

Functional and taxonomic significance of seed structure in *Salix mucronata* (Salicaceae)

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ABSTRACT

The polymorphic African willow, *Salix mucronata* Thunb., is a widely distributed African tree and a riparian rheophyte. Ovule-to-seed development is reported for *Salix mucronata* subsp. *woodii* (Seemen) Immelman. Contrary to some existing reports, the tuft of silky hairs enveloping the seed in *Salix* is derived from the funicle and not the placenta. The micromorphological structure of the hilar aril and funicular-placental and arillate hairs is described and illustrated for the first time. Willow seeds are primarily wind-dispersed, but have additional characters, such as a hydrophobic seed coat and an unwettable, hairy, hilar aril as specific adaptations for distribution by water, perhaps even chance dispersal by animal visitors to the riverine habitat. Seed adaptations linked to different dispersal strategies may account for seemingly marked differences in ovule/seed structure between Salicaceae *s. str.* and related, mainly zoochorous flacourtiaceous taxa, recently classified with the former in a more inclusively circumscribed Salicaceae *s.l.*

INTRODUCTION

Salicaceae, a classical family recently drastically redefined and classified in the order Malpighiales (Chase *et al.* 2002), is now considered a cosmopolitan group comprising about 53 genera with $\pm 2\ 415$ species of woody perennials. Apart from *Salix* L. (willows) and *Populus* L. (poplars, cottonwoods), the two genera traditionally making up the family (Salicaceae *s.str.*), the newly proposed circumscription now also includes most of the genera formerly placed in Flacourtiaceae *sensu* Lemke (1988). With 400–450 species included in *Salix*, this speciose genus of dioecious, catkin-bearing shrubs and trees is by far the largest in Salicaceae *s.l. sensu* Chase *et al.* (2002).

Salix, commonly known as willows, is the most widely dispersed genus in the family. Currently, most willow species occur in cold temperate to arctic regions of the northern hemisphere, but some grow in warm temperate to tropical climates (Wilmot-Dear 1985, 1991; Friis 1992; Judd *et al.* 2002) where the genus possibly originated (Skvortsov 1968; Dorn 1976). The genus is absent from Australasia and New Guinea (Wilmot-Dear 1985), a few species are found in South America (Zuloaga & Morrone 1999) and one species occurs naturally in Africa (M. Jordaan pers. comm.). This African species, *Salix mucronata* Thunb. (= *S. subserrata* Willd.) is widely distributed, extending from southern Arabia (McKean 1996) and Egypt southwestwards to Senegal and southwards through Ethiopia to Namibia and South Africa (Friis 1992). It is a polymorphic species and, in southern Africa, four (Coates Palgrave 2002; Jordaan 2002) or five (Immelman 1987) subspecies are recognized.

Characteristically, *Salix* prefer wet to moist, open habitats (Judd *et al.* 2002). In almost all African phytochoria,

representatives of the genus are riverine in distribution (Friis 1992). Indeed, many *Salix* species throughout the world are riparian rheophytes, i.e. plants growing along swift-running watercourses and on the banks up to flood level, but not beyond the reach of regularly occurring flash floods (Van Steenis 1981; Jordaan 2002). One such species is the widely dispersed African endemic, *S. mucronata* (Van Steenis 1978).

It is generally assumed that the plumed seeds of willows are wind-dispersed (Ridley 1930; Van der Pijl 1969; Johri *et al.* 1992; Judd *et al.* 2002), but the issue is whether wind is the principal dispersal agent involved in the wide geographical distribution of *S. mucronata*. Our observations on seed dispersal in *Salix mucronata* subsp. *woodii* (Seemen) Immelman showed that upon shedding, the seed does not remain airborne for long, despite the cover of loose wool that initially surrounds the seed and expedites its release from the capsule. In this contribution we present data on seed structure, supplemented by a study of capsule and seed development, suggesting that although willows are adapted to wind dispersal, the seed has additional modifications for dispersal by water and fortuitously by waterfowl or other animal visitors to the rheophytic habitat. We also comment on the taxonomic significance of seed structure in *Salix*, considering its recent association with members traditionally placed in Flacourtiaceae.

MATERIAL AND METHODS

Catkins in most developmental stages were collected from a female tree of *S. mucronata* subsp. *woodii* (accession number: GPTA 495) in the Pretoria National Botanical Garden. The plant was grown from seed, collected by Dr L.E. Codd in 1953 from a tree (*Codd 8246* PRE) on the bank of the Buffalo River, Natal [KwaZulu-Natal]. Floral buds, mature flowers, developing fruit and dehiscing capsules were fixed in a 0.1 M cacodylate-buffered solution (pH 7.4) containing 2.5% glutaraldehyde and 4% formaldehyde. Standard procedures were followed for dehydrating, infiltrating and imbedding the material in glycol methacrylate (GMA). For light microscope (LM) study,

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sagittal sections of ovules and seeds were obtained by sectioning flowers and capsules longitudinally, perpendicular to the subtending bract. Selected sections were stained with the periodic acid/Schiff reaction and counterstained with toluidine blue O (pH 4.4) by using the protocols of O'Brien & McCully (1981). Seed with mature embryos were obtained from herbarium sheets (*Codd 8246* PRE; *Obermeyer TM31027* PRE) and processed for GMA sectioning and staining as described above.

Tests for flight distance of seed were performed on windy days in an open part of the Pretoria National Botanical Garden. Dehiscent capsules containing wool-covered, fertile seed were collected from *Codd 8246* and *Obermeyer TM31027*, held between tweezers and exposed to the wind. Sterile 'seed' (unfertilized, shriveled ovules covered in wool) produced by Tree No. GPTA 495 were tested on the same days. Tests for wettability and buoyancy were conducted indoors by blowing loose wool and plumed, fertile seed onto the surface of muddy or clear, distilled water kept in containers in the laboratory and noting the flotation period.

For scanning electron microscope (SEM) studies, seeds from the above-mentioned herbarium specimens were carefully removed from dehiscent capsules, stuck onto aluminum stubs, sputter-coated with gold and viewed in an ISI SX 25 SEM.

RESULTS

Placentation, development and structure of ovules

Catkins on female trees contain a varying number (\pm 10–50) of flowers. Each flower is borne in the axil of a bract and consists of an adaxial nectary and a syncarpous, bicarpellate gynoecium (Figure 1A). The two carpels of the salicaceous pistil meet in the medium plane of symmetry of the flower (Meeuse 1975: 450) so that the parietal placentae, developing on the fused margins of the carpels, lie in this plane (Figure 1A). The ovuliferous zones of the placentae are restricted to the lower half of the unilocular ovary where eight to twelve ovules are formed.

Ovule primordia at the onset of meiosis (Figure 1B) were found inside floral buds still completely covered by the subtending bracts. In sagittal section (Figure 1A, B), such primordia consist of a large funicle, a developing outer integument (Corner 1976: 237) and a nucellus containing an enlarging megaspore mother cell covered by at least three layers of parietal nucellar cells (Figure 1A). An inner integument is absent, without any vestiges remaining. Meiosis results in four megaspores of which the chalazal one becomes functional (Figure 1C). Linear tetrads were not found in our material; the three micropylar megaspores lie obliquely to one another and possibly represent a stage intermediate between linear and T-shaped tetrads. At the completion of the meiotic process the integument has reached its full length, it covers the nucellus and forms the micropyle (Figure 1C).

Mature ovules are small (\pm 20–25 μ m in length, funicle excluded), anatropous and ovoid (Figure 2A). The lengths of the funicles vary (compare Figure 2A & C); ovules in the basal-parietal position usually have much shorter funicles than ovules nearer to the style. The

integument consists of three to four layers of thin-walled parenchyma. After the elements of the eight-nucleate embryo sac have been formed, the tip of the sac keeps intruding into the micropylar nucellus, later breaking through the nucellus epidermis and reaching the inner opening of the micropyle canal (Figure 2B).

During the elongation of the embryo sac, a plate-like intercalary meristem develops in the distal part of the funicle, forming a narrow band of flattened cells directly below the ovular body (Figure 2A). This region eventually forms a small, ring-like structure in the hilar region of the seed (see further on). At a slightly later stage, the epidermis cells of the placenta, funicle and hilar meristem form long, unicellular, intra-ovarian hairs, but the surface of the enlarging ovule remains glabrous (Figure 2C). In developing capsules collected from the female tree (GPTA No. 495) fertilization did not take place and the ovules aborted (Figure 2D). In such ovules the cells of the hilar meristem have disintegrated (Figure 2D). Seed abscission takes place at the funicular side of the aborted meristem so that the greater part of the funicle remains connected to the placenta (Figure 2C, D).

It is interesting that the capsule with its intra-ovarian hairs keeps developing and later dehisces in a normal manner, despite the abortion of the ovules. This parthenocarpic development of *Salix* capsules deserves further investigation.

Structure of the plumed seed and seed coat

SEM micrographs of fertile seed taken from herbarium sheets (*Codd 8246* PRE; *Obermeyer TM31027* PRE) show a small, annular structure with numerous long hairs attached to its perimeter, positioned at the micropylar side of the seed (Figure 3A, D). These hairs form the plume or coma on the seed. The free underside of the ring has a rough surface of broken cells (Figure 3B). When eased away from the seed (Figure 3C), the upper (micropylar) side of the ring displays an entire, glabrous exterior (Figure 3D), suggesting that the ring has enveloped the base of the seed, without forming an integral part of it. In structure, origin and position the hairy hilar ring represents a kind of seed appendage known as a funicular or hilar aril (Boesewinkel & Bouman 1984: 592). We propose that this ring has developed from the hilar meristem in the distal part of the funicle and, during abscission of the seed, has broken away from the funicle.

Seeds are small (1.3–1.6 mm long), exalbuminous and contain straight, chlorophyllous embryos almost filling the embryo sac, except for an air space underneath the seed coat (Figure 3E). The seed coat is undifferentiated and the number of layers has not increased during ovule-to-seed development (compare Figures 2A, B; 3E). The outer epidermis has unevenly thickened outer periclinal walls and, in surface view, the uneven thickenings form an irregular micro-morphological pattern (Figure 4A). Between the thickened parts of the walls the thinner parts collapse so that numerous, minute depressions are formed on the seed surface (Figure 4A).

The hairs on the aril resemble the placental-funicular hairs (loose wool) and consists of a mass of seemingly

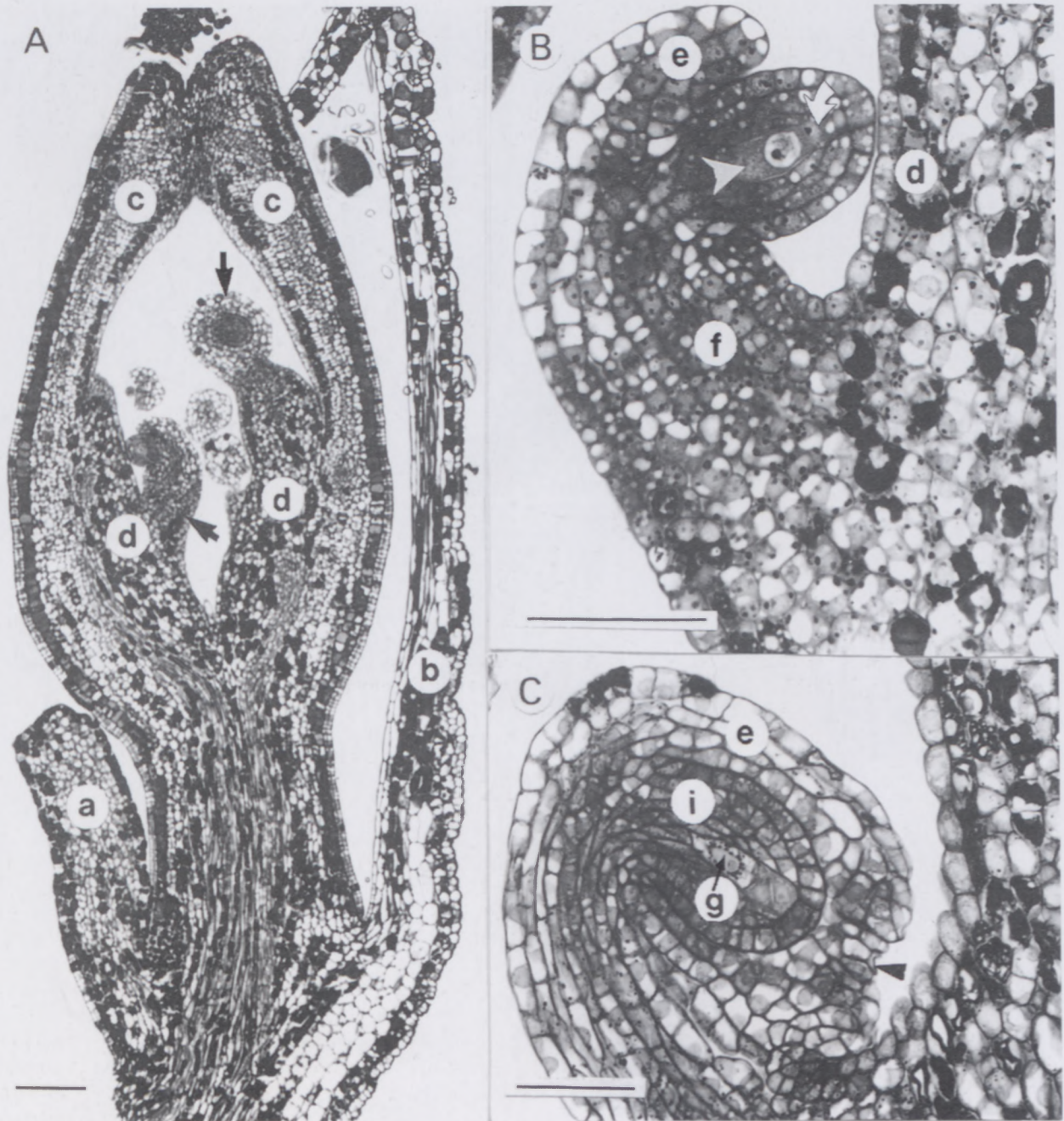


FIGURE 1.—Structure, position and placentation of ovules in *Salix mucronata* as seen in median sagittal sections. A, young female flower, note stalked ovule primordia (black arrows); B, ovule primordium in megaspore mother cell stage (white arrowhead) showing parietal nucellar cells (curved white arrow); C, young, anatropous ovule in megaspore tetrad stage, position of micropyle indicated by black arrowhead. a, adaxial nectary; b, subtending bract; c, bicarpellate ovary; d, parietal placenta; e, integument; f, funicle; g, functional chalazal megaspore; i, nucellus. Scale bars: A, 100 μ m; B, C, 50 μ m.

structureless, cylindrical fibres about 3–4 mm long, with smooth, transparent, thin walls without pits (Figures 3A–D; 4B). The walls stain blue-green with toluidine blue and yellow with aniline sulfate, indicating the presence of lignin. The fibres taper to a point and have a slightly bulbous base. When immersed in water, numerous air bubbles are trapped in the wide lumen (Figure 4B).

Distance of flight, buoyancy and wettability of seeds and hairs

Experiments in the garden and laboratory showed that fertile, wool-covered seeds do not remain airborne for more than ten metres in a moderately strong wind; after the loose

wool (intra-ovarian hairs supporting the seed) has been blown apart, the seed with hairy aril (plume) still attached, slowly descends. The flight distance of sterile 'seeds' could not be determined; they flew away so fast that they could not be retrieved. When the wool-covered seed lands in water, the loose hairs rapidly float away, but the plume remains attached to the seed. Loose wool, plumed seed and deplumed seed remain buoyant in clear and muddy water until the water in the containers has evaporated (about five days). The seed coats of floating seeds are unwettable (hydrophobic) and appear translucent white in water because of the numerous, minute air bubbles trapped in the depressions of the outer periclinal wall. By the time the muddy water in the containers has evaporated, the plumes have got stuck in the mud and the seeds separate easily from the arils.



FIGURE 2.—Development of ovule and intra-ovarian hairs in *Salix mucronata*. A, mature ovule in sagittal section showing hilar meristem (black arrows) in distal part of funicle; B, 1/s micropylar part of ovule with tip of embryo sac breaking through epidermis of nucellus, but staying inside integument; C, 1/s developing capsule showing intra-ovarian hairs originating from placenta and funicle. D, part of sterile capsule with abortive, stalked ovule imbedded in intra-ovarian hairs, note position of disintegrated hilar meristem (small black arrows), black arrowhead indicates position of micropyle. e, integument; f, funicle, i, nucellus; j, embryo sac; k, intra-ovarian hairs; o, ovule; ol, abortive ovule; w, ovary wall. Scale bars: A, B, D, 50 μ m; C, 100 μ m.

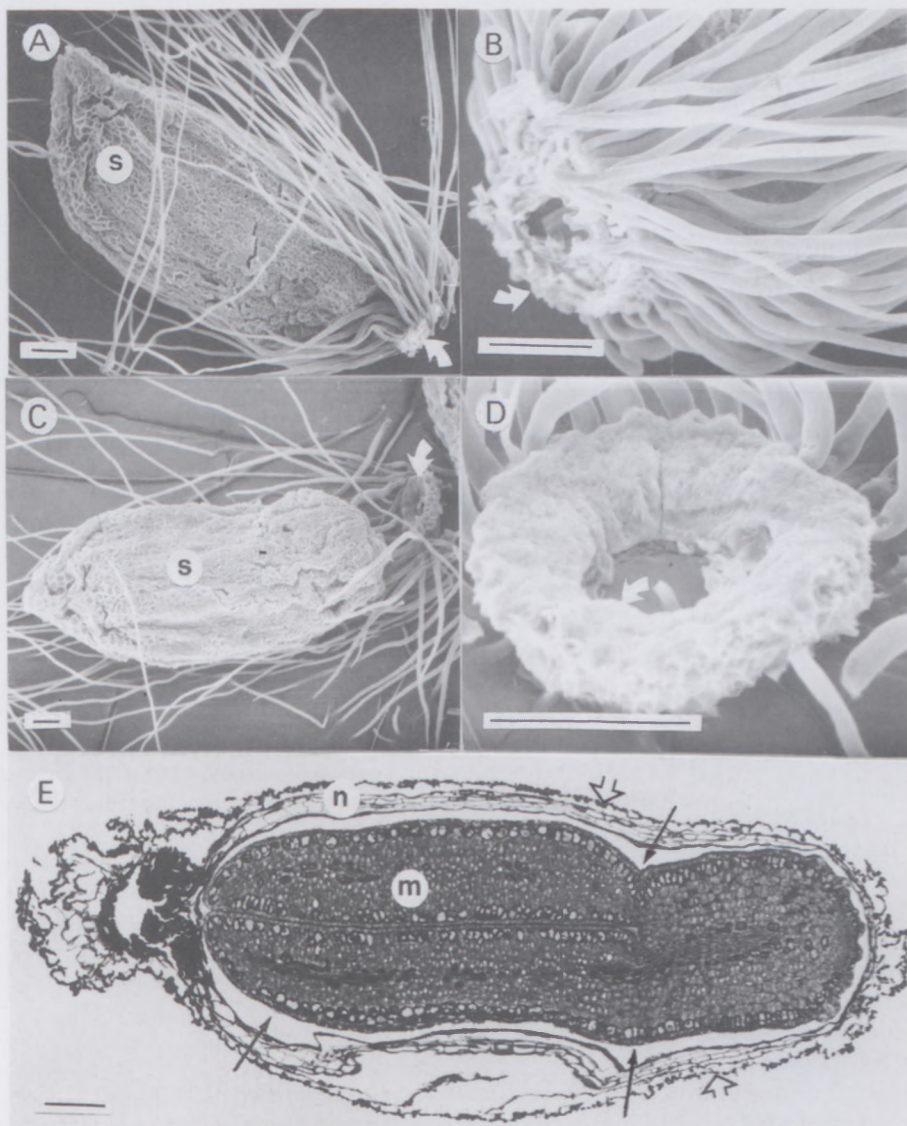


FIGURE 3.—Seed structure in *Salix mucronata* as seen in SEM micrographs (A–D) and LM photographs (E). A, plumed seed with coma of hairs attached to hilar aril; B, micropylar seed region showing aril and hairs at higher magnification than in A; C, aril detached from micropylar part of seed; D, aril as seen from above at higher magnification than in C; E, 1/3 fertile seed showing large chlorophyllous embryo surrounded by air space (black arrows), note irregular wall thickenings (open black arrow) on outer periclinal walls of epidermis, curved white arrow, aril. m, embryo; n, undifferentiated seed coat; s, seed. All scale bars: 100 μ m.

DISCUSSION

The coma of hairs on Salix seed

It has often been alleged that the tuft of silky hairs enveloping the seed of willows is placental in origin (Takeda 1936; Van der Pijl 1969; Corner 1976; Johri *et al.* 1992). Others (Ridley 1930; Wilmot-Dear 1991; McKean 1996; Boulos 1999) mention that the hairs are derived from the funicle. Our observations on ovule-to-

seed development in *Salix* lend support to the latter view: sagittally sectioned, developing capsules distinctly show the presence of stalked ovules with the coma of hairs resulting from epidermal cells on the most distal part of the funicle. Takeda's (1936) erroneous conclusion that *Salix* ovules have no funicles and that the hairy tuft on the seed is part of the placenta was based on incorrectly sectioned capsules. His line drawings (Takeda 1936: 285, figs 1 & 4) show ovules in longitudinal (not sagittal) section in which the funicular connections to the placenta

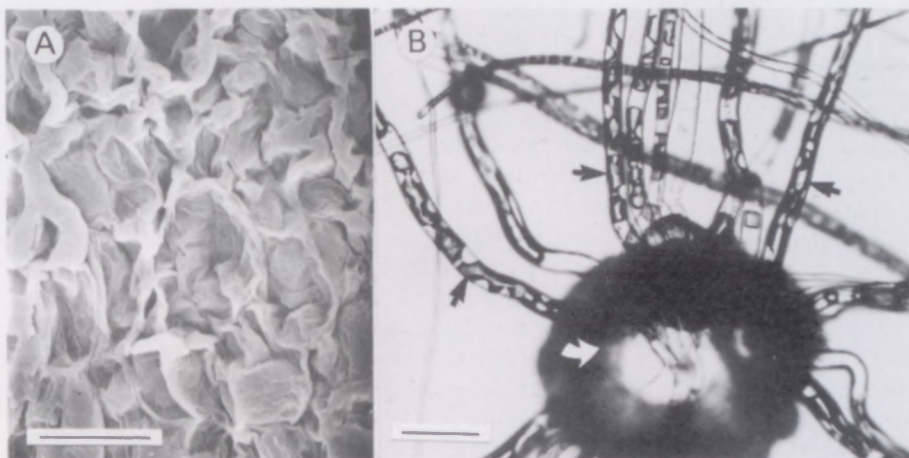


FIGURE 4.—Seed structure in *Salix mucronata* as seen in SEM micrograph (A) and LM photograph (B). A, structure of seed surface; B, hilar aril (curved white arrow) with air-filled hairs (black arrows). Scale bars: A, 20 μ m; B, 50 μ m.

were not visible. Later, well-known embryologists (Van der Pijl 1969; Corner 1976; Johri *et al.* 1992), accepted Takeda's (1936) interpretation, without re-investigating the matter.

The present report provides the first evidence for the occurrence of arillate seeds in *Salix*. The presence of hairy arils in Salicaceae was suspected, but not substantiated by Corner (1953), or mentioned in subsequent work (Corner 1976) and was not reconcilable with the supposed placental origin of the coma (Van der Pijl 1969). Since it is from the narrow distal region of the funicle that the small, annular and tufted aril arises and breaks away to form an appendage to the seed during seed abscission, we have referred to it as a hilar aril.

The micromorphological structure of the funicular-placental and arillate hairs in *Salix* is here described and illustrated for the first time. LM photographs and SEM micrographs show the mass of hairs consisting of cylindrical, structureless, unpitted, lignified and thin-walled fibres that remain filled with air when immersed in water. In these characters, *Salix* fibres closely resemble those found in the capsules of Bombacaceae, e.g. *Ceiba pentandra* Gaertn. (kapok tree) and *Bombax malabaricum* DC. (Indian kapok or Semal tree) as described by Kirby (1963: 389) and Ilvessalo-Pfäffli (1995: 358) and in *Chorisia speciosa* A.St.-Hil., the silk-floss tree (E.M.A. Steyn pers. obs.). Before being largely replaced by synthetic materials, kapok fibres were used for insulating and stuffing purposes (Kirby 1963). Kapok owes its use in e.g. life-saving equipment to the fact that the fibres remain buoyant after long periods in water (owing to its property of repelling water) and because it can easily be dried when it has become wet (Kirby 1963). According to Ilvessalo-Pfäffli (1995) the high buoyancy of kapok is due to the presence of air bubbles in the lumen of the fibres which apparently is also the case in *Salix* fibres.

Dispersal by wind (anemochory)

Confined to the rheophytic habitat, i.e. in the beds of swift-running rivers and streams and on the banks up to flood level (Jordaan 2002), *Salix mucronata* is exposed to up-and-down-stream breezes all the year round. When the capsules ripen and dehisce, the placental-funicular fibres dry out, break loose from the subepidermal tissue, expand and protrude from the bivalvate fruit. During tests on dehisced fruit, gusts of wind jerked the seed-bearing wool from the capsule, carrying it into the air and keeping fertile seeds airborne for about ten metres. At that distance the loose wool was blown apart, the hairy arils alone could not keep fertile seeds airborne and they descended. We propose that the same occurs in nature. Wind is therefore the releasing and the primary dispersal agent of *Salix* seed. It dislodges the seed from the capsule and scatters it some distance away from the parent plant. If the landing surface is not wet, the plumed seed may be blown further along the ground, but will stick to a wet substrate, e.g. mud, feathers or hair of wading birds and animals, bringing the role of wind to an end.

Characters enabling the seed to become airborne include its relative smallness, the absence of a large, heavy funicle and low specific weight. The latter is achieved by the thin, undifferentiated seed coat (testa) with air-filled

cells, an air space below the testa caused by the early disappearance of endosperm and enlargement of the seed surface by the long, smooth, air-filled hairs of the aril and seed-bearing wool.

Dispersal by water (hydrochory)

In its rheophytic habitat, the most important secondary dispersal agent for *Salix* seed is water. Our tests suggest that seed, landing in the bed of the stream or on the banks when the waters are in spate, will have the ability to float for days. In this way seeds may spread along the river edge far away from the parent plant or, caught in a strong current, they may migrate for many kilometres. Structural modifications for anemochory listed above, would increase buoyancy (Melcher *et al.* 2000). An additional adaptation for hydrochory in *Salix mucronata* is the unwettable seed surface. Van der Pijl (1969: 63) and Rauh *et al.* (1975: 372) reasoned that air bubbles, trapped in the numerous depressions in the seed coat epidermis, would have such an effect. In *Salix* this characteristic is aided by the presence of a unique floating apparatus in the form of a small (so as not to unduly increase seed weight), hilar aril with unwettable, air-filled hairs. The coma of hairs also ensures that the floating seed is not taken beyond the boundaries of the rheophytic habitat; when floodwaters recede, the fibres stick to wet mud, retaining the seed (Ridley 1930: 226). In these watery surroundings, the thin testa does not need to protect the embryo against desiccation and offers little resistance to germination. *Salix* seed germinates easily, seedlings have strong root systems and rapidly develop their first leaves (Pax 1894).

Fortuitous dispersal by animals (epizoochory)

Distribution of seed to upstream locations cannot occur by means of water and animal visitors to the water may play an important role here; *Salix* seeds have been removed from the coats of animals when the plants were in fruit (Ridley 1930: 554). It was found that the plumes attach themselves easily to the hair of animals when the vegetation is wet. The plumed seed may also become entangled in the feathers of waterfowl. To be carried in the mud on the feet of birds and animals, seeds have to be small and *Salix* seed certainly falls in this size group. While the plumes remain stuck in the mud, the small seeds may be picked up by the feet of waterfowl, hippopotamus, elephant and other animals and conveyed to another suitable rheophytic habitat.

Taxonomic implications

In a report on the phylogenetic relationships of *Salix* based on *rbcL* sequence data, Azuma *et al.* (2000: 71) stated that in their analysis 'Idesia and Dovyalis of Flacourtiaceae are the sister groups of the Salicaceae'. Leskinen & Alström-Rapaport (1999) found that *Idesia polycarpa* Maxim. shows great sequence similarity with Salicaceae and that the 5.8S rDNA sequences in their study suggest that Flacourtiaceae and Salicaceae may have shared a common ancestor within the order Violales. Chase *et al.* (2002) provide evidence that if a wider range of flacourt genera is included in an analysis, *Itoa* Hemsl. and *Poliothyrsis* Oliv. (Flacourtiaceae: Flacourtiaceae) seem to be the closest relatives of Salicaceae *s.str.*

As far as embryological data are concerned, Meeuse (1975) compared anther and ovule characters of Salicaceae *s.str.* and Flacourtiaceae *s.l.* and found 'many points of agreement' (Meeuse 1975: table 1). To these shared characters should be added the presence of arillate seeds. The presence of an aril on the seed of *Salix* offers some morphological support for combining on phylogenetic grounds Salicaceae *s.str.* with several flacourtiaceous taxa, members of which are reported to often have arillate seed (Chase *et al.* 2002). Several other authors who have previously suggested a close relationship between Salicaceae and some Flacourtiaceae are listed in Chase *et al.* (2002). However, if the putative close relationship between Salicaceae *s.str.* and Flacourtiaceae (Meeuse 1975; Chase *et al.* 1996; Nandi *et al.* 1998; Chase *et al.* 2002) is accepted, a radical change must have occurred during the evolution of the unitegmic, salicaceous seed with its undifferentiated seed coat. In Flacourtiaceae the seed coat develops from a bitegmic ovule and contains a fibrous exotegmen (Comer 1976; Johri *et al.* 1992) that protects the zoochorous seed, often produced in edible berries (e.g. *Idestia*, *Flacourtia* L'Hér., *Dovyalis*) against animal feeders. No rheophytes have been reported in Flacourtiaceae (Van Steenis 1981) and anemochorous seed is extremely rare but may, according to Sleumer (1954) be granted to the winged seed of *Itoa*. *Poliothyrsis* also has winged seed (Judd *et al.* 2002). It is noteworthy that these two anemochorous genera are probably the sister groups of Sailicaceae *s.str.* (Chase *et al.* 2002)—both are from China with *Itoa* also in tropical Asia. To our knowledge, their seed coat structure has not been reported.

CONCLUSION

We propose, therefore, that the total absence of an inner integument in *Salix* ovules and its suppression in early ovular stages in *Populus* (Nagaraj 1952) might be due to an adaptive change from animal to wind and water dispersal. This integument with its exotegmic protective layers was no longer necessary and would only increase seed weight. This could be another example of the well-known evolutionary tendency for unused structures, or unnecessary complication of structures, to degenerate (Cronquist 1988: 232). A study of ovule-to-seed development in *Dovyalis* is in progress and may shed more light on the possible evolutionary changes that have led to the Salicaceae *s.str.* clade.

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