

The taxonomic value of fruit structure in the subfamily Saniculoideae and related African genera (Apiaceae)

Mei (Rebecca) Liu, Ben-Erik van Wyk & Patricia M. Tilney

Department of Botany, Rand Afrikaans University, P.O. Box 524, Auckland Park, Johannesburg, 2006 Republic of South Africa. *ogsa@icon.co.za* (author for correspondence); *bev@na.rau.ac.za*; *pmt@na.rau.ac.za*

All members of Saniculoideae *sensu stricto* are unique in their fruit structure, having the endocarp non-lignified, outgrowths on mericarps, usually prominent intrajugal secretory ducts, vallecular vittae totally absent, commissural vittae absent except in *Lagoecia* L. (which should be better placed in Apioideae), carpophore absent except in *Alepidea* F. Delaroché, and crystals dispersed throughout the mesocarp. The fruits of the African genus *Lichtensteinia* Cham. & Schltdl. are very similar to those of Saniculoideae, having very prominent intrajugal secretory ducts and lacking both vallecular and commissural vittae (the endocarp of one mericarp is lignified, the other not). Furthermore, scattered crystals are present in the mesocarp. Three other African genera (*Arctopus* L., *Polemanniopsis* B.L. Burtt and *Steganotaenia* Hochst.) also have some fruit characters that are similar to those of Saniculoideae, such as the total absence of vallecular and commissural vittae, combined with intrajugal cavities (which are enormous in the latter two genera). They differ in some respects, such as nearly always having lignified endocarps, non-functional intrajugal secretory ducts forming cavities, wings (in *Polemanniopsis* and *Steganotaenia*), and an absence of crystals. A cladistic analysis based on all anatomical characters shows that *Lichtensteinia*, *Polemanniopsis* and *Steganotaenia* are directly basal to the Saniculoideae, and that there is sufficient morphological evidence (in support of earlier molecular systematic studies) to expand the circumscription of the subfamily to include these genera.

KEYWORDS: Apiaceae, classification, fruit anatomy, phylogeny, Saniculoideae.

INTRODUCTION

The subfamily Saniculoideae is a more or less distinctive group of predominantly northern hemisphere Apiaceae with congested or capitate inflorescences, toothed or spiny leaves, and fruits with surface outgrowths (Figs. 1–4). As originally conceived by Drude (1898), the subfamily comprised the two tribes Saniculeae and Lagoecieae. Drude was the first to define this subfamily by fruit structural characters, using the parenchymatous endocarp, scattered druse crystals, uneven exocarp (covered with scales, prickles or bristles, or rarely smooth) and the usually prominent intrajugal secretory ducts (oil tubes developed in the main ribs, never in the furrows). Members of the tribe Saniculeae have fruits with two mericarps and usually very prominent vittae, whereas members of Lagoecieae have fruits with a single mericarp and indistinct vittae. Drude's description of the fruits is basically correct, except that prominent commissural vittae are present in *Lagoecia cuminoides* L. (Fig. 1B), and some details of the fruit anatomy were not studied. Wolff (1913) arrived at nearly the same circumscription as Drude by studying vegetative organs and flower features of this subfamily.

Froebe (1964) mentioned that the inflorescence of

Arctopus (an African endemic genus) was different from that of other members of Saniculoideae. Magin (1980) stressed that *Arctopus* displays many floral characteristics that are lacking in Saniculoideae but occur in Hydrocotyloideae. Pimenov & Leonov (1993) followed these authors and transferred *Arctopus* to the *incertae sedis* of the subfamily Hydrocotyloideae. The African endemic genus *Lichtensteinia* was placed in the tribe Apieae of subfamily Apioideae (Pimenov & Leonov, 1993), but it has toothed leaves and round cotyledons (Burtt, 1991) as in members of Saniculoideae. Morphological and phylogenetic studies (Burtt, 1991; Van Wyk, 2001) showed that it has important characters in common with Saniculoideae, despite the typical apioid inflorescence structure. *Polemanniopsis marlothii* and *Steganotaenia araliacea* are two woody African genera with deciduous leaves, dentate leaf margins (Burtt, 1988; Van Wyk, 2001), and flowers commonly appearing before the leaves (sometimes co-occurring; Townsend, 1989; Glen & Onderstall, 1991). Norman (1934) observed that the fruit anatomy of these two genera is very peculiar (such as the presence of large cavities in the wings), and Burtt (1991) pointed out that the chromosome number of $n = 12$ agrees more with Araliaceae than Apiaceae, where $n = 11$ is typical. Further evidence of

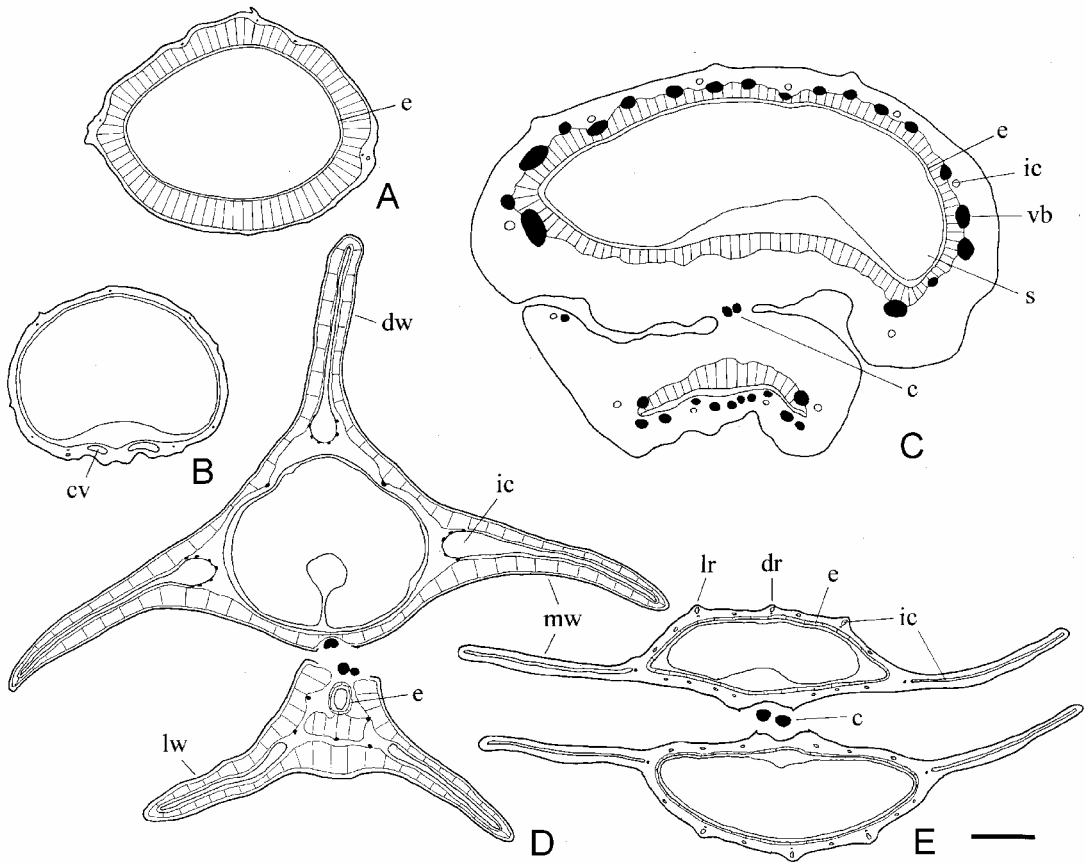


Fig. 1. Fruit structure of representatives of subfamily Saniculoideae sensu lato as seen in transverse section showing variation in mericarp surfaces, size of intrajugal secretory ducts, presence or absence of small vittae scattered in the mesocarp, lignification or otherwise of the mesocarp, commissural width, presence or absence of a carpophore, and seed shape. A, *Petagnaea saniculifolia*; B, *Lagoecia cuminoides*; C, *Arctopus echinatus*; D, *Polemanniopsis marlothii*; E, *Steganotaenia araliacea*. Hatching - lignification; dots - vascular bundles (vb); circles - secretory ducts; dr - dorsal rib; lr - lateral rib; e - endocarp; s - seed; c - carpophore; dw - dorsal wing; lw - lateral wing; mw - marginal wing; ic - intrajugal cavity; cv - commissural vitta. Scale bar = 0.5 mm in A & B, 1 mm in C–E.

the anomalous taxonomic positions of *Polemanniopsis* and *Steganotaenia* came through an important molecular systematic study of woody southern African Apiaceae (Downie & Katz-Downie, 1999), in which the two genera were placed basal to Saniculoideae. Such an affinity was contrary to expectation, but Plunkett (2001) confirmed the relationship. Van Wyk (2001) pointed out that there are indeed potential synapomorphies for this novel rearrangement, if less emphasis is placed on inflorescence structure.

From the above discussion it can be seen that (1) the circumscription of the subfamily needs to be re-evaluated, (2) the position of certain anomalous genera needs to be explored, and (3) possible morphological/ structural evidence should be found to evaluate recent hypotheses based on DNA evidence. Details of the taxa traditionally included in the subfamily and four related genera are given in Table 1.

MATERIALS AND METHODS

Materials. — At least two mature fruits of each of the following 21 species, representative of all genera of Saniculoideae and four putative African relatives (*Arctopus*, *Lichtensteinia*, *Polemanniopsis* and *Steganotaenia*) were studied. One species each of the genera *Tana* (Apioideae) and *Azorella* (Hydrocotyloideae) were used for comparative studies. Voucher specimens are included in Table 2. Authorities for generic and specific names are given in Tables 1 and 2, respectively. These samples form part of a much larger sample of 700 fruits from more than 300 genera.

Anatomical studies. — All materials were rehydrated and placed in FAA for a minimum of 24h and then treated according to the method of Feder & O'Brien (1968) for embedding in glycol methacrylate (GMA). However, a minimum of 24h was used for the first two

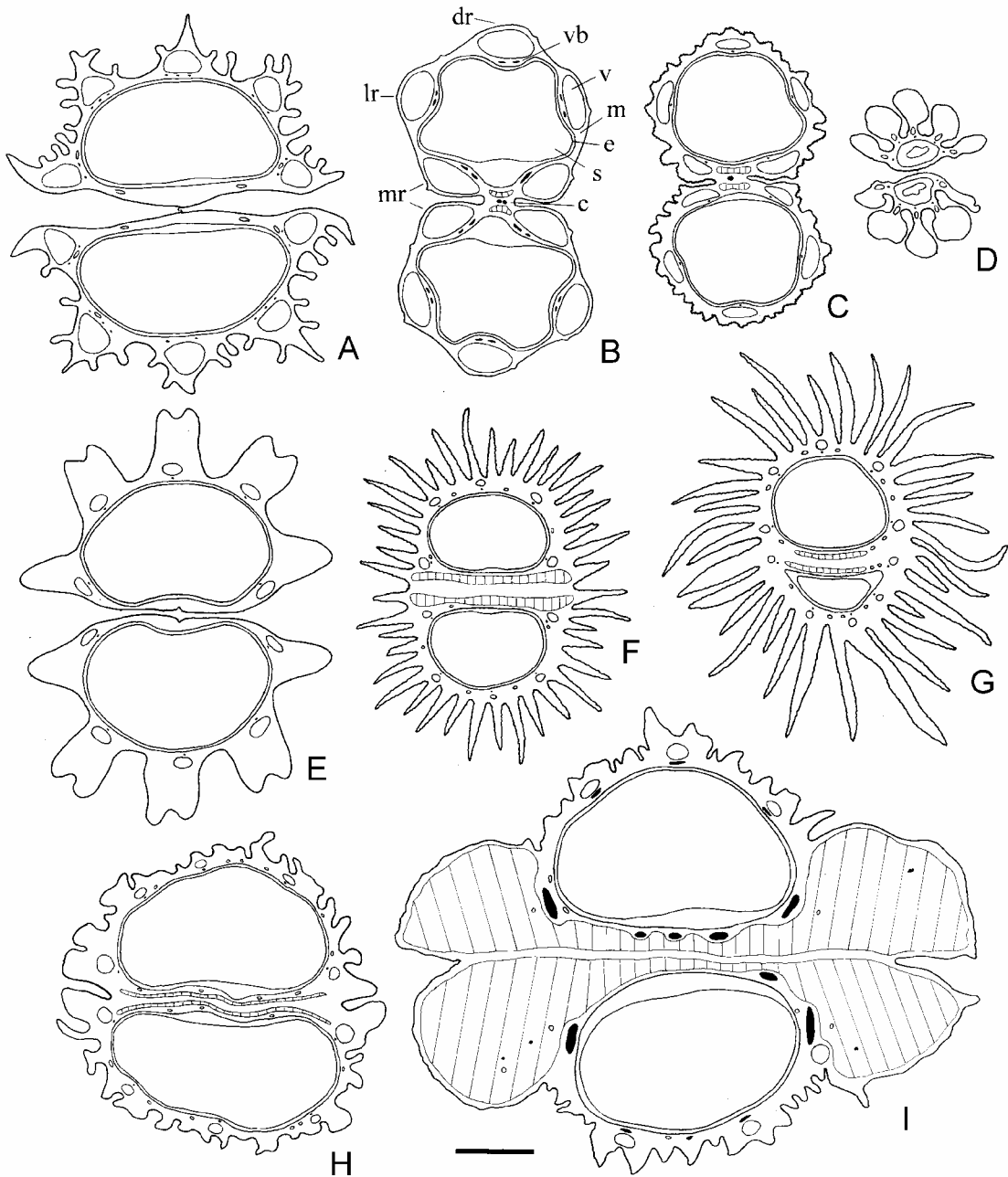


Fig. 2. Fruit structure of representatives of subfamily Saniculoideae s.l. as seen in transverse section. A, *Actinolema macrolema*; B, *Alepidea amatymbica*; C, *A. setifera*; D, *Astrantia major*; E, *A. maxima*; F, *Eryngium planum*; G, *E. campestre*; H, *E. giganteum*; I, *E. maritimum*. Hatching - lignification; dots - vascular bundles (vb); circles - secretory ducts (v); mr - marginal rib; m - mesocarp. Other abbreviations and details as in Fig. 1. Scale bar = 1 mm.

infiltrations in GMA and a minimum of five days for the third infiltration. The capsules containing the material and GMA were placed in an oven at 60° for 24h. Medial transverse sections, about 5 µm thick, were cut using a Porter-Blum ultramicrotome. The periodic acid-Schiff/toluidine blue staining method was used. With this method, lignified cells (green in colour) can easily be

distinguished from non-lignified ones (purple in colour); there are no intermediates. The wall thickness of lignified cells varies greatly, so that we have avoided using wall thickness as a character. The phloroglucin test (Morholt & al., 1966) was performed on all the samples to confirm that green-stained cells are indeed lignified. Photographs were taken using a Leitz Wetzlar micro-

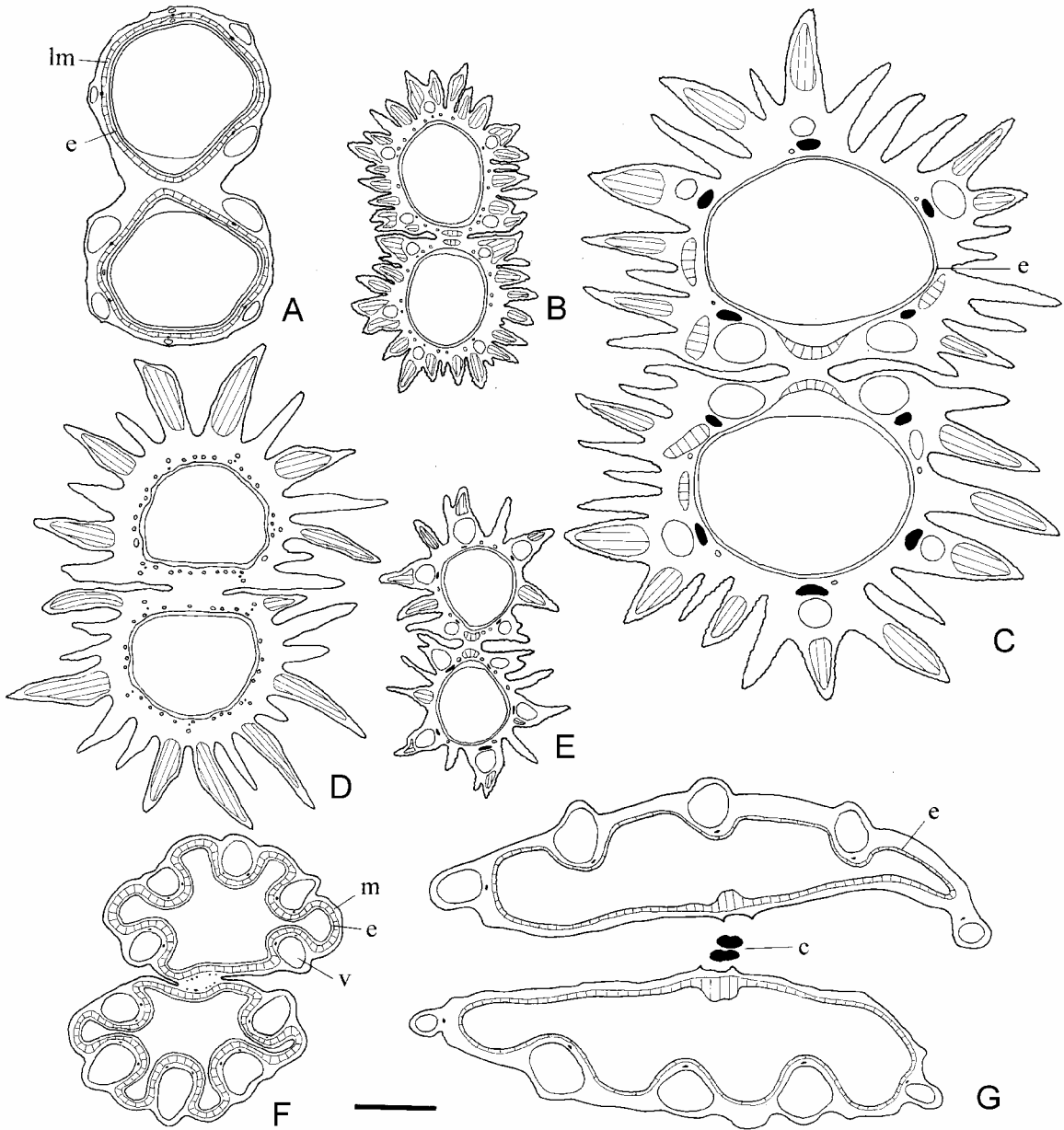


Fig. 3. Fruit structure of representatives of subfamily Saniculoideae sensu lato as seen in transverse section. A, *Hacquetia epipactis*; B, *Sanicula coerulescens*; C, *S. rubiflora*; D, *S. europaea*; E, *S. lamelligera*; F, *Lichtensteinia obscura*; G, *L. lacera*. Circles - secretory ducts (v); lm - lignified mesocarp; other abbreviations and details as in Fig. 1. Scale bar = 1 mm.

scope and Ilford Pan F film. Drawings were done using a camera lucida (Figs. 1–3).

Cladistic analyses. — All fruit anatomical characters (as listed in Table 3) were considered, but only 12 could be logically polarized for cladistic analyses (listed in Table 4). *Azorella* and *Tana* were chosen to serve as place markers for, respectively, Hydrocotyloideae and Apioideae in the cladistic analysis. The former was chosen as outgroup partly because it was also included in the

study of Valiejo-Roman & al. (2002), where it was shown to be basal to Saniculoideae and Apioideae. The data were repeatedly analysed using the computer program HENNIG86 Version 1.5 (Farris, 1988). The “ie” command gave four most parsimonious trees with a length of 22 and a consistency index of 0.78. A strict consensus tree is shown in Fig. 5. Readers may wish to explore the pattern in the data by using other programmes, but the partially resolved consensus tree in

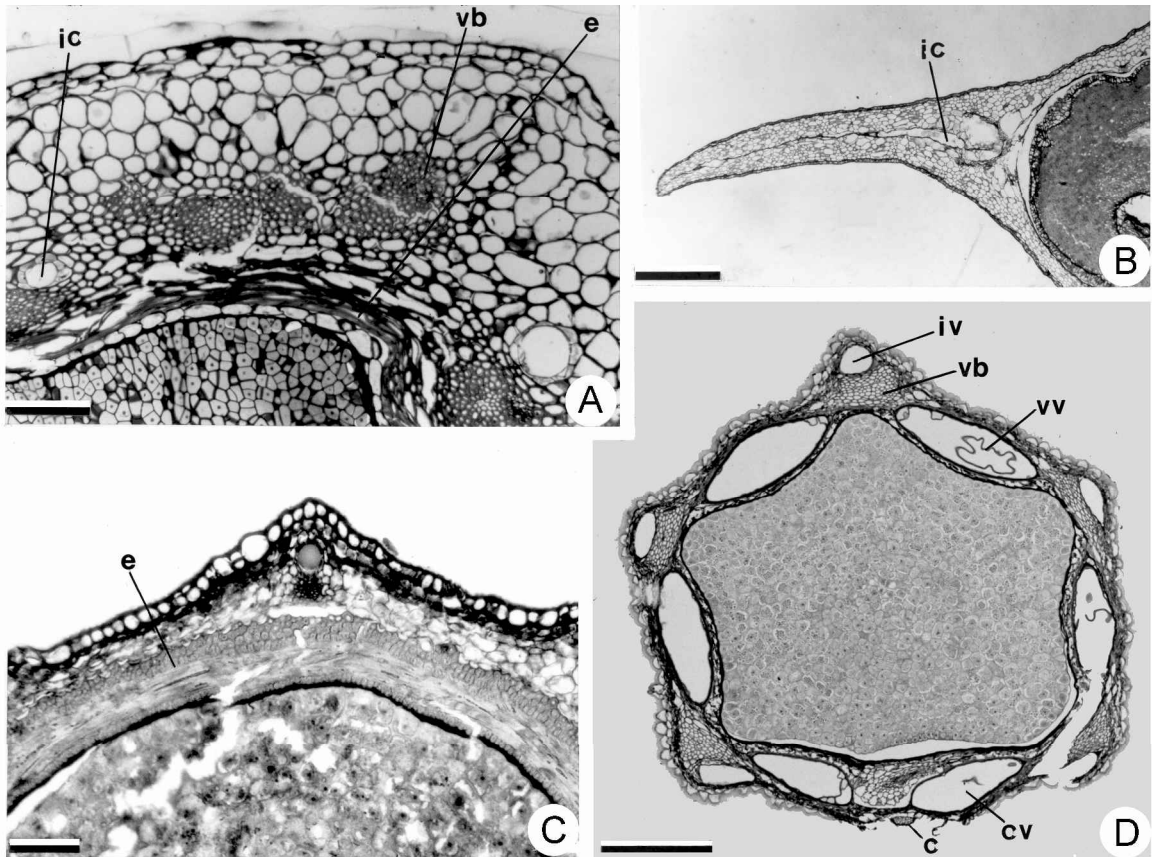


Fig. 4. Detail of the fruit anatomy of some species of Apiaceae as seen in transverse section. A, *Arctopus echinatus* with an intra-jugal cavity and lignified cells of the endocarp (single layer) and the first few layers of the mesocarp; B, *Polemanniopsis marlothii* showing an intra-jugal cavity; C, *Azorella pedunculata* showing several lignified layers of endocarp cells; D, *Tana bojeriana* with the commissural and vallecular vittae much larger than the intra-jugal secretory ducts. iv - intra-jugal secretory duct; vv - vallecular vitta. Other abbreviations as in Fig. 1. Scale bar = 0.3 mm in A & D, 0.1 mm in C and 1 mm in B.

Table 1. Genera and species of the subfamily Saniculoideae (Apiaceae) according to Pimenov & Leonov (1993). Four related African genera are also included. The number of species studied is shown in parentheses.

Tribe	Genera	Number of species	Geographical distribution
Saniculeae W.D.J. Koch	<i>Actinolema</i> Fenzl	2 (1)	Asia
	<i>Alepidea</i> F. Delaroché	20 (2)	Africa
	<i>Astrantia</i> L.	8–9 (2)	Europe, Asia
	<i>Eryngium</i> L.	230–250 (4)	Europe, Asia, Africa, N. America, C. America, S. America, Australia, Australasia
	<i>Hacquetia</i> Neck. ex DC.	1 (1)	Europe
	<i>Sanicula</i> L.	39 (4)	Europe, Asia, N. America, C. America, S. America, Africa, Oceania
Lagoecieae Dumort.	<i>Lagoecia</i> L.	1 (1)	Europe, Asia
	<i>Petagnaea</i> Caruel	1 (1)	Europe
Incertae sedis	<i>Oligocladus</i> Chodat & Wilczek	2 (0)	S. America
Related genera	<i>Arctopus</i> L. *	3 (1)	Africa
	<i>Lichtensteinia</i> Cham. & Schltdl.	7 (2)	Africa
	<i>Polemanniopsis</i> B.L. Burt	1 (1)	Africa
	<i>Steganotaenia</i> Hochst.	2 (1)	Africa

*Pimenov & Leonov (1993) placed this genus in *Incertae sedis* of *Hydrocotyloideae*.

Table 2. Voucher specimens of Apioideae species used in the anatomical study. Numbers not italicized are institutional accession numbers.

Species	Voucher specimens or accession number & herbarium	Origin
<i>Actinolema macrolema</i> Boiss.	<i>Bornmul 14119</i> (PE)	Turkey
<i>Alepidea amatymbica</i> Eckl. & Zeyh.	<i>Schelphe 97</i> (JRAU)	South Africa
<i>A. setifera</i> N.E. Br.	<i>Victor 1196</i> (PRE)	South Africa
<i>Arctopus echinatus</i> L.	<i>Van Wyk & al. s.n.</i> (Oct 1993) (JRAU)	Arendskraal, South Africa
<i>Astrantia major</i> L.	<i>Pauca 165b</i> (PE)	Romania
<i>A. maxima</i> Pall.	K 1969 50623 (K)	ex hort. Kew
<i>Azorella pedunculata</i> Willd. ex DC.	<i>Luteyn 6709</i> (F)	Ecuador
<i>Eryngium campestre</i> L.	<i>Medwecka-Kornas & al. 552</i> (PE)	Polonia
<i>E. giganteum</i> Bieb.	K 1990 3722 (K)	ex hort. Kew
<i>E. maritimum</i> L.	<i>Devon 1989</i> (K)	England
<i>E. planum</i> L.	NAS 446828 (NAS)	Xinjiang, China
<i>Hacquetia epipactis</i> (Scop.) DC.	LJU s.n. (27 May 2000) (LJU)	near Visnja Gara, Russia
<i>Lagoecia cuminooides</i> L.	NAS 465901 (NAS)	unknown
<i>Lichtensteinia obscura</i> (Spreng.) Koso-Pol.	NBG 341023 (NBG)	South Africa
<i>L. lacera</i> Cham. & Schldtl.	<i>Boucher 1818</i> (PRE)	S.W. Cape, South Africa
<i>Petagnaena saniculifolia</i> Guss.	<i>Ross s.n.</i> (Jun 1885) (AMD)	Sicily, Valdemone, Italy
<i>Polemanniopsis marlothii</i> (H. Wolff) B.L. Burt	<i>Taylor 11269</i> (PRE)	S.W. Cape, South Africa
<i>Sanicula coerulescens</i> Franch.	NAS 476419 (NAS)	Sichuan, China
<i>S. europaea</i> L.	PE 207845 (PE)	Romania
<i>S. lamelligera</i> Hance	NAS 067298 (NAS)	Jiangxi, China
<i>S. rubriflora</i> F. Schmidt	IFP 18712 (IFP)	Changbaishan, China
<i>Steganoaenia araliacea</i> Hochst.	<i>Taylor 11269</i> (PRE)	South Africa
<i>Tana bojeriana</i> (Baker) B.-E. van Wyk	<i>Baron 5185</i> (P)	Madagascar

Fig. 5 accurately reflects the uncertainty of the relationship between Saniculoideae *sensu stricto* (excluding *Lagoecia*) and some anomalous genera (*Arctopus*, *Lagoecia* and *Petagnaena*).

RESULTS

A summary of morphological and anatomical characters of the fruits of Saniculoideae and four related genera is given in Table 3. The taxonomic implications of these characters are briefly discussed below.

Mericarps of Saniculoideae are dorsally compressed (Figs. 2A, D–I) or round (Figs. 2B, C; 3A–E). Two mericarps are present in Saniculeae (Fig. 2A–I; 3A–E) and a single one in Lagoecieae (Figs. 1A & B). In the cladistic analysis, a single mericarp was interpreted as derived (present in *Arctopus*, *Lagoecia*, and *Petagnaena*). The mericarp surface has blisters, scales, bristles, papillae, tuberculae, pusticulae or wrinkles, or is rarely smooth. The presence of surface features was accepted as an apomorphy for the purpose of the cladistic analysis (a possible synapomorphy for Saniculoideae). Wings are absent or weakly developed (see *Eryngium maritimum* in Fig. 2I). The mesocarp may be unligified (Figs. 1B; 2A, D, E) or partially (Fig. 2B & C, F–I; 3A–E) or nearly completely lignified (Fig. 1A, where lignification is indicated by hatching). The latter state was taken as apomor-

phic. Intrajugal secretory ducts (oil ducts in the ribs) are usually large in Saniculeae (a potential synapomorphy) and small or indistinct in Lagoecieae (Figs. 1A & B). There are small secretory ducts dispersed in the mesocarp in some genera of Saniculeae (here interpreted as a derived feature; Figs. 2A, F–I; 3A–E). Vittae are absent in the commissure (the area where two mericarps join) except in *Lagoecia* (Fig. 1B). Drude's (1898) description of the vittae as being indistinct in *Lagoecia* is therefore not quite accurate. This is an important result, as it supports the exclusion of *Lagoecia* from Saniculoideae and at the same time provides a potentially valuable synapomorphy for *Lagoecia* and Apioideae, where commissural vittae are almost invariably present. *Lagoecia* is also said to have small vallecular vittae restricted to the apex of the fruit (T. Ostroumova, pers. comm.), and which we have confirmed, but in our median sections these are not visible. Vallecular vittae (oil ducts in the furrows between the ribs) are completely absent in all the genera traditionally placed in Saniculoideae (Figs. 1A & B; 2A–I; 3A–E). Each mericarp generally has five ribs (rarely seven, in *Lagoecia* only; Fig. 1B). The endocarp consists of one layer of parenchymatous cells (a few endocarp cells in the commissural side of the fruit of *Sanicula rubriflora* are lignified; Figs. 3C). The commissure is very narrow (Figs. 2A, D, E), narrow (Fig. 2B & C; 3B–E), or half or more than half the width of the mericarp (Figs. 2F–I; 3A). The very narrow commissure

Table 3. Summary of fruit characters of representatives of subfamily Saniculoideae and four related African genera.

Species	Fruit shape	Mericarp surface	Mesocarp lignification	Endocarp lignification	Intrajugal secretory ducts/cavities*	Vittae scattered in mesocarp	Commissural vittae	Carpophore	Crystals dispersed in mesocarp
<i>Actinolema macrolema</i>	elliptic	papillae & bristles	absent	absent	450; 650	present	absent	absent	present
<i>Alepidea amatymbica</i>	oval	wrinkles	present	absent	450; 900	absent	absent	present	present
<i>A. setifera</i>	oval	pusticulae	present	absent	200; 500	absent	absent	present	present
<i>Arctopus echinatus</i>	oval	pusticulae	present	present	150; 150	absent	absent	present	absent
<i>Astrantia major</i>	elliptic	blisters	absent	absent	150; 50	absent	absent	absent	present
<i>A. maxima</i>	elliptic	blisters	absent	absent	150; 350	absent	absent	absent	present
<i>Azorella pedunculata</i>	elliptic	smooth	absent	present	40; 40	absent	absent	absent	absent
<i>Eryngium campestre</i>	cuneate	scales	present	absent	150; 180	present	absent	absent	present
<i>E. giganteum</i>	obvate	scales	present	absent	150; 200	present	absent	absent	present
<i>E. maritimum</i>	obvate	scales	present	absent	250; 300	present	absent	absent	present
<i>E. planum</i>	cuneate	scales	present	absent	150; 200	present	absent	absent	present
<i>Hacquetia epipactis</i>	elliptic	wrinkles	present	absent	500; 700	present	absent	absent	present
<i>Lagoecia cuminoides</i>	elliptic	tuberculae	absent	absent	10; 10	absent	present	?	absent
<i>Lichtensteinia obscura</i>	elliptic	smooth	present	absent	500; 450	absent	absent	absent	present
<i>L. lacera</i>	elliptic	smooth	present	present	700; 700	absent	absent	present	absent
<i>Petagnaea saniculifolia</i>	obovate	smooth	present	absent	10; 10	absent	absent	?	absent
<i>Polemanniopsis marlothii</i>	obovate-cordate	smooth	present	present	2700–4200; 100–600	absent	absent	present	absent
<i>Sanicula coerulescens</i>	oval	blisters	present	absent	160; 140	present	absent	absent	present
<i>S. europaea</i>	elliptic	blisters	present	absent	50; 50	present	absent	absent	present
<i>S. lamelligera</i>	elliptic	blisters	present	absent	300; 250	present	absent	absent	present
<i>S. rubriflora</i>	oval	blisters	present	absent**	400; 600	present	absent	absent	absent
<i>Steganotaenia araliacea</i>	oval-obovate	smooth	absent	present	2500–3000; 20–40	present	absent	present	absent
<i>Tana bojeriana</i>	elliptic	smooth	absent	absent	100–130; 35–90	absent	present	present	present

* Measurements in μm give length; width.

**A few endocarp cells in the commissural area are lignified.

(only a few cells wide) is unusual and occurs only in *Astrantia* and *Actinolema* and has been interpreted as a synapomorphy. A carpophore is absent except in *Alepidea* (Figs. 2B & C). This is clearly a potentially important character because it supports the monophyly of a large part of Saniculoideae. Crystals are dispersed in the mesocarp in Saniculeae or absent in Lagoeciae. The presence of crystals appears to be a derived feature in Saniculoideae (see cladistic analysis). Most seeds are flat on the commissural side except those of *Astrantia maxima* (Fig. 2E) and *Lagoecia cuminoides* (Fig. 1B), where the seeds are concave. The seed of *Petagnaea saniculifolia* was not visible in median transverse section (Fig. 1A).

The mericarp surface of the fruits of *Lichtensteinia* (Figs. 3F & G) is smooth. Very large intrajugal secretory ducts are present, while vallecular and commissural vittae are absent. The mesocarp is lignified adjacent to the endocarp and parenchymatous in the outer layers (*L. obscura*, Fig. 3F) or lignified mainly on the commissural side (*L. lacera*, Fig. 3G). Note that the endocarp is non-lignified in *L. obscura* (Fig. 3F) and lignified in the other species (Fig. 3G). It is very interesting to note that in the species studied of the African genera *Steganotaenia*, *Polemanniopsis* and *Arctopus*, all the endocarp cells

are slightly thickened and lignified (Figs. 1C–E), thereby supporting a basal position for these genera. Some species of other African genera, such as *Glia* Sond. and *Anginon* Raf. are similarly lignified or some of the endocarp cells are unligified. From a phylogenetic point of view, this appears to be an intermediate state between the complete lignification in *Azorella* and other “Hydrocotyloideae”, and the complete absence of lignification as in most Saniculoideae and most Apioideae. The commissure is narrow in both species of *Lichtensteinia*. A free carpophore may be completely lacking or may be represented by only a few xylem elements (Fig. 3F), or a free carpophore may be present (Fig. 3G). Crystals are dispersed in the mesocarp in *L. obscura* or absent in *L. lacera*. The seed is not visible in median transverse sections in both these species.

The fruits of *Arctopus echinatus* (Fig. 1C) have two mericarps but one mericarp invariably remains undeveloped. Small pusticulae are present on the dorsal surface of the mericarp. A variable number of vascular bundles are present, some of which are associated with a single cavity surrounded by epithelial cells, but lacking any visible deposit (Fig. 4A). These cavities are referred to as intrajugal cavities. The single layer of endocarp cells and the first few cell layers adjacent to the endocarp are lig-

Table 4. Polarization of characters and character states* for genera of Saniculoideae and some related African genera. *Azorella* and *Tana* were selected as place markers for the subfamilies Hydrocotyloideae and Apioideae.

Genera	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Actinolema</i>	0	2	0	0	1	1	0	0	0	1	1	2
<i>Alepidea</i>	0	1	1	0	1	0	0	0	1	0	1	2
<i>Arctopus</i>	1	1	1	0	0	0	0	0	1	0	0	1
<i>Astrantia</i>	0	2	0	0	1	0	0	0	0	1	1	2
<i>Azorella</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eryngium</i>	0	2	1	0	1	1	0	0	0	0	1	2
<i>Hacquetia</i>	0	1	1	0	1	1	0	0	0	0	1	2
<i>Lagoecia</i>	1	1	0	0	0	0	0	1	?	0	0	2
<i>Lichtensteinia</i>	0	0	1	0	1	0	0	0	1	0	1	1
<i>Petagnaëa</i>	1	1	1	0	0	0	0	0	?	0	0	2
<i>Polemanniopsis</i>	0	0	1	1	2	0	0	0	1	0	0	1
<i>Sanicula</i>	0	2	1	0	1	1	0	0	0	0	1	2
<i>Steganotaenia</i>	0	0	0	1	2	1	0	0	1	0	0	1
<i>Tana</i>	0	0	0	0	0	0	1	1	1	0	0	2

*1. Number of mericarps: two (0); one (1). 2. Fruit surface: more or less smooth (0); minutely ornamented (1); with large outgrowths (2). 3. Mesocarp lignification: not lignified (0); lignified (at least partly, i.e., some of the cells lignified) (1). 4. Fruit wings: small or absent (less than 30% of mericarp width) (0); large, distinct (more or less equal to mericarp width) (1). 5. Intrajugal secretory ducts small or absent (< 0.1 mm in diameter) (0); very large (0.2–0.8 mm) (1); enormous, forming cavities (>2 mm) (2). 6. Scattered vittae: absent (0); present (1). 7. Vallecular vittae: absent (0); present (1). 8. Commissural vittae: absent (0); present (1). 9. Carpophore: absent (0); present (1). 10. Commissural width: broad to narrow (> 10 cells wide) (0); very narrow (< 3 cells wide) (1). 11. Crystals: absent (0); present (1). 12. Endocarp type: more than one cell layer, lignified (0); single cell layer, lignified (1); single cell layer, not lignified (2).

nified and are predominantly transversely orientated, as shown in Fig. 4A. As can be seen in Fig. 1C, the seed is concave on the commissural side. The commissure is narrow and the carpophore is free. Crystals are absent from the mesocarp.

The mericarps of *Polemanniopsis marlothii* (Fig. 1D) are strongly heteromorphic, with a smooth surface. One mericarp has three wings—a dorsal and two marginal wings (lateral ribs are not visible), and the other has two lateral wings (dorsal and marginal ribs are not evident). Each wing has an intrajugal cavity (Fig. 4B) surrounded by apparently non-secretory epithelial cells only in the immature fruit (Liu, Van Wyk & Tilney, in prep.). Nearly all the cells of the mesocarp are lignified but relatively thin-walled. A parenchymatous endocarp is present in the three-winged mericarp whereas in the two-winged mericarp the endocarp consists of relatively thick-walled, lignified cells. The seed of the three-winged mericarp has a narrow commissural groove and is much larger than the seed of the two-winged mericarp. The commissure is narrow and the carpophore is free. Crystals are absent.

The two mericarps of *Steganotaenia araliacea* (Fig. 1E) are strongly compressed dorsally and have smooth surfaces. Each mericarp has prominent marginal wings. Only species of *Polemanniopsis* and *Steganotaenia* have large, distinct wings (interpreted as a synapomorphy).

Median and lateral ribs are inconspicuous or almost absent. Enormous intrajugal cavities are present in the wings (as in *P. marlothii*) and represent a seemingly convincing synapomorphy for the two genera. Small intrajugal cavities are present in the dorsal and lateral ribs of *S. araliacea*. Some small vittae containing a yellow deposit are scattered in the mesocarp. The mesocarp is non-lignified, but the endocarp is composed of relatively thin-walled lignified cells in both mericarps. Seeds are concave on the commissural side. The commissure is narrow and the carpophore is free. Crystals are absent.

All anatomical characters that could be logically polarized were selected for cladistic analysis, using *Azorella* as outgroup. The 12 characters chosen and the polarization of character states are given in Table 4. The “ie” option of HENNIG86 produced four equally parsimonious trees with a consistency index of 0.50, a retention index of 0.62 and a length of 28 steps. Since only a limited number of anatomical characters could be included in the analysis, the lack of resolution comes as no surprise. Nevertheless, some interesting groupings emerged (*Lagoecia* and *Petagnaëa*, for example, did not group with other Saniculoideae) that give new ideas about how fruit characters could be interpreted from a phylogenetic point of view. A strict consensus tree of the four trees is shown in Fig. 5. This tree is presented here as a working hypothesis for future studies. It may be interesting to see

how other characters (e.g., DNA sequences) agree with this hypothesis. Unfortunately some critical genera were not included in the analysis of Valiejo-Roman & al. (2002), but our results are quite similar to theirs. Note, for example, the sister group relationship between *Astrantia* and *Actinolema*, the exclusion of *Lagoecia* from Saniculoideae and the sequence of genera sister to the *Astrantia-Actinolema* clade (*Eryngium*, *Sanicula* and *Hacquetia*). What appears to be a strongly monophyletic Saniculoideae in their analysis is likely to be merely a subclade within a larger, less well-defined Saniculoideae complex, which will include some (if not all) of the anomalous African genera included in this study.

DISCUSSION

This study shows that the subfamily Saniculoideae *sensu stricto* is unique in its fruit structure, with a non-lignified endocarp, outgrowths on the mericarps, usually prominent intrajugal secretory ducts, vallecular vittae totally absent, and commissural vittae absent except in *Lagoecia cuminoides*. Drude's (1898) description of the vittae being indistinct in *Lagoecia* is therefore not quite accurate. *Lagoecia cuminoides* should be better placed in the subfamily Apioideae since it is the only taxon with commissural vittae, a character state which is widely present in Apioideae (Fig. 4D). This is supported by DNA studies, in which this genus was placed in

Apioideae very close to *Crithmum maritimum* L. (Plunkett & al., 1996; Valiejo-Roman & al., 2002). According to fruit characters, *Lichtensteinia* appears to be more closely related to Saniculoideae than to Apioideae, where it was placed by Pimenov & Leonov (1993). Almost all genera in Apioideae have large vallecular and commissural vittae, with some having small intrajugal secretory ducts as well (Fig. 4D). *Lichtensteinia*, if left in Apioideae, would be the only genus with large intrajugal secretory ducts, and without vallecular and commissural vittae. It would also be, as far as we know, the only genus with scattered crystals throughout the mesocarp all around the seed. Most genera of Apioideae do not have crystals, whereas some have crystals only on the commissural side (Drude, 1898; Burtt, 1991). In the "Hydrocotyloideae", crystals (if present) are confined to the inner layer of the mesocarp, immediately adjacent to the endocarp.

Arctopus has a lignified endocarp comprised of one layer of cells that is different from the soft endocarp found in Saniculoideae and the woody endocarp consisting of several layers of cells in "Hydrocotyloideae" (Fig. 4C), but similar to that of *Polemanniopsis marlothii* and *Steganotaenia araliacea*. Therefore this genus should not be placed in "Hydrocotyloideae" (Drude, 1898; Wolff, 1913; Pimenov & Leonov, 1993). Intrajugal cavities are present in *A. echinatus*, *P. marlothii* and *S. araliacea*. In *A. echinatus*, distinct epithelial cells surround the small cavities whereas in the latter two taxa, no such cells surround the cavities in mature fruits (but were seen in the immature state). Cavities are also found in *Bowlesia incana* Ruiz & Pav., which has a large cavity under the median rib (Tseng, 1967). The monotypic *Scandix pecten-veneris* L. has a single vascular bundle associated with many cavities. It is unlikely that the cavities in the latter two taxa are homologous with the intrajugal cavities found in *Arctopus*, *Polemanniopsis* and *Steganotaenia*. The species studied of the latter three genera do not have vallecular or commissural vittae and therefore fit comfortably in Saniculoideae on the basis of this character. However, none of them have crystals, a typical feature of Saniculoideae. The lack of convincing synapomorphies for the inclusion of *Arctopus* and *Petagnaea* in Saniculoideae *sensu stricto* is clearly reflected in the consensus tree in Fig. 5. When considering morphological characters (such as the shared presence of sessile female flowers and marginal setae on the leaves of *Arctopus* and *Alepidea*) and chemical characters (such as the shared presence of kaurenoic acids in *Arctopus* and *Alepidea*), then it seems likely that *Arctopus* could be easily accommodated within a broadened Saniculoideae concept.

In all genera studied, only species of *Alepidea*, *Arctopus*, *Lichtensteinia*, *Polemanniopsis* and *Steganotaenia* have free carpophores. On the basis of this char-

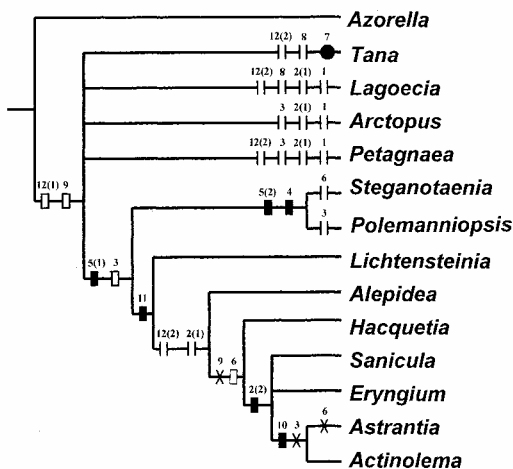


Fig. 5. Consensus tree of the four trees obtained in a cladistic analysis (exhaustive search, using the implicit enumeration option of HENNIG86) of the data in Table 4, showing relationships amongst Saniculoideae genera and putative relatives. All character state changes are plotted on the tree, numbered as in Table 4: ■, synapomorphy without homoplasy; □, synapomorphy with reversal(s); x, reversal; ||, convergence; ●, autapomorphy.

acter, it seems that *Arctopus*, *Lichtensteinia*, *Polemanniopsis* and *Steganotaenia* are more closely related to *Alepidea* than to any other genera of Saniculoideae *sensu stricto*. In addition, it is interesting to note that all the genera with carpophores in the fruit are endemic to Africa.

It is here proposed that the subfamily Saniculoideae be expanded to include the anomalous African genera discussed in this paper. Also of interest is the diversity of chromosome numbers in the group. The Saniculoideae *sensu stricto* typically have $n = 8$, while the anomalous African genera have $n = 9$ (*Arctopus*), $n = 11$ (*Lichtensteinia* and *Polemanniopsis* P. Winter, unpubl.) or $n = 12$ (*Steganotaenia*). The number in *Lichtensteinia* and *Polemanniopsis* is the same as in Apioideae, but in view of the convincing evidence (e.g., Downie & Katz-Downie, 1999) for a relation between *Polemanniopsis* ($n = 11$) and the Saniculoideae, the transfer of *Lichtensteinia* to this assemblage now seems quite reasonable.

The emphasis on condensed inflorescences as a diagnostic feature of Saniculoideae appears to be a northern hemisphere perspective (but note that the female flowers in *Arctopus* are sessile!). The fruit structure provides some supporting evidence for broadening the concept of the subfamily as was first hinted at by some morphological anomalies and later clearly evident from DNA phylogenies. The cladogram in Plunkett (2001), for example, is congruent with our result (Fig. 5) showing that supportive evidence from morphology can be found for the emerging DNA phylogeny of the family. It is a matter of improving our interpretation of the structural diversity (or perhaps abandoning some traditional diagnostic characters that no longer seem to work). New insight will come when the right taxa are included in comparative studies and also when characters are compared more rigorously across many taxa.

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