Wulfenia **13** (2006): 207–215

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

Some morphological basics for a revision of the tribe Celastreae Loes. (Celastraceae R. Br.)

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Summary: The large family Celastraceae is taxonomically difficult. Published revisions are incongruent and especially the relationships of the taxa within the tribe Celastreae are quite unclear. Morphological and anatomical analyses emphasizing on fruits and seeds revealed a set of characters, which can be used – in combination with molecular studies – for a highly desired new monographical treatment of Celastraceae.

Keywords: Celastraceae, Celastreae, morphological analysis, fruit and seed morphology, anatomy

The family Celastraceae comprises about 60(–90) genera and more than 1000 species (Hou 1962, 1964; Simmons 2004). Candolle (1825), and later on Bentham & Hooker (1862) published the first taxonomical treatment of the family. Although the system of Celastraceae has passed through several revisions based on molecular and cladistic data (Simmons & Hedin 1999; Simmons at al. 2001a,b; APG 2003; Simmons 2004) during the last years, the last comprehensive revision was made by Loesener in 1942. It was adopted by modern taxonomists (i.e. Takhtajan 1997) indeed, but no extensive taxonomical treatment of Celastraceae was published up to now (Simmons 2004).

The tribe Celastreae is very interesting, because it is a difficult taxonomical group (Simmons 2004). It comprises about 25 genera and 300 species and is widely distributed in temperate, subtropical and tropical zones of the world, especially in South-East Asia, Australia, Africa and Central America. Several anatomical and morphological characters show significant differences and allow groupings within the tribe. In our studies, we focused primarily on fruit anatomy and fruit morphology to get a basis for further investigations.

Materials and methods

Our investigations include 39 genera (represented by 108 species) with a special focus on *Apatophyllum*, *Bhesa*, *Catha*, *Celastrus*, *Denhamia*, *Gymnosporia*, *Lydenburgia*, *Maytenus*, *Paxistima*, *Polycardia*, *Psammomoya*, *Pterocelastrus*, and *Putterlickia*. We analyzed herbarium samples of the following herbaria: MW, MHA, MOSP, LE, KW and W. Especially for inflorescence and flower studies, we used living plants obtained from several Botanical Gardens of Russia, Ukraine, Greece, the Czech Republic, Austria, and Italy. All samples were fixed in alcohol. Morphological and anatomical studies, and the investigation of seed surfaces were made by means of light microscopy and scanning electron microscopy (SEM). Results were tested according to Vavilov's law of homologous series (Vavilov 1922).

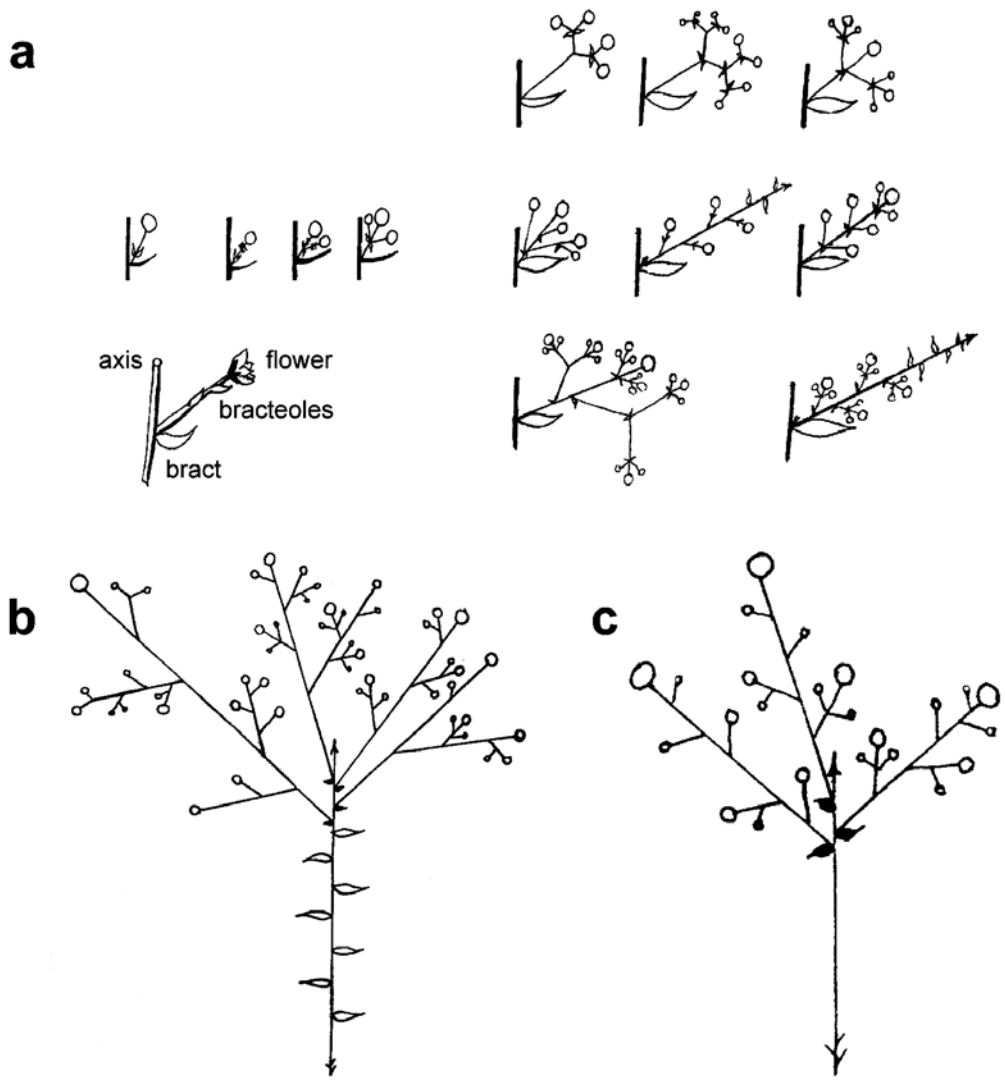

Figure 1: Structure of inflorescences in representatives of the Celastreae tribe: a: axillar floral position in different genera; b–c: pseudoterminal inflorescences in *Bhesa paniculata* Wall. (b) and *B. ceylanica* Arn. (c).

Results

Life-forms: Shrubs, small or big trees, and lianas are represented in Celastraceae. According to Loesener's (1942) classification, members of the subfamily Cassinoideae, consisting of the tribes Cassineae and Perrottetieae, are shrubs and trees; Hippocrateoideae are lianas, rarely erect shrubs and trees; and Tripterygioideae are trees, erect and scandent shrubs. In Celastroideae, representatives of the tribe Lophopetaleae are big trees in tropical rain forests, the tribes Celastreae and Euonymeae consist of big trees, shrubs, and scandent shrubs. The South African genus *Empleuridium* is an ericoid subshrub.

Inflorescences and flowers: Inflorescences are terminal and/or axillary. Thyrsoids as well as simple and umbellate dichasia occur. Structural units of the inflorescences are solitary flowers or simple dichasia. Serial complexes in inflorescences, and in vegetative shoots, too, (spines,

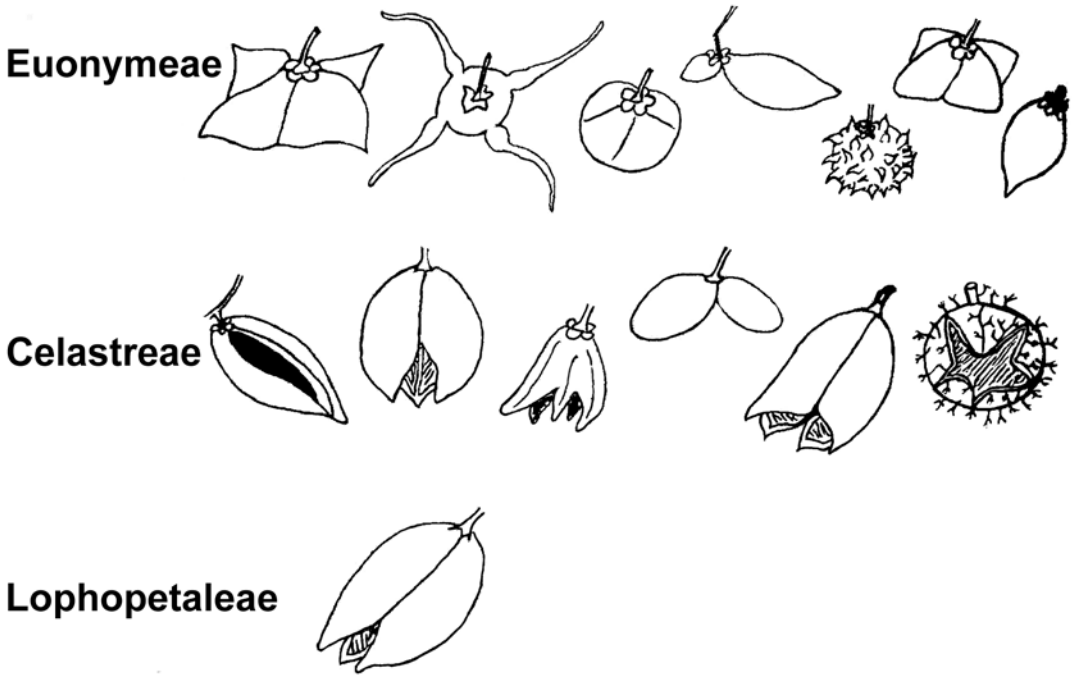

Figure 2: Morphological diversity of fruits in the tribes Euonymeae, Celastreae and Lophopetaleae.

brachyblasts, few floral shoots) are developed very often. Flowers are actinomorphic or rarely zygomorphic; usually 5- or 3-merous. The nectariferous disk is intrastaminal or extrastaminal, sometimes lobed or lacerated. It is flat, concave or glass-like. At the flower pedicel usually two bracteoles occur. Further details are listed in comparative floral studies of Berkeley (1953), and Matthews & Endress (2005).

General types of fruits and seeds: Five general fruit-types occur in Celastraceae: follicular divided (septifragal) capsules in the subfamily Hippocrateoideae and the tribe Lophopetaleae; loculicidal oligo- and many-seeded capsules in the tribes Celastreae and Euonymeae; samaras or nut-like one-seeded fruits in the subfamily Tripterygioideae; pyrenes (coenocarpous more-seeded drupes) in the subfamilies Hippocrateoideae and Siphonodontoideae, and in the tribe Cassineae; and berries in the tribe Perrottetieae.

Three general types of seeds can be found in Celastraceae: seeds with an aril or an arilloid in the tribes Celastreae and Euonymeae; winged seeds in the subfamily Hippocrateoideae, and in the tribes Celastreae and Lophopetaleae; and naked (bare) seeds. In the subfamily Hippocrateoideae, and in the tribes Euonymeae and Perrottetieae bare seeds possess a distinct sarcotesta, whereas in the subfamilies Tripterygioideae and Siphonodontoideae, and in the tribe Cassineae a sarcotesta is absent.

In the course of our studies on the disseminules of Celastraceae, we found out that those seed structures in *Sarawakodendron* and *Polycardia* (in particular, the presence of a filamentous aril like in *Empleuridium* too) have not been found in other families of flowering plants until now. The fruit of *Sarawakodendron* is a loculicidal capsule, opening with three locules and containing about 8 seeds in two series. It resembles capsules of the tribe Lophopetaleae. The sclerification of the

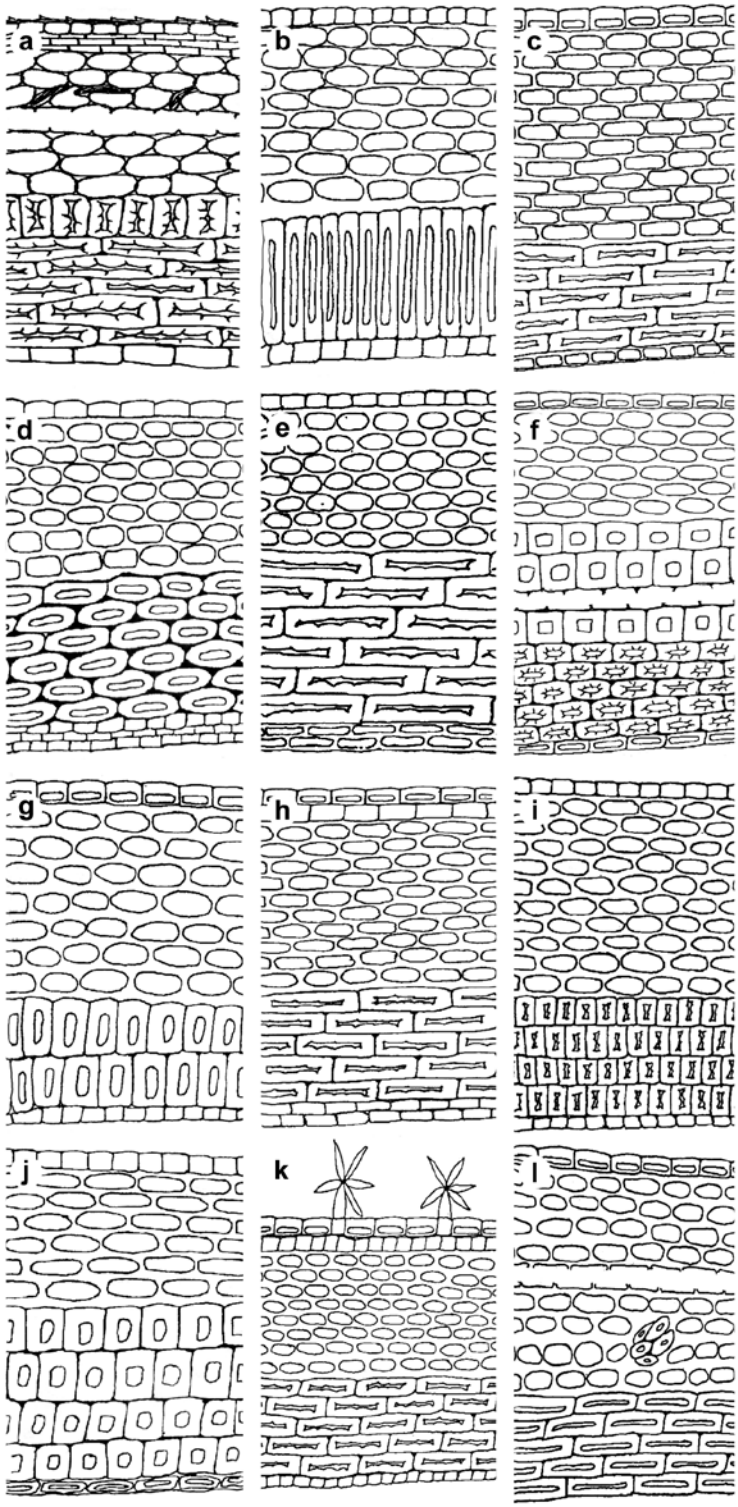

Figure 3: Anatomical structure of pericarp in representatives of the tribe Celastreae. a: *Putterlickia myracantha* Endl.; b: *Bhesa paniculata* Wall.; c: *Catha edulis* Forsk.; d: *Celastrus monosperma* Roxb.; e: *C. scandens* L.; f: *Denhamia obscura* (A.Rich) Meissn.; g: *Gymnosporia* sp.; h: *Lydenburgia cassinoides* N. Robson; i: *Paxistima myrsinites* (Pursh) Raf.; j: *Maytenus boaria* Molina; k: *Polycardia echinata* Forst.; l: *Pterocelastrus rostrata* Walp.

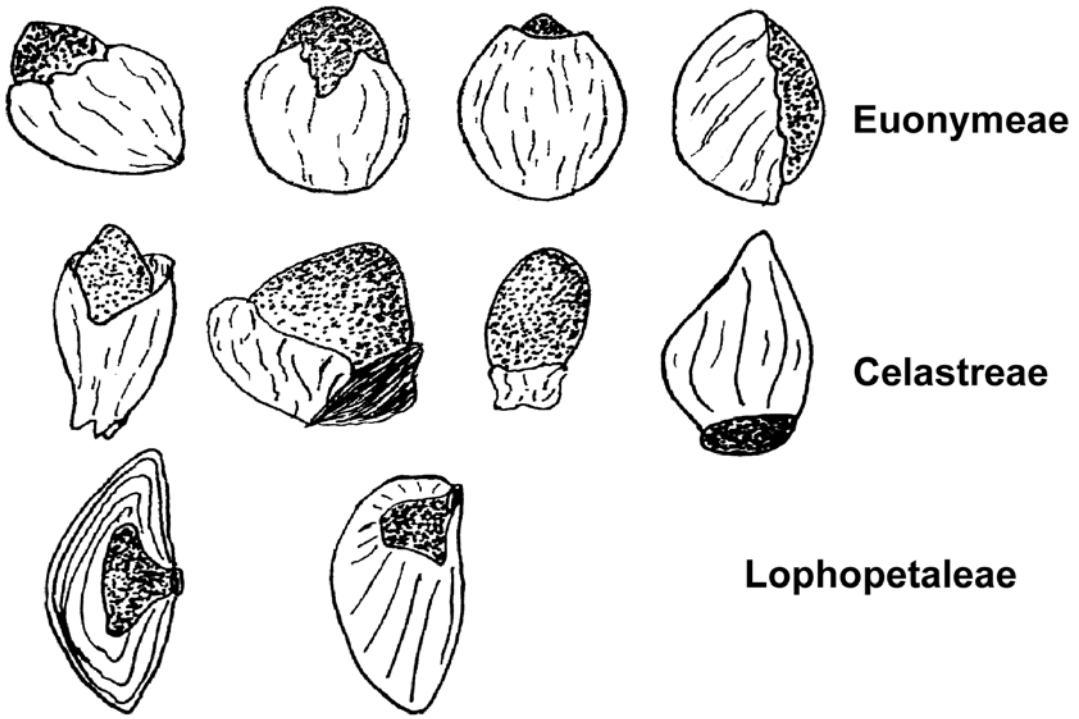

Figure 4: Morphological diversity of seeds in the tribes Euonymeae, Celastreae and Lophopetaleae.

pericarp of *Sarawakodendron* fruits is also very similar to other species of Lophopetaleae. From this point of view, *Sarawakodendron,* as well as *Brassiantha* and *Dicarpellum* are isolated genera within Celastraceae.

Floral, fruit and seed characters in the tribe Celastreae: Inflorescences are axillary or sometimes terminal. Thyrsoids, dichasia or rarely solitary flowers are developed. Flowers are actinomorphic, 4–5-merous, with an intrastaminal nectariferous disk. Pedicels usually have a pair of bracteoles at their base or at their middle part (fig. 1).

Fruit types in the tribe Celastreae are various (fig. 2). The majority of the genera possess one-, oligo- and many-seeded capsules. *Celastrus* has a berry-like fruit. Pericarp structure is diverse (fig. 3): usually it consists of a well differentiated many-layered to one-layered exocarp, a many-layered parenchymal mesocarp (sometimes with sclereid-groups) and a sclerotized many-layered endocarp. Macrosclereids extend tangential or radial.

Seeds have a well developed aril, an arilloid (the majority of the genera) or a wing (*Catha* and *Lydenburgia*) (fig. 4). The spermoderm is few- to many-layered (fig. 5).

The two Australian genera, *Apatophyllum* and *Psammomoya*, have an ephedroid habit and one-flowered (or few-flowered in *P. choretroides*), axillary inflorescences. Flowers are pedunculate (*Apatophyllum*) or sessile (*Psammomoya*), with a pair of bracteoles at the base of the pedicel. Capsules are loculicide and 1(2)-seeded.

Gymnosporia (non *Maytenus* s.str.; see Archer & Jordaan 2000; Jordaan & Wyk 2003) and *Putterlickia* have brachyblast-bearing, spiny branches. *Putterlickia* is very closely related to the

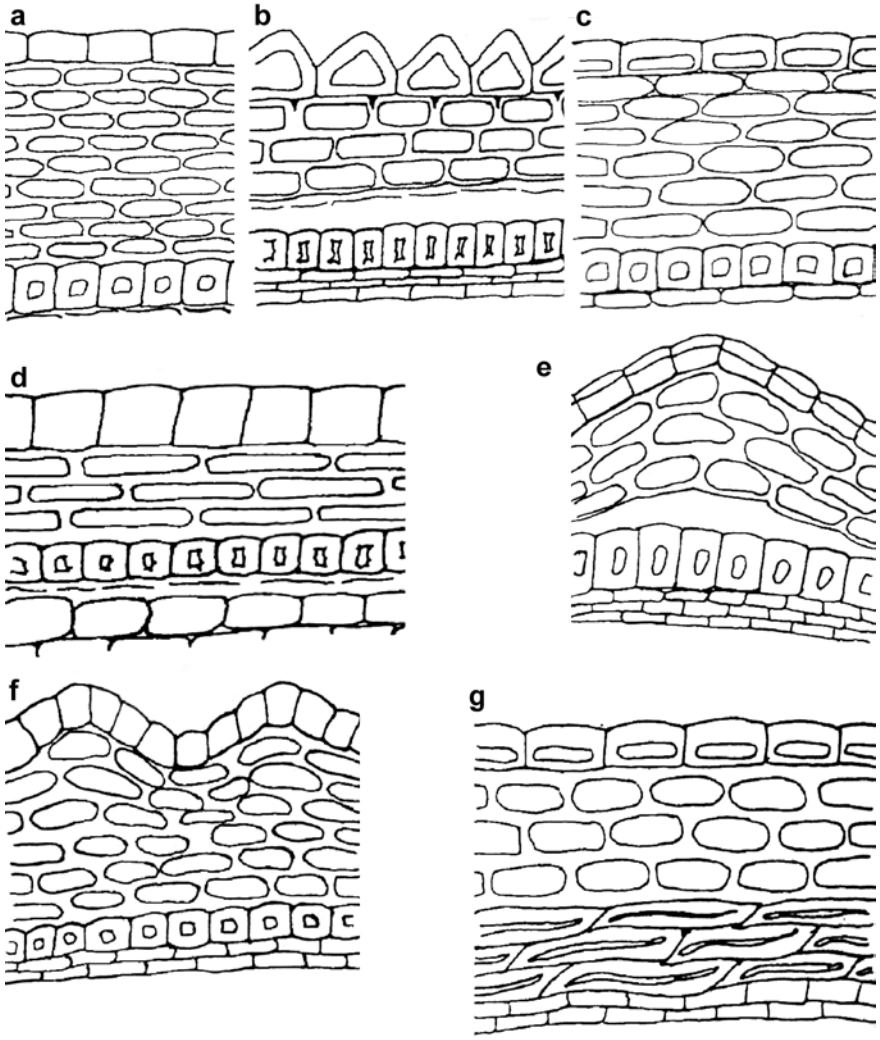

Figure 5: Anatomical structure of spermoderm in representatives of the Celastreae tribe. a: *Bhesa paniculata* Wall.; b: *Catha edulis* Forsk.; c: *Celastrus monosperma* Roxb.; d: *C. scandens* L.; e: *Lydenburgia cassinoides* N. Robson; f: *Maytenus boaria* Molina; g: *Polycardia echinata* Forst.

Australian genus *Denhamia*. Both taxa have a similar fruit structure (topography of the histological zones in the pericarp), and seeds with an unusual protuberant aril (fig. 6).

Similarities in inflorescence, fruit and seed structures allow the interpretation that *Bhesa*, *Celastrus*, *Catha*, *Lydenburgia* and *Pterocelastrus* are closely related and form a distinct group. In our studies, *Paxistima* appears to be very isolated in the tribe Celastreae.

Discussion

Our results confirm the taxonomical importance of inflorescence-, fruit- and seed-structures, which correlate in most cases very well with types of life-forms, texture of the stomatal complex, structure of flowers, and pollen grains (Berkeley 1953; Lobreau 1969; Corner 1976; Hartog & Baas 1978; Melikian & Savinov 2000; Savinov 2004, 2005).

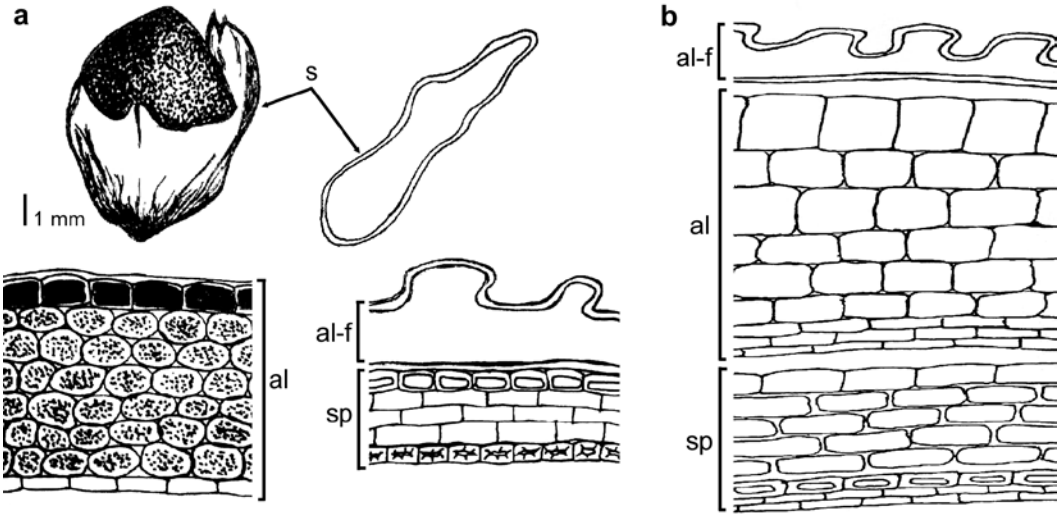

Figure 6: Seed and aril structures in *Putterlickia myracantha* Endl.(a) and *Denhamia obscura* (A.Rich.) Meissn. (b): al – aril, al-f – aril sculpture form, s – seed, sp – spermoderm.

Preliminary, we can conclude: the family Celastraceae R.Br. has to be treated in a wide sense, including Hippocrateaceae A. Juss.; the tribe Lophopetaleae Loes. forms a clade with Hippocrateaceae; the subfamily Tripterygioideae Loes. is monophyletic and monothetic, characterized by one-seeded nut-like fruits; and *Sarawakodendron, Brassiantha* and *Dicarpellum* are closely related, but isolated within Celastraceae. They represent the subfamily Sarawakodendroideae I. Savinov et Melikian. Sarawakodendroideae are very closely related to Hippocrateoideae and the tribe Lophopetaleae.

The studied genera form within the tribe Celastreae several circles of relationship: 1) *Bhesa*, *Celastrus*, *Catha*, *Lydenburgia*, *Pterocelastrus*; 2) *Denhamia*, *Putterlickia*; 3) *Gymnosporia*, *Maytenus*; 4) *Polycardia*; 5) *Psammomoya*, *Apatophyllum*; and 6) *Paxistima*. Although *Paxistima* forms an isolated group within Celastreae in our studies, structure of fruits and seeds of *Paxistima* demonstrate a relationship closer to Celastreae than to Euonymeae. This is supported by an identical chromosome number 2n=32, as in tribe Euonymeae (Darlington & Wylie 1955). According to morphological analyses, the Australian genera *Apatophyllum* and *Psammomoya* are closely related, but isolated taxa within the tribe Celastreae (McGillivray 1971).

Further studies should combine morphological, anatomical, and molecular data to answer the question of paraphyly within Celastroideae (Simmons 2004) and give rise to a comprehensive, monographical treatment of the family. Ultrasculptural characters of fruits and seeds (SEM) should be considered in taxonomical revisions.

Acknowledgements

The author is very grateful to Alexey K. Skvortsov (Main Botanical Garden RAS, Moscow, Russia), Alexander P. Melikian (Moscow State University, Moscow, Russia), Mark P. Simmons (Colorado State University, Fort Collins, USA), Peter K. Endress (Institute of Systematic Botany, University of Zurich, Zurich, Switzerland) and to Marie Jordaan (National Botanical Institute, Pretoria, Republic of South Africa) for extensive discussions.

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