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The taxonomic value of fruit wall structure in the genus *Annesorhiza* (Apiaceae)

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A study of the fruit wall structure of 12 species of *Annesorhiza* Cham. & Schlechtd. has shown a wealth of taxonomically useful characters at both the generic and infrageneric levels: firstly, the presence of enormously expanded and lignified vascular bundles, which appears to be a unique generic character; secondly, a remarkable type of heteromorphic wing symmetry [only in *A. macrocarpa* Eckl. & Zeyh. and *A. nuda* (Ait.) B.L. Burtt], in which all the sepaline ribs and the two commissural petaline ribs have expanded to form wings; and thirdly, the presence of lignified cells in various positions, which can be used to distinguish some of the species. The genus *Annesorhiza* is poorly known but the external and internal fruit wall structure provide valuable information which contributes to a better understanding of infrageneric relationships.

'n Studie van die struktuur van die vrugwand in 12 spesies van *Annesorhiza* Cham. & Schlechtd. het 'n rykdom van taksonomiese kenmerke aangetoon wat op generiese sowel as infrageneriese vlak bruikbaar is: eerstens, die teenwoordigheid van ontsaglik ontwikkelde en gelignifiseerde vaatbondels, wat skynbaar 'n unieke generiese kenmerk is; tweedens, 'n merkwaardige tipe heteromorfiese vlerksimmetrie [slegs in *A. macrocarpa* Eckl. & Zeyh. en *A. nuda* (Ait.) B.L. Burtt], waar al die kelkriwwe sowel as die twee kommissurale kroonriwwe vergroot het om vlerke te vorm; en derdens, die teenwoordigheid van gelignifiseerde selle in verskillende posisies, wat gebruik kan word om sommige spesies van mekaar te onderskei. Die genus *Annesorhiza* is swak bekend maar die uitwendige en inwendige bou van die vrugwand bied waardevolle inligting wat bydra tot 'n beter begrip van infrageneriese verwantskappe.

Keywords: *Annesorhiza*, Apiaceae, fruit wall anatomy, southern Africa, taxonomy.

Introduction

Annesorhiza Cham. & Schlechtd. is a genus with hysteranthous leaves comprising about 12 to 15 species endemic to southern Africa (Burtt 1991). Since it is not possible to collect leaves and fruits together, the species are notoriously difficult to identify from herbarium specimens. As a first step towards a complete revision of *Annesorhiza*, we have evaluated the taxonomic utility of fruit wall structure at the generic and infrageneric levels.

Fruit characters have traditionally been used in tribal and generic delimitations in the Apiaceae, but anatomical details of most of the African genera have remained unknown. The fruit wing symmetry in *Annesorhiza* is variable, with some species homomorphic and others heteromorphic (Sonder 1862; Drude 1898; Dyer 1975; Burtt 1988). The species with heteromorphic mericarps display a unique fruit wing configuration similar to that found in *Heteromorpha* Cham. & Schlechtd. (Winter *et al.* 1993). A study of the changes during different developmental stages of the two basic fruit types in *Annesorhiza* was needed, so that the homology of the wing symmetry of this genus and *Heteromorpha* could be compared.

Materials and Methods

Flowers, young fruits and mature fruits were removed from rich herbarium collections, rehydrated by placing in tubes with distilled water and heating slowly to boiling point for approximately 1 h, and then fixed in FAA for at least 24 h. Some fresh material preserved in FAA was also used. A complete list of material together with correct names and author citations are given in Table 1. Authorities for names are not repeated elsewhere. Some species are poorly known so that sample limitations are a real problem. Nevertheless, most of the species are represented, several of them by at least three different collections. The material was embedded in glycol methacrylate (GMA) according to a modification of the method of Feder and O'Brien (1968) for sectioning on a Porter Blum MT-1 ultramicrotome. This modification involves infiltrating the material in the GMA for a minimum of 24 h between the first two changes and for a longer period (usually at least five days) before placing in the gelatin capsules, which are then heated in an oven at 60°C for 24 h to polymerize. Mounted sections were stained according to the so-called Periodic Acid – Schiff/Toluidine Blue (PAS/TB) staining method and photographed using a Leitz Wetzlar microscope and Ilford PAN F (ASA 50) and Ilford FP4 (ASA 125) film.

Results and Discussion

A summary of various structural characters and their distribution in 12 species of *Annesorhiza* is given in Table 2. The results clearly show that the wall structure of the mericarps is useful at the generic and infrageneric levels. Characters and character states are discussed below.

Wing configuration

Two different types of wing configurations are found in *Annesorhiza* (Figure 1). In most of the species, the mericarps are homomorphic and more or less wingless (e.g. *A. altiscapa*, see Figure 2c). In some of these species [e.g. *A. flagellifolia* (Figure 1a), *A. wilmsii* (Figure 1b) and *A. schlechteri* (Figure 1c)], each vascular bundle is expanded into a distinct rib, with the four commissural (marginal) ribs more prominent than the other ribs. The larger size of the commissural ribs is typical of *Peucedanum* L. (Theobald 1971). *A. grandiflora* (Figure 1d) has the ribs enlarged and somewhat wing-like but the mericarps are still more or less homomorphic. In *A. nuda* (Figure 1e) and *A. macrocarpa* (Figure 1f), however, the mericarps are distinctly heteromorphic and winged; one mericarp has three wings, the other four. The mericarps of *A. hirsuta* are reported to be heteromorphic (Sonder 1862; Drude 1898), but we could not find any specimens of this species where this was the case. The heteromorphy in *A. macrocarpa* and *A. nuda* is reminiscent of the condition in *Heteromorpha* (Winter *et al.* 1993), where one mericarp has three sepaline wings and two petaline

Table 1 Voucher specimens of the flowers, young fruit and mature fruit of *Annesorhiza* that were used for anatomical studies

Species	Voucher specimen(s)	Flowers	Young fruit	Mature fruit
Annesorhiza altiscapa H. Wolff	*Acocks 14848* (PRE)			+
	Acocks 18558 (PRE)	+		+
	Van Wyk 3533 (JRAU)	+	+	
A. elata Eckl. & Zeyh.	*Adamson s.n.* (BOL)		+	
A. filicaulis Eckl. & Zeyh.	*Shearing 857* (PRE)	+	+	
A. flagellifolia Burtt Davy	*Compton 31804* (PRE)			+
	Mohle 116 (PRE)	+	+	
	Acocks 20878 (PRE)		+	+
A. grandiflora (Thunb.) Hiroe	*Marloth 10177b* (PRE)	+	+	
A. hirsuta Eckl. & Zeyh.	*Acocks 24522* (PRE)	+	+	
	Acocks 17566 (PRE)			+
	Marloth 7673 (PRE)			+
	Stirton & Zantovska 11422 (PRE)	+	+	
A. latifolia Adamson	*Adamson 1482* (BOL)		+	
	Van Berkel 468 (NBG)			+
A. macrocarpa Eckl. & Zeyh.	*Batten s.n. sub Hilliard & Burtt 14816*			+
	Van Wyk, Winter & Tilney 3483 (JRAU)	+	+	+
	Rourke 1700 (NBG)			+
A. marlothii H. Wolff	(poorly known; no fruit available)			
A. nuda (Ait.) B.L. Burtt	*Fellingham 930* (PRE)			+
	Flanagan 2432 (PRE)	+		+
	Esterhuysen 85 (PRE)			+
	Marloth 7429 (PRE)			+
	Bohnen 7541 (PRE)	+		+
A. schlechteri H. Wolff	*Flanagan 2685* (PRE)	+	+	+
	Germishuizen 1784 (PRE)	+	+	+
A. thunbergii B.L. Burtt	*Esterhuysen 23945* (BOL)		+	
A. villosa (Thunb.) Sonder	(poorly known; *A. hirsuta*?)			
A. wilmsii H. Wolff	*Hilliard & Burtt 18470* (PRE)	+	+	+

Table 2 Summary of taxonomically useful fruit structural characters in 12 species of *Annesorhiza* (authorities for names and voucher specimen details are given in Table 1)

Species	Fruit wings	Mericarp symmetry	Fruit wall characters: Groups of lignified cells	Fruit wall characters: Hypoderm lignified	Fruit wall characters: Endocarp lignified
A. altiscapa	–	homomorphic	+	±	±
A. elata	–	homomorphic	–	–	–
A. filicaulis	–	homomorphic	–	–	–
A. flagellifolia	–	homomorphic	+	–	–
A. grandiflora	+ small	± homomorphic	–	+	–
A. hirsuta	–	homomorphic	–	+	±
A. latifolia	–	homomorphic	–	+	+
A. macrocarpa	+ large	heteromorphic	–	–	±
A. nuda	+ large	heteromorphic	–	+	–
A. schlechteri	–	homomorphic	±	–	–
A. thunbergii	–	homomorphic	–	+	–
A. wilmsii	–	homomorphic	+	–	–

ribs, while the other mericarp has two sepaline wings and three petaline ribs. As was pointed out by Burtt (1991), *Annesorhiza* (and *Heptaptera* Margot & Reuter) never exhibit the strict sepal-wing correlation and always retain the two pairs of commissural wings. It thus appears that the '*Peucedanum*-type' wing expansion, as described by Theobald (1971), is here superimposed on the '*Heteromorpha*-type' wing configuration as described by Burtt (1991) and Winter *et al.* (1993).

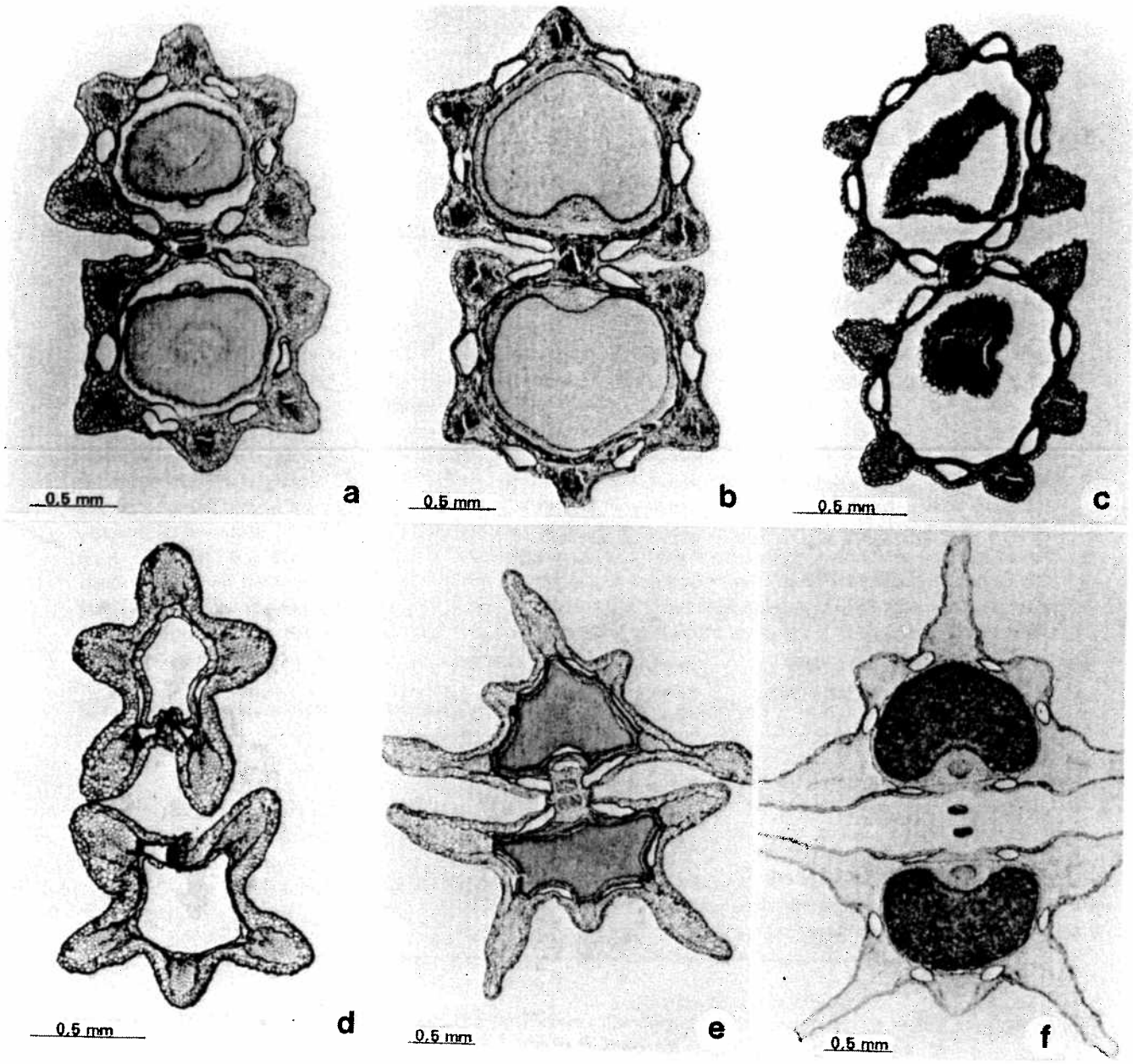

Figure 1 Homomorphic and heteromorphic wing configuration in the mericarps of *Annesorhiza* species, as seen in transverse section (note that the commissural ribs are at least slightly larger than the other ribs). **a.** Homomorphic, wingless (*A. flagellifolia*). **b.** Homomorphic, wingless (*A. wilmsii*). **c.** Homomorphic, wingless (*A. schlechteri*). **d.** More or less homomorphic, with small wings (*A. grandiflora*). **e.** Heteromorphic, winged (*A. nuda*). **f.** Heteromorphic, winged (*A. macrocarpa*). (a, from *Acocks 20878*; b, from *Hilliard & Burtt 18470*; c, from *Flanagan 2685*; d, from *Marloth 10177b*; e, from *Flanagan 2432*; f, from *Van Wyk, Winter & Tilney 3483*.)

The development of *Annesorhiza* fruit was studied in some detail by comparing the structure of flowers, young fruit and mature fruit (Figures 2a–f). The heteromorphic and homomorphic wing types are already distinct in the flower (Figures 2a&d), showing that the heteromorphic configuration is congenital and not a result of early development. The same was found in *Heteromorpha* (Winter *et al.* 1993). As in *Heteromorpha*, the wings are associated with sepaline ribs (Figure 2f), except that two of the four commissural wings arise from petaline ribs. Lignification, in contrast, occurs late in fruit development — just prior to maturity as the fruits start to dry out. Green fruits are only slightly lignified.

Vascular bundles

In all the specimens studied, the ten vascular bundles associated with the sepals and petals are enormously expanded and lignified (Figures 3a–c). These expanded vascular bundles make up the bulk of the tissue within the ribs or wings. In other genera of Apiaceae, the vascular bundles are inconspicuous and the wings comprise mostly parenchymatous cells, as in *Heteromorpha* and *Peucedanum*, or the wings may rarely be hollow (empty) structures, as in *Polemanniopsis* B.L. Burtt. Expanded, lignified vascular bundles are clearly conservative in *Annesorhiza* and appear to be a reliable diagnostic character at the generic level.

Fruit wall characters

The presence or absence of single lignified cells or groups of lignified cells are useful characters at the specific level. A subepidermal layer of lignified cells is present in *A. grandiflora*, *A. hirsuta*, *A. latifolia*, *A. nuda*, *A. thunbergii* and in some specimens of *A. altiscapa* (Figure 3d). A lignified endocarp

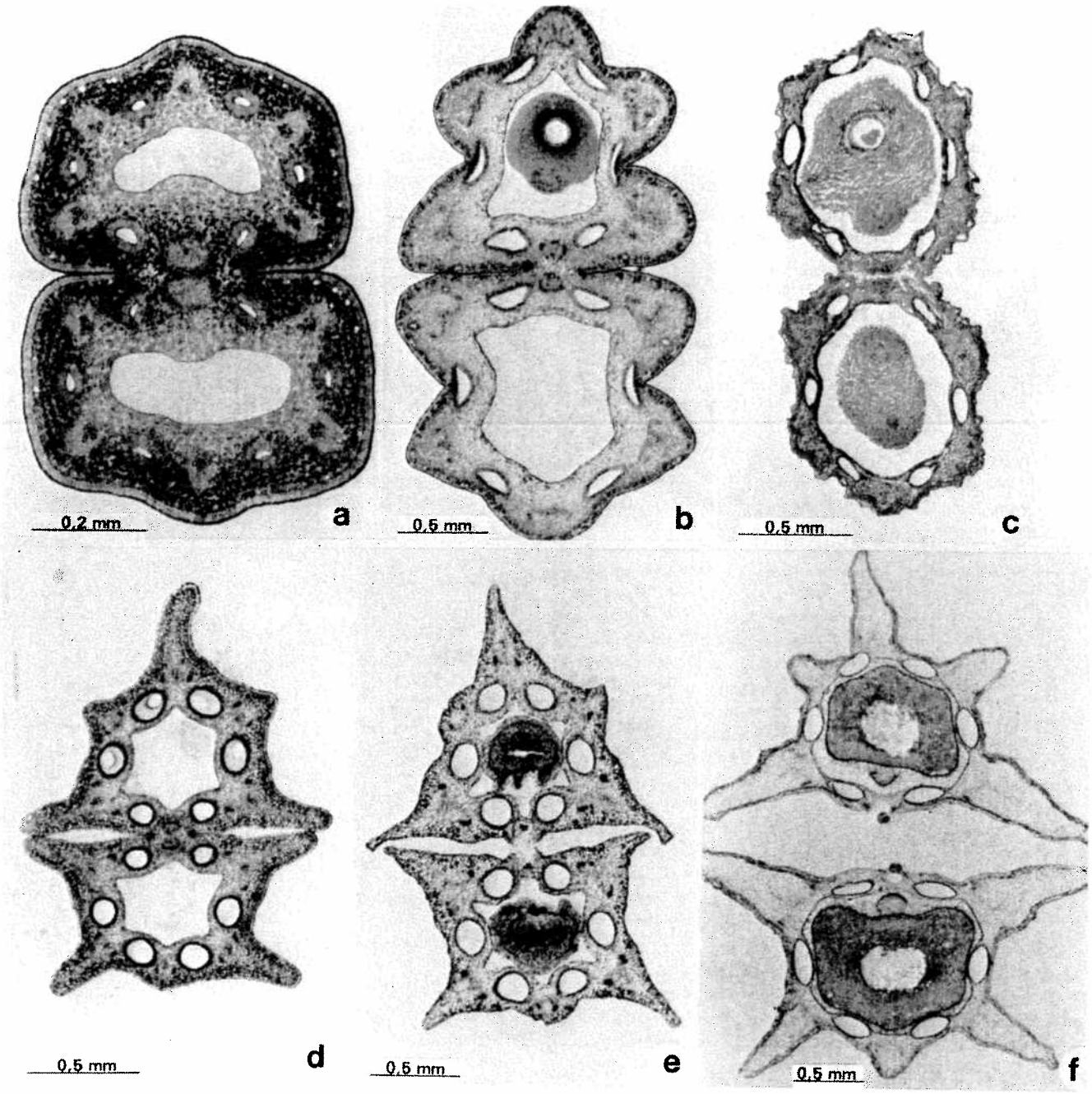

Figure 2 Fruit development in two species of *Annesorhiza* to show the difference in symmetry and wing configuration (all transverse sections). **a – c.** Ovary (a), young fruit (b) and mature fruit (c) of *A. altiscapa* (homomorphic, without wings). **d – f.** Ovary (d), young fruit (e) and mature fruit (f) of *A. macrocarpa* (heteromorphic, winged). (a and b, from *Van Wyk 3533*; c, from *Acocks 18558*; d – f, from *Van Wyk, Winter & Tilney 3483*.)

was found only in *A. macrocarpa* (Figure 3e), *A. latifolia* and in one specimen of *A. altiscapa* and one of *A. hirsuta*. The endocarp varies from a few lignified cells to several layers of lignified cells, as in Figure 3e. Groups of lignified cells are usually present between the vascular bundles and the vittae in *A. altiscapa, A. flagellifolia* (Figure 3f), *A. schlechteri* and *A. wilmsii* and frequently in the commissural region in most species (invariably in *A. altiscapa*, Figure 3d).

Individually and in combination, these characters of the fruit wall (presence or absence of various lignified cells) are of diagnostic value to distinguish some of the species.

Conclusions

A wealth of taxonomic information is found in the fruit anatomy of *Annesorhiza* species.

The wing configuration shows similarities with both the *Heteromorpha*-type' and the '*Peucedanum*-type', but the heteromorphous condition seems to have developed independently in *Heteromorpha* and *Annesorhiza*. Only two species show this peculiar '*Annesorhiza*-type' heteromorphous wing configuration, namely *A. macrocarpa* and *A. nuda*. In both of them, all the sepaline ribs and only two of the petaline ribs (the commissural ones) are developed into wings.

Distinct vascular bundles, each comprising a large group of lignified cells, appear to be a unique character for *Annesorhiza*. Other cell layers may also be lignified and these provide useful diagnostic characters for some of the species.

Anatomical characters, in combination with leaf and root characters, may eventually allow us to derive a convincing phylogeny for the genus *Annesorhiza* despite practical problems in obtaining suitable material for study.

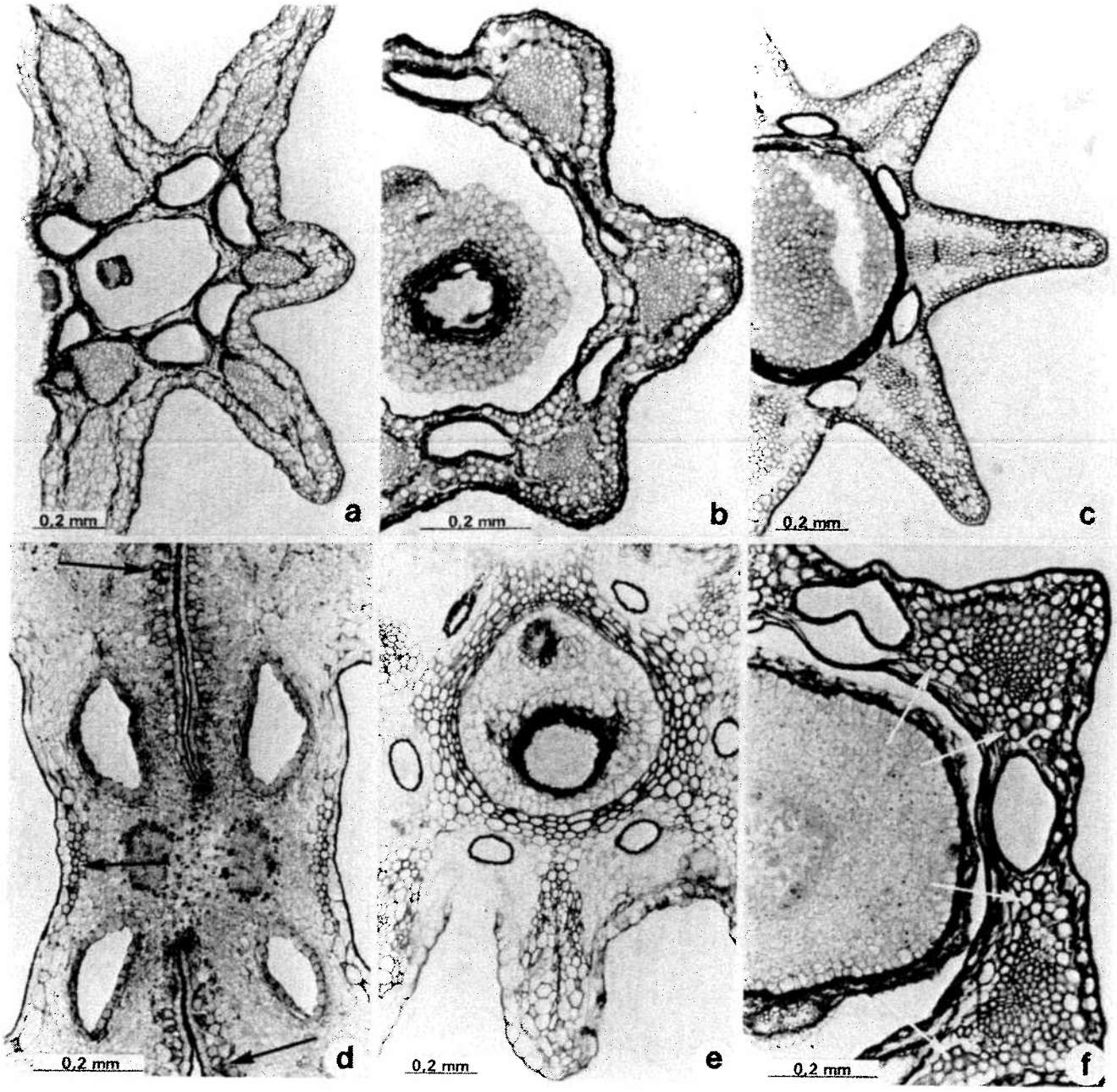

Figure 3 Fruit wall characters in *Annesorhiza* species (all transverse sections), showing the enormously expanded and lignified vascular bundles (a – c) and the presence of lignified cells (d – f). **a.** *A. nuda.* **b.** *A. latifolia.* **c.** *A. nuda.* **d.** *A. altiscapa* (note the lignified hypoderm and also the lignified cells in the commissural area, indicated by arrows). **e.** *A. macrocarpa* (note the layers of lignified endocarp). **f.** *A. flagellifolia* (note the groups of lignified cells near the vascular bundles, indicated by arrows). (a, from *Bohnen 7541*; b, from *Van Berkel 468*; c, from *Fellingham 930*; d, from *Van Wyk 3533*; e, from *Batten s.n. sub Hilliard & Burtt 14816*; f, from *Acocks 20878*.)

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References

BURTT, B.L. 1988. A new shrubby genus of African Umbelliferae. *Notes RBG Edinb.* 45: 493 – 501.

BURTT, B.L. 1991. Umbelliferae of southern Africa: an introduction and annotated checklist. *Edinb. J. Bot.* 48: 133 – 282.

DRUDE, O. 1898. Umbelliferae. In: Die natürlichen Pflanzenfamilien, eds. A. Engler & K. Prantl, No. 3(8), pp. 63 – 250. Engelmann, Leipzig.

DYER, R.A. 1975. The genera of southern African flowering plants, Vol. 1, pp. 425 – 426. Botanical Research Institute, Pretoria.

FEDER, N. & O'BRIEN, T.P. 1968. Plant microtechnique: some principles and new methods. *Am. J. Bot.* 55: 123 – 142.

SONDER, O.W. 1862. *Annesorhiza.* In: Flora Capensis, eds. W.H. Harvey & O.W. Sonder, Vol. 2, pp. 544 – 547. Hodges Smith, Dublin.

THEOBALD, W.L. 1971. Comparative anatomical and developmental studies in the Umbelliferae. In: The biology and chemistry of the Umbelliferae, ed. V.H. Heywood, pp. 177 – 197 (Suppl. 1 to *Bot. J. Linn. Soc.* 64).

WINTER, P.J.D., VAN WYK, B.-E. & TILNEY, P.M. 1993. The morphology and development of the fruit of *Heteromorpha* (Apiaceae). *S. Afr. J. Bot.* 59: 336 – 341.