THE CARPOLOGY AND TAXONOMIC RELATIONSHIPS OF BRETSCHNEIDERA (BRETSCHNEIDERACEAE)

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SUMMARY. The carpology and taxonomic relationships of Bretschneidera (Bretschneideraceae). The fruit and seed anatomy and morphology of Bretschneidera sinensis Hemsl., the monotypic genus in the Bretschneideraceae, have been studied in order to clarify its phylogenetic relationships. The loculicidal trilocular syncarpous fruit has unusual unspecialised, aerenchymatous fibrous 12-14-layered endocarp and sclerified innermost part of the mesocarp with numerous radially elongated bundles pervading the parenchyma of mesocarp. Such a distribution of mechanical elements is indicative of the derivation of the Bretschneidera fruit from a drupaceous fruit of the «durian» type. In order to emphasise hard differences in pericarpic mechanical system of between drupe, capsule and this specialised type it is proposed to establish a new type of fruits - ascade (aseada, lat.) - to accommodate all fruits originated from the superior ovary with sclerified mechanical system located in the mesocarp. Thus the fruit of Bretschneidera is defined as a loculicidal ascade instead of loculicidal capsule. Seeds of Bretschneidera are relatively large, practically exalbuminous, with straight dicotyledonous embryo. The spermoderm of Bretschneidera is exomesotestal with unspecialised crushed tegmen, 40-45-layered, traversed by 8 postchalazal vascular bundles. Evidence mainly from seed morphology and anatomy of seed coats emphasises the somewhat anomaly of the traditional inclusion of Bretschneideraceae in the Sapindales, being quite distinct in spermoderm structure and origin from both Sapindaceae and Hippocastanaceae as well as from other families of the order, excepting anomalous exo-mesotestal Akaniaceae. Furthermore, seed anatomy does not confirm any relationships with Capparales. It is suggested that Bretschneideraceae with Akaniaceae constitute a distinct relict side-branch of connaraceous-sapindaceous ancestry. It can by no means be considered as a basal clade to Capparales. It is suggested to keep Bretschneideraceae with Akaniaceae separately from Sapindales and Capparales before more comprehensive studies of seedcoat anatomy of other orders of Rosidae.

Key words. Carpology, Bretschneidera, Bretschneideraceae, phylogeny, seed.
Bretschneidera es definido como una ascada loculicida y no una cápsula loculicida. Las semillas de Bretschneiderae son relativamente anchas, prácticamente exalbuminosas con embrión dicotiledóneo recto. El espermodermo de Bretschneiderae es exomesotestal, con un tegumento no especializado, aplastado, con 40-45 capas, atravesado por 8 haces vasculares postchalaza. La morfología y anatomía de las semillas evidencia, hasta cierto punto, la anomalía de la tradicional inclusión de Bretschneiderae en Sapindales y la distinta estructura del espermodermo y origen de Sapindales e Hippocastanaceae, así como otras familias de este orden, excepto las anomalías mesotestales de Akaniaceae. La anatomía de semillas no confirma ninguna relación con las Capparales. Se sugiere que Bretschneiderae, junto con Akaniaceae, constituye una rama relicta de ancestros connaraceo-sapindaceo. Se puede considerar como una rama basal de Capparales. Se sugiere conservar Bretschneiderae con Akaniaceae, separadamente de Sapindales y Capparales, pevio a la realización de más estudios sobre la anatomía de semillas de otros órdenes de Rosidae.

Palabras clave. Carpología, filogenia, Bretschneidera. Bretneideraceae, semillas.

INTRODUCTION

Bretschneidera Hemsl., the only monotypic genus in the Bretschneideraceae described by Hemsley (1901), is generally treated as a natural member of Sapindales (Takhtajan, 1987; Cronquist, 1992; Thorne, 1992) or rather doubtful (Dahlgren, 1983, 1989). Bretschneidera has been included in Hippocastanaceae (Engler, 1919) or in Sapindaceae (Hemsley, 1901; Hutchinson, 1926), but nevertheless it has been segregated into a distinct family Bretschneideraceae Radlk. (Radlkofer, 1908; Engler, 1924) accepted in all modern systems. At present time Rodman (1991, a, b), Rodman et al. (1993) and then Gadek et al. (1992, 1996) advanced a hypothesis of its closer affinity with Capparales basing their arguments on cladistic, phenetic and molecular analyses in spite of recently studied embryology of the genus (Tobe & Peng, 1990) showed a reasonable gap between Bretschneidera and the families of highly advanced Capparales. The latter is characterised by a very specialised exotegmic seedcoat construction and paracarpous fruits. Nevertheless, the problem of the proper systematic position of Bretschneidera is remained unsolved especially in the context of its supposed affinities with other 15 myrosin-producing angiosperm families (Goldberg, 1986; Rodman, 1991, a,b; Gadek et al., 1992, 1996; Rodman et al., 1993) and the lack of likeness in terms of embryology (Tobe & Peng, 1990). The available data on pollen morphology (Liu, 1986; Chaw & Peng, 1987), chromosome numbers (Yang & Hu, 1985), timber anatomy (Tang, 1935; Heimsch, 1942; Zeng & Tong, 1984; Lü & Hu, 1994, 1999), phytochemistry (Boufford et al. 1989), and embryology (Tobe & Peng, 1990) are also insufficiently wide to provide clear relationships of Bretschneidera. Tobe & Peng (1990) reported for first time on the seedcoat structure of Bretschneidera and found it similar to other sapindalean seed coats. However, the occurrence of pachytestal seedcoat construction within typical Sapindales (Corner, 1976; Doweld, 1996 a, b) questioned such a close relationship. In this connection we attempt to elucidate phylogenetic relationships of Bretschneideraceae using the carpological features of Bretschneidera.

MATERIAL AND METHODS

Fruits and seeds of Bretschneidera sinensis Hemsl. were kindly provided for this study by Prof. H. Tobe (voucher at the Gaertnerian Institution, NICAR) being collected in the Yangmingshan National Park,
Taipei Co., Taiwan (voucher: Peng 9855 at HAST, KYO & NICAR). Drawings were made from cross-sections prepared by the usual paraffin method (O’Brien & McCully, 1981). Scanning electron microscope observations were made with a HITACHI S-405A at 15 kV.

**OBSERVATIONS**

**Fruit**

Mature fruit (fig. 1). This is 4-4.5 cm long and 3-3.5 cm wide, brown, pubescent, with numerous lenticels, oblong-obovate, or of irregular shape owing to abortion of locules. It is originated from the trimerous syncarpous gynoecium, with non-persisting style and axile placentation of 2 ascending ovules; it is loculicidally dehiscent. The vascular skeleton of the fruit (fig. 2) consists of central trimerous vascular system and 4-5, occasionally more (to 8) vascular bundles around the locules and sometimes recorded 2 or 4 vascular bundles in the outermost part of mesocarp.

**Pericarp** (fig. 3). This is trizonate: 8-10-layered exocarp, 50-55 layers of parenchymatous mesocarp traversed by numerous fibrous bundles from the diffusively wooded innermost mesocarp, and diffusively fibrous, but not lignified endocarp.

The exocarp is composed of 8-10 parenchymatous layers with numerous rows of myroinsiferous cells; the epidermal cells are differentiated into specialised thick-walled 2-4-celled trichomes (fig. 4). There are numerous lenticels. The mesocarp is bizonate: innermost sclerified part is composed of 8-12 layers of thick-walled fibres, the other part of mesocarp represented by parenchymatous cells, being radially traversed by numerous fibrous bundles originated in the innermost part of mesocarp. The endocarp is composed of 12-14 layers of non-lignified and relatively thick-walled fibres, aerenchymatous; the innermost part is represented by a thick-walled cells in the inner epidermis with numerous 3-4-celled specialised trichomes which are separated from the fibrous endocarp by a single layer of thick-walled, occasionally lignified cells (endocarpic hypoderma).

**Seed.**

Mature seed (fig. 5a). This is relatively large, 10-12 mm wide and 12-15 mm long, red, rounded, exarillate; hilum subbasal, with a single vascular bundle entering the seed and pervading through the slightly differentiated raphe to chalaza and then splitting into 8 postchalazal bundles which extend through the outer integument up to micropyle (fig. 5b). A micropyle is formed by both integuments; the antiraphe is not clearly differentiated. After fertilisation the massive cup-shaped hypostase is formed in the chalazal part of seed (Tobe, Peng, 1990), in the mature seed consisting of
Figure 2. Cross-section of the fruit of *Bretschneidera sinensis*, x 3. Abbreviations: cvb, central vascular bundles; lvb, lateral vascular bundles; dl, dehiscence lines; s, seed; tr, trichomes; excp, exocarp; endcp, endocarp; imscp, inner sclerified part of mesocarp (intensively dotted).

**SUMMARY OF CARPOLOGICAL FEATURES**

The seed is formed from campylotropous (Tobe, Peng, 1990) bitegmic ovule; spermoderm is a derivative of multiplicative outer integument (2-3-layered inner integument is unspecialised and crushed), exo-mesotestal. The seed coats are vascularised by a single raphal bundle splitting into 8 postchalazal vascular bundles penetrating the outer integument. The endosperm absent; embryo dicotyledonous, massive, straight, with a differentiated plumule and two leaves.

The fruit is formed from the trimerous syncarpous gynoecium with axile placentation of 2 ovules per locule; style non-persistent; it is loculicidally dehiscent. The unusual construction of the mechanical system of fruit (aerenchymatous unspecialised fibrous endocarp with the lignified innermost part of the mesocarp consisting of numerous radially elongated bundles of fibres) indicates for a necessity to clarify the fruit type of *Bretschneidera*. From one hand, the unspecialised fibrous endocarp suggests its evolutionary history from a capsular fruit with a well differentiated sclerocarp serving as only mechanical system of capsules or dry follicles (Leclerc du Sablon, 1884; Weberbauer, 1898). From another hand, the presence of sclerified mesocarpic innermost layers with numerous fibrous bundles radially pervading mesocarpic parenchyma (like in many durian-like fruits: Corner, 1976) together with a lack of any rudiments in the parenchyma of exocarp.
Figure 3. Cross-section of the pericarp of Bretschneidera sinensis, x 7. Abbreviations: exocp, excarp, mscp, mesocarp, endcp, endocarp.

Sección transversal del pericarpo de Bretschneidera sinensis, x 7. Abreviaciones: exocp, excarp, mscp, mesocarpo, endcp, endocarpo.
Figure 4. SEM sculpture of the fruit of *Bretschneidera sinensis*. - 4a. Surface of the pericarp with numerous epidermal trichomes and lenticel, x 50. - 4b. the same, enlarged, x 380. - 4c. Cross-section of exocarp with numerous trichomes, x 250. - 4d. Cross-section of endocarp with numerous epidermal trichomes, x 200.

Escultura a SEM del fruto de *Bretschneidera sinensis*: -4a. Superficie de el pericarpo con numerosos tricomas de la epidermis y lenticelas, x 50.-4b. el mismo, ampliado, x 380. -4c. Corte transversal del exocarpo con numerosos tricomas, x 250. -4d. Corte transversal del endocarpo con numerosos tricomas de la epidermis, x 200.
suggests the origin of such a complicatedly differentiated pericarp construction from a drupe-like type of fruits («noyaux a structure hétérogène»: Garcin, 1891: 29). Thus it became evident that fleshy, dehiscent fruit of Bretschneidera is a specialised derivative of capsule-drupeous morphogenetic series, occupying a rather distinct, intermediate position between drupe-like fruits (‘dry drupes’) and capsular fruits (‘fleshy capsules’). The available anatomical structure of the mesocarp suggests that it is appropriate to segregate this type of fruit with a mesocarpic specialised mechanical system (exocarp and endocarp despecialised or unspecialised) into a distinct type of fruits - ascade (ascada, lat.) - to accommodate all superior fruits with a mesocarpic mechanical system. Thus it would emphasise the essential, mostly overlooked, hard differences between capsules, drupes and ascales in the localisation of the mechanical layers in pericarp. A new classification of the fruits basing mostly on the anatomical features of the differentiation of pericarp, like it has been advanced and recommended for description and analysis of seed coats by Corner (1976) and Schmid (1986), would be published elsewhere.

In summary, it is also necessary to notice that the Bretschneidera fruit treated as a loculicidal ascale has nothing in common with carcerulus, as it has been proposed by Spjut
Figure 6. Cross-section of the spermoderm of *Bretschneidera sinensis*, x 10. Abbreviations: extt, exotesta, scltt, sclerotesta, endtt, endotesta, tg, tegmen, hyp, layer of hypostase, endsp, endosperm, embr, tissue of embryo. Sección transversal del espermodermo de *Bretschneidera sinensis*, x 10. Abreviaciones: extt, exotesta, scltt, esclerotesta, endtt, endotesta, tg, tegumento, hyp, capa de hipostasa, endsp, endospermo, embr, tejido embrionario.
Fruits of Bretschneidera (1994). He defined carcerulus as a plurilocular indehiscent fruit with 'undifferentiated pericarp' (Spjut, 1994: 49). Since the fruit of Bretschneidera is loculicidally dehiscent and has complicatedly differentiated pericarp, it is out of question to suggest any relationships with carceruli representing in itself a highly variable and quite artificial assemblage of dry indehiscent coenocarpous fruits (Kaden, 1964).

DISCUSSION

So far as our real knowledge of the anatomy and morphology of fruits in general as well as the distribution of ascades among the families of the angiosperms is very limited, further discussion on the systematic position of Bretschneideraceae would be practically based on its seed anatomy and morphology.

Relationships with Sapindales. The exo-mesotestal spermoderm of Bretschneidera is not so closely related to similar exo-mesotestal construction of the seed coats of both Hippocastanaceae (Guérin, 1901; Doweld, 1996a) and Sapindaceae (Corner, 1976; Doweld, 1996a) as it has been stated previously (Tobe, Peng, 1990). These families have very specialised pachytestal coats (pachychalazal sensu Corner (1976) in mature seeds). The exo-mesotestal seeds of Bretschneideraceae reveal only remote relationships with the exo-mesotestal-endotegmic (Staphylea, Turpinia p.p.) or more advanced mesotestal-endotegmic (Euscaphis) seeds of the Staphyleaceae (Corner, 1976; Doweld, 1996a). The vascularization of the staphyleaceous seeds, preserving the vascular system derivative from the pachytestal seed type (Le Monnier, 1872; Doweld, 1996a), has nothing in common with a more simply organised vascular skeleton of Bretschneidera seeds. The same is true for more simplified and reduced exo-mesotestal seed coats of Aceraceae (Magen, 1912). The exotegmic seeds of Tapisciaceae (Corner, 1976), aberrant within the whole order (Doweld, 1996b), are far from being comparable with quite different exo-mesotestal seeds of Bretschneideraceae. The Melianthaceae possessing advanced an exotestal type of seed coats with unspecialised, as a rule, crushed tegmen show only distant relationships with a more archaic exo-mesotestal construction of Bretschneidera spermoderm, and furthermore, the occurrence of abundant endosperm, small embryo, another type of seed vascularization (Corner, 1976) indicates in addition of its affiliation with a somewhat another phylum. It is out of the question also to propose any relationships of the Bretschneideraceae with unitegmic (? pachytestal) Sabiaceae. The available data on the seedcoat structure of other sapindalean families (Stylobasiaceae, Emblingiaceae and Physenaceae) are too insufficient to be discussed in present paper.

However, the exo-mesotestal seed coats of Bretschneideraceae reveal a similarity with that of exo-mesotestal Akaniaceae (Doweld, 1996a, c) having a somewhat doubtful position within the order. But the occurrence of copious endosperm, smaller embryo, more complicatedly differentiated palisade of columellar, heavily thickened exotestal cells within Akaniaceae indicates that Akania retains more primitive features in seed construction. With the data on seed structure at hand, it seems that Bretschneideraceae with Akaniaceae form a common lineage. But the community of this phylum with sapindalean line of evolution (Tobe & Peng, 1990; Tobe & Raven, 1995) is not supported by their seedcoat anatomy (Doweld, 1996c). The archaic representatives of the Sapindaceae (tribes Koelreuterieae, Dodonaeae, etc.) usually have thickened cells in the outer epidermis of inner integument (Guérin, 1901; Doweld, 1996a), indicative of ancestral exotegmic construction of the inner integument (Corner (1976) reported even unusual exotegmic fibres in Alectryon).
This circumstance avails to connect Sapindaceae directly with Connaraceae having testal-exotegmic spermoderm, arillate seeds with copious endosperm and follicular fruits (Corner, 1976; Takhtajan, 1987). It is probable that Bretschneidera and Akania possessing unspecialised tegmen with no rudiments of its exotegmic construction, exo-mesotestal non-pachytestal seeds with abundant endosperm (Akania), have begun to go by another morphogenetic way of seedcoat evolution which is characterised by the obliteration of tegmen in early stages of development. This mode has nothing in common with the gradual despecialization of the exotegmic seed construction (traced in archaic Dodonaeoideae) and with the formation of pachytesta or even highly specialised sarcopachytesta within Sapindaceae (Corner, 1976; Doweld, 1996a).

Thus, on the basis of the seed anatomical data now available, practically none of the sapindalean families, excepting Akaniaceae, are revealed any close relationships with the Bretschneideraceae. It is essential for Sapindaceae and Hippocastanaceae in the structure of which Bretschneidera has been sometimes placed (Engler, 1919; Hutchinson, 1926). It seems that more specialised and advanced Bretschneideraceae with relictual Akaniaceae (Doweld, 1996c) form a distinct side-branch of pro-sapindalean ancestry, diverging very early from a common ancestor with Connarales/Sapindales. At present time it seems better to keep separately Bretschneideraceae with Akaniaceae from Sapindales.

Relationships with Capparales/ Moringales. As it has been proposed by Rodman (1991a, b), Rodman et al. (1993) and then Gadek et al. (1992, 1996) using phenetical, cladistic and biomolecular analyses, Bretschneidera being one of 15 myrosin-producing families of flowering plants, should constitute a single clade with Tropaeolales and be closely related to Capparales. Judging by seed anatomy only, excepting other exomorphic essential differences (Radkofer, 1908), it is hard to connect exalbuminous, pachytestal seeds with simplified thin-walled 10-15-layered seed coats of Tropaeolum (Corner, 1976) with the exo-mesotestal, lacking of pachytesta, thick-walled and multilayered spermoderm of Bretschneidera. The morphogenetic hiatus is so great that it is quite impossible even to suggest any relationships between these families as well as with Capparaceae (Rodionova, 1992a) and highly advanced Resedaceae (Czerniakowskaya, 1992) and Tovariaceae (Boesewinkel, 1990; Rodionova, 1992b) having endotestal-exotegmic (Cadaba) or mostly exotegmic spermoderm. They are too far from being closely related to Bretschneidera with quite different exo-mesotestal seed coats. The endotestal seeds and specialised paracarpous fruits (siliquas) of Brassicaceae (Rodionova, 1992c) also do not show any relationships with exo-mesotestal seeds and loculicidal ascade of Bretschneidera. Moringaceae which is characterised by a very advanced, secondary multiplicative and complicatedly differentiated mesotesta (Komar, Rodionova, 1992) also have nothing in common with Bretschneideraceae.

Thus it becomes evident from the viewpoint of seed anatomy that the recently advanced hypothesis of the affinities between Bretschneideraceae and Capparales/ Tropaeolales (Goldberg, 1986; Rodman, 1991, a, b; Gadek et al., 1992, 1996; Rodman et al., 1993) is exclusively artificial, and all attempts to 'constitute' a single evolutionary line of glucosinolate-producing angiosperms, probably polyphyletically originated (Harbourne, Turner, 1984), should be abandoned. However, our real knowledge of the spermoderm structure of the related orders Rosales and Rutales (Corner, 1976) does not allow to compare adequately its seedcoat structure with Bretschneidera. Thus the true systematic position of Bretschneideraceae is
remained till uncertain awaiting further comprehensive studies of seed and fruit anatomy of basal Rosidae, but being clearly far from Capparales and Sapindales.

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