



## Carpology, Seed Anatomy and Taxonomic Relationships of *Tetracentron* (Tetracentraceae) and *Trochodendron* (Trochodendraceae)

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This study of the anatomy and morphology of fruits and seeds of *Trochodendron aralioides* Sieb. & Zucc. and *Tetracentron sinense* Oliv. has revealed significant new data in the understanding of their systematic and phylogenetic relationships. The correction of the seed coat type for *Trochodendron* as (endotestal-) exotegmic (instead of endotestal) and for *Tetracentron* as exotegmic (instead of endotestal) documents a large morphogenetic gap between these putatively advanced types of seed coat and those of other Hamamelididae. Among primitive angiosperms, the combination of a few-layered testa with a markedly differentiated endotesta and a relatively multilayered tegmen with a sclerified tracheidal exotegmen occurs only in the seeds of the family Dilleniaceae (Dilleniales), which occupies a somewhat isolated position within the subclass Dilleniidae. The former features, as well as characteristics of node anatomy, anther dehiscence, pollen, floral and fruit morphology, suggest a close relationship between Trochodendrales and Dilleniales. The intermediate position of Trochodendrales between Magnoliidae and Hamamelididae is rejected, and Trochodendrales are taxonomically transferred from Hamamelididae to Dilleniidae in the rank of a distinct superorder: Trochodendranae. It is considered necessary to reform further the systematics of the artificial complex of the so-called 'lower' Hamamelididae and Dilleniidae. The suggested relationship between *Trochodendron* and fossil forms such as *Trochodendroides*, *Nordenskiöldia*, *Trochodendrocarpus* and *Trochodendrospermum* is also found untenable in light of the carpological survey of modern forms presented here.

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**Key words:** *Trochodendron aralioides* Sieb. & Zucc., *Tetracentron sinense* Oliv., carpology, pericarp anatomy, seed anatomy, systematics, phylogenetic relationships, palaeobotany, Trochodendraceae, Tetracentraceae, Dilleniaceae, Hamamelidaceae, Altingiaceae, Bucklandiaceae, Rhodoleiaceae, Platanaceae, Cercidiphyllaceae, Eupteleaceae, Trochodendrales, Dilleniales, Theales, Hamamelidales, *Trochodendroides*, *Nordenskiöldia*, *Trochodendrocarpus*, *Trochodendrospermum*, *Trochodendroides*, *Zizyphoides*.

### INTRODUCTION

The homoxylc genera *Tetracentron* Oliv. and *Trochodendron* Sieb. & Zucc., included in monotypic families Tetracentraceae A. C. Smith and Trochodendraceae Prantl, respectively (Smith, 1945, 1972), occupy a relatively stable and unquestioned position among primitive, 'lower' Hamamelididae. They are usually considered as a connecting link between the putatively archaic Magnoliidae and apetalous 'amentiferous' Hamamelididae (Dahlgren, 1989; Cronquist, 1992; Thorne, 1992; Takhtajan, 1997). In the original description of *Trochodendron*, Siebold and Zuccarini (Siebold, 1838) placed the genus in the Winteraneae of Magnoliaceae Juss. Oliver (1889) assigned the newly described genus *Tetracentron* to Magnoliaceae (tribe Trochodendreae). However, Seeman (1864), Eichler (1865*a, b*) and van Tieghem (1900) emphasized the anomalous position of *Trochodendron* in Magnoliaceae by its segregation into a distinct taxon (Seeman's 'order', van Tieghem's 'family') [Prantl (1888) was the first to validly publish a family name for Trochodendraceae according to the rules of botanical nomenclature]. Harms (1897) provisionally stated that *Tetracentron* merits familial rank, although he continued to treat the genus as belonging to a subfamily of Magnoliaceae.

Van Tieghem (1900) was the first to accept family status for *Tetracentron*. [Smith (1945) was the first to validly publish a family name for Tetracentraceae according to the rules of botanical nomenclature.] Nevertheless, Hallier (1901, 1903, 1904, 1912) removed both genera from Magnoliaceae and placed them into a distinct tribe of Hamamelidaceae R. Br. [as tribe Trochodendreae (Hallier, 1903)]. However, Bailey and Nast (1945) and Nast and Bailey (1945, 1946) continued to treat *Trochodendron* and *Tetracentron* in Ranales *s.l.* This view point was accepted for a long time (e.g. Pervukhina, 1963), but was rejected after radical reforms of Ranales (Takhtajan, 1966; Cronquist, 1968). The inclusion of *Trochodendron* and *Tetracentron* in Hamamelididae is supported by modern studies of floral morphology and anatomy (Endress, 1986), phenetic, cladistic and molecular analyses (Barabé, Bergeron and Vincent, 1982, 1987; Zavada and Dilcher, 1986; Donoghue and Doyle, 1989; Hufford and Crane, 1989; Hufford, 1992; Chase *et al.*, 1993; Doyle, Donoghue and Zimmer, 1994; Soltis *et al.*, 1997). Some of these authors (Barabé *et al.*, 1982, 1987; Donoghue and Doyle, 1989; Hufford and Crane, 1989) demonstrated a highly isolated, basal position of *Trochodendron* and *Tetracentron* within their subclass, but continued to treat them as 'natural hamamelids'. On the basis of *rbcL* molecular analyses, *Trochodendron* and *Tetracentron* are now considered as part of a monophyletic

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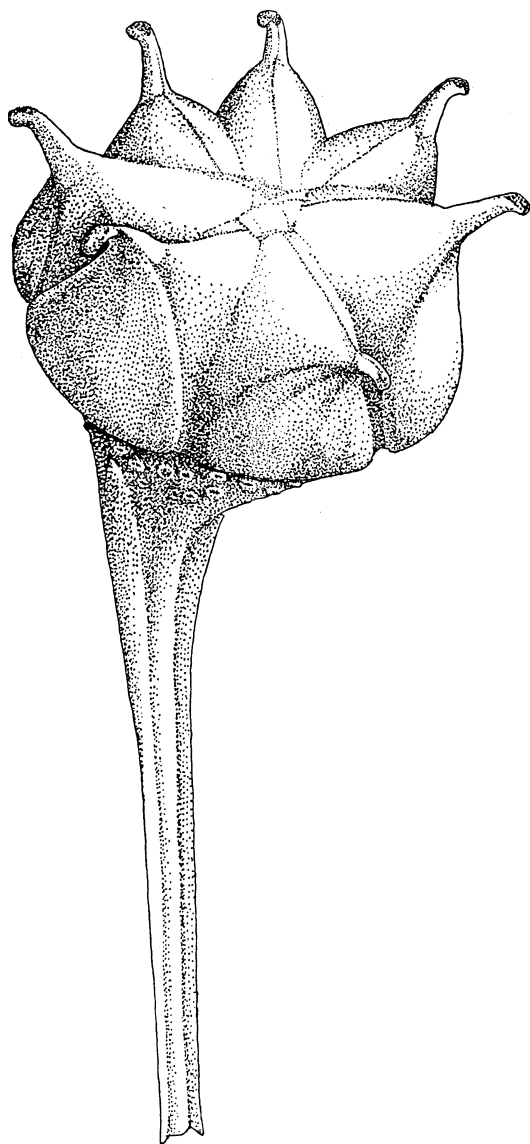


FIG. 1. Indehiscent capsule of *Trochodendron aralioides* Sieb. & Zucc.,  
× 20.

line sister to 'paleoherbs' (Soltis *et al.*, 1997), and a relationship with other typical hamamelids (Hamamelidaceae, Daphniphyllaceae, Cercidiphyllaceae) is questioned. Also, *rbcL* analyses (Chase *et al.*, 1993) demonstrated the polyphyly of Hamamelididae and proposed an affinity of Trochodendrales with 'eudicots' (Rosidae–Asteridae). In addition, Leroy (1988*a, b*, 1993) stated that, from floral morphology, Trochodendrales may not have originated from Magnoliales or related groups, but may represent one of the most archaic living angiosperms. Finally, from vegetative morphology, Hickey and Wolfe (1975) suggested that Trochodendrales (together with Cercidiphyllales) form a separate clade derived from prehamamelid ancestry.

The putative phylogenetic relationships of *Trochodendron* and *Tetracentron* with Hamamelidales in part found support from the conclusion of Melikian (1969, 1973*a, b*, 1991*a*), who studied seed anatomy of both genera. Nast and Bailey

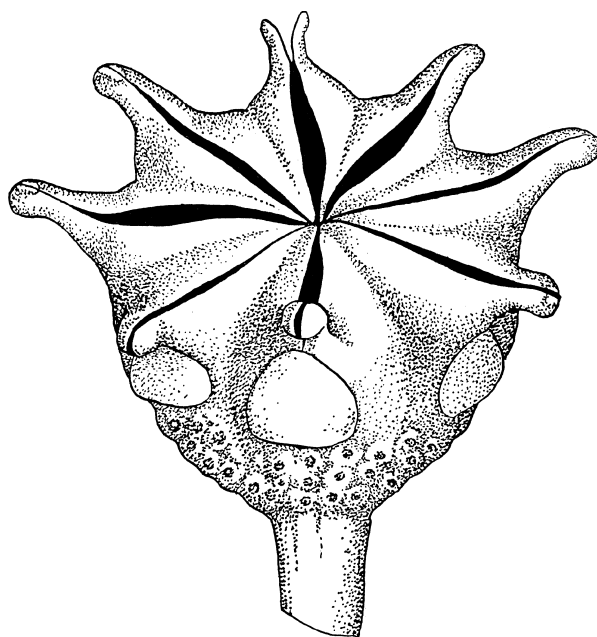


FIG. 2. Dehiscent capsule of *Trochodendron aralioides* Sieb. & Zucc.,  
× 20.

(1945) corrected van Tieghem's descriptions of trochodendraceous seed coats as bitegmic mesotestal [the seed coat of *Tetracentron* was not studied by van Tieghem (1900)]. They reported an exotegmic construction of seed coat for both genera. However, Melikian (1969, 1973*a, b*) described the seed coats of both *Trochodendron* and *Tetracentron* as strongly endotestal, supporting in part the putative phylogenetic relationships of *Trochodendron* and *Tetracentron*. Mohana Rao (1983), not citing works of Melikian (1969, 1973*a, b*), described the seed coat of *Trochodendron* as exotegmic, following in part Nast and Bailey (1945). Nevertheless, based on the original drawings of M. Plisko in the second volume of the modern encyclopedia of seed anatomy, *Anatomia seminum comparativa*, Danilova and Plisko (1991) referred to the seed coats of Trochodendraceae as the endotestal type, thereby confirming Melikian's point of view. In this volume, Tetracentraceae was also described as endotestal (Melikian, 1991*a*). Thus, three radically different descriptions of the seed coat anatomy of *Trochodendron* have been provided: (1) exotegmic, advanced by Nast and Bailey (1945) and followed by Mohana Rao (1983); (2) endotestal, proposed by Melikian (1969, 1973*a, b*, 1991*a*) and Danilova and Plisko (1991); and (3) mesotestal, erroneously advanced by van Tieghem (1900) and having only historical interest. Clarification of seed coat features is justified by quite differing views on the systematic relationships of these genera and different interpretations of seed coat features. Endotestal, mesotestal and exotegmic types of seed coat correspond to distinct and taxonomically remote morphogenetic types of seed coats (Corner, 1976). Therefore, different interpretations of type of seed coat for *Trochodendron* and *Tetracentron* may suggest different general systematic affinity. In this respect, I re-evaluate seed anatomy of *Tetracentron* and *Trochodendron* with detailed carpological descriptions. Few previous carpological de-

scriptions for Trochodendrales have been made, and *Tetracentron* has not been studied at all. *Trochodendron* was recently studied by Mohana Rao (1983), but the specialized features of the endocarp (sclerification) were not mentioned.

## MATERIALS AND METHODS

Mature fruits and seeds of *Trochodendron aralioides* Sieb. & Zucc. and *Tetracentron sinense* Oliv. were obtained from the Herbarium of the V. L. Komarov Botanical Institute of the Russian Academy of Sciences, St.-Petersburg (LE) and the D. Syreiščikov Herbarium of the Moscow M. V. Lomonosov State University (MW):

*Trochodendron aralioides* Sieb. & Zucc.—Japan, C. Houshu, Kyoto Pref., 3.06.1973, Y. Tateichi & J. Murata 4180 (LE);—Japan, Kyoto, Kitakuwata-gûn, Miyama-chô, Ashû Exp. Forest of Kyoto Univ. Agric., 1.10.1987, S. Masuda s.n. (LE, MW);

*Tetracentron sinense* Oliv.—China, Hupeh, Huantsao, 25.04.1930, W. Y. Chun 4138 (LE);—China, Yunnan, Mekong Valley, mountains of K'ang-pu, Yeh-chih, and An-wa, 5.05.1935, J. F. Rock 8932 (LE).

Drawings were made with [PA-4<sup>®</sup>] camera lucida from microtome serial cross-sections (5–10 µm) prepared by the usual paraffin method and stained with safranin-fast green (O'Brien and McCully, 1981). Scanning electron microscope (SEM) observations were made with a HITACHI S-405 A at 15 kV after sputtercoating with gold-palladium.

## OBSERVATIONS

*Trochodendron aralioides* Sieb. & Zucc.

*Mature fruit.* Fruits (Fig. 1) are 0.5–0.8 cm long and 0.5–0.8 cm wide, dark brown, rounded, with free styles, dorsiventrihiscent (dihiscent)\* capsules (Fig. 2) formed from a (4–) 7–11 (–17)-merous syncarpous gynoecium (Smith, 1945; Pervukhina and Yoffe, 1962) [not a *syncarpous multifolliculus* (Takhtajan, 1966, 1997), nor a *septicidal capsule* (van Tieghem, 1900: 269), and not a *follicetum* (Nast and Bailey, 1945; Spjut, 1994)]. The capsules are sometimes broken off with a long pedicel (two accrescent scales are visible) and a slightly expanded receptacle with numerous traces of stamens and staminodes, in which the carpels are basally embedded. The gynoecium is partially inferior. Each carpel has a prominent succulent nectariferous dorsal bulge (Fig. 3A and B) for insect attraction (van Tieghem, 1900; Endress, 1986). During anthesis there is an abaxial deformation of carpels, caused by the enhanced growth of the adaxial sides of the carpel, resulting in the displacement of the free styles to the outermost, upper part of the distally flattened fruit. The fruit sculpturing is papillate, with small

trichomes, laterocytic stomata and faceted cuticular sculpturing (Fig. 3C and D).

The vasculature of each carpel (Fig. 4) consists of five main vascular bundles (two ventral and three dorsal ones each originating from different sympodia). The dorsal system produces numerous lateral strands ending blindly in the dorsal bulge of every carpel (Nast and Bailey, 1945; Pervukhina and Yoffe, 1962; Melville, 1969). The dorsal bundles anastomose with adjacent dorsal strands, but then split again, and further anastomose with one of the ventrals (at upper levels), thus producing a partial common vascular supply to the ovules. The ventral traces, originating independently from the stelar bundles, anastomose with adjacent ventral strands in the region of lateral concrescence of carpels, and then again split into two independent ventral carpellary strands, each of them entering its own carpel. Pervukhina and Yoffe (1962) characterized such a type of coenocarpy as a '*deep syncarpy*'.

*Pericarp.* The pericarp (Fig. 5) is differentiated into a two–three layered endocarp, up to eight–ten layers of parenchymatous mesocarp and a three–four layered exocarp. The pericarp has a sclerendocarp-like construction typical of capsular fruits (Leclerc du Sablon, 1884; Weberbauer, 1898).

The epidermal cells of the parenchymatous exocarp are differentiated into one-celled thick-walled trichomes (Fig. 3C and D) with large cavities lacking dark tannin-like substances, in contrast to the two–three subepidermal layers of exocarp which contain tannin-like substances. The mesocarp is clearly differentiated into two zones. The outer region includes numerous slightly thickened 'oil' cells ['Sekretschläuche' of Harms (1897)] and cells filled with dark contents. The innermost part of the mesocarp is represented by (one–) two–three discontinuous layers of radially and irregularly branched osteosclereids (similar to that reported for leaves by Foster, 1945), adjoining fibres of sclerendocarp. The endocarp is composed of longitudinally oriented, heavily lignified, thick-walled and pitted fibres. As a rule, the single layer of thin-walled, unligified cells of the inner epidermis is obliterated.

Mohana Rao (1983) did not mention the presence of a sclerified endocarp, perhaps because he only examined immature fruits.

*Mature seed.* (Figs 6 and 7). The seeds (Fig. 6A) are relatively small, (3–4 mm long × 0.5–0.8 mm wide × 0.2–0.5 mm thick), dark brown to black and originate from anatropous, crassinucellate, bitegmic ovules. There are 15 to 25 seeds in each locule, arranged in two rows along the carpellary ventral suture, including numerous sterile seeds. Seeds are elongate, with a raphe ridge and a prominent subchalazal projection (Fig. 7A). The single vascular bundle makes a hair-pin loop in the subchalazal appendage of the ovule and ends blindly in the chalaza near the cup of hypostase (Fig. 6B). The mature seeds are abundantly albuminous and oily, with a small, straight dicotyledonous embryo (Fig. 6C). The micropyle is formed by the inner integument only (Yoffe, 1965), and not by both integuments (Nast and Bailey, 1945).

*Spermoderm.* The seed coat (Figs 8 and 9) is formed from both integuments. It is (endotestal-) exotegmic, and with

\* According to a new, improved terminology of fruit dehiscence (Doweld, 1997a) modern epithets for description of *dehiscencia fructuum* are formed with the base of Latin participle *-hiscens* (from Latin verb *hisco*—to open, yawn, split), thus avoiding ambiguous usage of former element *-cid* (from Latin verb *caedo*—to beat, break, cut): dorsicidal—dorsihiscent, ventricidal—ventrihiscent, dorsiventricidal—dihiscent, septicidal—lobihiscent.

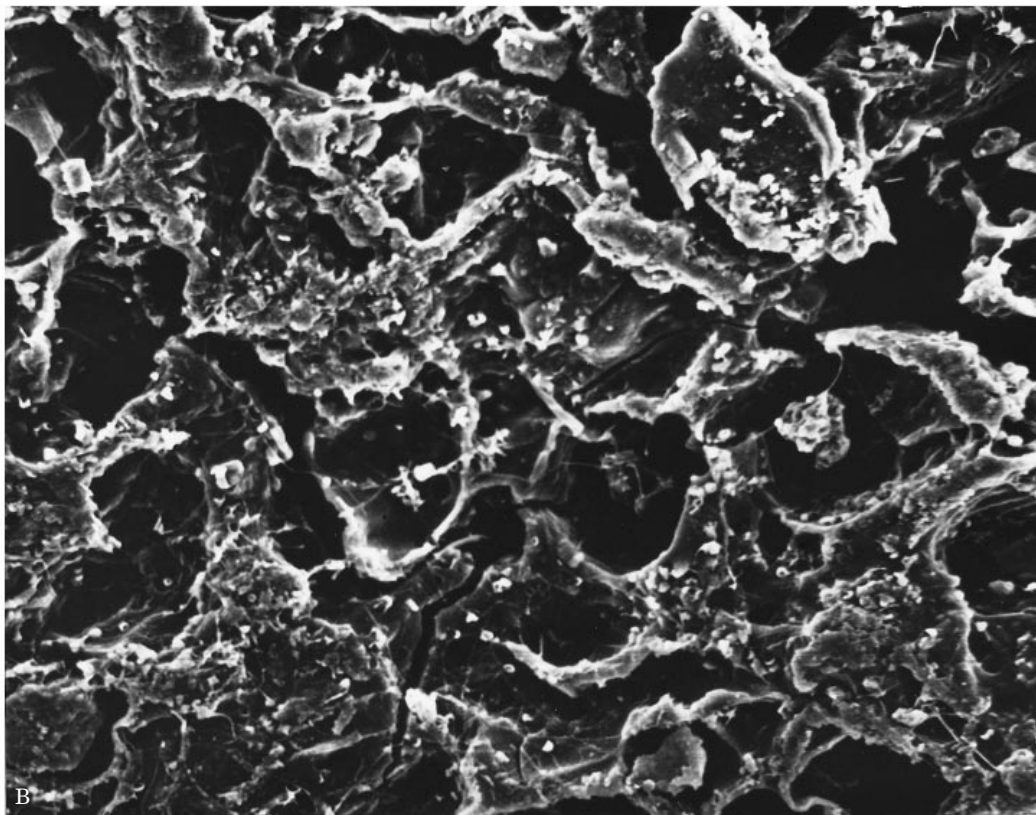
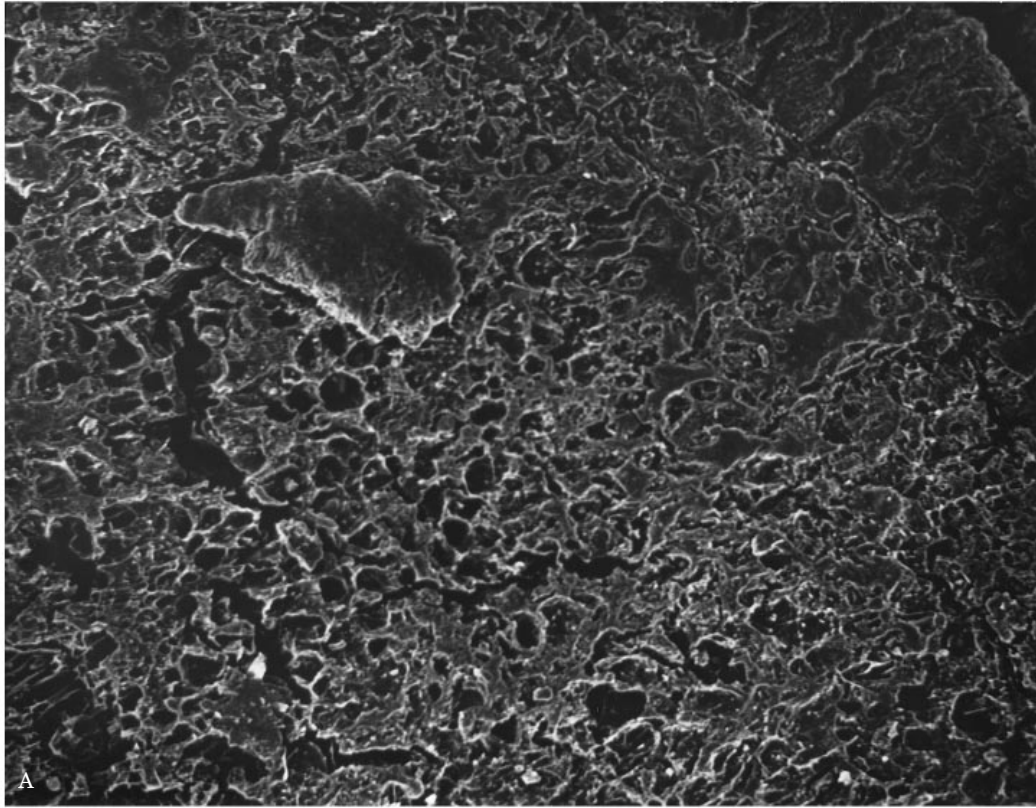


FIG. 3. A & B. For legend see facing page.

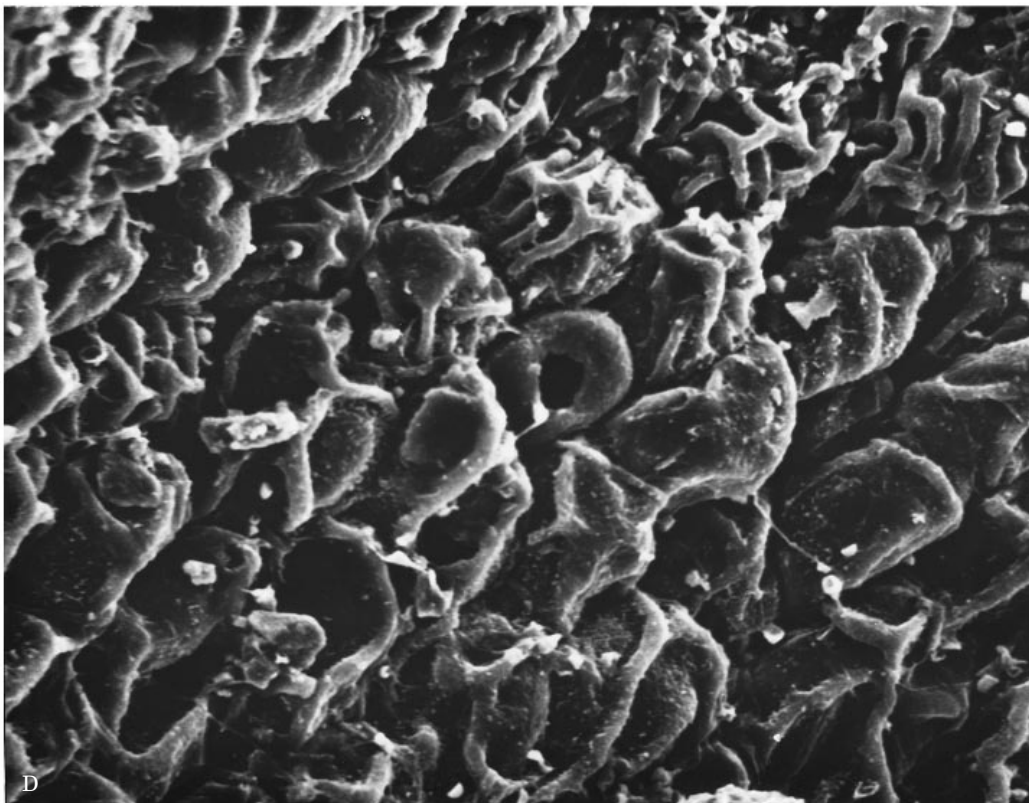
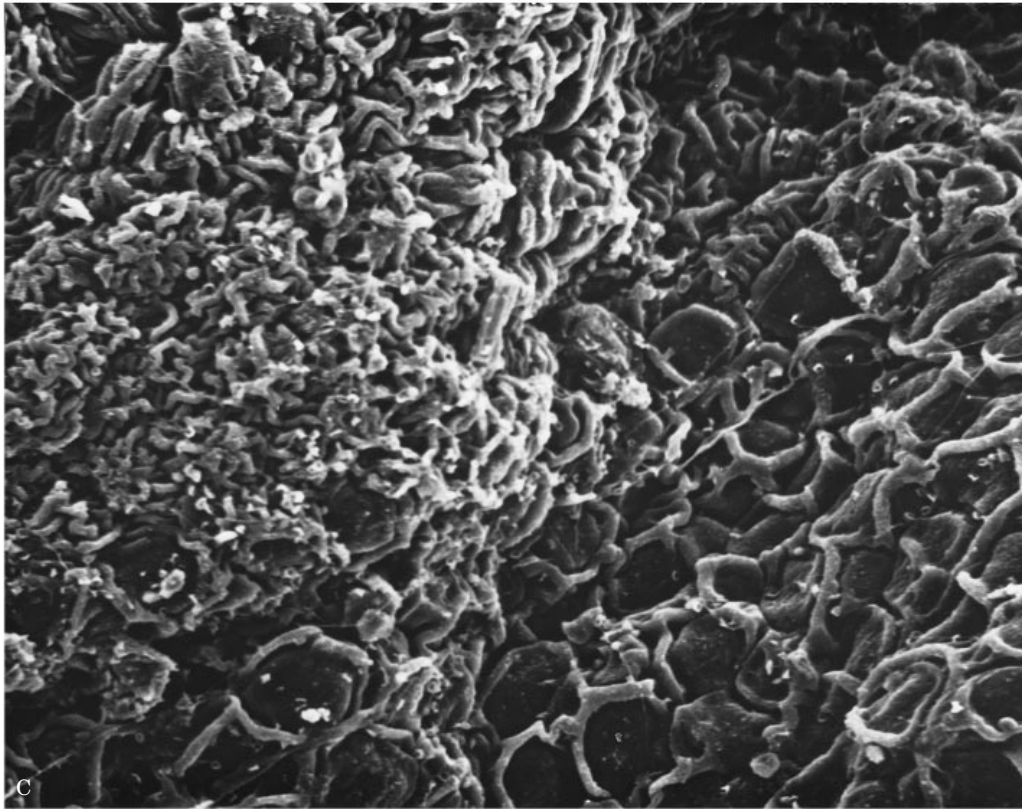


FIG. 3. SEM photographs of the fruit surface of the capsule of *Trochodendron aralioides* Sieb. & Zucc. A, General view of the dorsal nectariferous bulge,  $\times 100$ ; B, the same, enlarged,  $\times 500$ ; C, fruit surface,  $\times 500$ ; D, the same, enlarged,  $\times 750$ .

almost smooth seed sculpturing (Fig. 7B) and less differentiated striate cuticular sculpturing (Fig. 7C) owing to the tight packing of seeds within a locule.

The testa is composed of two layers: (1) the exotesta, which originates from the epidermis of the outer integument, and is formed by large, somewhat tangentially oblong, thin-walled cells filled with brown contents; and (2) the endotesta, which is formed by a single layer of prosenchymatous cells with numerous crystals and thickened outer periclinal and anticlinal walls. Cell wall thickness is more pronounced in the chalazal end of the seed, appearing as a despecialized sclerified endotestal mechanical system.

The tegmen is three to four-layered and clearly differentiated into three zones: an outer sclerified exotegmen; a middle colourless mesotegmen; and an inner brown endotegmen. The exotegmen is composed of strongly tangentially elongated cells with spiral thickenings on cell walls [tracheidal exotegmen] (Fig. 9C). The exotegmen is thinner at the chalazal end of seed. The cells of the exotegmen are oriented at right angles to the cells of the endotesta. The mesotegmen is formed by one or two layers of longitudinally oblong, colourless, thin-walled cells. The cells of this layer are usually collapsed. The endotegmen is represented by a single layer of large, longitudinally elongated thin-walled cells filled with tannin-like substances. This layer may penetrate into the endosperm region.

It is likely that the tanniferous endotegmen was misidentified by Nast and Bailey (1945: 273) as derived from the 'nucellus'. The polymorphism of the endotestal/exotegmic cell thickness, correlated with the proximity to the micropyle (exotegmen is more differentiated) or to the chalazal part of seed (endotesta is more differentiated) perhaps misled Melikian (1969, 1973*a, b*; Fig. 9A) and Danilova and Plisko (1991; Fig. 9C) when identifying the layers involved in the formation of the mature seed coat. The endotestal mechanical system of the trochodendraceous seeds is vestigial and reminiscent only of the ancestral state of integumentary differentiation. It is not equal to the mechanical function of the exotegmen, and therefore the trochodendraceous seed coats should be re-defined as (endotestal-) exotegmic. The descriptions of Mohana Rao (1983) proved to be the most accurate (Fig. 9B).

#### *Tetracentron sinense Oliv.*

*Mature fruit.* The fruit (Fig. 10) is a 0.3–0.5 cm long × 0.3–0.4 cm wide, brown to dull red, four-lobed, ventrihiscent capsule with four free styles (Fig. 11) formed from a 4-merous basally syncarpous gynoecium [not a *follicetum* (Nast and Bailey, 1945; Spjut, 1994), nor a '4-lobed berry' (*baie quadrilobée*) (van Tieghem, 1900: 359), and not a *syncarpous multifolliculus* (Takhtajan, 1966; 1997)]. Each carpel has a nectariferous dorsal bulge (Nast and Bailey, 1945; Endress, 1986). There is also a great abaxial deformation of carpels during anthesis: ventral parts of the capsule increase to such an enormous extent that the styles are displaced to occupy an external, apparently abaxial, and basal position in the mature fruit. The fruit sculpturing is smooth with a faceted-reticulate cuticular sculpturing (Fig. 12A and B).

The vasculature of the carpel (Fig. 13) consists of five main vascular bundles: two ventral and three dorsal ones originating respectively from the stelar and cortical vascular systems (Melville, 1969). The dorsal system produces a very small number of phloic strands vascularizing the small dorsal nectariferous bulge. The three dorsal strands sometimes anastomose with each other, but never with any ventral traces (Nast and Bailey, 1945) or adjacent dorsal traces, as observed in *Trochodendron*. The ventral traces, originating independently from the stelar bundles, anastomose with adjacent ventral traces at the septae of the capsule, and once again split into two distinct ventral carpellary strands, as observed in *Trochodendron*.

*Pericarp.* The pericarp (Fig. 14) is differentiated into a two-layered exocarp, up to a four–five layered parenchymatous mesocarp and a three–four layered sclerified endocarp. The sclerendocarp-like construction of the whole pericarp is typical of capsular fruits (Leclerc du Sablon, 1884; Weberbauer, 1898), but not of berry-like fruits [van Tieghem's (1900) description].

The epidermal cells of the parenchymatous exocarp are differentiated into one-celled thick-walled small trichomes with large cavities lacking tannin-like dark contents, and a subepidermal exocarpic parenchyma, composed of large, slightly oblong tanniferous cells. The mesocarp is formed by numerous tanniferous cells, and very rarely 'oil' cells with somewhat thickened walls. The branched osteosclereids are practically absent in the pericarp of *Tetracentron*. The endocarp is represented by three (–four) layers of thickened, sclerified, pitted colourless longitudinal fibres. The cells of the innermost layer of the endocarp have prominently thickened walls.

*Mature seeds* (Figs 15 and 17). The seeds (Fig. 15A) are relatively small (3–4 mm long × 0.4–0.7 mm wide × 0.3–0.4 mm thick), yellow to brownish and originate from the anatropous, crassinucellate, bitegmic ovules. There are five–eight (–ten) seeds per carpel, arranged in two rows along the carpellary ventral suture. Seeds are long, with a raphal ridge and a prominent subchalazal projection (Fig. 17A). The single vascular strand makes a hair-pin loop in the subchalazal protrusion and ends blindly in the chalaza, near the cup of hypostase (Fig. 15B). The mature seeds are abundantly albuminous, oily, with a straight small dicotyledonous embryo (Fig. 15C). The micropyle is formed only by the inner integument.

*Spermoderm.* The seed coat (Figs 16 and 18) originates from both integuments and has a distinctive faceted sculpturing (Fig. 17B and C).

The testa consists of two layers. The exotesta is represented by very large, sharply radially elongated, thin-walled cells filled with nearly colourless contents. The endotesta is composed of slightly tangentially oblong thin-walled cells, in which crystals are sometimes present. Their external periclinal walls, as well as the anticlinal walls, are somewhat thickened (but not sclerified). These cells are thicker in the chalazal region of the seed. The endotestal layer is partially reminiscent of the more thickened endotesta of *Trochodendron*, but in fact, the cells of the endotesta of *Tetracentron* are less specialized.

The tegmen is three-layered (three–four layers at micro-

TABLE 1. Summary of some characters differing between *Tetracentron* and *Trochodendron*

	<i>Trochodendron</i>	<i>Tetracentron</i>
Inflorescences	Botryoid	Spike
Flowers		
Tepals	In bud enclosed by cataphylls 1–5 (rudimentary)	In bud enclosed by tepals 4 in 2 alternate pairs
Stamens	Numerous	4
Gynoecium	(4–) 7–11 (–17)-carpellary	4-carpellary
Styles	Displaced to the outermost, upper part of fruit	Displaced to abaxial-basal part of fruit
Capsules		
Pedicel	Long with two accrescent scales and expanding receptacle	Sessile
Shape	Rounded	4-lobed
Fruit sculpturing	Papillate	Smooth
Cuticular sculpturing	Faceted	Faceted-reticulate
Dehiscence	Dorsiventrihiscent	Ventrihiscent
Pericarp		
Exocarp	3–4 layers	2 layers
Tanniferous hypoderma	2–3-layered	1-layered
Mesocarp	8–10 layers	4–5 layers
	Differentiated into 2 zones, innermost part represented by branched osteosclereids (2–3 discontinuous layers)	No differentiation into 2 zones, no osteosclereids or their discontinuous layers
Endocarp	2–3 layers	3–4 layers
Seeds		
Number, per locule	15–25	5–8 (–10)
Vascular supply	By ventrals and partially by common (dorsals anastomose with ventrals)	By ventrals only
Spermoderm	(Endotestal-) exotegmic	Exotegmic
Seed sculpturing	Almost smooth	Faceted
Cuticular sculpturing	Striate	Smooth
Testa		
Exotesta	1 tanniferous layer	1 colourless layer
Endotesta	1 layer of prosenchymatous thickened cells	1 layer of prosenchymatous cells with slightly thickened walls
Tegmen	3–4-layered	3-layered
Exotegmen	Tracheidal	Tracheidal
Endotegmen	1 layer penetrating into endosperm	1 layer not penetrating into endosperm

pile only) and differentiated into three distinct zones: a sclerified exotegmen, a colourless mesotegmen and a brown endotegmen. The exotegmen is represented by sharply tangentially elongated cells with strongly thickened walls [tracheidal exotegmen]. Cell walls have small invaginations and a somewhat striate appearance caused by numerous spiral thickenings. The spiral thickenings are less differentiated than in *Trochodendron*, and look comparatively reduced (vestigial). The exotegmic cells are somewhat thinner at the chalazal end of the seed. The exotegmic sclereids are oriented perpendicularly to the oblong cells of the endotesta, and to all other cells of the tegmen. The colourless mesotegmen is composed of thin-walled, longitudinally elongated cells, which are usually collapsed. In contrast, the single layer of thin, longitudinally oblong tanniferous cells of the endotegmen does not undergo destruction. In contrast to *Trochodendron*, the endotegmen of *Tetracentron* does not project into the endosperm region.

The rudimentary endotestal thickenings represent a connecting link between the more archaic (endotestal-) exotegmic seed coats of *Trochodendron* and the strongly exotegmic spermoderm of *Tetracentron*. The polymorphism of endotestal/exotegmic cell thickness is not so readily visible in *Tetracentron* as it is in *Trochodendron*, and

therefore, Melikian's (1991*a*) descriptions of the seed coats of *Tetracentron* as endotestal are shown to be completely erroneous (Fig. 18). The attribution of the tanniferous endotegmen as a nucellar derivative (Nast and Bailey, 1945: 273) is also shown to be erroneous.

## DISCUSSION

The present study of the carpology and seed anatomy of *Trochodendron* and *Tetracentron* supports the standpoint of Smith (1945, 1972) and his successors (Cronquist, 1992; Takhtajan, 1997) that both genera deserve a distinct familial rank, as suggested by van Tieghem (1900) and should be placed in a single order Trochodendrales *sensu* Takhtajan (1997). Differences in spermoderm and pericarp anatomy supplement previously recognized differences in vegetative and productive features between the two genera (Table 1). The most significant differences in seed coat anatomy are the (endotestal-) exotegmic *vs.* exotegmic construction and different seed and cuticular sculpturings. Significant differences in pericarp anatomy are the lack of differentiation of the mesocarp into two zones (no osteosclereids and their discontinuous layers within *Tetracentron*), a reduced number of layers in the exocarp and mesocarp, and an enlarged



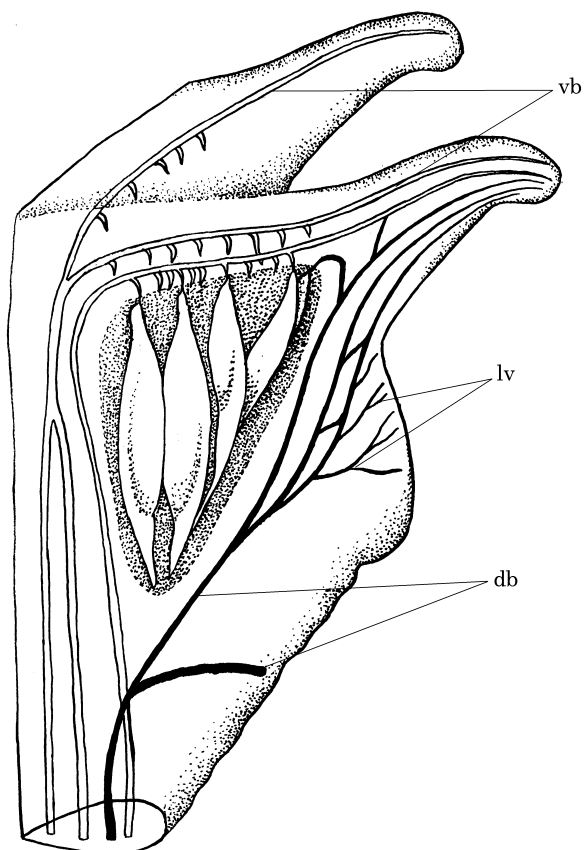


FIG. 4. Vascular skeleton of the fruit of *Trochodendron aralioides* Sieb. & Zucc.,  $\times 25$ . vb, Ventral bundles; lv, lateral bundles; db, dorsal bundles.

sclerendocarp within *Tetracentron*. The new observations of seed coat type and pericarp structure of *Trochodendron* and *Tetracentron* allow a re-evaluation of the systematic position of both genera within the system of flowering plants.

#### Relationships with Eupteleales

The order Eupteleales, comprising a single family Eupteleaceae Wilhelm (Takhtajan, 1997), occupies an isolated position in the 'lower' Hamamelididae. Corner (1976) suggested that the seed coat structure of *Euptelea* Sieb. & Zucc. resembles that of *Trochodendron* and *Tetracentron*. However, in light of present carpological and seed anatomical studies of both genera, this view is questioned. The eupteleaceous seed coat is reportedly formed from both integuments, with a solitary layer of sclereids in the endotesta (Corner, 1976), not in the exotegmen, as observed in *Tetracentron/Trochodendron*, and with greatly enlarged thin-walled exotestal cells (Melikian and Korčagina, 1991). The inner integument of *Euptelea* is composed only of two–three layers of tanniniferous, tangentially oblong parenchymatous cells (sometimes partially obliterated); no sclereids are visible. The endotestal seed coats of *Euptelea* could be considered to be derived from a common ancestral stock with *Tetracentron/Trochodendron*, if it was possible to suggest at least an endotestal-exotegmic seed coat prototype. The remnants of such a construction are clearly observed

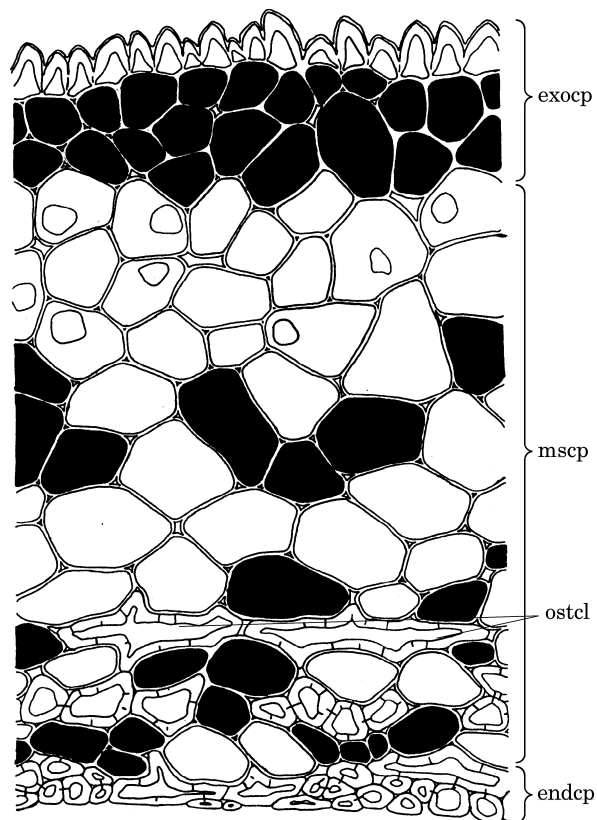


FIG. 5. Cross-section of the pericarp of *Trochodendron aralioides* Sieb. & Zucc.,  $\times 20$ . Exocp, exocarp; mscp, mesocarp; endcp, endocarp; ostcl, osteosclereids.

within the (endotestal-) exotegmic seed coats of *Trochodendron*, which retain a certain thickness of cells in the endotesta. This may suggest that a putative ancestral seed coat construction may have undergone different modes of specialization, resulting in the highly specialized seed structure of *Euptelea*. However, the transference of the mechanical function from endotesta to exotegmen, as observed in *Trochodendron/Tetracentron*, indicates a different type of seed coat to that of endotestal *Euptelea*, which lacks any mechanical elements in the tegmen. A close phylogenetic relationship between *Euptelea* and *Tetracentron/Trochodendron* is therefore not supported by seed coat anatomy. The same is true from the stand point of carpology: the pericarp of samaroid flattened follicles in a capsetum (follicetum) of *Euptelea* has no sclerendocarp, which is typical for capsules in Trochodendrales. Differences in fruit type, vascular skeleton, together with a distinctive archaic coincidence of the stigma with ovule placentation in *Euptelea* (Doweld, 1996a) emphasize a morphogenetic gap between these taxa. Recent molecular studies (Chase *et al.*, 1993; Doyle *et al.*, 1994; Soltis *et al.*, 1997) confirm this view, suggesting a ranunculid affinity of *Euptelea* rather than a hamamelidid one.

#### Relationships with Cercidiphyllales

The genus *Cercidiphyllum* Sieb. & Zucc., comprising the distinct monotypic family Cercidiphyllaceae Engl., is mor-



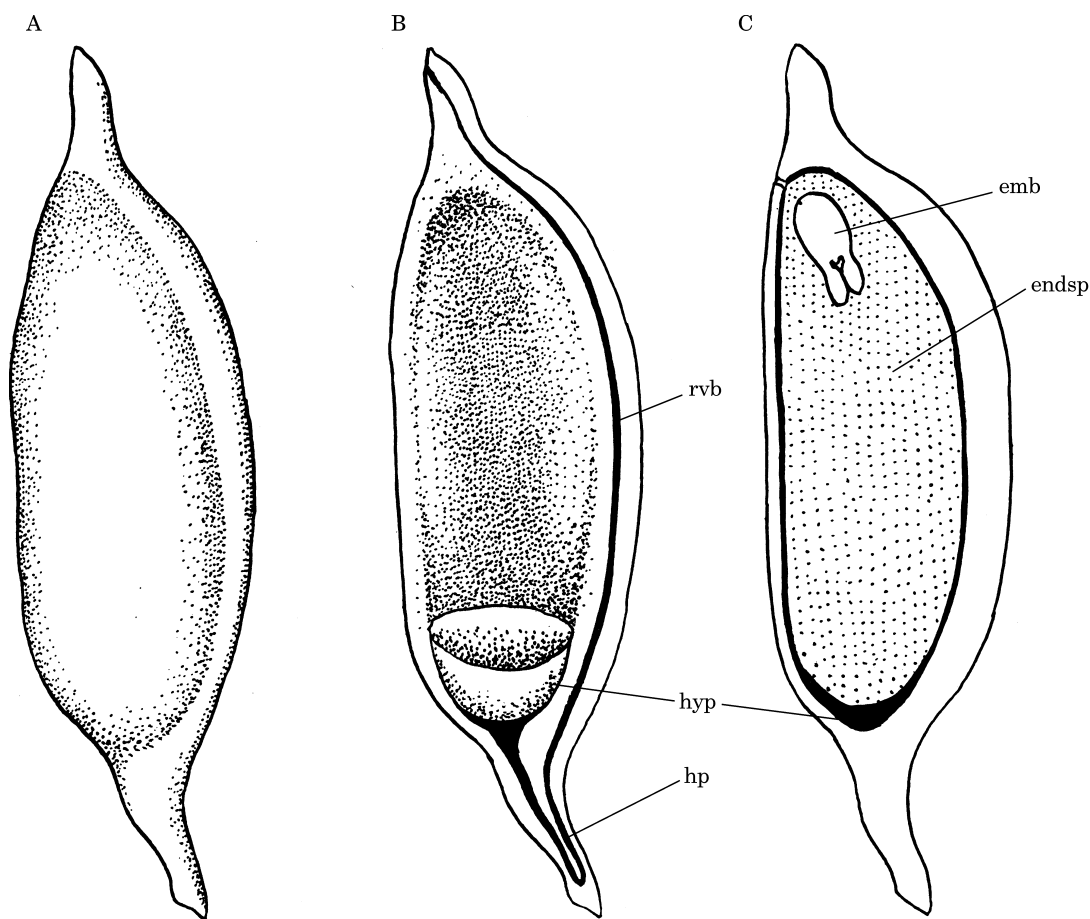


FIG. 6. Seeds of *Trochodendron aralioides* Sieb. & Zucc.,  $\times 50$ . A, General view; B, vascularization of the seed; C, longitudinal section of seed showing minute embryo (emb) and abundant endosperm (endsp). rvb, Raphal vascular bundle; hp, vascular hair-pin loop; hyp, hypostase.

phologically distinct from its putative hamamelid relatives (Harms, 1916, 1918). The family Cercidiphyllaceae is therefore usually treated as a separate monotypic order Cercidiphyllales within Hamamelididae (Takhtajan, 1997) or placed within Hamamelidales and related both to Hamamelidaceae (especially *Disanthus* Maxim.) and to Trochodendrales and Magnoliales (Cronquist, 1992). Maximowicz (1872) pointed out a close relationship among *Cercidiphyllum*, *Trochodendron* and *Euptelea*, but this is not supported by carpology and seed anatomy. The fruits of *Cercidiphyllum* are follicles associated in distinctive racemoid free infructescences—follicaria; they have nothing in common with the syncarpous capsules of *Trochodendron* and *Tetracentron*, except for ventrihiscent opening. The spermoderm of Cercidiphyllaceae is formed from two integuments, is almost parenchymatous, thin-walled (Swamy and Bailey, 1949) or with a solitary mesotestal (?) layer of slightly thickened rectangular cells (Melikian, 1969, 1973b, 1991e). The number of layers in the testa (six–seven) and tegmen (two–three) is different from that found in *Trochodendron* and *Tetracentron*. The massive embryo of *Cercidiphyllum* has two differentiated flat cotyledons, a long hypocotyl and scanty endosperm, in contrast with a

small embryo and copious endosperm in seeds of *Trochodendron/Tetracentron*. The only similarity between seeds of Cercidiphyllales and Trochodendrales is found in the presence of a distinctive vascular hair-pin loop in the prominent subchalazal projection, but this is a common occurrence in different families and orders of angiosperms (e.g. Greiaceae Hutchins.—Nemirovič-Dančenko, 1996; Rosaceae Juss.—Melikian and Bondar, 1996; Butomaceae L. C. Rich.—Croizat, 1947; Thymelaeaceae Juss.—Corner, 1976; Nemirovič-Dančenko, 1992) and even gymnosperms (*Podocarpus ferrugineus*—Croizat, 1947). The presence of such a complicated vascular structure is not in itself necessarily indicative of a close relationship between these taxa. Pervukhina and Yoffe (1962) suggested that the presence of a subchalazal projection, which is elongated and transformed into a wing-like appendage, is correlated with the occurrence of mucilaginous substances in the developing ovary. In this connection the subchalazal protrusion may serve as a haustorium. In my opinion, its origin may be better explained by the reduction of chalazal arilloids (or arils), as in Thymelaeaceae (Corner, 1976; Nemirovič-Dančenko, 1992). For example, the seeds of *Aquilaria malaccensis* Lamk. and *A. hirta* Lamk. have a prominent

TABLE 2. Summary of principal carpological and permatological<sup>1</sup> features of the orders of Hamamelididae (sensu Takhtajan, 1997)

Taxon	Fruit	Pericarp*			Ovule	Spermoderm	Endosperm	Embryo
		Exocarp	Mesocarp	Endocarp				
Trochodendrales Trochodendraceae	Capsule	—	—	+	Anatropous crassinucellate bitegmic	(Endotestal- exotegmic	Copious	Small, differentiated
Tetracentraceae	Capsule	—	—	+	Anatropous crassinucellate bitegmic	Exotegmic	Copious	Small, differentiated
Cercidiphyllales Cercidiphyllaceae <sup>2</sup>	Follicles in a follicarium (infructescence)	—	—	+	Anatropous crassinucellate bitegmic	(?) Mesotestal- endotegmic	Wanting	Massive, differentiated
Eupteleales Eupteleaceae <sup>3</sup>	Capsetum (= follicetum)	—	—	+	(Ana-) epitropous crassinucellate bitegmic	Endotestal	Copious	Small, differentiated
Eucommiales Eucommiaceae <sup>4</sup>	Capsule	—	—	+	Anatropous crassinucellate unitegmic (pachychalazal?)	Exotestal (parenchotestal) or pachytestal (?)	Wanting	Massive, differentiated
Hamamelidales Hamamelidaceae <sup>5</sup> Hamamelidoideae	Capsule (drupe?)	—	— (+?)	+	Anatropous crassinucellate bitegmic	Sclerotestal, sarcotestal ( <i>Trichocladus</i> , <i>Sinowilsonia</i> )	Copious	Small, slightly differentiated
Disanthoideae	Capsule (drupe?)	—	— (+?)	+	Anatropous crassinucellate bitegmic	Mesendotestal (sarcotestal?)	Copious	Small, slightly differentiated
Exbucklandioideae (= Bucklandiaceae)	Capsules in a capsarium (infructescence) Capsules	—	—	+	Anatropous crassinucellate bitegmic	Exo-endotestal ( <i>Exbucklandia</i> ), Exotestal ( <i>Chumia</i> ) Exotestal	Scanty	Large
Rhodoleiaceae <sup>6</sup>	Capsules in a capsarium (infructescence)	—	—	+	Anatropous crassinucellate bitegmic	Exotestal	Copious	Large
Altingiaceae <sup>7</sup>	Capsules in a capsarium (infructescence)	—	—	+	Anatropous tenuinucellate bitegmic	Endotestal (exotegmic?)	Copious	Large
Platanaceae <sup>8</sup>	Capsetum	—	—	+	Orthotropous crassinucellate bitegmic	Mesotestal (exotegmic?)	Wanting	Large, straight

Daphniphyllales Daphniphyllaceae <sup>9</sup>	Drupe	—	+	+	Anatropous crassinucellate bitegmic	Parenchotestal, endotegmic	Copious	Small, straight
Balanopales Balanopaceae <sup>10</sup>	Drupe (?)	— (?)	+	+	Anatropous unitegmic (pachychalazal?)	Parenchotestal (pachytetal?)	Wanting	Large, straight
Didymelales Didymelaceae <sup>11</sup>	Drupeole (monomerous drupetum)	—	+	+	(Epi-) hemitropous bitegmic	Parenchotestal	Absent	Massive
Myrothamniales Myrothamnaceae <sup>12</sup>	Capsules	—	—	—	Anatropous crassinucellate bitegmic	Unspecialized (exotegmic?)	Copious	Small, straight
Buxales Buxaceae <sup>13</sup>	Drupe	—	+	+	Anatropous crassinucellate bitegmic	Exotestal, exomesotestal- exotegmic, parenchotestal ( <i>Notobuxus</i> ) Unknown (exotestal?)	Copious ( <i>Buxus</i> , <i>Notobuxus</i> ) or wanting ( <i>Sarcococca</i> )	Large or small, straight
Stylocerateales <sup>14</sup> Simmondsiales Simmondsiaceae <sup>15</sup>	Drupe (?) Capsules	— (?) —	+	+	Anatropous, bitegmic crassinucellate bitegmic	Exotestal-endotegmic	Copious Wanting or absent	Large, straight Large, straight
Casuarinales Casuarinaceae <sup>16</sup>	Ascades	—	—	+	(Ana-) hemitropous crassinucellate bitegmic	Exotestal	Absent	Large, straight

[continued overleaf]

TABLE 2 (cont.)

Taxon	Fruit	Pericarp*			Ovule	Spermoderm	Endosperm	Embryo
		Exocarp	Mesocarp	Endocarp				
Fagales								
Fagaceae <sup>17</sup>								
Fagoideae	Rindine	+	—	—	(Ana-) hemitropous crassinucellate bitegmic	Exotestal or parenchotestal	Wanting or absent	Massive
Castaneoideae	Rindine	+	—	—				
Trigonobalanoidae	Rindine	+	—	—				
Quercoidae	Rindine	+	—	—				
Nothofagoideae (= Nothofagaceae)	Ascadine	—	+	—	(?) Tenuinucellate unitegmic (pachychalazal?)	Parenchotestal (pachytetal?)	Wanting	Large
Betules								
Betulaceae <sup>18</sup>								
Betuloideae	Drupine	—	+	+	(Epi-) anatropous, hemitropous ( <i>Duschekia</i> ) crassinucellate unitegmic (pachychalazal?)	Exo-endotestal (pachytetal?)	Wanting	Massive, straight
Carpinoideae (= Carpinaceae)	Drupine	—	+	+	(Epi-) anatropous crassinucellate bitegmic	Parenchotestal (exotestal?)	Wanting	Massive, straight
Coryloideae (= Corylaceae)	Caryine	+	+	—	Campylotropous crassinucellate unitegmic (pachychalazal?)	Exo-endotestal (exopachytetal?)	Wanting	Massive, straight
Myricales								
Myricaceae <sup>19</sup>								
Myricoidae	Assare (sometimes associated in infructescences—assaria)	+	—	+	Orthotropous crassinucellate pachychalazal	Exopachytetal, parencho-pachytetal ( <i>Comptonia</i> )	Wanting or absent	Massive, straight
Canacomyricoidae (= Canacomyricaceae)	Berry	—	—	—	Orthotropous crassinucellate pachychalazal	Accrescent with a pericarp, parencho-pachytetal	Wanting or absent	Massive, straight
Rhoipteleales								
Rhoipteleaceae <sup>20</sup>	Drupe	—	+	+	(Hemi-) anatropous crassinucellate bitegmic	Exotestal	Wanting	Massive, straight

Juglandales Juglandaceae <sup>21</sup>	Ascadine	—	+	—	Orthotropic crassinucellate pachychalazal	Exopachytestal	Wanting	Massive, straight
Juglandoideae	Ascadine (?)	— (?)	+ (?)	— (?)	Orthotropic crassinucellate pachychalazal	Exopachytestal	Wanting	Massive, straight
Platycaryoideae (= Platycaryaceae)	Ascadine (?)	— (?)	+ (?)	— (?)	Orthotropic crassinucellate pachychalazal	Exopachytestal	Wanting	Massive, straight

\* Pericarp: sclerified (+), non sclerified (—).

<sup>1</sup> *Phermatology, adj.*—*phermatology* (from Greek φέρμα—'that which is borne' and λόγος—'discourse')—a new adopted name for the science of seeds, instead of unmanageable *spermatology* (Doweld, 1997*b*).

<sup>2</sup> Melikian (1991*e*).

<sup>3</sup> Melikian and Korčagina (1991); the fruit type is corrected (not a '1-seeded nucule' or 'indehiscent capsule').

<sup>4</sup> Melikian (1991*f*); the fruit type is corrected (not a 'leathery samaroid nucule'). The term *pachytesta* (*pachytestal, adj.*) is introduced by Doweld (1996*b, c*; in Čerňakovskaya and Doweld, 1996; Doweld, 1998*b*) for description of the pachychalazal seed coats in mature seeds.

<sup>5</sup> Melikian (1972, 1973*a, b, c*, 1991*b*); the histological differentiation of pericarp is poorly known, and it may be possible to find a typical drupaceous (mesendocarpic) structure of the whole pericarp within so-called 'woody capsules'.

<sup>6</sup> Melikian (1972, 1991*g*).

<sup>7</sup> Melikian (1971, 1991*d*).

<sup>8</sup> Melikian (1991*c*); the fruit type is corrected (not 'multinuculae' or 'multifolliculus'); it is formed from the apocarpous gynoeccium and has a sclerified endocarp-like pericarp construction (Bretzler, 1924), which is typical of capsular fruits (*capsules*) according to a new system of classification of the fruits (Doweld and Sorokina, 1997).

<sup>9</sup> Petrova (1991*a*); Bhatnagar and Kapil (1982).

<sup>10</sup> Nemirovič-Dančenko (1991).

<sup>11</sup> Kravzova (1991*a*); the fruit type is corrected (not a 'drupe' restricted only to the superior coenocarpous fruits), it is a monomeric drupetum comprising of a single drupeole (monocarpeal gynoeccium).

<sup>12</sup> Petrova (1991*b*); Jäger-Zürm (1966).

<sup>13</sup> Petrova (1991*c*); Baillon (1859); the fruit type is corrected (not 'capsules') because all so-called 'capsules' have a typical drupaceous (mesendocarpic) differentiation of the pericarp.

<sup>14</sup> Kravzova (1991*b*); Baillon (1859).

<sup>15</sup> Petrova (1991*d*); Wunderlich (1967).

<sup>16</sup> Korčagina (1991*a*); the fruit type is corrected according to a new system of classification of the fruits (Doweld and Sorokina, 1997) (not a 'nut-like', a '2-4-seeded capsule' or even 'follicle'), being re-named on 'ascade'—an adopted term for all superior coenocarpous fruits having a mechanical system (sclerification) in the mesocarp only (Doweld, 1996*d*; Doweld and Sorokina, 1997).

<sup>17</sup> Korčagina (1991*b*); Langdon (1939); Soepadmo (1968), the fruit types are corrected according to a new system of classification of the fruits (Doweld and Sorokina, 1997) (not 'nuts'). In Fagoideae, Trigonobalanoidae, Castaneoideae and Quercoidae the sclerification occurs in the exocarp only (Soepadmo, 1968), and therefore these fruits should be termed 'rindines' (suffix *-ine* is used to separate inferior fruits from superior ones); in contrast, in Nothofagoideae (*Nothofagus*) there is a sclerified mesocarp only, and these fruits should be named as 'ascadines' (Doweld, 1996*d*).

<sup>18</sup> Korčagina (1991*c*); Melikian (1973*b*); the fruit types are corrected (not 'nuts') because the usually sclerified mesendocarp-like pericarp is typical of drupaceous (*drupa*) fruits (*Alnus, Betula, Carpinus*) or sclerified exomesocarp-like pericarp construction is typical of caryaceous (*Caryum*) fruits. The last term has been adopted in the new system of classification of the fruits (Doweld and Sorokina, 1997) for the fruits having the mechanical system (sclerification) in the exocarp and mesocarp. The suffix *-in(e)* is used to separate inferior forms of fruits from superior ones.

<sup>19</sup> Vyšenskaya (1991*a*); Corner (1976); the fruit type is corrected (not a 'drupe' or 'nut') because the pericarp is clearly differentiated into a sclerified exocarp (?), parenchymatous mesocarp and sclerified endocarp. Such a pericarp structure is clearly of assaraceous (*assarae*) fruits [assare (кожыпет)—an adopted term for all superior coenocarpous fruits having the mechanical system (sclerification) in the exocarp and endocarp (Doweld and Sorokina, 1997)]. We adopted the interpretation of Corner (1976) that the myricaceous seed coats are pachychalazal, not unitegmic or bitegmic (*cf.* Vikhireva, 1957; Macdonald and Sattler, 1973).

<sup>20</sup> Vyšenskaya (1991*b*); the fruit type is corrected (not a 'nut'), having a typical mesendocarpic stone.

<sup>21</sup> Vyšenskaya (1991*c*); Vaughan (1970), Leroy (1955); the fruit type is corrected according to a new system of classification of the fruits (Doweld and Sorokina, 1997) because the pericarp is clearly differentiated into a parenchymatous exocarp and endocarp (?), and sclerified mesocarp. Such a pericarp structure is of ascadaceous (*ascada*) fruits (Doweld, 1996*d*). Data on the histological differentiation of the pericarp in Platycaryoideae are missing.

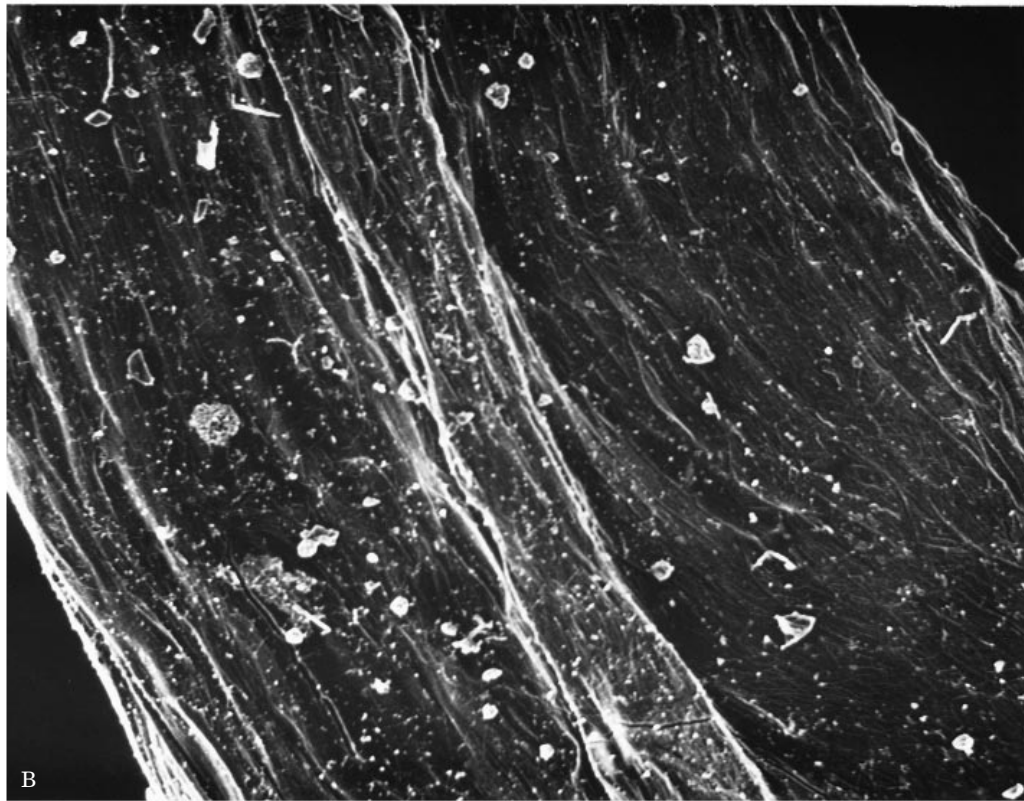
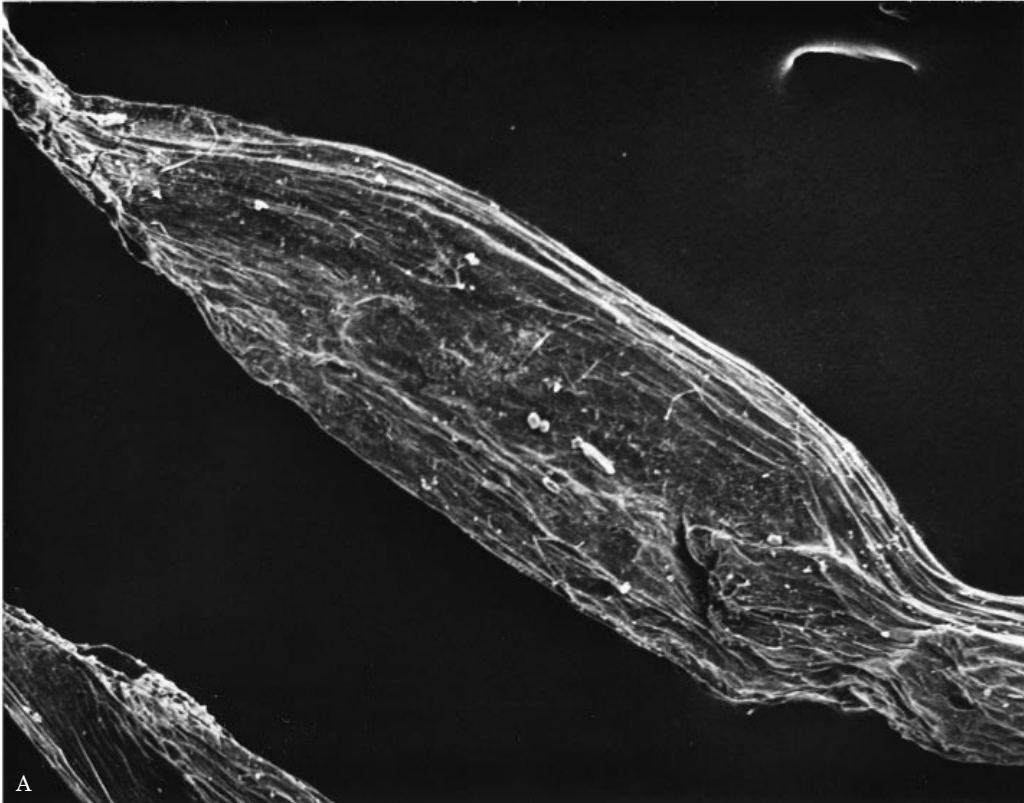


FIG. 7. A & B. For legend see facing page.

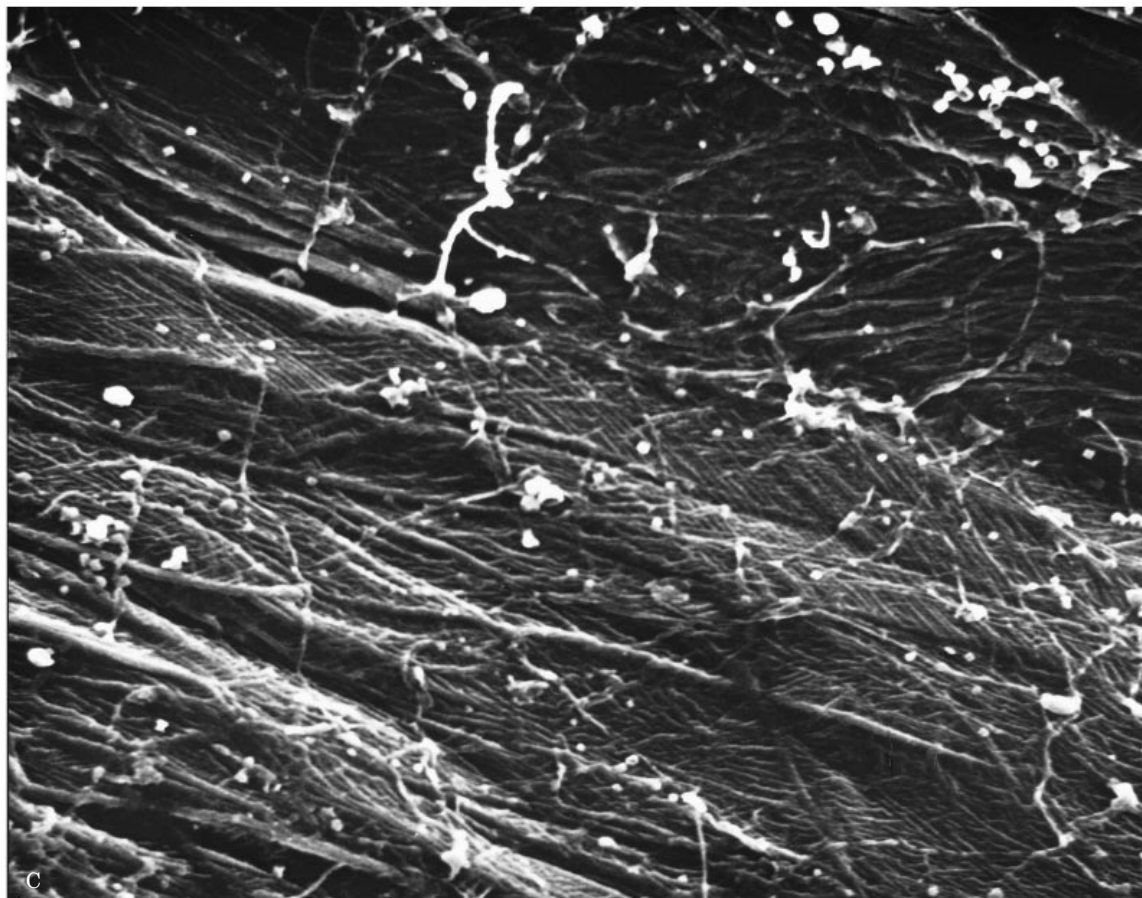


FIG. 7. SEM photographs of the seed surface of *Trochodendron aralioides* Sieb. & Zucc. A, General view,  $\times 50$ ; B, seed sculpturing,  $\times 150$ ; C, cuticular sculpturing,  $\times 750$ .

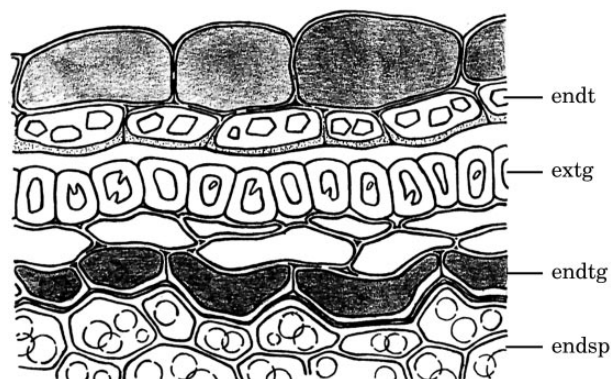


FIG. 8. Cross-section of the spermoderm of *Trochodendron aralioides* Sieb. & Zucc.,  $\times 40$ . extg, Exotegmen; endt, endotesta; endtg, endotegmen; endsp, endosperm.

subchalazal appendage (varying from a small fold to a tail-like protrusion); the vascular bundle leaving the placenta enters a massive arilloid (or aril), makes a loop and ends blindly in the chalaza. Further reduction may lead to the formation of the trochodendraceous type of subchalazal protrusion with a vascular hair-pin loop. The relationship with Dilleniaceae having seeds with arils and/or arilloids proposed below may support this.

#### Relationships with Hamamelidales

The (endotestal-) exotegmic seed coats of *Trochodendron* and most exotegmic seed coats of *Tetracentron* are histologically very different from the seed coats of Hamamelidales, comprising four diverse families: Hamamelidaceae R. Br., Rhodoleiaceae Nakai, Altingiaceae Lindl. and Platanaceae Dum. (Takhtajan, 1997). The seed coat in Hamamelidaceae (except for subfamily Exbucklandioideae) (Melikian, 1973*a, b, c*; Mohana Rao, 1974) is represented by a distinctive, multilayered exo-mesotestal or mesotestal (*Disanthus*: Disanthoideae–Hamamelidaceae) type with an unspecialized endotesta usually composed of two–four depressed layers of thin-walled cells (Fig. 19). Differences between the seed coats of *Trochodendron* and *Tetracentron* are obvious. Within Trochodendrales, the endotesta is represented by a single layer of unspecialized, slightly thickened cells with the progressive development of an exotegmic mechanical system. Moreover, the inner integument of *Trochodendron* and *Tetracentron* is differentiated and well preserved in the mature spermoderm; in contrast it is usually obliterated in Hamamelidaceae. The differences between seed coat types of these representatives of Hamamelidales and Trochodendrales are so great that it is possible to reduce such a distance only by several revolutionary reorganizations of the mechanical construc-



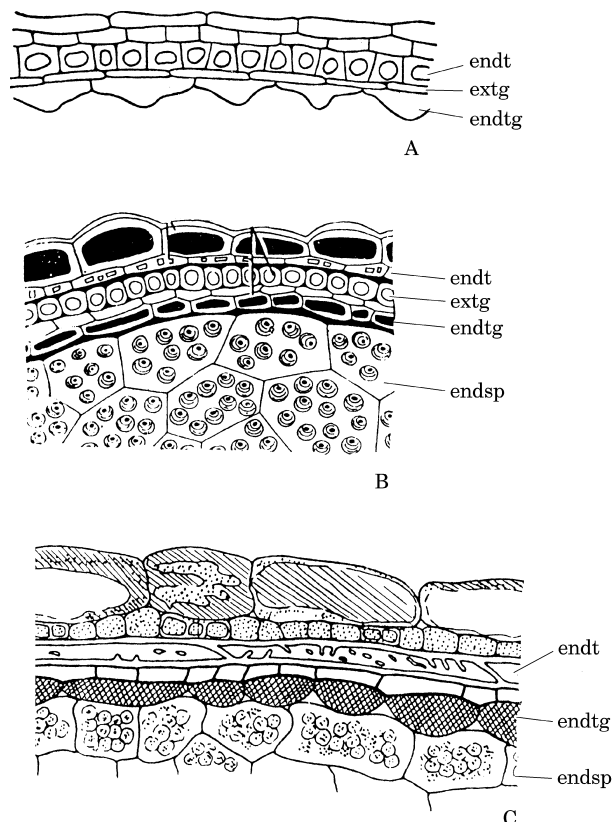


FIG. 9. Cross-sections of seed coats of *Trochodendron aralioides* Sieb. & Zucc. by various students. A, After Melikian (1973b); B, after Mohana Rao (1983); C, after Danilova and Plisko (1991). endt, Endotesta; extg, exotegmen; endsp, endosperm; endtg, endotegmen.

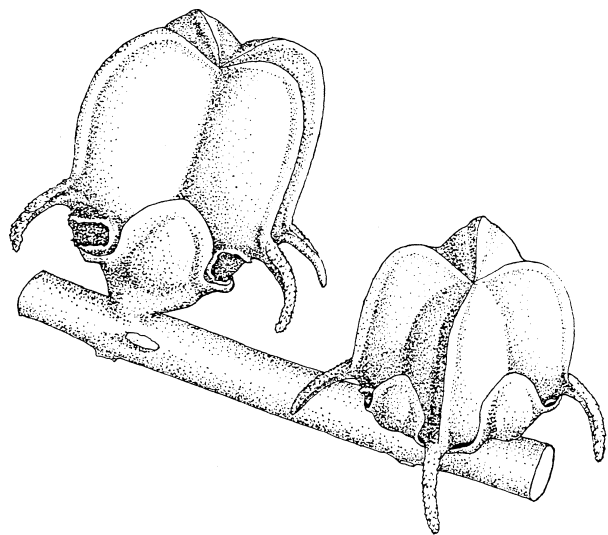


FIG. 10. Indehiscent capsules of *Tetracentron sinense* Oliv.,  $\times 15$ .

tion of the integumentary system. Under such a condition, a close relationship between these two taxa seems highly improbable.

The discovery of a sarcotesta of the magnolialian type in the hamamelidaceous genera *Sinowilsonia* Hemsl. and *Trichocladus* Pers. (Melikian, 1973a, b, c; 1991b) (Fig. 19)

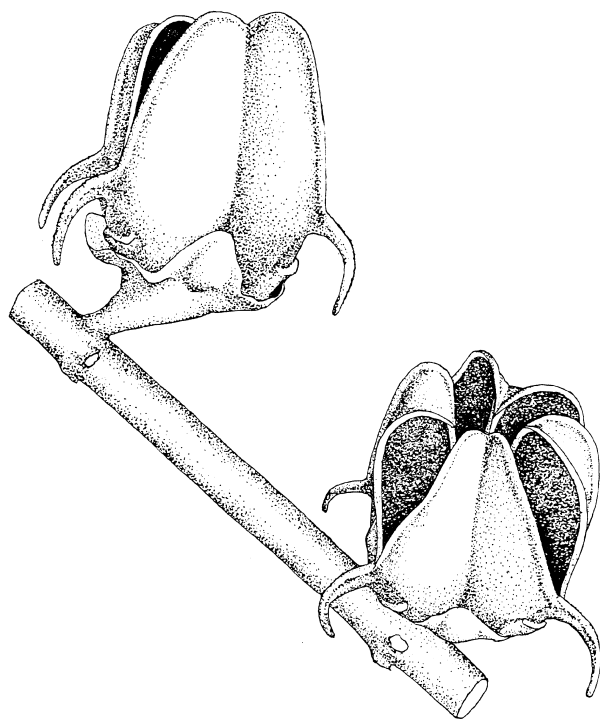


FIG. 11. Dehiscent capsules of *Tetracentron sinense* Oliv.,  $\times 15$ .

indicates a possible origin for these Hamamelidaceae genera (excl. Exbucklandioideae) directly from Magnoliales, as suggested by Hallier (1903, 1904, 1912) and supported by studies of floral anatomy (Endress, 1967, 1970, 1977, 1978, 1989). In contrast, the (endotestal-) exotegmic seed of *Trochodendron*, being of a more primitive type than the exotegmic seed of *Tetracentron*, reveals only very remote relationships with morphological reorganizations in the Magnoliales–Hamamelidaceae line. The rudimentary endotestal construction of the trochodendraceous outer integument may resemble in part the sclerendotesta of Magnoliaceae (Melikian and Plisko, 1988), but the differentiation of the sclerotic exotegmen only as a mechanical system, emphasizes a great distance between the Trochodendrales and Magnoliaceae. However, the occurrence of a depressed sclerotic exotegmen in Magnoliaceae does not exclude a possible relationship between Magnoliales and Trochodendrales in the remote past. This is also supported by the frequent occurrence of distinctive, sometimes sclerified ‘oil’ cells [‘Sekretschläuche’ of Harms (1897)] in Magnoliales and Trochodendrales, which are absent from Hamamelidales. Seed coat structure in *Tetracentron* and *Trochodendron* (in comparison to that of Hamamelidales and Magnoliales) is indicative of a distinct evolutionary line rooting in some pro-magnoliids. A recent 18S sequence analysis (Soltis *et al.*, 1997) and a survey of vegetative morphology (Hickey and Wolfe, 1975) also indicates that Trochodendraceae and Tetracentraceae constitute a distinct clade within archaic dicotyledons.

Additional comparisons with taxa assigned to the Hamamelidales also indicate differences in fruit and seed characters. Several unusual seed coat types are known in genera of Hamamelidales Melikian (1973a, b, c): endo-

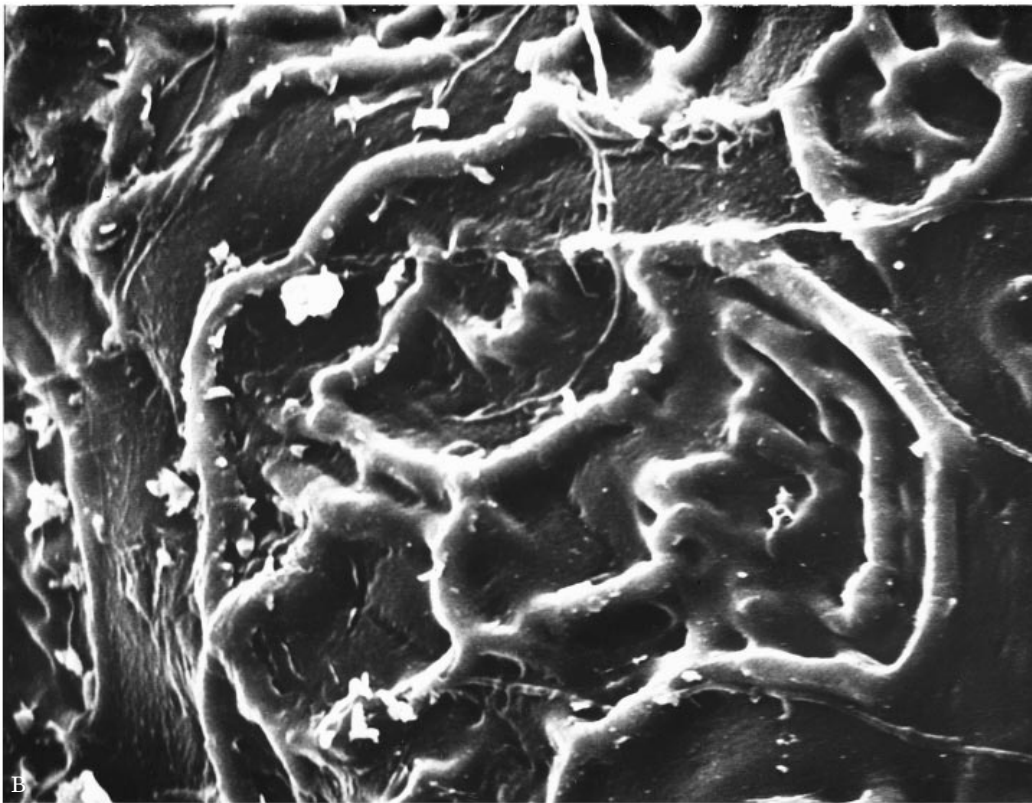
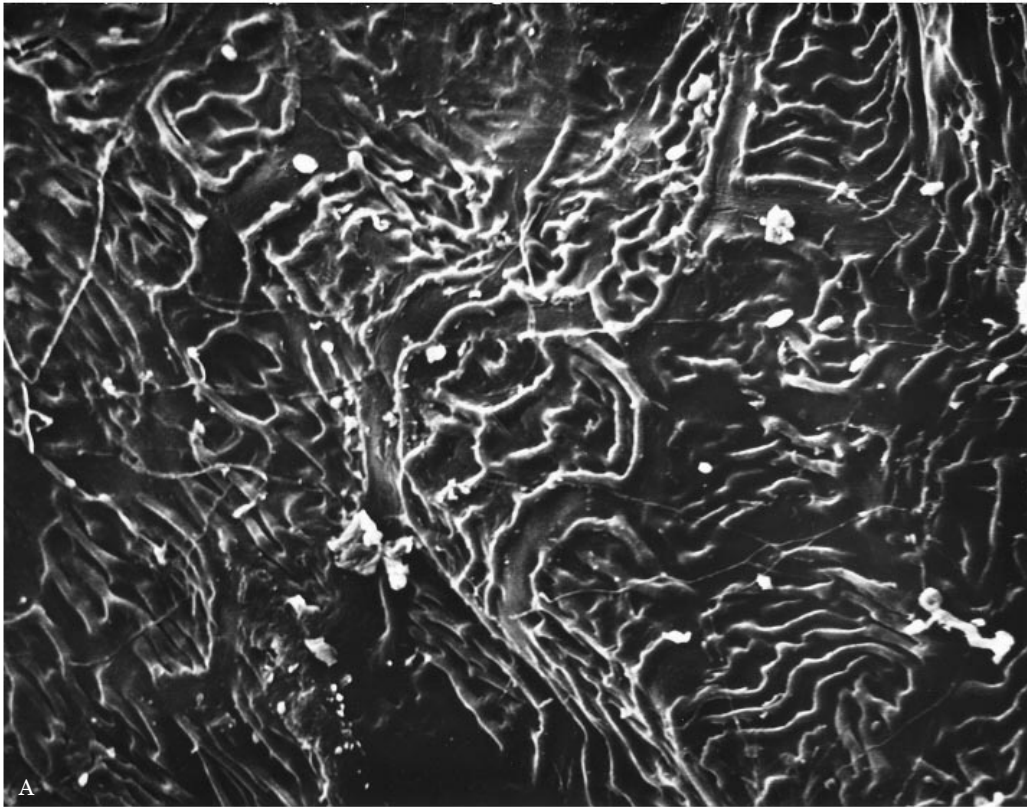


FIG. 12. SEM photographs of the fruit surface of the capsule of *Tetracentron sinense* Oliv. A, Fruit sculpturing,  $\times 500$ ; B, the same enlarged,  $\times 1500$ .

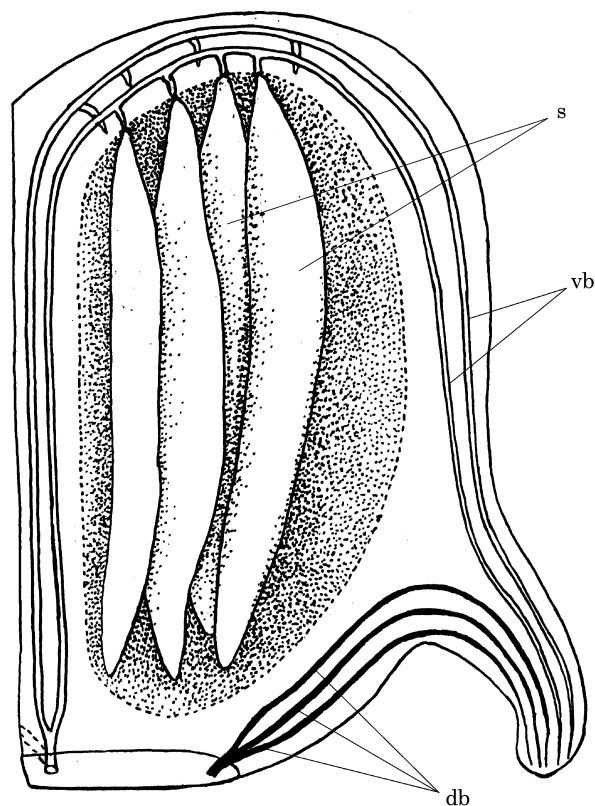


FIG. 13. Vascular skeleton of the fruit of *Tetracentron sinense* Oliv.,  $\times 35$ . vb, Ventral bundles; db, dorsal bundles; s, seeds.

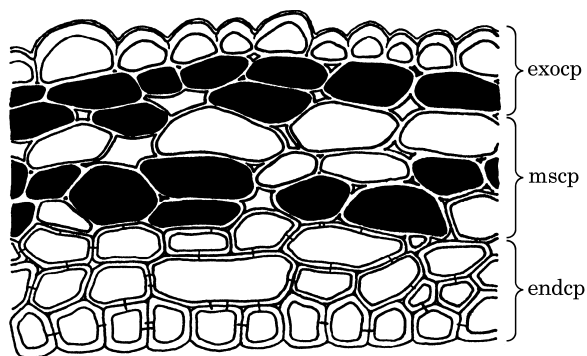


FIG. 14. Cross-section of the pericarp of *Tetracentron sinense* Oliv.,  $\times 30$ . exocp, Exocarp; mscp, mesocarp; endcp, endocarp.

testal (*Altingia* Nor., *Liquidambar* L.: Altingiaceae), mesotestal (*Platanus* L.: Platanaceae), exotestal (*Rhodoleia* Champ. ex Hook. f., *Chunia* Chang: Rhodoleiaceae) and exo-endotestal (*Exbucklandia* R. Br. in Wall.: Exbucklandioideae–Hamamelidaceae). All of them are markedly different from the exo-mesotestal seed coats of Hamamelidoideae–Hamamelidaceae and mesotestal ones of Disanthoideae–Hamamelidaceae. Only the exotestal seeds of *Rhodoleia* (Rhodoleiaceae) and *Chunia* (Hamamelidaceae: Exbucklandioideae) may be considered to be modified from an exo-mesotestal seed coat construction (Melikian, 1973*a, b, c*, 1991*b*). Melikian (1971) emphasized a close phylogenetic relationship between Trochodendrales and Altingiaceae (*Altingia*, *Liquidambar*), and later added

Platanaceae (Melikian, 1973*a, b, c*, 1991*c*). Platanaceae have an unusual mesotestal seed coat type, very different from the seed coat of Trochodendrales, which is usually exotegmic. There are no sustainable reasons for such an affiliation.

The resemblance of Trochodendraceae with Altingiaceae is supported only in part by the structure of their spermoderm, although the spermoderm of Altingiaceae is more specialized by formation of endotesta, and lacks mechanical elements in the tegmen (Melikian, 1971, 1973*a, b, c*, 1991*d*). Amongst Hamamelidales, only *Altingia* and *Liquidambar*, having an anomalous seed type, show a somewhat remote resemblance to Trochodendrales. The occurrence of a vestigial endotestal seed coat construction in *Trochodendron* may support a common origin of the endotestal seed coat of Altingiaceae and the (endotestal-) exotegmic seed coat of Trochodendrales from a putative ancestral stock with endotestal-exotegmic seed coats. Furthermore, distinct endotestal and exotegmic seed types have apparently appeared in different cases of seedcoat specialization. [However, I am not sure that studies of Melikian (1971, 1973*a, b*) on the seed coats of Altingiaceae have been validated; Mohana Rao (1974: 130), following Netolitzky (1926), reported an exotegmic seed coat construction for *Altingia* and *Liquidambar*, but no illustrative material was provided. If true, the similarity in seedcoat construction between Trochodendrales and Altingiaceae appears to be very strong, and the phylogenetic relationships compelling.]

The genera *Exbucklandia* and *Chunia*, usually treated as constituting a distinct subfamily Exbucklandioideae with Hamamelidaceae (Takhtajan, 1997), or even as the distinct family Bucklandiaceae Agardh, together with its close ally Rhodoleiaceae (*Rhodoleia*), could also be affiliated with the altingiaceous line of endotestal seed coat evolution, because *Exbucklandia* has been reported as having a distinctive one–two (–three?)–layered endotestal mechanical system (Melikian, 1972, 1973*a, b*, 1991*b*). If so, then the seed coats of Bucklandiaceae could not be direct derivatives of the exomesotestal and mesotestal seed coats of other Hamamelidaceae (Hamamelidoideae, Disanthoideae), which have a parenchymatous, unspecialized endotesta. Nevertheless, the presence of exotesta and reduction of the endotesta (and tegmic mechanical system?) in favour of exotesta look very different from the purely endotestal condition in the Altingiaceae and, moreover, from the strongly exotegmic Trochodendrales. The relationship of Bucklandiaceae with the taxa with endotestal seed coats should be re-investigated. In any case, based on observations of seed coat anatomy, Bucklandiaceae (incl. *Chunia*!), Rhodoleiaceae and Altingiaceae should be removed from the Hamamelidales; similarities in seed coat anatomy suggest the association of Altingiaceae and Trochodendraceae and Tetracentraceae.

Summarizing all current knowledge on the carpology and seed anatomy of Hamamelididae (Table 2), there are apparently no close relatives of *Trochodendron* and *Tetracentron* among the other representatives of this subclass. This view is supported in part by phenetic and cladistic analyses (Barabé *et al.*, 1982, 1987; Donoghue and Doyle, 1989; Hufford and Crane, 1989), in vegetative (Hickey and Wolfe, 1975) and floral (Leroy, 1988*a, b*, 1993) morphology,

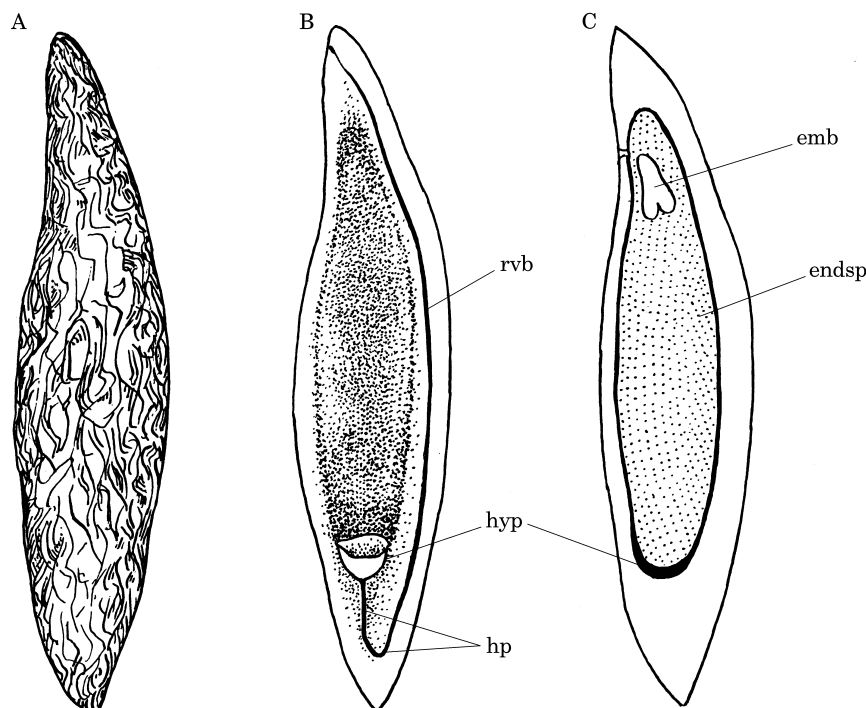


FIG. 15. Seeds of *Tetracentron sinense* Oliv.,  $\times 50$ . A, General view; B, vascularization of the seed; C, longitudinal section of seed showing minute embryo (emb) and abundant endosperm (endsp). rvb, Raphal vascular bundle; hp, vascular hair-pin loop; hyp, hypostase.

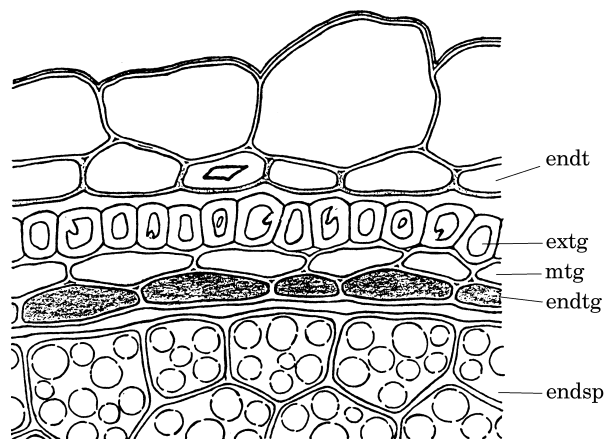


FIG. 16. Cross-sections of seed coats of *Tetracentron sinense* Oliv.,  $\times 45$ . extg, Exotegmen; endt, endotesta; endtg, endotegmen; endsp, endosperm; mtg, mesotegmen.

and recently by molecular analysis (Soltis *et al.*, 1997) which questioned the monophyly of the whole subclass. The distinctive trachotegmen of *Trochodendron/Tetracentron* has no morphologic analogue in the seed coats of any orders in Hamamelididae, and this important feature precludes any possibility of relating Trochodendrales with the subclass. This is a case when a sole important feature of the spermoderm in particular—a derivative of the organ *sui generis* (Smith, 1964; Doweld 1998c), not just a coat of seed as traditionally treated by some botanists—may weigh down all other characters or their complex. The totality of other characters may only indicate a convergent resemblance rather than a real phylogenetic relationship.

#### Relationships with Dilleniales

The diversity of fruit morphological types within Altingiaceae [dihiscent capsules (sometimes erroneously described as *nutlets* or *follicles*) associated in globose head infructescences—*capsaria*] and Trochodendrales (dihiscent/ventrihiscent capsules) may support an ancient, remote relationship, in which one or both lineages have acquired multiple, important modifications in reproductive and vegetative features. Amongst all follicular/capsular ranaleans we could find similar capsular fruits (capsules described as '*folliceta*') and a similar archaic endotestal-exotegmic seed coat type only in Dilleniaceae Salisb. (Dilleniales). Corner (1976, 1: 29) considered the dilleniaceous seed coat type as 'a short blind alley of evolution'. The characteristic endotestal seeds of Dilleniaceae with a tracheidal exotegmen (trachotegmen) differ in most details from the seeds of suggested close allies such as most exo-mesotestal Theanae. Amongst archaic angiosperms, only Dilleniaceae have a striking resemblance with the (endotestal-) exotegmic seed coat of Trochodendrales.

The characteristic feature of the seed coat of Dilleniaceae is a combination of sclerified endotesta and tracheidal exotegmen (Fig. 20). The seed is vascularized by a simple vascular strand (which sometimes splits in the massive chalaza), as also reported for Trochodendrales. The outer integument is few-layered: usually having two, but sometimes three layers. The inner integument is more extensively layered, with the number of layers varying from two to three (as in Trochodendrales) to six (de Cordemoy, 1859; Sastri, 1958; Corner, 1976). The exotesta is formed by thin-walled large cells filled with tannin-like substances, and crystals are

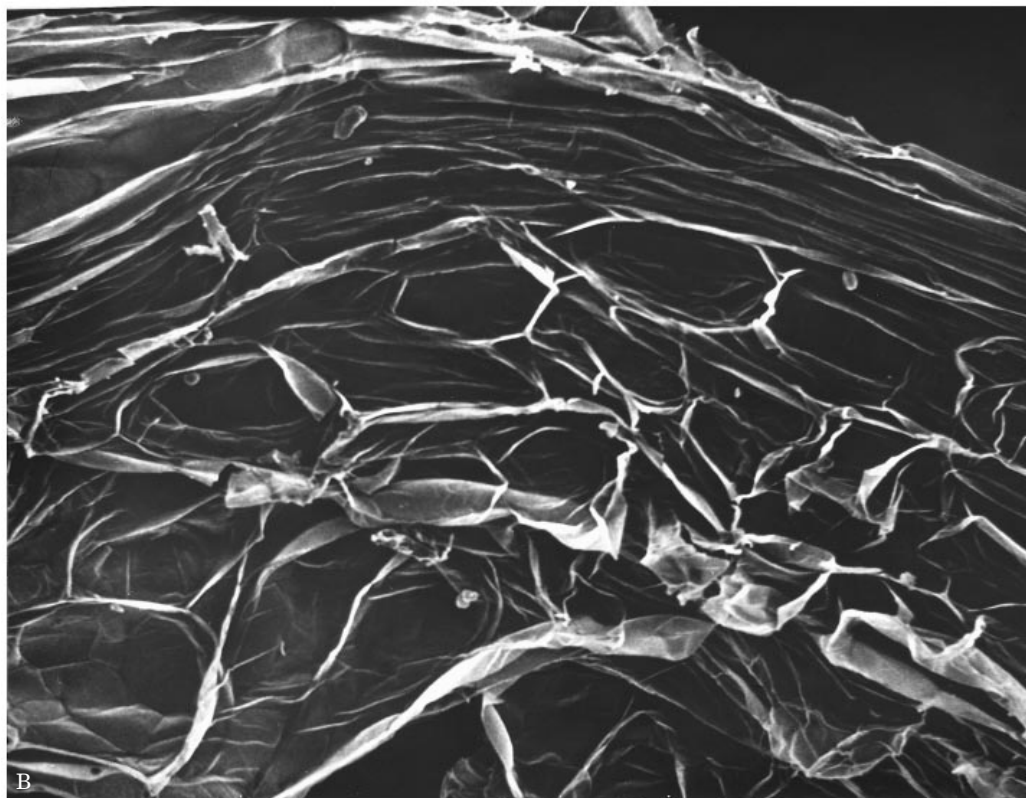
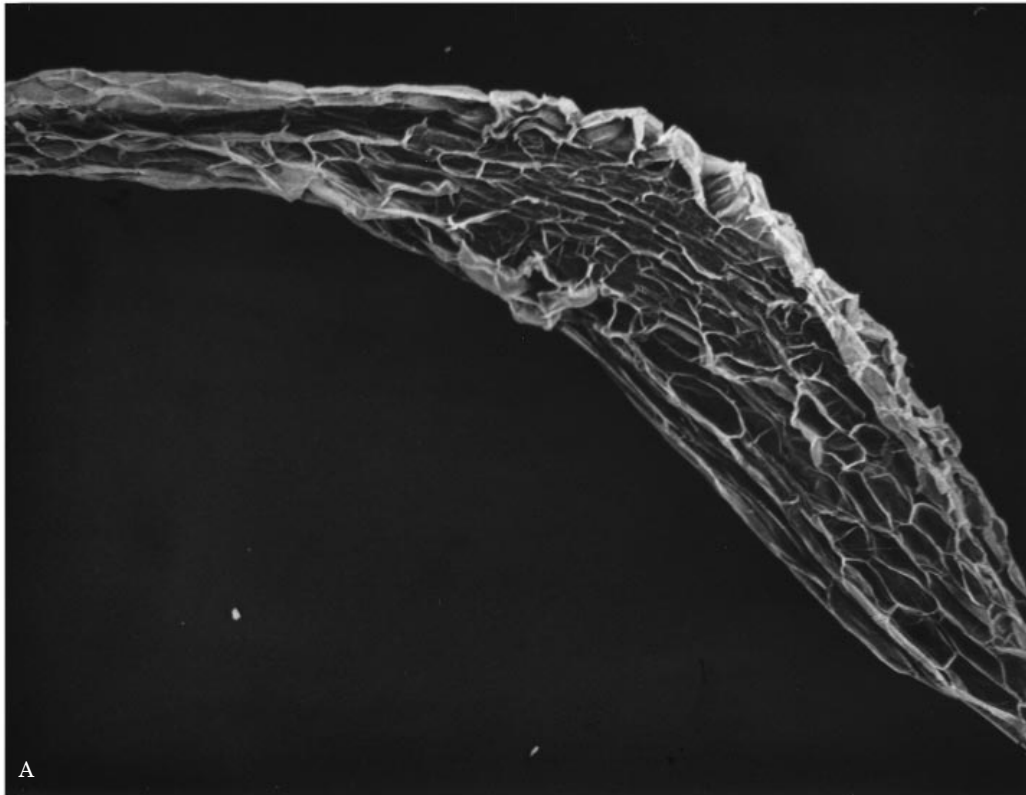


FIG. 17A & B. For legend see facing page

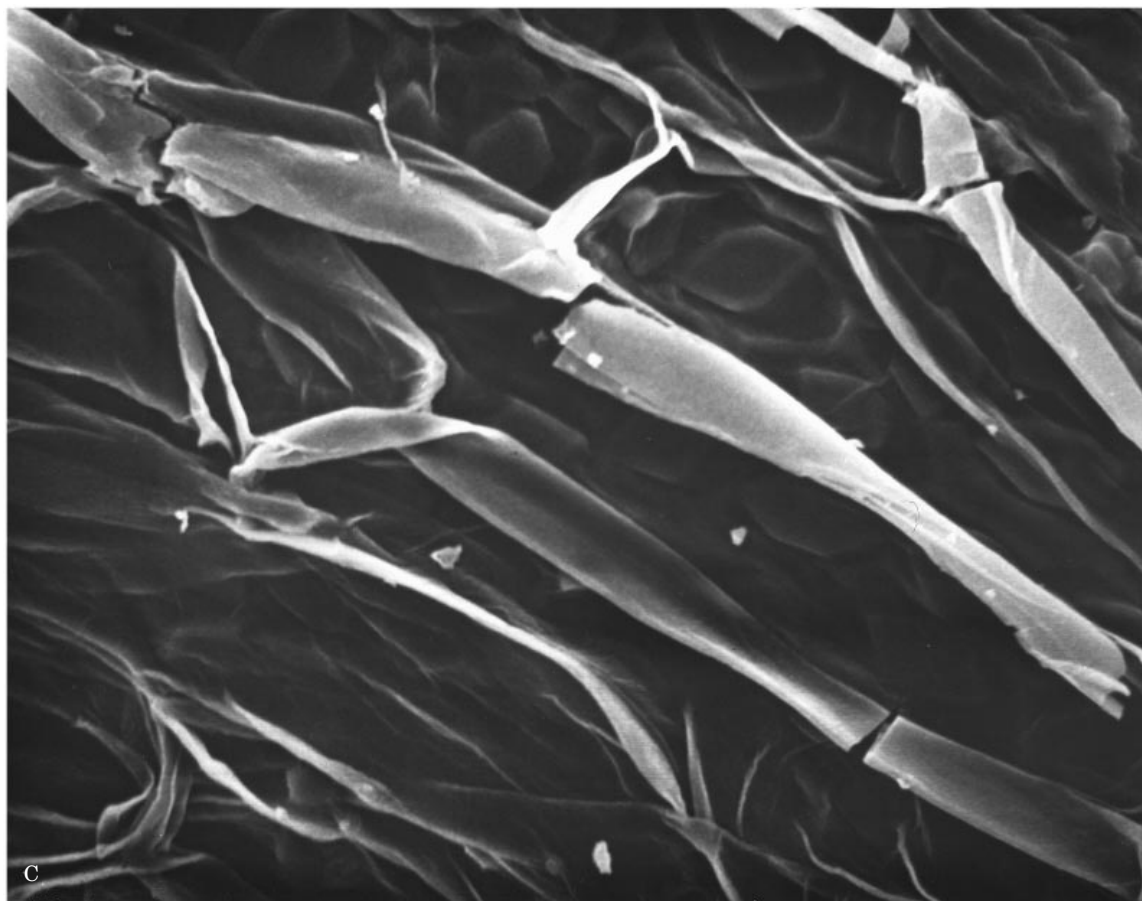


FIG. 17. SEM photographs of the seed surface of *Tetracentron sinense* Oliv. A, General view,  $\times 50$ ; B, seed sculpturing,  $\times 200$ ; C, the same enlarged,  $\times 750$ .

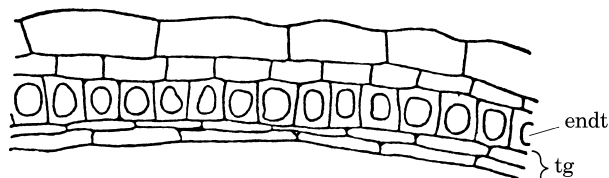


FIG. 18. Cross-section of seed coats of *Tetracentron sinense* Oliv. after Melikian (1973*b*). endt, Endotesta; tg, tegmen.

present in the testa (Corner, 1976). The endotesta consists of one layer (sometimes with one–two sclerified layers of mesotesta within advanced Tetraceroideae–Dilleniaceae) of sclerified thick-walled, pitted cells with coloured (yellow-brown) walls (Vyšenskaya and Oganezova, 1991). They are similar in form to endotestal cells of *Trochodendron*, if we could assume a reduction of its thickened walls. Another characteristic feature of the seed coat in Dilleniaceae (as in *Trochodendron* and *Tetracentron*) is the presence of a distinctive tracheidal exotegmen [*trachotegmen*] (Corner, 1976; Vyšenskaya and Oganezova, 1991), consisting of tangentially elongated, thick-walled cells with spiral thickenings and small invaginations of cell walls (Fig. 20). The endotegmen is also similar to that of *Trochodendron* and *Tetracentron*: it is formed by one layer of large, thin-walled cells with tannin-like dark brown contents. However, contrary to the similar seed coat histology found between

TABLE 3. A modern synopsis of main suprafamilial taxa in 'lower' Dilleniidae

Subclass Dilleniidae
Superorder Trochodendranae (Takhtajan, 1966)
Order <i>Trochodendrales</i> (Hu, 1950)
Family Trochodendraceae Prantl (Prantl, 1888)
Family Tetracentraceae (Smith, 1945)
Order <i>Altingiales</i> (Doweld, <i>ord. nov.</i> )
Family Altingiaceae (Lindley, 1846)
Family Rhodoleiaceae (Nakai, 1943)
Superorder Dilleniaceae (Takhtajan, 1966)
Order <i>Dilleniales</i> (Hutchinson, 1926)
Family Dilleniaceae (Salisbury, 1807)

*Trochodendrales* and *Dilleniaceae*, there are a number of differences in their respective seed characters, e.g. occurrence of arils, sarcotesta, exotestal trichomes, testa or tegmen, sometimes destroyed, or additionally differentiated one–two layers of sclerified mesotesta. These differences show only a different level of specialization of *Trochodendrales* and *Dilleniaceae*, which possibly originated from a common endotestal-exotegmic proto-magnolialian condition.

Other similarities between *Trochodendrales* and *Dilleniaceae* include node anatomy, microsporogenesis, anther dehiscence, pollen morphology [*cf.* Pragłowski (1974) and Walker (1976) for *Trochodendron* and *Tetracentron*, and

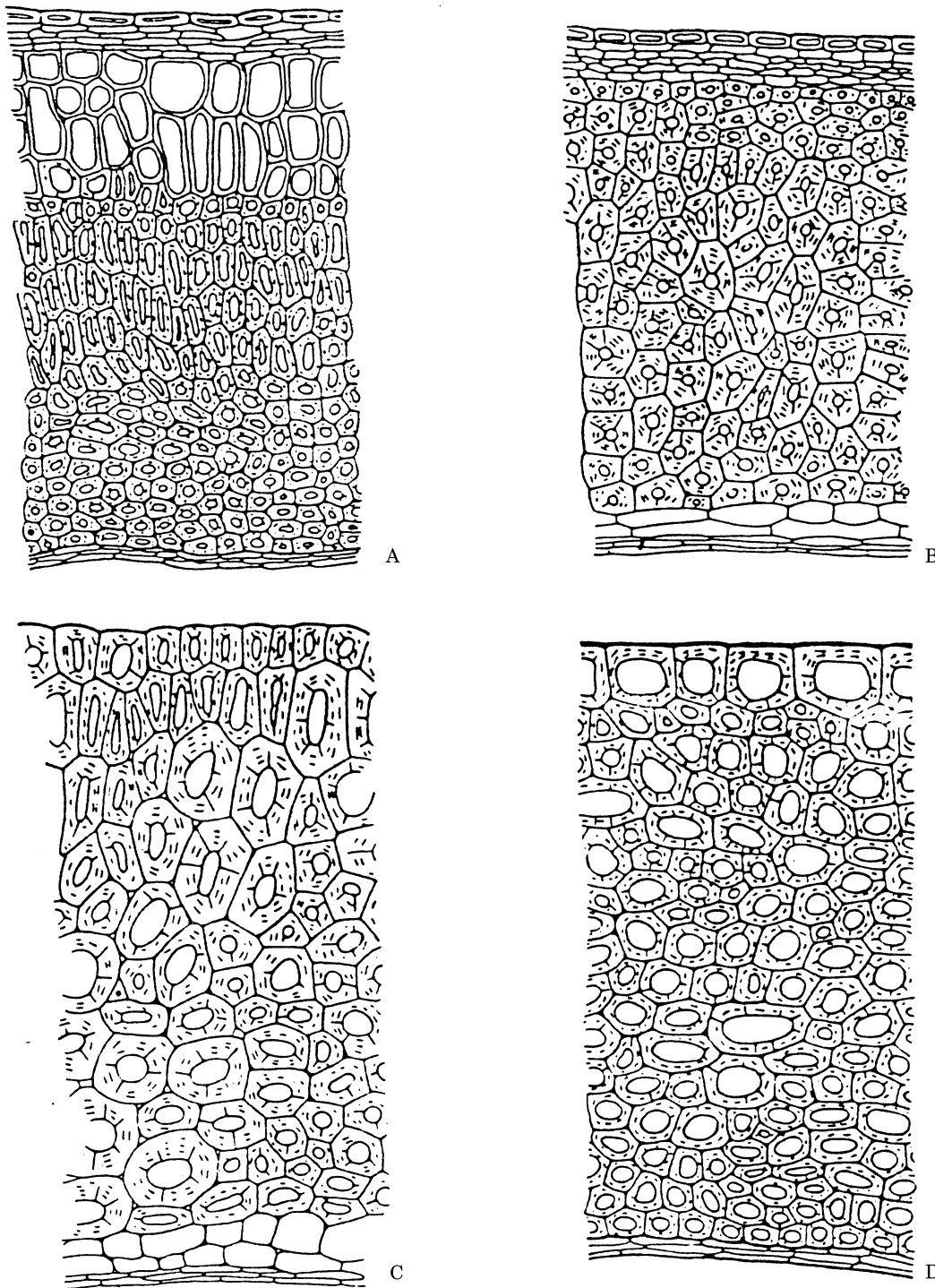


FIG. 19. Cross-sections of the spermoderm of some Hamamelidaceae after Melikian (1991b). A, *Sinowilsonia henryi*; B, *Trichocladus crinitus*; C, *Maingaya malayana*; D, *Mytilaria mollis*.

Dickison (1967b) and Dickison, Nowicke and Skvarla (1982) for Dilleniaceae], basic anatropous, crassinucellate ovule type, *Polygonum*-type of female gametophyte, capsular fruits (folliceta) and albuminous seeds (Sastri, 1958; Wilson, 1965, 1973; Dickison, 1967a, b; 1968, 1969, 1970). These, and numerous additional similarities, suggest a possible common origin of both orders from the protomagnolian stock independently from the hamamelidalian

one. It should be noted that some features of Trochodendrales (e.g. homoxily, distinctive reticulate-striate tectal sculpturing on its pollen grains, expanded nectarial tissue on the dorsal parts of carpels, seed coat construction, etc.) distance them from the rest of Hamamelididae and place them in an isolated position. At the same time, these characters support the proposed relationships with Dilleniales, releasing Trochodendrales from this problematical



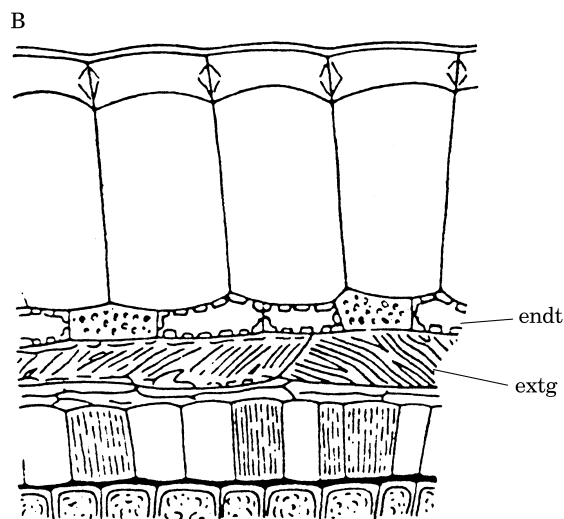
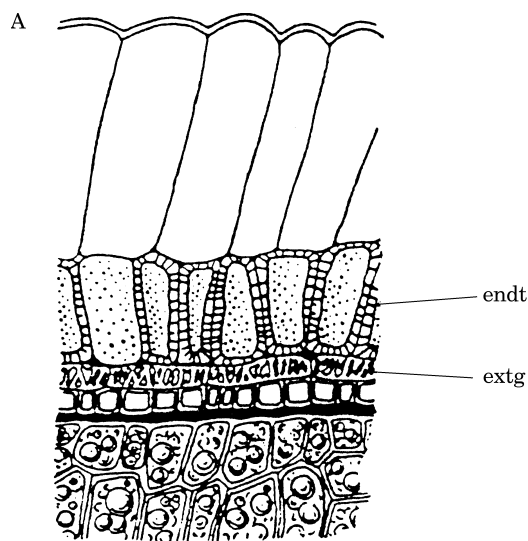


FIG. 20. Cross-sections of the spermoderm of some Dilleniaceae after Corner (1976). A, *Davilla* sp.; B, *Tetracera indica*. endt, Endotesta; extg, exotegmen.

'isolated position'. Croizat (1947) sharply criticized the affinities of *Trochodendron* and *Tetracentron* with other woody Ranales like Winteraceae or Magnoliaceae and suggested a relationship with Hamamelidales, but later (Croizat, 1960, 1a: 369) refuted this and proposed another 'platanaceous' or 'flacourtiaceous' [dilleniidalean line of evolution!] affinity of Trochodendrales. This magnificent prevision has been overlooked in recent systems of angiosperms (Dahlgren, 1989; Cronquist, 1992; Thorne, 1992; Takhtajan, 1997), even in the special case of the reform of the Hamamelididae as 'an artificial group' (Thorne, 1973).

Based on seed coat and pericarp features, Trochodendrales and Tetracentraceae should be assigned to the order Trochodendrales, superorder Trochodendranae (Takhtajan, 1997), and removed from Hamamelididae to Dilleniidae close to the superorder Dilleniaceae, which comprises a

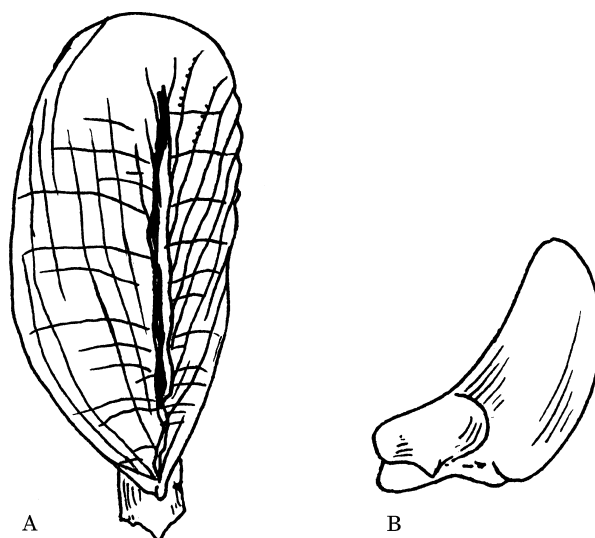


FIG. 21. General view of *Trochodendrocarpus* and *Trochodendrospermum*. A, *Trochodendrocarpus arcticus* Krysht.,  $\times 10$ ; B, *Trochodendrospermum arcticus* Krysht. ex Krassilov. [All figures redrawn from the original drawings of Baykovskaya and Kryshtofovich (1966)].

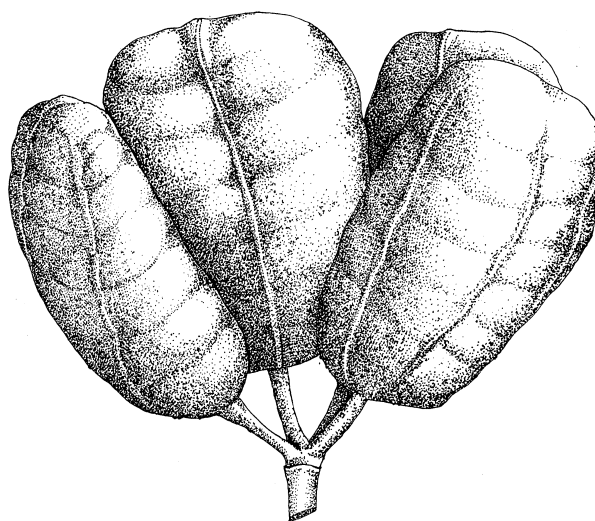


FIG. 22. Capsetum (follicetum) of *Drimys stipitata* Vickery,  $\times 10$ .

single order and family. Furthermore, Altingiaceae should be removed from Hamamelidales and assigned to Dilleniidae within Trochodendranae, occupying a distinct ordinal rank: Altingiales\*. These four families (Trochodendrales, Tetracentraceae, Altingiaceae and Dilleniaceae), each exhibiting different pathways of specialization may thus constitute a single, relic, isolated distinct side-branch of putative protomagnolian ancestry (Table 3).

\* Altingiales A. Doweld, ord. nov. *Arbores* 20 m alt., *rami floriferi rigidi, recti, folia alterna, petiolata, tenuia, chartacea, eleganter lanceolata, petioli gracillimi, pedunculi florum feminiorem pseudoterminales, erecti, monocephali, amenta masculina carent, capitula feminea pauciflora, sepalata atque petala nulla, ovaria inter se arcte confluentia, bilocularia, stylis 2 ligulatis obtusis recurvis, ovula in quoque loculo numerosa, fructus capsularis, dihiscentes*. TYPE: *Altingia* Noronha, Verh. Batav. genootsch. kunst. wetensch. 5(2): 1. 1790; Altingiaceae Lindley, 1846.

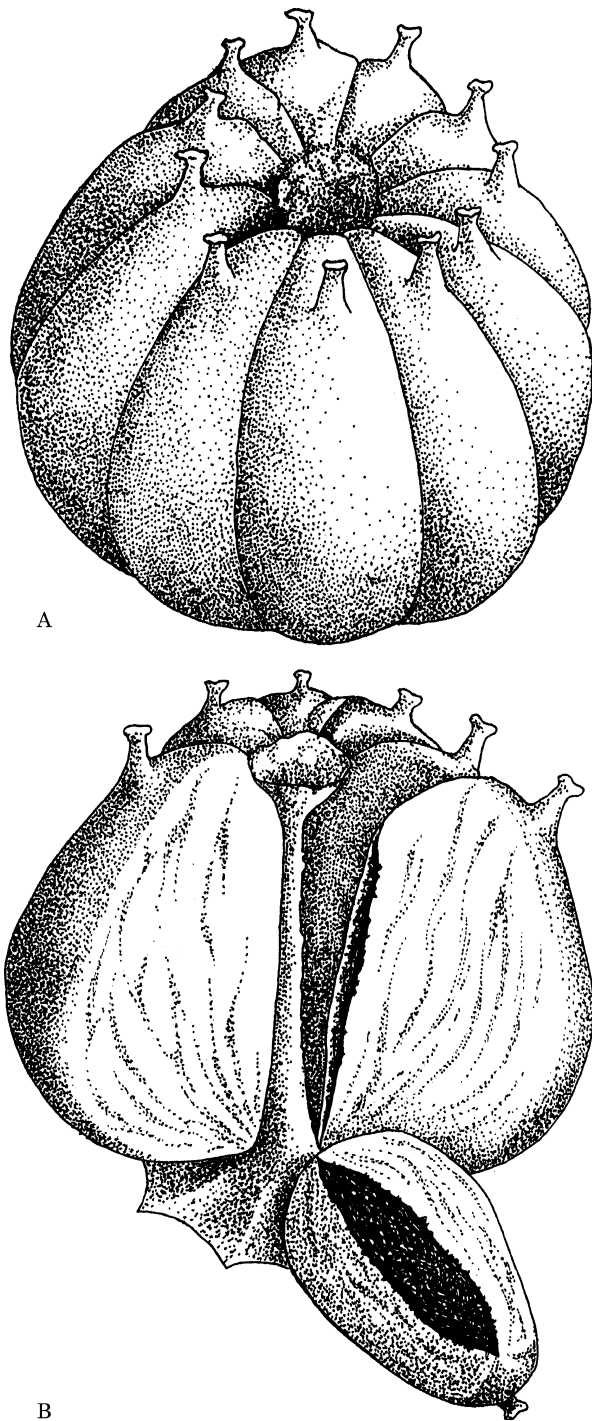


FIG. 23. Amended reconstructions of the fruit of *Nordenskiöldia borealis* Heer. A, Immature fruit,  $\times 15$ ; B, general view of the septicid-laterally dehiscent fruit with a detached dehiscent carpel and showing fruit columella and umbrella-like expanded receptacle,  $\times 15$ . [The fruit surface might be similar to that of the mature fruits of *Medusagyne* (Fig. 25B) as evidenced by the durian pericarp anatomy].

Seed coat and pericarp features also demonstrate inaccuracy and some vagueness of the limits among current subclasses of angiosperms. I am not sure that Dilleniales, occupying a rather isolated position within the subclass Dilleniidae, naturally relate to this subclass. In any case, as

categorically evidenced by seed coat anatomy, Trochodendrales should be considered together with Dilleniaceae, constituting a suprafamilial taxonomic entity. It is possible that this taxonomic re-arrangement may split the heterogeneous Dilleniidae *sensu* Takhtajan (1997) into several, more natural entities, in a similar way as for Asteridae/Lamiidae.

#### Relationships with fossil forms

*Trochodendroides*. In 1922 Edward Berry created a new genus *Trochodendroides* Berry for some fossil leaves described formerly as *Populus* (!) *arctica* (Heer, 1868), and tried to emphasize the likeness of these fossils with leaves of the extant Trochodendraceae. However, this likening was unfortunate because the leaves of *Trochodendroides* are more similar to those of *Cercidiphyllum* than to *Trochodendron* or *Tetracentron*. This resemblance with Cercidiphyllaceae led Brown (1939) to include all species recognized as *Trochodendroides* in the extant genus *Cercidiphyllum*. This radical step was highly criticized by Kryshtofovich (1958), Baykovskaya and Kryshtofovich (1966), and some of their successors (Iljinskaja, 1972, 1974; Krassilov, 1976). Extant *Trochodendron*, *Tetracentron* or even *Cercidiphyllum* lack features typical of *Trochodendroides*: long-petiolate broad leaves with a wide wedge-shaped truncated base and massive basal veins diverging from the leaf base, craspedodromous venation, large mamillate teeth, and a truncated apex of the leaf. Brown (1939) ignored these essential differences in the vegetative morphology. Also the reported association of some follicle-bearing racemose infructescences with leaves of *Trochodendroides* (Brown, 1939) has not been recognized as similar to extant capsaria (infructescences) of *Cercidiphyllum* (Kryshtofovich, 1958; Iljinskaja, 1972, 1974).

*Trochodendrocarpus*. Kryshtofovich (1958; cf. also Baykovskaya and Kryshtofovich, 1966) did not accept the transference of all species of *Trochodendroides* into *Cercidiphyllum*, (Brown, 1939), and furthermore created a new genus *Trochodendrocarpus* Krysht. (= *Nyssidium* Heer *sensu* Iljinskaja, 1974), for the fossil follicles associated spirally in the distinctive racemose infructescences of nearly 14 fruits (Iljinskaja, 1974; Krassilov, 1976; Krassilov and Fotyanova, 1996). The follicles are arranged in pairs on the short pedicels; they are elliptic or elongated-elliptic, up to 3 cm long, with a longitudinal striateness and transverse ribbing (wrinkling) (Fig. 21A). Baykovskaya and Kryshtofovich (1966: 274) described this 'transverse wrinkling' as 'some deeper structure which is later (in time of its full ripening) sharply developed from the outside, possibly analogous to the fleshy pericarp of *Juglans*'. From the standpoint of the carpology of extant forms, this 'transverse wrinkling' represents prominences formed by the developing seeds in the follicles with non-thick pericarp (e.g. as in *Drimys*: Fig. 22). In addition, Krassilov (1976) reported the dihiscent opening of these follicles, which is also typical of legumes. This feature (Mädler, 1939) finally debunks any ideas of a likeness of *Trochodendrocarpus* with capsules of Trochodendrales or even follicles of Cercidiphyllaceae. Iljinskaja (1974) synonymized the genus with *Nyssidium* Heer, which

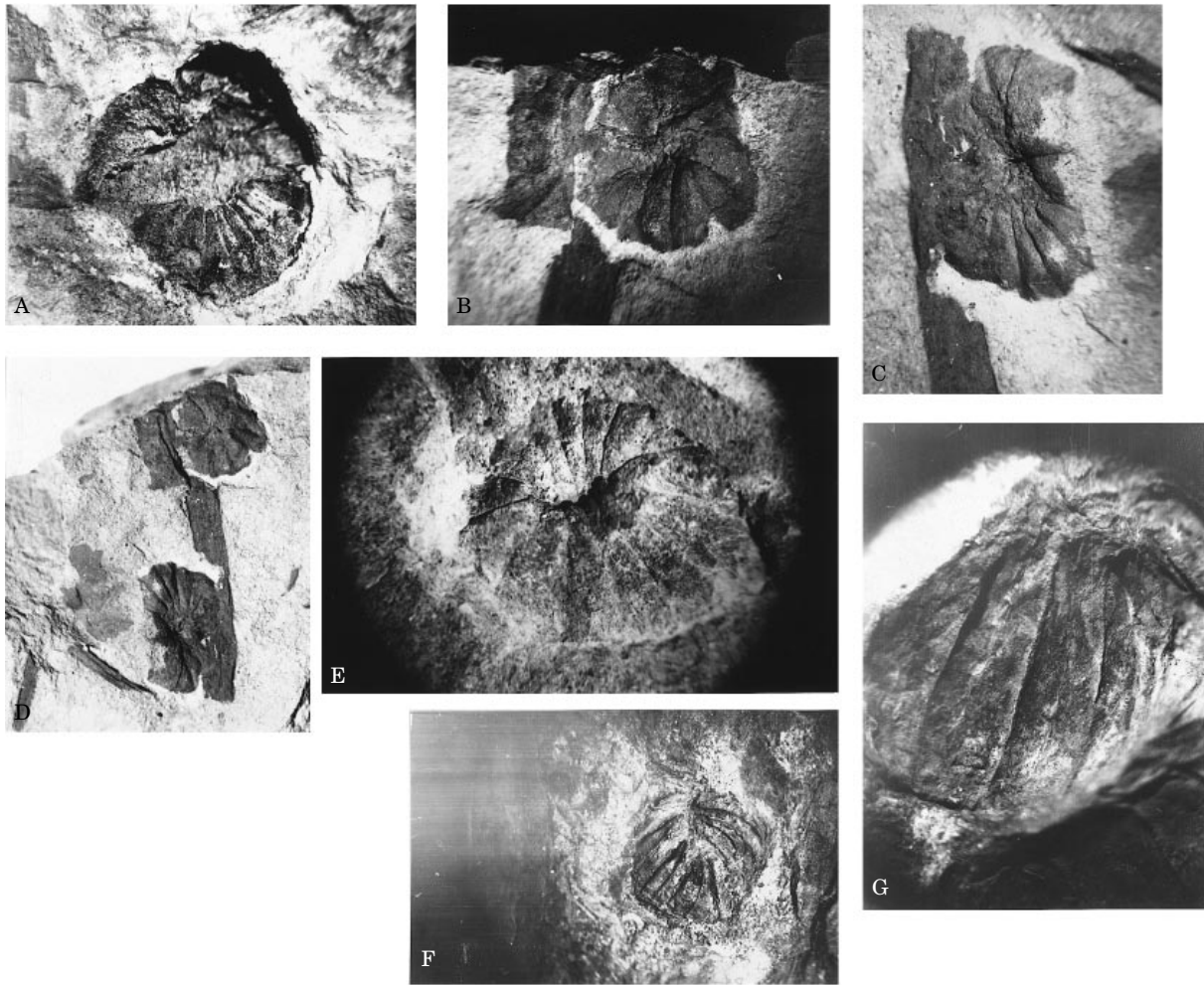


FIG. 24. Fossil fruits of *Nordenskiöldia borealis* Heer from the Tsagayan flora of Amur region, Far Eastern Russia. A, Capsule,  $\times 15$ ; B, uppermost part of capsule,  $\times 15$ ; C, As B, but another specimen,  $\times 20$ ; D, two capsules arranged on the inflorescence axis,  $\times 7$ ; E, uppermost part of capsule,  $\times 12$ ; F, dehiscent fruit,  $\times 10$ ; G, fragment of the distal part of the capsule with preserved styloids,  $\times 25$ . (All photographs kindly provided by V. Krassilov).

is affiliated taxonomically with Cercidiphyllaceae, not with Trochodendrales *s. str.* (Crane and Stockey, 1986), although Krassilov (1973) referred it to the ancestry of the Hamamelidaceae and Platanaceae, which is not supported by inflorescence morphology.

*Trochodendrospermum*. The name *Trochodendrospermum* was introduced by Baykovskaya and Kryshthovitch (1966) for some strange remnants, which were characterized as 'winged seeds' (Fig. 21 B), associated with *Trochodendrocarpus*. These were sickle-shaped, oblique seeds (up to 4 mm long) with a large wing. Iljinskaja (1974) described them as an indefinite 'pair of scales', supposedly of even animal (!) origin. These remnants are absolutely unlike seeds of Trochodendrales, and Krassilov (1976) pointed out their likeness to seeds of *Liquidambar*. Krassilov (1976) and Krassilov and Fotyanova (1996) did not agree with the conclusions of Iljinskaja (1974), and confirmed the seed nature of these fossils and especially their association with the fruits of *Trochodendrocarpus*, not at all related to Trochodendrales.

*Trochodendroxylon and Trochodendron*. The fossil homoxyllic wood known as *Trochodendroxylon beckii* Hergert & Phinney, similar to *Trochodendron*, has been recorded in Eocene and Oligocene of Oregon (Hergert and Phinney, 1954; Scott and Wheeler, 1982). The association of fruits and infructescences with a *Trochodendron*-like foliage, known as *Trochodendron protoaralioides* Murai (Uemura, 1988), has been recorded from the Miocene of Japan (Manchester, Crane and Dilcher, 1991). This fossil remnant is undoubtedly similar to extant *Trochodendron*.

*Nordenskiöldia*. Recently Crane (1989), Crane, Manchester and Dilcher (1991) and Manchester *et al.* (1991) assigned *Nordenskiöldia* Heer, known from fossil fruits and infructescences, to Trochodendrales. These authors followed Berry (1922) who suggested that *Nordenskiöldia* Heer (1870) from the Paleocene has an affinity with extant *Trochodendron* and *Tetracentron*. This point of view has been shared by most palaeobotanists (Kryshthovitch, 1958; Baykovskaya and Kryshthovitch, 1966), but was questioned by Krassilov (1971), Iljinskaja (1974), and Krassilov and Fotyanova

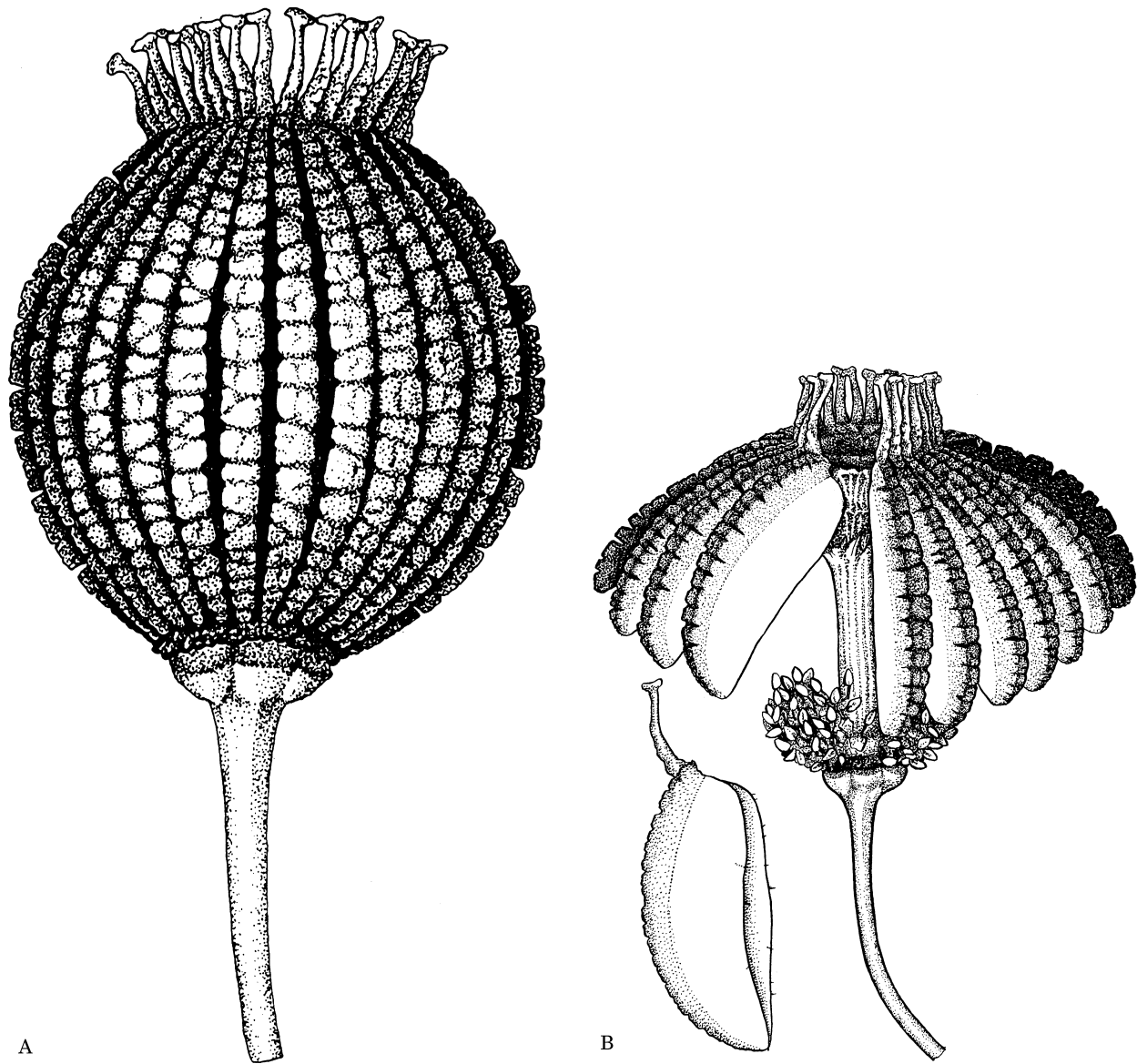


FIG. 25. The fruit (*sciridium*) of *Medusagyne oppositifolia* J. G. Baker (Medusagynaceae). A, Immature fruit,  $\times 15$ ; B, general view of the incompletely septicid-laterally dehiscent fruit with a detached dehiscent carpel and showing a columella,  $\times 10$ . [From Doweld (1998*a*), by permission of 'Botaničeskij Žurnal' (St.-Petersburg)].

(1996). In discussing *Nordenskiöldia*, the cited authors pointed out the lack of an obvious similarity with extant Trochodendraceae, but Crane (1989: 174) stated that '*Nordenskiöldia* is clearly related to *Trochodendron* and *Tetracentron*'. I disagree with such an interpretation. In such an assignment, a very important fruit feature has been generally overlooked. The fruits of *Nordenskiöldia borealis* Heer and *Nordenskiöldia interglacialis* (Hollick) Manch., Crane & Dilch., as seen from illustrations and descriptions (Crane, 1989; Crane *et al.*, 1991; Manchester *et al.*, 1991) as well as from the Heer's classical monograph *Flora Fossilis Arctica* (1870), are clearly capsules of a columellate type (Figs 23 and 24). After fruit dehiscence, there is a clearly differentiated columella on the axis of the flower. In Trochodendrales there is no such columella. Trochodendrales have a primitive type of capsular fruit (dihiscent/

ventrihiscent capsules), which has nothing in common with the very specialized and advanced lobihiscent-lateral (= septicid-lateral) columellate capsules of *Nordenskiöldia*. In an amended diagnosis, the cited authors described *Nordenskiöldia* as having 'schizocarpic' fruits, at the same time pointing out that 'dispersed fruitlets...[are]...dehiscent...' (Crane *et al.*, 1991: 1316). The schizocarpy presupposes only the splitting of the fruit into *closed* mericarps (Winkler, 1936; Kaden, 1962), and should not thus be confused with the lobihiscent-lateral mode of fruit opening. Therefore, the dehiscent fruits of *Nordenskiöldia* are not schizocarpic, but syncarpous lobilaterihiscent capsules. It has also become clear that the opinion of Kryshtofovich (1958) that the fruits of *Nordenskiöldia* are derived from *apocarpous* gynoeceum is mistaken. In recent reconstructions of *Nordenskiöldia* the separation of the exocarp from the base of mericarp as a

mode of dehiscence appears highly improbable. Palaeobotanists suggested that the exocarp (correctly, a basal part of it) remains attached with the remnant of the receptacle on the axis of flower in the form of an umbrella-shaped cup with a central columella. Among extant forms, such a ‘dehiscence’ or ‘splitting’ is absolutely unknown and morphogenetically unlikely (Stopp, 1950), and therefore the umbrellas of *Nordenskiöldia* possibly represent only remnants of expanded receptacle.

There are many seeds in the locules of trochodendraceous capsules, unlike the ‘one-seeded’ fruitlets of *Nordenskiöldia*. In addition, the pericarp anatomy of *Nordenskiöldia* is unlike that of *Trochodendron* or *Tetracentron*: there are numerous radially elongated fibrous osteosclereids (‘discrete bands’) forming ‘distinct oblique ridges’ (resembling so-called highly specialized durian fruits; Corner, 1976), three–five-layered parenchymatous exocarp (‘outer tissue of dorsal surface’), five–six-layered sclerendocarp (no sclereids at the ventral margins of carpels near central columella of fruit). A very distinctive feature of trochodendraceous seeds is apparently absent from seeds of *Nordenskiöldia*: no vascular hair-pin loop has been recorded in the chalazal part of seed. Moreover, there are some essential differences in spermoderm anatomy between *Nordenskiöldia* and Trochodendrales. As seen from the descriptions and illustrations of the seed coat of *Nordenskiöldia* (Crane *et al.*, 1991: 1321), there is a one-layered exotesta with somewhat thickened anticlinal and inner periclinal walls (‘outermost layer’) and a one-layered exotegmen (‘inner layer... not extending into the wing’), and therefore the spermoderm is exotestal-exotegmic (the so-called ‘middle layer’ represents crushed remnants of testal parenchyma). Considering all mentioned differences and summarizing all important details of fruit and seed anatomy of *Nordenskiöldia*, I consider that the affinity of *Nordenskiöldia* is not close to *Trochodendron* and *Tetracentron*.

In my opinion, *Nordenskiöldia* might represent a possible ancestral form for Theales, which are characterized by columellar, lobihiscent-lateral capsules. The homoxylous wood of *Nordenskiöldia* might also be closely related to Theales, which have an archaic wood type (Gottwald, 1977). It is noteworthy that Gottwald mentioned (*ibid.*: 119) that ‘the most primitive structures (of xylem) of vessel-bearing taxa can be found in the ‘Dillennial-Hamamelidal’ and the ‘Theal’ structural groups outside the Magnoliales *sensu* Takhtajan’ (my italics). Some families of thealean affinity (i.e. Bonnetiaceae, Clusiaceae, Hypericaceae, Medusagynaceae) have a characteristic exotestal-exotegmic seed coat and syncarpous capsules opening lobihiscent-laterally and thus leaving a columella on the axis of the flower (Doweld, 1998a). For instance, the syncarpous polymerous capsule of *Medusagyne* (Medusagynaceae) opens lobihiscently and laterally, but the carpels remain united distally (Doweld, 1998a), thus forming an umbrella-like type of fruit (*sciridium*) (Fig. 25). In Bonnetiaceae, syncarpous capsules have a complete lobihiscent-lateral dehiscence, leaving only a columella. The seed coat in both families is exotestal-exotegmic (Fedotova, 1991; Doweld, 1998a); in the pericarp there are similar, numerous osteosclereids forming ‘distinct oblique ridges’ on the fruit surface,

five–six-layered sclerified endocarp; one–two winged seeds per locule with a simple (no hair-pin loop) seed vascular skeleton. The faceted seed sculpturing of *Nordenskiöldia* (Crane *et al.*, 1991) is like that of *Medusagyne* (Doweld, 1998a). These numerous similarities indicate the general similarity of *Nordenskiöldia* to Theales *s.l.* *Nordenskiöldia* has a unique combination of advanced features [lobihiscent-lateral (columellate) capsules, one-seeded locules, durian-like pericarp (with osteosclereids), exotestal-exotegmic spermoderm, winged seeds, (?) expanded receptacle (= ‘umbrella’)], that preclude its affiliation with any ranalian or hamamelidalian line of evolution. Its systematic position, based on all these characters, is definitely among higher dicotyledonous orders (Theales *s.l.*, Paracryphiales, Medusagynales, Ochnales *s.l.*, (?) Malvales, etc.). In this connection the lack of vessels in the wood of *Nordenskiöldia* might only illustrate the polyphyletic origin (or lack: Young, 1981) of vessels in dicotyledons, which is absolutely uncorrelated with the evolution of the reproductive sphere (fruits and seeds) in flowering plants. It is necessary to study in detail the vegetative morphology and anatomy of *Nordenskiöldia* and associated leaves *Zizyphoides flabella* (Newb.) Crane, Manch. & Dilch. and *Zizyphoides auriculata* (Heer) Manch., Crane & Dilch. with reference to possible thealean affinity. It is likely that palaeobotanists have found a vesselless precursor to recent Theanae, retaining archaic vessel elements with simple scalariform perforation plates, rather than a link to Hamamelidids.

*Tetracentron*. Fossil remnants assigned to *Tetracentron* are rather few. From the Burean Tsagayan (Paleocene, Far Eastern Russia) Baykovskaya and Kryshthovich (1966) described leaves under *Tetracentron amurense* Kryshth., which are more similar to leaves of the formal genus *Trochodendroides*, than to *Tetracentron*. Iljinskaja (1972) described two more species. *Tetracentron potomacense* (Ward) Iljinsk. (formerly known as *Populus potomacensis* Ward from USA and Eastern Siberia of Russia) and *Tetracentron vachrameevianum* Iljinsk. from the Albian of Kazakhstan. The leaves of these species show some differences in venation which led Vakhrameyev (1952) to conclude the species belonged in the genus *Cercidiphyllum*, but Iljinskaja (1974) continued to treat them as *Tetracentron*. The fossil wood of *Tetracentron*-like plants has been described from the Upper Cretaceous of California (Page, 1968). The fossil fruits and seeds of *Tetracentron* are unknown.

With the refutation of the relationships with *Nordenskiöldia*, *Trochodendroides*, *Trochodendrocarpus* and *Trochodendrospermum*, the fossil forerunners of recent Trochodendrales, except for *Trochodendroxylon beckii* and *Trochodendron protoaralioides*, remain undescribed or unrecognized. In this respect, carpology and seed anatomy studies on *Trochodendron* and *Tetracentron* have proved to be useful instruments in the postulation of phylogenetic relationships between recent and fossil forms.

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