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The taxonomic significance of fruit morphology and anatomy in the genus *Alepidea* Delaroche (Apiaceae, subfamily Saniculoideae)

By **Elena Yu. Yembaturova, Ben-Erik van Wyk, Patricia M. Tilney** and **Pieter J.D. Winter**

With 4 figures and 2 tables

Abstract

Yembaturova, E.Y., van Wyk, B.-E., Tilney, P.M. & Winter, P.J.D: The taxonomic significance of fruit morphology and anatomy in the genus *Alepidea* Delaroche (Apiaceae, subfamily Saniculoideae). — Plant Div. Evol. **128**: 369–385. 2010. — ISSN 1869-6155.

The African endemic genus *Alepidea* Delaroche has been revised several times but relationships within the genus and circumscriptions of the species remain problematic. A detailed study of the morphology and anatomy of the fruits of *Alepidea* species was done to evaluate the taxonomic value of fruit characters at both generic and infrageneric levels. The sporadic occurrence of both regular vittae and cyclic vittae (paraendocarpic ducts) in *Alepidea* species is reported for the first time. The fruit structure is highly polymorphic and very variable within species and only a limited number of carpological traits appear to be of taxonomic value (presence or absence of vittae, surface sculpturing). At the generic level, the fruit structure in *Alepidea* can now be more accurately characterized. *Alepidea* differs from all other genera of the tribe Saniculeae (subfamily Saniculoideae) in the presence (albeit sporadic) of regular vittae (intervallecular as well as commissural vittae), at least in some of the species. The presence of vittae in *Alepidea* greatly reduces the apparent taxonomic distance between the subfamilies Saniculoideae (where regular vittae were hitherto thought to be absent) and the Apioideae (where regular vittae are diagnostic).

Keywords: *Alepidea*, fruit structure, Saniculoideae, surface sculpturing, vittae.

Introduction

The genus *Alepidea* is restricted to the African continent and consists of approximately 25 species (Klopper et al. 2006), most of which are endemic to southern Africa. Only one species, *A. peduncularis* Steud. ex A. Rich., extends as far north as the highlands of Kenya and Ethiopia (Hedberg & Hedberg 2003). The species are perennial rhizomatous herbs with simple leaves, markedly ciliate or bristly leaf margins, peculiar capitate inflorescences (pseudanthia) surrounded by showy bracts and small clustered

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schizocarps of typically 'saniculoid' appearance (i.e., sessile, with conspicuous surface protuberances). *Alepidea* remains taxonomically difficult despite revisions by Dümmer (1913), Wolff (1913) and Weimarck (1949), as well as taxonomic notes by Hilliard & Burtt (1982). Burtt (1991) enumerated the taxa and pointed out the need for further study on the variation of species and the delimitation of taxa. Several studies have been done on characters of potential taxonomic value, including vegetative morphology (leaf shape and margins, petiole, root and rhizome anatomy) (De Castro & Van Wyk 1994; De Castro, unpublished data), terpenoid chemistry (Rustaiyan & Sadjada 1987, Holzapfel et al. 1995), molecular phylogenetics (Calviño & Downie 2007) and biogeography (Calviño et al. 2008). Carpological features were also taken into consideration to some extent. Weimarck (1949), for example, based his sectional division of *Alepidea* on fruit surface sculpturing (smooth fruits versus squamose, tuberculate, knobby or with various types of appendages). Subsequent studies focused on fruit structure (Liu et al. 2003, Liu 2004, Calviño et al. 2008) and provided more details on the fruit anatomy but without giving an overview of the carpology of the entire genus.

Given the exceptional importance of fruit structural traits for both Apiaceae and angiosperms in general, our study aimed at investigating the fruit anatomy of a large and representative sample of *Alepidea* species. The sampling covered all six of Weimarck's (1949) sections in order to evaluate the taxonomic significance of fruit structure and to determine if it can be used to distinguish between species. Also, more information was needed to allow for comparisons at the generic level between *Alepidea* and other saniculoid genera of the tribe Saniculeae (e.g., *Eryngium* L., *Sanicula* L., *Arctopus* L.). Data on the fruit anatomy of these genera are already available (Liu et al. 2003, Liu 2004, Magee at al. 2008).

Materials and methods

Mature fruits were obtained from herbarium specimens (see Table 1 for the list of taxa examined with voucher specimens), rehydrated, fixed in FAA (for a minimum of 24 h) and then treated according to the method of Feder & O'Brien (1968) for embedding in glycol methacrylate (GMA). Fruits and flowers of some *Alepidea* species were collected fresh and fixed in FAA. A Porter-Blüm ultramicrotome was used to cut medial transverse sections of the fruits from 3 to 5 µm thick, and the periodic acid-Schiff/toluidine blue staining method (Feder & O'Brien 1968) applied. Suitable sections were photographed. To reveal the vittae, the outer cell layers of the pericarp of FAA-preserved material were carefully removed and the remaining fruit studied with a light microscope as suggested by Liu et al. (2007). The terminology used is illustrated in the figures. Author citations for all *Alepidea* names are given in Table 1 and are not repeated hereafter.

Results

Fruit morphology

Fruits of *Alepidea* are schizocarps consisting of two equally-sized and -shaped mericarps, usually not compressed (sometimes slightly flattened), mostly with inconspicuous ribs (Fig. 1). Mature fruit length varies from 2.5 mm in *A. setifera* (Fig. 1G, H) to

Table 1. List of *Alepidea* species (arranged by section) and specimens examined (with voucher specimens), with a summary of the main characters and character states of calcium oxalate crystals [crystal number; crystal type; location pattern: comm = mainly in commissural area, prot = mainly in protuberances, outer = mainly in outer pericarp layers, scattered = scattered throughout the pericarp] and exomesocarp protuberances [abundance: absent, sparse (two or less per rib, none between ribs), common = moderately abundant, abundant (more than two per rib, more than three between ribs); branching: undivided or divided (branched); shape]. N/A = not available (crystals not visible in stained sections).

Section	Species and varieties	Voucher specimen and herbarium	Crystals:			Exomesocarp protuberances		
			number	type	location	abundance	branching	shape
Leiocarpae Weim.	*A. amatymbica* Eckl. & Zeyh.	*Bokelman 1-PL55* (NBG)	scarce	solitary	scattered	absent		
	A. amatymbica	*Galpin 6641* (PRE)	N/A	N/A	N/A	absent		
	A. cordifolia B.-E.van Wyk	*Jacobsz 2521* (NBG)	scarce	solitary	scattered	sparse	undivided	triangular
	A. cordifolia	*Van Wyk & Yembaturova 4232* (JRAU)	abundant	solitary	scattered	absent		
Longifoliae Weim	*A. peduncularis* A.Rich.	*Barker 4409* (NBG)	common	solitary	outer	sparse	undivided	triangular
	A. peduncularis	*De Castro 192* (JRAU)	N/A	N/A	N/A	common	undivided	square
	A. peduncularis	*Gillbert & Phillips* 9213 (K)	scarce	solitary	scattered	common	undivided	irregular
	A. peduncularis	*Abbott & Yembaturova 8872* (JRAU)	scarce	solitary	scattered	common	undivided	triangular and square
	A. woodii Oliv.	*Wood 1845* (SAM, isotype)	common	solitary	prot	sparse	undivided	irregular
Alepidea	*A. capensis* (P.J.Bergius) R.A.Dyer	*Victor 1196* (PRE);	N/A	N/A	N/A	abundant	undivided and divided	square and irregular
	A. galpinii Dümmer	*De Castro 224* (JRAU)	N/A	N/A	N/A	N/A	N/A	N/A
	A. galpinii Dümmer	*Hilliard & Burtt* 16428 (NBG)	common	solitary	outer	abundant	divided	irregular
	A. longeciliata Schinz ex Dümmer	*Schlechter 4044* (NBG)	abundant	clustered	comm and prot	abundant	undivided	triangular and irregular

Setiferae Weim	*A. basinuda* Pott var. *basinuda*	*Venter 11739* (JRAU)	abundant	solitary and clustered	scattered prot and comm	common	undivided	triangular, finger-like and irregular
	A. setifera N.E.Br.	*Steyn 1033* (NBG)	abundant	solitary and clustered	prot	N/A	N/A	N/A
	A. setifera	*Jacobsz 2178* (NBG)	abundant	solitary and clustered	scattered	abundant	divided and undivided	finger-like and irregular
	A. setifera	*Compton 28714* (NBG)	scarce	solitary	prot	abundant	undivided	triangular and finger-like
Stellatae Weim	*A. natalensis* J.M.Wood & M.S.Evans	*De Castro 186* (JRAU)	common	solitary	scattered	sparse	undivided	triangular and finger-like
	A. natalensis	*Lewis 1790* (SAM)	common	solitary	scattered	sparse	undivided	triangular
Heterotrichae Weim	*A. serrata* Eckl. & Zeyh. *var. serrata*	*De Castro 261* (JRAU)	N/A	N/A	N/A	sparse	undivided	triangular and square
	A. serrata var. serrata	*De Castro 265* (JRAU)	scarce	solitary	prot	sparse	undivided	triangular and square
	A. serrata var. cathcartensis (Kuntze) Weim.	*De Castro 281* (JRAU),	common	solitary and clustered	outer	common	undivided	square
	A. serrata var. cathcartensis	*Flanagan 2292* (JRAU)	common	clustered	comm. and prot	abundant	undivided	finger-like
	A. cirsiifolia Schltr. & H.Wolff	*Hilliard & Burtt 6510* (NBG)	abundant	solitary	prot and outer	common	undivided	triangular and irregular
	A. cirsiifolia	*AE van Wyk 7131* (KEI)	common	solitary	prot	common	undivided	finger-like

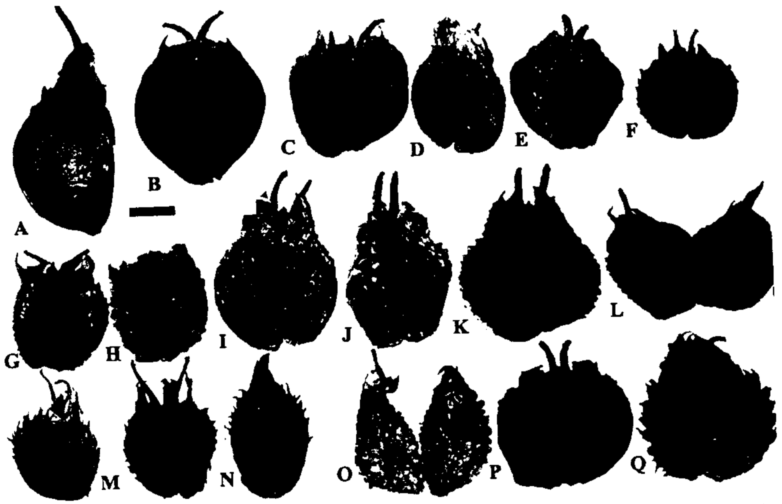

Fig. 1. External fruit morphology of *Alepidea* in lateral view unless otherwise indicated. — A, *A. amatymbica*. — B, *A. cordifolia*. — C–D, *A. peduncularis*. — E, *A. woodii*. — F, *A. basinuda*. — G–H, *A. setifera*. — I–J, *A. serrata* var. *serrata*. — K, *A. serrata* var. *cathcartensis*. — L, *A. cirsiifolia*. — M, *A. natalensis*. dorsal (left) and side view (right). — N, *A. natalensis*, ventral view. — O, *A. capensis*. — P, *A. galpinii*. — Q, *A. longeciliata*. Scale bar: 1 mm.

5.0 mm in *A. amatymbica* (Fig. 1A) and *A. cordifolia* (Fig. 1B); the width and thickness varies from 1.6 to 2.2 mm. Fruits usually range from a light colour in *A. setifera* (Fig. 1H) to a dark brown in *A. serrata* var. *cathcartensis* at maturity (Fig. 1K). The fruit is crowned with dried papery calyx teeth which may be prominent, as in *A. serrata* (Fig. 1I, J, K), somewhat inconspicuous as in *A. galpinii* (Fig. 1P) and *A. setifera* (Fig. 1G, H) or rarely absent as in *A. woodii* (Fig. 1E). The two stylopodia (one per mericarp) are persistent. Surface sculpturing shows a wide range of variation: from almost smooth or slightly wrinkled in *A. amatymbica* (Fig. 1A), *A. cordifolia* (Fig. 1B); to longitudinally somewhat grooved in *A. woodii* (Fig. 1E), *A. cordifolia* (Fig. 1B) and *A. amatymbica*, and tuberculate or verrucose in *A. cirsiifolia* (Fig. 1L), *A. setifera* (Fig. 1G, H) and *A. serrata* (Fig. 1I, J, K). As summarized in Table 1, the appendages vary in abundance, branching and shape. They may even be squamose (scaly) as in *A. longeciliata* (Fig. 1Q) and *A. natalensis* (Fig. 1M, N). The surface sculpturing pattern and the size of the ribs are more pronounced around the apex and base of the fruit.

As is common for African saniculoid genera, *Alepidea* species possess distinct carpophores, visible as multicellular vascular structures in transverse sections (Liu et al. 2003). These carpophores remain attached to one of the mericarps when the fruit breaks apart at maturity (visible in Fig. 1N).

Fruit anatomy (in medial transverse section)

Mericarps. The shapes of mericarps are summarized in Table 1. The mericarps are isodiametric as in *A. basinuda* (Fig. 2I), *A. galpinii* (Fig. 2M), *A. peduncularis* (Fig. 2D, E) and *A. setifera* (Fig. 2H), oval as in *A. amatymbica* (Fig. 2A), *A. capensis* (Fig. 2L), *A. cirsiifolia* (Fig. 2N), *A. cordifolia* (Fig. 2B, C), *A. longeciliata* (Fig. 2K), *A. natalensis* (Fig. 2J) and *A. woodii* (Fig. 2F) or sometimes almost pentagonal in outline e.g. in *A. natalensis* (Fig. 2J) and *A. serrata* (Fig. 2O, P).

Ribs. Fruits of many Apiaceae are characterized by five prominent ribs, one above each vascular bundle. In *Alepidea*, ribs are less prominent. *A. woodii* is an exception in having peculiar bifurcate ribs (Fig. 2F). In *A. cordifolia* (Fig. 2C) and in *A. amatymbica* similar longitudinal grooves are clearly observed in the field as well as in transverse section (Winter, pers. obs.) — they seem to be partly formed due to a sulcate outer wall of the large rib oil duct and partly by blunt ribs on either side of the oil ducts.

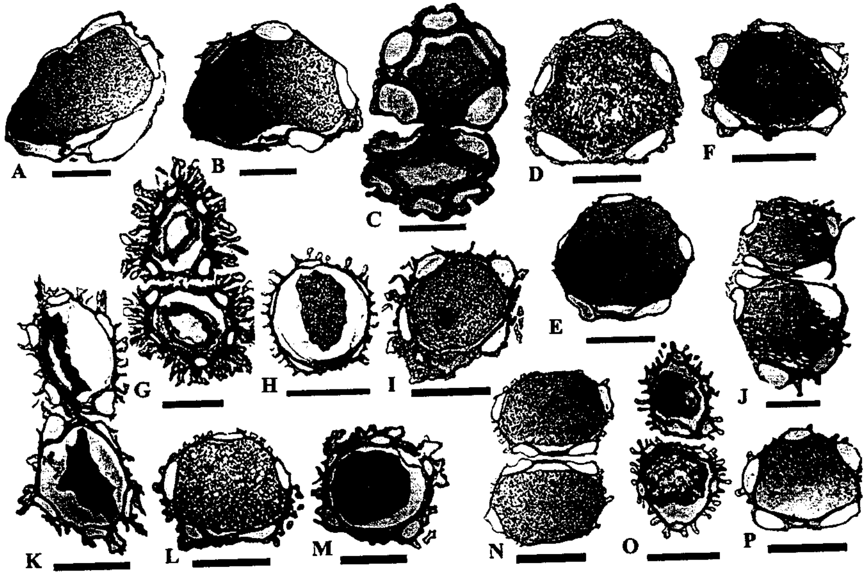

Fig. 2. Transverse sections of fruits in various sections of *Alepidea*. Sect. *Leiocarpae*. — (A) *A. amatymbica*; (B), (C) *A. cordifolia* (note the well-developed vallecular and commissural vittae in the latter). Sect. *Longifoliae*: (D), (E) *A. peduncularis*; (F) *A. woodii*. Sect. *Setiferae*: (G), (H) *A. setifera*; (I) *A. basinuda*. Sect. *Stellatae*: (J) *A. natalensis*. Sect. *Alepidea*: (K) *A. longeciliata*; (L) *A. capensis*; (M) *A. galpinii*. Sect. *Heterotrichae*: (N) *A. cirsiifolia*; (O) *A. serrata* var. *cathcartensis*; (P) *A. serrata* var. *serrata*. Scale bars: 0.8 mm.

Rib oil ducts. These structures are typically well-developed in most members of the subfamily Saniculoideae and a few anomalous African genera of uncertain placement at the rank of subfamily. In subfamily Apioideae, they are typically absent or, if present, very small. In *Alepidea*, conspicuous rib ducts are invariably present. They vary in size and shape as shown in Fig. 2 and summarized in Table 2. The large oil ducts in *A. cordifolia* have sulcate outer walls. This is apparent in transverse section (Fig. 2C). Though this may appear to be an artefact, this interesting feature was observed in fresh fruits, where the sulcate outer walls of the oil ducts result in distinct longitudinal grooves along the fruit surface. In some specimens, there may be less than five oil ducts e.g. *A. cirsiifolia* (Fig. 2N), which may have only three or four oil ducts per mericarp and *A. natalensis* which sometimes has only four per mericarp. A reduced number of rib oil ducts was also noted by Liu (2004) in *Hacquetia epipactis* Scop., currently re-included in the genus *Sanicula* [as *S. epipactis* (Scop.) E.H. Krause] by Calviño & Downie (2007) on the basis of molecular evidence. It is possible that the reduction in the number of rib oil ducts in *Alepidea* (and *Sanicula*) is due to the large number of fruits that develop in a single compact inflorescence at the same time.

Vascular bundles. The rib oil ducts (intrajugal oil ducts) in *Alepidea* are always associated with vascular bundles but the size of the bundles varies considerably. In some taxa, the number of bundles is reduced (i.e., less than five) and they are also greatly reduced in size, the lignified elements being represented by only a few cells below the duct. There may be two or three solitary lignified elements below each oil duct as in *A. cirsiifolia* (Fig. 3D), *A. cordifolia* and *A. setifera*, or five to seven clustered elements as in *A. serrata* (Fig. 3C) or *A. setifera*. In other species studied, more or less regular and multicellular strands can be observed, which may be rather small in *A. natalensis*, and *A. peduncularis*, medium-sized in *A. galpinii* or fairly large, with numerous lignified cells as in *A. amatymbica* (visible in Fig. 2A), *A. capensis*, and *A. serrata* var. *serrata*. In *A. longeciliata* (Fig. 3A, B), transverse sections in the apical and basal parts of the fruit revealed rather well developed vascular bundles while in the medial part they appeared to be reduced. The most pronounced of all vascular bundles in a mericarp were found to be nearly always the ventral ones. Our observations show that this trait is present in *A. cirsiifolia* and *A. galpinii* (i.e. the ventral bundles are the most prominent), whereas *A. natalensis* and *A. peduncularis* are polymorphic (ventral bundles sometimes large, sometimes small). Fig. 3A–D illustrates various types of lignified elements associated with the rib oil ducts in *Alepidea*. A summary of the various character states is given in Table 2.

Commissure. In *Alepidea*, the commissure occupies approximately 17–25% of the mericarp width [the narrowest in *A. longeciliata* (Fig. 2K) and the widest — close to 30% — in *A. cirsiifolia* (Fig. 2N)].

Vittae. Surprisingly, we have found regular vittae in *Alepidea*, apparently reported here for the first time. They were observed in several species but are not always clearly visible in rehydrated mature fruits. *A. cordifolia* (*Van Wyk & Yembaturova 4232*) has conspicuous vallecular and commissural vittae (Fig. 2C). *A. amatymbica* (*Galpin 6641*) shows compressed vallecular vittae and *A. galpinii* (*Hilliard & Burtt 16428*)

Table 2. Summary of anatomical characters and character states in *Alepidea* species (arranged by section). Mericarp shape (transverse section); rib oil ducts size, shape and number; vascular bundles; vallecular vittae and commissural vittae (in mature fruits).

Section	**Species and varieties**	**Voucher specimen**	**Mericarp shape**	**Rib oil duct size**	**Rib oil duct shape and number**	**Lignified xylem elements per oil duct**	**Vallecular vittae**	**Commissural vittae**
Leiocarpae	*A. amatymbica*	*Bokelman 1-PL55*	oval	large	irregular, 5	very large no.	absent/ not visible	absent/ not visible
	A. amatymbica	*Galpin 6641*	oval	large	irregular, 5	medium-sized multicellular strands	present and compressed	absent/ not visible
	A. cordifolia	*Jacobsz 2521*	oval	large	oval and slightly angular, 5	5-7 clustered elements	present and branched; compressed	absent/ not visible
	A. cordifolia	*Van Wyk & Yembaturova 4232*	oval or isodiametric	large	oval, compressed (concave) or irregular, 5	2-3 solitary elements	present and rounded	present
Longifoliae	*A. peduncularis*	*Barker 4409*	isodiametric	medium-sized	oval or compressed, 5	5-7 clustered elements	absent / not visible	absent / not visible
	A. peduncularis	*De Castro 192*	oval or isodiametric	medium-sized	oval or triangular, 5	2-3 solitary elements	absent / not visible	absent / not visible
	A. peduncularis	*Gillbert & Phillips*	isodiametric	medium-sized to large	oval, 5	2-3 solitary elements	absent / not visible	absent / not visible
	A. peduncularis	*Abbott & Yembaturova 8872*	isodiametric	medium-sized	oval or triangular, 5	2-3 solitary elements	absent / not visible	absent / not visible
	A. woodii	*Wood 1845*	oval	medium-sized to large	oval and slightly angular, 5	2-3 solitary elements to 5-7 clustered elements in commissural zone	absent / not visible	absent / not visible
Alepidea	*A. capensis*	*Victor 1196*	oval	medium-sized to large	oval or compressed, 5	2-3 solitary elements to 5-7 clustered elements / small multicellular strands in commissural zone	present	absent / not visible
	A. galpinii	*De Castro 224*	oval to isodiametric	small to medium-sized	oval or compressed, 5	small multicellular strands	absent / not visible	absent / not visible
	A. galpinii	*Hillard & Burtt 16428*	isodiametric	small to medium-sized	oval, 5	5-7 clustered elements	absent / not visible	present and branched
	A. longeciliata	*Schlechter 4044*	oval and angular	medium-sized to large	oval and slightly angular, triangular or compressed, 5	small to large multicellular strands	absent / not visible	absent / not visible
Setiferae	*A. basinuda* var. *basinuda*	*Venter 11739*	isodiametric	large	triangular, 5	2-3 solitary elements or small multicellular strands in commissural area	present and branched	present
	A. setifera	*Jacobsz 2178*	isodiametric to triangular	medium-sized	oval, 5	2-3 solitary elements	present and branched	present and branched
	A. setifera	*Compton 28714*	isodiametric	small	compressed, 5	5-7 clustered elements	absent / not visible	absent / not visible
Stellatae Weim	*A. natalensis*	*De Castro 186*	isodiametric	large	oval and slightly angular, 4 or 5	2-3 solitary elements to 5-7 clustered elements	absent / not visible	absent / not visible
	A. natalensis	*Lewis 1790*	isodiametric to oval	medium-sized to large	oval, triangular or compressed, 4 or 5	5-7 clustered elements	absent / not visible	absent / not visible
Heterotrichae	*A. serrata* var. *serrata*	*De Castro 261*	isodiametric	large	oval or triangular, 5	2-3 solitary elements	absent / not visible	absent / not visible
	A. serrata var. *serrata*	*De Castro 265*	pentagonal	large to medium-sized	oval and slightly angular, 5	2-3 solitary elements	absent / not visible	absent / not visible
	A. serrata var. *cathcartensis*	*De Castro 281*	oval	small	oval, 5	n/a	absent / not visible	absent / not visible
	A. serrata var. *cathcartensis*	*Flanagan 2292*	isodiametric to isodiametric	medium-sized	oval anr slightly angular or irregular, 5	2-3 solitary elements to 5-7 clustered elements in commissural area	absent / not visible	absent / not visible
	A. cirsiifolia	*Hilliard & Burtt 6510*	oval to isodiametric	large or obsolete	triangular, irregular or compressed, 3, 4 or 5	2-3 solitary elements	absent / not visible	absent / not visible
	A. cirsiifolia	*AE van Wyk 7131*	isodiametric	small	circular, 3, 4 or 5	2-3 solitary elements	absent / not visible	absent / not visible

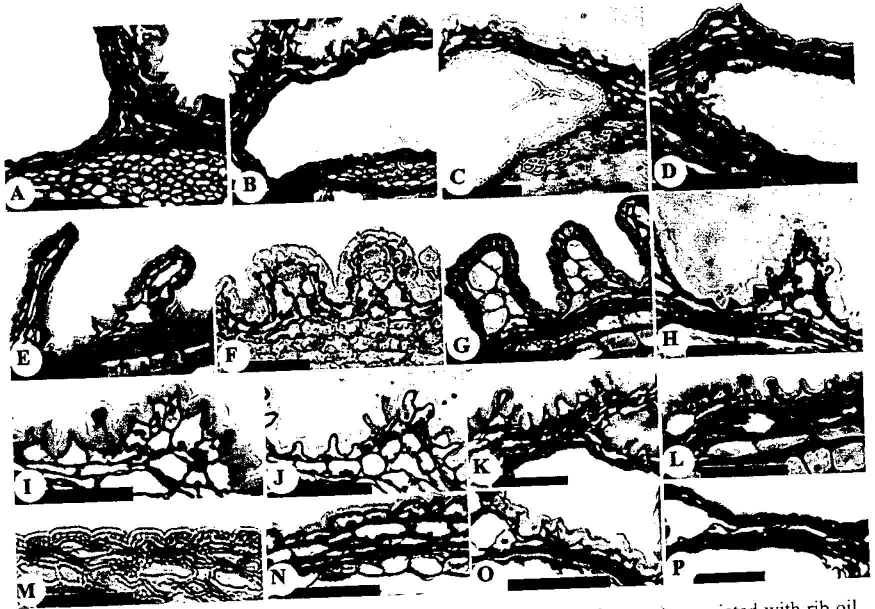

Fig. 3. Details of pericarp anatomy in *Alepidea*. Vascular bundles (elements) associated with rib oil ducts: (A) *A. longeciliata*, large vascular strand near the commissural area; (B) *A. longeciliata*, vascular strand below rib duct; (C) *A. serrata* var. *serrata*, clustered vascular elements; (D) *A. cirsiifolia*, solitary vascular elements. Exomesocarp protuberances: (E) *A. galpinii*, irregularly-shaped outgrowths; (F) *A. peduncularis*, rounded square projections; (G) *A. cirsiifolia*, finger-like multiseriate protuberances; (H) *A. serrata* var. *serrata*, triangular appendages. Exocarp cells: (I), (L) *A. peduncularis*; (J) *A. serrata* var. *serrata*; (K) *A. longeciliata*; (M) *A. galpinii*; (N) *A. natalensis*; (O) *A. serrata* var. *cathcartensis*; (P) *A. cordifolia*. Scale bars: 0.07 mm.

shows branched and compressed commissural vittae (Fig. 4J). *A. capensis* (*Victor 1196*) appears to have numerous vallecular vittae in the upper part of the fruit (one of them is shown in Fig. 4K). *A. basinuda* (*Venter 11739*) (Fig. 4I) and *A. setifera* (*Jacobsz 2178*) also have both types of vittae, with the vallecular ones being branched (Fig. 2G, 4L). A summary of the variation in vallecular and commissural vittae is presented in Table 2.

A study of the flowers as well as the immature and mature fruits of *A. peduncularis* (*Abbott & Yembaturova 8872*; a species lacking vittae at maturity) and *A. cordifolia* (*van Wyk & Yembaturova 4232*; a species which may have pronounced vittae in mature fruits) was undertaken to reveal the origin and early developmental stages of vittae (Fig. 4A-H). In *A. cordifolia*, regular vittae were conspicuous in all stages (Fig. 4G, H), whereas in *A. peduncularis*, regular vittae were absent. In this latter species, however, numerous small, vittae-like structures were discovered, but only in flowers (Fig. 4A, B) and very immature fruits (*De Castro 192*; Fig. 4C, D). They occur in a continuous zone that completely surrounds the endocarp. At a more advanced stage of maturity,

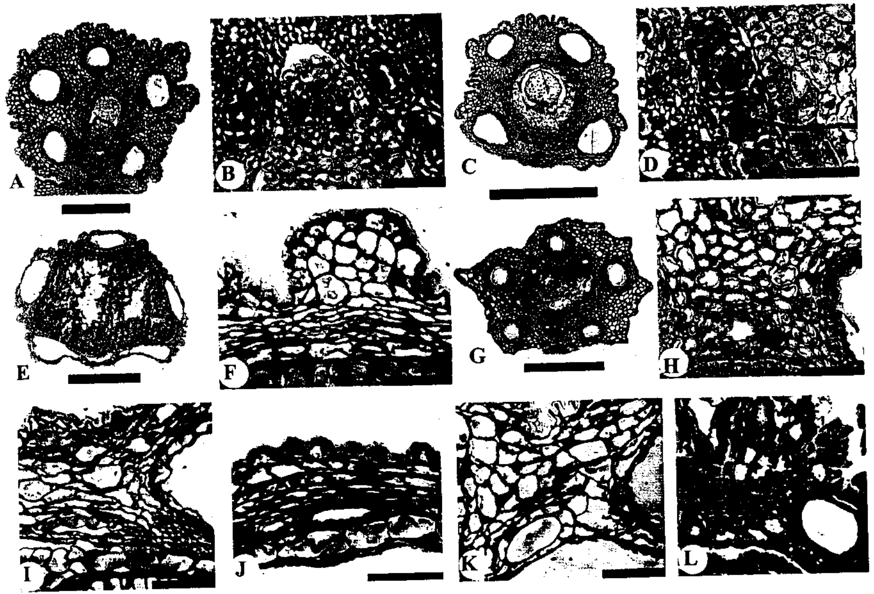

Fig. 4. Vittae in *Alepidea* (in transverse section). Development of vittae in *A. peduncularis* (A) — (F), and in *A. cordifolia* (G) and (H): (A) ovary (one carpel) showing cyclic vittae (paraendocarpic ducts); (B) close-up view of cyclic vittae in a flower; (C) very young fruit with a discernible zone of cyclic vittae; (D) close-up view of cyclic vittae in a very young fruit; (E) young fruit with no visible vittae; (F) details of fruit wall structure between rib oil ducts in a young fruit. (G) a very young fruit of *A. cordifolia* (Van Wyk 4232) showing conspicuous vittae; (H) a vallecular vitta in a very young fruit of *A. cordifolia*. Vittae of mature fruits (I) — (L): (I) *A. basinuda* (Venter 11, 739), vallecular vittae; (J) *A. galpinii* (Hilliard & Burtt 16428), commissural vittae; (K) *A. capensis* (Victor 1169), a vallecular vitta in the apical part of the fruit; (L) *A. setifera* (Jacobsz 2178), branched vallecular vittae. Scale bars: (A), (G) — 0.4 mm; (C), (E) — 0.8 mm; (B), (D), (F), (H) — (L) — 0.07 mm.

these vittae-like structures apparently become obliterated (Fig. 4E, F) leaving no traces in fully mature fruits (Fig. 2D, E). Such structures have been variously referred to as 'irregular vittae' (Liu et al. 2004, 2007), 'cyclic vittae' (Kljuykov et al. 2004) or as 'paraendocarpic ducts' (Denisova 1961). In the Russian literature, various other terms are also used, including 'endocarpic ducts' (Alexandrov & Klimochkina 1947, Tikhomirov 1959), 'vittae endocarpicae cyclicae' (Koso-Poljansky, *Sciadophytorum systematis lineamenta*, cited by Pervukhina 1950) and 'cyclic ducts' (Shishkin 1950). Paraendocarpic ducts typically occur only in young fruits and become obliterated in mature ones.

Exocarp. This layer is sometimes referred to as the epidermis. It is uniserial, consisting of cells varying greatly in shape (see Fig. 3 for the variation in this character): radially-elongated, almost finger-like in *A. basinuda*, *A. serrata*, resembling equilateral triangles in *A. galpinii* (Fig. 3E), *A. serrata* var. *serrata* (Fig. 3J) and *A. natalensis* (in

Fig. 3N amongst other types), or bottle-shaped, as in *A. peduncularis* (Fig. 3I) and *A. serrata* var. *serrata* (Fig. 3J). Some species possess two (*A. setifera*) or three [*A. longeciliata* (Fig. 3K)] of these cell types together (see Table 1), or there may be additional tangentially-flattened cells, as in *A. amatymbica, A. cirsiifolia* (Fig. 3G), *A. galpinii* (Fig. 3M) and *A. peduncularis* (Fig. 3L). The cell walls are markedly thickened, sometimes to the extent that the cell lumen is almost obscured, as seen in *A. cirsiifolia* (Fig. 3G), and they have thick cuticles. Variations in cell shape are shown in Fig. 3I–P and the main types are summarized in Table 1.

Mesocarp. The mesocarp is composed of about two layers of parenchymatous cells in *A. amatymbica* (Fig. 2A) but may have as many as 10 tangentially flattened layers, as in *A. cordifolia* (Fig. 2C). In common with other members of the Saniculoideae (Liu et al. 2004), dispersed druse crystals (calcium oxalate) are found in the pericarp of *Alepidea* species. As shown in Table 1, crystals vary greatly in their distribution and there are no obvious discontinuities among the species or sections. Note that the data in Table 1 is incomplete for some samples because unstained sections were not available (crystals are frequently dissolved during the staining process and ghost cells may be difficult to distinguish in rehydrated material).

Our anatomical study revealed that the protuberances found in most *Alepidea* species are not strictly 'exocarp outgrowths' (Calviño et al. 2008) but are partly formed by the mesocarp as well (and should therefore be treated as parts of the exomesocarp rather than solely as exocarp). The different outgrowth types are shown in Fig. 3E–H and are summarized in Table 1.

Endocarp. In *Alepidea*, the endocarp is one-layered, parenchymatous and may adhere tightly to the seed in some specimens. Endocarp cells are almost square in outline (most species examined) or tangentially elongated (*A. setifera*).

Discussion

The genus *Alepidea*, despite being the subject of several taxonomic studies, still lacks suitable characters which can be used phylogenetically (to clarify interspecific relationships) as well as practically (e.g., to complete keys or descriptions in reference books, to help identify medicinally utilized species). The characters used in previous treatments of *Alepidea* have proven to be inadequate (Dümmer 1913, Wolff 1913, Weimarck 1949), so that the sectional division of *Alepidea*, especially that of Weimarck (1949), has been recently criticized for being artificial (Burtt 1991, Calviño & Downie 2007, De Castro & Winter unpublished data). However, to date no reasonable alternative has been offered.

Our research has revealed a wide range of variation in fruit structural characters, but apparently only a few are of taxonomic value. The most variable traits are discussed below, some of which may contribute to a better understanding of the diversity pattern in the genus.

External features. Species of *Alepidea* differ slightly in fruit size, shape and colour.

Representatives of the sect. *Leiocarpae* (especially *A. amatymbica*) appear to have the largest fruits, whilst the smallest ones are found in *A. natalensis* (Fig. 1M, N) and *A. setifera*.

Surface sculpturing. This feature was traditionally used in taxonomic studies of *Alepidea*. The first section (*Leiocarpae*) in Weimarck's (1949) revision is comprised of the smooth-fruited species, whereas all other species with uneven pericarp surfaces were distributed amongst five other sections. Our study once again confirmed the taxonomic significance of smooth fruits, at least at species level. *A. amatymbica* can be recognized by its smooth fruits that totally lack outgrowths (Fig. 2A), while the fruits of *A. cordifolia* (Fig. 2B) are almost smooth, having only inconspicuous protuberances.

Fruits of *Alepidea* rarely appear grooved in dorsal view as a result of either somewhat sulcate rib oil ducts, as in some individuals of *A. cordifolia* (Fig. 2C), or a ridge on either side of each rib duct, as in *A. woodii* (Fig. 2F).

For the uneven-surfaced fruits, it was revealed that various elements contribute to the surface sculpturing, including the exomesocarp protuberances, the exocarp cell shapes and the cuticle. Exomesocarp protuberances, sometimes very pronounced, are commonly found in many other Saniculoideae (*Actinolema* Fenzl., *Eryngium, Sanicula*, etc.) and represent the greatest diversity. Externally, the outgrowths in *Alepidea* can have different shapes (mainly scales or tubercles) and sizes, and can also vary in arrangement (either vertical rows, evenly distributed over the fruit surface or restricted to the apical or basal parts of the fruit). Many anatomical characters and characters states can be reported for the protuberances (see Table 1), but no particular patterns of outgrowths are characteristic for any of the sections. The only section showing relative consistency in the exomesocarp projections is sect. *Alepidea*. The studied members of this section all possess abundant, mostly branched protuberances of irregular, or less often, triangular shape as seen in transverse section. Exocarp cells also contribute to surface sculpturing, forming the primary surface ultrasculpture. In addition, the cuticle represents the secondary ultrasculpture. These traits, especially when studied by scanning electron microscopy, can be of some use for taxonomic studies at the specific level and may have a practical application (for compiling keys) but they rarely have phylogenetic significance (e.g. Yembaturova 2001, 2004).

The patterns of druse crystal distribution in the mesocarp, characterized as 'dispersed', also appear to be very variable. Crystals vary in abundance and location and therefore have little or no diagnostic value within *Alepidea*. According to Liu et al. (2003) and Liu (2004), dispersed druse crystals are commonly found in many other Saniculoideae sensu lato [*Actinolema, Astrantia* L., *Eryngium, Sanicula* (incl. *Hacquetia* Neck. ex DC.)], but can also be absent (*Arctopus, Petagnaea* Caruel). This character is variable in *Alepidea*, as some species have numerous druse crystals while others have very few (see Table 1).

Our research revealed the sporadic occurrence of regular vittae in *Alepidea*. Vittae (regular or irregular) have never been recorded in this genus before. Vittae are typically absent in the subfamily Saniculoideae or are small and irregular, as was reported by Liu et al. (2003) and Liu (2004). Regular vittae, i.e., vittae differentiated into four vallecular (between the ribs) and two commissural vittae (one on either side of the ventral vascular bundle), are so far known only from the subfamily Apioideae, where they are usually very conspicuous.

There seems to be no obvious relation between the presence of vittae and the current taxonomic divisions in *Alepidea* and they appear to be present in all or most of Weimarck's (1949) sections. To date, regular vittae have been recorded in several species but they may often not be clearly visible in mature, rehydrated fruits. Vittae are clearly visible in samples of *A. cordifolia* and *A. amatymbica* (sect. *Leiocarpae*), *A. galpinii* and *A. capensis* (sect. *Alepidea*), and *A. setifera* (sect. *Setiferae*).

In the polymorphic and geographically widespread *A. peduncularis* (sect. *Longifoliae*), cyclic vittae are present in a continuous zone around the endocarp but become obliterated as the fruit matures. Cyclic vittae were clearly visible only in two of the specimens of *A. peduncularis* studied. We also observed cyclic vittae in immature fruits of *Sanicula elata* Buch.-Ham. ex D.Don (Saniculoideae) and species of *Conium* L. Hilliard & Burtt (1985) referred to these structures as 'schizogenous canals'; Kljuykov et al. (2004) used the term 'cyclic vittae'. Liu et al. (2003, 2007) called them 'irregular vittae' and reported their presence in mature fruits of several genera of the subfamily Saniculoideae [*Actinolema, Eryngium* and *Sanicula* (incl. *Hacquetia*)] and also in the anomalous woody African genera *Steganotaenia* Hochst. and *Pseudocarum* C.Norman. Cyclic vittae ('irregular vittae') in these genera were described by Liu et al. (2003, 2007) as branching and anastomosing structures that may form a network around the endocarp. Both cyclic (irregular) and regular vittae were reported to be absent in *Alepidea, Astrantia* and *Polemanniopsis* B.L.Burtt (Liu et al. 2003; Liu 2004). Cyclic vittae are also known from a few members of the subfamily Apioideae, e.g. *Archangelica decurrens* Ledeb. (Denisova 1961), *Prangos pabularia* Lindl. (Alexandrov & Klimochkina 1947; Tikhomirov 1959); *P. lipskyi* Korovin (Kljuikov et al. 2004), species of *Ligusticum* L. (Tikhomirov & Konstantinova 2000) and *Aegopodium podagraria* L. (Alexandrov & Klimochkina 1947). The South African endemic *Arctopus* is known to have a well-developed branched network of vascular bundles in the pericarp so the rib oil ducts associated with them often have rather unusual location patterns (Magee unpublished data) but vittae appear to be absent. *Alepidea* seems to be the only genus in the subfamily Saniculoideae with regular vittae.

Conclusions

Although fruit structural characters are highly variable in *Alepidea*, only a limited number appear to have taxonomic significance. The surface sculpturing, formed by multiple components (exomesocarp protuberances, exocarp cell shape and cuticle) is one of the most useful carpological characters for the infrageneric taxonomy of *Alepidea*, despite its variability. The uniqueness of the smooth-fruited species (*A. amatymbica, A. cordifolia*), which also possess the largest fruits in the genus, is again confirmed. In view of substantial variation in surface sculpturing, an extensive sampling, representative of the full geographical range and diversity of each species, will be necessary to confirm apparent discontinuities.

This study, originally aimed at contributing to the intrageneric taxonomy of *Alepidea*, has unexpectedly provided us with a deeper insight into the presence and distribution of secretory structures in the fruits of Apiaceae. The difference between so-called 'irregular vittae' and 'regular', or 'true vittae', has now been clarified. The term 'irregular vittae' may be somewhat confusing because true vittae that vary in size and number are present in some apioid genera (e.g., the tribe Heteromorpheae). We therefore propose that the term 'dispersed paraendocarpic vittae be used for the structures found in *Alepidea* and other members of Saniculoideae as well as in some members of Apioideae (e.g. Conium, see Corsi & Biasci 1998). Since flowers and young fruits are rarely studied anatomically, paraendocarpic ducts may be more widespread in *Alepidea*, the Saniculoideae and even other Apiaceae. It is noteworthy that vittae and paraendocarpic ducts do not co-occur in any *Alepidea* samples we have investigated. This indicates that these two structures are not homologous, i.e. paraendocarpic ducts apparently do not develop into regular vittae.

The presence of regular vittae in *Alepidea* species is of considerable interest, as it reduces the taxonomic distance between the subfamilies Apioideae and Saniculoideae. The co-occurrence of large rib ducts and vittae is a very rare combination, so far found only in the genus *Phlyctidocarpa* Cannon & W.L.Theob. Furthermore, the rows of surface protuberances that result in longitudinal grooves in the fruits of some species of *Alepidea* (notably *A. woodii*, see Fig. 2F) are similar to the rows of seemingly unique blisters on the fruits of *Phlyctidocarpa flava* Cannon & W.L.Theob. The similarities between *Alepidea* and *Phlyctidocarpa*, and their respective relations to the subfamilies Saniculoideae and Apioideae, need to be taken into consideration when a new phylogenetic system for the family is devised. The presence of cyclic vittae in *Alepidea* species (at least in flowers and immature fruits) supports its relation to other members of the tribe Saniculeae, where cyclic vittae are fairly common, even in mature fruits. The sporadic occurrence of cyclic vittae in members of the subfamily Apioideae indicates that a wider survey of flowers and young fruits may provide a better understanding of the distribution pattern and homology of this character across the entire family.

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