When did the mistletoe family Loranthaceae become extinct in Tasmania? Review and conjecture

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Introduction

‘Mistletoe’ is the common name for a diverse group of hemi-parasitic shrublets that grow attached to and within the branches of trees and shrubs. Vidal-Russell and Nickrent (2008a) and Nickrent et al. (2010) infer that the mistletoe habit has evolved five times in the sandalwood order Santalales. The first of these clades is the family Misodendraceae, which is endemic to southern South America and whose species grow mainly on *Nothofagus*. The habit evolved three times within the Santalaceae – in the cosmopolitan tribe Visceae, which includes the ‘archetypal’ European Mistletoe *Viscum album*, in tropical American species of Santaleae that were formerly placed into a separate family, the Eremolepidaceae, and in the tropical tribe Amphorogyneae. The third clade comprises all members of the Loranthaceae except the early diverging genera *Nuytsia* and *Atkinsonia*. The family is restricted to the Southern Hemisphere except for a few

genera growing north of the equator in the tropics and around the Mediterranean.

Two mistletoe clades are extant in Australia. These are (1) *Visceae* (three genera including *Viscum*), which is restricted to rainforests, monsoon forests and woodlands along the northern and eastern margins, and (2) *Loranthaceae* (12 genera), which is widely distributed across mainland Australia, with hosts ranging from coastal mangrove forests to mulga (*Acacia aneura*) woodlands in the arid zone (www.anbg.gov.au/abrs/online-resources/flora/redirect.jsp). Two Australian species are root parasites and for this reason give the appearance of being stand-alone shrubs or small trees – *Nuytsia floribunda*, which is endemic to southwest Western Australia, and *Atkinsonia ligustrina*, which is confined to exposed habitats in the Blue Mountains of NSW (Barlow 1984).

No mistletoes now occur in Tasmania. The reason(s) for this remain obscure given the wide ecological tolerance of many genera within the *Loranthaceae* and their observed dispersal over long distances by birds (www.anbg.gov.au/mistletoe/remote-islands.html). In this review, we illustrate and discuss the implications of *Loranthaceae*-type pollen recovered from a range of offshore and onshore sites around Tasmania (Figure 1). Unlike many fossil angiosperm pollen types, the morphology of these specimens is sufficiently distinctive to allow them to be assigned to this family and one of the six fossil species possibly to an extant genus.

Figure 1. Location of sites mentioned in the text.

Loranthaceae pollen

Modern Loranthaceae pollen comprise two morphologically distinct types, one of which is a $\pm$ convex triangular, oblate grain with simple to complex tricolpate (rarely syncolpate) apertures, e.g. *Alepis*, *Amyema*, *Amylothea*, *Decaisnia*, *Peraxilla* and *Nuytsia*, and the other of which is a sphaeroidal, triporate to tricolporoidate grain ornamented with stout spines (baculae, echini), e.g. *Lepidoceras* (Chile) and *Tupeia* (NZ) (see Erdtman 1966; Heusser 1971; Moar 1993; Beug 2004).

Pollen produced by Loranthaceae genera (Figures 2a-o) are easily distinguished from other Australian pollen morphotypes. Key characteristics are: (a) the oblate, triangular to lobate shape, (b) thin exine except across the poles where distinctively sculptured or thickened exine may form a bluntly triangular 'bridge' (Pocknall and Mildenhall 1984) or 'apical cushion' (Mildenhall and Pocknall, 1989), respectively, and (c) apertures (colpi) located at the tips (angles) of rounded to truncated apices. The usually gaping, colpate to demicolpate apertures vary in length from relatively short, in, for example, *Amylothea*, to extremely long, in, for example, *Amyema* and *Peraxilla*. Ornamentation in the mesocolpial regions varies from psilate-scabrate to verrucate-baculate. In some genera, the tectum breaks down to form a pseudo-reticulum, e.g. *Nuytsia*; more rarely, the colpi are bordered by very short parallel rods (striae) that may extend close to the poles, e.g. *Alepis* and *Peraxilla*.

Australian fossil pollen types displaying the same morphological characteristics have been assigned to, or compared with, six formally described species: '*Amylothea*' *pliocenica* Cookson 1957, *Gothanipollis bassensis* Stover and Partridge 1973, *Gothanipollis gothani* Krutzsch 1959, *Gothanipollis perplexus* Mildenhall and Pocknall 1984, *Tricolpites simatus* Stover and Partridge 1973, and *T. thomasii* Cookson and Pike 1954. Examples of these morphospecies and their time distribution in southeast Australian sedimentary basins are shown in Figure 3 and Table 1, respectively. Additional specimens are illustrated in Stover and Partridge 1973, Martin 1978, Pocknall and Mildenhall 1984, Hill and Macphail 1985, Mildenhall and Pocknall 1989, Macphail et al. 1994 and Macphail 1999. *Cranwellia striata* (Couper) Srivastava 1966 and a related but more coarsely striate morphospecies, *C. costata* Mildenhall 1978 are assumed to be fossil Loranthaceae, e.g. by Askin (1990). The relationship has yet to be confirmed. However, in terms of amb shape and ornamentation, we note that both morphospecies more closely resemble pollen of Krameriaceae, a monogeneric family that is endemic to the southwest United States, Argentina and Chile (see Plate 31: Figure 378 in Heusser 1971).

Table 1. First (FA) and Last (LA) appearance of Loranthaceae-type morphospecies in southeast Australian sedimentary basins (north to south). ¹ Data from Macphail (1999), ² Data from Partridge (1999), ³ Data from Partridge (2002).

Fossil species	Murray ¹		Gippsland ²		Bass ³	
	FA	LA	FA	LA	FA	LA
<i>Tricolpites simatus</i>	middle Eocene	late Miocene	middle Eocene	late Eocene	middle Eocene	late Eocene
<i>Tricolpites thomasii</i>	late Eocene	early Oligocene	late Mid. Eocene	late Eocene	late mid. Eocene	late Eocene
<i>Cranwellia striata</i>	middle Eocene	late Miocene	late Eocene	late Eocene	late Eocene	late Eocene
<i>Gothanipollis bassensis</i>	middle Eocene	late Miocene	late early Eocene	early Miocene	middle Eocene	early Miocene
<i>Gothanipollis</i> cf. <i>gothani</i>	late Eocene	late Miocene	not recorded	not recorded	not recorded	not recorded
<i>Gothanipollis perplexus</i>	late Miocene	early Pliocene	not recorded	not recorded	not recorded	not recorded
' <i>Amylothea</i> ' <i>pliocenica</i>	late Miocene	early Pliocene	late Pliocene	Quaternary?	not recorded	not recorded

Figure 2. Photomicrographs of modern Lorantheaceae pollen. **a.** *Amyema pendula* (Sieb. Ex Spreng.) Tiegh., NSW. **b.** *Amyema congener* (Sieb. Ex Schult. and Schult.f.) Tiegh., Queensland. **c.** *Amyema miquelli* (Lehm. Ex Miq.) Tiegh., NSW. **d.** *Amylotheca dictyophleba* (F. Muell.) Tiegh. Queensland. **e.** *Decaisnina signata* (F. Muell. ex benth.) Tiegh., Western Australia. **f.** *Dactyliophora novae-guineae* (F.M. Bail.) Dans, New Guinea. **g.** *Helixanthera sessiliflora* Danser, Philippines. **h.** *Ileostylus micranthus* (Hook.f.) Tiegh., New Zealand. **i.** *Lysiana* sp. cf. *L. spathula* (Blakey) Barlow, Western Australia. **j.** *Lysiana murrayi* (Tate) Tiegh., Western Australia. **k.** *Muellerina eucalyptoides* (DC) Barlow, NSW. **l.** *Nuytsia floribunda* (Labill.) R.Br., Western Australia. **m.** *Peraxilla colensoi* (Hook.f.) Tiegh., New Zealand. **n.** *Plicosepalus curviflorus* Tiegh., South Africa. **o.** *Tupeia antarctica* (Forst.f) Cham. and Schlecht., New Zealand.

Figure 3. Fossil Loranthaceae pollen (SE Australia). **a.** *Anacolosidites sectus*. Late Eocene, BMR DDH 36-839 121-122 m, Darling Basin. **b.** *Tricolpites simatus*. Oligocene-Early Miocene, Marma-1 268-269 m, Murray Basin. **c.** *Tricolpites simatus*. Late Eocene, Hatfield-1 384 m, Murray Basin. **d.** *Tricolpites thomasi*. Late Eocene, Booligal-1 362-363 m, Murray Basin. **e.** *Gothanipollis bassensis*. Early Oligocene, HEC DDH 5825 131 ft., Tasmania. **f.** *Gothanipollis* cf. *gothani*. Oligocene-Early Miocene, Leaghur-1 177-178 m, Murray Basin. **g.** *Gothanipollis perplexus*. Early to late Miocene, Scotia-1 9.60 m, Murray Basin. **h.** *Gothanipollis* cf. *perplexus*. Early-Late Miocene, Tyntynder West-2 61-64 m, Murray Basin. **i.** *'Amylothea' pliocenica*. Early Pliocene, Cal Lal-1 80-81 m, Murray Basin.

A comparison with pollen produced by extant Loranthaceae genera indicates that *Gothanipollis bassensis* has no close living analogue in Australia due to its very small size (<20 µm) and strongly lobate shape. Nevertheless, this species and its larger relative *Gothanipollis* cf. *gothani* bear a general resemblance to pollen produced by extant species such as *Amyema congener* and *Dactyliophora novae-guineae* (Figures 2b, f): The same qualification applies to *Tricolpites simatus* and *T. thomasi*. Ornamentation on the latter species includes coarse striae bordering the colpi (cf. *Decaisnina signata* and *Peraxilla colensoi*: (Figures 2e, m) but, as far as we are aware, no living Loranthaceae produce pollen with medium to coarse reticulate sculpturing of exine in the mesocolpial regions. The largest morphotypes found in southeast Australia, *'Amylothea' pliocenica* and *Gothanipollis perplexus* closely resemble pollen of *Amylothea*, and *Peraxilla*, respectively (cf. Martin, 1978; Pocknall & Mildenhall, 1984). The latter genus is endemic to New Zealand.

Chronostratigraphic distribution of fossil Loranthaceae pollen in Tasmania

At present, there are no records of Loranthaceae at Tertiary or Quaternary sites in southeast Tasmania, and the selection of fossil Loranthaceae pollen types illustrated in Figures 4a-o comes from sites in the north and west of the state: The stratigraphic distribution of these species in

Figure 4. Fossil Loranthaceae pollen (Tasmania). **a.** *Gothanipollis bassensis*. Early Oligocene, Lemonthyme Creek DDH5825 131 ft. **b.** *Gothanipollis* cf. *bassensis*. Early Oligocene, Lemonthyme Creek DDH5825 131 ft. **c.** *Gothanipollis bassensis*. Early Eocene, outcrop Macquarie Harbour Beds, Strahan. **d.** *Gothanipollis* cf. *gothani*. Middle Pleistocene, Darwin Crater core 61.5 m. **e.** *Gothanipollis* cf. *gothani*. Early-Middle Pleistocene, outcrop Regatta Point, Strahan. **f.** *Gothanipollis* cf. *gothani*. Middle Pleistocene, Darwin Crater 61.5 m. **g.** *Gothanipollis* cf. *gothani*. Middle Pleistocene, Darwin Crater core 61.0 m. **h.** *Gothanipollis* cf. *gothani*. Early Oligocene, outcrop, Lea River. **i.** *Gothanipollis* cf. *gothani*. Early Eocene, outcrop Macquarie Harbour Beds, Strahan. **j.** *Gothanipollis* cf. *gothani*. Early Oligocene, Wilmot Dam DDH 4558 77.5 ft. **k.** *Gothanipollis* cf. *perplexus*. Early Oligocene, Lemonthyme Creek DDH5825 97 ft. **l.** *Gothanipollis* cf. *perplexus*. Early Oligocene, Lemonthyme Creek DDH5825 131 ft. **m.** *Gothanipollis* cf. *T. thomasi*. Early-Middle Pleistocene alluvium Regatta Point. **n.** *Gothanipollis* aff. '*A.*' *pliocenica*. Early-Middle Pleistocene alluvium, Regatta Point. **o.** Loranthaceae. Last Glacial, Core GC 320 cm, Lake St. Clair.

Table 2. Chronostratigraphic distribution of Loranthaceae pollen in the Bass and Sorell Basins and onshore sites in Tasmania.

Basin/Area	Well/locality	Age	Zone	Morphospecies	Reference	Comment
offshore Bass	Chat-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Gothanipollis bassensis</i>	Partridge et al. 2002	data from Morgan 1986
	Cormorant-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites simatus</i> , <i>T. thomasii</i>	M.K. Macphail, unpubl.	see Partridge et al. 2002
	Dondu-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Gothanipollis bassensis</i> , <i>Tricolpites simatus</i>	Partridge et al. 2002	data from Stover 1973
	Kon Kon-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites simatus</i> , <i>T. thomasii</i>	Partridge et al. 2002	data from Stover 1973
		middle Eocene	lower <i>Nothofagidites asperus</i>	<i>Gothanipollis bassensis</i>	Partridge et al. 2002	unconfirmed record
	Narimba-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites thomasii</i>	Partridge et al. 2002	data from Morgan 1986
		middle Eocene	lower <i>Nothofagidites asperus</i>	<i>Tricolpites simatus</i>	Partridge et al. 2002	
	Pelican-2	early Eocene?	<i>Proteacidites asperopolus?</i>	<i>Tricolpites thomasii</i>	Partridge et al. 2002	middle Eocene?
	Pelican-5	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites simatus</i>	Partridge et al. 2002	data from Morgan 1986
	Toolka-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites simatus</i>	Partridge et al. 2002	data from Stover 1974
	Yolla-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites thomasii</i>	Partridge et al. 2002	see Partridge et al. 2002
		early Oligocene	upper <i>Nothofagidites asperus</i>	<i>Gothanipollis bassensis</i>	Partridge et al. 2002	
	Yurongi-1	late Eocene	middle <i>Nothofagidites asperus</i>	<i>Tricolpites thomasii</i>	Partridge et al. 2002	data from Stover 1973
offshore Sorell		middle Eocene	lower <i>Nothofagidites asperus</i>	<i>Gothanipollis bassensis</i> , <i>Tricolpites thomasii</i>	Partridge et al. 2002	
	Cape Sorell-1	early Eocene?	middle <i>Malvacipollis diversus</i>	<i>Tricolpites simatus</i>	M.K. Macphail, unpubl.	caved specimen
West Coast	Coal Head	late Quaternary	-	<i>Gothanipollis</i> cf. <i>gothani</i>	M.K. Macphail, unpubl.	reworked specimen
	Darwin Crater	middle Pleistocene	core samples at 22.0-44.7 m, 61.0-61.5 m. Absent above 22 m.	<i>Gothanipollis</i> cf. <i>bassensis</i> , <i>G. cf. gothani</i> and <i>perplexus</i>	M.K. Macphail, unpubl. E.A. Colhoun, unpubl.	interval between 44.7 and 61.0 m not yet analysed
	King River	middle Pleistocene	Regency site at 0, 15, 40, 60 cm	<i>Gothanipollis perplexus</i>	E.A. Colhoun, unpubl.	Fitzsimmons et al. 1990
	Lowana Road	late Early Eocene	<i>Proteacidites asperopolus</i>	<i>Gothanipollis</i> cf. <i>bassensis</i>	M.K. Macphail, unpubl.	collected by G. Jordan
	Regatta Pt.,	early? Quaternary	<i>Tubulifloridites pleistocenicus?</i>	<i>Gothanipollis bassensis</i> , <i>Tricolpites simatus</i>	Hill and Macphail 1985	reworked specimen
	Strahan	late early Eocene	<i>Proteacidites asperopolus</i>	<i>Gothanipollis bassensis</i> , <i>G. cf. gothani</i>	Macphail et al. 1993a	Macquarie Harbour Beds
	Zeehan	Oligo-Miocene	<i>Proteacidites tuberculatus</i>	<i>Gothanipollis</i> cf. <i>gothani</i>	M.K. Macphail, unpubl.	collected by M. Pole

Table 2. *Continued*

Basin/Area	Well/locality	Age	Zone	Morphospecies	Reference	Comment
Northeast	Loch Aber	mid late Eocene	<i>Nothofagidites asperus</i>	<i>Gothanipollis</i> cf. <i>bassensis</i>	M.K. Macphail, unpubl.	
northwest Central Plateau	Cradle Mt.	recent	core LDGS at 7, 33, 38 cm	<i>Loranthaceae</i>	Dyson 1995	Dove Lake
	Lake St. Clair	late Pleistocene	core CG at 320 cm	<i>Loranthaceae</i> cf. <i>Amyema</i>	F. Hopf, unpubl.	Narcissus Bay
	Lemonthyme Creek	early Oligocene	<i>Proteacidites tuberculatus</i>	<i>Gothanipollis bassensis</i> , <i>G.</i> cf. <i>gothani</i> , <i>G. perplexus</i> , <i>G.</i> cf. <i>perplexus</i> .	Macphail et al. 1993b M.K. Macphail, unpubl.	HEC DDH 5825
	Lea River	Oligo-Miocene	<i>Proteacidites tuberculatus</i>	<i>Gothanipollis</i> cf. <i>gothani</i>	M.K. Macphail, unpubl.	collected by R. Hill
	Tyndall Ranges	Holocene	-	<i>Gothanipollis</i> cf. <i>gothani</i>	Macphail and Colhoun 1982	peat in summit tarn
	Wilmot Dam	early Oligocene	<i>Proteacidites tuberculatus</i>	<i>Gothanipollis bassensis</i> , <i>G.</i> cf. <i>gothani</i>	Macphail and Hill 1994	HEC DDH 4558

the Bass Basin and onshore sites in Tasmania is given in Table 2. We emphasise that absence of evidence is not necessarily evidence of absence. Reasons are small morphospecies such as *Gothanipollis bassensis* are easily overlooked, especially if partly obscured by plant detritus, and also can be lost during processing if the organic extracts are filtered through 10 to 20 µm sieve cloth. Nevertheless, the records are adequate to confirm (numerical ages after Ogg et al. 2008):

1. The oldest reliable records of Loranthaceae species in Tasmania (and probably Australia as a whole) are specimens of *Gothanipollis bassensis* and *Tricolpites simatus* preserved in the late early Eocene (ca. 50.5–51.5 million years ago) Macquarie Harbour Formation at Regatta Point and Lowana Road near Strahan, western Tasmania. Specimens of *Tricolpites simatus* in the same sections appear to pre-date the first appearance of the species in the offshore Bass and Gippsland Basins in Bass Strait, although the converse applies to *Gothanipollis bassensis*. Both species grew in complex evergreen mesotherm to megatherm (subtropical–tropical) rainforest communities (Macphail 2007) that began developing at relatively high (60–65°S) palaeolatitudes in southern Australia following rapid greenhouse warming of the planet by 5°C to 10°C at the Paleocene/Eocene boundary ca. 55.8 million years ago (Paleocene–Eocene Thermal Maximum) and subsequent hyperthermal events that characterised the Early Eocene (see Dickens 2009). Presumed reworked specimens occur in Quaternary deposits at Coal Head in Macquarie Harbour and in cuttings along the road between Strahan and Lowana Road, e.g. behind the Cool Store at Regatta Point (Macphail et al., 1993a)
2. Except in the offshore Bass Basin and onshore extensions in northern Tasmania, middle to late Eocene deposits are rare (see Macphail 2007) and there is insufficient evidence to determine whether Loranthaceae species such as *Tricolpites thomasi* ever extended southwards into the mountainous interior or along the west or east coasts. Stratigraphic evidence from the Bass Basin indicates *Tricolpites thomasi* became extinct at about the major cooling event that marks the Eocene/Oligocene boundary at 33.9 million years ago (references in Wei 1991; Exon et al. 2004). *Tricolpites simatus* is recorded in early Oligocene sediments at Lemonthyme Creek (see Plate 5, Figure D in Macphail and Hill 1994): *Gothanipollis bassensis* survived into Oligo-Miocene time in western Tasmania and also in the Bass, Gippsland and Murray Basins in mainland southeast Australia.

3. *Gothanipollis perplexus* and a complex of morphotypes centred on this species and *G. gothani* first appear in the early Oligocene in Tasmania, with the majority of records coming from the disputed glacial sequences at Lemonthyme Creek and Wilmot Dam in the Mersey-Forth Valleys (cf. Paterson 1965; Paterson et al. 1967; Fitzsimons et al. 1993; Macphail et al. 1993b; Macphail and Hill 1994). These and other records from correlative sediments from the Lea River and near Zeehan provide compelling evidence that at least three species of Loranthaceae were growing in *Nothofagus* warm temperate rainforest in western Tasmania during the late Paleogene: It is possible that the host trees included *Nothofagus* spp. (cf. Vidal-Russell and Nickrent 2008b).
4. *Gothanipollis perplexus* may have reached Tasmania by trans-oceanic dispersal, since the morphospecies first occurs in late Eocene deposits in New Zealand (Pocknall and Mildenhall 1984) but is absent in late Eocene deposits at Prydz Bay, East Antarctica (see Macphail and Truswell, 2004; Truswell and Macphail 2008). The Lemonthyme Creek records of *Gothanipollis perplexus* and *G. cf. perplexus* are significantly older than the earliest records of *Gothanipollis perplexus* in the epicontinental Murray Basin in southeast Australia (Table 2). It is unlikely any of the currently known *Gothanipollis* species evolved in Tasmania, although the migration route(s) are unknown.
5. Fossil Loranthaceae pollen have not been recorded in the late Oligocene-early Miocene cool-climate flora at Monpeelyata (920 m elevation) on the eastern Central Plateau (Macphail et al. 1991), nor at the one known late Pliocene site in western Tasmania, the Linda Valley palaeosol (Macphail et al. 1995).
6. At least one fossil species, '*Amylothea* *pliocenica*', which first appears in the late Pliocene in eastern Australia and New Guinea, did not extend as far south as Tasmania or the Bass and Gippsland Basins (Macphail 1997, 2007). The reason for this may be cool to cold climates, since *Amylothea* is restricted to coastal rainforest from central NSW northwards into southern New Guinea (Barlow 1966; Henty 1995). Fossil specimens are found in late Pliocene assemblages from the northwest Murray Basin (Scotia Province) to the Atherton Tableland in northeast Queensland Australia (Kershaw and Sluiter 1982; Macphail 1999).
7. Specimens belonging to the complex of morphotypes centred on *Gothanipollis bassensis*, *G. gothanii* and *G. perplexus* are rare but ubiquitous in (1) the middle Pleistocene Regency interglacial sequence in the King River Valley near Queenstown (Fitzsimons et al. 1990), and (2) in the lower ca. 40 m of a 62 m thick sequence of lacustrine clays at Darwin Crater in the Andrew River Valley ca. 20 km east of Macquarie Harbour (Howard and Haines, 2007). The lake sediments show normal magnetic polarity, the Brunhes-Matuyama Boundary is not recorded (Barton 1987) and, based on K/Ar fission-track dates of 0.82 million years ago on a siliceous impact glass (Darwin Glass) associated with the crater, are middle to late Pleistocene (Lo et al. 2002): The section has yet to be fully pollen-analysed, but Loranthaceae pollen commence at 22.0 m and are consistently present down to 44.7 m, and occur between 61.0 m and 61.5 m, immediately above the contact with poorly sorted, coarser crater fill deposits (Colhoun 1988; Colhoun and Van der Geer 1998; E.A. Colhoun and M.K. Macphail, unpubl. data). The section between 44.7 m and 61 m has not been analysed but we anticipate Loranthaceae pollen will be present.
8. The Regency sequence represents the replacement of montane scrub rainforest by *Nothofagus cunninghamii*-Podocarpaceae cool temperate rainforest. Specimens of *Gothanipollis perplexus*

and *G. cf. perplexus* occurring between c. 22 m and 45 m in Darwin Crater mostly occur in cool temperate rainforest pollen assemblages dominated by Huon Pine *Lagarostrobos franklinii*, associated with lesser amounts of Subantarctic Beech (*Nothofagus cunninghamii*) and Celery-top Pine (*Phyllocladus aspleniifolius*) and occasional tree-fern (*Cyathea* spp.) spores, but are absent in assemblages representing lower, more open vegetation types such as wet scrub/heath and herbfield (E.A. Colhoun, unpubl. data). A not unreasonable interpretation is that mistletoes were growing on trees at the margins of temperate rainforest during the middle Pleistocene and the host species may have included *Lagarostrobos* and *Nothofagus*.

9. The top 20 m of sediment in Darwin Crater is believed to have accumulated between Oxygen Isotope Stages (OIS) 1 to OIS 7, indicating that Loranthaceae became locally? extinct in the Andrew River Valley sometime before the OIS 7 Interglacial, i.e. before 0.24–0.25 million years ago.
10. Four specimens of Loranthaceae pollen have been found in last glacial and postglacial sediments in western Tasmania – at Lake St. Clair on the Central Plateau (F. Hopf, unpubl. data), at Dove Lake, Cradle Mountain (Dyson 1995), and at an unnamed tarn on the summit of the Tyndall Ranges (Macphail and Colhoun 1982). Since the two Dove Lake specimens occur in near surface muds, it is equally likely that the Lake St. Clair and Tyndall Ranges specimens have been long-distance transported, e.g. by migrating birds.

Discussion

All mistletoe lineages within the Santalales appear to have evolved from root parasite ancestors (Vidal-Russell and Nickrent, 2008a, b). Molecular dating of genera divergence times indicates that the ‘aerial’ parasitic habit evolved in the Misodendraceae sometime between ca. 80 and 25 million years ago (early Campanian to late Oligocene), in the Viscaceae between ca. 72 and 43 million years ago (late Campanian to middle Eocene), in the Santaleae between ca. 46 and 53 million years ago (middle to early Eocene), in Amphorogyneae between ca. 53 and 22 million years ago (early Eocene to early Miocene), and the Loranthaceae at ca. 27 to 28 million years ago (mid Oligocene). On this model, ‘*Amylotheca*’ *pliocenic*a and? *Gothanipollis perplexus* are likely to represent hemi-parasitic shrublets growing on and within the branches of trees and shrubs: Whether the Eocene parent plants of *Gothanipollis bassensis*, *G. cf. gothani*, *Tricopites simatus*, *T. thomasi* and early Oligocene parent plant(s) of *G. cf. perplexus* were root parasites or represent wholly extinct clades of aerial parasites is unknown, and likely to remain so without macrofossil evidence.

Pollen evidence for the origins of the Loranthaceae per se is complicated by the uncertain evolutionary relationship of the family to late Cretaceous taxa, in particular *Cranwellia*, a morphogenus that first occurs in the Campanian in Antarctica (Askin 1990), and *Aquilapollenites*, one of many extinct angiosperm genera within the *Triprojectacites* group that dominated Northern Hemisphere Maastrichtian palynofloras (see Farabee 1993). However, there is compelling pollen evidence in the form of an extinct morphospecies of *Anacolosa* (*Anacolosidites acutullus* Cookson and Pike 1954) that one clade within the Santalales was present in northwest Australia during the late Cretaceous (see Macphail 2007). The *Anacolosidites* species that most closely resembles modern Loranthaceae pollen (*A. sectus* Stover and Partridge 1973: Figure 3a) does not appear before the middle Eocene in southeast Australia. Whether late Cretaceous morphotypes assigned to *Cranwellia* and *G. gothani* ssp. *plicus* in China (see Plate 150: Figures 1–3 in Song et al. 2004) are in fact fossil members of the Loranthaceae has yet to be confirmed.

Phylogenetic and fossil evidence (Vidal-Russell and Nickrent 2008a, b) suggests that the family evolved in East Gondwana (Australia-New Guinea, New Zealand, South America) during the late Cretaceous, with relatively late dispersals into Africa, India, Asia and Europe. For example, the genus *Loranthus* occurs in Europe and Asia, but the split between it and *Cecarria* (a monotypic genus spanning Australia to the Philippines) has been estimated at less than 30 million years ago. Several other clades of similar or younger age have members in both Australasia and Asia (Vidal-Russell and Nickrent 2008a, b). Nevertheless, morphospecies resembling modern Loranthaceae pollen have been recorded from early to late Eocene deposits in northern and central Europe, the United States and China (references in Muller 1981; Song et al. 2004) and it is possible that the family first appeared in both hemispheres about the same time but the ancient Northern Hemisphere lineages subsequently became extinct. Whether such speculations are an artefact of inadequate fossil data is unknown. However, it is tempting to hypothesise that the migration of birds and possibly bats (see Archer et al. 1991:137, 230) across the equator is a plausible reason for the near-contemporaneous first appearance of Loranthaceae in both hemispheres. This conjecture is reinforced by records of Loranthaceae pollen at sites where alternative modes of transport are improbable. Examples are the now-submerged Ninetyeast Ridge in the remote Indian Ocean where *Gothanipollis* cf. *gothani* occurs in Oligocene sediments (see Kemp and Harris 1975), and the summits of mountains in tropical South America, where Loranthaceae pollen has been recovered from modern snow samples (see Reese et al. 2003).

The data demonstrate that fossil species of Loranthaceae in Tasmania were tolerant of megatherm and then mesotherm climates during the Paleogene. For example, macro- and microfossils from late-early Eocene deposits at Regatta Point and Lowana Road confirm that the tropical mangrove palm *Nypa* lined tidal channels within Macquarie Harbour (Partridge 1976; Pole and Macphail 1997). Other mesotherm-megatherm rainforest taxa associated with *Tricolpites simatus* and *Gothanipollis bassensis* include *Anacolosia*, Arecaceae (*Arecipites*, *Dicolpopollis*), *Ascarina*, Cunoniaceae, *Dysoxylum*, *Freycinetia*, *Ilex*, Meliaceae and Strasburgeriaceae (*Bluffopollis scabratus*). In contrast, Loranthaceae pollen (*Gothanipollis bassensis*) found at the middle-late Eocene Loch Aber site in northeast Tasmania (M.K. Macphail, unpubl. data) grew in floristically diverse, warm temperate rainforest dominated by *Nothofagus* and gymnosperms that are now extinct in Tasmania. For example, trees included a species similar to *Nothofagus moorei*, now endemic to NSW, Podocarpaceae, including *Acmophyle*, now endemic to New Caledonia and Fiji, and an extinct *Araucaria* belonging to the South American section *Columba*. Average leaf lengths in the Loch Aber fossil flora are smaller than in early Eocene floras, consistent with a general decrease in mean air temperatures from the early to middle Eocene (Hill and Carpenter 1991; Carpenter et al. 1994).

Major global cooling that followed subsidence of the South Tasman Rise and Drake Passage to abyssal depths and formation of the Circumantarctic Current during the Eocene-Oligocene transition meant Loranthaceae species growing in cool temperate rainforest in the Mersey-Forth River Valleys had become resilient to even cooler (microtherm) conditions by about 33 million years ago (see Macphail et al. 1993b; Exon et al. 2004). Whether Loranthaceae were continuously present in Tasmania from the early Oligocene to Early Miocene and Quaternary is unclear due to lack of tightly dated palynosequences south of the offshore Bass Basin. Clusters of *Gothanipollis* spp. found in the basal 40 m of lake sediments in Darwin Crater and in the Regency Interglacial deposit indicate that Loranthaceae were growing in cool temperate rainforest in western Tasmania during the middle Pleistocene. We note that these rainforest communities differed from modern *Nothofagus cunninghamii*-Podocarpaceae closed forest in Tasmania in two minor aspects only – the tree-fern stratum was dominated by *Cyathea* spp., not *Dicksonia antarctica*, and in some areas the subcanopy stratum included several small tree

and shrub genera that are now restricted to mainland Australia (*Haloragodendron*, *Quintinia*, *Symplocos*).

A number of taxa now endemic to South America became established in Tasmania during the Paleogene. Examples (fossil species in parentheses) are: *Nothofagus* subgenus *Nothofagus* (*Nothofagidites flemingii*) in the earliest Paleocene, *Embothrium* (*Granodiporites nebulosus* Stover and Partridge 1973) in the earliest Oligocene, and the tribe Mutisieae of the Asteraceae (*Mutisiapollis patersonii* Macphail and Hill 1994) and the ground fern *Lophosoria quadrapinnata* (*Cyatheacidites annulatus* Cookson 1947) by the early Oligocene. Given the observed close relationship of *Misodendron* with *Nothofagus* in southern South America, it seems reasonable to speculate that this mistletoe family also could have been present in Tasmania in the past.

Misodendron pollen are distinctive due to their sphaeroidal shape and apiculate sculpture. However, confirming the presence of this genus in Tasmania will be difficult since the small size (19–22 µm) of its pollen grains means specimens can be easily lost during processing, or overlooked, or the pollen type may have evolved after the split between *Misodendron* and other Santalaceae. Fossil specimens are likely to be assigned to the morphogenus *Compositoipollenites* Potonié ex Potonié 1960 (see Macphail and Cantrill 2006). At present, the only species of *Compositoipollenites* that has been formally described in Australia is *C. tarrogoensis* Truswell and Owen 1988 from a middle Eocene palynosequence at Bungonia on the Southern Tablelands of NSW (cf. Plate 38, Figure 462 in Heusser 1971, Figure 8 H–U in Truswell and Owen 1988). Similar morphotypes occur in late Maastrichtian sediments in the Bonaparte Basin in northern Australia, an early Eocene sample from the Cape Sorell-1 petroleum exploration well in the offshore Sorell Basin (Figure 1), and a probable early Eocene deposit in the Styx River Valley in southeast Tasmania (Macphail 2007). *Viscum* pollen are easily recognised by the presence of stout spines (see Tafel 35: 1–4 in Beug 2004), but, as yet, no fossil specimens have been recorded in Australia (G.S. Hope pers. comm.).

Reconstructing and interpreting the history of mistletoes in Tasmania will continue to depend on the slow accumulation of microfossil evidence, often from sites that have been uncovered by chance events (see Hill 1987). We consider it unlikely that palynologists working on Tertiary to late Quaternary deposits will have mis-identified or overlooked larger morphospecies such as *Gothanipollis perplexus* or ‘*Amylotheca*’ *pliocenica*, and therefore conclude that, even when establishment was successful, Loranaceae always were rare elements in the Tasmanian flora. Why this should be so is more likely to be a consequence of cool/wet climates than a lack of suitable host species. If correct, then any climatic barriers that have prevented the establishment of mistletoes during the Holocene may well be breached through warming/drying of Tasmania in the near future.

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