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Pod Characters of the Mulga Group (*Acacia aneura* and Close Relatives), an Important Arid Zone Species-complex from Australia

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With 6 Figures

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Summary

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Mulga (*Acacia aneura* F. MUELL. ex BENTH. and its close relatives) is a very diverse, taxonomically complex and important group of species that is wide-spread and common in many parts of the inland, arid Australia. This preliminary morpho-anatomical examination of Mulga pods is based on selection of taxa that represent the range of carpological and taxonomic variation within the group. Although Mulga pods are somewhat variable they are always laterally flattened structures that are relatively short and broad, normally thin-textured, reticulately veined and possess either a wing or rim along their ventral and dorsal sides. This contrasts with the presumed closest relatives of Mulga which have ± terete or quadrangular pods that

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are more elongate (i.e. have a greater length : width ratio) and which are never winged. From both a taxonomic and phylogenetic perspective the most important Mulga carpological character relates to structure of the pod margins, whether they are winged or rimmed (i.e. wingless). Although wings and rims normally look very dissimilar, anatomically these structures appear to be homologous. In an associated study these pod margin characters, in conjunction with attributes of the branchlet resin, are used to define three major taxonomic assemblages within Mulga, namely, the Green alliance (pods rimmed, resin translucent), the Grey-green alliance (pods winged, resin translucent) and the Blue alliance (pods winged, resin opaque).

Zusammenfassung

RUTISHAUSER R., PFEIFER E., REID J. E. & MASLIN B. R. 2010. Pod characters of the Mulga group (*Acacia aneura* and close relatives), an important arid zone species-complex from Australia. [Hülsenmerkmale der Mulga-Gruppe (*Acacia aneura* und nahe Verwandte), ein wichtiger Artenkomplex im ariden Australien]. – Phyton (Horn, Austria) 50 (1): 69–89, mit 6 Abbildungen.

Mulga (*Acacia aneura* F. MUELL. ex BENTH. und Verwandte) ist eine vielgestaltige, taxonomisch komplexe und wichtige Artengruppe der Gattung *Acacia*. Mulga kommt in zahlreichen Regionen des ariden Australiens vor und prägt stellenweise die Vegetation. Die hier vorliegende morphologische Untersuchung von Früchten basiert auf einer Auswahl von Taxa, welche das ganze Variationsspektrum der Fruchtmorphologie und Taxonomie innerhalb der Mulga-Gruppe abdeckt. Obwohl Mulga-Hülsen recht vielgestaltig sind, zeigen sie doch folgende gemeinsame Merkmale. Es sind immer seitlich abgeflachte Früchte, die relativ kurz und breit sind. Die üblicherweise dünnen Fruchtklappen zeigen Netznervatur und besitzen entlang von Ventral- und Dorsalrand entweder einen Flügel oder (seltener) nur einen Wulst. Diese Fruchtmorphologie unterscheidet sie deutlich vom oft annähernd zylindrischen Hülsenbau der vermutlich nächstverwandten Akazien, welche oft länger und dünner sind und nie Randflügel aufweisen. Obwohl Randflügel und Randwulst bei Mulga-Hülsen sehr verschieden aussehen können, sind diese Strukturen anscheinend einander homolog (positionsäquivalent). In einer weiteren Publikation (in Vorbereitung) werden die Fruchtmerkmale, kombiniert mit Eigenschaften des aus den Zweigen austretenden Harzes, für die Abgrenzung von drei Mulga-Allianzen verwendet: die Grüne Allianz (mit flügellosen, nur mit Wulst versehenen Hülsen, Harz durchsichtig), die Grau-grüne Allianz (mit geflügelten Hülsen, Harz durchsichtig) und die Blaue Allianz (mit geflügelten Hülsen, Harz weisslich-trüb und undurchsichtig).

1. Introduction

The following paper focuses on the morphology and anatomy of pods of the Mulga group (i.e. *Acacia aneura* F. MUELL. ex BENTH. and its close relatives). Pods have long been used in the taxonomy of this very complex group of Australian species (PEDLEY 1973 & 2001, RANDELL 1992). They are of seminal importance to understanding the classification and phylogeny

of the group and to the discrimination and identification of the species. This group is currently under investigation as part of the 'Understanding Mulga' project (Maslin & van Leeuwen 2006) that was established in 2006 and is near completion. The present paper is produced under the auspices of this collaborative research program.

1.1. What is Mulga?

Mulga is a name that is most commonly applied to the large, woody, perennial, Australian species *Acacia aneura* and some of its close relatives. The name is also used to denote the vegetation type that is dominated by these species. Mulga communities are a very common component of the Australian arid zone where they occupy about 20% of the land surface (Everist 1949) and are critically important to the ecology, functioning and viability of rangeland landscapes and ecosystems. Economically Mulga is the most significant species group of *Acacia* of the arid zone, primarily because it is an important source of fodder, especially during times of drought.

1.2. Variation in Mulga

Species of the Mulga group, especially *A. aneura* itself, are notoriously variable and identification of these taxa, both in the field and from herbarium material, is often very difficult. Different species of Mulga commonly co-occur to form bewilderingly complex mixed populations that dominate many parts of the arid zone. Understanding this variation and its causal factors, and being able to identify well-defined taxa reliably, are critically important to the effective management, conservation and utilisation of this valuable resource. These were the primary drivers for the 'Understanding Mulga' project referred to above. An overview of variation in Mulga, including a discussion of factors such as polyploidy, hybridization, apomixis and neoteny that may be responsible for its creation and maintenance, is presented in Miller & al. 2002.

1.3. Taxonomy of Mulga

Despite taxonomic revisions of Mulga by Randell 1992 and Pedley 2001 uncertainties remained regarding the definition of many taxa and classification of the group. This prompted a detailed taxonomic revision of Mulga in Western Australian (which is the centre of diversity for the group) by Maslin and Reid as part of the 'Understanding Mulga' project. The broad species-groupings and nomenclature of Mulga used in the present paper is based on this work.

Acacia aneura and its relatives are members of *Acacia* section *Juliflorae* DC. within the family *Leguminosae*, subfamily *Mimosoideae*. The *Juliflorae* is a group of about 235 species which is defined by spicate inflorescences and plurinerved phyllodes (MASLIN 2001) but its phylogenetic position within the context of the Australian acacias is presently unresolved. Nevertheless, current morphological evidence shows that, broadly speaking, there exists within this section a discrete 'Mulga complex' comprising a core group, referred to here-in as the 'Mulga group', of about 15 species (some of which are presently unpublished) and a related out-group of at least eight species. For the Mulga group MASLIN & REID (in prep.) have established a broad framework that accommodates the 15 species within three major alliances, the Blue, Grey-green and Green alliance. These alliances are defined by a combination of pod and branchlet resin attributes (see below).

The following list summarizes the Mulga group taxa that are included in this paper, arranged according to their alliance. In this list we have followed the nomenclature of PEDLEY 2001, however, it should be noted that when the MASLIN & REID revision is published many of the varieties will be afforded species status.

1. Green Alliance (branchlet resin translucent; pods not winged)
   Acacia aneura F. MUELL. ex BENTH. var. *macrocarpa* RANDELL
   Acacia aneura var. *tenuis* PEDLEY
   Acacia aneura var. *tenuis* (?)
2. Grey-green Alliance (branchlet resin translucent; pods winged)
   Acacia aneura F. MUELL. ex BENTH. var. *aneura*
   Acacia aneura var. *aneura* (?)
   Acacia ayersiana MACONOCHIE
   Acacia craspedocarpa F. MUELL.
   Acacia paraneura RANDELL
3. Blue Alliance (branchlet resin opaque; pods winged)
   Acacia aneura var. *argentea* PEDLEY
   Acacia aneura var. *argentea* (hybrid)
   Acacia aneura var. *microcarpa* PEDLEY

As noted in MILLER & al. 2002 there is no known morphological character that uniquely defines the Mulga group. However, there are characters which, when used in combination, appear to define the group; some of the more important of these attributes are the following ones (see MILLER & al. 2002 for additional characters):

> New shoots often resinous, invested with short, appressed, normally white hairs and minute, circular, red-brown to blackish resin hairlets.
>
> Phyllodes striate by numerous, fine, closely-spaced, longitudinal nerves (except *A. craspedocarpa* which has reticulately nerved phyllodes).

Flowers arranged in cylindrical spikes or rarely in obloid (= very short cylinder with rounded ends; never globular) heads, the sepals free or shortly united at their base.

Pod flat, normally thin-textured (often ± papery, never woody), commonly reticulately veined and with or without a narrow marginal 'wing'.

Mulga out-group taxa that are mentioned in this paper include the following ones: *A. atopa* PEDLEY, *A. brachystachya* BENTH., *A. catenulata* C.T. WHITE subsp. *occidentalis* MASLIN, *A. coolgardiensis* MAIDEN, *A. effusifolia* MASLIN & BUSCUMB, *A. latior* (R.S. COWAN & MASLIN) MASLIN & BUSCUMB, *A. ramulosa* W. FITZG. var. *linophylla* (W. FITZG.) PEDLEY, *A. subtessaragona* TINDALE & MASLIN and *A. thoma* MASLIN (see Fig. 2).

1.4. The *Leguminosae* Pod (Legumen)

Most *Leguminosae* have flowers with a single carpel containing several ovules along the ventral pod margin. Mature pods of most *Leguminosae* dehisce along both the ventral and the dorsal suture into two equal valves. Tensions in the mechanical tissue (fibre stratum) of the drying pericarp promote dehiscence and (occasionally) results in an explosive release of the seeds (FAHN & ZOHARY 1955, ROBBERTSE 1975, ROTH 1977, DUDIK 1981).

PATE & KUO 1981 described the pod wall (pericarp) of various *Leguminosae* (*Fabaceae*), but did not include *Acacia*. Similar to FAHN & ZOHARY 1955 they distinguished three layers in the pericarp: (1) The exocarp usually comprises an outer (abaxial) epidermis, and perhaps also a hypodermis of one or more layers of thick-walled cells (called stone-cell or sclereid stratum by FAHN & ZOHARY 1955). (2) The mesocarp comprises parenchyma with thin-walled, large vacuolated cells; the main vascular network ('anastomosing network of veins') is situated within the mesocarp. (3) The endocarp comprising a thin-walled inner (adaxial) epidermis and a fibre stratum ('sclerenchyma') just beneath it as inner hypodermis; upon drying of the pod, this fibre stratum contributes to its dehiscence.

1.5. Mulga Pods

The production of pods by Mulga plants is erratic and appears to be closely correlated with the timing and intensity of rainfall events. Similarly, the numbers of pods produced by individual plants is variable, even between individuals of the one species within the same population where some plants may have exceedingly large pod crops while adjacent plants may have few or no pods at all. Following dehiscence Mulga pods are normally readily shed from the plants. These phenomena are not particular to Mulga and are commonly observed in many other Australian arid zone species of *Acacia*.

Typical Mulga pods are flattened, relatively thin-textured (often chartaceous) structures that dehisce into two valves without any twisting tendency. The pod valves have a reticulate venation pattern that may be obscure or pronounced and the nerves may vary from transverse to longitudinal. As can be seen from the descriptions provided by RANDELL 1992, PEDLEY 2001 and MILLER & al. 2002 Mulga pods are variable with respect to their size, colour and indumentum. Unlike the marginal 'wing' which is discussed below, the aforementioned carpological attributes are not especially informative from a taxonomic perspective.

Many (but not all) Mulga pods are invested with a marginal 'wing'. The term 'rimmed' is used for pods that lack a wing (following PEDLEY 2001). Although RANDELL 1992 considered that 'wing' was an incorrect term she, like PEDLEY 2001, MILLER & al. 2002 and ourselves in the present paper use it as convenient descriptor. The wing is a band of tissue of variable width that occurs between the outer margin of the pod and the intramarginal vein that extends around the pod. In the present paper we use the term 'seed-feeding vein' to describe that portion of the intra-marginal vein along the ventral side of the pod because it is from this region that veins supply the placenta of the developing seed via the funicle.

1.6. Aim of Paper

The aims of the present study are twofold:

(1) to describe and discuss the morphological and anatomical characteristics of Mulga pods with particular to their margins;

(2) to discuss the utility of pod characters in relation to the taxonomy of the Mulga group.

2. Material and Methods

Voucher material used for this study has been lodged at the Western Australian Herbarium (PERTH) and the Herbarium of Zurich Universities (Z/ZT). Both herbarium and spirit collections were used with the latter fixed and preserved in 70% ethyl alcohol. For microtome sections, specimens were embedded in Kulzer's Technovit (2-hydroethyl methacrylate), and sectioned with a MICROM HM 355 rotary microtome and conventional microtome knife types C and D. The mostly 7 μm thick sections were stained with ruthenium red and toluidine blue. Vouchers for pod images illustrated in Figs. 1 & 2 are included in the respective captions. Anatomical voucher material used in this study include the following:

Green alliance

Acacia aneura var. *tenuis* (B. R. MASLIN 9441 & 9442)

Acacia aneura var. *tenuis* (?) (B. R. MASLIN, J. MILLER & J. E. REID BRM 9202)

Grey-green alliance

Acacia aneura var. *aneura* (R. HILL 1222)

Acacia aneura var. *aneura* (?) (B. R. MASLIN & J.E. REID BRM 9631)

Acacia craspedocarpa (B. R. MASLIN 9434)
Acacia paraneura (B. R. MASLIN 9436)

Blue alliance
Acacia aneura var. *argentea* (hybrid) (B. R. MASLIN 9433)

3. Results

3.1. General Pod Morphology

In all Mulga species examined the mature pods were laterally flattened and possessed either a wing or rim along their ventral and dorsal sides (Fig. 1). By way of contrast the pods of Mulga out-group taxa are ± terete or quadrangular and never winged (Fig. 2). The Mulga pod wing and rim are discussed in detail below.

Tab. 1 summarizes salient features of Mulga pods that are briefly discussed below based on our examination of selected taxa that typify the range of variation found in the entire group. Mulga pods dimensions are variable, even within a single species, but they are generally about 10–40 mm long and 5–10 mm wide. However, there are notable exceptions such as *A. aneura* var. *macrocarpa* (pods mostly 25–60 x 10–20 mm) and *A. craspedocarpa* (20–60 × 15–30 mm). As shown in Fig 1 and Tab. 1 there is variation in pod colour. In most species the pods are brown to grey-brown, with the colour seemingly influenced to some degree by the density of the indumentum (which comprises minute, white, appressed hairs). In a few species, however, the pods are of a distinctive, different colour, often orange in *A. aneura* var. *tenuis* (Fig. 1B) and yellow in *A. aneura* var. *macrocarpa* (Fig. 1A) and *A. craspedocarpa* (Fig. 1I). Typically Mulga pods are thin-textured (ranging from chartaceous to thinly coriaceous) and pliable. However, in some species such as *A. paraneura* they can be slightly crustaceous while in *A. craspedocarpa* the pods are noticeable thick and rigid, ranging from thickly coriaceous to sub-woody. These textual differences are reflected in the anatomical features of the pericarp as noted below. The pods of all Mulga species are reticulately veined but there is variation in the degree of prominence of the nerves. In many of the taxa (typified by *A. aneura* var. *argentea* and var. *microcarpa*) the anastomosing veins are best described as obscurely to moderately prominent, however, in *A. aneura* var. *tenuis* and *A. aneura* var. *macrocarpa* the veins are often almost absent. At the other end of the spectrum *A. craspedocarpa* has the most pronounced veins; this is the only species of Mulga where the veins are raised above the surface pod. The orientation of the most prominent veins in the reticulum is either mostly transverse (Fig. 1A-B), mostly longitudinal or intermediate (Fig. 1C-I; compare Tab. 1). As already noted the indumentum of Mulga pods, when present, comprises minute, white, appressed hairs which are sometimes obscured by a thin layer of resin (and sometimes intermixed

Table 1. Pod morphological characteristics of selected representatives of the Mulga group that are discussed in the text. Data derived from MASLIN & REID (in prep.) except for *Acacia aneura* var. *aneura* (see footnotes D and E below).

Taxon (arranged by Alliance defined by MASLIN & REID, in prep.)	Figure	Pods							
		Margins		Size (mm)[A]		Texture	Colour	Indumentum	Venation
		Type	Width[B] (mm)	Length (mm)	Width (mm)				
Green Alliance									
Acacia aneura var. *macrocarpa*	1A	Rimmed	to 0.4	(20–) 25–60 (–100)	10–20	Thinly coriaceous	Yellowish to light brown	Glabrous	Obscurely transversely reticulate
Acacia aneura var. *tenuis*[C]	1B, 3D-E, 4A-C	Rimmed	to 0.3	20–45	6–10 (–11)	Chartaceous	Light brown, often tinged orange	Glabrous to subglabrous	± nerveless or obscurely transversely reticulate
Grey-green Alliance									
Acacia aneura var. *aneura*[D]	1E, 3A-C	Winged	to 0.4	to 40	6–10	Chartaceous	Brown	Sparsely hairy	Reticulate
Acacia aneura var. *aneura* (?)[E]	1F, 5C-D	Winged	0.5–1 (–1.5)	(10–) 20–40	5–7 (–11)	Chartaceous to thinly coriaceous	Brown to grey-brown	Hairy	Obscurely longitudinally reticulate
Acacia ayersiana	1G	Winged	1–2	10–40	10–14 (–17)	Chartaceous	Brown to grey-brown	Glabrous or minutely hairy	± obscurely openly reticulate
Acacia craspedocarpa	1I, 6B-C	Winged	1.5–4 (–5)	20–60 (–75)	15–30	Thickly coriaceous to sub-woody	Yellowish to light brown	Sub-glabrous to sparsely-hairy	Openly reticulate, the nerves prominent
Acacia paraneura	1H, 6A	Winged	1–2.5	20–60 (–90)	7–12 (–17)	Thinly coriaceous to ± crustaceous	Greyish brown or red-brown	Sparsely to moderately hairy	± obscurely openly reticulate

Blue Alliance									
Acacia aneura var. *argentea*[F]	1C, 5A-B	Winged	1–2 (–2.5)	10–20 (–30)	(9–) 10–15 (–20)	Firmly chartaceous	Greyish brown	± sparsely hairy	± obscurely reticulate
Acacia aneura var. *microcarpa*	1D	Winged	0.5–1	10–40	(4–) 5–8 (–10)	Chartaceous	Brown to grey-brown	Glabrous or obscurely hairy	± longitudinally reticulate

[A] Pod width values included the marginal wing if present. – [B] Width values are for diameter of rim or wing as measured on inside of pod valve. – [C] Note that the rimmed pod margins shown in Fig. 3D-E belong to a specimen (B. R. MASLIN, J. MILLER & J. E. REID BRM 9202) that we labelled as *"Acacia aneura* var. *tenuis* (?)" because it is similar but not identical to the typical variety. – [D] Variety *aneura* is currently under review by MASLIN & REID; the data presented here for this taxon are taken from PEDLEY 2001 . – [E] What we label here as *"Acacia aneura* var. *aneura* (?)" (B. R. MASLIN & J. E. REID BRM 9631) is similar but not identical to the typical variety. – [F] Data presented here refers only to typical representatives of this highly variable taxon. Note that the pod microtome sections shown in Fig. 5A-B belong to a specimen (B. R. MASLIN 9433) that we labelled as *"Acacia aneura* var. *argentea* (hybrid)" because it appears to be a hybrid quite similar to the typical variety.

with minute, reddish glandular hairlets). The density of the indumentum is variable and appears to have no particular taxonomic significance although in *A. aneura* var. *tenuis* and var. *macrocarpa* glabrous pods seem more common than in most other taxa of the group.

3.2. Characteristics of Mulga Pods with Emphasis on their Margins

The most important carpological character in Mulga is whether or not the pod margins are invested with a wing or a rim (i.e. wingless). However, when viewing the outer surface of the pod it is often difficult to determine with certainty whether or not a wing is present. The most reliable way to assess this character is to split the pod open and examine the marginal zone on the inside of the valve.

3.2.1. Rimmed Mulga Pods

In *A. aneura* var. *macrocarpa* and var. *tenuis* the pods are not winged (Fig. 1A-B), instead they have a rim that extends along both the ventral and dorsal margins (see Fig. 3D-E). As measured on the inside of the valve the differentiated tissue of the rim measures less than 0.5 mm in width. Anatomical details of immature rimmed pods are shown in stained microtome sections of *A. aneura* var. *tenuis* (Fig. 4A–C). These immature pods consist of two valves which closely attach to each other by their inner narrow-celled epidermis. Parenchyma is present in these pod valves forming c. 7–10 cell layers (p in Fig. 4A, C). Continuous layers of narrow-celled sclerenchyma fibres are found just beneath the outer epidermis of the pod valve (see 's' in Fig. 4B–C). This peripheral tissue is better differentiated in nearly mature pods (Fig. 4B–C), less so in young ones (Fig. 4A). Few inconspicuous vascular bundles are found next to this peripheral sclerenchyma (see asterisks in Fig. 4A–B) but do not transcend the smooth outer surface of the pod valves. Mechanical (sclerenchyma) tissue and vascular bundles are more prominent towards the marginal rims. There are about 3 or 4 prominent vascular bundles inside each rim (Fig. 4A–C). Occasionally we found an additional vascular bundle exactly in the center of the marginal rim (see arrowhead in Fig. 4B). This central bundle seems to act as the 'seed-feeding vein' because a funicle (f) supplying an ovule (the latter not shown in section) is derived from it. The margin rims of nearly mature pods (Fig. 4B–C) mainly consist of fibres (sclerenchyma) filling the gaps between the somewhat distinct 3 or 4 vascular bundles. This sclerenchyma is not fully differentiated in immature pods which may even show a longitudinal furrow (see arrows in Fig. 4A). A dehiscence line (i.e. a central thin-walled separation layer) has not yet been observed in these immature rimmed pods, and mature pods were not cut by microtome.

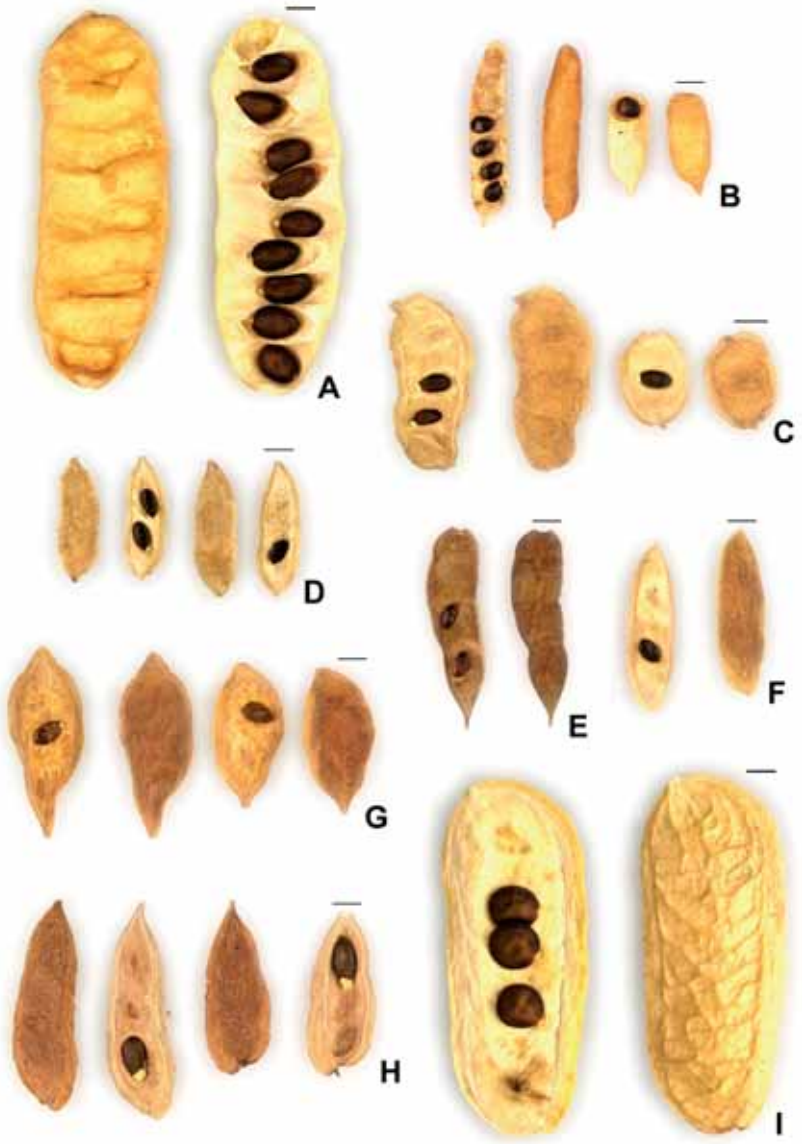

Fig. 1. Mature pods from a selection of Mulga group taxa. – A *Acacia aneura* var. *macrocarpa* (J. E. Reid 6). – B *Acacia aneura* var. *tenuis* (B. R. Maslin, J. Miller & J. E. Reid BRM 9222F). – C *Acacia aneura* var. *argentea* (B. R. Maslin 9932). – D *Acacia aneura* var. *microcarpa* (B. R. Maslin 9913). – E *Acacia aneura* var. *aneura* (R. Hill 1222). – F *Acacia aneura* var. *aneura* (?) (B. R. Maslin 9927). – G *Acacia ayersiana* (S. Midgely 630). – H *Acacia paraneura* (B. R. Maslin 7915). – I *Acacia craspedocarpa* (A. Markey & S. Dillon 4564). – All scales represent 4 mm. Photos Fiona McCallum.

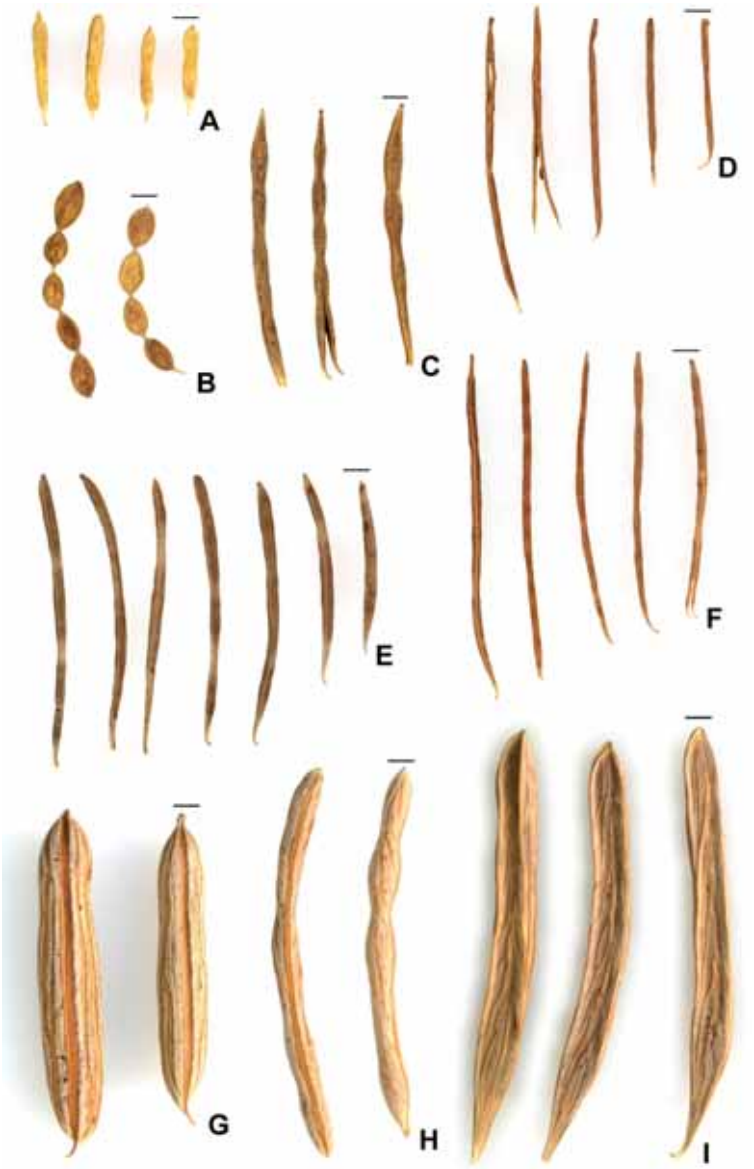

Fig. 2. Mature pods from a selection of Mulga out-group taxa. – A *Acacia atopa* (B. R. Maslin & J. E. Reid BRM 9584). – B *Acacia catenulata* subsp. *occidentalis* (S. van Leeuwen 1291). – C *Acacia thoma* (B. R. Maslin 9077). – D *Acacia coolgardiensis* (B. R. Maslin 7914). – E *Acacia latior* (B. R. Maslin 5076). – F *Acacia effusifolia* (B. R. Maslin 7516). – G *Acacia ramulosa* var. *linophylla* (B. R. Maslin 9068). – H *Acacia brachystachya* (B. R. Maslin 8128). – I *Acacia subtessarogona* (B. R. Maslin, J. Miller & J. E. Reid BRM 9174). – All scales represent 4 mm. Photos Fiona McCallum.

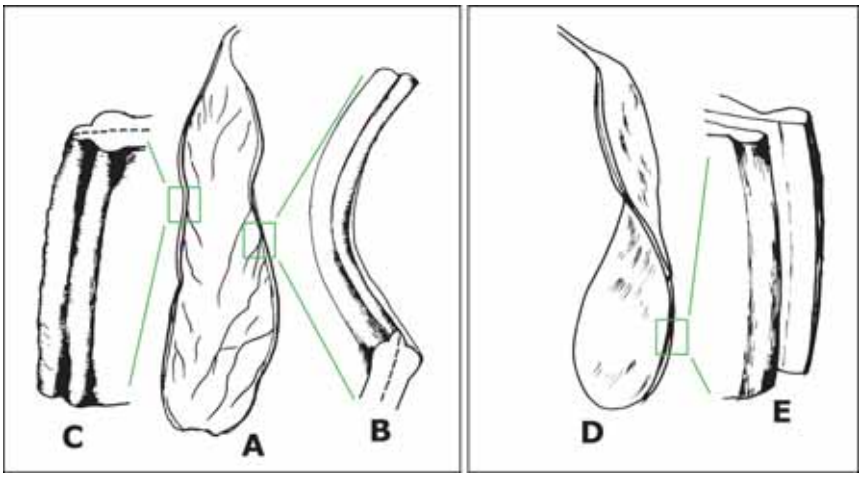

Fig. 3. Line drawings of mature pods of two *Acacia aneura* variants showing different margins types. – A – C *Acacia aneura* var. *aneura* (R. Hill 1222) showing a narrow wing as yellow crest along both pod margins (A: overview, B & C: close-ups of ventral and dorsal margin, respectively). – D & E *Acacia aneura* var. *tenuis* (?) (B. R Maslin, J. Miller & J. E. Reid BRM 9202) showing a simple, slightly raised rim without additional yellow crest (D: overview, E: close-up of margin after dehiscence of valves). – Line-drawings Rolf Rutishauser & Konrad Huber.

3.2.2. Winged Mulga Pods

All remaining Mulga taxa that we studied have pods with a narrow to wide wing along their dorsal and ventral margins (Fig. 1C–I). Anatomical details of winged pods are shown in Figs. 3A–C, 5 and 6, the widest being *A. craspedocarpa* (Figs. 1I, 6B–C) where the wings reach 5 mm across. More normal wing widths are shown by *A. ayersiana* (Fig. 1G), *A. paraneura* (Fig. 1H) and winged varieties of *A. aneura* (e.g. var. *argentea*) where the wings are 1–2.5 mm wide (Fig. 1C–F). The pods of *A. aneura* var. *aneura* (?) have narrow wings which show a dorsiventral asymmetry, with the dorsal one narrower (and nearly lacking) compared to the ventral one (Fig. 5C–D). This dorsiventral asymmetry is not uncommon in other winged Mulga species.

Anatomical details of winged pods are as follows (Figs. 3, 5 and 6). In *A. aneura* var. *argentea* (hybrid) (Fig. 5A–B) and *A. aneura* var. *aneura* (?) (Fig. 5C–D) the tissue arrangement in the pericarp is quite similar to that observed in the rimmed pods of var. *tenuis* (see above). The immature pods consist of two valves which are closely attached to each other by their inner narrow-celled epidermis, except for the spaces filled with young seeds (Fig. 5A–D). Parenchyma is present in the pod valves forming c. 7–10 cell layers (p in Fig. 5A, C) whereas the inner epidermis is accompanied by a

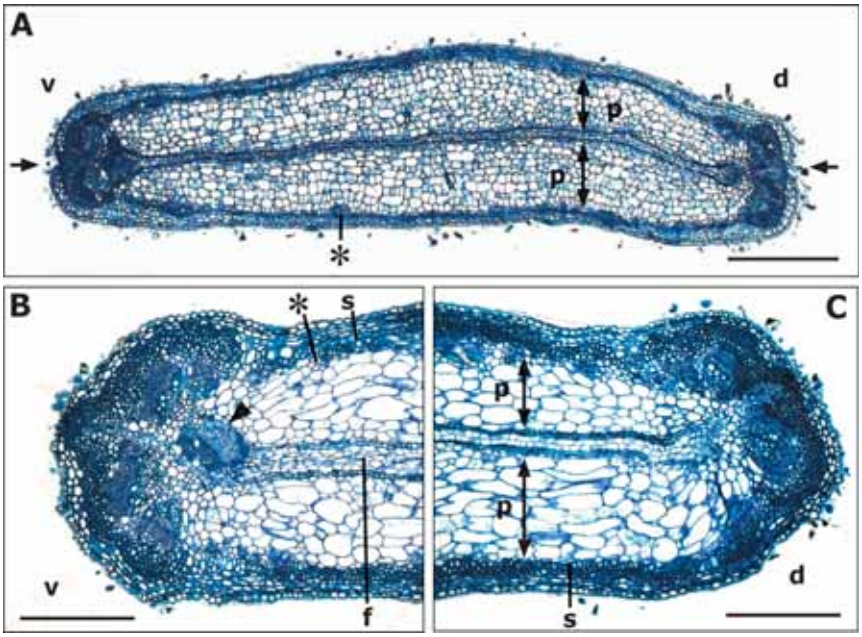

Fig. 4. Transversal microtome sections of rimmed pods of *Acacia aneura* var. *tenuis* (B. R. MASLIN 9441). – A Complete cross-section illustrates marginal rim formation in rather young pod. Note incision of marginal rim on both the ventral (v) and the dorsal (d) side (as indicated by arrows). The two valves are firmly attached to each other. Scale represents 0.5 mm. – B & C Close-ups of the rimmed marginal regions (v = ventral, d = dorsal) of a nearly mature pod. Note presence of prominent vascular bundles (about 3 or 4) inside each marginal rim. An arrowhead points to the vascular bundle that act as 'seed-feeding vein' with a funicle (f) cut longitudinally next to it. The peripheral zone of the valve surfaces contains continuous layers of sclerenchyma fibres (s) with few inconspicuous vascular bundles (see asterisks) next to it. Parenchyma layers of pericarp (valves) are shown by 'p'. – Scales represent 0.25 mm.

hypodermal sclerenchyma layer. A continuous layer of prominent fibres (sclerenchyma) is found adjacent to the outer epidermis of the pod valve. This peripheral mechanical tissue is more differentiated in *A. aneura* var. *aneura* (?) than in *A. aneura* var. *argentea* (hybrid). Few inconspicuous vascular bundles are found next to this peripheral sclerenchyma (see asterisks in Fig. 5A). Notwithstanding the pericarp similarities the winged pod margins of *A aneura* var. *aneura* (?) and *A. aneura* var. *argentea* (hybrid) are completely unlike the rimmed pod margins of *A. aneura* var. *tenuis*. In the former two taxa prominent mechanical tissue (sclerenchyma) and vascular tissue are present adjacent to the pod wings inside a swollen zone (indicated by arrowheads in Fig. 5A–D). This sub-marginal zone is interpreted here as equivalent ('homologous') to the marginal pod rim of *A.*

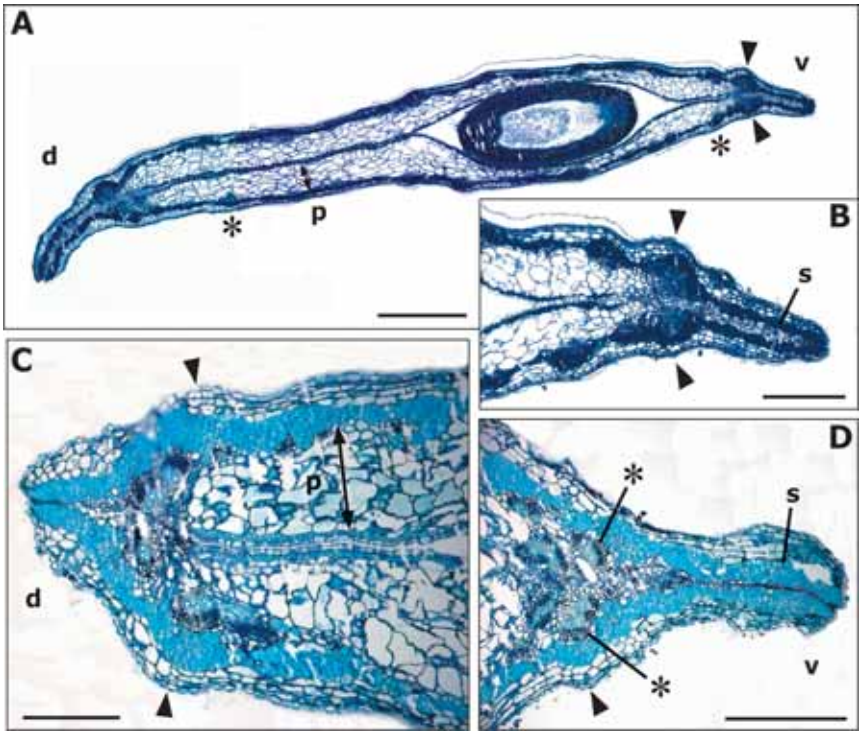

Fig. 5. Transversal microtome sections of winged pods of two *Acacia aneura* variants. – A & B *Acacia aneura* var. *argentea* (hybrid) (B. R. Maslin 9433). – A Complete cross-section illustrates prominent wing formation along both dorsal (d) and ventral (v) margins of immature pod. The two valves attach each other firmly, except for the area that contains a seed. Asterisks indicate weak vascular bundles in pod valves below continuous hypodermal sclerenchyma layer. Parenchyma layers of pericarp (valves) are shown by 'p'. Scale represents 1mm. – B Close-up of the ventral marginal region (with wing) of pod shown above. The 'seed-feeding vein' actually consists of two vascular bundles inside the sub-marginal swollen zone (marked with arrowheads) which are more prominent than additional bundles along the valve surfaces (indicated by asterisks in A). The wing tissue beyond the 'seed-feeding vein' consists of two layers of sclerenchyma (stained dark) with unlignified small-celled tissue ('dehiscence line') in between and additional parenchyma layers towards the periphery. Sclerenchyma tissue is shown by 's'. Scale represents 0.25 mm. – C & D *Acacia aneura* var. *aneura* (?) (B. R. Maslin & J. E. Reid BRM 9631). Close-up of dorsal (C) and ventral (D) margins of nearly mature pod. The dorsal wing is only narrow whereas the ventral one is wide. Two layers of lignified sclerenchyma (s) enter the marginal wing regions, with crashed unlignified cells ('dehiscence line') in between. Note complex of vascular tissue which is separated into 2–4 separate bundles in region of 'seed-feeding vein' (marked with arrowheads) below sclerenchyma. Asterisks indicate additional weak vascular bundles of pod valves below continuous hypodermal sclerenchyma layer. – Scales represent 0.25 mm.

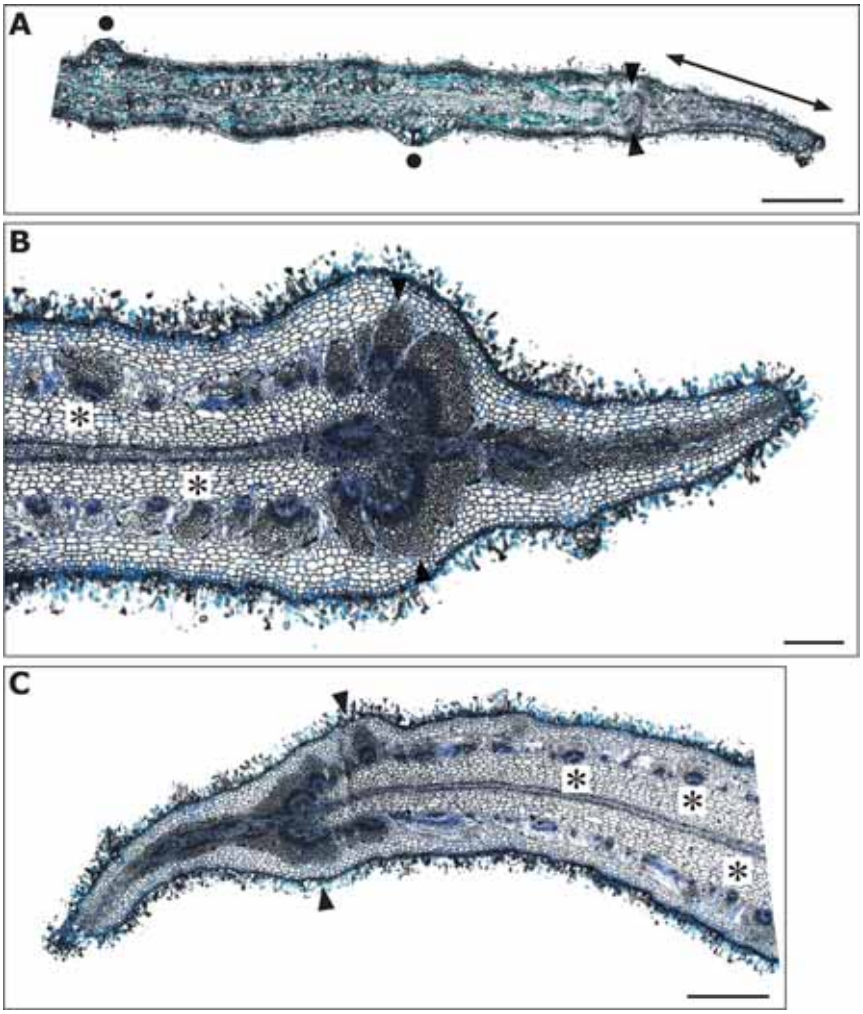

Fig. 6. Transversal microtome sections of winged pods of two Mulga group species. – A *Acacia paraneura* (B. R. Maslin 9436). Portion of cross-section of nearly mature pod. Note presence of a wide wing (indicated by double-arrow), including region of vascular tissue forming the 'seed-feeding vein' (marked with arrowheads). Black circles indicate tubercle-like swellings on the outer pod surfaces. Scale represents 1 mm. – B & C *Acacia craspedocarpa* (B. R. Maslin 9434). Portions of cross-sections through immature pod, showing close-ups of ventral (B) and dorsal (C) pod margin with wide wings. Note complex of vascular tissue adjacent to the wing (marked with arrowheads), surrounded by narrow-celled sclerenchyma. Note also presence of many minor vascular bundles inside surface of pod valves (some indicated by asterisks). Outer surfaces of valves and wings densely covered by hairs. – Scales represent 0.25 mm (B) and 0.5 mm (C).

aneura var. *tenuis* (Fig. 4). In the winged pods it is quite difficult to separate the sub-marginal vascular complex into single bundles (as indicated by asterisks in Fig. 5D). However, it is this sub-marginal vascular region that contains the 'seed-feeding vein' on the ventral ('v') side of the pod (Fig. 5A). Typical Mulga pod wings protrude beyond the swollen sub-marginal zone and resemble a 'bird's beak' when viewed in cross-section (Fig. 5B, D). In species such as *A. paraneura* and *A. craspedocarpa* which have very wide wings the area beyond the sub-marginal zone resembles an elongated 'bird's beak' when viewed in cross-section (Fig. 6A-C). The wings usually do not contain vascular tissue. They mainly consist of two sclerenchyma layers (one per valve) and a central thin-walled separation layer in between that serves as the dehiscence line (Fig. 5B-D). The wings show unlignified peripheral layers, i.e. an outer epidermis and about 2–3 layers of hypodermal parenchyma.

Narrow pod wings such as those found in *A. aneura* var. *aneura* (?) (Fig. 5C-D) are anatomically identical to wide pod wings that occur in species such as *A. paraneura* (Fig. 6A). In a few cases the pod wings are extremely reduced and as such require particular comment. In *A. aneura* var. *aneura* (?) for example, the wing zone of the dorsal margin is inconspicuous but still present as an often yellowish crest that protrudes beyond the usually brown sub-marginal swollen zone (i.e. resembling a very short 'bird's beak' in cross-section, Fig. 5C). Very narrow wings similar to those found in *A. aneura* var. *aneura* (?) occur along both the dorsal and ventral pod margins in *A. aneura* var. *aneura*, and here again a short yellowish crest of tissue protrudes beyond the usually brown sub-marginal swollen zone (as illustrated by drawings in Fig. 3A-C). Anatomically these extremely narrow wings which are identified by their very short marginal crest line (forming a 'bird's beak') are different structures from the rimmed pod margins of *A. aneura* var. *tenuis* (Fig. 3D-E) even though the two may macroscopically look superficially very similar.

Acacia craspedocarpa has especially wide pod wings (1.5–5 mm, Fig. 1I; see Tab. 1). Anatomically the pods of this species have many clearly distinct vascular bundles that are differentiated inside the pericarp (valve) parenchyma; each bundle is provided with a prominent sclerenchyma (fibre) cap towards the outer periphery (indicated by asterisks in Fig. 6B–C). It is probably due to the lack of a continuous sclerenchyma layer (i.e. lack of a continuous stone-cell stratum sensu Robbertse 1975) that the various vascular bundles are present as very conspicuous and raised veins in the pods of this species. In most other Mulga group members that show continuous sclerenchyma layers, the valve bundles are less prominent (or at least less visible) on the pod surface. In *A. craspedocarpa* this layer of pericarp (valve) bundles gradually continues into a very well differentiated vascular complex along both the dorsal and ventral pod margin. This bow-

shaped vascular complex consists of about 5–7 not clearly separated vascular bundles and is situated inside the swollen sub-marginal zone which again resembles a 'bird's beak', when seen in cross-section (Fig. 6B). Typical for *A. paraneura* are (besides few hairs) tubercle-like swellings ('warts') on the outer pod surfaces (indicated by black circles in Fig. 6A), whereas the pod valves of *A. craspedocarpa* have outer surfaces that are hairy with mixed simple and glandular hairs (Fig. 6B–C).

4. Discussion

Although this is not a comprehensive morpho-anatomical study of Mulga pods the taxa examined here do represent the major pod types and illustrate the main variational trends that exist within the group. Therefore, the information presented in this paper provides a good basis for anticipated more detailed studies in the future.

4.1. General Mulga Pod Morphology

The pods of all Mulga group taxa are laterally flattened and possessed either a wing or rim along on their ventral and dorsal sides. By way of contrast the pods of Mulga out-group taxa are ± terete or quadrangular in cross-section and are never winged (compare Figs. 1 and 2). Furthermore, the pods of the out-group taxa are more elongate than those of the Mulga group (i.e. they have a greater length : width ratio). This pod cross-sectional shape as well as length : width characters are very useful from a taxonomic perspective in identifying members of the Mulga group. They will be discussed, together with other morphological attributes, by MASLIN & REID (in prep.).

With the exception of *A. craspedocarpa* the pods of all species of the Mulga group are rather thin-textured, ranging from chartaceous to thinly coriaceous or slightly crustaceous, and somewhat obscurely reticulately veined. Thin-textured pods are commonly found in many other Australian species of *Acacia*. As shown in Tab. 1 Mulga pods vary considerably with respect to their size but most are relatively short and moderately broad. In a study of Mulga from Leonora, Western Australia, CODY 1989 quantified co-variation between phyllode and pod morphology and observed that "wider pods are found chiefly on individuals with wider and somewhat shorter phyllodes." However, results of the present study and those of MASLIN & REID (in prep.) which use a more representative sample of the variation in Mulga, illustrate that this correlation does not hold true across the entire group. Mulga pods also vary in their colour (often brown to grey-brown) and indumentum (often sparsely to moderately minutely appressed-hairy) and these attributes are not especially informative from a taxonomic perspective. Nevertheless, the above characters can be useful in helping to recognize certain Mulga taxa, for example, in *A. aneura* var.

microcarpa the pods are often narrow, in *A. aneura* var. *macrocarpa* they are wide and commonly yellow while in *A. aneura* var. *tenuis* the pods are often orange, glabrous and very obscurely nerved.

Acacia craspedocarpa differs from the other Mulga group taxa in having thick-textured (coriaceous to sub-woody) pods that are very prominently reticulately veined (it is the only member of the group where the veins are significantly raised above the surface of the pod). It also has the widest pod wings of any Mulga species (1.5–5 mm). Despite these differences the basic structure of the *A. craspedocarpa* winged pod clearly shows that it is closely related to other members of the group. Nevertheless, *A. craspedocarpa* differs significantly from other members of the Mulga group in another way, namely, its reticulately veined phyllodes (parallel veined in all other members of the group). This character influenced MILLER & al. 2002 to exclude *A. craspedocarpa* from their 'Mulga core group', instead placing it with out-group taxa such *A. ramulosa*. However, judging from our pod data *A. craspedocarpa* is more correctly placed within the Mulga group, within the Grey-green alliance (see below).

4.2. Interpretation of Mulga Pod Wings and Rims

The pods of Mulga species posses either a rim (following the terminology of PEDLEY 2001) or a wing along their ventral and dorsal sides. As can be seen from the discussions below these pod margin characters are the most important carpological features of Mulga pods from both a taxonomic and phylogenetic viewpoint. Although a majority of Mulga species have winged pods this character alone does not define the group. RANDELL 1992 considered that 'wing' was an inappropriate term to use in relation to Mulga pods, but for convenience sake continued to use the term as did PEDLEY 2001 and MILLER & al. 2002. We too regard the term wing as a convenient descriptor. Based on evidence from the present preliminary study of Mulga pods, it appears that the rim and the wing are anatomically equivalent ('homologous') structures even though morphologically they normally look quite dissimilar.

It is often difficult to determine with certainty the margin type (rim or wing) from an external examination of the pod valve. The best way to assess this character is to split the pod open and examine the marginal zone on the inside of the valve because there the differentiated tissue of the wing or rim is readily visible. Normally the wing tissue is clearly broader than that of the rim, commonly about 1–2 mm and 0.2–0.4 mm wide respectively. However, in a few taxa the wings are extremely reduced (about 0.5 mm wide) and in these cases it can be very difficult deciding on the margin type. *Acacia aneura* var. *aneura* is a case in point. Specimens of this taxon which correspond to some of those from the type locality (i.e. Flinders Range, South Australia) have extremely narrow wings that super-

ficially could be misinterpreted as a rim. However, close inspection of the pod marginal zone shows a sub-marginal vein located about 0.5 mm internal from the edge of the pod. Because of this vein and its location the pod margins assume a 'beveled' appearance when viewed externally. When viewed in cross-section the region between the intra-marginal vein and the margin protrude as a short yellowish crest of tissue that extends the length of the pod (see Fig. 3A–C). Anatomically these very narrow wings are identical to broad pod wings and understanding this homology can have important taxonomic implications. For example, MASLIN & REID (in prep.) consider *A. aneura* var. *intermedia* PEDLEY which was described as having wings 'usually at least 1 mm wide' (PEDLEY 2001) to be conspecific with *A. aneura* var. *aneura*.

4.3. Correlation of Pod Anatomy with Major Groupings of Mulga Taxa

Pod marginal characteristics together with branchlet resin type are seminal features used by MASLIN & REID (in prep.) to define major species assemblages within the Mulga group. These assemblages are the Blue alliance (winged pods, opaque resin), the Grey-green alliance (winged pods, translucent resin) and the Green alliance (rimmed pods, translucent resin). These alliances appear to be robust because most Mulga taxa can confidently be assigned to one or other of them, and furthermore, they are broadly supported by genetic data (MILLER, pers. comm.). Further discussion of these Mulga alliances will be presented in MASLIN & REID (in prep.).

5. Acknowledgments

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