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## NOTE

# FOSSIL FRUIT OF THE GREVILLEEAE (PROTEACEAE) IN THE TERTIARY OF EASTERN AUSTRALIA

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*Conchotheca rotundata* F.Muell., 1873 a fossil fruit taxon described from mid-Tertiary deep lead sediments at Haddon, Victoria is morphologically and anatomically consistent with fruits of extant *Grevillea* (Tribe Grevilleeae). The fossil taxon, which is redefined on the basis of the type and other specimens, accommodates uniloculate, tardily dehiscent, ellipsoidal fruits with stalk attachment displaced laterally towards the style and a thick, woody pericarp that is radially structured. The fossil fruit evidence taken together with that of fossil leaves and pollen associated with *Grevillea* demonstrate a history of the Tribe to at least the latest Cretaceous (Maastrichtian) in the Australian vegetation. *Conchocaryon smithii* F.Muell., 1879, a fossil fruit from Miocene sediments at Gulgong, New South Wales may also have affinities with Tribe Grevilleeae, but the protocol specimen, which is refigured herein, has not been located and is believed lost. For comparative purposes, fruit and seed structure is documented of extant members of Tribe Grevilleeae (*Grevillea*, *Hakea*, *Finschia*) and of *Buckinghamia* (sister to Grevilleeae on molecular evidence). ❏ *Proteaceae, Grevilleeae, Grevillea, Conchotheca, Conchocaryon, fossil fruit, Australia, Tertiary.*

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The Tribe Grevilleeae comprises three genera, two of which (*Grevillea* Knight ~363 spp., *Hakea* Schrad. & J.C. Wendl. ~150 spp.) are the most species-rich of the Proteaceae in the Australian flora, plus *Finschia* Warb.with four species centred in New Guinea and adjacent islands in the Western Pacific region (Fig. 1). Whereas *Finschia* are mostly tall trees of rainforests, open woodlands and swamp forests in high rainfall areas, *Hakea* (endemic to Australia) has near pan- Australian distribution and is concentrated in the drier regions, occurring as low trees and shrubs in open woodlands, heathlands, and coastal communities. *Grevillea*, with its distribution centred in Australia (357 spp.), extends to New Caledonia, New Guinea and Sulawesi, includes tall trees and shrubs of closed to open forests and woodlands (mostly in high rainfall or monsoonal regions of northern and eastern areas of its range), and small trees to spreading and prostrate shrubs especially under lower rainfall regimes in southern and Western Australia.

By contrast to the high diversity levels and almost pan-Australian distribution of *Grevillea* and *Hakea* in the present-day vegetation, their past history is virtually unknown from the fossil record. The possible occurrence of the genera in Australia during the Tertiary was first hinted at by Mueller (1873: 41). He noted the 'general appearance' of fossil fruits attributed to *Conchotheca rotundata* F.Muell. to pericarps of three extant *Grevillea* species. Although arguing against assigning the fossils to *Grevillea*, he later (1882: 44) noted that they, like the pericarps of *Grevillea*, are attached to stipes that are laterally displaced with respect to the style. The fossils were recovered from deep lead sediments during gold mining activities in the 1850's-1870's near Haddon, Victoria (Mueller, 1873, 1874a,b), and subsequently reported (Mueller, 1879; Barnard, 1881) to have been recovered from beneath Tertiary basalts at Beaconsfield near Launceston (Tasmania), Clifton (Queensland) and Gulgong (New South Wales). Another fossil fruit taxon, *Conchocaryon smithii* F.Muell. (1879: 39) most likely from the Gulgong locality was described as resembling pericarps of *Grevillea* and *Hakea*. The enclosed seed, which was reported with a 'terminal wing-like appendage', intimated a closer resemblance to *Hakea* than *Grevillea*. The fossil taxon was discriminated from *Hakea* on account of possessing only one seed, and a pericarp with a 'lesser degree' of dehiscence. No further evaluation of the systematic affinities of either *Conchotheca rotundata* or *Conchocaryon smithii* has been undertaken and there is no reference to them in reviews of the macrofossil

FIG. 1. Map of the southwestern Pacific region showing present distribution range of *Grevillea*, *Hakea* and *Finschia* and locations from which fossil fruits, leaves and pollen that conforms with Tribe Grevilleeae have been reported; also indicated are doubtful fossil records of the Tribe.

record of Australian Proteaceae (Carpenter, 1994; Hill et al., 1995).

In order to clarify the status and affinity of Mueller's taxa, protocol specimens were sought from museums in Victoria and New South Wales. The single specimen on which *Conchotheca rotundata* was based was located in the Museum of Victoria together with several other specimens subsequently collected. No specimens of *Conchocaryon smithii* were found; the species was defined on the basis of one specimen, but neither it nor subsequently reported specimens were located. Comparisons have been undertaken of available fossil material with fruits of the three Grevilleeae genera (*Grevillea*, *Hakea*, *Finschia*), and of *Buckinghamia* F.Muell. (Tribe Embothrieae), which on molecular

evidence is the sister group to Grevilleeae (Hoot & Douglas, 1998). Fruits of the extant genera are described and figured and the fossil record of Grevilleeae is reviewed.

## MATERIAL

Fossil fruits investigated include the protocol material and other specimens of *Conchotheca rotundata* F.Muell.,1873 housed in the collections of the Museum of Victoria (catalogue numbers prefixed NMVP). The fruits are woody, some retaining well preserved anatomical characters, and others are vitrinised and/or pyritised with few anatomical features preserved. None retains original seed material, which appears to have been lost since investigated by Mueller (1873). Specimens examined are from Smythe's Creek (Reform Co. Shaft, ~47.5m) and

Nintingbool (Crucible Co. Shaft ~ 23.2m), near Haddon (37°18'S 146°32'E), SW of Ballarat, Victoria. These were collected from deep lead sediments that underlie basalts of Late Miocene age. An Oligocene or Early-Middle Miocene age of the sediments has been considered most likely (Rozefelds & Christophel, 1996; Dettmann & Clifford, 2001). Specimens were reported from probable Oligocene sediments at Ophir Gold Mine, Beaconsfield, Tasmania (Mueller, 1879), Middle Miocene sediments in Black Lead, Gulgong, New South Wales (Barnard, 1881) and Clifton, Queensland (Mueller, 1879), but these have not been located. No material of *Conchocaryon smithii* has been located; the single specimen described and illustrated by Mueller (1879) probably came from deep lead sediments of Middle Miocene age at Gulgong, New South Wales (Dettmann & Clifford, 2001).

Comparative material investigated and detailed in Appendix I include fruits of several *Grevillea* and *Hakea* species and of *Buckinghamia celsissima* F.Muell. cultivated or from the wild in south east Queensland. Developmental stages of fruit maturation were traced for several of these species whose identities were verified by reference to the collections of the Queensland Herbarium. Additionally mature fruit of *Grevillea candicans* C.A. Gardner were obtained from Kings Park, Perth, Western Australia, and of *Finschia chloroxantha* Diels from the Singapore Herbarium, Singapore.

## METHODS

Fossil and modern fruits were studied using a binocular dissecting microscope. Several of the woody fruits were sectioned in the transverse and longitudinal planes using a jeweller's saw, and the resulting surfaces polished on fine emery paper to reveal details of anatomy. Specimens photographed include the type specimen of *Conchotheca rotundata* illustrated by (Mueller, 1873, 1874b); this specimen is depicted in Figs 2B-G, 4C,D together with reproductions of the original lithographic illustrations (Fig. 2A). Additional anatomical detail was obtained for fruits of *Grevillea heliosperma* R.Br., *Hakea laurina* R.Br., *Finschia chloroxantha*, and *Conchotheca rotundata* from fragments mounted on stubs and gold plated for scanning electron microscope analysis using a Phillips instrument.

Several developmental stages of fruits and seeds were studied in *Grevillea robusta* A.Cunn. ex R.Br., *G. hilliana* Maiden, *Hakea actites*

W.R.Barker, and *Buckinghamia celsissima*. Dissected ovaries and hand cut sections of young fruits were cleared in a weak solution of sodium hypochlorite for 1-2 hours, followed by thorough washing in distilled water and mounting in glycerine jelly on glass microscope slides. Anatomical characters of mature seed coats were examined in transmitted light after clearing as designated above.

To provide a basis for the comparison of fossil and living fruits, morphological and anatomical features of fruits of several modern species of *Grevillea, Hakea, Finschia* and *Buckinghamia* are outlined in Appendix 1.

## SYSTEMATIC PALAEOBOTANY

### Conchotheca F.Muell., 1873, emend.

1873 *Conchotheca* F.Muell., p.41.

TYPE SPECIES (by monotypy). *Conchotheca rotundata* F.Muell., 1873, emend.

EMENDED DIAGNOSIS. Fruit laterally compressed prolate ellipsoidal or spheroidal, with bilateral symmetry only about the plane that includes stalk, style base, and ventral suture (potential dehiscence line); indehiscent or tardily dehiscent, splitting into 2 equal portions; unilocular. Stalk base displaced dorsiventrally (laterally towards style), the ventral suture longer than dorsal hinge line. Surface smooth or near-smooth. Fruit wall in transverse section radially structured, the outer pericarp with radially aligned fibres, the middle pericarp with radially aligned fibres associated with predominantly longitudinal vascular bundles, and the inner pericarp predominantly of parenchyma. Seed laterally attached, solitary filling, or almost so, locule. Seed flat, roundish, unwinged.

REMARKS AND COMPARISON. When proposed the genus was monotypic and based on a single specimen (Mueller, 1873: 41, pl. VI, figs 9-11), which is re-figured herein (Figs 2A-G, 4C,D); the seed referred to by Mueller has not been located. Additional specimens were subsequently collected (Mueller, 1882: 44; 1883), but none was illustrated. Mueller (1882) noted further characters of the seed (flat-compressed, almost truncate at one extremity, slightly apiculate at the other; testa membranous, minutely granular), but none of the specimens we examined possesses seed tissue. Nevertheless, the vascular trace from the ovary wall to the placenta confirms lateral
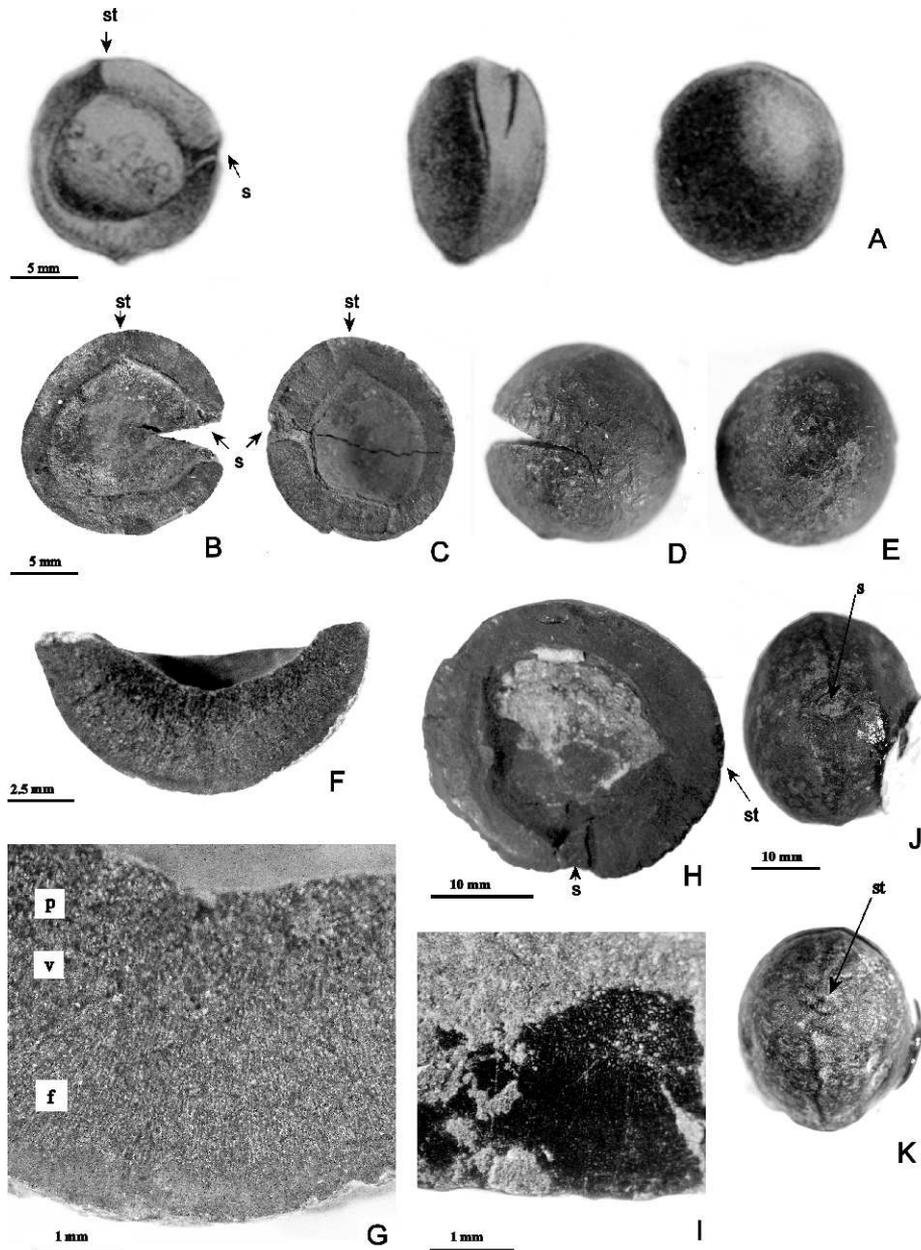
FIG. 2. *Conchotheca rotundata* F.Muell., Holotype (NMVP53971), A-G, and two other specimens, H-K, from Nintingbool (Crucible Co. Shaft, ~23.2m), Victoria. A, Lateral views showing interior of locule, and external views showing dorso-ventral suture before separation into two valves and lateral surface respectively as illustrated by Mueller (1873, pl. VI, figs 9-11), arrows indicate position of stalk (s) and stigma (st); B,C, interior views of locule, arrows point to stalk (s) and stigma (st); D,E, external views of lateral surfaces; F,G, section of valve cut transverse to ventral suture and dorsal hinge line showing inner pericarp with isodiametric cells (p), and middle and outer pericarp with vasculature (v) and radially aligned fibres (f); H,I, NMVP206494, lateral view of interior of valve showing locule with infilling of sulphur and detail of pericarp wall in longitudinal section respectively; J,K, NMVP53972, basal and apical views showing scars of stalk (s) and stigma (st).

attachment of the seed. A second species, *C. turgida*, referred to the genus by Mueller (1874a: 42, 1874b: 24) was differentiated from *C. rotundata* in being smaller and with a thinner-walled pericarp. Illustrated specimens of *C. turgida* comprise two morphologically distinct forms, each of which differs from *Conchotheca* F.Muell. emend., in that their styles and stalks are in vertical alignment, their ventral sutures and dorsal hinge lines are equal in length, and their seeds are apically attached. Both forms are excluded from *Conchotheca* as emended herein, and will be transferred to a new genus (Dettmann & Clifford, in prep.).

*Conchocaryon* F.Muell. 1879, a monotypic genus based on a single specimen of *C. smithii* F.Muell. 1879, was described as possessing several of the characters displayed by *Conchotheca*, but was segregated on account of its shape being 'unsymmetrical' rather than ellipsoidal. A further distinction noted between the two genera was that the seed of *Conchocaryon* was described as possessing 'a flat terminal appendage' (wing) in contrast to the unwinged seed of *Conchotheca* (Mueller, 1879: 39). The specimen on which *Conchocaryon* was based has not been located in museums in Sydney or Melbourne, and is presumed lost. Detailed comparisons between the two genera were thus precluded.

### Conchotheca rotundata F.Muell. 1873, emend.
### (Figs 2A-K, 3A-D, 4C,D)

MATERIAL. HOLOTYPE (by monotypy): NMVP53971 (2 valves of follicle; vertical axis 14mm; lateral axes, 12.5mm (in plane of dehiscence) x 10mm; pericarp wall 2-3mm thick), Figs 2A-G, 4C,D. OTHER MATERIAL. NMVP53972, NMVP53553, NMVP206494 (Coll. R.A. Lock, Nintingbool, but identified by F.Mueller as *Conchotheca turgida*).

TYPE LOCALITY. Deep leads at Haddon, Nintingbool (Crucible Co. Shaft, ~23.2m), Victoria; ?Early-Middle Miocene.

DESCRIPTION. Fruit prolate ellipsoidal to subspheroidal, bilaterally symmetrical about the plane that includes stalk, stigma, and potential dehiscence line or ventral suture; indehiscent or tardily dehiscent; unilocular, with 1 laterally inserted seed. Stalk attachment displaced dorsiventrally; ventral suture twice length of dorsal hinge line. Stalk base circular, 1-2mm in diameter; style base inconspicuous, represented by faint scar. Fruit with a smooth or near-smooth surface. Pericarp up to 2-3mm thick at midpoint of lateral surfaces, tapering to 1.5-2mm at ventral suture and dorsal hinge line. In section pericarp radially structured, the outer and middle pericarp with radially aligned fibres directed outwards from the predominantly vertically aligned vasculature that demarcates the boundary between the middle and inner pericarp, the latter of which is composed predominantly of parenchyma. Seed flat, roundish, unwinged.

DIMENSIONS. Fruit; length 11.5 (12.8) 14mm; lateral axes, 10 (11.8) 13.5mm (in plane of dehiscence) x 9 (10.6) 13mm (at right angles to dorsal-ventral plane). Seed dimensions unknown.

REMARKS. One valve of the holotype has cracked and split since illustrated (Mueller, 1873, pl. 6, figs 9-11; Mueller, 1874b, pl.6, figs 9-11).

The dorsiventral displacement of the stalk with respect to the style in the fruits was not specified in the original diagnosis, but was hinted at by Mueller's comparison of the fossils with fruits of three species of tropical *Grevillea* (Mueller, 1873: 41). He subsequently emphasised (Mueller, 1882: 44) the asymmetry of *Concotheca rotundata* in lateral views noting that it 'seems to have its fruit laterally affixed to a stipes (sic)'. Thus, the dorsal hinge line is considerably shorter than the ventral suture (Figs 2A,B,C,H, 4C), a feature of fruits of extant *Grevillea*, and here illustrated for *G. candicans* (Fig. 5H), *G. heliosperma* (Figs 4A, 5A,B), and *G. robusta* (Fig. 5L,M).

Mueller's characterisation of the seed is accepted herein even though no seed material has been observed in the holotype and other specimens studied; it appears that the seed material described by Mueller has been lost or destroyed. Mueller (1873: 41) stated that the fruit possessed one 'flat, roundish' seed, and later remarked (Mueller, 1882: 44) that 'the well-developed seed completely fills the cavity, is flat-compressed, almost truncate at one extremity and slightly apiculate at the other'. He further noted (1882: 44) that 'the testa is membranous, minutely rough from granular elevations, which are mostly arranged in short lines, giving to the outside of the seeds a pretty appearance'.

DISTRIBUTION. (Fig. 1): Haddon (Smythe's Creek, Reform Co. Shaft, ~47.5m; Ningtingbool, Crucible Co. Shaft ~ 23.2m), Victoria (Mueller, 1873, 1874a); Ophir Gold Mine, Beaconsfield, Tasmania (Mueller, 1879b); Black Lead, Gulgong, New South Wales (Barnard, 1881).
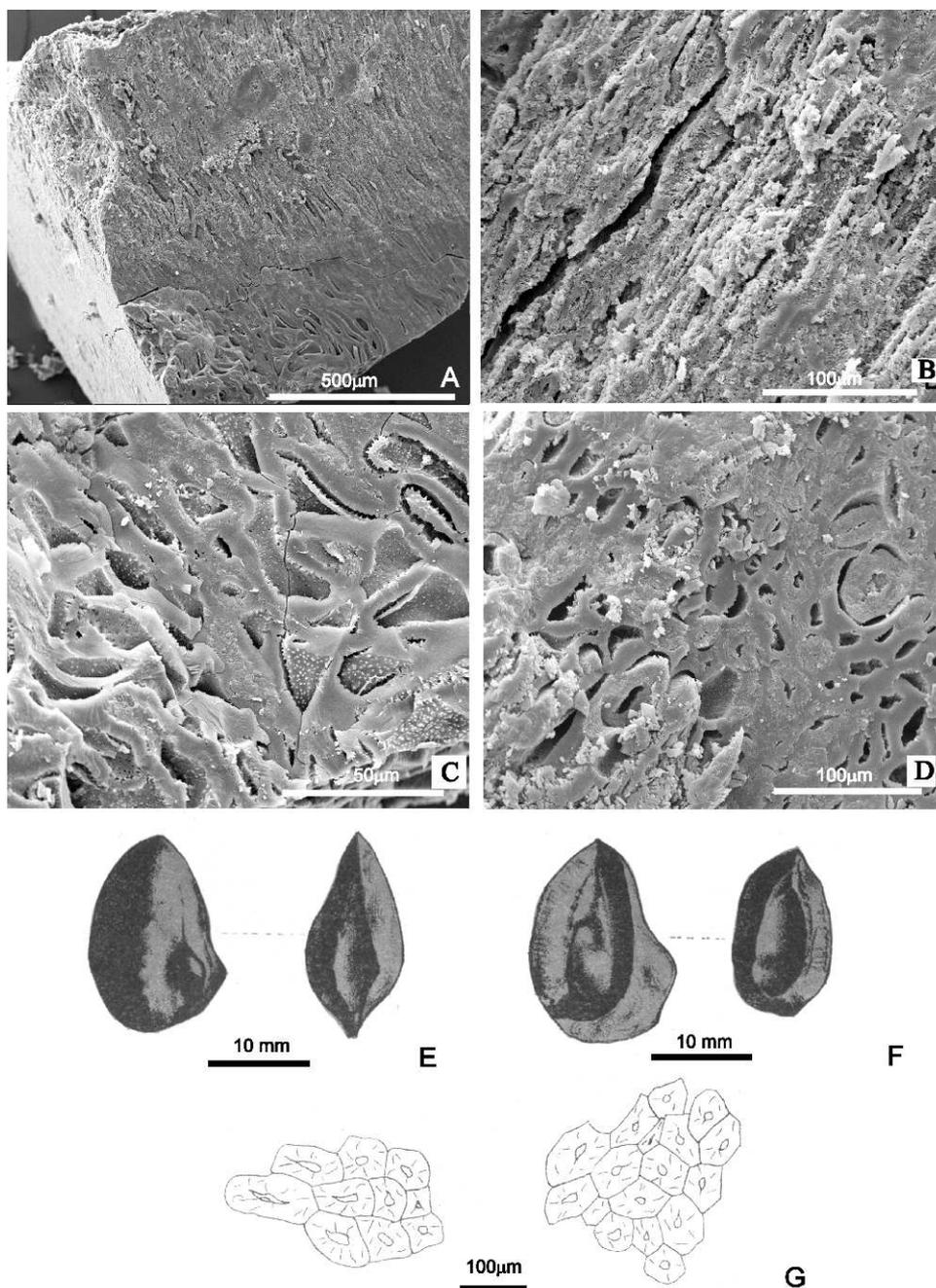
AGE RANGE. ?Oligocene-Miocene

FIG. 3. *Conchotheca rotundata* F.Muell. (A-D) and *Conchocaryon smithii* F.Muell. (E-G). A-D. *Conchotheca rotundata*, NMVP206494 from Ningtinbool (Crucible Co. Shaft, ~23.2m), Victoria. A, Portion of pericarp in transverse (large face) and longitudinal (face on left) section; B, radially aligned fibres in middle and outer pericarp; C-D, fibres in oblique and transverse section surrounding vasculature in mid region of pericarp. E-G, *Conchocaryon smithii*, holotype. E,F, oblique, basal and lateral views as illustrated by Mueller (1879, pl. 17, figs 4,5); G, detail of pericarp fibres as illustrated by Mueller (1879, pl. 17, fig.6).

AFFINITY. Initially, Mueller (1873: 41) considered *C. rotundata* distinct from *Grevillea*, Mueller (1873: 41) in lacking a 'conspicuous stipe' (gynophore), but subsequently acknowledged that '*Conchotheca rotundata* seems to have its fruit laterally affixed to a stipe, as in the case with many Grevilleas' (Mueller, 1882: 44; 1883: 21). In the absence of flowers and leaves he cautioned against placing the species in the genus *Grevillea*.

We confirm that the *C. rotundata* fruit is morphologically consistent with those of *Grevillea*, and shares with them the following characters: asymmetrical except about the plane of potential dehiscence; dorsal hinge line shorter than ventral suture; lateral attachment of seeds; and radially aligned fibres in the middle and outer pericarp. *C. rotundata* is tardily dehiscent in contrast to *Grevillea* fruits, which have readily dehiscent follicles except for fruits of *G. candicans*, which are indehiscent.

In terms of size and shape Mueller (1873) noted resemblance of *C. rotundata* to fruits of several taxa of *Grevillea* referred to the Hilliana and Heliosperma Groups (sensu Makinson, 2000), and especially *Grevillea refracta* R.Br.*, G. mimosoides* R.Br., and *G. polystachya* R.Br. (= *G. parallela* Knight). These and other species of the Hilliana and Heliosperma Groups of *Grevillea* have fruits in which the stalk attachment is dorsiventral with respect to the style base, and the thick pericarp wall is composed predominantly of radially aligned fibres in the middle and outer zones external to the vascular bundles (Fig. 5D-F) as described and illustrated by Filla (1926, figs 36-38, 70d). In these respects the fruit wall of *Conchotheca rotundata* is comparable (Figs 2F,G,I, 3A-D), and moreover, as in *Grevillea* fruits, the wall is thickest midway between the ventral suture and dorsal hinge line (Figs 2F, 4D). However, fruits of all extant taxa other than those of *G. candicans* (Fig. 5H-I) are readily dehiscent, although is some species like *G. heliosperma,* (Figs 4A,B, 5A-C) and *G. refracta*, the suture may be barely evident until the latest stages of ripening.

Most *Grevillea* fruits have two laterally attached seeds, but the number may be reduced to one by abortion. In some species the seeds have a broad peripheral wing (Fig. 5G,N), but in the majority of species, the seeds are unwinged (Fig. 5K). Although the unwinged seeds lack a broad peripheral papery wing, they have a circumferential structure such as a 'rib' or 'ruff' that may be a wing-homologue. One-seededness

is far more common amongst species with unwinged seeds than in species with winged seeds. *C. rotundata* was described (Mueller, 1873) as having one, unwinged seed, but seed material is absent from specimens examined, and thus unambiguous verification of a *Grevillea* affinity for *C. rotundata* is precluded.

Tardily dehiscent, usually one-seeded fruits that are borne on lateral stipes also occur in *Finschia* (Sleumer, 1955) and *Hakea* (Barker et al., 1999). *Finschia* is distinct in possessing a corky pericarp comprising an exocarp of corky cells and a thick mesocarp of large stone cell complexes interspersed with corky tissue external to the vasculature of the mesocarp (Fig. 6I,J). *Hakea* fruits are dehiscent, but at maturity the two portions remain united at the base and attached to the plant stem. In many species the fruit has pronounced humps on the lateral faces resulting from secondary thickening of the pericarp (Filla, 1926; Johnson & Briggs, 1963; Barker et al., 1999). The pericarp, whether significantly secondarily thickened or not, comprises stone cell complexes instead of radially arranged fibres adjacent to the ventral suture and external to the vasculature in the mesocarp (Fig. 6B). In these respects *Hakea* fruits differ from *Conchotheca*.

Fruits of *Buckinghamia* differ from those of *Grevillea* and *Conchotheca* in that the dorsal hinge line is longer than the ventral suture (Fig. 5Q,R). Moreover, in *Buckinghamia* the radially directed vascular bundles of the middle and outer pericarp are themselves branched (Filla, 1926, fig.70f) as opposed to the unbranched radial vasculature of *Grevillea* (Filla, 1926, fig. 70d; Fig. 5E,F herein) and *Conchotheca* (Figs 2G, 3A).

## Conchocaryon F.Muell., 1879

TYPE SPECIES (by monotypy)*. Conchocaryon smithii* F.Muell., 1879.

DIAGNOSIS (Mueller, 1879: 39). 'Fruit hard, oblique-ovate, considerably compressed, one-celled, almost smooth, dehiscent only along the anterior (ventral) margin, produced at the lower portion of the back into two acute ridges. Placenta narrow, dorsal in the cavity; its point of attachment to the seed about midway up at the dorsal inner angle of the pericarp. Seed solitary, ovate, turgid, filling the lower part of the cavity, extended at the summit into a flat short triangular appendage'.
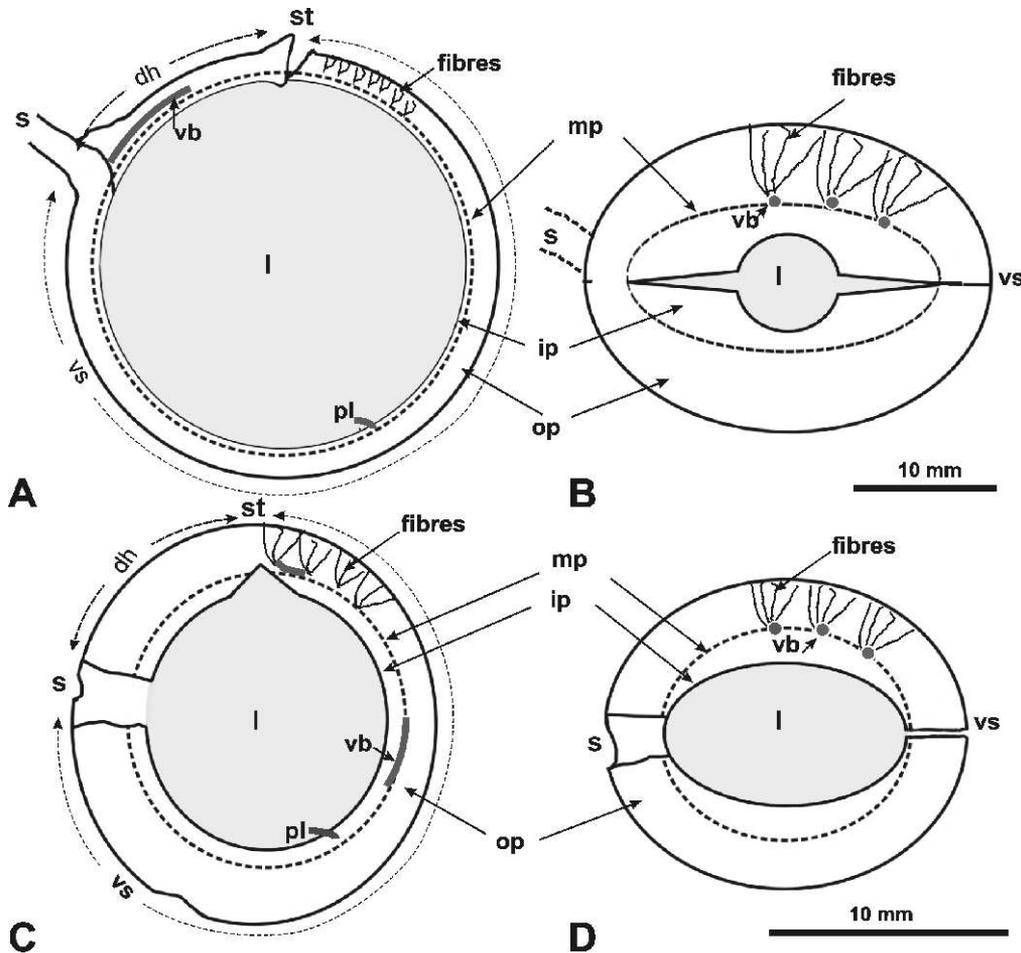
FIG. 4. Diagrammatic outline of longitudinal and transverse sections of fruit of *Grevillea heliosperma* (A,B) and holotype, NMVP53971, of *Conchotheca rotundata* (C,D); dh, dorsal hinge; l, locule; ip, inner pericarp; mp, middle pericarp; op, outer pericarp; pl, placenta; s, stalk; st, stigma; vb, vascular bundle; vs, ventral suture. Note, fibres illustrated in upper right segment only.

FIG. 5. Fruits and seeds of *Grevillea* (A-P) and *Buckinghamia* (Q-T). A-G. *Grevillea heliosperma* R.Br. A,B, lateral views showing exterior of fruit (d, dorsal hinge, v, ventral suture) and interior of locule containing winged seed, arrows indicate position of stalk (s) and stigma (st); C, section of fruit cut transverse to ventral suture and dorsal hinge line showing two winged seeds cut transversely; D-F, portion of pericarp in transverse section showing radially aligned fibres in middle and outer pericarp (D) and vasculature surrounded by fibres in mid regions of pericarp (E,F); G, winged seed showing raphe trace (t) and seed body. H-J, *Grevillea candicans* C.A.Gardner. H-I, longitudinal and transverse sections of fruit showing interior of locule (s, stalk, st, stigma) and unwinged seeds cut transversely (note only one seed with embryo); J, transverse section of fruit wall showing radial structure of middle and outer regions of pericarp, parenchymatous inner pericarp, and underlying section of seed coat (darker layer); K, seed, lateral view. L, *Grevillea robusta* A.Cunn. ex R.Br. lateral view of fruit (d, dorsal hinge line, v, ventral suture). M,N,P, *Grevillea hilliana* F.Muell. M, lateral view of interior of fruit (d, dorsal hinge, v, ventral suture); N, winged seed showing branched raphe trace (t); P, cells of locule lining; Q, inner epidermis of testa with cells containing crystals of calcium oxalate. O, *Grevillea pteridifolia* Knight, hemitropous ovule showing ovule trace (t) passing through outer integument to chalaza and hypostase. R-T, *Buckinghamia celsissima* F.Muell. R,S, exterior and interior of fruit in lateral view (d, dorsal hinge, v, ventral suture); T, winged seed showing raphe trace (t) at margin of wing.
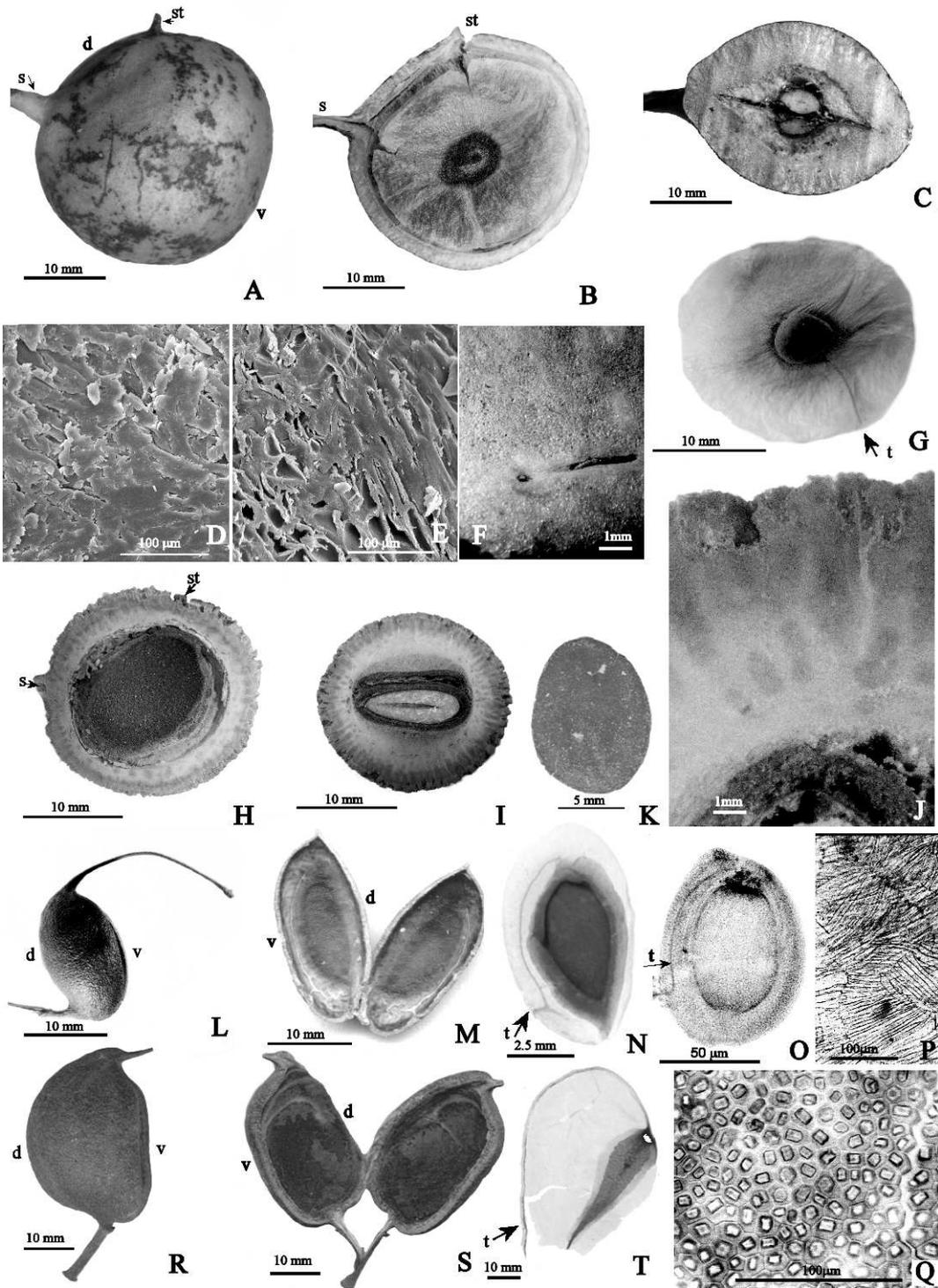
REMARKS AND COMPARISON. The genus was proposed on the basis of one specimen and was distinguished from *Conchotheca* on its 'unsymmetrical form', the fruit bulbous in basal regions and tapering towards the apex (Mueller, 1879: 39). Further systematic evaluation of the taxon is precluded as neither the type specimen nor any subsequently collected material has been located. Illustrations of the type, *C. smithii,* (Mueller, 1879, pl. 17, figs 4-6; 1883, pl.17, figs 4-6; Fig. 3E-G herein) imply bilateral symmetry and a fruit wall thickest on basal areas of the valve faces.

### Conchocaryon smithii F.Muell. 1879
### (Fig. 3F-G)

HOLOTYPE (by monotypy). Mueller, 1879: 39; pl. 17, figs 4-6.

TYPE LOCALITY. Gulgong, New South Wales, or 'from a Victorian locality' (Mueller, 1879: 39); Middle Miocene (Gulgong) or uncertain (Victorian locality).

DESCRIPTION (after Mueller, 1879: 39). Fruit asymmetrical about lateral axes, bilaterally symmetrical about vertical plane that includes stalk, stigma and potential dehiscence line; ovate with base broader than apex; edge at ventral suture acute and obtuse at dorsal hinge line; vertical axis 20mm, lateral axes 10-12mm. Stalk scar inset at base; fruit wall ~ 2mm thick, composed of thick-walled (15ìm thick) fibres and/or sclereids up to 75ìm in diameter; surface slightly rough. Seed attached laterally, the seed body filling basal portion of cavity and with a short wing directed towards apex of fruit.

DISTRIBUTION. Gulgong (Mueller, 1879; Barnard, 1881),?Victorian locality (Mueller, 1879: 39).

AGE. Middle Miocene (Gulgong) or uncertain (Victorian locality).

REMARKS. Characterisation of the species is based entirely on Mueller's description and illustrations, and is provided should specimens conforming to the holotype be located. Mueller (1879) introduced uncertainty as to the location of the described specimen; Gulgong is specified, and then qualified as possibly Victoria.

AFFINITY. With the Proteaceae (Tribe Grevilleeae) as suggested by Mueller (1879: 39), notwithstanding his suggestion the placenta is 'dorsal in the cavity'. Mueller compared the fossil with *Hakea* on the basis of the winged seed and woody fruit wall, which is swollen towards the base, but as noted by him, living species of *Hakea* possess two seeds, not one, as observed in the fossil.

### DISCUSSION

As observed by Mueller (1873) *Conchotheca rotundata* is morphologically and anatomically consonant with fruits of the Proteaceae (Subfamily Grevillioideae), and is more similar to those of *Grevillea*, Tribe Grevilleeae than to other members of the family. Less certain is the detailed morphology and affinities of *Conchocaryon smithii*. Mueller (1879) believed the sole specimen resembled fruits of *Hakea* and to a lesser extent *Grevillea*, and an affinity with Tribe Grevilleeae is cautiously accepted on the basis of the original descriptions and illustrations. Thus, irrespective of uncertainties surrounding affinities of *Conchocaryon smithii*, the Tribe has a history in Australia that extends to at least the mid-Tertiary.

All records of the fossil fruits are from south-eastern Australia, but fossil leaves and pollen that may represent the Grevilleeae are known from other Australian localities in sediments of latest Cretaceous and Tertiary age (Fig. 1). The most securely founded identifications are of leaf compressions (*Maslinia grevilleoides* Blackburn) from the Middle Eocene of South Australia; these are similar in architecture and cuticular features to *Grevillea hilliana* Maiden*,* a northern Australian species (Blackburn, 1981). Less certain are the leaf impressions recorded from Vegetable Creek (Late Eocene), New South Wales, Melville Island (?Paleogene), Northern Territory, and Muradup (Late Eocene), south Western Australia each of which was likened to *Grevillea* (Deane, 1903; Pole, 1998a; McLoughlin & McNamara, 2001). Fossil pollen that is similar to that of *Grevillea exul* Lindl., a species endemic to New Caledonia, occurs in Maastrichtian sediments of the Otway Basin (as *Propylipollis* sp. B of Dettmann & Jarzen, 1996, 1998). *Grevillea*-and *Hakea*-type pollen referred respectively to *Hakeidites* (*Grevillea*) sp. and *Hakeidites (Hakea)* sp. by Macphail (1996) occurs in Miocene and younger sediments of the Murray Basin. To the north, in Papua New Guinea, Pliocene pollen attributed to *Hakeidites martinii* Khan, 1976 may represent the Tribe Grevilleeae. The fossil pollen was compared with pollen of extant *Hakea gibbosa* (Khan, 1976), but also resembles that of *Grevillea*.

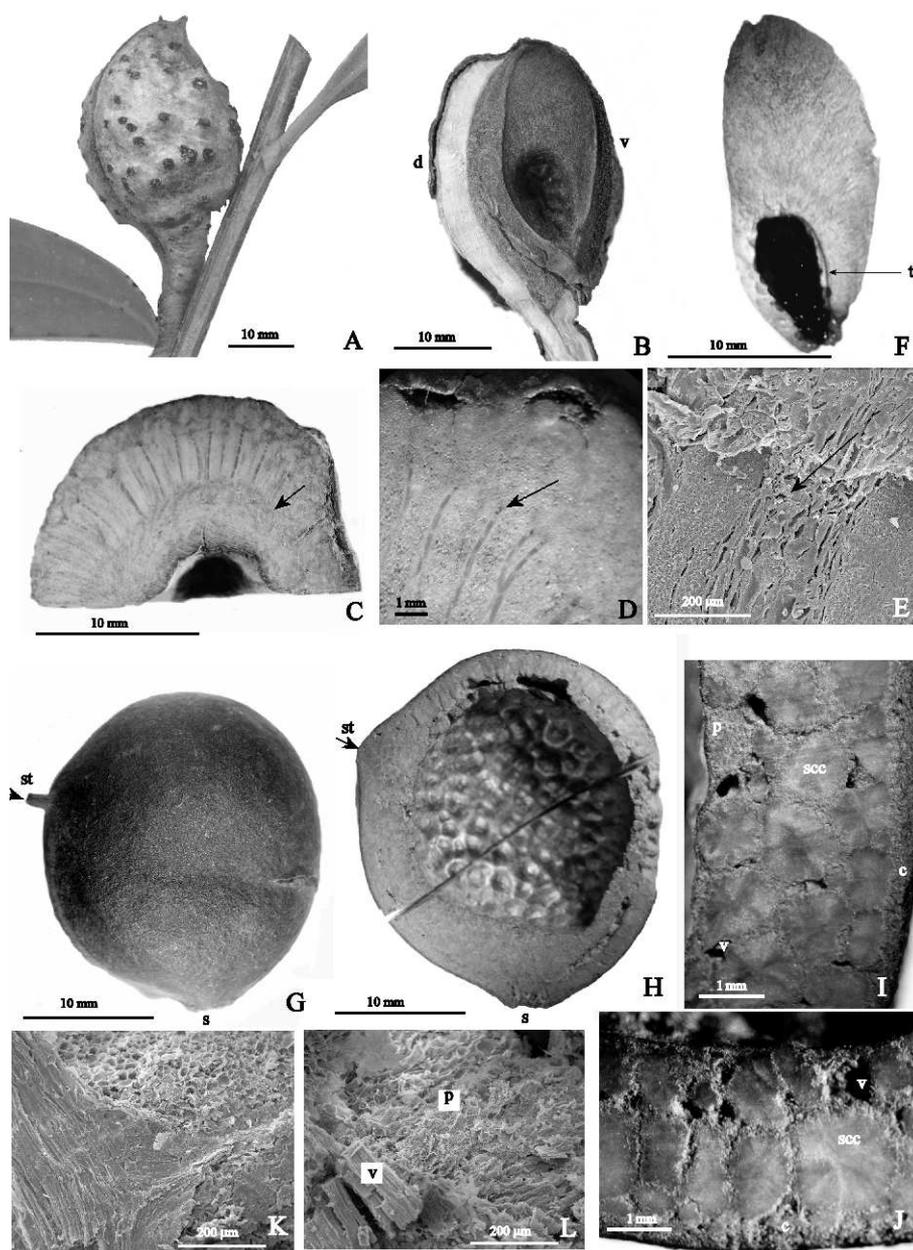There is no confirmed fossil record of the Grevilleeae from New Zealand. Fruits from the

Fig. 6. Fruits and seeds of *Hakea* (A-F) and *Finschia* (G-K). A, *Hakea laurina* R.Br. lateral view; B-F, *H. actites* W.R.Barker; B, lateral view showing interior of locule showing abrupt demarcation between 'dark' and 'light' or secondary wood adjacent to dorsal hinge line (d) and stone cells at ventral suture (v); C, transverse section showing seed cavity (bottom centre), and sharp demarcation (arrow) between primary (inner darker zone) and overlying paler secondary wood of pericarp. D-E, detail of secondary wood showing libriform fibres (arrow) and overlying cork tissue; F, seed showing basal wing and raphe trace (t). G-L, *Finschia chloroxantha* Diels; G,H, lateral views showing exterior and interior of fruit, stigma (st), stalk (s); I,J, longitudinal and transverse sections of fruit wall showing stone cell complexes (scc), vasculature (v), parenchyma (p) and cork tissue (c); K,L, detail of vasculature (v) and parenchyma (p).

Pliocene near Auckland, and the Miocene of Otago were compared with those of *Hakea* (Moore &McKelvey, 1971; Pole, 1993, 1998b), but their morphological and anatomical characters are insufficiently known to verify this affinity. Similarly, the pollen taxon, *Proteacidites hakeoides* described by Couper (1960) from Eocene sediments of New Zealand, is insufficiently known to confirm identity with *Hakea*.

Fossils morphologically and anatomically congruent with Grevilleeae indicate that the Tribe was represented in Australia by latest Cretaceous (Maastrichtian) times and persisted, at least in southern areas, through the Tertiary to the present day. The majority of fossils have been allied with rainforest or monsoon forest representatives of *Grevillea* that today are restricted to northern parts of the genus' distribution range (Fig.1). Fossils that may represent *Hakea* are unknown from pre-Miocene sediments, which may relate to lack of suitable habitats adjacent to depositional sites.

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## APPENDIX 1

## FRUIT AND SEED STRUCTURE IN THE GREVILLEEAE

### Grevillea R.Br.ex Knight (Figs 4,B, 5A-K)

Fruits of the majority of species are prolate ellipsoidal follicles. The majority of species (~265 spp.) contain seeds that lack a circumferential papery wing and of these most have a plump ellipsoidal seed body (Fig. 5K); two-seededness is the usual condition but one-seededness (by abortion) occurs in many species. A minority of species (~90 spp.) have a flat circumferential wing, and this is strongly associated with a flat seed body (Fig. 5G,N). The wingless, plump-seeded condition is typical of most species from the southeastern and south-western temperate regions of Australia, and is less common in the northern monsoon tropics and in the Eremaean, where winged-seeded species are more numerous. Fruits are borne on stalks that are lateral with respect to the stigma, with the ventral suture longer than the dorsal hinge line. Follicles and tardily dehiscent fruits are bilaterally symmetrical and split into equal portions along the ventral suture, but may remain conjoined along the dorsal hinge line adjacent to the stalk. The seeds are laterally attached and develop from hemitropous ovules (Brough, 1933). *Pericarp*. Filla (1926) detailed development of follicles of *G. rosmarinifolia* A.Cunn. noting the progressive radial elongation and subsequent

lignification of cells in the outer mesocarp between the outer epidermis and the vascular bundles; these lignified cells form a near continuous zone external to the longitudinally and laterally (tangential sensu Johnson and Briggs, 1975) aligned vascular bundles of the middle mesocarp (Filla, 1926, figs 36-38, 70d; Figs 4A,B, 5D-F herein). Cells of the inner mesocarp and the inner epidermis are tannin-filled and remain parenchymatous. This developmental pattern also has been observed by the authors in *G. hilliana* F.Muell.*, G. pteridifolia* Knight*, G. banksii* R.Br. and *G. robusta* A.Cunn.ex R.Br. Mature follicles of these and other species investigated are characterised by fibre complexes of radially and longitudinally aligned components that cap the vascular bundles and radiate towards the external surface of the pericarp which has a smooth, rough, or hair encrusted surface (Filla, 1926). The inner mesocarp between the inner epidermis and vascular bundles consists predominantly of parenchyma, the cells of which may be tannin infilled as in *G. heliosperma* R.Br.*, G. robusta*, and *G. candicans* (Fig. 5F,J).

*Seeds.* Seeds of *Grevillea* are winged, rimmed, or wingless. The wing, if present, is situated in the plane of flattening of the seed (ie. the plane that includes the hilum, chalaza, and micropyle) and encircles or forms a partial border to the exotesta around the embryo sheath (Fig. 5G,N). In *G. robusta*, the wing and exotesta, which surrounds the embryo sheath, develops from the outer epidermis of the outer integument, and through it passes the ovule trace, which branches dichotomously near the margin of the wing (Fig. 5N). One branch passes through the raphe to the chalaza, and the other branch passes in the opposite direction and terminates within the wing (Brough, 1933). The inner epidermis of the outer integument is a prismatic layer (Brough, 1933); the cells of this, the crystal layer (Fig. 5Q), contain calcium oxalate crystals, which are laid down in the developing ovule 2-3 weeks after anthesis in species examined. At this stage of development, the inner integument disintegrates, except for the cuticles separating it from the outer integument and the nucellus. These two cuticles form the embryo sheath, in which the micropyle is situated (Fig. 5N). This developmental pattern has been confirmed by us for the winged seeds of *Grevillea heliosperma, G. pteridifolia, G. banksii* and *G. hilliana*. The elaborate ruff-like structure that forms the wing about the margin of *G. hookeriana* seeds is located on their

topologically inner surface. Mature seeds are non-endospermic.

*Remarks*. In all species examined the raphe is branched near its point of entry in the marginal wing or rim; the branch traces are opposed, the main branch directed towards the chalaza, the other in the opposite direction where it terminates within the wing or rim (Fig. 5N). The palisade layer described by Brough (1933) in the seeds of *G. robusta* consists of a single layer of cells containing crystals of calcium oxalate. Seeds of other species examined possess a crystal layer, which comprises transfer cells in which calcium oxalate crystals or granules accumulate (Fig. 5Q; Léon et al., fig. 8). This layer invariably develops from the inner epidermis of the outer integument in *Grevillea* and other taxa of the Proteaceae (Neolitzky, 1926; Manning & Brits, 1993; Stroschen, 1986a,b,c; Clifford & Dettmann, 2005).

### *Hakea* Schrad. & J.C.Wendl. (Fig. 6A-E)

Fruits of *Hakea* are woody, tardily dehiscent, modified follicles usually containing 2 winged-seeds. The follicles are prolate ellipsoidal, subspheroidal or spheroidal, often with a beak or paired horns at or near the apex (Fig. 6A); they split fully or partly down the ventral or both sutures into equal portions, the ventral suture being shorter than the dorsal hinge line (Fig. 6B). The follicles are secondarily thickened, the thickening greatest on the faces of the valves and adjacent to the dorsal hinge line (Fig. 6B); surface is smooth or variously sculptured, and the outer bark may break away from the underlying mesocarp. The seeds are laterally attached near the base of the follicle and develop from hemitropous ovules (Kausik, 1949; Venkato Rao, 1971; Johnson & Briggs, 1975; Barker et al., 1999).

*Pericarp*. Filla (1926) traced pericarp development in *Hakea suaveolens* R.Br. (=*Hakea drupacea* C.F.Gaertn.) Roem.&Schu. and *H. microcarpa* R.Br., noting that after initial primary growth of the mesocarp vasculature and radial elongation of stone cells between the vasculature and the epidermis, there is considerable enlargement of the follicle resulting from secondary growth generated from a fascicular and interfascicular cambium layer (Filla, 1926, figs 41-45; fig. 6C-E herein). The pale secondary wood is generated from the interfascicular cambium and rows of libriform fibres from the vascular cambium; a meristem external to the secondary wood and beneath the epidermis generates cork tissue, which may

absciss at maturity. The boundary between the primary and secondary wood is expressed as a sharp demarcation between the layers of dark and pale wood exposed in open follicles (Fig. 6B). Dark wood surrounds the seed cavity and forms the mesocarp at the ventral suture; pale wood overlies the dark wood about the dorsal hinge line and may envelop the dark wood except along the ventral suture, or it may be limited to regions immediately adjacent to the dorsal hinge line. The width and surface extent of the pale wood zone is taxonomically significant for discriminating between some taxa (Barker et al., 1999).

*Seeds.* Seeds of *Hakea* are winged, the wing terminal or more rarely at one side or encircling seed body, which is convex on the face adjacent to the seed cavity of the follicle and flattened on the other surface (Fig.6F). Wing situated in the plane of flattening of the seed (ie. the plane that includes the hilum, chalaza, and micropyle); develops from basal tissues of ovule (Kausik, 1949). The ovule trace from the hilum passes through the outer integument and radiates into the tannin-rich hypostase near wing base. Seed coat often sculptured on convex surface, exotestal; comprising outer layer that develops from outer epidermis of outer integument and an inner crystal layer of transfer cells that contain crystals of calcium oxalate and derive from the inner epidermis. These surround the embryo sheath in which the micropyle is situated and is formed as in *Grevillea* from cuticles between the outer integument and the embryo. Mature seeds are non-endospermic.

*Remarks.* The woody follicles of *Hakea* are unique in the Proteaceae in possessing secondary wood. Seed development was detailed by Kausik (1949), who, although not recognising the presence of calcium oxalate, noted tearing of tissues during attempts to section developing ovules of *Hakea saligna* Knight.

### Finschia Warb. (Fig. 6G-L)

Fruits of *Finschia* are tardily dehiscent subspheroidal or ellipsoidal follicles borne on lateral stalks and contain 2 wingless seeds (Fig. 6G,H). The fruits are bilaterally symmetrical about the dorso-ventral plane and the seeds are laterally attached. Pericarp and seed morphology/anatomy was briefly outlined by Sleumer (1955) and Johnston & Briggs (1975); mature fruits of *F. chloroxantha* Diels have been investigated herein.

*Pericarp.* Mature pericarps of *F. chloroxantha* have large stone-cell complexes that cap the vascular bundles and radiate towards the smooth external surface (Fig. 6I,J). Between the stone-cell complexes are thin-walled, isodiametric parenchymatous cells; parenchymatous cells also occur in inner regions of the pericarp, whereas the outer regions comprise corky tissue (Fig. 6K,L).

*Seeds.* Seeds are flattened and wingless, but almost encircled by the raphe, which branches near its entry into the chalaza. The exotesta comprises tannin filled thick-walled cells that overlie a layer of pentagonal cells containing crystals of calcium oxalate. The underlying embryo sheath in which the micropyle is situated comprises two cuticles as in seeds of *Grevillea* and *Hakea*. The mature seeds are non-endospermic.

*Remarks.* Fruits of *Finschia chloroxantha* differ from those of *Grevillea* in possessing large clusters of stone-cells in the middle and outer parts of the pericarp and wingless seeds.

### Buckinghamia F.Muell. (Fig. 5R-T)

The genus comprises two species endemic to north-eastern Queensland. Fruits and seeds examined are from the type species, *B. celsissima* F.Muell., which has fruits similar to those of *B. ferruginiflora* Foreman & Hyland, except they are smaller. Fruits are prolate ellipsoidal follicles containing 4 winged-seeds that develop from hemitropous ovules with near basal attachment.

*Pericarp.* Mature follicles are bilaterally symmetrical about the vertical plane including the pedicel, dorsal hinge line and ventral suture; ventral suture shorter than the dorsal hinge line (Fig. 5R,S). Pericarp wall predominantly of mesocarp with longitudinal, lateral, and third-order radial vasculature, the bundles mostly capped by radially aligned fibres and sclereids interspersed with tannin-filled parenchyma. The inner mesocarp between the inner epidermis and vascular bundles is predominantly of tannin-filled parenchymatous cells.

*Seeds.* Seeds have near-basal attachment, are near-rhomboidal and flattened in shape, and have a marginal wing in the plane that includes micropyle, chalaza and raphe (Fig. 5T). Raphe trace marginal to wing, extending from hilum to chalaza where the vascular bundle branches and radiates into hypostase. Outer epidermis of testa, which develops from the outer epidermis of the outer integument, is composed of loose

tannin-filled isodiametric sclereids and parenchyma that separate from seed coat at maturity. Inner epidermis of testa develops from inner epidermis of outer integument, and is composed of isodiametric pentagonal-hexagonal cells each with a prismatic crystal of calcium oxalate. The crystal layer forms the wing and envelops seed sheath, which consists of two cuticles, the outer derived from inner epidermis of inner integument and the inner from that of the nucellus. The seeds are non-endospermic.

*Remarks*. *Buckinghamia* follicles superficially resemble those of some *Grevillea* species, but differ in possessing branched lateral vascular bundles in the mesocarp and a ventral suture shorter than the dorsal hinge line. In mature *Buckinghamia* seeds loose sclereids of the outer testa are shed, whereas in *Grevillea* seeds the outer testa that envelops the crystal layer and embryo sheath is retained.