

Proliferated megasporangiate strobili of *Zamia furfuracea* (Zamiaceae, Cycadales) and its possible evolutionary implications for the origin of cycad-megasporophylls

VEIT MARTIN DÖRKEN & BRIGITTE ROZYNEK

Abstract

At a 30-years-old individual of *Zamia furfuracea* (Zamiaceae, Cycadales) cultivated in the Botanic Garden Bochum (Germany), several proliferated megasporangiate strobili were found. The morphology of normal and proliferated strobili was compared. Within the proliferated strobili the sequence of megasporophylls, cataphylls, trophophyll-like leaves, followed again by a flush of cataphylls, was similar to those developed at the stems of extant *Cycas* species. However, all proliferated megasporangiate strobili were sterile. Within the proliferated strobili the pinnate trophophyll-like leaves that were replacing the terminal megasporophylls can be regarded as an atavism possibly reflecting the primitive character of megasporophylls in cycads. Thus, the results of the morphological examinations and also the comparison with fossil taxa may deliver new data supporting the idea that pinnate cycad-megasporophylls are a plesiomorphic feature within cycads.

Key words: *Zamia*, Cycadales, strobilus, megasporophyll, proliferation.

1. Introduction

Due to the morphology of megasporangiate strobili, megasporophylls and the attachment of ovules, the systematics among extant cycads is still debated. Some authors suggest a concept composing of three families: Cycadaceae, Stangeriaceae, and Zamiaceae (e.g. BIERHORST 1971; STEVENSON 1990; WINK 2006). However, other authors suggest a concept with only two families: Cycadaceae, composing only *Cycas*, and Zamiaceae including all remaining cycads (e.g. STEVENS 2001; HILL et al. 2003; CHAW et al. 2005). In the second concept, which is followed in this study, *Cycas* represents a distinctly separated sister group to all remaining cycads.

All Recent cycads are dioecious. Among both families the microsporophylls are arranged in compact strobili, as is also the case for the megasporophylls in the Zamiaceae (Fig. 1A). Mega- and microsporangiate cycad-strobili are unbranched structures, insofar as they reflect the morphology required for the strobilus- or euanthium-concept of the evolution of the angiospermous flower. Such strobili represent unisotomous branches, terminating the activity of the apical meristem (STEVENSON 1988). The vertical growth of the main stem is, however, continued by a new meristem, finally shifting the strobili in a seemingly lateral position (GAO & THOMAS 1989). Within zamiaceous megasporangiate strobili a large number of megasporophylls are inserted more or less compact (e.g. STEVENSON 1988, 1990; GIFFORD & FOSTER 1989; JONES 1993; OBERMANN 2003; KUNZE 2008). Among the Zamiaceae, megasporophylls have a strongly reduced and entire distal lamina. They are

often wedge-shaped with a hexagonal outer face. In some species they have one or two distal spine-like appendages. Each megasporophyll bears only two ovules, which are developed deeply within the strobilus. The micropyles are pointing towards the axis of the strobilus.

In contrast with the Zamiaceae, among the Cycadaceae such compact megasporangiate strobili are not developed (e.g. GIFFORD & FOSTER 1989; STEVENSON 1990). In the Cycadaceae, megasporophylls are inserted in a loose crown surrounding the apex of the stem (Fig. 1B). Among Cycadaceae, megasporophylls and trophophylls are both developed from the same apical stem meristem. Among *Cycas* trophophylls are followed by several strongly reduced mucronate to rostrate cataphylls, which are followed by a flush of megasporophylls. In all *Cycas* species, megasporophylls represent more or less strongly reduced pinnate leaves. In the position of basal leaflets (2)4–8 ovules are inserted at the rachis of each megasporophyll (Fig. 2). The micropyles point away from the rachis and also from the stem. In extant *Cycas* species the distal incision of the lamina varies strongly among species. For example, in *Cycas revoluta* (Fig. 2A) the distal part is distinctly lobed, while it is nearly entire in *Cycas circinalis* (Fig. 2C). In this respect species such as *Cycas rumphii* represent intermediate forms (Fig. 2B).

Today, cycads are cultivated worldwide in botanical collections and Mediterranean gardens and parks (e.g. SCHNEIDER & MIKA 2012; DÖRKEN & STEINECKE 2012). Apart from *Cycas revoluta*, the Mexican *Zamia furfuracea* L.f. especially became a standard organism for representing morphology, anatomy, and also the lifecycle of

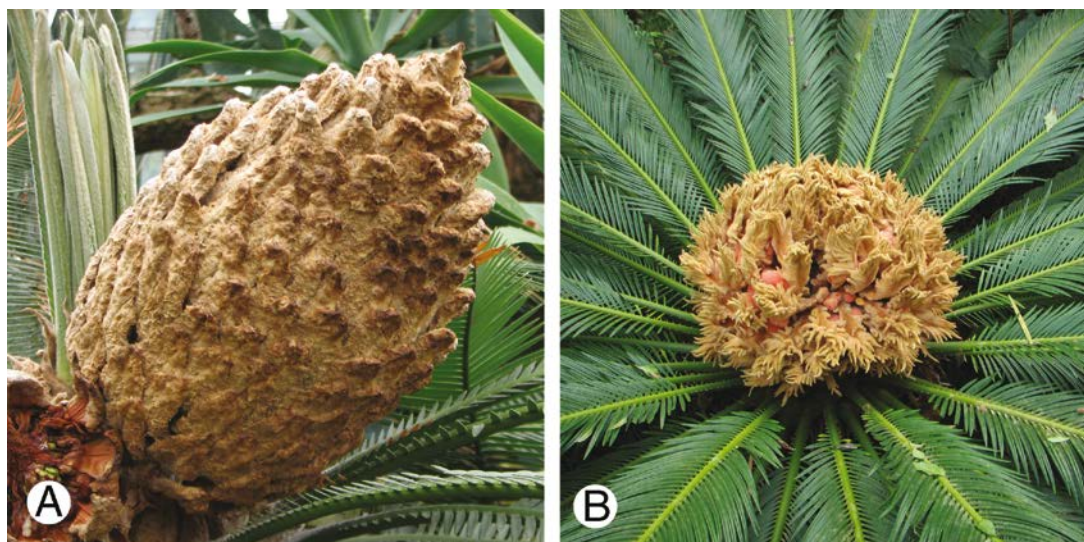


Fig. 1. In Zamiaceae megasporophylls are arranged in more or less compact strobili; in Cycadaceae they are developed in a loose crown surrounding the apex of the stem. **A.** *Dioon edule* (Zamiaceae); **B.** *Cycas revoluta* (Cycadaceae).

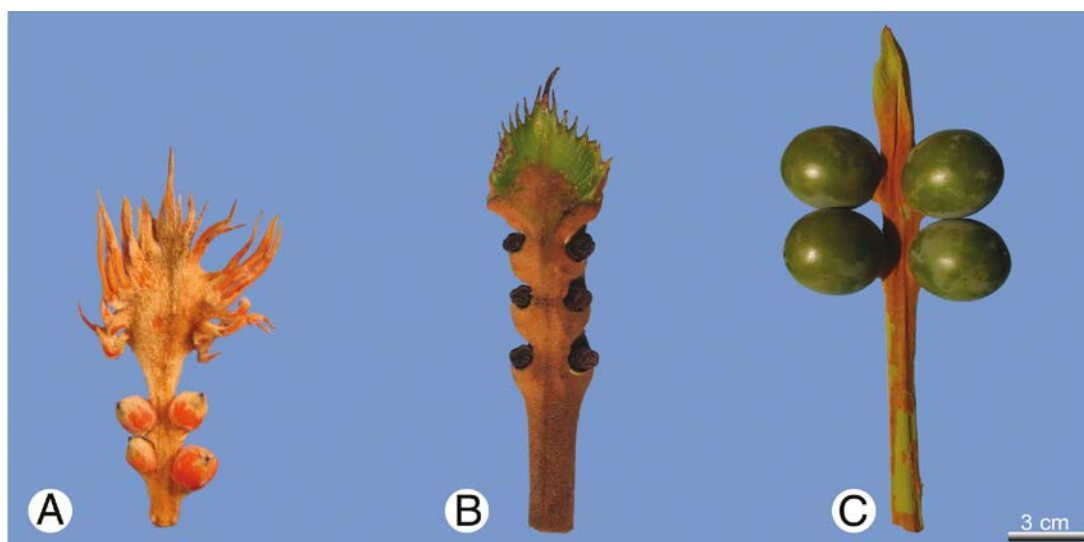


Fig. 2. Megasporophylls of different *Cycas* species; the incision of the lamina varies interspecific strongly; **A.** *Cycas revoluta*; **B.** *Cycas rumphii*; **C.** *Cycas circinalis*.

cycads. At a 30-years-old individual of *Zamia furfuracea* cultivated in the Botanic Garden Bochum (Germany), in addition to the majority of normal megasporangiate strobili, some abnormal proliferated strobili were found. Their morphology was examined in detail and the collected data were compared with other cycads, both extant and fossil. In earlier studies about proliferated coniferous “seed-cones” it could be shown that such malformations are especially helpful for suggesting evolutionary scenarios, if otherwise simultaneous developmental steps are uncoupled, leading

to two or more subsequent steps (DÖRKEN 2012). Therefore the examination of the proliferated strobili seems to be promising for collecting new data that might be helpful for elucidating the evolutionary pathway of megasporophylls in cycads.

Acknowledgements

We are grateful to Mr. WOLFGANG SCHLESIES and Mrs. ANNETTE HÖGEMEIER (Botanic Garden of the Ruhr-University Bochum, Germany), Dr. RALF OMLOR (Botanic Garden Johannes

Tab. 1. Material used in this study (BG BOCH = Botanic Garden Ruhr-University Bochum; BG GIESS = Botanic Garden Justus-Liebig-University Gießen; BG MZ = Botanic Garden Johannes Gutenberg-University Mainz; PG F = Palmengarten Frankfurt a. M.).

taxon	material	location
<i>Cycas circinalis</i>	megasporophyll	BG GIESS
<i>Cycas revoluta</i>	megasporophyll	BG BOCH
<i>Cycas rumphii</i>	megasporophyll	PG F
<i>Zamia furfuracea</i>	female strobili (wild-type)	BG BOCH; BG MZ
<i>Zamia furfuracea</i>	proliferated female strobili	BG BOCH

Gutenberg-University Mainz, Germany), Dr. HILKE STEINECKE (Palmengarten Frankfurt a. M., Germany) and Dipl.-Ing. HOLGER LAAKE (Botanic Garden Justus-Liebig-University Gießen, Germany) for their generous providing of research material and to Prof. RICHARD M. BATEMAN DSc (Kew, Richmond, UK) for critical comments on an earlier version of the manuscript and Dr. WAYNE DAWSON (Ecology, University of Konstanz, Germany) for his linguistic support. The numerous and detailed comments on an earlier version of the manuscript by the two anonymous reviewers helped us to improve the manuscript significantly.

2. Material and methods

All material was collected from specimens cultivated in temperate houses in different German Botanic Gardens (Tab. 1). Macrophotography was done with a digital camera (CANON POWERSHOT IS2), microphotography with a digital microscope (KEYENCE VHX 500 F).

3. Results

3.1. Morphology and anatomy of megasporangiate strobili (wild-type)

In *Zamia furfuracea* megasporangiate strobili are erect and arise after a flush of brownish mucronate to rostrate cataphylls. The strobili are *c.* 20–25 cm long and 6–7 cm in width. They have a peduncle 5–10 cm long (Fig. 3A). The strobili are composed of about 80–120 wedge-shaped megasporophylls with a hexagonal outer face (Fig. 3C). Megasporophylls have nearly no chlorophyll. The most proximal megasporophylls are sterile and partly to entirely fused congenitally with each other (Fig. 3B). The most distal megasporophylls are also sterile but not fused with each other. Only megasporophylls in the middle of the strobili have fertile ovules developing megaprothalli, and later forming embryos. At each megasporophyll two ovules are inserted (Fig. 3D). The ovules are developed deep inside the strobili

with micropyles pointing towards the axis of the strobilus. Within the strobili no bracts are developed.

3.2. Morphology and anatomy of proliferated megasporangiate strobili

On a 30-years-old individual cultivated in the Botanic Garden Bochum, apart from normal-shaped strobili several malformed ones had developed. The latter showed proliferations of different intensity (Figs. 4, 5, 8). Contrasting to normal-shaped megasporangiate strobili, all found proliferated strobili were notably smaller and consisted of significantly less megasporophylls. Furthermore, all proliferated strobili were sterile.

3.2.1. Weakly proliferated megasporangiate strobili

In basal parts these weakly proliferated, sterile strobili are similar to normal-shaped ones (Fig. 4A). Most basal megasporophylls are congenitally fused with each other (Fig. 4B). Megasporophylls inserted in the middle of the strobili are wedge-shaped, with a more or less hexagonal and hairy outer face (Fig. 4A). They are peltate leaf-like with a central stalk (Fig. 4C). They are followed by some green, linear, and approximately 5 cm long leaves (Fig. 4D), which are followed by green, *c.* 3–8 cm long, flattened and prominently hairy, mucronate to rostrate cataphylls (Fig. 4E). Some of them did not have completely separated lateral leaflets at their base (Fig. 4F).

3.2.2. Strongly proliferated megasporangiate strobili

In strobili showing the strongest proliferations (Figs. 5, 8), the basal part (Figs. 5B, 8B) is similar to those developed within normal-shaped strobili. Megasporophylls are wedge-shaped, poor in chlorophyll, and with a more or less hexagonal hairy outer face (Fig. 6A). Some of them terminate in two free ends (Figs. 5D, 6B, C). In more distal parts megasporophylls are followed by several linear about 5 cm

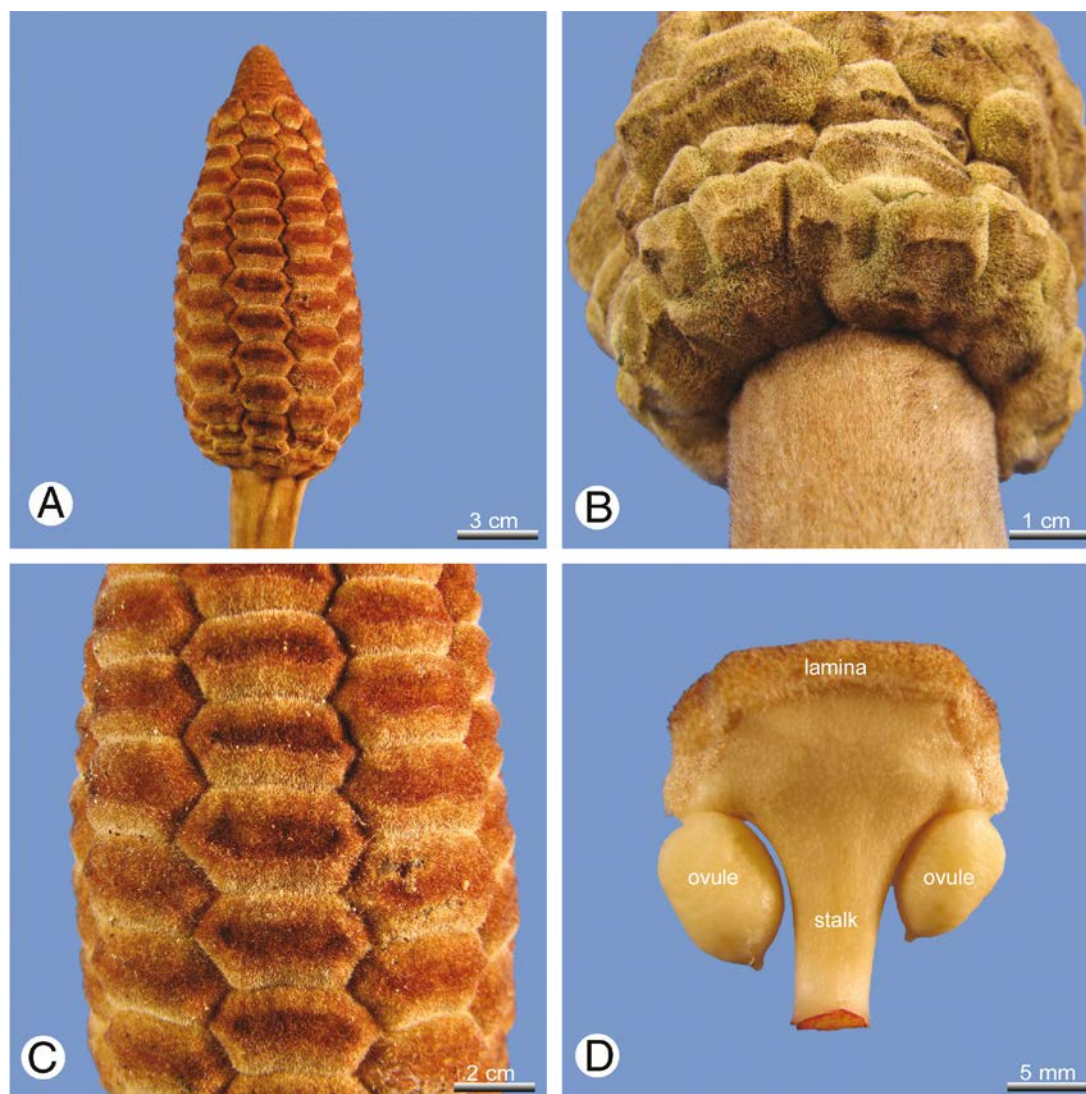


Fig. 3. *Zamia furfuracea*; normal-shaped, fertile megasporangiate strobilus. **A.** Compact strobilus with determinate growth and several strongly reduced megasporophylls; **B.** Most proximal megasporophylls are sterile and fused with each other; **C.** Fertile megasporophylls in the middle of the strobilus with a wedge-shaped distal part; **D.** Detail of a fertile megasporophyll with a central stalk and two ovules; micropyles pointing towards the axis of the strobilus.

long green leaves (Fig. 5C, 8C, D). These leaves are part of a transition series towards small pinnate leaves, which are 4–6 cm in length. These leaves have 4–8 leaflets (Fig. 6D, E). The following leaves are similar to normal trophophylls (Figs. 5A, 6F, 8A). They are *c.* 20–100 cm long with 9 to 23 leaflets. Some of the leaflets are deeply lobed or even pinnate again (Fig. 7). The leaflets and the rachis are slightly covered with brownish hairs. The margins of the leaflets are slightly serrate. In basal parts of the pinnate leaves the rachis is carrying several spines. These leaves are followed again by a flush of mucronate to rostrate cataphylls (Fig. 5C).

4. Discussion

4.1. Comparative morphology between normal and proliferated cycad-strobili and the possible evolutionary implications

Among extant seed plants, the mega- and microsporangiate cycad-strobili represent relatively primitive unbranched structures that are composed of several fertile leaves. In the *Zamiaceae* the strobili have a determinate growth. Therefore they correspond to the definition of a “single flower” in angiospermous taxa. In all proliferated



Fig. 4. *Zamia furfuracea*; weakly proliferated, sterile megasporangiate strobilus. **A.** Basal part with several wedge-shaped megasporophylls, followed by a flush of linear green leaves and a flush of mucronate to rostrate cataphylls; **B.** Most proximal megasporophylls fused with each other; **C.** Detail of a basal sterile megasporophyll; **D.** Detail of a linear green leaf; **E, F.** Details of distal mucronate to rostrate cataphylls, some of them with not fully separated basal leaflets (**F**).

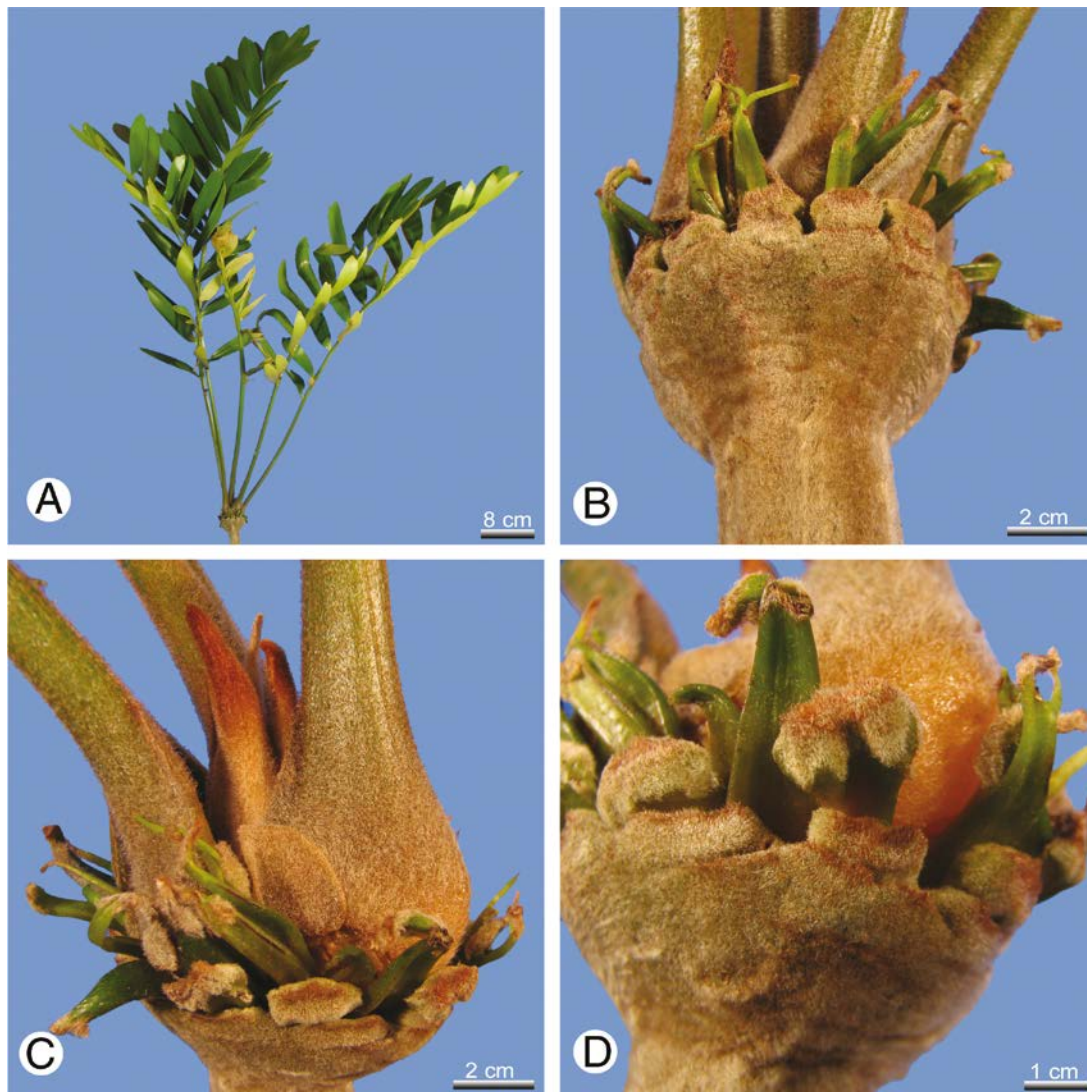


Fig. 5. *Zamia furfuracea*; strongly proliferated, sterile megasporangiate strobilus. **A.** Habitus; **B.** Most proximal megasporophylls fused with each other; **C.** Proximal megasporophylls followed by a flush of green, linear leaves and a flush of large trophophyll-like pinnate leaves; the strobilus terminates with several mucronate to rostrate cataphylls; **D.** Detail of the basal part; several intermediate forms between typical wedge-shaped megasporophylls and linear leaves are developed; some of the linear leaves with two distinct free ends.

strobili of *Zamia furfuracea* examined, a similar distinct developmental sequence was found: megasporophylls > cataphylls > trophophyll-like leaves > cataphylls. Zamia-ceous megasporangiate strobili result from unisotomous branching of the stem. Therefore the proliferated strobili represent a strongly reduced lateral branch. The developmental sequence of megasporophylls, mucronate to rostrate cataphylls and trophophylls is similar to those developed at the stems of *Cycas*. It seems that within the proliferated strobili, the number of fertile megasporophylls is strongly reduced and the terminal ones that are generally reduced in normal-shaped strobili are replaced by developing large pinnate, green leaves. These leaves are similar in size and

shape to normal-shaped trophophylls. Therefore, these pinnate leaves might be green, sterile megasporophylls, representing an atavism and perhaps a primitive feature of megasporophylls among cycads. This idea is supported by the fact that in all proliferated strobili the same transitional serial is apparent, beginning with normal wedge-shaped, but sterile megasporophylls and ending with fully developed pinnate sometimes bi- or multipinnate, green trophophyll-like leaves (Figs. 6, 7).

Within all proliferated megasporangiate strobili the basal wedge-shaped megasporophylls are followed by a flush of mucronate to rostrate cataphylls, which are followed by a flush of mostly non-pinnate, linear, green leaves.



Fig. 6. *Zamia furfuracea*; foliar details within the proliferated megasporangiatic strobilus represented in Fig. 5; a complete transitional serial from proximal wedge-shaped but sterile megasporophylls (A) to large pinnate trophophyll-like leaves (E, F) can be found; remarkable, that some of the linear, green leaves, which are leading over to rudimentary pinnate leaves (D) are terminating in two free ends (B, C).

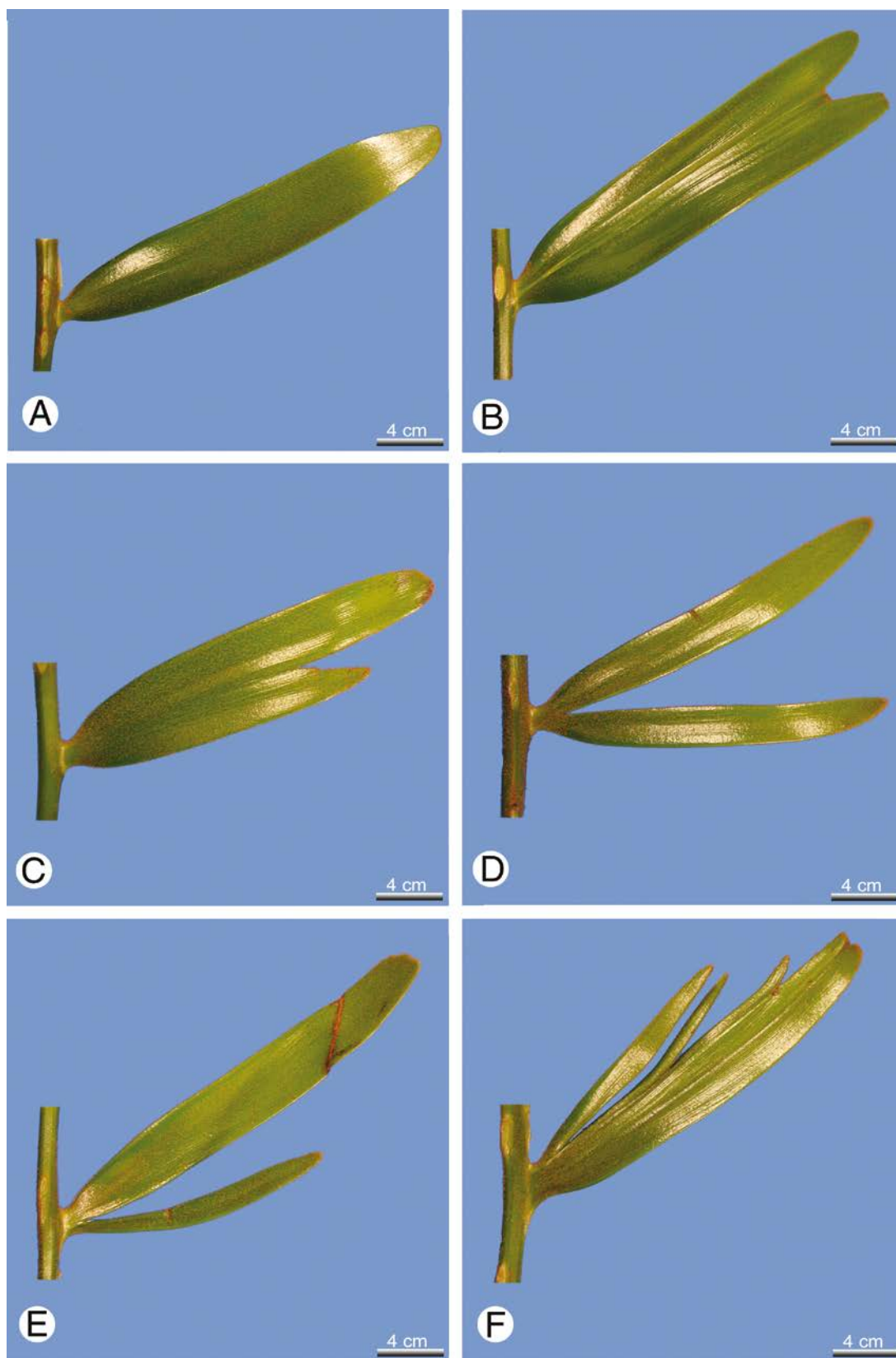


Fig. 7. *Zamia furfuracea*; foliar details of the pinnate green trophophyll-like leaves developed within the proliferated strobilus represented in fig. 5 (neighbored leaflets for a better overview removed). **A.** Typical undivided leaflet; **B–F.** Transitional serial from deeply notched (**B**, **C**) to somewhat like bi- (**D**, **E**) or even multipinnate leaves (**F**).

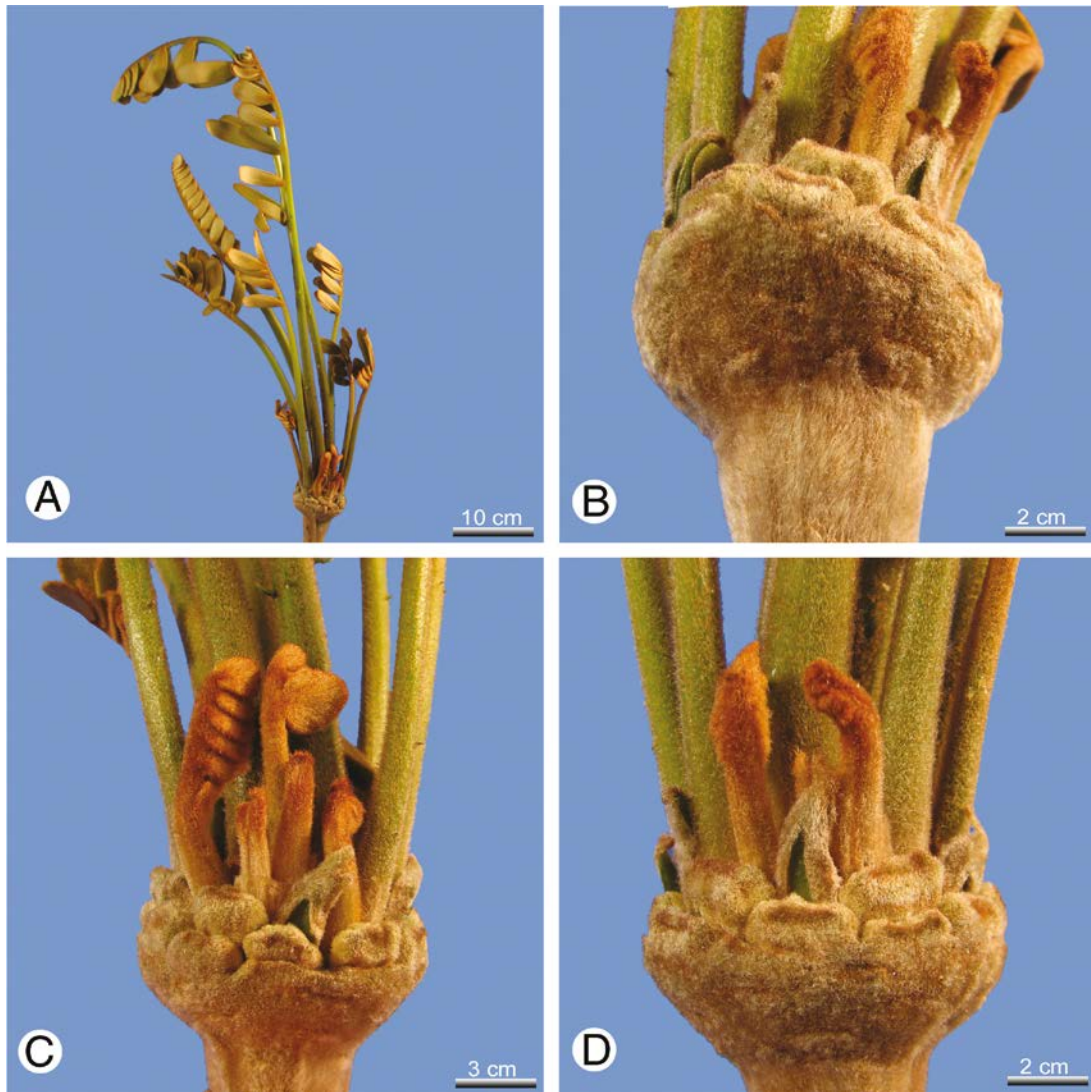


Fig. 8. *Zamia furfuracea*, strongly proliferated, sterile megasporangiate strobilus; strobilus with a developmental sequence of leaves quite similar to the situation at a stem of *Cycas*: megasporophylls > mucronate to rostrate cataphylls > trophophyll-like leaves > mucronate to rostrate cataphylls. **A.** Habitus; **B.** Most proximal megasporophylls strongly reduced and fused with each other; **C, D.** Within the strobilus a full transitional serial from normal megasporophylls to large pinnate trophophyll-like green leaves can be found.

These linear leaves might represent rudimentary midribs of strongly reduced pinnate leaves and can therefore be regarded as intermediate forms between the wedge-shaped megasporophylls and the pinnate trophophyll-like leaves. Some of these linear leaves terminated in two distinct free ends as is also the case for some of the proximal wedge-shaped megasporophylls. Therefore, it seems that the distal wedge-shaped part of zamiaceous megasporophylls might be formed by the two most distal leaflets of a strongly reduced pinnate leaf. In this case, each of the free ends would represent a strongly reduced rudimentary leaflet.

Regarding the fully developed, pinnate, green trophophyll-like leaves within the proliferated *Zamia*-strobili as

an atavism, fits quite well to the evolutionary concept for the origin of megasporophylls in cycads, as suggested by GAO & THOMAS (1989). They described an evolutionary concept beginning with a type of ovuliferous leaf as was developed in the fossil Chinese taxon *Crossozamia*. From this *Crossozamia*-type they described two evolutionary lineages. The first one leads to the situation as can be found in extant *Cycas* species with pinnate megasporophylls that are arranged in a loose crown surrounding the stem apex. These megasporophylls carried several ovules at their base. In this lineage *Crossozamia chinensis* would represent an intermediate form preceding the extant *Cycas* megasporophyll. The second lineage leads to the situa-

tion as represented in extant *Zamia* species, where several strongly reduced megasporophylls are arranged in compact strobili. In this second lineage several intermediate forms of megasporophylls have developed between the *Crossozamia*-type and the *Zamia*-type. One of them was e.g. *Crossozamia minor*, with pinnate megasporophylls. In *Beania gracilis* the number of ovules and the distal part of the megasporophyll were already strongly reduced. The distal sterile part was entire and expanded, with a peltate shape. At the inner surface of each megasporophyll only two sessile, orthotropous ovules were inserted. Contrasting to the situation among extant *Zamia* species, the reduced megasporophylls were arranged widely separated from each other at the axis of the strobilus (e.g. CARRUTHERS 1869; HARRIS 1964; SCHWEITZER 2000; TAYLOR & TAYLOR 1993; TAYLOR et al 2009). From *Beania gracilis* it was only a small step to the compact strobili of extant *Zamia* species by progressive reductions of the megasporophylls and their compaction at the axis of the strobilus. Following these evolutionary concepts extant *Cycas* species would reflect the most primitive condition compared with the compact megasporangiate strobili of *Zamia*, which would represent a strongly derived feature. Thus, HERMSEN et al. (2006) regarded *Crossozamia* as sister to extant *Cycas*.

CHAMBERLAIN (1913) and STEWART (1983) also proposed an evolutionary concept for megasporophylls and megasporangiate strobili, beginning with the most primitive type of megasporophylls comparable to those as developed in extant *Cycas* and ending in the strongly reduced and specialized megasporophylls of extant *Zamia*. In this scenario megasporophylls of e.g. *Macrozamia* with a reduced but entire blade are suggested as intermediate stages.

Several authors suggest trophophylls and sporophylls of primitive cycads as frond-like structures, as is still the case for trophophylls of all extant cycads and also for megasporophylls of *Cycas*. Thus, Palaeozoic (Late Pennsylvanian and Early Permian) taeniopterid pteridosperms are often regarded as being closely related to cycads (e.g. MAMAY 1969, 1973, 1976). Therefore DELEVORYAS & ARBOR (1955), DELEVORYAS (1982) and DELEVORYAS & HOPE (1976) suggested Late Palaeozoic pteridosperms with pinnate megasporophylls as the ones representing most of the features necessary to be considered precursors to cycads. Thus, these authors suggested only a small gap from Permian medullosean to extant cycads, with e.g. *Colpoxylon* representing a taxon that has anatomically much in common with cycads.

However, STEWART (1983) regarded the presence of specialized pollen and strobili, both features absent in pteridosperms, as one of the obvious difference between cycads and pteridosperms. In pteridosperms microsporangia as well as ovules were developed on unmodified or only slightly modified fronds. Among medullosean pteri-

dosperms, both fertile and sterile fronds developed closely to each other at the stem. STEWART (1983) described the tendency towards condensation of fronds (not apparent in other pteridosperms), as “foreshadowing” the consolidation and reconstruction of a frond required to produce the micro- and megasporangiate strobili of cycads. However, STEWART (1983) regarded the origin of the entire cycad-microsporophylls as the largest “roadblock” in deriving cycads from medullosean pteridosperms. However, MUNDRY & STÜTZEL (2003) demonstrated that microsporophylls in *Zamia* are also derived from a pinnate leaf. The results of their ontogenetic studies on the morphogenesis of male sporangiophores of *Zamia amblyphyllidia* have shown that microsporophylls have a pinnate structure, with synangia inserted at strongly reduced and condensed lateral leaflets. Thus, in cycads no significant differences between micro- and megasporophylls, as they have been previously often been suggested, do exist. Moreover they could show that the pinnate microsporophyll can be regarded as being derived from a pteridospermous ancestor, where synangia were inserted in radial groups. Thus, MUNDRY & STÜTZEL’s results also point to the Medullosaceae.

Contrasting with the evolutionary concept suggested by GAO & THOMAS (1989), MAMAY (1969, 1973, 1976) regarded megasporophylls in cycads as being derived from the Carboniferous *Spermopteris*. MAMAY’s reconstructions of megasporophylls in *Archaeocycas whitei* leads to the hypothesis that megasporophylls in cycads might be derived from those of pteridosperms, with an entire distal lamina. Among this group ovules were inserted in two longitudinal rows, in proximal involute parts of the sporophyll. The distal sterile part was widened and entire. MAMAY suggested three most important evolutionary steps towards modern *Cycas*-megasporophylls: (1) progressive reduction of proximal parts of the lamina; (2) insertion of megasporangia at the rachis; (3) progressive incision of distal parts of the lamina. But the extinct *Spermopteris* differs from extant cycads insofar that trophophylls and sporophylls have been entire and not pinnate. MAMAY (1976) suggested the Permian *Archeocycas* as well as *Phasmatocycas* as important intermediate transitions on the way from Upper Carboniferous pteridosperms with an entire lamina to a pinnate *Cycas*-megasporophyll. However, this reconstruction was hypothetical, because no fossil remains of the sterile distal part of the megasporophylls of *Archaeocycas whitei* have been found. Thus, its true morphology is still unknown. Furthermore, AXSMITH et al. (2003) who reinvestigated the original *Spermopteris*-specimen from the Lawrence Shale of Kansas came to another important conclusion. They have shown that in this fossil specimen ovules were attached to the rachis of the megasporophyll and not to the abaxial side of the lamina. Thus, *Spermopteris* and *Phasmatocycas* show only slight differences in their laminar morphology. Therefore AXSMITH et al. transferred *Sper-*

mopteris coriaceae as a new species in the already existing genus *Phasmatozycas* as *Phasmatozycas bridwelii*. Thus, in this new evolutionary concept of *Phasmatozycas* this taxon is less cycad-like than it was previously suggested to be. The phylogenetic position of *Phasmatozycas* is therefore relatively unclear now and a *Spermopteris*-origin of the cycad-megasporophyll should be excluded.

4.2. Comparison of proliferated megasporangiate cycad-strobili to proliferated coniferous “seed-cones”

The evolutionary relevance of proliferations within reproductive structures is generally highly debatable. Among extant conifers the rarely developed lateral proliferation of “seed-cones” are, in contrast to the much more frequent terminal proliferations, more useful for suggesting evolutionary scenarios (e.g. TOSH & POWELL 1986; CARON & POWELL 1991; JAGEL & STÜTZEL 2001; FARJON 2008; OWENS 2008; BATEMAN et al. 2011; RUDALL et al. 2011; DÖRKEN 2012). Among extant conifers terminal proliferations of “seed-cones” result from a simple change in the internode length and leaf shape of units that have always been regarded as foliar shoots. The life span of such terminal proliferations is often limited. This is especially the case, when the proliferated “seed-cones” are fertile and the cone axis dries out to allow seed release. In contrast to terminal proliferations, lateral proliferations are different. Here ovules are replaced by leaves that might support the homology of leaf and ovule in conifers.

Among extant conifers the “seed-cone” consists of two types of scales: (1) bract-scales, representing reduced leaves; (2) flattened and condensed seed-scales representing axillary shoots (phylloclades). They are inserted in the axils of the bract-scales. This morphology gives rise to the idea that “seed-cones” in conifers represent branched systems, corresponding to the definition given for an inflorescence in angiospermous taxa (SCHUHMAN 1902; HERZFELD 1914; PILGER 1926; FLORIN 1951, 1954; SCHWEITZER 1963; FARJON 1984, 2005; STÜTZEL & RÖWEKAMP 1997, 1999; MUNDY 2000; FARJON & GARCIA 2003; ECKENWALDER 2009; DÖRKEN 2012). Such a coniferous bract-/seed-scale complex is always absent in cycads. In the examined proliferated cycad-strobili only one type of leaf is replaced by another one. Due to the fact that in conifers, megasporangia are inserted at a phylloclade-like ovuliferous short-shoot and in cycads at an ovuliferous leaf, the evolutionary relevance of terminal proliferations should urgently be considered different for each group. Contrasting to conifers, among cycads terminal proliferations of strobili, as represented by those of the examined *Zamia furfuracea*, are therefore useful for suggesting evolutionary scenarios.

5. Conclusions

The results of the examined proliferated megasporangiate strobili of *Zamia furfuracea* show, that within these anomalous strobili the developmental sequence of megasporophylls, cataphylls, trophophyll-like leaves, followed again by a flush of cataphylls, is quite similar to those developed at the stems of extant *Cycas* species. Contrasting to normal shaped strobili, the terminal megasporophylls within the proliferated strobili were replaced by large pinnate trophophyll-like leaves, possibly representing an atavism and therefore reflecting the primitive character of megasporophylls in cycads. Due to the results of the morphological examinations and their comparison with fossil data, it seems that the plesiomorphic feature of cycad-megasporophylls was pinnate as is still the case in extant *Cycas* species. The entire megasporophylls developed among all other remaining cycads would reflect a derived feature from a former pinnate ovuliferous leaf. This hypothesis conflicts with older interpretations of e.g. MAMAY, which regard an entire megasporophyll as the primitive feature.

6. References

- AXSMITH, B. J., SERBET, R., KRINGS, M., TAYLOR, T. N., TAYLOR, E. L. & MAMAY, S. H. (2003): The enigmatic Paleozoic plants *Spermopteris* and *Phasmatozycas* reconsidered. – *American Journal of Botany*, **90** (11): 1585–1595.
- BATEMAN, R. M., HILTON, J. & RUDALL, P. J. (2011): Spatial separation and developmental divergence of male and female reproductive units in gymnosperms, and their relevance to the origin of the angiosperm flower. In: WANNTORP, L. & RONSE DE CRAENE, L. P. (eds.): *Flowers on the tree of life*. – Systematics Association, Special Volumes, **80**: 8–48; Cambridge (Cambridge University Press).
- BIERHORST, D. W. (1971): *Morphology of vascular plants*. – New York (Macmillan).
- CARON, G. E. & POWELL, G. R. (1991): Proliferated seed cones and pollen cones in young black spruce. – *Trees*, **5**: 65–74.
- CARRUTHERS, W. (1869): On *Beania* a new genus of cycadean fruit from the Yorkshire Oolite. – *Geological Magazine*, **6**: 97–99.
- CHAMBERLAIN, C. T. (1913): *Macrozamia moorei*, a connecting link between living and fossil cycads. – *Botanical Gazette*, **55** (2): 141–154.
- CHAW, S.-M., WALTERS, T. W., CHANG, C.-C., HU, S.-H. & CHEN, S.-H. (2005): A phylogeny of cycads (Cycadales) inferred from chloroplast matK gene, trnK intron, and nuclear rDNA ITS region. – *Molecular Phylogenetics and Evolution*, **37**: 214–234.
- DELEVORYAS, T. (1982): Perspectives on the origin of Cycads and Cycadeoids. – *Review of Palaeobotany and Palynology*, **37**: 115–132.
- DELEVORYAS, T. & ARBOR, A. (1955): The Medullosae-structure and relationships. – *Palaeontographica*, (B), **97**: 114–167.

- DELEVORYAS, T. & HOPE, R. C. (1976): More evidence for a slender growth habit in Mesozoic Cycadophytes. – Review of Palaeobotany and Palynology, **21**: 93–100.
- DÖRKEN, V. M. & STEINECKE, H. (2012): Palmfarne im Palmengarten – eine einzigartige Nacktsamer-Gruppe. – Palmengarten, **76** (2): 105–115.
- DÖRKEN, V. M. (2012): Proliferating seed cones in *Metasequoia glyptostroboides* HU & CHENG (Cupressaceae s.l., Coniferales) elucidate the evolution of seed cones and ovules in Cupressaceae s.l. – Feddes Repertorium, **122**: 409–420.
- ECKENWALDER, J. E. (2009): Conifers of the world. Portland (Timber Press).
- FARJON, A. (1984): Pines, drawings and descriptions of the genus *Pinus*. Leiden (Brill).
- FARJON, A. (2005): A monograph of Cupressaceae and Sciadopityaceae. Richmond (Royal Botanic Gardens Kew).
- FARJON, A. (2008): A natural history of Conifers. Portland (Timber Press).
- FARJON, A. & GARCIA, S. O. (2003): Cone and ovule development in *Cunninghamia* and *Taiwania* (Cupressaceae sensu lato) and its significance for conifer evolution. – American Journal of Botany, **90** (1): 8–16.
- FLORIN, R. (1951): Evolution in cordaites and conifers. – Acta Horti Bergiani, **17**: 7–37.
- FLORIN, R. (1954): The female reproductive organs of conifers and taxads. – Biological Reviews of the Cambridge Philosophical Society, **29**: 367–389.
- GAO, Z. & THOMAS, B. A. (1989): A review of fossil Cycad megasporophylls with new evidence of *Crossozamia* POMEL and its associated leaves from the Lower Permian of Taiyuan, China. – Reviews of Palaeobotany and Palynology, **60**: 205–223.
- GIFFORD, E. M. & FOSTER, A. S. (1989): Morphology and evolution of vascular plants. New York (Freeman & Co.).
- HARRIS, T. M. (1964): The Yorkshire Jurassic Flora. II. Caytoniales, Cycadales and Pteridosperms. 38 pp.; London (British Museum, Natural History).
- HERMSEN, E. J., TAYLOR, T., TAYLOR, E. L. & STEVENSON, D. W. (2006): Cataphylls of the middle Triassic Cycad *Antarcticycas shoppii* and new insights into Cycad evolution. – American Journal of Botany, **93** (5): 724–738.
- HERZFELD, S. (1914): Die weibliche Koniferenblüte. – Österreichische Botanische Zeitschrift, **64** (8): 321–358.
- HILL, K. D., CHASE, M. W., STEVENSON, D. W., HILLS, H. G. & SCHUTZMAN, B. (2003): The families and genera of Cycads: A molecular phylogenetic analysis of Cycadophytina based on nuclear and plastid DNA Sequences. – International Journal of Plant Sciences, **164** (6): 933–948.
- JAGEL, A. & STÜTZEL, T. (2001): Zur Abgrenzung von *Chamaecyparis* SPACH und *Cupressus* L. (Cupressaceae) und die systematische Stellung von *Cupressus nootkatensis* D. DON [= *Chamaecyparis nootkatensis* (D. DON) SPACH]. – Feddes Repertorium, **112**: 179–229.
- JONES, D. C. (1993): Cycads of the World. Washington D.C. (Smithsonian Institution Press).
- KUNZE, J. (2008): Vergleichende morphogenetische und entwicklungsgeschichtliche Untersuchungen an Samenanlagen. PhD-thesis, Ruhr University Bochum.
- MAMAY, S. H. (1969): Cycads: Fossil evidence of Late Paleozoic origin. – Science, **164**: 295–296.
- MAMAY, S. H. (1973): *Archaeocycas* and *Phasmatoicycas* – new genera of Permian cycads. – Journal of Research of the U.S. Geological Survey, **1**: 687–689.
- MAMAY, S. H. (1976): Paleozoic origin of Cycads. – U.S. Geological Survey, Professional Papers, **934**: 1–48.
- MUNDRY, I. (2000): Morphologische und morphogenetische Untersuchungen zur Evolution der Gymnospermen. – Bibliotheca Botanica, **152**: 1–90.
- MUNDRY, M. & STÜTZEL, T. (2003): Morphogenesis of male sporangiophores of *Zamia amblyphyllidia* D.W. STEV. – Plant Biology, **5**: 297–310.
- OBERMANN, J. (2003): Vergleichende Untersuchungen an den Samenanlagen spermatozoidbefruchteter Gymnospermen mit REM und Anatomie unter Berücksichtigung fossiler Strukturen. – Diploma thesis, Ruhr University Bochum.
- OWENS, J. N. (2008): The reproductive biology of western larch. Victoria (The Inland Empire Tree Improvement Cooperative).
- PILGER, R. (1926): Coniferae. – In: ENGLER, A. (ed.): Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere der Nutzpflanzen. Leipzig (Engelmann).
- RUDALL, P. J., HILTON, J., VERGARA-SILVA, F. & BATMEMANN, R. M. (2011): Recurrent abnormalities in conifer cones and the evolutionary origins of flower-like structures. – Trends in Plant Science, **16** (3): 151–159.
- SCHNEIDER, J. V. & MIKA, M. (2012): Mexikanische Cycadeen und deren Schutzsammlung im Botanischen Garten von Xalapa, Veracruz, Mexiko. – Palmengarten **76** (1): 5–11.
- SCHUHMAN, K. (1902): Über die weiblichen Blüten der Coniferen. – Verhandlungen des Botanischen Vereins der Provinz Brandenburg, **44**: 5–79.
- SCHWEITZER, H.-J. (1963): Der weibliche Zapfen von *Pseudovoltzia liebeana* und seine Bedeutung für die Phylogenie der Koniferen. – Palaeontographica, (B), **113**: 1–9.
- SCHWEITZER, H.-J. (2000): Neue Pflanzenfunde im Unterdevon der Eifel (Deutschland). – Senckenbergiana Lethaea, **80**: 371–395.
- STEVENS, P. F. (2001, onwards): Cycadales. Angiosperm Phylogeny Website. Version 12, July 2012. <http://www.mobot.org/mobot/research/apweb/>
- STEVENSON, D. W. (1988): Strobilar ontogeny in Cycadales. – In: LEINS, P., TUCKER, S. C. & ENDRESS, P. K. (eds.): Aspects of floral development, 205–224. Berlin & Stuttgart (Borntraeger).
- STEVENSON, D. W. (1990): Morphology and systematics of Cycadales. – Memoirs of the New York Botanical Garden, **57**: 8–55.
- STEWART, W. N. (1983): Palaeobotany and the evolution of plants. Cambridge (Cambridge University Press).
- STÜTZEL, T. & RÖWEKAMP, I. (1997): Bestäubungsbiologie bei Nacktsamern. – Palmengarten, **61** (2): 100–110.
- STÜTZEL, T. & RÖWEKAMP, I. (1999): Bestäubungsbiologie bei Nacktsamern (Gymnospermen). – In: ZIZKA, G. & SCHNECKENBURGER, S. (eds.): Blütenbiologie – faszinierendes Miteinander von Pflanzen und Tieren. – Kleine Senckenberg-Reihe, **33**: 107–117.
- TAYLOR, T. N. & TAYLOR, E. L. (1993): The biology and evolution of fossil plants. Englewood Cliffs (Prentice Hall).
- TAYLOR, T. N., TAYLOR, E. L. & KRINGS, M. (2009): Palaeobotany: The Biology and evolution of fossil plants. Burlington, London, San Diego & New York (Academic Press).

- TOSH, K.J. & POWELL, G.R. (1986): Proliferated, bisporangiate, and other atypical cones occurring on young, plantation-grown *Larix laricina*. – Canadian Journal of Botany, **64**: 469–475.
- WINK, M. (2006): Evolution and phylogeny of Cycads. In: SHARMA, A. K. & SHARMA, A. (eds.): Plant Genome: Biodiversity and Evolution, Vol. 1. Part D, 1–28. Enfield (Science Publishers).

Addresses of the authors:

VEIT MARTIN DÖRKEN, Department of Biology, University of Konstanz; M 613; Universitätsstr. 10; 78457 Konstanz, Germany

E-mail: veit.doerken@uni-konstanz.de

BRIGITTE ROZYNEK, Ina-Seidel-Str. 4, 74405 Gaildorf, Germany

E-mail: info@rozynek.net

Manuscript received: 22 May 2013, accepted: 26 September 2013.

