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The systematic significance of morphological and anatomical variation in fruits of *Crotalaria* and related genera of tribe Crotalarieae (Fabaceae)

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The phylogenetic and taxonomic significance of morphological and anatomical trends in fruits of tribe Crotalarieae has been evaluated, with emphasis on the genus *Crotalaria* and its seemingly distinctive, inflated and balloon-shaped pods. In addition to the normal explosive dehiscence as a means of dispersal, several genera (including *Crotalaria*) show independent evolution of modifications apparently adapted for dispersal by wind, water and gravity. Transverse sections were made of mature pods of 142 species from the 12 currently recognized genera of Crotalarieae. The taxa differ in the orientation of the fibres (related to dehiscence or non-dehiscence), the overall thickness of the fruit wall, the relative proportions of the pericarp layers, the degree of lignification and the presence or absence of trichomes. Three basic pericarp types can be distinguished: type I, with one, two or three zones of various numbers of cell layers of fibres (almost all genera); type II, with a single cell layer of fibres (only in *Rothia, Robynsiophyton, Lebeckia* and *Lotononis* sections *Listia* and *Leobordea*); and type III, with one zone of several cell layers of gelatinous fibres and multicellular trichomes associated with the endocarp (only in some species of *Calobota* and *Wiborgiella*). Considerable variation was encountered in the tribe, but *Crotalaria* appears to be rather uniform, with type I predominating.

ADDITIONAL KEYWORDS: anatomy – dehiscence – endocarp – exocarp – fibres –indehiscence – mesocarp – rattlepod – wind-dispersal.

INTRODUCTION

Crotalarieae (Benth.) Hutch. are the largest tribe of papilionoid legumes in Africa (Polhill, 1968; Van Wyk & Schutte, 1995) with *c.* 1204 species (Van Wyk, 2005). The tribe is closely related to Genisteae Bronn and Podalyrieae Benth., all of which form part of the genistoid alliance (*sensu* Polhill, 1976), more specifically the core genistoids (Crisp, Gilmore & Van Wyk, 2000). The monophyly of Crotalarieae is well supported by molecular, morphological, cytological and chemical data (Van Wyk & Schutte, 1995; Crisp *et al.*, 2000; Wink & Mohamed, 2003; Boatwright *et al.*, 2008a; Boatwright, Tilney & Van Wyk, 2009). Combined analyses of molecular and morphological data of this tribe indicated that there are three clades and, because of the polyphyly of some of the genera, changes at the generic level resulted in 12 genera being recognized (Boatwright *et al.*, 2008a, 2009). Crotalarieae (Fig. 1) comprise three clades. The 'Cape' clade includes six genera: (1) *Aspalathus* L.; (2) *Wiborgia* Thunb.; (3) *Wiborgiella* Boatwr. & B.-E.van Wyk; (4) *Calobota* Eckl. & Zey.; (5) *Lebeckia* Thunb; and (6) *Rafnia* Thunb. The poorly known *Lotononis macrocarpa* Eckl. & Zeyh. on its own represents a

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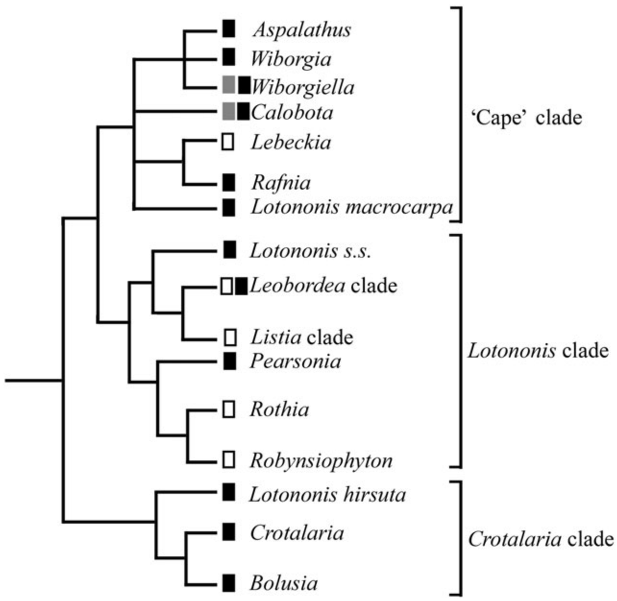

Figure 1. Pericarp structure indicated on a phylogenetic tree for tribe Crotalarieae: type I pericarp (black rectangle); type II pericarp (grey rectangle); type III pericarp (white rectangle).

seventh lineage in this clade. The *Lotononis* clade includes four genera (Boatwright, Wink & Van Wyk, in press): (1) *Lotononis* (DC.) Eckl. & Zeyh.; (2) *Pearsonia* Dümmer; (3) *Robynsiophyton* R.Wilczek; and (4) *Rothia* Pers. The *Crotalaria* clade includes: (1) *Lotononis hirsuta* (Thunb.) D.Dietr.; (2) *Crotalaria* L.; and (3) *Bolusia* Benth. (Boatwright *et al*., 2008a). All of these lineages have recently been given generic status and the necessary nomenclatural changes have been proposed (Boatwright *et al*., in press). As the concepts are not yet formalized, we refer to the groups as the *Lotononis hirsuta* clade (genus '*Euchlora*' in Boatwright *et al*., in press), the *Listia* clade (genus '*Listia*' in Boatwright *et al*., in press), the *Leobordea* clade (genus '*Leobordea*' in Boatwright *et al*., in press) and the *Lotononis macrocarpa* clade (genus '*Ezoloba*' in Boatwright *et al*., in press).

Crotalaria, *Bolusia* and *Lotononis hirsuta* together form the sister group of the remainder of tribe Crotalarieae and include > 700 species, widely distributed across the southern hemisphere. Approximately 500 species are endemic to Africa and Madagascar (Polhill, 1982). *Crotalaria* is commonly known as 'rattlepod' because of the sound produced by the ripe seeds when the inflated fruits are shaken. The generic name is derived from the Greek word *crotalon* (*κροταλου*), which means castanet, also referring to this rattling sound. Polhill divided the genus into eight sections based on taximetric analyses (Bisby, 1973; Bisby & Polhill, 1973, Polhill 1982) of morphological, chemical and seed anatomical characters.

Kirkbride, Gunn & Weitzman (2003) published generic descriptions of the fruit morphology and some anatomy for the papilionoid legumes. The pericarp anatomy and dehiscence mechanisms have been described several times for the family (Fahn & Zohary, 1955; Esau, 1962; Fahn, 1967, 1982; Pate & Kuo, 1981). The pericarp consists of an exocarp (single epidermal cell layer), mesocarp (multiple parenchyma and collenchyma cell layers) and endocarp (single or multiple sclerenchyma cell layers with a single inner epidermal cell layer, or multiple parenchyma cell layers with a single epidermal cell layer). Dehiscence is caused by the anisotrophic shrinkage of thickened cell walls in the pericarp. The greatest expansion is at right angles to the longitudinal axis of the fruits and microfibrils. When fruits mature, the cell walls dry out and shrink, causing an explosion. Variations of the pericarp structure and modes of dehiscence are numerous (Fahn & Zohary, 1955; Fahn, 1982).

With the clarification of phylogenetic relationships within Crotalarieae (Boatwright *et al*., 2008a), an opportunity exists to evaluate potentially useful taxonomic characters further. As *Crotalaria* is now known to be one of the early diverging lineages, a comparison of the fruit morphology and anatomy with other genera was expected to yield phylogenetically informative results. This study is aimed at determining the taxonomic value of pericarp anatomical structure at the generic level within Crotalarieae, and at the sectional and species levels, with emphasis on the genus *Crotalaria*. Furthermore, we wished to evaluate the overall pattern in the evolution of fruits in the tribe and explore possible links between the structure of the fruits and the main adaptations to seed dispersal: dehiscence, where the seeds are expelled, or indehiscence, where the whole fruit (diaspore) is dispersed by wind, water or gravity. Anatomical features of dehiscence mechanisms in the tribe were also investigated and compared with those that have previously been reported for legumes in general.

MATERIAL AND METHODS

Taxon sampling

Fruits of 142 species from all 12 genera of Crotalarieae and two of Genisteae were obtained through fieldwork and from specimens from the following herbaria: BOL, JRAU, K, MEL, NBG (including SAM), PRE, UPS and WIND. This sampling represents all or most of the taxonomic diversity in Crotalarieae and also the extremes of the variation in the individual genera. Two species of Genisteae, one of *Dichilus* DC. and one of *Melolobium* Eckl. & Zeyh., were sampled as outgroup taxa. In molecular systematic studies

Figure 2. Morphological variation of fruits in Crotalarieae: A, *Aspalathus linearis* [*Van Wyk 3617* (JRAU)]; B, *Wiborgia monoptera* [*Schutte 296* (JRAU)]; C, *Wiborgiella leipoldtiana* [*Van Wyk et al. 3278* (JRAU)]; D, *Calobota sericea* [*Van Wyk et al. 2353* (JRAU)]; E, *C. cuspidosa* [*Boatwright et al. 92* (JRAU)]; F, *Lebeckia sepiaria* (L.) Thunb. [*Van Wyk et al. 2979* (JRAU)]; G, *L. ambigua* [*Van Wyk et al. 2900* (JRAU)]; H, *Rafnia capensis* [*Campbell et al. 11* (JRAU)]; I, *Pearsonia sessilifolia* [*Van Wyk et al. 3192* (JRAU)]; J, *P. cajanifolia* [*Posthumus 1a* (JRAU)]; K, *Lotononis densa* [*Van Wyk 3122* (JRAU)]; L, *L. globulosa* [*Van Wyk 2211* (JRAU)]; M, *L. listii* [*Schutte 354* (JRAU)]; N, *L. subulata* [*Van Wyk 2884* (JRAU)]; O, *L. macrocarpa* [*Schlechter 4925* (BOL)]; P, *L. benthamiana* [*Van Wyk 2538* (JRAU)]; Q, *L. hirsuta* [*Van Wyk 1338* (JRAU)]; R, *Bolusia amboensis* [*Boatwright et al. 248* (WIND)]; S, *Crotalaria lotoides* [*Germishuizen 3790* (PRE)]; T, *C. damarensis* [*Germishuizen 9247* (PRE)]; U, *C. vasculosa* [*De Winter 9460* (PRE)]; V, *C. pisicarpa* [*Le Roux et al. 79* (WIND)]; W, *C. longidens* Burtt Davy ex Verdoorn [*Le Roux et al. 101* (JRAU)]; X, *C. virgulata* [*Van Wyk 3044* (JRAU)]; Y, *C. laburnifolia* [*Van Wyk et al. 4334* (JRAU)]. Scale bar, 10 mm.

(Crisp *et al.*, 2000; Boatwright *et al.*, 2008b), these two southern African genera were the earliest divergent lineages in Genisteae. They may show the original character states for Genisteae, avoiding the complication of having to consider further possible modifications higher up in the phylogenetic tree. Voucher specimen information is listed in the Appendix. Author citations for the individual species are also listed in the Appendix.

Anatomy

Anatomical sections were performed both by hand and with a Porter-Blüm ultramicrotome. For microtome sections, material of 83 species was prepared using a modification of the method of Feder & O'Brien (1968) for embedding in glycol methacrylate (GMA). This involved a final infiltration in GMA for 5 days. Dried material was rehydrated and fixed in formaldehyde–acetic acid–**a**lcohol (FAA; formaldehyde:acetic acid:96% alcohol:water; 10:5:50:35) for 24 h, whereas fresh material was directly fixed in FAA before dehydrating and embedding in GMA. Sections of 3–5 μm were cut and stained using the periodic acid Schiff/toluidine blue (PAS/TB) staining method (Feder & O'Brien, 1968) and mounted. Photographs were taken with a JVC KY-F1030 digital camera. For hand sections, fruit material of 61 species was rehydrated in hot water for approximately 15 min, sectioned with a sharp blade, stained with toluidine blue and scanned for diagnostic characters.

RESULTS

Fruit morphology in tribe Crotalarieae was found to be variable. Figure 2 illustrates some of the variation that was observed in the different genera in terms of size, shape, degree of inflation, presence or absence of a stipe, vestiture, presence or absence of a margin or wing and constrictions between the seeds. Fruits of *Crotalaria* are generally larger than those of most other genera and are typically much inflated or balloon-shaped (there are a few exceptions, e.g. *C. coursii* M.Peltier, *C. cytisoides* DC., *C. leptocarpa* Balf.f. ssp. *leptocarpa*, *C. leptocarpa* Balf.f. ssp. *contracta* Polhill and *C. linearifoliolata* Chiov., which have laterally compressed fruits), with the base and/or apex rounded and bulging. Similar fruits occur in the related genus *Bolusia* and in *Lotononis hirsuta*. The fruit may rarely also be small in *Crotalaria* (e.g. *C. vasculosa* Graham and *C. pisicarpa* Welw. ex Baker, Fig. 2U and V, respectively) and similar in size to those of other genera in the tribe. *Crotalaria* fruits in general lack adaptations to wind dispersal (except in a few species where the calyx is persistent, e.g. *C. berteroana* DC., *C. chinensis* L., *C. dubia* Graham and *C. sessiliflora* L.) as seen in other genera (Fig. 3). *Wiborgia*, for example, has fruits with broad wings (Figs 2B and 3E) and similar but narrower wings are found along the upper suture in *Lebeckia meyeriana* Eckl. & Zeyh. (Fig. 3I). Fruits of *Lotononis* section *Digitata* B.-E.van Wyk (Fig. 3A, D) and *L.* section *Synclistus* B.-E.van Wyk (Fig. 3B, C) have small, lightweight, indehiscent fruits with persistent calyces and corollas so that they are easily blown about by the wind. The species of section *Digitata* grow almost exclusively in the cracks of large granite domes, and in this habitat the fruits are highly mobile and easily 'caught' in the cracks (B.-E. van Wyk, pers. observ.). Another adaptation is the 'rolling' fruits of section *Synclistus* (e.g. *L. longicephala* B.-E.van Wyk, Fig. 3B and *L. polycephala* Benth., Fig. 3C). These species occur in bare sandy habitats (mostly inland sand dunes) and the fruits are rolled around by the wind (B.-E. van Wyk, pers. observ.). Similar are the fruits of *Calobota elongata* (Thunb.) Boatwr. & B.-E.van Wyk, also an inhabitant of inland sand dunes. This is the only species of *Calobota* with small, indehiscent, single-seeded fruits enclosed in a persistent calyx and corolla. The similarity with species of *Lotononis* section *Synclistus* is striking. A few species of *Crotalaria* are similar in having small, indehiscent, few-seeded pods that appear to be adapted to dispersal by wind, water or gravity, perhaps with a rolling action.


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Figure 3. Fruits with different dispersal methods in Crotalarieae. (A–D) and (H) show a series of three photographs where the fruits are firstly enclosed in persistent calyx and corolla, secondly where the calyx and corolla are removed and thirdly where the fruit is opened. (E–G) and (I) show a series of two photographs where the fruits are firstly closed and secondly opened. A, *Lotononis digitata* [*Van Wyk 2341* (JRAU)]; B, *L. longicephala* [*Van Wyk 2241* (JRAU)]; C, *L. polycephala* [*Van Wyk 2394* (JRAU)]; D, *L. benthamiana* [*Van Wyk 2538* (JRAU)]; E, *Wiborgia fusca* [*Van Wyk 3213* (JRAU)]; F, *Crotalaria sphaerocarpa* [*Le Roux et al. 74* (WIND)]; G, *C. pisicarpa* [*Le Roux et al. 78* (WIND)]; H, *Calobota elongata* [*Van Wyk 2562b* (JRAU)]; I, *Lebeckia meyeriana* [*Van Wyk 3351a* (JRAU)]. Scale bar, 5 mm.

As *Crotalaria* fruits are typically much inflated, it is of interest to consider the overall pattern in the tribe. The shape of the fruit in transverse section is determined by the orientation of the upper and lower sutures, which can be raised or sunken in various combinations, as shown in Figure 4. In *Crotalaria*, the fruits are often perfectly round in transverse section (Fig. 4O, L) or they may be ellipsoid (Fig. 4H), cordate (Fig. 4K) or somewhat didymous when both the upper and lower sutures are sunken (Fig. 4N). Inflated fruits are also found in other genera of the tribe and are thus not unique to *Crotalaria*. *Bolusia* (Fig. 4Q), *Lotononis hirsuta* (Fig. 4P), *Wiborgiella* and several other species of *Lotononis* have inflated fruits (Fig. 4E, F). In *Crotalaria* section *Hedriocarpae* Wight & Arn., some species have the seeds surrounded by trichomes, which often fill the cavity completely (Fig. 4J). The same is true for species of *Calobota* (Fig. 4C, D). In *Crotalaria* section *Chrysocalycinae* (Benth.) Bak.f. subsection *Glaucae* (Benth.) Bisby & Polhill and section *Crotalaria* subsection *Longirostres* (Benth.) Polhill, a few species have a line of trichomes inside the fruit along the lower suture. Superficially, the species of *Calobota* (Fig. 4C, D) are similar to some species of *Lebeckia* (Fig. 4A, B) in having inflated, spongy fruits, but these are not homologous: the spongy texture is because of spongy parenchyma in the mesocarp in *Lebeckia*, whereas it is because of a dense layer of endodermal trichomes in *Calobota*.

Diagnostically informative characters of the pericarp that were identified include the number of fibre cell layers in the endocarp, the type of fibres and the presence or absence of multicellular trichomes composing the endocarp cells. Three basic fruit types were identified:

1. Type I – one, two or three zones of various numbers of cell layers of fibres within the endocarp; trichomes (formed from the endocarp cells) occasionally present.
2. Type II – single cell layer of normal fibres within the endocarp; trichomes absent.
3. Type III – one zone of several cell layers of gelatinous fibres; trichomes (formed from the endocarp cells) invariably present.

A short fruit anatomical description for each genus is given below (summarized in Table 1) with an indication of the classification of the fruit wall type (fruit type classification for all species investigated is listed in the Appendix). The distribution of fruit wall types within the tribe is shown in Figure 1.

GENERIC FRUIT ANATOMICAL DESCRIPTIONS

'Cape' clade – type I and type III fruit walls are present

Aspalathus: Fruits relatively uniform, thick-walled (Fig. 5A–C). *Exocarp*: Epidermal cells with highly thickened cell walls; mucilage cells absent. *Mesocarp*: Only collenchyma cells present. *Endocarp*: One or two zones of various numbers of cell layers of fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

Wiborgia: Fruits relatively thin- to thick-walled (Fig. 5D, E). *Exocarp*: Epidermal cells with slightly thickened cell walls; mucilage cells absent. *Mesocarp*: Only parenchyma cells present. *Endocarp*: One or two zones of various numbers of cell layers of fibres arranged in one direction, parallel to the longitudinal axis of the fruits, or two directions, parallel and perpendicular to the longitudinal axis of the fruits; trichomes absent.

Wiborgiella: Fruits thick-walled (Fig. 5F–I). *Exocarp*: Epidermal cells with slightly to highly thickened cell walls; mucilage cells present or absent. *Mesocarp*: Parenchyma and collenchyma cells present or only collenchyma cells present. *Endocarp*: One or two zones of various numbers of cell layers of fibres or one zone (except *W. vlokii* Boatwr. & B.-E.van Wyk, with two zones) of several cell layers of gelatinous fibres arranged in one direction, parallel or at 45° angle to the longitudinal axis of the fruits; trichomes mostly absent (but present in *W. inflata* (Bolus) Boatwr. & B.-E.van Wyk and *W. bowieana* (Benth.) Boatwr. & B.-E.van Wyk, Fig. 5G and H, respectively). *Wiborgiella humilis* (Thunb.) Boatwr. & B.-E.van Wyk has exceptionally thin-walled fibre cells (Fig. 5F).

Calobota: Fruits relatively thin- to thick-walled (Fig. 6A–I). *Exocarp*: Epidermal cells with slightly to


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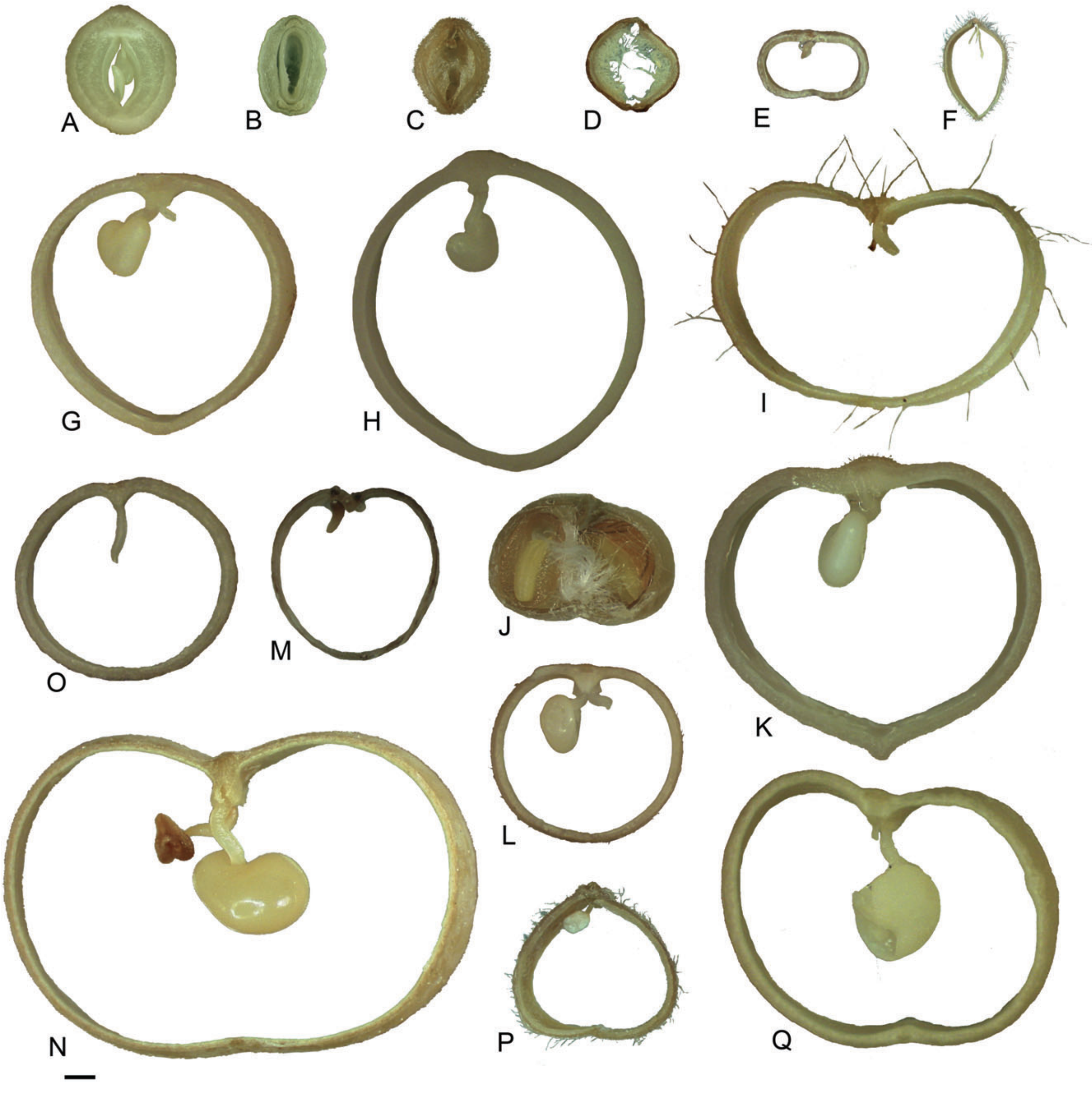

Figure 4. A comparison of inflated fruits in Crotalarieae. A, *Lebeckia brevicarpa* [*Le Roux et al. 4* (JRAU)]; B, *L. pauciflora* [*Le Roux et al. 12* (JRAU)]; C, *Calobota cinerea* [*Boatwright et al. 150* (JRAU)]; D, *C. thunbergii* [*Boatwright et al. 140* (JRAU)]; E, *Lotononis nutans* [*Van Wyk 3442* (JRAU)]; F, *L. pungens* [*Vlok 1646* (JRAU)]; G, *Crotalaria laburnifolia* [*Van Wyk et al. 4333* (JRAU)]; H, *C. damarensis* [*Le Roux et al. 65* (WIND)]; I, *C. obscura* [*Le Roux et al. 109* (JRAU)]; J, *C. somalensis* [*Gillett 21175* (PRE)]; K, *C. argyraea* [*Le Roux et al. 82* (WIND)]; L, *C. flavicarinata* [*Le Roux et al. 72* (WIND)]; M, *C. excisa* [*Le Roux et al. 108* (JRAU)]; N, *C. recta* [*Le Roux 42* (JRAU)]; O, *C. virgulata* [*Le Roux et al. 38* (JRAU)]; P, *Lotononis hirsuta* [*Van Wyk 1338* (JRAU)]; Q, *Bolusia amboensis* [*Boatwright et al.* 248 (WIND)]. Scale bar, 1 mm.

highly thickened cell walls; mucilage cells absent. *Mesocarp*: Parenchyma and collenchyma cells present or only collenchyma cells present. *Endocarp*: One or rarely two zones of various numbers of cell layers of fibres or one zone of several cell layers of gelatinous fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes only present in fruits with gelatinous fibres.

Table 1. Summary of pericarp characters of *Crotalaria* and all other genera of the tribe Crotalarieae (and two genera of the tribe Genisteae). Authorities for the names of taxa and data for the individual species of each genus are provided in the Appendix. Type I – one, two or three zones of various numbers of cell layers of fibres within the endocarp; trichomes (formed from the endocarp cells) occasionally present. Type II – single cell layer of normal fibres within the endocarp; trichomes absent. Type III – single zone of several cell layers of gelatinous fibres; trichomes (formed from the endocarp cells) invariably present

	Pericarp	Exocarp		Mesocarp		Fruit type
Genus and infrageneric group (where available)	Fruit wall thickness – thin (< 140 μm) + thick (> 140 μm)	Cell walls – thin + thick	Mucilage – absent + present	Parenchyma – absent + present	Collenchyma – absent + present	+ Type I ++ Type II +++ Type III
Aspalathus	+	+	–	–	+	+
Bolusia	+	–	–	–	+	+
Calobota	+	–	–	–/+	+	+/+++
Crotalaria						
Section *Calycinae*	–/+	–/+	–/+	–	+	+
Section *Chrysocalycinae*	+	–/+	–	–	+	+
Section *Crotalaria*	+	–	–/+	–	+	+
Section *Dispermae*	–/+	–	–/(+)	–	+	+
Section *Geniculatae*	+	–	–	+	+	+
Section *Grandiflorae*	+	+	–	–	+	+
Section *Hedriocarpae*	+	–/+	–	–	+	+
Section *Schizostigma*	–	–	+	–	+	+
Dichilus	+	–	–	+	+	+
Lebeckia	+	–	+	+	+	++
Lebeckia wrightii	+	–	+	–	+	+
Lotononis						
Section *Aulacinthus*	+	+	–	–	+	+
Section *Buchenroedera*	+					+
Section *Digitata*	–					+/++
Section *Euchlora*	+	+	–	–	+	+
Section *Krebsia*	+					+
Section *Leobordea*	–					+
Section *Leptis*	–					+
Section *Lipozygis*	+	+	–	–	+	+
Section *Listia*	–	–	–	–/+	+	++
Section *Lotononis*	+					+
Section *Oxydium*	+	+	–	+	+	+
Section *Polylobium*	+					+
Section *Synclistus*	–	–	–	+	+	++
Melolobium	+	+	–	–	+	+
Pearsonia	+	–/+	–	–	+	+
Rafnia						
Section *Colobotropis*	–	+	–	–	+	+
Section *Rafnia*	+	–	–	–/+	+	+
Robynsiophyton	–	–	+	–	+	++
Rothia	–	–	–	–	+	++
Wiborgia	+	–	–	+	–	+
Wiborgiella	+	–	–/+	–/+	+	+/+++
Wiborgiella inflata	+	–	–	+	+	+++
Wiborgiella vlokii	+	–	+	–	+	+

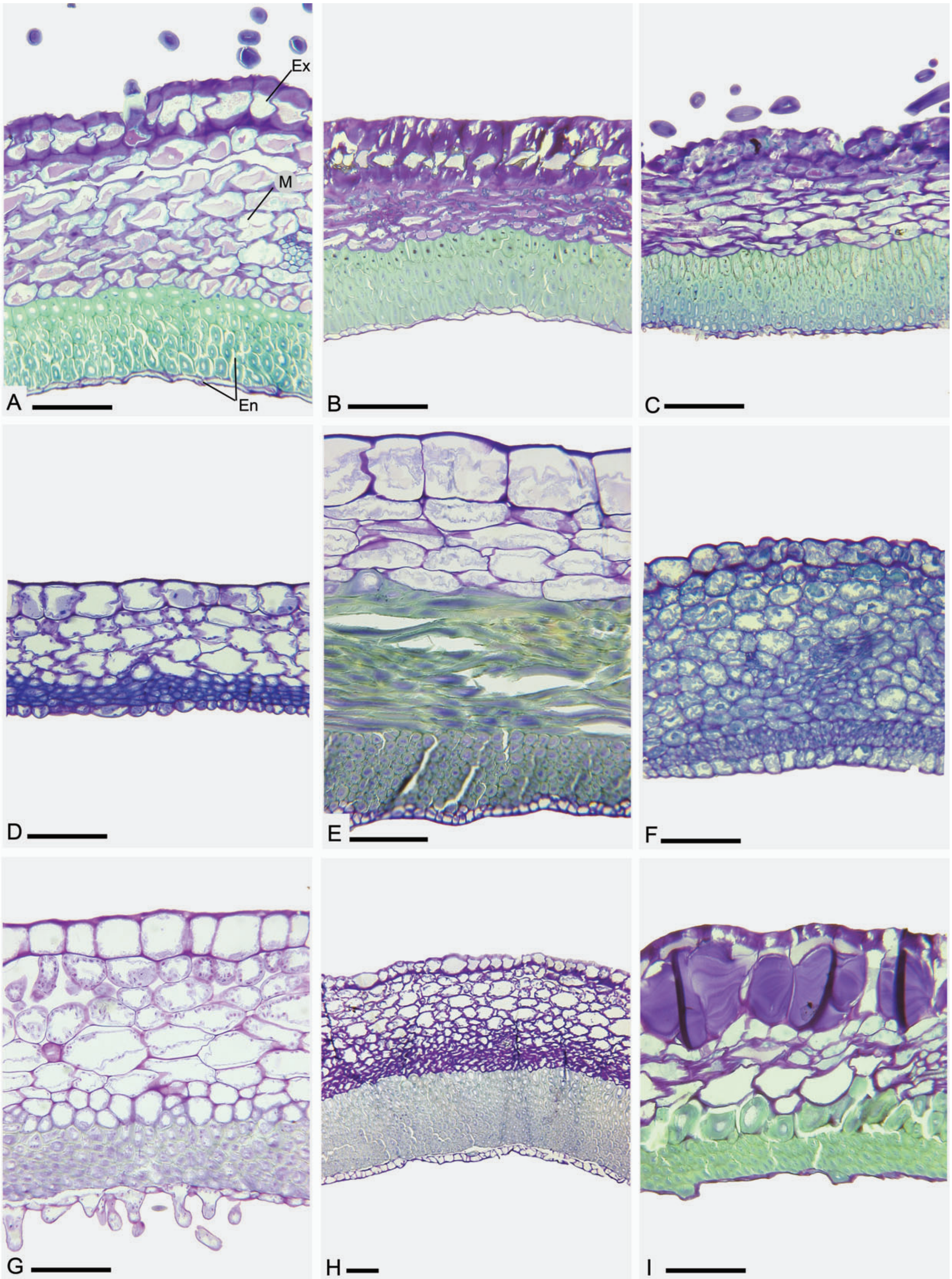
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Figure 5. Transverse sections of fruits in Crotalarieae, all with a type I pericarp: A, *Aspalathus teres* [*Van Wyk 1329* (JRAU)]; B, *A. linearis* [*Van Wyk 3617* (JRAU)]; C, *A.spinosa* [*Van Wyk 2935* (JRAU)]; D, *Wiborgia monoptera* [*Boatwright et al. 152* (JRAU)]; E, *W. sericea* [*Boatwright et al. 124* (JRAU)]; F, *Wiborgiella humilis* [*Boatwright et al. 212* (JRAU)]; G, *W. inflata* [*Johns 162* (JRAU)]; H, *W. bowieana* [*Streicher s.n. sub Schutte 831* (JRAU)]; I, *W. vlokii* [*Vlok 2045* (PRE)]. Pericarp layers: Exocarp (Ex); Mesocarp (M); Endocarp (En). Scale bar, 0.1 mm.

Lebeckia: Fruits thin- to thick-walled (Fig. 7A–C). *Exocarp*: Epidermal cells with slightly thickened cell walls; mucilage cells present. *Mesocarp*: Parenchyma and collenchyma cells present. *Endocarp*: A single cell layer of normal fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent. *L. wrightii* Bolus (Fig. 7C) has a type I pericarp structure. It differs from the other *Lebeckia* spp. in having only collenchyma cells present in the mesocarp and one zone of multiple numbers of cell layers of fibres and trichomes in the endocarp.

Rafnia: Fruits thin- to thick-walled (Fig. 7D, E). *Exocarp*: Epidermal cells with slightly to highly thickened cell walls; mucilage cells absent. *Mesocarp*: Parenchyma and collenchyma cells present or only collenchyma cells present. *Endocarp*: One or two zones of various numbers of cell layers of fibres arranged in one direction, parallel or at a 45° angle to the longitudinal axis of the fruits; trichomes absent. *Rafnia amplexicaulis* Thunb. has fibre cells that are only slightly lignified (Fig. 7D).

Lotononis clade – type I and type II fruit walls are present

Lotononis: Fruits thin- to thick-walled (Figs 7F–I, 8A–C and 9A). *Exocarp*: Epidermal cells with slightly to highly thickened cell walls; mucilage cells usually absent. *Mesocarp*: Parenchyma and collenchyma cells present or only collenchyma cells present. *Endocarp*: One or rarely two zones of various numbers of cell layers of fibres or a single cell layer of normal fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent. *Lotononis macrocarpa* Eckl. & Zeyh. (Fig. 7F) has slightly lignified fibres and forms part of the 'Cape' clade. *Lotononis hirsute* Schinz (Fig. 9A) forms part of the *Crotalaria* clade and has a type I fruit wall structure.

Pearsonia: Fruits thick-walled (Fig. 8D–F). *Exocarp*: Epidermal cells with slightly to highly thickened cell walls; mucilage cells absent. *Mesocarp*: Only collenchyma cells present. *Endocarp*: One zone of various numbers of cell layers of fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

Rothia: Fruits thin-walled (Fig. 8G–H). *Exocarp*: Epidermal cells with slightly thickened cell walls; mucilage cells usually absent. *Mesocarp*: Only collenchyma cells present. *Endocarp*: A single cell layer of normal fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

Robynsiophyton: Fruits thin-walled (Fig. 8I). *Exocarp*: Epidermal cells with slightly thickened cell walls; mucilage cells present. *Mesocarp*: Only collenchyma cells present. *Endocarp*: Usually a single cell layer of normal fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

Crotalaria clade – type I fruit walls are present

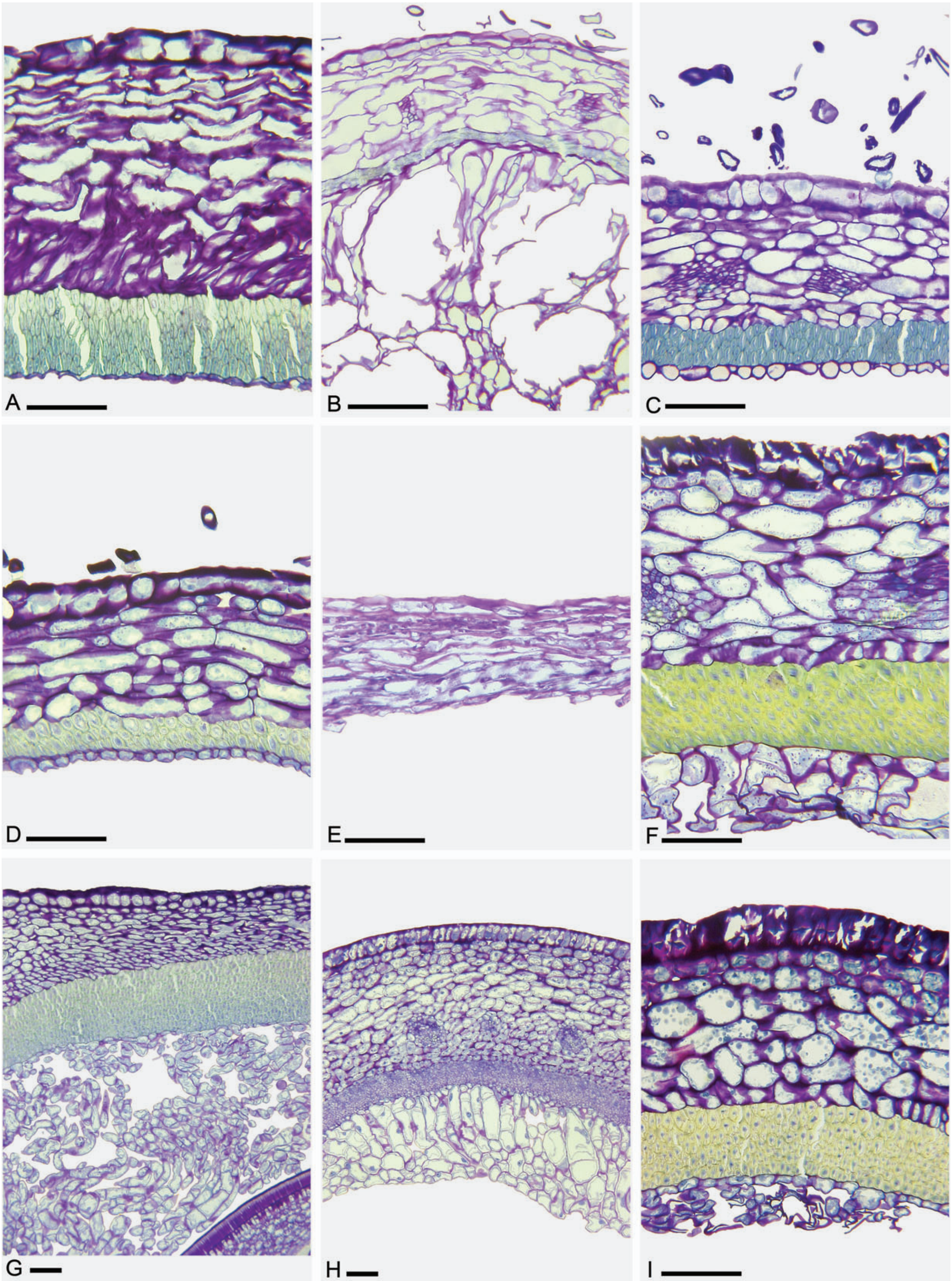
Crotalaria: Fruits usually thick-walled (Figs 9B–I and 10A–F). *Exocarp*: Epidermal cells with slightly to highly thickened cell walls; mucilage cells sometimes present. *Mesocarp*: Parenchyma cells rarely present, collenchyma cells present. *Endocarp*: One, two or three zones of various numbers of cell layers of fibres arranged in one direction, parallel or two directions, parallel and perpendicular to the longitudinal axis of the fruits; trichomes occasionally present.

Bolusia: Fruits thick-walled (Fig. 10G). *Exocarp*: Epidermal cells with somewhat thickened cell walls; mucilage cells absent. *Mesocarp*: Only collenchyma cells present. *Endocarp*: One or two zones of various numbers of cell layers of fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

Genisteae – type I fruit walls are present

Melolobium: Fruits thick-walled (Fig. 10H). *Exocarp*: Epidermal cells with highly thickened cell walls; mucilage cells absent. *Mesocarp*: Only collenchyma cells present. *Endocarp*: One zone of various numbers of cell layers of fibres arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

Dichilus: Fruits thick-walled (Fig. 10I). *Exocarp*: Epidermal cells with somewhat thickened cell walls; mucilage cells absent. *Mesocarp*: Parenchyma and collenchyma cells present. *Endocarp*: One or two zones of various numbers of cell layers of fibres


A
B
C
D
E
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I

Figure 6. Transverse sections of fruits in Crotalarieae with a type I pericarp (A–F) and a type III pericarp (G–I): A, *Calobota linearifolia* [*Giess et al. 6180* (WIND)]; B, *C. elongata* [*Van Wyk 2562b* (JRAU)]; C, *C. pungens* [*Boatwright et al. 106* (JRAU)]; D, *C. spinescens* [*Boatwright et al. 158* (JRAU)]; E, *C. saharae* [*Davies 49564* (K)]; F, *C. lotononoides* [*Boatwright et al. 142* (JRAU)]; G, *C. sericea* [*Boatwright et al. 151* (JRAU)]; H, *C. cytisoides* [*Boatwright et al. 114* (JRAU)]; I, *C. halenbergensis* [*Boatwright et al. 149* (JRAU)]. Scale bar, 0.1 mm.

arranged in one direction, parallel to the longitudinal axis of the fruits; trichomes absent.

DISCUSSION

Fruit morphology is variable and characters sometimes have diagnostic value at the generic level. Examples are the indehiscent, winged, samara-like fruits of *Wiborgia* (Van Wyk, 2005; Boatwright *et al*., 2009) and the inflated and usually dehiscent fruits of *Crotalaria* (Polhill, 1982). Detailed studies by Polhill (1976) and a taxonomic review by Van Wyk (1991) have shown that genera can usually only be identified by a combination of characters and that fruit characters on their own have limited value. However, the present results have contributed to a better understanding of the relation between form and function in the fruits of *Crotalaria* and related genera.

The anatomy of the pericarp is too conservative to be used diagnostically at the generic level. However, some trends were observed and three basic pericarp types were identified within the tribe. The distribution of these types across the tribe is somewhat congruent with the current phylogenetic analyses, as shown in Figure 1. Note that type I is predominant, type II occurs in three independent lineages (*Lebeckia*, *Leobordea-Listia* and *Rothia-Robynsiophyton*) and type III is found in only two genera (*Calobota* and *Wiborgiella,* albeit only in some species).

'CAPE' CLADE

Aspalathus (Fig. 5A–C), *Wiborgia* (Fig. 5D–F), *Wiborgiella* (Fig. 5G–I), *Rafnia* (Fig. 7D–E) and some species of *Calobota* all have a type I pericarp, and *Lebeckia* spp. (Fig. 7A–C), with the exception of *L. wrightii*, all have a type II pericarp. *Lebeckia wrightii* is a short-lived fireweed with several unusual morphological features, such as stipules, spirally twisted keel petals and black seeds (Le Roux & Van Wyk, 2009). A comparison with its close relative, *L. uniflora* B-E. van Wyk & M.M. le Roux, may yield interesting results. *Aspalathus* seemingly has a uniform pericarp structure (type I), despite the large number of variable species in the genus. No diagnostic differences were observed among species from different groups within the genus. *Wiborgiella humilis* (Fig. 5F) was transferred to the genus *Wiborgiella* based on molecular data, together with fruit and androecial characters to support the generic change (Boatwright *et al*., 2009; Boatwright, Tilney & Van Wyk, 2010). The present fruit anatomical study revealed that there are multiple cell layers of only somewhat lignified cells as opposed to the thick-walled fibres of *Wiborgiella* and *Wiborgia*. Of particular interest is the discovery of an unexpected anatomical difference between *Wiborgiella inflata* and *W. vlokii*, two closely related and anomalous species. They are the only short-lived perennials in the genus and also differ in having gelatinous fibres (elsewhere found only in *Calobota* spp.). Furthermore, *W. vlokii* differs from *W. inflata* in the absence of the endodermal trichomes that are invariably associated with gelatinous fibres in other species investigated. In *Calobota* (Fig. 6A–I) both type I and type III pericarps are found. This is the only other genus in which gelatinous fibres (present in type III) are present and correlates with the two informal groups found within the genus. The one group has thin-walled fruits (type I pericarp) and the second has thick-walled fruits with trichomes associated with the endocarp (type III pericarp), with the exception of *C. elongata* (Thunb.) Boatwr. & B.-E.van Wyk and *C. namibensis* Boatwr. & B.-E.van Wyk, which have type I pericarps. *Calobota saharae* (Coss. & Durieu) Boatwr. & B.-E.van Wyk (Fig. 6E) has two cell layers of only somewhat lignified cells and has a type I pericarp.

LOTONONIS CLADE

Recent molecular studies (Boatwright *et al*., 2008a, in press) have indicated that *Lotononis* is polyphyletic and three clades were identified (Fig. 1): (1) the *Lotononis s.s.* clade (*L.* section *Lotononis* and allies); (2) the *Leobordea* clade [*L.* section *Leobordea* and allies]; and (3) the *Listia* clade (*L.* section *Listia*). These three clades are now considered to be distinct at generic level and formal new circumscriptions were proposed by Boatwright *et al*. (in press), respectively, as '*Lotononis*', '*Leobordea*' and '*Listia*'. The *Lotononis s.s.* clade (Fig. 7G–H) has a type I pericarp, the *Leobordea* clade (Figs 7I and 8A) has both type I and type II pericarps and the *Listia* clade has exclusively type II pericarps (Fig. 8B, C). Sections within the *Leobordea* clade can be recognized using pericarp structure; for example, all species of section *Synclistus* have a type II pericarp. Compared with *Aspalathus*, that has a rather uniform pericarp structure throughout, differences within the *Leobordea* clade are diagnostically

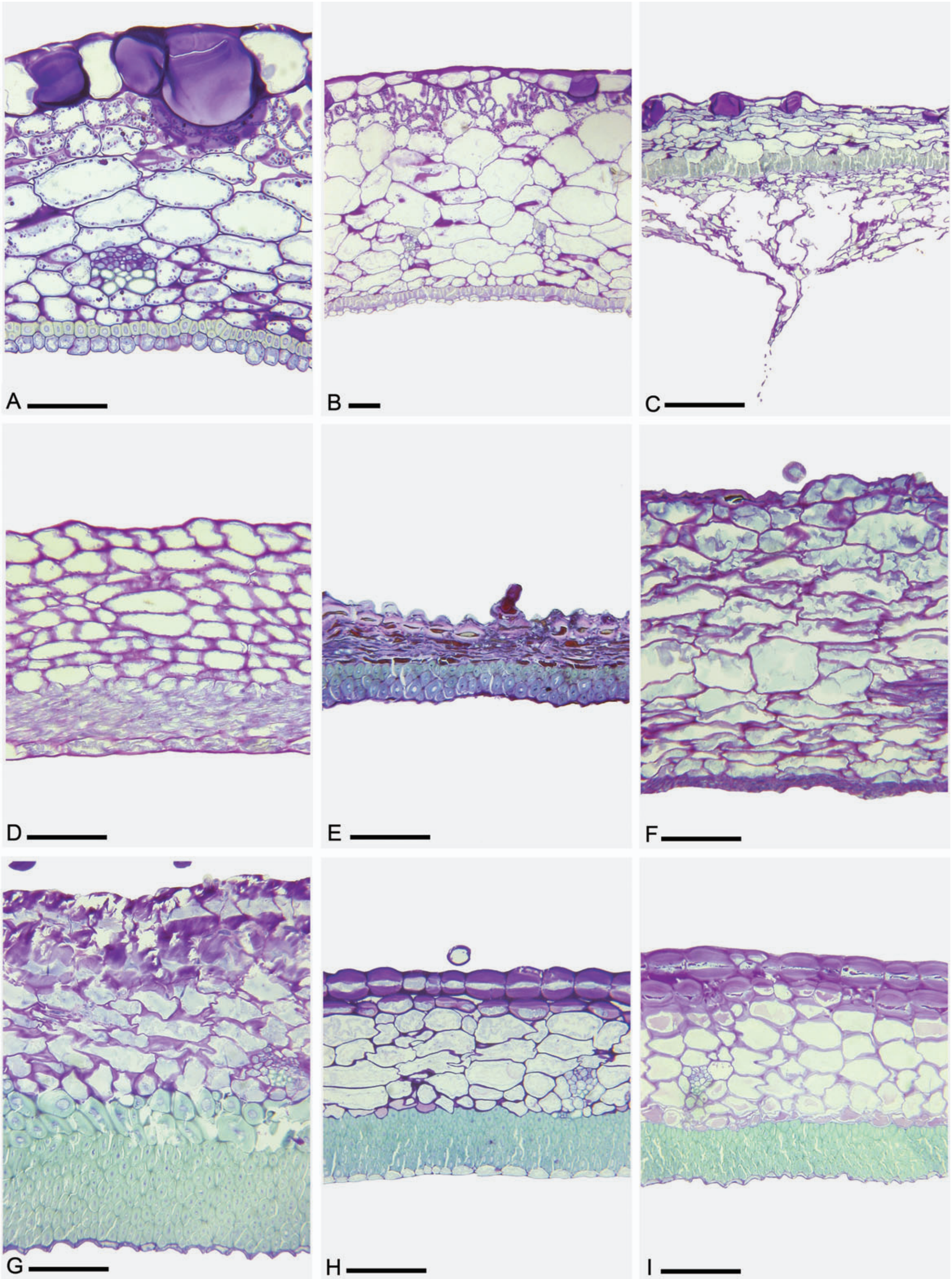

Figure 7. Transverse sections of fruits in Crotalarieae with a type II pericarp (A–B) and a type I pericarp (C–I): A, *Lebeckia contaminata* [*Le Roux et al*. *16* (JRAU)]; B, *L. pauciflora* [*Le Roux et al*. *12* (JRAU)]; C, *L. wrightii* [*Johns 163* (JRAU)]; D, *Rafnia amplexicaulis* [*Campbell et al*. *40* (JRAU)]; E, *R. capensis* [*Campbell et al*. *11* (JRAU)]; F, *Lotononis macrocarpa* [*Schlechter 4925* (NBG)]; G, *L. densa* [*Van Wyk 3122* (JRAU)]; H, *L. lenticula* [*Schutte 300* (JRAU)]; I, *L. eriantha* [*Van Wyk 2631b* (JRAU)]. Scale bar, 0.1 mm.

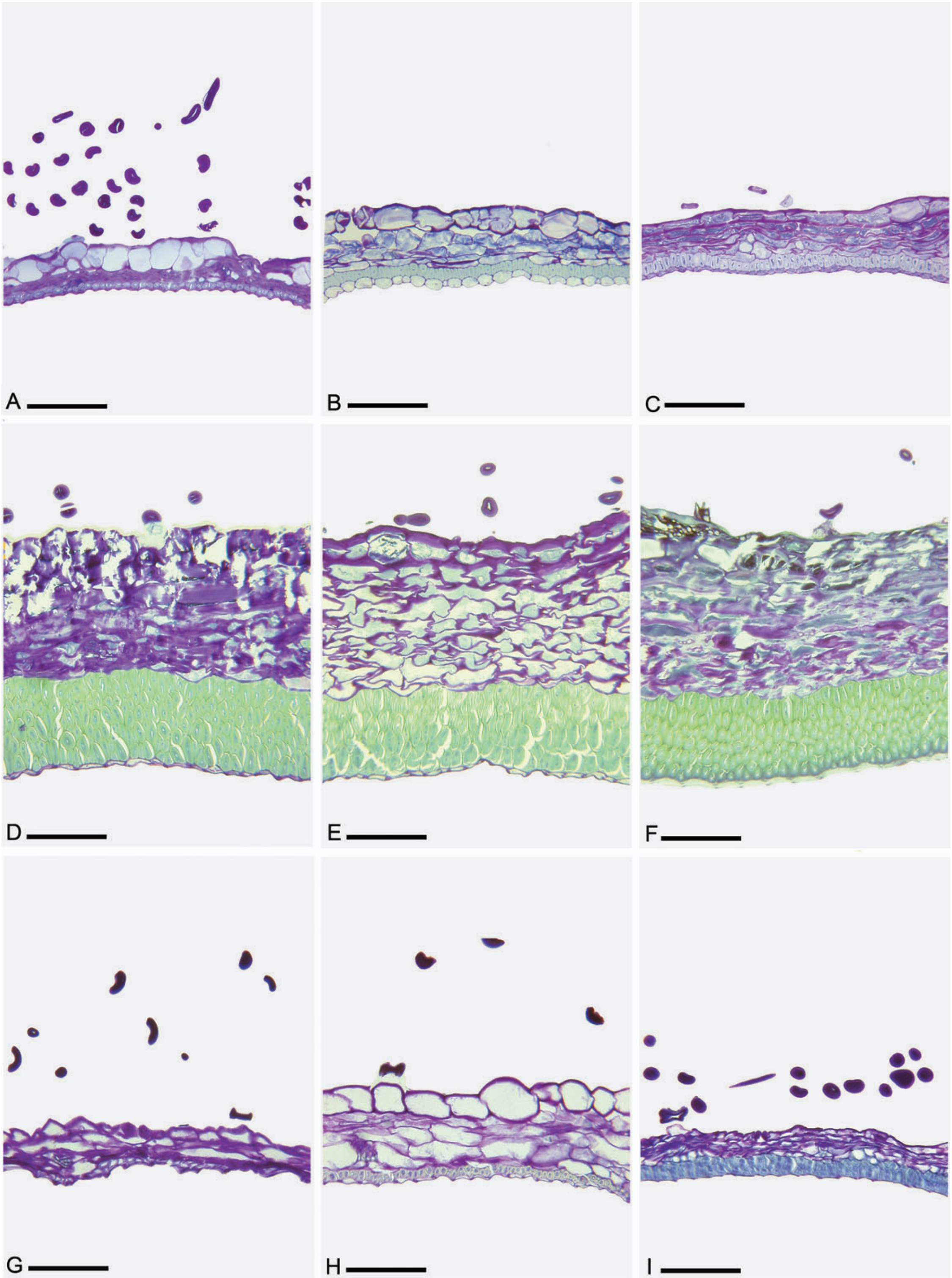

Figure 8. Transverse sections of fruits in Crotalarieae with a type II pericarp (A–C, G–I) and a type I pericarp (D–F): A, *Lotononis globulosa* [*Van Wyk 2211* (JRAU)]; B, *L. listii* [*Schutte 354* (JRAU)]; C, *L. subulata* [*Van Wyk 2884* (JRAU)]; D, *Pearsonia sessilifolia* [*Van Wyk 3192* (JRAU)]; E, *P. cajanifolia* [*Posthumus 1a* (JRAU)]; F, *P. aristata* [*De Castro 346* (JRAU)]; G, *Rothia hirsuta* [*Bogdon 2205* (K)]; H, *R. indica* [*Latz 16126* (MEL)]; I, *Robynsiophyton vanderystii* [*Lisowski 20326* (K)]. Scale bar, 0.1 mm.

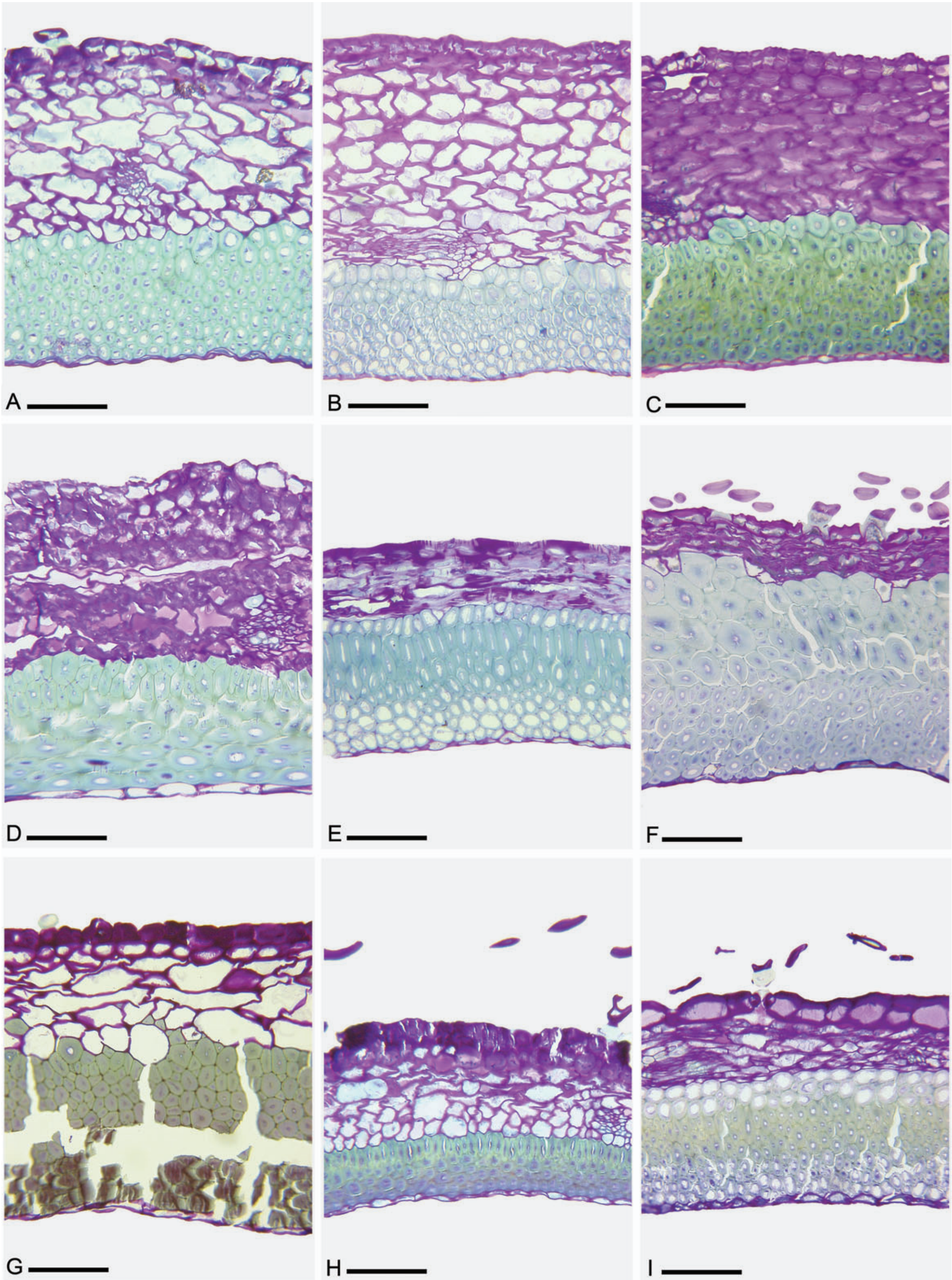

Figure 9. Transverse sections of fruits in Crotalarieae, all with a type I pericarp: A, *Lotononis hirsuta* [*Van Wyk 1338* (JRAU)]; B, *Crotalaria doidgeae* [*Viljoen 52* (PRE)]; C, *C. lebeckioides* [*Van Wyk 3315* (JRAU)]; D, *C. burkeana* [*Nienaber EN 126* (PRE)]; E, *C. natalitia* [*Mogg 34335* (JRAU)]; F, *C. dura* [*Ward 11910* (PRE)]; G, *C. pisicarpa* [*Klaasen et al. 107* (WIND)]; H, *C. burtii* [*Grundy L96* (PRE)]; I, *C. pallida* [*Germishuizen 1146* (PRE)]. Scale bar, 0.1 mm.

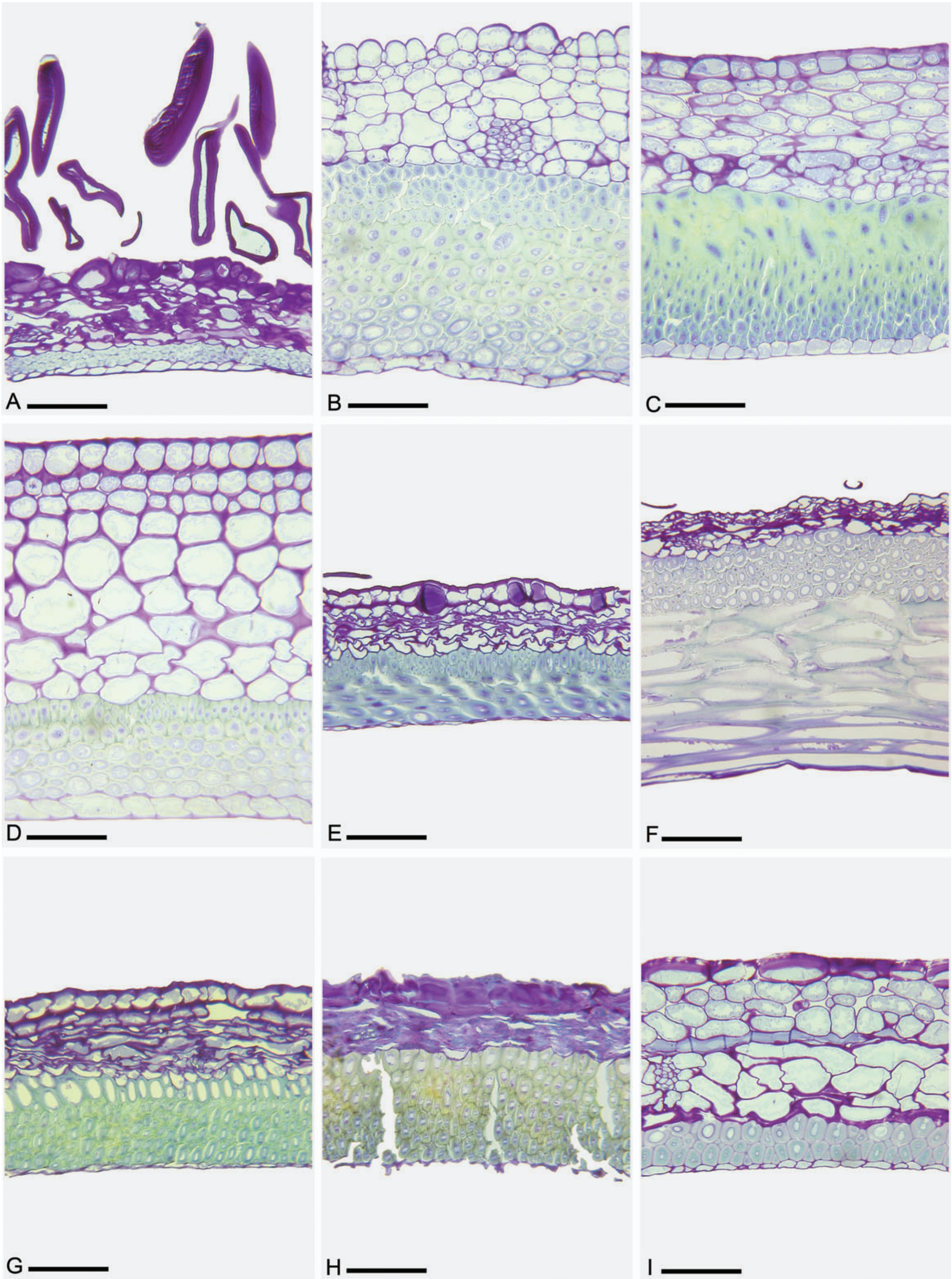

Figure 10. Transverse sections of fruits in Crotalarieae (A–G) and Genisteae (H–I), all with a type I pericarp: A, *Crotalaria vasculosa* [*De Winter 9460* (PRE)]; B, *C. virgultalis* [*Le Roux 38* (JRAU)]; C, *C. spartioides* [*Le Roux et al. 84* (WIND)]; D, *C. recta* [*Le Roux 42* (JRAU)]; E, *C. humilis* [*Thorne 52437* (NBG)]; F, *C. globifera* [*Pienaar 532* (PRE)]; G, *Bolusia amboensis* [*Boatwright et al. 248* (WIND)]; H, *Melolobium alpinum* [*Schutte 160* (JRAU)]; I, *Dichilus strictus* [*Schutte 376* (JRAU)]. Scale bar, 0.1 mm.

useful at an infrageneric level. Species of the *Leobordea* clade are more widely distributed and adaptations to various habitats could account for the observed variation. *Lotononis macrocarpa* (Fig. 7F), an anomalous species of the genus, is placed closer to the 'Cape' group of Crotalarieae (Boatwright *et al*., in press) and has a type I pericarp with multiple cell layers of not highly sclerified cells in the endocarp, which differs from *Lotononis s.s. Rothia* and *Robynsiophyton* have been reported to be closely related to *Pearsonia* (Van Wyk, 1991), which is supported by molecular (Boatwright *et al*., 2008a) and morphological data (Boatwright, Tilney & Van Wyk, 2008c). A sister relationship between *Rothia* and *Robynsiophyton* (and their generic status, i.e. being distinct from *Pearsonia*), as indicated by Boatwright & Van Wyk (2009) and Boatwright *et al*. (2008a), is here also supported by the fruit anatomy.

CROTALARIA CLADE

The taxa of the earliest diverging clade of Crotalarieae, *Lotononis hirsuta* (Fig. 9A), *Crotalaria* (Figs 9B–I and 10A–F) and (3) *Bolusia*, all have a type I pericarp and strongly inflated pods. Molecular and morphological data (Boatwright *et al*., 2008a, in press) indicated that *L. hirsuta* should be excluded from the genus *Lotononis* and its placement within the *Crotalaria* clade is also supported by the fruit anatomy.

It is difficult to identify apomorphies for the sections within *Crotalaria*. Species from sections *Grandiflorae* (Bak.f.) Polhill and *Geniculatae* Polhill show some uniformity in the pericarp thickness, ratio of the pericarp layers and fibre orientation (Figs 9B, C and 10B, C). These pericarp characters are also similar to those of some individual species from other sections within *Crotalaria* (e.g. *C. recta* Steud. ex A.Rich., Fig. 10D) and other genera, e.g. *Aspalathus* (Fig. 5A–C) and *Pearsonia* (Fig. 8D–F). Other sections in *Crotalaria* display too much variation and it is difficult to find characters to use as apomorphies for specific groups; for example, section *Crotalaria* (Fig. 10C–F) or section *Hedriocarpae* (Figs 9I and 10A). In these cases, fruit characters could be useful diagnostically at the species level.

Fahn & Zohary (1955) considered the presence of multiple cell layers of fibres to be the primitive state in legume fruit and its loss to be derived. The type I pericarp (present in the early diverging lineages of the tribe) therefore represents the most primitive state, whereas the type II, as found in the *Listia* clade, is clearly derived. The plesiomorphic state is also present in *Melolobium* and *Dichilus* (Fig. 10H and I, respectively) of Genisteae.

DEHISCENCE

The mechanism of dehiscence and the function of fibre orientation in this process were described by Fahn & Zohary (1955) and several variations of the basic dehiscence model, which can exist within one genus (Fahn & Zohary, 1955; Fahn, 1982). In the type I pericarp, all fibres within a single zone are generally arranged in one direction parallel to the longitudinal axis of the fruits. When the fruits mature, the cells dry out and the cell walls shrink in a perpendicular direction to the longitudinal axis, creating tension and resulting in dehiscence (Fig. 10A–C). Fibres may also be directed at a 45° angle to the longitudinal axis, and the elongated epidermal and hypodermal cells of the exocarp and mesocarp are also orientated at a 45° angle, but in the opposite direction to the fibres. This arrangement of fibres results in the twisting of the valves and the dehiscence of the fruits. Fibre cell layers with different cell wall thicknesses can be arranged in two or more zones. When these cells dry out, each zone creates a different strength of tension, resulting in dehiscence (Fig. 9E, I). Indehiscent fruits appear to have two zones; an outer zone of various numbers of cell layers of fibres oriented parallel to the longitudinal axis and an inner zone of various numbers of cell layers of fibres oriented perpendicular to the longitudinal axis (Figs 9G and 10F).

In the type III pericarp, fibres (all forming one zone) are mostly arranged in a single direction parallel to the longitudinal axis, resulting in dehiscence (Fig. 6G–I). In type II, the fibres are all orientated in the same direction in a single layer of fibres, parallel to the longitudinal axis, and the fruits are sometimes dehiscent.

There are some exceptions to the dehiscence or indehiscence model. Other factors that could influence dehiscence are fruit morphology and additional anatomical features. These modifications were probably necessitated by a need for seed protection and dispersal. Type II pericarp fruits should dehisce, for example, *Lotononis globulosa* B.-E.van Wyk (Fig. 8A), but stay intact. This could be because of the presence of large epidermal cells in the exocarp, which could absorb some of the tension created by the single layer of fibres. *Wiborgia monoptera* E.Mey. is an example of an indehiscent fruit with a type I pericarp. The fruits have multiple layers of fibres orientated at 45° angles to the longitudinal axis and should dehisce; the tension created by the shrinking fibres is possibly absorbed and counteracted by the presence of a wing along the zone of dehiscence.

CONCLUSIONS

Fruit morphology in Crotalarieae is diverse and of limited systematic value. However, there are convergent trends in the size, shape and general morphology that can be linked to dispersal and seed protection. In general, the inflated, balloon-shaped fruits typical of *Crotalaria* are a useful diagnostic character and represent the ground plan for further structural modifications seen in other genera of the tribe.

Three different pericarp types are recognized within the tribe: (1) type I, with one, two or three zones of various numbers of cell layers of normal fibres and trichomes occasionally associated with the endocarp; (2) type II, with a single cell layer of normal fibres and (3) type III, with one zone of several cell layers of gelatinous fibres and trichomes associated with the endocarp. The type I pericarp is most widely distributed throughout the tribe. There are some potentially useful generic apomorphies. The lack of monophyly of both *Lebeckia s.l and Lotononis s.l.* is supported by the results presented here. Species of *Lebeckia sensu stricto* (Le Roux & Van Wyk, 2009) almost invariably have a type II pericarp, whereas types I and III are present in the segregate genera *Wiborgiella* and *Calobota* (Boatwright *et al*., 2009, 2010). Species of *Lotononis s.s.* have type I pericarps, whereas the section *Listia* invariably has type II. Although all *Crotalaria* spp. have a type I pericarp, there is some structural variation that may be of value in distinguishing between some of the species. There are no apparent discontinuities between any of the sections.

An example of non-homologous similarity was revealed by comparing pericarp structure of the small, indehiscent, globose and few-seeded fruits (presumably all wind or water dispersed) that are found in species of *Crotalaria*, *Lotononis* section *Synclistus* and one species of *Calobota* (*C. elongata*). These have types I, II and III pericarps, respectively. Also noteworthy is the fact that this seemingly identical dispersal mechanism has evolved independently in each of the three main clades in the tribe.

The pattern of dehiscence and indehiscence in *Crotalaria* and other genera of the tribe seems to conform to the general pattern reported for other legume genera. The orientation of the fibres in the endocarp relative to the longitudinal axis of the fruits is the major determinant, but the presence of different zones of fibres and their orientation relative to one another are also important. Our study has revealed other morphological and anatomical features that may counteract dehiscence, such as the presence of wing tissue along the line of the suture (e.g. *Wiborgia*) or the relative thickness of the single fibre cell layer in relation to the adjoining mesocarp tissue, which seems to be independent of the absolute thickness, or the fibre cell layer (thick in, e.g. *Lebeckia brevicarpa* M.M.le Roux & B.-E.van Wyk, but thin in *Lotononis* section *Synclistus*). Fruit anatomical characters are of potential value not only for new taxonomic interpretations but also to deepen our understanding of various morphological and functional adaptations in tribe Crotalarieae.

ACKNOWLEDGEMENTS

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APPENDIX

List of fruit pericarp types and voucher specimens used for fruit anatomical studies in the tribe Crotalarieae. The species are arranged according to the phylogeny of Boatwright *et al*. (2008a)

Species	Infrageneric group (if applicable)	Voucher specimen	Pericarp thickness (mm)	Fruit classification	Dehiscence
Aspalathus angustifolia (Lam.) Dahlgr.		*Van Wyk 2592* (JRAU)	182	Type I	Dehiscent
Aspalathus bracteata Thunb.		*Van Wyk 914* (JRAU)	169	Type I	Dehiscent
Aspalathus carnosa Berg.		*Van Wyk 3006* (JRAU)	240	Type I	Dehiscent
Aspalathus cf. hirta E.Mey.		*Van Wyk 3295* (JRAU)	353	Type I	Dehiscent
Aspalathus chortophila Eckl. & Zeyh.		*Van Wyk et al. 831* (JRAU)	235	Type I	Dehiscent
Aspalathus intermedia Eckl. & Zeyh.		*Schutte 522* (JRAU)	219	Type I	Dehiscent
Aspalathus juniperina Thunb. subsp. *juniperina*		*Van Wyk 2756* (JRAU)	339	Type I	Dehiscent
Aspalathus lactea Thunb. subsp. *adelphea* (Eckl. & Zeyh.) Dahlgr.		*Van Wyk et al. 1564* (JRAU)	266	Type I	Tardily dehiscent
Aspalathus linearis (Burm.f) Dahlgr.		*Van Wyk 3617* (JRAU)	262	Type I	Dehiscent
Aspalathus longifolia Benth.		*Van Wyk 2799* (JRAU)	452	Type I	Dehiscent
Aspalathus pendula Dahlgr.		*Van Wyk 3346* (JRAU)	530	Type I	Dehiscent
Aspalathus perfoliata (Lam.) Dahlgr.		*Van Wyk 2786* (JRAU)	417	Type I	Dehiscent
Aspalathus spinosa L.		*Van Wyk 2935* (JRAU)	273	Type I	Dehiscent
Aspalathus teres Eckl. & Zeyh.		*Van Wyk et al. 1329* (JRAU)	405	Type I	Dehiscent
Bolusia amboensis (Schinz) Harms		*Boatwright et al. 248* (WIND)	233	Type I	Dehiscent
Calobota angustifolia (E.Mey.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 138* (JRAU)	385	Type III	Dehiscent
Calobota cinerea (E.Mey.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 150* (JRAU)	491	Type III	Dehiscent
Calobota cuspidosa (Burch.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 92* (JRAU)	265	Type I	Indehiscent
Calobota cytisoides (Berg.) Eckl. & Zeyh.		*Boatwright et al. 114* (JRAU)	506	Type III	Dehiscent
Calobota elongata (Thunb.) Boatwr. & B.-E.van Wyk		*Van Wyk 2562b* (JRAU)	203	Type I	Indehiscent
Calobota halenbergensis (Merxm. & Schreib.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 149* (JRAU)	328	Type III	Dehiscent
Calobota linearifolia (E.Mey.) Boatwr. & B.-E.van Wyk		*Giess et al. 6180* (WIND)	270	Type I	Dehiscent
Calobota lotononoides (Schltr.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 142* (JRAU)	397	Type III	Dehiscent
Calobota namibensis Boatwr. & B.-E.van Wyk, ined.		*De Winter et al. 7919* (WIND)		Type I	?Dehiscent
Calobota psiloloba (E.Mey.) Boatwr. & B.-E.van Wyk		*Le Roux et al. 20* (JRAU)	291	Type I	Indehiscent
Calobota pungens (Thunb.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 106* (JRAU)	305	Type I	Indehiscent
Calobota saharae (Coss. & Dur.) Boatwr. & B.-E.van Wyk		*Davies 49564* (K)	141	Type I	Indehiscent
Calobota sericea (Thunb.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 151* (JRAU)	479	Type III	Dehiscent
Calobota spinescens (Harv.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 158* (JRAU)	230	Type I	Tardily dehiscent
Crotalaria agatiflora Schweinf.	Section *Grandiflorae* (Bak.f.) Polhill	*Le Roux 45* (JRAU)	531	Type I	Dehiscent
Crotalaria alata Ham. ex D. Don	Section *Calycinae* Wight & Arn.	*Rwaburindore 2628* (PRE)	395	Type I	Dehiscent
Crotalaria alexandri Bak. f.	Section *Dispermae* Wight & Arn.	*Pope 15* (PRE)	117	Type I	Dehiscent
Crotalaria argyraea Welw. ex Bak.	Section *Hedriocarpae* Wight & Arn.	*Van Slageren MSJB011* (WIND)	334	Type I	Indehiscent
Crotalaria brachycarpa (Benth.) Burtt Davy ex Verdoorn	Section *Crotalaria*	*Le Roux 49* (JRAU)	771	Type I	Indehiscent
Crotalaria burkeana Benth.	Section *Chrysocalycinae* (Benth.) Bak.f.	*Nienaber EN 126* (PRE)	422	Type I	Dehiscent
Crotalaria burttii Bak.f.	Section *Hedriocarpae*	*Grundy L96* (PRE)	223	Type I	Tardily dehiscent
Crotalaria calycina Schrank	Section *Calycinae*	*De Nevers et al. 3310* (PRE)	359	Type I	Dehiscent
Crotalaria cephalotes Steud. ex A.Rich.	Section *Dispermae*	*Schmidt et al.1912* (PRE)	338	Type I	Dehiscent
Crotalaria damarensis Engl.	Section *Chrysocalycinae*	*Leippert 4608* (WIND)	488	Type I	Tardily dehiscent
Crotalaria dinteri Schinz	Section *Crotalaria*	*Giess 11637* (PRE)	304	Type I	Dehiscent

APPENDIX *Continued*

Species	Infrageneric group (if applicable)	Voucher specimen	Pericarp thickness (mm)	Fruit classification	Dehiscence
Crotalaria doidgeae Verdoorn	Section *Grandiflorae*	*Viljoen 52* (PRE)	437	Type I	Dehiscent
Crotalaria dura Wood & Evans	Section *Chrysocalycinae*	*Ward 11910* (PRE)	347	Type I	Indehiscent
Crotalaria ephemera Polhill	Section *Dispermae*	*Brooks et al. 93* (PRE)	183	Type I	Tardily dehiscent
Crotalaria excisa (Thunb.) Bak.f.	Section *Crotalaria*	*Le Roux 108* (JRAU)	342	Type I	Dehiscent
Crotalaria filicaulis Welw. ex Bak.	Section *Dispermae*	*Teixeira et al. 4463* (PRE)	207	Type I	Indehiscent to tardily dehiscent
Crotalaria flavicarninata Bak.f.	Section *Geniculatae* Polhill	*Le Roux et al. 72* (WIND)	330	Type I	Dehiscent
Crotalaria globifera E.Mey.	Section *Crotalaria*	*Pienaar 532* (PRE)	398	Type I	Tardily dehiscent
Crotalaria goetzei Harms	Section *Chrysocalycinae*	*Thulin 7826* (UPS)	226	Type I	Dehiscent
Crotalaria griquensis Bolus	Section *Crotalaria*	*Gubb s.n. PRE 825170* (PRE)	187	Type I	Indehiscent
Crotalaria heidmannii Schinz	Section *Geniculatea*	*Le Roux et al. 69* (WIND)	502	Type I	Dehiscent
Crotalaria humilis Eckl. & Zeyh.	Section *Crotalaria*	*Thorne 52437* (NBG)	169	Type I	Dehiscent
Crotalaria hyssopifolia Klotzsch	Section *Dispermae*	*Faulkner 208* (PRE)	119	Type I	Tardily dehiscent
Crotalaria incana L.	Section *Chrysocalycinae*	*Thulin et al. 9114* (UPS)	254	Type I	Tardily dehiscent
Crotalaria juncea L.	Section *Calycinae*	*Arnola 9991* (PRE)	290	Type I	Dehiscent
Crotalaria kirkii Bak.	Section *Hedriocarpae*	*Markström et al. MN215A* (UPS)	232	Type I	Dehiscent
Crotalaria laburnifolia L.	Section *Grandiflorae*	*Van Wyk et al. 4333* (JRAU)	441	Type I	Dehiscent
Crotalaria lanceolata E.Mey.	Section *Hedriocarpae*	*Le Roux 37* (JRAU)	385	Type I	Dehiscent
Crotalaria lebeckioides Bond	Section *Grandiflorae*	*Van Wyk 3315* (JRAU)	397	Type I	Dehiscent
Crotalaria leptocarpa Balf. f.	Section *Schizostigma* Polhill	*Van Wyk et al. 4650* (JRAU)	125	Type I	Tardily dehiscent
Crotalaria lotoides Benth.	Section *Chrysocalycinae*	*Le Roux 47* (JRAU)	300	Type I	Dehiscent
Crotalaria mesopontica Taub.	Section *Hedriocarpae*	*Rwaburindore 2340* (UPS)	326	Type I	Dehiscent
Crotalaria monteiroi Taub. ex Bak.f.	Section *Grandiflorae*	*Le Roux 95* (JRAU)	736	Type I	Dehiscent
Crotalaria natalitia Meisner	Section *Chrysocalycinae*	*Mogg 34335* (JRAU)	268	Type I	Tardily dehiscent
Crotalaria occidentalis Hepper	Section *Calycinae*	*? 3765* (PRE)	123	Type I	Dehiscent
Crotalaria orientalis Burtt Davy ex Verdoorn	Section *Geniculatea*	*Le Roux et al. 91* (JRAU)	449	Type I	Dehiscent
Crotalaria pallida Ait.	Section *Hedriocarpae*	*Germishuizen 1146* (PRE)	272	Type I	Dehiscent
Crotalaria pearsonii Bak.f.	Section *Crotalaria*	*Marloth 12445* (PRE)	266	Type I	Dehiscent
Crotalaria pisicarpa Welw. ex Bak.	Section *Chrysocalycinae*	*Klaasen et al. 107* (WIND)	346	Type I	Indehiscent
Crotalaria platysepala Harv.	Section *Crotalaria*	*Le Roux et al. 73* (WIND)	342	Type I	Tardily dehiscent
Crotalaria prittwitzii Bak.f.	Section *Chrysocalycinae*	*Bidgood et al. 3597* (UPS)	359	Type I	Indehiscent to tardily dehiscent
Crotalaria pseudotenuirama Torre	Section *Dispermae*	*Greenway et al. 11682* (PRE)	218	Type I	Indehiscent to tardily dehiscent
Crotalaria recta Steud. ex A.Rich.	Section *Crotalaria*	*Le Roux 42* (JRAU)	490	Type I	Dehiscent
Crotalaria saltiana Andr.	Section *Hedriocarpae*	*Hemming 3056* (PRE)	336	Type I	Dehiscent
Crotalaria somalensis Chiov.	Section *Hedriocarpae*	*Gillett 21175* (PRE)	255	Type I	Tardily dehiscent
Crotalaria spartioides DC.	Section *Geniculatea*	*Le Roux et al. 84* (WIND)	422	Type I	Dehiscent
Crotalaria spectabilis Roth.	Section *Crotalaria*	*Le Roux et al. 98* (JRAU)	596	Type I	Dehiscent
Crotalaria sphaerocarpa Perr. ex DC.	Section *Geniculatea*	*Le Roux et al. 74* (WIND)	161	Type I	Indehiscent
Crotalaria steudneri Schweinf.	Section *Hedriocarpae*	*Le Roux 80* (WIND)	196	Type I	Tardily dehiscent
Crotalaria tenuirama Welw. ex Bak.	Section *Dispermae*	*Teixeira 3.391* (PRE)	192	Type I	Dehiscent
Crotalaria vasculosa Wall. ex Benth.	Section *Hedriocarpae*	*De Winter 9460* (PRE)	132	Type I	Dehiscent
Crotalaria virgulata Klotzsch	Section *Crotalaria*	*Le Roux 38* (JRAU)	377	Type I	Dehiscent
Crotalaria xanthoclada Boj. ex Benth.	Section *Chrysocalycinae*	*Hedrén et al. 665* (UPS)	295	Type I	Dehiscent
Dichilus strictus E.Mey.		*Schutte 376* (JRAU)	271	Type I	Dehiscent
Lebeckia ambigua E.Mey.		*Boatwright et al. 131* (JRAU)	456	Type II	Tardily dehiscent
Lebeckia brevicarpa M.M.le Roux & B.-E.van Wyk		*Le Roux et al. 4* (JRAU)	886	Type II	Indehiscent
Lebeckia contaminata (L.) Thunb.		*Le Roux et al. 16* (JRAU)	269	Type II	Tardily dehiscent

Lebeckia pauciflora Eckl. & Zeyh.		*Le Roux et al. 12* (JRAU)	831	Type II	Tardily dehiscent
Lebeckia wrightii (Harv.) Bolus		*Johns 163* (JRAU)	94	Type I	Tardily dehiscent
Lotononis acuminata Eckl. & Zeyh.	Section *Lotononis*	*Van Wyk 2587* (JRAU)	284	Type I	Dehiscent
Lotononis alpina (Eckl. & Zeyh.) B.-E.van Wyk subsp. *multiflora* (Eckl. & Zeyh.) B.-E.van Wyk	Section *Buchenroedera* (Eckl. & Zeyh.) B.-E.van Wyk	*Stirton 12484* (JRAU)	364	Type I	Dehiscent
Lotononis bachmaniana Dümmer	Section *Krebsia* (Eckl.& Zeyh.) Benth.	*Van Wyk 4011* (JRAU)	386	Type I	Dehiscent
Lotononis bainesii Bak.	Section *Listia* (E.Mey.) B.-E.van Wyk	*Schutte 462c* (JRAU)	85	Type II	Indehiscent
Lotononis benthamiana Dümmer	Section *Digitata* B.-E.van Wyk	*Van Wyk 2538* (JRAU)	86	Type II	Dehiscent along one suture (corolla persistant)
Lotononis bolusii Dümmer	Section *Synclistus* B.-E.van Wyk	*Van Wyk 2444* (JRAU)	74	Type II	Indehiscent (calyx and seemingly corolla persistant)
Lotononis brevicaulis B.-E.van Wyk	Section *Polylobium* (Eckl. & Zeyh.) Benth.	*Schutte 447* (JRAU)	430	Type I	Dehiscent
Lotononis complanata B.-E.van Wyk	Section *Lotononis*	*Van Wyk 2879* (JRAU)	448	Type I/Type II	Indehiscent
Lotononis comptonii B.-E.van Wyk	Section *Aulacinthus* (E.Mey.) Benth.	*Van Wyk 2190* (JRAU)	205	Type I	?
Lotononis corymbosa (E.Mey.) Benth.	Section *Lipozygis* (E.Mey.) Benth.	*Stirton 11819* (JRAU)	164	Type I	Dehiscent
Lotononis decumbens (Thunb.) B.-E.van Wyk subsp. *decumbens*	Section *Leptis*	*Van Wyk 1699* (JRAU)	133	Type I	Dehiscent
Lotononis densa (Thunb.) Harv.	Section *Aulacinthus*	*Van Wyk 3122* (JRAU)	470	Type I	Dehiscent
Lotononis elongata (Thunb.) D.Dietr.	Section *Lotononis*	*Van Wyk 2573* (JRAU)	191	Type I	?Indehiscent
Lotononis eriantha Benth.	Section *Lipozygis*	*Van Wyk 2631b* (JRAU)	313	Type I	Dehiscent (corolla seemingly persistent)
Lotononia foliosa Bolus	Section *Lipozygis*	*Maguire 8691* (JRAU)	227	Type I	Dehiscent
Lotononis globulosa B.-E.van Wyk	Section *Synclistus*	*Van Wyk 2211* (JRAU)	66	Type II	Indehiscent (calyx and seemingly corolla persistent)
Lotononis hirsuta (Thunb.) D.Dietr.	Section *Euchlora* (Eckl. & Zeyh.) B.-E.van Wyk	*Van Wyk 1338* (JRAU)	448	Type I	Tardily dehiscent
Lotononis lanceolata (E.Mey.) Benth.	Section *Lipozygis*	*Van Wyk 1884* (JRAU)	156	Type I	Dehiscent
Lotononis laxa Eckl. & Zeyh.	Section *Oxydium* Benth.	*Van Wyk 1315* (JRAU)	251	Type I	Dehiscent
Lotononis lenticula (E.Mey.) Benth.	Section *Oxydium*	*Schutte 300* (JRAU)	258	Type I	Dehiscent
Lotononis listii Polhill	Section *Listia*	*Schutte 354* (JRAU)	100	Type II	Indehiscent
Lotononis longicephala B.-E.van Wyk	Section *Synclistus*	*Van Wyk 2209* (JRAU)	56	Type II	Indehiscent
Lotononis lotononoides (Scott Elliot) B.-E.van Wyk	Section *Buchenroedera*	*Van Wyk 1938* (JRAU)	235	Type I	Dehiscent
Lotononis macrocarpa Eckl. & Zeyh.	Section *Listia*	*Schlechter 4925* (NBG)	415	Type I	?Indehiscent
Lotononis magnifica B.-E.van Wyk	Section *Digitata*	*Van Wyk 2552* (JRAU)	85	Type I	Dehiscent
Lotononis pentaphylla (E.Mey.) Benth.	Section *Synclistus*	*Van Wyk 2379* (JRAU)	116	Type II	Indehiscent
Lotononis platycarpa (Viv.) Pic.-Serm.	Section *Leobordea* (Del.) Benth.	*Viviers 2039* (JRAU)	106	Type I	Dehiscent
Lotononis plicata B.-E.van Wyk	Section *Digitata*	*Van Wyk 3282* (JRAU)	74	Type II	Indehiscent
Lotononis prolifera (E.Mey.) B.-E.van Wyk	Section *Leptis* (E.Mey. ex Eckl. & Zeyh.) Benth.	*Van Wyk 1700* (JRAU)	69	Type I	Late dehiscent
Lotononis prostrata (L.) Benth.	Section *Lotononis*	*Van Wyk 3494* (JRAU)	568	Type I	Dehiscent
Lotononis quinata (Thunb.) Benth.	Section *Digitata*	*Van Wyk 2416* (RJAU)	95	Type I	Dehiscent
Lotononis rosea Dümmer	Section *Synclistus*	*Van Wyk 2905* (JRAU)	77	Type II	Indehiscent
Lotononis stricta (Eckl. & Zeyh.) B.-E.van Wyk	Section *Krebsia*	*Van Wyk 1720* (JRAU)	227	Type I	Dehiscent
Lotononis subulata B.-E.van Wyk	Section *Listia*	*Van Wyk 2884* (JRAU)	124	Type II	Indehiscent
Melolobium alpinum Eckl. & Zeyh.		*Schutte 160* (JRAU)	218	Type I	Dehiscent
Pearsonia aristata (Schinz) Dümmer		*De Castro 346* (JRAU)	364	Type I	Dehiscent
Pearsonia bracteata Benth. (Polhill)		*Schutte 202* (JRAU)	466	Type I	Dehiscent
Pearsonia cajanifolia (Harv.) Polhill		*Posthumus 1a* (JRAU)	346	Type I	Indehiscent or very tardily dehiscent
Pearsonia sessilifolia (Harv.) Dümmer		*Van Wyk 3192* (JRAU)	318	Type I	Dehiscent
Rafnia angulata Thunb.	Section *Rafnia*	*Campbell et al. 23* (JRAU)	388	Type I	Dehiscent

APPENDIX *Continued*

Species	Infrageneric group (if applicable)	Voucher specimen	Pericarp thickness (mm)	Fruit classification	Dehiscence
Rafnia amplexicaulis Thunb.	Section *Rafnia*	*Campbell et al. 40* (JRAU)	305	Type I	Dehiscent
Rafnia capensis (L.) Schinz	Section *Colobotropis* E.Mey.	*Campbell et al. 11* (JRAU)	115	Type I	Dehiscent
Rafnia rostrata G.J.Campbell & B.-E.van Wyk	Section *Rafnia*	*Van Wyk 2175* (JRAU)	218	Type I	Dehiscent
Robynsiophyton vanderystii Wilczek		*Lisowski 20326* (K)	79	Type II	Dehiscent
Rothia hirsuta (Guill. & Perr.) Baker		*Bogdon 2205* (K)	109	Type II	Dehiscent
Rothia indica (L.) Druce		*Latz 16126* (MEL)	123	Type II	Dehiscent
Wiborgia monoptera E.Mey.	Subgenus *Pterocarpia* Dahlgr.	*Boatwright et al. 152* (JRAU)	180	Type I	Indehiscent
Wiborgia sericea Thunb.	Subgenus *Pterocarpia*	*Boatwright et al. 124* (JRAU)	468	Type I	Indehiscent
Wiborgia tetraptera E.Mey.	Subgenus *Pterocarpia*	*Schutte 737* (JRAU)	225	Type I	Indehiscent
Wiborgiella bowieana (Benth.) Boatwr. & B.-E.van Wyk		*Streicher s.n. sub Schutte 831* (JRAU)	571	Type I	Dehiscent
Wiborgiella humilis (Thunb.) Boatwr. & B.-E.van Wyk		*Boatwright et al. 212* (JRAU)	296	Type I	Indehiscent
Wiborgiella inflata (H.Bolus) Boatwr. & B.-E.van Wyk		*Johns 162* (JRAU)	462	Type III	Dehiscent
Wiborgiella leipoldtiana (Schltr. ex R.Dahlgren) Boatwr. & B.-E.van Wyk		*Boatwright et al. 123* (JRAU)	412	Type III	Dehiscent
Wiborgiella mucronata (Benth.) Boatwr. & B.-E.van Wyk		*Esterhuysen 6880* (BOL)	297	Type I	Dehiscent
Wiborgiella sessilifolia (Eckl. and Zeyh.) Boatwr. & B.-E.van Wyk		*Taylor 4329* (PRE)	375	Type I	Dehiscent
Wiborgiella vlokii Boatwr. & B.-E.van Wyk, ined.		*Vlok 2045* (PRE)	312	Type I	Dehiscent

