

## THE MELIANTHACEOUS SEED AND ITS RHAMNACEOUS AFFINITY

ALEXANDER B. DOWELD

**ABSTRACT.** *The Melianthaceous seed and its Rhamnaceous affinity.* The seed anatomy and morphology of *Bersama* (*Bersamataceae*) and *Melianthus* (*Melianthaceae*) have been studied in an effort to clarify their phylogenetic position. The exotestal seed coats of *Bersama* and *Melianthus* with a differentiated palisade of Malpighian cells in exotesta, dimerous raphal vascular skeleton, abundant endosperm, and small differentiated straight embryo show a resemblance with exotestal albuminous seeds of *Rhamnaceae* and *Elaeagnaceae*. Using also additional data on carpology, floral and vegetative morphology it is suggested that *Bersamataceae* with *Melianthaceae* and *Rhamnaceae/Elaeagnaceae* constitute a distinct relict side-branch of exo-mesotestal rosidaeceous ancestry. Evidence from seed anatomy and morphology emphasizes the anomaly of the traditional inclusion of *Bersama* and *Melianthus* in the *Sapindales*, since they have a distinct spermoderm structure and seed vascularization. The seed anatomy does not confirm any relationships with alternatively suggested exo-mesotestal *Lardizabalaceae*. The formerly suggested relationships of this clade with exotegmic *Malvales* are also not supported by seed anatomy. The affinity with exotegmic *Celastrales* which are considered as a possible connecting link between archaic exo-mesotestal *Rosales* and exotestal *Rhamnales/Elaeagnales* is also found untenable. It is suggested that both families, *Bersamataceae* and *Melianthaceae*, constituting a distinct order *Meliantales*, together with *Rhamnaceae* (*Rhamnales* s.str.) and *Elaeagnaceae* (*Elaeagnales*) represent advanced remanants of the massive, much branched phylum tracing back directly to *Fabales*, passed by specialized *Rosales*, *Sapindales*, *Icacinales*, and *Celastrales*.

**Key words.** Carpology, pericarp, seed anatomy, phylogenetic relationships, *Elaeagnaceae*, *Greyiaceae*, *Lardizabalaceae*, *Leeaceae*, *Rhamnaceae*, *Sapindaceae*, *Vitaceae*, *Elaeagnales*, *Rhamnales*, *Sapindales*, *Vitales*.

**RESUMEN.** *La semilla de Melianthaceae y su afinidad con Rhamnaceae.* En el presente trabajo, se ha estudiado la anatomía y morfología de la semilla de *Bersama* (*Bersamataceae*) y *Melianthus* (*Melianthaceae*) con el objeto de clarificar su posición sistemática. La exotesta de *Bersama* y *Melianthus*, con una empalizada de células de Malpighi bien diferenciada, abundante endosperma y embrión recto y escasamente diferenciado, muestra ciertas afinidades con la exotesta albuminosa de las semillas de *Rhamnaceae* y *Elaeagnaceae*. Utilizando también datos carpológicos, florales y morfológico-vegetativos adicionales, se sugiere que *Bersamataceae*, junto con *Melianthaceae* y *Rhamnaceae/Elaeagnaceae* constituyen una ramificación lateral relictica de un ancestro rosidae exo-mesotestado. La morfología y anatomía de las semillas evidencian la anómala y tradicional inclusión de *Bersama* y *Melianthus* en el orden *Sapindales*, cuyas semillas presentan diferente pautas en la estructura de la espermodermis y en la vascularización de

la misma. La anatomía de la semilla, no confirma ninguna de las relaciones que se han sugerido, alternativamente, con *Lardizabalaceae* exo-mesotestales ni con *Malvales* exotegmicos. Por otra parte, consideramos insostenibles las afinidades con *Celastrales* exotégmicos, que han sido consideradas como una posible conexión entre *Rosales* arcaicos exo-mesotestados y *Rhamnales/Elaeagnales* exotestados. Se sugiere que ambas familias, *Bersamataceae* y *Melianthaceae*, constituyen el orden *Meliantales* que, junto con *Rhamnaceae* (*Rhamnales*, s. e.) y *Elaeagnaceae* (*Elaeagnales*) representan remanentes avanzados de un phylum profusamente ramificado, cuyas relaciones se remontan directamente hacia *Fabales*, pasando por *Rosales*, *Sapindales*, *Icacinales* y *Celastrales*.

Palabras clave. Carpología, pericarpo, anatomía de la semilla, relaciones filogenéticas, *Elaeagnaceae*, *Greyiaceae*, *Lardizabalaceae*, *Leeaceae*, *Rhamnaceae*, *Sapindaceae*, *Vitaceae*, *Elaeagnales*, *Rhamnales*, *Sapindales*, *Vitales*.

## INTRODUCTION

The genus *Melianthus* T. ex L. has been described by Pitton de Tournefort (1694) still in pre-linnean times. The genus *Bersama* affiliated with *Melianthus* from the original description (Fresenius, 1837) as well as *Melianthus* alone have never had a stable and clear position within angiosperms.

A. L. de Jussieu (1789: 297) considered *Melianthus* in the 'genera affinia' of his more natural *Rutaceae* s.l. (incl. *Zygophylleae* R. Brown), that is looked more convincing: «Genus *Tropaeolo calicis cucullo, petalorum et staminum situ*». This viewpoint has been shared by his son A. de Jussieu (1825). In contrast, Reichenbach (1828) revived the idea of the taxonomic affinity of *Melianthus* with *Sapindaceae* Juss. (Tournefort's '*Corindus*'). Thus, two contradictory stand points on the relationships of *Melianthus* and *Bersama* have been formed: first, with *Rutaceae-Zygophyllaceae* (A. L. de Jussieu, 1789; A. de Jussieu, 1825; Endlicher, 1840; Lindley, 1846; Radlkofer, 1891) and second, with *Sapindaceae* (Reichenbach, 1828; Bentham and Hooker, 1862-1867; Baillon, 1874; Hallier, 1912; Hutchinson, 1926). The only exception was a curious suggestion of the meliaceous relationship (Richard, 1847/1851) and vitaceous ('*Ampelideae*') for *Bersama* (Endlicher, 1836-1840).

In order to emphasize a certain distinctness of *Melianthus* and *Bersama* from both suggested close allies, Planchon (1851), being unaware of the earlier suggestion of Link (1831), proposed a new 'order' (family) '*Meliantheae*'. The genus *Greyia*, originally described by Hooker and Harvey (Harvey, 1859) and placed provisionally in '*Saxifrageae*', also has been later added to *Melianthaceae* by Hooker (Bentham and Hooker, 1862-1867; Hooker, 1873). The segregation of *Greyia* into a distinct family *Greyiaceae*, made by Hutchinson (1926: 202), and even its exclusion from the order *Sapindales* is accepted in all modern systems of angiosperms (Dahlgren, 1989; Cronquist, 1992; Thorne, 1992; Takhtajan, 1997). This was also recently confirmed by its seed anatomy in particular (Nemirovicz-Danczenko, 1995, 1996 a), linking the genus with the family *Frankoaceae* Juss. (Nemirovicz-Danczenko, 1994, 1996 b) of the order *Saxifragales*. The other two melianthaceous genera *Diplerisma* (Planchon, 1851) and *Natalia* (Hochstetter, 1841) have been considered clearly congeneric with *Melianthus* and *Bersama* respectively (Bentham and Hooker, 1862-1867; Hooker, 1873; Baker, 1907; von Brehmer, 1919).

Nevertheless, Planchon was inclined to relate his new 'order' with *Sapindaceae*. But later, '*Meliantheae*' have been reduced to a 'suborder' (tribe) of the family ('order')

*Sapindaceae* by Hooker (Bentham & Hooker, 1862-1867). However, such a conservative and artificial treatment has not been longer continued and the familial status has been restored (Radlkofer, 1891; Gürke, 1896; Hallier, 1912; Hutchinson, 1926; Wettstein, 1935). The segregation of both *Melianthus* and *Bersama* into a distinct family is also accepted in all modern systems of angiosperms (Umadevi *et al.*, 1986; Dahlgren, 1989; Cronquist, 1992; Thorne, 1992; Takhtajan, 1997) as well as their remaining close relationships with *Sapindaceae*.

Corner (1976) was the first in more recent times who has questioned such a close affinity. Based on the seed anatomy, he proposed to exclude *Melianthaceae* from the *Sapindales* and place it near the family *Lardizabalaceae* Decne. Dahlgren (1983) also regarded *Melianthaceae* as a doubtful element of the whole order *Sapindales*, but the arillate seeds of *Bersama* and some other characters looked as a certain possible link to *Sapindaceae*. Recently we confirmed the anomaly of *Melianthaceae* within *Sapindales* (Doweld, 1996 a, b, 1998) from the stand point of carpology and phermatology. *Phermatology* (from Greek φέρμα — ‘that which is borne’ and λόγος — ‘discourse’) — a new adopted name for the science of seeds, instead of unmanageable *spermatology* (Doweld, 1997).

Based on the differences in the structure of fruits and seeds of *Bersama* and *Melianthus* as wells as other differences in habit, stipules, flower, stigma, etc., listed by van Wyk (1988), we segregated *Bersama* into a family of its own, *Bersamataceae* Dwd. (Doweld, 1998), in order to emphasize the advance and high specialization of the genus. It has been also suggested to segregate both families into a distinct order *Meliantales* Dwd., which reveals some phylogenetic relationships with *Rhamnales* and *Elaeagnales*. Here we attempt to elucidate the phylogenetic relationships and roots of *Meliantales*.

## MATERIALS AND METHODS

Seeds of the *Bersamataceae* and *Melianthaceae* were obtained from the herbarium of the V. L. Komarov Botanical Institute, Russian Academy of Sciences, St.-Petersburg (LE). Voucher specimens were housed in the Carpotheca of National Institute of Carpology (Gaertnerian Institution), Moscow, NICAR:

*Bersamataceae*: *Bersama abyssinica* Fresen. «Abyssinia, in regione media montis Scholoda, Oct. 1837, W. Schimper 942»; *Melianthaceae*: *Melianthus comosus* Vahl. «Caput bonae spei, s.d., Ecklon 777»; *Melianthus major* L. «Africa australis s.d., Ecklon 787».

Drawings were made from serial cross-sections 5—10 μm thick, prepared by the usual paraffin method and stained with safranin-fast green (O'Brien and McCully, 1981). The seed vascularization has been observed after dissection of dry seeds, both parts of which were heated in water and then transferred to a dilute solution of NaOH until cleared to the desired degree. A further employing of the classical reaction for lignification (O'Brien and McCully, 1981) reveals all details of the seed vascular skeleton. Scanning electron microscope (SEM) observations were made with a HITACHI S-405A at 15 kV after sputtercoating with platinum-palladium.

## OBSERVATIONS

*Bersama abyssinica* Fresen.

*Mature seed.* (fig. 1). This is relatively large, 12-15 mm long, 8-10 mm wide and 6-9 mm thick. It is rounded, ovoid, slightly oblong at the chalazal tip; dark brown to black. The seed has a funicular massive yellow aril at the base, it is developing late in half-grown seeds, arising as a broad annulus (Corner, 1976). The vascular skeleton of seed consists of a single

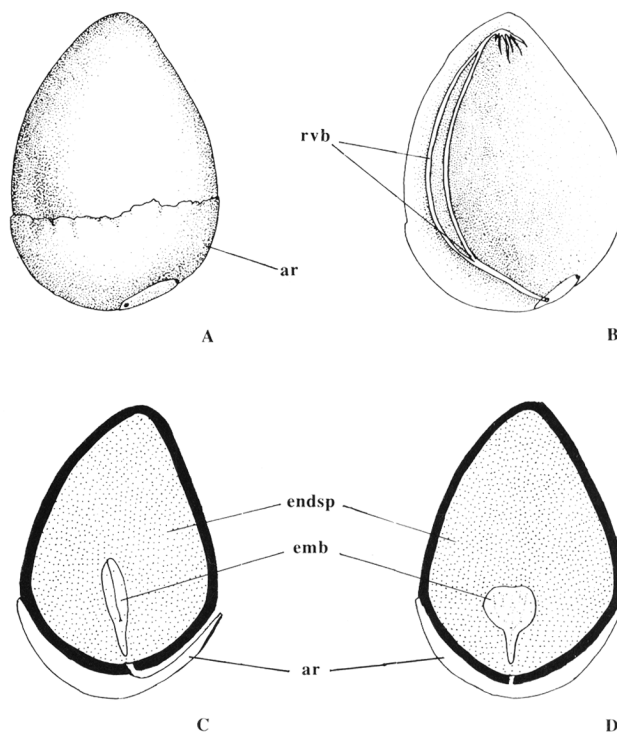


Figure 1. Seeds of *Bersama abyssinica* Fresen., x 30. A. General view. B. Vascularization of the seed. C-D. Longitudinal sections of seed showing small embryo and abundant endosperm. Abbreviations: rvb, raphal vascular bundles; emb, embryo; endsp, endosperm.

raphal vascular bundle bifurcating into two large branches that form a small plexus at the chalazal tip of seed. The endosperm is copious, oily, horny, composed of thick-walled cells with starch granules (fig. 3d). The embryo is small (Steyn, Robbertse and van der Schijft, 1986), with two flat, narrow, spade-like cotyledons and a long hypocotyl. A micropyle is formed by the outer integument only (exostome).

**Spermoderm.** (figs 2-3). The seed coat is formed from both integuments of the anatropous ovule. It is exotestal, with a fully obliterated tegmen in the early stages of seed development (Corner, 1976). The seed sculpturing is rectangular-faceted (fig. 3 A-B).

The *testa* is differentiated into outer (exotesta) and the rest, more massive (15-18

layers) parenchymatous part. The exotesta is composed of a single layer (palisade) of columellar thick-walled, but unligified cells (Malpighian cells) filled with orange granular contents. Van Wyk (1988: 50) erroneously stated the lack of 'macroscleireid layer' in *Bersama*. The remainder of the outer integument (mesotesta & endotesta) consists of thin-walled parenchymatous cells, tangentially elongate and with numerous long styloids and crystals of calcium oxalate (fig. 3 C-D). The endotesta (derivative of the inner epidermis of the outer integument) is not differentiated, because it and the adjacent layers of mesotesta collapse in the mature seed.

The *tegmen* is formed from 2-4-layered inner integument, but fully obliterated in mature seeds.

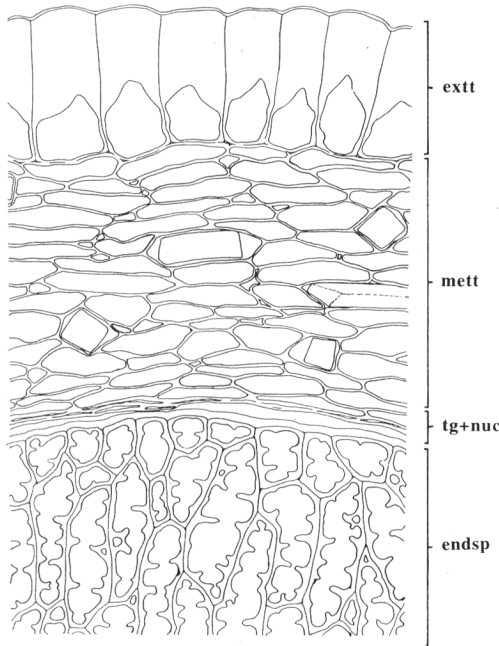


Figure 2. Cross-section of the spermoderm of *Bersama abyssinica* Fresen., x 40. Abbreviations: extt, exotesta; mett, mesendotesta; tg, tegmen; nuc, nucellus; endsp, endosperm.

There are also some remnants of the *nucellus* (2-3 layers of very thin-walled cells) adjoining the crushed tegmen.

### *Melanthus major* L., *M. comosus* Vahl.

*Mature seed.* (fig. 4). This is relatively small, 8610 mm long, 567 mm wide and 5-7 mm thick. It is oblong-ovoid, exarillate, black. The hilum is basal, small, with a single vascular bundle dichotomising in the raphe and expanding in the chalaza by two massive branches. They form a small plexus at the chalazal tip of seed. The mature seeds are abundantly albuminous, with starch grains and oil. The small embryo (Steyn, 1975) is straight, symmetrical, with two flat, spade-like

cotyledons and long hypocotyl. A micropyle is formed by the inner integument only.

*Spermoderm.* The seed coats (figs. 5-6) are exotestal, formed from two integuments of the anatropous ovule, but the inner integument (except for its micropylar part) becomes collapsed in mature seeds. The seed sculpturing is granular (fig. 6 A-B).

The *testa* is differentiated into a 1-layered exotesta (epidermis) and the mesendotestal unspecialized parenchyma. The exotesta (fig. 6C) is represented by a palisade of longitudinally elongate, narrow thick-walled, but unligified macrosclereids (Malpighian cells) filled with tannin-like substances. The remaining part of the testa (fig. 6D) is composed of thin-walled, somewhat tangentially elongate cells with dispersed crystals of calcium oxalate, located mostly in the 2-4 subepidermal layers of mesotesta. The endotesta is undifferentiated, being composed of unspecialized parenchymatous cells; in mature seeds the endotesta and several (1-3) layers of adjacent mesotestal parenchyma are undergone to partial destruction.

The *tegmen* is a derivative of a two-layered inner integument (Khushalani, 1963), collapsed in mature seeds, except for an endostome consisting of 3-5 layers of thin-walled cells. In the micropylar region the cells of the inner epidermis of the inner integument are more differentiated being somewhat larger, thus giving the appearance of a remnant of the ancestral endotegmic seed coat construction.

Adjacent to the tegmen the (3-5) layers of the *nucellus* are clearly visible.

## DISCUSSION

### Relationships with *Greyiaceae*

The affinity of *Greyia* (*Greyiaceae*) with the melianthaceous genera was suggested first by Hooker (in Bentham and Hooker, 1862-

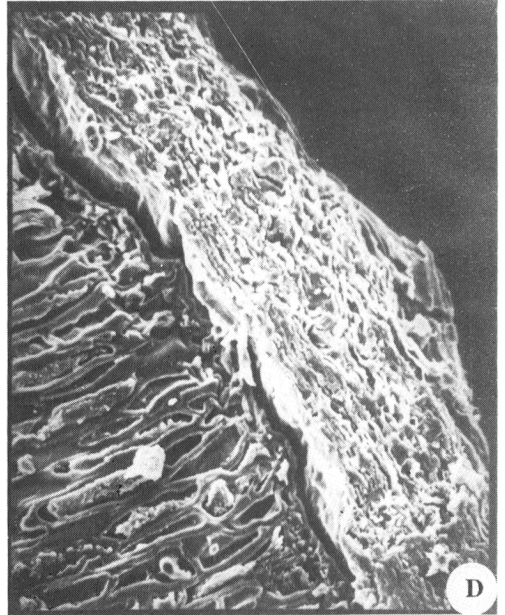
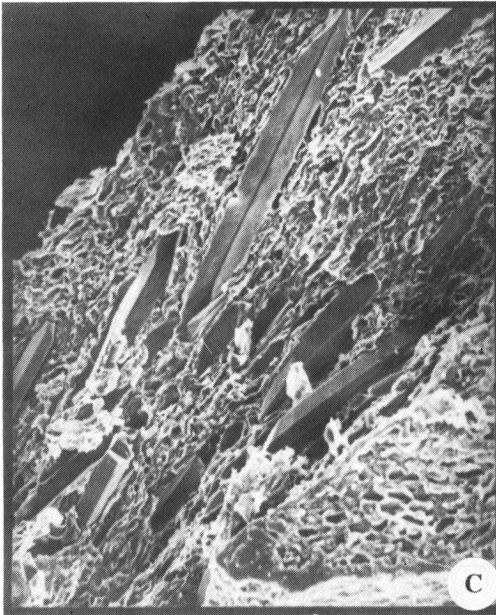
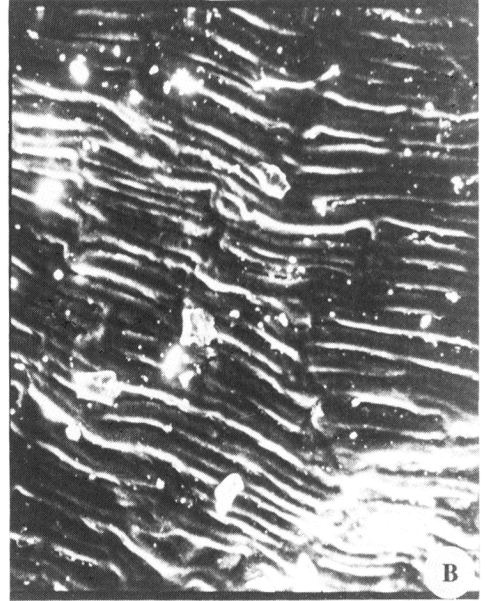


Figure 3. SEMgraphs of the seed of *Bersama abyssinica* Fresen. A. Surface of the seed, x 300. B. The same, enlarged, x 1000. C. Cross-section of the aril (left) and testa with numerous styloids, x 300. D. Cross-section of the spermoderm and horny thick-walled endosperm, x 300.

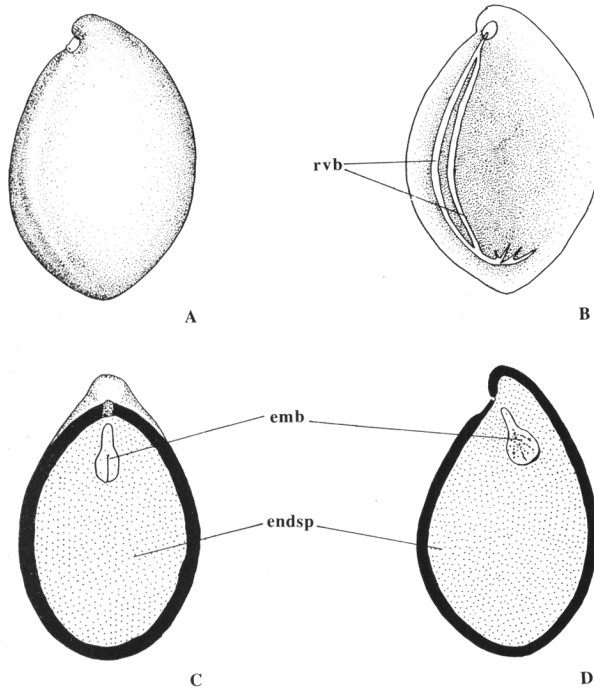


Figure 4. Seeds of *Melianthus comosus* Vahl, x 50. A. General view. B. Vascularization of the seed. C-D. Longitudinal sections of seed showing embryo and abundant endosperm. Abbreviations: rvb, raphal vascular bundles; emb, embryo; endsp, endosperm.

1867), although Harvey (1859) formerly put it in the neighbourhood of 'Saxifrageae'. This view point has been adopted by Baillon (1874, 1897), who suggested a frankoaceous affinity upon the basis of remarkable foliage, and later also by Hutchinson (1926, 1973), Thorne (1992), Cronquist (1992) and Takhtajan (1997). Hooker based his suggestion on the resemblance between *Greyia* and *Melianthus-Bersama* in 4-5-locular, deeply grooved ovary with numerous 2-seriate ovules (*Melianthus* only) and axial placentation, copiously albuminous seeds with small straight embryos, and also in habit, inflorescence, bracts, stamens, etc. (Hooker, 1873: 357). In addition, he has listed some characters of floral morphology (irregular perianth, remarkable form and elongation of stamens during anthesis,

grooved style, etc.), which are directly connected with ornithophilous adaptive floral syndrome typical for *Greyiaceae* and *Melianthaceae*, rather than with the fundamental nature of floral construction. Endress and Stumpf (1991) also mentioned the resemblance in stamen morphology which is affected by a similar floral syndrome. Thus, these characters of floral organization are valueless in this case.

The recent studies of seed and fruit anatomy and morphology of both *Greyiaceae* (Nemirovicz-Danczenko, 1995, 1996 *a*) and *Melianthaceae* (Doweld, 1996 *a*, 1998, present study) show the groundlessness of the suggested affinity between both families in contrast to the molecular studies of Gadek *et al.* (1996). The lobilaterihiscent capsules of

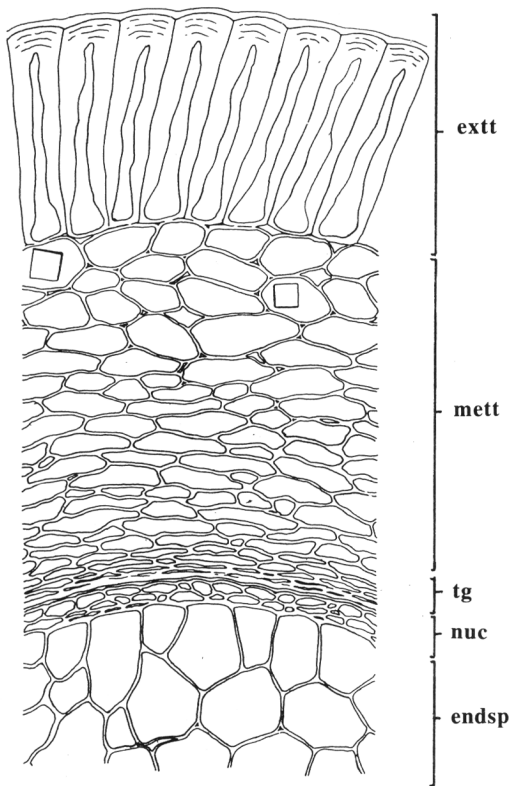


Figure 5. Cross-section of the seed coats of *Melianthus major* L., x 45. Abbreviations: extt, exotesta; mett, mesendotesta; tg, tegmen; nuc, nucellus; endsp, endosperm.

*Greyia* have only superficial resemblance with dorsihiscent capsules of *Melianthus* and *Bersama* (Doweld, 1998). The seeds of *Greyiaceae* are not like that of *Melanthaceae*: they are planate, smooth, elongate, with a long chalazal appendage, semitransparent (tannin-rich endotegmen and massive hypostase of suberitized thick-walled cells (absolutely lacking within *Bersama-Melianthus*) are visible through testa), with a massive, non-branching raphal vascular bundle making a hair-pin loop in the chalazal appendage and ending blindly near hypostase cup, with a thick-walled endosperm, straight embryo, and micropyle

formed by two integuments. The seed coats of *Greyia* are composed of 4-5-layered testa and 2-3-layered tegmen (Nemirovicz-Danczenko, 1995, 1996 a); the testa is differentiated into a single-layered exotesta having thickened outer periclinal walls and a solitary crystal of calcium oxalate per cell, and also a single-layered remarkable endotesta with heavily thickened lignified anticlinal walls (other walls are thin-walled); the tegmen has a differentiated endotegmen composed of tangentially elongate, large cells filled with tannins. Such a specialized construction of the greyiaceous exo-endotestal-endotegmic seed coats and a specialized construction of its vascular skeleton have nothing in common neither with *Melianthus* nor with *Bersama*, which are characterized by a simple dimerous raphal vascular system and strongly exotestal spermoderm. The essential differences in the anatomy of fruits and seeds of *Greyiaceae* and *Melanthaceae-Bersamataceae* preclude any possibilities to suggest a close relationship.

#### Relationships with *Lardizabalaceae*

Corner (1976) suggested an affinity of *Bersama* and *Melianthus* to *Lardizabalaceae*. He homologized a rudimentary aril of *Akebia* with that of *Bersama*, and noted a similar histological differentiation of the seed coats and raphal seed vascular skeleton of *Decaisnea* with that of *Melianthus*. The resemblance was supplemented by the occurrence of copious endosperm and small differentiated straight embryos, remnants of nucellus and thin unspecialized tegmen. Corner also stated that exotestal seed coats of *Bersama-Melianthus* are more advanced than archaic exo-mesotestal spermoderm of *Lardizabalaceae* (Miers, 1858, 1861; Réaumur, 1906; Melikian and Komar, 1988). These somewhat thickened walls in several subexotestal cells of mesotesta within both *Bersama* and *Melianthus* are clearly



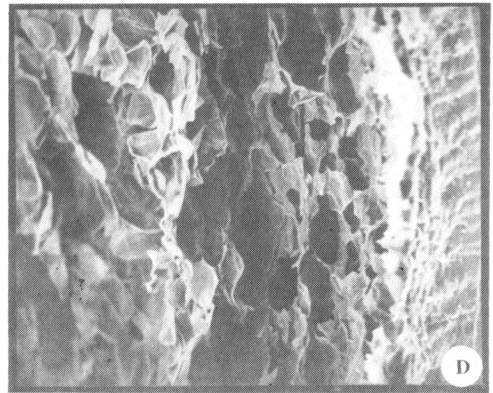
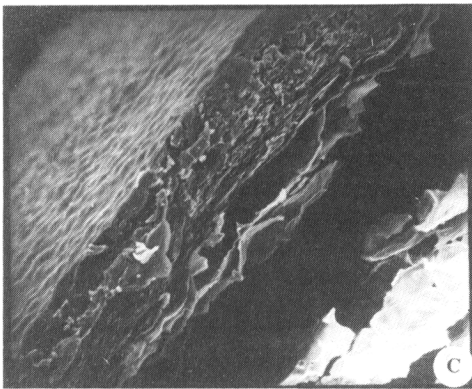
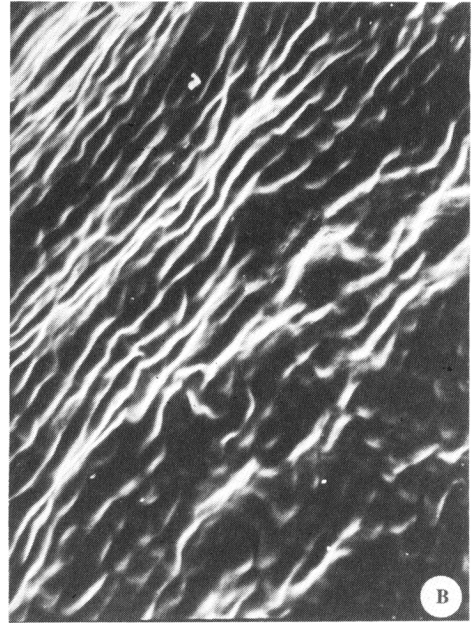
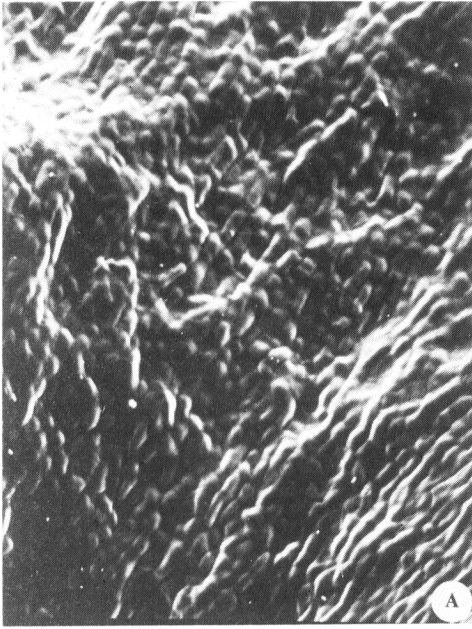


Figure 6. SEMgraphs of seeds of *Melianthus major* L. A. Surface of the seed, x 300. B. The same, enlarged, x 1000. C. Cross-section of the exotesta and several adjoining subexotestal layers of testa (others are obliterated), x 300. D. Parenchyma of testa, x 380.

vestiges of ancestral exo-mesotestal construction of seed coats. The very high and narrow exotestal (Malpighian) cells of *Decaisnea* with 6-8 mesotestal layers of thick-walled macrosclereids (Melikian and Komar, 1988) may serve a prototype of the ancestral structure of spermoderm for *Melianthus*. The same is true for *Bersama*: the seed coats of *Akebia* have a similar single-layered exotesta represented by rectangular, large macrosclereids with thickened outer periclinal and anticlinal walls, and 10-14 layers of thick-walled, unligified cells of mesotesta. However, the fruit morphology and anatomy of *Bersama-Melianthus* and *Lardizabalaceae* compel one to doubt on the suggested (Corner, 1976) close relationships of these three taxa. The pericarp structure of the berrieta of *Lardizabalaceae* (Qin, 1989) has nothing in common with capsules of *Bersama-Melianthus*: in the pericarp there is no evidence of either mesocarpic fibro-vascular osteosclereids (*Bersama*), or multiseriate endocarp composed of lignified macrosclereids (Doweld, 1998). The lack of crystals of calcium oxalate in the seed coats of *Lardizabalaceae* does not also support a close affinity between these taxa. All this emphasizes an exclusively superficial likeness of the structure of spermoderm in *Bersama-Melianthus* and *Lardizabalaceae*, not indicative of close phylogenetic relationships.

### Relationships with *Sapindales*

The putative relationships of *Bersama* and *Melianthus* with *Sapindales* have been questioned by Corner (1976) and again recently by Doweld (1996 *a, b*, 1998) upon the basis of seed anatomy; and this affinity has been also questioned by molecular analysis of *Sapindales* (Gadek *et al.*, 1996 : 807), suggesting the exclusion of *Bersama* and *Melianthus* from the order.

*Bersama* and *Melianthus* possess an

exotestal type of seed coats that is not like to that of other representatives of the order *Sapindales* (*sensu* Takhtajan, 1997). As in case of *Lardizabalaceae*, on the basis of the somewhat thickened cell walls in the subexotestal layers of spermoderm in extant taxa we may suggest the ancestral, exo-mesotestal construction of seed coats for *Bersamataceae/Melianthaceae*. Thus, the sole sapindalean candidate for the affinity with *Bersama-Melianthus* would be exo-mesotestal *Akaniaceae* Stapf, *Bretschneideraceae* Engl. et Gilg, *Staphyleaceae* Lindl., *Sapindaceae* Juss., and *Hippocastanaceae* DC.

*Tapisciaceae* Takht. (Corner, 1976; Doweld, 1996 *c*) having an advanced exotegmic spermoderm are quite anomalous within the whole order and therefore do not show any relationships with other testal *Sapindales*. Their placement in the *Sapindales* (Takhtajan, 1997) is quite erroneous, and it seems that they should be placed into *Euphorbiales*, near *Phyllanthaceae* Agardh (Doweld, 1996 *b*), which are also characterized by distinctive exotegmic seed coats and specialized bullate chalaza.

*Aceraceae* (Magen, 1912; Shabes and Morozova, 1996) are characterized by exalbuminous seeds with a large curved embryo and very advanced and simplified seed coats lacking any sclereidal elements. Their seed coats have fewer layers (testa: 3-6; tegmen: 3-4), partially obliterated in nut-like (correctly, assare-like) samaroid fruits; the exotesta (in contrast to Malpighian cells of *Bersama-Melianthus*) is composed of large cuboid thin-walled cells, the mesotesta consists of small, thin-walled crushed cells; there are usually many crystals of calcium oxalate in the endotesta (*Dipteronia sinensis*, *Acer pseudoplatanus*). Such an advanced construction of the seed coats are far morphogenetically from exotestal *Bersamataceae* and *Melianthaceae*.

However, other sapindalean exo-

mesotestal representatives also reveal very remote relationships with exotestal *Bersamataceae* and *Melianthaceae*. The somewhat similar exo-mesotestal *Akaniaceae* (Doweld, 1996 *d, e*) and *Bretschneideraceae* (Doweld, 1996 *f, g*) are strongly distinct in the structure of seed vascular skeleton from the endosperm-rich seeds of *Bersama* and *Melianthus*. In contrast to melianthaceous seeds possessing a distinctive dimerous raphal vascular skeleton, *Akaniaceae* and *Bretschneideraceae* have a greatly differentiated postchalazal vascular system consisting of 6-8 massive bundles. This fundamental difference is also supplemented by the development of hypostase in *Bretschneidera* Hemsl. and by the occurrence of a rather scanty endosperm (except for *Akania* F. v. Muell.).

The resemblance of the exotestal seed coats of *Bersama-Melianthus* with exo-mesotestal ones of *Staphyleaceae* (*Staphylea* L., *Turpinia* Vent. p.p.) is also artificial because they possess a very complicated seed vascular skeleton with both differentiated postchalazal vascular bundles and several bundles directly vascularizing the outer integument (not forming a chalazal plexus) (Doweld, 1996 *h*). This type of vascular system has been regarded as a regressive derivative of specialized pachytestal seed construction (Doweld, 1996 *b*). Thus, in spite of some likeness in the histological differentiation of spermoderm, *Staphyleaceae* are not closely related to *Meliantales*.

Rejecting a pachytestal ancestry for more primitive *Bersama-Melianthus* (no rudiments of pachychalaza as in staphyleaceous seeds have been found), it would be unwise to relate the mostly pachytestal exo-mesotestal *Sapindaceae* (Guérin, 1901; Corner, 1976; Doweld, 1996 *i*) and *Hippocastanaceae* (Doweld, 1996 *k*). In addition, they are characterized by practically exalbuminous seeds with massive curved embryos in contrast to the melianthaceous exotestal seeds with

abundant endosperm and small straight embryos. Thus, the available evidence from seed coat anatomy suggests that it is more appropriate to segregate *Bersama* and *Melianthus* from the *Sapindales*.

### Relationships with *Rhamnales*/*Elaeagnales*

The order *Rhamnales* is usually treated as consisting of a single family *Rhamnaceae* Juss. (Takhtajan, 1997), or as consisting of three different families: *Rhamnaceae*, *Vitaceae* Juss., and *Leeaceae* Dum. (Cronquist, 1992). It is noteworthy that such irreconcilable opponents as Hallier (1897, 1912) and Wettstein (1935), adhered to quite different systematic doctrines in the classification of flowering plants, equally considered *Vitaceae* s.l. (incl. *Leeaceae*) and *Rhamnaceae* in the single order *Rhamnales*. The last redaction looks very artificial from the stand point of seed anatomy. It is quite impossible to accept that *Rhamnaceae* having exotestal, scanty albuminous seeds may be closely allied to highly specialized families *Vitaceae* and *Leeaceae*, which are characterized by sarcotestal, endotestal seeds, with specific tracheidal tegmen (trachotegmen) in *Vitaceae*, and developed perichalazy in some *Vitaceae* (*Cissus* L., *Cyphostemma* (Planch.) Alston, etc.) and *Leeaceae*, both with abundant endosperm (even ruminant in *Vitaceae*) (Berlese, 1892; Nair and Nambisan, 1957; Nair and Parasuraman, 1962; Periasamy, 1962, 1990; Nair and Bajaj, 1966; Nair, 1968; Corner, 1976). The morphogenetic hiatus between the seeds of buckthorn family and the grape and the *Leea* families is so great that it may be bridged by several radical and therefore highly improbable steps in the morphogenetic reorganization of the integument mechanical structure. In this connection it seems to be more natural to segregate the latter two families, *Leeaceae* and *Vitaceae*, into a distinct order *Vitales* (Takhtajan, 1997), directly related

with endotestal *Proteales*. Thus, the order *Rhamnales* consisting of a single family is more logical to treat as monotypic, revealing only a certain relationship with the neighboring monotypic order *Elaeagnales* (*Elaeagnaceae* Juss.), which is also characterized by the similar advanced exotestal albuminous seeds with undifferentiated, crushed tegmen and differentiated straight embryos (Servettaz, 1909; Corner, 1976).

Cronquist (1992) and Takhtajan (1997) followed Bessey (1915) in trying to see the origin of *Rhamnales* and *Elaeagnales* directly in the highly specialized exotegmic *Celastrales* (Magen 1912; Netolitzky, 1926; Corner, 1976), but it appears highly improbable from the stand point of seed anatomy. Alternatively, Dahlgren (1983, 1989) and Thorne (1976, 1992) tried to connect *Rhamnales* (incl. *Elaeagnales*) directly with again exotegmic *Malvales*: «*The relationships of the Rhamnales, especially the Rhamnaceae, to the Malvales can hardly be questioned if one takes into account the shared obdiplostemonous stamens, anomocytic stomata, mucilage receptacles, phloem fibers, cluster crystals, similar vessel elements, lepidote vesture, other anatomical features, and the unusual peptide alkaloids*» (Thorne, 1976: 79). However, the whole stated 'complex of characters' is weighed down by a sole important feature of seed structure: the malvalean seeds are strongly exotegmic (Rolfs, 1892; Corner, 1976; Plisko, 1992), having a solitary mechanical layer of high Malpighian cells (150-220  $\mu\text{m}$ ) in exotegmen; the seeds are practically exalbuminous, with large, mostly curved embryos, raphal or mainly postchalazal (6-8 branches) seed vascular skeleton. These differences in seed construction preclude any possibilities to relate *Rhamnales*/*Elaeagnales* with *Malvales*.

Nemejc (1956) tried to root *Elaeagnaceae* (treated as a distinct order *Elaeagnales*) in *Dilleniales*, but specialized endotestal-exotegmic (trachotegmic) seed coat

construction of *Dilleniaceae* (Sastri, 1958; Corner, 1976; Vyshenskaya and Oganezova, 1991) may not be an ancestral for *Elaeagnaceae* or *Rhamnaceae*, and thus this suggestion should be ruled out. The phylogenetic roots of the *Rhamnales*/*Elaeagnales* remain rather indefinite, so far as we showed above, the most various current views are chiefly untenable.

Among all known exotestal and exomesotestal representatives of *Rosidae* (*Rosales*, *Fabales*, *Sapindales*, *Rhamnales*, *Elaeagnales*, etc.), the *Rhamnales* and closely allied *Elaeagnales* only possess a distinctive combination of the sclereidal exotestal (with Malpighian cells) seed coats (plus crystals of calcium oxalate), obliterated tegmen, abundant endosperm, straight differentiated embryo, and specific two-branched raphal seed vascular skeleton (Ward and Dunlop, 1888; Servettaz, 1909; Vikhireva, 1951; Corner, 1976). These fundamental features are similar to that of melianthaceous seeds. The typical seed of the buckthorn family is a straight, somewhat flattened, with a large, well differentiated embryo and massive spade-like cotyledons (up to  $1/3$  of the whole seed volume), but with small thick hypocotyl, abundant endosperm; the spermoderm is composed of the derivatives of both integuments: exotestal (typical Malpighian cells) or exotestal-endotegmic, with numerous crystals of calcium oxalate, and remnants of nucellus; seed vascular skeleton is represented by two bundles in raphe (Kajale, 1944; Vikhireva, 1951). The exceptions are: *Reynosia* Griseb. with small embryo and therefore more abundant endosperm, and with thin-walled (!) exotesta; the exalbuminous seeds of *Ventilago* Gaertn.; *Karwinskia* Zucc. with thick-walled, but unligified exotestal cells; *Rhamnus* L., *Frangula* Mill., *Sageretia* Brongn., *Scutia* Comm. ex Brongn., etc., having an exotesta composed of short, rectangular macrosclereids. These insignificant deviations from the typical rhamnaceous seed construction are indicative

of the advance of some *Rhamnaceae*.

It is noteworthy that the resemblance is also revealed in the structure and differentiation of inner integument: the rudiments of the exotestal-endotegmic seed construction within *Melianthus* (endotegmic layer in the micropylar part of seed: Khushalani, 1963) suggests a close affinity with the exotestal-endotegmic *Rhamnaceae* (*Hovenia dulcis* Thunb., *Rhamnus cathartica* L., *Zizyphus jujuba* Mill.: Vikhireva, 1951). The studies of Juel (1929) and Vikhireva (1951) did not confirm the occurrence of perisperm, erroneously ascribed by Lindau (1891) as well as a solitary integument (Brandza, 1891); they simplified a compound unmanageable terminology used by Miers (1860) and corrected rather schematical drawings and descriptions of Godfrin (1880). It permitted the re-evaluation of the significance of seed anatomy for systematics and phylogeny of the *Rhamnaceae*.

Miers (1860), Pammel (1899) and Vikhireva (1951) also discovered a distinctive *linea lucida* (Targioni-Tozzetti, 1855; Junowicz, 1877; Mattiolo, 1886; Mattiolo and Buscalioni, 1890) in the exotestal palisade of Malpighian cells within rhamnaceous seeds. The lack of *linea lucida* in the seed coats of *Bersama* and *Melianthus* may not be considered as a feature questioned a close affinity between *Rhamnaceae* and *Bersama-Melianthus*, so far as in some rhamnaceous seeds there are also no vestiges of *linea lucida* (*Reynosia*, *Cendalia*, *Scutia*, etc.) (Pammel, 1899). The Malpighian cells in exotesta (alike those of *Bersama-Melianthus*) have been also recorded in *Zizyphus* Mill., *Paliurus* Mill., *Hovenia* Thunb., *Ceanothus* L., *Pomaderris* Labill., *Colletia* Comm., *Colubrina* L. C. Rich., *Phylica* L., *Trymalium* Fenzl, *Discaria* Hook., *Helinus* E. Meyer, *Gouania* Jacq., *Reissekia* Endl., and *Alphitonia* Reissek.

The seed coat structure of the closely allied *Elaeagnaceae* (*Elaeagnales*) also shows a great resemblance with spermoderm of

*Bersama-Melianthus*: they have a similar exotestal palisade of Malpighian cells with *linea lucida*, 14-40 layers of thin-walled mesendotestal parenchyma with crystals of calcium oxalate, unspecialized, obliterated tegmen, simple chalaza, seed vascular skeleton consisting of two-branched raphal vascular system, scanty endosperm, and straight, large embryo (Servettaz, 1909; Corner, 1976). The resemblance in main features of seed construction are undoubtedly indicative of a close relationship with *Bersama-Melianthus*.

The characters of seed anatomy, suggesting a close affinity between *Bersama-Melianthus* and *Rhamnales/Elaeagnales*, are supplemented by the likeness in habit (woody or shrubby), in having stipulate foliage, anomocytic stomata (*Rhamnaceae* also possesses paracytic or rarely anomocytic types), 3-locular nodes, vessels with simple perforation, pentamerous floral construction (4-5 sepals, 4-5 petals, 4-5 antisepalous stamens) excepting for occurrence of hypanthium in advanced *Rhamnaceae*, secretory tapetum, simultaneous microsporogenesis, anatropous bitegmic, crassinucellate ovules, *Polygonum*-type of female gametophyte (*Allium*-type is also recorded for *Rhamnaceae*), nuclear *ab initio* endosperm, occurrence of calcium oxalate crystals. The rhamnaceous flowers have an extrastaminal nectary disc (Prichard, 1955; Nair and Sarma, 1961) in contrast to intrastaminal one of *Bersama-Melianthus*, which may have arisen independently as a modification of a fifth perianth lobe receiving a vascular supply from the combined sepal and petal traces, and thus this feature may not have a high systematic value (Khushalani, 1963).

The gynoecium of *Rhamnaceae* appears more specialized than subfollicular (*Melianthus*) or lobed (*Bersama*) 4-5-carpellary ovary: the carpel number may be reduced to 2-3 only, it may be even pseudomonorous (*Microrhamnus* A.Gray, *Rhamnidium* Reissek,

*Maesopsis* Engl.: Süssenguth, 1953). The coalescence of the ovary by hypanthium may be incomplete (semi-inferior *Ceanothus*, *Colletia*, *Colubrina*, *Discaria*, *Ventilago*, *Alphitonia*, *Paliurus*, *Zizyphus*, *Hovenia*, *Pomaderris*, *Trymalium*, etc.) or complete (inferior *Helinus*, *Phylica*, *Gouania*, and *Reissekia*). In spite of the resemblance between *Rhamnaceae* and *Bersamataceae* in basal-axial ovule placentation and low ovule number per locule (1-2: *Rhamnaceae*, 1: *Bersama*), the buckthorn family appears more advanced than *Bersamataceae*. It is also supported by its fruit anatomy and morphology: in *Rhamnaceae*, in addition to above mentioned capsules we may notice the occurrence of typical drupaceous fruits with mesendocarpic pyrens (*Paliurus*, *Zizyphus*, etc.), which are dehiscent (lobi-ventrally in contrast to dorsal or dorsilateral of *Melianthus* and *Bersama* respectively), or even splitting (schizocarpic) (*Pomaderris*, *Trymalium*, *Gouania*, etc.) and columellar schizocarpic (cremocarp-like *Gouania* and *Reissekia*) (Vikhireva, 1952). Nevertheless, it should be noted that in spite of high specialisation there are no postdurian mesocarpic fibro-vascular osteosclereids in the pericarp of rhamnaceous capsules or drupes (Ward and Dunlop, 1888; Vikhireva, 1952). The differences in the fruit structure of *Rhamnaceae* and *Bersamataceae*/*Melianthaceae* are not fundamental, but they emphasize only a certain morphogenetic distance between advanced *Rhamnaceae* and more archaic *Bersama-Melianthus*, that does not upset the integrity of the suggested evolutionary line.

The family *Elaeagnaceae* is somewhat more distanced from the proposed alliance of *Rhamnaceae* and *Bersamataceae*/*Melianthaceae* in having exstipulate leaves, unilocular nodes, mostly tetramerous flowers with reduced petals and funnel-like calyx, varying stamen number from 4 (*Elaeagnus* L., *Hippophaë* L.) to even 12 (*Shepherdia* Nutt.),

monocarpellary gynoecium transformed into monomerous nucetum (nuceole) inferred into fleshy funnel-like calyx ('spurious drupe' after Takhtajan, 1997). Nevertheless, the seed structure is typically rhamnaceous (Corner, 1976), and this important feature weighs down all mentioned differences.

In summary, on the basis of phermatological data now available, *Bersama-Melianthus*, *Rhamnaceae* and *Elaeagnaceae* represent highly specialized fragmentary remnants of the once massive, much branched phylum tracing back directly to *Fabales* having also exo-mesotestal spermoderm with Malpighian cells and *linea lucida*, but never to exotegmic *Celastrales* or *Malvales*, as has been suggested by Dahlgren (1983, 1989) and Thorne (1992). The segregation of the families *Bersamataceae* and *Melianthaceae* into a distinct order *Meliantales* (Doweld, 1998) is fully justified from the stand point of phermatology. By seed structure *Meliantales* are affiliated with an exotestal or/and exo-mesotestal bitegmic line of seed evolution in *Rosidae*, the main representatives of which are *Fabales*, *Rosales p.p.*, *Connarales*, *Sapindales p.p.*, *Rutales*, *Icacinales p.p.*, *Rhamnales*, and *Elaeagnales*. The appearance of the distinctive fibrous exotegmen in *Connarales*, pachytestal seed construction in *Rosales*, *Sapindales*, and *Icacinales*, highly multiplicative sclerified mesotesta and tracheidal exo-endotegmen (or mostly rudimentary endotegmic) in *Rutales* points to a some distance between these exo(meso)testal orders of *Rosidae* and alliance of *Meliantales*, *Rhamnales*, and *Elaeagnales*. They represent a distinct evolutionary line in exotestal *Rosidae*, having a common ancestry with *Fabales*.

ACKNOWLEDGEMENTS. I am indebted to Dr Dmitry Geltman, Curator of the Herbarium, The V. L. Komarov Botanical Institute of the Russian Academy of Sciences, St.-Petersburg (LE), for providing fruits and seeds of *Bersama* and

*Melianthus*. I wish to thank Ms Natalie Shevryyova for excellent morphological drawings used in paper. Special thanks go to Mrs Francesca B. Yakovleva for invaluable SEM assistance. I acknowledge with a gratitude the kind assistance of the Staff of the Library of the Moscow Society of Naturalists providing necessary botanical literature.

### LITERATURE CITED

- BAILLON, H.É. -1874- Monographie des Térébinthacées et des Sapindacées. In: Baillon H.É. *Histoire des plantes*. Vol. 5. Paris, 257-428.
- BAILLON, H.É. -1897- Note sur l'organisation florale du *Greyia sutherlandi*. *Bull. Soc. Linn. Paris* 2(1891): 950-951.
- BAKER, E.G. -1907- A revision of *Bersama*. *J. Bot. (London)* 45: 12-21.
- BENTHAM, G. & J.D. HOOKER -1862/1867- *Genera plantarum ad exemplaria imprimis in Herbarii Kewensibus servata definita*. Vol. 1. *Sistens dicotyledonum polypetalorum ordines LXXXIII: Ranunculaceas-Cornaceas*. Londini.
- BERLESE, A.N. -1892- Studi sulla forma, struttura e sviluppo del seme nelle Ampelidee. *Malpighia* 6: 293-324, 482-536.
- BESSEY, C.E. -1915- The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109-164.
- BRANDZA, M. -1891- Développement des téguments de la graine. *Rev. Gén. Bot.* 3: 229-240.
- BREHMER, W. von. -1919- Neue Arten der Gattung *Bersama*. *Bot. Jahrb. Syst.* 54 (1917): 393-415.
- CORNER, E.J.H. -1976- *The Seeds of Dicotyledons*. Vols 1, 2. Cambridge.
- CRONQUIST, A. -1992- *An integrated system of classification of flowering plants*. 2nd ed. New York.
- DAHLGREN, G. -1989- An updated angiosperm classification. *Bot. J. Linn. Soc.* 100: 197-203.
- DAHLGREN, R. -1983- General aspects of angiosperm evolution and macrosystematics. *Nord. J. Bot.* 3: 119-149.
- DOWELD, A.B. -1996a- Melianthaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 348-351. [In Russian].
- DOWELD, A.B. -1996b- Conclusions on the order Sapindales. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 360. [In Russian].
- DOWELD, A.B. -1996c- Tapisciaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 315-317. [In Russian].
- DOWELD, A.B. -1996d- The systematic relevance of fruit and seed anatomy and morphology of *Akania* (Akaniaceae). *Bot. J. Linn. Soc.* 120: 379-389.
- DOWELD, A.B. -1996e- Akaniaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 352-354. [In Russian].
- DOWELD, A.B. -1996f- The carpology and taxonomic relationships of *Bretschneidera* (Bretschneideraceae). *Acta Bot. Malacitana* 21: 79-90.
- DOWELD, A.B. -1996g- Bretschneideraceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 346-348. [In Russian].
- DOWELD, A.B. -1996h- Staphyleaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 312-315. [In Russian].
- DOWELD, A.B. -1996i- Sapindaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 317-338. [In Russian].
- DOWELD, A.B. -1996k- Hippocastanaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 343-346. [In Russian].
- DOWELD, A.B. -1997- Phermatology, a new name for the science of seeds. *Taxon* 46: 539-540.
- DOWELD, A.B. -1998- The systematic relevance of phermatology and carpology of *Bersama* and *Melianthus* (Melianthaceae). *Ann. Bot. (London)* 83: 321-333.
- ENDLICHER, S. -1836/1840- *Genera plantarum secundum ordines naturales disposita*. Vindobonae.
- ENDRESS, P.K. & S. STUMPF -1991- The diversity of stamen structure in 'Lower' Rosidae (Rosales, Fabales, Proteales, Sapindales). *Bot. J. Linn. Soc.* 107: 217-293.
- FRESENIUS, G. -1837- Über die Gattung *Bersama*. *Mus. Senckenberg.* 2: 279-282.
- GADEK, P.A. E.S. FERNANDO, C.J. QUINN, S.B. HOOT, T. TERRAZAS, M.C. SHEAHAN & M.W. CHASE -1996- Sapindales: molecular delimitation and infraordinal groups. *Amer. J. Bot.* 83: 802-811.

- GODFRIN, J. -1880- Étude histologique sur les téguments séminaux des Angiospermes. *Bull. Soc. Sci. Nancy, Sér. 2, Ann. 13, 5*: 109-219.
- GUÉRIN, P. -1901- Développement de la graine et en particulier du tégument séminale de quelques Sapindacées. *J. Bot. (Morot) 15*: 336-362.
- GÜRKE, M. -1896- Melianthaceae. In: Engler A, Prantl K, eds. *Die natürlichen Pflanzenfamilien*. Abt. 3, Teil 5. Leipzig, 374-383.
- HALLIER, H. -1897- Betrachtungen über die Verwandtschaftsbeziehungen der Ampelideen und anderer Pflanzenfamilien. *Natuurk. Tijdschr. Nederl.-Indië, N.S. (5)56*: 300-331.
- HALLIER, H. -1912- L'origine et le système phylétique des Angiospermes exposés à l'aide de leur arbre généalogique. *Arch. Néerl. Sci. Exact. Nat., Sér. 3B (Sci. Nat.) 1*: 146-234.
- HARVEY, W.H. -1859- Three new species of South African plants. *Proc. Dublin Univ. Zool. Bot. Assoc. 1(1857-1859)*: 135-141.
- HOCHSTETTER, C.F. -1841- Nova genera plantarum Africae tum australis tum tropicæ borealis proponit et describit Ch. F. Hochstetter. *Flora 24 Jahrg. 2(42)*: 657-672.
- HOOKER, J.D. -1873- On Melianthus trimenianus H. f. and the affinities of Greyia sutherlandii. *J. Bot. (Trimen), N.S. 2*: 353-358.
- HUTCHINSON, J. -1926- *The families of flowering plants. I. Dicotyledons. Arranged according to a new system based on their probable phylogeny*. London.
- HUTCHINSON, J. -1973- *The families of flowering plants arranged according to a new system based on their probable phylogeny*. 3<sup>rd</sup> ed. Oxford.
- JUEL, H.O. -1929- Beiträge zur Morphologie und Entwicklungsgeschichte der Rhamnaceen. *Kungl. Svenska Vetenskapsakad. Handl., Ser. 3, 7(3)*: 1-13.
- JUNOWICZ, R. -1877- Die Lichtlinie in den Prismenzellen der Samenschalen. *Sber. Math.-naturwiss. Cl. K. Akad. Wiss. Wien, Abth. I, 76*: 335-352.
- JUSSIEU, A. de. -1825- *Mémoires sur les Rutacées; ou, Considérations sur ce groupe de plantes, suivies de l'exposition des genres qui le composent*. Paris.
- JUSSIEU, A.L. de. -1789- *Genera plantarum secundum ordines naturales disposita, juxta methodum in Horto regio parisiensi exaratum, anno M.DCC.LXXIV*. Paris.
- KAJALE, L.B. -1944- A contribution to the life-history of Zizyphus jujuba Lamk. *Proc. Nat. Inst. Sci. India 10*: 387-391.
- KHUSHALANI, I. -1963- Floral morphology and embryology of Melianthus major Linnaeus. *Phyton 10*: 145-156.
- LINDAU, G. -1891- Zur Entwicklungsgeschichte einiger Samen. *Ber. Dtsch. Bot. Ges. 9*: 274-279.
- LINDLEY, J. -1846- *The Vegetable Kingdom; or, The structure, classification and uses of plants, illustrated upon the natural system*. 2nd ed. London.
- LINK, H.F. -1831- *Handbuch der Erkennung der nutzbarsten und am häufigsten vorkommenden Gewächse*. Bd. 2. Berlin.
- MAGEN, K. -1912- *Beiträge zur vergleichenden Anatomie der Samenschalen einiger Familien aus der Engler'schen Reihe der Sapindales*. Inaug.-Diss. Univ. Zürich. Borna-Leipzig.
- MATTIROLLO, O. -1886- La linea lucida nelle cellule malpighiane degli integumenti seminali. *Mem. R. Accad. Sci. Torino, Ser. 2, 37*: 219-246.
- MATTIROLLO, O. & L. BUSCALIONI -1890- Sulla funzione della linea lucida nelle cellule malpighiane. *Atti R. Accad. Sci. Torino 25*: 310-315.
- MELIKIAN, A.P. & G.A. KOMAR -1988- Lardizabalaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 2. Leningrad, 163-165. [In Russian].
- MIERS, J. -1858- On a new species of Lardizabala, and on the structure of the seed in that genus. *Ann. Mag. Nat. Hist., Ser. 3, 2*: 183-192.
- MIERS, J. -1860- On the tribe Colletia, with some observations on the structure of the seed of the family of the Rhamnaceae. *Ann. Mag. Nat. Hist., Ser. 3, 5*: 76-95, 200-216, 267-273, 370-381, 482-492; 6: 5-14.
- MIERS, J. -1861- On a new species of Lardizabala, and on the structure of the seed in that genus. In: Miers J. *Contributions to botany, iconographic and descriptive, detailing the characters of plants that are either new or imperfectly described; to which are added remarks on their affinities*. Vol. 1. London & Edinburgh, 145-155.
- NAIR, N.C. -1968- Contribution to the floral morphology and embryology of two species of



- Leea with a discussion on the taxonomic position of the genus. *J. Ind. Bot. Soc.* 47: 193-205.
- NAIR, N.C. & Y.P.S. BAJAJ -1966- Floral morphology and embryology of *Cyphostemma setosum* (Wall.) Alston and a discussion on the taxonomic position of the genus *Cyphostemma* (Planch.) Alston. *J. Ind. Bot. Soc.* 45: 103-115.
- NAIR, N.C. & P.N.N. NAMBIAN -1957- Contribution to the floral morphology and embryology of *Leea sambucina* Wild. *Bot. Not. (Lund)* 110: 160-172.
- NAIR, N.C. & V. PARASURAMAN -1962- Contribution to the embryology of *Vitis pallida* W. et A. *phyton* 18: 157-164.
- NAIR, N.C. & V.S. SARMA -1961- Organography and floral anatomy of some members of the Rhamnaceae. *J. Ind. Bot. Soc.* 40: 47-55.
- NEMEJC, B. -1956- Studie k otázce o puvodu a fylogenetickém vyvoji krytosemenných rostlin. *Sborn. Národn. Musea Praze, Přírodov.*, 12B: 59-144. [In Engl.].
- NEMIROVICZ-DANCZENKO, E.N. -1994- Structure of the seeds of species of the genera *Frankoa* and *Tetilla*. *Bot. Zh. (St.-Petersburg)* 79(7): 28-34. [In Russian].
- NEMIROVICZ-DANCZENKO, E.N. -1995- Structure of the seeds of *Greyia sutherlandii* (Greyiaceae). *Bot. Zh. (St.-Petersburg)* 80(1): 99-104. [In Russian].
- NEMIROVICZ-DANCZENKO, E.N. -1996a- Greyiaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 79-82. [In Russian].
- NEMIROVICZ-DANCZENKO, E.N. -1996b- Frankoaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 82-88. [In Russian].
- NETOLITZKY, F. -1926- *Anatomie der Angiospermen-Samen*. In: Linsbauer K, ed. *Handbuch der Pflanzenanatomie*. II Abteilung, 2 Teil, *Pteridophyten und Anthophyten*. Bd. 10. Berlin, 1-364.
- O'BRIEN, T.P. & McCULLY, M.E. -1981- *The Study of Plant Structure: Principles and Selected Methods*. Melbourne.
- PAMMEL, L.H. -1899- Anatomical characters of the seeds of Leguminosae, chiefly genera of Gray's Manual. *Trans. Acad. Sci. St. Louis* 9: 91-263.
- PERIASAMY, K. -1962- Studies on the seeds with ruminant endosperm. II. Development of rumination in the Vitaceae. *Proc. Ind. Acad. Sciences, Sect. B, Biol. Sci.* 56: 13-26.
- PERIASAMY, K. -1990- The ruminant seed. *Ind. Rev. Life Sci.* 10: 141-168.
- PLANCHON, J.E. -1851- On Meliantheae, a new natural order, proposed and defined by J.E. Planchon. *Trans. Linn. Soc. London* 20: 403-418.
- PLISKO, M.A. -1992- Malvaceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 4. St.-Petersburg, 325-363. [In Russian].
- PRICHARD, E.C. -1955- Morphological studies in Rhamnaceae. *J. Elisha Mitchell Sci. Soc.* 71: 82-106.
- QIN, H-N. -1989- An investigation on carpels of Lardizabalaceae in relation to taxonomy and phylogeny. *Cathaya* 1: 61-82.
- RADLKOFER, L. von. -1891- Über die Gliederung der Familie der Sapindaceen. *Sber. Math.-physik. Cl. K. Bayer. Akad. Wiss. München* 20(1890): 105-379.
- RÉAUBOURG, G. -1906- *Étude organographique et anatomique de la famille des Lardizabalées*. Thèse Univ. de Paris. Mantes-sur-Seine.
- REICHENBACH, H. -1828- *Conspectus regni vegetabilis per gradus naturales evoluti*. Pt. 1. Lipsiae.
- RICHARD, A. -1847/1851- *Tentamen flora abyssinica; seu Enumeratio plantarum hucusque in plerisque Abyssiniae provinciis detectarum et praecipue a beatis doctoribus Richardo Quartin Dillon et Antonio Petit annis 1838-1843 lectorum*. Vol. 1. Paris.
- ROLFS, P. H. -1892- The seed coats of Malvaceae. *Bot. Gaz. (Crawfordsville)*, 17: 33-39.
- SERVETTAZ, C. -1909- Monographie des Éléagnacées. Partie 2. Anatomie et biologie. *Beih. Bot. Centralbl., Abt. 2*, 25: 129-421.
- SHABES, L.K. & A.A. MOROZOVA -1996- Aceraceae. In: Takhtajan AL, ed. *Anatomia Seminum Comparativa*. Vol. 5. St.-Petersburg, 339-343. [In Russian].
- SPJUT, R.W. -1994- A systematic treatment of fruit types. *Mem. N. Y. Bot. Gard.* 70: 1-182.
- STEYN, E.M.A. -1975- Embriogenie van *Melianthus major* L. *J. S. Afr. Bot.* 41: 199-205.
- STEYN, E.M.A., ROBBERTSE, P. J. & SCHIJFT, H. P. VANDER -1986- An embryogenetic study of *Bersama transvaalensis* and *Greyia*

- sutherlandii. *S.-Afr. Tydskr. Plantk.* 52: 25-29.
- SÜSSENGUTH, K. -1953- Rhamnaceae. In: Engler A, Prantl K, eds. *Die natürlichen Pflanzenfamilien*. 2 Aufl. Bd. 20d. Berlin, 7-173.
- TAKHTAJAN, A.L. -1997- *Diversity and classification of flowering plants*. New York.
- TARGIONI-TOZZETTI, A. -1855- Saggioni di studi intorno al guscio dei semi. *Mem. R. Accad. Sci. Torino, Ser. 2*, 15: 359-445.
- THORNE, R.F. -1976- A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9: 35-106.
- THORNE, R.F. -1992- Classification and geography of the flowering plants. *Bot. Rev. (Lancaster)* 58: 225-348.
- TOURNEFORT, J.P. de. -1694- *Éléments de botanique ou Méthode pour conoître les plantes*. T. 1, 3. Paris.
- UMADEVI, I., M. DANIEL & S.D. SABNIS -1986- Interrelationships among the families Aceraceae, Hippocastanaceae, Melianthaceae, and Staphyleaceae. *J. Plant Anat. Morph.* 3: 169-172.
- VIKHIREVA, V.V. -1951- Development of the seed within the buckthorn family. *Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 7, Morf. Anat. Rast.* 2: 221-227. [In Russian].
- VIKHIREVA, V.V. -1952- Morphologico-anatomical study of the fruits in the buckthorn family. *Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 7, Morf. Anat. Rast.* 3: 241-292. [In Russian].
- VYSHENSKAYA, T.D. & G.G. OGANEZOVA - 1991- Dilleniaceae. In: TAKHTAJAN AL, ed. *Anatomia Seminum Comparativa*. Vol. 3. Leningrad, 163-171. [In Russian].
- WARD, H.M. & J. DUNLOP -1888- On some points in the histology and physiology of the fruits and seeds of Rhamnus. *Ann. Bot.* 1(1887): 1-26.
- WETTSTEIN, R. R. von. -1935- *Handbuch der systematischen Botanik*. 4 Aufl. Leipzig-Wien.
- WYK, A.E. van. -1988- Melianthaceae. In: DAHLGREN R, WYK AE van. Structures and relationships of families endemic to or centered in southern Africa. *Monogr. Syst. Bot. Missouri Bot. Gard.* 25: 48-52.

Acceptado para su publicación en Junio de 1998

Author's address. National Institute of Carpology (Gaertnerian Institution), PO Box 72, RUS-119517, Moscow, Russian Federation; Fax +7(095)9258607. email: mts6@mts6.mmtel.msk.su