

## 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 trilobular 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 (ascada, 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.

**RESUMEN.** *Estudio carpológico en Bretschneidera (Bretschneideraceae) y sus relaciones taxonómicas. Se ha estudiado el fruto, anatomía y morfología de las semillas de Bretschneidera sinensis Hemsl., género monotípico de Bretschneideraceae, con objeto de clarificar sus relaciones filogenéticas. El fruto de tipo sincárpico, trilobular y loculicida tiene un inusual endocarpo parenquimatoso, no especializado, fibroso con 12-14 capas; mesocarpo esclerificado en su parte más interna con numerosos haces elongados y radiales en toda la extensión de su parénquima. Cada una de las distribuciones de los elementos mecánicos es indicativa de la derivación del fruto de Bretschneidera a partir de un fruto drupáceo o de tipo "durian". Con objeto de resaltar las diferencias del sistema mecánico del pericarpo entre drupa, cápsula y este tipo especializado, se propone establecer un nuevo tipo de fruto -ascada- para acomodar todos los frutos originados a partir de un ovario súpero con sistemas mecánicos esclerificados en el mesocarpo. El fruto de*

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*Bretschneidera* es definido como una ascada loculicida y no una cápsula loculicida. Las semillas de *Bretschneideraceae* son relativamente anchas, prácticamente exalbuminosas con embrión dicotiledóneo recto. El espermodermo de *Bretschneideraceae* 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 *Bretschneideraceae* 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 *Bretschneideraceae*, junto con *Akaniaceae*, constituye una rama relicta de ancestros conaraceo-sapindaceo. Se puede considerar como una rama basal de *Capparales*. Se sugiere conservar *Bretschneideraceae* con *Akaniaceae*, separadamente de *Sapindales* y *Capparales*, previo a la realización de más estudios sobre la anatomía de semillas de otros órdenes de *Rosidae*.

Palabras clave. Carpología, filogenia, *Bretschneidera*. *Bretschneideraceae*, 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; Lü & Hu, 1994), 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-ovovate, 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

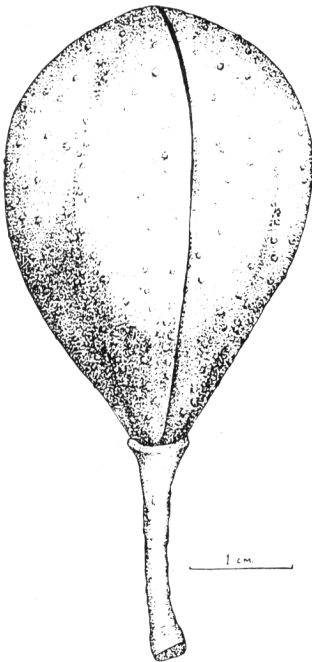


Figure 1. Loculicidally dehiscent syncarpous ascade of *Bretschneidera sinensis*, x 3. *Dehiscencia loculicida de la ascada sincárpica de Bretschneidera sinensis*, x 3.

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 myrosiniferous 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

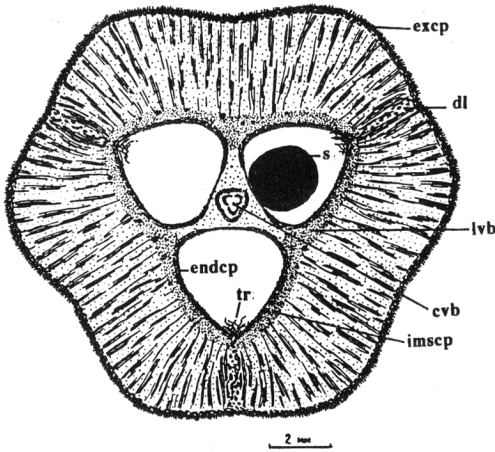


Figure 2. Cross-section of the fruit of *Bretschneidera sinensis*, x 3. Abbreviations: cvb, central vascular bundles; lvb, lateral vascular bundles; dl, dehiscence lines; s, seed; tr, trichomes; excp, exocarp; endcp, endocarp; imscp, inner sclerified part of mesocarp (intensively dotted). *Corte transversal del fruto de Bretschneidera sinensis*, x 3. Abreviaciones: cvb, Haces vasculares centrales; lvb, haces vasculares laterales; dl, líneas de dehiscencia; s, semillas; tr., tricomas; excp, exocarpo; endcp, endocarpo; imscp, parte interior esclerificada del mesocarpo (bandas oscuras).

tanniferous thick-walled cells. The mature seeds are practically exalbuminous: only 2-4 layers of endosperm are preserved and visible in cross-sections (fig. 6). The dicotyledonous embryo is large, straight (fig. 5 c, d), with a clearly differentiated plumule and two leaves.

**Spermoderm.** The seed coat (fig. 6) is formed by both outer and inner integuments. It is exo-mesotestal with unspecialised crushed tegmen (Tobe, Peng, 1990).

The testa is differentiated into a one-layered exotesta (derivative of the outer epidermis of outer integument) and 40-45 sclerified layers of mesotesta, superseded by 1-2-layered endotesta composed of unspecialised cells with slightly thickened walls. The exotesta is composed of high (up to 250  $\mu$ m) columellar cells with heavily thickened outer periclinal and radial walls.

The mesotesta is represented by small cells with strongly thickened, but not lignified walls, slightly oblong in tangential direction; the innermost part of mesotesta is aerenchymatous.

The tegmen is fully obliterated, but sometimes retains structure (2-3 unspecialised layers) near the hypostase.

### 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 gynoeceium 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 sclerendocarp 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

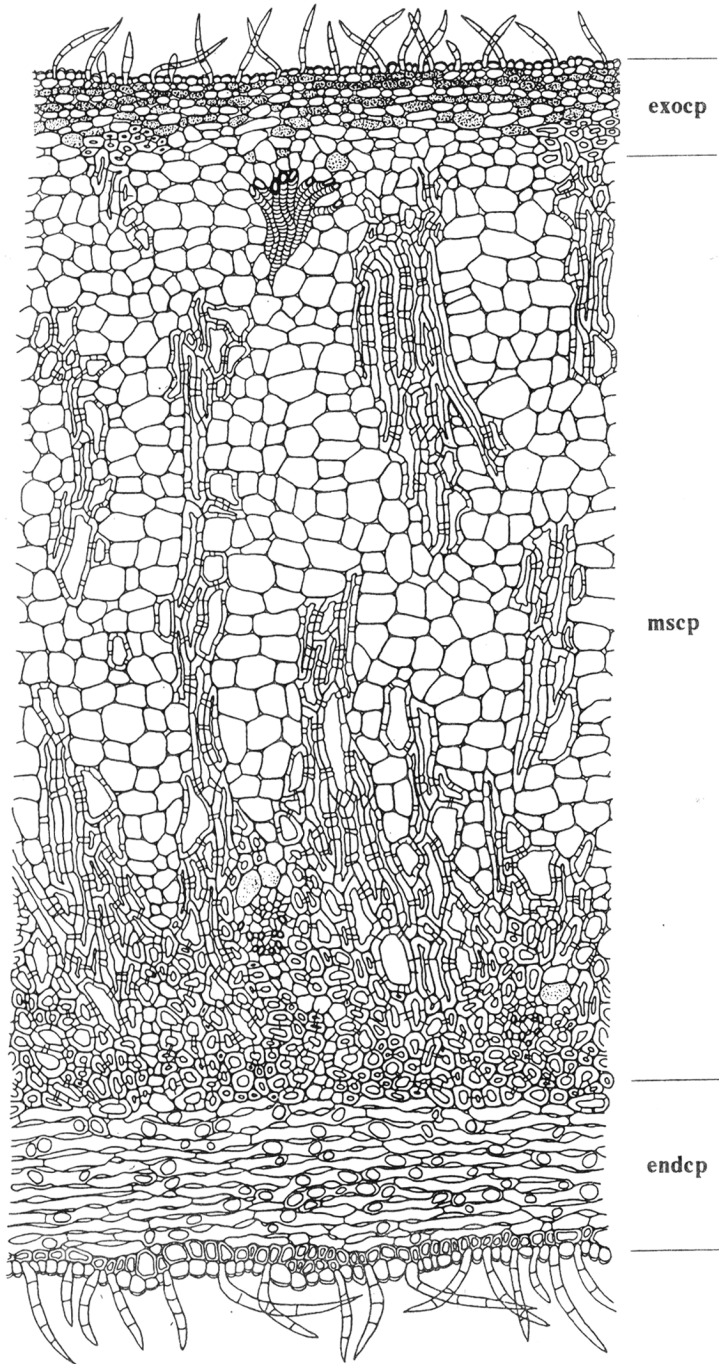


Figure 3. Cross-section of the pericarp of *Bretschneidera sinensis*, x 7. Abbreviations: exocp, excarp, mscp, mesocarp, endcp, endocarp. *Sección transversal del pericarp de Bretschneidera sinensis, x 7. Abreviaciones: exocp, excarp, mscp, mesocarp, endcp, endocarp.*

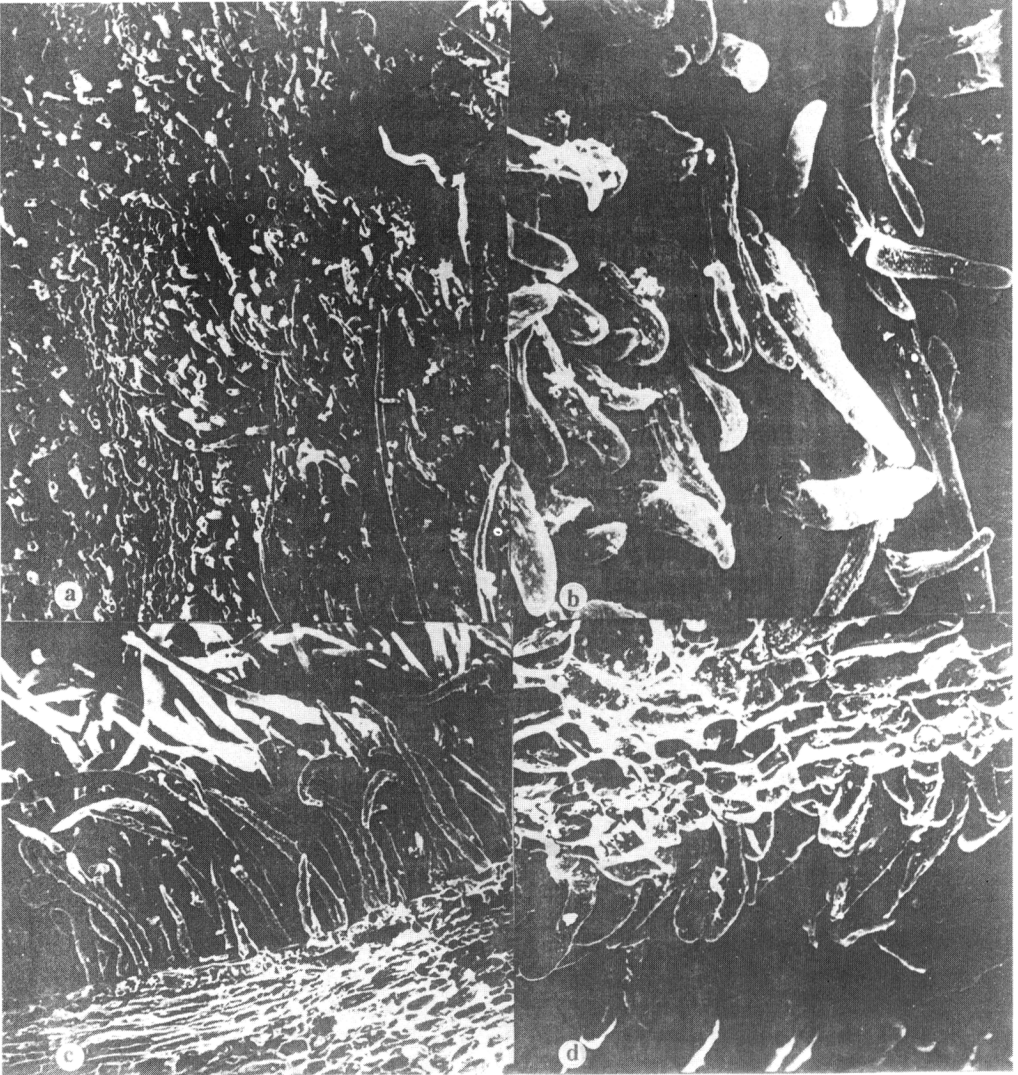


Figure 4. SEM sculpture of the fruit of *Bretschneidera sinensis*. - 4a. Surface of the pericarp with numerous epidermal trichomes and lenticel, x 50. - 4b. the same, enlarged, x 380. - 4c. Cross-section of exocarp with numerous trichomes, x 250. - 4d. Cross-section of endocarp with numerous epidermal trichomes, x 200. *Escultura a SEM del fruto de Bretschneidera sinensis*: -4a. Superficie de el pericarp con numerosos tricomas de la epidermis y lenticelas, x 50.-4b. el mismo, ampliado, x 380. -4c. Corte transversal del exocarp con numerosos tricomas, x 250. -4d. Corte transversal del endocarp con numerosos tricomas de la epidermis, x 200.

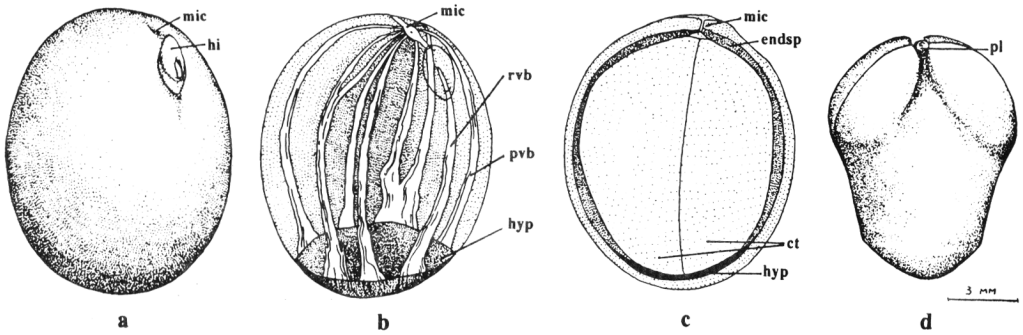


Figure 5. Mature seed of *Bretschneidera sinensis*. - 5a. General view, x 7. - 5b. Vascularization of seed, x 7. - 5c. Longitudinal section of seed showing embryo (half removed), x 7. - 5d. General view of dicotyledonous embryo, x 7. Abbreviations: rvb, raphal vascular bundles; pvb, postchalazal vascular bundles; ct, cotyledons; endsp, endosperm; hyp, hypostase; mic, micropyle; hi, hilum; pl, plumule. *Semillas maduras de Bretschneidera sinensis*. -5a. Vista general, x7. -5b. Vascularización de las semillas, x 7. -5c. Sección longitudinal de la semilla mostrando el embrión, x 7. - 5d. Vista general del dicotiledón embrionario, x 7. Abreviaciones: rvb, haces vasculares; pvb, haces vasculares postchalaza; ct, cotiledones; endsp, endosperma; hyp, hipostasa; mic, microfillo; hi, hilo; pl, plúmula.

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-drupaceous 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 ascades 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 ascade has nothing in common with carcerulus, as it has been proposed by Spjut

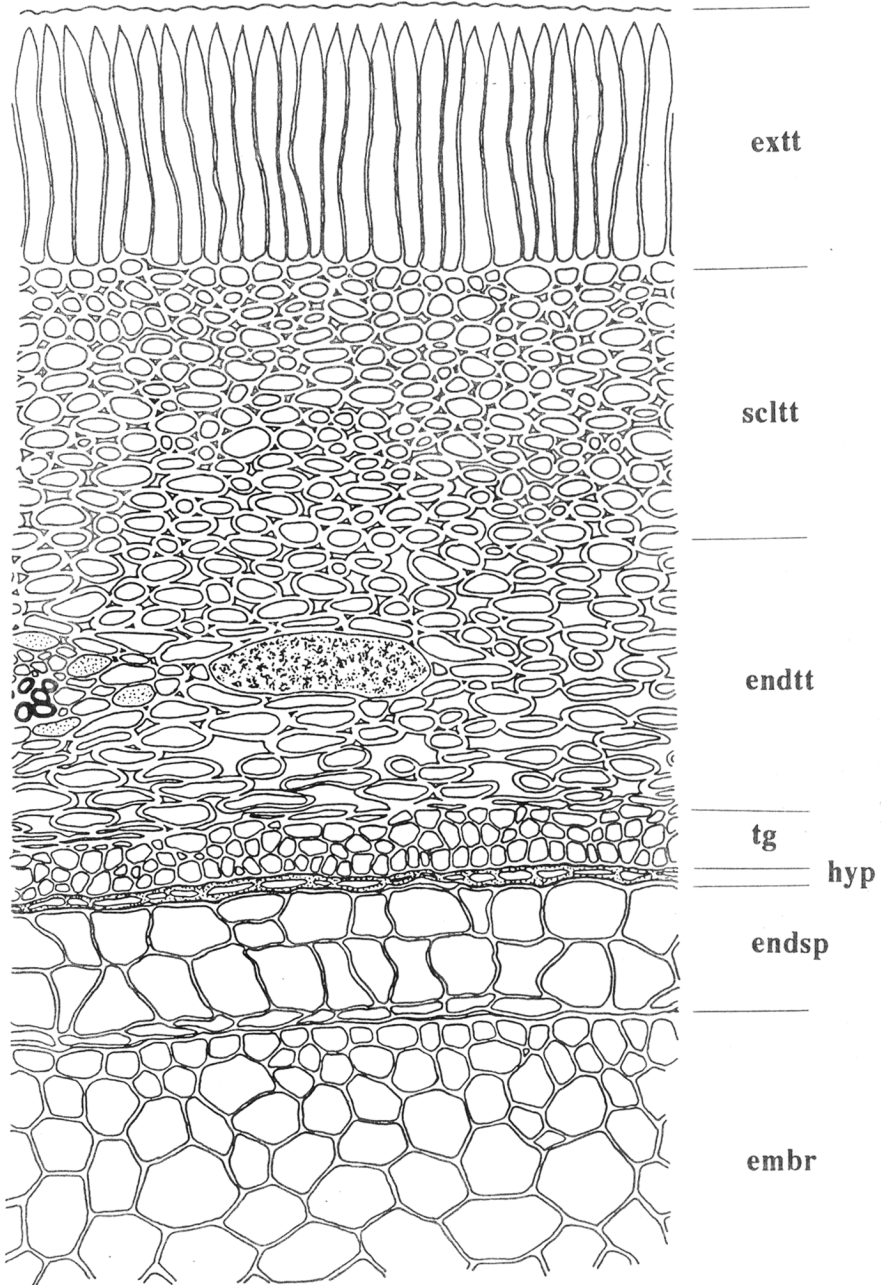


Figure 6. Cross-section of the spermoderm of *Bretschneidera sinensis*, x 10. Abbreviations: extt, exotesta, scltt, sclerotesta, endtt, endotesta, tg, tegmen, hyp, layer of hypostase, endsp, endosperm, embr, tissue of embryo. Sección transversal del espermodermo de *Bretschneidera sinensis*, x 10. Abreviaciones: extt, exotesta, scltt, esclerotesta, endtt, endotesta, tg, tegmento, hyp, capa de hipostasa, endsp, endospermo, embr, tejido embrionario.



(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 pachytetal 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 pachytetal 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 *Meliantaceae* 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 (? pachytetal) *Sabiaceae*. The available data on the seedcoat structure of other sapindalean families (*Stylobasiaceae*, *Emblingiaceae* and *Phytenaceae*) 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*, *Dodonaceae*, 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 (1991 a, 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 *Tropaeolaceae* and be closely related to *Capparales*. Judging

by seed anatomy only, excepting other exomorphic essential differences (Radlkofer, 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 (siliques) 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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## REFERENCES

- BOESEWINKEL, F.D. -1990- Ovule and seed development of *Tovaria pendula* Ruiz et Pavon. *Bot. Jahrb. Syst.*, 111: 389-401.
- BOUFFORD, D. E., KJAER, A., MADSEN, J. O. & SKRYDSTRUP, T. -1989- Glucosinolates in *Bretschneideraceae*. *Biochem Syst. Ecol.*, 17: 375-379.
- CHAW, S.-M. & PENG, C.-I. -1987- Palynological notes on *Bretschneidera sinensis* Hemsl. *Bot. Bull. Acad. Sin.*, 28: 55-60.
- CORNER, E. J. H. -1976- *The seeds of dicotyledons*. Vols. 1, 2. Cambridge: Cambridge University Press.
- CRONQUIST, A. -1992- *An integrated system of classification of flowering plants*. 2nd ed. New York: Columbia University Press.
- CZERNIAKOWSKAYA, E. F. -1992- *Resedaceae*. Pp. 202-208 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 4. St.-Petersburg: Nauka. [In Russian].
- DAHLGREN, G. -1989- The last Dahlgrenogram. System of classification of the dicotyledons. Pp. 249-260 in K. Tan (Ed.), *Plant taxonomy, phytogeography and related subjects*. The Davis and Hedge Festschrift. Edinburgh: Edinburgh University Press.
- DAHLGREN, R. -1983- General aspects of angiosperm evolution and macrosystematics. *Nord. J. Bot.*, 3: 119-149.
- DOWELD, A. B. -1996a- *Staphyleaceae, Tapisciaceae, Sapindaceae, Hippocastanaceae, Melianthaceae, Akaniaceae*. Pp. 306-341, 343-349 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg: Nauka. [In Russian].
- DOWELD, A. B. -1996b- *Zaklyucheniye k poriadku Sapindales [Conclusions on the order Sapindales]*. Pp. 349-350 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg: Nauka [In Russian].
- DOWELD, A. B. -1996c- The systematic relevance of fruit and seed anatomy and morphology of *Akania* (*Akaniaceae*). *Bot. J. Linn. Soc.*, 120: 379-389.
- ENGLER, A. -1919- *Syllabus der Pflanzenfamilien; eine Übersicht über das gesamte Pflanzensystem mit besonderer Berücksichtigung der Medizinal- und Nutzpflanzen, nebst einer Übersicht über die Florenreiche und Florengebiete der Erde, zum gebrauch bei Vorlesungen und Studien über spezielle und medizinisch-pharmazeutische Botanik*. 8 Aufl. Berlin: Gebrüder Borntraeger.
- ENGLER, A. -1924- *Syllabus der Pflanzenfamilien; eine Übersicht über das gesamte Pflanzensystem mit besonderer Berücksichtigung der Medizinal- und Nutzpflanzen, nebst einer Übersicht über die Florenreiche und Florengebiete der Erde, zum gebrauch bei Vorlesungen und Studien über spezielle und medizinisch-pharmazeutische Botanik*. 9 & 10 Aufl. Berlin: Gebrüder Borntraeger.
- GADEK, P.A., E.S. FERNANDO, C.J. QUINN, S.B. HOOT, T. TERRAZAS, M.C. SHEANAN & M.W. CHASE -1996- *Sapindales: molecular delimitation and infraordinal groups*. *Amer. J. Bot.*, 83: 802-811.
- GADEK, P. A., C.J. QUINN, J.E. RODMAN, K.G. KAROL, E. CONTI, R.A. PRICE, & F.S. FERNANDO -1992- Affinities of the Australian endemic *Akaniaceae*: new evidence from the *rbcL* sequences. *Austr. Syst. Bot.*, 15: 717-724.
- GARCIN, A.-G. -1891- Contribution a l'étude des péricarpes charnus. Du noyau des drupes. Histologie et histogénèse. *Ann. Soc. Bot. Lyon*, 17 (1890): 27-39.
- GOLDBERG, A. -1986- Classification, evolution, and phylogeny of the families of dicotyledons. *Smiths. Contr. Bot.*, 58: 1-314.
- GUÉRIN, P. -1901- Développement de la graine et en particulier du tégument séminal de quelques Sapindacées. *J. Bot. (Morot)*, 15: 336-362.
- HARBOURNE, J.B., B.L. TURNER -1984- *Plant chemosystematics*. London: Academic Press.
- HEIMSCH, C. -1942- Comparative anatomy of the secondary xylem in the «Gruinales» and «Terebinthales» of Wettstein with reference to taxonomic grouping. *Lilloa*, 8: 83-198.
- HEMSLEY, W.B. -1901- *Bretschneidera sinensis*. *Hooker's Icon. Pl. Ser. 4*. 8(28): 2708.

- HUTCHINSON, J. -1926- The families of flowering plants. I. Dicotyledons. Arranged according to a new system based on their probable phylogeny. London: MacMillan & Co.
- KADEN, N.N. -1964- Osnovy evolyutsionnoy morfologii plodov [Fundamentals of the evolutionary morphology of fruits]. Vol. I. Doct. Sci. Diss. Moscow: Moscow M. V. Lomonosov State University, Dept. of Higher Plants. [In Russian].
- KOMAR, G.A., G.B. RODIONOVA -1992- Moringaceae. Pp. 209-212 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 4. St.-Petersburg: Nauka. [In Russian].
- LE MONNIER, G. -1872- Recherches sur la nervation de la graine. *Ann. Sci. Nat. Bot. Sér.* 5, 16: 233-305.
- LECLERC DU SABLON, M. -1884- Sur la déhiscence du fruits à péricarpe sec. *Ann. Sci. Nat. Bot. Sér.* 6, 18: 5-104.
- LIU, C. -1986- Studies of pollen morphology in the Bretschneideraceae and the relative families. *Acta Bot. Yunnan.*, 8: 441-450. [In Chinese].
- LÜ, J. & Y.S. HU -1994- Structural study of secondary xylem in *Bretschneidera sinensis* Hemsl. *Acta Bot. Sin.*, 36: 459-465. [In Chinese].
- LÜ, J. & Y.-X. HU -1994- Anatomy of the young stem and secondary phloem in *Bretschneidera sinensis* Hemsl. *Chin. J. Bot.*, 6: 112-117.
- MAGEN, K. -1912- Beiträge zur vergleichenden Anatomie der Samenschalen einiger Familien aus der Engler'schen Reihe der Sapindales. Inaug.-Diss. Univ. Zürich. Borna-Leipzig: Buchdruckerei R. Noske.
- O'BRIEN, T.P. & M.E. MCCULLY -1981- The study of plant structure: principles and selected methods. Melbourne: Termarcaphi and Pty. Ltd.
- RADLKOFER, L. -1908- *Bretschneidera*. Pp. 208-209 in A. Engler & K. Prantl (Eds), *Die natürlichen Pflanzenfamilien*. Nachträge 3. Leipzig: W. Englemann.
- RODIONOVA, G.B. -1992a- Capparaceae. Pp. 183-191 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 4. St.-Petersburg: Nauka. [In Russian].
- RODIONOVA, G.B. -1992b- Tovariaceae. P. 202 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 4. St.-Petersburg: Nauka. [In Russian].
- RODIONOVA, G.B. -1992c- Brassicaceae. Pp. 191-201 in A. L. Takhtajan (Ed.), *Anatomia Seminum Comparativa*. Vol. 4. St.-Petersburg: Nauka. [In Russian].
- RODMAN, J.E. -1991a- A taxonomic analysis of glucosinolate-producing plants. Part 1. *Phenetics. Syst. Bot.*, 16: 589-618.
- RODMAN, J.E. -1991b- A taxonomic analysis of glucosinolate-producing plants. Part 2. *Cladistics. Syst. Bot.*, 16: 619-629.
- RODMAN J.E., R.A. PRICE, K. KAROL, E. CONTI, K.J. SYTSMA & J.D. PALMER -1993- Nucleotide sequences of the *rbcL* gene indicate monophyly of mustard oil plants. *Ann. Missouri Bot. Gard.*, 80: 686-699.
- SCHMID, R. -1986- On Cornerian and other terminology of angiospermous and gymnospermous seed coats: historical perspective and terminological recommendations. *Taxon*, 35: 476-491.
- SPJUT, R.W. -1994- A systematic treatment of fruit types. *Mem. N.Y. Bot. Gard.*, 70: 1-182.
- TAKHTAJAN, A.L. -1987- *Systema Magnoliophytorum*. Leningrad: Nauka. [In Russian].
- TANG, W. -1935- Timber studies of Chinese trees. VII. Notes on the systematic position of *Bretschneideraceae* as shown by its timber anatomy. *Bull. Fan Mem. Inst. Biol.*, 6: 153-159.
- THORNE, R.F. -1992- An updated phylogenetic classification of the flowering plants. *Aliso*, 13: 365-389.
- TOBE, H. & C.-I. PENG -1990- The embryology and taxonomic relationships of *Bretschneidera* (*Bretschneideraceae*). *Bot. J. Linn. Soc.*, 103: 139-152.
- TOBE, H. & P.H. RAVEN -1995- Embryology and relationships of *Akania* (*Akaniaceae*). *Bot. J. Linn. Soc.*, 118: 261-274.
- YANG, D.-Q. & C.-M. HU -1985- The chromosomes of *Bretschneidera* Hemsl. *Notes Roy. Bot. Gard. Edinb.*, 42: 347-349.
- WEBERBAUER, A. -1898- Beiträge zur Anatomie der Kapsel Früchte. *Bot. Centralbl.*, 73: 54-59, 81-105, 135-142, 161-168, 193-202, 250-257, 296-302.
- ZENG, M.X. & Z.L. TONG -1984- Anatomical study of the stem of *Bretschneidera sinensis*. *S.W. Agric. Coll. Bull.*, 1984(1): 42-46. [In Chinese].

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