

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/285653155>

Structure and relationships of primitive conifers

Article · January 1991

CITATIONS

61

READS

328

2 authors:



Gene Mapes

Ohio University

65 PUBLICATIONS 1,403 CITATIONS

[SEE PROFILE](#)



G.W. Rothwell

Ohio University and Oregon State University

341 PUBLICATIONS 7,522 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Taxodiaceous seed cones from Japan, Cornales morphological matrix, Pinaceous leaves from the Cretaceous of Hokkaido, Araucarian cones from Hokkaido and Argentina, etc. [View project](#)



Conifer Evolution [View project](#)

Herrn Prof. Dr. Winfried Remy
zum 65. Geburtstag gewidmet

Structure and relationships of primitive conifers

By

Gene Mapes and Gar W. Rothwell, Athens, Ohio

With 17 figures and 2 tables in the text

MAPES, G. & ROTHWELL, G. W. (1991): Structure and relationships of primitive conifers. – N. Jb. Geol. Paläont., Abh., 183: 269–287; Stuttgart.

Abstract: Fossil evidence for the most primitive conifers is summarized, and the structure of permineralized North American specimens is emphasized. Some produce compound cones in which inverted ovules are borne at the tips of sporophylls. These are interpreted to be more primitive than previously known conifers, and are assigned to *Emporia* n. g. of the Emporiaceae n. fam. The historical development of primitive conifer systematics is reviewed, and the recent systematic scheme of CLEMENT-WESTERHOF and colleagues is emended to include *Utrechtia* n. g. of the Utrechtiaceae n. fam. for the illegitimate genus *Lebachia* FLORIN. *Walchia* STERNBERG is retained as a form genus for primitive conifer remains.

Zusammenfassung: Im Rahmen einer Übersicht werden die Kenntnisse über die frühesten Koniferen zusammengefaßt. Dabei wird insbesondere auf strukturbietend erhaltene Funde aus Nordamerika eingegangen. Sie bildeten zusammengesetzte Zapfen bei denen sich die zurückgekrümmten Samenanlagen an den Spitzen der Sporophylle befinden. Als bislang primitivste Koniferen werden sie als neue Gattung *Emporia* in die neue Familie der Emporiaceae gestellt. In diesem Zusammenhang wird ein Überblick zur historischen Entwicklung in der Systematik früher Koniferen gegeben. Die neue Systematik von CLEMENT-WESTERHOF und Kollegen wird dahingehend erweitert, daß an Stelle der ungültigen Gattung *Lebachia* FLORIN die neue Gattung *UTRECHTIA* aus der neuen Familie der Utrechtiaceae tritt. Die Gattung *Walchia* STERNBERG wird als Formgattung für primitive Koniferenreste beibehalten.

Contents

1. Introduction	270
2. Paleozoic North American conifers	270
3. Background to the systematics of primitive conifers	273
4. Systematic interpretations	274
5. Taxonomic discussions and nomenclatural revisions	277
6. Rationale for taxonomy and nomenclature in the classification of primitive conifers	281
7. Acknowledgements	285
8. Literature	285

1. Introduction

Recent descriptions of conifer remains in Upper Carboniferous and Lower Permian deposits of Europe, North America and South America generally support the interpretations by FLORIN regarding the structure and homologies of the most ancient conifers. These studies also reveal a far greater diversity of taxa than recognized earlier, as well as several features that previously were either unknown or inaccurately interpreted.

The new family Ferugliocladaeae has been described from Argentina (ARCHANGELSKY & CUNEO 1987), and together with the Buriadiaceae from India (PANT 1977, 1982) demonstrate that conifers were present on the Gondwana continent by Permian time. Permineralized remains from North America yield the first extensive anatomical evidence of primitive conifers (MILLER & BROWN 1973, ROTHWELL 1982, MAPES & ROTHWELL 1984, 1988, MAPES 1987). The North American fossils further heighten our appreciation of taxonomic diversity, and allow for the interpretation of several structural, developmental and reproductive features that clarify early conifer characters and systematic relationships.

Some of the most abundant new material consists of coalified compressions and cuticular envelopes from Europe. Such material provides the basis for the description of several new species, new genera and a new family of primitive conifers (CLEMENT-WESTERHOF 1984, 1987, 1988, VISSCHER, KERP & CLEMENT-WESTERHOF 1986, KERP & CLEMENT-WESTERHOF this volume, KERP et al. 1990). These authors also have recognized that FLORIN's well known and extensively studied genus *Lebachia* FLORIN (1938) is both nomenclaturally illegitimate and includes several genera (e. g. CLEMENT-WESTERHOF 1988). As a result, a far more accurate and inclusive systematics of primitive conifers has begun to emerge (Table 1).

In this paper we emphasize several unique characters of the primitive North American conifers, and employ these data to further extend and emend the recently proposed systematic revisions of CLEMENT-WESTERHOF and colleagues (CLEMENT-WESTERHOF 1984, 1987, 1988, VISSCHER et al. 1986, KERP & CLEMENT-WESTERHOF, this volume, KERP et al. 1990; Table 1).

2. Paleozoic North American conifers

Primitive conifer remains have been recovered from North American deposits in the Cordilleran, Midcontinent and Appalachian regions, and range from Middle Pennsylvanian through Early Permian in age (MAPES & GASTALDO 1986). Most of the reports are based on a small number of fragments of vegetative shoots that are preserved by impression or coalified compression and are lacking in cuticle (e. g. DARRAH 1936). As a result, they conform to the form genus *Walchia* STERNBERG as employed by FLORIN and others (e. g. FLORIN 1951). Other remains are more informative. These include isolated leafy twig

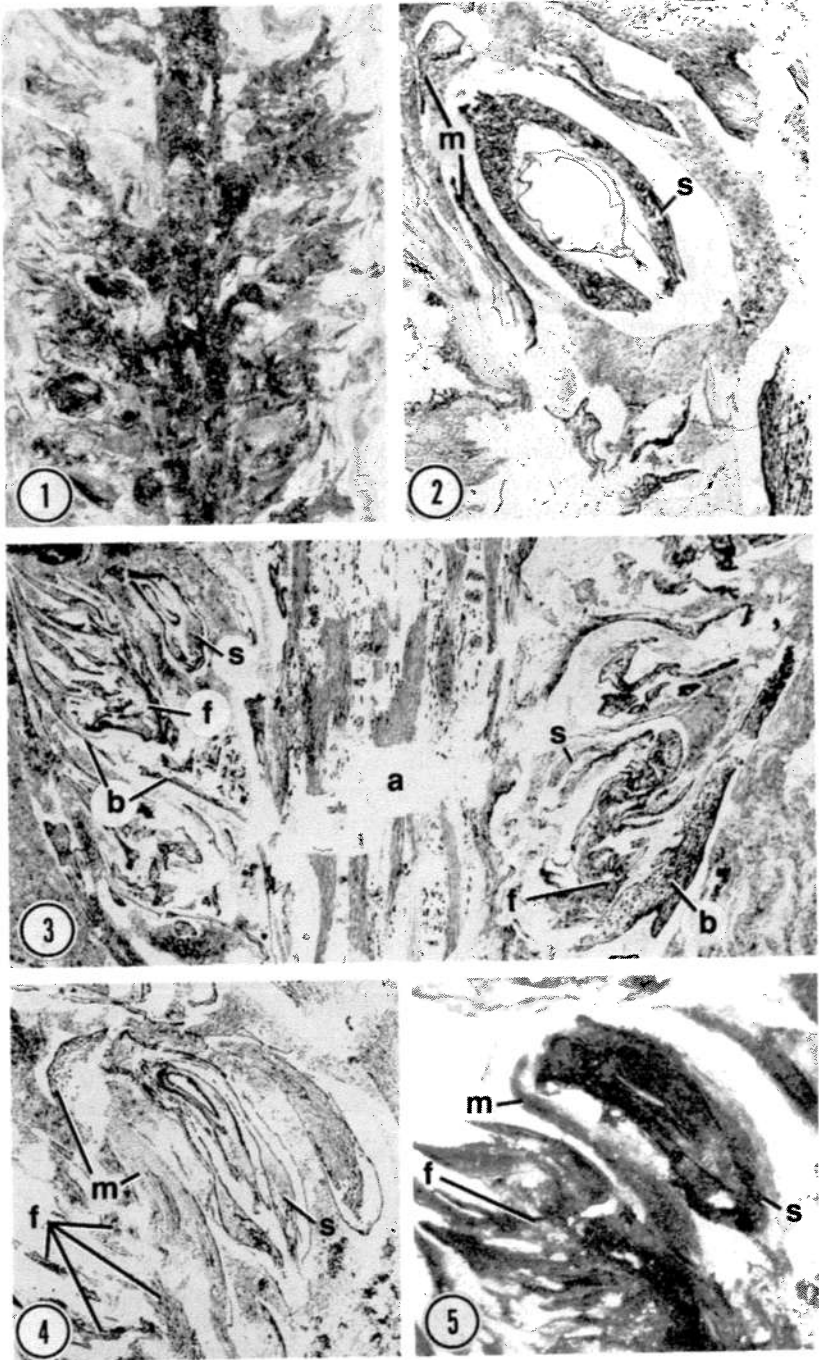
(ELIAS 1948, ROTHWELL 1982) and cones (MILLER & BROWN 1973, MAPES 1983) that show internal cellular preservation, and large collections of compressed vegetative and fertile remains that display some cuticular features (TIDWELL & ASH 1980, ASH & TIDWELL 1982, WINSTON 1984). The most informative material reveals internal cellular preservation as well as external morphology and cuticular detail (MAPES & ROTHWELL 1988, McCOMAS 1988). Fossil conifer remains with this suite of features yield valuable information that is not available from specimens preserved by other modes. These fossils allow us to interpret the biology of ancient conifers by direct comparisons with extant conifers, and significantly extend the suite of characters available for phylogenetic analyses.

Many of the North American fossils have been described earlier or are being prepared for publication elsewhere, so we restrict our descriptions to specimens that are crucial for clarifying features of systematic importance. Material from Hamilton Quarry in southeastern Kansas consists of woody logs with orthotropic branching, leafy shoots with plagiotropic branching, leafy shoots with irregular branching, pollen cones with saccate pollen, compound ovulate cones with attached ovules, and seeds that bear polycotyledonary embryos (MAPES & ROTHWELL 1984, 1988, MAPES 1987, MAPES, ROTHWELL & HAWORTH 1989). Among vegetative shoots with essentially identical internal anatomy and cuticular features of leaves in the ultimate branches, there is a wider range of variation in leaf morphology (MAPES & ROTHWELL 1988) than recognized for individual species of European conifers (FLORIN 1938-1945). Other shoots with essentially identical leaf morphology differ anatomically (MAPES & ROTHWELL 1988). Pollen cones consist of a non-woody axis that bears helically arranged sporophylls with adaxial clusters of pollen sacs that contain sacate grains (e. g. *Potomiesporites*; MAPES 1983, MAPES & ROTHWELL 1988).

Of perhaps greatest systematic interest are the anatomically preserved ovulate cones (Figs. 1-5, 9-16). One species was originally described as *Lebachia lockardii* (Figs. 9-16; MAPES & ROTHWELL 1984). A second undescribed species (Figs. 1-5) contains polycotyledonary embryos that provide the first evidence for the evolution of seed dormancy (MAPES et al. 1989). Cones of these species are borne on leafy shoots and consist of a woody axis that bears helically-arranged, forked bracts with axillary fertile shoots (Figs. 1, 3). The fertile shoots are bilaterally symmetrical and somewhat flattened, and each bears numerous sterile scales and several distinctive sporophylls (Figs. 16, 17b).

The sterile scales fan outward from the fertile shoot axis and are leaf-like (Figs. 16, 17b). Most are relatively narrow and flat (Fig. 16), with an acutely pointed apex or apical protuberance (Figs. 9-10, 14). Some of the sterile scales are more or less fused (Figs. 10, 14).

Sporophylls are also narrow and leaf-like (Figs. 11-13), though generally more terete in transverse sections (Plate 13, Figs. 2-4 of MAPES & ROTHWELL 1984). Sporophylls are attached to the side of the fertile shoot that faces the primary cone axis (Figs. 3, 17b). Each sporophyll separates from the fertile shoot and extends 3 to 4.5 mm before terminating in the base of a single in-



Figs. 1-5 (Legends see p. 273)

verted ovule (Figs. 2-5). The tip of each sporophyll is more or less recurved (Figs. 2-5), but ovule attachment is always terminal. Because the angle of recurvation varies, however, in maceration preparations the abscission scar often appears at the side of the sporophyll apex (Fig. 11-13).

Within each cone, the angle of ovule attachment is determined by the degree of sporophyll recurvation. As a result, the position of the abscission scar on the ovule ranges from basal (Figs. 2, 4) to lateral (Fig. 15). Likewise, the attachment scar on the sporophyll ranges from apical to lateral. In the first instance the scar is perpendicular to the long axis of the ovule, whereas in the latter it is not. The extremes in this range of variation are what CLEMENT-WESTERHOF refers to as "seed axis is straight" or "seed axis is bent" respectively (CLEMENT-WESTERHOF 1988, p. 320).

3. Background to the systematics of primitive conifers

In his investigations of primitive conifers FLORIN (1931, 1938-45, 1950) interpreted external morphology, cuticular anatomy, wood anatomy and reproductive features to be characters of taxonomic significance. Florin recognized two families of primitive Northern Hemisphere conifers, Lebachiaceae and Voltziaceae, as well as several form genera (Table 1). More recent studies have led to the establishment of two new families of Gondwana conifers, the Buriadiaceae PANT (1977) and the Ferugliocladaceae ARCHANGELSKY & CUNEO (1987), that appear to produce either solitary stalked ovules or simple (not compound) ovulate cones.

Figs. 1-5. *Emporia* sp. ovulate cone, Hamilton, Kansas specimen No. M1613 in the Ohio University Paleobotanical Herbarium; all in longitudinal view. Abbreviations for Figs. 1-5. a = axis of cone, b = bract, f = fertile axillary shoot, m = megasporophyll, s = seed.

Fig. 1. Fractured interior of cone midregion showing cone axis, bracts and axillary fertile shoots. Note ovules at left, X 2.

Fig. 2. Close up of fertile shoot showing one recurved sporophyll with abscised seed facing cone axis at right. Note open micropyle, pollen chamber and megaspore membrane within nucellus. Note also that nucellus is free from integument distal to chalaza. Cellulose acetate peel MP20 X 9.

Fig. 3. Midlongitudinal section of cone midregion showing bracts and axillary fertile shoots diverging from cone axis. Note seeds attached to the tips of recurved sporophylls. Cellulose acetate peel BL15 X 7.

Fig. 4. Section view of axillary fertile shoot with one recurved sporophyll and abscised terminal seed. Cellulose acetate peel BL13 X 10.

Fig. 5. Surface view of axillary fertile shoot with one recurved sporophyll and terminal seed for comparison to comparable features as seed in section views (e. g., Fig. 4). X 10.

In their ongoing revision of primitive conifer systematics CLEMENT-WESTERHOF and colleagues (CLEMENT-WESTERHOF 1984, 1986, 1988, VISSCHER et al. 1986, KERP & CLEMENT-WESTERHOF this volume, KERP et al. 1990) agree with FLORIN (1931, 1938-45, 1950) and others that external morphology alone is inadequate for delimiting genera and families of plants. These authors consider a wide array of both vegetative and reproductive characters to have systematic significance, but in practice they delimit families primarily by the morphology of the ovulate cones. This practice appears to be more valid than earlier approaches and reveals greater diversity than previously had been recognized among primitive conifers (Table 1).

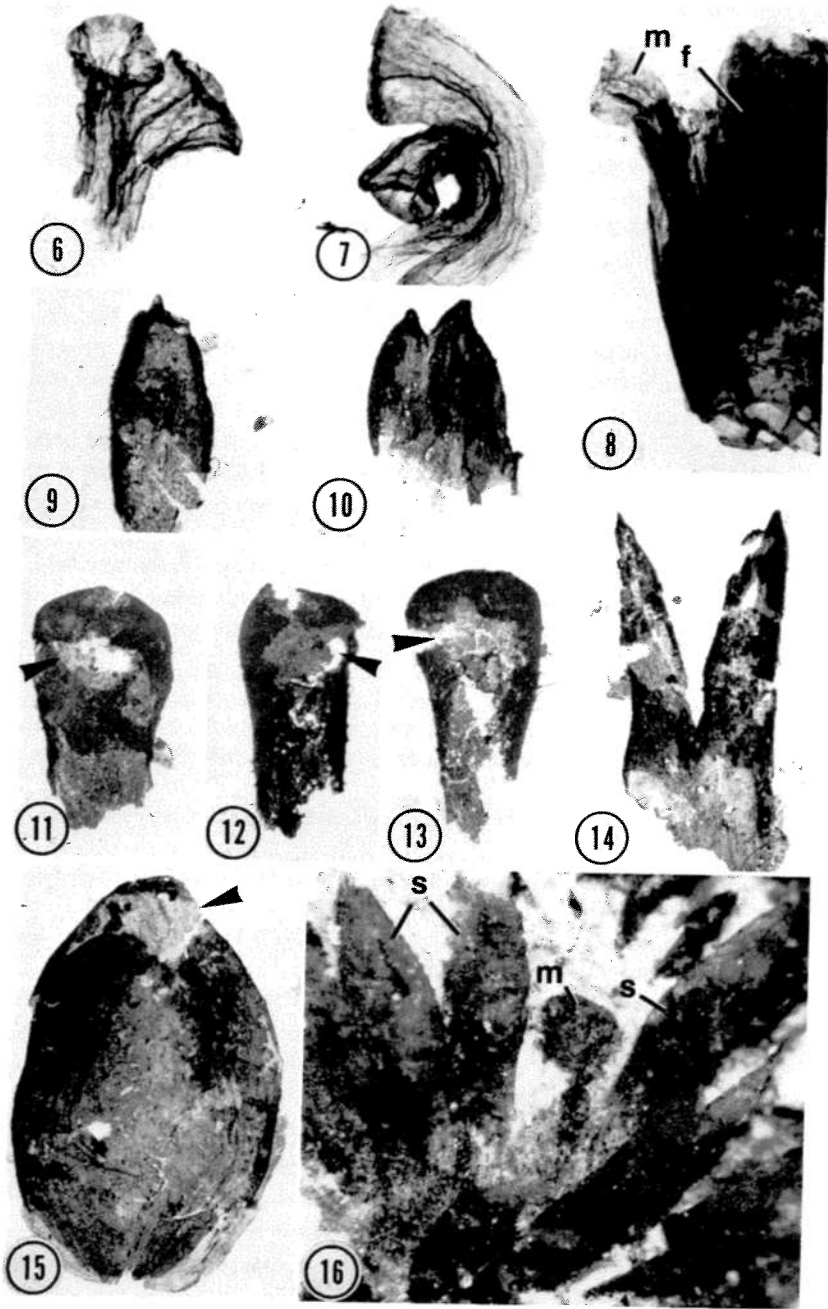
CLEMENT-WESTERHOF and colleagues recognize the two families of Gondwana conifers and several families of Euramerican conifers (Table 1). These are the Buriadiaceae PANT (1977), Ferugliocladaceae ARCHANGELSKY & CUNEO (1987), Walchiaceae (= Lebachiaceae of FLORIN), Ullmanniaceae ZIMMERMANN, Majonicaceae CLEMENT-WESTERHOF, and by implication Voltziaceae (sensu FLORIN 1963, in part). They also recognize several form genera of primitive conifer remains (Table 1; CLEMENT-WESTERHOF 1984, 1987, 1988, KERP & CLEMENT-WESTERHOF this volume, KERP et al. 1990).

One species left unclassified by CLEMENT-WESTERHOF and colleagues (e. g. CLEMENT-WESTERHOF 1988) is the anatomically preserved ovulate cone (Figs. 9-16) originally described as *Lebachia lockardii* MAPES & ROTHWELL 1984. CLEMENT-WESTERHOF (1984) recognized that a new generic name is needed for cones of this type, and excluded *L. lockardii* from the Walchiaceae (sensu VISSCHER et al. 1986) because there is commonly more than one ovule borne on each axillary fertile shoot (Fig. 17b; MAPES & ROTHWELL 1984). Now that the features of ovulate cones assigned to the Lebachiaceae by FLORIN (1938) have been clarified, we agree with CLEMENT-WESTERHOF (1984, 1988) that specimens like those described earlier as *L. lockardii* are distinct at the family level. However, we consider them to be distinct for reasons other than that stated by CLEMENT-WESTERHOF 1984, p. 110; 1988, p. 320). Both species of Hamilton Quarry cones described in this report are of this type (Figs. 1-5, 9-16, 17b).

Our interpretation is based on the distinctive morphology of the axillary fertile shoots, and particularly that of the ovulate sporophylls. As detailed above, the ovulate sporophylls of these Hamilton conifers diverge from the axillary fertile shoot well below the level where the ovule is attached terminally (Figs. 5, 17b). The sporophylls are also quite narrow, and in these features are remarkably similar to ovulate sporophylls of most cordaites (Figs. 6-8, 17a; ROTHWELL 1988, IGNATIEV & MEYEN 1989).

4. Systematic interpretations

Since the studies of FLORIN, cordaites cones have been considered as the archetype for the ovulate cones of conifers. Using phylogenetic rationale this is



Figs. 6-16 (Legends see p. 276)

appropriate because cordaites and conifers are considered to be sister groups (MILLER 1982, CRANE 1985, DOYLE & DONOGHUE 1986), and therefore cordaites may be used as an outgroup for assessing character state polarities among primitive conifers. FLORIN (1951) demonstrated that the ovulate cones of cordaites and most conifers are compound structures that consist of a primary axis that bears bracts with axillary fertile shoots. In the Cordaitales the fertile shoots bear both sterile scales and distinct fertile scales (sporophylls) with terminal ovules (Figs. 6-8, 17a), but in conifers there is a wide array of morphologies that are considered to represent different degrees of fusion and reduction among the fertile shoot axis, sterile scales and sporophylls (e. g. Fig. 17b-e; FLORIN 1951). In the most highly modified of these (e. g. *Ullmania*, Fig. 17e) the entire axillary fertile shoot is represented by a simple structure (= cone scale of PINUS) with an inverted seed (or seeds) attached laterally to the surface that faces the cone axis.

Recently, the ovules of even the most ancient of conifer cones have been recognized as inverted (CLEMENT-WESTERHOF 1984, MAPES & ROTHWELL 1984). However, the axillary fertile shoots of most genera (e. g. *Ortiseia*, Fig. 17c; *Pseudovoltzia*, Fig. 17d; MAPES 1987) are modified to such a degree that, without anatomical details of vascularization, one can not determine with certainty if the ovules are attached to the surface of a reduced and modified sporophyll, attached to a lobe that consists of the fusion of the sporophyll to the

Figs. 6-16. Maceration preparations of cuticular envelopes from cordaites ovulate cones (Figs. 6-8) and from *Emporia lockardii* (Figs. 9-16), all deposited in the Ohio University Paleobotanical Herbarium. Abbreviations for Figs. 6-16. f = fertile shoot, m = megasporophyll, s = sterile scale.

Fig. 6. Cordaites megasporophyll with forked tip and terminal attachment scars of two ovules. Lonestar Lake CM11 X 12.

Fig. 7. Cordaites sporophyll similar to that in Fig. 6, but with more or less recurved tip. Lonestar Lake CM11A X 12.

Fig. 8. Cordaites axillary fertile shoot with numerous sterile scales and one extended megasporophyll. Lonestar Lake CM12 #3 X 9.

Figs. 9-16. *Emporia lockardii* from Hamilton Quarry, specimen M1775.

Fig. 9. Sterile scale with apiculate tip, or sporophyll with aborted ovule primordium. 2nd. Mac. #11 X 16.

Fig. 10. Connate sterile scales. Mac. #6 X 16.

Fig. 11. Sporophyll with attachment scar at arrow point. 2nd. Mac. #29 X 16.

Fig. 12. Sporophyll with attachment scar at arrow point. 2nd. Mac. #29 X 16.

Fig. 13. Sporophyll with attachment scar at arrow point. 2nd. Mac. #29 X 16.

Fig. 14. Lanceolate sterile scales fused basally. 2nd. Mac. #26 X 16.

Fig. 15. Inverted ovule or seed with attachment scar at arrow and micropyle at bottom. Mac. #3 X 10.

Fig. 16. Surface view of axillary fertile shoot as seen from exterior of cone with bract removed. Note several sterile scales and one sporophyll. Mac. #3 X 5.

fertile shoot axis, or borne on a highly reduced axillary fertile shoot (= cone scale). In other words, the homologies of structures described by the term „fertile scale“ are not clear (MAPES 1987).

The Hamilton cones described in this chapter bear ovules at the tip of distinct sporophylls (Fig. 17b). We interpret these species to represent a new genus and a new family with a larger number of ancestral characters than any other family of primitive conifers. For plants previously described as *Lebachia lockardii* MAPES & ROTHWELL 1984, we propose the genus *Emporia* n. g. and *Emporia lockardii* (MAPES & ROTHWELL) n. comb. in the new family Emporiaceae. Additional conifer material illustrated here (Figs. 1-5) represents an unnamed new species of *Emporia* that will be formally described elsewhere.

Order Coniferales

Emporiaceae n. fam.

Familial Diagnosis: Coniferous trees with orthotropic stems and plagiotropic or irregularly branched lateral leafy shoots. Penultimate vegetative shoots with helically arranged simple and/or bifid leaves; leaves on ultimate branches simple with one collateral bundle. Leaves usually amphistomatic with stomata in bands or rows, stomatal complexes comprising 4-10 subsidiary cells with sunken guard cells. Papillae and trichomes present on epidermis of stems and leaves. Stems with endarch eustele and wood of narrow tracheids with uniseriate-biseriate bordered pits, rays 1-2 cells wide and 1-8 cells high. Cortex, pith and mesophyll with secretory cells, nests of sclereids and hypodermal sclerenchyma. Ovulate cones compound on leafy shoots; woody cone axis bearing bifid bracts and axillary fertile shoots. Fertile shoots bilaterally symmetrical and somewhat flattened, with 15-30 sterile scales and one or more leafy sporophylls. Sporophylls narrow, diverging from shoot for 3 to 5 mm, more or less recurving, each bearing apically one inverted ovule or seed. Seeds bilaterally symmetrical and flattened with rounded-subcordate base, attachment scar basal to sublateral; bearing polycotyledonary embryos at maturity. Pollen cones simple, cylindrical and elongated, constructed of herbaceous axis bearing helically arranged amphistomatic sporophylls with adaxial clusters of sporangia containing monosaccate prepollen.

Emporia n. g.

Type Species: *Emporia lockardii* (MAPES and ROTHWELL) comb. n.

Etymology: The genus name refers to Emporia, Kansas, where the Geology Museum at Emporia State University houses a significant collection of specimens from the Hamilton Quarry.

Remarks: This genus and species are proposed for specimens originally described as *Lebachia lockardii* MAPES & ROTHWELL 1984. The diagnosis, type specimens and locality data for *Emporia lockardii* are as stated previously for *Lebachia lockardii* Mapes & Rothwell 1984.

5. Taxonomic decisions and nomenclatural revisions

CLEMENT-WESTERHOF has proposed that the form genus *Walchia* be elevated to a genus of plants in the Walchiaceae, and that several of the species included

Table 1. Families and genera of primitive conifers from the Northern Hemisphere as they are recognized in this paper (at left), by FLORIN and those who followed his classification (at center), and by CLEMENT-WESTERHOF and colleagues (at right). Gondwana conifers (not included in Table) are the same in the three classifications. See text for details.

<u>Mapes and Rothwell</u>	<u>sensu Florin</u>	<u>Clement-Westerhof, & Colleagues</u>
Utrechtiaceae	Lebachiaceae	Walchiaceae
<u>Utrechtia</u> Mapes and Rothwell	<u>Lebachia</u> Florin	Walchia Sternberg
Ortiseia Florin	Ortiseia Florin	Ortiseia Florin
<u>Moyliostrobus</u> Miller and Brown	<u>Moyliostrobus</u> Miller	<u>Otovicia</u> Kerp et al.
Ernestiodendron Florin (?)	and Brown	<u>Moyliostrobus</u> Miller and Brown
<u>Otovicia</u> Kerp, et al. (?)	<u>Ernestiodendron</u> Florin	<u>Ernestiodendron</u> Florin
Emporiaceae	Voltziaceae	<u>Walchiostrobus</u> Florin*
<u>Emporia</u> Mapes and Rothwell	<u>Voltzia</u> Brongniart	<u>Culmitzchia</u> Ullrich*
Voltziaceae	<u>Pseudovoltzia</u> Florin	Majoniaceae
<u>Voltzia</u> Brongniart	<u>Ullmannia</u> Goepfert	<u>Majonica</u> Clement-Westerhof
Majoniaceae	Form Genera	<u>Dolomitia</u> Clement-Westerhof
<u>Majonica</u> Clement-Westerhof	<u>Walchia</u> Sternberg	<u>Pseudovoltzia</u> Florin
<u>Dolomitia</u> Clement-Westerhof	<u>Walchiostrobus</u> Florin	Ullmanniaceae
<u>Pseudovoltzia</u> Florin	<u>Walchianthus</u> Florin	<u>Ullmannia</u> Goepfert
Ullmanniaceae	<u>Gomphostrobus</u> Marion	Form Genera
<u>Ullmannia</u> Goepfert	<u>Lecrosia</u> Florin	<u>Walchianthus</u> Florin
Form Genera	Form Genera	<u>Thuringiostrobus</u> Kerp and Clement-
<u>Walchia</u> Sternberg	<u>Walchia</u> Sternberg	Westerhof
<u>Culmitzchia</u> Ullrich	<u>Culmitzchia</u> Ullrich	<u>Hermitia</u> Visscher et al.
<u>Walchiostrobus</u> Florin	<u>Walchiostrobus</u> Florin	Not Classified
<u>Walchianthus</u> Florin	<u>Walchianthus</u> Florin	<u>Lebachia</u> <u>lockardii</u> Mapes and Rothwell

that proposal (JONGMANS, HALLE & GOTHAN 1935) been adopted, then the genus *Lebachia* would not have been typified by the same specimen as a previously established legitimate species. This is because, as the type species of a form genus (sensu FLORIN), *Walchia piniformis* would not have been typified by a specimen. However, the proposal was not adopted, so that despite an apparently logical and reasonable basis for FLORIN's approach, *Lebachia* FLORIN was typified by the same specimen as *Walchia* STERNBERG and is therefore illegitimate (CLEMENT-WESTERHOF 1984).

For this reason, CLEMENT-WESTERHOF has correctly rejected *Lebachia* FLORIN (1938) as illegitimate. Together with her colleagues at Utrecht, CLEMENT-WESTERHOF ascribes to a system of classification where one recognizes "natural taxa" and "artificial taxa" (VISSCHER et al. 1986). Their concept of "natural taxa" is essentially equivalent to that of genera and species of living plants and to genera and species of fossilized plants as employed for nomenclatural purposes (Article 3.1 of the I.C.B.N.; Voss et al. 1983). Their concept of "artificial taxa" is more complex. As explained by VISSCHER et al. (1986) fossils interpreted as "artificial taxa" comprise a broad spectrum of concepts, ranging from plant fragments that can only tentatively be assigned to a major group (e. g. presumed conifer remains) to those that can be assigned to a "natural" family. At one end of their spectrum "artificial genera" are not assignable to a family of plants, and therefore are equivalent to the concept of form genera (Article 3.1 of the I.C.B.N.; Voss et al. 1983), whereas at the other end of the spectrum these authors consider the remains to be assignable to a family. This last category has given rise to their concept of "form genera that can be attributed to a natural family".

This system provides a laudable level of taxonomic precision for understanding the information content implied by each genus of fossil plants. It also sets up a system whereby as one learns progressively more about a genus, it can be progressively "promoted" to successively higher taxonomic categories (i. e. from a form genus not assignable to a family, to a form genus assignable to a family, to a natural genus of plants; VISSCHER et al. 1986). As attractive as this scheme may appear for taxonomic purposes, however, it creates nomenclatural difficulties and necessitates several confusing changes in names and generic concepts that introduce unnecessary nomenclatural instability into the systematics of primitive conifers (Table 2).

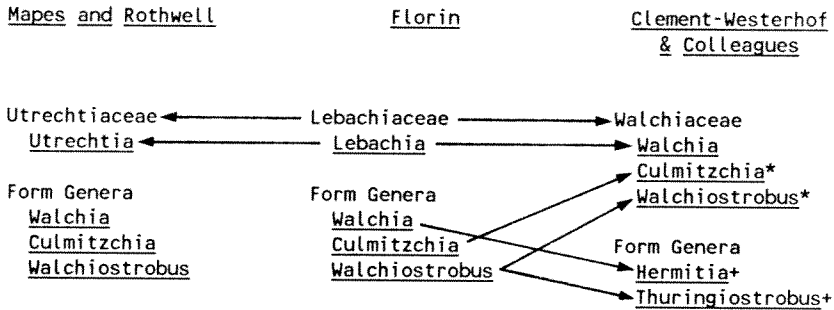
While we applaud the practice of promoting form genera to genera of plants where possible, we do not consider the type specimen of the form genus *Walchia* STERNBERG to display the features necessary to justify promoting it to the status of a genus of plants. There are two circumstances under which we would consider it appropriate to promote *Walchia* STERNBERG to the status of a genus of plants. The first would be if reexamination of the specimen that typifies *Walchia* STERNBERG (i. e. Pl. 1/2, Fig. 1-5 of FLORIN 1938-45) were to reveal new and diagnostic features of a genus of plants. The second would be if additional specimens are found that display both features that are diagnostic of a genus of

plants and features that identify them unequivocally as belonging to the same species as the specimen that typifies *Walchia*. However, since neither of these circumstances applies, the proposal to promote the form genus *Walchia* to the status of a genus of plants is based on a taxonomic guess rather than on evidence from the fossils. We consider this to be the difficulty with the proposal to promote *Walchia* STERNBERG to the status of a genus of plants (CLEMENT-WESTERHOF 1984), and therefore view the proposal as unwarranted.

There are additional nomenclatural difficulties that would result from promotion of the form genus *Walchia* to a genus of plants and adoption of the systematic scheme proposed by CLEMENT-WESTERHOF and colleagues (i. e. VISSCHER et al. 1986, KERP & CLEMENT-WESTERHOF this volume, KERP, et al. 1990; Table 1). That scheme would create considerable confusion about which names apply to which concepts of primitive conifers (Table 2), because their proposal that *Walchia* STERNBERG be promoted to a genus of plants requires that a new name (viz. *Hermitia* VISSCHER et al. 1986) be proposed for specimens that previously were assigned to the form genus *Walchia* STERNBERG. We also are troubled by their proposal to recognize some form genera as belonging to specific families of primitive conifers (Table 1). Under the current rules of botanical nomenclature the taxonomic concept of a "form genus that is assignable to a family" (VISSCHER et al. 1986; Table 2) has no nomenclatural status. Indeed, the definition of a form genus as "not assignable to a family" (Article 3.1 of the I.C.B.N., Voss et al. 1983) specifically precludes such a concept for nomenclatural purposes.

In our revision of primitive conifers (Table 1), *Walchia* STERNBERG is retained as a form genus, and *Utrechtia* and *Utrechtiaceae* are proposed for the illegitimate genus *Lebachia* FLORIN and part of his family *Lebachiaceae*. The new genus *Emporia* and family *Emporiaceae* are proposed for conifers of the type that previously were described as *Lebachia lockardii* MAPES & ROTHWELL, and not classified by CLEMENT-WESTERHOF (1988). We accept and adopt the remainder of the systematic scheme of CLEMENT-WESTERHOF and colleagues with the exception of certain form genera (Table 2). *Walchia* STERNBERG is used for vegetative shoots with no preserved cuticular detail. *Culmitzschia* ULLRICH is used for vegetative shoots with cuticular detail preserved. *Walchiostrobus* FLORIN is recognized for ovulate cones lacking the morphological details needed to assign them to a family, and *Walchianthus* FLORIN is recognized for pollen cones of uncertain familial affinities (Table 1). *Hermitia* KERP & CLEMENT-WESTERHOF (in VISSCHER et al. 1986) and *Thuringiostrobus* KERP & CLEMENT-WESTERHOF (1989) are synonymous with the form genera *Walchia* STERNBERG and *Walchiostrobus* FLORIN respectively, and therefore are not recognized because they are superfluous as later synonyms. In the system proposed here nomenclatural stability is promoted and confusion is minimized because far fewer name and concept changes are required to adequately assign all of the currently known primitive conifers to legitimate genera and families or to form genera (Table 2).

Table 2. Changes in the names and concepts of primitive conifer genera and families from those of FLORIN (at center) that result from the proposed system of CLEMENT-WESTERHOF and colleagues (at right) and from the system proposed in this paper (at left). Only those genera and families whose names or concepts are affected by one or both of the proposals are included. Arrows extend between taxa recognized by Florin, and those whose names or concepts have been changed in each of the proposed systems. "*" identifies form genera that we consider to have been inappropriately placed within families. "+" identifies form genera that have been proposed to replace other form genera that have been included in families, and therefore, are superfluous. See text for detailed explanation.



7. Acknowledgements

This study was supported in part by grants from the National Science Foundation (BSR86-00660), the Ohio University Research Committee (#9783) and the Kansas Geological Survey.

8. Literature

- ARCHANGELSKY, S. & CUNEO, R. (1987): Ferugliocladaeaceae, a new conifer family from the Permian of Gondwana. — *Rev. Palaeobot. Palynol.*, **51**: 3-30; Amsterdam.
- ASH, S. & TIDWELL, W. D. (1982): Notes on the Upper Paleozoic plants of central New Mexico. — *New Mexico Geol. Soc. Guidebook*, 33rd Field Conference: 245-248; Albuquerque.
- CLEMENT-WESTERHOF, J. A. (1984): Aspects of Permian palaeobotany and palynology. IV. The conifer *Ortiseia* FLORIN from the Val Gardena Formation of the Dolomites and the Vicentian Alps (Italy) with special reference to a revised concept of the Walchiaceae (GOEPPERT) SCHIMPER. — *Rev. Palaeobot. Palynol.*, **41**: 51-166; Amsterdam.
- , — (1987): Aspects of Permian palaeobotany and palynology. VII. The Majonicaceae, a new family of Late Permian conifers. — *Rev. Palaeobot. Palynol.*, **52**: 375-402; Amsterdam.
- , — (1988): Morphology and phylogeny of Paleozoic conifers. — In: Beck, C. B. [Ed.]: *Origin and evolution of gymnosperms*: 298-337; New York (Columbia Univ. Press).
- CRANE, P. R. (1985): Phylogenetic analysis of seed plants and the origin of angiosperms. — *Ann. Missouri Bot. Garden*, **72**: 715-793; St. Louis.
- DARRAH, W. C. (1936): Permian elements in the fossil flora of the Appalachian province, II. *Walchia*. — *Bot. Mus. Leaflets*, Harvard Univ., **4**: 9-19; Cambridge.
- ELIAS, M. K. (1948): *Walchia*: anatomy of branch and leaf. — *Bull. Geol. Soc. Amer.*, **59**: 1319-1320; Boulder. — [Abstract]

