

Memoirs of the Queensland Museum | **Nature**

59

© The State of Queensland, Queensland Museum 2014

PO Box 3300, South Brisbane 4101, Australia
Phone 06 7 3840 7555
Fax 06 7 3846 1226
Email qmlib@qm.qld.gov.au
Website www.qm.qld.gov.au

National Library of Australia card number
ISSN 0079-8835 Print
ISSN 2204-1478 Online

NOTE

Papers published in this volume and in all previous volumes of the *Memoirs of the Queensland Museum* may be reproduced for scientific research, individual study or other educational purposes. Properly acknowledged quotations may be made but queries regarding the republication of any papers should be addressed to the Editor in Chief. Copies of the journal can be purchased from the Queensland Museum Shop.

A Guide to Authors is displayed at the Queensland Museum web site www.qm.qld.gov.au

A Queensland Government Project
Typeset at the Queensland Museum

Numerical analysis of the inter-relationships of some extinct and extant taxa of Araucariaceae

H. Trevor CLIFFORD

Mary E. DETTMANN

Scott A. HOCKNULL

Ancient Environments Program, Queensland Museum, Hendra Facility, 122 Gerler Rd, Hendra, Qld 4011 Australia. Email: scott.hocknull@qm.qld.gov.au

<http://dx.doi.org/10.17082/j.2204-1478.59.2015.2013-04>

LSID urn:lsid:zoobank.org:pub:1A1AF2E1-951D-4366-8COA-1D8E8A23A2CD

Citation: Clifford, H.T., Dettmann, M.E. & Hocknull, S.A. 2015. Numerical analysis of the inter-relationships of some extinct and extant taxa of Araucariaceae. *Memoirs of the Queensland Museum – Nature* 59: 27–38. Brisbane, ISSN 2204-1478 (Online), ISSN 0079-8835 (Print). Accepted: 20 October 2014. First published online: 20 February 2015.

ABSTRACT

The inter-relationships between extant and selected extinct taxa of Araucariaceae were explored using thirty morphological and anatomical characters. The sample of Araucariaceae included all three extant genera of the family with three extinct species of *Araucaria* and the fossil genera *Emwadea* and *Wairarapaia*. The data were analysed using phenetic and cladistic methodology which revealed there was close agreement between the two when applied to extant taxa but not to extant plus extinct taxa. All analyses recognised that the araucarioid taxa with embedded seeds formed a group separate from the agathoid taxa whose seeds at maturity separate from the seed-scale. However, whereas the parsimony (cladistic) analyses failed to distinguish clades within *Araucaria* the phenetic analyses recognised four Sections within the genus and placed the three fossil species of *Araucaria* in Sect. *Eutacta*. The fossil genera *Emwadea* and *Wairarapaia* united with *Agathis* and *Wollemia*. □ *Araucariaceae*, *Wollemia*, *Emwadea*, *Wairarapaia*, seed-cones, phylogeny.

The description of *Emwadea microcarpa* Dettmann *et al.* (2012) based on permineralised seed-cones with preserved anatomy, from the mid-Cretaceous (late Albian) of western Queensland, adds to the data base of confirmed araucarian remains worldwide and supports the widely held view that during the Mesozoic and early Tertiary the family was more diverse than at present (Hill 1990; Cantrill 1992; Stockey 1994; Stockey *et al.* 1994; Pole 1995; Chambers *et al.* 1998; Hill & Brodribb 1999; Cantrill & Raine 2006; Dettmann *et al.* 2012)

Whilst the araucarian affinities of many well preserved fossil seed-cones is not in doubt, their relationships with each other and with extant

taxa has not been explored, until recently, by quantitative phenetic or cladistic analyses (Escapa & Catalano 2013). The extant Araucariaceae are represented by three genera *Araucaria*, *Agathis* and *Wollemia* (Farjon 2010), whose relationships have not been unambiguously established by cladistic studies based on gene sequencing data (Gilmore & Hill 1997; Stephanovic *et al.* 1998; Setoguchi *et al.* 1998; Codrington *et al.* 2002; Rai *et al.* 2008). Furthermore, these cladistic studies do not strongly support either the widely accepted four Sections into which extant *Araucaria* species were grouped by Wilde & Eames (1952) or the two Section grouping espoused by Laubenfels (1988). For example, whereas according to Setoguchi *et al.* (1998) Sect. *Araucaria* is the

sister group to the clade Sects *Bunya* and *Intermedia* according to Gilmore & Hill (1997) it is the sister group to Sect. *Eutacta*.

Such disparity may be a consequence of the current Sections being based on morphological and anatomical data derived from extant taxa and so do not take into account the structure of Mesozoic seed-cones that may share characters with more than one extant Section of *Araucaria* (Stockey 1994; Stockey *et al.* 1994; Ohsawa *et al.* 1995).

In view of the uncertainty of the interrelationship within Araucariaceae it was decided to investigate relationships between the three extant genera and five fossil taxa of the family incorporating morphological and anatomical data for all extant taxa and those fossils for which adequate descriptions are available. Both phenetic and cladistic analyses were undertaken.

MATERIAL AND METHODS

Fourteen taxa, of which nine are extant, were selected for study. They were the genera *Pinus*, *Podocarpus*, *Phyllocladus*, *Agathis* and *Wollemia* together with the four currently accepted Sections of extant *Araucaria* (Wilde & Eames 1955). Following Farjon (2010) no subgeneric ranks were recognised within *Agathis*. The five fossil taxa, namely *Emwadea microcarpa* Dettmann, Clifford & Peters, *Wairarapaia mildenhallii* Cantrill & Raine, *Araucaria mirabilis* (Spegazzini) Windhausen, *A. nipponensis* Stockey, H. Nishida & M. Nishida and *A. vulgaris* (Stopes & Fujii) Ohsawa, H. Nishida & M. Nishida were chosen because the anatomical details of their ovule/seed-cones are available.

Since the development of the seed-cones of most araucarian taxa has not been studied the homologies of their characters could not be determined directly. Instead, it was necessary to choose a theoretical model against which to make comparisons. The model accepted was that proposed by Florin (1944) as it provides a suitable framework for this purpose, notwithstanding it is predicated on the structure of mature cones. Allowance therefore has to be made for the considerable changes in

structure that may occur following pollination (Tomlinson & Takaso 2002). For example, the ovules of young seed-cones of extant conifers are often initially orthotropous but are later inverted.

Here it has been accepted that the ovules derive from an axillary complex which is subtended by a scale, and that each ovule is sessile or terminal on a more or less developed axis terminating in a pair of bracts fused marginally to form an integument around the nucellus. The axis may or may not bear lateral appendages below the integumentary bracts. If present, these appendages may generate secondary axes. Such a modular construction of the cone is supported by the recent studies of developmental genetics reviewed by Mathews & Kramer (2012).

Although all ovules are postulated to arise directly from the axils of bracts or from axillary complexes, due to the activity of intercalary meristems at the complex or bract bases, they may appear to arise from the adaxial surface of the bract rather than its subtending axis.

The interpretation of the bract-ovule complex can be resolved only through a study of its ontogeny. Although the pattern of vascular traces in the mature complexes may reflect their ontogeny, this assumption cannot be justified *a priori* because primordia, at least those of ovules, may develop from almost any tissue and generate their own vascular tissues (Bouman in Johri 1984). Furthermore, the formation of adventitious buds on wound callus tissues and the development of ovules from single epidermal cells, both of which may become vascularized (Romberger *et al.* 1993), suggests that the arrangement of the vascular tissues may not always be phylogenetically informative.

However, the situation is much less clear with the interpretation of the 'ligule' which is restricted to araucarian seed scale where the ovule is always inverted. Although generally accepted as arising from the ovule stalk it has recently been reinterpreted as an extension of the chalaza (Dettmann *et al.* 2012) or a stigma (Krassilov & Barinova 2014). To distinguish between these hypotheses the development of the ligule must be determined, but as cautioned by Tomlinson & Takaso (2002, p. 1251), 'If part-for-part

Extant and extinct taxa of Araucariaceae

equivalence is assumed, one has to invoke both heterochrony (i.e. changes in developmental timing among parts) and heterotopy (i.e. spatial transference of characters), but only with considerable manipulation of the original model.' Due to such developmental flexibility, 'plants become so transformed by meristematic invocation that to expect to be able to identify all structures of a putative ancestor is unrealistic.' (Tomlinson & Takaso 2002, p. 1272). An example of heterochrony such as that postulated by Tomlinson & Takaso (2002) is the reversal of the sepaline and petaline whorls in *Xyris* and other monocot flowers with a double perianth (Remizowa *et al.* 2012).

The seeds of many conifer species are accompanied by accessory structures variously described as teeth (*Cryptomeria*), appendages (*Cunninghamia*), arils (*Taxus* and *Phyllocladus*) or 'ligules' (*Araucaria*). As these structures, with the possible exception of the ligule, arise from immediately below the integuments they are accepted as homologous.

The difficulty of interpreting characters is furthermore compounded by the lack of a definite sister group for the conifers (Taylor *et al.* 2009, pp. 870-871) which, in the literature, has led to conflicting reports of character states. The two following examples illustrate the problem.

The cotyledon numbers of *Araucaria* species are given as 4 by Kindel (2001), 2-4 by Laubenfels (1988) or in 2 free and 2 fused and 2 fused pairs, with 4 free, or 4 fused into 2 pairs at the base. (Farjon 2010, p. 185). A similar diversity of ovule number per ovuliferous scale has also been reported for the genus. Whereas *Araucaria* species usually bear only one ovule per scale, both 2 and 3 ovules have been reported (Wilde & Eames 1955; Mitra 1927). Numbers of ovules in excess of 1 per scale may be teratological malformations and so may be ignored if not regarded as atavistic.

Because the best preserved fossil taxa are represented by ovuliferous cones these provided most of the characters studied. For each of the 14 taxa included in the analysis information, where available, was collated for 30 characters, of which at least one was known for each fossil

taxon. This stricture was introduced so as to ensure the fossil and extant taxa are not *ab initio* members of unrelated taxa. The characters and their states are given in Appendix 1 and the taxa together with their character scores are listed in Appendix 2.

Due to the paucity of character states available for the fossil taxa evidence of structure within the data matrix was investigated using only simple phenetic and phylogenetic methods. The former were based upon a Similarity Index (S.I.) defined as the percentage of characters shared by two taxa and so varies from zero when they share no character states to 100% when they are identical.

Two types of phenetic analyses were undertaken. One analysis constructed a Constellation Diagram in which those taxa with arbitrarily high similarity values were linked to each other; the other was the formation of a dendrogram using a simple distance measure and group average as the clustering strategy (Swofford & Olse 1990). This clustering strategy tends to preserve the spatial interrelationships of the taxa with a minimum of distortion because it uses all distances available at each step in the development of the dendrogram and the distances depend upon all characters.

In contrast every step of the cladistic analyses was based on parsimony settings within the software program PAUP 4.0.8. (Swofford 2003) which forms a dendrogram whose ultimate branches imply relationships between taxa but more accurately, as stressed by Farjon (2010, p. 1035), the interrelationships that are generated from analysis of the selected characters.

Characters assumed to be phylogenetically informative were scored in MacClade 4 (Maddison & Maddison 2005), and subject to two tree generating analyses. One was based on phenetic (UPGM) and the other on cladistics principles using parsimony settings within the software program PAUP 4.0.8 (Swofford 2003). Each analysis was undertaken first with extant taxa only, then repeated with the addition of the extinct taxa.

Where required character states were polarised by setting *Pinus* as the outgroup taxon, with all ingroup taxa monophyletic. All character states were unordered and unweighted, consisting of up to three character states. Each analysis used the Tree Bisection and analysis bootstraps were calculated from 1000 replicates where only values of exceeding 50% were recorded.

RESULTS

Pair-wise comparisons of all taxa as measured by the S.I. are given in Table 1. These values varied from 23% (*Pinus* – *Araucaria*, Sect. *Araucaria*) to 94% (*A. mirabilis* – *A. vulgaris* and *A. mirabilis* – *A. nipponensis*). Choosing an arbitrary value of 75% the Constellation Diagram was drawn which linked all taxa with this or a higher score (Fig. 1). At this level of similarity four groups of taxa emerged of which one included only *Pinus*. In another *Phyllocladus* was linked to *Podocarpus*. The remaining taxa had either embedded or stalked seeds. The former were all the members

of *Araucaria* and were linked to one another through *A. mirabilis*, an extinct taxon, the latter comprised four genera inter-linked through *Wairarapaia*, another extinct taxon (Fig. 1).

On subjecting the nine extant taxa to a group average clustering program (UPGMA) a dendrogram with four major branches emerged (Fig. 2). Their terminal taxa were as follows: *Pinus*; *Podocarpus* and *Phyllocladus*; *Araucaria* (all Sects); *Agathis* and *Wollemia*. The four Sections of *Araucaria* were united into two pairs, namely Sects *Eutacta* plus *Intermedia* and Sects *Araucaria* plus *Bunya*.

When the UPGMA analysis was repeated with the addition of five extra, less well-described, extinct araucarian taxa *Araucaria* again separated into two groups one of which included all the fossil species plus the Section *Eutacta* and the other included the Sections *Intermedia*, *Araucaria* and *Bunya*. The agathoid genera again formed a close-knit group but with *Wollemia* linked to *Wairarapaia* instead of to *Agathis* (Fig. 3).

Table 1. Indices of Similarity below and the numbers of characters used in their calculation above the diagonal. *Ar.* abbreviation of *Araucaria*.

Taxon	Similarity Index \ Number of Comparisons													
<i>Pinus</i>	X	30	29	30	30	33	27	30	27	26	19	21	21	21
<i>Ar. Sect. Eutacta</i>	33	X	29	30	30	30	28	30	27	26	10	22	21	20
<i>Ar. Sect. Intermedia</i>	38	19	X	29	19	29	27	29	25	25	19	22	21	19
<i>Ar. Sect. Araucaria</i>	23	73	90	X	30	30	28	30	27	26	20	24	21	20
<i>Ar. Sect. Bunya</i>	27	63	76	83	X	30	28	30	27	26	20	22	21	30
<i>Agathis</i>	57	53	59	50	67	X	27	30	26	26	20	22	21	21
<i>Wollemia</i>	41	61	70	56	61	78	X	27	25	23	19	20	18	19
<i>Podocarpus</i>	73	35	38	23	23	47	39	X	26	26	20	22	20	21
<i>Phyllocladus</i>	66	37	44	26	22	54	52	88	X	24	20	19	19	21
<i>Emwadea</i>	38	62	56	50	38	73	70	38	54	X	19	21	20	19
<i>Wairarapaia</i>	49	74	74	65	60	80	84	40	55	79	X	15	16	15
<i>Ar. vulgaris</i>	38	86	64	68	73	41	60	18	37	57	67	X	16	15
<i>Ar. nipponensis</i>	43	71	67	67	71	48	61	30	37	60	63	88	X	15
<i>Ar. mirabilis</i>	43	80	79	80	90	43	63	24	24	47	67	93	93	X

Extant and extinct taxa of Araucariaceae

Parsimony analysis (PAUP) of the data for extant taxa generated a cladogram which was in most respects similar to the dendrogram generated by group average clustering (UPGMA). The genera *Podocarpus* and *Phyllocladus* constituted a single clade whilst the four Sections of *Araucaria* were resolved into three clades with the Sects *Araucaria* and *Bunya* sharing a common ancestor (Fig. 4)

Repeating the parsimony analysis with the addition of the five fossil taxa resulted in the loss of much of the structure present evident in Fig. 4. As before *Podocarpus* and *Phyllocladus* formed a clade with strong bootstrap support. However, although there was still strong bootstrap support for recognising the Araucariaceae and *Araucaria* as monophyletic there was no bootstrap support above 50% for

recognising Sections within the genus. Nor was there any strong support for recognising separate clades amongst the agathoid genera all of which shared a common ancestor (Fig. 5).

That different tree topologies were generated is not surprising given the considerable morphological difference exhibited by taxa in characters other than those of the ovuliferous-cone which were here emphasised because of the decision to restrict the data to characters that were available for at least one fossil taxon. For example, had seedlings been considered those of *Araucaria*, *Agathis* and *Wollemia* are quite different. Whereas the first plumular leaves of *Wollemia nobilis* are opposite decussate cataphylls with an abrupt transition to adult-like foliage (Offord *et al.* 1999) those of *Agathis* spp. are a mixture of alternately arranged

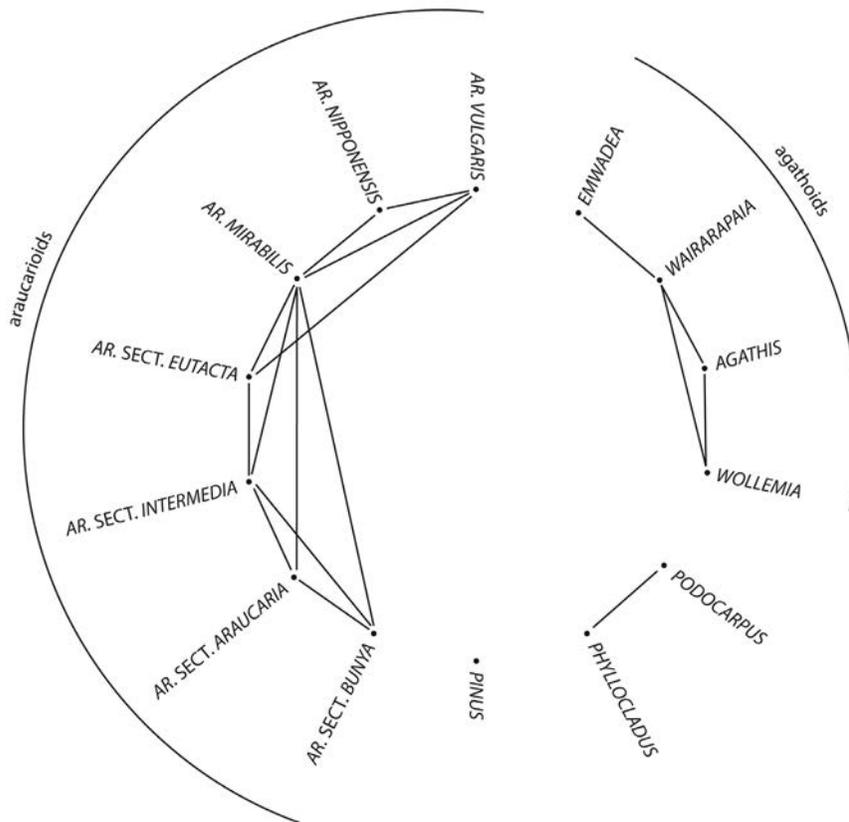


FIG. 1. Constellation Diagram in which those taxa with pair-wise Similarity Index values of 75% or more linked with straight lines. *Ar.* Abbreviation of *Araucaria*.

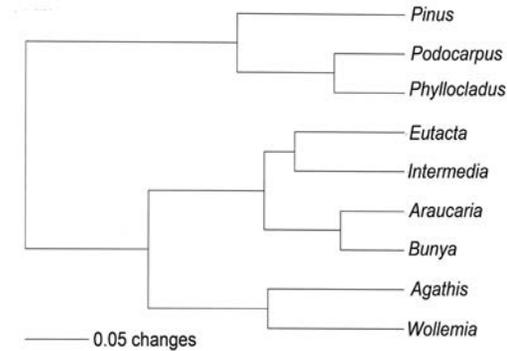


FIG. 2. Relationships of extant taxa expressed as a dendrogram generated by a UPGMA analysis of data in Appendix 2.

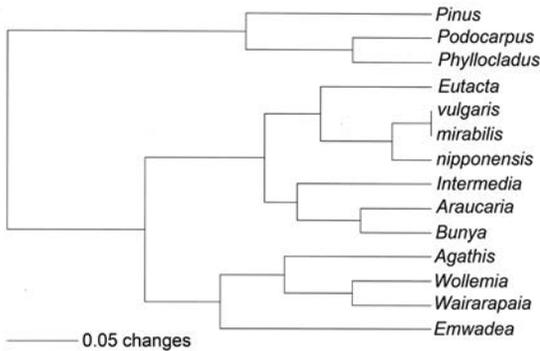


FIG. 3. Relationships of extant and fossil taxa expressed as dendrogram generated by a UPGMA analysis of the data in Appendix 2.

leaves, similar in shape to, but smaller than those of the adult plant. In contrast the initial plumular leaves of *Araucaria* spp. have needle-shaped leaves.

GENERAL DISCUSSION

Though the above analyses produced different results they share much in common in that *Phyllocladus* and *Podocarpus* are consistently associated and separated from the Araucariaceae whose taxa always divide into two groups the araucarioid with sessile seeds and the other the agathoid with seeds that,

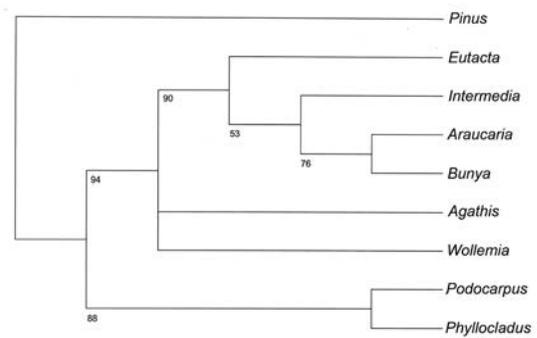


FIG. 4. Relationships of extant taxa expressed as a cladogram generated by the parsimony program PAUP employing data of Appendix 2. Numbers represent bootstrap values returned greater than 50%.

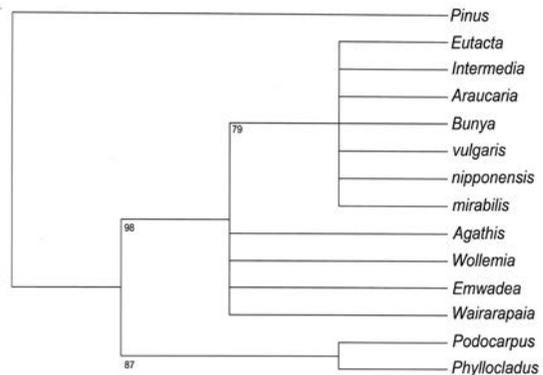


FIG. 5. Relationships of extant and fossil taxa expressed as a cladogram generated by the parsimony program PAUP employing data from appendix 2. Numbers represent bootstrap values returned greater than 50%.

at maturity, separate from their subtending scales. Within these two clades the taxa are aligned somewhat differently in the above and published analyses.

Furthermore, the agathoid genera, *Agathis* and *Wollemia*, behaved less consistently than did the araucarioid taxa. In six of the eleven cladistic analyses available *Agathis* and *Wollemia* are in different clades (Setoguchi *et al.* 1988; Codrington *et al.* 2002; Stephanović *et al.* 1998; Biffin *et al.* 2010; Escapa & Catalano 2013; herein Figs 4 & 5), and in five the same clade (Kunzmann 2007; Leslie *et al.* 2012; Liu *et*

al. 2009; Rai *et al.* 2008; Gilmour & Hill 1997). The reasons for this disparity are not clear. They may reflect that the analyses are not based on the same taxa, and characters, or that the analyses are based on different amounts of data. As shown by Liu *et al.* (2009) parsimony analyses undertaken on the basis of single gene sequences favoured the tree topology ((*Agathis*, *Wollemia*) *Araucaria*), but on statistical grounds neither ((*Agathis*, *Araucaria*) *Wollemia*) nor ((*Araucaria*, *Wollemia*) *Agathis*) could be rejected when the analyses were based on the sequences of eight genes.

Although the parsimony analyses, which involved both extinct and extant taxa, detected no clades within *Araucaria* those based solely on extant taxa recognised the presence of two clades. One was Sect. *Eutacta* and the other clade resolved into three subclades, corresponding with the currently recognised Sections in the genus (Fig. 4). Therefore, as proposed by Axsmith *et al.* (2008) and Leslie *et al.* (2012), Sect. *Eutacta* is the oldest of those recognised in the genus.

This conclusion is supported by the result of the group average clustering analysis (UPGMA) which assigned all three of the extinct species of *Araucaria* to the Sect. *Eutacta*. Two of these species, *A. nipponensis* (Setoguchi *et al.* 1988) and *A. vulgaris* (Ohsawa *et al.* 1995) had been reported as sharing seed-cone characters with members of the Sect. *Eutacta*. The third *A. mirabilis*, has hitherto been closely allied with *A. bidwillii*, an extant species and sole representative of *Araucaria* Sect. *Bunya* (Calder 1953; Stockey 1978). Both these authors, writing before cladistics methodology became widely accepted, laid great stress on 'the separate origins of the bract and ovulate-scale vascular supplies which seem to ally *A. mirabilis* with this species,' (Stockey 1975, p. 865, referring to *A. bidwillii*). Nonetheless, their support was not fully forthcoming in that the vasculature only 'seemed' to ally *A. mirabilis* and *A. bidwillii*. Furthermore, 20 years later Stockey *et al.* (1994, p. 813) noted the double cone-scale trace, 'is exceedingly difficult to interpret in fossil cones,' thereby casting doubt

on the reliability of the origin of the vascular trace as a taxonomic character.

Attempts to fix the absolute age of the crown groups Sects *Eutacta* and *Bunya*, using sequencing data and the fossil record have produced conflicting results. Axsmith *et al.* (2008) concluded that the araucarian crown group arose in the Late Triassic with the crown groups for the Sects *Eutacta* and *Bunya* arising in the Middle and Late Jurassic respectively. That is their relative ages were in the same order as that postulated by the cladistic analyses. Using similar data Biffin *et al.* (2010) and Leslie *et al.* (2012) concluded the araucarian crown group was much younger and developed in the Middle Jurassic. According to the former authors the crown group of Sect. *Bunya* arose in the mid Cretaceous and Sect. *Eutacta* in the early Paleogene a reversal in the order of appearance to that proposed by Axsmith *et al.* (2008). In contrast, Leslie *et al.* (2012) agreed with the relative ages of Sects *Eutacta* and *Bunya*, as proposed by Axsmith *et al.* (2008), but postulated that they arose towards the end of the Paleogene and the beginning of the Neogene respectively.

To resolve these differences much more work is required to encompass the diversity existing amongst extant taxa and the discovery of fossil specimens of mature ovuliferous cones with attached foliage. The emended description of *Araucaria vulgaris* by Ohsawa *et al.* (1995), incorporating foliage characters, led to the recognition of new Section (*Yezonia*) of *Araucaria* and further Sections may be required to accommodate the diversity predicted to exist amongst Jurassic and Cretaceous araucarians known presently only from ovuliferous cones (Stockey 1994; Stockey *et al.* 1992, 1994).

Furthermore, since the double origin of the vascular strands to the ovuliferous cone scale complex of *A. bidwillii* depends largely on the single elegant study of Eames (1913) it needs independent confirmation. In their treatment of the taxonomy of the conifers Pilger & Melchior (1954) provide a diagrammatic longitudinal section of a seed-cone scale of *A. bidwillii* which shows the origin of the vascular strand as single but branching close to the stele. The lack of

certainty of the double origin of the ovuliferous cone vascular strands casts doubt on its value as a diagnostic character.

The failure of the cladistic analyses to recognise clades in the combined sample of extant and fossil taxa suggest that the data are inadequate or that the Sections of *Araucaria* are in need of recircumscription taking into account fossil material. As Axsmith *et al.* (2008, p. 7) pointed out 'it is likely that phylogenetic studies based only on extant taxa underestimate the true complexity, as the fossil record indicated high levels of extinct diversity, including completely extinct Sections'.

The emergence in the parsimony analyses of four possible new clades of seed shedding Araucariaceae, (*Agathis*, *Wollemia*, *Emwadea* and *Wairarapaia*) and the recognition that the extinct species assigned to *Araucaria* do not form a single clade support the view that in Jurassic and Cretaceous times there were species whose seed-cones differed from those of all extant species. Furthermore, the parsimony analyses involving both extant and extinct taxa offer no conclusive evidence of possible phylogenetic relationships within the Araucariaceae other than that agathoid and araucarioid taxa constitute separate sister clades and that the agathoid is the older of the two clades (Fig. 5).

Until data are available from ovuliferous cones with fully developed seeds and attached foliage any formal classification of the family incorporating extinct taxa must be regarded as tentative. As noted by Bigwood and Hill (1985) the three species they allotted to the foliage form genus *Araucarioides* could not be assigned, with confidence, to either *Agathis* or *Araucaria* as there are few differences in leaf and cuticle morphology between these genera (Burrows & Bullock 1999). Therefore, the foliage of some species of *Araucarioides* may belong to other araucarian genera including the extant *Wollemia* or the fossil *Wairarapaia* and *Emwadea*, for which foliage characters are presently limited. The Section (*Perpendiculare*) of *Araucaria* proposed by Pole (1995), based solely on cuticle characters, is questionable.

Given the plethora of cladistic and phenetic analytical techniques available (Felsenstein 2004) the choice of characters and taxa included in the analysis will determine the phylogenetic relationships that are generated. Therefore, it is not surprising, that studies on the araucarians using different data sets, and taxa, have produced differing although not always inconsistent results. Although recourse to genomic data may be helpful as noted by Soltis *et al.* (2004), referring to extant taxa, even complete genomic data by themselves are not a panacea for phylogenetic reconstructions. Therefore, although it is unfortunate that genomic data are unlikely to become available for Paleozoic conifers and Cretaceous araucarians this lack of data is not a major problem when combining genomic and morphological data. Instead it is the inadequate fossil record. In particular there is a lack of specimens with foliage connected to ovuliferous cones.

ACKNOWLEDGEMENTS

The authors thank Ross McKinnon, Curator of the Brisbane Botanic Gardens for providing living material; Gordon Guymmer, for allowing us access to the Queensland Herbarium Library; Andrew Rozefelds, Ancient Environments Section, Queensland Museum for providing living plant material and offering helpful comments on an early draft of the manuscript; Bryan Simon, Queensland Herbarium for advice on nomenclatural problems.

LITERATURE CITED

- Axsmith, B.J., Escapa, I.H. & Huber, P. 2008. An araucarian bract-scale complex from the lower Jurassic of Massachusetts: Implications for estimating phylogenetic and stratigraphic congruence in Araucariaceae. *Palaeontologica Electronica* PE11.3.13A: 1–9.
- Bigwood, A.J. & Hill, R.S. 1985. Tertiary araucarian macrofossils from Tasmania. *Australian Journal of Botany* 33: 645–656.
- Biffin, E., Hill, R.S. & Lowe A.T. 2010. Did Kauri (*Agathis*: Araucariaceae) survive the Oligocene drowning of New Zealand? *Systematic Botany* 59(5): 594–602.

Extant and extinct taxa of Araucariaceae

- Bouman, F. 1984. The Ovule. pp. 123–57. In Johri, B.M. (ed.). *Embryology of the Angiosperms*. Springer-Verlag, Berlin.
- Burrows, G.E. & Bullock S. 1999. Leaf anatomy of Wollemi pine (*Wollemia nobilis*), Araucariaceae. *Australian Journal of Botany* **47**: 795–806.
- Calder, M.G. 1953. A coniferous petrified forest in Patagonia. *Bulletin of the British Museum (Nat. Hist.) Geology* **2**: 99–138.
- Cantrill, D.J. 1992. Araucarian foliage from the Lower Cretaceous of southern Australia. *International Journal of Plant Science* **153**: 622–645.
- Cantrill, D.J. & Raine, J.I. 2006. *Wairarapaia mildenhallii* gen. et sp. nov. a new araucarian cone related to *Wollemia* from the Cretaceous of New Zealand. *International Journal of Plant Science* **16**: 1259–1269.
- Chambers, T.C., Drinnen, A.N. & McLoughlin, S. 1998. Some morphological features of Wollemi pine (*Wollemia nobilis*: Araucariaceae) and their comparison to Cretaceous plant fossils. *International Journal of Plant Science* **159**: 160–171.
- Codrington, T.A., Scott, L.J., Scott, K.D., Graham, G.C., Rossetto, M., Ryan, M., Whiffin, T., Henry, R.J. & Hill, K. 2002. Unresolved phylogenetic position of *Wollemia*, *Araucaria* and *Agathis*. pp. 69–73. In Wilcox, M. & Bielecki, R. (eds) *International Araucariaceae Symposium*. Auckland. New Zealand.
- Dettmann, M.E., Clifford, H.T. & Peters, M. 2012. *Emwadea microcarpa* gen. et sp. nov. – anatomically preserved araucarian seed cones from the Winton Formation (late Albian), western Queensland, Australia. *Alcheringa* **36**: 217–237.
- Eames, A.J. 1913. The morphology of *Agathis australis*. *Annals of Botany* **27**: 1–38.
- Escapa, I.H. & Catalano, S.A. 2013. Phylogenetic analysis of Araucariaceae: integrating molecules, morphology, and fossils. *International Journal of Plant Science* **174**: 1153–1170.
- Farjon, A. 2010. *A Handbook of the World's Conifers*. Brill. Leiden-Boston.
- Felsenstein, J. 2004. *Inferring Phylogenies*. Sinauer Associates. Sunderland, Mass.
- Florin, R. 1944. Die Koniferen des Oberkarbon und des unteren Perms. Heft 7. *Palaeontographica* **85** Abt. B.: 457–64.
- Gilmore, S. & Hill, K.D. 1997. Relationships of the Wollemi pine (*Wollemia nobilis*) and a molecular phylogeny of the Araucariaceae. *Telopea* **7**: 275–291.
- Hill, R.S. 1990. *Araucaria* (Araucariaceae) Species from Australian Tertiary Sediments – a micromorphological study. *Australian Systematic Botany* **3**: 203–220.
- Hill, R.S. & Brodribb, T.J. 1999. Turner Review No.2: Southern conifers in time and space. *Australian Journal of Botany* **47**: 639–696.
- Holloway, J.T. 1937. Ovule anatomy and development and embryology in *Phyllocladus alpinus* (Hook.) and *P. glaucus* (Carr.). *Transactions of the Royal Society of New Zealand* **67**: 149–165.
- Kindel, K-H. 2001. Die Gattung *Araucaria*. *Mitteilungen der Deutsche Dendrologische Gesellschaft* **86**: 191–218.
- Krassilov, V. & Barinova, S. 2014. Carpel-fruit in a coniferous genus *Araucaria* and the enigma of the angiosperm origin. *Journal of Plant Sciences* **2(5)**: 159–166.
- Kunzmann, L. 2007. Araucariaceae (Pinopsida) Aspects in palaeobiogeography, paleodiversity in the Mesozoic. *Zoologischer Anzeiger* **246**: 257–277.
- Laubenfels, D.J. de 1988. Coniferales In: Flora Malesiana ser.1, **10**: 337–453. Kluwer. Academic Publishers Dordrecht.
- Leslie, A.B., Beaulieu, J.M., Rai, H.S., Crane, P.R., Donoghue, M.J. & Mathews, S. 2012. Hemisphere-scale differences in conifer evolutionary dynamics. *Proceedings National Academy of Science* **100**: 16217–16221.
- Liu, N., Zhu, Y., Wei, Z-X., Chen, J., Wang, Q-B., Jian, S-G., Zhou, D-W., Shi, J., Yang, Y. & Zhong, Y. 2009. Phylogenetic relationships and divergence times of the family Araucariaceae based on DNA sequences of eight genes. *Chinese Science Bulletin* **54**: 2648–2655.
- Maddison, D.R. & Maddison, W.P. 2005. *MacClade 4: Analysis of phylogeny and character evolution*. Version 4.08a. <http://macclade.org>.
- Mathews, S. & Kramer, E.M. 2012. The evolution of reproductive structures in seed plants are-examination based on insights from developmental genetics. *New Phytologist* **194**: 910–923.
- Mitra, A.K. 1927. On the occurrence of two ovules on araucarian cone-scales. *Annals of Botany (N.S.)* **41**: 461–471.
- Offord, C.A., Porter, C.L., Meagher, P.F. & Errington, G. 1999. Sexual reproduction and early plant growth of the Wollemi Pine (*Wollemia nobilis*), a rare and threatened Australian conifer. *Annals of Botany* **84**: 1–9.
- Ohsawa, T., Nishida, H. & Nishida, M. 1995. *Yezonia*, a new Section of *Araucaria* (Araucariaceae) based on permineralised vegetative and reproductive organs of *A. vulgaris* comb. nov. from the upper Cretaceous of Hokkaido, Japan. *Journal of Plant Research* **108**: 25–39.
- Page, C.N. 1990. Gymnosperms: Coniferophytina (Conifers and Ginkgoales). pp. 279–361. In Kubitzki, K. & Green, P.S. (eds) *The families and*

- genera of vascular plants. Vol. 1, Pteridophytes and Gymnosperms. Koeltz, Koenigstein.
- Pilger, R. & Melchior, H. 1954. Gymnospermae. In A. Engler's, *Syllabus der Pflanzen-Familien. Band 1. Abteilung xvi*. Berlin-Nikolassee. Gebruder Borntrager.
- Pole, M. 1995. Late Cretaceous macrofloras of Eastern Otago, New Zealand, Gymnosperms. *Australian Systematic Botany* **8**: 1067–1106.
- Rai, H.S., Reeves, P.A., Peakall, R., Olmstead, R.G., & Graham, S.W. 2008. Inference of higher order conifer relationships from a multi-locus plastid data set. *Botany* **86**: 658–669
- Remizowa, M.V., Kuznetsov, A.N., Kunetsova, P.S., Rudall, P.J., Nuraliev, M.S. & Soksdoff, D.D. 2012. Flower development and vasculature in *Xyris grandis* (Xyridaceae, Poales); a case study for examining petal diversity in monocot flowers with a double perianth. *Botanical Journal of the Linnean Society* **169**: 93–111.
- Romberger, J.A., Hejnowicz, Z. & Hill, J.F. 1993. *Plant structure: function and development. A treatise on anatomy and vegetative development, with special reference to Woody Plants*. Springer-Verlag, Berlin.
- Rouane, M.L., Gondran, M. & Woltz, P.H. 1988. Heterocotyle et évolution cotyledonaire chez les Podocarpaceae. *Gaussenia* **4**: 7–15
- Rouane, M-L. & Woltz, P.H. 1980. Intérêt évolution des Araucariacées. *Bulletin de la Societe de Histoire Naturelle de Toulouse* **116**: 120–136.
- Setoguchi, H., Ohsawa, T.A., Pintaud, J-C., Joffré, T. & Vaillon, J.M. 1998. Phylogenetic relationships within Araucariaceae based on rbcL gene sequences. *American Journal of Botany* **85**: 1507–1516.
- Soltis, D.E., Albert, V.A., Savolainen, V., Hilu, K., Qui, Y-L., Chase, M.A., Farris, J.S., Stephanović, S., Rice, D.A., Palmer, J.D. & Soltis, P.S. 2004. Genome-scale data, angiosperm relationships, and 'ending congruence': a cautionary tale in phylogenetics. *Trends in Plant Science* **9**: 477–483.
- Stephanović, S., Jager, M., Deutsch, J., Broutin, M. & Masselot, M. 1998. Phylogenetic relationships of conifers inferred from partial 28S rRNA gene sequences. *American Journal of Botany* **85**: 688–697.
- Stockey, R.A. 1975. Seeds and embryos of *Araucaria mirabilis*. *American Journal of Botany* **62**: 856–858.
1978. Reproductive biology of Cerro Cuadrado fossil conifers: Ontogeny and reproductive strategies in *Araucaria mirabilis* (Spegazzini) Windhausen. *Palaeontographica Abt.* **166B**: 1–15.
1978. On the structure and evolutionary relationships of the Cerro Cuadrado fossil conifer seedlings. *Journal of the Linnean Society Botany* **76**: 167–176.
1982. The Araucariaceae: An evolutionary perspective. *Review of Palaeobotany and Palynology* **37**: 133–154
1994. Mesozoic Araucariaceae: morphology and systematic relationships. *International Plant Research* **107**: 493–502.
- Stockey, R.A., Nishida, H. & Nishida, M. 1992. Upper Cretaceous araucarian cones from Hokkaido: *Araucaria nihongii* sp. nov. *Review of Palaeobotany and Palynology* **72**: 27–40.
1994. Upper Cretaceous araucarian cones from Hokkaido and Saghalien: *Araucaria nipponensis* sp. nov. *International Journal of Plant Science* **155**: 806–815.
- Swofford, D.L. 2003. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Taylor, T.N., Taylor, E.L. & Krings, M. 2009. *Paleobotany: The Biology and Evolution of Fossil Plants*. Academic Press, New York.
- Tomlinson, P.B. & Takaso, T. 2002. Seed cone structure in conifers in relation to development pollination: a biological response. *Canadian Journal of Botany* **80**: 1250–1273.
- Wilde, M.H. & Eames, A.J. 1952. The ovule and seed of *Araucaria bidwillii* with discussion of the taxonomy of the genus. III. Taxonomy. *Annals of Botany (N.S.)* **16**: 27–47.
1955. The ovule and 'seed' of *Araucaria bidwillii* with discussion of the taxonomy of the genus. III. Anatomy of ovulate scales. *Annals of Botany (N.S.)* **47**: 343–349.

Extant and extinct taxa of Araucariaceae

APPENDIX 1

Character states according to original authors or as subsequently recorded. The principal authors consulted were the following and the numbers in brackets after each are the characters involved; Dettmann *et al.* 2012 (11, 17); Farjon 2010 (27); Holloway 1937 (28); Wilde & Eames 1952 (29); Stockey 1975 (19, 24); Stockey 1982 (25); Rouane *et al.* 1988, Rouane & Woltz 1980 (24)

Leaf anatomy

1. Compartmented cells: present 0, absent 1.
2. Nerve number at maximum leaf width: single 0, two or more 1.
3. Adult foliage: epi- 0, hypo- 1, amphistomatic 2.

Vegetative morphology

4. Adult leaf attachment: decurrent 0, petiolate 1.
5. Lamina shape: flat 0, awl-shaped and beaked 1, cylindrical 2.
6. Apophysis: present 0, absent or inconspicuous 1.
7. Leaf disposition with respect to axis: appressed 0, spreading 1.

Ovuliferous cone

8. Bract-scale at maturity: separating from cone axis 0, retained on cone axis 1.
9. Bract-scale length at maturity: longer than ovuliferous complex 0, shorter than ovuliferous complex 1.
10. Ovules per bract-scale: one 0, two or more 1.
11. Vasculature of ovuliferous complex: arising within cone axis 0, arising within bract-scale 1.
12. Fertile bracts per ovuliferous cone: 20 or less 0, 21 or more 1.
13. Apex of bract-scale: acute 0, apiculate 1, obtuse 2.
14. Apex of bract-scale: deciduous 0, not deciduous 1.
15. Ovuliferous complex at maturity: succulent 0, not succulent 1.
16. Ovuliferous cone: terminal 0, axillary 1.

17. Vascular strands to cone-scale complex: one 0, two 1.

18. Bract-scale base: auriculate 0, non auriculate 1
19. Cotyledon length as a fraction of embryo length: less half 0, more than half 1.

Ovule and seed anatomy

20. Ovules at maturity: free of bract 0, embedded in bract 1.
21. Ovule integument: winged laterally 0, not winged laterally 1.
22. Ovule accessory structures: more or less fused to bract-scale 0, separate from bract-scale 1.
23. Nucellus: stipitate 0, non-stipitate 1.
24. Cotyledon numbers: two 0, three or more 1.

Seeds and seedlings

25. Hypocotyl: fleshy 0, not fleshy.
26. Cotyledon vein number: one or two 0, three or more 1.
27. Seed shape in transverse section: laterally compressed 0, dorsally compressed 1, not compressed 2.
28. Mesotesta anatomy: simple sclereids 0, branched cylindrical sclereids 1, parenchyma 2.
29. Cotyledon petioles of seedlings: long 0, short 1.
30. Seed length: less than 30mm 0, 30mm or more 1.

APPENDIX 2

Appendix 2. Taxa and their character states as defined in Table 1. Ar. abbreviation of *Araucaria*.

Character states	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29		
<i>Pinus</i>	1	0	0/2	1	2	1	1	1	1	1	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	0		
Ar. Sect. <i>Eutacta</i>	0	1	2	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	1	1	0	0	0/1	1	1	1	0	1	0	
Ar. Sect. <i>Intermedia</i>	0	1	2	0	0	0	1	0	0	0	1	1	1	1	1	1	0	1	?	1	1	0	0	0	1	1	1	2	1	0	
Ar. Sect. <i>Araucaria</i>	0	1	2	0	0	0	1	0	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	1	
Ar. Sect. <i>Bunya</i>	0	1	2	0	0	0	1	0	0	0/1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1/2	0	0	1	
<i>Agathis</i>	1	1	2	1	0	1	1	0	0	0	1	1	2	1	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	
<i>Wollemia</i>	0	1	2	0	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	0	0	1	?	0	1	1	1	1	?	1	0
<i>Podocarpus</i>	1	0	½	1	0	1	1	1	1	0	0	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	0	2	1	1	0
<i>Phyllocladus</i>	1	?	?	0	0	1	?	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0
<i>Emuadea</i>	0	?	0	0	1	1	0	1	0	0	1	1	2	1	1	0	0	1	0	0	0	1	0	0	?	?	1	0	?	0	
<i>Wairarapaia</i>	?	1	?	0	0	?	?	?	0	0	1	1	1	?	1	0	?	1	1	0	0	1	0	0	?	?	?	1	?	0	
<i>Ar. vulgaris</i>	?	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1	?	?	1	0	0	?	?	?	1	0	?	?	
<i>Ar. nipponensis</i>	?	?	?	0	1	?	0	0	0	0	0	1	?	1	1	0	?	?	1	1	1	0	0	?	?	?	2	0	?	0	
<i>Ar. mirabilis</i>	?	?	?	?	?	0	?	0	0	0	0	1	?	1	1	?	1	1	1	1	1	0	0	0	0	1	1/2	0	?	0	