Woody angiosperm taxa of the Canarian laurel forests: Leaf morphology and cuticular structures

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Abstract

Systematic-taxonomic investigations of fossil foliage are based on leaf morphology including the details of higher order venation and on cuticular structures. These features are rarely taken into account for the determination of modern plant taxa. Hence, they are usually not included in the systematic literature. It has long been known that the laurel forests of the Canary Islands bear similarities to the Neogene European plant record. Here, we describe in detail the foliage morphology, especially the venation details and cuticular features, of the woody angiosperm taxa of the Canarian laurel forests (27 species/subspecies from 18 families). Additionally, possible ancestral plants of the European Neogene are discussed.

K e y w o r d s : Canary Islands, laurel forests, woody angiosperm taxa, cleared leaves, venation details, cuticle structures, determination of foliage, fossil record.

Zusammenfassung

Die systematisch-taxonomische Bestimmung fossiler Blätter erfolgt nach Blattmorphologie und Kutikular-strukturen. Diese Merkmale werden jedoch bei der Bestimmung rezenter Pflanzen kaum jemals berücksichtigt und sind in der Bestimmungsliteratur meist nicht enthalten. Seit langem ist bekannt, dass die Zusammensetzung der Lorbeerwälder der Kanarischen Inseln Ähnlichkeiten zu den Pflanzengemeinschaften Europas während des Neogens aufweisen. In dieser Arbeit wird nun erstmals die Blattmorphologie der Gehölze der kanarischen Lorbeer-wälder (27 Arten/Unterarten aus 18 Familien) beschrieben und dabei spezielles Augenmerk auf Feinnervatur und Kutikularstrukturen gelegt. Anschließend werden ihre möglichen Vorläufer diskutiert.

Contents

1 Introduction

The determination of modern plants is more strongly based on generative than on vegetative features. Details of leaf morphology, especially venation details and cuticular features, are rarely included in the description of modern species. KLUCKING (1986–1995) dealt extensively with leaf venation patterns on the family level but did not go deeper than to the second-order venation. HÖGERMANN (1987) dealt with Lauraceae from tropical Venezualian Guyana. The fossil plant record is hampered by the detachment and fragmentation of the plant organs prior to fossilisation. Leaf assemblages are common in the fossil record, and the systematic assignment of detached plant organs is largely based on comparison with corresponding organs of modern plants. Consequently, there is a strong need to describe the morphological foliar features of modern plant species, especially venation details along with cuticular structures.

Traditionally, comparative investigations for the systematic identification of fossil plants usually start with different modern species of one genus, largely disregarding their habitat. The present approach, however, starts from the sociological viewpoint: species that co-occur in one forest type today. The argument for this procedure is the fact that the composition of Paleogene and Neogene plant assemblages shows strong relations to different forest types of the northern hemisphere, e. g. broad-leaved evergreen forests, mixed mesophytic forests or broad-leaved deciduous forests.

The Canarian laurel forests have often served for comparison with the Neogene European plant record, but leaf morphological and cuticular traits of their taxa remained largely unexamined. In this study we therefore focus on leaf morphology and cuticle structures of the woody taxa of the Canarian laurel forests. This is designed to enlarge our knowledge of diagnostic foliar features and to provide a sound basis for further comparisons of the fossil plant record.

2 Material and methods

Material

All leaves investigated here derive from herbarium material housed in the State Museum of Natural History Stuttgart (STU). A big part has been specially collected by the second author for comparison with the fossil record (here herbarium EDER). Most cuticle preparations were performed from this material.

Preparation techniques

For the investigation of the venation details, cleared leaves were prepared. The methods described by FOSTER (1952) modified by HICKEY (1973), the method of PAYNE (1969) modified by SHEFFY (1972) and a recipe of WOLFE used by DILCHER (1974) were initially applied. None of them was appropriate for the hard and resistant leaves of the laurel forest taxa. An optimised method was therefore developed based on the tested techniques. The proposed bleaching substance chloral hydrate was replaced by ordinary chloral bleach. The proposed cooking of the samples was abandoned because it caused shrinkage and in some cases severely damaged the foliage. The mounting of the leaves between two glass plates in glycerine gelatine was replaced by mounting in glycerol and coverage by a thin plastic wrap. This enabled samples to be taken at a later time. The method has been described in detail by RASCHE & KOVAR-EDER (2008).

Cuticle preparation was performed with Schulze's reagents ($KClO_3$ plus HNO_3), subsequent rinsing in water, followed by treatment in a 5 %-solution of KOH and renewed rinsing in water. The cuticles were stained with Safranin, mounted in glycerol-gelatine and sealed with nail polish.

Descriptions

Descriptions of gross morphology and venation follow the "Manual of Leaf Architecture" (WING et al. 1999), that of cuticles DILCHER (1974) and STACE (1965). Stoma and trichome frequency are calculated using DILCHER's formula of $I = (S/(E+S))*100$ for an area of $100\,\mu m^2$ where S is the number of stomata or trichomes per area and E is the corresponding number of non-modified epidermal cells.

In every taxon, 20 measurements for leaf size and petiole length were taken from at least five different herbarium sheets (the exact number of herbarium sheets is given with the specific description). Ten measurements were taken for every cuticular cell type, if possible from three different herbarium sheets. Minimum and maximum values are given along with mean values in brackets. Five measurements of the distances between the secondary veins were measured in one leaf.

When selecting the herbarium material for this study, high priority was given to cover species variability. Nevertheless, the herbarium material did not enable clear differentiation between canopy and understorey leaves or unambiguous distinction of material from different exposures, e. g. north/south exposed ridges, slopes, valleys. That these environmental parameters may influence leaf morphology and physiology has recently been demonstrated by OHSAWA & NITTA (1999). KVAČEK (2004) added that non-modified epidermal cells of understorey leaves are bigger than those of canopy leaves and more often show undulations. Therefore, the parameter ranges given in the descriptions probably reflect trends and ranges rather than full character variability.

Photographic documentation

The cleared leaves were examined under a Novex Holland-binocular microscope, photos of details were taken through a phototube. For the photos of the entire leaves, the slides were put on a phototable with transmitted light. All photos were taken with a Nikon Coolpix 4500.

The cuticles were examined under a Leica DM R-microscope with interference contrast, and photos were taken with a Canon PowerShot S45 digital camera through a phototube. Measurements were performed on the digital photos using the software Leica IM50.

General layout

In chapter 3, families, genera and species/subspecies are arranged in alphabetical order. In the figure captions numbers of herbarium sheets are given in brackets; the little arrow in the figures points towards the leaf apex.

3 Systematic part

Aquifoliaceae
Ilex canariensis Poiret
(Figs. 1–7)

Material: Herbarium EDER nos. 18, 31, 32, 57–59, 60, 65 (16 herbarium sheets, cuticles from 8 sheets).

Leaf attachment alternate, leaf organization simple, petiole 1.0–1.8 cm (1.3 cm) long, marginal petiolar attachment, laminar size microphyll – 2 : 1, length 2.7–10.2 cm (7.3 cm), width 1.5–4.5 cm (3.3 cm), shape elliptic, symmetrical, base and apex angle both acute, base and apex shape convex, margin entire or serrate, revolute; tooth shape: basal side retroflexed (= apically convex, basally concave), apical side concave, sinus rounded, apex spinose, a veinlet running directly in the tooth apex.

Venation: primary vein pinnate; secondaries festooned brochidodromous, in most cases recurved, sometimes straight, secondary vein spacing irregular, 0.6–1.0 cm, secondary vein angle smoothly decreasing towards the base, inter-secondaries not developed; tertiaries random reticulate, admedially ramified; fourth-order veins alternate percurrent, areolation well developed; fifth-order veins dichotomizing; freely ending ultimate veinlets twice or more times branched, ultimate marginal venation consisting of incomplete loops.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells 21–67 µm (36 µm) in diameter, anticlines undu-

late to almost straight, undulation U-shaped, wave length 16–32 µm (24 µm), amplitude 7–12 µm (10 µm); surface sometimes striate. Marginal cells polygonal, rarely elongated, 19–58 µm (39 µm) long, anticlines straight, cell surface occasionally striate.

Abaxial cuticle: thick, glabrous, non-modified epidermal cells 18–48 µm (39 µm) in diameter, shape variable, anticlines strongly undulate to almost straight, undulation U-shaped, wave length 13–24 µm (19 µm), amplitude 4–21 µm (10 µm); stomatal complexes cyclocytic to incomplete amphicyclocytic; subsidiary cells slightly elongated tangentially; stomata roundish to oval, 26–48 µm (32 µm) long, 23–37 µm (29 µm) wide, polar I-pieces slender, outer stomatal ledges thick; stomatal aperture oval, 13–29 µm (20 µm) long; stomata frequently arranged in groups partly sharing the outer ring of subsidiary cells; stomatal frequency 20, stomata less densely spaced when the anticlines of the non-modified epidermal cells are almost straight; few giant stomata observed, size about 45 × 35 µm, non-modified epidermal cells surrounding the giant stomata thicker than normal; distinct idiocuticular foldings developed, running almost circular around the stomata; cork warts also occasionally developed, surrounding epidermal cells thickened, sometimes flattened and tangentially oriented around the warts.

Remarks: Differential features of this species from the following are the recurved secondaries, the admedially ramified tertiaries, and the ultimate marginal venation, which is composed of incomplete loops.

Ilex platyphylla Webb & Berthet
(Figs. 8–14)

Material: Herbarium EDER nos. 10, 56 (11 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate, leaf organization simple, petiole 0.8–1.5 cm (1.0 cm) long, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 8.4–13.7 cm (10.8 cm), width 3.7–8.0 cm (5.9 cm), shape elliptic, symmetrical, base and apex angle both acute, base shape rounded, apex shape acuminate, forming a spinose apex, margin entire or serrate, revolute, almost always one tooth per centimetre, spacing almost regular, tooth shape: basal side convex, apical side concave, sinus rounded to nearly angular, apex spinose.

Venation: primary vein pinnate; secondaries festooned brochidodromous, near their origin somewhat recurved to straight, near the margin somewhat convex, secondary vein spacing irregular, 0.6–1.5 cm, secondary vein angle rather uniform, inter-secondaries developed; tertiaries alternate to opposite percurrent, straight to convex, tertiary

vein angle to primary vein obtuse to acute, tertiary vein angle decreasing exmedially; fourth-order veins regular polygonal reticulate, areolation moderately developed (4- to more-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets twice or more times branched, ultimate marginal venation a fimbrial vein.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells 17–44 µm (29 µm) in diameter, anticlines straight or weakly undulate, undulation U-shaped, wave length 16–24 µm (19 µm), amplitude 6–11 µm (8 µm). Marginal cells polygonal to elongated and linear, 18–55 µm (34 µm) long, 13–34 µm (19 µm) wide, anticlines straight to weakly undulate.

Abaxial cuticle: thick, glabrous, non-modified epidermal cells 14–38 µm (26 µm) in diameter, anticlines straight or undulate, undulation U-shaped, wave length 13–22 µm (17 µm), amplitude 3–8 µm (5 µm); stomatal complexes – sometimes incomplete – amphicyclocytic, anticlines of subsidiary cells straight, even when surrounded by non-modified epidermal cells with undulate anticlines, subsidiary cells staining more intensely than non-modified cells, 13–37 µm (23 µm) long, 5–12 µm (8 µm) wide; stomata wide oval, 27–37 µm (33 µm) long, 20–29 µm (25 µm) wide, poles sometimes marked by thickened I-piece; stomatal aperture wide oval, 15–21 µm (17 µm) long, outer stomatal ledges well developed; stomata frequently arranged in groups of two to five; stomatal frequency 8, stomata less densely spaced when the anticlines of non-modified epidermal cells are straight; giant stomata present (one observed, 48 × 37 µm); large, multicellular cork warts occasionally developed.

Remarks: The foliage of *I. platyphylla* differs from *I. canariensis* by marginal teeth with a spinose apex, the presence of intersecondaries and a fimbrial vein. The cuticular features of both species are very similar and are not suitable for specific differentiation.

C a p r i f o l i a c e a e
Sambucus nigra L. ssp. *palmensis* (Link) Bolli
(Figs. 15–20)

Material: Herbarium EDER nos. 48, 49 (6 herbarium sheets, cuticles from 2 sheets).

Leaf attachment opposite, odd-pinnately compound, 7 to 9 leaflets, petiole 6.7–13.5 cm (10.2 cm) long, pilose, laminar size mesophyll – 1.5 : 1, leaves 8.3–22.8 cm (14.6 cm) long, 6–10 cm (11 cm) wide; leaflets: petiolule of the terminal one usually about 1 cm long, petiolule of the lateral leaflets 0.2–0.3 cm long, marginal petiolar attachment, leaflet size microphyll – 2 : 1; leaflets 3.7–9.5 cm (6.8 cm) long, 1.6–3.9 cm (2.9 cm) wide, shape elliptic to

ovate, base symmetrical to asymmetrical, base and apex angle both acute, base shape convex to rounded, apex shape straight to slightly convex; margin simple to occasionally double serrate, 4 teeth per centimetre on average, rather regularly spaced; tooth shape: basal side convex to flexuous (= basally convex, apically concave), apical side straight to flexuous, sinus angular, apex mucronate.

Venation: primary vein pinnate; secondaries curved and somewhat zig-zag, festooned semicraspedodromous, secondary vein spacing 0.5–1.3 cm, decreasing towards the base, no inter-secondaries developed; tertiaries partly alternate to opposite percurrent, partly reticulate, generally widely spaced, tertiary vein course variable, tertiary vein angle to primary vein obtuse to acute, tertiary vein angle inconsistent; fourth-order veins regular polygonal reticulate, areolation weakly developed (mostly 5-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets unbranched to once branched, ultimate marginal venation consisting of incomplete loops, a veinlet running directly in the tooth apex.

Adaxial cuticle: extremely delicate, non-modified epidermal cells not always visible, if recognizable widely U- to Ω-shaped undulate. Surface finely striate, striae running in rather parallel bundles. Two types of trichomes developed: one-celled conical trichomes positioned above very large simple, roundish bases (see Fig. 20), base diameter $>80\,\mu m$, trichome body $>500\,\mu m$ long, fine but distinct striation developed around the trichome base and on the lower part of the trichome body, furthermore pluricellular club-shaped glandular trichomes developed, 117–139 μm (130 μm) long, head 51–65 μm (58 μm) wide and 61–95 μm (77 μm) long (Fig. 18).

Abaxial cuticle: also very delicate, non-modified epidermal cells hardly visible on the cuticle; stomatal complexes probably anomocytic; stomata elliptic, 14–35 μm (22 μm) long, 9–21 μm (14 μm) wide; stomatal aperture elliptic, 8–24 μm (14 μm) long, outer stomatal ledges well developed and strongly staining; both trichome types as described above present, surface finely striate.

Remarks: Isolated leaflets of *S. nigra* ssp. *palmensis* may be mistaken for a Rosaceae species. Characteristic for *S. nigra* ssp. *palmensis* is the low number of secondaries resulting from the relatively wide spacing and the rather coarse pattern of the tertiaries. The most remarkable cuticular features are the extremely large trichome bases and the very long trichomes.

Viburnum tinus L. ssp. *rigidum* (Vent) Silva
(Figs. 21–27)

Material: Herbarium EDER nos. 20, 33, 34 (5 herbarium sheets, cuticles from 3 sheets).

Leaf attachment opposite, leaf organization simple, petiole 1.5–2.1 cm (1.9 cm) long, densely pilose, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 6.9–15.0 cm (9.9 cm), width 3.4–7.3 cm (5.2 cm), shape elliptic, symmetrical to asymmetrical, base angle obtuse, apex angle acute, base shape convex, apex shape slightly convex to almost straight, margin entire to erose; lower leaf surface densely pubescent, especially on veins, occasionally axillary domatia developed, upper leaf surface less densely pubescent; two types of trichomes present: simple long filiform and shorter stellate ones.

Venation: primary vein pinnate; secondaries smoothly curved, festooned brochidodromous, secondary vein spacing irregular, 1.3–2.5 cm, secondary vein angle decreasing towards the base, inter-secondaries developed; tertiaries mixed opposite/alternate percurrent, tertiary vein course straight, convex or sinuous, tertiary veins sometimes hardly distinguishable from inter-secondaries, tertiary vein angle to primary vein slightly acute to almost perpendicular, tertiary vein angle uniform; fourth-order veins alternate percurrent, towards the margin polygonal reticulate, areolation moderately to weakly developed (mostly 4-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets unbranched to once branched, ultimate marginal venation consisting of loops; all veins protuberant and densely pilose.

Adaxial cuticle: thick, non-modified epidermal cells polygonal, 16–47 μm (28 μm) in diameter, anticlines straight to undulate, undulation U-shaped, wave length 15–26 μm (19 μm), amplitude 4–7 μm (5 μm); very characteristic trichome bases present, diameter 49–99 μm (74 μm), densely spaced, mainly upon veins, consisting of (5) 6–7 (8) radially arranged cells and one or more central cells, outer margin of trichome base thickened, occasionally surrounded by slender, tangentially elongated epidermal cells; additionally, small, simple, thickened trichome bases scattered, diameter 13–22 μm (17 μm). Marginal cells rectangular, rather slender long and short cells randomly alternating, 22–70 μm (39 μm) long, 9–22 μm (14 μm) wide, oblique or horizontal anticlines; trichome bases as described above.

Abaxial cuticle: thinner than adaxial one, non-modified epidermal cells 8–43 μm (24 μm) in diameter, anticlines straight or undulate, undulation U-shaped, wave length 16–38 μm (24 μm), amplitude 5–11 μm (7 μm); stomatal complexes brachypara- to incompletely paracytic; stomata slender oval, 21–31 μm (27 μm) long, 17–27 μm (21 μm) wide; stomatal aperture oval, 11–19 μm (15 μm) long, outer stomatal ledges smooth and slightly thickened; stomatal frequency 21; trichome bases scattered as on the adaxial cuticle, both complex and simple ones, simple ones sometimes with a basal trichome body remnant still adhering.

Remarks: At a first glance this foliage may be mistaken for a laurel species. The stomatal complexes are paracytic, as in the Lauraceae. Distinctive features are the more asymmetrical leaf shape, the presence of freely ending ultimate veinlets, the pilosity, the trichome types and the absence of oil cells in the mesophyll. The multicellular trichome bases may be correlated to the stellate trichomes, while the simple bases probably derive from the simple filiform ones.

Celastraceae

Maytenus canariensis Kunkel & Sunding
(Figs. 28–33)

Material: STU 5336, 862 (5 herbarium sheets, cuticles from 2 sheets).

Leaf attachment opposite, leaf organization simple, petiole 0.5–1.0 cm (0.8 cm) long, base slightly swollen, marginal petiolar attachment, laminar size microphyll – 2 : 1, length 4.5–10.0 cm (6.4 cm), width 2.4–4.4 cm (3.2 cm), laminar shape elliptic, symmetrical, base and apex angle both acute, base shape concavo-convex, apex shape convex; margin serrate to crenate, 3–4 teeth per centimetre, rather regularly spaced; tooth shape: basal side retroflexed, apical side concave, sinus rounded, apex non-specific glandular, a veinlet ending directly in the tooth apex.

Venation: primary vein pinnate; secondaries curved, festooned semicraspedodromous, curved and slightly wavy, secondary vein spacing 0.4–1.9 cm, decreasing towards the base, secondary vein angle relatively uniform, inter-secondaries weakly developed; tertiaries opposite to alternate percurrent, tertiary vein course sinuous, tertiary vein angle to primary vein almost perpendicular, tertiary vein angle decreasing exmedially; fourth-order veins regular polygonal reticulate, areolation poorly developed (4- to > 7-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets twice or more times branched, ultimate marginal venation consisting of incomplete loops.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells mostly penta- to hexagonal, 16–42 μm (27 μm) in diameter, anticlines straight to very slightly curved or undulate. Marginal cells with the same characteristics as mentioned above but slightly smaller, 6–26 μm (13 μm) long.

Abaxial cuticle: thick, glabrous, non-modified epidermal cells 12–43 μm (23 μm) in diameter, anticlines straight, sometimes slightly wavy; stomatal complexes anisocytic, anomotetracytic to cyclocytic, subsidiary cells almost identical to normal epidermal cells; stomata oval, 21–27 μm (25 μm) long, 18–27 μm (22 μm) wide; stomatal aperture short, slender oval, 9–15 μm (11 μm) long, poles thickened; stomatal frequency 12–19 (15).

Remarks: The foliage resembles to some degree that of *Visnea mocanera*. It may be distinguished by the rather regular spacing of the secondaries, the regular meshes of the tertiary veins, and by the smaller stomata.

Ericaceae

Arbutus canariensis Veill.
(Figs. 34–40)

Material: Herbarium EDER nos. 28, 29 (10 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate, leaf organization simple, petiole 1.2–2.0 cm (1.6 cm) long, covered by (long) glandular trichomes, (stalk variable in length, head rounded) extending into the basal part of the lamina mainly along the midvein and the leaf margin, marginal petiolar attachment, leaf size notophyll – 3 : 1, length 9.4–17.0 cm (13.4 cm), width 2.5–6.0 cm (4.3 cm), elliptic to obovate, symmetrical, base and apex angle both acute, base shape straight to cuneate, apex shape convex; margin crenate to serrate, teeth variable in size and shape, densely spaced, basal side convex or straight, apical side concave, straight or retroflexed, sinus almost angular or rounded, apex rounded to acute, partly non-glandular, partly non-specific glandular.

Venation: primary vein pinnate; secondaries semicraspedodromous, straight to moderately curved, secondary vein spacing dense, 0.3–0.6 cm, course not evenly parallel among each other, secondary vein angle relatively uniform, inter-secondaries occasionally developed; tertiaries alternate percurrent, tertiary vein course sinuous, tertiary vein angle to primary vein obtuse, tertiary vein angle decreasing exmedially; fourth-order veins reticulate to opposite percurrent, areolation moderately developed (5-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets unbranched to twice branched, ultimate marginal venation consisting of incomplete loops, veinlets running towards the teeth either ending in the sinus or the apex or sometimes touching first the sinus and ending finally in the apex.

Adaxial cuticle: moderately thick, non-modified epidermal cells almost isodiametric, 12–34 μm (23 μm) in diameter, polygonal, anticlines straight, cuticle striation developed above veins and often short epicuticular foldings on single cells. Rarely, simple, roundish, thick-walled trichome bases present, diameter 16–30 μm (23 μm), two- to three- (to four-?)celled trichome bases scattered, trichome bodies absent. Marginal cells elongated, long and short cells randomly alternating, 13–39 μm (24 μm) long, 7–13 μm (9 μm) wide, anticlines straight, end anticlines square to oblique.

Abaxial cuticle: thinner than adaxial one, glabrous, non-modified epidermal cells elongated to polygonal, 10–

35 μm (21 μm) in diameter, anticlines straight to rounded; epicuticular striation sometimes developed over veins and in intercostal areas, running concentrically upon guard cells; stomatal complexes cyclocytic with a ring of 6–8 elongated and slender subsidiary cells similar to non-modified epidermal cells but more intensively staining; stomata roundish to oval, 24–39 μm (31 μm) long, 17–32 μm (24 μm) wide; stomatal aperture oval to spindle-shaped, 13–21 μm (17 μm) long, outer stomatal ledges slightly thickened; stomatal frequency 11–20 (15), stomata clustered in distinct groups; giant amphicyclocytic stomatal complexes present, two observed 47 × 26 μm and 25 × 20 μm, surrounded by radially oriented striation.

Remarks: The gross morphology of this foliage is fairly characteristic due to the densely spaced secondaries and the uniform, dense, partly glandular crenation/serration. In addition, the characteristic cyclocytic stomatal complexes with intensively staining subsidiaries and the striation are valuable diagnostic features. The scattered multi-celled trichome bases on the adaxial cuticle probably stem from glanduliferous trichomes that are developed mainly on the petiole but extend somewhat into the lamina and which are visible on the blade using a hand lens.

E u p h o r b i a c e a e
Euphorbia mellifera Ait.
(Figs. 41–45)

Material: STU 7179, 15070 (5 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate, leaves concentrated at the end of the branch, leaf organization simple, petiole 0.3–1.8 cm (0.9 cm) long, marginal petiolar attachment, laminar size microphyll – 5–6 : 1, length 5.4–16.6 cm (12.2 cm), width 1.1–2.8 cm (2.0 cm), shape slender oblong, symmetrical, base and apex angle both acute, base shape straight to decurrent, apex shape straight to slightly convex, leaf blade merges into the petiole, margin entire.

Venation: primary vein pinnate; secondaries already very thin and poorly visible, straight to slightly curved, weakly brochidodromous, secondary vein spacing increasing towards the base, 0.3–0.4 cm, secondary veins arising almost perpendicular, inter-secondaries occasionally developed; tertiaries dichotomizing, tertiary vein course admedially ramified, tertiary vein angle to primary vein acute, tertiary vein angle uniform, areolation rare to poorly developed (many-sided); fourth-order veins dichotomizing; fifth-order veins not developed; freely ending ultimate veinlets twice or more times branched, ultimate marginal venation consisting of incomplete loops.

Adaxial cuticle: delicate, glabrous, non-modified epidermal cells polygonal, 17–46 μm (28 μm) in diameter, anticlines straight to very slightly zig-zag undulate, wave length 13–22 μm (18 μm), amplitude 2–5 μm (4 μm). Hypodermis well developed.

Abaxial cuticle: delicate, glabrous, non-modified epidermal cells penta- to hexagonal, 15–35 μm (25 μm) in diameter, anticlines undulate (U-shaped), wave length 9–15 μm (13 μm), amplitude 2–4 μm (3 μm); stomatal complexes brachypara-, para- or anisocytic, subsidiary cells less intensively staining than non-modified epidermal cells; stomata oval, 17–23 μm (20 μm) long, 20–25 μm (23 μm) wide; stomatal aperture slender spindle-shaped, 11–12 μm (12 μm) long, outer stomatal ledges bordering the apertures distinct; stomatal frequency 13.

Remarks: Remarkable are the indistinct secondary veins arising almost perpendicular to the midvein. The tertiaries are already dichotomizing, as are the fourth-order veins, but fifth-order veins are not developed.

H y p e r i c a c e a e
Hypericum canariense L.
(Figs. 46–51)

Material: Herbarium EDER no. 21 (5 herbarium sheets, cuticle from one sheet).

Leaf attachment opposite, leaf organization simple, petiole very short to almost sessile, base swollen, marginal petiolar attachment, laminar size nanophyll – 3 : 1, length 4.4–6.5 cm (5.4 cm), width 0.8–1.5 cm (1.0 cm), elliptic, symmetrical, base and apex angle both acute, base shape cuneate, apex shape straight, margin entire and occasionally revolute; mesophyllous resinuous globuli abundant, resolving during the preparation of the cleared leaf.

Venation: primary vein pinnate; secondaries curved, festooned brochidodromous, running in variable courses across the lamina, secondary vein spacing irregular, 0.3–0.6 cm, secondary vein angle smoothly decreasing towards the base, inter-secondaries occasionally developed; tertiaries already weakly developed, mixed opposite/alternate percurrent, tertiary vein course almost straight, tertiary vein angle to primary vein obtuse to perpendicular, tertiary vein angle inconsistent, poorly developed; fourth-order veins dichotomizing; fifth-order veins not developed, areolation poorly developed; freely ending ultimate veinlets twice or more times branched, ultimate marginal venation consisting of incomplete loops.

Adaxial cuticle: delicate, glabrous, non-modified epidermal cells rather isodiametric, quadrangular to hexagonal, 12–25 μm (18 μm) in diameter, anticlines thick and straight. Marginal cuticle thicker than adaxial cuticle,

marginal cells slightly elongated, end anticlines square to rounded, 19–46 µm (28 µm) long, 8–16 µm (11 µm) wide.

Abaxial cuticle: delicate, glabrous, non-modified epidermal cells polygonal, 11–28 µm (18 µm) in diameter, anticlines slender and straight; stomatal complexes paracytic, but sometimes instead of one lateral cell two may be developed; stomata slender elliptic, 11–20 µm (16 µm) long, 7–12 µm (10 µm) wide, partly overlapped by neighbouring cells, epidermal wall of guard cells mostly not visible; stomatal aperture slender oval, 5–11 µm (9 µm) long; stomatal frequency 21.

Remarks: *H. canariensis* is distinguishable from other entire-margined species of the Canarian laurel forests by its nanophyll laminar size (length/width ratio 3 : 1). Although very distinct in leaf gross morphology, *Hypericum canariense* and *H. grandifolium* are similar in their cuticular structure regarding the rather small paracytic stomatal complexes.

Hypericum grandifolium Choisy
(Figs. 52–57)

Material: Herbarium EDER nos. 6, 35 (5 herbarium sheets, cuticles from 2 sheets).

Leaf attachment opposite, leaf organization simple, petiole very short to almost sessile, marginal petiolar attachment, laminar size microphyll – 1.5 : 1, length 3.2–6.3 cm (4.5 cm), width 1.8–3.8 cm (2.6 cm), ovate, symmetrical, base angle obtuse, apex angle acute, base shape rounded, apex shape convex, margin entire.

Venation: primary vein pinnate; secondaries thick, brochidodromous, running in wide and smooth curves across the lamina, secondary vein spacing decreasing towards the base, 0.8–1.4 cm, inter-secondaries hardly developed; tertiaries mixed opposite/alternate percurrent, tertiary vein course straight, convex to slightly sinuous, tertiary vein angle to primary vein slightly acute to almost perpendicular, tertiary vein angle rather inconsistent; fourth-order veins regular polygonal reticulate; fifth-order veins forming polygons or dichotomizing, areolation well developed; freely ending ultimate veinlets unbranched to once branched, ultimate marginal venation consisting of loops.

Adaxial cuticle: delicate, glabrous, non-modified epidermal cells quadrangular to polygonal, 11–41 µm (22 µm) in diameter, anticlines straight. Marginal cells slightly elongated, linear, end anticlines square to oblique, 35–189 µm (87 µm) long, 10–25 µm (17 µm) wide.

Abaxial cuticle: delicate, glabrous, non-modified epidermal cells dome-shaped, rather variable in diameter, 17–38 µm (22 µm), anticlines straight to rounded; stomatal complexes anomocytic; stomata oval to spindle-shaped, partially overlapped by non-modified epidermal cells, 8–26 µm (16 µm) long, 4–18 µm (11 µm) wide; stomatal aperture narrow, 9–19 µm (14 µm) long; stomatal frequency 13.

Remarks: Isolated leaves of *H. grandifolium* may be mistaken for laurel foliage. However, these leaves are almost sessile, and their shape is distinctly ovate with a rounded base. Contrary to Lauraceae, they show unbranched or once branched freely ending ultimate veinlets and no oil cells in the mesophyll. The stomatal complex type is paracytic as in the Lauraceae, but the stomata are smaller than in the laurel family.

L a u r a c e a e
Apollonias barbujana (Cav.) Born.
(Figs. 58–63)

Material: Herbarium EDER nos. 5, 17, 45 (13 herbarium sheets, cuticles from 3 sheets).

Leaf attachment alternate to almost opposite, leaf organization simple, petiole 0.6–2.6 cm (1.2 cm) long, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 7.8–16.0 cm (10.5 cm), width 2.8–6.8 cm (4.1 cm), elliptic to slightly obovate, symmetrical, base and apex angle both acute, base shape cuneate, apex shape acuminate, margin entire to finely erose; mesophyllous resinuous bodies present but small and indistinct, discernible vaguely only in the cleared leaf; leaf blade may show bulges caused by mites.

Venation: primary vein pinnate; secondaries curved, festooned brochidodromous, secondary vein spacing rather regular, 0.7–1.1 cm, one pair of acute basal secondaries, inter-secondaries developed; tertiaries almost regular polygonal reticulate to alternate percurrent, tertiary vein course straight, convex or sinuous, tertiary vein angle inconsistent; fourth-order veins regular polygonal reticulate, forming the areoles; no fifth-order veins developed; freely ending ultimate veinlets absent, ultimate marginal venation a fimbrial vein.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells 12–34 µm (19 µm) in diameter, tri- to pentagonal, anticlines sometimes undulate (U-shaped), partly knobbed or thickened and sometimes with double contour, wave length of undulation 14–27 µm (20 µm), amplitude 3–9 µm (5 µm). Marginal cells slender elongated with oblique end anticlines, 85–209 µm (138 µm) long, 10–31 µm (19 µm) wide.

Abaxial cuticle: medium thick to thick, glabrous, non-modified epidermal cells 9–40 µm (19 µm) in diameter, penta- to hexagonal, anticlines partly knobbed or thickened and sometimes with double contour but more weakly

developed than adaxially, anticlines rather straight, sometimes weakly U-shaped undulate, wave length 12–29 μm (19 μm), amplitude 3–8 μm (5 μm); stomatal complexes paracytic, subsidiary cells staining exactly as the non-modified epidermal cells, shape triangular to square, partly overlapping the guard cells; stomata 15–27 μm (22 μm) long, 9–25 μm (16 μm) wide; stomatal aperture slit-like, deeply staining, 6–11 μm (8 μm) long; stomatal frequency 15. Epidermal secretory cells developed above veins recognizable by their very thin cuticle.

Remarks: Among entire-margined coriaceous foliage, that of Lauraceae is distinctive by either the absence or poor development of ultimate veinlets in the areoles. In *A. barbujana* the tertiaries form a fine and rather regular polygonal network, contrary to *Laurus azorica* and *Ocotea foetens*. Regarding the cuticular structures, the Canarian laurel species are well distinguishable from each other. Though paracytic, the stomatal complexes are of quite different shape in all four species. For *A. barbujana* the occasional presence of epidermal secretory cells on the abaxial cuticle and anticlines with double contour are noteworthy.

Laurus azorica (Seub.) Franco
(Figs. 64–69)

Material: Herbarium EDER nos. 4, 11, 38, 55 (16 herbarium sheets, cuticles from 4 sheets).

Leaf attachment alternate, leaf organization simple, petiole 0.5–2.5 cm (1.5 cm) long, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 7–16 cm (10.7 cm), width 2.4–8.2 cm (4.4 cm), elliptic, symmetrical, base and apex angle both acute, base shape convex to complex, apex shape convex to rounded, margin entire, mesophyllous secretory bodies well developed.

Venation: primary vein pinnate, pilose, abaxially axillary glanduliferous domatia developed mainly along the primary vein but also occasionally in axils of higher order veins; secondaries curved, weakly brochidodromous, secondary vein spacing irregular, 0.6–1.2 cm, two pairs of short acute basal secondaries, inter-secondaries occasionally developed; tertiaries mixed opposite/alternate percurrent, tertiary vein course sinuous, tertiary vein angle to primary vein obtuse, tertiary vein angle increasing basally; fourth-order veins regular polygonal reticulate; fifth-order veins regular polygonal reticulate, areolation well developed (mostly 4- to 5-sided); freely ending ultimate veinlets absent to unbranched, ultimate marginal venation a fimbrial vein.

Adaxial cuticle: thick, non-modified epidermal cells 19–61 μm (35 μm) in diameter, anticlines strongly Ω-shaped undulate, wave length 14–33 μm (21 μm), ampli-

tude 6–15 μm (10 μm); simple trichome bases present, often situated upon veins, trichome pore round to slightly elongated, cells surrounding the pore thicker and more deeply staining than non-modified epidermal cells. Marginal cells elongated with oblique end anticlines, becoming undulate in transition to ad- and abaxial cuticle, 15–58 μm (39 μm) long, 10–20 μm (16 μm) wide.

Abaxial cuticle: thick, non-modified epidermal cells 10–66 μm (34 μm) in diameter, anticlines strongly undulate, undulation Ω-shaped, wave length 5–15 μm (9 μm), thus smaller than adaxially, amplitude 4–12 μm (7 μm); trichome bases with the same characteristics as described above; stomatal complexes paracytic, mostly rhomboidal, 23–40 μm (32 μm) long, 19–47 μm (28 μm) wide; subsidiary cells less intensively staining than non-modified epidermal cells; stomatal aperture a slender slit, 14–25 μm (18 μm) long, poles often indented and sometimes marked by a T-piece of thickened cutin; stomatal frequency 28.

Remarks: In *L. azorica* two basal pairs of slender, steeply ascending secondaries are noteworthy, as is the presence of axillary glanduliferous domatia on the lower leaf surface. During the clearing process the trichomes become detached and only axillary depressions remain visible. Among the Lauraceae of the Canary Islands, FERGUSON (1974) mentions the existence of hairs on young leaves. They have entirely disappeared by the time the leaf is mature, leaving behind trichome bases that mark their point of leaf attachment.

Ocotea foetens (Ait.) Baill.
(Figs. 70–75)

Material: Herbarium EDER no. 47 (13 herbarium sheets, cuticle from one sheet).

Leaf attachment alternate, leaf organization simple, petiole 0.9–2.0 cm (1.3 cm) long, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 8.3–13.5 cm (11.1 cm), width 3.3–6.4 cm (4.8 cm), oblong to elliptic, symmetrical, base and apex angle both acute, base shape straight to slightly convex, apex shape convex to acuminate, margin entire, mesophyllous resinuous bodies present.

Venation: primary vein pinnate; secondaries curved, festooned brochidodromous, secondary vein spacing rather regular, 1.1–2.0 cm, secondary vein angle relatively uniform, 2–3 distinct domatia in the axils of the lower secondaries, each covering an axillary gland, inter-secondaries present; tertiaries regular polygonal reticulate, tertiary vein course straight to curved; fourth-order veins regular polygonal reticulate; fifth-order veins regular polygonal reticulate or dichotomizing, areolation well developed (4- to 5-sided); freely ending ultimate veinlets

absent to once branched, ultimate marginal venation formed by loops.

Adaxial cuticle: thick, non-modified epidermal cells polygonal, diameter 12–23 µm (18 µm), anticlines clear cut and straight; simple roundish pores (?trichome bases, Fig. 75) rarely present, diameter about 13 µm. Marginal cells elongated, distinctly linear with horizontal anticlines, 12–34 µm (25 µm) long, 8–15 µm (12 µm) wide.

Abaxial cuticle: medium thick, non-modified epidermal cells centrally thickened, elongated, diameter 7–38 µm (21 µm), anticlines straight, rounded or weakly undulate, undulation U-shaped, wave length 10–20 µm (15 µm), amplitude 3–7 µm (5 µm); stomatal complexes paracytic, appearing broadly oval to almost square, 19–28 µm (23 µm) long, 17–28 µm (22 µm) wide; stomatal aperture short, narrow and spindle-shaped, 10–14 µm (12 µm) long, bordered by extremely thickened cuticular ledges; stomatal frequency 14; giant stomata present (one observed, 34 × 33 µm); sometimes trichome bases present as described above.

Remarks: For this Lauraceae, big domatia in the basal part of the lamina are distinctive. The tertiaries are regular polygonal reticulate, whereas they are percurrent in *Laurus azorica* and *Persea indica* and alternate percurrent to random reticulate in *Apollonias barbujana.*

Persea indica (L.) Spreng
(Figs. 76–82)

Material: Herbarium EDER nos. 15, 16, 44 (13 herbarium sheets, 3 cuticles).

Leaf attachment alternate, leaf organization simple, petiole 1.3–3.3 cm (2.4 cm) long, marginal petiolar attachment, laminar size mesophyll – 3 : 1, length 9.5–20.2 cm (15.2 cm), width 3.0–7.5 cm (5.2 cm), elliptic to oblong, symmetrical, base occasionally asymmetrical, base and apex angle both acute, base shape concavo-convex to decurrent, apex shape almost straight to slightly convex or acuminate, margin entire and revolute.

Venation: primary vein pinnate; secondaries brochidodromous, smoothly curved, secondary vein spacing rather regular, 0.6–1.2 cm, secondary vein angle almost uniform, inter-secondaries developed; tertiaries mixed opposite/alternate percurrent, tertiary vein course almost straight to sinuous, tertiary vein angle to primary vein obtuse, tertiary vein angle decreasing exmedially; fourth-order veins opposite to alternate percurrent; fifth-order veins regular polygonal reticulate, areolation well developed (4- to 6-sided); freely ending ultimate veinlets absent to unbranched, ultimate marginal venation consisting of loops.

Adaxial cuticle: moderately thick, glabrous, non-modified epidermal cells polygonal, very variable in size,

9–40 µm (19 µm), anticlines distinct and straight. Marginal cells elongated, linear with horizontal to oblique end anticlines, anticlines of adjoining non-modified epidermal cells often thickened; trichomes simple, one-celled, 27–142 µm (60 µm) long.

Abaxial cuticle: thinner than adaxial one, pubescent, non-modified epidermal cells dome-shaped, diameter 7–27 µm (19 µm), anticlines straight to smoothly rounded; stomatal complexes paracytic; stomata oval to rhomboidal, overlapped by surrounding cells, frequently asymmetrical, 13–23 µm (19 µm) long, 12–27 µm (16 µm) wide; stomatal aperture a slender, spindle-shaped slit, 7–15 µm (10 µm) long, often indistinct; stomatal frequency 15; anticlines of adjoining non-modified epidermal cells often thickened, one-celled trichome bases rather densely spaced, intensively staining, shape roundish to oval, diameter 8–17 µm (12 µm), trichome 10–30 µm (20 µm) long, 7–16 µm (11 µm) wide.

Remarks: Among the laurels on the Canary Islands, *P. indica* is the only deciduous one, characterized by an occasionally asymmetrical leaf base, denser and more regular spacing of secondary veins as well as by the very regular pattern of the percurrent tertiaries. Mesophyllous resinous bodies are absent. On the abaxial cuticle the non-modified epidermal cells are dome-shaped, overlapping the stomata. This feature is also known from the fossil *Laurophyllum acutimontanum* Mai. An indumentum of simple and short trichomes is developed especially on the abaxial surface.

M y r i c a c e a e
Myrica faya Ait.
(Figs. 83–88)

Material: Herbarium EDER nos. 14, 22, 36, 37, 51–53, 61 (15 herbarium sheets, cuticles from 8 sheets).

Leaf attachment alternate, leaf organization simple, short petiole 0.2–1.0 cm (0.7 cm), marginal petiolar attachment, laminar size microphyll – 3 : 1, length 4.3–10.4 cm (6.6 cm), width 1.1–3.1 cm (2.1 cm), elliptic, symmetrical, base and apex angle both acute, base shape decurrent, apex shape concave to almost straight, margin crenate, serrate, almost entire to slightly erose, revolute, 2–5 teeth per centimetre, spacing irregular; tooth shape: basal side convex or retroflexed, apical side convex or straight, sinus angular, apex weakly spinose on serrate leaves, teeth often non-specific glandular.

Venation: primary vein pinnate; secondaries festooned brochidodromous, almost straight to moderately curved, secondary vein spacing 0.4–0.8 cm, one pair of acute basal secondaries, inter-secondaries present; tertiaries regular

polygonal reticulate; fourth-order veins regular polygonal reticulate; fifth-order veins dichotomizing or forming polygons, areolation well developed (4- to 5-sided); freely ending ultimate veinlets unbranched to twice branched, ultimate marginal venation consisting of loops; as variable as the leaf margin is the venation of the teeth: veinlets may run into the sinus and the apex, but loops may also enter the teeth and approach the sinus, sometimes from such loops veinlets arise that enter the sinus or the apex.

Adaxial cuticle: medium thick, non-modified epidermal cells polygonal, sometimes nearly isodiametric, diameter 10–33 µm (21 µm), anticlines straight and distinct. Two-celled, well-cutinized, oval to roundish trichome bases present, diameter 12–29 µm (20 µm), peltate, glandular trichomes ca. 60–80 µm in diameter, surrounding epidermal cells less intensively staining than non-modified epidermal cells; marginal cells identical, anticlines slightly more rounded, 11–26 µm (20 µm) wide, trichome bases as mentioned above.

Abaxial cuticle: medium thick, non-modified epidermal cells polygonal, diameter 9–28 µm (18 µm), anticlines straight to curved or wavy; stomatal complexes anomocytic; stomata roundish, 20–34 µm (28 µm) in diameter, guard cells deeply staining; stomatal aperture often formed like the greek Φ; outer stomatal ledges raised and deeply staining; stomatal frequency variable, 6 to 11 (9); two-celled trichome bases slightly bigger than on the adaxial cuticle, 21–33 µm (27 µm) in diameter.

Remarks: Isolated foliage of *M. faya* may be easily identified by the two-celled bases of peltate glandular trichomes characteristic for the whole genus.

Myrsinaceae
Heberdenia excelsa (Ait.) Banks ex DC.
(Figs. 89–94)

Material: STU 7559, 9258 (5 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate, leaf organization simple, short petiole 0.4–1.2 cm (0.7 cm), marginal petiolar attachment, laminar size notophyll – 2 : 1, length 5.9–14.8 cm (9.1 cm), width 2.6–5.2 cm (4.1 cm), elliptic, symmetrical, base and apex angle both acute, base shape almost cuneate, apex shape convex, margin entire but slightly wavy; big roundish to oval mesophyllous resinuous bodies are located in the poorly developed areoles.

Venation: somewhat erratic in appearance, primary vein pinnate; secondaries festooned brochidodromous, slightly recurved near the primary vein, secondaries sometimes forking in very different distances from the primary vein, running somewhat fluttery across the lamina, sec-

ondary vein spacing rather dense, irregular, 0.1–0.5 cm, secondary vein angle slightly increasing towards the base, one pair of very short acute basal secondaries, intersecondaries developed; tertiaries regular polygonal reticulate to mixed opposite/alternate percurrent, tertiary vein course sinuous to straight, tertiary vein angle inconsistent, areolation poorly developed; fourth-order veins dichotomizing; fifth-order veins not developed; freely ending ultimate veinlets unbranched to twice or more times branched, ultimate marginal venation consisting of both complete and incomplete loops.

Adaxial cuticle: medium thick, glabrous, non-modified epidermal cells polygonal, diameter variable, 10–33 µm (19 µm), less strongly cutinized and somewhat bigger (secretory?) cells scattered, anticlines thick, straight to slightly curved; marginal cells with the same attributes.

Abaxial cuticle: medium thick, non-modified epidermal cells polygonal, diameter variable, 13–51 µm (27 µm), anticlines thick, straight to somewhat curved; stomatal complexes mostly anisocytic, rarely anomotetracytic; stomata oval to almost round, 16–28 µm (20 µm) long, 13–23 µm (18 µm) wide; stomatal aperture also oval to almost round, 7–12 µm (9 µm) long, outer stomatal ledges thickened and raised, poles with thickened T-piece; stomatal frequency 21; scattered are peltate trichomes, head multicellular, diameter 22–43 µm (31 µm), cells radially arranged, segment-shaped, trichome bases more or less roundish, relatively small, 20–28 µm (23 µm), one-celled, strongly thickened, surrounded by normal-sized but slightly thickened epidermal cells.

Remarks: Distinctive venation features are the densely spaced, basally recurved and forking secondaries that loop in rather heterogeneous distances from the margin, causing a somewhat irregular venation picture. Already fourth-order veins dichotomize, whereas fifth-order veins are absent and areolation is hardly developed. Small peltate trichomes are also developed in the following species, *Pleiomeris canariensis.*

Pleiomeris canariensis (Willd.) DC.
(Figs. 95–100)

Material: STU 8665, 579 (5 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate, leaf organization simple, petiole short, 0.5–1.4 cm (1.0 cm) long, marginal petiolar attachment, laminar size mesophyll – 3 : 1, length 11.9–24.6 cm (17.7 cm), width 3.9–7.6 cm (6.0 cm), elliptic, symmetrical, base and apex angle both acute, base shape slightly concavo-convex to almost cuneate, apex shape almost straight to convex, margin entire to slightly erose and sometimes revolute.

Venation: primary vein pinnate; secondaries weakly brochidodromous, curved, secondary vein spacing rather dense and more or less regular, 0.5–1.1 cm, secondary vein angle almost uniform, one to two inter-secondaries well developed, one to several intersecondaries between two secondaries; tertiaries regular polygonal reticulate, forming the well developed areolation (mostly 4-sided); fourth-order veins dichotomizing; no fifth-order veins developed; freely ending ultimate veinlets absent to unbranched to twice branched, ultimate marginal venation consisting of loops.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells 20–50 µm (31 µm) in diameter, anticlines undulate (U-shaped), wave length 15–28 µm (21 µm), amplitude 4–9 µm (6 µm). Marginal cells slightly elongated, anticlines straight to rounded, not arranged in distinct rows, 11–39 µm (22 µm) long, 8–26 µm (14 µm) wide.

Abaxial cuticle: thick, non-modified epidermal cells 17–57 µm (32 µm) in diameter, anticlines curved to undulate (U-shaped), wave length 19–31 µm (22 µm), amplitude 4–7 µm (6 µm); stomatal complexes anisocytic to anomotetracytic, subsidiaries hardly distinguishable in staining from non-modified epidermal cells but only about half the size; stomata oval to roundish, 17–23 µm (20 µm) long, 13–24 µm (18 µm) wide, poles indented and marked by a T-piece of cutin; stomatal aperture oval, 5–10 µm (7 µm) long, outer stomatal ledges thickened; stomatal frequency 16; peltate trichomes scattered, diameter 25–39 µm (34 µm), numerous narrow, radially arranged, segment-shaped cells forming the head, trichome bases one-celled, strongly thickened, diameter 11–22 (18 µm).

Remarks: The foliage is bigger than in *H. excelsa*; secondaries and intersecondaries are densely spaced, forming a very regular pattern. The secondaries are not recurved as in *Heberdenia excelsa*. A network of tertiaries is hardly distinctive from higher order venation. Remarkable is the small size of the stomata compared to the size of the non-modified epidermal cells.

O l e a c e a e

Jasminum odoratissimum L.
(Figs. 101–106)

Material: Herbarium EDER no. 27 (7 herbarium sheets, cuticle from one sheet).

Leaf attachment alternate, leaf organization ternate or less frequently odd-pinnate (5 leaflets), petiole winged, 1.8–4.0 cm (2.7 cm) long, marginal petiolar attachment, laminar size microphyll – 1 : 1, 3.6–6.8 cm (5.0 cm) long, 3.0–8.1 cm (5.2 cm) wide, ovate, symmetrical, base angle obtuse, apex angle acute.

Leaflets: petiolule of terminal leaflet 1.0–1.2 cm, of lateral leaflets 0.2 cm, marginal petiolar attachment, leaflet size microphyll – 2 : 1, 2.0–5.2 cm (3.6 cm) long, 0.9–2.8 cm (1.7 cm) wide, leaflets elliptic to somewhat ovate, terminal leaflet symmetrical, lateral leaflets base asymmetrical (apical side shorter), both base and apex angle acute, base shape concavo-convex and convex, apex shape slightly convex to straight, margin entire.

Venation: primary vein pinnate; secondaries (weakly) festooned brochidodromous, straight to slightly curved, the basal pair of secondaries ascending quite close to the leaf margin, secondary vein spacing rather irregular, 0.4–1.4 cm, secondary vein angle decreasing towards the base, inter-secondaries well developed; tertiaries regular polygonal reticulate; fourth-order veins regular polygonal reticulate or dichotomizing, almost identical to the dichotomizing fifth-order veins, areolation moderately developed (4- to 5-sided), freely ending ultimate veinlets unbranched to twice or more times branched, ultimate marginal venation consisting of sometimes complete, sometimes incomplete loops.

Adaxial cuticle: medium thick, non-modified epidermal cells often almost isodiametric, polygonal, 12–33 µm (23 µm) in diameter, centrally thickened, anticlines almost straight; trichome bases scattered in intercostal areas, base thickened, simple and roundish or polygonal, diameter 17–30 µm (20 µm). Marginal cells slightly elongated, anticlines straight to slightly rounded, 11–36 µm (21 µm); trichome bases as described above.

Abaxial cuticle: medium thick, non-modified epidermal cells polygonal, diameter 14–33 µm (21 µm), anticlines straight; stomatal complexes brachyparacytic, but sometimes two lateral subsidiaries instead of one, subsidiaries slightly less staining than non-modified epidermal cells; stomata oval, 23–33 µm (27 µm) long, 18–25 µm (23 µm) wide, sometimes partly overlapped by subsidiary cells; aperture oval, 12–20 µm (16 µm) long, poles marked by thickened I-piece of cutin; stomatal frequency 12; trichome bases as described above.

Remarks: This is the only species with ternate foliage. Isolated lateral leaflets are easily recognizable by their strongly asymmetrical base, terminal leaflets are distinguishable from other entire-margined foliage by the smaller laminar size. Moreover, *J. odoratissmum* differs from Lauraceae foliage by the presence of un- to multi-branched, freely ending ultimate veinlets.

Picconia excelsa (Ait.) DC.
(Figs. 107–116)

Material: Herbarium EDER nos. 23, 24, 40–43 (20 herbarium sheets, cuticles from 6 sheets).
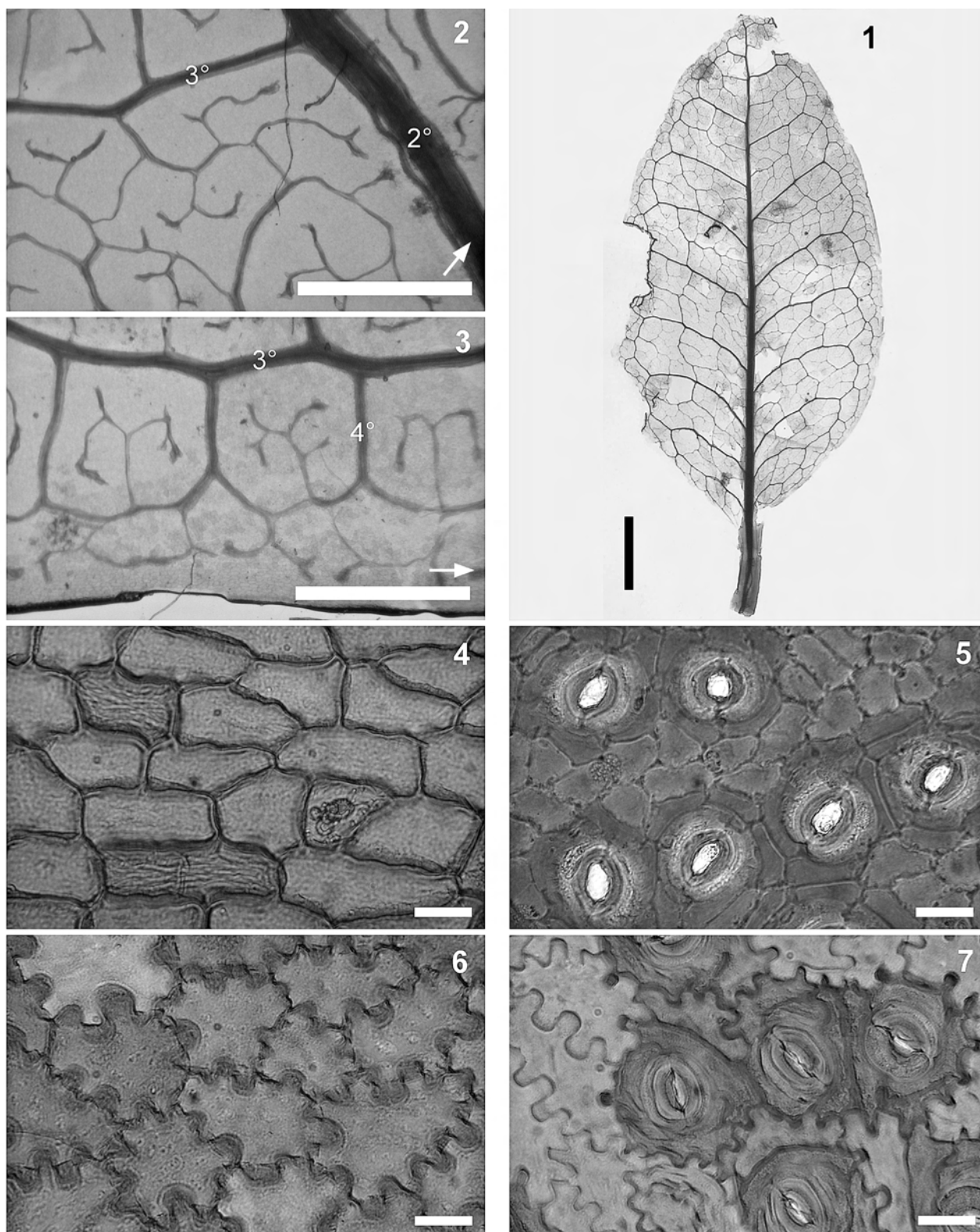
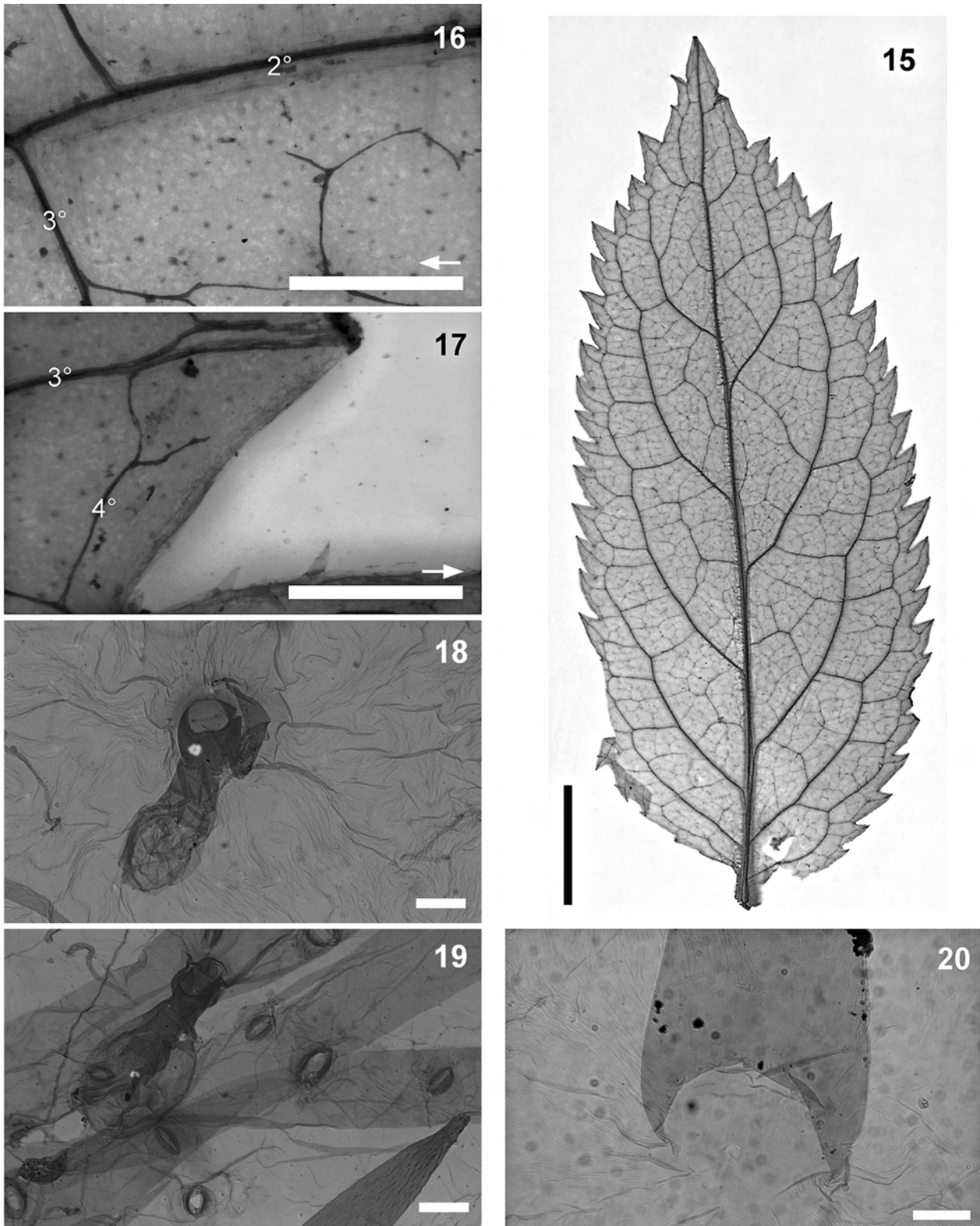**Figs. 1–7.** *Ilex canariensis.* – **1**. Cleared leaf [32]. **2**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [32]. **3**. Ultimate marginal venation, incomplete loops [32]. **4**. Margin [31]. **5**. Abaxial cuticle, straight anticlines [60]. **6**. Adaxial cuticle [65]. **7**. Abaxial cuticle, undulate anticlines [65]. – Scales: 1 cm (1), 1 mm (2–3), 25 µm (4–7).
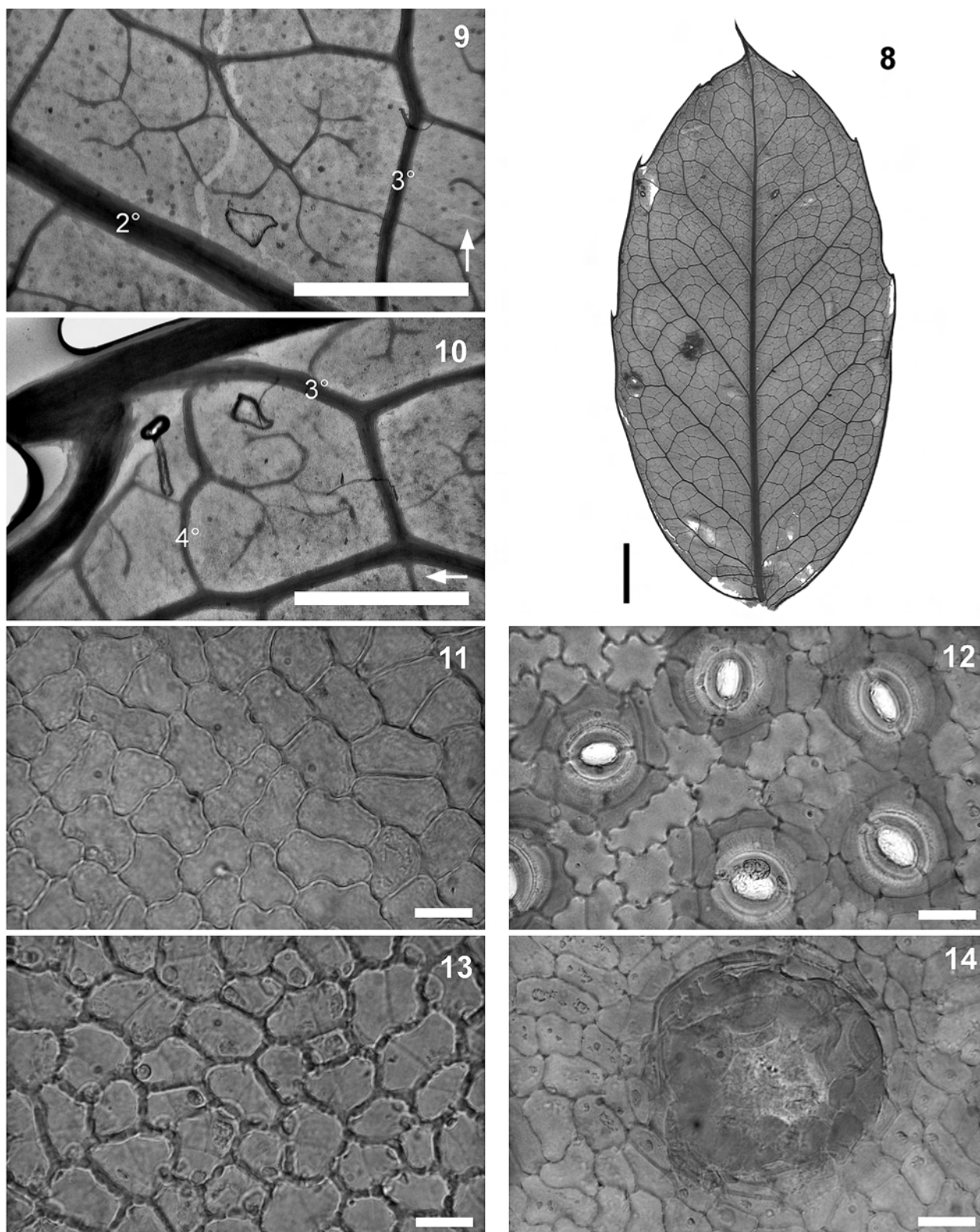
Figs. 8–14. *Ilex platyphylla.* – **8**. Cleared leaf [10]. **9**. Secondary to fifth-order veins [10]. **10**. Ultimate marginal venation, fimbrial vein [10]. **11**. Margin, transition of undulate to straight anticlines [10]. **12**. Abaxial cuticle [10]. **13**. Adaxial cuticle [56]. **14**. Abaxial cuticle, multicellular cork-wart [10]. – Scales: 1 cm (8), 1 mm (9–10), 25 µm (11–14).

Figs. 15–20. *Sambucus nigra* ssp. *palmensis.* – **15**. Cleared leaf [49]. **16**. Secondary to fifth-order veins, freely ending ultimate vein-lets dichotomizing [49]. **17**. Ultimate marginal venation, incomplete loops, tooth [49]. **18**. Adaxial cuticle, glandular trichome, stria-tion [48]. **19**. Abaxial cuticle, stomata, glandular trichome, simple trichomes [48]. **20**. Adaxial cuticle, trichome, trichome base [48]. – Scales: 1 cm (15), 1 mm (16–17), 25 µm (18–20).
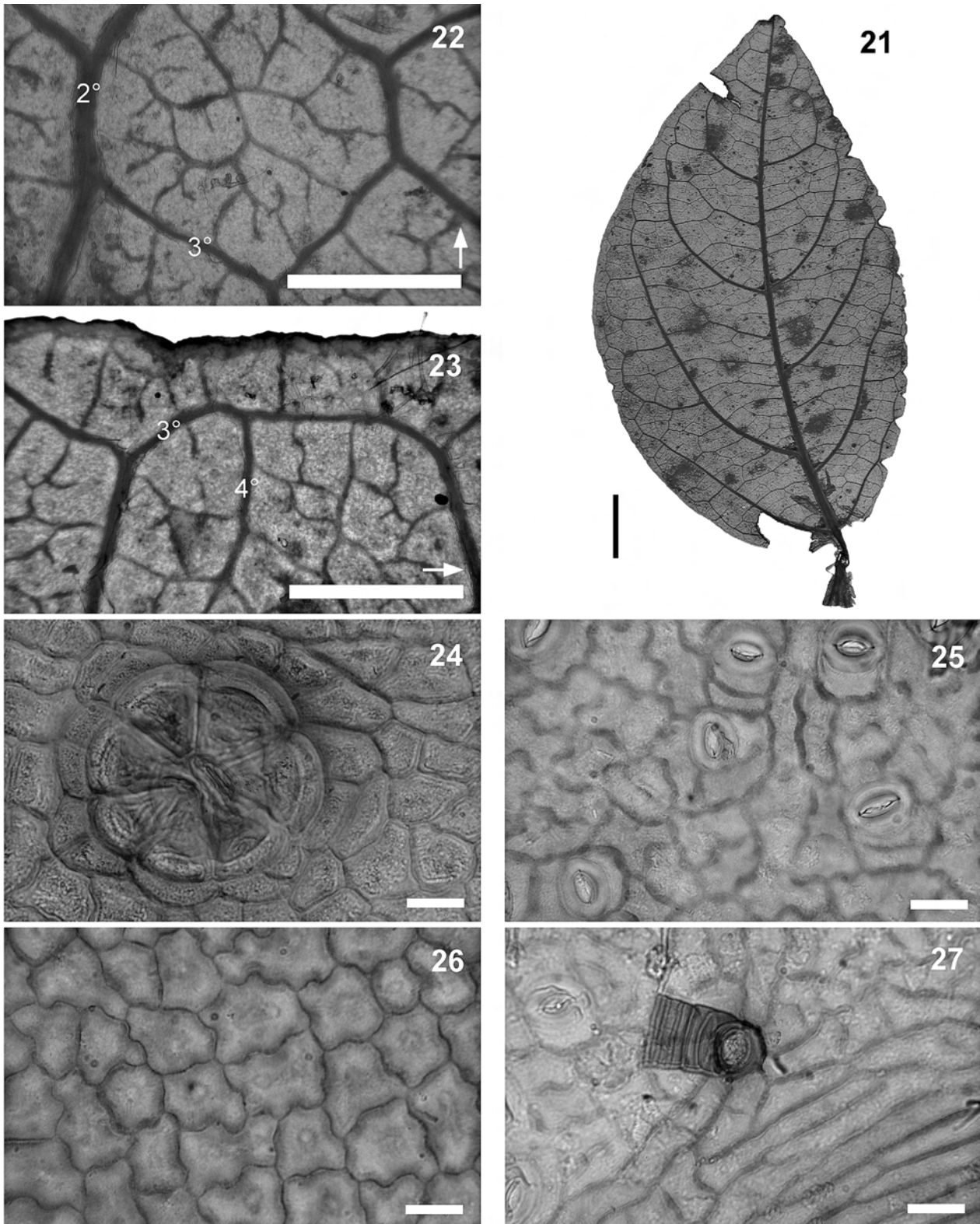
Figs. 21–27. *Viburnum tinus* ssp. *rigidum*. – **21**. Cleared leaf [34]. **22**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [34]. **23**. Ultimate marginal venation, complete loops [34]. **24**. Adaxial cuticle, multicellular trichome base [20]. **25**. Abaxial cuticle [33]. **26**. Adaxial cuticle [34]. **27**. Abaxial cuticle, simple trichome base, part of multicellular trichome [33]. – Scales: 1 cm (21), 1 mm (22–23), 25 µm (24–27).
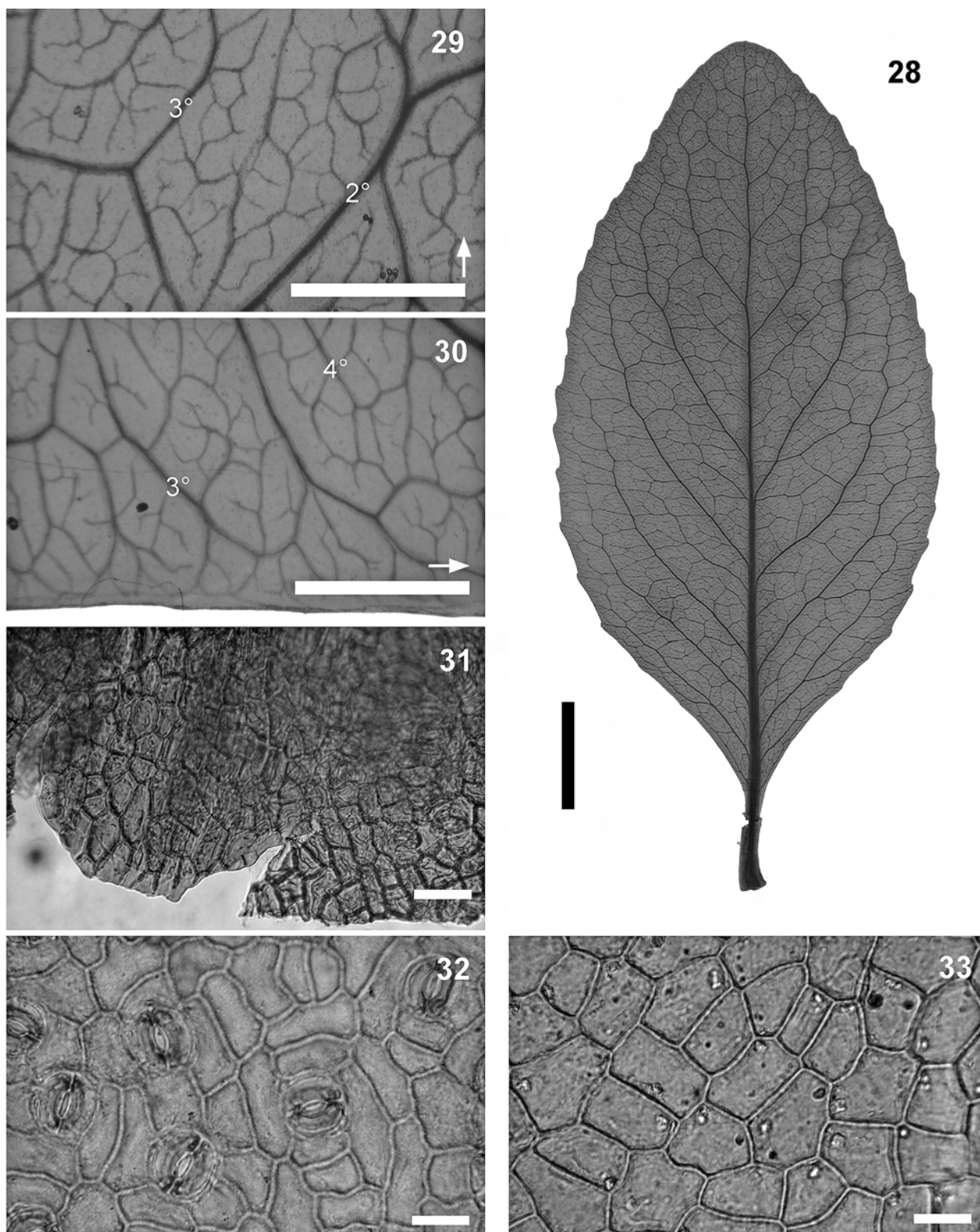
Figs. 28–33. *Maytenus canariensis.* – **28**. Cleared leaf [STU 5336]. **29**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [STU 5336]. **30**. Ultimate marginal venation, incomplete loops [STU 5336]. **31**. Margin [STU 5336]. **32**. Abaxial cuticle [STU 5336]. **33**. Adaxial cuticle [STU 5336]. – Scales: 1 cm (28), 1 mm (29–30), 25 µm (31–33).
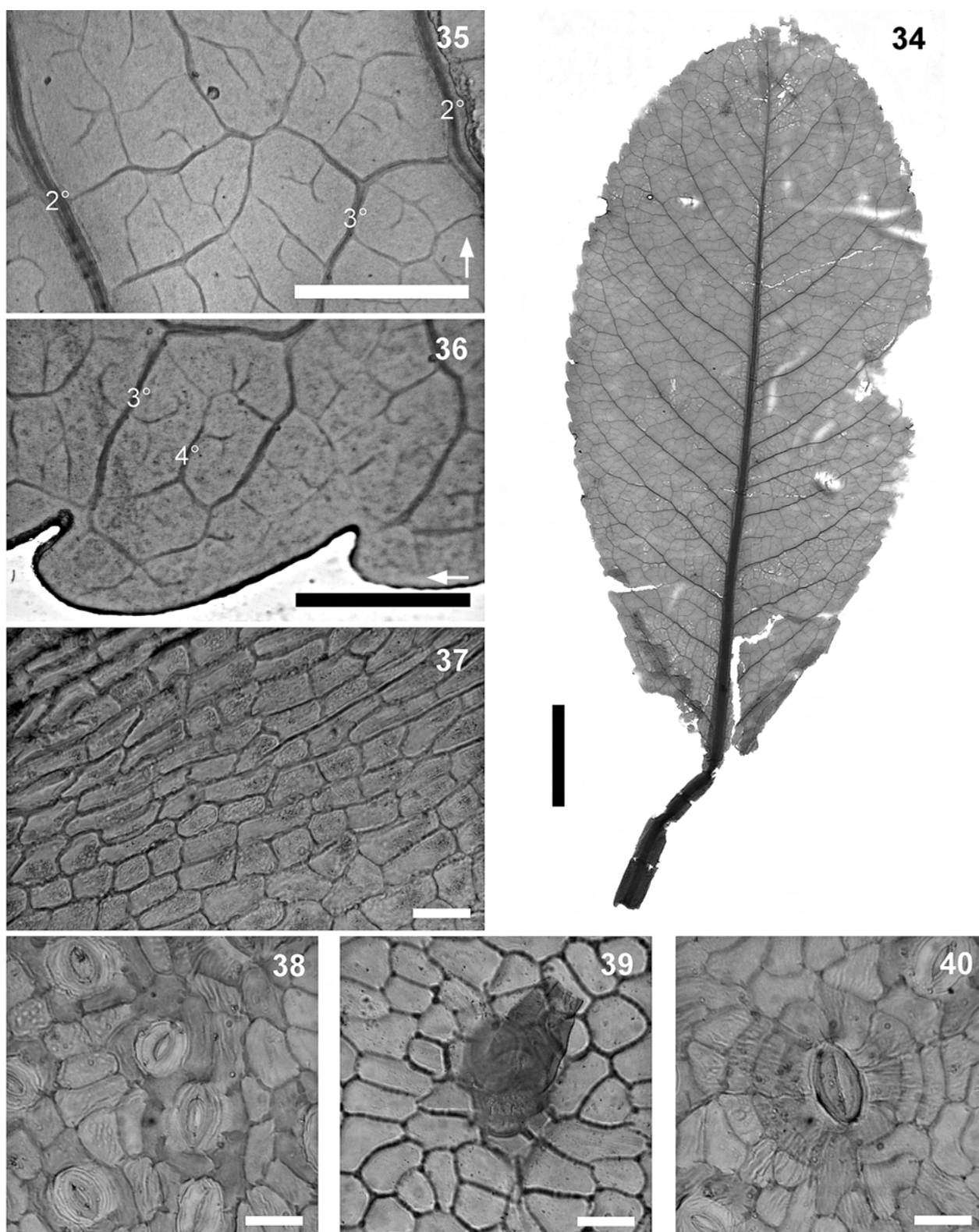
Figs. 34–40. *Arbutus canariensis*. – **34**. Cleared leaf [28]. **35**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [28]. **36**. Ultimate marginal venation, incomplete loops, tooth [28]. **37**. Margin [29]. **38**. Abaxial cuticle [29]. **39**. Adaxial cuticle, trichome, trichome base [29]. **40**. Abaxial cuticle, giant stoma [29]. – Scales: 1 cm (34), 1 mm (35–36), 25 µm (37–40).
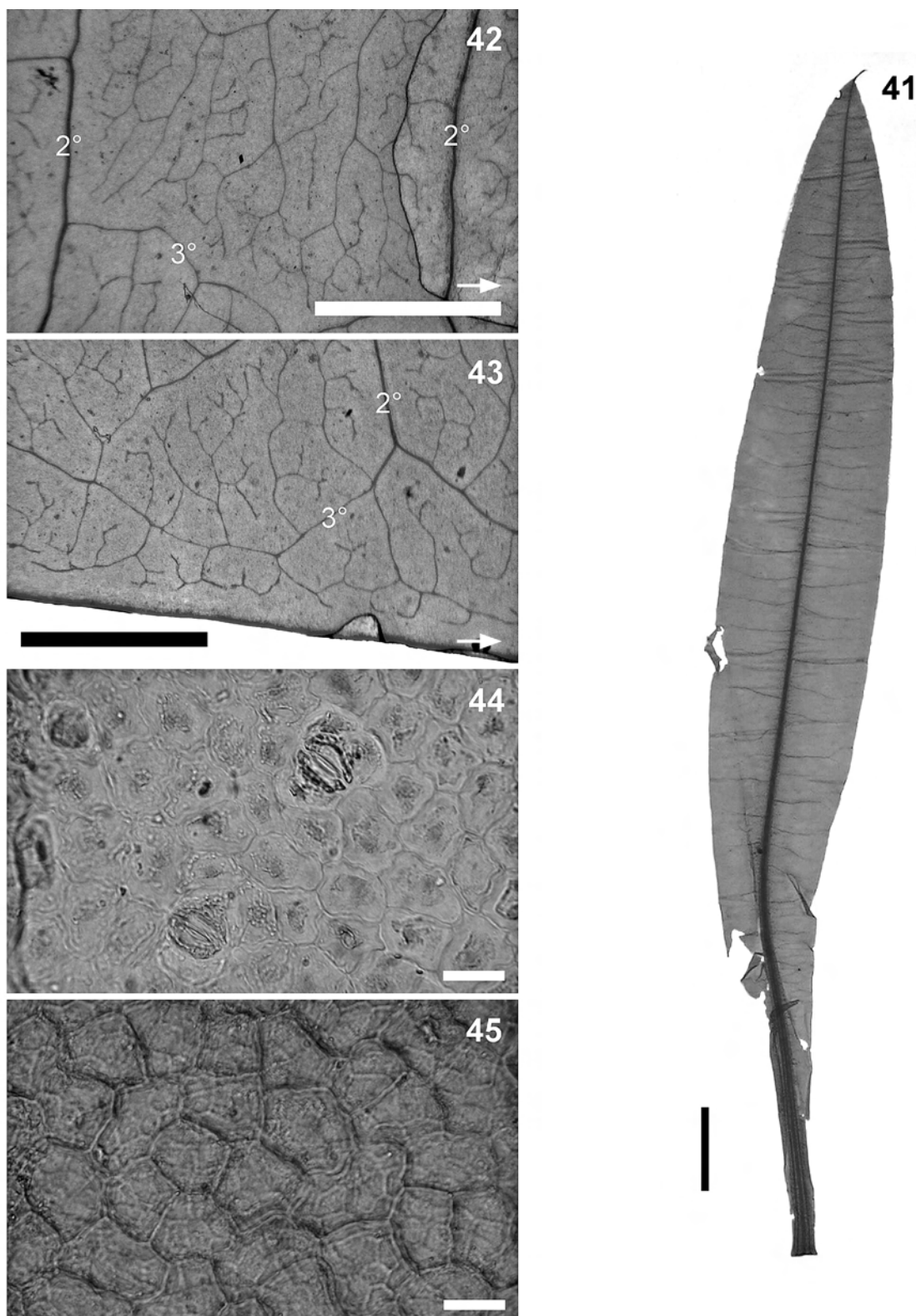
Figs. 41–45. *Euphorbia mellifera*. – **41**. Cleared leaf [STU 7179]. **42**. Secondary to fourth-order veins, freely ending ultimate veinlets dichotomizing [STU 7179]. **43**. Ultimate marginal venation, incomplete loops [STU 7179]. **44**. Abaxial cuticle [STU 15070]. **45**. Adaxial cuticle with hypodermis [STU 15070]. – Scales: 1 cm (41), 1 mm (42–43), 25 µm (44–45).
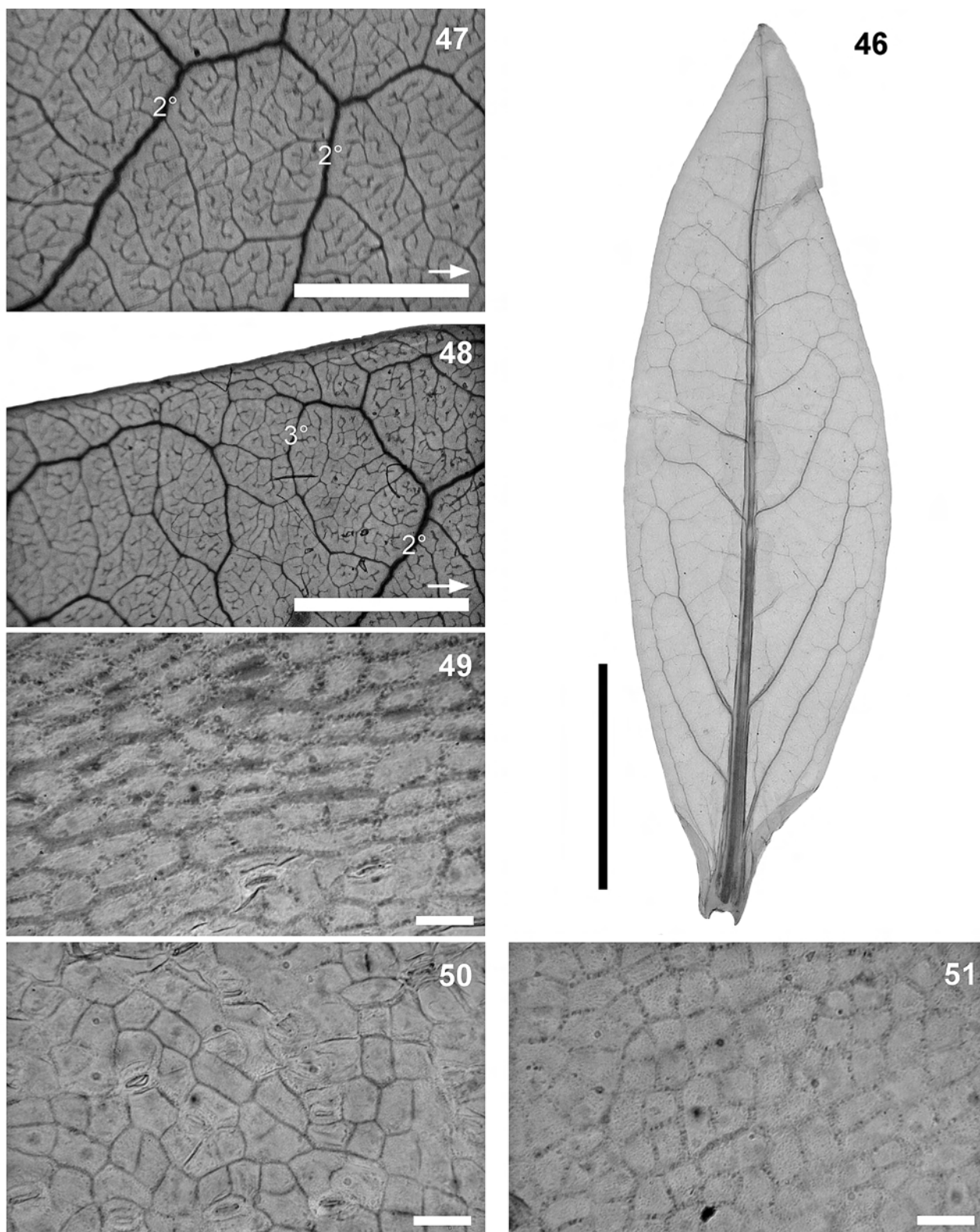
Figs. 46–51. *Hypericum canariense*. – **46**. Cleared leaf [21]. **47**. Secondary to fourth-order veins, freely ending ultimate veinlets dichotomizing [21]. **48**. Ultimate marginal venation, incomplete loops [21]. **49**. Margin [21]. **50**. Abaxial cuticle [21]. **51**. Adaxial cuticle [21]. – Scales: 1 cm (46), 1 mm (47–48), 25 µm (49–51).
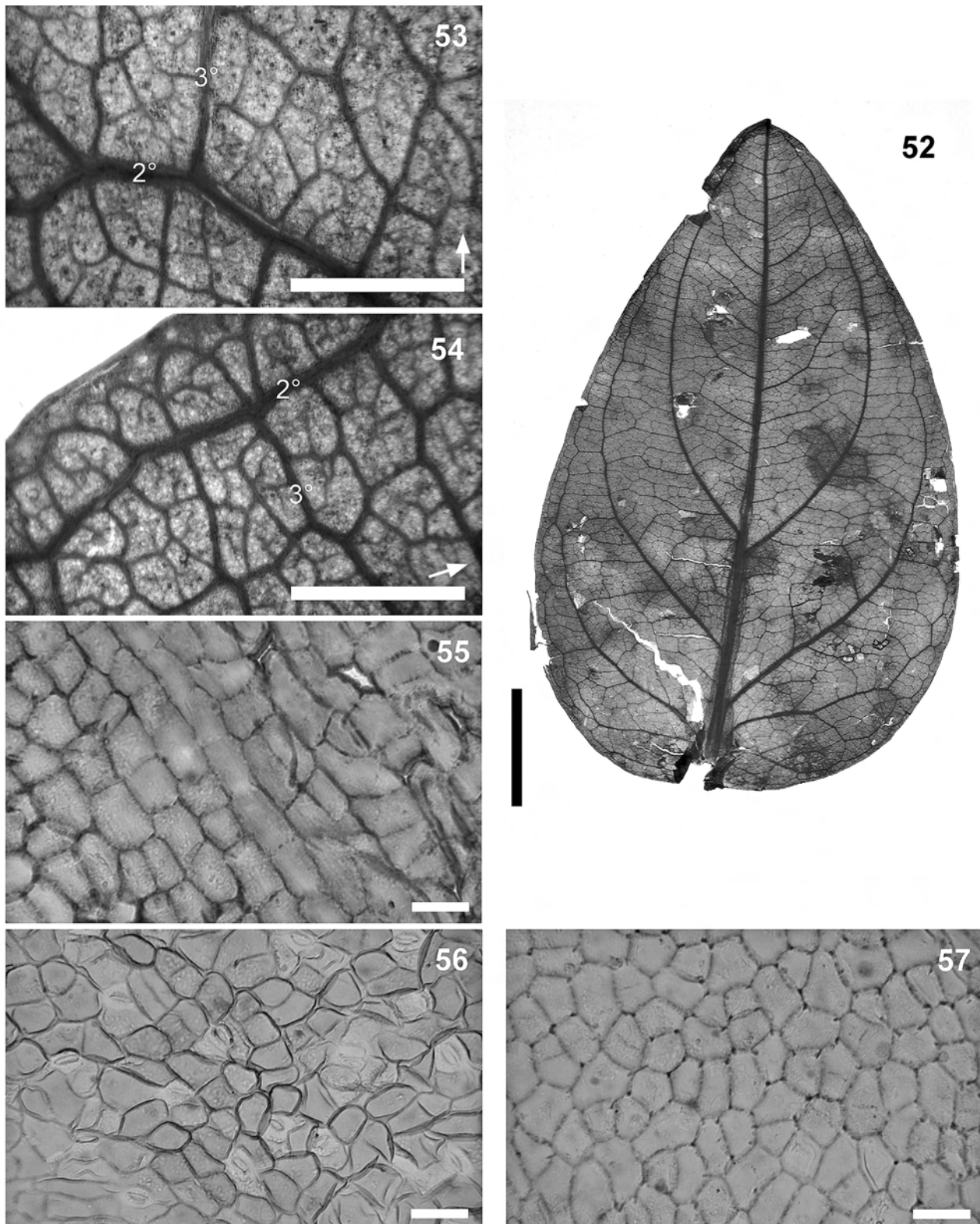
Figs. 52–57. *Hypericum grandifolium*. – **52**. Cleared leaf [6]. **53**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing or forming polygons [6]. **54**. Ultimate marginal venation, complete loops [6]. **55**. Margin [6]. **56**. Abaxial cuticle [6]. **57**. Adaxial cuticle [6]. – Scales: 1 cm (52), 1 mm (53–54), 25 µm (55–57).
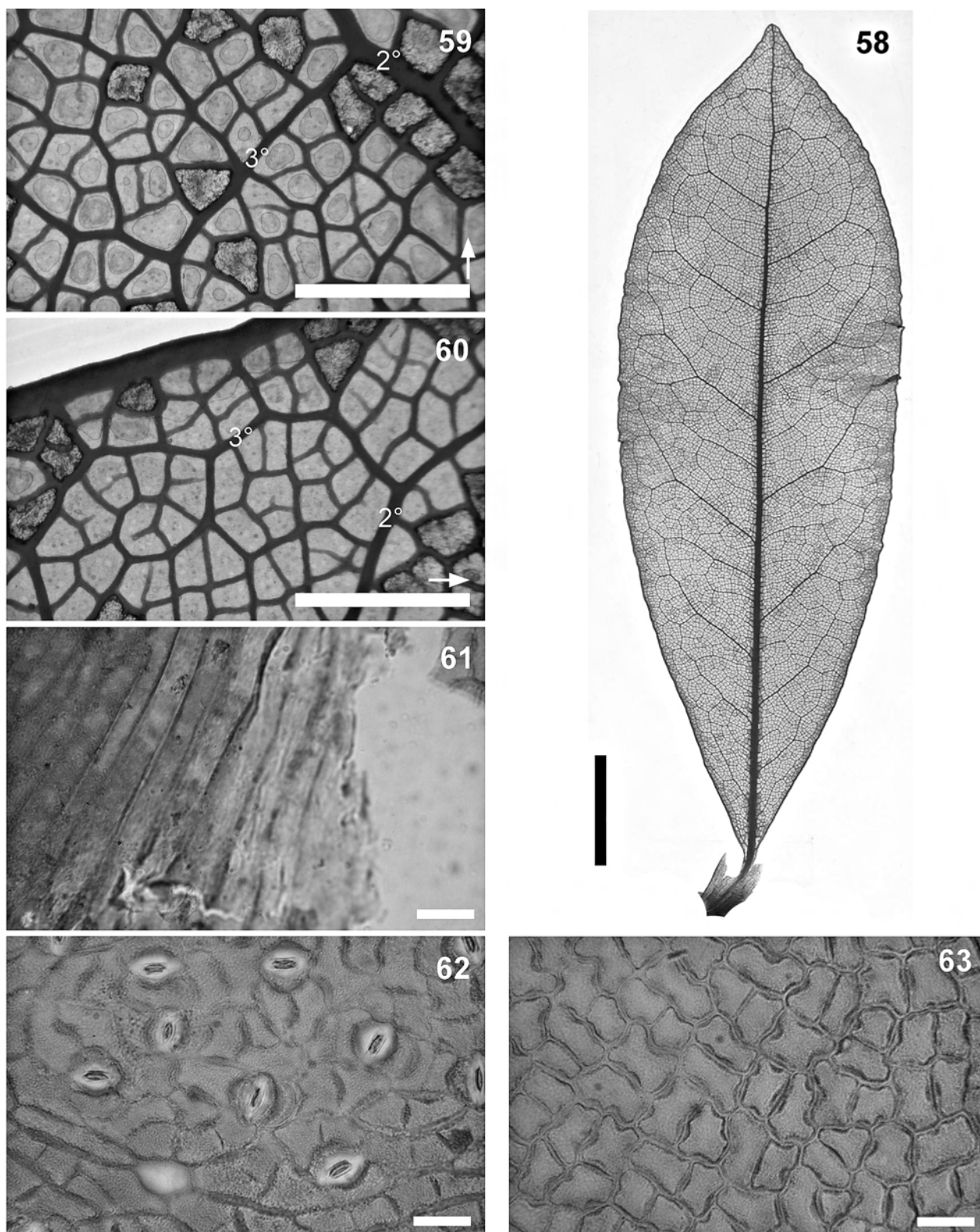
Figs. 58–63. *Apollonias barbujana*. – **58**. Cleared leaf [17]. **59**. Secondary to fourth-order veins, freely ending ultimate veinlets forming polygons [17]. **60**. Ultimate marginal venation, fimbrial vein [17]. **61**. Margin [45]. **62**. Abaxial cuticle, secretory body [5]. **63**. Adaxial cuticle [5]. – Scales: 1 cm (58), 1 mm (59–60), 25 µm (61–63).
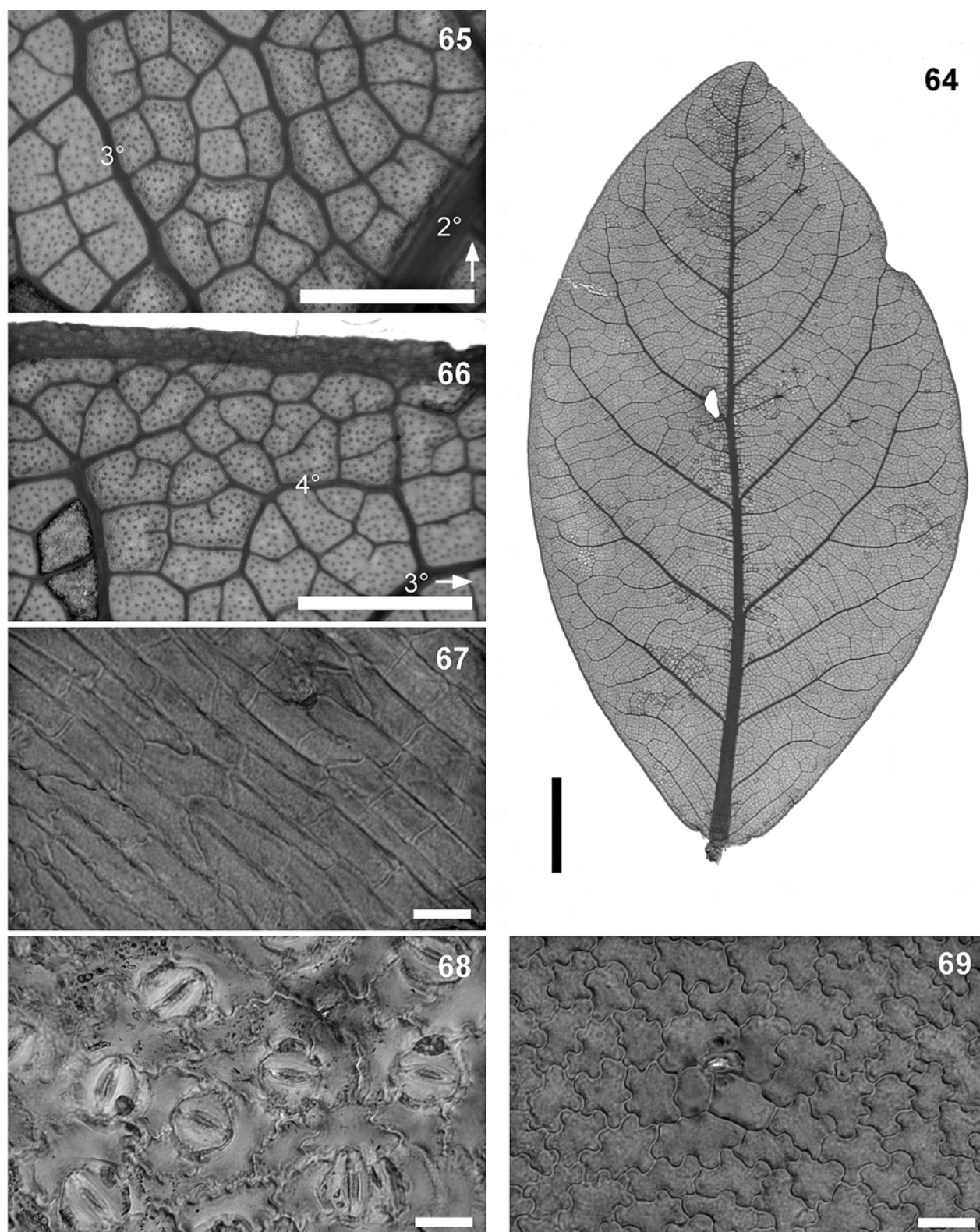
Figs. 64–69. *Laurus azorica.* – **64**. Cleared leaf [38]. **65**. Secondary to fifth-order veins, freely ending ultimate veinlets forming polygons, secretory bodies [38]. **66**. Ultimate marginal venation, fimbrial vein [38]. **67**. Margin [11]. **68**. Abaxial cuticle [4]. **69**. Adaxial cuticle [55]. – Scales: 1 cm (64), 1 mm (65–66), 25 µm (67–69).
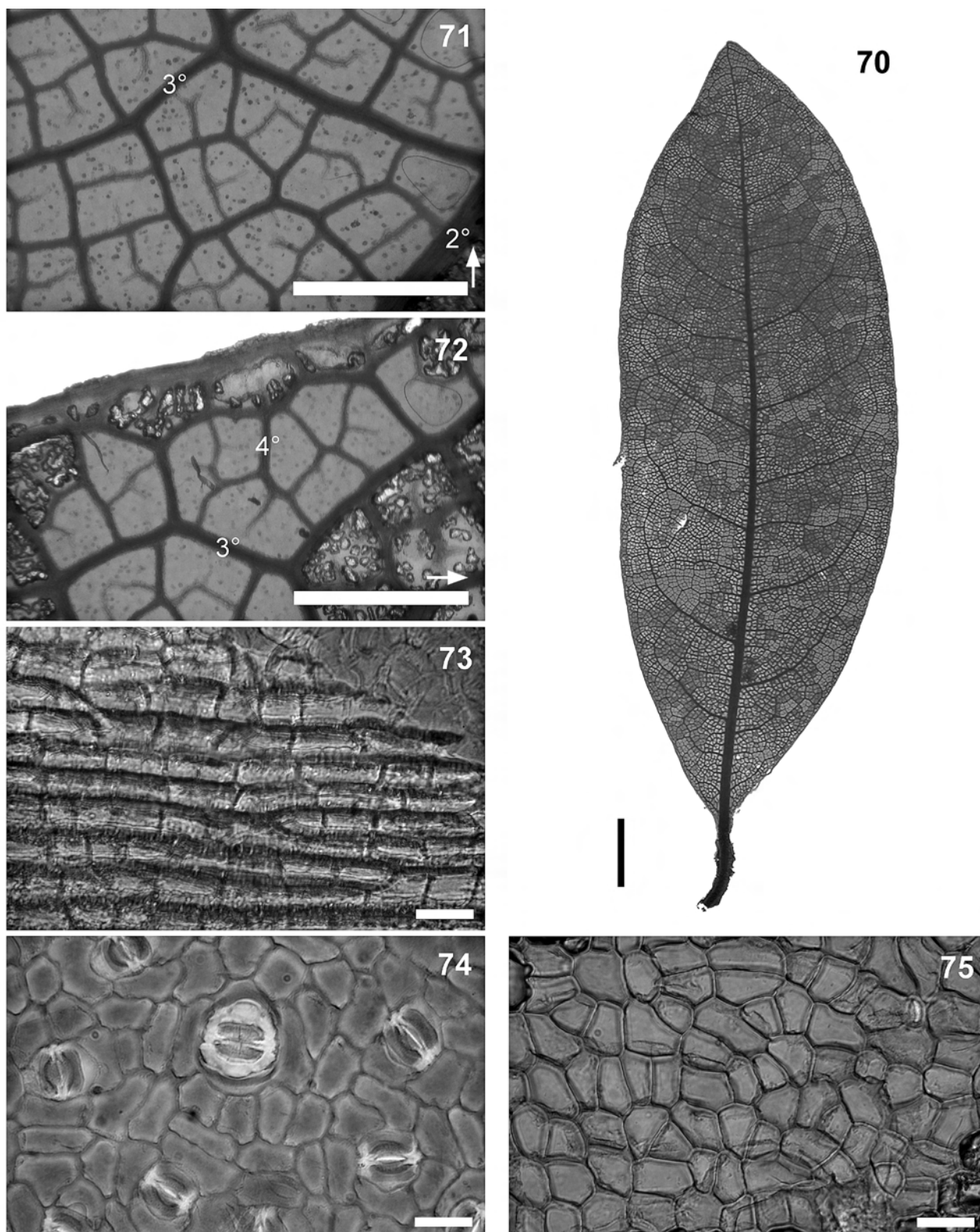
Figs. 70–75. *Ocotea foetens*. – **70**. Cleared leaf [47]. **71**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing or forming polygons, secretory bodies [47]. **72**. Ultimate marginal venation, complete loops [47]. **73**. Margin [47]. **74**. Abaxial cuticle [47]. **75**. Adaxial cuticle [47]. – Scales: 1 cm (70), 1 mm (71–72), 25 µm (73–75).
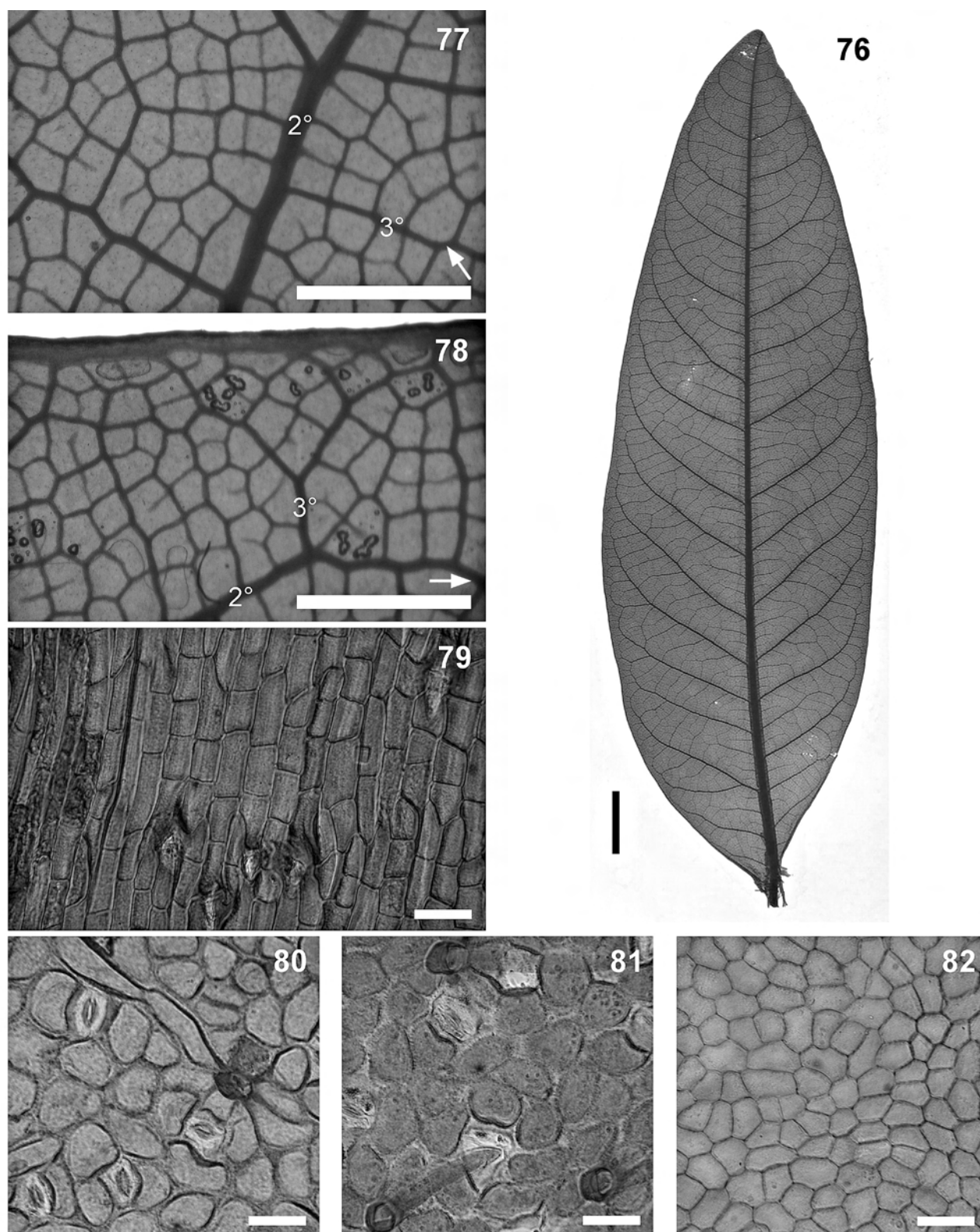
Figs. 76–82. *Persea indica.* – **76**. Cleared leaf [16]. **77**. Secondary to fifth-order veins, freely ending ultimate veinlets forming polygons [16]. **78**. Ultimate marginal venation, complete loops [16]. **79**. Margin [44]. **80**. Abaxial cuticle [44]. **81**. Abaxial cuticle [16]. **82**. Adaxial cuticle [16]. – Scales: 1 cm (76), 1 mm (77–78), 25 µm (79–82).

Figs. 83–88. *Myrica faya*. – **83**. Cleared leaf [51]. **84**. Tertiary to fifth-order veins, freely ending ultimate veinlets dichotomizing [51]. **85**. Ultimate marginal venation, complete loops [51]. **86**. Margin [22]. **87**. Abaxial cuticle [36]. **88**. Adaxial cuticle [22]. – Scales: 1 cm (83), 1 mm (84–85), 25 µm (86–88).
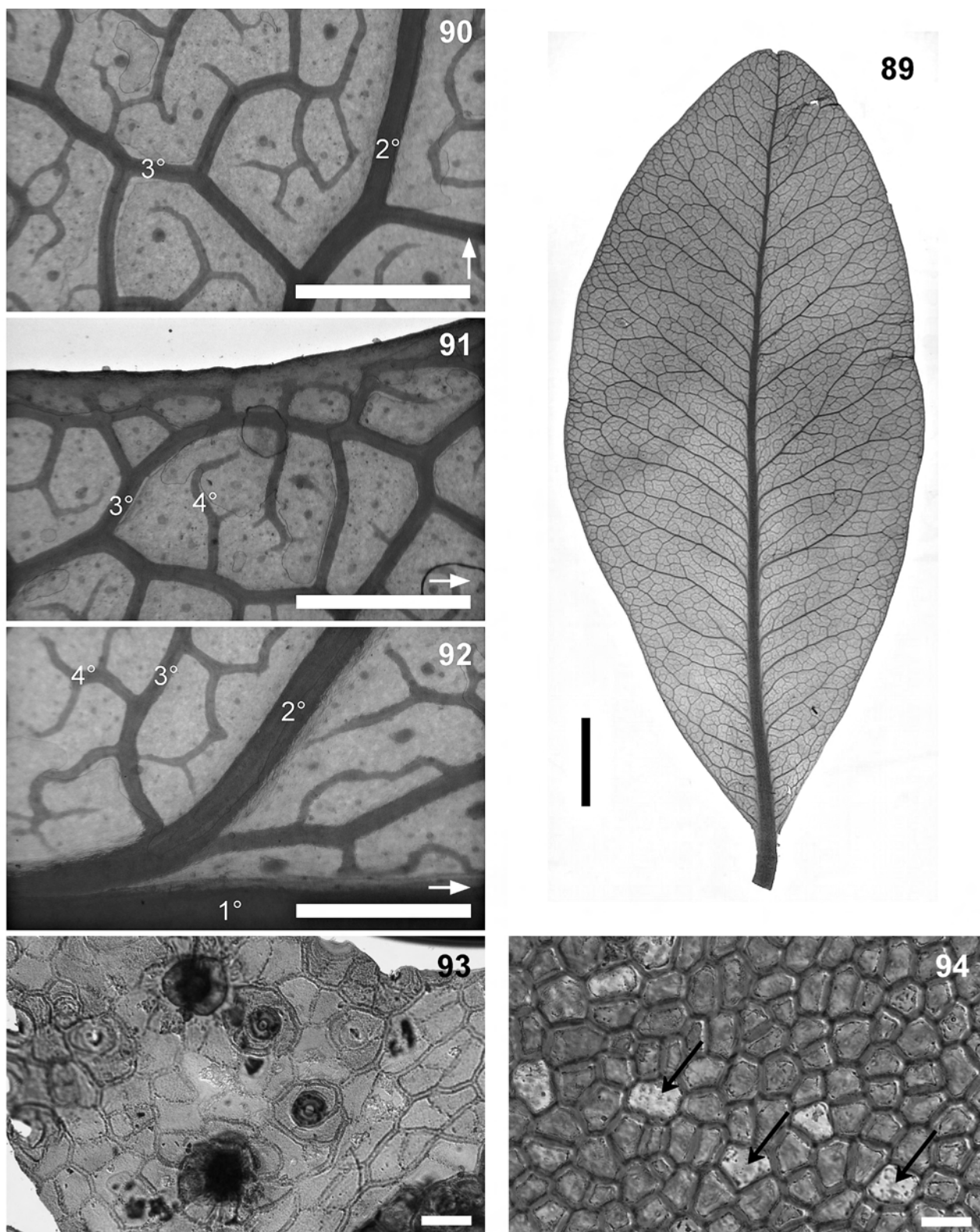
Figs. 89–94. *Heberdenia excelsa*. – **89**. Cleared leaf [STU 9258]. **90**. Secondary to fourth-order veins, freely ending ultimate veinlets dichotomizing [STU 9258]. **91**. Ultimate marginal venation, incomplete to complete loops [STU 9258]. **92**. Primary vein [STU 9258]. **93**. Abaxial cuticle, peltate trichomes [STU 7559]. **94**. Adaxial cuticle, bigger cells (see arrows) scattered [STU 7559]. – Scales: 1 cm (89), 1 mm (90–92), 25 µm (93–94).
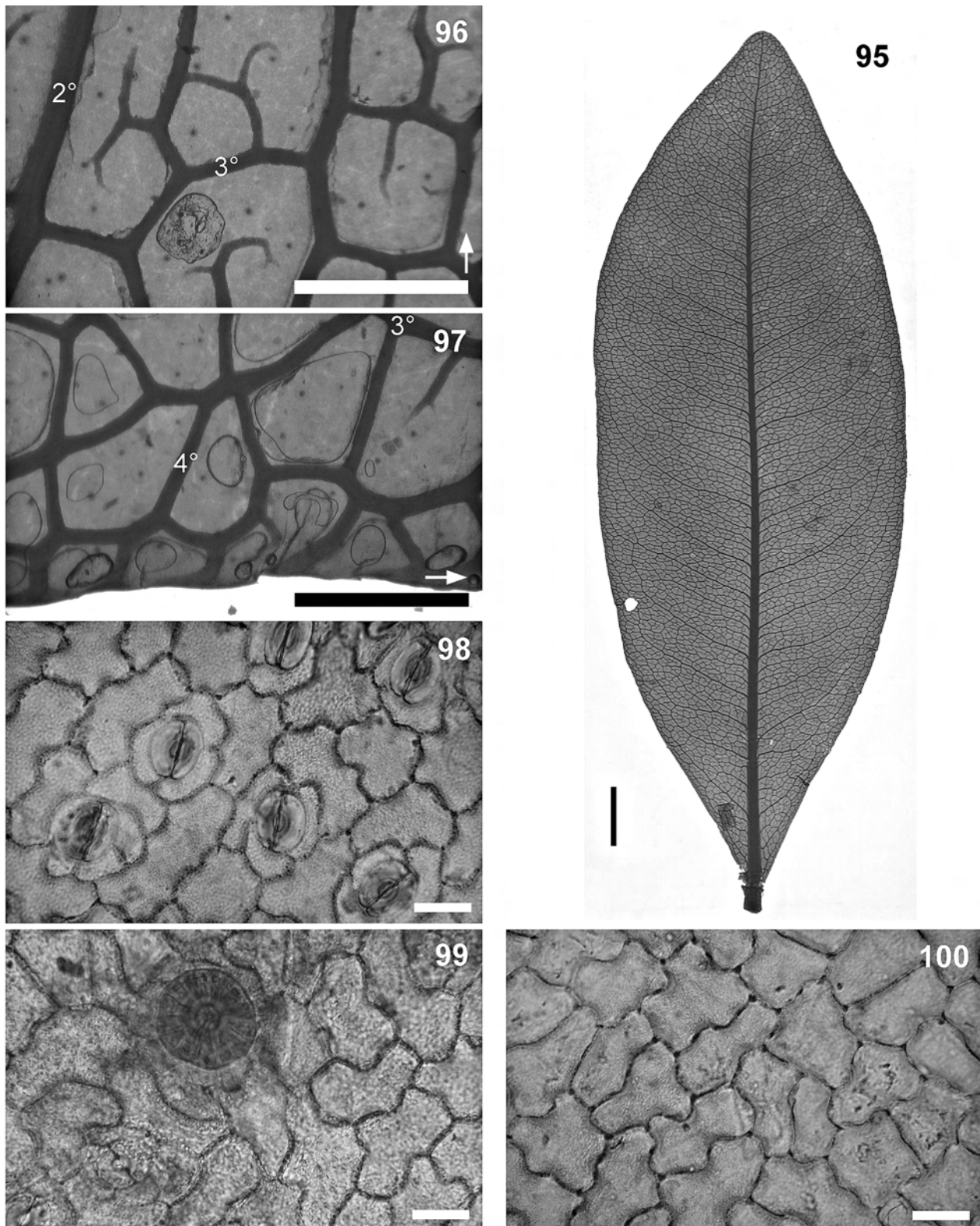
Figs. 95–100. *Pleiomeris canariensis.* – **95**. Cleared leaf [STU 8665]. **96**. Secondary to fourth-order veins, freely ending ultimate veinlets dichotomizing or forming polygons [STU 8665]. **97**. Ultimate marginal venation, complete loops [STU 8665]. **98**. Abaxial cuticle [STU 8665]. **99**. Abaxial cuticle, multicellular trichome [STU 8665]. **100**. Adaxial cuticle [STU 8665]. – Scales: 1 cm (95), 1 mm (96–97), 25 µm (98–100).
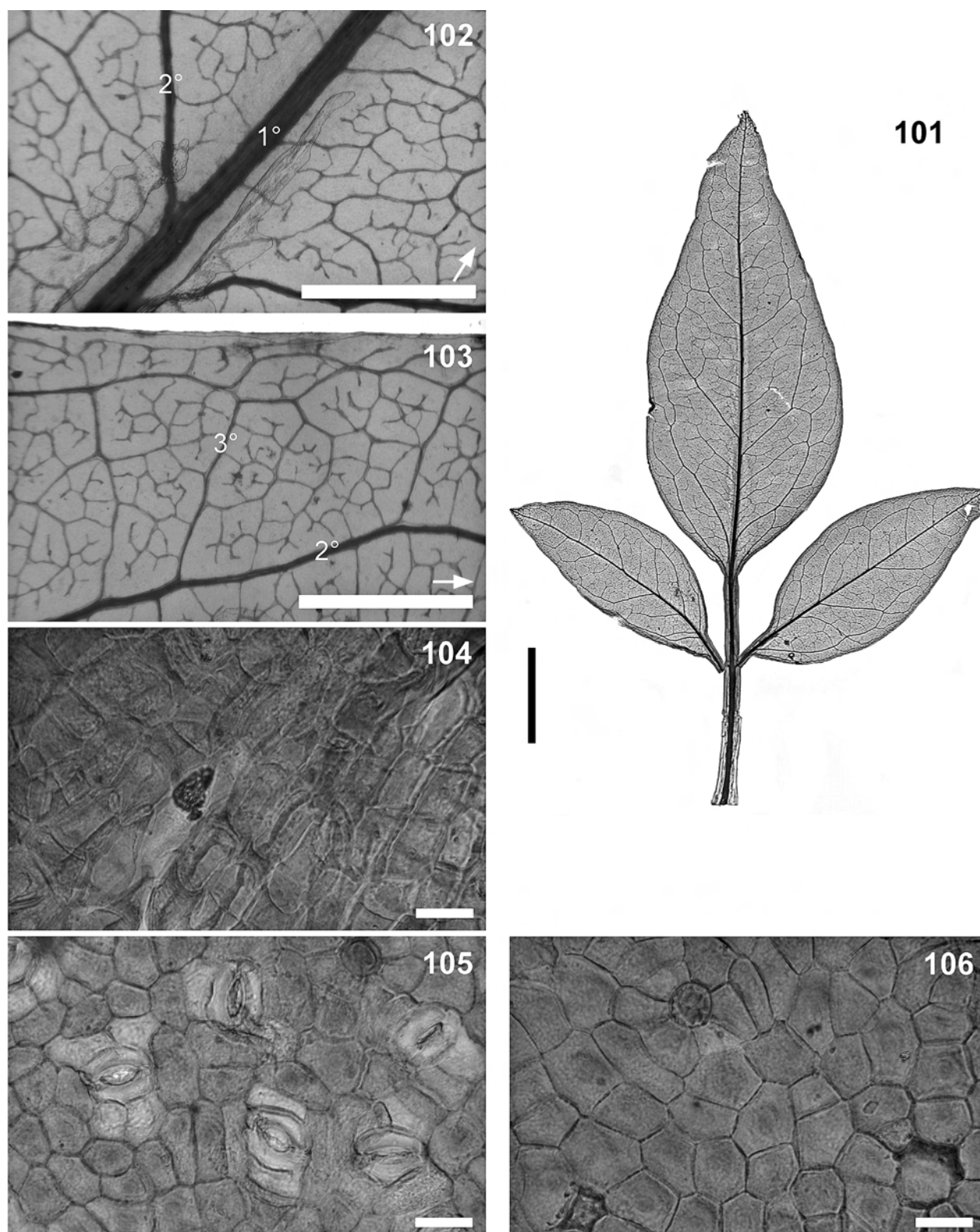
Figs. 101–106. *Jasminum odoratissimum*. – **101**. Cleared leaf [27]. **102**. Secondary to fourth-order veins, freely ending ultimate veinlets dichotomizing [27]. **103**. Ultimate marginal venation, complete or incomplete loops [27]. **104**. Margin [27]. **105**. Abaxial cuticle [27]. **106**. Adaxial cuticle [27]. – Scales: 1 cm (101), 1 mm (102–103), 25 µm (104–106).
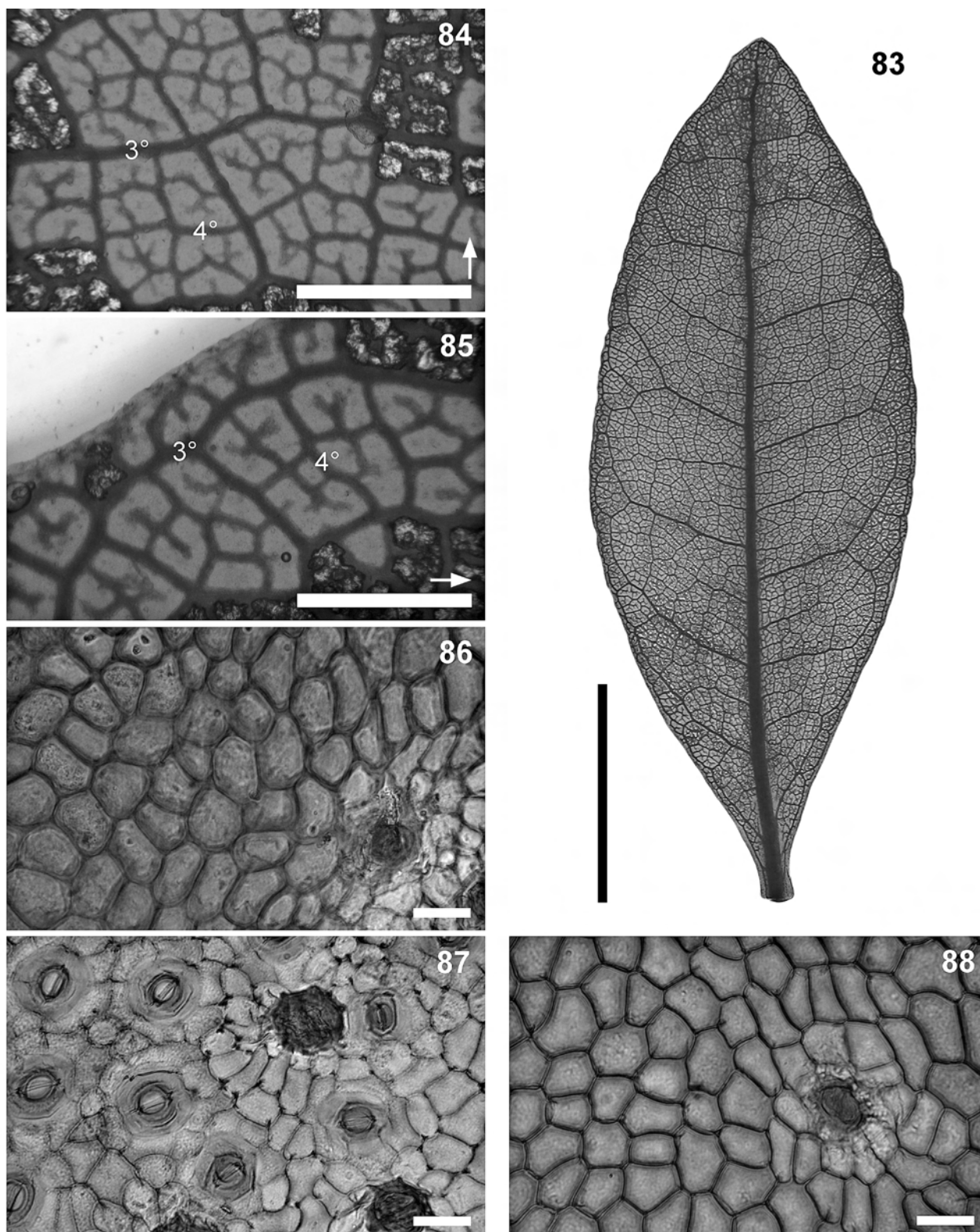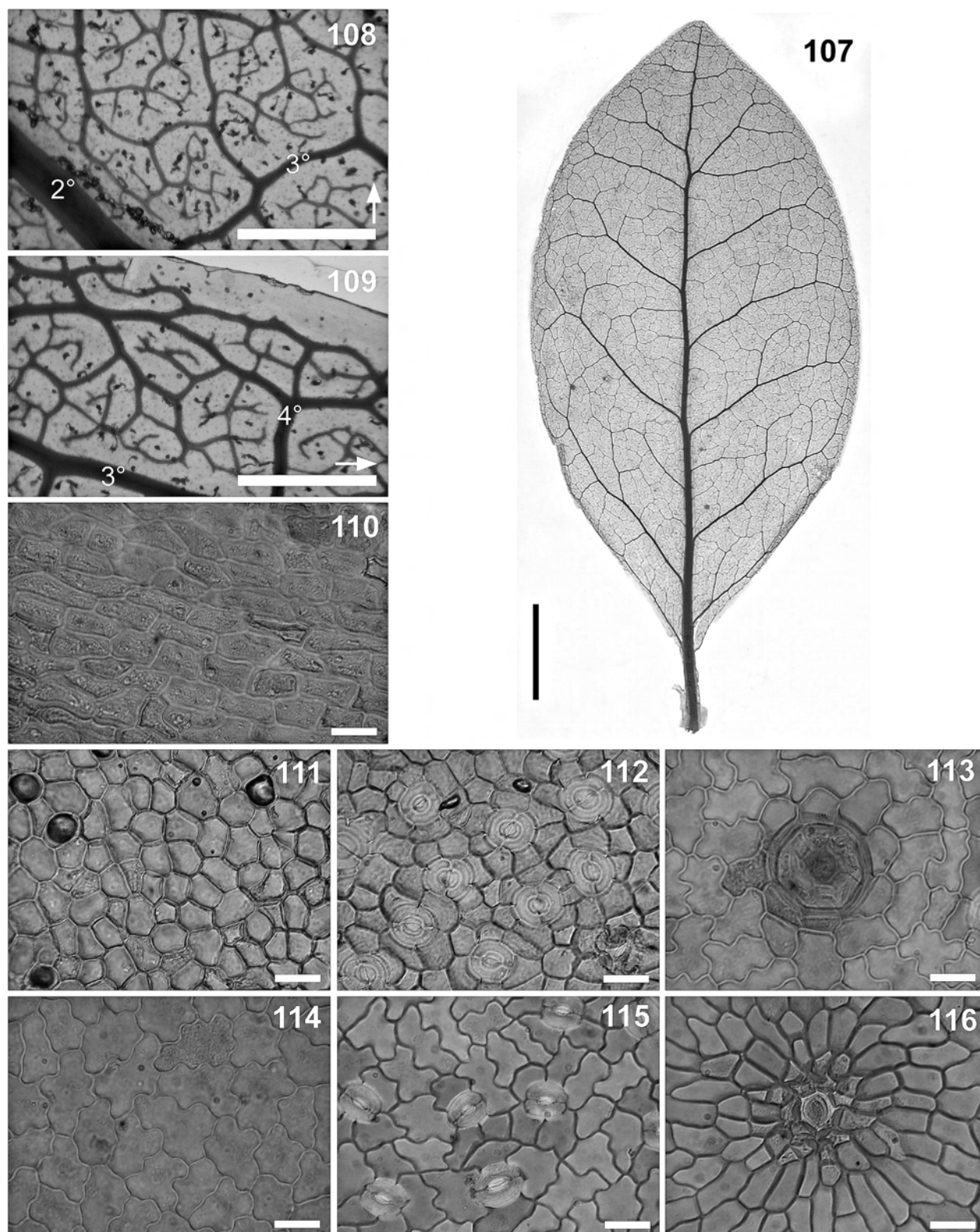
Figs. 107–116. *Picconia excelsa.* – **107**. Cleared leaf [24]. **108**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [24]. **109**. Ultimate marginal venation, complete or incomplete loops [24]. **110**. Margin [42]. **111**. Adaxial cuticle, straight anticlines [40]. **112**. Abaxial cuticle [40]. **113**. Abaxial cuticle, glandular peltate trichome [43]. **114**. Adaxial cuticle, undulate anticlines [43]. **115**. Abaxial cuticle [43]. **116**. Abaxial cuticle, gland [43]. – Scales: 1 cm (107), 1 mm (108–109), 25 µm (110–116).
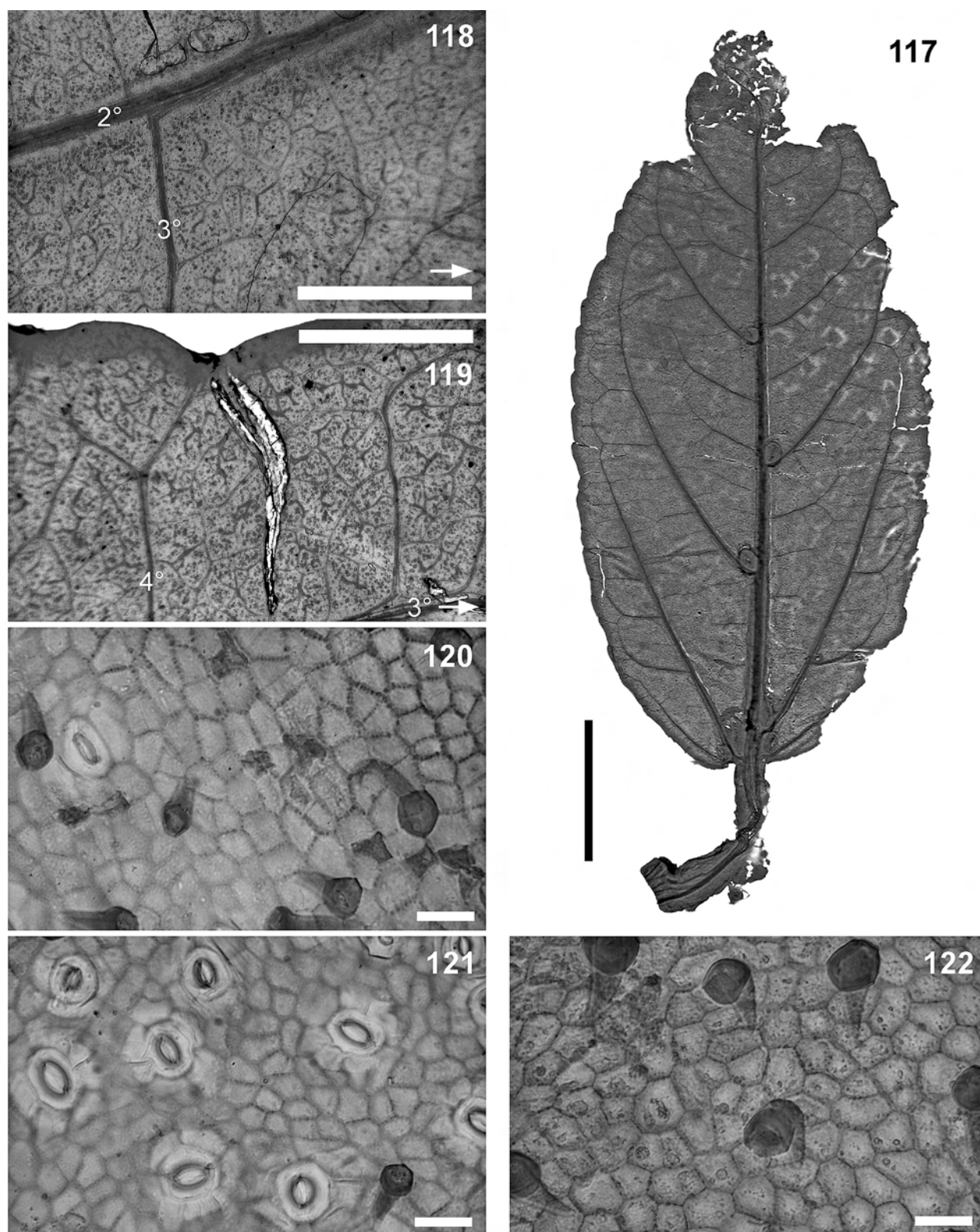
Figs. 117–122. *Rhamnus glandulosa*. – **117**. Cleared leaf [3]. **118**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [3]. **119**. Ultimate marginal venation, complete loops, tooth [3]. **120**. Margin [9]. **121**. Abaxial cuticle [9]. **122**. Adaxial cuticle [3]. – Scales: 1 cm (117), 1 mm (118–119), 25 μm (120–122).
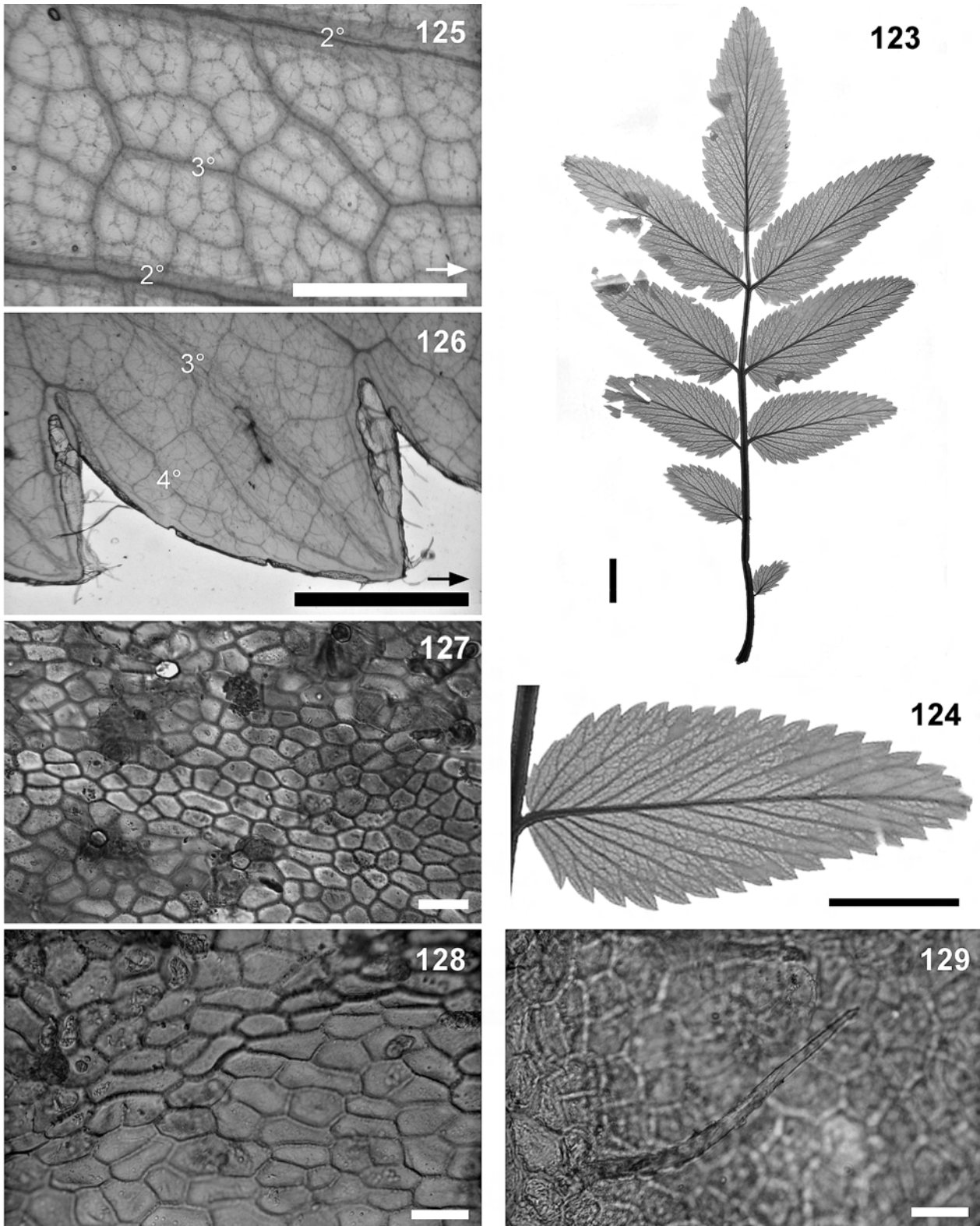
Figs. 123–129. *Bencomia caudata.* – **123**. Cleared leaf [STU 5352]. **124**. Cleared leaflet [STU 5352]. **125**. Secondary to sixth-order veins, freely ending ultimate veinlets dichotomizing [STU 5352]. **126**. Ultimate marginal venation, complete loops, fifth-order veins may protrude, tooth [STU 5352]. **127**. Abaxial cuticle, glandular trichome [STU 5352]. **128**. Adaxial cuticle [STU 8676]. **129**. Adaxial cuticle, trichome [STU 8676]. – Scales: 1 cm (123–124), 1 mm (125–126), 25 µm (127–129).
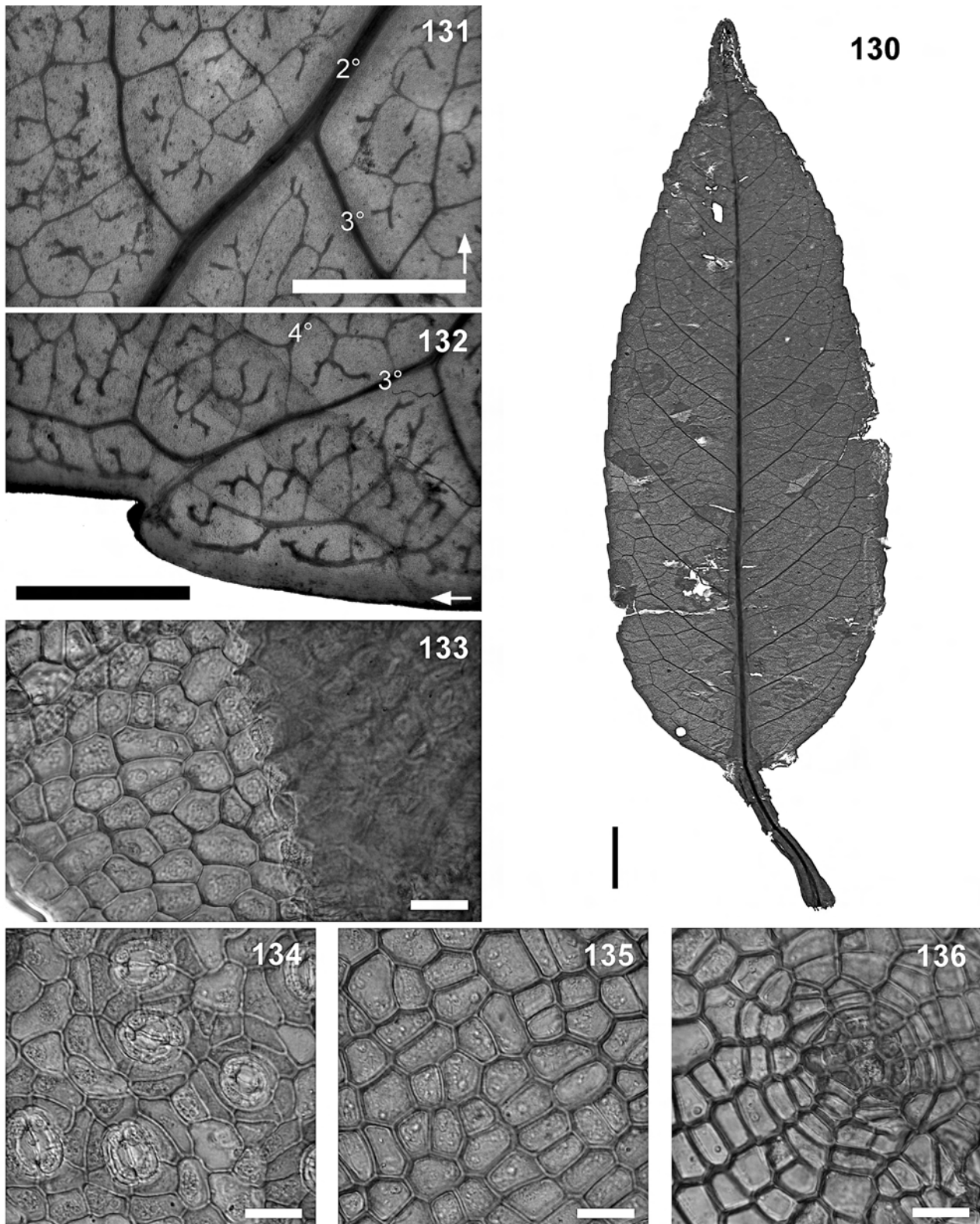
Figs. 130–136. *Prunus lusitanica*. – **130**. Cleared leaf [1]. **131**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [1]. **132**. Ultimate marginal venation, incomplete loops, tooth [1]. **133**. Margin [1]. **134**. Abaxial cuticle [1]. **135**. Adaxial cuticle [1]. **136**. Adaxial cuticle, cork-wart [1]. – Scales: 1 cm (130), 1 mm (131–132), 25 µm (134–136).
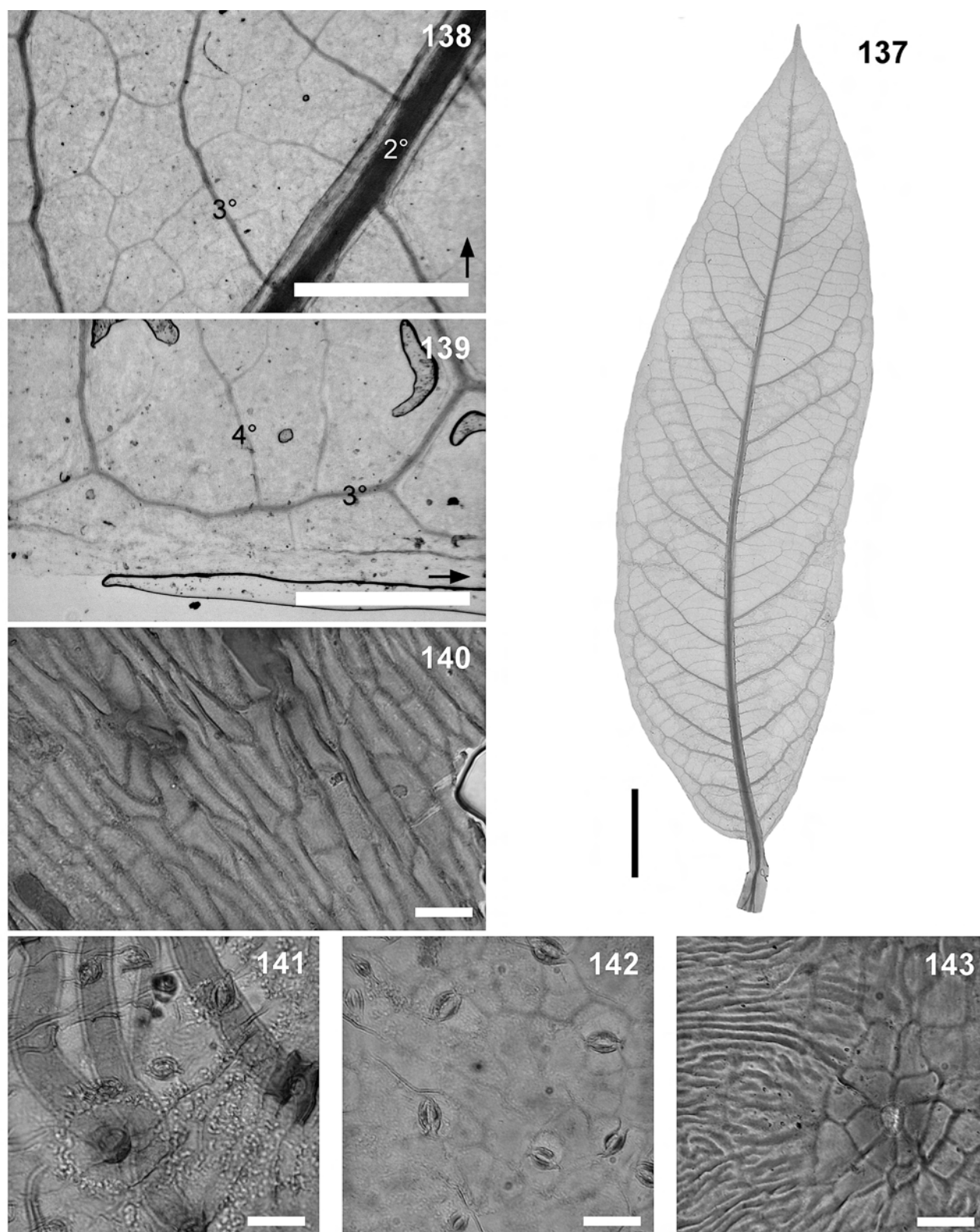
Figs. 137–143. *Salix canariensis.* – **137**. Cleared leaf [64]. **138**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [64]. **139**. Ultimate marginal venation, incomplete loops [64]. **140**. Margin [64]. **141**. Abaxial cuticle, trichomes [63]. **142**. Abaxial cuticle [64]. **143**. Adaxial cuticle, trichome bases [63]. – Scales: 1 cm (137), 1 mm (138–139), 25 µm (140–143).
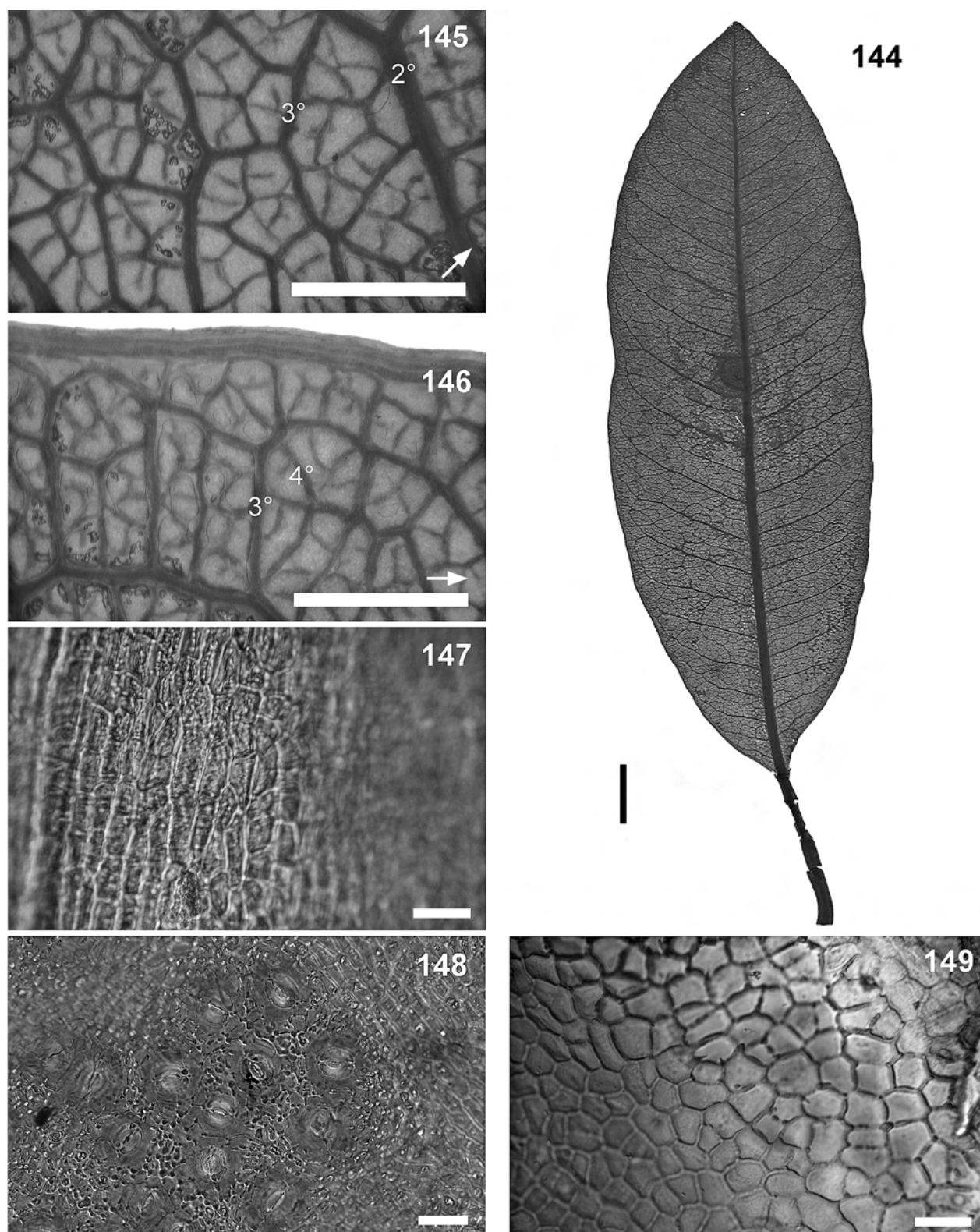
Figs. 144–149. *Sideroxylon marmulano.* – **144**. Cleared leaf [STU 1041]. **145**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [STU 1041]. **146**. Ultimate marginal venation, complete loops [STU 1041]. **147**. Margin [STU 1041]. **148**. Abaxial cuticle [STU 1041]. **149**. Adaxial cuticle [STU 7550]. – Scales: 1 cm (144), 1 mm (145–146), 25 µm (147–149).
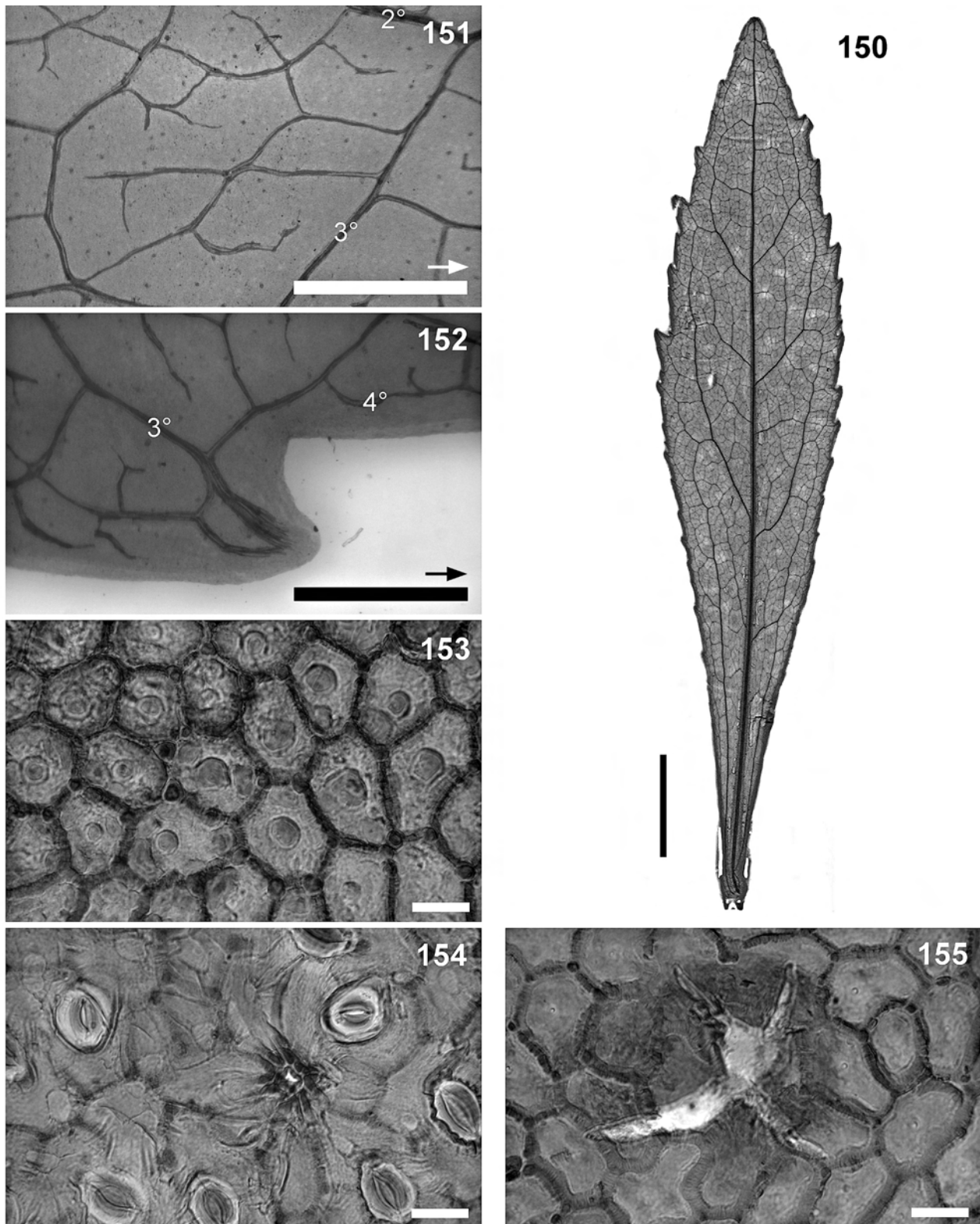
Figs. 150–155. *Isoplexis canariensis.* – **150**. Cleared leaf [26]. **151**. Secondary to fifth-order veins, freely ending ultimate veinlets forming polygons or dichotomizing [26]. **152**. Ultimate marginal venation, incomplete loops, tooth [26]. **153**. Margin [26]. **154**. Abaxial cuticle, small trichome base [26]. **155**. Adaxial cuticle, large trichome base [26]. – Scales: 1 cm (150), 1 mm (151–152), 25 µm (153–155).
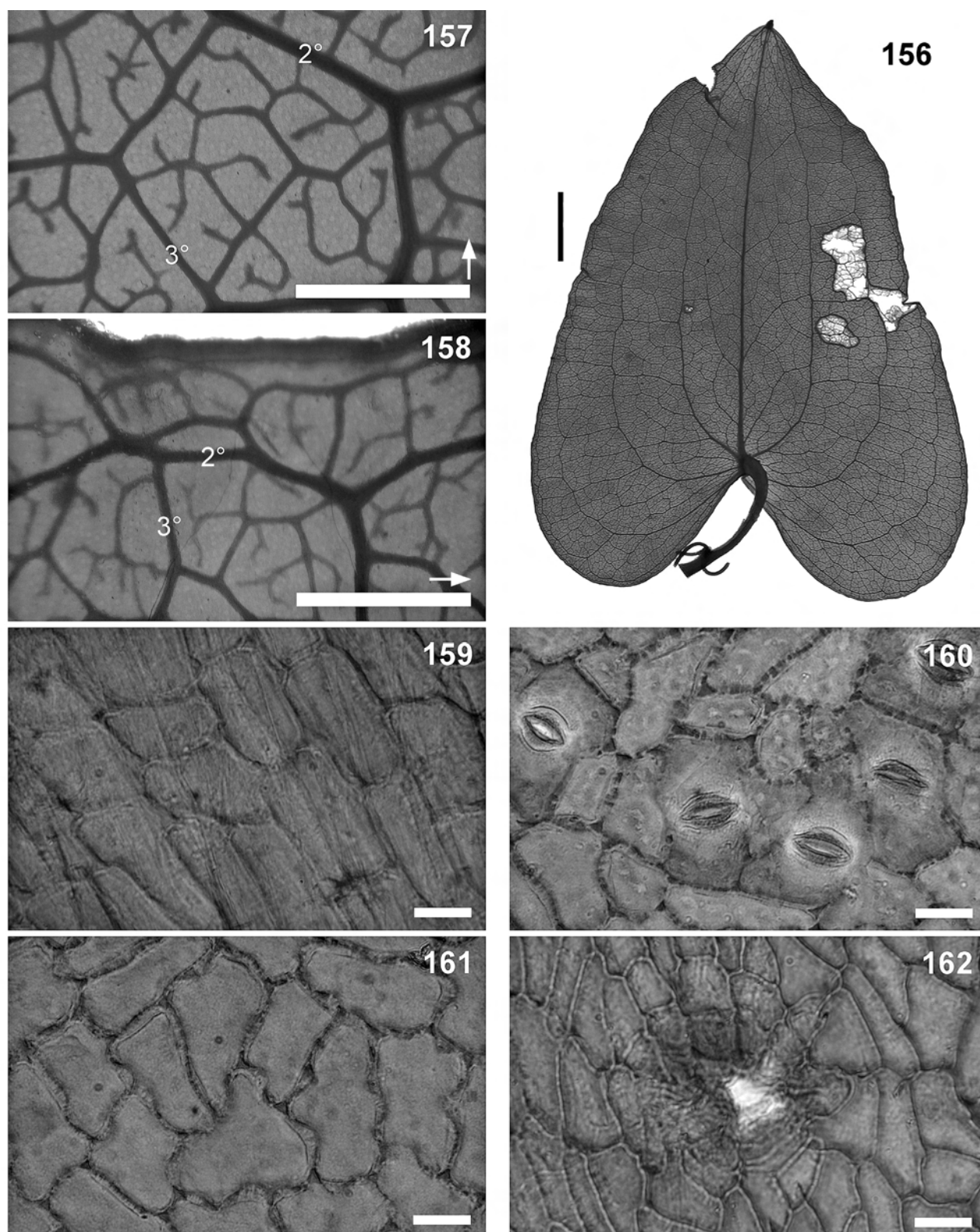
Figs. 156–162. *Smilax canariensis*. – **156**. Cleared leaf [13]. **157**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [13]. **158**. Ultimate marginal venation, complete or incomplete loops [13]. **159**. Margin [13]. **160**. Abaxial cuticle [13]. **161**. Adaxial cuticle [13]. **162**. Abaxial cuticle, secretory pore(?) [13]. – Scales: 1 cm (156), 1 mm (157–158), 25 µm (159–162).
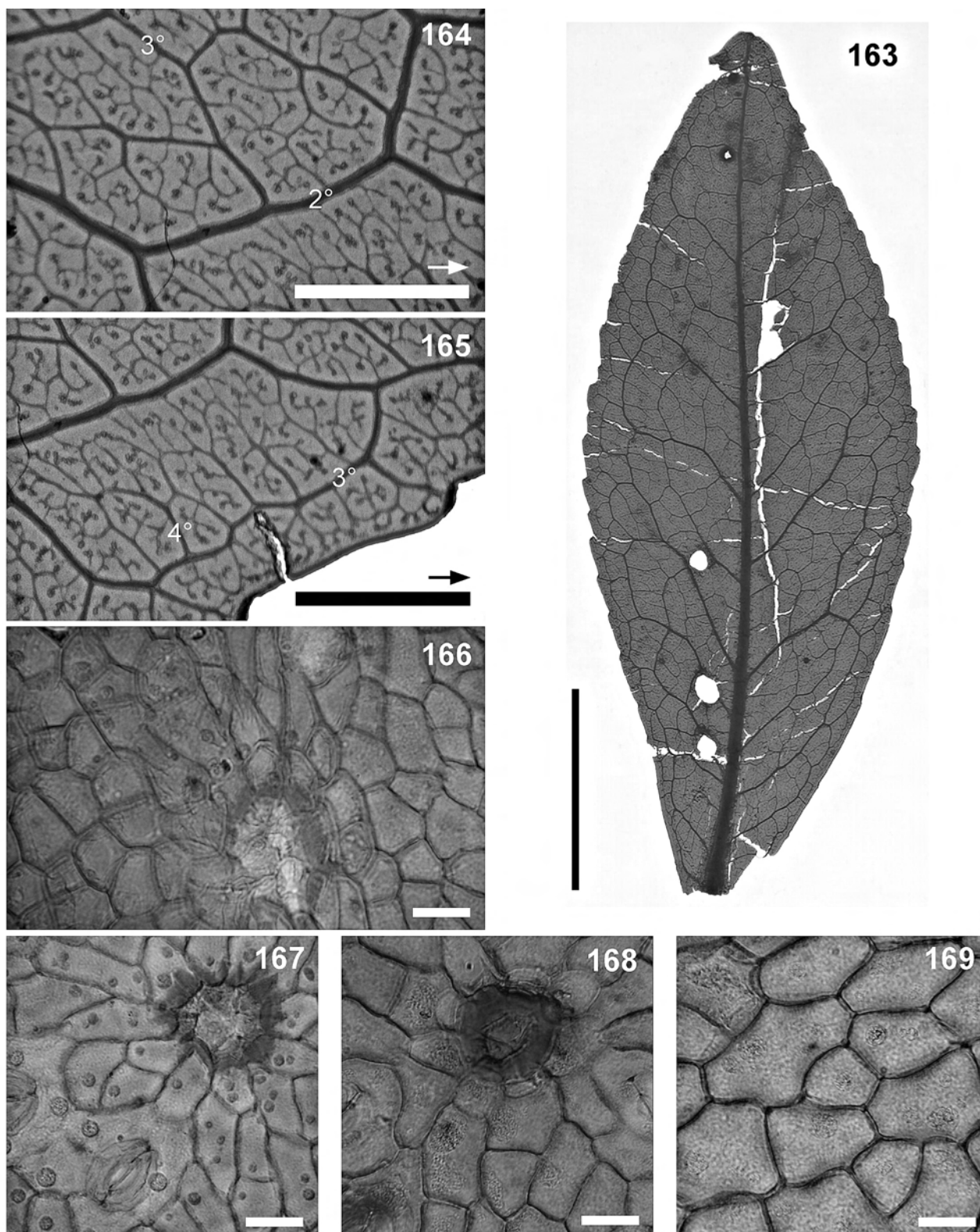
Figs. 163–169. *Visnea mocanera*. – **163**. Cleared leaf [8]. **164**. Secondary to fifth-order veins, freely ending ultimate veinlets dichotomizing [8]. **165**. Ultimate marginal venation, incomplete loops, tooth [8]. **166**. Margin, cork-wart [8]. **167**. Abaxial cuticle, cork-wart [8]. **168**. Abaxial cuticle, trichome base [25]. **169**. Adaxial cuticle [25]. – Scales: 1 cm (163), 1 mm (164–165), 25 µm (166–169).
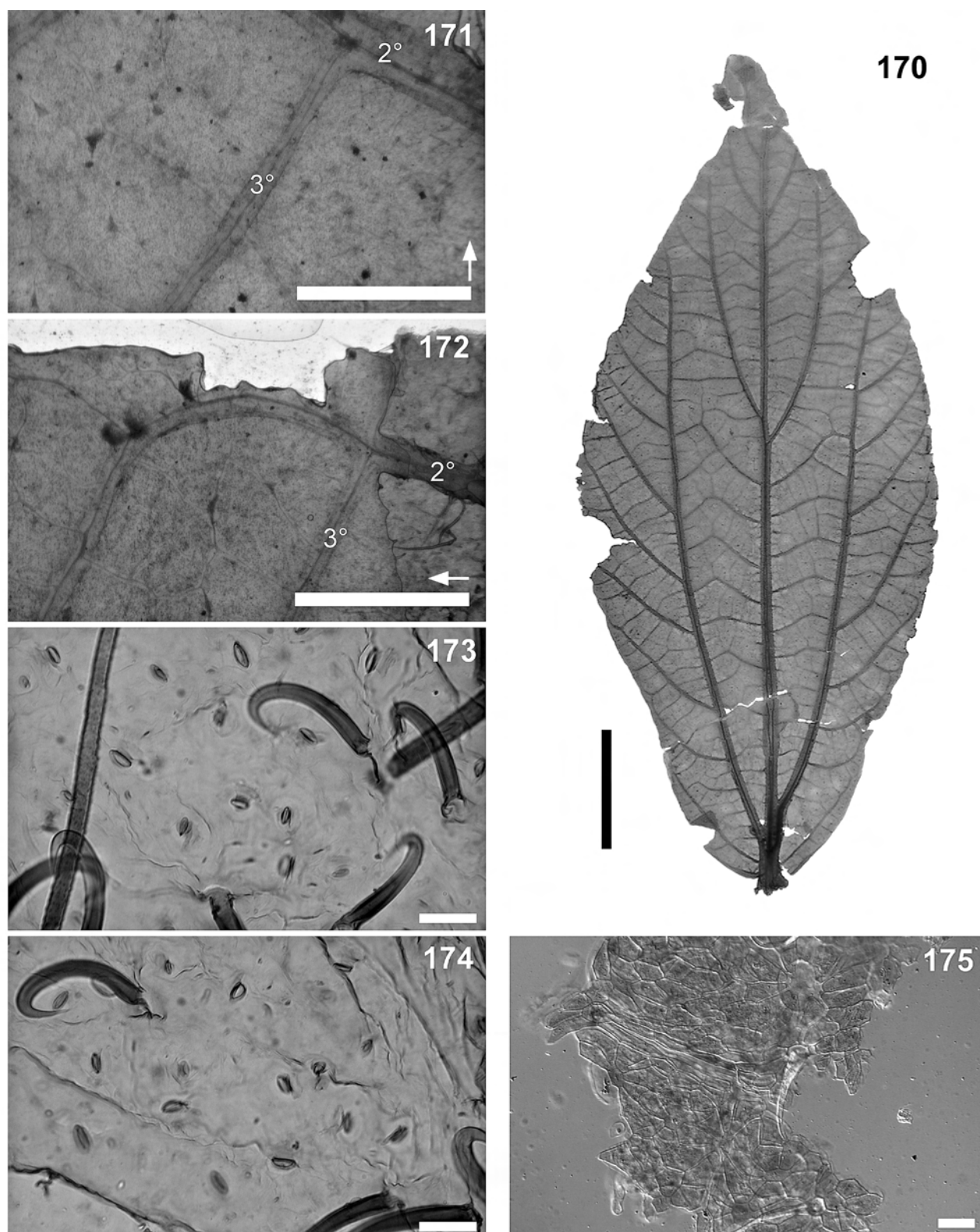
Figs. 170–175. *Gesnouinia arborea.* – **170**. Cleared leaf [STU 8669]. **171**. Secondary to tertiary veins [STU 8669]. **172**. Ultimate marginal venation, complete loops [STU 8669]. **173**. Abaxial cuticle, stomata, trichomes [STU 8669]. **174**. Abaxial cuticle, stomata, trichomes [STU 8669]. **175**. Adaxial cuticle, resinous bodies [STU 885]. – Scales: 1 cm (170), 1 mm (171–172), 25 µm (173–174), 50 µm (175).

Leaf attachment opposite, leaf organization simple, petiole short, 0.4–1.6 cm (0.8 cm) long, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 7.4–13.5 cm (9.6 cm), width 3.1–6.2 cm (4.5 cm), elliptic, symmetrical, base and apex angle both acute, base shape almost straight to slightly concavo-convex, apex shape convex, margin entire and somewhat revolute.

Venation: primary vein pinnate; secondaries weakly brochidodromous, curved to recurved, course irregular, secondary vein spacing irregular, 0.9–1.4 cm, one pair of acute basal secondaries running parallel to the margin, secondary vein angle smoothly decreasing towards the base, inter-secondaries occasionally developed; tertiaries polygonal reticulate, sometimes alternate percurrent, tertiary vein angle to primary vein obtuse to sometimes acute, tertiary vein angle variability inconsistent; fourth-order veins regular polygonal reticulate, areolation poorly to moderately developed (5- to more-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets once to twice branched, ultimate marginal venation consisting of sometimes complete, sometimes incomplete loops.

Adaxial cuticle: medium thick, non-modified epidermal cells 19–25 µm (21 µm) in diameter, anticlines straight to undulate, undulation U-shaped, wave length 12–26 µm (19 µm), amplitude 3–9 µm (5 µm); peltate glands scattered, sunken in the cuticle but still somewhat raised, surrounding non-modified epidermal cells arranged circularly, diameter 17–46 µm (27 µm). Marginal cells elongated, end anticlines square to oblique, 21–57 µm (33 µm) long, 6–18 µm (11 µm) wide.

Abaxial cuticle: thin to medium thick, non-modified epidermal cells 9–26 µm (16 µm) in diameter, anticlines straight to undulate, undulation U-shaped, wave length 13–23 µm (16 µm), amplitude 3–8 µm (5 µm); stomatal complexes cyclocytic, 5–6 subsidiary cells, more intensively staining than the non-modified epidermal cells; stomata oval to roundish, 18–26 µm (21 µm) long, 16–26 µm (21 µm) wide with thickened polar I- to T-pieces; stomatal aperture oval, 8–15 µm (10 µm) long; giant stomata present (one observed, 33 × 25 µm); stomatal frequency 8–14 (11); faint but clearly visible striation developed. Glands as described above but more densely spaced, diameter about 45 µm, surrounded by a ring of more intensively staining, slightly elongated epidermal cells (Fig. 113).

Remarks: This foliage is characterized by a basal pair of secondaries running parallel to the margin, by irregularly and widely spaced, somewhat recurved secondaries forking and looping in different distances from the margin, and the slender but distinctive polygonal reticulate network of the tertiaries. Additional diagnostically relevant features are the cyclocytic stomata with thickened and therefore well-staining subsidiary cells and peltate trichomes.

Rhamnaceae
Rhamnus glandulosa Ait.
(Figs. 117–122)

Material: Herbarium EDER nos. 3, 9, 19 (10 herbarium sheets, cuticles from 3 sheets).

Leaf attachment alternate, leaf organization simple, petiole long, 1.0–2.2 cm (1.6 cm), base slightly swollen, marginal petiolar attachment, laminar size microphyll – 2 : 1, length 2.8–10.1 cm (6.7 cm), width 2.0–4.8 cm (3.4 cm), elliptic, symmetrical, base and apex angle both acute, base shape convex, apex shape acuminate to convex, margin crenate and revolute, circa 3 teeth per centimetre; tooth shape: basally retroflexed to convex, apically convex, sinus rounded, apex non-specific glandular, veinlet ending in the sinus.

Venation: primary vein pinnate, very strong, in the axils of the secondaries big and distinct glands present; secondaries semicraspedodromous, smoothly curved, secondary vein spacing irregular, increasing towards the base, 1.0–2.3 cm, two pairs of basal secondaries, the lower one thin and short running near the margin, the upper one prominent and running steeply into the upper half of the lamina, secondary vein angle smoothly decreasing towards the base, inter-secondaries well developed, often more than one between two adjacent secondaries; tertiaries mixed opposite/alternate percurrent, tertiary vein course straight, tertiary vein angle to primary vein mostly obtuse, tertiary vein angle variability inconsistent; fourth-order veins alternate percurrent, areolation moderately developed; fifth-order veins dichotomizing; freely ending ultimate veinlets twice or more times branched, ultimate marginal venation consisting of loops.

Adaxial cuticle: thick, non-modified epidermal cells polygonal, diameter 11–38 µm (21 µm), anticlines straight; simple trichomes scattered, trichome base a single modified cell, size coherent to normal epidermal cells, trichome body one-celled, cone-shaped, short, the single cell often crooked, length 17–99 µm (34 µm), considerably longer above veins 31–312 µm (94 µm); trichome frequency 9.4. Marginal cells polygonal, anticlines straight, 8–42 µm (18 µm).

Abaxial cuticle: thinner than adaxial one, non-modified epidermal cells polygonal, diameter 9–31 µm (17 µm), anticlines straight; stomatal complexes cyclocytic with 5–7 almost rectangular subsidiary cells which stain less intensively than the non-modified epidermal cells, subsidiaries 11–27 µm (19 µm) long, 7–14 µm (10 µm) wide; stomata oval, 23–35 µm (28 µm) long, 16–27 µm (22 µm) wide; stomatal aperture oval with prominent outer stomatal ledge, aperture 8–18 µm (12 µm) long, 3–10 µm (7 µm) wide, poles more intensively staining than the guard and subsidiary cells; sometimes cuticular striation

present (radially oriented around stomata); stomatal frequency 8; trichomes as described above, trichome frequency 3.1.

Remarks: Apart from the few, widely spaced and steeply ascending secondaries, the large axillary glands are characteristic. Diagnostically valuable are also the cyclocytic stomatal complexes with a ring of only faintly staining subsidiaries and the mostly short, cone-shaped trichomes positioned on comparably large bases.

Rosaceae
Bencomia caudata Webb & Berthet
(Figs. 123–129)

Material: STU 5352, 8676 (9 herbarium sheets, 2 cuticles).

Leaf organization odd-pinnate (7–13 leaflets), petiole 4.9–25.0 cm (13.1 cm), petiole base swollen, marginal petiolar attachment, laminar size mesophyll – 2 : 1, length 5.5–34.0 cm (16.3 cm), width 4–15 cm (7.2 cm), obovate, symmetrical, base angle acute, apex angle obtuse.

Leaflets: simple, almost sessile or petiolules very short, marginal petiolar attachment, leaflets all sizes from microphyll – 2 : 1 to nanophyll – 1 : 1 (stipules), 0.8–5.0 cm (3.5 cm) long, 0.6–2.2 cm (1.5 cm) wide, ovate, terminal leaflet symmetrical, lateral leaflets base asymmetrical (apical side shorter), base angle obtuse, apex angle acute, base shape rounded, apex shape almost straight to slightly convex, margin simple serrate, 4 teeth per centimetre, spacing regular; tooth shape: basal side convex, apical side slightly flexuous, sinus angular, apex simple.

Venation: primary vein pinnate; secondaries craspedodromous, straight to minimally recurved, secondary vein spacing very dense and uniform, 0.1–0.3 cm, secondaries running parallel to each other, slightly diverging near the margin, secondary vein angle uniform, slightly increasing towards the base; tertiaries alternate percurrent, forming "composite" inter-secondaries, tertiary vein course sinuous, tertiary vein angle to primary vein obtuse, tertiary vein angle relatively uniform; fourth and fifth-order veins regular polygonal reticulate, areolation moderately developed (4- to 5-sided); sixth-order veins dichotomizing; freely ending ultimate veinlets unbranched to once branched, ultimate marginal venation consisting of loops with some fifth-order veins outside of the loops, branches of the secondaries and two tertiaries enter the marginal teeth and fuse directly at the apex.

Adaxial cuticle: medium thick, non-modified epidermal cells polygonal, diameter 13–34 µm (19 µm), anticlines straight; filiform trichomes present, mainly situated above veins, one-celled, about 150 µm long, trichome bases one-celled and circular, small (10 µm in diameter); further-

more, glandular trichomes developed, base simple, quite indistinct, trichome composed of one row of several short cells and an almost spherical head, which is often missing.

Abaxial cuticle: preparation remained unsuccessful.

Remarks: Remarkable are the very densely spaced, straight, and strongly parallel secondaries as well as the inter-secondaries which are composed of alternate percurrent tertiaries. Up to six orders of veins can be discriminated. The abaxial cuticle poorly withstands maceration.

Prunus (Laurocerasus) lusitanica L.
(Figs. 130–136)

Material: Herbarium EDER no. 1 (12 herbarium sheets, cuticle from one sheet).

Leaf attachment alternate, leaf organization simple, petiole 0.4–2.9 cm (1.8 cm) long, base slightly swollen, marginal petiolar attachment, laminar size notophyll – 2 : 1, length 7.4–14.8 cm (10.5 cm), width 2.8–5.5 cm (4.2 cm), elliptic to slightly oval, symmetrical to basally asymmetrical, base and apex angle both acute, base shape convex to rounded, apex shape acuminate, margin crenate, teeth regularly spaced, 2–4 teeth per centimetre; tooth shape: basal side straight to slightly convex, apical side convex, sinus rounded, apex non-specific glandular.

Venation: primary vein pinnate, at the base two glands situated left- and right-hand of the primary vein; secondaries semicraspedodromous, straight to slightly curved, secondary vein spacing rather uniform, 0.8–1.1 cm, secondary vein angle smoothly increasing towards the base, inter-secondaries occasionally developed to absent; tertiaries mixed opposite/alternate percurrent, tertiary vein course sinuous, tertiary vein angle to primary vein obtuse, tertiary vein angle rather uniform; fourth-order veins opposite percurrent, areolation poorly developed (4- to more-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets once to more times branched, ultimate marginal venation consisting of incomplete loops, loops developing close to the marginal teeth sending a short veinlet directly into the tooth apex.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells polygonal, diameter 9–37 µm (23 µm), anticlines straight; cork warts present, raised above the cuticle surface, surrounded by several rings of tangentially elongated cells. Marginal cells somewhat elongated, anticlines straight, 13–30 µm (24 µm) long, 10–25 µm (17 µm) wide.

Abaxial cuticle: thick, glabrous, non-modified epidermal cells polygonal, diameter 12–39 µm (24 µm), anticlines straight to rounded, sometimes weakly undulate, wave length 14–27 µm (19 µm), amplitude 2–7 µm (5 µm);

stomatal complexes incompletely amphicyclocytic with an inner five- to six-celled ring and an incomplete outer ring of subsidiary cells, the outer ring sometimes shared by neighbouring stomata; subsidiaries tangentially slightly elongated, staining more intensely than non-modified cells; stomata oval to roundish, 23–33 µm (28 µm) long, 18–31 µm (25 µm) wide; stomatal aperture oval, bordered by thick outer stomatal ledges, aperture 10–15 µm (13 µm) long, 4–8 µm (6 µm) wide, poles marked by an I-piece of thickened cutin, above the guard cells distinct circular cuticular folds developed; stomata frequently clustered in groups of two to five; stomatal frequency 11; two giant stomata observed (45×26 µm and 42×29 µm).

Remarks: Among the woody taxa of the Canarian laurel forests, *Maytenus canariensis* and *Visnea mocanera* resemble each other in their rather regular marginal crenation with glandular non-specific apices. Among others, *P. lusitanica* differs by regularly spaced and marginally regularly looping secondaries. The incomplete amphicyclic stomatal complexes are a further distinctive criterion. The glands near the petiole attachment in *P. lusitanica* are a diagnostic feature of the genus *Prunus*.

Salicaceae

Salix canariensis C. Sm. ex Link
(Figs. 137–143)

Material: Herbarium EDER nos. 63, 64 (13 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate to nearly opposite, leaf organization simple, petiole 0.5–1.5 cm (1.1 cm) long, base swollen, marginal petiolar attachment, laminar size microphyll – 3 : 1, length 6–10.1 cm (8.4 cm), width 1.1–3.5 cm (2.5 cm), oblong, almost symmetrical, base and apex angle both acute, base shape convex, apex shape convex to slightly acuminate, margin revolute, entire to crenate, about 4 teeth per centimetre, regularly spaced; tooth shape: basal side convex, apical side concave to straight, sinus rounded, apex simple.

Venation: primary vein pinnate; secondaries festooned brochidodromous, curved and slightly zig-zag, secondary vein spacing irregular, relatively dense, 0.5–0.9 cm, secondary vein angle uniform to increasing towards the base, inter-secondaries well developed, often more than one between two adjacent secondaries; tertiaries mostly opposite percurrent, sometimes alternate percurrent, tertiary vein course sinuous to convex, tertiary vein angle to primary vein obtuse, tertiary vein angle decreasing exmedially; fourth-order veins mixed opposite/alternate percurrent, areolation moderately developed (3- to 5-sided); fifth-order veins rather indistinct, dichotomizing; freely ending

ultimate veinlets twice or more times branched, ultimate marginal venation consisting of incomplete loops.

Adaxial cuticle: thick, non-modified epidermal cells almost isodiametric, polygonal, diameter 5–33 µm (15 µm), anticlines straight, cuticle strongly folded. Very long, thin, one-celled trichomes present, base roundish, one-celled with thickened poral rim, diameter 8–21 µm (14 µm), situated mainly upon the veins, surrounding cells deeply staining. Marginal cells distinctly elongated, linear, anticlines straight, end anticlines square to oblique, 16–57 µm (34 µm) long, 6–15 µm (11 µm) wide, with trichomes as described above.

Abaxial cuticle: thinner than adaxial one, non-modified epidermal cells polygonal, diameter 8–35 µm (16 µm), anticlines weakly developed, straight to very slightly rounded, cuticle slightly folded; stomatal complexes brachypara- to paracytic; stomata very small, oval, 9–17 µm (13 µm) long, 5–11 µm (8 µm) wide; stomatal aperture slit-like to oval, almost as long as the stomata, outer stomatal ledges thick and deeply staining, not meeting at the poles; stomatal frequency 16; trichome bases as described above, often in groups of two to four.

Remarks: Foliage of willow is usually distinctive by a combination of traits including regular, largely parallel and curved secondaries, the regular presence of inter-secondaries as well as percurrent tertiaries. The leaf margin is mostly crenate but sometimes entire as in *S. canariensis*. The tertiaries form regular meshes, while higher order veins are less distinctive. Furthermore, diagnostically relevant are the paracytic stomatal complexes in which the subsidiary cells stain less intensively than the non-modified cells.

Sapotaceae

Sideroxylon marmulano Banks
(Figs. 144–149)

Material: STU 1041, 7550 (5 herbarium sheets, cuticles from 2 sheets).

Leaf attachment opposite to nearly decussate, leaf organization simple, petiole 1.1–4.0 cm (2.6 cm) long, pilose, marginal petiolar attachment, laminar size notophyll – 3 : 1, length 7.2–13.0 cm (10.1 cm), width 3.1–4.5 cm (3.8 cm), elliptic, symmetrical, base and apex angle both acute, base shape slightly convex to concavo-convex, apex shape slightly convex (young leaves emarginate), margin entire and slightly revolute.

Venation: primary vein pinnate; secondaries brochidodromous, curved and faintly zig-zag, secondary vein spacing dense and uniform, 0.4–0.6 cm, secondary vein angle rather uniform, slightly increasing towards the base, one

to several inter-secondaries regularly and well developed; tertiaries and fourth-order veins regular polgygonal reticulate; fifth-order veins partly polygonal, partly dichotomizing, areolation well developed (4- to 5-sided); freely ending ultimate veinlets unbranched to once branched, ultimate marginal venation consisting of loops.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells polygonal, diameter 7–23 µm (13 µm), anticlines straight; margin slightly thickened. Marginal cells somewhat elongated, disorderly linear, end anticlines oblique or square, 8–26 µm (14 µm) long, 6–12 µm (9 µm) wide.

Abaxial cuticle: thick, glabrous, non-modified epidermal cells polygonal, diameter 5–14 µm (10 µm), anticlines straight; stomatal complexes cyclocytic, 7–8 slightly thicker subsidiary cells surrounding the guard cells; stomata broadly oval, 14–24 µm (21 µm) long, 15–23 µm (19 µm) wide; stomatal aperture slender oval, 6–14 µm (10 µm) long, poles with thickened I-piece of cutin; stomatal frequency 6.

Remarks: Gross-morphologically this foliage resembles *Pleiomeris canariensis* in leaf shape and venation pattern, although leaves of *S. marmulano* are usually smaller. Both species are distinctive by the shape of the leaf base (slightly convex to concavo-convex in *S. marmulano*, slightly concavo-convex to cuneate in *P. canariensis*) and fifth-order venation, which develops in *S. marmulano* only. The ultimate veinlets are unbranched to once branched in *S. marmulano* but unbranched to twice branched in *P. canariensis*. Cyclocytic stomatal complexes are characteristic of *S. marmulano*, whereas anisocytic to anomotetracytic complexes are present in *P. canariensis*. Only the latter species bears peltate trichomes.

Scrophulariaceae

Isoplexis canariensis (L.) Loud.
(Figs. 150–155)

Material: Herbarium EDER no. 26 (11 herbarium sheets, 1 cuticle).

Leaf attachment alternate, forming rosettes at the top of the branches, leaf organization simple, leaf sessile, microphyll – 3 : 1, length 8.1–15.0 cm (11.1 cm), width 1.4–4.0 cm (2.6 cm), elliptic, symmetrical, base and apex angle both acute, base shape decurrent, apex shape straight, margin irregularly crenate/serrate, 1–2 orders of teeth, about 4 teeth per centimetre, spacing and size variable; tooth shape: basal side slightly retroflexed to slightly convex or straight, apical side slightly retroflexed or concave, sinus rounded, apex simple.

Venation: primary vein pinnate; secondaries festooned semicraspedodromous, curved, one pair of slender sec-

ondaries running steeply upwards starting from the base until about half the length of the blade, secondary vein spacing wide and irregular, 1.3–3.4 cm, secondary vein angle abruptly decreasing towards the base, inter-secondaries developed; tertiaries random reticulate; fourth-order veins regular polygonal reticulate, areolation well developed; fifth-order veins dichotomizing; freely ending ultimate veinlets unbranched to once branched, ultimate marginal venation consisting of incomplete loops, veinlets originating from the marginal loops enter the teeth, almost touching the apex.

Adaxial cuticle: thick, non-modified epidermal cells tetra- to octogonal, diameter 23–51 µm (36 µm), anticlines thick and straight; cuticle over epidermal secretory bodies intensively staining, ruptured, small, simple trichome bases scattered, surrounded by distinct radial cuticular folding. Marginal cells polygonal, anticlines thick and straight, diameter 25–58 µm (36 µm).

Abaxial cuticle: thinner than adaxial one, non-modified epidermal cells, diameter 3–46 µm (33 µm), anticlines straight to somewhat curved; stomatal complexes anomocytic; stomata oval, often overlapped by epidermal cells and cuticular folds, 23–32 µm (28 µm) long, 18–25 µm (21 µm) wide; stomatal aperture spindle-shaped, 11–19 µm (15 µm) long, outer stomatal ledges thick, deeply staining; stomatal frequency 21; well cutinized, small, and simple trichome bases present, diameter 13–18 µm (15 µm). Cuticle distinctly but finely folded, folds radially oriented around stomata and trichome bases.

Remarks: Due to the traits complex of the cuneate base, the steeply ascending pair of secondary veins, and the irregularly crenate/serrate margin, this foliage cannot be mistaken for any other of the woody taxa of the Canarian laurel forests.

Smilacaceae

Smilax canariensis Willd.
(Figs. 156–162)

Material: Herbarium EDER no. 13 (11 herbarium sheets, cuticle from one sheet).

Leaf attachment alternate, leaf organization simple, petiole with climbing tendrils, 1.1–2.3 cm (1.8 cm) long, marginal petiolar attachment, laminar size notophyll – 1.5 : 1, length 4.3–10.0 cm (7.4 cm), width 2.5–11.2 cm (5.8 cm), ovate to elliptic, symmetrical, base angle wide obtuse, base shape cordate to hastate to convex, at the base above the veins some spines developed, apex angle acute, apex shape acuminate to straight to convex, margin entire and revolute.

Venation: basal actinodromous/campylodromous, bro-

chidodromous, 3–7 main veins originating at the base, medial one stronger than the lateral ones (= secondaries); secondaries basally recurved then straight, running into the leaf apex; tertiaries connecting the medial vein with the first pair of secondaries, tertiaries originating in acute angles from the medial vein, forming a network with wide meshes, tertiaries interconnecting the secondaries opposite to alternate percurrent, course straight to slightly sinuous; fourth and fifth-order veins regular polygonal reticulate, areolation moderately developed (4- to 5-sided); sixth-order veins dichotomizing; freely ending ultimate veinlets absent, un- to multi-branched, ultimate marginal venation mostly consisting of loops.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells often slightly elongated, 22–76 µm (48 µm) long, 18–39 µm (27 µm) wide, weakly undulate, anticlines very thick and U-shaped, wave length 26–49 µm (34 µm), amplitude 7–12 µm (9 µm). Marginal cells rectangular to isodiametric, long and short cells randomly alternating, anticlines straight, 19–62 µm (48 µm) long, 18–39 µm (26 µm) wide, distinctly striate, striation running parallel to the leaf margin.

Abaxial cuticle: thick, glabrous, non-modified epidermal cells 25–65 µm (43 µm) long, 10–31 µm (22 µm) wide, anticlines very weakly undulate; stomatal complexes (brachy)paracytic; stomata 21–32 µm (26 µm) long, 12–20 µm (15 µm) wide, epidermal wall of guard cells not distinguishable; stomatal aperture spindle-shaped, 13–22 µm (16 µm) long, outer stomatal ledges prominent, accompanied laterally by fine cuticular folds; stomatal frequency variable, 11–20 (16). Secretory pores(?) on veins occasionally present.

Remarks: Due to the basal actino-/campylodromous venation the leaves of this species cannot be mistaken for any other woody taxon of the Canarian laurel forests.

T h e a c e a e
Visnea mocanera L.
(Figs. 163–169)

Material: Herbarium EDER nos. 8, 25 (17 herbarium sheets, cuticles from 2 sheets).

Leaf attachment alternate, leaf organization simple, petiole short, 0.2–0.7 cm (0.4 cm) long, marginal petiolar attachment, laminar size microphyll – 2 : 1, length 2.9–6.8 cm (5.2 cm), width 1.4–3.1 cm (2.4 cm), elliptic, symmetrical, base and apex angle both acute, base shape convex to straight, apex shape straight and in the uppermost part convex, margin crenate, 6–7 teeth per centimetre, spacing somewhat irregular; tooth shape: basal side straight to convex, apical side convex, sinus rounded, apex non-specific glandular.

Venation: primary vein pinnate; secondaries festooned semicraspedodromous, course irregular, straight, curved to recurved, secondary vein spacing irregular, 0.4–0.8 cm, secondary vein angle decreasing towards the base, intersecondaries present; tertiaries mixed opposite/alternate percurrent, tertiary vein course convex to sinuous, very variable, tertiary vein angle to primary vein very variable, obtuse to sometimes acute, tertiary vein angle variability very inconsistent; fourth-order veins mixed opposite/alternate percurrent to polygonal reticulate, areolation moderately developed (5- to more-sided); fifth-order veins dichotomizing; freely ending ultimate veinlets unbranched to once or more times branched, ultimate marginal venation consisting of incomplete loops, veinlets which originate from loops formed by tertiaries enter the marginal teeth randomly between sinus and apex.

Adaxial cuticle: thick, glabrous, non-modified epidermal cells polygonal, diameter 20–56 µm (34 µm), anticlines straight to curved; marginal cells with the same characteristics, 14–44 µm (26 µm).

Abaxial cuticle: thick, non-modified epidermal cells polygonal, 16–43 µm (29 µm) in diameter, anticlines straight to slightly curved; stomatal complexes aniso-, anomotetracytic to cyclocytic with 3–5 subsidiary cells, subsidiaries staining slightly less intensely than non-modified epidermal cells; stomata oval to roundish, 26–37 µm (30 µm) long, 23–32 µm (27 µm) wide, epidermal wall of guard cells weakly developed; stomatal aperture oval, 11–19 µm (14 µm) long, outer stomatal ledges distinct, bordered by faint folds upon the guard cells, polar T- or I-pieces developed; stomatal frequency 15; simple trichome bases with strongly thickened margin scattered across the surface, trichomes not preserved; solitary, thick-walled, raised, multicellular cork-warts present, diameter of 28–45 µm (35 µm).

Remarks: *V. mocanera* foliage resembles *Prunus lusitanica* and *Maytenus canariensis* of the Canarian laurel forests. Differential characteristics to *P. lusitanica* are discussed above. *V. mocanera* can be distinguished from *M. canariensis* by the shape of the leaf base, which is convex to straight in *V. mocanera* but concavo-convex in *M. canariensis*. *V. mocanera* is characterized by the inconsistent network of the secondary and third-order veins, and by the the percurrent fourth-order venation. In *M. canariensis* the secondaries run in much smoother curves across the lamina, the secondary vein angle is rather uniform, the tertiary vein angle decreases slightly exmedially, and fourth-order veins are regular polygonal reticulate. Among the cuticular features, the stomata are distinctly bigger in *V. mocanera* than in *M. canariensis*.

Ur t i c a c e a e
Gesnouinia arborea (L. fil.) Gaudich
(Figs. 170–175)

Material: STU 8669, 885 (10 herbarium sheets, 2 cuticles).

Leaf attachment alternate, leaf organization simple, petiole 0.7–4.9 cm (2.1 cm) long, pilose, marginal petiolar attachment, laminar size microphyll – 2.5 : 1, length 4.2–10.8 cm (7.1 cm), width 1.8–4.8 cm (2.8 cm), elliptic, symmetrical, base and apex angle both acute, base shape convex to concave, apex shape straight, margin entire to erose; adaxial surface covered by secretory (white) dots.

Venation: suprabasal acrodromous, the central vein ending in the apex, the lateral ones ending in the apical third of the blade; secondaries weakly brochidodromous, one pair (sometimes two pairs) of fine and short secondary veins developed near the very base, running parallel to the leaf margin, secondary vein spacing increasing towards the base, 1.4–2.7 cm, secondary vein angle uniform, intersecondaries not developed; tertiaries opposite percurrent, tertiaries between the main veins hill-shaped, otherwise almost straight, convex to sinuous, tertiary vein spacing irregular, tertiary vein angle increasing towards the base, tertiary vein angle to primary vein mostly obtuse to sometimes acute; fourth-order veins sinuous and opposite percurrent; further venation not developed, ultimate marginal venation consisting of loops.

Adaxial cuticle: extremely delicate, non-modified epidermal cells polygonal with straight-running anticlines, cell arrangement radial around and over mesophyllous resinuous bodies, leaving a central pore for secretion discharge, diameter of non-modified epidermal cells 16–36 µm (27 µm); simple, one-celled, filiform trichomes abundant, often crooked, 73–167 µm (106 µm) long, slightly longer over veins; trichome bases simple, roundish, one-celled, marginally slightly thickened, diameter 6–21 µm (10 µm).

Abaxial cuticle: also extremely delicate, non-modified epidermal cells not discernible; stomata faintly visible, oval to roundish, 11–21 µm (16 µm) long, 9–15 µm (11 µm) wide, epidermal wall of guard cells indistinct, aperture oval, variable in shape, 4–13 µm (8 µm) long, outer stomatal ledges distinct, staining intensely; trichome bases and trichomes as described above.

Remarks: At first glance, isolated litter may resemble laurel foliage with suprabasal acrodromous venation. Even the areolation lacks ultimate veinlets, as in most of the Canarian Lauraceae. However, distinctive gross morphological traits are the thin texture and the thin basal veins running parallel to the margin. The cuticles are very delicate, and the stomatal complexes are not paracytic as in laurels. Moreover, the petiolar and laminar indumentum

are distinctive, and the trichome bases are very large. In untreated foliage, the adaxial leaf surface appears densely covered by secretory remains (white dots) when viewed with a hand lens. Cuticular investigation shows circular arrangement of non-modified epidermal cells around densely spaced mesophyllous resinuous bodies bordering a central opening which serves for secretory discharge (Fig. 175). The "white dots" visible in the untreated foliage are clearly situated above these openings. They become removed during the preparation process. It is remarkable that the mesophyllous secretory cells are visible neither in the untreated foliage nor in the cleared leaf under the binocular microscope but are evident when investigating the cuticle.

4 Results

The woody species of the Canarian laurel forests are mostly characterized by foliage with unlobed, simple leaf organization. Leaf margin variability is also rather limited, most taxa bearing either entire or crenate/serrate margins. Only three species/subspecies – *Jasminum odoratissimum*, *Bencomia caudata*, and *Sambucus nigra* ssp. *palmensis* – have compound leaves with serrate margin. Thus, gross-morphologically, easily recognizable variability is definitely more limited than in woody floras of temperate climates. For the here-presented study the specific foliar traits have been investigated thoroughly applying the cleared leaf method and cuticular analysis. The trait complexes are described in detail. Based on these results, an identification key relying exclusively on foliage has been developed. In detached and already decaying leaf litter, not all morphological features visible on in situ foliage may be preserved. For example, leaf arrangement on the twig remains unknown in isolated foliage; if leaflets are isolated, then leaf organisation (simple or compound) may be unclear. Also, the freely ending ultimate veinlets may no longer be preserved. The here-presented identification key considers these deficiencies to the extent possible.

5 Identification key for litter of isolated foliage

1 Blade with 3–7 main veins arising at the base and running into the leaf apex. . . . . . . **Smilax canariensis** (Figs. 156–162)
– Venation suprabasal acrodromous, the lateral main veins steeply ascending into the apical part of the lamina. – Leaf surface rough. . . . . **Gesnouinia arborea** (Figs. 170–175)
– Other. **2**

2 Leaf margin clearly serrate. **3**
– Leaf margin clearly crenate. **4**
– Leaf margin crenate/serrate. **7**
– Leaf margin entire. **8**
– Leaf margin variable or not unambiguous. **21**

3 Margin simple serrate, teeth regularly, densely and evenly

developed; secondary veins craspedodromous. . . . .
. . . . *Bencomia caudata* (Figs. 123–129)

– Margin simple to double serrate, teeth shape variable; secondary venation festooned semicraspedodromous. . . . .
. . . . *Sambucus nigra* ssp. *palmensis* (Figs. 15–20)

4 Tooth apices partly glandular. – Laminar size notophyll – 3 : 1; shape elliptic to obovate; secondaries numerous, densely spaced, not evenly parallel among each other. . . . .
. . . . *Arbutus canariensis* (Figs. 34–40)

– Tooth apices glandular. **5**

5 Distinct axillary glands developed at the origin of the secondaries; few secondaries, widely spaced, rather steeply ascending, inter-secondaries present. . . . .
. . . . *Rhamnus glandulosa* (Figs. 117–122)

– Two glands situated at the leaf base to the right and left of the midvein; secondaries numerous, regularly spaced and parallel among each other. . . . *Prunus lusitanica* (Figs. 130–136)

– Neither petiolar nor axillary glands. **6**

6 Secondaries rather regularly spaced, course regular, network of tertiaries regular; abaxial and adaxial cuticle glabrous. . . . . *Maytenus canariensis* (Figs. 28–33)

– Secondaries irregularly spaced, course irregular, network of tertiaries irregular; abaxial cuticle with simple, strongly thickened trichome bases. . . . .
. . . . *Visnea mocanera* (Figs. 163–169)

7 Laminar size notophyll; secondaries numerous, densely spaced; teeth regularly spaced and evenly sized, tooth apices partly glandular. . . . . *Arbutus canariensis* (Figs. 34–40)

– Laminar size microphyll; base decurrent, secondaries widely spaced, the basal pair steeply ascending; teeth shape and size variable, tooth apices non-glandular. . . . .
. . . . *Isoplexis canariensis* (Figs. 150–155)

8 Laminar size nanophyll – 3 : 1, laminar shape elliptic, base shape cuneate. . . . . . *Hypericum canariense* (Figs. 46–51)

– Laminar size microphyll. **9**

– Other. **13**

9 Laminar shape oblong. **10**

– Other. **11**

10 Laminar size 5–6 : 1; only mid vein distinct, secondaries hardly visible. . . . . *Euphorbia mellifera* (Figs. 41–45)

– Laminar size 3 : 1; secondaries distinct, regularly festooned brochidodromous, inter-secondaries developed. . . . .
. . . *Salix canariensis* (entire-margined leaf; Figs. 137–143)

11 Laminar size 1.5 : 1, laminar shape distinctly ovate; tertiaries percurrent. . . . . *Hypericum grandifolium* (Figs. 52–57)

– Laminar size 2 : 1, shape elliptic; secondaries recurved, tertiaries random reticulate, stomatal complexes (incomplete) amphicyclocytic to cyclocytic. . . . .
. . . . *Ilex canariensis* (entire-margined leaf; Figs. 1–7)

– Laminar size 2 : 1, shape ovate to somewhat elliptic; tertiaries regular polygonal reticulate, stomatal complexes paracytic. **12**

12 Leaf base symmetrical. . . . .
Jasminum odoratissimum (terminal leaflet; Figs. 101–106)

– Leaf base distinctly asymmetrical. . . . .
. . *Jasminum odoratissimum* (lateral leaflet; Figs. 101–106)

13 With a marginal fimbrial vein. . . . .
. . . . *Ilex platyphylla* (entire-margined leaf; Figs. 8–14)

– No fimbrial vein developed. **14**

14 Secondaries rather densely spaced and numerous. **15**

– Secondaries not densely spaced. **17**

15 Course irregular, somewhat fluttery, partly forking, partly recurved. – Mesophyllous secretory cells situated in the

areoles, peltate trichomes on the abaxial leaf surface. . . . . .
. . . . *Heberdenia excelsa* (Figs. 89–94)

– Course of secondaries regular, curved, rather parallel to each other. **16**

16 One to two inter-secondaries developed, stomatal complexes cyclocytic. . . . . . . *Sideroxylon marmulano* (Figs. 144–149)

– One to several inter-secondaries well developed, abaxial leaf surface covered by small peltate trichomes. . . . .
. . . . *Pleiomeris canariensis* (Figs. 95–100)

17 Stomatal complexes paracytic. **18**

– Other. **20**

18 Stellate trichomes positioned above complex trichome bases. – Laminar shape elliptic symmetrical to asymmetrical . . . .
. . . . *Viburnum tinus* ssp. *rigidum* (Figs. 21–27)

– Glabrous or simple trichomes positioned above simple trichome bases. **19**

19 Abaxial surface with epidermal resinuous cells. . . . .
. . *Apollonias barbujana* (entire-margined leaf; Figs. 58–63)

– Shape of stomatal complexes rhomboidal, anticlines strongly undulate, with several to numerous (indistinct) axillary glanduliferous domatia. . . . . . *Laurus azorica* (Figs. 64–69)

– Shape of stomatal complexes rather quadrangular, strongly thickened cuticular ledges bordering the stomatal aperture, in the basal part of the lamina with 2–3 distinct axillary domatia along the midvein. . . . . *Ocotea foetens* (Figs. 70–75)

– Non-modified epidermal cells dome-shaped and somewhat overlapping the stomata, anticlines straight to curved. . . . . .
. . . . *Persea indica* (Figs. 76–82)

20 Stomatal complexes anomocytic, peltate trichomes on two-celled trichome bases. . . . .
. . . . *Myrica faya* (entire-margined leaf; Figs. 83–88)

– Stomatal complexes cyclocytic, peltate glands ad- and abaxially developed, secondaries widely spaced, curved to recurved, course irregular. . . . . *Picconia excelsa* (Figs. 107–116)

21 Leaf margin entire to apically crenate to distinctly serrate; stomatal complexes anomocytic, peltate trichomes positioned on two-celled trichome bases. . . . .
. . . . *Myrica faya* (Figs. 83–88)

– Leaf margin entire to finely, hardly visible, crenate; laminar size microphyll – 3 : 1, shape oblong. . . . .
. . . . *Salix canariensis* (Figs. 137–143)

– Leaf margin finely erose to almost entire; laminar size notophyll – 2 : 1, shape elliptic; stomatal complexes paracytic, with epidermal resinuous cells. . . . .
. . . . *Apollonias barbujana* (Figs. 58–63)

– Leaf margin entire or with spiny, irregularly spaced or single teeth. **22**

22 Laminar size notophyll; margin revolute, with a marginal fimbrial vein. . . . . *Ilex platyphylla* (Figs. 8–14)

– Laminar size microphyll; no marginal fimbrial vein, secondaries recurved. . . . . *Ilex canariensis* (Figs. 1–7)

6 The fossil record

As mentioned in the introduction, some Canarian laurel forest species serve for comparison with Palaeogene and Neogene taxa of Europe and are regarded as relicts of the European Paleogene and Neogene laurel forests, e. g. *Visnea mocanera* (MAI 1995). The Cenozoic plant record includes many taxa of yet unknown systematic affinity on

the generic as well as on the family level. This study was designed to provide a better basis for their identification. We therefore briefly summarize the European fossil record of the families present today in the laurel forests of the Canary Islands. This summary follows BENTON (1993) and MAI (1995) and also adds new records.

A q u i f o l i a c e a e : Fruits resembling those of modern *Ilex* have occurred in Europe since the Maastrichtian, and leaves have been described repeatedly from the Upper Paleocene onwards. Although carpological remains of *Ilex* are well known from the European Palaeo- and Neogene, e. g. MAI & WALTHER (1991), unambiguous leaf remains are not as abundant, e. g. MÄDLER (1939), KVAČEK & WALTHER (1981, 1998), KVAČEK et al. (2008), WALTHER & KVAČEK (2008).

C a p r i f o l i a c e a e : Cretaceous leaf remains have been repeatedly assigned to *Viburnum*, but carpological remains are not older than Miocene. Seeds identical with those of modern *Sambucus* occur from the early Eocene onwards, but leaf records remain ambiguous.

C e l a s t r a c e a e : In Europe, *Celastrus*, *Euonymus*, and *Maytenus* have been reported since Paleogene time. However, there are hardly any reliable records of foliage.

E r i c a c e a e : Fossil flowers of an Ericalean s. l. affinity have been described from the Upper Cretaceous of Sweden (SCHÖNENBERGER & FRIIS 2001). First fruit- and seed remains are reported from the Upper Cretaceous of Europe, i. e. *Leucothoe*. Seeds resembling modern *Rhododendron* occur in the Upper Paleocene of Great Britain. The oldest record of *Kalmiophyllum* Kräusel & Weyland (emend. Schneider) derives from Eocene deposits of Ukraine (SCHNEIDER 2004). *Kalmiophyllum* and seeds of *Kalmia* are characteristic of Paleogene and Neogene lignite deposits of Germany. *Arbutus* has been repeatedly listed from Eocene through Pliocene time. By fructifications, the family shows great diversity, especially in the European Middle Miocene whereas the assignment of foliage to the generic level is usually difficult, e. g. KVAČEK & WALTHER (1990), KOVAR-EDER & HABLY (2006).

E u p h o r b i a c e a e : Flowers and fruits of Hippomaneae have been recorded from the Lower Eocene of Great Britain. *Euphorbia* is accounted for in the Paleogene and Neogene of Europe.

H y p e r i c a c e a e : Remains of *Hypericum* are known in Europe since Paleogene time.

L a u r a c e a e : Flower and remains of inflorescences of *Mauldinia* have been reported from the Cenomanian of Bohemia (ECKLUND & KVAČEK 1998). For secure botanical assignment of foliage to the family level, cuticle analysis is an indispensable tool. During the Paleogene and Neogene the family is widely documented, whereby the best and most diverse records are based on foliage but also on wood, fruits, and sometimes even flowers. With few exceptions, however, the assignment of foliage to modern genera is rather problematic, and the numerous fossil morphospecies are usually summarized as *Laurophyllum*. – *L. azorica* is regarded as the next living relative of *L. abchasica* (Kolakovsky & Shakryl) Ferguson (FERGUSON 1974). BŮŽEK et al. (1996) assigned the former *Laurophyllum hradekense* Kvaček & Bůžek to *Ocotea* based on axillary thickenings interpreted as axillary glands and the stomatal structures. The authors stated a close relationship to *O. foetens*. UZUNOVA & STOJANOVA (1999) proposed assigning *Laurophyllum pseudoprinceps* Weyland & Kilpper, among others, to *Ocotea*. This view is yet not widely accepted. The distinctive fruits of *Ocotea* prove the existence of at least four species of this genus from the Lower Eocene to the Upper Pliocene of Europe, of which *O. rhenana* Menzel and *O. heeri* (Gaudin) Mai are regarded as being direct fossil ancestors of *O. foetens* (MAI 1995).

M y r i c a c e a e : Leaves and fruits of Myricaceae are known since the late Cretaceous. Endocarps prove the existence of *Myrica* in Europe since early Eocene time. *Comptonia* (documented by foliage and endocarps) has a richer record in the Paleogene than during the Neogene.

M y r s i n a c e a e : The European record of this family, whose modern distribution is concentrated mainly in the southern hemisphere, is somewhat ambiguous and requires revision. *Pleiomerites reticulatus* Ettinghausen (foliage) derives from the Bohemian Paleogene. *Pleiomeropsis rottensis* Weyland, an inflorescence, has been described from the Siebengebirge, Germany. In the European Paleogene and Neogene, the Myrsinaceae are recorded as *Berendtia*, *Myrsinophyllum*, *Myrsinopsis*, *Pleiomeropsis*, and *Rapanea*.

O l e a c e a e : Foliage from the Cretaceous of Greenland has been assigned to *Fraxinus*, but these records are ambiguous. Winged fruits are as old as Oligocene. *Chionanthus* and *Forestiera* are known since Miocene time. The occurrence of *Olea* and *Syringa* is likely, but the records of *Ligustrum* and *Phillyrea* are doubtful. *Notelea* may be the fossil counterpart of *Picconia* (MAI 1995). Recently, foliage from different Paleogene and Neogene stratigraphic levels has been assigned to the morphogenus *Oleinites* because the exact generic assignment within the Oleaceae is ambiguous (e. g. SACHSE 2001, KVAČEK 2004, KOVAR-EDER & HABLY 2006).

R h a m n a c e a e : The fossil history of this family is rather difficult to unravel because numerous problematic fossils from Upper Cretaceous onwards have been assigned to it. Well-founded are the occurrences of *Frangula* fruit remains from the Eocene. Earliest records of *Paliurus tiliifolius* (Unger) Bůžek (foliage) derive from Europe and Siberia (Oligocene). Early Oligocene findings of *Ziziphus zizyphoides* (Unger) Weyland (foliage, fruits) are known from the Paratethys region. *Berchemia* foliage has been described from the Miocene and fruit records are known from the Pliocene.

Rosaceae: *Rubus* and *Prunus* have been reported since Eocene time, *Pyracantha*, *Rosa*, and *Crataegus* since the early Oligocene. MAI (1995) lists *Comarum*, *Mespilus*, *Potentilla*, and *Pyrus* as immigrants in Europe during Miocene time; in the Pliocene this is additionally true for *Agrimonia*, *Filipendula*, *Cotoneaster*, *Physocarpus*, and *Stephanandra*. Genera recorded exclusively based on foliar gross morphology are *Amelanchier*, *Cydonia*, *Fragaria*, *Malus*, *Spiraea*, and *Sorbaria*.

Salicaceae: Cretaceous records of foliage from Greenland and Bohemia assigned to *Populophyllum*, *Populites* and *Saliciphyllum* remain ambiguous. In Central Europe both *Salix* and *Populus* occur during the early Oligocene for the first time. Later, both genera are certainly species-rich, but due to leaf variability the species number remains unclear.

Sapotaceae: For this tropical family, MAI (1995) lists *Chrysophyllum*, *Dipholis*, *Illipophyllum*, *Palaquiophyllum*, *Sapotacites*, *Sapotispermum*, *Siderophyllum*, *Sideroxylon* and *Tetracolporopollenites* as having been reported from the Paleogene and Neogene of Europe. Especially Neogene records are ambiguous.

Scrophulariaceae: *Asarina*, *Gratiola*, *Limosella*, *Paulownia*, *Scrophularia*, and *Verbascum* have been described from the Paleogene and Neogene of Europe.

Smilacaceae: Leaves of *Smilax* are recorded since Cretaceous time, not only from Europe but also from North America and Armenia. Usually the foliage constitutes an accessory component at single sites. In Europe, *Smilax* already becomes extremely rare in the Middle Miocene. Late Miocene records were detected from the Pannonian basin (HABLY 1992; KOVAR-EDER & HABLY 2006).

Theaceae: According to carpological remains, Ternstroemioideae (*Eurya*, *Ternstroemia*, *Visnea*) and Camellioideae (*Gordonia*, *Polyspora*, *Hartia*, *Schima*) were widespread in Europe from the Paleogene onwards. Based on cuticle diversity, the fossil leaf record reflects a high diversity of this family as well. Modern Theaceae are one of the very few families whose cuticles have been investigated systematically (KVAČEK & WALTHER 1984a) as a basis for the identification of fossil foliage. Nevertheless, the assignment to modern taxa often remained vague, and foliage is often summarized as *Ternstroemites*. KVAČEK & WALTHER (1984b) were also unable to assign fossil material to the genus *Visnea*. The Theaceae leaf record of Bulgaria was investigated by BOZUKOV & PALAMAREV (1995), but *Visnea* was not discovered among the leaf remains. Since Middle Miocene time, the Theaceae record decreased in Europe due to climatic deterioration. Pliocene findings are already restricted to southern Europe.

Urticaceae: The oldest though not unambiguous record of the family is fruits of *Urticarpum* from the Cretaceous of Great Britain. The Boehmerieae have a continuous European record from the Paleocene to the Pliocene but lack any modern representative. Carpologically, *Fleurya*, *Laportea*, *Parietaria*, *Pilea*, and *Urtica* are present especially in the European Miocene. They are represented by herbaceous species in the modern European flora.

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