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Short communication

Irregular vittae and druse crystals in *Steganotaenia* fruits support a taxonomic affinity with the subfamily Saniculoideae (Apiaceae)

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Abstract

The three-dimensional structure of the vittae and crystals of *Steganotaenia araliacea* was studied for the first time to allow a rigorous comparison with members of the subfamily Saniculoideae, where these two characters are of diagnostic value. The irregular vittae were found to be branching and anastomosing and druse crystals dispersed in the mesocarp. Both these states are predominant in the Saniculoideae but very rare in Apioideae. In the subfamily Apioideae, regular vittae (vallecular and commissural, or cyclic) are present and druse crystals, if present, occur in the commissural side only. The absence of regular vittae and the presence of irregular vittae and dispersed druse crystals further support the exclusion of *Steganotaenia* from the subfamily Apioideae but support its hypothesized relation to the Saniculoideae, where large rib ducts combined with irregular vittae (branching or anastomosing) and dispersed druse crystals are typical. This study has led to a better understanding of the taxonomic value of irregular vittae and crystals.

Keywords: Apiaceae; Fruit anatomy; *Steganotaenia araliacea*; Vittae; Umbelliferae

Steganotaenia araliacea Hochst. is an anomalous woody African taxon with deciduous, hysteranthous leaves and dentate-aristate leaf margins (Norman, 1934; Burtt, 1988; Townsend, 1989; Glen and Onderstall, 1991; Van Wyk, 2001). These characters can also be found in *Polemanniopsis marlothii* (H.Wolff) B.L.Burtt. Based on molecular evidence, Downie and Katz-Downie (1999) and Plunkett (2001) proposed that these two genera, previously placed in the subfamily Apioideae Drude (Pimenov and Leonov, 1993), are sister taxa and that they are closely associated with the subfamily Saniculoideae Burnett. Liu et al. (2003a, b) used fruit structural evidence to evaluate this hypothesis. The fruits of both genera were shown to have large rib cavities but no vallecular or commissural vittae. Irregular vittae are absent in *P. marlothii*, but present in *S. araliacea*. Large rib ducts, irregular vittae and dispersed crystals are present in several genera and species of the Saniculoideae. Details of the vittae of *S. araliacea* and members of Saniculoideae and the presence of crystals in *S. araliacea* were not previously studied or reported. In this investigation we present the details of the three-dimensional structure of the irregular vittae and crystals of this taxon and all genera of the subfamily Saniculoideae with irregular vittae for the first time. Our aims were to see if there are any common structural features of the vittae and crystals between *Steganotaenia* and Saniculoideae and to gain new insight into the diversity of these characters. In addition, we wanted to ascertain whether or not details of vittae and crystal structure would provide further supporting evidence for the suggestion [based on molecular evidence of Downie and Katz-Downie (1999) and Plunkett (2001)] that *Steganotaenia* should be excluded from the subfamily Apioideae.

The external and internal structure of at least three different mature fruits of each sample was investigated (Figs. 1, 2 and 3). Fruits of *S. araliacea* (voucher specimens: *Winter 273*, SAM; *Taylor 11269*, PRE), *Actinolema macrolema* Boiss. (voucher specimen: *Bornmul 14119*, PE), *Eryngium planum* L. (voucher specimen: *NAS 446828*) and *Sanicula europaea* L. (voucher specimen: *PE 207845*) were rehydrated and the exocarps carefully removed. The three-dimensional appearance of the rib

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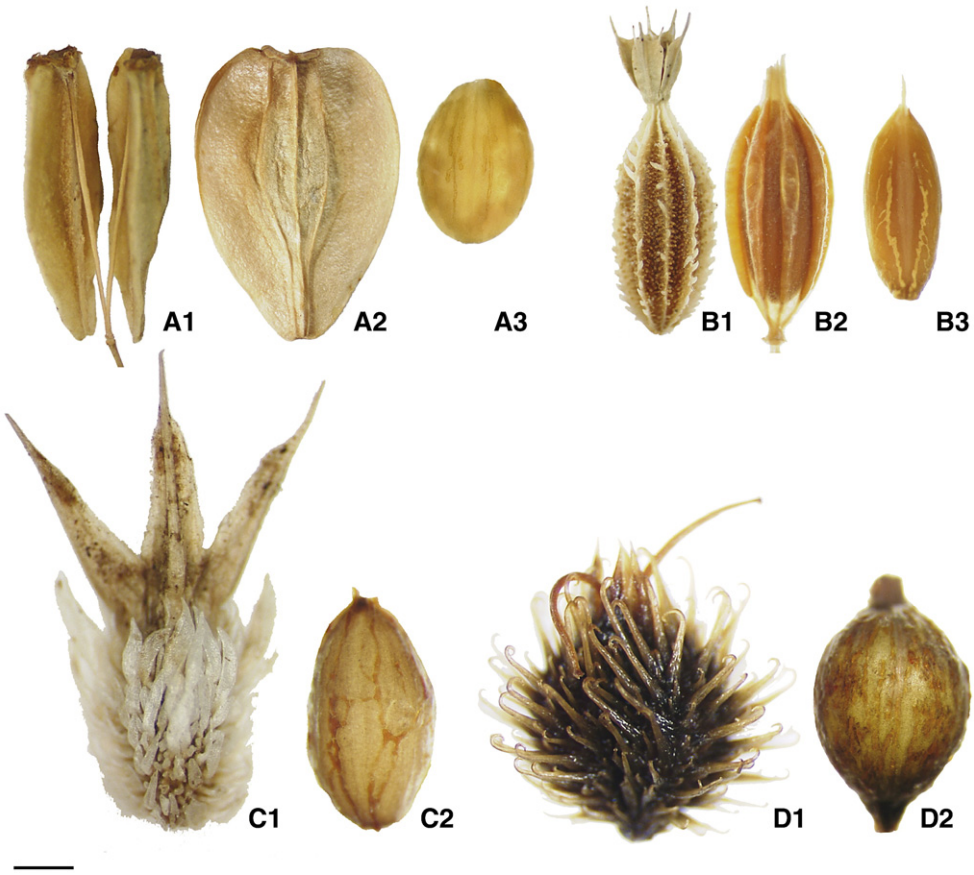

Fig. 1. Fruits of *Steganotaenia araliacea* and some taxa of Saniculoideae (shown in dorsal view, except for A1 = lateral view and B3 = commissural view) showing the variation in structure. Exocarps have been removed in A3, B2, B3, C2 and D2 to expose secretory structures. (A) *S. araliacea*, carpophore present (A1), mericarp surface smooth (A1, 2), branching vittae (A3); (B) *Actinolema macrolema*, surface appendages (B1), large rib ducts (B2), branching and anastomosing vittae (B3); (C) *Eryngium planum*, surface appendages (C1), anastomosing vittae (C2); (D) *Sanicula europaea*, surface appendages (D1), branching vittae (D2). Scale bar = 2 mm in A1–3 and B1–3; 800 μm in C1, 2 and D1, 2.

ducts and vittae and the crystal structure was observed and photographed. Additional fruits were placed in FAA for a minimum of 24 h after rehydration and then treated according to the method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA). Transverse sections, about 5 μm thick, were cut using a Porter-Blüm ultramicrotome. Samples were stained using the periodic acid-Schiff/toluidine blue staining method (Feder and O'Brien, 1968) and photographed. Terminology is illustrated in Fig. 3. A summary of characters is provided in Table 1.

In *S. araliacea* regular vittae (vallecular and commissural) are absent (Liu et al., 2003a,b), but surprisingly, the removal of the exocarp revealed branching and anastomosing irregular vittae (Figs. 1A3 and 2A, B) (Table 1). Both types of irregular vittae appear in the saniculoid taxon *A. macrolema* (Figs. 1B3 and 2C). Anastomosing vittae are found in *E. planum* (Fig. 1C) and branching vittae in *S. europaea* (Figs. 1D2, and 2D). These irregular vittae are shown in transverse section in Fig. 3A–D. Vittae are absent in the other genera of Saniculoideae and in *P. marlothii* (Liu et al., 2003a,b). In earlier studies (Liu et al., 2002; pers. obs.), anastomosing and branching vittae were observed in three genera (*Dickinsia* Franch., *Hermas* L. and *Klotzschia* Cham.) of the subfamily Azorelloideae Plunkett and Lowry, in *Pseudocarum* C. Norman of Apioideae tribe Heteromorpheae M.F. Watson and S.R. Downie, and in *Bupleurum* L., e.g. *Bupleurum chinense* DC. and *B. scorzonerifolium* Willd. of the Apioideae tribe Bupleurieae Spreng. In the above groups, Azorelloideae are easily distinguished by a woody endocarp which is non-woody in all other groups. Regular vittae are absent from fruits of all Azorelloideae and Saniculoideae but present in Heteromorpheae and *Bupleurum*. Anastomosing and branching vittae were observed in a few taxa of Apioideae, e.g. *Cachrys* L., *Fuernrohria* K. Koch and *Eremodaucus* Bunge, but these irregular vittae are invariably combined with regular vittae. *Cachrys* has cyclic vittae and *Fuernrohria* and *Eremodaucus* have commissural vittae. Regular vittae (vallecular and commissural, and cyclic) are normally present in Apioideae (Liu, 2004; pers. obs.). The absence of regular vittae and the presence of irregular vittae are therefore typical of the Azolloideae and Saniculoideae. In the subfamily Mackinlayoideae Plunkett and Lowry, vittae are completely absent.

Two types of crystals (single and druse) are present in Apiaceae. Druse crystals are dispersed in the mesocarp in

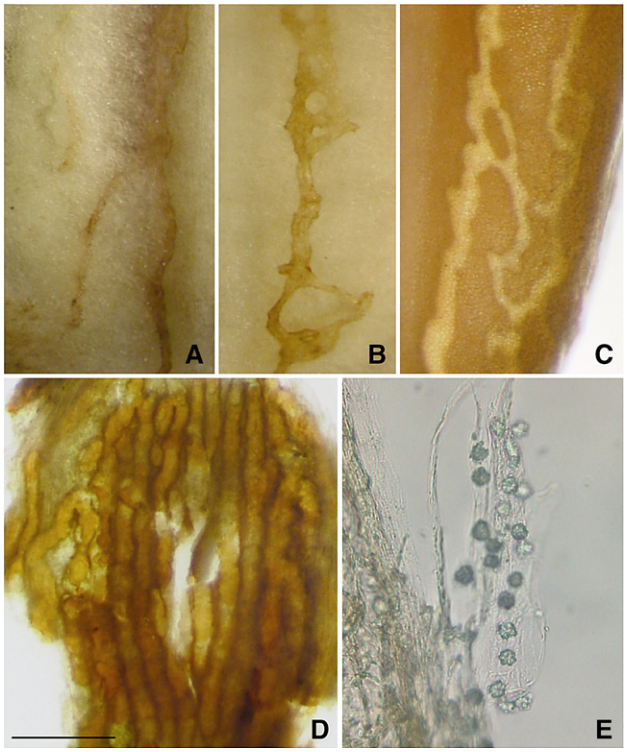

Fig. 2. Portions of the mesocarp showing irregular vittae or crystals. (A, B) *Steganotaenia araliacea* with branching and anastomosing vittae; (C) *Actinolema macrolema*, showing anastomosing vittae; (D) *Sanicula europaea*, with branching vittae; (E) *S. araliacea*, with druse crystals. Scale bar = 1 mm in A and B; 300 μm in C and D.

S. araliacea (Fig. 2E) as in *P. marlothii* and almost all taxa of Saniculoideae and Heteromorpheae. Crystals appear to be absent in *Bupleurum*. However, they are normally absent in Apioideae but, if present, are restricted to the commissural side of the mericarp (e.g. in *Torilis arvensis* Link and *Caucalis leptaphylla* L.). Single crystals are present in the outer layer of the endocarp in Azorelloideae and Mackinlayoideae.

Previous studies showed that the mericarp surface is smooth in *S. araliacea* (Fig. 1A2) unlike that in almost all taxa of Saniculoideae e.g. *A. macrolema* (Fig. 1B1), *E. planum* (Fig. 1C1) and *S. europaea* (Fig. 1D1) (Liu et al., 2003a,b). *S. araliacea* (Fig. 1B) differs from Saniculoideae in having two large marginal wings (Liu et al., 2003a,b). Rib ducts in Saniculoideae are usually large as in *A. macrolema* (Figs. 1B2 and 3B) and *E. planum* (Fig. 3C). In *S. araliacea* rib ducts occur in the median and lateral ribs and form large cavities in the marginal wings. Large cavities are also present in the wings of *P. marlothii* (Liu et al., 2003a,b). Note that in *E. planum* (Fig. 1C2) and *S. europaea* (Fig. 1D2) the rib ducts were removed together with the exocarps. A paired carpophore is present in *S. araliacea* (Fig. 1A1) as in *P. marlothii*, Heteromorpheae, *Bupleurum* and most genera of Apioideae (Liu et al., 2003a,b; pers. obs.). A carpophore is lacking in all Saniculoideae and Mackinlayoideae, but a single carpophore is usually present in Azorelloideae.

This study therefore supports the exclusion of *Steganotaenia* from the subfamily Apioideae and its inclusion in the subfamily Saniculoideae, as was suggested by molecular evidence (Downie and Katz-Downie, 1999; Plunkett, 2001).

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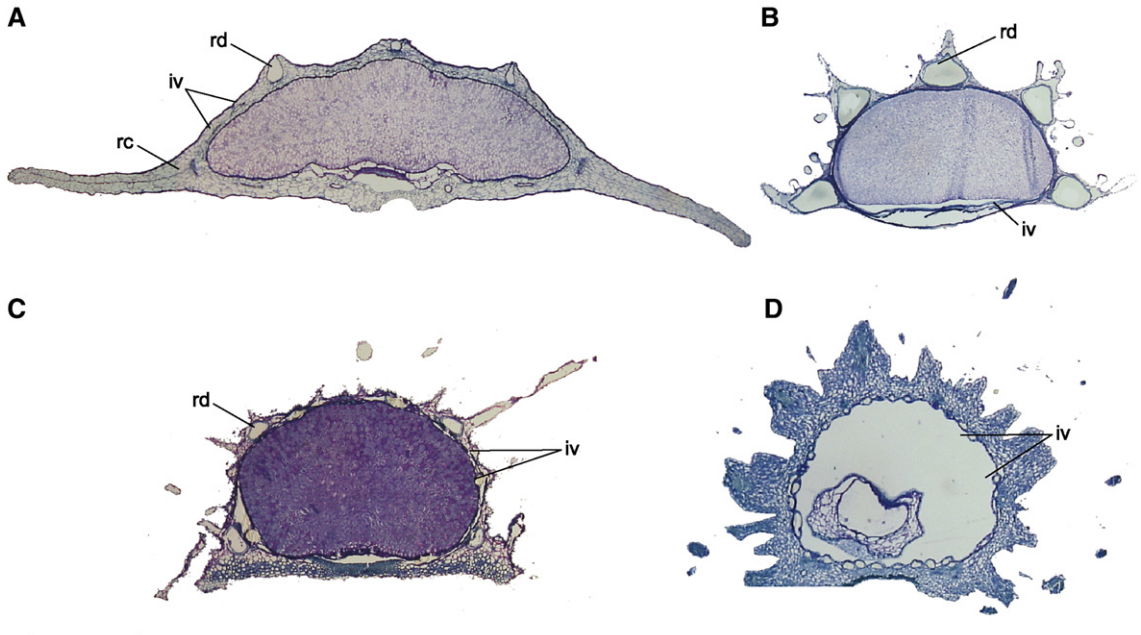

Fig. 3. Transverse sections of mericarps of *Steganotaenia araliacea* and some taxa of Saniculoideae showing the rib ducts (rd), rib cavities (rc) and irregular vittae (iv). (A) *S. araliacea*; (B) *Actinolema macrolema*; (C) *Eryngium planum*; (D) *Sanicula europaea*. Scale bar = 1 mm in A; 800 μm in B, C and D.

Table 1
Summary of fruit characters of *Steganotaenia araliacea* and three taxa of the subfamily Saniculoideae

Species	Vittae	Crystals	Rib ducts	Epidermal appendages	Marginal wings	Carpophores
Steganotaenia araliacea	Branching and anastomosing	Dispersed	Present and form cavities in marginal wings	Absent	Present	Present
Actinolema macrolema	Branching and anastomosing	Dispersed	Present	Present	Absent	Absent
Eryngium planum	Anastomosing	Dispersed	Present	Present	Absent	Absent
Sanicula europaea	Branching	Dispersed	Present	Present	Absent	Absent

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