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The imbricate-leaved dacrydiums – identifying the adult foliage

R. O. Gardner

"Dear Mr Phillips Turner

I have given this morning to the study of your specimens, and to comparing them with the types in my herbarium. First of all, I may say that the adult foliage of several of our Coniferae is very difficult to distinguish. Dacrydium bidwillii, D. intermedium and D. colensoi have adult leaves so similar to one another that dried specimens can barely be separated..."

So wrote T. F. Cheeseman in 1922 (letter filed with unnumbered specimens in AK). These plants, and our two other native species, are now placed as *Halocarpus bidwillii*, *H. biformis* and *H. kirkii*, *Lagarostrobos colensoi*, and *Lepidothamnus intermedius* and *L. laxifolius*, the three genera here being distinguished principally on features of the female cone. The species themselves have very characteristic juvenile foliage and rather different adult growth forms – see, for example, the descriptions and key of Wilson and Galloway (1993). But, as Cheeseman states, there is quite a problem identifying collections of sterile (or male) adult foliage, such as may be represented by ecological survey vouchers or old herbarium material. Nor do the distributions help much in deciding what an unknown collection "should" be, since the species have a common preference for open, cool or cold, moist habitats.

Even with the best binocular microscope in the herbarium, identifying a particular collection from the subtle differences in leaf shape and size among these plants is still a good morning's work. In AK, Cheeseman's (few) sterile sheets were correctly named by him, but of the more modern collections nearly half have received either the wrong name or none at all.

The following discussion, mostly on anatomical characters, is based on my examination of the AK and AKU collections. As well as confirming the characterisations of Tengnér (1965) it adds some new data.

Characters of the foliage

Morphology
The margin of the adult leaf in all these plants is extended slightly by translucent epidermal cells to form a border known as the "marginal frill". It varies in width from species to species, being readily visible to the naked eye only in *Halocarpus kirkii*. Measurements given below apply to the frill a short way down from the leaf apex, where it is most easily seen in intact shoots. The frill is more or less entire (x 40) except in *L. intermedius*, *L. laxifolius* (especially), and their hybrids, where it may be sinuous to serrate.

In dried material of *Lepidothamnus intermedius* the flanks of the leaves, where the stomata are borne, tend to be pock-marked or even irregularly and somewhat transversely wrinkled. Note that this texture is additional to the minute sinking of the stomata, which is uniform in these genera. I have not been able to examine fresh material for texture.

Anatomy
Three features are especially useful here. Firstly, in nearly all conifers, resin canals occur in the stem and leaf, just exterior to the vascular tissue. They can usually be seen (x 10) on cutting a fresh shoot (or at least the clear or milky resin itself can be seen) and are even more apparent in preserved or rehydrated foliage. All the species investigated here have a single canal in their leaves, with the remarkable exception of *Lepidothamnus intermedius* and *L. laxifolius*, which invariably lack canals from their stems and leaves.

The second valuable feature is the presence of large sclereids (lignified cells) in the mesophyll of the leaf in adult shoots. These can be seen under a compound microscope, either in section or in a squash preparation (made by softening a length of shoot in bleach or strong alkali). In the three *Halocarpus* species these cells are irregularly shaped, with swellings and conical projections ("dinosauriform"), and have very thick sparsely pitted walls. In *Lagarostrobos colensoi* they are regularly subcylindrical and rounded, their long axis being more or less radially directed; their walls are only somewhat thickened and are not pitted. *Lepidothamnus intermedius* and *L. laxifolius* are again anomalous in not usually having sclereids; however, a few specimens (some juvenile and some adult) had infrequent shortly oblong weakly-angled sclereids.

In two of the c. 30 specimens of *Halocarpus bidwillii* examined, mesophyll sclereids were very rare or lacking. This is the condition of the juvenile foliage in *H. bidwillii* (and in *H. biforme* and *H. kirkii*) and though it was their adult parts that were examined both specimens also bore juvenile sprigs. This phenomenon should be kept in mind when selecting material.

In the three *Halocarpus* species sclereids also occur in the pith. In *H. kirkii* they are quite frequent, though they may not be present in every section made. In *H. biformis* they are much less common, and are perhaps missing entirely from some shoots or parts of these. In *H. bidwillii* they seem to be very rare, being noted by me only in three out of several hundred sections made from seven specimens.

The third feature is the presence of fibres at the exterior of the stem's vascular system. In *Lagarostrobos colensoi* these "phloem fibres" soon form a more or less continuous layer one to several cells deep outside each vascular arc. Stems of *Halocarpus* species lack phloem fibres. The two *Lepidothamnus* species usually have a few, but they never occur in a continuous layer. Phloem

fibres are well-developed even in the feathery early-juvenile shoot of *L. colensoi* and so help one distinguish this from the very similar *Lepidothamnus intermedius* juvenile.

Further study may show that *Halocarpus bidwillii* and *H. biformis* differ in the amount of extra-cellular space in their leaf mesophyll. This seems to be greater in *H. biformis* leaves, which would account for their more deeply sunken flanks (at least in dried material).

Chemistry
A short time before beginning this project I happened to collect *Halocarpus biformis* and *Lepidothamnus intermedius* and not being able to identify them straight away I kept them for a few days in plastic bags, lightly doused with methylated spirits, before examining them at home. On opening the bags I encountered two different odours. *H. biformis* smelt something like leather and pine and perhaps seaweed, while the odour of *L. intermedius* was very distinctly sweeter and fruitier. I have since found that the odours of *H. bidwillii* and *H. kirkii* are quite like that of *H. biformis*, *Lepidothamnus laxifolius* is sweet like *L. intermedius*, though perhaps with more "plum" and "lemon", and that *Lagarostrobos colensoi* has a smell something like witch-hazel. This identification technique is demanding but seems worthy of wider trial.

Critical notes on the species

Note that a difficulty with the anatomical method is in assessing variation, because this would require the examination of numerous samples, preferably those whose identity is beyond doubt. I have not been able to do this and so have indicated relative differences only, or have queried particular points.

Halocarpus bidwillii Adult leaf: marginal frill very obscure, to c. 0.025 (-0.05) mm wide; resin canal large; mesophyll sclereids irregular, walls thick, with a few pits, the cell lumen quite often ± obscured. Stem: pith sclereids rare (in the order of 1 in every 100 sections made?); phloem fibres lacking. Bark of young ± leafless shoots (such as often found near the base of herbarium specimens) thin and smooth compared with that of *Lagarostrobos colensoi.*

Halocarpus biformis Adult leaf: marginal frill barely visible to naked eye, to c. 0.075 (- 0.1) mm wide; resin canal large; mesophyll sclereids irregular, walls thick, with a few pits, the cell lumen quite often ± obscured. Stem: pith sclereids occasional (in the order of 1 in every 10 sections made?); phloem fibres lacking. Bark as in *H. bidwillii.*
Shoots of this species, as measured a few centimetres back from the tips, are usually much more robust than those of *H. bidwillii*, and I think it likely that shoots greater than 1.7 mm in diameter will prove to belong to *H. biformis.* However it is relevant to note that Druce (unpub.) believes that these species can hybridise, despite their having different chromosome numbers. It can be speculated then that possibly the rare pith sclereids of "*H. bidwillii*" actually occur only in hybrid plants.

Halocarpus kirkii Adult leaf: marginal frill comparatively conspicuous, to c. 0.2 mm wide; resin canal large, mesophyll sclereids irregular, walls thick, with a few pits, cell lumen quite often ± obscured. Stem: pith sclereids quite common (in the order of several every 10 sections made?); phloem fibres lacking. Bark as in *H. bidwillii.*
The northern distribution of this species means that one usually needs to distinguish it only from *Lagarostrobos colensoi* and *Lepidothamnus intermedius.*

Lagarostrobos colensoi Adult leaf: marginal frill barely visible to naked eye, to c. 0.05 (-0.075) mm wide; resin canal small compared with those of *Halocarpus* spp.; mesophyll sclereids cylindrical or slightly tapered or almost suborbicular, walls thickened but only about half as thick as those in *Halocarpus* spp., and not pitted, the cell lumen never obscured. Stem: pith lacking sclereids; phloem fibres abundant, soon forming a ± continuous sheath outside each vascular arc. Bark of ± leafless shoots much thicker than that of *Halocarpus* spp. and somewhat annulate.

Lepidothamnus intermedius Adult leaf: marginal frill barely visible to naked eye, to c. 0.05 (-0.075) mm wide, sometimes minutely irregularly sinuate or almost toothed; flanks of leaf minutely pitted and folded (just visible to naked eye); resin canals lacking; mesophyll sclereids rare (often lacking?),

shortly oblong and not as irregular in outline as those of *Halocarpus* spp., walls thickened (about as in *Lagarostrobos colensoi*), pitted, the cell lumen not obscured. Stem: pith lacking sclereids; phloem fibres few (occ. lacking?). Bark of ± leafless shoots ± smooth and thin, like that of *Halocarpus* spp. I have seen only a single specimen of *Lepidothamnus intermedius* from north of the Barrier Islands - it is "North Cape, J. Adams" AK 14270. Unfortunately, there are numerous dubious localities in Adam's herbarium and I think that this may be another.

Lepidothamnus laxifolius As *L. intermedius*, but the marginal frill on adult leaves often with minute irregularly spaced ± serrate teeth (x 25), the leaf flank pitting sometimes obscure or lacking. Usually the presence of juvenile linear, spreading leaves even on fertile shoots will distinguish this species – fully adult (imbricate) leaves are often found only for a few millimetres just below the cones. Wells & Hill (1986) described *L. laxifolius* leaves as being without a marginal frill, but this is true for juvenile leaves only.

Hybrids between *L. laxifolius* and *L. intermedius* have a marginal frill that perhaps is usually wider than in the parents (but the toothing is not similarly over-developed), and adult leaves may occur for several centimetres; however I am not at all sure whether an extensive length of imbricate-leaved shoot indicates that the material is hybrid.

Additional Notes

Mr Cheeseman's letter quoted at the beginning of this article goes on to note that foliage of the imbricate dacrydiums is also very much like that of *Libocedrus bidwillii*. This however has the opposite and decussate leaf arrangement of most members of Cupressaceae, and the leaves have a raised midrib on their adaxial surface, rather compact mesophyll sclereids, and thick-walled fibres in the hypodermis.

One recent AK specimen from Northland, "on cutting beside farm track", was identified as *Lagarostrobos colensoi* but is actually *Cupressus macrocarpa*; its leaves have a finely denticulate marginal frill (x40).

It is conceivable, particularly if fragmentary or subfossil material is being dealt with, that foliage of *Dacrydium cupressinum* or *Dacrycarpus dacrydioides* might be mistaken for one of the other species, especially *Lepidothamnus intermedius* or (subjuvenile) *Lagarostrobos colensoi*. The former two species are like *L. colensoi* in having conspicuous phloem fibres in their stems and a single smallish resin canal in their leaves, but they lack mesophyll sclereids and have a fibrous hypodermis.

Figure 1 illustrates the following:-

Vascular tissue cross-hatched; resin canals with dashed outline; mesophyll sclereids (x c. 250) partly in optical section to show concentric thickening, pits, degree of occlusion of lumen.
Halocarpus bidwillii. Shoot t.s (1.6 mm diam.).
Halocarpus biformis. Shoot t.s. (2.0 mm diam.).
Halocarpus kirkii. Shoot t.s. (2.2 mm diam.), the pith with two sclereids. Broken shoot of same size, and enlargement of marginal frill (x c. 170).
Lagarostrobos colensoi. Shoot t.s (1.8 mm diam.), phloem fibres (dark) as a sheath between rest of vascular cylinder and resin canals.

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Figure 1: