



The family Myodocarpaceae: looking at the system from the standpoint of comparative carpology

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With 24 figures and 3 tables

Abstract

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The fruit structure of five *Myodocarpus* species and four *Delarbreia* species (Myodocarpaceae, Apiales) was studied. It was found that the species studied share several fruit structure traits, such as: dimerous gynoeceum, presence of peculiar secretory cavities (“oil vesicles”) and a free column separating from mericarp tissues. However, many distinctions in fruit structure of *Myodocarpus* and *Delarbreia* were also revealed: pericarp consistence (dry versus fleshy), dispersal type (anemochory versus zoochory) and details of column separation mode, presence or absence of sclereids, groups of “hydrocyte parenchyma” cells and tannins in the pericarp as well as secretory canals location pattern. *Myodocarpus* and *Delarbreia* also show some differences in the seed coat structure. Data from comparative carpology confirm that Myodocarpaceae comprises modern remnants of an ancient branch of Apiales evolutionary tree. *Myodocarpus* and *Delarbreia*, closely related to Araliaceae and Apiaceae, share some features of both families, although they are obviously distinct. Within Myodocarpaceae, *Myodocarpus* and *Delarbreia* represent different phylogenetic lineages and their fruit structure provides evidence for that. Moreover, carpological data strongly support the presence of two groups within *Myodocarpus*.

Keywords: *Delarbreia*, *Myodocarpus*, anatomy and morphology, fruit structure, dispersal pattern, phylogenetic lineages.

Introduction

Myodocarpus Brongn. & Gris and *Delarbreia* Vieill. are closely related genera distributed mainly in New Caledonia. All ten (Lowry 1993) or eight (Frodin & Govaerts 2003) *Myodocarpus* species and four out of six known species of *Delarbreia* (Lowry 1986, Van Balgooy & Lowry 1993), as well as the monotypic genus *Pseudosciadium* Baill., recently included into *Delarbreia* as *D. balansae* (Baill.) Lowry & Plunkett (Lowry et al. 2004b) are endemic to this island with unique flora. Outside of New

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Caledonia, only *D. paradoxa* Vieill. ssp. *paradoxa* (through Vanuatu and Solomon Islands to Moluccas and Lesser Sunda islands) and *D. michieana* (F. Muell.) F. Muell. (Queensland, Australia) can be found. The latter species was earlier regarded as a separate monotypic genus *Porospermum* F. Muell., which, unlike other representatives of the studied group, does not occur in New Caledonia (Lowry 1986). The species of *Myodocarpus* and *Delarbrea* are monocaulous or slightly branched trees, up to 12 m (*Delarbrea*) or 20 m (*Myodocarpus*) high (Lowry 1993). *Delarbrea* has large pinnate compound leaves, clustered at the top of braches while *Myodocarpus* species can possess either pinnate compound leaves (*M. pinnatus* Brongn. & Gris, *M. fraxinifolius* Brongn. & Gris), or simple ones. In some species of *Delarbrea* and *Myodocarpus* (Lowry 1986) juvenile foliage differs slightly from that of mature plants. A number of features are usually pointed out as shared by both *Myodocarpus* and *Delarbrea*, such as apotracheal axial parenchyma in secondary xylem (Oskolski 1994, Oskolski et al. 1997), similar inflorescence structure, broadened petiole bases, articulate flower stalks, five stamens and a gynoeceum of two carpels, as well as “large secretory oil ducts” in the fleshy part of the fruit (Lowry 1986) or “distinctive oil vesicles in the endocarp” (Lowry et al. 2004b). The latter are considered to be a unique trait for araliads and have not been found in any other member of this group (Lowry et al. 2004b). Traditionally, *Myodocarpus* and *Delarbrea* were either placed in the tribe Araliaceae (Bentham 1867, Harms 1894–1897, Hutchinson 1967, Tseng & Hoo 1982) or treated as a separate tribe “Myodocarpaceae” (Viguié 1906) = Myodocarpeae (Takhtajan 1987, Plunkett & Lowry 2001, Lowry et al. 2001). Today, the two genera *Delarbrea* and *Myodocarpus* constitute the family Myodocarpaceae (see Lowry et al. 2004a, Plunkett et al. 2004).

However, it cannot seem a coincidence that the position of *Myodocarpus* within Apiales as well as its relation to *Delarbrea* has been a matter of discussions throughout the entire 20th century. When originally describing *Myodocarpus*, A. Brongniart and A. Gris placed it in Apiaceae. Later on, however, the position of *Myodocarpus* within Araliaceae had been “secured” (Bentham 1867, Viguié 1906), but the scholars kept finding traits of typological resemblance with Apiaceae in its fruit structure (Baumann 1946). To a certain extent, it gave motivation for another discussion concerning the necessity of reconsidering the entire order’s system. Not coincidentally, R. Thorne, who proposed a revolutionary system including four subfamilies — Aralioidae, Apioideae, Hydrocotyloideae and Saniculoideae — in Araliaceae, mentioned *Myodocarpus* among the plants that had made a crucial change in his concepts: “It is much harder to ignore intermediate when one has studied and collected them where they are indigenous” (Thorne 1973: p. 162)”. Latest molecular research suggested polyphyletic origin of Apiaceae subfamily Hydrocotyloideae (sensu Drude 1897) and the paraphyly of Araliaceae (Plunkett et al. 1996, 1997, Plunkett & Downie 1999), therefore supporting Thorne’s standpoint regarding the absence of a big phylogenetic gap between Araliaceae and Apiaceae. Thanks to these and other works botanists today have a different understanding of the evolution in Apiales. The majority of them are ready to acknowledge several evolutionary lines within the order, which gave rise to many more contemporary taxa of familial rank than two (Araliaceae and Apiaceae) traditionally recognized (Chandler & Plunkett 2004). Thus, presently the researchers acknowledge the existence of 7 families, 4 of those (Apiaceae, Araliaceae, Myodocarpaceae и Pittospor-

Table 1. Names, voucher and source for the taxa analyzed with notes of the material condition.

Taxon	Condition	Voucher and source
<i>Myodocarpus fraxinifolius</i> Brongn. & Gris	dry	Lowry no. 3820, LE; Bonati no. 930, L
<i>M. involucratus</i> Dubard & R.Vig.	dry	LE
<i>M. pinnatus</i> Brongn. & Gris	dry	McKee no. 3734, K; LE
<i>M. simplicifolius</i> Brongn. & Gris	dry	LE
	fixed	Lowry no. 4746
<i>M. viellardii</i> Brongn. & Gris	dry	LE
<i>Delarabrea harmsii</i> R.Vig.	dry	New Caledonia, McPherson no. 6279, K
	fixed	New Caledonia, Lowry no. 4732
<i>D. michieana</i> (F. Muell) F. Muell	fixed	Australia, Plunkett no. 1502
<i>D. montana</i> R.Vig. ssp. <i>montana</i>	dry	<i>D. montana</i> ssp. <i>montana</i> , New Caledonia, McPherson no. 4782, K
<i>D. montana</i> R.Vig.	fixed	New Caledonia, Lowry 4759
<i>D. paradoxa</i> Vieill. ssp. <i>paradoxa</i>	dry	Novae Ebudae (New Hebrides), Bernardi no. 12945, K
	dry	New Britain, Lae no. 58532, L
	fixed	New Caledonia, Lowry no. 4791

raceae) belong to the suborder Apiineae (Plunkett et al. 2004). Some so-called “intermediate” taxa are presently recognized not as “bridges” or “links”, but as direct descendants of ancient developmental lineages (Plunkett & Lowry 2001).

Although *Myodocarpus* and *Delarabrea* are definitely very closely related, they also differ in some characters, e.g., calyprate (rather than free) petals and distinctly joined stylodia (Lowry et al. 2001, p. 211) in *Myodocarpus* and non-calyptrate petals and non-joined stylodia in *Delarabrea*. Other traits of difference include; the stipe at the base of the fruits in several species of *Delarabrea* (Lowry et al. 2004a, p. 253), which does not occur in *Myodocarpus*, some wood characters (Oskolski et al. 1997) and some conspicuous fruit traits, such as fleshy pericarp consistence versus dry. Certain distinctions in leaf types of *Myodocarpus* (pinnate compound in *M. pinnatus* and *M. fraxinifolius* and simple in other species) and wood structure [shape of intervessel and vessel-ray pits — only oval and rounded in *M. pinnatus* and *M. fraxinifolius* and scalariform as well as oval and rounded” in *M. simplicifolius* Brongn. & Gris (Oskolski et al. 1997)] led to the conclusion that there are two groups within this genus. This point of view was later strongly supported by molecular data (Lowry et al. 2004b).

We are convinced that, given all above listed facts, a detailed carpological study, specifically focused on *Myodocarpus*, *Delarabrea* as well as *Mackinlaya* F. Muell., *Apiopetalum* Baill., *Astrotricha* DC. and other genera of uncertain position within the system of Apiales would be extremely timely now. This activity has been already started in regards to the genus *Harmsioplanax* Warb. (Konstantinova 2008). Regretfully, previously published data on fruit structure of *Myodocarpus* and *Delarabrea* (Baumann 1946, Lowry 1986) are insufficient to be used in taxonomy and phylogenetics; moreover, they require some corrections and updating.

Unfortunately, due to lack of up-to-date data on fruit structure, molecular researchers have to use for their phylogenetic conclusions data on fruit morphology taken from the late 19th — early 20th century literature (Baillon 1878, Viguier 1906). Meanwhile, the phylogenetic value of such characters (e.g. fruit shape) often needs to be rethought. Also, a modern approach is necessary when it comes to revealing the origin of and distinguishing various pericarp zones. Thus, prominent secretory “oil vesicles” of *Delarbrea* and *Myodocarpus* do not belong to the endocarp however, in mature fruits they indeed look like as if they are part of it — e.g., Lowry with co-authors believes they are included in the endocarp (Lowry et al. 2001, p. 209–210; Plunkett & Lowry 2001, p. 267; Lowry et al. 2004a, p. 252). That is why thorough carpological studies, based on the analysis of as many taxa as available, are important and necessary to possibly clarify the results obtained from molecular studies. The present research is focused on the fruit structure of Myodocarpaceae and is aimed to obtain additional morphological data to be used for taxonomic and phylogenetic purposes.

Materials and methods

Fruits of five species of *Myodocarpus* and four species of *Delarbrea* were studied. The material for this research was collected and graciously provided by A.A.Oskolski, P.P. Lowry II, and G.M. Plunkett (alcohol-preserved). Mature fruits in dry condition were obtained from the Herbarium of the Royal Botanic Gardens, Kew (K), from the Rijksherbarium, Leiden (L) and also from the Herbarium of the Komarov Botanical Institute, St. Petersburg (LE).

Dry fruits were kept in the mixture of 96% ethanol, glycerol, and distilled water in equal proportions for several days. For studying the fruit anatomy transverse sections (sometimes also longitudinal sections) in the middle part of fruits were prepared and examined by light and scanning electron microscopes (JSM 6380 LA) at different magnifications. When necessary, the fruits at different developmental stages were examined. Traditional anatomical techniques were used to prepare the material for research. Histochemical reactions were conducted to determine the degree of cell walls lignification as well as to locate tannins and oils (Prozina 1969, Furst 1979, O’Brien & McCully 1981, Barykina et al. 2000).

Terminology

The term “carpophore”, widely used in contemporary literature on Apiaceae does not seem completely suitable to us. The term suggests the AXIAL origin of the structure, whereas in Apiales the biggest part (lengthwise) of the “carpophore” is made out of tissues of carpel margins (Jackson 1933). Meanwhile, there are certain taxa (e.g. Capparaceae) the representatives of which bear true carpophores of axial origin, developing from a gynophore or an androgynophore (Tikhomirov, unpublished data; Rankin Rodriguez & Greuter, 2004). We believe that the term “carpophore” should rather be used to describe structures of these plants as they are of true axial origin whereas for Apiales the term “column” (Tikhomirov & Konstantinova 1995, 2000) will be used in the present paper as seemingly more appropriate.

In fruits of Apiaceae, different types of secretory structures are traditionally recognized. Transverse sections of fruits clearly show, that some of them are in direct connection with vascular bundles and tend to be located in the outer pericarp layers (“companion canals”; Tseng 1967) or “rib oil ducts”; Kljuiikov et al. 2004), while the other (usually larger ones) occur in inner pericarp layers between ribs (“vittae”; Tseng 1967, or “vallecular vittae” and “commissural vittae”; Kljuiikov et al. 2004). These types apparently differ in the composition of the substances secreted (Pervukhina 1950, Eyde & Tseng 1971). Also, the former (“oil ducts”) are usually longer than the fruit itself extending into the fruit

stalk whereas the latter (“vittae”) are shorter, equaling to the fruit in length (Roth 1977) or shorter than that. In fruits of the vast majority of Araliaceae scattered secretory canals are found. They do not show noticeable tendency to accompany major vascular bundles — such a correlation can only be observed in a limited number of taxa (Eyde & Tseng 1971, Konstantinova & Yembaturova 2002, 2005).

The above mentioned types of “canals” should be distinguished from the “reservoirs” (“oil cavities” or “oil vesicles”). These are large inflated, pustule-like structures filled with essential oils, found in the inner pericarp layers in the fruits of *Delaribrea* and *Myodocarpus* (Lowry et al. 2001, Plunkett & Lowry 2001, Lowry et al. 2004a). Similar pustule-like structures, however localized in the outer mesocarp layers (closer to the periphery), can be found in some Apiaceae-Saniculoideae and Apiaceae-Apioideae (Baumann 1946, Pervukhina 1950). Obviously, the difference between a “canal” and a “reservoir” is a quantitative factor: “reservoirs” or “vesicles” can be formed through the process of septation, as in *Seseli* L. species (Pervukhina 1950) or by shortening of canals due to delay in their growth when the fruit itself grows faster than the canals, as in *Heracleum* L. (Alexandrov & Klimochkina 1947). We believe, however, that it is incorrect to call an isodiametric structure “a canal”.

“Hydrocyte parenchyma” (Klimochkina 1950) refers to groups of almost isodiametric cells with lignified walls and numerous pores in them, located in the commissural zone of *Myodocarpus* fruits. The term “stereom” (Kozo-Polyanski 1916) is used for groups of sclerenchymal fibers, derived from vascular bundles and surrounding areas of small-celled lignified parenchyma. These terms are used to display significant differences between the two types of supporting tissue (first of all, in the shape of cells and the ratio of these cells’ dimensions).

To make it convenient, when describing fruits of *Delaribrea* species, we also use such terms as “outer”, “middle” and “inner” mesocarp. Regretfully, to date there is no agreement amongst botanists on how pericarp zones should be named correctly in fruits derived from superior and inferior ovary while the difference between them is obvious. Thus, if in superior fruits the mesocarp is derived solely from the ovary tissues, in the ones derived from the inferior ovary, it develops from the tissues of both the ovary and the floral tube (Esau 1977). Since fruits of the vast majority of Apiales (excluding only two species of *Tetraplasandra* A. Gray, Eyde & Tseng 1969, Costello & Motley 2004) are inferior, and the demarcation lines between the tissues of different origin are not always noticeable in mature fruit mesocarp, we find it advisable to follow Shibakina’s (1984) treatment suggesting the use of the terms “exocarp”, “mesocarp” and “endocarp” only in very general topographic sense. In the present paper we adhere to the same “topographic” approach when describing the “pyrene” rather than “endocarp”, since, strictly speaking, “endocarp” refers to the pericarp zone derived from the inner epiderm of a carpel (Sitte et al. 2007). Speaking about a “pyrene”, we refer to the overall sclerenchymal sheath surrounding the seed cavity. This sclerenchyma often differs in appearance and origin during fruit development. Thus, in species of *Delaribrea*, the endocarp proper (in strict sense) composes only the inner part of the pyrene, while the outer part is made of mesocarp elements, so the pyrene is of combined “mesoendocarpic origin”.

When describing *Myodocarpus* and *Delaribrea* fruits, following S.G. Tamamshyan (1951), we speak about so-called “false”(ruminatio spuria), or, to be more exact, “false canaliculated” (r.s. *canaliculata*) endosperm rumination. We distinguish this type of rumination from the true (*ruminatio vera*) or the funiculate one (*ruminatio funiculata*). This type of rumination occurs as a result of a very early initiation of secretory cavities in a very immature ovary and the mechanical pressure they put on the tender tissues of the seed which only starts to develop. Pericarp supporting tissues begin their development much later and therefore do not significantly affect the endosperm shape (Tamamshyan 1951). The false canaliculated rumination is found in many Apiaceae (Tikhomirov & Konstantinova 2000), however in Araliaceae another kind of false rumination mainly occurs — the one caused by the invaginations of inner lignified pericarp (pyrene) layers, which are not associated with canals or reservoirs in their origin (e.g., *Schefflera heptaphylla* (L.) Frodin, *S. pubigera* (Brongn. ex Planch.) Frodin). In the latter, true rumination can also be found (species of *Arthrophyllum* Blume, *S. chinensis* (Dunn) H.L. Li, *S. hypoleucoides* Harms, etc.; Konstantinova & Suchorukow 2010). We have reported a combination of the true and the false rumination in the structure of a single fruit in *Macropanax* (*M. oreophilus* Miq., *M. undulatas* (Wall. ex G. Don) Seem) and *Brassaiopsis variabilis* C.B. Shang (Konstantinova & Groshnikova 2006).

Results

Delarbrea

Fruit morphology

The fleshy fruit of *Delarbrea* consists of two mericarps of the same shape and size, seemingly remaining together at maturity (Fig. 1a, 12).

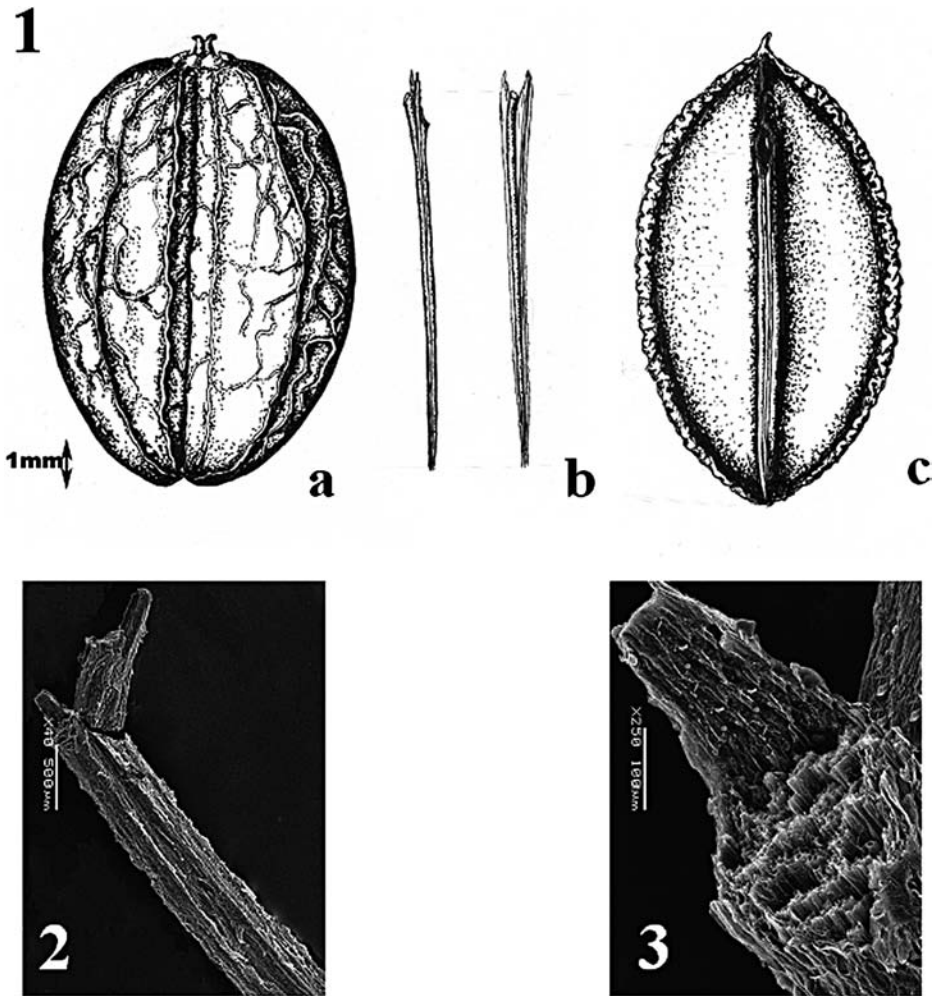


Fig. 1–3. *Delarbrea michieana*. — 1, External fruit morphology: a, entire fruit; b, column separating from mericarp tissues; c, mericarp, commissural view; note the scar remaining from the detached column. — 2, Upper part of the column — 3, Vascular bundles' derivatives in the upper part of the column.

However, there is a free filiform column, potentially able to separate from mericarp tissues and suggesting an ability of the fruit to dissociate into one-seeded diaspores after drying out (Fig. 1b, 2, 3). Mericarps vary in size from 27–31 mm x 4–6 mm (*D. harmsii*) to 11–15 mm x 3–5 mm (*D. montana*). From the dorsal view, the mericarp shape appears to be of a wide oval, with convex dorsal surface and flat commissural one (Fig. 1c). The fruit surface is grooved; the ribs are usually well-defined, shaped as five longitudinal filiform projections. A groove separating two mericarps is often quite conspicuous (*D. michieana*, *D. paradoxa*, *D. harmsii*), but sometimes almost unpronounced (*D. montana*). Unlike *Myodocarpus*, large secretory reservoirs, localized in the pericarp of the seed-bearing part cannot be seen from the outside (Fig 1a). Stylopodia are flattened and quite small (up to 0,5 mm high in *D. michieana*) or, more often, conical in shape and somewhat bigger, up to 2 mm in height (*D. paradoxa*, *D. harmsii*, *D. montana*). The stylopodia are crowned with a wreath of calyx teeth (sepals), fused to a greater (*D. montana*, *D. harmsii*) or lesser (*D. michieana*, *D. paradoxa*) extent; the sepals have wide bases and are narrowed towards the tops. Stylodia are up to 2 mm long, hook-shaped, with decurrent stigmata (Fig. 4).

Fruit anatomy: In transverse section made in the middle of the mericarp the outline of the latter is oval or semi-circular, with a flat commissural side. The exocarp is one-layered, or rarely two-layered (*D. michieana*) (Fig. 5, 6). The tannin content can be present in all exocarp cells (*D. harmsii*), or in few exocarp cells either only as the impregnation of cell walls or the content of cell cavities (*D. montana* and *D. paradoxa*) or, finally, completely absent in larger outer cells of the two-layered exocarp (*D. michieana*).

The mesocarp is rather thick (Fig. 5–9), and distinctively divided into two subzones (inner and outer ones; Fig. 5–7) in *D. michieana*, and into 3 subzones in other species. The outer subzone (“outer mesocarp” — “OM”) comprises sclereids, scarce (*D. michieana*) or numerous (*D. paradoxa*, *D. harmsii*, *D. montana*), alternating with large thin-walled cells of mesocarp parenchyma, which are sometimes tanniferous (*D. paradoxa*, *D. harmsii*). The middle subzone, or “middle mesocarp” — “MM”, is made of large thin-walled cells, often compressed and obliterated. The inner subzone (“inner mesocarp” — “IM”; Fig. 8, 9) is found to possess large secretory reservoirs, surrounded by lignified parenchymatous cells of almost isodiametric shape (*D. michieana*, *D. montana*, *D. paradoxa*) or by markedly elongated ones, as in *D. harmsii*. The “IM” is relatively thin (up to one third of the pericarp thickness) in *D. michieana*, *D. montana*, and *D. paradoxa*, or very thick (more than a half of the pericarp thickness) in *D. harmsii*, Fig. 8). Secretory reservoirs protrude into the seed cavity, causing “false” rumination of the endosperm in all species but in *D. harmsii*. However, between the cells of the reservoirs’ lining and the seedcoat, as a rule, one to three layers of compressed mesocarp parenchyma cells and thin fibrous endocarp are present. In *D. harmsii*, the reservoirs do not form invaginations towards the endosperm, but are completely submerged in the “inner mesocarp” (Fig. 8). Secretory canals, situated in the “OM” and “MM” subzones, do not show any visible connection with vascular bundles (“scattered secretory canals”) (Fig. 11). These bundles can be seen in the “MM” subzone, as well as in the outer parts of the “IM” subzone, almost where the “middle” mesocarp borders with the “inner” one.

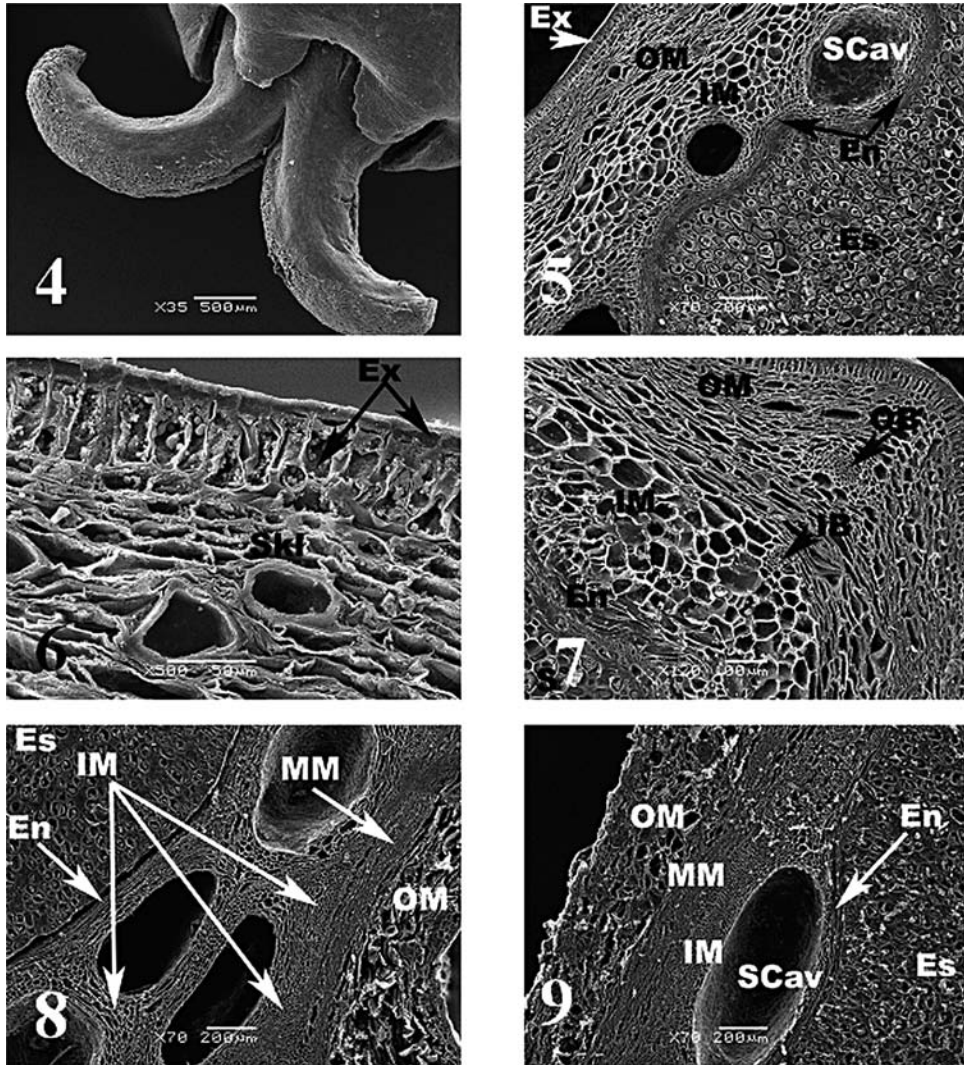


Fig. 4. *Delarbreia montana*. — Stylodia, external morphology. — 5–7, *Delarbreia michieana*. — Transverse section (TS) of the middle part of the mericarp. — Ex = exocarp, OM = “outer mesocarp” layers, IM = “inner mesocarp” layers, En = endocarp, OB = vascular bundles of the outer circle, IB = vascular bundles of the inner circle, SCav = secretory cavities in “inner mesocarp” layers, S = seed, Es = endosperm. — 8, 9, *Delarbreia harmsii*. — TS of the middle part of the mericarp — MM = “middle mesocarp” layers.

In *Delarbreia*, neither a seed, nor a single mericarp, not even the fruit itself serves as a dissemination unit (= diaspore). This function is overtaken by the seed-containing pyrene, i.e. the inner part of the pericarp, consisting of the endocarp (2 to 5 layers of poorly lignified fibers) and the “inner mesocarp” with secretory cavities (Fig. 13–15).

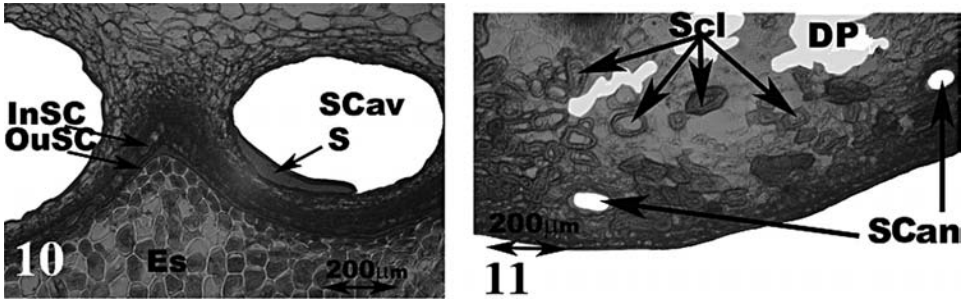


Fig. 10. *Delarbreia michieana*. —TS of the middle part of the mericarp. — OuSC = outer layer of the seed coat, InSC = inner layer of the seed coat. — 11, *D. montana*. — TS of the middle part of the mericarp. — Scl = sclereids in the “outer mesocarp”, SCan = secretory canals in the “outer mesocarp”, DP = destroyed parenchyma of the “middle mesocarp”.

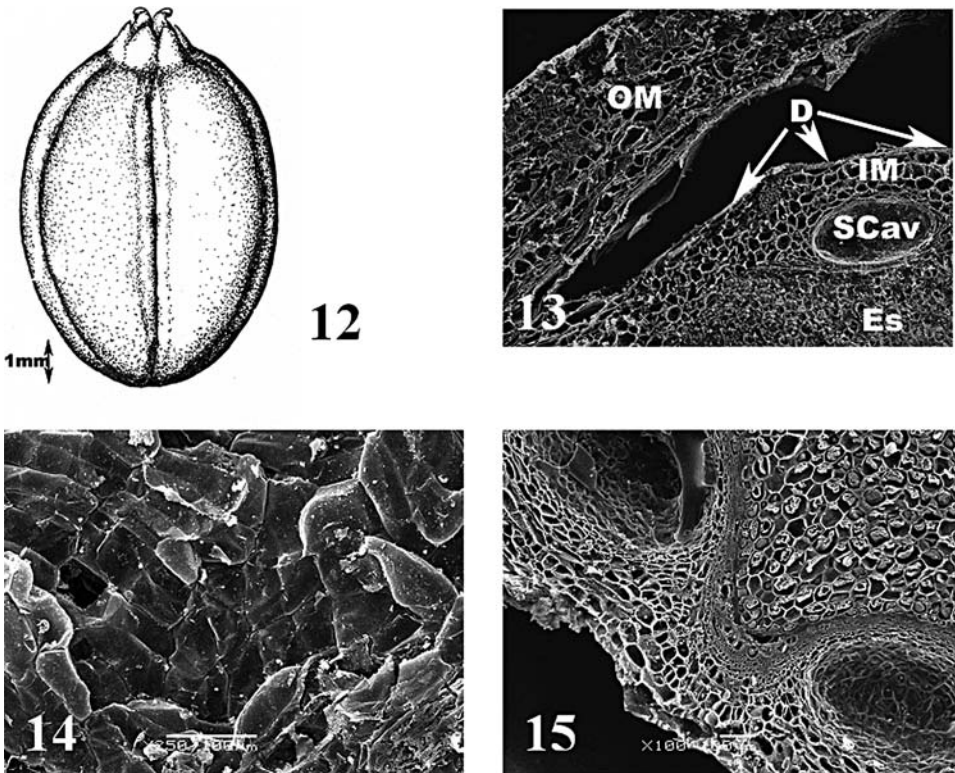


Fig. 12–13. *Delarbreia paradoxa*. — 12, External fruit morphology — entire fruit. 13, Lamination of the “outer mesocarp” and “inner mesocarp” layers and diaspore detachment. D = diaspore. — 14–15. *D. michieana*. — 14, Diaspore surface, note almost isodiametric cells of the “Inner mesocarp”, surface view. —15, TS of the middle of the diaspore.

The transition from the pyrene to thin-walled isodiametric cells of the “outer mesocarp” is, as a rule, gradual, and therefore, the pyrene boundaries (Fig. 5, 8) are indistinct.

The spermoderm is well-developed, thick, two-layered, with the outer layer of large thick-walled cells which are: almost square in transverse section in *D. michieana*; slightly elongated with straight anticlinal walls in *D. harmsii* and *D. montana*, or with extremely tortuous anticlinal walls in *D. paradoxa*. The inner layer is amorphous, with the cells boundaries undistinguished (Fig. 10).

At the transverse section, the column in *D. michieana* and *D. montana* is usually comprised of one or two large stereomes that seem to be made of a few vascular bundles' derivatives (two from each mericarp) and of lignified parenchymal cells. A zone of small, compressed, partly destroyed cells of mesocarp parenchyma surrounds these stereomes. Closer to the stylopodium, in the upper third of the fruit, the stereomes split into the derivatives of separate vascular bundles, a pair of which goes into each mericarp. The bundles can be more or less detached; morphologically, the degree of detachment determines the number of strands going into each mericarp (two or four).

Myodocarpus

Fruit morphology

Dry fruit consists of two mericarps of the same shape and size, easily separating at maturity (Fig. 16). The mericarps separate due to the specific “column” that does not split into two longitudinal parts, as it is typical of Apioideae, but remains solid (Fig. 17). In *M. fraxinifolius*, *M. involucratus* and *M. pinnatus* the mericarps are approximately of the same size (10–13 mm × 4,5–5,5 mm); in *M. viellardii* and *M. simplicifolius* they are a bit smaller (9–11 mm × 3–4 mm and 7–8 mm × 1,3–1,7 mm respectively) and flattened from the side. Due to the presence of the wing, the mericarps are narrow-ovate or rounded-ovate in outline, with slightly outstanding marginal and intermediate ribs. The wing develops on the basis of the mericarp's dorsal rib, just under its seed-bearing part (Fig. 16). Thus, it is not surprising that R. Viguier (1906) described the fruit of *Myodocarpus* as resembling “... *une mouche au repos* ...”. Large pericarp secretory cavities, located in its seed-bearing part, are well seen from the outside, thus giving the fruit surface its peculiar tuberculate outlook (Fig. 16b). Distinct stylopodia (Fig. 18, 19) are conical and large (up to 1 mm high in *M. fraxinifolius*, *M. involucratus* and *M. pinnatus*; up to 0,5 mm in *M. simplicifolius* and *M. viellardii*). Large calyx teeth (sepals) reach 1 mm in *M. pinnatus*, 0,8 mm in *M. fraxinifolius*, *M. involucratus* and *M. simplicifolius* and 0,5 mm in *M. viellardii*; they are wide at the base and smoothly rounded or narrowed at the top, but not acuminate (Fig. 18, 19). Distinctly joined stylochia (curved in the middle part), with decurrent stigmata, are up to 1,5 mm (*M. simplicifolius*, *M. involucratus*) or 2 mm (*M. fraxinifolius*, *M. viellardii*) long; in *M. pinnatus* they can reach 2,5 mm (Fig. 20).

Fruit anatomy

At the transverse section, the mericarps are almost oval or of the shape of an elongated triangle (Fig. 22, 23) One-layered exocarp consists of minute cells, slightly elongated

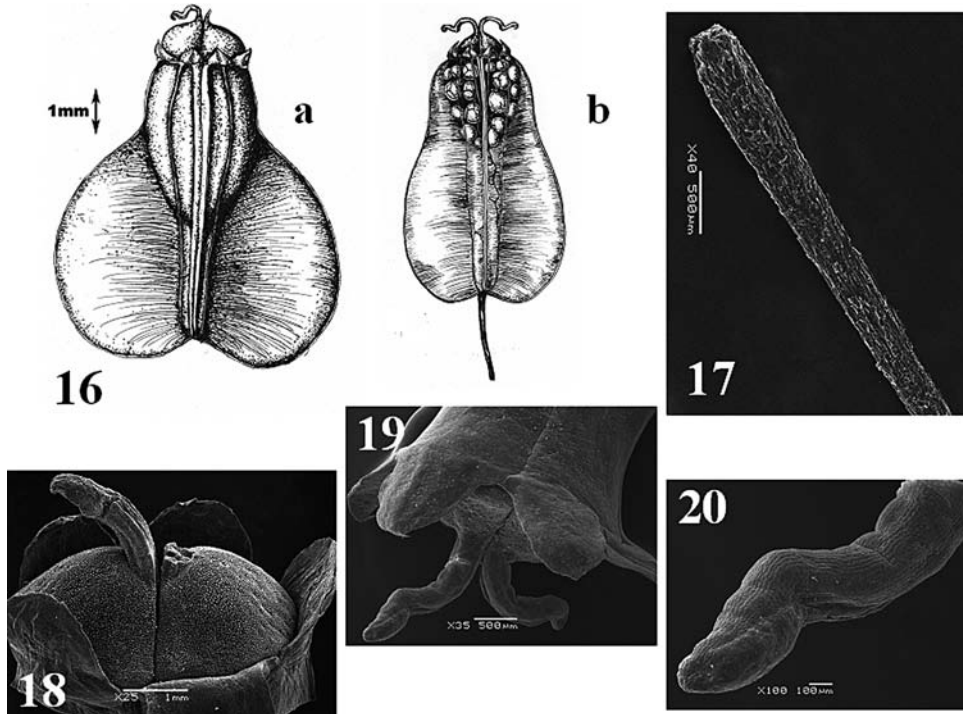


Fig. 16–20. *Myodocarpus*. — 16, External fruit morphology: a, *M. fraxinifolius*, b, *M. simplicifolius*. — 17, Column of *M. pinnatus*. — 18, Calyx, stylopodium and stylodia of *M. pinnatus*. — 19, Calyx, stylopodium and stylodia of *M. simplicifolius*. — 20, Stylodium of *M. simplicifolius*.

tangentially. The outer walls are insignificantly thickened and covered with a thin cuticle layer (Fig. 21). No tannins are found in exocarp cells.

The mesocarp is not divided into distinct subzones. The vascular bundles in the studied species are forming two to three clearly visible circles; those of the outer circle and of the middle circle (perianth bundles) are located close to each other and sometimes are fused into a single stereom (Fig. 24) to a lesser (*M. pinnatus*) or a greater (*M. viellardii*) extent. Secretory canals, occurring commonly near the vascular bundles (“companion canals” or “rib oil ducts” — Fig. 21), as in *M. involucratus*, *M. pinnatus*, are sometimes absent completely (*M. fraxinifolius*, *M. viellardii*), or enlarged and extremely numerous (*M. simplicifolius*). Since in the latter case they do not display any connection with vascular bundles and are located irregularly, we doubt it is advisable to interpret them as “companion canals” or “rib oil ducts”. We believe they better should be treated as “scattered secretory canals” as per *Delarabrea*-type. In the innermost mesocarp layers very large secretory reservoirs, markedly protruding into the endocarp and the seed-bearing cavity, are located. These reservoirs are usually very well seen from the outside. Due to this, the “false” endosperm rumination occurs, very clearly expressed in *M. fraxinifolius* and *M. pinnatus* (Fig. 23, 24).

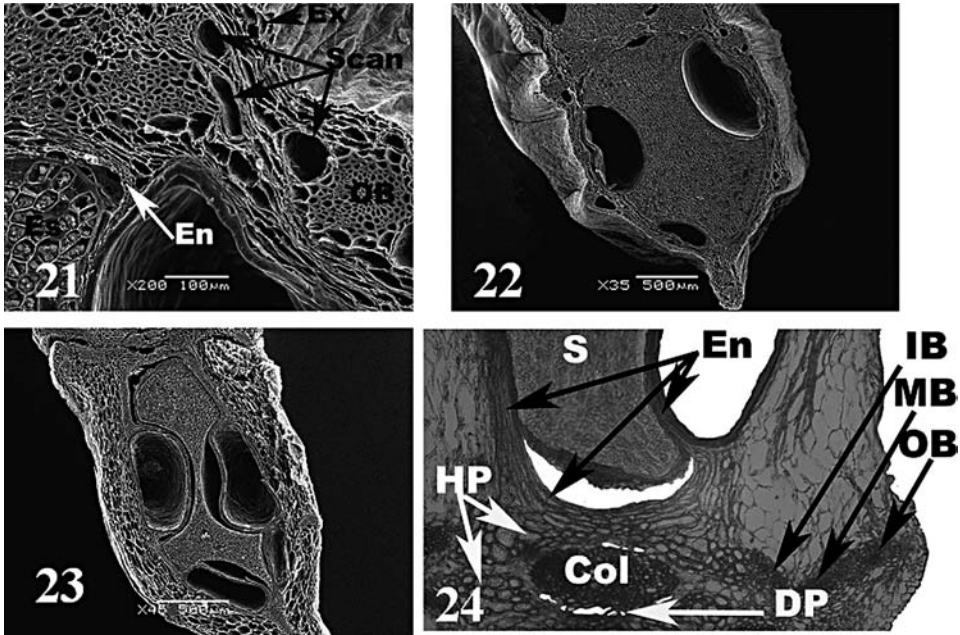


Fig. 21–22. *Myodocarpus involucratus*: — 21, TS of the middle of the seed-bearing part of a mericarp near a marginal rib. — 22, Mericarp, TS; note large secretory cavities creating “false” endosperm rumination. — 23–24. *Myodocarpus pinnatus*: — 23, TS of through the middle of the seed-bearing part of a mericarp; note large secretory cavities. — 24, Mericarp, TS. — Col = column, HP = “hydrocyte parenchyma”, DP = destroyed parenchyma.

In *Myodocarpus*, the entire mericarp apparently serves as a diaspore. The thin pyrene is composed of several (2–5) layers of endocarp fibers of different length. Their cell walls are rather thick but seemingly only slightly lignified (Fig. 21, 24). The endocarp becomes even thinner under the secretory cavities and, at some areas represented by only one or two layers of fibers, is hardly discernible. The pyrene is enlarged near the marginal ribs not only due to numerous elongated endocarp elements, but also because of adjacent groups of almost isodiametric cells, resembling those of “hydrocyte parenchyma” (Fig. 24). The transition from typical fibers to the “hydrocyte parenchyma” cells is sometimes very gradual and often it is not easy to put a clear-cut demarcation line between these two types of supporting elements. However, it is noticeable that in the pericarps of *M. pinnatus* and *M. fraxinifolius* the “hydrocyte parenchyma” is very abundant and constitutes the entire commissural area of the pyrene, whereas *M. simplicifolius* lacks it and the entire supporting tissue (including that of the commissural area) is made of fibers. The seed coat is without a distinct structure, consists of a few layers of cells destroyed due to compression, so cell boundaries are not discernible. Near the vascular bundle of the pedicel the cells can still remain undamaged. They are more or less isodiametric.

Table 2. The fruit structure traits in the species of the genus *Delarbrea*.

Species	Exocarp	Presence of tannins in exocarp cells	Sclereids in the outer mesocarp zone (OM)	Borders between pericarp zones	Endosperm rumination	Number of column stereoms going into each mericarp
<i>D. michieana</i>	2-layered	Present in the inner layer of exocarp cells	Few in number	Indistinct E-IM; IM-OM	Distinct	1 (corresponding to two bundles)
<i>D. montana</i>	1-layered	Present in few exocarp cells	Numerous	Indistinct E-IM; IM-MM	Distinct	2 (each corresponding to a bundle)
<i>D. paradoxa</i> ssp. <i>paradoxa</i>	1-layered	Present in few exocarp cells	Numerous	Distinct E-IM; IM-MM	Distinct	2 (each corresponding to a bundle)
<i>D. harmsii</i>	1-layered	Present in all exocarp cells	Numerous	Indistinct (smooth or gradual) E-IM; distinct IM-MM	Indistinct	1 (corresponding to two bundles)

Comments: — Indistinct boundary = gradual and smooth type of transition; distinct boundary = abrupt type of transition; E-IM — transition from endocarp fibers to the inner mesocarp layers; IM-MM - transition from the inner mesocarp layers to the middle mesocarp layers; IM-OM — transition from the inner mesocarp layers to the outer mesocarp layers in case the mesocarp is of two zones (IM and OM) in *D. michieana*; — Number of stereoms going into each mericarp = in the upper third of the mericarps the column splits into 2 stereoms (each corresponding to 2 bundles) or into 4 stereoms (each corresponding to a bundle).

In transverse section the column is represented by one or two fused stereoms, made of four (two from each mericarp) ventral derivatives plus the lignified parenchyma surrounding the vascular bundles in the commissural zone (Fig. 4). The location of the stereoms can vary — either along the line connecting the mericarps (*M. fraxinifolius*, *M. pinnatus*) or perpendicular to this line (*M. simplicifolius*, *M. involucratus*).

Discussion

The evolutionary affinity of *Myodocarpus* and *Delarbrea* has never been seriously questioned. However, there are quite few carpological characters shared by the studied genera and showing their resemblance. Among them we note dimerous fruits (bicarpellate gynoecium), the presence of peculiar secretory cavities and the free column, capable of separating from the mericarp tissues. Let us take a deeper insight into each of these features.

The bicarpellate gynoecium is a feature shared by almost all representatives of Apiaceae. Many genera of Araliaceae are known to have it, too — e.g., the vast majority of species in *Astrotricha*, *Brassaiopsis* Decne. & Planch., *Cephalalaria* Harms, *Harmsioplanax*, *Heteroplanax* Seem., *Kaloplanax* Miq., *Mackinlaya*, *Motherwellia* F.

Table 3. The fruit structure traits in the species of the genus *Myodocarpus*.

Species	Presence of “hydrocyte parenchyma” in the commissural zone	Secretory canals “companion canals” or “scattered secretory canals” in mesocarp; association with vascular bundles	Vascular bundles of the outer and the middle circle; fusion into stereoms	Location of ventral vascular bundles
<i>M. involucratus</i>	Present; few cells	Scarce; mostly associated with bundles (“companion canals”)	No fusion	Collateral
<i>M. fraxinifolius</i>	Present; numerous cells	Missing or inconspicuous	No fusion	Sagittal
<i>M. pinnatus</i>	Present; numerous cells	Scarce; mostly associated with bundles (“companion canals”)	Bundles located close together; partially fused	Sagittal
<i>M. simplicifolius</i>	Missing	Extremely numerous; no association (“scattered secretory canals”)	No fusion	Collateral
<i>M. viellardii</i>	Present; few cells	Missing or inconspicuous	Bundles completely fused into stereoms	N/A

Comments: — Secretory canals — here we do not mean large secretory “oil vesicles” in the innermost mesocarp layers, but rather secretory structures in its outer layers: “companion canals” — the localization of secretory canals according to Apiaceae-type, “scattered secretory canals” — according to Araliaceae and *Delarbraea*-type; — Collateral location of the ventral vascular bundles = perpendicular to the line connecting mericarps, sagittal = along the line connecting mericarps.

Muell., *Oplopanax* Miq., *Panax* L., *Tetrapanax* K. Koch (K. Koch) as well as some species of *Cheirodendron* Nutt. ex Seem., *Eleutherococcus* Maxim., *Polyscias* Forst., *Schefflera* J.R. Forst. & G. Forst. All representatives of Myodocarpaceae also possess dimeric ovaries, but, as one can see from the above given examples, this trait is not exceptional and cannot be solitarily used as an argument to support the phylogenetic unity of *Myodocarpus* and *Delarbraea*.

All studied species of *Myodocarpus* and *Delarbraea* show “oil vesicles” in the inner mesocarp layers (Fig. 5, 8, 10) and in each of them, except in *D. harmsii*, this fact has caused the “false” endosperm ruminations (Tamamshyan 1951). Supposedly, the process of merging the secretory vesicles into the endocarp in ontogeny is gradual but at the same time very efficient, so in a mature fruits these reservoirs appear to be surrounded by fibers. Some authors even interpret them as a part of the endocarp (Lowry 1986, Lowry et al. 2001, Lowry et al. 2004a).

Since the fruit of *Delarbraea* is fleshy, with thick, well-hydrated pericarp, the “oil vesicles” usually cannot be seen from the outer surface, whereas in *Myodocarpus* species they are usually very conspicuous due to drier and thinner fruit wall. In fruits of Araliaceae, described in literature or studied by us before, no similar secretory reservoirs in the inner pericarp have been reported. Seemingly, this trait is unique within Myodocarpaceae, but similar structures can be observed in fruits of some apioideid and saniculoid genera, too. The secretory reservoirs isolated from the vascular bundles resembling the “vallecular vittae” in most Apioideae are known in *Smyrniopsis* Boiss.

(Pervukhina 1950). In *Pastinaca* L., as a fruit reaches maturity, “commissural vittae” move deeper into the fibrous (though lacking lignification) “hypoendocarp”, surrounding the parenchymous endocarp and the seed, ending up adhering directly to the endosperm (Alexandrov & Klimochkina 1947). In some species of *Sanicula* L. similar reservoirs also exist, but they do not lose connection with vascular bundles (Pervukhina 1950, Yembaturova unpublished data).

Functions of these secretory structures are a matter of discussions. Liu (2004) suggests that the belt of “oil vesicles” ensures the mechanical strength and support for the fruits of *Myodocarpus* and *Delarabrea*, which, unlike most closely related Araliaceae, lack a pronounced sclerenchymous endocarp. However, we believe that here this belt of “vesicles” rather serves protective purposes than mechanical support. Obviously, fruits of *Myodocarpus* and *Delarabrea* reach the ground in different ways: through anemochorous dispersal (spinning around when falling down from the mother tree due to the peculiar one-sided wing position) in the former and via synzoochorous (birds peck on them, tear the fruits apart and spread the fruit parts around) or endozoochorous (the diaspores go through the birds’ digestive tract) dispersal in the latter. Depending on which way is taken, the outer mesocarp layers become more (*Delarabrea*) or less (*Myodocarpus*) deteriorated, but apparently undergo further decomposition while remaining on the soil surface. This decomposition process should not however affect the diaspore itself (the seed-bearing part, including the seed, the pyrene and the “oil vesicles”).

We believe that in the extant representatives of *Myodocarpus* as well as their closest ancestors the embryo was initially underdeveloped continuing to develop after the seed is detached from the mother plant, i.e. on the soil surface. This hypothesis was suggested by the fact that underdeveloped embryos occur in the most ancient flowering plants with many archaic traits (Amborellaceae, Degeneriaceae, Himantandraceae, Illiciaceae, Magnoliaceae, Winteraceae, etc.). Seeds with underdeveloped embryos were also reported in the majority of Araliaceae, including rather highly specialized *Aralia*, *Kalopanax*, *Panax* and in the genus *Hydrocotyle* (Grushvitsky 1961). The fact that embryo of such type was found in Myodocarpaceae, closely related to Araliaceae and representing one of basally branching lineages within Apiales (Plunkett & Lowry 2001, Lowry et al. 2001) seems more therefore more obvious. In case of prolonged and slow embryo development one can logically presume that the terpenoid substances in the vesicles (mainly essential oils) provide protection from the intrusion of pathogenic fungi, germs and from decomposition (Denisova 1961, Vasiliev 1977). Further investigations are certainly required on that matter, but this character (the presence of such “oil vesicles”) is unique within Myodocarpaceae.

The column, separating from the mericarp tissues is very common amongst Apiales, but the ways of separating and the structure of the column itself vary markedly (Fig. 2, 17). To illustrate the highest level of specialization of the column in the schizocarp structure in Apiales, a long list of genera can be given. In Apiaceae subfamily Apioideae, the column serves not only for the separation but also the dispersal of mericarps, ensuring ballistochory (*Angelica* L., *Heracleum* L., *Pastinaca* L.). For that, the column splits into two parts in its upper third, so that two separated mericarps are hanging on them (Levina 1987). Numerous representatives of hydrocotyloid genera

(sensu Drude 1897) also possess a free (i.e. separating) column, which, however, does not bifurcate in its upper part, so no ballistochory occurs in this case — this takes place in *Asteriscium* Cham. & Schltdl., *Gymnophyton* Clos, *Hermas* L., *Homalocarpus* Hook. & Arn., *Pozoa* Lag., *Trachymene* Rudge. The presence of a free column in fruits of some of them (*Asteriscium*, *Gymnophyton*) correlates with the presence of wings, developed to a lesser or a greater extent and ensuring mericarp detachment and anemochorous dispersal (Tikhomirov & Konstantinova 1995). Since the wing is located on one side, it causes mericarps to rotate when falling down, therefore decreasing their speed and allowing the air currents to carry them further away from the mother plant.

Fruits of *Myodocarpus* also have the free column, which separates from the mericarp tissues as a solid structure, and, as in some hydrocotyloid genera, ensures the separation (but not the ballistochory). In *Delaribrea*, the column apparently does not always separate from the mericarps, and, if it does, it splits into two to four branches. It is formed by the ventral bundles, enclosed into a thick sheath of lignified parenchyma, thus forming a stereom, surrounded by the obliterated ground parenchyma cells. So, the presence of the free column itself cannot testify neither of the evolutionary affinity of *Myodocarpus* and *Delaribrea*, nor the isolated position of the family Myodocarpaceae.

Summarizing, we can state that our data of fruit anatomy presented in this study support the advisability of placing *Myodocarpus* and *Delaribrea* into a separate family, representing contemporary remnants, or “pieces” of such an early lineage of the evolutionary tree of Apiales (Lowry et al. 2001, Plunkett & Lowry 2001). No doubt that these two closely related genera are not part of Araliaceae. Neither should they be placed in Apiaceae, although, they are rather close to both above mentioned groups, because they definitely have certain characters in common with representatives of these families.

Surprising as it may seem, there are many more traits to be discussed in this paper that demonstrate the difference between fruits of *Myodocarpus* and *Delaribrea*.

It has already been shown that the dispersal mode is principally different between *Myodocarpus* and *Delaribrea*. They differ greatly from Apiaceae subfamily Apioideae in how the mericarps attach to the column. In *Myodocarpus* species, the mericarps remain attached to its lower part, directly over the area of connection with the pedicel (Baumann 1946, Vyshenskaya 2000, Yembaturova & Konstantinova, unpublished data): this peculiar way of attachment inspired Baumann (1946) to call the column in *Myodocarpus* “procarpophore” (Fig. 17). In *Delaribrea* fruits, column-forming vascular bundles grow into the mericarp tissues near their upper part, just under the stylopodium (Fig. 2, 3), just like in Apiaceae-Apioideae. However, unlike that in the latter, the column in *Delaribrea* does not bifurcate at maturity. The presence of the separating column can be easily explained for the dry, anemochorous, bicarpellate schizocarp of *Myodocarpus*, but appears to be much more questionable from the functional standpoint in the genus *Delaribrea*, known to be dispersed by birds (Lowry 1986). A similar column was reported previously in fleshy dimerous fruits of *Stilbocarpa lyalii* I. B. Armst. (Apiaceae-Azorelloideae) (Grushvitsky et al. 1969), where its presence raises a number of questions, still unanswered (Tikhomirov & Konstantinova 1995). We can consider the column formation in the evolution of *Myodocarpus* and *Delaribrea* as two

completely independent processes, therefore treating the columns as analogous structures. Alternatively, we can assume that their common ancestor possessed some unspecialized column-like structures (e.g., ventral bundles, separating to a greater or a lesser extent) — in this case, homology can be spoken about. The assumption about an independent progressive evolutionary development of the column in *Delarbraea* seems to be doubtful as it is not supported by a function the column could possibly perform. Moreover, there is no clear evidence that the evolution of the column in *Delarbraea* was directed by adaptive forces. The second suggestion, however, perfectly falls into the concept of monophyly in Myodocarpaceae. The presence of the column in *Delarbraea* can readily be interpreted as a result of stagnation and incomplete development of a morphological structure (an organ) without performing its function. Treating *Delarbraea*'s column as a rudiment corresponds well with the concept of a very ancient origin of this genus. Due to the fact that endozoochorously dispersed fruits of *Delarbraea* most evidently require a long dormancy period for the embryo to develop (Grushvitsky 1961), *Delarbraea* fruits should: 1) possess a thicker pyrene, 2) create the mechanism protecting the seed from decomposing when kept on the soil surface. On the contrary, for the anemochorous fruits of *Myodocarpus* only condition (2) is important, because they do not go through the birds' digestive tract.

The ways of increasing mechanical strength of the fruit structure are also very different in *Myodocarpus* and *Delarbraea*. The outer pericarp subzone in *Delarbraea* possesses sclereids while *Myodocarpus* fruits lack them completely. Apparently, the fruits of *Myodocarpus* are strengthened by stereoms. "Hydrocyte parenchyma" cell groups, adhering to the endocarp in the commissural area, also contribute to it. In *Delarbraea*, no such "hydrocyte parenchyma" is found.

In the majority of studied *Myodocarpus* species (excluding *M. simplicifolius*), the secretory canals in the outer part of the mesocarp definitely appear to be associated with vascular bundles, but no such connection is found in *Delarbraea*, where the canals are usually scattered throughout the pericarp. That is why in the former case we speak about the "companion canals" (Tseng 1967) or "rib oil ducts (Kljuykov et al. 2004) of *Myodocarpus*-type, in the latter we consider "scattered secretory canals" (Eyde & Tseng 1971) of *Delarbraea*-type. It is noteworthy, that most Apiaceae are known to have their secretory structures associated with vascular strands, whereas in most Araliaceae no such ties are noticed (Tseng 1967, Eyde & Tseng 1971, Tikhomirov & Konstantinova 2000, Konstantinova & Yembaturova 2002, 2005).

Tannins occur in exocarp cells (either as impregnations of cell walls, or as cell content) in all studied *Delarbraea* species, but are missing in the corresponding parts of *Myodocarpus* fruits.

Anatomical distinctions in fruits of *Myodocarpus* and *Delarbraea* also apply to the spermoderm structure. The seed coat in Araliaceae is derived from the single integument and consists of the testa only (Baumann 1946, Vyshenskaya 2000). In all investigated *Delarbraea* species the exotesta is composed of large, almost isodiametric cells and is distinct from the amorphous endotesta. In *Myodocarpus* both exotesta and endotesta are amorphous, consisting of compressed and destroyed cells, where no cell boundaries can be distinguished. Only near the funicular vascular bundle the exotestal cells become close to isodiametric, resembling those of *Delarbraea*.

Therefore, most distinctions between *Myodocarpus* and *Delarbreia* are also shared between *Myodocarpus* and representatives of Apiaceae-Apioideae. *Myodocarpus*, as we believe, is a modern example of that ancestral araliaceous lineage. Within it, a set of pro-apioideid (ancestral for Apioideae) traits had been developing. These traits involve dry pericarp and the column usually separating to ensure fruit disintegration, thin pyrene, which does not increase the fruit weight, “hydrocyte parenchyma”, tight connection between the secretory and vascular systems, obliterated and destroyed exotesta, etc. This set of traits could be somehow connected to anemochorous dispersal. Another evolutionary pathway was taken by *Delarbreia*'s ancestors — and, due to a different way of dispersal (zoochory), a set of pro-aralioid features (fleshy mesocarp and the solid column potentially capable of separating from the mericarp tissue, but which often remains attached, no obvious connection between secretory structures and vascular bundles, thick pyrene of various supporting elements, but with no “hydrocyte parenchyma”, large-celled exotesta) had been developed. Thus, one can see how extant taxa can demonstrate the results of ancient evolutionary bifurcation, which apparently existed in the ancestors of modern Apiaceae and Araliaceae. The type of dissemination might have played the key role in the evolution of these taxa. Earlier, the idea of acknowledging *Myodocarpus* and *Delarbreia* (including *Pseudosciadium*) as isolated subclades or clades within Myodocarpeae (Lowry et al. 2001) or Myodocarpaceae (Lowry et al. 2004a) has been proposed. Our findings bring us to the same conclusion.

Moreover, carpological evidence strongly supports the presence of two groups within *Myodocarpus* (Lowry et al. 2001): simple-leaved species *M. fraxinifolius* and *M. pinnatus* are found to have certain fruit structure traits in common (the presence of large “hydrocyte parenchyma” complexes, the location of ventral vascular bundles) and due to this, slightly differ from other studied representatives of the genus. This interesting fact requires further investigations with more representative material collected.

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