Micromorphological structure of the fruit and seed of *Smodingium argutum* (Anacardiaceae), as an adaptation to its natural habitat

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Smodingium argutum E. Mey. ex Sond. is very closely allied to the genus *Rhus* L., but easily distinguished from it by the inflorescence which is a thyrse; its pendulous ovule; an 'apical-lateral' style; winged fruit; a sap (noxious secretion from all organs) which turns black on exposure to air; indumentum on the pedicel, bracteoles and calyx, as well as an unique, papery pericarp. The latter comprises a uniseriate exocarp, a mesocarp with large secretory ducts and a mostly two-layered, weakly developed endocarp. An anatropous, bitegmic, crassinucellate ovule develops into a small, partially pachychalazal, exalbuminous seed, also characterized by an endotegmen and lipidic nutrient reserves. The following characters are obviously of crucial importance for the survival of this species: efficient fruit dispersal, aided by the samaroid drupe; easy germination; the well-developed cuticles on the calyx, ovary wall and exocarp; and the thick cuticular layer delimiting the mature integumentary seed coat, which, together with cell wall impregnations in the physiologically mature hypostase cells, protects the embryo against dehydration.

Keywords: Callose, hypostase, lipids, pericarp, samara, seed coat.

Introduction

According to Mabberley (1987) the Anacardiaceae, which is mainly tropical and subtropical, comprises 73 genera. In southern Africa this family is represented by ten indigenous genera, five of which are monotypic (Arnold & De Wet 1993). One of these is the endemic *Smodingium* E.Mey. ex Sond. which was placed in the tribe Rhoeae by Engler (1892). The only species, *Smodingium argutum* E.Mey. ex Sond., is closely allied to and resembles the genus *Rhus* L., but was previously easily distinguished by its winged fruit, a pendulous ovule, 'lateral' style and the sap which turns black on exposure to air. Characteristics of the fruit and seed of *S. argutum* will be compared with those of the genus *Rhus*. However, for the sake of brevity, only those characteristics of *Rhus* that differ significantly from those of *Smodingium*, are specifically mentioned. Ovary, pericarp and seed coat anatomy of several species of *Rhus* has been studied previously (e.g. Pienaar & Von Teichman 1998; Von Teichman 1991a; Von Teichman & Robbertse 1986; Von Teichman & Van Wyk 1991; Wannan & Quinn 1990, 1991). Watt and Breyer-Brandwijk (1962) mention contact dermatitis in susceptible individuals caused by the poisonous sap occurring in all parts of *S. argutum*. Findlay *et al.* (1974) found a close chemical relationship between the allergens from, amongst others, the American Poison Ivy (*Toxicodendron radicans* (L.) Kuntze) and *S. argutum* (henceforth referred to as *Smodingium*). Two heptadecyl catechols constitute the main components of their noxious secretions. These authors also refer to the treatment of *Smodingium* dermatitis. *Smodingium* is the only known indigenous species of the Anacardiaceae causing dermatitis, i.e. severe erythema with oedema and blistering. Most American researchers in this field consider *Toxicodendron* Mill. (comprising the notorious species) to be separate from *Rhus* (Mitchell 1990; Reveal 1990). On the other hand, authors from the United Kingdom mostly do not segregate *Toxicodendron* from *Rhus* (e.g. Mabberley 1987).

The common names of *Smodingium*, African Poison Oak, Pain Bush, inTovane and Rainbow Leaf, reflect its poisonous nature and beautiful autumn foliage (e.g. Pooley 1993). The frost-resistant shrubs or small trees (up to six m high) are characterized by their drooping habit and occur mostly in stony soil. They are found in *Acacia*-dominated and riverine thorn bush and on forest margins. The natural distribution of the species extends from the midlands of the Eastern Cape and KwaZulu-Natal, into the eastern Free State and the lowveld of Mpumalanga. A distribution map is supplied by Wells (1988).

The importance of data on seed structure for taxonomic revision has been stressed repeatedly (e.g. Boesewinkel & Bouman 1984; Corner 1976; Groenendijk *et al.* 1996). These authors also suggested that seed studies began with the ovule and ended with germination, and that a correct interpretation of mature seed coat structure necessitated ontogenetic studies. In a recent encyclopaedic work, Werker (1997) followed the holistic approach by relating seed anatomy to various physiological processes. In the present paper, the contribution of the micromorphological structure of the fruit and seed to the adaptation of *Smodingium* to its natural habitat is discussed. Information on the position of the styles, structure of the ovule and notes on germination are also supplied for the first time. This study is part of a comprehensive survey of the fruit and seed structure of the Anacardiaceae. It aims to supply new data required for a revised infra-familial classification of this family as envisaged by Wannan and Quinn (1990, 1991).

Materials and Methods

Floral buds, flowers and fruit of *Smodingium*, in various stages of development, were collected from trees in the Pretoria National Botanical Garden (voucher specimens: *Von Teichman 536, 546 & 548* in PRU). Material for anatomical studies was fixed in 2.5% caffeinated, sodium phosphate-buffered glutaraldehyde. Dehydration, infiltration and embedding in glycolmethacrylate (GMA) were done according to Feder and O'Brien (1968).

Composition of the monomer mixture, preparation and staining of the 3 μm-thick GMA sections, as well as the histochemical test for cutin, are described by Von Teichman (1987). However, in the present study the sections were cut on a Reichert-Jung Autocut 2040 ultramicrotome. Histochemical staining for proteins was done with amido black 10B according to Bullock *et al.* (1980). For the detection of callose, semi-thin sections were mounted in 0.1% water-soluble aniline blue in 0.1 M K_3PO_4 buffer at pH 12.4, and examined with a Nikon Optiphot light microscope equipped with

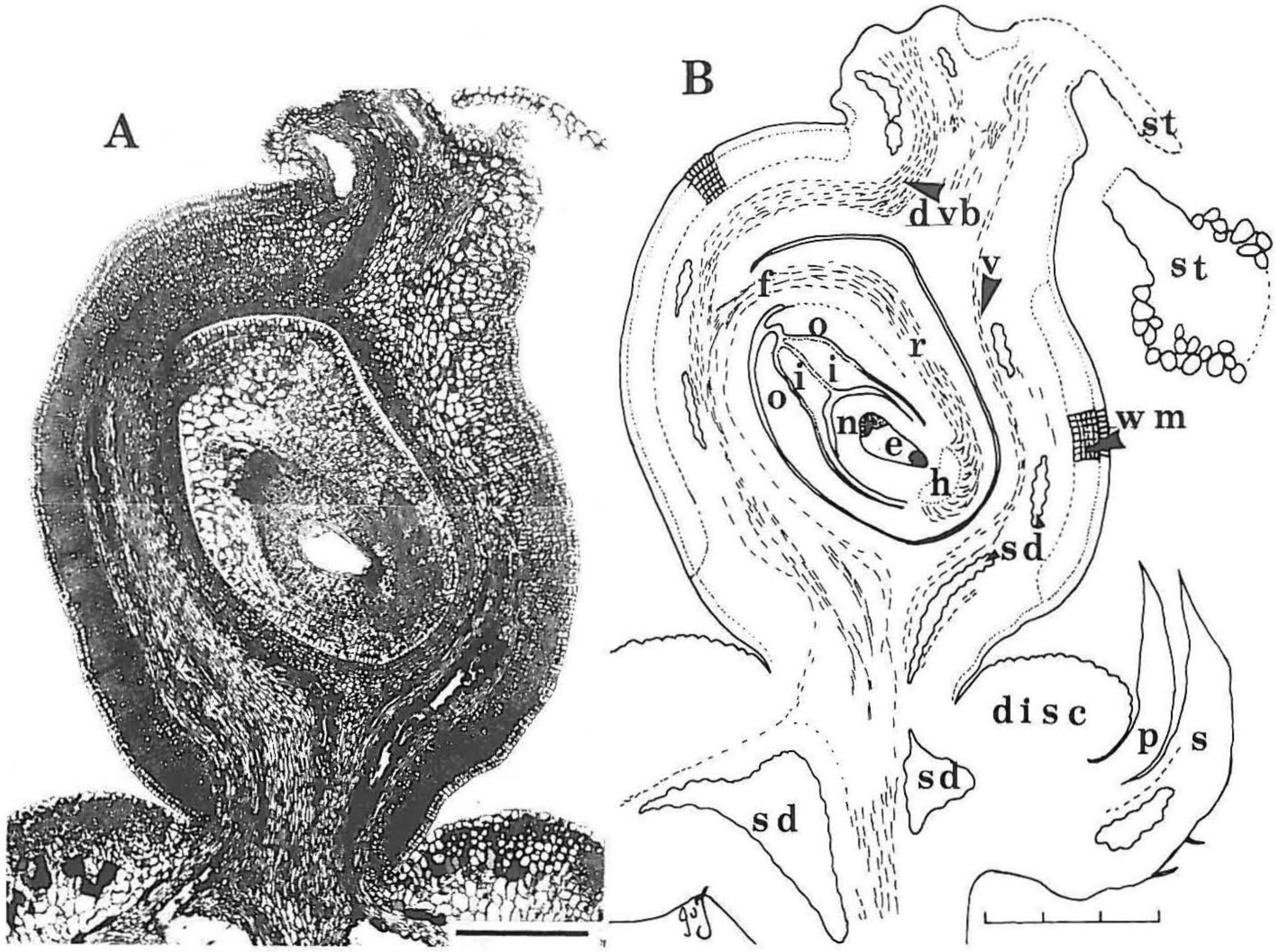

Figure 1 The ovary of *Smodingium* in the flower at anthesis. **A**, one of the longitudinal sections (ls), **B**, a reconstruction from a series of ls. Abbreviations: d vb, dorsal vascular bundle; e, embryo sac; f, funicle; h, hypostase; i, inner integument; n, nucellus; o, outer integument; p, petal; r, raphe vascular bundle; s, sepal; sd, secretory duct; st, part of recurved style with stigma; v, ventral vascular bundle; wm, wing meristem. Scale bar: A = 200 μm, B = 300 μm.

epifluorescence optics (450–490 nm = B-2A excitation filter and 520 nm barrier filter). For the microphotography, CF N PLAN APO objectives were used with the Nikon microscope. Crystals and starch grains were observed under crossed polarized filters.

Results and Discussion

Morphology of flowers, fruit and seed

Smodingium is dioecious. According to the interpretation of Weberling (1992), the inflorescence is a many-flowered, axillary and terminal, determinate (double) thyrse. Barfod (1988:8) states that the 'inflorescences of the tribe Rhoeae are typically thyrsoid'. This applies to a number of North American species of *Rhus*, but *Toxicodendron* is an exception, having a panicle. Female flowers of *Smodingium* are functionally unisexual, very small, *ca.* 2 mm in diameter, and whitish to cream-coloured. Pedicels are articulated near the apex. The pedicel, the two minute bracteoles and the sepals have numerous, straight or variously bent, stiff, lignified, mostly unicellular hairs. In *Rhus lancea* L.f., the perianth is glabrous. In *Smodingium* the calyx and corolla are pentamerous. The abaxial epidermis of the perianth has a very well-developed, serrated cuticle. Five well-developed antisepalous staminodes, situated at the deeper notches of the disc, alternate with the reflexed petals. An orange, annular, 10-crenate intrastaminal disc is present (Figure 1). It is characterized by a well-developed cuticle on the non-papillate epidermal cells. Abundant, mostly open stomata occur within the epidermis. The hypodermal parenchyma cells seem to be metabolically active, judged by the large nuclei and abundant cytoplasm. Whether these cells function as a secretory tissue, is not known.

The tricarpellary gynoecium is characterized by a unilocular, ellipsoidal, laterally compressed ovary (*ca.* 1.5 mm high and 1 mm in diameter). In flowers at anthesis, the ovary wall (Figures 1–3) comprises the following:

a) an outer epidermis (future exocarp *sensu stricto*) with slightly radially elongated cells and well-developed cuticle;

b) a parenchymatous ground tissue with crystalliferous cells containing calcium oxalate; on the lateral sides of the ovary the outer part of the ground tissue represents a 'wing meristem', consisting of small, metabolically active parenchyma cells lying in distinct radial rows; the ground tissue is furthermore characterized by one row of very large secretory ducts surrounded by cytoplasmic-rich epithelial cells and two or three cell layers of small, thin-walled parenchyma cells forming a distinct sheath, as well as by the vascular tissue; and

c) the innermost epidermis, which has formed two distinctly meristematic cell layers by means of periclinal divisions. In some places even three cells may lie in radial rows after a further periclinal division has taken place.

This vascular tissue in the ovary of *Smodingium* comprises

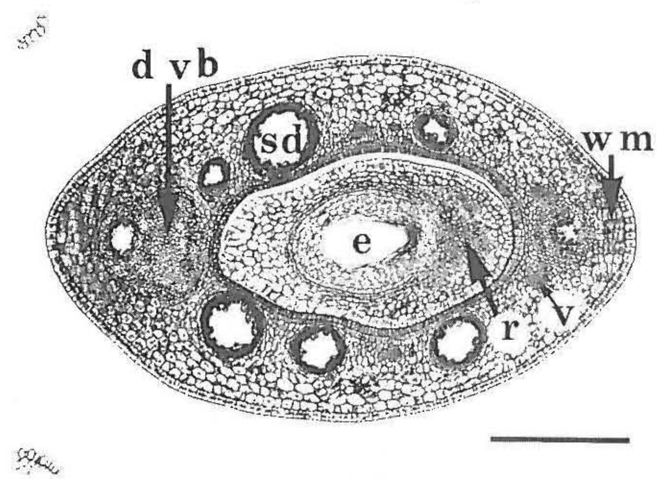

Figure 2 Transverse section of the ovary at anthesis. Abbreviations as in Figure 1. Scale bar = 200 µm.

one large dorsal, two distinct ventral bundles (Figures 1–3) and lateral procambium strands, mostly alternating with the secretory ducts or distinguishable as a few xylem elements lying near the secretory duct sheath. This vasculature in the ovary and stylar base is of significance, as already in 1883 Engler described *Smodingium* with lateral styles. However, he did not state whether they were dorsally or ventrally positioned. Wannan and Quinn (1991) have already described and amply illustrated very similar dorsal and ventral vascular bundles in various taxa of the Anacardiaceae, amongst others, in the genera *Blepharocarya* F.Muell. and *Mangifera* L. Comparing the present Figure 1 with that of *Mangifera indica* L. by Wannan and Quinn (1991, amongst others, Figures 21K & 27), the style base in *Smodingium* may be described as 'apical-lateral', since it is not as pronouncedly 'lateral' as that of *Mangifera indica*. The larger, dorsal vascular bundle does not bend over the ovule to the same great extent as in *Mangifera*. Again the concept of a continuum applies, as the style in *Smodingium* is an intermediate form between distinctly apical and distinctly lateral. In *Smodingium* the styles are situated on the ventral side of the ovary (Figure 1B). The three styles are free (fused only basally) and recurved. Three functional and capitate stigmata, with a non-papillate epidermis, terminate the styles.

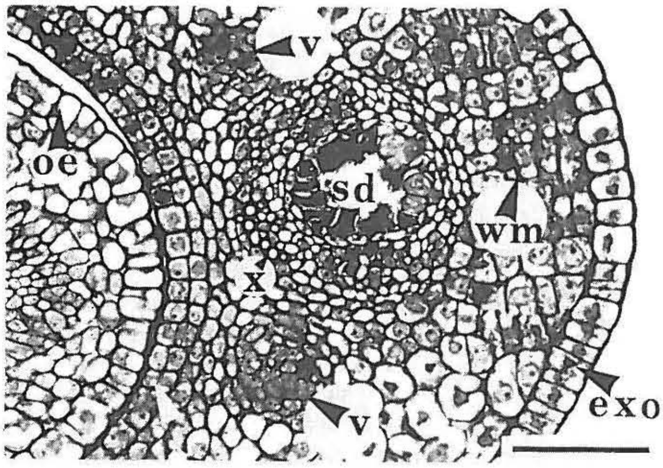

Figure 3 Transverse section (ts) of a small part of the ovary wall at higher magnification, illustrating, amongst others, the future endocarp, *white arrow heads*; future exocarp, *exo*; outer epidermis of ovule in the chalazal region, *oe*; wing meristem, *wm*; and xylem elements *x*, close to the secretory duct (*sd*) between the two ventral vascular bundles (*v*). Scale bar = 50 µm.

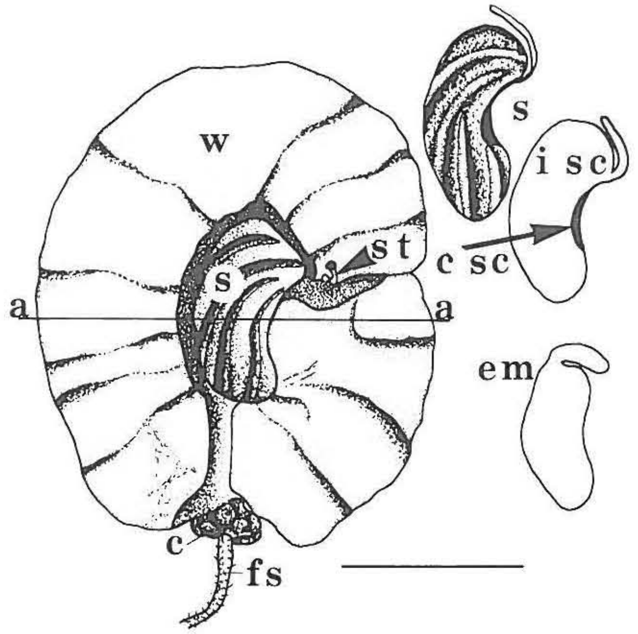

Figure 4 Morphology of the fruit, seed and embryo of *Smodingium*. Abbreviations: line at **a**, indicates the position of the ts in Figure 5; c, persistent calyx; c sc, chalazal seed coat; em, embryo; fs, fruit stalk; i sc, integumentary seed coat; s, seed (one showing the impressions of secretory ducts in the mesocarp); st, remnants of persistent style and stigma; w, wing. Scale bar = 4 mm.

The single pendulous ovule is very small (*ca.* 0.7 mm long), bitegmic, anatropous, crassinucellar, with a ventral raphe (Figure 1). As in most ovules/seeds of the Anacardiaceae studied previously, the raphe has an amphicribral vascular bundle. A hypostase *sensu lato*, consisting of a group of metabolically active parenchyma cells, is present. Although this hypostase *sensu lato* is not as sharply demarcated as in *Ozoroa* Delile (Von Teichman 1993: Figure 4), it characterizes the chalazal-nucellar tissue. The distinction between a hypostase *sensu lato* and *sensu stricto* in the Anacardiaceae is explained by Von Teichman (1988). It is only the hypostase *sensu lato* which takes part in the formation of the seed coat. In *Smodingium* the outer integument (o) is proximally four or five cell layers thick, while the inner integument (i) consists proximally of only two epidermal layers, with the inner epidermis (ie ii), i.e. the future endotegmen, easily distinguishable due to its meristematic character.

Fruitset can be so high that great parts of the plant are draped with light brown infructescences. Drupes are laterally compressed, samaroid, subcircular (*ca.* 11 × 9 mm), light brown when ripe, indehiscent, with a conspicuous circular, papery wing which developed from the 'wing meristem', secretory ducts and persistent styles and calyx (Figure 4). In contrast to the observations of Engler (1892), who most probably used dry herbarium material, it was found that the seed coat is not attached to the pericarp. The partially pachychalazal seeds are kidney-shaped and show the impressions of the secretory ducts occurring in the mesocarp (Figures 4 and 5). The seed coat is light brown (integumentary part) with a dark brown, saddle-shaped part (the chalazal seed coat) - the dark colour is due to the presence of the tanniniferous cells in the hypostase *sensu lato*. This seed coat is very similar to that of *Rhus lancea* (Von Teichman 1991a), as well as those of the other species of *Rhus* studied previously.

Anatomy of the pericarp

In order to be useful in phylogenetic considerations, i.e. comparing homologous parts in different taxa, the pericarp in

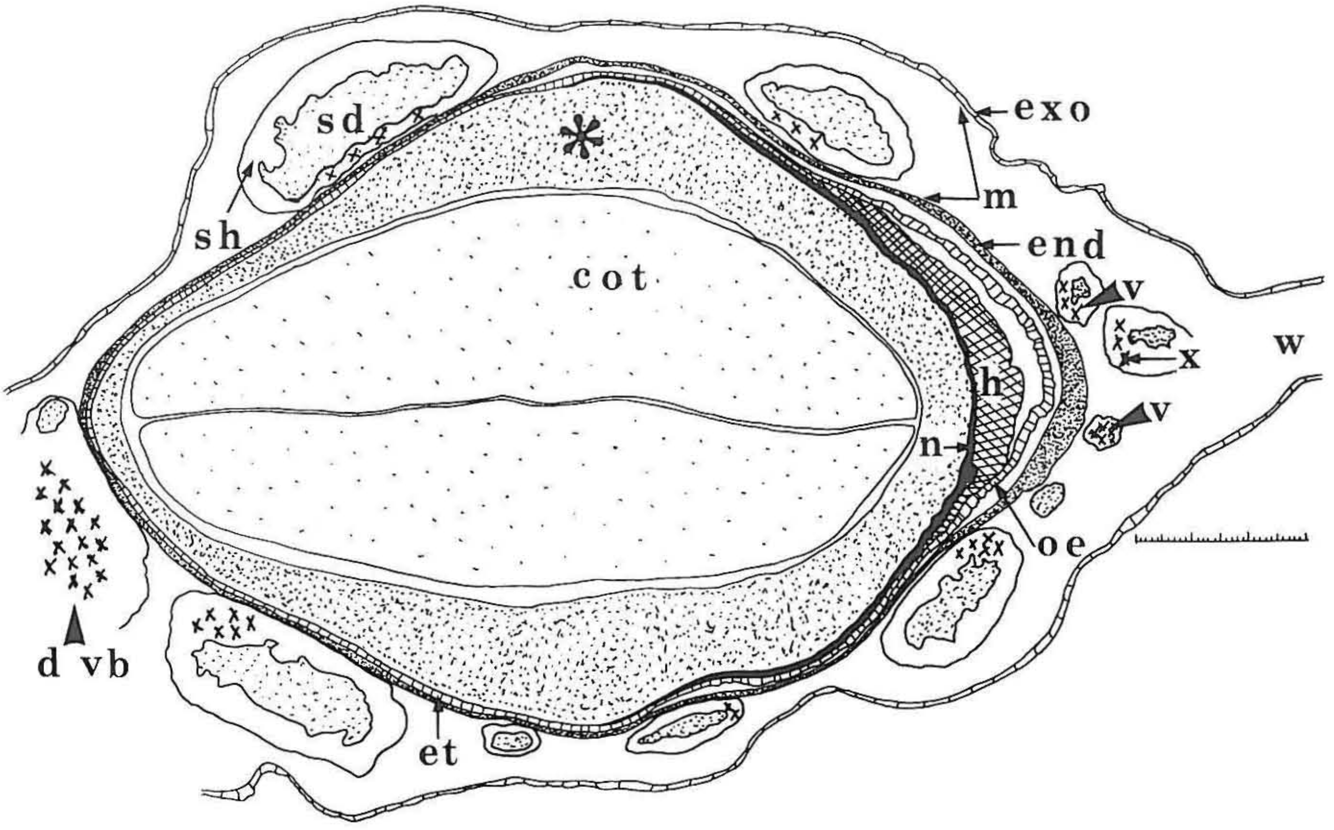

Figure 5 Ts of mature pericarp and seed. Abbreviations: cot, cotyledon; d vb, large dorsal vascular bundle; end, endocarp; asterisk, cellular remnants of the endosperm; et, endotegmen in integumentary seed coat; exo, exocarp; h, hypostase in chalazal seed coat; m, mesocarp; n, nucellar remnants; oe, outer epidermis of seed coat; sd, secretory duct; sh, parenchyma sheath; v, ventral vascular bundle; w, wing; x, xylem elements within vascular tissue. Scale bar = 300 µm.

Smodingium is interpreted *sensu stricto*. My reasons have been published previously in a paper on the reinterpretation of the pericarp of *Rhus lancea* (Von Teichman 1989). In *Smodingium* the exocarp (Figures 5–7) with its well-developed cuticle comprises relatively thin-walled parenchyma. It originated from the outer epidermis (oe) of the ovary wall. The mesocarp *s. str.* is characterized by large secretory ducts (Figures 5–7), the vasculature, thin-walled parenchyma and crystalliferous cells. This vasculature comprises a large dorsal and two ventral vascular bundles, as well as vascular tissue which usually, together with the epithelial cells and parenchymatous sheath cells, surrounds the secretory ducts. The wing is formed by the exocarp and the outer parenchyma of the mesocarp. The thin, slightly leathery endocarp *s. str.* consists of one or mostly two layers of relatively thin-walled brachysclereids (Figures 5–7). Parenchyma cells adjacent to the ventral vascular bundles (Figure 6) have formed thin-walled brachysclereids.

In the pericarp of *Rhus lancea*, the exocarp is very similar to that of *Smodingium*. However, the outermost layer of the mesocarp of *Rhus lancea* forms a sclerenchymatous hypodermis, followed by parenchyma and pronounced inner sclerenchymatous ridges, associated with the secretory ducts and vascular bundles (Von Teichman & Robbertse 1986). In *R. lancea* and *R. problematodes* Merxm. & Roessler (Von Teichman & Van Wyk 1991), as well as in *Lithraea brasiliensis* Marchand, which should rather be classified under the genus *Rhus* (Pienaar & Von Teichman in press), the thick, stony endocarp *sensu stricto* is three- or four-layered (stratified), consisting of an innermost layer of palisade-like macrosclereids, a layer of osteosclereids, followed by a layer of brachysclereids. A distinct fourth crystalliferous layer, with cell walls also slightly thickened, occurs in *R. lancea* and *L. brasiliensis*. Such a distinctly layered (stratified) endocarp *sensu stricto* as in *R. lancea* represents the *Anacardium*-type endocarp *sensu* Wannan and Quinn (1990). Under the *Anacardium*-type, these authors recognize three endocarpal sub-types (or taxon groups) in the tribe Rhoeae. An endocarp of four discrete layers as in *Rhus, Ozoroa, Schinus* L. and seven other genera, forms Group A. A two-layered endocarp, as was found in *Smodingium* during the present study, which is also present in *Protorhus longifolia* (Bernh.) Engl. (Von Teichman 1991b) and *Heeria argentea* (Thunb.) Meisn. (Von Teichman & Van Wyk 1996) does not fit any of the sub-types or Groups of Wannan and Quinn (1990). Therefore, as proposed by Von Teichman and Van Wyk (1996) for *H. argentea*, this type of endocarp in *Smodingium*, represents a fourth Rhoeae endocarpal sub-type (Group D). The latter is also derived from the Group A-type.

Anatomy of the seed

The seed of *Smodingium*, which is very similar to that of the species of *Rhus* mentioned above, is partially pachychalazal, the seed coat being of dual origin, since the secondarily extended chalaza takes part in the development of the mature seed coat. Anatomically the chalazal seed coat comprises the outer epidermis, a few layers of hypodermal, thin-walled, tanniniferous and slightly compressed parenchyma and the hypostase. The latter conforms to the Anacardiaceae-type described for all the previously studied taxa (e.g. Von Teichman 1991a,c; Von Teichman & van Wyk 1996). Its cells are contiguous, thin-walled, distinctly tanniniferous and form a zone which is easily distinguishable (Figures 5 and 6). Cell walls of the hypostase in the mature, physiologically ripe seed remained unstained in periodic acid-Schiff's reagent and in toluidine blue (Figure 6). However, in the tests for lipids, namely cutin, and also callose, these cell walls

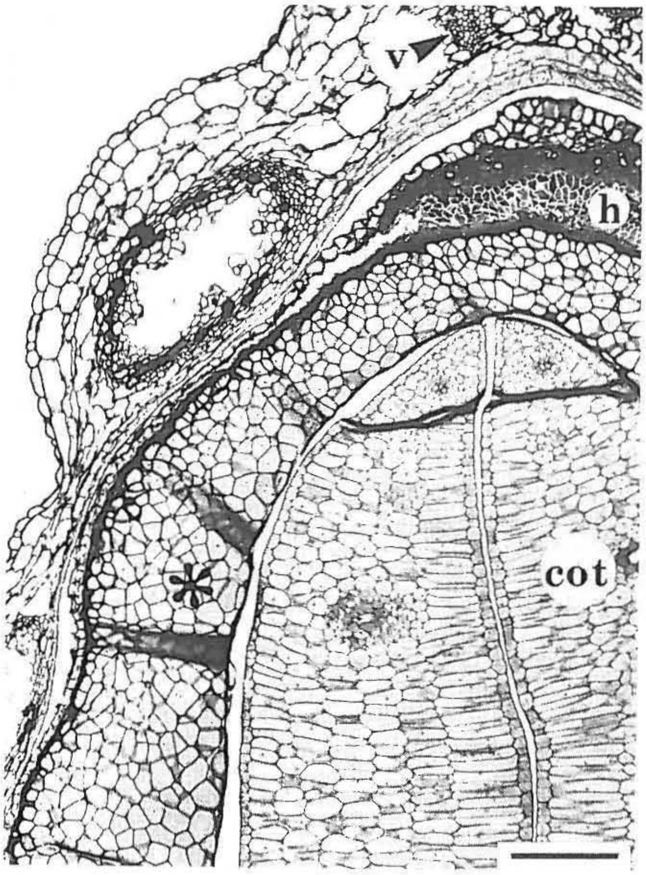

Figure 6 A part of the ts shown in Figure 5, at higher magnification. Abbreviations as in Figure 5. Scale bar = 150 μm.

reacted positively.

The periphery of the hypostase, covered only by the outer epidermis, merges with the integumentary seed coat. A well-developed cuticular layer (Figure 7), comprising the cuticles of the inner epidermis of the inner integument as well as the nucellar epidermis, forms the innermost part of the integumentary seed coat (Figure 7). At maturity the latter consists of the endotegmen, namely the differentiated inner epidermis of the inner integument, and very compressed, minute remnants of the outer epidermis of the inner integument as well as remnants of the whole outer integument. Radial and tangential cell walls of the endotegmen are secondarily thickened, lignified, and abundantly pitted (Figure 7). The well-developed cuticular layer, which merges into the hypostase, as well as the cutinized cell walls of the hypostase, forms a continuous lipidic layer protecting the whole, physiologically mature embryo against dehydration.

At the anti-raphal side the endotegmen abuts directly on the cellular endosperm remnants (to the inside) and the endocarp (on the outside) (Figure 5). In *Smodingium*, in contrast to other taxa of the tribe Rhoeae, the extent of the endosperm remnants is more significant, since at the anti-raphal side of the seed they are practically absent in e.g. *Rhus, Ozoroa, Protorhus* Engl. and *Heeria* Meisn. (Pienaar & Von Teichman 1998; Von Teichman 1991a & c, 1993, 1994; Von Teichman & Van Wyk 1996). According to Boesewinkel and Bouman (1984), seeds are called exalbuminous or exendospermous if the endosperm is (almost) completely used up by the developing embryo. In *Smodingium* the remnants are more extensive and the seeds may therefore possibly be called semi-exalbuminous. This surely represents a continuum, as the presence of endosperm in *Smodingium* is the intermediate form. Functionally the lipids within these endosperm remnants possibly also serve to prevent the dehydration of the embryo.

The white, bent embryo is laterally compressed. Its cotyledons consist of parenchymatous epidermal cells which are distinctly smaller than the storage parenchyma cells. In the centre of this storage tissue is a row of about five secretory ducts. Protein bodies, which fill all these cells, and also fats constitute the food reserves in this semi- exalbuminous seed (Figures 6 and 7). This small, partially pachychalazal seed, with lipids as main food reserve, is also typical of several other indigenous or even endemic species of the Anacardiaceae from savanna or extremely arid desert regions, where plants are periodically subjected to drought. These species, in contrast to those with large, pachychalazal, recalcitrant (also exalbuminous) seeds which mainly store starch, are considered more derived. Large seeds characterize, amongst others, *Heeria argentea, Protorhus longifolia* and *Mangifera indica.* The results obtained in this study therefore support the hypothesis of Von Teichman and Van Wyk (1994) that pachychalazy with associated greater seed size and the recalcitrant seed viability behaviour may be regarded as ancestral character states in dicotyledons.

Notes on seed germination

When whole fruit were planted in sand, the seeds started to germinate after seven days. As shown in Figure 8, germination in *Smodingium* is epigeal. The same applies to *Rhus lancea, Loxostylis alata* Spreng.f. ex Rchb. and *Laurophyllus capensis* Thunb. (both also dispersed by wind), *Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro (the marula), *Harpephyllum caffrum* Bernh. ex Krauss and *Ozoroa paniculosa* (Sond.) R. & A. Fern. On the other hand, *Heeria argentea* and *Protorhus*

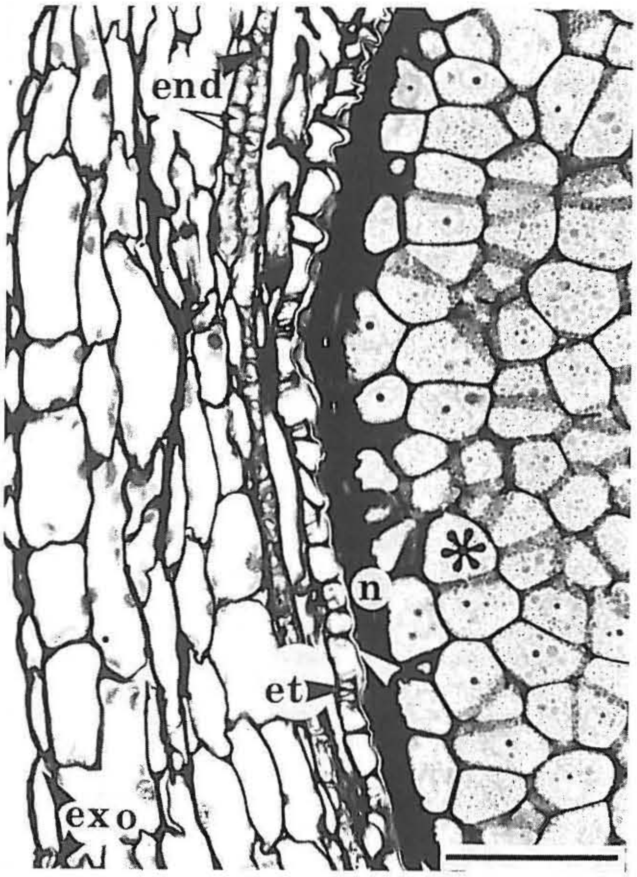

Figure 7 Another part of the ts shown in Figure 5, at higher magnification. Abbreviations as in Figure 5, with the white arrow head points to the cuticular layer. Scale bar = 50 μm.

Figure 8 Seedling of *Smodingium* grown in a plastic bag with a sandy soil mixture, with the cotyledons distinctly above the surface of the soil. Scale bar = 10 mm.

longifolia (with large, pachychalazal and recalcitrant seeds) and *Lannea discolor* (with small, partially pachychalazal seed) germinate hypogeally (Von Teichman & Logischen 1988). The small seeds of *Smodingium, Rhus* and *Ozoroa*, store mainly lipids, comprising a higher energy reserve. *Smodingium* usually produces abundant seeds which germinate easily, and since the fruits are very effectively dispersed by wind, the survival of the species is ensured. It has been reported that small, light, wind-dispersed fruits are often associated with epigeal germination. This is indeed the case in *Smodingium, Loxostylis alata* and *Laurophyllus capensis*. On the other hand, the larger, heavier, animal-distributed seeds usually exhibit hypogeal germination (*P. longifolia* and *H. argentea*). However, the animal-dispersed *L. discolor*, the marula and *H. caffrum* do not fit into this generalized scheme (Von Teichman & Logischen 1988).

Conclusions

Smodingium is not only easily distinguished from *Rhus* species (especially *R. leptodictya* Diels) by its pendulous ovule, 'apical-lateral' styles, winged fruit with persistent styles and calyx, and sap which turns black on exposure to air - but also by the following: an inflorescence which is a determinate (double) thyrse, not thyrsoid; hairs on the pedicel, bracteoles and calyx, which may possibly dissipate heat by scattering/reflecting the light; shape of the ovary; and a unique pericarp structure. Fruit and seed characters are relevant ecologically since they represent adaptive features which contribute to the survival of indigenous/endemic species in their natural habitat. Adaptation can be circumscribed as any heritable character or a set of such associated characters, which increase the probability that the specific individual can survive or reproduce more successfully under its specific environmental conditions (Niklas 1997). Obviously of crucial importance for the survival of *Smodingium* are the following characters: fruit dispersal aided by the structure of the samaroid drupe; easy germination; the mentioned indumentum; the well-developed cuticles on the calyx, ovary wall and later on the exocarp, and the cuticular layer delimiting the mature integumentary seed coat as well as the impregnation of the cell walls of the hypostase cells with cutin and callose in the physiologically mature seed.

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References

ARNOLD, T.H. & DE WET, B.C. (Eds) 1993. Plants of southern Africa: names and distribution. Memoirs of the Botanical Survey of South Africa, No. 62. National Botanical Institute, Pretoria.

BARFOD, A. 1988. Inflorescence morphology of some South American Anacardiaceae and the possible phylogenetic trends. *Nord. J. Bot.* 8: 3–11.

BOESEWINKEL, F.D. & BOUMAN, F. 1984. The seed: structure. In: Embryology of angiosperms, ed. B.M. Johri, Ch. 12, pp. 567–610. Springer-Verlag, Berlin.

BULLOCK, S., ASHFORD, A.E. & WILLETTS, H.J. 1980. The structure and histochemistry of sclerotia of *Sclerotinia minor* Jagger II. Histochemistry of extracellular substances and cytoplasmic reserves. *Protoplasma* 104: 333–351.

CORNER, E.J.H. 1976. The seeds of dicotyledons. Vols I & II. Cambridge University Press, Cambridge.

ENGLER, A. 1883. Anacardiaceae. In: Monographiae Phanerogamarum, eds A.P. & A.C. De Candolle, Vol. 4, pp. 171–546. S.G. Masson, Paris.

ENGLER, A. 1892. Anacardiaceae. In: Die natürlichen Pflanzenfamilien, eds A. Engler & K. Prantl, III (4 & 5), pp. 138–178. Engelmann, Leipzig.

FEDER, N. & O'BRIEN, T.P. 1968. Plant microtechnique: some principles and new methods. *Am. J. Bot.* 55: 123–142.

FINDLAY, G.H., WHITING, D.A., EGGERS, S.H. & ELLIS, R.P. 1974. *Smodingium* (African 'poison ivy') dermatitis: history, comparative plant chemistry and anatomy, clinical and histological features. *Br. J. Dermatol.* 90: 535–541.

GROENENDIJK, J.P., BOUMAN, F. & CLEEF, A.M. 1996. An exploratory study on seed morphology of *Miconia* Ruiz & Pavón (Melastomataceae), with taxonomic and ecological implications. *Acta bot. neerl.* 45: 323–344.

MABBERLEY, D.J. 1987. The plant-book. Cambridge University Press, Cambridge.

MITCHELL, J.D. 1990. The poisonous Anacardiaceae genera of the world. *Adv. Econ. Bot.* 8: 103–129.

NIKLAS, K.J. 1997. The evolutionary biology of plants. The University of Chicago Press, Chicago.

PIENAAR, M.E. & VON TEICHMAN, I. 1998. The generic position of *Lithraea brasiliensis* Marchand (Anacardiaceae): evidence from fruit and seed structure. *Bot. J. Linn. Soc.*

POOLEY, E. 1993. The complete field guide to trees of Natal, Zululand & Transkei. Natal Flora Publications Trust, Durban.

REVEAL, J.L. 1990. Minor new combinations in *Toxicodendron* (Anacardiaceae). *Phytologia* 69: 275.

VON TEICHMAN, I. 1987. Development and structure of the pericarp of *Lannea discolor* (Sonder) Engl. (Anacardiaceae). *Bot. J. Linn. Soc.* 95: 125–135.

VON TEICHMAN UND LOGISCHEN, I. 1988. A morphological study of the fruit and seed of certain southern African members of the Anacardiaceae. D.Sc. thesis, University of Pretoria, Pretoria.

VON TEICHMAN, I. 1988. Development and structure of the seed-coat of *Lannea discolor* (Sonder) Engl. (Anacardiaceae). *Bot. J. Linn. Soc.* 96: 105–117.

VON TEICHMAN, I. 1989. Re-interpretation of the pericarp of *Rhus lancea* (Anacardiaceae). *S. Afr. J. Bot.* 55: 383–384.

VON TEICHMAN, I. 1991a. Ontogeny of the seed-coat of *Rhus lancea* L. fil., and pachychalazy in the Anacardiaceae. *Bot. J. Linn. Soc.* 107: 35–47.

VON TEICHMAN, I. 1991b. Pericarp strucutre in *Protorhus longifolia*

(Bernh.) Engl. (Anacardiaceae) and its taxonomic significance. *Bot. Bull. Acad. Sci.* 32: 121–128.

VON TEICHMAN, I. 1991c. The pachychalazal seed of *Protorhus longifolia* (Bernh.) Engl. (Anacardiaceae) and its taxonomic significance. *Bot. Bull. Acad. Sin.* 32: 145–152.

VON TEICHMAN, I. 1993. Development and structure of the seed of *Ozoroa paniculosa* (Anacardiaceae) and taxonomic notes. *Bot. J. Linn. Soc.* 111: 463–470.

VON TEICHMAN, I. 1994. Generic position of *Protorhus namaquensis* Sprague (Anacardiaceae): evidence from seed structure. *Bot. Bull. Acad. Sin.* 35: 53–60.

VON TEICHMAN, I. & ROBBERTSE, P.J. 1986. Development and structure of the pericarp and seed of *Rhus lancea* L. fil. (Anacardiaceae), with taxonomic notes. *Bot. J. Linn. Soc.* 93: 291–306.

VON TEICHMAN, I. & VAN WYK, A.E. 1991. Taxonomic position of *Rhus problematodes* (Anacardiaceae): evidence from fruit and seed structure. *S. Afr. J. Bot.* 57: 29–33.

VON TEICHMAN, I. & VAN WYK, A.E. 1994. Structural aspects and trends in the evolution of recalcitrant seeds in dicotyledons. *Seed Sci. Res.* 4: 225–239.

VON TEICHMAN, I. & VAN WYK, A.E. 1996. Taxonomic significance of pericarp and seed structure in *Heeria argentea* (Thunb.) Meisn. (Anacardiaceae), including reference to pachychalazy and recalcitrance. *Bot. J. Linn. Soc.* 122: 335–352.

WANNAN, B.S. & QUINN, C.J. 1990. Pericarp structure and generic affinities in the Anacardiaceae. *Bot. J. Linn. Soc.* 102: 225–252.

WANNAN, B.S. & QUINN, C.J. 1991. Floral structure and evolution in the Anacardiaceae. *Bot. J. Linn. Soc.* 107: 349–385.

WATT, J.M. & BREYER-BRANDWIJK, M.G. 1962. The medicinal and poisonous plants of southern and eastern Africa. 2nd edn. E. & S. Livingstone Ltd., Edinburgh.

WEBERLING, F. 1992. Morphology of flowers and inflorescences. Paperback ed. Cambridge University Press, Cambridge.

WELLS, M.J. 1988. *Smodingium argutum*. Flowering Plants of Africa 50(1): t. 1968.

WERKER, E. 1997. Seed anatomy. In: Encyclopedia of plant anatomy, eds. S. Carlquist, D.F. Cutler, S. Fink, P. Ozenda, I. Roth & H. Ziegler. Special part, Vol. 10, part 3, pp. 424. Gebrüder Bornträger, Berlin.