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The Triassic conifer seed cone *Glyptolepis*

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Abstract

A new species of the voltzialean seed cone *Glyptolepis* is described from the Late Triassic of Germany. Specimens of *Glyptolepis richteri* sp. nov. are large (up to 14.0 cm long, 3.5 cm wide) and contain numerous small, helically arranged bract scale complexes. Each cone scale is composed of eight uniform lobes, each with an obtuse apex. The bract is fused to the long cone scale stalk and expands distally into a somewhat diamond-shaped laminar unit that completely covered the underlying cone scale. A reconsideration of other fossils assigned to *Glyptolepis* suggests that all except the type material of *Glyptolepis keuperiana* Schimper, are erroneously assigned to the genus. Although *Glyptolepis* is considered a key taxon in some concepts of conifer phylogeny, evidence is presented to suggest that most reconstructions of this genus are based on inaccurate interpretations of unrelated cones.

Keywords: *Glyptolepis*; Coniferales; Triassic; Keuper

1. Introduction

The highly artificial family Voltziaceae, sometimes termed the 'transitional conifers', represents a heterogeneous assemblage of mostly Early Mesozoic conifers, some of which have been interpreted as morphologically intermediate between Paleozoic conifers and their modern relatives. This hypothesis has been based primarily on the classic works of Florin (1938–1945) in which the ovulate scales of several voltzialean genera have been interpreted as representing various stages in the modification of a fertile dwarf shoot. Despite the important role the 'Voltziaceae' have played in this influential model, several pivotal genera remain poorly understood or variously interpreted. Problems in the interpretation of early Mesozoic conifers are particularly evident in the genus *Glyptolepis*.

Glyptolepis was established by Schimper (1870) for ovulate conifer cones from the Late Triassic of Germany. Cones of the type species (*G. keuperiana*) were described as elongate and lax with small, grooved scales. According to Florin's reconstruction (Florin, 1944), the inverted ovules were born terminally on stalk-like megasporophylls. The sporophylls were lateral to the central sterile scales (Fig. 2A). He also interpreted *G. longibracteata*, *G. hungarica* and *G. winsheimensis* as possessing lateral, stalk-like megasporophylls. We suggest below that the fossils assigned to *Glyptolepis* by Florin are not closely related to those described by Schimper.

The suggestion that some fossil conifers had stalk-like megasporophylls with terminally attached ovules has been controversial, and remains unresolved in many forms including some of the earliest taxa from the Upper Carboniferous

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and Lower Permian of North America and Europe (Mapes and Rothwell, 1991; Kerp and Clement-Westerhof, 1991). Schweitzer's (1963) study of the Upper Permian conifer *Pseudovoltzia* clearly demonstrated that the ovules of this genus were attached by their bases to broad fertile scales rather than terminally on stalks as initially proposed by Florin (1944). Although Schweitzer's interpretation of *Pseudovoltzia* became widely accepted, the fact that he proposed a similar interpretation for several species of *Glyptolepis* is rarely noted. Moreover, Mägdefrau (1963), Bock (1969) and Cornet (1977) have described and figured specimens that do not conform to any earlier interpretation of the genus. Despite this, Florin's concept of *Glyptolepis* remains unchallenged in most subsequent treatments of the Mesozoic conifers (e.g., Miller, 1977, 1988).

The primary focus of this paper is to describe and illustrate specimens of a new species of *Glyptolepis* from the Triassic of Germany. We also reconsider several other fossil conifer cones currently referred to *Glyptolepis*, and suggest that most of these, including those upon which the Florin (1944) reconstructions were based, are misinterpreted morphologically and are probably not related to *Glyptolepis*.

2. Materials and methods

The specimens used in this study are part of the P.B. Richter collection housed at the Swedish Museum of Natural History, Stockholm. Richter amassed a large private collection of Triassic and Cretaceous fossil plants which was subsequently purchased by the Swedish Museum shortly after his death in 1911 (Nathorst, 1912).

The Triassic cones were recovered from sandstones of the middle Keuper exposed north and east of Thale in the Hartz region of central Germany. The only components of Richter's Triassic collection described to date are the putative cycadophytes *Sphenozamites tener* (Linnell, 1932) and *Scytophyllum bornem* (Linnell, 1933). It should be noted that Dobruskina (1975) regards *Scytophyllum* as a peltasperm. Other elements of Richter's Triassic plant collection as identified by Linnell (1933) include: *Equisetites arenaceus*, *Neuropteridium* sp., *Pecopteris latepinnata*, *P. schoenleiniana*, *Cladophlebis remota*, *Bernoullia helvetica*, *Pseudodanaeopsis marantacea*, *Macrotaeniopteris* sp., *Pterophyllum jaegeri*, and *Dioonitocarpidium pennaeforme*. The conifers are represented by ovulate cones of *Pachylepis quinquies* and over 60 specimens of the large strobilus described here as a new species of *Glyptolepis*. It is interesting that these cones were not mentioned by Linnell (1932,1933). Franke (1936) described a new species, *Equisetites asperrimus*, from collections made by Gothan from the same localities.

Preservation of most specimens is generally poor. The appearances of several features, including the size and shape of the bract, and relative size and number of cone scale lobes, are strongly affected by the position in the cone through which the matrix was split. Examination of the counterparts would have been useful in this regard but none were found in the collection. The only organic material consists of thick coaly fragments in some spaces on the cone surface. Interestingly, no conifer foliage or pollen cones are included in the collection.

Cones useful for comparative purposes were collected from gray shales of the New Oxford Formation (late Carnian) in York County, Pennsylvania (USA). Although attempts at clearing the cuticle for epidermal studies were unsuccessful, excellent Bioplastic transfers were produced. This was accomplished by first embedding the specimen in Ward's Bioplastic embedding medium. The hardened block was then cut longitudinally through the matrix behind the cone. The matrix was then dissolved in 49% HF. The remaining Bioplastic block with embedded cuticle was rinsed in several water baths and subsequently examined and photographed in reflected light.

3. Systematics

Order CONIFERALES

Genus ***Glyptolepis*** Schimper, 1872

Glyptolepis richteri Axsmith et Taylor, *sp. nov.* (Plate 1, 1–5)

Holotype: No. S50052 (Plate I, 2, 4, 5).
Paratypes: No. S50051 (Plate I, 1); No. S50054 (Plate I, 3).
Disposition of specimens: All specimens are deposited in the Swedish Museum of Natural History in Stockholm, Sweden.
Locality: North and east of Thale in central Germany.
Stratigraphy: Middle Keuper.
Age: Late Triassic (Carnian).
Etymology: The specific epithet *richteri* is proposed in honor of P.B. Richter who collected the cones sometime before 1911.
Diagnosis: Ovulate cones at least 14.0 cm long and 1.5–3.5 cm in diameter, born terminally on a naked axis; cone axis typically 3.5 mm wide, bearing numerous small, tightly aggregated, helically arranged bract scale complexes, cone scale stalks up to 6.0 mm long and 0.5 mm wide, distal part of cone scale expanded, typically 4.0 mm long and 6.0 mm wide, consisting of eight equal-sized lobes each with an obtuse apex; bract base fused to cone scale stalk, bract apex expanding into a somewhat diamond-shaped laminar unit up to 5.0 mm tall and 6.0 mm wide which completely covers the underlying scale, bract apices tightly appressed.
Description: The morphology of these cones is difficult to interpret due to the generally poor preservation in a rather course sandstone matrix. Most of the specimens are represented by impressions of the outer cone surface that show only the general size and shape of the cones, and the outlines of the expanded bract apices. The most complete such specimen is 14.0 cm long and approximately 3.0 wide, and is terminally attached to a naked axis 9.0 mm wide (Plate I, 1). The smallest specimen is only 1.5 cm wide and of unknown length due to fracturing (Plate I, 3). It is uncertain if such size differences represent different developmental stages or variations in mature cones.

One specimen is fractured in such a way as to reveal the long, narrow cone scale stalks (6.0 mm × 0.5 mm) which are attached to the cone axis in a tight helix (Plate I, 3). In another specimen, some bract apices in the upper part of the cone are partially broken away revealing the underlying cone scales (Plate I, 2, 4, 5). The upper portion of the scale is expanded (4.0 mm tall and 6.0 mm wide) and consists of eight equal-sized lobes, each with an obtuse apex (Plate I, 4, 5). All eight lobes are rarely visible on a single cone scale. The lobes are separated by deep suture lines that extend the length of the expanded portion of the cone scale. No attached ovules or attachment scars have been identified.

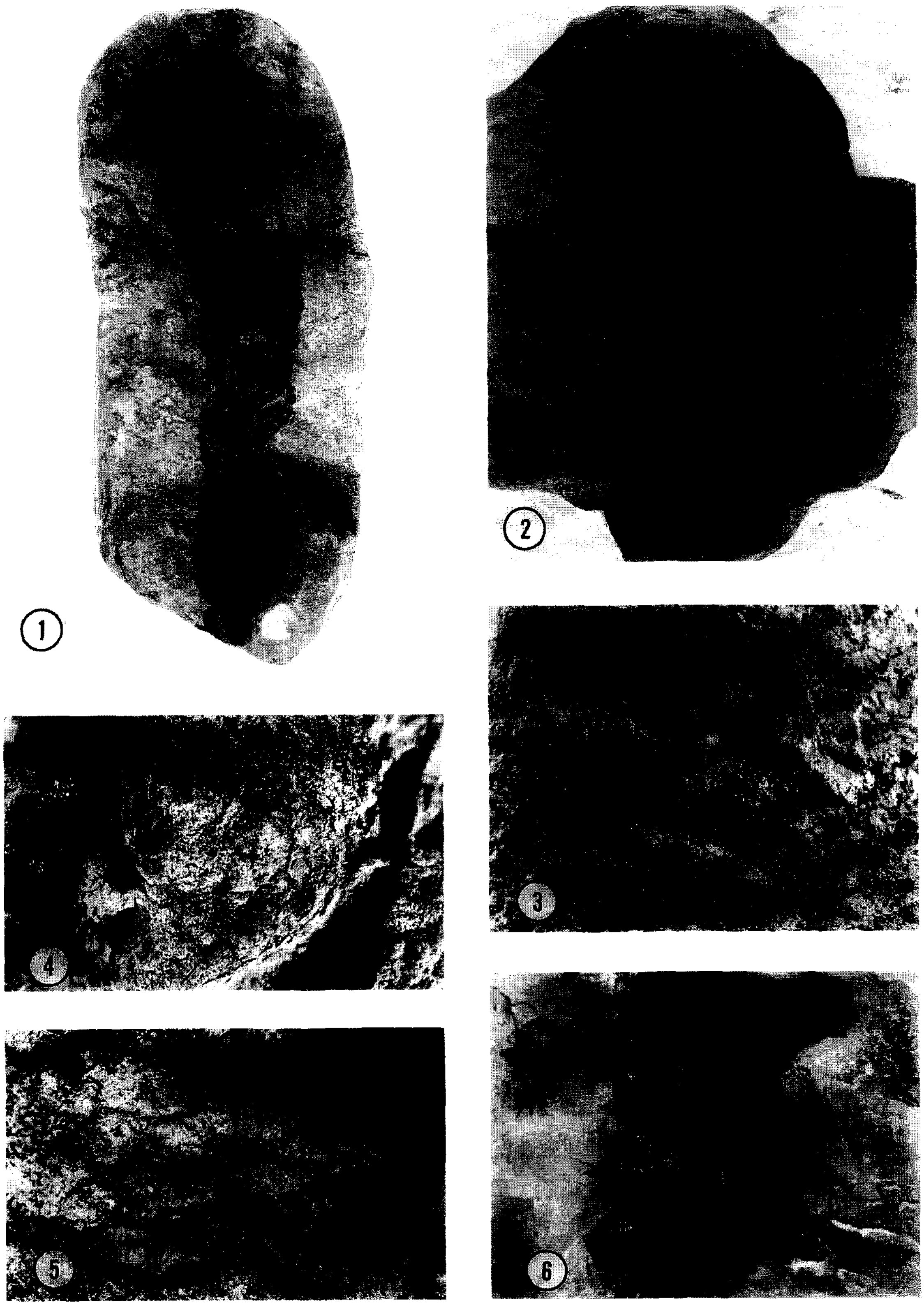
The bract base is fused to the narrow cone scale stalk. The upper part of the bract expands into a somewhat diamond-shaped laminar unit that is up to 5 mm tall and 6 mm wide. These bract apices are tightly packed together and collectively form an outer armor to the cone that completely covers the underlying scales (Plate I, 1; Fig. 1).

4. Discussion

There are several interpretations of the *Glyptolepis* seed cone in the primary literature (Table 1). We believe that the majority of these are inaccurate, and based on numerous unrelated conifer cones. Schimper (1870) depicted the type species, *Glyptolepis keuperiana*, as elongate (approximately 18 cm) and narrow (approximately 2 cm wide). The scales have long stalks and are helically arranged, but lax on the cone axis. Based on the illustrations, the expanded part of the cone scale is composed of 15 equal lobes; bracts were neither described nor figured. The description of two oval, basal seeds was apparently uncertain since it is followed by a question mark; moreover, there is no figure for this feature. In light of Schimper's ambiguity regarding seeds, it is noteworthy that Florin (1944) and Mägdefrau (1963) considered the presence of two seeds to be an important character of *Glyptolepis* and assigned several species to the genus based principally on this character.

The type material of *Glyptolepis keuperiana* has recently been reexamined and figured by Schweitzer (1996, Tafel 3, figs. 2–4). Based on this material it appears that Schimper's (1870) recon-

PLATE I



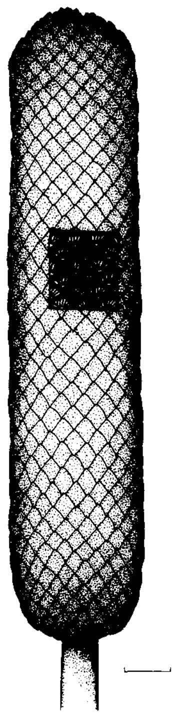


Fig. 1. Reconstruction of *Glyptolepis richteri* seed cone. Cutaway of expanded bract apices reveals underlying lobed cone scales. Scale bar = 1 cm.

struction is correct in showing long, narrow cone scale stalks; however, there are only eight lobes comprising the expanded portion of the scale rather than fifteen. The lobes are separated by suture lines running to the base of the expanded portion of the scale as in *G. richteri*. No bracts are visible. Schweitzer's (1996, fig. 34b) reconstruction depicts two large ovules attached laterally to the base of the expanded portion of the cone scale. However, ovules are not apparent in his line drawings and photographs of the type material.

According to Schimper (1870) cones of *G. keuperiana* were born in clusters; cones of *Glyptolepis richteri* were apparently born singly. This, along with the more lax cone scale arrangement and smaller bracts of *G. keuperiana*, are the primary justifications for erecting a new species for the Richter specimens. It is possible that the more compact cones of *G. richteri* merely represent immature developmental stages. This is unlikely though due to the large size of the cones. We propose that the genus *Glyptolepis* be restricted to Triassic conifers with elongate ovulate cones bearing cone scales consisting of eight equal lobes with obtuse apices.

4.1. 'Glyptolepis' cones with doubtful affinities

Florin (1944) transferred several cones to *Glyptolepis keuperiana* that were previously identified as *Voltzia coburgensis* (Kräusel, 1939). The cone scales display large lateral structures that Kräusel (1939) identified as seeds attached directly to the scale. However, Florin suggested that the seeds were actually born terminally on stalk-like megasporophylls (Fig. 2A). Schweitzer (1963) reexamined Kräusel's material and concluded that no stalks could be found, suggesting that the ovules were actually attached directly to the scale surface.

Mägdefrau (1963) described several similar cones from the middle Keuper of Haßfurt, Germany as *Glyptolepis keuperiana*. The cone scales are typically composed of seven lobes, and

PLATE I

1–5. *Glyptolepis richteri*. 6. Unnamed North American cone.

1. Complete cone with outer layer of expanded bract heads visible in upper region (arrow). No. S50051. ×0.63.
2. Cone with partially exposed cone scales in upper region and layer of intact, expanded bract apices in lower region. No. S50052. ×0.82.
3. Detail of upper region of cone in Fig. 2 showing partially exposed cone scales. Bracket encloses a relatively intact scale. No. S50052. ×2.7.
4. Fractured cone showing cone axis (*A*) and long, narrow cone scale stalks (arrow). No. S50054. ×3.0.
5. Detail of cone scale indicated by bracket in 3. Note the eight scale lobes (arrows) and remnants of the expanded bract head (*B*). No. S50052. ×5.8
6. Bioplastic transfer of North American cone erroneously assigned to *Glyptolepis*. Arrow indicates large, lateral fertile lobe of a cone scale. ×4.2.

Table 1
Various interpretations of ovuliferous cone scales assigned to *Glyptolepis*

Species and reference	Character: Scale lobe arrangement	Ovule attachment
G. delawarensis Bock (1969)	five equal-sized lobes	in two depressions in middle of upper scale surface
G. hungarica Florin (1944)	five sterile lobes; two lateral, stalk-like sporophylls	terminal on the lateral sporophylls
G. keuperiana Schimper (1870)	fifteen equal-sized lobes (based on illustration)	'basal'
G. keuperiana Mägdefrau (1963)	seven lobes; arrangement not specified	not described; figures indicate large, lateral lobes
G. keuperiana Schweitzer (1996)	eight equal-sized lobes	on lateral surface of lateral lobes
G. keuperiana Schweitzer (1963)	five or six sterile lobes; two larger, lateral, fertile lobes	on surface of lateral lobes
G. longibracteata Florin (1944)	five equal-sized sterile lobes; two lateral, stalk-like sporophylls	terminal on the lateral sporophylls
G. longibracteata Schweitzer (1963)	?	probably near base of lateral lobes
G. platysperma Mägdefrau (1963)	five central lobes; two larger lateral lobes (based on illustration)	in middle of scale surface
G. richteri This paper	eight equal-sized lobes	?
G. 'unnamed' Cornet (1977)	three or four central sterile lobes, two larger lateral lobes	on surface of lateral lobes
G. windsheimensis Kräusel (1939)	five equal-sized lobes	attached to sides of cone scale stalk
G. windsheimensis Florin (1944)	five equal-sized sterile lobes, two lateral, stalk-like megasporophylls	terminal on the lateral sporophylls

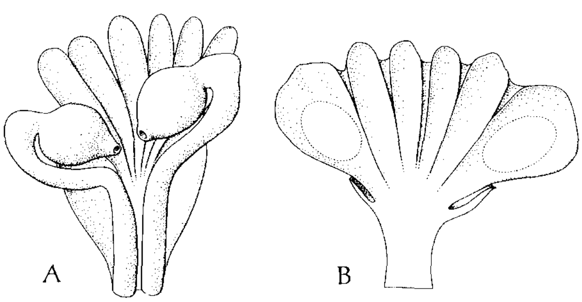


Fig. 2. (A) Florin's concept of a cone scale erroneously assigned to *Glyptolepis keuperiana*. Redrawn from Florin (1944). (B) Reconstruction of a similar cone scale from a North American specimen. Circles represent sites of ovule attachment. See text for details.

two large lateral seeds. He was unable to identify stalk-like megasporophylls but attributed this to poor preservation. His illustrations, however, suggest that the two lateral lobes are approximately twice as large as the central lobes and bear an ovule or large ovule attachment scar directly on their surfaces. This material was also examined by Schweitzer (1963) who did not find evidence for stalk-like megasporophylls.

Seed cones from the Late Triassic (late Carnian) New Oxford Formation of York County, Pennsylvania (USA) were assigned to *Glyptolepis* by Cornet (1977) based on their similarity to Mägdefrau's (1963) specimens. Similar cones occur in the Upper Stockton Formation in Chester County, Pennsylvania (Axsmith and Kroehler, 1989). Bioplastic transfers of additional specimens collected from the York County locality clearly show that the cone scale consists of five small central sterile scales and two large, laterally diverging fertile scales (Plate I, 6). We suggest that the stalk-like, recurved megasporophylls of Florin's (1944) reconstruction are actually the outer edges of the large, lateral fertile lobes as suggested by comparison with the better preserved North American material (Fig. 2B). Such a cone scale structure suggests affinity with the Late Permian family Majonicaceae (Clement-Westerhof, 1987), but bears little similarity to *Glyptolepis* as described here.

4.2. *Glyptolepis windsheimensis*

Kräusel (1939) described seed cones from the middle Keuper of Windsheim in Oberfranken, Germany as *Voltzia windsheimensis*. Florin (1944) transferred these cones to *Glyptolepis* based primarily on the presence of two seeds. Although little is known about these cones, the small size (5.25 cm × 3.5 cm) and five-lobed cone scale arrangement precludes any close relationship to *Glyptolepis*.

4.3. *Glyptolepis platysperma* and *G. delawarensis*

Glyptolepis platysperma is known from cone scales from the middle Keuper of Ziegelanger, Germany (Mägdefrau, 1963). These are probably the same as some of the scales assigned to *Voltzia coburgensis* by Kräusel (1939). Bock (1969) described similar cone scales from the Late Triassic Passaic Formation in New Jersey, USA as *Glyptolepis delawarensis*. The scales of both species are five-lobed with the ovules born in two depressions on the adaxial surface of the scale. It is probable that Mägdefrau (1963) interpreted molds of the depressions as ovules. These isolated cone scales have no stalks and were probably sessile on the cone axis. This feature, along with the two ovules born in depressions, suggests affinity with the Cheirolepidiaceae. Bock (1969) noted the similarity of these scales to those of the cheirolepidiaceous genus *Hirmeriella*, but nevertheless placed them in the genus *Glyptolepis*. Although Bock's specimens of '*Glyptolepis*' *delawarensis* are lost (Spamer, 1995), newly collected material is currently under study. Although these cone scales are presently poorly understood, there is little reason to consider them any further as members of *Glyptolepis*.

4.4. *Glyptolepis hungarica* and *G. longibracteata*

These taxa were considered by Florin (1944) to be the earliest known representatives of the genus. *Glyptolepis hungarica* comes from the Upper Permian of southern Hungary and was first described as *Voltzia hungarica* by Heer (1876). Heer's illustrations indicate a five-lobed cone scale but no information regarding the number and placement of the seeds is provided. Florin reexamined Heer's collection and illustrated a specimen he interpreted as bearing inverted seeds terminally attached to lateral, stalk-like megasporophylls. The figured specimen (Florin, 1944, plate 179/180, fig. 16) is poorly preserved with the putative seed and stalk visible only on one side. Schweitzer (1963) concluded that it was impossible to determine the placement of the seeds. Florin (1944) provided a similar interpretation of *Glyptolepis longibracteata* (Lower Triassic of Fürstenberg, Germany). After examination of the type material Schweitzer (1963) concluded that the seeds were not born on lateral stalk-like megasporophylls, but rather directly on the surface of lateral fertile scales. This agrees with the earlier interpretation of these cones by Schlüter and Schmidt (1927). Schweitzer (1963) further suggested that the structures identified as stalk-like megasporophylls by Florin (1944) are actually the edges of a relatively large bract that extends beyond the cone scale stalk as is the case in *Pseudovoltzia*.

5. Conclusions

Despite the uncertain nature of many fossils assigned to *Glyptolepis*, Florin's (1944, fig. 54, a, b) line drawings have been frequently reproduced as representative of the genus (e.g., Miller, 1977), and have influenced concepts of conifer phylogeny and functional morphology. For example, Niklas (1985) constructed scale models of *Glyptolepis hungarica* based on Florin's drawings for use in his studies of the aerodynamics of wind pollination in conifers. In addition, Miller (1988) has hypothesized that with more information *Glyptolepis* may make a good outgroup in phylogenetic analysis of modern conifer families. Based on the uncertain nature of these taxa as discussed above, we suggest that further use of Florin's (1944) reconstructions should be discontinued.

Although Schimper's (1870) description of *Glyptolepis* included some inaccuracies, the above analysis suggests that the major misinterpretations of the genus began when certain Triassic ovulate cone scales with two large, lateral, fertile lobes were erroneously assigned to *Glyptolepis keuperiana* by Florin (1944), and subsequently by Mägdefrau (1963) and Cornet (1977). Based on our analysis, it appears that the only published material that should presently be included in *Glyptolepis* are the specimens assigned to *G. keup-*

eriana by Schimper (1870) and recently refigured by Schweitzer (1996), and the cones described here as *G. richteri*.

The lack of information regarding important features such as the number and position of ovules, morphology of pollen cones, and vegetative features precludes a detailed consideration of the affinities of these cones at this time. Comparisons are also hampered by the ambiguous interpretations of many other early Mesozoic conifer genera. For example, it is difficult to evaluate Schimper's (1870) description of *Glyptolepis* as *Voltzia*-like since nearly every early Mesozoic conifer with lobed cone scales has at some time been included in *Voltzia*. Although several genera have subsequently been removed from *Voltzia*, there can be little doubt that the genus remains highly artificial (Delevoryas and Hope, 1987). *Glyptolepis richteri* exhibits several unusual features that make comparison with other taxa difficult. The eight-lobed cone scales of both *Glyptolepis richteri* and *G. keuperiana* are unusual since most Triassic conifers have five or fewer lobes. Exceptions include the cones erroneously assigned to *Glyptolepis* by Florin (1944) and Cornet (1977). As discussed above, however, these cones display dimorphism of fertile and sterile lobes, and probably represent late ranging members of the otherwise Permian family Majonicaceae. Assuming that loss and/or fusion of cone scale lobes is irreversible, the relatively low number of cone scale lobes in early Mesozoic conifers is problematic since some modern genera like *Sciadopitys* and *Taxodium* can have up to 11 and 12 lobes, respectively (Takaso and Tomlinson, 1990, Takaso and Tomlinson, 1991). Although *Glyptolepis* has too few cone scale lobes to be considered a precursor to such modern forms, it does demonstrate that conifers with more than five equal cone scale lobes existed in the Triassic. This raises the possibility that potential ancestral morphologies for modern conifers with numerous cone scale lobes may be found in the Triassic thus eliminating the need to postulate a reversal in this character transformation. Schweitzer (1996) suggests that *Glyptolepis* may be descended from some member of the family Majonicaceae. We believe that this is unlikely since the currently recognized members of this family have dimorphic fertile and sterile cone scale lobes. Schweitzer (1996, p. 2) also proposes that the cone scale lobes of *Glyptolepis* are 'nearly completely coalescaent'. However, the deep furrows between the cone scale lobes of *Glyptolepis* suggest less fusion of parts than found in the cone scales of most members of the Majonicaceae.

The outer layer of expanded bract apices is a conspicuous feature of *G. richteri*. Bracts in the Araucariaceae are large compared with the cone scale and often have protracted apices. However, there is no lobed cone scale known in the Araucareaceae. The taxodiaceous conifer *Cunninghamia* has a relatively large bract and a three-lobed cone scale, but there is little else upon which to compare it with *Glyptolepis*. The current lack of data on important aspects of the morphology of *Glyptolepis* precludes any other meaningful comparisons with fossil or living forms. Miller (1988) suggested the necessity of keeping an open mind regarding concepts of conifer phylogeny due to our imperfect knowledge of both fossil and recent forms. Although progress has been made recently in our understanding of the earliest conifers (Kerp and Clement-Westerhof, 1991; Mapes and Rothwell, 1991), current understanding of most early Mesozoic forms is less precise. A major finding of Paleozoic conifer research has been the recognition of greater diversity than previously thought. Although the great diversity of early Mesozoic conifers has been recognized for some time (Miller, 1977), it is likely that much more diversity is still conceptually hidden within overly circumscriptive genera such as *Glyptolepis* and *Voltzia*. A recognition of greater conifer diversity in the early Mesozoic will exasperate an already confusing picture that Miller (1977, p. 219) has called, "...a jigsaw puzzle with too many pieces". Nevertheless, it is clear that what is now needed is a case by case reinvestigation of all known early Mesozoic conifers. It is only as a result of such studies that it will be possible to develop a robust estimate of conifer phylogeny.

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References

Axsmith, B.J. and Kroehler, P.A., 1989. Upper Triassic *Dinophyton* Zone plant fossil from the Stockton Formation in southeastern Pennsylvania. Mosasaur, 4: 45–48.

Bock, W., 1969. The American Triassic Flora and Global Distribution, Vols. 3 and 4. Geological Center, North Wales, PA, 406 pp.

Clement-Westerhof, J.A., 1987. Aspects of Permian palaeobotany and palynology, VII. The Majonicaceae, a new family of late Permian conifers. Rev. Palaeobot. Palynol., 52: 357–402.

Cornet, B., 1977. Preliminary investigation of two Late Triassic conifers from York County, Pennsylvania. In: R.C. Romans (Editor), Geobotany. Plenum, New York, NY, pp. 165–172.

Delevoryas, T. and Hope, R.C., 1987. Further observations on the Late Triassic conifers *Compsostrobus neotericus* and *Voltzia andrewsii*. Rev. Palaeobot. Palynol., 51: 59–64.

Dobruskina, I.A., 1975. The role of peltaspermacean pteridosperms in Late Permian and Triassic floras. Paleontol. J., 9: 536–548.

Florin, R., 1938–1945. Die Koniferen des Oberkarbons und des unteren Perms. Paleontographica B, 85(1–8): 1–729.

Florin, R., 1944. Die Koniferen des Oberkarbons und des unteren Perms. Paleontographica B, 85: 366–456.

Franke, F., 1936. *Equisetites asperrimus*, ein neuer Equisetit aus dem Keuper Mitteldeutschlands. Jahrb. Preuß. Geol. Landesanst. Berlin, 1935, 56: 219–221.

Heer, O., 1876. Ueber permische Pflanzen von Fünfkirchen. Mitt. Jahrb. K. Ung. Geol. Anst., 5: 1–18.

Kerp, H. and Clement-Westerhof, J.A., 1991. Aspects of Permian palaeobotany and palynology, XII. The form-genus *Walchiostrobus* Florin reconsidered. Neus Jahrb. Geol. Paläontol. Abh., 183(1/3): 257–268.

Kräusel, R., 1939. Die Windsheimer Ähren ein Beitrag zur Kenntnis der Koniferen des süd-Deuschen Mesozoikums. Palaeontographica, 84: 21–41.

Linnell, T., 1932. Zur morphologie und systematik Triassischer cycadophyten, I. Die gattung *Sphenozamites* Brogn. Sven. Bot. Tidskr., 26: 241–263.

Linnell, T., 1933. Zur Morphologie und Systematik Triassischer Cycadophyten, II. Über *Scytophyllum* Bornem., eine wenig bekannte Cycadophytengattung aus dem Keuper. Sven. Bot. Tidskr., 27: 310–331.

Mägdefrau, K., 1963. Die gattungen *Voltzia* und *Glyptolepis* im mittleren Keuper von Haßfurt (Main). Geol. Bl. NO Bayern, 13: 95–98.

Mapes, G. and Rothwell, G.W., 1991. Structure and relationships of primitive conifers. Neues Jahrb. Geol. Paläontol. Abh., 183(1/3): 269–287.

Miller, C.N., 1977. Mesozoic conifers. Bot. Rev., 43(2): 218–271.

Miller, C.N., 1988. Origin of modern conifer families. In: C.B. Beck (Editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York, NY, pp. 448–486.

Nathorst, A.G., 1912. P.B. Richter's paläobotanische Sammlungen. Sonderabdruck Palaeobot. Z., 1.

Niklas, K.J., 1985. The aerodynamics of wind pollination. Bot. Rev., 51(3): 329–383.

Schimper, W.P., 1870–1872. Traité de Paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel, 2. Baillière, Paris, 966 pp.

Schlüter, H. and Schmidt, H., 1927. *Voltzia*, *Yuccites* und andere neue Funde aus dem Südhannoverschen Buntsandstein. Neues Jahrb. Mineral., Geol. Paläontol., Beilagebd. 57B Abt. B. Stuttgart.

Schweitzer, H.J., 1963. Der weibliche Zapfen von *Pseudovoltzia liebeana* und seine Bedeutung für die Phylogenie der Koniferen. Palaeontographica B, 113: 1–29.

Schweitzer, H.J., 1996. *Voltzia hexagona* (Bischoff) Geinitz aus dem mittleren Perm Westdeutschlands. Palaeontographica B, 239: 1–22.

Spamer, E.E., 1995. The surviving component of the Wilhelm Bock collection of fossils (invertebrates, vertebrates, and plants) held at the Academy of Natural Sciences of Philadelphia. Notulae Naturae, 473: 1–16.

Takaso, T. and Tomlinson, P.B., 1990. Cone and ovule ontogeny in *Taxodium* and *Glyptostrobus* (Taxodiaceae–Coniferales). Am. J. Bot., 77(9): 1209–1221.

Takaso, T. and Tomlinson, P.B., 1991. Cone and ovule development in *Sciadopitys* (Taxodiaceae–Coniferales). Am. J. Bot., 78(3): 417–428.