Palaeontologia Electronica
http://palaeo-electronica.org

AN ARAUCARIAN CONIFER BRACT-SCALE COMPLEX FROM THE LOWER JURASSIC OF MASSACHUSETTS: IMPLICATIONS FOR ESTIMATING PHYLOGENETIC AND STRATIGRAPHIC CONGRUENCE IN THE ARAUCARIACEAE

Brian J. Axsmith, Ignacio H. Escapa, and Phillip Huber

ABSTRACT

The conifer family Araucariaceae has an extensive Mesozoic fossil record, but no unambiguous megafossils of this group have been described from the Newark Supergroup of eastern North America. A bract-scale complex attributable to *Araucaria* is described from the Lower Jurassic Portland Formation of Massachusetts. Although known from a single specimen, this discovery is significant as the first *bona fide* megafossil of the Araucariaceae from the Newark Supergroup and one of the few early Mesozoic examples from all of North America. Furthermore, this bract-scale complex is proposed as the earliest known occurrence of *Araucaria* section *Eutacta* based on its wedge-like shape, the centrally placed ovule that was retained at maturity, and lateral wings. An analysis of the relationship between the most current phylogenetic hypotheses for the sections of *Araucaria* and the temporal information from the rich fossil record of the genus indicates low levels of congruence. Clearly, more paleobotantical and phylogenetic research is needed to provide a robust estimate of this important conifer family's evolutionary history.

Brian J. Axsmith. Department of Biology, University of South Alabama, LSCB 124, Mobile, AL 36688, USA, baxsmith@jaguar1.usouthal.edu
Ignacio H. Escapa. CONICET, Museo Paleontologico Egidio Feruglio, Fontana 140, Trelew, Chubut, Argentina, iescapa@mef.org.ar
Phillip Huber. GeoScience Books, P.O. Box 1036, Faribault, MN 55021 raregeologybooks@earthlink.net

KEY WORDS: *Eutacta*; phylogenetics; Mesozoic; Newark Supergroup; Portland Formation

INTRODUCTION

The conifer family Araucariaceae occurs exclusively in the Southern Hemisphere today, but it was widely distributed in both hemispheres during the Mesozoic (Stockey 1982, 1994; Stockey and Ko 1986; Hill 1995; Del Fueyo and Archangelsky 2002; Kunzman 2007a, 2007b). The mid-Jurassic through Cretaceous record is particularly rich in many regions, but early Mesozoic occurrences are uncommon and often ambiguous, especially in North America. Rare araucarian ovulate cones and cone scales have recently been described from the Late Triassic Chinle Formation of Arizona and New Mexico (Axsmith and Ash

PE Article Number: 11.3.13A

Submission: 29 December 2007. Acceptance: 29 April 2008

Axsmith, Brian J., Escapa, Ignacio H., and Huber, Phillip. 2008. An Araucarian Conifer Bract-scale Complex from the Lower Jurassic of Massachusetts: Implications for Estimating Phylogenetic and Stratigraphic Congruence in the Araucariaceae. *Palaeontologia Electronica* Vol. 11, Issue 3; 13A:9p; http://palaeo-electronica.org/2008_3/153/index.html

2006) and the Lower Jurassic Moenave Formation of Utah (Tidwell and Ash 2006). Putative araucarian megafossils have also been reported from the Newark Supergroup of eastern North American (e.g., Wanner and Fontaine 1900; Bock 1954), but these are not generally accepted as convincing evidence for the family (Cornet 1986; Stockey 1994; Axsmith and Ash 2006). It is in this context that an unambiguous araucarian bract-scale complex from the Lower Jurassic Holyoke Dam locality of Massachusetts is described. Although known from a single specimen, this discovery is significant as the first certain megafossil of the Araucariaceae from the Newark Supergroup and one of the few early Mesozoic examples from all of North America. Furthermore, this bract-scale is similar to those of *Araucaria* section *Eutacta* and may represent the earliest known representative of this clade.

The extant species of *Araucaria* are commonly placed taxonomically among four sections; *Eutacta*, *Intermedia*, *Araucaria* (= *Columbea*) and *Bunya* (Endlicher 1847; Wilde and Eames 1952). Several characters, including aspects of the bract-scale morphology, are often used to distinguish among the sections. These classic delimitations are generally concordant with more recent molecular phylogenies (Gilmore and Hill 1997; Setoguchi et al. 1998; Kunzmann 2007b); however, relationships within the genus (i.e., between the sections) remain unclear. Fossil species of *Araucaria* (as well as *Araucarites* – see below) are represented by impression/compression remains of vegetative and reproductive organs from the Jurassic of the Northern and Southern Hemispheres, and most of these have been assigned to one of the sections of *Araucaria* (see Stockey 1982; Del Fueyo and Archangelsky 2002). These early records, along with the fossil described here, allow for estimates of phylogenetic/stratigraphic congruence, such as that presented below.

MATERIALS AND METHODS

Nomenclatural Considerations

Historically, vegetative shoots ascribed to the Araucariaceae have sometimes been described using the generic name *Araucarites*; however, Zijlstra and Konijnenburg-van Cittert (2000) proposed that this name be restricted to megasporangiate cones and isolated bract-scale complexes. This practice is acceptable when applied to early representatives of the Araucariaceae with uncertain sectional affinities or to more poorly preserved material. However, the name *Araucarites* should not be applied to material assigned to a particular section, as such a determination must indicate affinity with the genus *Araucaria*.

The generic name *Araucaria* is used here with reference to the new Holyoke specimen, but it is not formally named as a new species as it is represented by a single, isolated specimen that cannot be definitively diagnosed from several *Araucaria* section *Eutacta* bract-scale complexes. Some other comparative taxa are referred to here as *Araucarites* based on the original descriptions until a thorough revision of the fossil record of the family is available.

Locality and Geological Setting

The new *Araucaria* bract-scale complex was collected from the South Hadley Falls Member of the Portland Formation (Olsen et al. 2003, 2005), from strata that crop out just below the dam in the middle of the Connecticut River at Holyoke, Massachusetts (Figure 1). The Portland Formation contains the youngest rocks of the Hartford Group, Newark Supergroup and has been dated by palynostratigraphy (Cornet and Waanders 2006) and vertebrate biochronology (Lucas and Huber 2002) to span the Hettangian, Sinemurian, and possibly Pliensbachian stages of the Early Jurassic. The South Hadley Falls Member is of Hettangian age, and consists of gray and red lacustrine shale and siltstone beds arranged in ~20 m thick cycles, each of which has been interpreted as the depositional product of the 20 Ky precessional cycle (Olsen 1986; Olsen et al. 2003, 2005). At Holyoke Dam and nearby exposures, the South Hadley Falls Member contains an abundant, allochthonous, low-diversity flora strongly dominated by conifer branches with common equisetalian stem fragments and some cycadeoid leaves. Other fossils from the South Hadley Falls Member include fossil insect larvae (Huber et al. 2003), fragmentary fishes, and occasional theropod dinosaur and crocodilian footprints (Olsen et al. 2003, 2005). Although this locality has been known for some time (see discussion in McDonald 1992) no detailed systematic work on the plant material has been published despite the use of the conifer shoots in paleoecological studies (e.g., Cornet and Waanders 2006). Based on the abundance of *Pagiophyllum* and *Brachyphyllum* morphotype leafy shoots, ovulate cone scales putatively similar to *Hirmeriella*, and the dominance of dispersed *Classopollis* pollen (Cornet et al 1973) at this and coeval localities in the Hartford and Deerfield Basins, most of this material has been assumed to

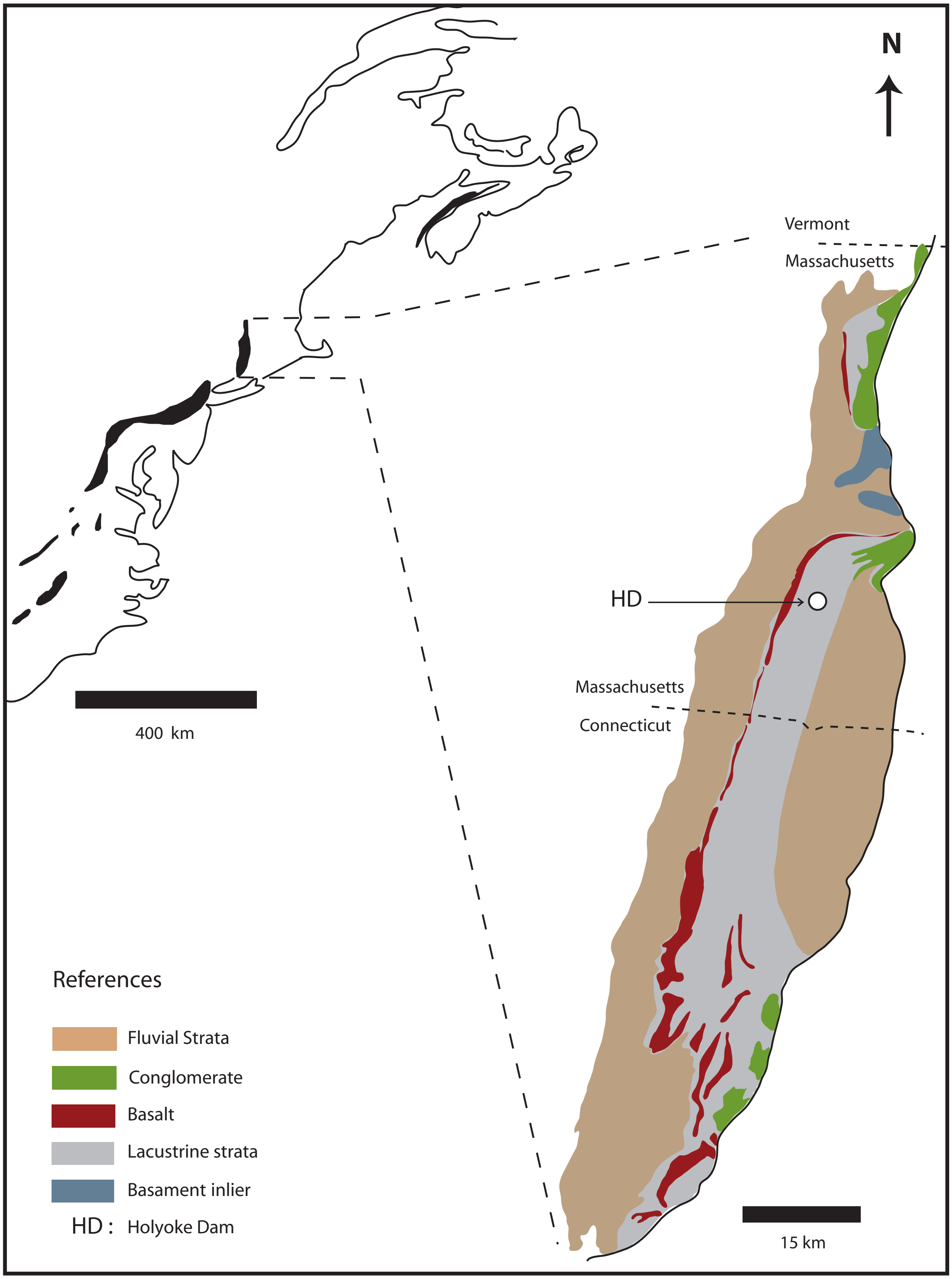

Figure 1. Map of Newark Supergroup basins (left) and inset detail of Hartford Basin (right). Location of Holyoke Dam locality (HD) indicated by arrow. Figure modified from Olsen, Whiteside, and Huber (2003).

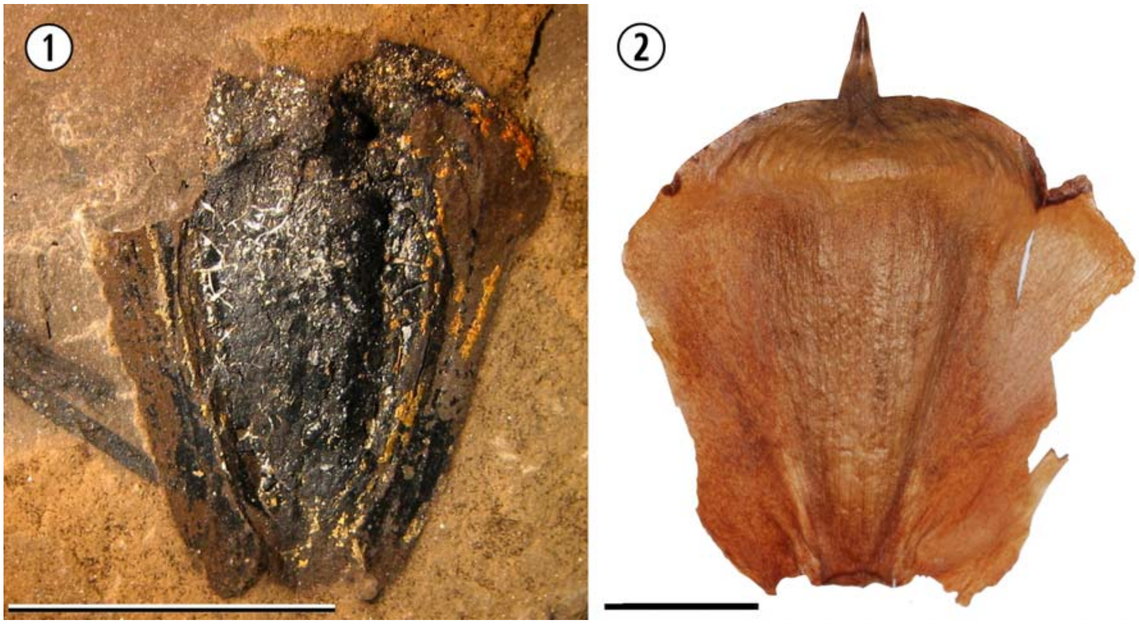

Figure 2. Fossil and extant *Araucaria* bract-scale complexes. (1) Fossil *Araucaria* bract-scale complex from the Lower Portland Formation of Massachusetts. Note the central seed-bearing region and lateral wings. # J 1430. (2) Bract-scale complex of extant *Araucaria heterophylla*. (From specimen # BH 2732.) Note similarity to fossil in Figure 1.1. Scale bars = 1.0 cm.

represent the important Mesozoic conifer family Cheirolepidiaceae. However, it has been previously suggested that some of the shoots may be araucarian (Cornet and Waanders 2006). In fact, the cuticular preservation of the leafy shoots is poor (*contra* Cornet and Waanders 2006) and the familial affinities of any of the specific leafy shoots remain uncertain. An ongoing restudy of ovulate cone scales and pollen cones from Holyoke Dam does suggest dominance of the Cheirolepidiaceae; however, the bract-scale complex described here provides unequivocal macrofossil evidence of the Araucariaceae in this flora.

Fossil Preparation and Study Methods

No special preparation of the fossil was performed; however, it was immersed in ethanol to increase contrast for photography (Figure 2.1). The specimen exhibits considerable relief, which makes it possible to delimit several important characters under incident light, such as the position of the ovule and the presence and orientation of the wings. A thin layer of carbonaceous material is present, but the application of the transfer technique was not attempted because it is the only specimen, and attempts at transferring other fossils from this locality were unsuccessful. The fossil bract-scale complex specimen (# J 1430) will be deposited in the collections of the Paleobotany Division of the Natural History Museum and Biodiversity Research Center at the University of Kansas. Comparative material of extant *Araurcaria* species was examined and photographed in the L.H. Bailey Hortorium of Cornell University.

Phylogenetic and Statistical Methods

Although the value of fossils in phylogenetic reconstruction is controversial, the time of first appearance of groups in the geological record is widely used in calibrating phylogenies based on molecular evidence. Furthermore, fossils are sometimes used to describe the level of agreement between the temporal sequence of taxa in the fossil record and the order of branching on phylogenic trees. Such congruence studies normally employ one of two approaches; 1) methods that evaluate the number of inconsistencies between the phylogeny and temporal data (Norell and Novaceck 1992; Huelsenbeck 1994), and 2) methods that measure calibrated “ghost lineages” or phylogenetically implied gaps (Sidall 1998; Wills 1999; Pol and Norell 2001) by which the absolute temporal disparity is evaluated (Brochu and Norell 2000). In this paper, the second approach is used to evaluate the congruence between the current phylogenetic hypotheses for the sections of *Araucaria* and the temporal information from the fossil record of the genus. Specifically, we used the analysis of Setoguchi et al. (1998), which produced one hypothesis of relationships between the sections of *Araucaria* and that of Gilmore and Hill (1997), which produced two topologies–one perfectly congruent with that of Setoguchi et al. (1998) in terms of the sectional relationships and one different. The Gilmore and Hill (1997) study used fewer *Araucaria* species, but it included at least one species of each monophyletic section of the genus (*sensu* Setoguchi et al. 1998).

The first appearance datum (FAD) used for each taxon is based on the literature for sections *Araucaria, Bunya*, and *Intermedia* (e.g., Stockey 1994; Setoguchi et al. 1998). The FAD for section *Eutacta* is based on the Holyoke bract-scale complex described here. The Manhattan Stratigraphic Measure (MSM) method originally proposed by Sidall (1998) and later modified by Pol and Norell (2001) designated as MSM* was utilized. In addition, the age uncertainty was considered with the randomization approach for age ranges (Pol and Norell 2006) using the MSM* to calculate the stratigraphic fit for each of 1000 random replicates. This analysis was performed using the phylogenetic analysis software program TNT (Goloboff et al. in press).

DESCRIPTION AND COMPARISONS

The Holyoke *Araucaria* bract-scale complex is about 1.67 cm long, with only the most distal portion missing (Figure 2.1). It is 0.8 cm wide at the base and expands distally to 1.37 cm wide near the apex. A single obovate seed, which is represented by a distinct thickening in the middle of the complex surface, is enclosed by the complex tissues. On each side of the central seed-bearing zone is a 0.2 cm wide wing with longitudinal striations. The seed-bearing zone is well defined due to the presence of two deep, longitudinal grooves that delineate it from the wings. The distal part of the complex shows a distinct thickening that is concave toward the base. No ligule (free portion of the ovuliferous scale) is visible, but this is probably due to preservational factors. The basal part of the complex shows three lobes; the central lobe is produced by the base of the seed-bearing region, and the smaller lateral lobes are formed from the bases of the wings.

The new *Araucaria* bract-scale complex is most similar in shape, wing morphology, and ovule disposition to those of section *Eutacta* of *Araucaria*. Among extant species, it is particularly similar to those of *Araucaria heterophylla* (Figure 2.2). In comparison, bract-scale complexes of section *Araucaria* (= *Columbea*) have a nut-like shape and entirely lack wings, and those of section *Bunya* have thicker woody wings, and the seed is shed from the complex. Finally, the bract-scale wings of section *Intermedia* are broader and thinner than those of *Eutacta*.

Araucaria section *Eutacta* has a rich fossil history, and during the Mesozoic it was present in both hemispheres (Stockey 1982; Hill and Brodribb 1999); however, most records are based on vegetative remains (Hill and Brodribb 1999). One exception is *Araucarites stockeyi* from the Lower Jurassic of Utah, which is suggested as a representative of section *Eutacta* by Tidwell and Ash (2006) based on the wedge-shaped bract-scale complex with a short apical point, and the centrally placed ovule that was apparently retained at maturity. Although this may indeed be the earliest record of section *Eutacta*, the wings of the Holyoke bract-scale complex described here make it an even more convincing representative. *Araucarites phillipsii* from the Jurassic of Yorkshire (Kendall 1949; Harris 1979; Van Konijnenburg-van Cittert and Morgans 1999) has been referred to section *Eutacta* based on characters of the ovuliferous cones and seedlings (Stockey 1982). Bract-scale complexes of *Araucarites phillipsii* are similar in shape and size to the Holyoke *Araucaria*; however, they do not show the clear delimitation of the seed-bearing zone, and no distal thickening has been observed. *Araucarites baqueroensis* and *Araucarites minimus* from the Cretaceous of Argentina have also been included in section *Eutacta* (Del Fueyo and Archangelsky 2002). The bract-scale complexes of these species are similar in general morphology to the Holyoke specimen, but *Araucarites minimus* is much smaller (nearly half of the size) while *Araucarite baqueroensis* is considerably larger. Another well-known species is *Araucarites brodiei*, from middle Jurassic of Oxfordshire (Cleal and Rees 2003). However, these fossils are notably larger than the Holyoke *Araucaria* bract-scale complex, the seed occupies the lower part of the complex rather than the middle, and no wings are present. In addition, the seed in *Araucarites brodiei* is born in a depression on the bract-scale but is not embedded in its tissues (Cleal and Rees 2003). In fact, this character suggests that this species may not be close to *Araucaria* at all, as the seeds of this genus are embedded in the tissues of the bract-scale complex at least during some ontogenetic stage. Based on these comparisons, it is proposed that the Holyoke *Araucaria* bract-scale complex provides enough features to be confi-

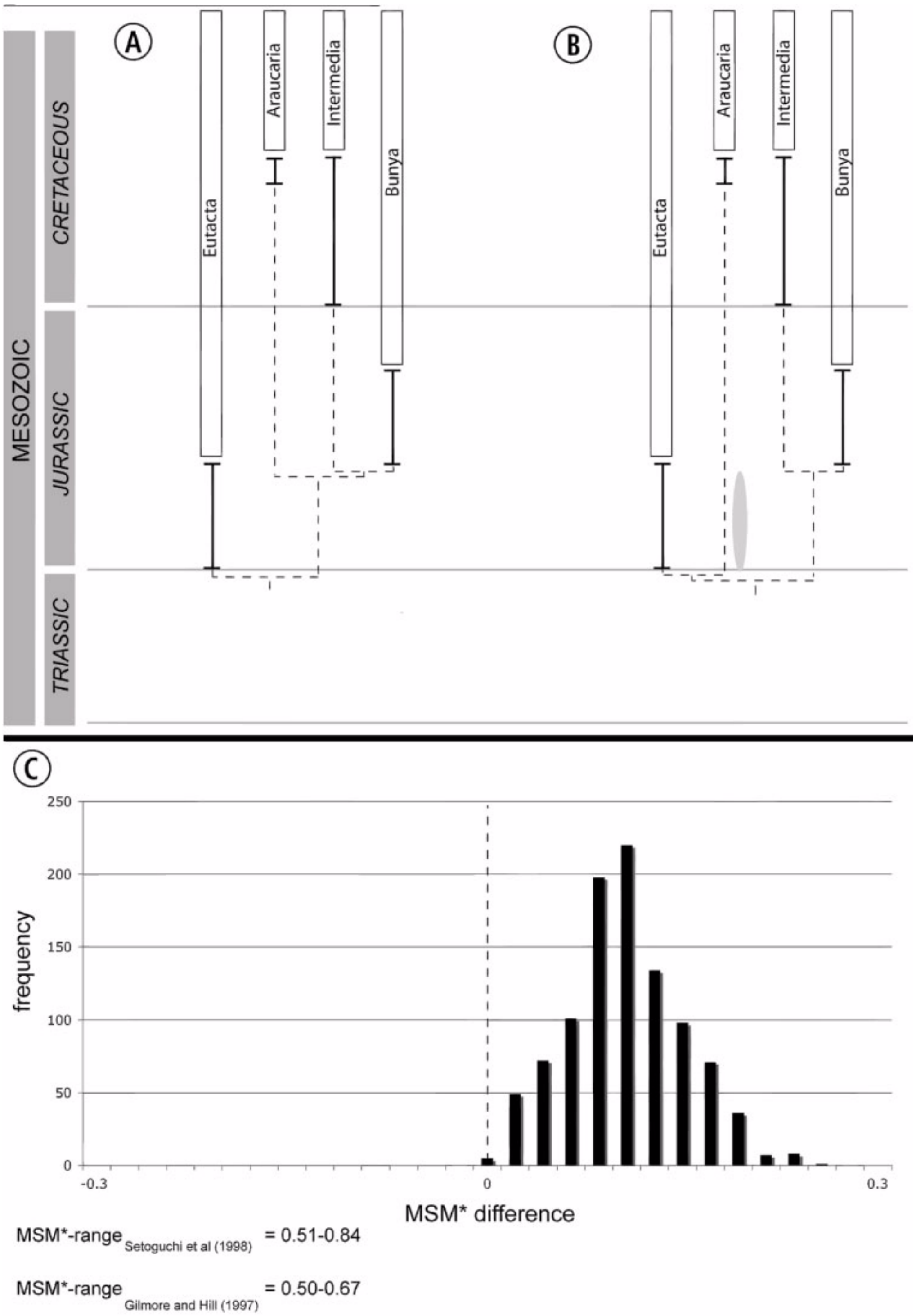

Figure 3. Stratigraphic fit of phylogenetic hypotheses for *Araucaria* sections. FADs are considered with uncertainty intervals (entire lines); the dashed lines represent ghost lineages. (1) Stratigraphic adjustment for the classical hypothesis (based on Gilmore and Hill 1997, Figures 3a, 4a, 4c and 4d; Setoguchi et al. 1998, Figure 1). (2) Stratigraphic adjustment for alternative hypothesis (from Gilmore and Hill 1997, Figures 3b, 4b). (3) Frequency histogram of the difference in MSM*values of both hypotheses obtained in each replicate of the randomization procedure. The MSM* difference between the classical and alternative hypothesis is positive (or zero) in all replicates indicating that the alternative hypothesis score is equal to or lower than the classical one in stratigraphic fit (represented by MSM*value).

dently assigned to *Araucaria* section *Eutacta* and represents the earliest record of this section.

DISCUSSION

Phylogenetic/stratigraphic Congruence

Measures of phylogenetic/stratigraphic congruence for the Araucariaceae utilizing the statistical tests, fossil taxa, and phylogenies described above were surprisingly low.

The range of MSM* values obtained for the sectional relationships within *Araucaria* is 0.51-0.84 for the classical phylogenetic hypothesis (Gilmore and Hill 1997, Figures 3a, 4a, 4c and 4d; Setoguchi et al. 1998, Figure 1) (Figures 3.1 and 3.3), and 0.5-0.67 for the alternative one (Gilmore and Hill 1997, Figures 3b, 4b) (Figures 3.2 and 3.3). These relatively low values are probably related to the incongruence between the FAD ranges of the sections and their position on both tree topologies (Figure 3.1-3.2), generating a long temporal ghost for some lineages. Alternatively, the broad MSM* range obtained with the FAD dates used in this study may reflect the high degree of uncertainty in determining the precise ages of most of the sections. For example, the Lower Cretaceous FAD range for Section *Intermedia* covers about 43 million years. Another potential problem is the lack of fossil taxa as terminals in the phylogenetic analyses utilized.

Conclusion

Ideally, a clade with a rich fossil record and a well-resolved phylogenetic hypothesis should show high levels of congruence among these data sets. The Araucariaceae would seem to satisfy the requirements for high phylogenetic/stratigraphic congruence, as the family is considered to have a particularly long and rich fossil record, and substantial living diversity to provide abundant data for phylogenetic studies. Nevertheless, the analysis presented here indicates that much more research is needed, probably in both areas, to provide a more consistent estimate of this important conifer family's evolutionary history. This will most likely entail the continued discovery and description of new fossils as well as a critical re-evaluation of known fossil taxa. In addition, it is likely that phylogenetic studies based only on extant taxa underestimate the true complexity of araucarian phylogeny, as the fossil record indicates high levels of extinct diversity, including completely extinct sections (e.g., *Yezonia*) with unique character combinations (Ohsawa et al. 1995). The inclusion of well-preserved and reconstructed fossil taxa in a combined analysis of the Araucariaceae should provide new data regarding those parts of the phylogeny currently represented by ghost lineages leading to a more robust phylogenetic hypothesis and improved phylogenetic/stratigraphic congruence.

Regardless of the causes of the current phylogenetic/stratigraphic incongruence for the Araucariaceae, the bract/scale complex described here is significant as the first *bona fide* megafossil of the Araucariaceae from the Newark Supergroup and one of the few early Mesozoic examples from all of North America. This fossil is also significant as the earliest record of *Araucaria* section *Eutacta*. Although plant fossils have been known from the Newark Supergroup for many years, there is little question that it remains an underutilized source of information regarding early Mesozoic plant evolution.

ACKNOWLEDGEMENTS

The authors are grateful to the staff of the L.H. Bailey Hortorium at Cornell University for access to herbarium specimens. This research was supported by a National Science Foundation Grant (EAR-0105476) to B.J.A.TNT is freely available, thanks to a subsidy from the Willi Hennig Society.

REFERENCES

Axsmith, B.J., and Ash, S.R. 2006. Two rare fossil cones from the Upper Triassic Chinle Formation in Petrified Forest National Park, Arizona, and New Mexico. *Museum of Northern Arizona Bulletin,* 62:82-94.

Bock, W. 1954. *Primaraucaria*, a new araucarian genus from the Virginia Triassic. *Journal of Paleontology,* 28:32-42.

Brochu, C.A., and Norell, M.A. 2000. Temporal congruence and the origin of birds. *Journal of Vertebrate Paleontology,* 20:197-200.

Cleal, C. J., and Rees, P.M. 2003. The Middle Jurassic flora from Stonesfield, Oxfordshire, UK. *Palaeontology,* 46:739-801.

Cornet, B. 1986. The leaf venation and reproductive structures of a Late Triassic angiosperm, *Sanmiguelia lewisii*. *Evolutionary Theory,* 7:231-309.

Cornet, B., and Waanders, G. 2006. Palynomorphs indicate Hettangian (Early Jurassic) age for Middle Whitmore Point Member of the Moenave Formation, Utah and Arizona. *New Mexico Museum of Natural History and Science Bulletin,* 37:1-17.

Cornet, B., Traverse, A., and McDonald, N.G. 1973. Fossil spores, pollen and fishes from Connecticut indicate Early Jurassic age for part of the Newark Group. *Science,* 182:1243-1246.

Del Fueyo G.M., and Archangelsky, S. 2002. *Araucaria grandifolia* Feruglio from the Lower Cretaceous of Patagonia, Argentina. *Cretaceous Research,* 23:265-277.

Endlicher, S. 1847. *Synopsis coniferarum*. Sankt Gallen, Switzerland.Del Fueyo, G.M., and Archangelsky, A. 2002. *Araucaria grandifolia* Feruglio from the Lower Cretaceous of Patagonia. *Cretaceous Research,* 23:265-277.

Gilmore, S., and Hill, K.D. 1997. Relationships of the Wollemi Pine (*Wollemia nobilis*) and a molecular phylogeny of the Araucariaceae. *Telopea,* 7:275-291.

Goloboff, P.A., Farris, F.S., and Nixon, K. in press. TNT: Tree analysis using new technologies. Program and documentation available from the authors at: <http://www.zmuc.dk/public/phylogeny>.

Harris, T.M. 1979. *The Yorkshire Jurassic flora, V, Coniferales*. British Museum (Natural History), London.

Hill, R.S., 1995. Conifer origin, evolution and diversification in the Southern hemisphere. p. 10-29, In Enright, N.J., and Hill, R.S. (eds.), *Ecology of Southern Conifers*. Melbourne University Press, Melbourne.

Hill, R.S., and Brodribb, T.J. 1999. Turner Review No. 2. Southern conifers in time and space. *Australian Journal of Botany,* 47:639-696.

Huber, P.N.G., McDonald, N., and Olsen, P.E. 2003, Early Jurassic insects from the Newark Supergroup, northeastern United States. p. 206-223. In LeTourneau, P.M., and Olsen, P.E. (eds.), *The great rift valleys of Pangea in eastern North America, vol. 2: sedimentology, stratigraphy, and paleontology.* Columbia University Press, New York.

Huelsenbeck, J.P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology,* 20:470-483.

Kendall, M.W. 1949. A Jurassic member of the Araucariaceae. *Annals of Botany, New Series,* 13:151-161.

Kunzmann, L. 2007a. Neue Untersuchungen zu *Araucaria* Jussieu aus der europäischen Kreide. *Palaeontographica,* B276:97-131.

Kunzmann, L. 2007b. Araucariaceae - aspects in palaeobiogeography and palaeobiodiversity in the Mesozoic. *Zoologischer Anzeiger,* 246:257-277.

Lucas, S.G., and Huber, P. 2002. Vertebrate biostratigraphy and biochronology of the nonmarine Late Triassic, p. 143-191. In LeTourneau, P.M., and Olsen, P.E. (eds.), *The great rift valleys of Pangea in eastern North America, vol. 2: sedimentology, stratigraphy, and paleontology.* Columbia University Press, New York.

McDonald, N.G. 1992. Paleontology of the early Mesozoic (Newark Supergroup) rocks of the Connecticut Valley. *Northeastern Geology,* 14:185-200.

Norell, M.A., and Novacek, M.J. 1992. Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics,* 8:319-337.

Ohsawa, T., Nishida, H., and Nishida, M. 1995. *Yezonia*, a new section of *Araucaria* (Araucariaceae) based on permineralized vegetative and reproductive organs of *A. vulgaris* comb. nov. from the Upper Cretaceous of Hokkaido, Japan. *Journal of Plant Research,* 108:25-39.

Olsen, P.E. 1986. Paleoecology and paleoenvironments of the continental early Mesozoic Newark Supergroup of eastern North America, p. 185-230. In Manspeizer, W. (ed.), *Triassic-Jurassic rifting: continental breakup and the origin of the Atlantic Ocean and passive margins*. Elsevier, Amsterdam.

Olsen, P.E., Whiteside, J.H., and Huber, P. 2003. Causes and consequences of the Triassic-Jurassic mass extinction as seen from the Hartford basin. p. B5-1 – B5-41. In Brady, J.B., and Cheney, J.T. (eds.), *Guidebook for field trips in the Five College Region, 95th New England Intercollegiate Geological Conference.* Department of Geology, Smith College, Northampton, Massachusetts.

Olsen, P.E., Whiteside, J.H., LeTourneau, P.M., and Huber, P. 2005. Jurassic cyclostratigraphy and paleontology of the Hartford basin. p. A4-1 – A4-5. In Skinner, B.J. and Philpotts, A.R. (eds.), *97th New England Intercollegiate Geological Conference*. Department of Geology and Geophysics, Yale University, New Haven, Connecticut.

Pol, D., and Norell, M.A. 2001. Comments on the Manhattan Stratigraphic Measure. *Cladistics,* 17:285-289.

Pol, D., and Norell, M.A. 2006. Uncertainty in the age of fossils and the stratigraphic fit to phylogenies. *Systematic Biology*, 55:512-521.

Setoguchi, H., Osawa, T.A., Pintaud, J.- C., Jaffre, T., and Veillon, J.-M. 1998. Phylogenetic relationships within Araucariaceae based on *rbcL* gene sequences. *American Journal of Botany,* 85:1507-1516.

Sidall, M.E. 1998. Stratigraphic fit to phylogenies: a proposed solution. *Cladistics,* 14:201-208.

Stockey, R.A. 1982. The Araucariaceae: an evolutionary perspective. *Review of Palaeobotany and Palynology,* 37:133-154.

Stockey, R.A. 1994. Mesozoic Araucariaceae: morphology and systematic relationships. *International Journal of Plant Sciences,* 107:493-502.

Stockey, R.A., and Ko, H. 1986. Cuticle micromorphology of *Araucaria* de Jussieu. *Botanical Gazette,* 147:508-548.

Tidwell, W.D., and Ash, S.R. 2006. Preliminary report on the Early Jurassic flora from the St. George dinosaur discovery site, Utah. *New Mexico Museum of Natural History and Science Bulletin,* 37:414-420.

Van Konijnenburg-van Cittert, J.H.A., and Morgans, H.S. 1999. *The Jurassic flora of Yorkshire.* Palaeontological Association field guides to fossils 8, The Palaeontological Association, London.

Wanner, A., and Fontaine, W.M. 1900. Triassic flora of York County, Pennsylvania. p. 233-255. In Ward, L.F. (ed.), *Status of the Mesozoic floras of the United States. First paper: The older Mesozoic*. Geological Survey Annual Report, 20. Washington D.C.

Wilde, M.H., and Eames, A.J. 1952. The ovule and 'seed' of *Araucaria bidwilli* with discussion of the taxonomy of the genus. II. Taxonomy. *Annals of Botany, New Series,* 16:27-47.

Wills, M.A. 1999. Congruence between phylogeny and stratigraphy: Randomization tests and the gap excess ration. *Systematic Biology,* 48:559-580.

Zijlstra, G., and Van Konijnenburg-van Cittert, J.H.A. 2000. Proposal to conserve the name *Araucarites* C. Presl (Fossil Gymnospermae, Coniferales, Araucariaceae) against *Araucarites* Endl. (Fossil Gymnospermae, Coniferales). *Taxon,* 49:279-280.