Plant macrofossils associated with the Riversleigh macrofauna

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Abstract
Fossil plant organs from the Oligocene aged Dunsinane Site of Riversleigh, Queensland, were studied. Several fossils provide evidence for climate. A leaf species was identified as Alectryon Gaertn., on the basis of the anatomy of abaxial cuticular features. Thorns, leaves and a fruit with affinities to Rubus L. and Capparis L. were also present. A species of Casuarinaceae common in the deposit has affinities with Casuarina L. and Allocasuarina L.A.S. Johnson in having greater than four teeth per whorl on the photosynthetic branchlets and stomata hidden in deep furrows filled with trichomes and as such represents the earliest known record of the sub-family Cryptostomae. The assemblage was interpreted as a low diversity open vegetation type with moisture limitation. No evidence for the presence of rainforest was found.

Introduction
The Riversleigh fossil site, located north of Mount Isa, Queensland, is well known for its vertebrate fossil record which provides an almost continuous record over the last 25 million years. The Tertiary records are deposited in extensive limestone formations and cave deposits.

Evidence on the nature of the vegetation and environment associated with these fossils is contradictory. The dominant view has been that the area was covered with a species-rich lowland tropical rainforest until these forests were forced into decline very late in the Tertiary (Archer et al. 1994). The evidence for this conclusion comes solely from the diversity and phylogenetic relationships of the fossil mammal species. In particular, the high species diversity, presence of feeding guilds of similar species, high number of sympatric obligate leaf eaters, presence of taxa known only from rainforests and the presence of browsers rather than grazers are cited as evidence (Archer et al. 1989).

Evidence of a similar nature from fossil turtles and birds present in the Riversleigh deposits seems to indicate that both open and closed vegetation types may have been present, based on comparisons of the physiology and functional anatomy of the fossils with modern taxa (Boles 1997; White 1997). But again, there are various exceptions and a number of fossil taxa are unidentified or unrelated to living taxa.

Reports on the geology and sedimentology of Riversleigh have also been collectively inconclusive. Megirian (1992) interpreted the D Site plateau at Riversleigh as being a semi-arid alluvial fan, formed in an environment where any rainforest must have been limited in extent. But in contradiction to this interpretation, Creaser (1997) argued that similar sediments are today being deposited in the Huon Terraces of New Guinea due to the local topographic conditions, despite rainfall in excess of 2000 mm per year.

In terms of evidence on a continent-wide scale, plant fossil records from central Australia are sparse whilst some areas of the continent have almost no known fossil record (Truswell 1993; Greenwood 1994). The more abundant record of southern Australia does not necessarily represent what was happening across the entire landmass. Eocene plant macrofossil
deposits near Lake Eyre South in South Australia show a different scenario to that depicted by more southerly deposits of similar age (Greenwood 1996). These deposits seem to represent a mosaic community in which gallery rainforest occurred in riparian areas with adjacent tropical/monsoonal type communities or sclerophyllous communities. These deposits indicate that rainfall was seasonal, even at this early time.

The discovery of plant remains at the Dunsinane site, located on the Gag Plateau, provides a unique opportunity to compare possibly contemporaneous fossil animal and plant assemblages at Riversleigh. The site has been dated at approximately 25 million years old via correlation of vertebrate material with the System A faunas of Riversleigh (Arena 1997) and the fossiliferous nodules themselves may be of that age or derived from an older Tertiary source (Rick Arena pers. comm.). Only those fossils that provide evidence for environmental conditions are considered here. A full account of the fossil flora will be given elsewhere.

Methods
The mineralised fossil material from Riversleigh is contained within rounded nodules of fluorapatite up to approximately 10 cm long (Fig. 1). These were originally embedded within a limestone matrix containing poorly preserved vertebrate bone material (Arena 1997). The material examined consisted of nodules or nodule fragments removed from this matrix and specimens removed from the loose weathered surface debris.

Initially, all available nodules were broken up and examined under a dissecting microscope and any samples with visible fossils were retained. Acid treatment was then applied to break them down. Nodules were soaked in a 10 percent aqueous solution of hydrochloric acid overnight to dissolve them. The dissolved nodules were transferred to a fine grade sieve and washed to remove the finer silt. The remaining material was then washed into a petri dish and examined under a dissecting microscope. Any fossils preserved well enough to be useful were removed and stored separately in ethanol.

Specimens were mounted on stubs with pipettes or brushes using double-sided adhesive tape. Once dried, the stubs were coated with carbon and gold and viewed with a Phillips XL20 scanning electron microscope (SEM) operated at 10kV.

In total, 240 nodule fragments were dissolved.

Results
Casuarinaceae fossil
The most common fossil in the deposit is known from fragmented vegetative branchlets (articles) (Figs 2, 3). It is clearly aligned with the Casuarinaceae family as the branchlets consist of articulated segments with leaves reduced to whorls of teeth at nodes and the stomata are found in grooves distributed radially around the stem in equal numbers to the teeth. In total, 36 specimens of this species were examined in detail.

The species consistently has five teeth. The furrows contain two bands of stomata, each with a single row of closely spaced stomata. The stomatal complexes have pronounced external florin rings.

The above characters demonstrate the clear affinities of this species with the subfamily Cryptostomae which comprises the living genera Ceuthostoma L.A.S. Johnson, Allocasuarina L.A.S. Johnson, and Casuarina L. The defining feature of this group is the deep, narrow furrows on photosynthetic branchlets containing the stomata which separates them from Gymnostoma which has shallow, open furrows with the stomata exposed (Johnson and Wilson 1989). Within the Cryptostomae, Ceuthostoma always has four teeth per whorl on the deciduous branchlets and can be removed from consideration. Features that the other two genera share with the fossil include greater than four teeth per whorl, stomata hidden in deep furrows with trichomes between bands, epidermal cell shape ranging from
circular to rectangular on the phyllchnia (photosynthetic branchlets) and concave between stomata within a row, similar article and tooth dimensions and presence of florin rings on the external cuticles of stomatal complexes (R.S. Hill, K. Wilson and D. Steane, unpublished data; Dilcher et al. 1990).

Under the current taxonomy, the genera Casuarina and Allocasuarina are separated mainly on fruiting characters (Torrey and Berg 1988) and there are no obvious vegetative morphological traits that can separate them. For this reason, although the fossil appears to be closely related to these genera, it cannot be placed within either at this stage.

Reconstruction of a fruit
In an oblique section of a fruit an apocarpous gynoecium consisting of four visible superior free carpels arranged spirally on the receptacle is preserved (Fig. 4). The fruit is derived from a single flower and is therefore an aggregate fruit (composed of many free carpels from a single flower). It is difficult to determine the original nature of the tissue in the fruit but the walls appear relatively robust. A visible sessile seed shows that the fruits were all single seeded with an erect ovule attached presumably basally but possibly apically. The gynoecium had a minimum of four carpels, but given the spiral arrangement there may have been a higher number.

Affinities of the fruit
In Ranunculaceae, when the superior gynoecium is apocarpous, the carpels are arranged spirally on the receptacle and in one genus, Ranunculus L., there is a single basally-attached ovule per carpel (Aston 1973; Bhattacharyya and Johri 1998). The general shape and size of the carpels in Ranunculus matches that of the carpels in the fossil. The fruit of Ranunculus is an achene, a single-seeded, dry, indehiscent fruit in which the seed is either fused to some extent with the carpel wall or closely fitted within it (Engler and Prantl 1995; Judd et al. 1999). This type of fruit could well match the Riversleigh fossil. The achenes, borne in a cluster, are sometimes adorned with various architectural features such as wrinkles and projections (pers. obs.; Engler and Prantl 1995) but since the fossil is embedded in rock it is impossible to check for the presence or absence of such features.

Gynoecia in Rosaceae may be superior, apocarpous with spirally-arranged carpels and single, pendulous seeds (Bhattacharyya and Johri 1998). A genus that matches the floral structure of the fossil closely is Rubus L., which has many free, spirally-arranged carpels, initially with two ovules but with only one maturing and persisting in the mature fruit (Kalkman 1993). The aggregate fruits are fleshy but in many species only moderately so (Kalkman 1993). The fossil seems to match the generic description quite well and may be either from a species with rather dry, woody fruits or have been preserved in an immature state, before the carpel walls became swollen and fleshy.

Based on comparisons to extant taxa, Ranunculaceae and Rosaceae seem to be the best candidates for this fossil and in particular the genera Ranunculus and Rubus. There is not enough information to take the identification any further. However, see later discussion on possible links between fruits, leaves and thorns.

Leaves
A leaf with distinct venation
A fossil leaf species known only from surface fossils on the nodules has craspedodromous venation featuring a prominent mid-rib with loosely paired secondary veins leading off from it at the same acute angle. Finer venation leaves these vascular bundles more or less perpendicularly. One specimen has a dentate margin preserved on one side. These features are common in many known taxa, but the various specimens are similar enough to be treated here as the same
species. However, there is not enough information obtainable from this species to place it with any certainty. But again, see later discussion on links between fossil organs.

A pubescent leaf

A second leaf species is defined by the abaxial features. The primary vascular bundles are extremely prominent with large hair bases which are also scattered less densely across the entire leaf surface (Fig. 5). The trichomes that left these conspicuous bases are not preserved but the size of the bases implies they supported relatively robust trichomes. On a smaller scale, the abaxial leaf surface is densely covered with papillate/glandular trichomes with striated cuticular markings.
These trichomes are sparser and apparently less developed on minor vascular tissue and are entirely absent from prominent vascular tissue.

**Affinities of the pubescent leaf**

In order to identify this species, cuticles from extant families were compared to the fossil. The fossil species has close affinities with the genus *Alectryon* Gaertn. (Sapindaceae) and in particular the species *A. affinis* Radlk.

Derived features shared between the fossil and the genus *Alectryon* (synapomorphs) include the presence of large, elongated trichomes with large, robust bases and minute striated glandular trichomes. The autapomorphs (unique derived features) unique to the fossil and *A. affinis* are the combination of prominent primary venation with slightly acute branching of secondary veins, moderate pubescence (more densely hairy over major vascular tissue), and a dense covering of the micro-trichomes between vascular bundles (less prominent on minor vascular tissue and entirely absent from major vascular tissue), only occasionally revealing the stomata. This combination of key features is shared with none of the other 17 species of *Alectryon* examined.

**Fossil thorns**

A number of thorns were removed from the nodules (Fig. 6). The thorns are small, 1-2 mm long, curved and ending in a pungent tip, with a broad base and relatively clean abscission zone. This type of thorn is characteristic of the family Rosaceae, particularly the general shape and presence of a clean abscission zone. Such thorns in similar dimensions are often present on the stems and/or leaves of *Rubus* species. Similarly, the genus *Capparis* L. (Capparaceae) has thorns almost indistinguishable from both *Rubus* and the fossil.

There is a possible link between unattached organs found in the deposit. In particular, the leaf with craspedodromous venation, the apocarpous fruit and the deciduous thorns may all belong to the genus *Rubus* and represent the same parent species. However, this possibility will remain as speculation as all three organs have affinities with other known taxa and cannot be shown to have been organically attached.

**Discussion**

The fossil species of Casuarinaceae is clearly adapted for xeric conditions with its stomata hidden in deep furrows with trichomes between the bands which are considered barriers against excessive water loss (Hill 1994). *Casuarina* and *Allocasuarina* today occur in open habitats that may be arid, saline or coastal, although some tree species occur commonly where water tables are high, such as along stream banks (Barlow 1983; Johnson and Wilson 1989). Neither genus is found in closed rainforests. The conclusion that must be drawn is that the species grew in a habitat at Riversleigh that was at least seasonally moisture-limited and a vegetation type that was open-canopied.

The *Alectryon* leaf fragments in the Dunsinane limestone represents the first fossil record of the genus. The habitat of the genus in general is largely areas receiving seasonal rainfall and includes monsoon forest, forest edges and river banks (Adema et al. 1994). Representatives of the genus in Australia occur from arid areas of the interior to rainforest (one species), but most commonly in habitat types intermediate between these extremes (Reynolds 1985; Dunlop and Bowman 1986; Barry 2000). Narrowing down the possible affinities of other fossils allows us to speculate on the nature of the plants and their environment. If fruits, leaves or thorns can be attributed to *Rubus* then conditions of strong sunlight reaching ground level would have been present as could be the case for disturbed areas, forest edges and open-canopied vegetation (Kalkman 1993). It is also possible that light entering the vegetation through the break created by the water body allowed such light-loving species to exist around its edge. The genus does have
a Quaternary fossil record in Australia, including leaves with thorns attached and is known from the Oligocene/Miocene of Antarctica (Jordan 1992), hence its presence at Riversleigh in the Oligocene is plausible in biogeographical terms.

As stated earlier, the fossil thorns in the deposit are also indistinguishable from the thorns found on the juvenile branches of the cosmopolitan genus *Capparis*. This genus occurs generally in lowlands and most species prefer conditions of seasonal drought (Jacobs 1964). Of those species that have different tolerances, some occur in wet forest whilst others occur in arid climates. Most likely, the confirmed presence of *Capparis* at Riversleigh would provide evidence against a tropical rainforest scenario.

The fossils from the Dunsinane deposit of Riversleigh are consistent with a seasonally dry vegetation type, such as monsoonal forest. The affinities of the species assigned to *Cryptostomae* (Casuarinaceae) and *Alectryon* (Sapindaceae) are clear and both are similar to modern taxa that occur in relatively dry, seasonal habitats. The strong possibility that either *Rubus* or *Capparis* was also present only reinforces the notion that the parent vegetation was open-canopied and not consistent with rainforest.

This recorded vegetation does not support the argument raised by Archer *et al.* (1989) that the high species diversity of mammals was due to a high species diversity of plants for this point in time. This must now be explained either in terms of the effects of habitat diversity (if there was any) or by other means.

The interpretation of Riversleigh's environment at this time as seasonally dry seems to be supported by the taphonomy of the Dunsinane nodules themselves. Arena (1997) described the likely scenario of their formation as a stagnant water body, rich in nutrients, becoming anoxic due to algal blooms. The subsequent anoxia and presence of concentrated phosphorous from decomposing algae created the conditions necessary for the microbially-induced precipitation of the fluorapatite which formed the nodules (Lucas and Prévôt 1991). This type of event is consistent with a marked dry season in which water bodies dry out and algae bloom.

If this was the case, any patches of rainforest present must have been limited in area and confined to permanent springs along the margins of streams. Indeed, this was the conclusion drawn by Megirian (1992) in his study of the geology of the D Site Plateau.

Speculation on the Riversleigh environment based on particular vertebrate fossil faunas suggesting open vegetation, at least in patches (such as Boles (1997) and White (1997)), is supported by the plant data, however the presence of patches of rainforest cannot be supported by the plant fossils. The plant material in the nodules represents only a snapshot on time so there remains the possibility moister conditions prevailed at Riversleigh at other times.

The only direct plant data we have indicate seasonally dry conditions and open canopied vegetation at Riversleigh during the late Oligocene or earlier in the Tertiary. The recorded vegetation was probably dominated by a species of Casuarinaceae with close affinities to *Casuarina* and *Allocasuarina* and the association also included a number of other species in smaller numbers including a species of *Alectryon*, possibly *A. affinis*, and possibly a species of either *Rubus* or *Capparis*.

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**References**


