Taxonomic significance of fruit and seed structure in the subfamily *Cassinoideae* (Celastraceae)

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Summary. The paper reports on the macro- and micromorphology and anatomy of fruits and seeds in 19 species representing 13 African and American genera of subfamily *Cassinoideae* (family Celastraceae). A diversity of carpological characters was identified: fruit type and peculiarities of its dehiscence; presence of trichomes on fruit surface; subtypes of pyrenaria (polymerous, olygomerous, dimerous, pseudomonomerous); number of seeds, morphology of the seed (shape, presence/absent of outgrowths); the ratio of parenchymatous (ground) and sclerenchymatous (supporting) cell elements in the pericarp, cell shape and number of cell layers in the seedcoat. Fruit and seed characters support the differences between genera, also reflect on their possible relationship. The traits revealed are also used to substantiate and support the recent taxonomic revision of many genera, primarily African. The array of revealed fruit and seed traits strongly support previous taxonomic decisions to define most genera of the subfamily *Cassinoideae* in a narrow sense. It is especially relevant in the taxonomy of the African representatives, characterizing among others the distinct indigenous flora of the Cape Floristic Region.

Таксономическая значимость структуры плодов и семян в подсемействе *Cassinoideae* (Celastraceae)

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Аннотация. В статье представлены новые сведения о макро- и микроморфологии, а также анатомии плодов и семян 19 видов, относимых к 13 африканским и американским родам подсемейства *Cassinoideae* (Celastraceae). Выявлено разнообразие карпологических признаков: тип плода и особенности его вскрывания, наличие трихом на поверхности плодов, подтипы пиренария (полимерный, олигомерный, димерный или псевдомономерный), число семян, морфология семян (форма, наличие/отсутствие выростов), соотношение паренхимных (основных) и склеренхимных (опорных) клеточных элементов в перикарпии, форма клеток и

число клеточных слоев в семенной кожуре. Признаки плодов и семян подтверждают различия между родами, а также отражают их возможное родство. Выявленные признаки также используются для обоснования и поддержки недавней таксономической ревизии многих родов, в первую очередь африканских. Множество выявленных признаков плодов и семян убедительно подтверждают предыдущие таксономические решения по пониманию большинства родов подсемейства *Cassinoideae* в узком смысле. Это особенно актуально в таксономии африканских представителей, характеризующих, среди прочего, самобытную местную флору Капской флористической области.

Introduction

The family Celastraceae R.Br., as currently treated, comprises 98 genera and about 1350 species (Simmons, 2004), primarily with a pantropical distribution. Within the family, members of subfamily *Cassinoideae* sensu Th. Loesener (1942) occupy a special position due to morphological peculiarities and geographic distribution. The subfamily consists of 23 genera (plus the *Canotia* Torr. – as genus with the questionable affiliation, but minus the *Cheiloclinium* Miers which later has been placed in *Salacioideae*) and about 140 species found in North, Central and South America, Africa, tropical Asia and Australia (Loesener, 1942). According to Loesener (1942), the subfamily comprises two tribes: *Cassineae* Loes. and a monotypic tribe *Perrottetieae* Loes. Plants of this subfamily demonstrate rather striking differences from other Celastraceae as they possess coenocarpous pyrenaria sensu Bobrov et Romanov (2019) (stone fruits) while their seeds lack arils, typical for other species and genera in the family. Considerable structural diversity of pyrenaria reflects different degree of the taxa's evolution. To clarify taxonomic and phylogenetic aspects in *Cassinoideae*, all available modern methods and tools have been implemented, including comparative morphological and anatomical studies of vegetative organs, pollen record, data of molecular phylogeny (Metcalfe, Chalk, 1950; Archer, Van Wyk, 1992, 1993; Islam et al., 2006; Simmons et al., 2012). Many authors concluded that an up-to-date revision of several genera, often mono- or oligotypic, is needed. These taxa are presented by species primarily confined to Africa and Central or South America (Archer, Jordaan, 2000; Archer, Lombardi, 2013). Additionally, African species of Celastraceae and *Cassinoideae* in particular (including a number of Madagascan genera) are found to possess some apparent ancestral traits which therefore can be treated as key for understanding early evolutionary stages of the family in general (Savinov, 2010).

A long-term debate about distinctions between such species as *Cassine* L., *Elaeodendron* Jacq., and *Mystroxylon* Eckl. (Ding Hou, 1962) is worth noting. Scholars either placed them in one polymor-phous genus, or, on the contrary, found differences among them. Sonder treated these genera as separate ones (five in total), pointing out the distinction in fruit structure of *Cassine* and *Elaeodendron*: "in *Cassine* the drupe was defined as juicy with a thin crust-like putamen, in *Elaeodendron* it being rather dry, with a very hard ligneous putamen" (Sonder, 1860: 451). Bentham, Hooker (1862) kept the latter two separate, however, Baillon (1877) accepted only *Elaeodendron*. Davison (1927) merged *Elaeodendron* and some other genera with *Cassine* concluding that there were no generic differences between them. Perrier de la Bathie (1942, 1946), though agreeing that these two genera cannot be distinguished, arranged all species of Madagascar under *Elaeodendron*. Metcalfe, Chalk (1950) found that the anatomical characters of the vessels did not hold in conjunction with other characters. The recognition of only one broadly defined genus, *Cassine*, seems therefore to be final, as Ding Hou thought (1962).

This discussion resumed at the transition of 20th and 21st century, and included the newest data, including phylogenetic and molecular evidence. Thus, a paper by Islam et al. (2006) dedicated to taxonomic problem solving in "*Elaeodendron* alliance": *Elaeodendron, Cassine, Pseudosalacia* Codd*, Pleurostylia* Wight et Arn.*, Mystroxylon, Robsonodendron* R. H. Archer, and *Lydenburgia* N. Robson, was recently published. The authors analyzed morphological data and four genes: ITS, 26S rDNA, *mat*K, *trn*L-F region. The necessity to consider hereby the "problem of a genus" in a strict sense, involving the separation of many independent taxa from this group, is hereby shown. Papers where several wood and bark structural types in some *Cassinoideae* are defined (Archer, Van Wyk, 1993b) are worth noting. In South African representatives of *Cassinoideae*, three types of pollen structure have been described (Archer, Van Wyk, 1992): with reticulate, smooth/minutely pitted and finely wrinkled to reticulate exine, moreover, they differ in terms of ectexine and endexine thickness (Archer, Van Wyk, 1992). Based on that, using also comparative bark and wood structure (Archer, Van Wyk, 1993a, 1993b), these authors suggest treating *Elaeodendron* (incl. *Crocoxylon* Eckl. et Zeyh.),

Cassine s. str., *Hartogiella* Codd, *Maurocenia* Mill., *Lauridia* Eckl. et Zeyh., *Allocassine* N. Robson, *Mystroxylon*, *Pleurostylia* as independent genera.

Despite various scholars' notable interest in African and American representatives of the studied group, fruit structure in these genera and species has not been sufficiently investigated: only morphological descriptions of fruits and seeds for some of them are available. Details of pericarp and seed coat anatomy have been completely neglected, yet they can,
on the one hand, help to identify the morphological fruit type and on the other hand, to potentially elucidate the taxonomic relationships within the studied group and serve as diagnostic traits to distinguish among taxa. This source of taxonomic evidence would be of considerable significance to modern researchers, in particular, since the earlier authors used traits of fruit morphology to substantiate and support their treatments and decisions to unite or to separate certain genera.

Table 1

Specimens of *Cassinoideae* examined

Species (Taxon)	Origin (herbarium housing voucher)	Distribution
Canotia holacantha Torr.	LE, Botanical museum of Komarov Botanical Institute, St. Petersburg	USA (Arizona and California)
Cassine schinoides (Spreng.) R. H. Archer (=*Hartogiella schinoides* (Spreng.) Codd)	KW, LE	South Africa
Crocoxylon excelsum Eckl. et Zeyh.(= *Cassine crocea* (Thunb.) C. Presl)	KW	South Africa
Crossopetalum rhacoma Crantz	LE	Carribean countries
Elaeodendron australe Vent.	Botanical museum of Komarov Botanical Institute, St. Petersburg	Australia
E. punctulatum Turcz.	KW	New Zealand
E. sp.	Botanical museum of Komarov Botanical Institute, St. Petersburg	Unknown
E. viburnifolium (Juss.) Merr.	SING	Andaman Islands, Thailand, Malaysia, Indonesia
E. aff. viburnifolium	SING	Solomon Islands
Gyminda latifolia (Sw.) Urban.	Botanical museum of Komarov Botanical Institute, St. Petersburg	Mexico, Trinidad, Cuba
Mortonia greggii A. Gray	Botanical museum of Komarov Botanical Institute, St. Petersburg	Northern Mexico
Myginda sp.	Botanical museum of Komarov Botanical Institute, St. Petersburg	Mexico
Mystroxylon aethiopicum (Thunb.) Loes.	Botanical museum of Komarov Botanical Institute, St. Petersburg	Africa, Madagascar, Comoros isl.
Orthosphenia mexicana Standley	LE	Mexico
Pleurostylia opposita (Wall.) Alston (= *P. wightii* W. et A.)	Botanical museum of Komarov Botanical Institute, St. Petersburg	E. Mozambique, Madagascar, India, Sri Lanka, Hainan, Tropical Asia to New Caledonia and Australia (Queensland)
Schaefferia buxifolia Nutt.	Botanical museum of Komarov Botanical Institute, St. Petersburg	Mexico
S. frutescens Jacq.	KW	Bahamas and Antilles (incl. Cuba)
Perrottetia alpestris (Bl.) Loes. (Dipentodontaceae)	Botanical museum of Komarov Botanical Institute, St. Petersburg	Malaysia, Sumatra, Java, Borneo, Philippines, Celebes, New Guinea, Solomon isl.
P. racemosa (Oliv.) Loes. (Dipentodontaceae)	Botanical museum of Komarov Botanical Institute, St. Petersburg	Central China

Materials and methods

The present investigation was carried out in the lab of the Department of Morphology and Systematics of Higher Plants (Moscow State University) and covered fruits and seeds of 19 species (from 13 genera) of *Cassinoideae*. Additionally, material from herbarium of the Singapore Botanic Gardens – National Parks Board (SING) has been studied, as one of the coauthors was able to work there in January 2020. Fruit samples were obtained from various sources (see Table 1). The fruits were fixed in 70 % ethanol (in case of fresh material) or in Strassburger mixture (in case of rehydrated material; 90 % ethanol, glycerol and distilled water in equal proportion).

To study fruit morphology, a binocular microscope MBS-2 was used; fruit structure descriptions are in accordance with generally accepted methodology and respective terminology (Melikian, Devyatov, 2001; Bobrov, Romanov, 2019); topographic zones of the seed coat according to E. J. H. Corner (1976). Fruit and seed anatomy was studied according to standard methods (O'Brien, McCully, 1981; Barykina et al., 2000) in cross (transverse) sections through the middle of mature fruits, freehand, by means of a razor blade. Temporarily microscopic preparations were made, treated with phloroglucinol +HCL to identify cell wall lignification in different pericarp zones and subsequently mounted in glycerol. Anatomical preparations (transverse sections) were observed using light microscopes MBB-1 and Biomed C-2.

The analysis of all results obtained was based upon the degree of variability of carpological traits, revealing of similarity/difference by comparing of all studied taxa and therefore, evaluating taxonomic significance of each trait (providing substantiation for possible homoplasy), interpreting possible adaptive advantages of the structural traits. The evolution of traits was modelled in accordance with molecular trees.

The scope of the *Cassinoideae* subfamily is taken here according to Th. Loesener (1942), with minor changes by A. Takhtajan (2009). The authors treated all studied taxa in a narrow sense, as in papers by R. Archer and colleagues (Archer, Van Wyk, 1996; Archer, Jordaan, 2000).

The nomenclatural information for the scientific names follows the International Plant Name Index (https://www.ipni.org/); when establishing priority species names – the World Flora Online (http://worldfloraonline.org), additionally also https:/powo.science.kew.org.

Results

Canotia Torr.
Canotia holacantha Torr. (fig. 1a; 2a; 3a; 4a; 5a)

The fruit of *C. holacantha* is an olygomerous, three-seeded dehiscent capsule, crowned with the stylar remnants. The pericarp is made up of 18 to 21 cell layers. A single-layered endocarp is formed by moderately sized cells, rectangular in cross section. The cuticle is rather thick. The mesocarp is presented by 5 layers of large tanniniferous parenchyma cells. The endocarp consists of 12 to 15 layers of macrosclereids, markedly elongated tangentially.

The winged seed possesses a wing of 7 to 8 mm long. The seed coat is composed of 6 or 7 tanniniferous cell layers. Single-layered exotesta is made of rather large mammillary cells; their outer and, to a lesser extent, lateral walls thickened. The cuticle is not pronounced. The mesotesta is of 2 or 3 layers of well-developed parenchyma cells, tangentially elongated. All other cell layers are completely crushed and destroyed. No endotesta is visible. The exotegmen is one-layered, made of small tabular cells with U-thickened walls. Meso- and endotegmen are formed of 2 layers of small parenchyma cells.

Cassine L. (incl. *Hartogiella* Codd)
*Cassine schinoides (*Spreng.) R. H. Archer (= *Hartogiella schinoides* (Spreng.) Codd) (fig. 1i; 4g; 5g)

The fruit is a relatively dry pyrenarium, with 17- or 18-layered pericarp. Single-layered exocarp consists of cells rectangular in cross section and thickened outer and lateral walls. The cuticle thickness is half the height of these cells. Ten layers of large parenchyma cells comprise the mesocarp. The endocarp is made of 6 layers of large sclereids; near the mesocarp, they are close to isodiametric in shape, next to the seed, they are tangentially elongated (1–2 innermost layers).

The seed is of the sarcotestal type, with 12- or 13-layered seed coat. One-layered exotesta is of tanniniferous cells, with thickened outer and lateral walls and rectangular in cross section. The cuticle thickness is half the height of these cells. 8 or 9 layers of large parenchyma cells, slightly elongated tangentially, form the mesotesta. The endotesta is not discernible. The exotegmen is single-layered and composed of nearly isodiametric sclereids with markedly thickened walls. The 2 remaining cell layers are greatly compressed. The endosperm is large-celled.

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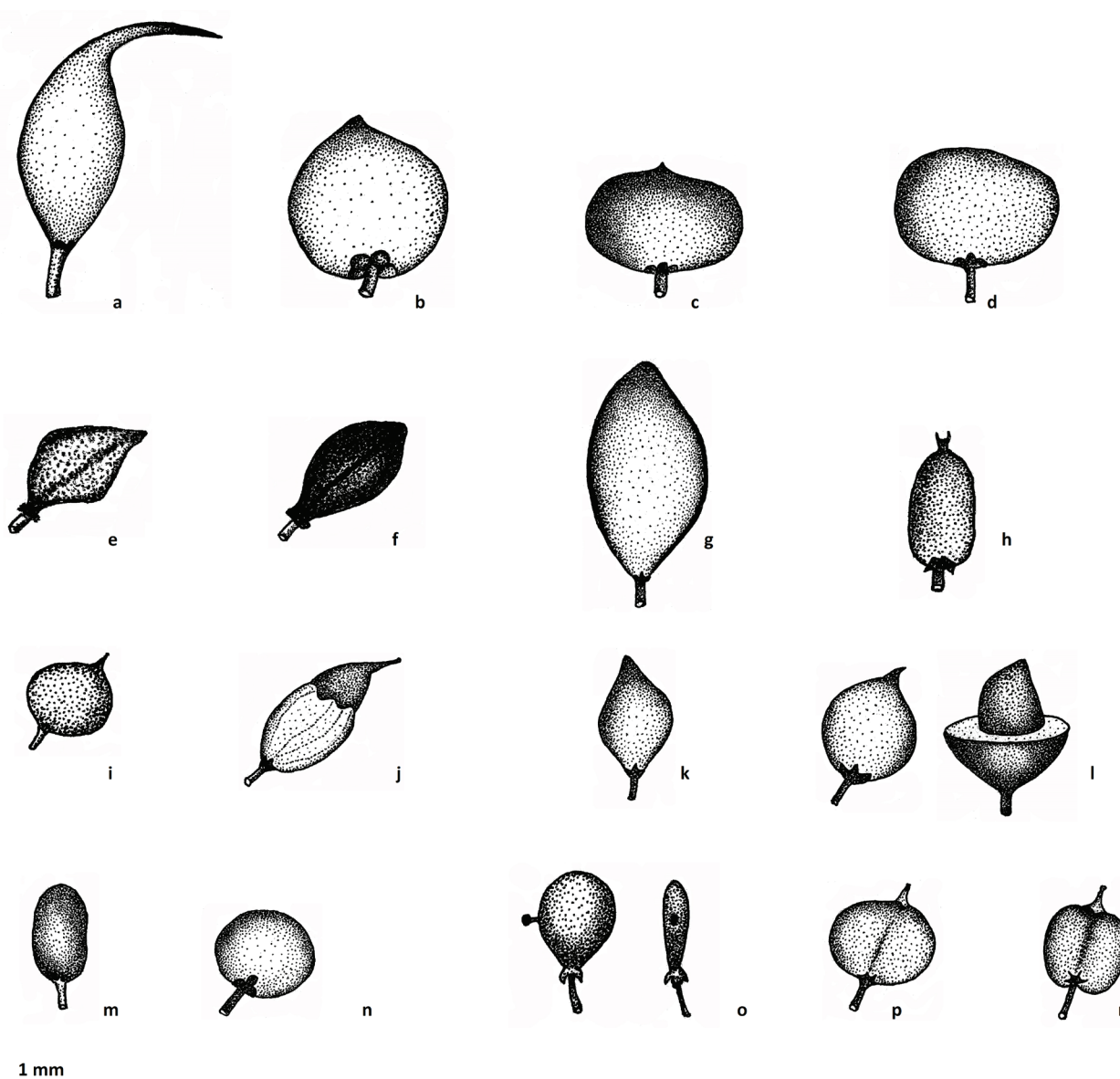
1 mm

Fig. 1. Fruit morphology of *Cassinoideae* (schematic): a – *Canotia holacantha*; b – *Crocoxylon excelsum*; c – *Crossopetalum rhacoma*; d – *Elaeodendron australe*; e – *E. viburnifolium*; f – *E.* aff. *viburnifolium*; g – *E. punctulatum*; h – *Gyminda latifolia*; i – *Cassine schinoides*; j – *Mortonia greggii*; k – *Myginda* sp.; l – *Mystroxylon aethiopicum*; m – *Orthosphenia mexicana*; n – *Perrottetia alpestris*; o – *Pleurostylia opposita*; p – *Shaefferia buxifolia*; r – *S. frutescens*. Scale bar – 1 mm.

***Crocoxylon* Eckl. et Zeyh.**

Crocoxylon excelsum Eckl. et Zeyh. (= *Cassine crocea* (Thunb.) C. Presl) (fig. 1b; 2b; 3b; 4b; 5b)

The fruit is an olygomerous, almost globose light brown pyrenarium, around 20 mm in diameter. The fruit possesses 4 pyrenes, each one containing 1(2) seeds. The pericarp is of 70–76 cell layers. Single-layered exocarp is represented by small cells, square to rectangular in cross section. The mesocarp is differentiated into two zones: the outer – 15 layers of minute tanniniferous parenchyma cells, and the inner one of 25 to 30 layers of large-celled loose parenchyma, with rounded vascular bundle derivatives throughout. The endocarp consists of 30 layers of large rounded "cartilaginous" sclereids forming the pyrene (stone).

The seed is obovate, approximately 8–9 mm in length. The seed coat is clearly differentiated and consists of 9 cell layers. One-layered exotesta is made of large cells with thickened outer cell walls; the cells are almost square in cross section and are filled with tannins. The outer cuticle layer is rather thin and even. The mesotesta consists of 4(5) layers of tangentially elongated parenchyma cells, containing tannins. Single-layered exotegmen is composed of medium-sized sclereids. Two layers of mesoteg-

men are also discernible – they are made of small parenchyma cells possessing tannins. The endosperm is large-celled. The embryo is relatively small.

Crossopetalum P. Br.

Crossopetalum rhacoma Crantz (fig. 1c; 2c; 4c; 5c)

The fruit is an olygo- or dimerous, one- or two-seeded globose pyrenarium. The pericarp is formed by 23–26 cell layers. Single-layered exocarp is composed of cells, almost rectangular in cross section and with their outer wall thickened. The cuticle is very thin and sometimes not detected. Two topographic zones can be distinguished in the mesocarp. Just beneath the exocarp, there are 2 or 3 layers of tanniniferous hypoderm cells, almost rectangular in cross section. The rest of the mesocarp is made of 10–12 layers of medium-sized parenchyma cells, with clusters of 6–8 sclereids located among them. The endocarp is of 9 sclereid layers, they are large, but short; also, an innermost layer of minute colourless cells of the internal zone is discernible.

Seeds are small, arils absent. The seed coat is made of 8(9) cell layers. Single-layered exotesta is represented by medium-sized cells, rectangular in cross sections. They are found to contain tannins. The cuticle is poorly developed. The mesotesta is composed of 4 layers of parenchyma cells, elongated tangentially and bearing tannins, too. The endotesta is just a single layer of smallish cells. The exotegmen, also one-layered, consists of minute tabular sclereids. Other cell layers of the tegmen are almost completely destroyed.

Elaeodendron Jacq.

Elaeodendron australe Vent. (= *Cassine australis* (Vent.) Kuntze) (fig. 1d; 3c; 4d; 5d)

The fruit is a polymerous succulent pyrenarium, red in colour, with leathery exocarp and fleshy mesocarp. Multi-layered pericarp consists of 30–35 cell layers. The mesocarp is formed by tiny tannin-containing parenchyma cells (up to 20 layers). The endocarp is composed of almost isodiametric sclereids, forming 10 to 12 layers, and 2 or 3 layers of tangentially elongated macrosclereids (the innermost zone).
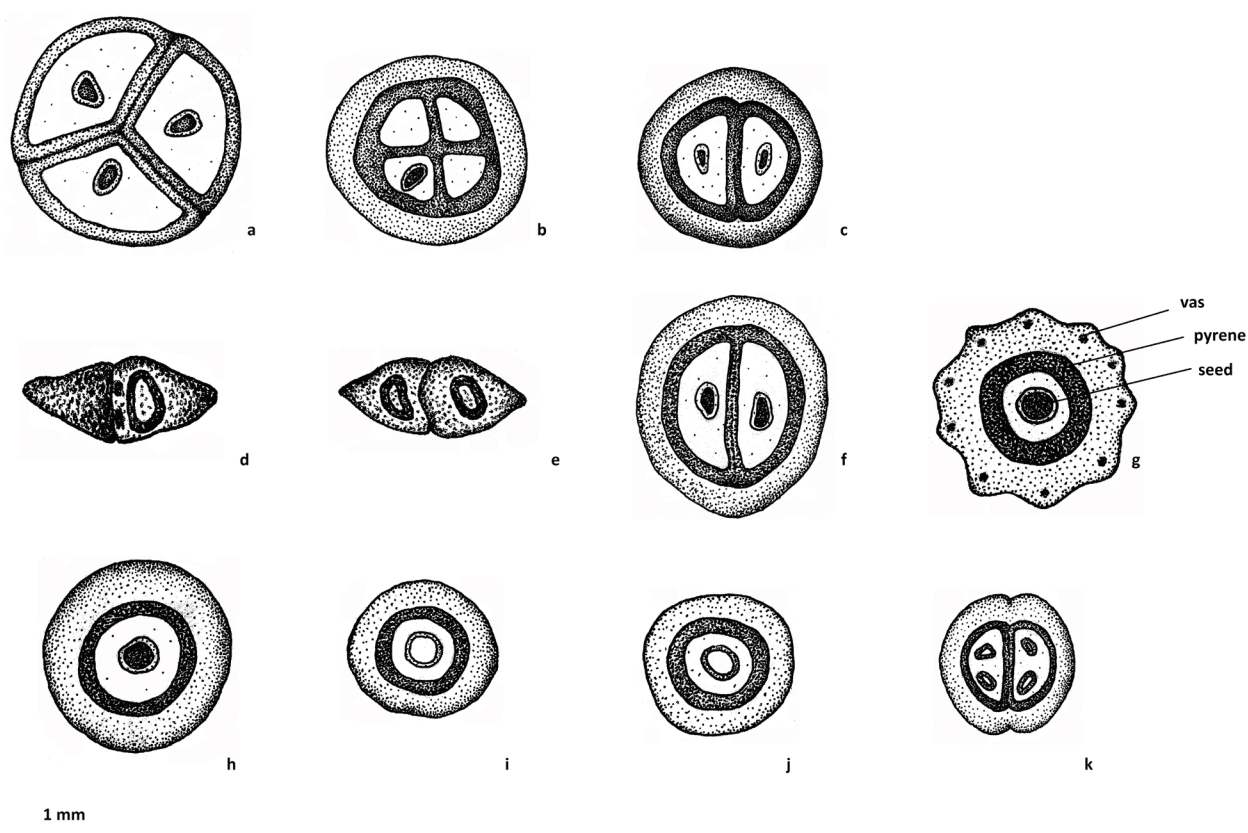

Fig. 2. Fruit cross-section of *Cassinoideae* (schematic): a – *Canotia holacantha*; b – *Crocoxylon excelsum*; c – *Crossopetalum rhacoma*; d – *Elaeodendron viburnifolium*; e – *E.* aff. *viburnifolium*; f – *E. punctulatum*; g – *Mortonia greggii*; h – *Mystroxylon aethiopicum*; i – *Orthosphenia mexicana*; j – *Shaefferia buxifolia*; k – *S. frutescens*. Symbol: vas – vascular bundle. Scale bar – 1 mm.

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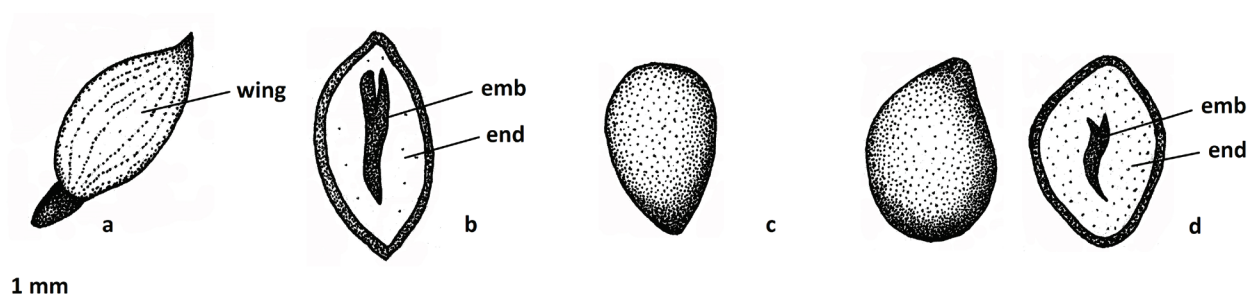
Fig. 3. Seed morphology of some *Cassinoideae* (schematic): a – *Canotia holacantha*; b – *Crocoxylon excelsum* (longitudinal section); c – *Elaeodendron australe*; d – *E. punctulatum* (general view and longitudinal section). Symbols: emb – embryo; end – endosperm. Scale bar – 1 mm.

Elaeodendron punctulatum Turcz. (fig. 1g, 2f, 3d, 4e, 5e)

The fruit is a dimerous pear-shaped pyrenarium, approximately 13 mm in length. The pericarp is found to consist of 15 to 21 cell layers in total. Single-layered exocarp is represented by medium-sized tannin-containing cells, markedly elongated tangentially. 10 to 15 layers of rather large parenchyma cells form the mesocarp; among these cells, clusters of 6–8 tanniniferous cells are located. The endocarp is composed of radially situated sclereids (one layer) and 3 to 4 layers of fibrous sclereids.

The seed is ovate in shape, about 8 mm long. The seed coat is quite uniform in structure, 10 cell layers in total. One-layered exotesta is made up of minute cells containing tannins. Eight layers of minute, rounded parenchyma cells, filled with tannins, compose the mesotesta. Single-layered tegmen is formed by dark rectangular cells. The endosperm is found to have cavities. The embryo is small.

Elaeodendron sp.

The fruit is a pyrenarium, fleshy and polymerous. The number of cell layers in the pericarp ranges from 30 to 33. One-layered exocarp is composed of minute cells with thickened outer walls; the cells are elongated tangentially. In the mesocarp, two zones can be identified. Beneath the exocarp, there are 10–15 layers of minute, thin-walled parenchyma cells, which are subsequently replaced by the cells with somewhat thickened walls. Among them, medium-sized vascular bundle derivatives are found. The endocarp consists of 10 layers of large sclereids; within the zone, they are gradually replaced by 5 to 7 layers of smaller sclereids. The innermost endocarp zone is of 3 or 4 layers of fibrous sclereids, extended tangentially.

Each pyrene possesses a single seed. The seed coat is formed by 8–11 cell layers. The exotesta is uniform, consisting of cells with evenly thickened walls, with marked radial elongation. The mesotesta is 3- or 4-layered, composed of almost isodiametric parenchyma cells, containing tannins. The endotesta is obsolete; the exotegmen is formed by 3 or 4 layers of fibrous cells. Other tegmen layers are compressed and obliterated.

Elaeodendron viburnifolium (Juss.) Merr. (= *Cassine viburnifolia* (Juss.) Ding Hou) (fig. 1e; 2d)

The fruit is a small 1(2)-locular one-seeded (rarely two-seeded) angular pear-shaped pyrenarium (in cross section it usually appears to be rhombic), around 13 mm in length. The fruit surface is papillose. As a rule, only one locule containing a single seed is visible in transverse section of the fruit, the second one being obsolete. The seed, obovate to oblong, 6 to 3 mm in dimensions, lacks an aril. The fruit can be easily sectioned. The pericarp is found to consist of thin exocarp, porous corky mesocarp and poorly developed pyrene enclosed by a poorly developed endocarp.

Elaeodendron aff. *viburnifolium* (fig. 1f; 2e)

The fruit is a small two-locular two-seeded pyrenarium, oval in shape, about 10(13) mm long. The fruit surface is papillose. Contrary to the previously described one, this fruit is hard to cut or section. The pericarp appears to be made of thin exocarp, thinner, but porous mesocarp (similar to that of *E. viburnifolia*), better developed pyrenes (thicker endocarp). Seeds are usually 2, lacking arils.

Gyminda (Griseb.) Sarg.

Gyminda latifolia Urb. (fig. 1h; 4f; 5f)

The fruit is a pseudomonomerous, single-seeded dark brown pyrenarium. Number of pericarp layers is 23–25. One-layered exocarp is formed by minute cells with thickened outer walls; these cells appear rectangular in cross section. The cuticle layer is moderate. The mesocarp is composed of 12 layers of large-celled, tanniniferous parenchyma. The en-

docarp is of 10–11 layers of macrosclereids forming the pyrene. Its outermost layer consists of very large, radially elongated macrosclereids, the middle zone – 6 to 7 layers of tangentially elongated macrosclereids in oblique position, and the inner zone – 3 layers of tangentially elongated macrosclereids in straight position.

The seed is small. The seed coat is of 6–7 cell layers. Single-layered exotesta is represented by rather large papillate cells with thickened outer and lateral walls. The cuticle reaches up to ¼ of their height. 3(4) tangentially elongated parenchyma cells constitute the mesotesta. Its inner zone, along with the endotesta, is obliterated. The exotegmen is one-layered, consisting of small tabular cells with evenly thickened walls. Rest of the tegmen layers are almost entirely crushed. Endosperm cells are minute.

Mortonia **A. Gray**
Mortonia greggii A. Gray (fig. 1j; 2g; 4h; 5h)

The fruit is a pseudomonomerous, one-seeded pyrenarium, crowned by the persisting style and surrounded by the "calyx", yellowish green in colour. The pericarp is of 17 or 18 cell layers. Single-layered exocarp is formed by medium-sized rectangular cells with greatly thickened walls, somewhat elongated radially. The cuticle on the surface is ½ of these cells' height. The mesocarp consists of 6 layers of rather large parenchyma cells, between which clusters of isodiametric sclereids, 6 to 8 in each, are located. The endocarp is composed of macrosclereids; in the outer layer, they are radially orientated, in the central zone, there are 5 or 6 layers of tangentially elongated ones in oblique position, and in the innermost – 4 layers of macrosclereids in straight position. The "calyx" is made up of large sclereids and provides additional support.

The small seed is slightly ribbed. The seed coat consists of 7 or 8 cell layers. The exotesta is one-layered, composed of rather large cells, rectangular in cross section and possessing slightly evenly thickened walls. The cuticle layer is thin. The mesotesta is formed by 3 or 4 layers of minute, partly compressed parenchyma cells, elongated in tangential direction and containing tannins. One-layered exotegmen consists of tangentially elongated cells with uniformly thickened walls. Only one layer (small parenchyma cells) persists of the rest of the tegmen.

Myginda **Jacq.**
Myginda sp. (fig. 1k; 4i; 5i)

The fruit is a pseudomonomerous one-seeded ribbed pyrenarium. Total number of pericarp layers ranges from 27 to 34. One-layered exocarp is of square-shaped cells. The mesocarp consists of 10 to 15 layers of medium-sized tanniniferous parenchyma cells. The endocarp forms a pyrene of sclereids and fibers. Directly beneath the mesocarp, there are around 10 layers of tangentially extended macrosclereids. The inner endocarp zone is formed by 6–8 fiber layers.

The moderately sized seed is ribbed, with an 8-layered seed coat. Single-layered exotesta is composed of rectangular (in cross section) cells with thickened outer and lateral walls. The cuticle is poorly developed. The mesotesta consists of 4 layers of slightly compressed parenchyma cells, elongated tangentially. The exotesta is not discernible. The exotegmen is one-layered, formed by tangentially extended sclereids. Meso- and endotegmen comprise of 2 layers of parenchyma cells.

Mystroxylon **Eckl.**
Mystroxylon aethiopicum (Thunb.) Loes. (= *M. confertiflorum* Tul. = *Cassine aethiopica* Thunb.) (fig. 1l; 2h; 4j; 5j)

The fruit is a pseudomonomerous one-seeded pyrenarium, greenish brown in colour, oval, about 12 mm in length and 6–7 mm in width, with wrinkled or crumpled surface. Total number of pericarp cell layers is 14 or 15. One-layered exocarp is covered by thick cuticle and is presented by tanniniferous cells, almost square in cross section. Undifferentiated mesocarp is composed of 10 layers of small tanniniferous cells, nearly isodiametric in shape. Three layers of endocarpic sclereids form the pyrene. A single layer of large, radially elongated sclereids is prominent, being surrounded by nearly isodiametric sclereids.

The medium-sized seed is oval or ovate, ribbed; no aril is present. Total number of cell layers in the seed coat ranges from 10 to 12. Single-layered exotesta is made of vast mammillary cells containing tannins; their outer and lateral walls are thickened. The outer cuticle layer is thin. The mesotesta is formed by 5 layers of tanniniferous parenchyma cells, elongated tangentially. One-layered endotesta is of smallish dark cells. The exotegmen, also single-layered, consists of porous sclereids, slightly elongated radially. In the tegmen, only the outermost mesotegmen layer of dark-coloured cells is clearly discernable, the other layers (3 or 4) are compressed.

Orthosphenia **Standl.**
Orthosphenia mexicana Standl. (fig. 1m; 2i; 4k; 5k)

The fruit is a pseudomonomerous one-seeded pale yellow pyrenarium. Total number of pericarp layers is 17. One-layered exocarp is of minute rectangular cells with thickened outer and lateral walls. The cuticle on the exocarp surface is equal to these cells' height. The mesocarp is formed by 10 layers of small-celled parenchyma, alternating with clusters of sclereids (5 or 6 in each). Two topographic zones can be distinguished in the endocarp: the outer one – 5 layers of tangentially extended sclereids, and the inner one – a single layer of medium-sized cells with evenly thickened walls.

The seed is small, oval in shape. Total number of cell layers in the seed coat is 5(6). One-layered exotesta is composed of minute rectangular cells, filled with tannins. Their walls are evenly thickened. The cuticle is barely visible. Two-layered mesotesta is formed by partly compressed parenchyma cells. The endotesta is not discernible. One-layered exotegmen consists of minute cells with evenly thickened walls. Only a single layer of parenchyma cells remains in the rest of the tegmen. Endosperm cells are rather large.

Pleurostylia Wight. et Arn.
Pleurostylia opposita (Wall.) Alston (= *P. wightii* W. et A.) (fig. 1o; 4m; 5m)

The fruit is a pseudomonomerous one-seeded (very rarely dimerous) pyrenarium, elliptic in shape, up to 7 mm long and 5 mm wide. Since it is derived from a 2-locular ovary, with 2 ovules per locule, it is defined as pseudomonomerous. The fruit bears a "prominent persistent hardened style on the lateral side" (Ding Hou, 1962: 288). The pericarp is of 18–20 cell layers. Single-layered exocarp consists of rectangular (in cross section) cells with thickened outer and lateral walls. A thin layer of cuticle is present on the surface. Undifferentiated mesocarp is formed by 10 layers of medium-sized isodiametric cells, containing tannins. Pyrene-forming endocarp is composed of sclereids, in 5 or 6 outer layers, they are elongated in radial, and in the inner 3 or 4 layers in tangentially direction.

The medium-sized seed lacks an aril. Total number of cell layers in the seed coat is 16 or 17. One-layered exotesta is composed of very large cells, square in cross section, with their walls evenly thickened. A thin cuticle layer is present. The mesotesta (parenchotesta) is formed by 10 layers of nearly isodiametric, tanniniferous parenchyma cells. Pronounced single-layered endotesta is made of tangentially elongated cells. The exotegmen, also one-layered, consists of tabular sclereids. The mesotegmen is of

2 or 3 layers of somewhat compressed parenchyma cells. The endotegmen is formed by dark cells of the integumentary tapetum.

Schaefferia Jacq.
Schaefferia buxifolia Nutt. (fig. 1p; 2j; 4n; 5n)

The fruit is nut-like, two-seeded, 3–4 mm in length and 2–2.5 mm in width, in the literature commonly referred to as a "drupe". Total number of pericarp cell layers is 12–14. Single-layered exocarp is of medium-sized cells, rectangular in cross section and with greatly thickened outer walls. The cuticle is quite massive (half of the exocarp cell height). Two zones can be distinguished in the mesocarp. The outer one is lignified, consisting of 2–6 layers of short sclereids. The inner zone is formed by 5 or 6 layers of minute, almost isodiametric cells. The endocarp is one- or two-layered, fibrous. Therefore, the sclerification pattern of the outer pericarp zones indicates a different fruit type – a nut or nuciform fruit (derived from superior ovary, two-seeded), as in drupes and pyrenaria, inner pericarp layers are sclerified.

The seed is small, ovate, and brownish in colour. The total number of cell layers in the seed coat ranges from 10 to 12. One-layered exotesta is composed of square cells, with markedly thickened outer and lateral walls ("horseshoe like" cell wall thickening). Meso- and endotesta consist of 3 layers of nearly isodiametric cells with slightly and evenly thickened walls and 4 layers of thin-walled tangentially elongated parenchyma cells. One-layered exotegmen is formed by medium-sized sclereids, elongated tangentially. Meso- and endotegmen are of 2 layers of two layers of tanniniferous parenchyma cells.

Schaefferia frutescens Jacq. (fig. 1r; 2k; 4o; 5o)

The fruit is a dimerous, almost globose pyrenarium, pale in colour, bearing 2 pyrenes with 1 or 2 seeds in each. Total number of pericarp cell layers is 17–19. One-layered exocarp is made of minute cells, square to rectangular in cross section. The mesocarp consists of 10–12 layers of smallish parenchyma cells containing tannins. In the endocarp, a layer of radially oriented sclereids, 4 or 5 layers of fibrous sclereids and the innermost layer of cells with evenly thickened walls can be seen.

The seed is minute, about 2 mm in length, with thin seed coat. One-layered exotesta is composed of cells almost square in cross section, with evenly thickened walls. The mesotesta is formed by 3 or 4 layers of somewhat compressed, tangentially elongated parenchyma cells. Single-layered exotegmen is of cells with evenly thickened walls, other tegmen layers are usually compressed and obliterated.
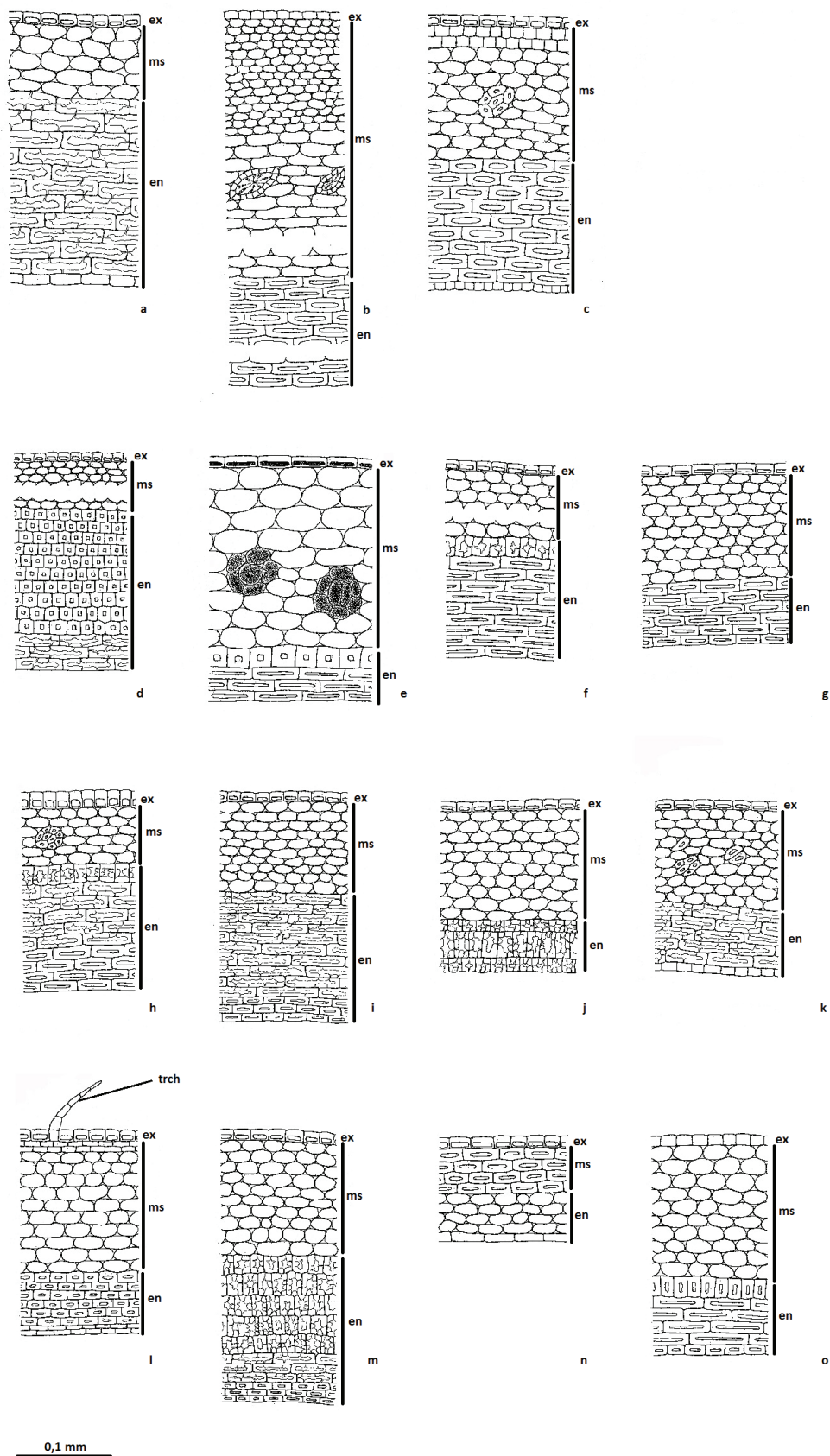
Fig. 4. Pericarp structure of *Cassinoideae* (schematic): a – *Canotia holacantha*; b – *Crocoxylon excelsum*; c – *Crossopetalum rhacoma*; d – *Elaeodendron australe*; e – *E. punctulatum*; f – *Gyminda latifolia*; g – *Cassine schinoides*; h – *Mortonia greggii*; i – *Myginda* sp.; j – *Mystroxylon aethiopicum*; k – *Orthosphenia mexicana*; l – *Perrottetia alpestris*; m – *Pleurostylia opposita*; n – *Shaefferia buxifolia*; o – *S. frutescens*. Symbols: ex – exocarp; ms – mesocarp; en – endocarp; trch – trichome. Scale bar – 0.1 mm.
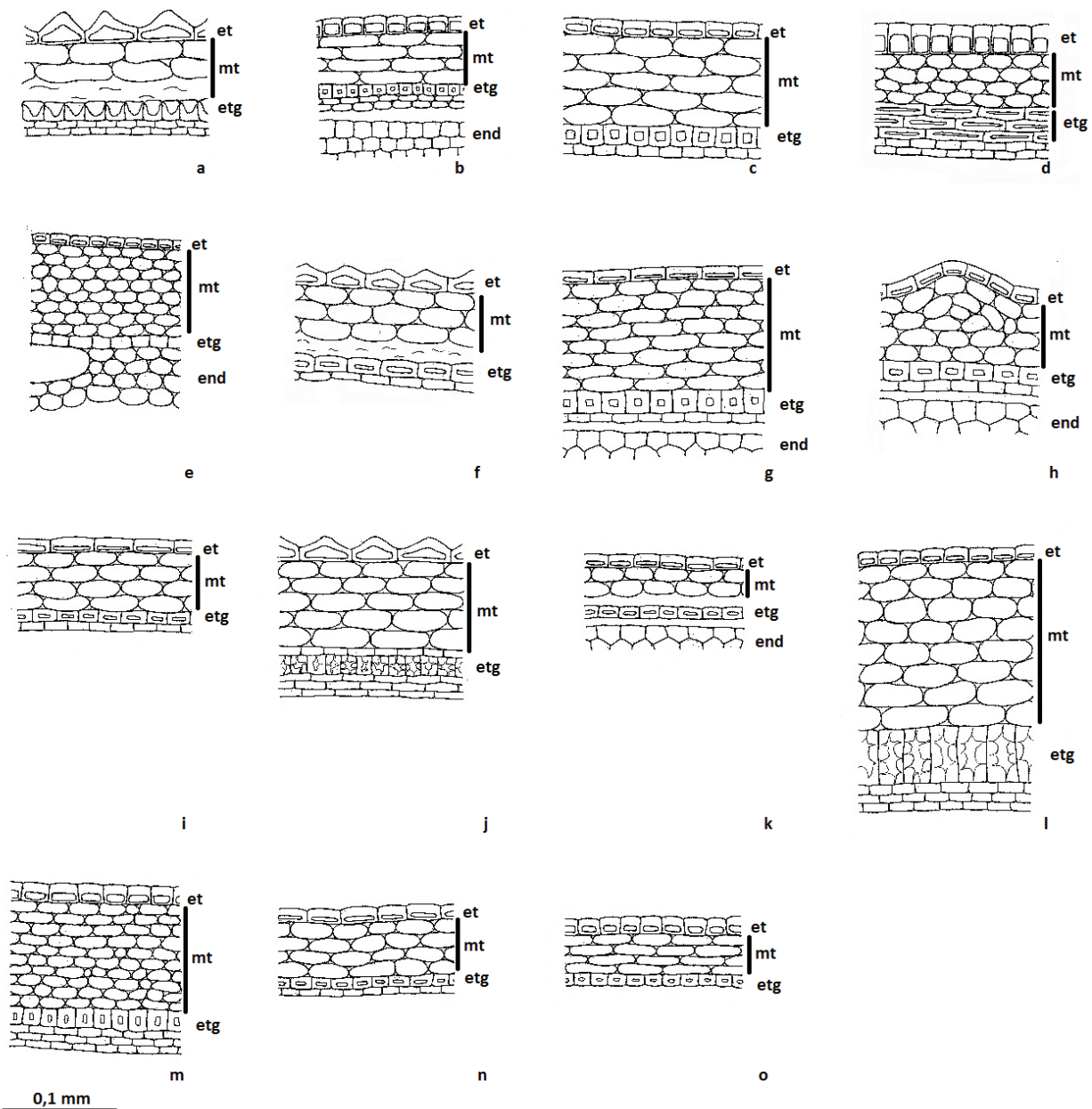
Fig. 5. Seed coat structure of *Cassinoideae* (schematic): a – *Canotia holacantha*; b – *Crocoxylon excelsum*; c – *Crossopetalum rhacoma*; d – *Elaeodendron australe*; e – *E. punctulatum*; f – *Gyminda latifolia*; g – *Cassine schinoides*; h – *Mortonia greggii*; i – *Myginda* sp.; j – *Mystroxylon aethiopicum*; k – *Orthosphenia mexicana*; l – *Perrottetia alpestris*; m – *Pleurostylia opposita*; n – *Shaefferia buxifolia*; o – *S. frutescens*. Symbols: et – exotesta; mt – mesotesta; etg – exotegmen; end – endosperm. Scale bar – 0.1 mm.

Perrottetia Kunth

Perrottetia alpestris (Blume) Loes. (fig. 1n; 4l; 5l)

The fruit is a berry, fleshy, globose, about 3–4 mm in diameter. Total number of pericarp cell layers is 22–27. One-layered exocarp is composed of square to rectangular (in cross section) cells with thickened outer and lateral walls. The fruit surface is covered by numerous elongated trichomes. The mesocarp is differentiated into two zones – one- to two-layered dark-celled hypoderm and 10–15 layers of large-celled parenchyma, containing abundant tannins.

The endocarp is made of 10 layers of medium-sized sclereids and single-layered inner epiderm.

The seed is minute, ovate, up to 2–2.5 mm long and around 1 mm wide, fleshy, with wrinkled to ribbed surface and large ribs, running parallel to the seed's longitudinal axis. Total number of cell layers in the seed coat is 12 or 13. Single-layered exotesta consists of medium-sized rectangular cells with evenly thickened walls. Cuticle strands and granules of epicuticular wax are well seen. Both mesotesta and endotesta form a succulent structure – sarcotes-

ta, composed of 8 or 9 layers of large parenchyma cells, slightly elongated tangentially. One-layered exotegmen is represented by large, radially extended sclereids. Other tegmen layers (1 or 2) are markedly compressed.

Additionally, a closely related species, *P. racemosa* (Oliv.) Loes., was investigated. It was also found to bear small one-celled superficial trichomes; its mesocarp is made of small-celled parenchyma, hypoderm is missing, and the seed coat structure is similar to that in *P. alpestris* – the only difference is the number of cell layers.

Discussion

Morphological fruit types. Data provided by various scholars in the relevant literature are conflicting. Thus, fruits of *Cassineae* were referred to as drupes, berries or even nuts, according to different authors (Loesener, 1942; Ding Hou, 1962; Archer, Jordaan, 2000). Following the terminology of, among others, Bobrov and Romanov (2019), the fruits are pyrenaria (except for *Canotia holacantha* with its olygomerous three-seeded dehiscent capsule) or berries (*Perrottetia* is also an exception). In the scientific literature, there is a challenging aspect of clearly defining types of dry fruit types such as "nut", "achene" (not cypsela-type) and dry drupe (Artyushenko, Konovalov, 1951), when the fruits are very similar in appearance but different in terms of pericarp and seed coat anatomy. The authors derive nut-like fruits directly from capsules, whereas drupes, both fleshy and dry, are said to have originated from a follicle. A typical syncarpous nut is formed of two or more carpels and is characterized by sclerification of the entire pericarp or its outer layers only, the inner ones remaining non-lignified. A nut is a one-seeded fruit. A drupe develops from a unilocular ovary, normally formed by a single carpel. Contrary to the nut, in the drupe (and also in pyrenarium), the inner part of the pericarp is lignified yet the outer parts remain fleshy (as in *Prunus* L.) or dry (*Amygdalus* L.). Depending on the consistency of the outer pericarp layers, the drupe is called dry or fleshy (succulent). There is also a syncarpous drupe-like fruit, derived from a multilocular, syncarpous ovary (Artyushenko, Konovalov, 1951). However, even in this case the drupe is formed by only one carpel: only one locule bearing a single ovule develops (as in *Viburnum, Linnaea, Valeriana*) or all locules develop equally, each forming a fruitlet (as in *Sambucus, Symphoricarpos*). Additional significant traits of such fruit formation (with Caprifoliaceae

taken as an example) are shown by one of the above co-authors in another paper (Artyushenko, 1951: 167): "lateral attachment of the ovule, development of a seed in each locule. In the typical drupe originating from a superior ovary, the ventral suture between the carpel margins would be detectable as well as the well-developed vascular system of the carpel". The above mentioned scholar (Artyushenko, 1951) identified three main fruit types in Caprifoliaceae: capsule, drupe and berry, and the other two types are shown to be derived from a multi-seeded multi-locular capsule plus the capsule with the reduction of locule number to two. This conclusion, according to our results, is quite consistent with morphological diversity of fruits and possible fruit evolution pathways in the family Celastraceae.

In the contemporary review of fruit morphogenesis (Bobrov et al., 2009), the authors consider one-seeded (rarely 2-seeded) fruits of *Mortonia* p. p. and *Pleurostylia* to be transitional from loculicidal capsules to true nuts. Fruits of *Perrottetia* are treated as superior syncarpous berries, and those of many *Cassineae* – as pseudomonomerous superior (one-seeded and with a single pyrene) syncarpous pyrenaria (*Cassine, Crossopetalum, Gyminda, Elaeodendron, Mystroxylon, Schaefferia*).

Cassineae are known to particularly have dry drupes (syncarpous pyrenaria), while fleshy drupe-like fruits and berries are also reported. *Pleurostylia* fruit was described as drupaceous (Robson et al., 1994), nut-like (Archer, Jordaan, 2000) or even a one- to two-locular nut (Ding Hou, 1962). The latter author provides details of its anatomy: exocarp + mesocarp are thin and leathery, the endocarp is hard (corky), thin, its inner side is shiny and irregularly crested, easily detaching from the mesocarp + exocarp, with several irregular fissures at the base of hilum (raphe) in the seed. The question of the fruit nature in the southern African *Cassinoideae* remains open: *Cassine, Maurocenia, Lauridia, Allocassine,* and *Robsonodendron.*

Anatomical structure of fruits and seeds. The pericarp has a varied structure and consists of 22 to 27 cell layers. The tribe *Cassineae* is of particular interest, because some representatives of the tribe are found to possess different structural subtypes of pyrenaria, such as: polymerous, olygomerous, dimerous, pseudomonomerous, with varying number of seeds and pyrenes and different degree of pulpiness in the pericarp middle zone (Table 2). The pericarp anatomy of the studied species differs markedly in terms of structure and location pattern of pyrene-forming cells (sclereids and fibers), presence of small

sclereid clusters, vascular bundle derivatives or cells with dark inclusions (tannins) in the mesocarp. It is not improbable that the pyrene origin can differ in different representatives of the group, and mesocarp and endocarp layers can differently contribute to the pyrene formation. To resolve this issue, further developmental (ontogenetic) studies of fruit wall formation are required.

Table 2

Summary of fruit types/subtypes and methods of seed dispersal in genera of the *Cassinoideae*

Genus and total the number of species	Fruit type	Fruit subtype (for pyrenaria only)	Adaptation for dispersal	Type of dissemination
Canotia 2 spp.	Loculicidal capsule		Winged seeds	Anemochory
Cassine L. 3 spp.	Pyrenarium	Di- or threemerous	Fleshy fruit; many-layers seed coat (sarcotesta)	Endo- and synzoochory
Crocoxylon Eckl. et Zeyh. 3 spp.		Olygomerous (with 4 stones)	Fleshy fruit	Endo- and synzoochory
Crossopetalum P. Browne 26 spp.		Dimerous	Dry fruit	Endo- and synzoochory
Elaeodendron Jacq. 40 spp.		Polymerous, rarely pseudomono-merous or dimerous	Fleshy fruit; many-layers seed coat (sarcotesta) or no; a corky porous mesocarp	Endo- and synzoochory, hydrochory
Gyminda Sarg. 4 spp.		Dimerous	Fleshy fruit	Endo- and synzoochory
Mortonia A. Gray 5 spp.		Pseudomono-merous	Dry fruit	Endo- and synzoochory
Myginda Jacq. 6 spp.		Pseudomono-merous	Dry fruit	Endo- and synzoochory
Mystroxylon Eckl. et Zeyh. 1 sp.		Pseudomono-merous	Fleshy fruit; many-layers seed coat (but no sarcotesta)	Endo- and synzoochory
Orthosphenia Standl. 1 sp.		Pseudomono-merous	Dry fruit	Endo- and synzoochory
Perrottetia Kunth 17 spp.	Berry		Fleshy fruit (berry), with trichomes on the surface; sarcotesta	Endozoochory
Pleurostylia Wight et Arn. 8 spp.	Pyrenarium	Pseudomono-merous	Dry fruit; sarcotesta	Endo- and synzoochory
Schaefferia Jacq. 23 spp.		Dimerous	Fleshy or dry fruit	Endo- and synzoochory

The studied member of the genus *Mystroxylon*, namely *Mystroxylon aethiopicum*, considering its fruit type (pseudomonomerous one-seeded), pericarp (only 3 sclereid layers in the endocarp) and seed coat structure (one-layered exotesta, radially oriented sclereids in the exotegmen), shows difference from the genus *Elaeodendron*, which is commonly characterized by polymerous pyrenaria, with well-developed endocarpic sclereids.

It was found that in the genus *Schaefferia* (*S. buxifolia*), the fruit is nut-like, due to sclerification of outer layers in the pericarp. Pericarp anatomy in *Perrottetia*, in particular, great number of sclereid layers in the endocarp, proves that its peculiar berry had been derived from a pyrenarium (no signs or remnants of dehiscence have been found in the present study).

Selected features of fruit morphogenesis. The fruits develop from syncarpous gynoecia, consisting of 2 or 3 (4 or 5) carpels. The ovary is 2 or 3 (4 or 5)-locular with (1)2 or 3 (up to 8) ovules per locule. Sometimes, the gynoecium can be pseudo-

monomerous, so then the ovary is unilocular as the second locule appears to be abortive (*Pleurostylia)*. The formation of pseudomonomerous one-seeded pyrenaria is very common in *Cassineae*, as well as the subfamily *Trypterygioideae*, where they develop wings. It is important to differentiate between the pseudomonomerous gynoecium (it has been recorded only in the genus *Pleurostylia*), when ovary locules are underdeveloped, and pseudomonomerous pyrenaria (fruits in many *Cassinoideae* – *Mortonia*, *Myginda*, *Mystroxylon*, *Orthosphenia*), when an originally olygomerous gynoecium transforms into a (pseudo-)monomerous fruit in the course of development.

Dispersal mode. Usually pyrenaria, just like true (monocarpous) drupes, are fleshy, which is traditionally interpreted as an adaptation to endozoochorous dispersal (Levina, 1957). However, considering the material of the current study and literature sources, it is obvious that approximately 50 % of *Cassinoideae* fruits are dry pyrenaria. This does not, though, rule out the possibility of endozoochorous fruit dispersal by herbivorous birds or mammals. Apparently, synzoochory can also be a possible dispersal mode; this is when animals actively carry fruits and seed away for storage and then forgetting to recover everything or dropping some on the way to the storage place. It is of special importance particularly in case of dry fruits and seeds (Levina, 1957).

Fleshy fruits attract animal dispersers by their bright coloration and flavour. In drupaceous fruits, both nutritive and protective tissues are part of the pericarp, in berries the nutritive tissues belong to the pericarp and the protective ones to the seed. Both dry and fleshy fruits attract herbivorous birds and mammals in case of endozoochory (Levina, 1957). As Zazhurilo's (1931) anatomical investigations revealed, fleshy fruits show remarkable uniformity of nutritive tissue structure while the protective tissue is extremely variable (in the latter, the basic and additional tissues can be distinguished). Both can develop from various flower parts. Nutritive and protective tissues differ by their consistency, coloration and microscopic structure. Certainly, the cell content is also important (cell sap, crystals, inclusions) because it defines nutritional properties of the tissue and its taste. Regarding the protective tissue, the diversity of its structure in different plants, as well as its different thickness, is taxonomically significant. The author provides a qualitative assessment of the relative thickness of nutritive and protective tissues in fruits and seeds, identifying three types: 1) fruits and seeds with thick nutritive and thin protective tissue; 2) fruits and seeds with the thickest protective tissue and the nutritive tissue intermediate between the 1st and 3rd type; 3) fruits and seeds in which both protective and nutritive tissues are thin. Then, a list of birds preferring fruits and seeds from each group is provided, the birds also being classified into 3 groups, according to how their digestion of plant tissues coupled with preserving the seed germination rate. Thus, they can: 1) destroy even the hardest fruits and seeds; 2) destroy only soft fruits and seeds; 3) no seeds or fruits are destroyed in the course of digestion. Zazhurilo (1931) describes aril-bearing seeds, too, with members of the celastraceous *Euonymus* among them (group 3). However, *Cassinoideae* lacks arils, so in realizing endozoochorous dispersal, the major role appears to be played by the outer layers of their pyrenaria, with well-developed pyrenes and pulpy mesocarps (the latter is not always pronounced in *Cassineae*!).

Among the representatives of the tribe *Cassineae*, some species are known to have very unusual dispersal modes. For example, in *Elaeodendron viburnifolium*, the pyrenarium has a corky porous mesocarp; due to its floating ability it can be dispersed in mangrove thickets (the fruit usually contains just one seed). Here, one can observe a case of true hydrochory. Ding Hou (1962: 286) showed that fruit structure in this genus is unique, yet our study revealed a new species of *Elaeodendron* from the Solomon Islands (specimen in SING) with a porous mesocarp, but in this taxon it is harder while the fruit is bilocular and 2-seeded. It is not easy to make deductions regarding its ecology and possible dispersal more, as we know that it grows in montane forests and along coastlines in the islands (according to herbarium specimens). Species of *Canotia* are known to be anemochorous, as their seeds have wing-like projections.

The role of a sarcotesta in indehiscent fruits. Another noteworthy morphological issue is related to the presence of a multi-layered fleshy testa in the seeds of many *Cassinoideae*: *Cassine*, *Elaeodendron*, *Perrottetia*, *Pleurostylia* (mainly on the basis exo- and mesotesta cell layers). Out of the studied species, the presence of a sarcotesta was previously reported only for *Perrottetia* (Corner, 1976). From the standpoint of dispersal modes and adaptations to zoochory, the sarcotesta is commonly found in plants with dehiscent fruits because this fleshy nutritive tissue is known to attract animal dispersal agents. Much less often it can be found in indehiscent fruits (Van der Pijl, 1955), e. g., in *Punica*, where the fruit either partly decays associated with cracking and/or is

opened by animals. A sarcotesta in berry-like fruits is quite an unusual phenomenon, although it was described in literature for some species (review see Van der Pijl, 1955). In Grossulariaceae, for instance, arils and arilloids have been reported (Komar, 1973: *Ribes, Grossularia*), but the presence of a sacrotesta in pyrenaria is rather unusual. Since a sarcotesta has been recorded in other Celastraceae from various subfamilies and tribes (unpublished data), we believe that the presence of a sarcotesta in the seeds is an ancestral trait for the entire family. Subsequently, in many other evolutionary lines, the sarcotesta is reduced and replaced by arils and arilloids, which corresponds to the evolutionary scheme of Van der Pijl (1955). However, in *Cassinoideae*, the seeds never possess any arils or arilloids. The sarcotesta in pyrenaria can seemingly be treated as a compensatory structure, supplementing fleshy pericarp tissues in case of zoochory (both synzoochory and endozoochory), which is especially relevant in the case of dry pyrenaria. This being said, according to recent molecular and phylogenetic research (Islam et al., 2006; Simmons et al., 2012), it originated within the subfamily *Cassinoideae* several times (in particular, in the genera *Cassine*, *Elaeodendron*, *Mystroxylon, Perrottetia, Pleurostylia*).

Fruit and seed structure and taxonomic status of genera. All in all, fruit structure traits strongly support the necessity to treat many genera of this group in the strict taxonomic sense (in particular, *Cassine*, *Elaeodendron*, *Crocoxylon*, *Mystroxylon)*. The studied genera can be well distinguished by details of their pericarp anatomy: number of cell layers, degree of histological differentiation in some pericarp zones, sclereid shape and number of layers, presence and shape of vascular bundle derivatives and various inclusions. Moreover, they belong to different structural subtypes of pyrenaria, which, in their turn, can be dry or fleshy. This partly corresponds with the results of molecular phylogenetic analyses (Islam et al., 2006; Simmons et al., 2012), although there was no evidence or attempt for the separation of e. g. *Crocoxylon*. Our paper was inspired by an earlier multi-disciplinary study towards a taxonomic revision of the southern African *Cassinoideae* (Archer, Van Wyk, 1996) and separate genera (Codd, 1966, 1983; Archer, Van Wyk, 1997, 1998).

Below, carpological traits supporting the treatment of the following genera as independent ones are listed:

Crocoxylon: olygomerous pulpy pyrenarium holding 4 pyrenes and "cartilaginous" endocarp.

Closely related to *Elaeodendron* and, possible, indistinguishable from him. Many-layers pericarp (70–76 vs 15–35 maximum in *Cassine*, *Elaeodendron*) – primitive character;

Elaeodendron: polymerous (rarely pseudomonomerous or dimerous) pyrenarium with well-developed endocarp sclereids;

Cassine s. str. (incl. *Hartogiella*): dimerous (or threemerous) fleshy or leathery pyrenarium, usually one- or two-seeded;

Mystroxylon: pseudomonomerous one-seeded pyrenarium (usually red or reddish in mature state), only 3 sclereid layers in the endocarp, single-layered endotesta, radially oriented sclereids in the exotegmen;

Pleurostylia: the fruit derived from pseudomonomerous gynoecium is a pseudomonomerous dry pyrenarium, commonly one-seeded (very rarely two-seeded), with "persisting floral parts – a small «nose» (style) – on the lateral side".

Perrottetia has unusual non-Celastraceous seed coat (Corner, 1976) and now placed in the Dipentodontaceae according to APG III and APG IV (Huerteales). Our research supports the decision.

Fruit and seed structure and phylogeny. The diversity of fruit anatomy and morphology in *Cassinoideae* allows us to apply the traits revealed in the current study in diagnosing species and when resolving phylogenetic matters. Thus, the revealed traits and their distribution in certain species coincide well with the molecular tree of *Cassinoideae* и *Tripterygioideae* based on molecular evidence (Simmons et al., 2012). Structural diversity of pyrenaria in the tribe *Cassineae*, demonstrated in the present paper, leads us to the following suggestion. According to the principle of economic evolution, the formation of 1(2)-seeded nut-like winged fruits in the subfamily *Tripterygioideae* from indehiscent dry pyrenaria of *Cassineae*-type through the seed number reduction and wing-like projection development appears to be the most probable. The emergence of various pyrenaria subtypes in the genera of *Cassineae* is apparently connected with improvement of adaptations to various dispersal agents. It also can be suggested that, in general, *Cassinoideae* seems to be a rather ancient group of Celastraceae, emerged very early in the family evolution. The above is supported, first of all, by geographical data (simultaneous presence of numerous genera in two continents – America and Africa) and structural organization of fruits and seeds.

Conclusion

The array of recorded fruit structure traits allows to strongly support previous taxonomic decisions to treat most genera of the subfamily *Cassinoideae* in a narrow sense. It especially concerns its African representatives, characterizing the peculiar indigenous flora of Cape Floristic Region. The key traits are: subtypes of pyrenaria (polymerous, olygomerous, dimerous, pseudomonomerous), number of seeds, the ratio of parenchyma (ground) and sclerenchyma (supporting) cell elements in the pericarp, cell shape, and number of cell layers in the seed coat.

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