

Leaf teeth in certain Salicaceae and ‘Flacourtiaceae’

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The leaf teeth glands in four taxa from Salicaceae and six from ‘Flacourtiaceae’ were examined using both light and scanning electron microscopes. There appears to be a progression from glands of simple structure in the flacourtiaceous taxa and a tendency to a more complicated development in morphology and anatomy of the salicaceous species. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 155, 241–256.

ADDITIONAL KEYWORDS: colleters – crystals – history – hydathodes – nectaries – resin.

INTRODUCTION

At the request of the herbarium staff at Kew, the leaf teeth of some ten taxa, four from Salicaceae (*s.s.*) and six from ‘Flacourtiaceae’ (*sensu* Lemke, 1988), were examined. The purpose was to show any similarities or differences between the marginal glands in these two ‘families’, and also to re-evaluate the term ‘salicoid tooth’ as used in various publications (for example, Hickey & Wolfe, 1975). The information was obtained from light and scanning electron microscopy as well as from the literature. The leaf glands of *Populus* and *Salix* have been observed and studied for over 100 years. The historical accounts given below show how much interest has been generated by these minute structures.

The first published references to resin secretion in *Populus* were by Hanstein (1868) on *Populus* bud scales. Secretion from leaf teeth was described accurately in *P. balsamifera* L. and *P. laurifolia* Ledeb. by Reinke (1876). Tschirch (1906), cited by Fehér (1923), recorded secretion in *P. balsamifera*, *P. nigra* L., *P. canadensis* Moench (? *deltoides* Marshall), *P. tremula* L., *P. alba* L., and *P. canescens* (Ait.) Smith, and described the tips of the leaf teeth. Trelease (1881) reported ‘nectar’ secretion from the same structures in *P. balsamifera*, *P. candicans* Aiton,

P. grandidentata Michx., *P. monilifer* Ait., *P. tremuloides* Michx., and *P. tremula*.

Edelstein (1902) induced guttation from the leaf teeth of *P. laurifolia*, and called the area in which this occurred a hydathode *without* an epithem (see Wilkinson, 1979). He also mentioned similar hydathodes in *P. balsamifera* and *P. tremula*, and was the first to suggest that a hydathode occurs next to each gland. Trelease was unaware of resin secretion and Fehér was equally unaware of nectar secretion. Lippman (1925) thought that guttation occurred from the glandular tips of the teeth.

According to Curtis & Lersten (1974), the first leaves to emerge on *P. deltoides* Marshall are covered with trichomes and lack a secretory epidermis. In successive leaves, the teeth become glandular and secrete resin as the lamina unrolls, and it is the marginal leaf glands which account for the resin. They also noted that each leaf tooth of mid-season leaves has a small outer vein that runs parallel to the leaf margin and ends near, but not in, the glands. A much larger, inner vein is closer to the sinus and ends within the gland. Later in the season, these authors state that, ‘Often, especially in leaves emerging in late summer and early fall, there are several stomata above the ending of the outer bundle (figs 17, 21). In some teeth the two veins merge into one large ending (fig. 15), the inner portion extends into the secretory gland, and the outer portion terminates below the stomata from which guttation presumably occurs.’

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This strongly suggests a hydathodic function, especially as the veins are composed mainly of tracheary elements. These authors indicate that the unspecialized type of hydathode found in *Populus* can also act as a nectary under certain conditions. They also state that the resin seems to function mainly as an insect repellent, but may also retard transpiration and reduce water loss from young leaves. Curtis & Lersten (1974) were unable to positively identify sieve tube members or companion cells, but found what could be interpreted as phloem parenchyma, or perhaps procambium, extending beyond the tracheary elements into the secretory glands (fig. 18). However, they thought it likely that guttation occurs through the large stomata proximal to the gland and that resin is secreted from the glandular teeth (fig. 19) of both early and later leaves. The resin first emerges as a milky, yellow–white liquid, but later turns to a clear yellow and is somewhat bitter to the taste. They also noted the following: (1) that secretion ceases at about the time the leaf finishes unrolling and when the teeth are no longer arched over the adaxial surface; (2) that within a few weeks the glandular tip of each tooth turns brown; (3) that the duration of secretion on an individual leaf is probably 8–10 days; and (4) that the secretory epidermis of the glandular teeth is composed of elongate, palisade-like cells perpendicular to the leaf surface. They also noticed that the gland cuticle separates from the cell wall.

Again according to Curtis & Lersten (1974), during the summer, resin is produced by both stipules and leaf teeth of *Populus*. The resin forms a thin coat over the entire leaf and probably has an effect similar to the cuticle in retarding transpiration from epidermal cells. It appears that the leaf teeth are capable of secreting more than one substance. The glandular tips secrete resin, and just below the tip nectar guttation may occur in the region of the stomata; however, they also thought that the rather unspecialized type of hydathode may also act as a nectary under certain conditions.

Wilson, Canny & McCully (1991) carried out some research on ‘Leaf teeth, transpiration and the retrieval of apoplastic solutes in balsam poplar’, that is *P. balsamifera*. These authors showed that the teeth in section have an upper portion (adaxial), which is a hydathode complete with an epithem of deeply lobed cells with large air spaces between the lobes, xylem elements below, and a stoma in the epidermis (figs 9–20). However, Pemberton (1992) performed glucose tests on the secretions from the basal leaf glands of eight *Populus* species and two hybrids, all of which gave strong positive glucose reactions.

Likewise, many authors have noticed or made more detailed studies of the leaf teeth glands of *Salix*. A

clear history of the discovery of the leaf teeth glands in *Salix* is given by Curtis & Lersten (1980), from whom the following references have been taken. Reinke (1876) seems to be the earliest author to describe the leaf teeth of *S. cinerea* L. as having ‘an epidermis of unusually long, slender, palisade-like cells subtended by a small group of polyhedral parenchyma cells’. Reinke mentioned that secretion occurred only on young leaves and that, in older leaves, the tip of each tooth was withered. This clear description holds good today. Lepeschkin (1921) recorded that, ‘Many species of *Salix* have marginal organs with the form of hemispheres. The external layer of elongated cells is well developed. One can frequently observe small particles or drops of gum on some of the organs, but the majority of these never secrete any substances.’ (translated by Curtis & Lersten, 1980). Metcalfe & Chalk (1950) state that Lutz (1938) reported glands with radially arranged secretory cells on the leaf teeth of *S. alba* L., *S. caprea* L., *S. nigricans* Sm., and *S. pentandra* L. An increase in the number and secretory activity of ‘extrafloral nectaries’ on successive leaves of *S. caprea*, *S. nigricans*, and *S. pentandra* during the growing season was reported by Ianishevskii (1941). By contrast, Frey-Wyssling (1941) listed *Salix* species amongst other Swiss alpine plants observed to be guttating, thus suggesting the presence of hydathodes. Schremmer (1970) made gross observations on the leaves of *S. elaeagnos* Scop. in Austria, on the marginal teeth of which a glistening drop of liquid could be seen. He reported that many kinds of insects, including bees, frequented the leaves. Twenty-eight species of Swiss *Salix* were studied by Weber (1978) from the cleared leaves of herbarium specimens. He showed that some species lacked glands, some had tiny and/or variably occurring glands, and, in other species, glands were large and always present. His figures on venation patterns are very clear, but those on the marginal teeth and glands are low-power morphological diagrams only.

Curtis & Lersten (1980) comment that the brief accounts of *Salix* glands given above suggest that hydathodes, extrafloral nectaries, and gum or resin glands may occur in various species of the genus. In the same paper, these authors made a detailed study of the morphology and anatomy of resin glands in *S. lucida* Muhl. The material examined with a light microscope was stained with safranin and chlorazol black E; other samples were examined with a Jeol scanning electron microscope. They describe and illustrate resin glands which occur at the tip of each marginal dentation of the lamina, and also the stipules and base of the lamina/distal end of the petiole. They record that glands in all locations are conical or domed (figs 7, 17, 18), with a palisade-like

epidermis subtended by five to six layers of parenchyma which contain druse crystals. There is one main vascular bundle (and occasionally one or two laterals) which ends in a small knob of tracheary elements. They studied glands from cleared leaves and from some excellent paraffin sections, in which they illustrate the 'palisade-like epidermal layer', tracheary elements at vein endings, and five to six layers of isodiametric parenchyma cells between the vascular tissue and the epidermis. They did not investigate the xylem and phloem of the bundle in any detail. They note that the relatively thick cuticle is usually distended by the resin beneath it, and that there is safranin-staining material in the parenchyma cells between the vascular bundle ending and epidermis, with smaller amounts of safranin-staining material in the epidermal cells (also confirmed by the current author).

With regard to the secretion of resin from the glands of *S. lucida*, Curtis & Lersten (1980) stated that the glands usually secrete liquid resin that covers the gland and surrounding area, which is shiny and sticky, and under certain conditions, particularly low humidity, resin is extruded as a filament from a pore in the gland apex on plants growing outdoors. Their scanning electron microscopy examination of uncoated glands of fresh leaves verified that filaments arise from a pore or dimple in the apex of the gland. The resin is colourless or yellowish, sticky until dry, has a faintly aromatic odour, and is insoluble in water but soluble in organic solvents, such as xylene, ethanol, and acetone. Fahn (1979) stated that the substances secreted by the young leaves of *Populus* contain flavonoid aglycones mixed with terpenes. He has redrawn a diagram from Fehér (1923) (Fahn, 1979: fig. 97B) of the palisade-like cells of a leaf tooth of *P. pyramidalis* Salisb., showing a ruptured cuticle through which the secreted substances pass to the leaf surface. According to Charrière-Ladreix (1973), the secretion is also extruded extracellularly into the parenchyma below the prismatic epidermis. This may account for the personal observation of darkly staining cells in this region.

Concerning the resinous secretion in *Salix*, Curtis & Lersten (1980: 1293) stated: 'As in *Populus*, we suspect that the resinous secretion of *Salix lucida* is responsible to a considerable degree for the small amount of damage we found from insects and other browsers.'. They also state that *S. lucida* glands are rather similar to those studied in *Populus* (Curtis & Lersten, 1974, 1978) and to those of other species of *Salix* as reported in the literature. In both genera, there is a palisade epidermis subtended by five to six layers of roughly isodiametric parenchyma cells. They also comment (Curtis & Lersten, 1980) that the vascular terminus in *Populus* glands is massive com-

pared with the rather small single bundle usually found in *S. lucida*, and also that no crystals are observed in *Populus* glands, whereas druse crystals are abundant in *S. lucida*.

The term 'salicoid teeth/tooth', used by Hickey & Wolfe (1975), is entirely morphological, in which the tooth is described as a seta with 'a dark, but not opaque, nondeciduous spherical callosity fused to the tooth apex'. These authors also stated that the salicoid teeth are 'inferred to be of common origin with those of *Idesia* in the Flacourtiaceae'. Hickey (1979: 30) repeated the same description of some marginal glands as his type VI, E, 2b: 'As a glandular seta or bristle (fig. 4.2(39), p. 29)'. Anatomical investigations were not made by these authors. Nandi, Chase & Endress (1998) included leaf teeth (character 200) and salicoid teeth (character 201) in their many nonmolecular characters, including those from palynology and relevant wood anatomy, for their data sets. Nandi *et al.* (1998) defined salicoid teeth as: 'leaf teeth showing a proximally rounded hyaline gland with concave gland body in herbarium specimens'. The differences in the appearance between dried and fresh material may be one of the sources of confusion in the use of the term. A full taxonomic and molecular systematics history concerning 'Flacourtiaceae' and Salicaceae, including references to palynology (Keating, 1973), wood anatomy (Miller, 1975), and chemical composition, is given by Chase *et al.* (2002).

There does not seem to be any publications on the leaf teeth anatomy of *Dovyalis*, *Carrierea*, *Olmediella*, *Oncoba*, or *Poliothyrsis*. Metcalfe & Chalk (1950) mention simple, unicellular hairs and 'rubiaceous' (paracytic) stomatal subsidiary cells in *Carrierea*, crystal idioblasts in the leaf epidermis and wax present on the leaf surface of *Oncoba*, and papillose epidermal cells in *Idesia*. With regard to the petiole, Metcalfe & Chalk (1950) categorized the different states of the median vascular strand for various 'Flacourtiaceae', in which *Dovyalis caffra* (Hook. f. & Harv.) Warb. has a solitary, shallow crescentic strand, *Carrierea calycina* has an arc-shaped median strand accompanied by small bundles towards the petiole wings, *Oncoba spinosa* has a circular, cylindrical median vascular strand, and *Poliothyrsis sinensis* has a median but adaxially flattened or slightly concave strand with noticeably thick-walled xylem vessels in well-marked radial multiples. These authors also mention that cluster crystals are common, often abundant in the cortical region of the petiole in *Dovyalis*, *Oncoba*, and *Poliothyrsis*.

The leaf tooth anatomy of *Idesia polycarpa* has been studied in detail and well illustrated with light micrographs (Belin-Depoux, 1982) and a diagram (Belin-Depoux, 1989: fig. 5). Belin-Depoux states in

Figure 1–6. Marginal leaf teeth palisade-like cells in various taxa, some with venation shown. Fig. 1. *Oncoba spinosa*; scale bar, 50 µm. Fig. 2. Part of Fig. 1 at adaxial surface with stomata(s); scale bar, 100 µm. Fig. 3. *Poliothyrsis sinensis* showing partial disintegration below palisade secretory cells and large numbers of rhombic crystals in the vein sheath. Fig. 4. *Olmediella betschleriana* adaxial surface showing a group of palisade cells a little inside the margin; epidermal cell walls very thick. Fig. 5. *Idesia polycarpa* showing disintegration of epidermis below palisade cells. Fig. 6. *Populus ciliata* with resin (r, represented by dotted area) outside palisade cells and epidermis. Scale bar, 50 µm for Figs 1, 3–6.

her summary (Belin-Depoux, 1982: 111) that the leaf teeth of *I. polycarpa* show, on each tooth, one abaxial nectary and one small adaxial hydathode, which she considered as relictual. Later, she states that: ‘The foliar glandularization is considered as more recent than hydatherous elements from [the] phylogenetical point of view’. (The author of this translation from the French is not given.) She also indicates that, below the lamina (distal end of the petiole) on the adaxial surface, two petiolar glands are occasionally present, and at the base (proximal part) of the petiole are one or two laterally placed glands. The latter are not stipules, which abscise very early, and their scars can be seen on either side of the petiole base.

MATERIAL AND METHODS

All the material examined was obtained from the living collections in the Royal Botanic Gardens at Kew. *C. calycina* Franch. (Kew accession number 2000-616), *I. polycarpa* Maxim (1987-8153), *Poliothyrsis sinensis* Hook. f. (1908-8807), *P. ciliata* Wall. (1966-7101), *P. trichocarpa* Torr. & Gray (1969-12838), *S. aurita* L. (2000-2570), and *S. lasiolepis* Benth. (1996-2606) were all grown outside. *Dovyalis hebecarpa* Warb. (1962-13001), *Olmediella betschleriana* Loes. (1969-12335), and *Oncoba spinosa* Forssk. (1949-63701) were grown under glass. Voucher specimens have been placed in the Kew Herbarium.

Cleared leaf preparations of all species were made as follows. Parts of leaves, particularly the margin, were placed in Petri dishes containing a 5% solution of sodium hydroxide and a little domestic bleach (sodium hypochlorite), and transferred to an oven at c. 55 °C until they became white. Next, they were removed from the solution and washed twice in distilled water, and then immersed in chloral hydrate until the leaves appeared glassy; they were then removed and washed in distilled water. Finally, the leaves were placed in Feulgen’s reagent for varying amounts of time (from 5 min upwards) until the veins gave a strong pink reaction when washed in distilled water. Permanent preparations were then made: leaf samples were taken through an increasing series of alcohol from 30 to 100%, and then mounted in Euparal. Light micrographs were taken on a Leica DMLB photomicroscope and, although the results were not good enough for publication, they were

useful for the interpretation of structures. Line drawings made with a Wild drawing tube proved more illuminating. Other samples of the marginal leaf area were critical point dried in an Autosamdri 815B machine, and then coated with platinum in an Emitech K 550 sputter coater for 4 min. These samples were then examined with a Hitachi S-4700 scanning electron microscope.

GENERAL DESCRIPTIONS (FIGS 1–25, TABLE 1)

Throughout the following descriptions below, ‘palisade-like cells’ in glands refer to the radially elongate glandular cells, not the palisade cells of the leaf mesophyll. TS, transverse section of leaf and petiole.

CARRIERIA CALYCINA FRANCH.

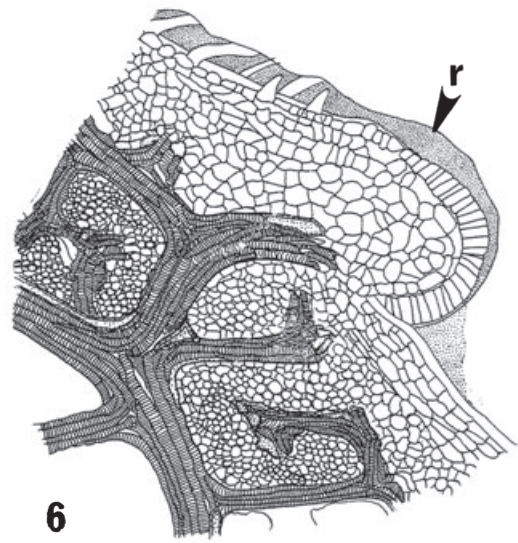
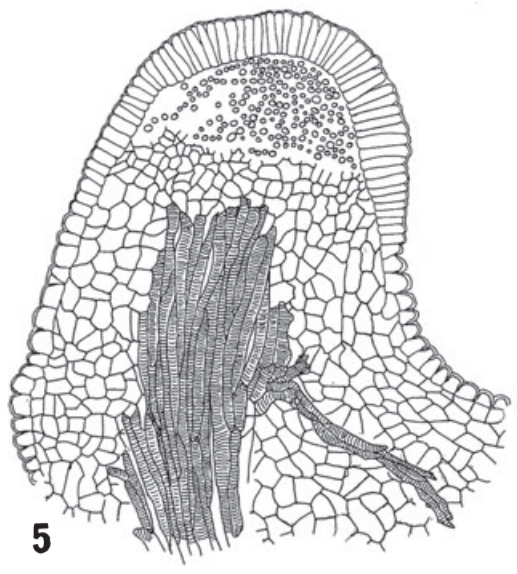
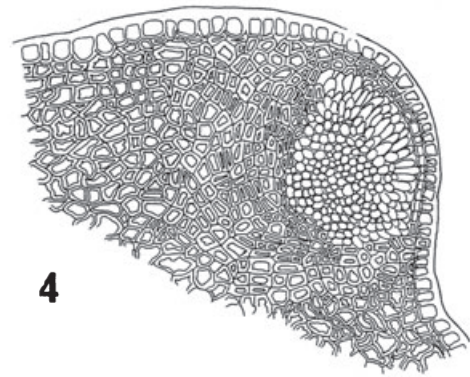
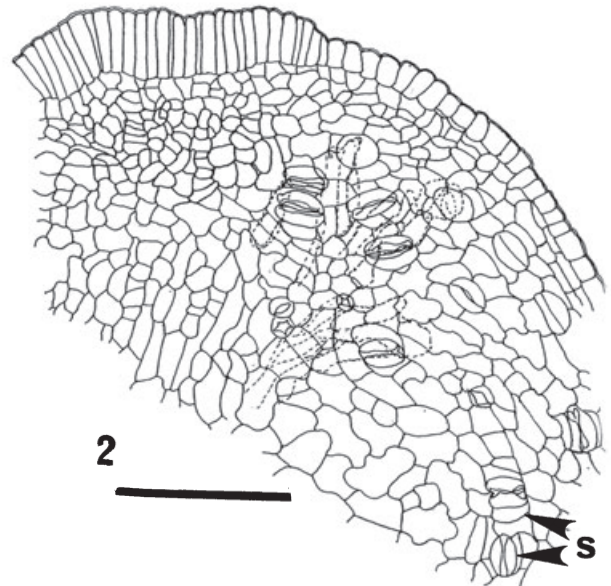
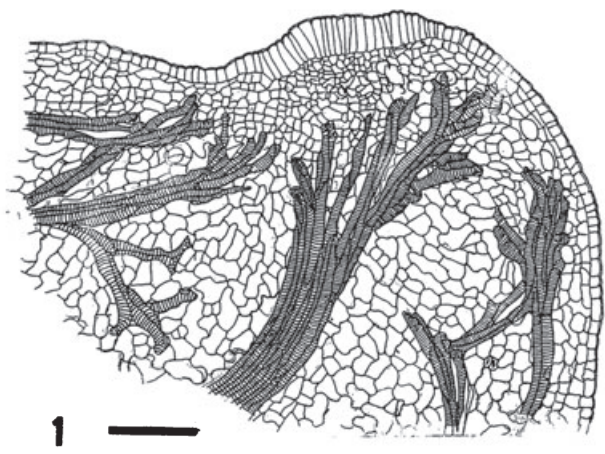
Leaves: Ovate; apex acuminate, base obtuse to truncate, margin crenate.

Marginal teeth glands: Large angular projections (Fig. 18); palisade-like cells not at margin but on abaxial sides of tooth in a circular patch; some cells with dark red-staining granular contents; supplied with three large veins. Large circular glandular patches on the adaxial surface at the base of the lamina or actually on the adjacent petiole.

Leaf surface: HAIRS: simple trichomes fairly abundant on adaxial, prolific on abaxial surface: stomata small, guard cells thin-walled, subsidiary cells brachyparacytic; ordinary cell walls slightly undulate; adaxial cell walls mostly straight. VENATION PATTERN: actinodromous, secondary veins more or less opposite, few; with wide curve from half to two-thirds length of lamina; tertiaries reaching to leaf teeth.

TS leaf

EPIDERMIS: Cells tabular on both surfaces, adaxial larger than abaxial; stomata flush with surface. MESOPHYLL: palisade tissue in two layers, outer very long forming one-third to one-half of leaf; spongy tissue loose. VEINS: MIDRIB: outline broadly angular obovate; vascular tissue a shallow crescent, xylem well developed; sclerenchymatous sheath; collen-



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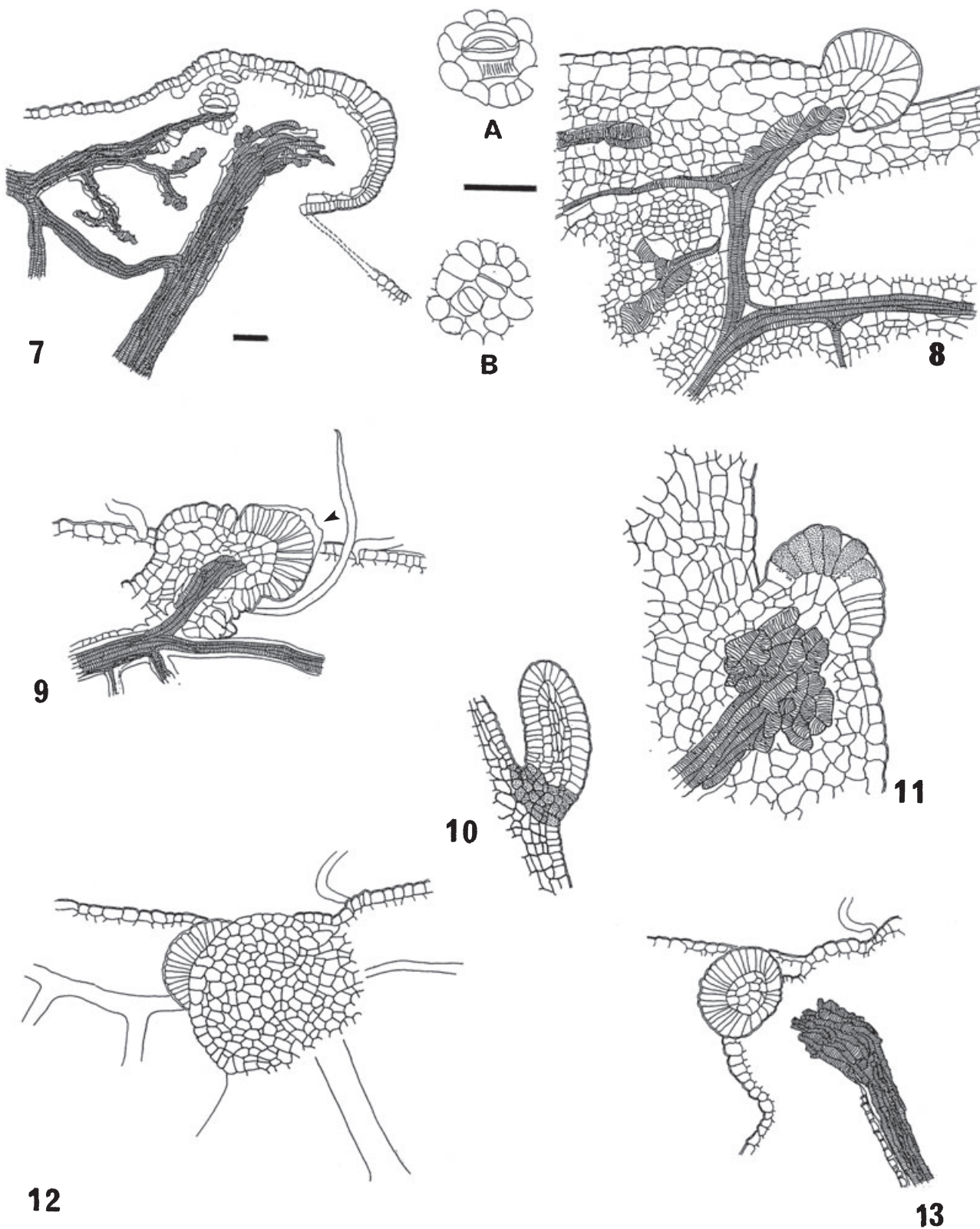


Figure 7–13. Marginal leaf teeth in *Populus*, *Salix*, and *Dovyalis*. Fig. 7. *P. trichocarpa* with three stomata indicated on the adaxial surface over vein tracheids; scale bar, 100 µm. A, B, stomata enlarged; scale bar, 50 µm. Fig. 8. *S. lasiolepis* gland with few tracheids on young leaf. Fig. 9. *S. aurita* showing optical section of gland on young leaf with developing hump of cells; depression (arrowhead) in cuticle and enlarged space between cuticle and glandular cells. Fig. 10. *D. hebecarpa* elongate gland with thick-walled stalk region with dark contents indicating where abscission will take place. Fig. 11. *S. lasiolepis* gland on mature leaf showing more tracheids in vein and coagulated resin (represented by dotted area) remaining in some gland palisade cells. Fig. 12. *S. aurita* showing well-developed hump of cells and part of gland in a mature leaf. Fig. 13. *S. aurita* gland seen in an optical section through the hump of cells in Fig. 12. Marginal glands in Figs 7, 9, 10, 12, 13 to same scale; Figs 8, 11 to same scale as Figs 7A, B.

chyma next to epidermis of ridges. Other veins: larger with increased amounts of sclerenchyma but collenchymatous girders to epidermis, only smallest veins embedded, sclerenchyma absent, sheath parenchymatous. MARGIN: vein absent, but small vein loops.

Petiole TS: Outline; base trigonous to depressed obovate to broadly obovate, middle region circular, distal longitudinally ovate. Vascular tissue: at base three veins, each a deep crescent, distally three to four veins, vascular tissue becoming a complete ring; no sclerenchyma around veins; most of groundmass collenchymatous.

Cell inclusions: CRYSTALS: druses in mesophyll of lamina, also some in leaf teeth; masses in phloem of midrib and petiole, less dense in parenchyma/collenchyma. Rhombohedra in sclerenchyma around larger veins of lamina. RESIN-LIKE contents in palisade-like cells in leaf teeth.

DOVYALIS HEBECARPA (GARDNER) WARB.

Leaves: Ovate-elongate, apex elongate-acuminate, base cuneate, margin with glands at widely spaced intervals giving a slightly crenate appearance.

Marginal teeth and glands: Multicellular stalked glands at intervals projecting towards adaxial side of leaf. Strictly speaking there are no ‘teeth’ on the leaf margin, as no part of the leaf mesophyll is involved. The broad base (stalk) is *c.* seven to nine cells wide and with stronger walls than the upper part of the hair which projects. Upper part elliptical with a central core of moderately thick-walled cells elongated to the long axis of the gland; at right angles to this are numerous radially elongated, palisade-like very thin-walled cells (Fig. 10). This upper part of the gland is very easily broken off, so that it is quite difficult to find a whole undamaged trichome (Fig. 24). Other species of this genus should be examined for the presence/absence of these glands or the presence/absence of ‘teeth’. There is usually a very slender vein ending near the base of these colleter-like glands,

which resemble the ‘standard type’ (S) colleter as described by Lersten (1974a, b) and illustrated in Thomas (1991: fig. 1A). No glands or nectaries seen at the base of the lamina or on the petiole.

Leaf surface: HAIRS: simple trichomes abundant on abaxial surface and leaf margin, fewer on adaxial. Colleters at margin only. Epidermal cells small with thin, straight/curved walls; stomata with brachyparacytic subsidiary cells. VENATION PATTERN A (according to Klucking, 1992): arcuate venation with mixed lineate and scalariform intercostals (Klucking, 1992: plate 20, fig. 1, p. 63). This is one of at least three different types of venation in this genus.

TS leaf

EPIDERMIS: Quadrangular cells; adaxial larger than abaxial; stomata not projecting. MESOPHYLL: palisade tissue in one layer of rather short palisade cells plus intermediate layer to rather compact spongy tissue. VEINS: MIDRIB: outline shield-shaped with prominent abaxial ridge and small adaxial ridge. Vascular tissue an abaxial crescent; both xylem and phloem well developed; sclerenchyma cap adaxial to vascular tissue; collenchyma adjacent to epidermis of both ridges. Other veins: larger veins smaller versions of midrib; some larger intermediate veins with collenchyma girders extending to adaxial and abaxial epidermis; smaller veins all embedded and with distinct parenchymatous sheaths.

Margin: No marginal vein.

Petiole TS: Outline; transversely broadly elliptical to circular; vascular tissue: crescentic; collenchyma beneath epidermis.

Cell inclusions: CRYSTALS: druses abundant in mesophyll, midrib, and petiole phloem and cortex.

IDESIA POLYCARPA MAXIM.

Leaves: Ovate, apex acuminate, base cordate, margin with many deep crenations.

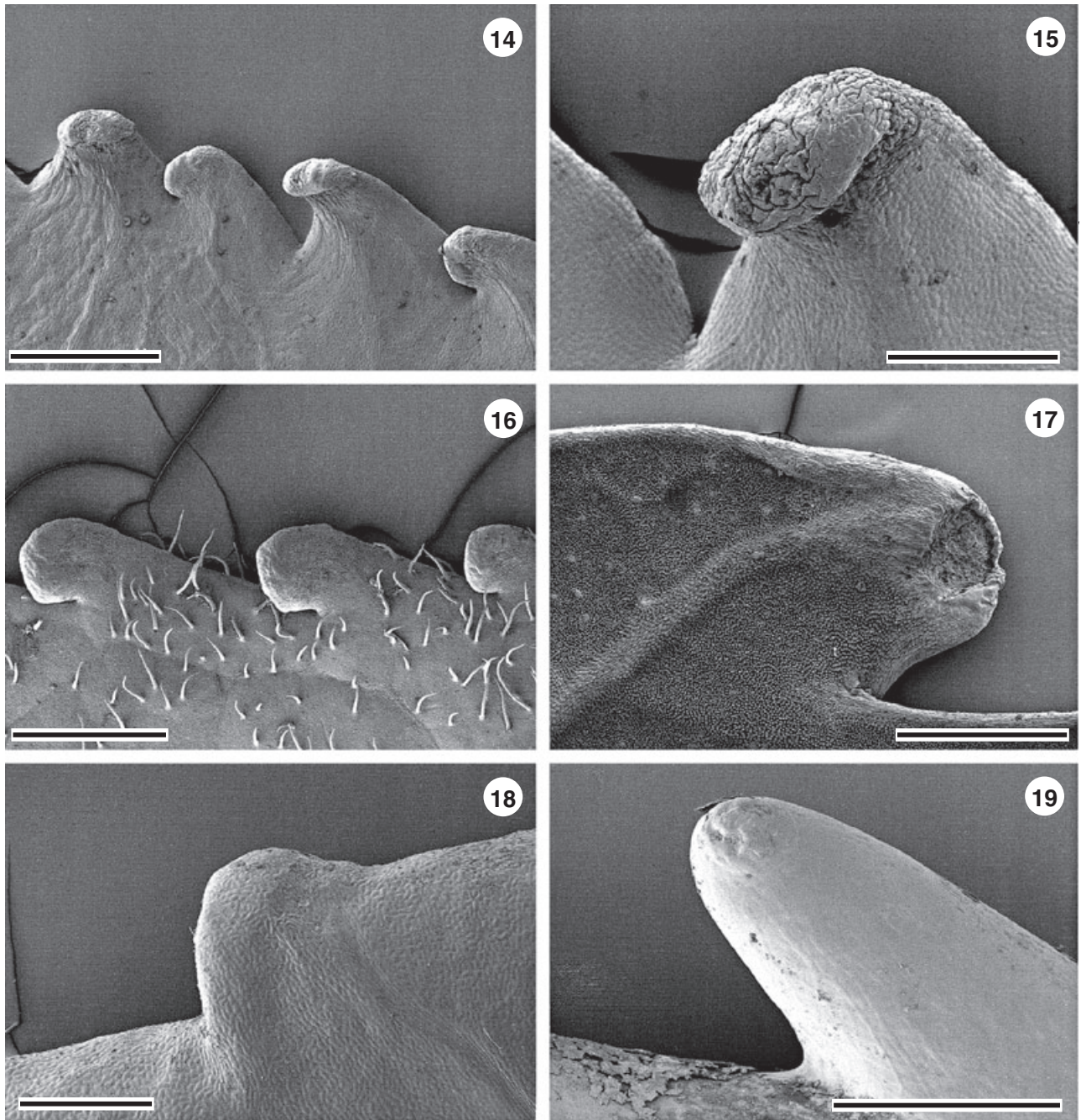


Figure 14–19. Scanning electron micrographs of marginal leaf teeth. Figs 14, 15. *Oncoba spinosa* teeth with glands on young leaves, adaxial surface. Fig. 14: scale bar, 500 μm . Fig. 15: scale bar, 200 μm . Figs 16, 17. *Idesia polycarpa*. Fig. 16. Marginal teeth glands on a young leaf, adaxial surface; scale bar, 100 μm . Fig. 17. Tooth on a mature leaf with most of gland gone; abaxial surface with papillae just visible; scale bar, 100 μm . Fig. 18. *Carrierea calycina* marginal tooth on a mature leaf; adaxial surface with some stomata visible at tooth apex; scale bar, 500 μm . Fig. 19. *Olmediella betschleriana* marginal tooth on a mature leaf, adaxial surface with glandular area slightly raised; scale bar, 300 μm . All micrographs taken by Greg Snowden.

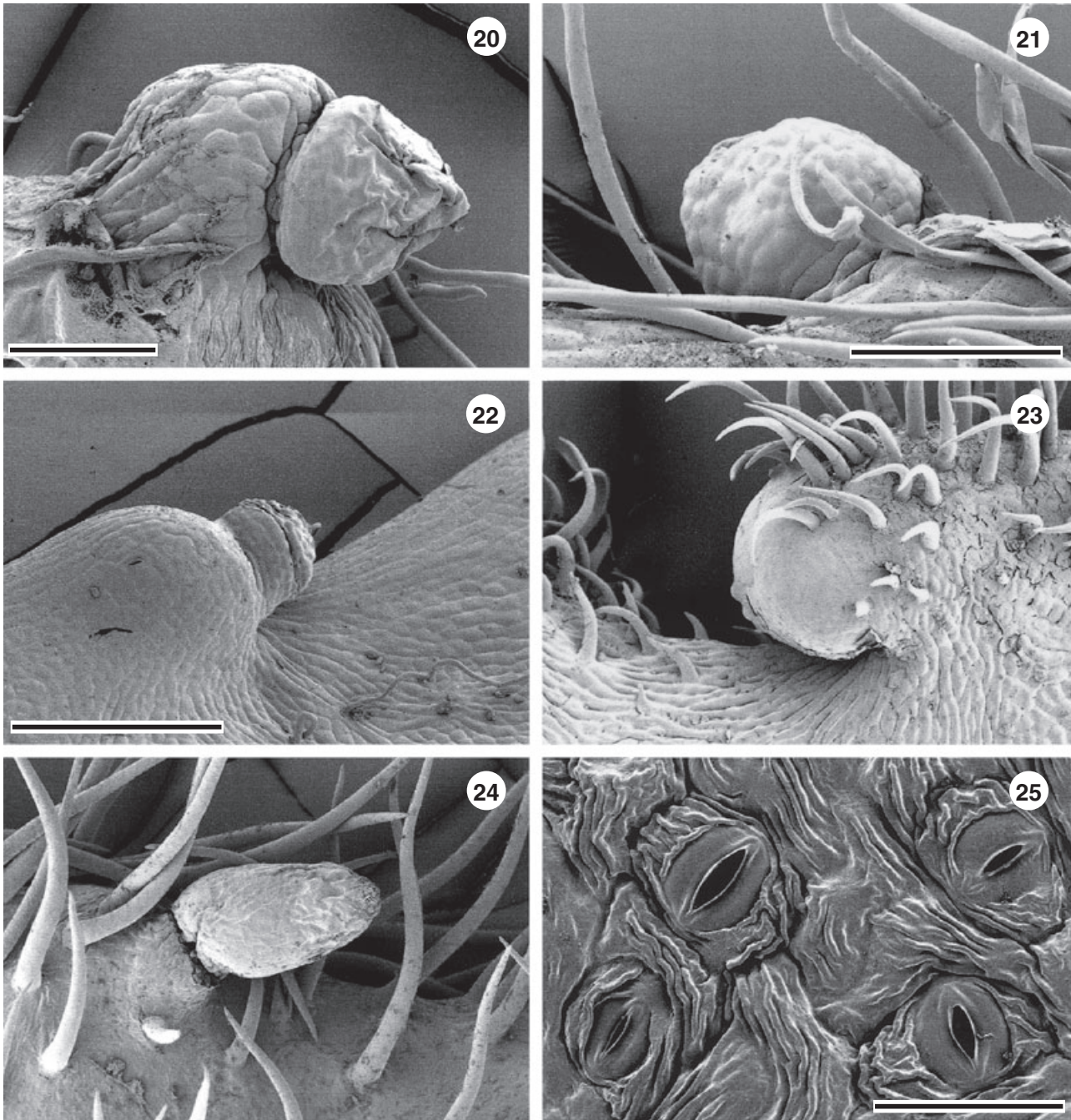


Figure 20–25. Scanning electron micrographs of marginal glands and stomata. Figs 20, 21. *Salix aurita*. Fig. 20. Marginal tooth and gland on a young leaf showing the distinct hump of cells, narrow neck capped by the gland, adaxial view; scale bar, 100 µm. Fig. 21. Globular gland with outlines of glandular cells visible and very short neck region, abaxial view; scale bar, 100 µm. Fig. 22. *Salix lasiolepis* marginal tooth with a less well-developed hump, distinct stalk-like neck region, and reduced remains of gland on a mature leaf; adaxial surface with one stoma visible on hump; scale bar, 200 µm. Fig. 23. *Populus ciliata* marginal tooth gland on a young leaf, adaxial surface. Fig. 24. *Dovyalis hebecarpa* marginal gland almost detached from stalk, on a young leaf, abaxial surface. Figs 22–24 to same scale. Fig. 25. *Oncoba spinosa* abaxial surface with stomata and striate cuticle; scale bar, 300 µm. All micrographs taken by Greg Snowden.

Table 1. Leaf marginal glands/hydathodes

Taxon	Marginal teeth glands	Teeth veins	Teeth stomata/lamina stomata	Crystals in teeth/lamina
<i>Carriera calycina</i> Franch. 2000-616	Massive; palisade-like cells at margin short or 0; masses in central zone	Large main and 2 laterals; played fan of vessels and tracheids	0/lamina brachyparacytic	Teeth masses of D in Y and O; lamina D +++; rhombs round veins
<i>Doyyalis hebecarpa</i> (Gardner) Warb. 1962-13001	Glands colleter-like, type A of Thomas (1991)	1 only; very fine	0/lamina brachyparacytic	Small D dense in O lamina; 0 in Y
<i>Idestia polycarpa</i> Maxim. 1987-8153	Domed; tall palisade-like cells in Y and some O; abscission layer in O	Very large main, 1 small lateral	+/lamina brachyparacytic	Teeth D ++, large in outer zone, smaller inner in Y; 0 in O
<i>Olmediella betscheriana</i> Loes. 1969-12335	Domed; palisade-like cells barely longer than other marginal cells	1 marginal and 1 lamina; large and with fibres; marginal veins wide and thick	?0/lamina brachyparacytic	Teeth 0; lamina D +++; large rhombs and irregular crystals around veins
<i>Oncoba spinosa</i> Forssk. 1949-63701	Curved; palisade-like cells tall, heavily pigmented in O abscission zone	1 main; 1-2 laterals	Adaxial side of gland/lamina brachyparacytic	0
<i>Poliothyrsis sinensis</i> Hook.f. 1988-8807	Very tall palisade-like cells in Y, shorter in O	1 large main and 1-2 smaller laterals	0/lamina brachyparacytic	0; rhombs (some large) around veins; D? only in Y
<i>Populus ciliata</i> Wall. 1966-7101	Domed; parenchymatous cells already thickened walls. Resin ++	1 Main vein only	0/very large stomata along and near abaxial margin; others brachyparacytic	0
<i>Populus trichocarpa</i> Torr. & A. Gray 1969-12838	Curved, tall palisade-like cells in Y	1 main vein, 1-2 laterals	0/very large stomata along abaxial margin; others brachyparacytic	0
<i>Salix aurita</i> L. 2000-2570	Hemispherical attached to hump of cells	1 rather slender	Teeth ? 0/lamina brachyparacytic	D in lamina ++; rhombs around veins
<i>Salix lasiolepis</i> Benth. 1996-2606	Spherical/hemispherical	1 moderately wide	Teeth ? 0/lamina brachyparacytic	0

D, druses; O, old; Y, young; +, few; ++, frequent; +++, abundant.

Marginal teeth and glands: In young leaves with flat, rounded glands curving over towards the abaxial leaf surface, in adult leaves glands damaged/abscised; teeth give margin crenate appearance; glands large (Figs 5, 16, 17); long palisade-like cells at margin and on abaxial side, many cells with dark-staining contents; supplied by one large main vein and one smaller lateral vein. Very large nectaries on petiole near base of lamina and also at various sites along the petiole length.

Leaf surface: HAIRS/PAPILLAE: long simple trichomes more abundant on abaxial surface; some tufts of septate hairs on adaxial surface; abaxial densely papillose, stomata mostly brachyparacytic; very large stomata with subsidiary cells divided at right angles to guard cell on one side of the stoma. Adaxial cell walls thin and mostly straight, abaxial straight/curved. VENATION PATTERN: not described by Klucking (1992). Pinnate, actinodromous; strong pair of secondary veins from cordate leaf base curving to margin between half to two-thirds towards apex, c. six others alternate or opposite; most tertiary veins scalariform; areolae large.

TS leaf

EPIDERMIS: Adaxial cells quadrangular and slightly domed, abaxial papillose. Stomata not projecting. MESOPHYLL: palisade tissue in one layer of very long cells, spongy compact. VEINS: MIDRIB: outline with prominent, broad abaxial ridge supported by collenchyma, small adaxial ridge supported mainly by collenchyma; small amount of sclerenchyma in abaxial/adaxial parts of sheath. Other veins: medium-sized with adaxial girder of sclerenchyma from vascular tissue to adaxial epidermis, collenchymatous girder on abaxial side; numerous smaller veins embedded and with sclerenchyma sheaths. MARGIN: no distinct marginal vein, only intermittent fine loops.

Petiole TS: Outline; lower base transversely elliptical with c. 14 bundles without sclerenchyma and with several corky areas around epidermis; more distally becoming stem-like with circular outline, a ring of c. 14 bundles, sometimes continuous, phloem surrounded by a continuous sheath of sclerenchyma. Pith large; cortex parenchymatous and collenchymatous under epidermis. Large, projecting glandular 'nectaries' with palisade-like cells and vascular supply, mostly necrotic with deep abscission zone in old petioles.

Cell inclusions: CRYSTALS: druses many in teeth of young leaves; none in teeth and few in mesophyll of adult leaves; many in petiole parenchyma, especially below projecting 'nectaries'. RESIN-LIKE cell contents staining dark red.

OLMEDIELLA BETSCHLERIANA LOES.

Leaves: Elongate elliptical, apex and base acute, margin with widely spaced shallow serrations (modified from Klucking, 1992).

Marginal teeth and glands: Straight, low-angled projection; palisade-like cells at margin and abaxial and a little on adaxial sides (Figs 4, 19); a massive marginal vein and another large vein from lamina. Marginal glands and leaf tip frequently have masses of dark brown amorphous material over them (? resin). Larger, lenticular glandular patches at base of lamina near the petiole.

Leaf surface: HAIRS: absent. VENATION PATTERN (according to Klucking, 1992: plate 44, fig. 3, p. 115): pinnate secondary venation with irregular intercostal pattern. The ultimate venation appears to be open with branching veinlets enclosed in relatively large areoles. Abaxial cell walls thin adjacent to stomata, thicker when not near stomata, undulate or curved; adaxial thick-walled, beaded, straight, curved or slightly undulate. Stomata with brachyparacytic subsidiary cells.

TS leaf

EPIDERMIS: Adaxial tabular, all walls thick; abaxial tabular thinner walled and smaller than adaxial; stomata flush with surface. MESOPHYLL: palisade tissue in one layer, spongy loose. VEINS: MIDRIB: very broadly obovate but with wide, low adaxial ridge. Vascular tissue wide crescent, with deep sclerenchymatous sheath; adaxial and abaxial ridges supported by collenchyma. Other veins embedded, with sclerenchymatous sheath, even smallest with some sclerenchyma and a distinct parenchymatous sheath. MARGIN: massive sclerenchymatous sheath round small vein.

Petiole TS: Outline; very broadly obovate; three veins, vascular tissue a curved deep crescent in central vein, forming a ring in two laterals; sclerenchyma absent; numerous groups of stone cells; collenchyma around periphery.

Cell inclusions: CRYSTALS: druses in mesophyll and in parenchyma/collenchyma and phloem of petiole.

ONCOBA SPINOSA FORSSK.

Leaves: Elongate to broadly elliptical, apex acuminate to acute, base obtuse rounded or slightly cordate, margin crenate, often with large and small crenations alternating.

Marginal teeth and glands: Successive curved over-arching teeth with terminal oval knob (Fig. 14) overlapping more onto adaxial than abaxial sides, palisade-like cells in knob area; one main vein plus one to two smaller lateral ones (Fig. 1). Stomata on adaxial surface of teeth immediately over or very near well-developed xylem; 11–17 stomata observed (Fig. 2). No nectaries seen at lamina base or on petiole.

Leaf surface: HAIRS: rather fine simple trichomes in young leaf, absent in adult but thick-walled insertion and rosette of surrounding cells frequent. VENATION PATTERN C (from Klucking, 1992: plate 46, fig. 3, pp. 117–118): pinnate secondary venation with mostly scalariform intercostal venation, some percurrent, moderate angled, narrowly spaced secondary veins. Abaxial cell walls thin, straight, curved to slightly undulate. Stomata with brachyparacytic subsidiary cells and striate cuticle (Fig. 25); adaxial walls similar but slightly thicker; stomata absent except over marginal teeth.

TS leaf

EPIDERMIS: Cells tabular and quadrangular on both surfaces; stomata flush with surface. MESOPHYLL: palisade tissue two-layered, spongy rather compact. VEINS: MIDRIB: outline rhombic with slight adaxial ridge. Vascular tissue a crescent but also some adaxial bundles; sclerenchyma between abaxial and adaxial vascular tissue and also outside abaxial. Other veins with some sclerenchyma as adaxial and abaxial caps in sheath and with collenchyma girders to epidermis; smallest without. MARGIN: no main vein, only fine loops (except leaf tooth supply).

Petiole TS: Outline; very broadly obovate with lateral adaxial wings; vascular tissue scroll shaped incomplete on adaxial side; this unrolls below leaf base with a lateral vein on each side; some sclerenchyma around vascular tissue in lower petiole, absent more distally; collenchyma as groundmass.

Cell inclusions: CRYSTALS: druses in midrib phloem; rhombs in lamina epidermis. RESIN?: red-staining contents in mesophyll cells.

POLIOTHYRSIS SINENSIS HOOK.F.

Leaves: Ovate with acute apices and rounded to truncate bases (Klucking, 1992), margin crenate.

Marginal teeth and glands: Broad, palisade-like cells at margin and on abaxial side; supplied by one large vein; mostly damaged/abscised in adult leaves (Fig. 3). Glandular teeth at base of lamina larger than

more distal regions; also at the junction with the petiole where they could be regarded as nectaries.

Leaf surface: HAIRS: absent. VENATION PATTERN (from Klucking, 1992): actinodromous secondary venation with essentially scalariform intercostals. Cell walls undulate, especially adaxial; stomatal subsidiary cells brachyparacytic.

TS leaf

EPIDERMIS: Adaxial tabular, round but all slightly domed; abaxial similar but not domed, smaller than adaxial; stomata flush. MESOPHYLL: palisade in two layers, outer long; spongy compact cells somewhat palisade-like. VEINS: MIDRIB: outline shield-shaped, prominent adaxial ridge; abaxial projection with subsidiary ridges. Vascular tissue a crescent; sheath of thick-walled sclerenchyma; ridges supported by collenchyma. Other veins all (except veinlets) with thick sclerenchymatous sheaths, often extending to epidermis. MARGIN: veins nearest to margin small, not far away, large with thick sclerenchymatous sheath.

Petiole TS: Outline; broadly obovate; vascular tissue shallow obtriangular with one to two small lateral adaxial bundles; groundmass mostly of collenchyma.

Cell inclusions: CRYSTALS: druses few in palisade tissue, abundant in petiole groundmass tissue, 'pith', and phloem. Rhombs dense in sheath around all veins.

POPULUS CILIATA WALL.

Leaves: Ovate-lanceolate, ciliate, base cordate, margin ciliate-serrate.

Marginal teeth and glands: Many all round leaf margin; curved over onto adaxial side of leaf (Fig. 23), domed; palisade-like cells all round periphery of dome; one large vein. Very hairy adjacent to but not on gland. Similar but larger glands also present at the base of the lamina, on the adaxial side near the petiole.

Leaf surface: HAIRS: simple trichomes at margin only. VENATION PATTERN: eucamptodromous. Cell walls on adaxial straight, on abaxial some straight but mostly curved to undulate; stomatal subsidiary cells brachyparacytic. On some leaves there are numerous very large stomata at the margin, over the marginal vein and adjacent areas.

TS leaf

EPIDERMIS: Adaxial cells tabloid to rectangular on both surfaces; cuticle of abaxial cells with finger-like vertical projections (striae in surface view). Large stomata raised above abaxial surface. MESOPHYLL: palisade tissue in two layers; spongy compact except above numerous stomata. VEINS: MIDRIB: broadly ovate with wide adaxial and abaxial ridges. Vascular tissue an almost flat plate and with two adaxial bundles; sclerenchymatous sheath with collenchyma to both ridges. MARGIN: with one moderately large vein and one smaller one (loop) nearer margin.

Petiole TS: Outline; base transversely broadly elliptical; vascular tissue one central and two lateral bundles with closed rings of xylem; distal portion vertically elliptical with two vertically superimposed main veins and two to three smaller adaxial veins with complete or incomplete rings of xylem.

Cell inclusions: CRYSTALS: druses few in lamina mesophyll; numerous in petiole cortex and especially dense around vascular bundles. Rhombs in bundle sheaths of veins. RESIN: seen outside the gland cuticle in some preparations (Fig. 6); usually removed by the use of the alcohols in the dehydration procedure of permanent preparations. TANNIN-LIKE contents staining red in all mesophyll palisade cells and, to a lesser extent, in the spongy tissue. Also present in some parenchyma cells of cortex, phloem, and ray cells of proximal petiole.

POPULUS TRICHOCARPA TORR. & A. GRAY

Similar to *P. ciliata*; a few minor differences given below.

Leaves: Broadly or narrowly ovate; apex shortly acute, base broadly cuneate, truncate, or very slightly cordate; margins shallowly and bluntly serrate.

Marginal teeth and glands: Depressed ovate-pyramidal curved towards adaxial side of leaf; palisade-like glandular cells at margin. Similar but larger glands at base of lamina on the adaxial side near the petiole. Thick-walled abscission layer cells apparent even in young leaves; one main vein and one to two laterals (Fig. 7). HAIRS: simple trichomes on abaxial surface.

Populus balsamifera L. and *P. schechuanica* Schneider, in Jodrell slide collection, also similar. CLEARED LEAF: tracheoidal cells absent from vein endings of *P. ciliata* and *P. trichocarpa*.

SALIX AURITA L.

Leaves: Oblong-ovoid, twice as long as wide, apex rounded or shortly acute, base cuneate; margins undulate-serrate, with short, rather irregular teeth.

Marginal teeth and glands: With massive barrel-shaped hump of cells, short stalk of strong-walled cells holding globular glandular region (Figs 20, 21) with the usual thin-walled palisade-like cells all around periphery (Figs 9, 12, 13). Bent over towards adaxial side of leaf. Supplied by one vein. No glands/nectaries seen at base of lamina or on petiole.

Leaf surface: HAIRS: on both surfaces, particularly long and abundant on abaxial midrib. VENATION PATTERN: eucamptodromous. Adaxial cell walls straight, abaxial curved and straight; stomatal subsidiary cells brachyparacytic. CLEARED LEAF: tracheoidal cells absent from vein endings.

TS leaf

EPIDERMIS: Adaxial large, ovoid; abaxial smaller and tabloid. MESOPHYLL: palisade of one outer layer and one shorter cell intermediate layer; spongy compact. VEINS: MIDRIB: outline broadly obovate, abaxial ridge very wide, adaxial small. Vascular tissue a complete oval of xylem and phloem continuous from abaxial to adaxial. Sclerenchymatous sheath on adaxial and at sides, abaxial collenchymatous. Both ridges supported by collenchyma. Other veins: larger veins slightly projecting abaxially; many veins with sclerenchymatous sheath, some with collenchyma connections to the epidermis, many small veins embedded. MARGIN: revolute; marginal vein small from fine loops.

Petiole TS: Outline; base depressed elliptical with three lobes and three bundles, main shaft depressed broadly obovate; adaxial surface very hairy. One main bundle and one lateral; xylem in flattened ring; sclerenchyma absent; collenchyma supporting abaxial ridge.

Cell inclusions: CRYSTALS: druses scattered throughout spongy mesophyll. Rhombs around a few veins.

SALIX LASIOLEPIS BENTH.

Leaves: Lanceolate; apex acuminate gradually tapering, base gradually narrowing into petiole, marginal teeth numerous and small.

Leaf surface: HAIRS: dense distribution especially on abaxial surface. VENATION PATTERN: eucamptodromous.

Marginal teeth and glands: Smaller than in *S. aurita* and without massive stalk, only a slight swelling or none but slightly curved over towards the adaxial side of the leaf; supplied by one vein (Figs 8, 11, 22), sometimes ending in a knot of red-staining tracheoidal cells and also sometimes red-staining parenchyma

cells forming the small core which supports the radiating palisade-like glandular layer. No glands/nectaries seen at base of lamina or on petiole.

Cleared leaf: Tracheoidal cells at veinlet endings a characteristic feature. Remaining details very similar to *S. aurita*.

TS leaf

EPIDERMIS: Cells on both surfaces tabular and quadrangular; abaxial smaller than adaxial. **MESOPHYLL:** palisade in two layers of equally long cells; 'spongy' very compact short rectangular cells, sometimes palisade-like. **VEINS:** MIDRIB: outline broadly obovate. Abaxial and adaxial plates of vascular tissue, very little sclerenchyma; usual collenchyma supporting ridges. Other veins: larger veins not projecting abaxially, reaching to epidermis with collenchymatous short girders. All other veins embedded. Tracheoidal cells scattered throughout middle mesophyll. **MARGIN:** with small vein.

Petiole TS: Outline; base somewhat crescentic and three lobulate ridges with three vascular bundles; central bundle an almost complete ring, open on adaxial side, lateral bundles usually a complete ring. Distal petiole flat on adaxial side, obovate, ridged, abaxial projection.

Cell inclusions: **CRYSTALS:** druses large, scattered throughout middle to lower mesophyll; few in collenchyma/parenchyma of petiole. Rhombs very frequent in bundle sheaths. **RESIN:** sometimes seen in a coagulated state in the gland palisade-like cells.

DISCUSSION AND RESULTS

The marginal glands in the taxa described above all have in common an area of secretory, palisade-like cells with a vascular supply of one to three veins (except *D. hebecarpa*). There appears to be a progression from glands of simple structure in the 'flacourtiaceous' taxa to a more complicated development in morphology and anatomy in the salicaceous species. There is a range from relatively simple structures, such as in *O. spinosa*, *Poliothyrsis sinensis*, *Olmediella betschleriana*, and *I. polycarpa* (Figs 1–5), to more complex structures, such as in some species of *Salix*, *Populus*, and, especially, *D. hebecarpa*. It seems that projecting leaf teeth involving a modified leaf mesophyll are apparent in *Carrierea*, *Idesia*, *Olmediella*, *Poliothyrsis*, and *Populus* spp. (Figs 1–7). They also have a wide area over which the secretory cells are spread, although less so in *Olmediella* (Fig. 4). The flat and cushion-like glandular areas seen in *I. polycarpa*, *Carrierea*, *Poliothyrsis*, and

Olmediella have the same palisade-like glandular cells, regardless of whether they are predominantly on the adaxial or abaxial surface, and are usually also at the margin; this is especially so in young leaves. In *Salix* species, there is a modification to a hump of cells below the gland, as in *S. aurita*, which is more reduced in *S. lasiolepis*; both have narrow neck or stalk regions. In the limited number of species examined in *Salix* and *Populus*, the actual glandular areas are globular or subglobular. This appears to be the 'salicoid' type of tooth. *D. hebecarpa* has even further modified glands which have wide basal stalks not involving the leaf lamina or a tooth projection, although each has a well-developed area of secretory cells around a central axis, the whole being an elongated ovoid. They are similar to the standard (S) type of colleter illustrated by Thomas (1991: fig. 1A). It seems quite likely that, when more taxa in the two families of Salicaceae and Flacourtiaceae are examined, the apparent difference from simple to more complex structures will be seen as a continuum, as the palisade-like secretory cells are common to all the taxa examined. Any future work on leaf teeth should include observations on young leaves, as some glands necrose or abscise very early. The definition of salicoid leaf teeth given by Nandi *et al.* (1998: appendix 4, 204) is: 'leaf teeth showing a proximally rounded hyaline gland with concave gland body in herbarium specimens'. The meaning of this description is not very clear. From the present study, the 'salicoid tooth' seems to be a projection at the apex of the leaf tooth, the outermost layer of which is composed of radially elongate, palisade-like cells which are subtended by several layers of parenchyma cells. This structure is of variable morphology and is supplied by one to three veins, mainly composed of xylem elements. This definition should be redefined after the glands of more genera and species in the salicoid/flacourtioid complex, and probably also the leaf teeth glands in other families, have been examined anatomically.

One of the striking features is the strong development of xylem tracheids supplying the leaf teeth in most specimens examined, although much finer and not reaching into the colleter-like gland of *D. hebecarpa*. Well-developed xylem is characteristic of hydathodes, whereas strongly developed phloem is indicative of nectaries. The presence of quite a large number of stomata on the adaxial surface of some of the leaf teeth of *O. spinosa* (Fig. 2), with fewer in *P. trichocarpa* (Fig. 7) and *S. lasiolepis* (Fig. 22), and the large number of tracheary elements supplying the leaf teeth, especially in *O. spinosa* (Fig. 1) and some species of *Populus* (Figs 6, 7), provide evidence of a hydathodic function, whereas the palisade-like cells

suggest a secretory function. The presence of resin in either a granular state outside the leaf tooth palisade cells of *P. ciliata* (Fig. 6) or in a coagulated state in *S. lasiolepis* (Fig. 11) is no surprise as many workers, especially Curtis & Lersten (1974, 1980), have reported the presence of resin in these genera for many years, as detailed in the 'Introduction'. Resin covering some glands of *Populus* (Fig. 6), extruded filaments of resin, and a pore or dimple in the glands (Fig. 9, arrowhead) of *Salix* have all been observed by the current author.

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