Wing structure in seeds of *Strangea* Meisn. and *Stenocarpus* R.Br. (Proteaceae)

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Summary

Clifford, H.T. & Dettman, M.E. (2005). Wing structure in seeds of *Strangea* Meisn. and *Stenocarpus* R.Br. (Proteaceae). *Austrobaileya* 7(1): 165–170. In *Stenocarpus* the inner wing of the seed derives from the mesophyll of the outer integument whereas with *Strangea* this wing develops from the inner epidermis of that integument. The outer wing in both genera derives from the outer epidermis of the outer integument. Contrary to the present circumscription of the Subtribe *Stenocarpinae* in neither genus is the inner integument involved in wing production. An emended diagnosis for the Subtribe *Stenocarpinae* is provided.

Key Words: Proteaceae, *Stenocarpus, Strangea*, seed morphology, subtribe *Stenocarpinae*

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Introduction

Strangea Meisn. and *Stenocarpus* R.Br. (Proteaceae) constitute the Subtribe *Stenocarpinae* L.A.S.Johnson & B.G.Briggs, within the Tribe *Embothrieae* Rchb. as defined by Johnson and Briggs (1975). The Subtribe is distinguished from the others of the *Embothrieae* in possessing, amongst other attributes, seeds with "2 adjacent wings; outer developed from the proximal part of the funicle and folded around the inner wing which is developed from the inner integument". Douglas (1995) stated that the *Stenocarpinae* "possess a fasciculate wheel-like or 1-flowered inflorescence and a distinctive interseminal layer". As shown below in neither genus is the inner wing derived from the inner integument.

The seed coats of these and other genera of Proteaceae are formed from the outer integument and the basal tissues of the ovule, so the seed is extotestal (Netolitzky 1926, Corner 1976, Manning & Brits 1993). The 'crystal layer' identified in the seeds of many genera develops from the inner epidermis of the outer integument (Corner 1976, Kausik 1940, Manning & Brits 1993, Netolitzky 1926, Strohschen 1986a,b,c) and is one cell thick. In the majority of these cells a single crystal and/or sand of calcium oxalate is present (Jordaan 1946a,b, Strohschen 1986a,b,c). Due to the breakdown of the inner integument the embryo sheath is formed largely from two cuticles. The outer forms between the two integuments and the inner between the inner epidermis of the inner integument and the nucellus (Strohschen 1986a,b,c). The embryo sheath is sac-like and envelops all tissues that lie within the outer cuticle and is usually stained with tannin especially about the hypostase. On account of its shape it is unfortunate the term embryo sac is not available for this structure.

In the current paper we describe the seed morphology of *Strangea* and *Stenocarpus* and provide an emended diagnosis for the tribe *Stenocarpinae*.

Materials and methods

The seeds and fruits of *Strangea linearis* (Voucher: *Dettmann s.n.* [AQ751259]) were collected from *Banksia aemula–Eucalyptus signata* woodland on North Stradbroke Island and those of *Stenocarpus sinuatus* (Louden) Endl. (Voucher: *Clifford s.n.* [AQ751257]) and *Stenocarpus salignus* (Voucher: *Clifford s.n.* [AQ751258]) from trees cultivated in Brisbane. Voucher specimens have been deposited in the Queensland Herbarium.

The structure of the seed wings was determined from a study of ovules and seeds

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made optically transparent by soaking in a dilute solution of commercial bleach and after rinsing thoroughly with water were stained with 1% safranin. They were mounted in glycerine jelly before examination in transmitted and reflected light at magnifications up to x200.

For purposes of comparison, the developing seed wings of several proteaceous genera, other than *Strangea* and *Stenocarpus*, were also investigated. These included *Banksia* L.f., *Buckinghamia* F.Muell., *Cardwellia* F.Muell., *Grevillea* R.Br. ex Knight, *Hakea* Schrad., *Lomatia* R.Br., *Orites* R.Br. and *Xylomelum* Sm.

Results

The seeds of both *Strangea* and S*tenocarpus* derive from ovules that are initially hemitropous but due to their differential growth and that of the follicle, the seeds, at maturity, may appear to be anatropous. This apparent change in the orientation of the ovule with age may result from the extension of the raphe relative to the distal portion of the ovule or from the anterior end of the sclereid strand being confused with the hilum (**Fig. 1**). The vascular trace in both genera is embedded in a strand of sclereids on the hilar side of the wing, but towards the base of the seed the strand reverses direction and, after passing through the tissue surrounded by the base of the outer integument, branches radially to form a radiating cap over the hypostase. On account of its change of direction the vascular trace assumes the form of a loop or sharp hook to which the name "hooked raphe" was given by Johnson & Briggs (1963).

Whereas the embryo is close to the chalazal region in the seeds of *Stenocarpus,* in *Strangea* it is quite distant therefrom (**Fig. 1**). This distinction between the genera was commented upon by Johnson & Briggs (1963) who noted that, "The most important difference lies in the downward projection of the vascular tissue in the chalazal region….".

The seeds of all species of *Strangea* are rectangular in outline and of those reported for

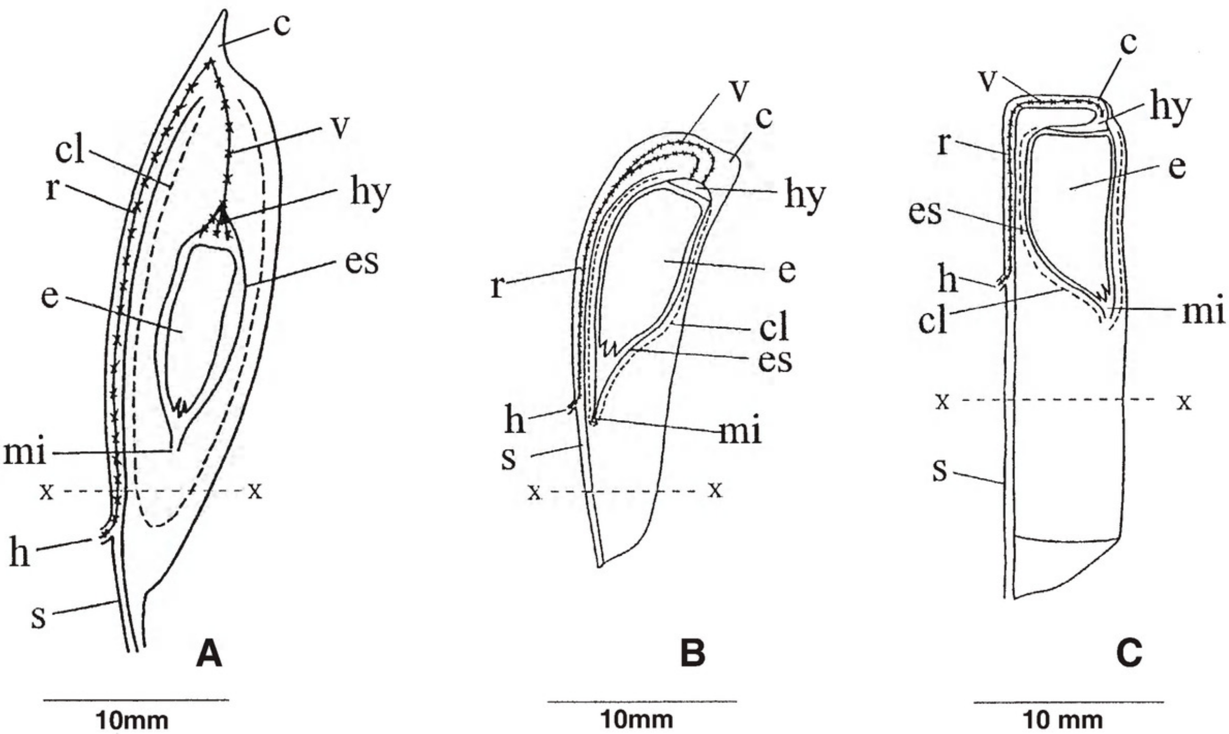

Fig.1. Longitudinal sections of mature seeds of *Strangea* and *Stenocarpus* species in the plane which includes the hilum, chalaza and micropyle , (diagrammatic and micropyle directed towards the base of the follicle). A. *Strangea linearis;* B. *Stenocarpus sinuatus;* C. S*tenocarpus salignus.*

Abbreviations: c, chalaza; cl, crystal layer; e, embryo; es, embryo sheath; h, hilum; hy, hypostase; me, mesophyll; mi, micropyle; oe, outer epidermis of outer integument; r, raphe; s, sclereid strand; v, vascular trace.

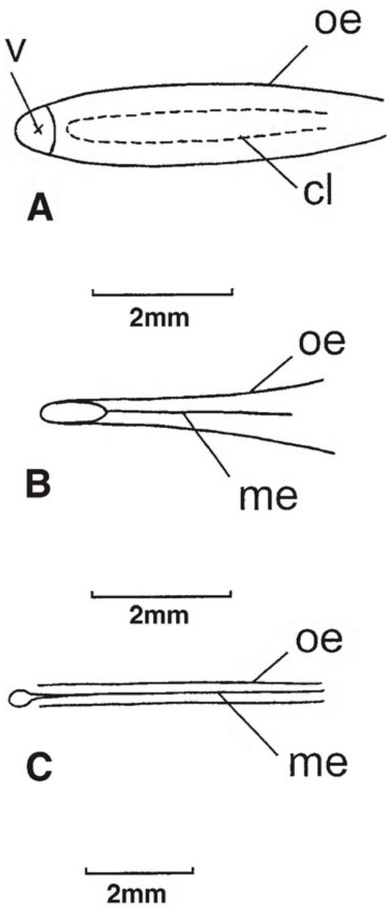

Fig. 2. Transverse sections of mature seed wings of *Strangea* and *Stenocarpus* species, (diagrammatic). A. *Strangea linearis*; B. *Stenocarpus sinuatus*; C. *Stenocarpus salignus*.

Stenocarpus they are either rectangular or sub-circular (Foreman 1995). All species of both genera are flattened in the plane that includes the micropyle, chalaza and hilum. In each genus the outer integument loosely invests the remainder of the seed in a membranous sheath. At maturity this splits longitudinally along the side opposite the hilum in all species of *Strangea* but in *Stenocarpus* splits across the apical end and the whole length of either the side opposite the hilum or along both sides of the sheath (**Fig. 2**).

With the seeds of *Strangea* the split penetrates the outer integument resulting in the formation of two membranous cloak-like open sheaths, commonly referred to as wings. The outer wing, which derives from the outer epidermis of the outer integument remains attached to the sclereid strand. Although separate from the inner wing it is folded along the line of the sclereid strand and is attached only at the chalaza. The inner wing is the crystalliferous inner epidermis of the same integument. The embryo and its enclosing sheath are suspended from the vascular trace that extends from behind the base of the outer integument to the hypostase (**Fig. 1A, 3A**) thereby resembling a seed on a long funicle and was so interpreted by Bailey (1913), Drummond (1853) and Gardner (1933,1942).

With the seeds of *Stenocarpus* the situation is more complex. Here the outer enveloping wing, as with *Strangea*, is formed from the outer epidermis of the outer integument but the inner develops from its mesophyll, a tissue not formed in *Strangea* seeds. The outer wing may split, as in *S. sinuatus,* from the base to the apex of the seed, along the side opposite the hilum, thereby forming a laterally compressed cowl-like sheath over the mesophyll as in *S. sinuatus*. In contrast, the outer epidermis of a *S. salignus* seed splits across its chalazal end and along both the hilum and non-hilum sides to produce two wing-like membranes (Maiden 1904, Schwartzbarth 1905), which are attached to a flap of tissue formed from the apex of the integument. On the hilum side of the seed a split develops on both sides of the sclereid strand. In both species the crystal layer (inner epidermis of the outer integument) immediately surrounds the embryo sheath to which it is tightly appressed. The mesophyll and outer epidermis (inner and outer wings) surround the crystal layer and are extended beyond the micropyle to form the apical half of the seed (**Fig. 3**).

Discussion

The origin of the two hinge-like wings surrounding the embryo sheath of *Strangea* seeds were misinterpreted by Gardner (1933, 1942) when he proposed *Diploptera* C.A.Gardner as a new genus to accommodate *Hakea stenocarpoides* Benth. Following Bailey (1913) and Drummond (1853) he regarded the wings as part of the fruit and the embryo sheath with its enclosed embryo as the seed. Later he appreciated that *Diploptera* and *Strangea* were congeneric (Gardner 1942). Initially *Strangea* was based on a single collection of *S. linearis*

Meisn., for which only one seed, "bordered on one side with a slightly thickened nerviform margin" (Meisner 1855, p.67), was available. As there was no mention of a wing the seed may have been immature. In the same paper Meisner described *Grevillea cynanchicarpa* Meisn. from Western Australia and although he was inclined to include it in *Strangea* did not do so because the specimen lacked seeds, the morphology of which he regarded as diagnostic of the genus.

However, the seeds had been described by Drummond (1853), the collector of the specimen, and Meisner quoted a portion of his description, after translating it into Latin. It read as follows "1-spermo, semine apice alato, samara *Fraxini* imitante". Unfortunately he left out the remainder of the sentence which read as follows, "each seed is enclosed by three membranous wings; the outer and inner are smooth and brown, not unlike the wings of the seed of *Hakea* and *Banksia* in substance; the middle membrane is of light brown colour and very brittle" (Drummond 1853, p.182). From one who possessed only a hand lens this description of the seed is amazingly accurate. Furthermore, in reporting that the middle wing, now known to be the crystal layer, is brittle, Drummond reveals he was exceptionally observant. Some years later Mueller (1871) transferred the species to *Strangea* and in an expanded description of the genus noted the seeds possessed two wings that were derived from the seed coat.

In the above account stress has been placed on the crystal layer for determining the structure of winged Proteaceae seeds, but Gardner (1933), when he described *Diploptera,* did not appear to have been aware of its taxonomic importance. At that date the presence of a crystal layer in some of these seed coats had been reported by Netolitzky (1926) who correctly placed the crystals in the inner epidermis of the outer integument. In the non-winged seeds of *Macadamia* F.Muell. a crystal layer had also been reported by Francis (1928) who incorrectly interpreted it as being the inner integument. Unaware that in some taxa of Proteoideae the outer integument and pericarp are fused, Filla (1926) regarded the crystal layer of *Serruria* Adans. *emend.* Salisb. seeds as part of the inner fruit wall. Although Brough (1933) described in detail both the anatomical and the morphological development of *Grevillea robusta* R.Br. seeds he did not report the presence of crystals in the inner epidermis of the outer integument. Not until the studies of Jordaan (1946a,b) was the taxonomic

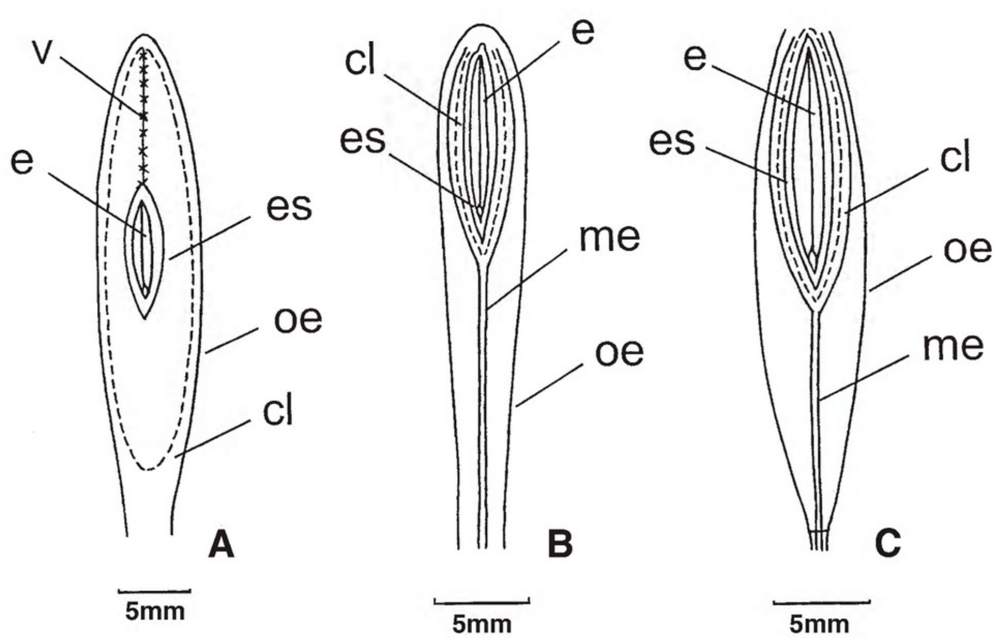

Fig. 3. Longitudinal section of mature seeds of *Strangea* and *Stenocarpus* species in the plane at right angles to that in Fig.1 (diagrammatic). A. *Strangea linearis;* B. *Stenocarpus sinuatus;* C. *Stenocarpus saligna*. Abbreviations as listed in Legend to Fig. 1.

All sections taken at level x——x of Fig. 1. Abbreviations as listed in Legend to Fig. 1.

significance of the crystal layer appreciated. Although the structure of the seed-wings of *Strangea* and *Stenocarpus* are not identical, in neither genus is the inner integument involved in their formation as claimed by Johnson and Briggs (1975) and *Flora of Australia* 16: 360 (1995), so the following emended diagnosis of the Subtribe *Stenocarpinae* is proposed:

Proteaceae, Subtribe **Stenocarpinae** L.A.S. Johnson & B.G. Briggs *emend.* H.T.Clifford & M.E.Dettmann

Conflorescentia fasciculiformis vel rotata vel floribus paucis aliquando unico; flores ± zygomorphi; ovula 1–2 vel 2 usque ad numerosa; semina 1 vel multa duo et alata. Chromosomata n=11. Genus typicum: *Stenocarpus* R.Br.

Conflorescence of fascicles or wheel-like or flowers few, sometimes solitary; flowers ± zygomorphic; ovules 1–2 or 2–many; seeds 1-several, two-winged.

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