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THE CARPOLOGY AND TAXONOMIC RELATIONSHIPS OF *DAVIDSONIA* (DAVIDSONIACEAE)

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The fruit of *Davidsonia pruriens* F. v. Muell. drying and splitting at maturity into two indehiscent mericarps is re-defined as a schizocarpic didrupe. The sclerified mesendocarpic construction of the whole pericarp supports its classification as a drupe. The peculiar fimbriate surface of the mericarp is caused by the destruction of parenchymatous exocarpic and mesocarpic tissues exposing radially elongated mesendocarpic osteosclereids. The seed coat is described as diffusive exotegmic with expanding pachychalaza substituting the two integuments in the chalazal half of the seed. The diffusive exotegmy of the spermoderm supports a close relationship with Cunoniaceae, but refutes any relationships with Saxifragales or with Staphyleaceae or any Hamamelidae. The seed-coat structure indicates advancement and specialization of *Davidsonia* among Cunoniales; its origin could trace back possibly to Rosales, but never to hamamelidalean stock.

Keywords. Carpology, Davidsoniaceae, Cunoniaceae, Hamamelidae, Rosidae, seed anatomy, taxonomic relationships.

INTRODUCTION

Over many years the systematic position of the monotypic endemic Australian genus *Davidsonia*, described by Mueller (1867), has been in doubt, although it has traditionally been associated with Cunoniaceae (Engler, 1928). It is distinct from Cunoniaceae in having alternate (not opposite) leaves, pendulous epitropous ovules and exalbuminous seeds. Bange (1952) established a new family, Davidsoniaceae, to accommodate this anomalous genus, thereby emphasizing its differences from Cunoniaceae. This taxonomic solution is accepted in most recent systematic classifications of flowering plants (Takhtajan, 1987; Dahlgren, 1989; Cronquist, 1992; Thorne, 1992), but the phylogenetic relationships of *Davidsonia* are still ill-understood, although Ingle & Dadswell (1956) and Dickison (1980) emphasize a certain similarity of *Davidsonia* to Cunoniaceae in xylem structure. In this respect carpological data, hitherto lacking for Davidsoniaceae (Czerniakowskaya & Doweld, 1996), are of great importance for clarifying its proper phylogenetic position.

MATERIALS AND METHODS

Mature dried fruits of *Davidsonia pruriens* F. v. Muell. var. *pruriens* were obtained from the North Coast Regional Botanic Garden, Coffs Harbour, Australia (voucher

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at the Carpotheca of the National Institute of Carpology (Gaertnerian Institution), Moscow, NICAR). Drawings were made from cross-sections prepared by the usual paraffin method (O'Brien & McCully, 1981). Scanning electron microscope (SEM) observations were made with an Hitachi S-405A at 15kV.

OBSERVATIONS

Fruit

Mature fruit. The mature fruit (Fig. 1) originates from the dimerous syncarpous gynoecium with two free styles and apical-axial placentation of 5–7 pendulous, epitropous ovules (only one or two of which mature into seeds) (Bange, 1952). Drying at maturity, the dimerous fruit splits into two dry indehiscent mericarps retaining apical remnants of the styles and with a nearly entirely obliterated parenchymatous exocarp and partially disintegrated drying mesocarpic parenchyma (fleshy when young) exposing radially elongated mesendocarpic bundles of fibres. Owing to these strands of fibres the surfaces of the mericarps are fimbriate. Taking into consideration the sclerification and lignification of mesendocarp (cf. pericarp, below) the fruit of *Davidsonia* should be re-defined as a schizocarpic didrupe in contrast to only didrupe (Bange, 1952).

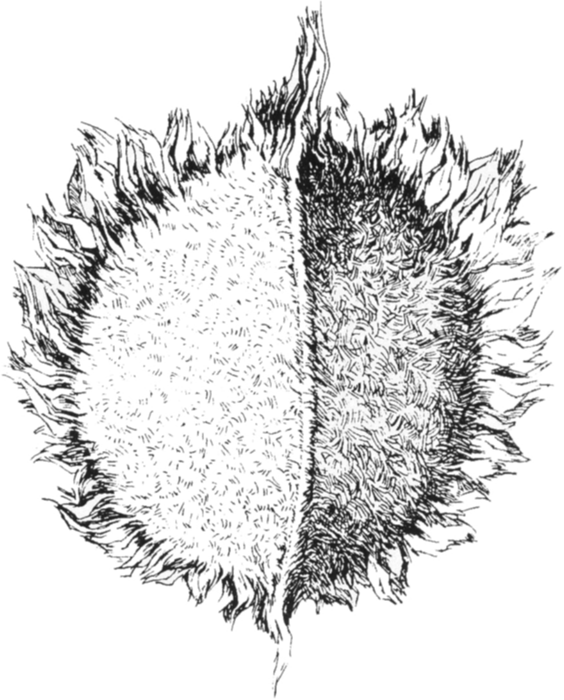

FIG. 1. Mericarp with apical remnant of a style of *Davidsonia pruriens* var. *pruriens*, ×3.

The mericarp is 16–20mm long, 15–20mm wide and 5–10mm thick, brown (red and fleshy when young), flattened, with the apical remnant of a style. The vasculature of the mericarp (Fig. 2) consists of three principal carpellary bundles (one dorsal, two ventrals) (Dickison, 1975). The ventral carpellary system produces numerous septal vascular bundles diverging from the main ventrals at right angles to the long axis of each mericarp. They form with numerous osteosclereids the distinctive wings of the mericarps. Dickison (1975: 447) has noticed that this feature of the gynoecial vasculature of *Davidsonia* distinguishes the latter from the Cunoniaceae where such a type of vasculature is absent. The dorsal trace also produces numerous fine vascular

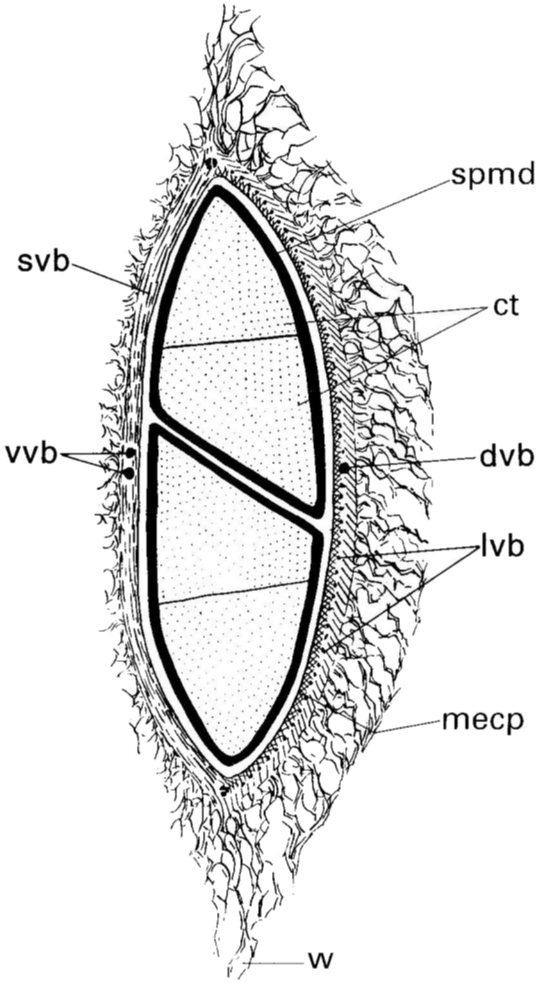

FIG. 2. Cross-section of the 2-seeded mericarp of *Davidsonia pruriens* var. *pruriens*, × 7. Abbreviations: dvb, dorsal vascular bundle; vvb, ventral vascular bundles; svb, septal vascular bundle; lvb, lateral vascular bundles; ct, cotyledons; spmd, spermoderm; w, wing; mecp, mesendocarp of dried mericarp.

strands (as a rule, 5–6 or more). At the narrow angles of every mericarp (near wings) there are 1–2(–3) big strands giving rise to numerous small bundles ended blindly in the mesendocarpic zone.

Pericarp. The pericarp (Fig. 3) is differentiated into a 6–8-layered endocarp, a 12–15-layered mesocarp and 3–5 layers of parenchymatous exocarp that breaks down in the mature fruit together with the mesocarpic parenchyma surrounding the radially elongated mesendocarpic fibres. Such a sclerified mesendocarp-like construction of the whole pericarp is typical of drupaceous fruits (Garcin, 1891).

The exocarp of mature dried fruits is practically completely destroyed although its remnants are sometimes visible (Fig. 4). By contrast, the endocarp is composed of longitudinal fibres, heavily lignified and thick-walled. The mesocarp is represented by 12–15 layers of thinner-walled, sclerified and slightly lignified fibres oriented at right angles to the endocarp; some of these are grouped into long (0.2–0.5cm),

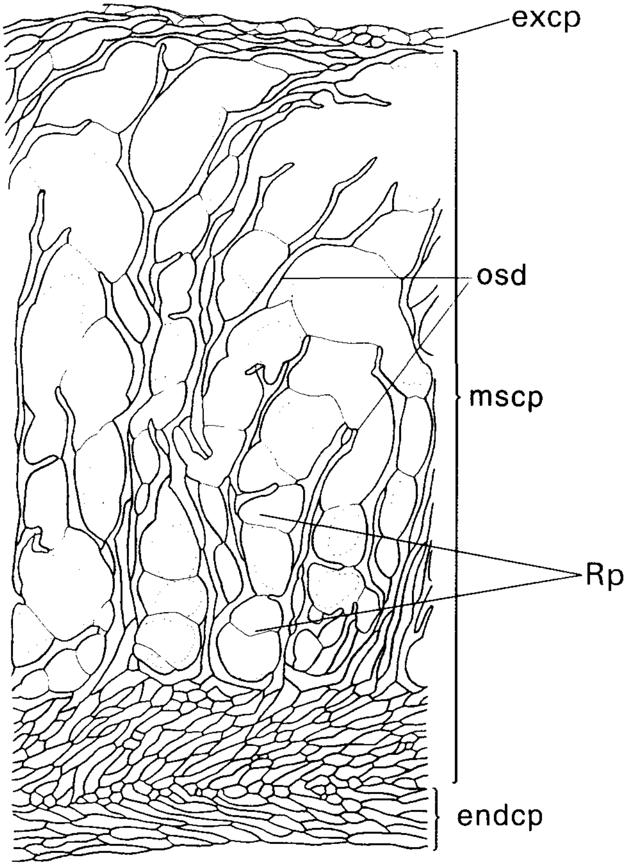

FIG. 3. Cross-section of the pericarp of *Davidsonia pruriens* var. *pruriens*, ×10. Abbreviations: endcp, endocarp; excp, exocarp; mscp, mesocarp; osd, osteosclereids; Rp, remnants of mesocarpic parenchyma.

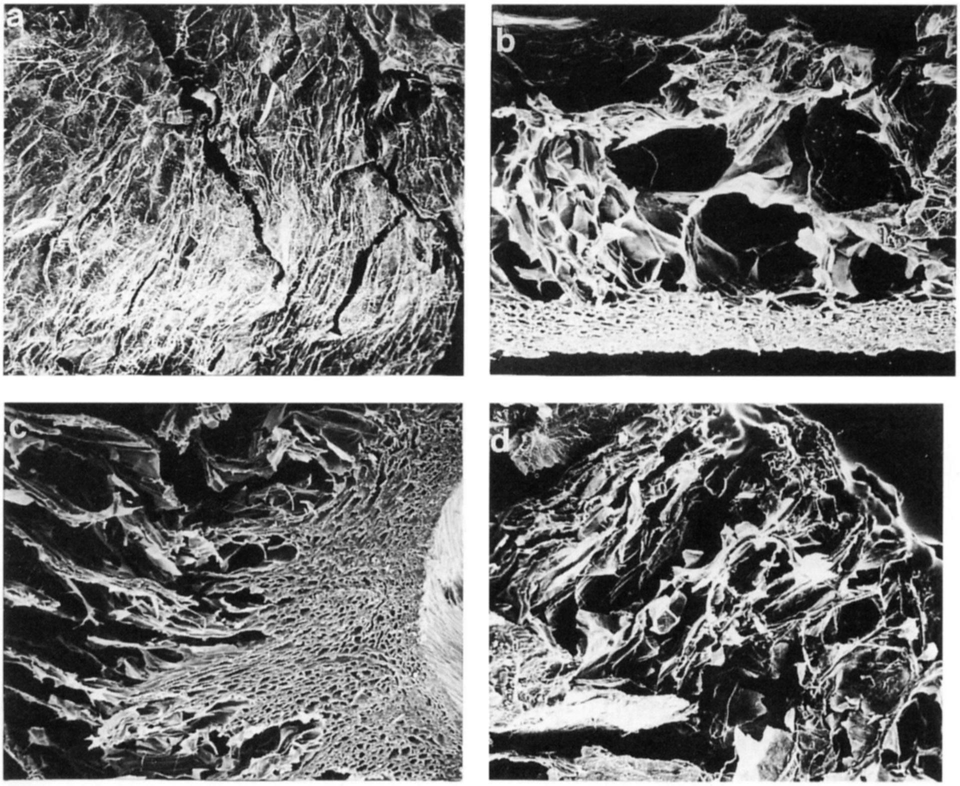

FIG. 4. SEM photographs of the pericarp of *Davidsonia pruriens* var. *pruriens*: a, surface of mature mericarp showing remnants of exocarp with fungi, × 210; b, cross-section of pericarp, × 110; c, cross-section of pericarp near wing, × 80; d, cross-section of pericarp showing broken down mesocarpic parenchyma, × 165.

relatively thick-walled, but scarcely, if at all, lignified osteosclereids, oriented at right angles to the long axis of the mericarp and pervading mesocarpic parenchyma (only remnants of which are represented in the dried mature fruit). These strands form a distinctive fimbriate surface of the fruit and the distinctive small wings of mericarps (Figs 1, 2, 4).

Seed

Mature seed. The mature seed (Fig. 5) is relatively large, 1.5–1.8cm long, 1.2–1.5cm wide and 0.5–0.8cm thick, brown, flattened, rounded cordate, exarillate, with undifferentiated raphe, smooth or slightly wrinkled at maturity (when drying). Seed sculpture finely papillate with faceted cuticular sculpture (Fig. 6). The boundary between the pachytesta (derivate of pachychalaza in mature seeds) and the rest of the seed coat formed of the two integuments is morphologically distinct and runs around the seed equator as a shallow groove (see Fig. 5a). The seed coat at the pointed end of the seed adjacent to the hilum consists of the two integuments and

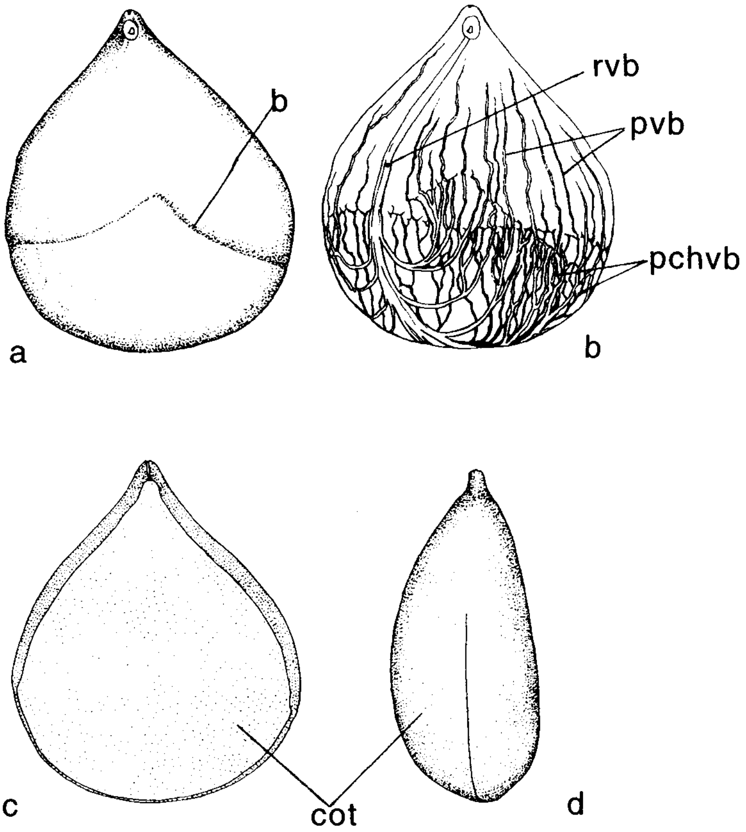

FIG. 5. Mature seed of *Davidsonia pruriens* var. *pruriens*: a, general view, × 3; b, vascularization of the seed, × 3; c, longitudinal section of seed showing embryo (half removed) and abundant endosperm, × 3; d, a dicotyledonous embryo, × 3. Abbreviations: b, border line between pachytesta and testa (upper part of seed); cot, cotyledons; pchvb, pachychalazal vascular bundles; pvb, postchalazal vascular bundles; rvb, raphal vascular bundle.

resembles an aril or arilloid. The hilum is sub-basal and long, with a slightly expanded micropylar rostrum, showing the track of the single vascular bundle entering the seed and giving off a branch system when it reaches the pachychalaza, densely vascularizing this region (Fig. 5b). However, only 8–12 larger bundles enter the true outer integument and reach the micropyle. The mature seeds are exalbuminous, with a straight massive embryo and two large cotyledons with a small radicle (Fig. 5c). The micropyle is formed by the inner integument only.

Spermoderm. The mature seed coat (Figs 7–9) is formed by both integuments and the expanded pachychalaza, diffusely exotegmic.

The *pachytesta*[1] (Fig. 7) substituting the bitegmic integumentary system in the

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[1] Pachytesta = pachychalaza in mature seeds sensu Corner (1976). The term was introduced by Doweld (1996a) for the description of some pachychalazal seed-coat systems of Sapindales.

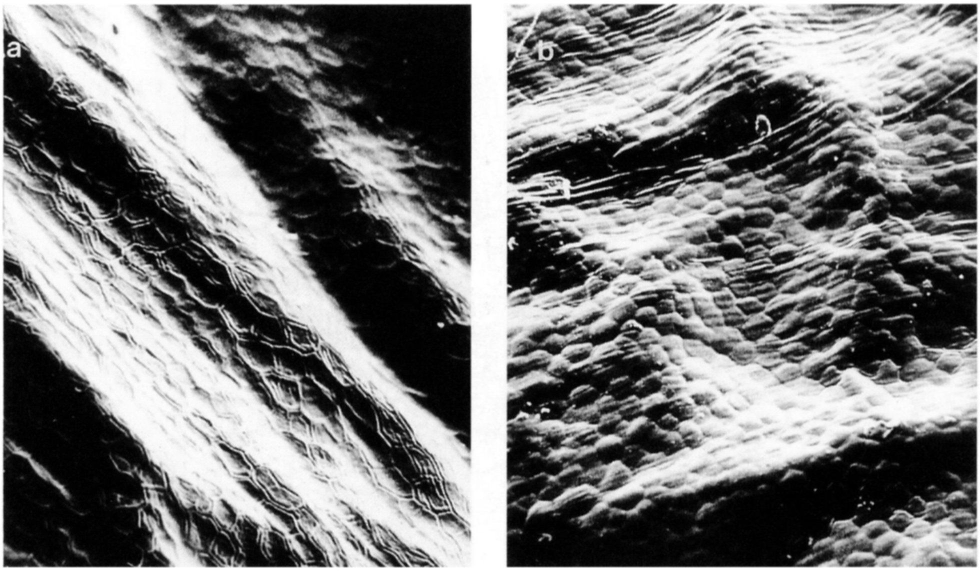

FIG. 6. SEM photographs showing the surface of the seed of *Davidsonia pruriens* var. *pruriens*: a, surface of testa, ×210; b, surface of pachytesta, ×210.

chalazal half of the seed coat is represented by 8–9 layers of tanniniferous cells with numerous anastomosing vascular bundles localized in the 6–7-layered mesopachytesta. The exopachytesta is formed from the epidermis of the pachychalaza and is composed of a single layer of thin-walled, cuboid cells filled with orange granular contents. The single-layered endopachytesta (derived from the innermost layer of the pachychalaza) consists of small cells accumulating tannin-like substances, with heavily thickened, but unlignified outer and radial walls.

In the zone of transition between the pachychalaza and the two integuments (Fig. 8), the thickened cells of the endopachytesta (in transition to the endotegmen) undergo despecialization, owing to the transference of mechanical function to the newly forming one-layered exotegmen. In contrast, the exopachytesta runs into the exotesta without any change in structure. The mesopachytesta divides into the layers constituting the tissues of the testa and the much thicker (multilayered) tegmen. The pachychalazal vasculature ends blindly in the zone of pachychalazal/integumental transition, and 8–12 large vascular bundles pervade the mesotestal tissue of the outer integument.

The *testa* (Fig. 9) is composed of 5–6 layers of small, thin-walled cells filled with tannin-like contents. The exotesta is identical to the exopachytesta; the mesotesta consists of thin-walled cells oblong in the tangential plane.

The *tegmen* (Fig. 9) varies from typically 5–6 layers to 10–12 layers in the zone of pachychalazal/integumental transition. In this area thickening of the walls of the exotegmic cells is practically lacking and correlates with the thickness of the walls of endotegmic cells (rudiment of the sclero-endopachychalazal construction of seed

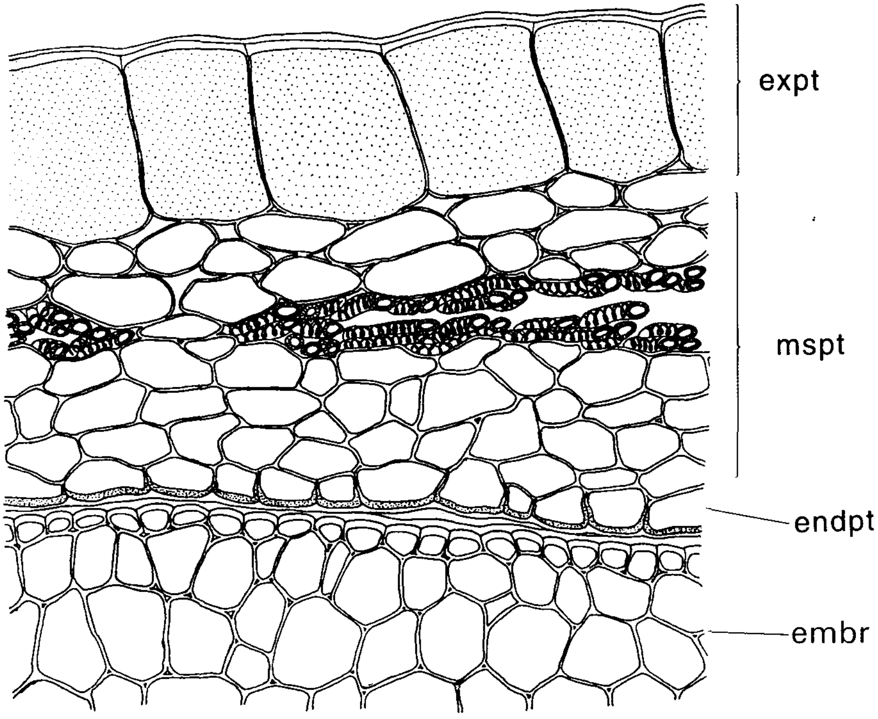

FIG. 7. Cross-section of the pachytesta of *Davidsonia pruriens* var. *pruriens*, ×40. Abbreviations: endpt, endopachytesta; expt, exopachytesta; mspt, mesopachytesta; embr, embryo.

coats). Further inside the seed there is progressive despecialization of the endotegmic layer, and the thickness of the whole exotegmen is greatly increased (tegmen is 2–4-layered at micropyle). A monolayered exotegmen is composed of small cells with heavily thickened and lignified outer periclinal and radial walls. The cells are filled with orange granular contents. The rest of the tegmen is represented by thin-walled parenchymatous cells.

DISCUSSION

The discovery of pachychalaza and exotegmic seed-coat structure in *Davidsonia* supports the affinity of the Davidsoniaceae with the Cunoniales. The exotegmy of the seed coat refutes any idea of close relationships with Saxifragales which are characterized by exotestal seeds (Krach, 1976, 1977; Kulbayeva, 1992a, b), having thus a quite distinct morphogenetic type of spermoderm (Corner, 1976). At the same time it is rather difficult to draw a clear distinction in structure of spermoderm between Davidsoniaceae and Cunoniaceae since Dickison (1984) does not mention the occurrence of a pachychalaza in the latter: however, indirect evidence for its occurrence

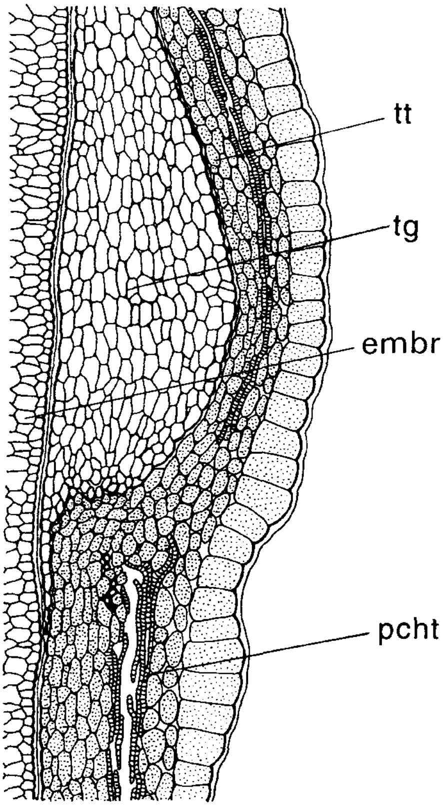

FIG. 8. Cross-section of the transition zone from pachytesta to the true integuments, ×25. Abbreviations: tt, testa; tg, tegmen; pcht, pachytesta; embr, embryo.

is indicated by the reported 'discontinuous [fibrous] layer'. It is comparable with recorded so-called diffusive exotegmy of the davidsoniaceous seed coats, which is caused by the expansion of pachychalaza and by the gradual transference of the mechanical function from the endopachychalaza to the exotegmen. In spite of the lack of adequate data on the cunoniaceous seed coats for comparison with that of *Davidsonia*, it seems that segregation of exalbuminous and strongly pachytestal *Davidsonia* into a family of its own (Bange, 1952) is rather reasonable, thereby emphasizing its advanced characteristics (Czerniakowskaya & Doweld, 1996).

The structure of the pachytesta is also of great interest since its exo-endopachychalazal construction indicates derivation from the exotestal-endotegmic structure of seed coats. This allows us to connect exotegmic Davidsoniaceae and Cunoniaceae with the exotestal-endotegmic Rosales which are also characterized by the occurrence of a pachychalaza (Corner, 1976). Thus the Cunoniales prove to be a more specialized and advanced order of the Rosidae than the Rosales themselves which retain a type of spermoderm ancestral to the Cunoniales. In this respect the treatment of the Cunoniales as the most primitive order of the whole Rosidae as

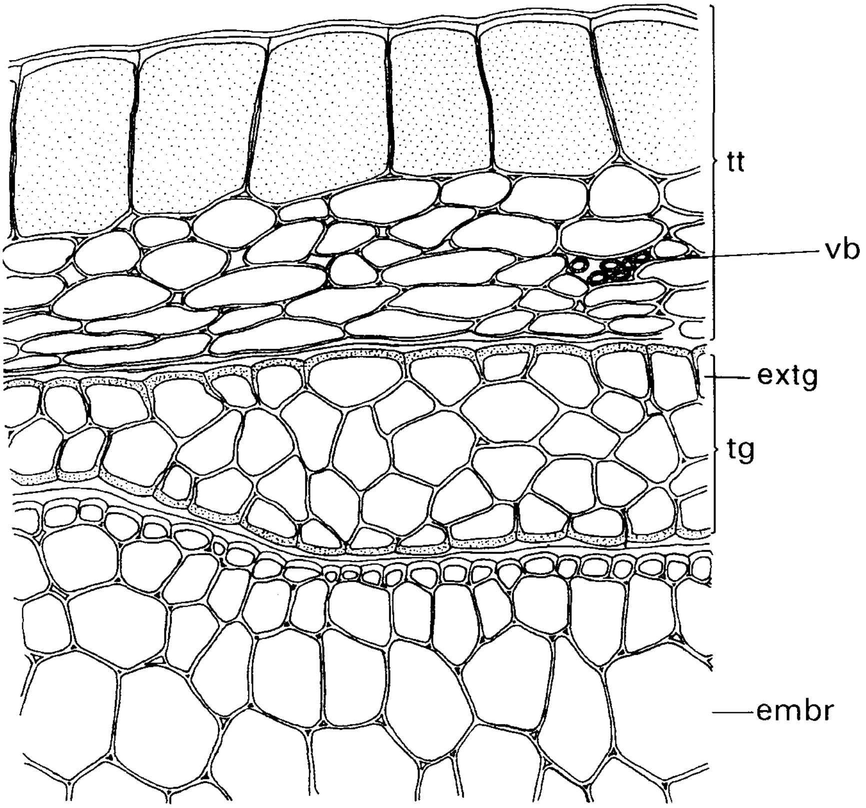

FIG. 9. Cross-section of the spermoderm (testa and tegmen) of *Davidsonia pruriens* var. *pruriens*, × 40. Abbreviations: extg, exotegmen; tt, testa; tg, tegmen; embr, embryo; vb, vascular bundle.

proposed by Takhtajan (1987: 142) is not supported. It seems possible that the highly specialized exotegmic Cunoniales represent a rather blind side-branch to Rosalean ancestry.

Hallier (1908, 1912) and more recently Takhtajan (1987), Cronquist (1992) and Thorne (1992) found it possible to connect the Staphyleaceae of the Sapindales with exotegmic Cunoniales ['its inclusion in Cunoniales would not be a big mistake' (Takhtajan, 1987: 170)]. However, there is a great morphogenetic gap between the exotegmic seed construction of the Cunoniales and that of the exo-mesotestal Staphyleaceae (Corner, 1976; Doweld, 1996b), the seed coats of which are formed from another (the outer) integument. Even the trend within the Staphyleaceae towards the despecialization of the outer epidermal cells of the outer integument and the formation of a fleshy layer (e.g. in *Euscaphis*) does not fit the suggested close relationship with Cunoniaceae. These fundamental differences completely debunk the concept of the close relationship of the two families. *Davidsonia* and Cunoniales, on one hand, and Staphyleaceae on another, represent quite distinct and distant evolutionary lines within Rosidae. This is strongly evidenced by differences in seed-coat anatomy that outweigh all similarities of exomorphic characters of mostly vegetative organs (Hallier, 1908, 1912; van der Linden, 1960).

Furthermore, the seed-coat anatomy also refutes the idea of the close relationship of *Davidsonia* and Cunoniales with the Hamamelidae as has been recently advocated by Dickison (1989). The primitive representatives of Hamamelidae (Hamamelidales) possess a very archaic and specialized exo-mesotestal type of seed coats (Melikian, 1973, 1991; Mohana Rao, 1974) derived from the sarcotestal magnolian or proto-magnolian type of spermoderm. This is illustrated by the occurrence of sarcotestal rudiments within *Trichocladus*, *Sinowilsonia* and *Disanthus* (Melikian, op. cit.). The hamamelidaceous seed coats are formed on the basis of multilayered outer integument (usually c.20–30 layers of heavily thickened macrosclereids), in contrast to the tegmic cunoniaceous type. In comparison with them it looks very simplified and advanced, having less multilayered exotegmic spermoderm (nearly 10–12 thin-walled layers only) with expanding pachychalaza. The probable relationships of *Davidsonia* and other Cunoniales with exotegmic Trochodendraceae and Tetracentraceae (Doweld, 1998) as well as with exotegmic Altingiaceae (Netolitzky, 1926; Mohana Rao, 1974) and also Bucklandiaceae (?) can be ruled out. The exotegmic construction of these hamamelidalian representatives is derived directly from the endotestal-exotegmic seed-coat type similar to that of Dilleniaceae (Dilleniales). It is supported by the occurrence of vestigial thickenings of the endotestal cells within *Trochodendron* (Doweld, 1998). By contrast, the seed coats of Davidsoniaceae are connected with the pachychalazal seed construction (absolutely lacking within the above-mentioned hamamelids) and directly originate from the rosalean pachytestal exotestal-endotegmic seed-coat type. This important difference precludes all possibilities of close relationships of *Davidsonia* and other Cunoniales in general with Hamamelidae. None of the hamamelidaceous families could resemble such a simplified and at the same time advanced type of pachychalazal exotegmic seed coat. In this connection any attempts to relate or group together archaic Hamamelidae and highly advanced Cunoniales look very artificial and untenable. The anatomy of seed coats clearly distinguishes the two groups, putting them into distinct, not closely allied phyla that are independently derived from the proto-magnolian stock. The seed-coat structure represents a delicate and at the same time unambiguous instrument for the delimitation of major patterns of evolution in putatively closely allied groups of flowering plants.

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