wider, thus the leaflets never overlap.

4.2. Comparison of *Schozachia donaea* n. gen., n. sp. with fertile leaves from the Upper Paleozoic

Pinnate cycad-like megasporophylls are known from layers as early as the paleozoic. DiMichele et al. (2001) mentioned a pinnate megasporophyll under the name *Dioonitocarpidium* sp. from the Early Perm of Texas (USA), resembling the Triassic morphogenus *Dioonitocarpidium*. Fertile leaves similar to megasporophylls of the extant genus *Cycas* have been recorded from the Lower Perm of China and classified as *Crossozamia* (Gao &

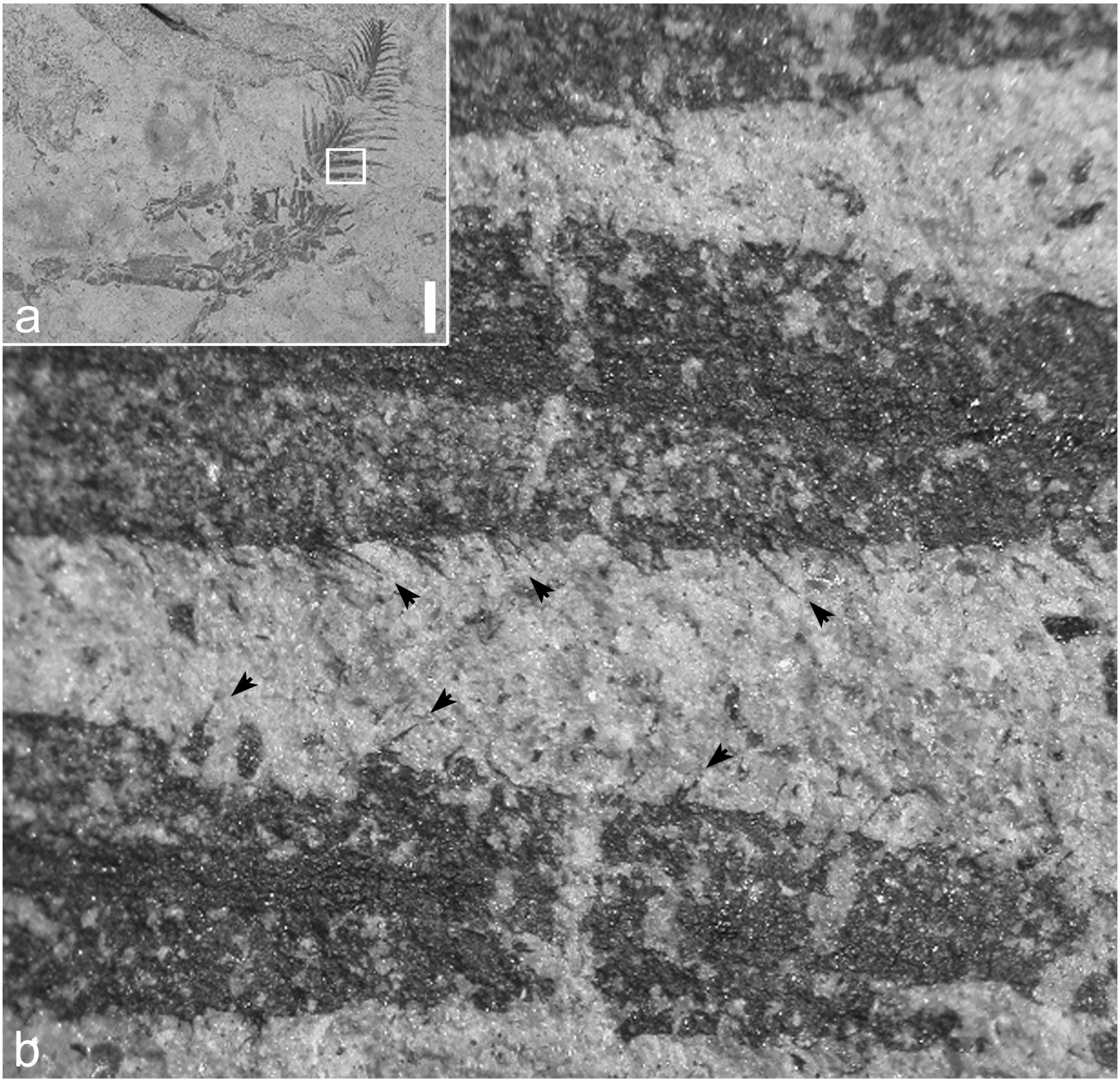

Fig. 6. Cycadales gen. et sp. indet.; Megasporophyll (SMNS P2097); Lower Keuper, Hauptsandstein (Ladinian, Middle Triassic); Rielingshausen, (Baden-Württemberg, Germany). – **a**. Complete specimen. **b**. Detail of the pinnately divided sterile lamina. Hairs are visible at the margins of the leaflets (arrows). – Scale: 10 mm.

THOMAS 1989, ZHU & DU 1981). Other fossil remains, which were discussed concerning possible origin and evolution of cycad megasporophylls are *Phasmatocycas kansana*, *P. bridwellii*, *Sobernheimia jonkeri*, *Archaeocycas whitei* and *Lesleya cheimarosa*.

***Dioonitocarpidium* sp.**

Early Permian (Late Leonardian Series), Texas (USA)

The megasporophyll mentioned by DIMICHELE et al. (2001) has a pinnate sterile lamina and a fertile basal part. Both rachis and pinnae are densely covered with short hairs. The Permian material differs from *S. donaea* n. gen., n. sp. by the relatively wide rachis and shorter leaflet with a broad mid-vein. In the Permian material, the longest leaflets are in the proximal part of the sterile lamina. Their length rapidly decreases distally. In *S. donaea* n. gen., n. sp., however, the longest leaflets are in the middle one-third of the long axis of the sterile part, and in the distal one-third the length of leaflets notably decreases. The completely bald leaflets arise in shorter distances, and have smaller mid-veins. In relation to the width of the sterile part the midrib is smaller.

Crossozamia POMEL, 1849 emend. GAO & THOMAS, 1989

The morphogenus *Crossozamia* consists of small cycad megasporophylls bearing fan-like to palmate lamina with the distal margin divided into segments, and a basal, ovule-bearing petiole. The morphospecies of *Crossozamia* are similar to megasporophylls of the extant Genus *Cycas*.

Crossozamia cucullata (HALLE) GAO & THOMAS, 1989 (Pl. 2, Fig. 5)

Permian (Shihhotse-Formation), Shanxi Province (China)

Megasporophylls approximately 30 mm long. The Lamina is fan-shaped, about 15 mm long and 16 mm wide, and deeply dissected into regular segments. The Petiole is about 15 mm long and 2 mm wide. Ovules about 4 × 3 mm in size, found in association with the petiole (ZHU & DU 1981; GAO & THOMAS 1989).

Crossozamia minor GAO & THOMAS, 1989 (Pl. 2, Fig. 6)

Lower Permian (Lower Shihhotse-Formation), Shanxi Province (China)

A megasporophyll with lamina extending about 10 × 10 mm. Lamina palmate, deeply divided into segments, the elongate central segment further divided pinnately. Petiole about 10 mm long and 1 mm wide. Ovules are circular (approximately 3 mm in diameter) laterally attached to the side of petiole. In one case specimens of *C. minor* were connected to an axis, at which the megasporophylls were spirally attached (GAO & THOMAS 1989).

Crossozamia chinensis (ZHU & DU) GAO & THOMAS, 1989 (Pl. 2, Fig. 7)

Lower Permian (Lower Shihhotse-Formation), Shanxi Province (China)

Megasporophylls with palmate lamina about 50 × 60 mm in size. Distal margins of lamina deeply segmented. Central segment oblong, and pinnately divided. Petiole more than 50 mm long and 10 mm wide. Ovules arranged in two rows, one row on each side of the petiole. Ovules ovoid to oblong, approximately 14 × 12 mm in size, arranged in nearly opposite pairs (GAO & THOMAS 1989).

Crossozamia and *Schozachia* n. gen. are clearly different, as *Crossozamia* megasporophylls have a fan-shaped or palmate lamina with a deeply divided distal margin, the ovules are attached in a distance on both sides of the petiole. The lamina of *Schozachia donaea* n. gen., n. sp., on the other hand, is oblong to ovate, pinnate, and has a distinct rachis. Its fertile part has a compact shape, with densely attached ovules. The megasporophyll proximally ends in a short petiole.

Phasmatocycas bridwellii AXSMITH et al., 2003 (Pl. 2, Fig. 8)

Carbon (Upper Pennsylvanian, Virgilian), Kansas (USA)

Phasmatocycas bridwellii has been described as a narrow, linear leaf, about 200 mm long and 10 mm wide, with a short (3–4 mm) petiole (AXSMITH et al. 2003). Complete fertile leaves are unknown. The leaf lamina is taeniopterid, with single or dichotomous forked veins emerging from the multi-stranded midrib. The ovules are arranged in two longitudinal rows, attached perpendicularly to the lateral sides of the midrib. They are found along the distal half of the leaf.

P. bridwelli differs from the cycadalean megasporophyll *Schozachia donaea* n. gen., n. sp. in its gross morphology, where the obliquely directed ovules are restricted to the proximal region, and the distal part is formed by a pinnate lamina.

Phasmatocycas kansana MAMAY, 1973 (Pl. 2, Fig. 10)

Lower Permian (Wellington Formation), Kansas (USA)

Phasmatocycas kansana is preserved as a slender 25 mm long and 2.5–4 mm wide fragment of a fertile axis. The specimen has two lateral rows of ovate to oblong ovules. In each row resinoid bodies are imbedded between the ovules. The ovules are broadly attached perpendicularly to the axis in an alternate to sub-opposite position. MAMAY (1969) reconstructed *P. kansana* as a cycadalean megasporophyll with a proximal elaminar fertil part and a distal taeniopterid steril lamina.

The fertile axis of *P. kansana* clearly differs from the fertile part of *Schozachia donaea* n. gen., n. sp. in the shape of the ovules and their perpendicular orientation at the mid-axis. In *S. donaea* n. gen., n. sp., no resinoid bodies are recognisable between the ovules. MAMAY's reconstruction of a taeniopterid lamina is based on the presence of resinoid bodies on taeniopterid sterile leaves found in association with *P. kansana*. There is no evidence for a real taeniopterid distal lamina in *P. kansana*; therefore, it cannot be compared in this respect with *Schozachia donaea* n. gen., n. sp.

Sobernheimia jonkeri KERP, 1983 (Pl. 2, Fig. 9)

Lower Permian (Autunian), Rheinland-Pfalz (Germany)

The only known specimen of *Sobernheimia jonkeri* is 105 mm long and 20 mm wide (KERP 1983). The leaf is incomplete due to the absence of the basal part and a damaged apical end. The lateral margins of the lamina are divided into elongate, apical rounded lobes of 11 × 1 mm. The lobes are alternating with ovoid bodies.

S. jonkeri and *Schozachia donaea* n. gen., n. sp. are morphologically clearly distinct. In *S. jonkeri*, the sterile and fertile structures alternate, while they are spatially separated in *Schozachia donaea* n. gen., n. sp., with the fertile part being restricted to the proximal region and the distal part produced as a sterile lamina.

Archaeocycas whitei MAMAY, 1973 (Pl. 2, Fig. 11)

Lower Permian (Petrolia Formation), Texas (USA)

The fossil material of *Archaeocycas whitei* consists of 17 to 23 mm long fertile segments, the sterile part is completely unknown. The ovules are arranged in two longitudinal rows with 4 to 6 ovules in each row. The tightly appressed ovules are in opposite position, obliquely orientated. Small circular structures on the surface of each ovule are interpreted as scars of ovule attachment to the lamina.

MAMAY (1969) reconstructed *Archaeocycas whitei* as a ca. 50 mm long cycadalean megasporophyll with a short petiole followed by a fertile part and a sterile distal end. He reconstructed the distal part of the fragmentary preserved material as an entire, taeniopterid sterile lamina.

Archaeocycas whitei, as reconstructed by MAMAY (1969), resembles *Schozachia donaea* n. gen., n. sp. in its gross morphology. In both megasporophylls, the fertile part is restricted to the proximal region, and a sterile lamina forms the distal area. The ovules are arranged in two longitudinal rows, tightly appressed to each other, and directed forwards to the midrib. In contrast, *A. whitei* is apparently a relatively small megasporophyll. The preserved fertile specimens are 17–23 mm long, with 4–6 ovules in each row, while the fertile portion of *S. donaea* n. gen., n. sp. is 38 mm long, bearing at least 16 ovules per row. The ovules are oppositely paired in *A. whitei*, but alternately in *S. donaea* n. gen., n. sp. The midrib of the fertile region of *A. whitei* is flat, while convex structures are visible between the ovule rows of *S. donaea* n. gen., n. sp. (Fig. 4c, e). Circular scars, as found on the ovule surface of *Archaeocycas whitei* and interpreted as attachment points of the ovules to the lamina margins by MAMAY (1969, 1973), are absent in *S. donaea* n. gen., n. sp. According to MAMAY (1969) the ovules of *A. whitei* are inserted at the margins of an involute lamina partly enclosing the fertile area. On the other hand the ovules in *S. donaea* n. gen., n. sp. are directly inserted at the midrib. In MAMAY's reconstruction of *A. whitei* the lamina enrolled distally forms a taeniopterid sterile blade. A constriction between the fertile and sterile parts, like in *S. donaea* n. gen., n. sp., is absent there. In *S. donaea* n. gen., n. sp., remains of an envelope layer surround the margins of the fertile part as well as the short petiole. The envelope layer is characterised by a conspicuous striation and gland-like dots (Fig. 4d), which are absent in the tissue of the pinnate sterile lamina.

Lesleya cheimarosa LEARY & PFEFFERKORN, 1977 (Pl. 2, Fig. 12)

Carbon (Lower Pennsylvanian, Namurian B or C), Illinois (USA)

The fossil material of *Lesleya cheimarosa* consists of few fertile fragments with only one specimen showing a sterile lamina (LEARY & PFEFFERKORN 1977). The 80 mm long taeniopterid lamina is incomplete and represents the basal portion of the sterile part of the leaf. The lamina is folded so that only one half is visible. The lateral veins are single or dichotomized. LEARY (1990) described the fertile part of this specimen as a 60 mm long fragmentarily preserved petiole bearing two longitudinal rows of ovuliferous receptacles.

According LEARY's description and illustrations, *L. cheimarosa* resembles *Schozachia donaea* n. gen., n. sp. in the position of the fertile part (proximal) and sterile lamina (distal). However, the sterile laminae differ as they are taeniopterid in *L. cheimarosa* but pinnate in *S. donaea* n. gen., n. sp. The fertile parts cannot compared. LEARY's documentation of the fertile part is vague, but he pictured a row of five ovuliferous receptacles over a distance of 60 mm, whereas the 38 mm long fertile area of *Schozachia donaea* n. gen., n. sp. at least contains 16 ovules per row.

4.3. General Discussion

Schozachia donaea n. gen., n. sp. is classified as a cycadalean megasporophyll due to its morphological resemblance with megasporophylls of the recent cycadalean genus *Cycas*. *Cycas* megasporophylls are leaf-like, with a sterile, more or less divided lamina and a proximal elaminar fertile part bearing two longitudinal rows of seeds. *Cycas* is the only extant cycad genus with megasporophylls arising directly from the stem apex. Megasporophylls of all other cycad genera differ in their arrangement on the cone axis, like the microsporophylls in all extant cycad genera.

Triassic pinnately compound fertile leaves, which are interpreted as cycad megasporophylls, are classified in the morphogenus *Dioonitocarpidium*, which is a heterogeneous group. With respect of so important features like laminar/elaminar fertile parts and one pair/several pairs of seeds the question arises if it is reasonable to arrange the four morphospecies of *Dioonitocarpidium* in a single morphogenus. A reinvestigation of the known material seems advisable, particularly regarding the question whether the type specimen *D. pennaeforme* is really a female reproductive organ.

Schozachia donaea n. gen., n. sp. resembles material from the Keuper beds of Bavaria (Pl. 2, Fig. 4) mentioned as Cycadales gen. et sp. indet. by KELBER (1990) and KELBER & HANSCH (1995). The leaflets of the sterile parts are similar in length, distance and orientation, and both forms have a distinct constriction between the fertile and sterile parts. On the other hand, these specimens are covered with hairs. *S. donaea* n. gen., n. sp. is completely bald, judging from the excellent preservation where such small structures as hairs would be recognisable if present. KELBER (1990) and KELBER & HANSCH (1995) referred that an envelope layer enclosed the fertile part. Remains of a thin layer bordering the fertile part and petiole of *S. donaea* n. gen., n. sp. might be relicts of an envelope layer originally enclosing the fertile part. Unfortunately, the absolute extension of this envelope in *S. donaea* n. gen., n. sp. is not recognisable. Nevertheless, the impression part shows a small stripe of tissue connected to the basal part of the petiole spreading out diametrically from the megasporophyll (Pl. 1, Fig. 2). Originally, the stripe seems to have covered the middle part of the petiole and at least half of the fertile portion in longitudinal direction. Thus possible the envelope layer has enclosed the entire fertile part during an early developmental stage, and later ripened and fell off by growing and widening of the fertile part. The specific structures like striations and gland-like dots indicate a function to protect against feeding damages. It is considered impossible that the 'protective layer' formed the sterile lamina, because both parts distinctly differ in their textures. Gland-like dots and parallel striations are absent in the distal sterile lamina.

Further investigations are needed to reveal if *S. donaea* n. gen., n. sp. and the material from Bavaria belong to the same morphogenus. Due to the envelope or 'protective lamina', Kelber (1990) and Kelber & Hansch (1995) discussed a possible phylogenetic relationship of their material with the Permian fertile leaf *Archaeocycas whitei*. Considering the circumstances mentioned above the new specimen described in the present paper cannot be classified as a morphospecies of either *Dioonitocarpidium* or *Archaeocycas*. Therefore, *Schozachia donaea* n. gen., n. sp. is described as a new morphogenus and morphospecies.

The attachment of the ovules on the leaf lamina is a characteristic feature of pteridosperms, whereas a subdivision of megasporophylls in a sterile distal lamina and a fertile part restricted to the proximal portion is characteristic to modern cycads. In Mamay's (1969) reconstruction of *Archaeocycas whitei* he combines characters of both plant groups, and interpreted *A. whitei* as an intermediate form between pteridosperms and modern cycads particularly as an early stage in the cycadalean lineage. Mamay (1969, 1976) supposed that cycads derived from pteridosperms with entire taeniopterid leaf lamina, and reconstructed *A. whitei* as a megasporophyll bearing ovules at the proximal involute part of the taeniopterid leaf lamina, which is distally widened to form a sterile blade (Pl. 2, Fig. 11). But the reconstruction is hypothetical. No remains of the sterile part of *A. whitei* have been found, so its shape, structure and morphology are really unknown.

Mamay's (1969) reconstructions of *Archaeocycas whitei* and *Phasmatocycas kansana* based on associated sterile leaf fragments showing similar features like vein curvature or resin-like bodies. Both morphospecies played a central role in Mamay's (1969) postulation of an evolutionary pathway of cycad megasporophylls with a '*Spermopteris*'-like origin. Without evidence of organic attachment, such reconstructions must be critically viewed. As it cannot be excluded that associated leaves belong to the same plant, it is not clear whether they are parts of a single leaf and the same organ, or not. In the case of *P. kansana*, additional fossil material demonstrated that associated sterile and fertile leaves were indeed parts of the same plant, but they also provided evidence that Mamay's (1969) reconstruction of *P. kansana* was erroneous. Furthermore, reinvestigations of the original specimens of '*Spermopteris*' (sensu Cridland & Morris 1960) by Axsmith et al. (2003) revealed a high similarity with *Phasmatocycas kansana*, thus '*Spermopteris*' was transferred as *P. bridwelii* to *Phasmatocycas*. So '*Spermopteris*' is excluded as a potential pteridospermous ancestor of cycad megasporophylls. Not only this, but also the real phylogenetic position of *Phasmatocycas*, previously regarded as cycadalean, is unclear now (Axsmith et al. 2003).

Associated fertile and sterile leaves were also combined by other authors. Rühle von Lilienstern (1928) combined the Middle Triassic sporophyll *Dioonitocarpidium pennaeforme* with the entire sterile leaf *Taeniopteris angustifolia* to a fertile organ. Kustatscher et al. (2004) correlated *D. moroderi* and the taeniopterid sterile leaves *Bjuvia dolomitica* due to their co-ocurrence at the same locality in Val Gardena (South Tyrol, Italy).

The question of what sort of sterile leaves belongs to *Schozachia donaea* n. gen., n. sp. cannot be answered yet. Although the type locality 'Bopp quarry' bears different plant fossils, pinnate or taeniopterid cycadalean leaves have not been found in direct association with *Schozachia donaea* n. gen., n. sp. Nevertheless, the future might reveal additional material of a similarly perfect preservation state as in *Schozachia donaea* n. gen., n. sp., which could help to solve this question.

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Plate 1

Schozachia donaea n. gen., n. sp., megasporophyll, holotype; Lower Keuper, Hauptsandstein (Ladinian, Middle Triassic), Bopp quarry near Ilsfeld (Baden-Württemberg, Germany).

Fig. 1. Compression fossil (SMNS P1994).

Fig. 2. Impression fossil (privat collection H. Donà) (arrow: stripe of tissue which possible envelopes the fertile part of the megasporophyll).

Scale (for both figures): 10 mm.

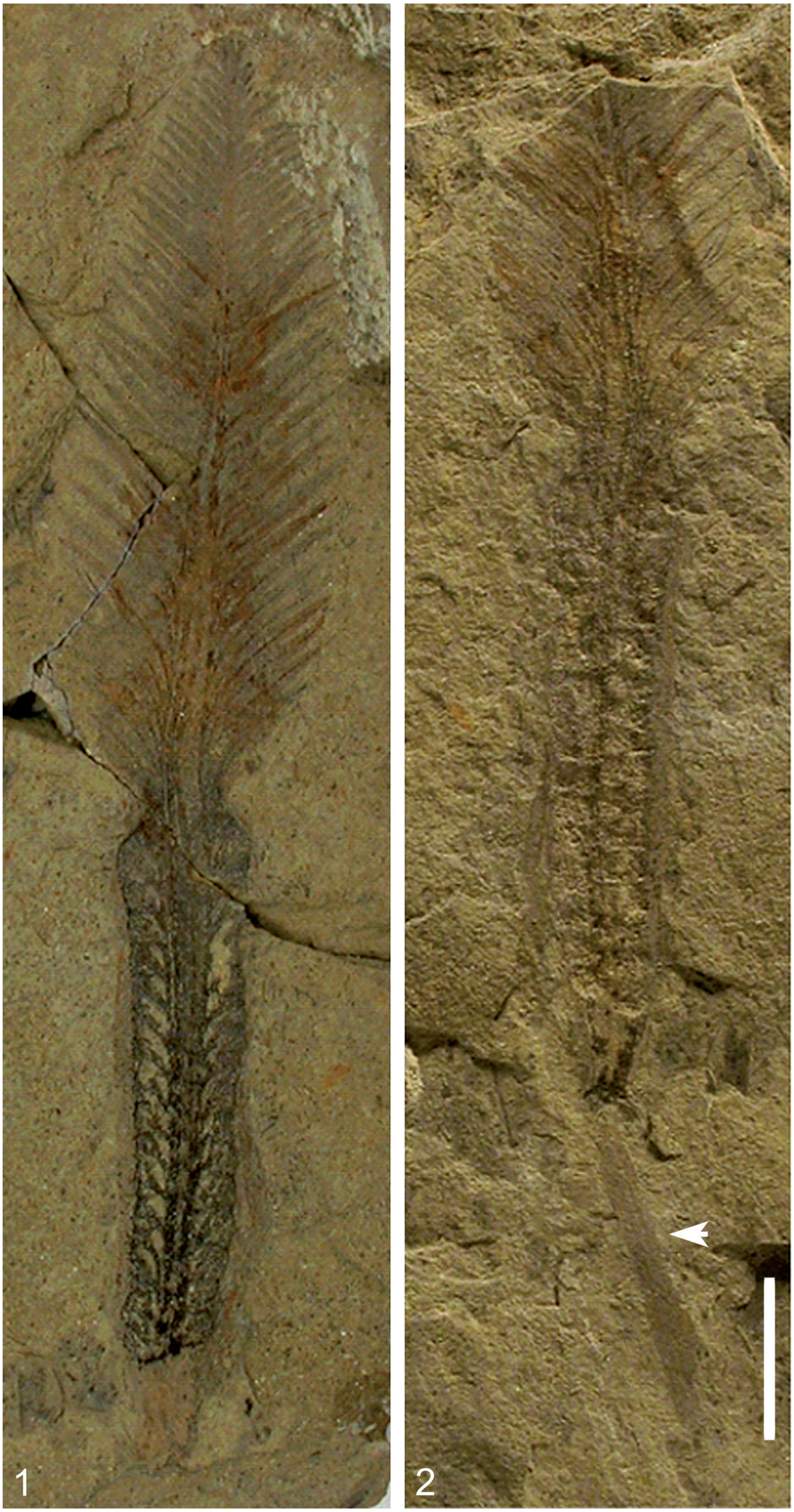
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Plate 2

Figs. 1–3. Reconstructed leaves of the Triassic morphogenus *Dioonitocarpidium*.

Fig. 1. *Dioonitocarpidium keuperianum* (Krasser) Kräusel; Upper Triassic, Carnian; Lunz (Austria) (Kräusel 1949). – Length ca. 120 mm.

Fig. 2. *Dioonitocarpidium liliensterni* Kräusel; Upper Triassic, Carnian; Lunz (Austria) (Kräusel 1953). – Length ca. 90 mm.

Fig. 3. *Dioonitocarpidium pennaeforme* (Schenk) Rühle von Lilienstern; Middle Triassic, Ladinian, Lower Keuper Hauptsandstein; Bavaria, Thuringia (Germany) (Rühle von Lilienstern 1928). – Length ca. 190 mm.

Fig. 4. Cycadales gen. et sp. indet.; Middle Triassic, Ladinian, Keuper; Bavaria (Germany) (Kelber 1990). – Length ca. 65 mm.

Figs. 5–7. Specimens of the Meso- and Palaeozoic morphogenus *Crossozamia* resembling megasporophylls of the recent cycad genera *Cycas* and *Dioon*.

Fig. 5. *Crossozamia cucullata* (Halle) Gao & Thomas; Permian, Shihhotse-Formation; Shanxi Province (China) (Zhu & Du 1981; Gao & Thomas 1989) – Lenght ca. 30 mm.

Fig. 6. *Crossozamia minor* Gao & Thomas; Lower Permian, Lower Shihhotse-Formation; Shanxi Province (China) (Gao & Thomas 1989). – Lenght ca. 15 mm.

Fig. 7. *Crossozamina chinensis* (Zhu & Du) Gao & Thomas*;* Lower Permian, Lower Shihhotse-Formation; Shanxi Province (China) (Zhu & Du 1981; Gao & Thomas 1989). – Length ca. 100 mm.

Figs. 8–12. Reconstructions of fertile leaves from the Palaeozoic.

Fig. 8. *Phasmatocycas bridwellii* Axsmith et al.; Carbon, Upper Pennsylvanian, Virgilian; Kansas (USA) (Axsmith et al. 2003). – Length ca. 300 mm.

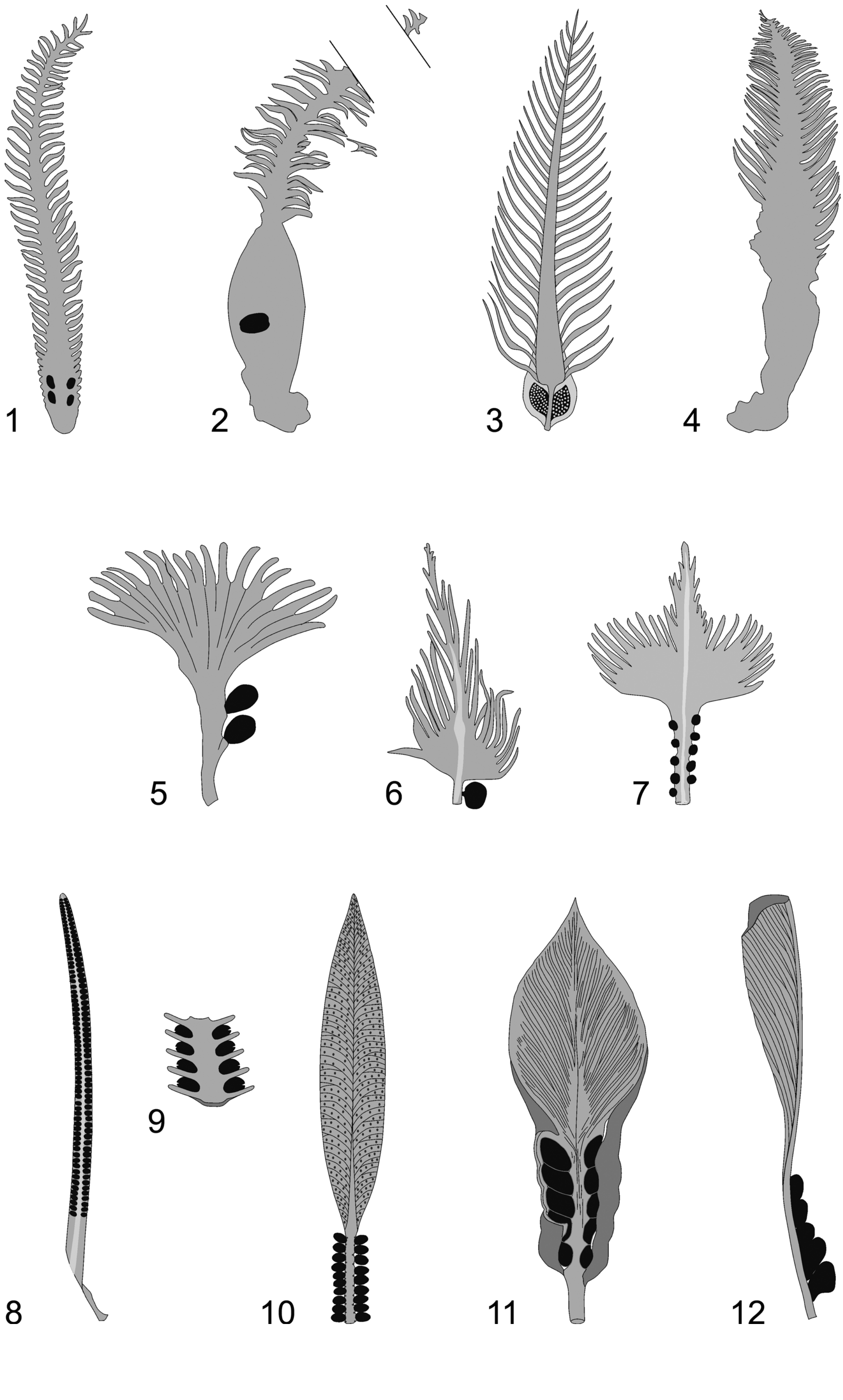
Fig. 9. *Sobernheimia jonkeri* Kerp, Lower Permian, Autunian; Rheinland-Pfalz (Germany) (Kerp 1983). – Lenght of the reconstructed leaf portion ca. 30 mm.

Fig. 10. *Phasmatocycas kansana* Mamay; Lower Permian, Wellington Formation, Kansas (USA) (Mamay 1969, 1973); sterile part hypothetical. – Lenght ca. 120 mm.

Fig. 11. *Archaeocycas whitei* Mamay; sterile part hypothetical; Lower Permian, Petrolia Formation; Texas (USA) (Mamay 1969, 1973). – Length ca. 50 mm.

Fig. 12. *Lesleya cheimarosa* Leary & Pfefferkorn; Carbon, Lower Pennsylvanian, Naumurian B or C; Illinois (USA) (Leary 1990). – Lenght ca. 150 mm.

All illustrations redrawn.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