(SS23) IOP Presidential Symposium: new concepts and discoveries in plant paleontology

Date: August 28
Place: Room 5334 (oral)
Organizers: Gar Rothwell & Ruth Stockey
Contact email address: rothwell@ohio.edu; rothwelg@science.oregonstate.edu
Purpose: This symposium focuses on important new concepts and discoveries in the areas of paleofloristics, systematics, and phylogeny over the past decade, by the current and past IOP Presidents as well as important contributors to the development of the field from around the world. The purpose is to highlight the breadth of new approaches and conceptual advancements that currently are, or recently have been developed in the field.

Oral Presentation

Aug. 28 [AM1] Room: 5334

Chair: Ruth Stockey

9:00-9:20 **[Introduction to the Symposium]** SS23-O01

Gar Rothwell

Chair: Gar Rothwell

9:20-10:00 **[Keynote] Reproductive anatomy of the conifer family Cheirolepidiaceae** SS23-O02 (497)

Ruth A. Stockey, Ignacio H. Escapa, Gar W. Rothwell

10:00-10:20 **Paleobotanical contributions to paleomycology** SS23-O03 (169)

Carla J. Harper, Michael Krings, Nora Dotzler

Aug. 28 [AM2] Room: 5334

Chair: Gar Rothwell

10:50-11:30 **[Keynote] Paleogene water ferns: turnovers, environments and biogeography** SS23-O04 (76)

Margaret E. Collinson, Selena Y. Smith, Han van Konijnenburg-van Cittert, David J. Batten, Johan van der Burgh, Judith Barke, Federica Marone

11:30-11:50 **Carboniferous bryophytes – perspectives of a hidden world?** SS23-O05 (236)

Hans Kerp, Maren Hübers, Olaf Glosny

11:50-12:10 **"Diversity of fungi and fungus-like organisms within the only known Mesozoic hot spring ecosystem (Patagonia, Argentina)"** SS23-O06 (145)

Juan García Massini, Alan Channing, Diego Guido, Alba Zamuner

Aug. 28 [PM2] Room: 5334

Chair: Ruth Stockey

14:30-15:10 **[Keynote] Square seeds and Early Cretaceous chlamydosperm diversity** SS23-O07 (132)

Else Marie Friis, Kaj Raunsgaard Pedersen, Peter R. Crane

15:10-15:30 **Fifty years of spore wall ultrastructure: what good is all this?** SS23-O08 (517)

Wilson A. Taylor

15:30-15:50 **Paleobotanical evidence for the origins of temperate hardwoods** SS23-O09 (97)

Melanie L. DeVore, Kathleen B. Pigg

Aug. 28 [PM3] Room: 5334

Chair: Ruth Stockey

16:20-16:40 **Whole-plant reconstruction of a Triassic voltzialean conifer from Antarctica** SS23-O10 (41)

Benjamin Bomfleur, Anne-Laure Decombeix, Ignacio H. Escapa, Andrew B. Schwendemann, Brian J. Axsmith

16:40-17:20 **[Keynote] The role of seed cones in resolving the overall pattern of conifer phylogeny** SS23-O11 (437)

Gar W. Rothwell, Ruth A. Stockey, Ignacio H. Escapa

Chair: Gar Rothwell

17:20-17:40 **[Summary and Conclusions]** SS23-O12

Ruth Stockey

SS23-O02 (497)

Reproductive anatomy of the conifer family Cheirolepidiaceae

Ruth A. Stockey[1], Ignacio H. Escapa[2], Gar W. Rothwell[3]

[1] *Oregon State University, USA, stockeyr@science.oregonstate.edu*
[2] *Museo Paleontologico Egidio Feruglio, Argentina*
[3] *Ohio University and Oregon State University, USA*

The Cheirolepidiaceae is a large family of extinct conifers of several genera that formed a dominant component of many Mesozoic floras worldwide. The unifying feature of these conifers is the unique pollen type, *Classopollis* (Upper Triassic-Upper Cretaceous). Until recently, the family has been represented primarily by compression/impression fossils with excellent cuticular remains. More recently, however both pollen and seed cones with excellent internal anatomy have been discovered. The pollen cone *Classostrobus crossii* from the Jurassic of the UK contains *Classopollis* pollen within clusters of pollen sacs that occur abaxially on the inner surface of the distal lamina on helically arranged sporophylls of simple cones. The permineralized seed cones described as *Pararaucaria* have recently been reexamined, and new specimens have allowed for their reinterpretation as cones of Cheirolepidiaceae showing for the first time anatomical characters of seed cones for this enigmatic family. The genus *Pararaucaria* was erected by for permineralized seed cones from the historic Jurassic Cerro Cuadrado Petrified Forest in the Santa Cruz Province of southern Argentina (Patagonia). New specimens of of *Pararaucaria patagonica* from the Cerro Cuadrado and cones of two new *Pararaucaria* species from the Late Jurassic Cañadón Calcáreo Formation (Chubut Province, Argentina) and the Middle Jurassic Trowbridge Formation (Oregon, USA), reveal previously unknown systematically informative characters. Whereas, the Argentine

fossils are preserved in a silica matrix like the type species, the Oregon cone occurs in a marine volcanoclastic carbonate concretion. Different preservational attributes of the three species provide complementary information about previously unknown or incompletely characterized features (e.g., the presence of distal ovuliferous scale lobes, distal branching of ovuliferous scale trace, number of seeds per bract/scale complex and a reinterpretation of the putative seed wing as a seed enclosing tissue), and allow for an improved understanding of the genus. Together, the newly interpreted characters demonstrate that *Pararaucaria* represents the conifer family Cheirolepidiaceae, thus providing the first anatomical information for seed cones of this important Mesozoic conifer family. This new information also emphasizes the dependence of conifer taxonomy on homology hypotheses, and on structural interpretations of the different seed cone structures. All three species of *Pararaucaria* occur in association with seed cones assignable to the genus *Araucaria*, demonstrating the geographical and chronological extension of Cheirolepidaceae-Araucariaceae forest biomes from the Middle Jurassic to the Late Jurassic and from the Southern Hemisphere to the Northern Hemisphere.

Keywords: Cheirolepidiaceae, *Classostrobus*, *Classopollis*, conifers, Jurassic.

SS23-O03 (169)

Paleobotanical contributions to paleomycology

Carla J. Harper[1], Michael Krings[1,2], Nora Dotzler[1]

[1] *Department of Ecology and Evolutionary Biology, and Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, Kansas 66045-7534, USA,* charper@ku.edu
[2] *Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany*

Fungi are one of the principal constituents in virtually all extant ecosystems. These organisms affect ecosystem structure and diversity through competition, antagonism, and varying degrees of mutualism. Thus, fungi play a major role in ecosystem functioning, today as well as in the past. The study of fossil fungi (paleomycology) is an emerging sub-discipline of paleontology. Paleomycology is generally associated with paleobotanical and palynological studies, and thus regarded as a subset of paleobotany. However, aspects of paleomycology such as fungal impacts on coal maceral development are also becoming increasingly important for other areas of Earth sciences. It was once believed that fungi were too fragile and delicate to be adequately preserved in the fossil record. However, this idea was disregarded as fungi were noted in early paleobotanical descriptive studies, mainly as dispersed fragments, spores, and other remnants. Many early investigators lacked the sufficient training in mycology to accurately interpret fossil fungi and thus, the taxonomic and ecological affinities were never described in great detail for these recorded fungi. Another limitation in the study of fossil fungi is a specimen collecting bias. Traditionally, paleobotanists seek out the best-preserved specimens and leave behind the defectives such as highly degraded material. These disregarded specimens though generally contain most fungal interactions. Furthermore, there has been an investigative and analysis bias. The time-consuming preparation of conventional thin-sections for permineralized plant-fossil analysis was considered obsolete after the introduction of the acetate peel technique in the 1950s. It has been shown, however, that the fine anatomical detail crucial for the description of fossil fungi is often lost during the etching process. Preparation of conventional thin-sections therefore plays a vital role in the accurate documentation and interpretation of fossil fungi. Despite the limitations in the study of fossil fungi, there has been a recent increase and interest in paleomycology. In this contribution we will review some of the recent advances in paleomycology, including novel discoveries of exceptionally well-preserved late

Paleozoic and Mesoszoic fungi and fungal associations and interactions with land plants, and assess how fungal interactions may have influenced the biology and evolutionary history of the host plants and ecosystems in which they lived.

Keywords: fungi, fossil fungi, plant-fungal interactions, Paleozoic, Mesozoic.

SS23-O04 (76)

Paleogene water ferns: turnovers, environments and biogeography

Margaret E. Collinson[1], Selena Y. Smith[2], Han van Konijnenburg-van Cittert[3,4], David J. Batten[5], Johan van der Burgh[3], Judith Barke[3], Federica Marone[6]

[1] *Royal Holloway University of London, UK, M.collinson@es.rhul.ac.uk*
[2] *University of Michigan, USA*
[3] *University of Utrecht, Holland*
[4] *National Centre for Biodiversity - Naturalis, Leiden, Netherlands*
[5] *University of Manchester, UK*
[6] *Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland*

The fossil record of heterosporous water ferns (Marsileaceae and Salviniaceae) is reviewed. Reproductive structures (sori, megaspores, megaspore apparatuses, microspore massulae and microspores) are widespread and abundant in plant mesofossil assemblages and the mega- and microspore-bearing components are often found in organic connection. In addition, at least for Salviniaceae, sufficient whole fertile fossil plants exist to ensure a good understanding of the plant morphology. Water ferns include excellent palaeoenvironmental indicator taxa and the good fossil record supports inferences on their origin, evolution and diversification. Recent research confirms previous work showing a major turnover across the Cretaceous / Tertiary transition with modern genera present in the Paleogene but several extinct sister taxa (and some modern genera) characterising the Cretaceous. In the Marsileaceae, Cretaceous *Molaspora* and Paleogene *Regnellidium* are a prime example, whilst in the Salviniaceae, *Azolla* and *Salvinia* occur in the Cretaceous and Paleogene but *Parazolla*, *Azollopsis* and *Glomerisporites* are restricted to the Cretaceous. Geographically widespread records of *Molaspora*, and the Eurasian records of fossil *Regnellidium,* show that the parent plants were widely dispersed in the past and that the current distribution of *Regnellidium* (Brazil, Uruguay, and Argentina) is relict. The recent discovery of abundant *Azolla* blooms, involving five species, in the Arctic and Nordic seas, during c. 1.2 myr in the earliest middle Eocene (c. 49 Ma), shows that *Azolla* grew on freshwater ocean surfaces and was widespread in surrounding continental wetlands. This '*Azolla* event' is an unpredicted and unexpected consequence of Eocene warm climates. *Azolla* and *Salvinia* appear and co-occur in the earliest part of the Paleocene-Eocene thermal maximum (PETM) lignite sequence at Cobham, Kent, UK. Co-occurrence of these genera is an extremely rare phenomenon in the fossil record and occurs here in parallel with major environmental shifts including increased rainfall and loss of the earlier episodic fire regime. The Cobham plant mesofossil assemblage also includes a single specimen that may be a coprolite containing fragments of *Salvinia* megaspores. SRXTM (synchrotron radiation X-ray tomographic microscopy; TOMCAT beamline, Swiss Light Source) is applied to *Azolla* in an attempt to digitally render the floats that are otherwise obscured by hairs. Hair diameters and smaller float vacuoles are similar in size (0.3 – 2.0 µm) and the theoretical pixel resolution is 0.35 µm with the x20 objective. However, if digital rendering can be achieved it will remove one major barrier to understanding *Azolla* phylogeny in the basal multifloated members of the genus.

Keywords: Marsileales, Salviniales, megaspore, microspore, SRXTM (synchrotron radiation x-ray tomographic microscopy).

SS23-O05 (236)

Carboniferous bryophytes – perspectives of a hidden world?

Hans Kerp[1], Maren Hübers[2], Olaf Glosny[1]

[1] *Forschungsstelle für Paläobotanik, Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität, Schlossplatz 9, 48143 Münster, Germany, kerp@uni-muenster.de*
[2] *Geologischer Dienst NRW, De-Greiff-Straße 195, 47803 Krefeld, Germany*

With ~20,000 extant species, bryophytes are the second most diverse group of plants after the flowering plants, and important constituents of most terrestrial ecosystems, from the tropics to boreal regions. In many modern wetland ecosystems bryophytes play a major role in nutrient cycling, water retention, and water availability. Peat bogs can only exist due to the enormous water storage capacity of peat mosses (Sphagnales). Unlike vascular land plants, bryophytes are predominantly poikilohydric, which means that their state of hydration is controlled by the environment and not by the plant itself. Moreover, the free-swimming sperm require water for the fertilization. Most bryophytes are bound to constantly moist habitats. Some can survive in temporarily drier habitats, but they must complete their life cycle to the production of dormant, desiccation-resistant spores prior to the dry season, or be desiccation tolerant. Recent molecular clock estimates indicate an age of ~449 Ma for the origin of liverworts and ~420 Ma for the divergence of mosses, predating vascular land plants. Despite their widespread occurrence today and the fact that bryophytes were among the earliest land plants, their fossil record is extremely poor. The extensive paleo-equatorial wetland environments of the Carboniferous coal basins with their unequalled accumulation of plant biomass likely provided ideal habitats for bryophytes. Nevertheless, the fossil record of Carboniferous bryophytes is remarkably meagre, although the very rich floras from this time interval, primarily consisting of compressions and anatomically preserved fossils, e.g. in coal balls, have been studied in great detail. We report three types of mosses from the upper Mississippian of Germany, being the oldest unequivocal mosses known to date. In addition, we present moss and liverwort remains from the upper Westphalian of Germany. These bryophyte remains were obtained by bulk maceration, a method that is not commonly used for studying Carboniferous floras. Although the material is fragmentary, these finds show that mosses formed part of Carboniferous ecosystems. We anticipate that applying this method on material from other Carboniferous localities will show that mosses were more widespread in the late Paleozoic than previously thought and that it will open perspectives to an important part of the ecosystem that remained hidden so far.

Keywords: palaeobotany, mesofossils, bryophytes, Carboniferous.

SS23-O06 (145)

"Diversity of fungi and fungus-like organisms within the only known Mesozoic hot spring ecosystem (Patagonia, Argentina)"

Juan García Massini[1], Alan Channing[2], Diego Guido[3], Alba Zamuner[4]

[1] *CONICET-CRILAR, Entre Ríos y Mendoza s/n (5301) Anillaco, La Rioja, Argentina, massini112@yahoo.com.ar*
[2] *School of Earth and Ocean Sciences, Cardiff University, Wales, CF10 3YE, UK*
[3] *CONICET-UNLP, Calle 64 esquina 120, (1900) La Plata, Buenos Aires, Argentina*

[4] *CONICET-UNLP, Paseo del Bosque s/n (1900) La Plata, Buenos Aires, Argentina*

Here, we report for the first time the presence of fungi and fungus-like microorganisms from a Mesozoic hot-spring ecosystem. This Jurassic hot spring deposit (Patagonia, Argentina) represents only the second known Phanerozoic hot spring ecosystem with an associated microflora and contains diverse, exceptionally-preserved microorganisms. Preserved remains include variously-shaped bodies, spores and hyphae that show affinities with ascomycetes, chytridiomycetes, oomycetes and others of uncertain affinity. Many of these microorganisms occur dispersed in chert matrix, but others are associated with variously decayed organic remains including animals and plants, mainly horsetails. This report expands the fungal fossil record and provides a unique opportunity to learn about the biology of Mesozoic microorganisms.

Keywords: Mesozoic ecosystems, cherts, fossil microorganisms.

SS23-O07 (132)

Square seeds and Early Cretaceous chlamydosperm diversity

Else Marie Friis[1], Kaj Raunsgaard Pedersen[2], Peter R. Crane[3]

[1] *Swedish Museum of Natural History, Stockholm, Sweden, else.marie.friis@nrm.se*
[2] *University of Aarhus, Denmark*
[3] *Yale University, New Haven, USA*

Plants related to the Bennettitales, Erdtmanithecales and Gnetales proliferated during the Early Cretaceous parallel to the early expansion of angiosperms. Vegetative remains of Bennettitales along with their flower-like reproductive organs have long been known from this time interval, while Erdtmanithecalean and Gnetalean diversity has mainly been documented from their extensive pollen record. There is however, and emerging record of gnetalean macrofossils and studies of mesofossil floras have now also revealed numerous and diverse assemblages of small isolated seeds from the Early Cretaceous with a unique chlamydospermous organisation that indicate monophyly for the Bennettitales-Erdtmanithecales-Gnetales complex. The seeds are often square and are characterised by having a thin, membranous integument extended into a long micropylar tube that project above the enclosing seed envelope. The seed envelope consists of an inner sclerenchyma zone and an outer parenchyma zone that is sometimes extensively developed into a layer of tubular cells. Sometimes the tubular cells also expand apically to form spiny projections. The recognition of the chlamydospermous organisation in this complex of seeds has been greatly facilitated by the use of synchrotron X-ray tomographic microscopy of exquisitely preserved charcoalified seeds that allows in depth comparison with fossils of different preservation.

Keywords: Bennettitales, Early Cretaceous, Erdtmanithecales, Gnetales, mesofossils.

SS23-O08 (517)

Fifty years of spore wall ultrastructure: what good is all this?

Wilson A. Taylor

University of Wisconsin-Eau Claire, USA, taylorwa@uwec.edu

Plant spores were among the first biological specimens to be sectioned and examined with the transmission electron microscope. From a heyday in the 70s and 80s, other techniques that analyze lower and lower levels of biological organization (i.e., chemistry) have mostly replaced ultrastructure as the subject of research focus. This is true everywhere but in the realm of paleontology. Cells and soft tissues decay, and the effects of diagenesis severely complicate reliable chemical analyses of biological materials that can persist. This uncertainty, combined with the extreme resistance of biomolecules like sporopollenin to diagenetic alteration, has kept ultrastructural data on fossils relatively more important than chemical as a source of information. A condensed historical survey of the contributions of spore wall ultrastructure in the past fifty years serves to illustrate the value of this approach. This survey will include: the initial realization that fossil spore walls preserve their ultrastructure for hundreds of millions of years; the fact that ultrastructural features in spore walls can be highly conserved in some lineages, thus serving as indicators of affinity of even dispersed spores; the utility of immature and aborted fossil spores for gaining insights on developmental phenomena; and the discovery of distinct and taxonomically diagnostic ultrastructural features in the walls of spores whose affinities were previously unknown, and in some cases predate any macrofossil record. In all of these cases, data from fossils add the element of time – often deep time – that serves to provide the context to analyses involving extant spores. Moreover, the widespread dispersal of spores and pollen has introduced them throughout the fossil record to an extent unparalleled by any other type of fossil. Thus, their various uses can become even more significant due to a sort of temporal and spatial multiplier effect. Additions to the data base of fossil and extant spore wall ultrastructure will ensure a continuing expansion of the knowledge and utility of this information, including but not limited to: reconstructions of earth's earliest terrestrial ecosystems, and furnishing additional characters (or dating points) for phylogenetic analyses.

Keywords: palynology, paleopalynology, phylogeny.

SS23-O09 (97)

Paleobotanical evidence for the origins of temperate hardwoods

Melanie L. DeVore[1], Kathleen B. Pigg[2]

[1] *Georgia College and State University, Milledgeville, GA USA, melanie.devore@gcsu.edu*
[2] *Arizona State University, Tempe, AZ USA*

Much attention in paleobotany has focused on the origins of tropical floras, and their range expansion and shrinking during the Tertiary. Considerably less emphasis has been placed on temperate floras. A critical question is how plants were able to transition from a greenhouse world with warm polar forests to one with temperate zones having distinct winter/summer seasonality. One way that plants appeared to make this shift is through shoot differentiation, into long and short shoot systems, a type of growth that results in heterophyllous leaf production. Both of these features are tied to endodormancy, a process signaled by both photoperiod and chilling. Long and short shoots and heterophylly can be recognized in the fossil record. The earliest angiosperm examples occur in Cretaceous and early Paleogene Northern Hemisphere plants of mid-high latitudes in such families as Cercidiphyllaceae and Trochodendraceae. As we progress into the early-mid Eocene, upland floras such as the Okanogan Highlands plants show a mix of these more archaic elements and taxa that today occur in temperate deciduous forests. We suggest that these upland mid-latitude plants were preadapted to survive cooler temperatures and unfavorable conditions as a result of earlier adaptations of their high latitude ancestors to pronounced photoperiods.

SS23-O10 (41)

Whole-plant reconstruction of a Triassic voltzialean conifer from Antarctica

Benjamin Bomfleur[1], Anne-Laure Decombeix[2], Ignacio H. Escapa[3], Andrew B. Schwendemann[1], Brian J. Axsmith[4]

[1] *University of Kansas, USA, bbomfleur@ku.edu*
[2] *CNRS, Montpellier University, France*
[3] *Museo Paleontológico Egidio Feruglio, Argentina*
[4] *University of South Alabama, USA*

We present a whole-plant reconstruction of a Triassic voltzialean conifer from Gondwana, based on a wealth of well-preserved material from Triassic deposits of the Transantarctic Mountains. Plant parts in compression/impression preservation include *Heidiphyllum* foliage, *Telemachus* seed cones, and *Switzianthus* pollen cones. Anatomically preserved taxa from permineralized peat deposits comprise *Notophytum* (stems, roots, and leaves) and *Parasciadopitys* seed cones. Associated pollen is of the *Alisporites* type. Evidence for the affiliation of these individual organs is comprehensive, and consists of a combination of organic connections, structural analogies, similarities in cuticles and epidermal morphologies, association/disassociation data, and palynology. The great amount of anatomical and morphological information on the individual organs enables a detailed habit reconstruction. The architecture of the plant corresponds to Rauh's model (essentially orthotropic branching and rhythmic growth) with a modification of long- and short-shoot growth. The largest axes known exceed 20 cm in diameter. By analogy with architecturally similar extant trees (e.g., *Larix*), we reconstruct this Gondwanan voltzialean conifer as a 15– 20 m tall forest tree. The occurrence in polar latitudes during the Triassic makes is highly likely that the crown shape was predominantly vertical and narrow-conical, as this shape is known to enable a much more efficient interception of the high amount of low-angle irradiation at such high latitudes. Leaves were up to 25 cm long, strap-shaped to narrow elliptical with about 8– 12 parallel veins, and borne in dense clusters on short shoots. Taphonomic and anatomical data indicate that these conifers were seasonally deciduous. Of special interest is the remarkably diverse set of evidence for biotic interactions, which include odonatan oviposition on leaves, two distinct types of mycorrhizal associations, and other endophytic as well as epiphyllous fungi. Altogether, we conclude that this conceptual whole-plant genus, referred to as 'a *Telemachus* conifer', probably represents one of the most completely known fossil conifers.

Keywords: *Heidiphyllum, Telemachus, Switzianthus, Notophytum, Parasciadopitys.*

SS23-O11 (437)

The role of seed cones in resolving the overall pattern of conifer phylogeny

Gar W. Rothwell[1], Ruth A. Stockey[2], Ignacio H. Escapa[3]

[1] *Ohio University and Oregon State University, USA, rothwell@ohio.edu*
[2] *Oregon State University, USA*
[3] *Museo Paleontologico Egidio Feruglio, Argentina*

Systematic relationships among living conifers have become highly resolved through analysis of nucleotide sequences, plant structure, and rare genetic markers, but relationships among living species do not always accurately reflect the overall pattern of phylogeny for an ancient clade in

which a great deal of extinction has occurred. Whole plant concepts for anatomically preserved conifer species from Paleozoic and Cenozoic strata have contributed to well-resolved phylogenies for species from each time span, but the almost total absence of whole plant reconstructions of anatomically preserved conifers from Triassic, Jurassic, and Lower Cretaceous sediments leaves relationships among the two groups in doubt. Up to the present, species that could link the two groups have been considered “transition conifers” of uncertain phylogenetic relationships. In an attempt to overcome this paucity of data we have hypothesized that anatomically preserved seed cones may be used as surrogates for whole plants to resolve the overall pattern of phylogeny for conifers. This approach relies heavily upon structural features of seed cones from a combination of fossil and living species. Through a program to describe more than 10 new species of Mesozoic conifer seed cones, and to reinterpret the structure of others, a data matrix of more than 40 species and 125 characters has been assembled and analyzed. Results of the phylogenetic analysis of this matrix resolve a conifer clade that is roughly concordant with results of analyses of living species only. Voltzialean conifers occur in a pectinate arrangement at the base of the tree, and more recent fossils plus crown group families form two clades. One clade includes several fossils and the Pinaceae while the other contains all of the non-pinoid living and extinct conifers. Placement of Cheirolepidiaceae within the tree is contingent on character scorings, and this emphasizes the importance of well-defined and explicit homology hypotheses for bract/scale complexes and other important seed cone structures.