



Convergent morphology and anatomy in the microphyllous leaves of selected heathland Myrtaceae and Asteraceae

Veit M. Dörken¹ · Philip G. Ladd² · Robert F. Parsons³

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Abstract

Key message We examined leaves of a suite of microphyllous woody plants and describe a little-known form of leaf peltation for the first time and also investigate strongly reflexed leaves in two distantly related lineages.

Abstract Plants cope with a range of environmental conditions, especially related to water relations, and have developed an array of physiological and structural solutions to maintain a functional water balance. There has been considerable recent work on physiological solutions to water deficit but little attention paid to leaf characteristics. In many species there is a change in leaf form from seedlings to adults. We examine such changes in several small-leaved species from the distantly related Asteraceae and Myrtaceae, some of which develop micropeltate or reflexed leaves as adults. All are native to dry or seasonally dry sites. Three major morphological groups were recognised as follows: (1) leaves erect, nonpeltate and scale-like (*Ozothamnus hookeri*), (2) leaves erect and peltate (*Phaenocoma prolifera*, *Regelia inops*), (3) Leaves reflexed (*Olearia lepidophylla*, *Ozothamnus scutellifolius*, *Ozothamnus reflexifolius*, *Melaleuca diosmifolia*). The microphyllous peltation in *P. prolifera* and *R. inops* in the absence of a meristematic fusion/bridge differs from typically peltate leaves. These small-leaved taxa occur in open, high light environments which are very different from the mesic, shaded understorey habitats of typical peltate-leaved plants. Many small-leaved species have leaves closely appressed to the stem and often with recurved margins. The erect leaves are functionally similar to reflexed leaves. Environmental filtering leads to superficially similar plant forms that may have somewhat different ontological origins. Such morphological forms are examples of convergent evolution in distantly related species but within each family are likely phylogenetically related.

Keywords Scleromorphy · Xeromorphy · Isobilateral · Bifacial · *Melaleuca* · *Regelia* · *Ozothamnus* · *Olearia* · *Phaenocoma*

Introduction

This paper is part of a series (Dörken 2013; Dörken and Parsons 2016, 2017, 2018; Dörken et al. 2017, 2018, 2019a, b, 2020) dealing with foliar changes, leaf reduction and peltation in woody seed plants. Numerous scale- or imbricate-leaved seed plants show a distinct shift in their foliage from juveniles to adults. In several taxa, seedlings develop needle or broad foliar leaves before shifting to the mature strongly reduced scale or imbricate leaf type. In conifers this occurs in scale-leaved Cupressaceae like *Thuja*, *Thujaopsis*, *Cupressus*, *Chamaecyparis*, *Callitris* (Baker and Smith 1910; Coulter and Chamberlain 1928; De Laubenfels 1953; McMillan 1956; Langner 1963; Foster and Gifford 1974; Schütt 2004; Little 2006; Eckenwalder 2009; Dörken 2013; Dörken et al. 2019a) and Podocarpaceae like *Dacrydium* and *Dacrycarpus* (Brodribb and Hill 1998; Biffin et al. 2012; Dörken and Parsons 2016). In angiosperms such a foliar shift

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✉ Veit M. Dörken
veit.doerken@uni-konstanz.de

Philip G. Ladd
P.Ladd@murdoch.edu.au

Robert F. Parsons
r.parsons@latrobe.edu.au

¹ Department of Biology, University of Konstanz, Constance, Germany

² School of Environment and Conservation Sciences, Murdoch University, Murdoch, WA 6150, Australia

³ Department of Environment and Genetics, La Trobe University, Bundoora, Melbourne, VIC 3086, Australia

is observable in, e.g. *Myricaria* (Tamaricaceae; Dörken et al. 2017), *Melaleuca* (Myrtaceae; Dörken and Parsons 2018) and members of the Casuarinaceae (*Casuarina*, *Gymnostoma*, *Allocasuarina*; Dörken and Parsons 2017; Dörken et al. 2018, 2019b), Elaeocarpaceae (*Tetralochea*) and Haloragaceae (e.g. *Glischrocaryon*; Dörken et al. 2020).

In all taxa mentioned above, leaf reduction affects the entire leaf, but it can also affect only parts of the leaf, mostly when the lamina becomes strongly reduced, in some cases even entirely, so that photosynthesis is carried out by green leaf-like petioles (= phylloides) as is the case for numerous *Acacia*, *Jacksonia* and *Labichea* species (Fabaceae, Cabbage 1914; Howchin 1930; Pedley 1986). In other taxa, leaf reduction is so strong, that photosynthesis is restricted to leaf-like two-dimensionally flattened short shoots called phylloclades, as in numerous Asparagaceae like *Asparagus*, *Danae*, *Simele* and *Ruscus* (Cooney-Sovetts and Sattler 1987; Hirayama et al. 2007; Dörken and Jagel 2022) or *Phyllanthus* species belonging to sections Choretropsis and Xylophylla (Euphorbiaceae, e.g. Keng 1974; Santiago et al. 2006, 2008). Such phylloclades can also be found in gymnosperms like *Phyllocladus* (Podocarpaceae), where they are a fusion product of lateral shoots and the inserted foliage (Keng 1963, 1974, 1979; Tetzlaff 2005; Dörken et al. 2021). A fusion of strongly reduced leaves to the shoot axis can also be seen in some angiosperms, e.g. the Casuarinaceae (Fagales), where leaves are not only fused to the shoot axis but also to each other, forming longitudinal ridges (= phyllichnia) on the shoot surface (Wilson and Johnson 1989; Zamalota et al. 2006). Only the tips of the leaves remain free. This makes members of the Casuarinaceae easily distinguished from all other living angiosperms (Rao 1972; Zimpfer et al. 2004; Niinemets et al. 2005; Warrier et al. 2013). Thus, in Casuarinaceae the shoot cortex is surrounded by a green photosynthetic chlorenchyma and it is impossible to distinguish between leaf and shoot tissue (Dörken and Parsons 2017; Dörken et al. 2018, 2019b).

The specialised photosynthetic organ reduction outlined above is restricted to only a minority of taxa in a few families. In this study, we largely focus on the more common situation of taxa with leaves of normal structure but strongly reduced in size and with steep leaf angles from the stem. Such taxa are found where soils are nutrient poor and/or seasonal climate fluctuates widely, e.g., *Melaleuca* and *Regelia* (both Myrtaceae), *Ozothamnus* and *Olearia* (both Asteraceae). In some cases, the leaf bases and petioles are strongly adnate to the stem, while in others the lamina is closely reflexed against the stem.

The divergence of leaf laminae from a position perpendicular to the stem varies considerably in plant species and is considered to influence efficiency of light interception. In a community of sclerophyll shrubs and trees, mean leaf angle (MLA) ranged from 17° to 78° (Falster and Westoby 2003)

but species with strongly reflexed leaves (greater than 70° from the horizontal) such as *Styphelia dielsiana* (E. Pritz.) Sleumer (https://www.flickr.com/photos/jean_hort/51822664862) are uncommon and the study of such morphology is understudied.

This brief summary shows the large variation of leaf reduction in today's land plants. In addition to reductions of the overall leaf size, in some woody taxa like *Melaleuca* species of Series Peltatae (e.g. *Melaleuca foliolosa* A.Cunn. ex. Benth., *Melaleuca micromera* Schauer, *Melaleuca tamari-scina* Hook. and *Melaleuca thyoides* Turcz.) (Bentham 1866) and also in some *Regelia* species, e.g. *R. inops* (Schauer) Schauer, an unusual leaf type is formed in adults. While juvenile leaves are bifacial, foliar and flattened, the mature type is a minute peltate leaf as in *Melaleuca micromera* (Bentham 1866; Brophy et al. 2013; Dörken and Parsons 2018). Such peltation is striking and interesting because peltate leaves usually occur in perennial herbs native to swampy or aquatic habitats (Wunnenberg et al. 2021) which lack any kind of leaf reduction. In contrast peltate *Melaleuca* species are woody and native to habitats showing either seasonal water stress, soil infertility or a combination of both, and these conditions are suggested as the evolutionary/ecological drivers for their leaf reduction (Dörken and Parsons 2018).

In general, a range of environmental conditions can lead to leaf reduction. The most important are: (1) water deficit (e.g. Thoday 1931; Blum and Arkin 1984; Blum 1996; Bosabalidis and Kofidis 2002; Korner 2003; Parsons 2010; Seidling et al. 2012); (2) low temperatures, in some cases combined with water deficit (e.g. Parsons 2010) and (3) infertile soils (e.g. Loveless 1961, 1962; Beadle 1966; Seddon 1974; Hill and Merrifield 1993; Hill 1998; Salleo and Nardini 2000; Düll and Kutzelnigg 2011; Dörken and Jagel 2014; Dörken and Parsons 2016, 2017; Dörken et al. 2017). In addition to leaf reduction many morphoanatomical leaf characteristics can also be correlated to edaphic conditions such as low soil nutrient availability or can be related to water deficit. Such characteristics of leaves of many species can be assigned to xeromorphy and/or scleromorphy (Beadle 1966; Hill 1998; De Micco and Aronne 2012) and can only be studied from anatomical sections. A relatively simple definition of the scleromorphic syndrome is of small evergreen leaves of high leaf mass/unit area (LMA), with revolute margins on highly branched shrubs (Onstein and Linder 2016). A similarly concise definition of xeromorphs is plants that can withstand long periods of drought without injury (Maximov 1931). However anatomical variation in structures such as distribution of chlorenchyma, cuticle thickness, stomatal location and presence of trichomes is often correlated with water availability to the plant. Some of these structures can also be correlated with low soil nutrient content along with others such as sclerenchyma, cells with abundant phenolics and epidermal thickness that are usually

not associated with water relations (Table 3, also Dörken et al. 2020).

In this study we examine these anatomical traits in species with microphyllous leaves.

Even today the evolutionary interpretation of the presence of broad-leaved juvenile leaves in taxa having a strongly reduced mature foliage is rarely considered (but see Dörken et al. 2019a). Thus, this present study represents an examination based on primary data about leaf reduction and peltation in woody species following on from information previously gained by Dörken and Parsons (2016, 2017, 2018) and Dörken et al. (2017, 2018, 2019a, b).

All seven species we studied had very small adult leaves mostly less than 5 mm long, but of these, only *Ozothamnus hookeri* (DC.) Hook. f. has scale-like leaves that are erect and closely appressed to the stem. Of the other six, four have reflexed adult leaves and are from the Asteraceae (*Olearia lepidophylla* (Pers.) Benth., *Ozothamnus reflexifolius* Leeson & Rozefelds, *Ozothamnus scutellifolius* Hook. f.) and Myrtaceae (*Melaleuca diosmifolia* Andrews) while *Regelia inops* (Schauer) Schauer (Myrtaceae) and *Phaenocoma prolifera* (L.) D. Don (Asteraceae) have peltate adult leaves. Thus, in this study, we document in detail leaf structure in a range of species in order to investigate the pattern of leaf reduction, reflexion and peltation in two phylogenetically distantly related families.

Material and methods

Material

Six of the species studied are shrubs from southern Australia between 29° and 44° S from lowlands with a summer dry season, except for the alpine to subalpine *Ozothamnus hookeri*, and are usually from heath, scrub or woodland (Tables 1 and 2) while *P. prolifera* occurs in fynbos in a similar latitude in the Cape of South Africa.

Origin of plant material

Seed of five species (*Olearia lepidophylla*, *Ozothamnus reflexifolius*, *Ozothamnus hookeri*, *Ozothamnus scutellifolius* and *Melaleuca diosmifolia*) was obtained from Nindethana Seed Service, Post Office Box 2121, Albany, Western Australia, 6331. *R. inops* (seeds and mature branches) was collected from the field in Perth, Western Australia and *P. prolifera* (mature branches) was collected from the field in South Africa. Mature material of *Ozothamnus*, *Olearia* and *Melaleuca diosmifolia* was collected in the Botanic Garden Konstanz where the plants are cultivated in a temperate house during winter. We acknowledge that material from plants periodically grown in a temperate house may show some small effect on the morphology and anatomical features of the leaves compared to plants grown in their native habitat. However, obtaining seedlings and adult material from the wild of species that occur in areas that are difficult to access such as Tasmania was not possible. We are convinced the morphology and anatomy of the leaves would not

Table 1 Distribution, plant form and habitat notes for the species studied

Family/species	Australian states ^a	Plant form	Vegetation types, etc.	Soil notes	Altitude	References
Asteraceae						
<i>Olearia lepidophylla</i>	N, S, T, V, W	Shrub to 1.5 m high	Scrub, heath	Sandy	Lowland	VicFlora (2023)
<i>Ozothamnus hookeri</i>	T	Shrub to 2 m high	Grassland, heath	Peaty	Alpine, subalpine	Ohlsen et al. (2010)
<i>Ozothamnus reflexifolius</i>	T	Shrub to 1.3 m high	Heath, woodland, forest	Various	Lowland	Leeson and Rozefelds (2003)
<i>Ozothamnus scutellifolius</i>	T	Shrub to 1 m high	Dry hill sides	Various	Lowland	Curtis (1963)
<i>Phaenocoma prolifera</i>	S Africa	Shrub to 0.6 m high	Heath	Rocky, sandy	Lowland to montane	Hind (1996)
Myrtaceae						
<i>Melaleuca diosmifolia</i>	W	Shrub 1–3 m high	Heath	Sandy, clay	Lowland	Brophy et al. (2013)
<i>Regelia inops</i>	W	Shrub to 2.5 m high	Open forests	Sandy	Lowland	Bentham (1866)

^aN = New South Wales, S = South Australia, T = Tasmania, V = Victoria, W = Western Australia

Table 2 Ranges for mean annual values for some climatic parameters in the distribution of the species studied

Climatic parameters	<i>Olearia lepidophylla</i>	<i>Ozothamnus hookeri</i>	<i>Ozothamnus reflexifolius</i>	<i>Ozothamnus scutellifolius</i>	<i>Phaenocoma prolifera</i> ^a	<i>Melaleuca diosmifolia</i>	<i>Regelia inops</i>
General							
Köppen climatic type	Cfb, Csb, Bsk—Oceanic, Mediterranean, Cold semi arid	Cfb—Oceanic	Cfb—Oceanic	Cfb—Oceanic	Csb, Csa, Bsk—Mediterranean, cold semi-arid	Csb—Mediterranean	Csb—Mediterranean
Latitude (°S)	28.7–43.6	39.5–42.9	42.8–42.8	41.3–43.5	33.5–34.5	34.8–35.1	30.0–34.6
Rainfall							
Annual (mm)	100–2310	549–2786	584–614	526–1163	200–600	433–925	275–998
Mean summer (mm)	23–350	108–472	135–151	98–245	No data available	81–122	34–100
Mean winter (mm)	67–670	154–887	159–179	141–349	No data available	161–368	98–452
Temperature							
Mean annual max (°C)	7.3–27.0	5.9–18.7	14.8–15.4	10.0–17.5	25–35	17.5–19.1	17.9–27.1
Mean annual min (°C)	0.4–12.6	−0.6–7.2	5.2–5.6	1.4–8.3	10–20	8.5–14.7	8.3–13.0

Climatic data for Australian species derived from ALA (2018). Accessed May, October 2022

^aData for *P. prolifera* from <https://www.south-africa-tours-and-travel.com/south-africa-climate.html#The%20Temperatures>. Accessed Nov 2022

be greatly different from that of wild-grown plants, particularly as the cultivated plants are removed from the temperate house into the open during the warmer seasons.

Methods

For species where seedlings were examined (*Olearia lepidophylla*, *Ozothamnus reflexifolius*, *Ozothamnus scutellifolius* and *Regelia inops*) seeds were germinated and 10 seedlings of each grown in a temperate glasshouse with long day conditions in the Botanic Garden of the University of Konstanz, Germany. They were sown in a mixture of compost and vermiculite (5:1). The glasshouse temperature ranged from 25 °C (day) to 15 °C (night).

The leaf collection time depended on the time the plants took to produce their first subsequent leaves, their juvenile leaves and their mature leaves. This varied greatly between the species and adult leaves were taken from plants that were between 2–7 years old. Cotyledons and primary leaves were collected from young seedlings. Freshly collected material was immediately examined and processed for further investigations without a break to avoid any artifacts caused by dehydration. It was photographed and then fixed in FAA (100 ml FAA = 90 ml ethanol 70% + 5 ml acetic acid 96% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol.

The leaf and stem anatomy was studied from representative tissues from one plant (seedling or adult) in serial sections using the paraffin technique and subsequent astrablue/safranin staining (Gerlach 1984). Sections were prepared

with a thickness between 12 and 16 µm. Several leaves were used because transverse and longitudinal sections and SEM samples were needed. *Phaenocoma prolifera* leaves were rinsed for 2 min in Trichloromethane (CHCl₃) > 99% (Carl Roth) to test for cuticular material.

For scanning electron microscopy (SEM) analysis, the FAA-material was dehydrated in formaldehyde dimethyl acetal (FDA) for 24 h (Gerstberger and Leins 1978) and later critical point dried. Sputter coating was done with a Sputter Coater SCD 50 Bal-tec (Balzers). The specimens were examined with an Auriga Zeiss TM.

Macrophotography used a digital camera (Canon PowerShot IS2) and microphotography a digital microscope (Keyence VHX 500F) equipped with a high-precision VH mounting stand with X–Y stage and bright-field illumination (Keyence VH-S5). Determination of the cuticle thickness and the size of the epidermal cells were carried out with the Keyence VHX-500F software tool box. For each feature 10 measurements were made on each of 10 leaves and maximum and minimum values reported.

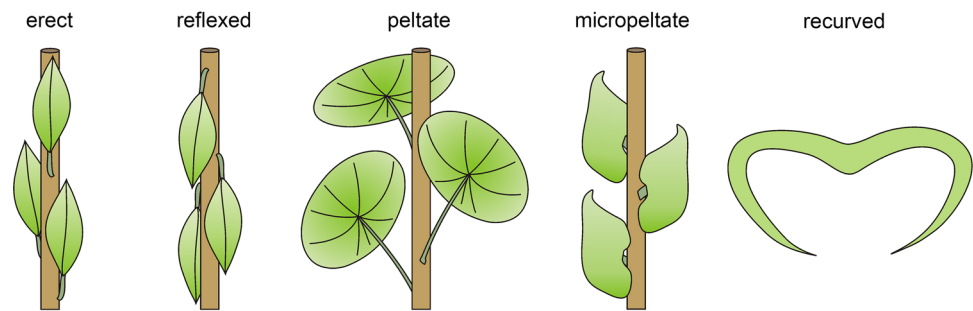
Special terms

Leaf morphology

Erect leaves: leaves that are either spreading at an upright angle from the shoot axis or have adaxial surfaces appressed to the shoot axis (Fig. 1).

Reflexed leaves: leaves are deflected down the stem more than 80 degrees from the horizontal (Fig. 1).

Fig. 1 Schematic drawings of the different leaf types examined and discussed in this study; in the micropeltate figure, the leaves are joined to the stem by minute petioles



Peltate leaves: large leaves with long petioles; the lamina is formed by a meristematic fusion/bridge and the petiole is attached within the leaf lamina rather than at the edge; due to the long petiole the lamina is located distantly from the stem, in some species e.g. waterlilies up to several meters (Fig. 1).

Micropeltate leaves: leaves that are strongly reduced in size with minute petioles and are formed in the absence of a meristematic fusion/bridge; due to the minute petiole the lamina is pressed closely to the stem or even appressed to it (Fig. 1).

Recurved leaves: the edge of the leaf curves towards the abaxial side to form an abaxial furrow (Fig. 1).

Leaf anatomy

There are three major terms describing leaf structure depending on abaxial–adaxial orientation: bifacial, isobilateral (aequifacial) and unifacial (e.g. Jurzitza 1987; Wagenitz 2008; Weiler and Nover 2008; Kück and Wolf 2009; Taiz et al. 2014; Kadereit et al. 2021). In English literature, the terms bi- and unifacial are common (e.g. Rudall 2007; Beck 2010), while aequifacial is rarely used and isobilateral is used instead.

Bifacial leaves: leaves with two clearly distinguishable surfaces, whose formation depends on their exposure to light. The upper light-exposed surface corresponds to the adaxial side, with strongly thickened epidermal cells, a thick cuticle and no or only few stomata. The lower surface corresponds to the abaxial side, with weakly thickened epidermal cells, a thinner cuticle and a high number of stomata. The mesophyll is dimorphic with palisade parenchyma towards the adaxial and spongy parenchyma towards the abaxial surface. Both leaf surfaces come into contact at the leaf margin. The vascular bundles are placed in a single plane, with xylem located towards the adaxial and phloem towards the abaxial side (Dörken and Parsons 2018).

Inverse bifacial leaves: these are similar to bifacial leaves. However, here the morphologically abaxial surface is the light-exposed one, and the morpho-anatomical structure becomes reversed, leading to the formation of an inverse structure, with palisade parenchyma towards the abaxial and spongy parenchyma towards the adaxial surface. The

vascular bundles are also placed in the same plane, but with xylem located towards the spongy parenchyma cells and phloem towards the palisade parenchyma (Dörken and Parsons 2018).

Isobilateral leaves (= aequifacial leaves): leaves that are mostly vertically orientated so that all parts are light-exposed, leading to the formation of the same morpho-anatomical features on both leaf surfaces. At the leaf margin both leaf surfaces come into contact. Stomata are developed on both sides with a similar density. Strongly thickened epidermal cells and thick cuticle are developed all over the surface and palisade parenchyma is developed on both sides. The vascular bundles are in the same plane. The part of the leaf that corresponds to the morphologically ad- or abaxial side can be recognized by the orientation of xylem (adaxial) and phloem (abaxial) (Dörken and Parsons 2018).

Unifacial leaves: leaves tubular in shape with no specific upper or lower side. Not relevant to plants in this study.

Phylogenetic relationships of the study species

The species we studied are in two widely separate families—the Myrtaceae in the Malvid/Rosid II clade and the Asteraceae in the Campanulid/Asterid II clade (Angiosperm Web Site 2023). The two Myrtaceae genera are closely related in the Melaleuceae that is considered to have separated from its sister taxon (*Osbornia*) in the early Eocene but did not begin to radiate in Australia until the Miocene (Thornhill et al. 2015) while the Asteraceae is considered to have originated on the South American plate in the late Cretaceous. However the tribes to which our species are assigned did not appear until the early Oligocene (Mandel et al. 2019) and likely began to radiate later. The Astereae (*Olearia*) and Gnaphalieae (*Ozothamnus*, *Phaenocoma*) are sister taxa so phylogenetically would be expected to show considerable similarity. The radiation of the groups to which our species belong is expected to have been primarily influenced by the aridification and soil nutrient loss of the southern Australia continent over the late Tertiary (see Byrne and Murphy 2020) so even in distantly related taxa this would have led to the evolution of species with similar morphologies due to adaptation to the prevailing environmental conditions.

Results

Foliar traits in the examined species

Morphological and anatomical features that relate to xeromorphy or scleromorphy of the species examined are listed in Table 3.

Olearia lepidophylla

Seedlings have 2 cotyledons and 2 primary leaves. These and the subsequent leaves on juvenile plants are small and spreading; however, they are distinctly larger (approximately 8 versus 1–2 mm long) than the adult leaves (Fig. 2a–c). Adults of *O. lepidophylla* are erect shrubs where the main stems have dense clusters of small leaves produced on short branchlets less than 4 mm long inserted in the axils of the larger leaves on the primary

stems (Fig. 2b, c). Later some axillary shoots become elongated. The leaves are alternate, and on strongly growing shoots they are somewhat spreading to reflexed. The leaf base is adnate to the shoot axis. The leaves on leading shoots (Fig. 2c) are orbicular to broadly ovate, flattened to slightly concave, 1.0–2.0 mm long and 0.5–1.2.0 mm wide. Those on the axillary shoots are narrowly ovate, flattened to cylindrical, 0.3–1.0 mm long and 0.3–0.5 mm wide. The leaf margin is slightly revolute. The adaxial surface is more or less glabrous (Fig. 2d), sometimes sparsely pubescent while the abaxial side is densely cottony-pubescent (Fig. 2e, f). The leaves are bifacial with a well-developed palisade parenchyma under the light exposed adaxial surface and spongy parenchyma located abaxially (Fig. 2f, g). There are no sclerenchymatic tissue layers; however, the outer periclinal cell walls of the epidermal cells are three times as thick as the other walls (Fig. 2g). Stomata are exclusively abaxial (Fig. 2f, h) and are not encrypted or deeply sunken in the epidermal layer

Table 3 Foliar traits in the examined species that are related to xeromorphy and scleromorphy

Trait	<i>Olearia lepidophylla</i>	<i>Ozothamnus hookeri</i>	<i>Ozothamnus reflexifolius</i>	<i>Ozothamnus scutellifolius</i>	<i>Phae-nocoma prolifera</i>	<i>Melaleuca diosmifolia</i>	<i>Regelia inops</i>
Xeromorphic trait							
Recurved leaf margins	Yes	Yes	Yes	Yes	Yes	No	No
Cuticle > 2 µm	Yes	No	Yes	Yes	Yes	Yes	Yes
Stomata surrounded by a cuticular rim	No	Yes	Yes	No	Yes	Yes	Yes
Stomata protected by cottony trichomes	No	No	Yes	No	Yes	No	No
Leaf amphistomatic	No	Yes	Yes	No	No	Yes	Yes
Presence of trichomes	Yes	Yes	Yes	Yes	Yes	No	No
Scleromorphic trait							
Abundant sclerenchyma	No	No	No	No	No	Minor	Minor
Cells rich in phenolic substances	No	No	No	No	No	Petiole	Yes
Thicker epidermis (> 20 µm)	Yes	No	No	Yes	Yes	No	No
Xero- and scleromorphic trait							
Denser leaf tissue (~ < 20% intercellular space in the leaf), often reduced spongy parenchyma compared with palisade	No	Yes	No	No	No	Yes	No
Large sub-stomatal cavity	Yes	No	Yes	Yes	Yes	Yes	Yes
Leaf type							
Leaves reflexed or peltate	Reflexed	Neither	Reflexed	Reflexed	Peltate	Reflexed	Peltate

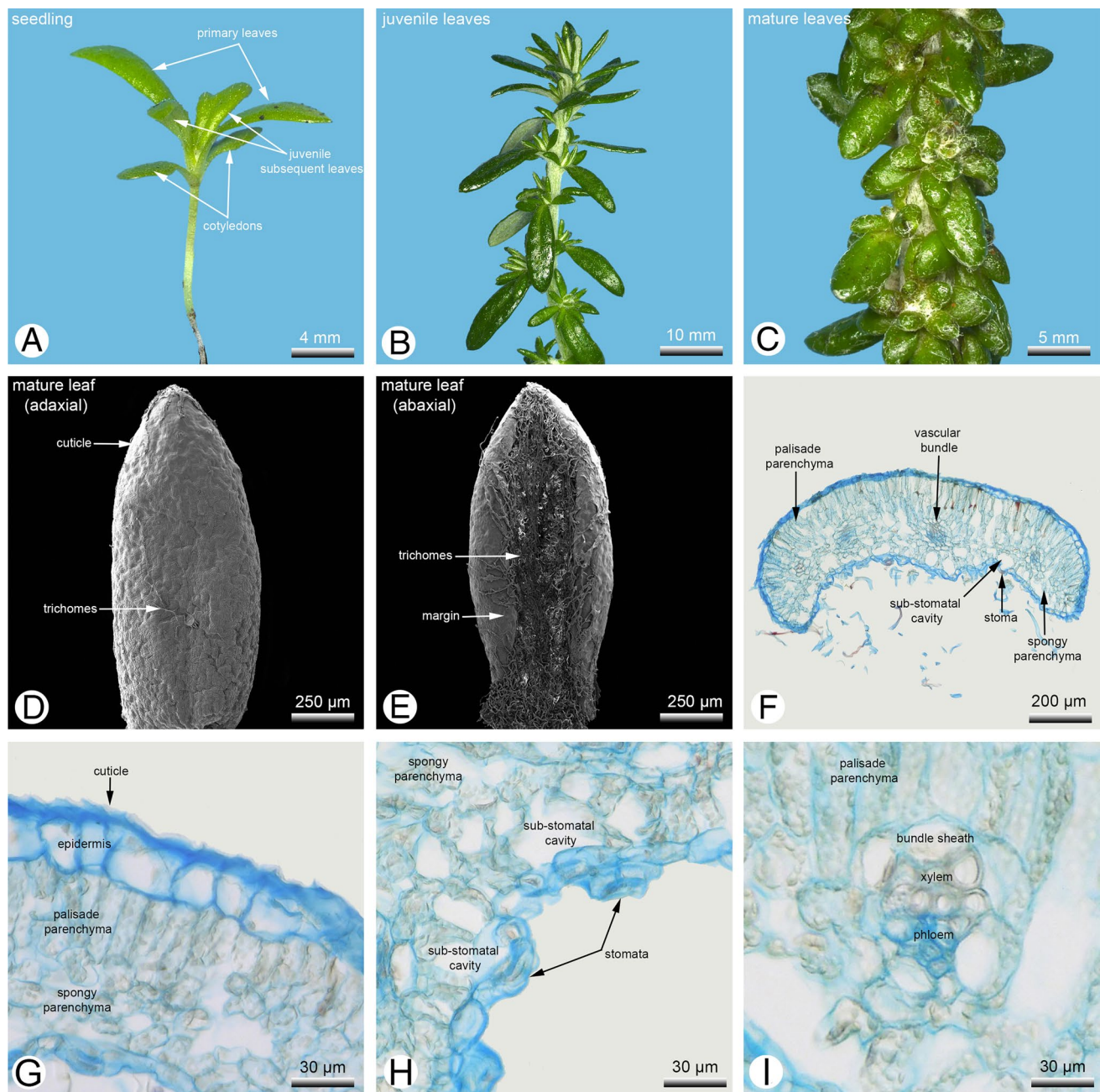


Fig. 2 *Olearia lepidophylla*, **a** seedling; **b** juvenile shoot; **c** foliate mature shoot axis; leaves reflexed; **d–i** mature leaves; **d** adaxial surface; (SEM-image); **e** abaxial surface; (SEM-image); **f** bifacial leaf

structure (microtome cross section); **g** epidermis with an approximately 2 µm cuticle; **h** stomata; **i** collateral vascular bundle showing the bundle sheath

(Fig. 2h) but each is surrounded by a distinct cuticular rim (Fig. 2h) and underlain by a large sub-stomatal cavity (~30 µm, Fig. 2h). There are several collateral vascular bundles in the central part of the mesophyll, with xylem located towards the adaxial and phloem towards the abaxial surface, and each bundle is surrounded by a bundle sheath (Fig. 2i).

Ozothamnus hookeri

Only the mature shoots and leaves of *O. hookeri* were examined as an example of an *Ozothamnus* species without reflexed leaves. There is no long-shoot/short-shoot differentiation (Fig. 3a). The shoot surface is covered with white, long, dense trichomes that are visible in the short

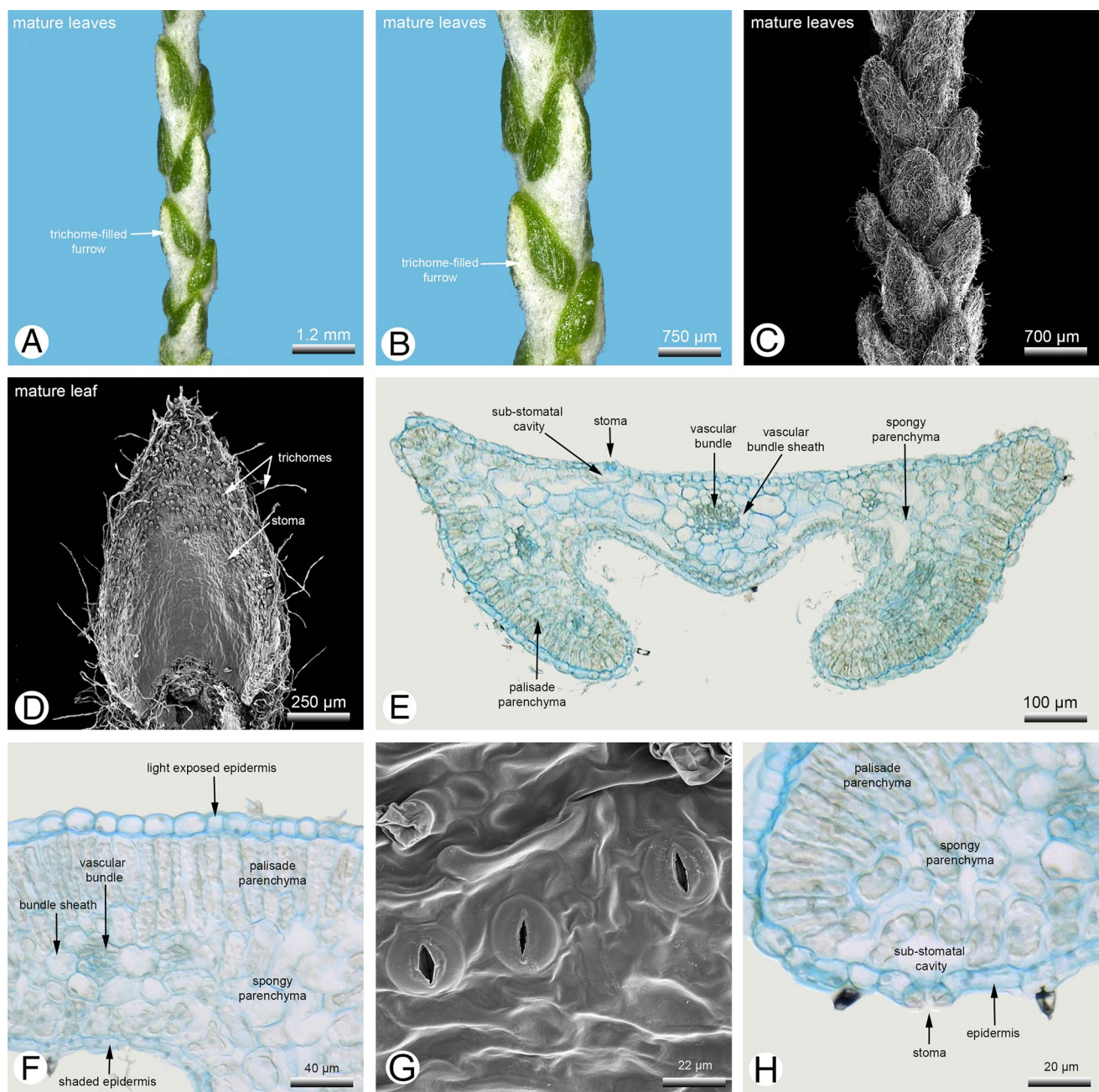


Fig. 3 *Ozothamnus hookeri*, shoots and foliage of mature individuals **a** mature shoot axis; **b** detail of **a**; **c** shoot axis with strongly appressed leaves (SEM-image); **d** adaxial leaf surface (SEM-image); **e** extreme recurving of the lamina. The abaxial surface is restricted to

the central furrow (microtome cross section); **f** detail of the leaf tissues; **g** stomata not encrypted but surrounded by a distinct cuticular rim (SEM-image); **h** stomata and epidermis in the same plane

internodes between the leaves (Fig. 3a–c). The leaves are erect, alternate, ovate-lanceolate, 1.0–1.5 mm long and 0.5–0.8 mm wide (Fig. 3a–d). The leaf lamina is markedly appressed to the shoot axis so that the central part of the adaxial surface becomes shaded while the edges of the adaxial and the abaxial surface are light exposed (Fig. 3a–c). Due to the recurved leaf margin the edge of the leaf curves into a large abaxial furrow, which is

filled with dense whitish trichomes (Fig. 3a, b). These trichomes, and those on the light exposed parts of the leaf margin are long, (up to 400 μ m) while those on the shaded parts of the leaf surface are shorter (100–300 μ m), cylindrical, strongly crinkled and multicellular. Palisade parenchyma is formed in the light-exposed curved parts of the adaxial side of the leaf, while it is absent from the central part. Spongy parenchyma is formed towards the

cottony abaxial furrow and the central part of the adaxial surface (Fig. 3e). There are no sclerenchymatic tissues (Fig. 3e, f). There is a thin adaxial cuticle (3.8–8.2 μm , Table 5) covering the epidermis (Fig. 3f). The leaves are amphistomatic with stomata developed all over the shaded adaxial surface (Fig. 3h) while on the abaxial surface they only occur in the trichome filled furrow and more or less

in the same plane as the epidermis (Fig. 3h). They are not encrypted but are covered by dense trichomes. Each stoma is surrounded by a distinct cuticular rim (Fig. 3g). The sub-stomatal cavity is from 20–30 μm (Fig. 3h). There are some collateral vascular bundles, with adaxial xylem and abaxial phloem. Each bundle is surrounded by a distinct bundle sheath (Fig. 3e).

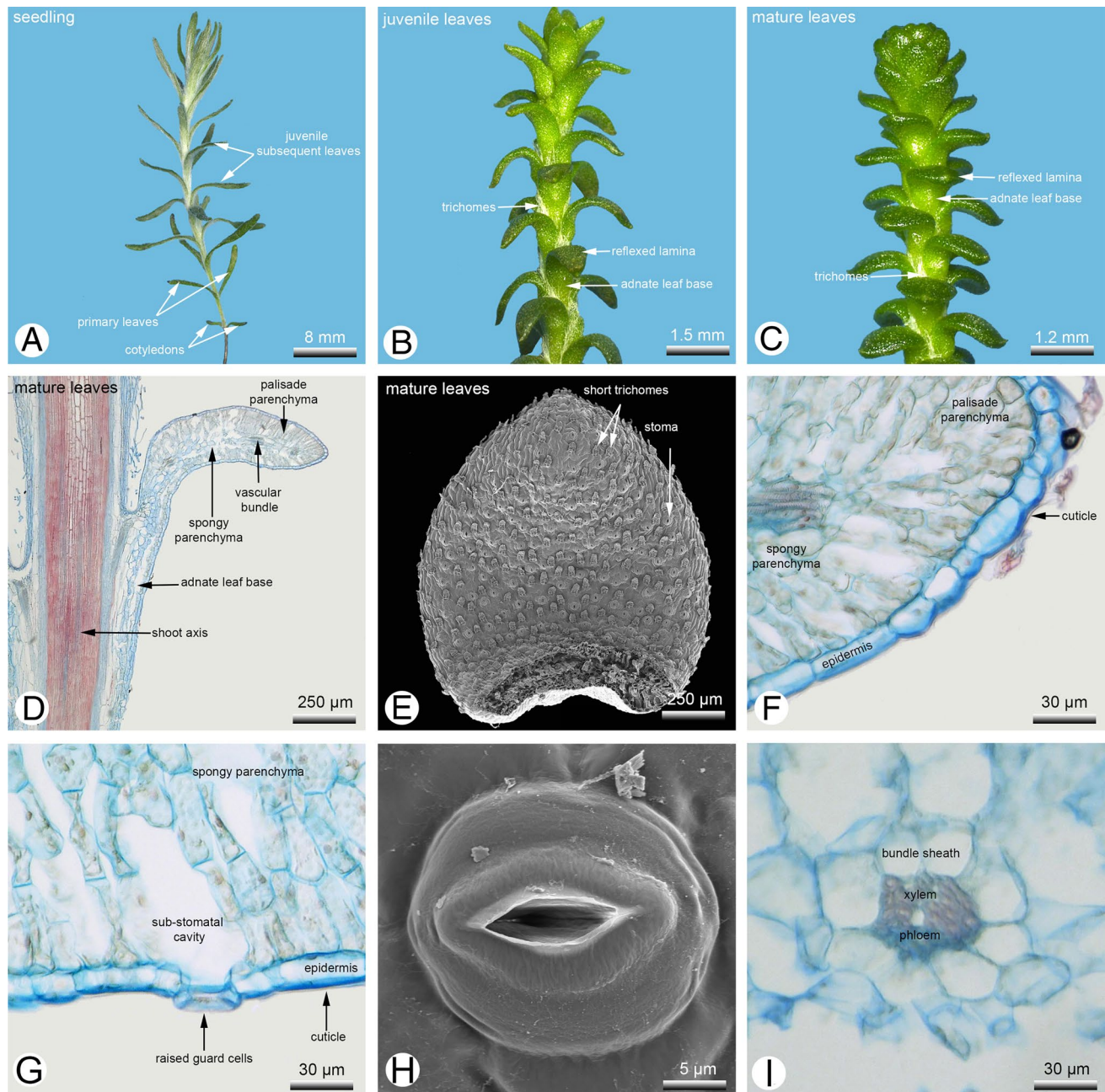


Fig. 4 *Ozothamnus reflexifolius*, **a** seedling; **b** shoot axis of a juvenile individual; **c–i** morphology/anatomy of mature shoots and leaves; **c** mature shoot; **d** longitudinal section of a shoot axis and an inserted leaf; **e** adaxial leaf surface (SEM-images); **f** epidermis; **g** the guard

cells of the stomata are slightly raised above the general level of the epidermis; **h** stoma surrounded by a distinct cuticular rim (SEM-image); **i** collateral vascular bundle

Ozothamnus reflexifolius

The 2 cotyledons, 2 primary leaves and the subsequent juvenile leaves are small, but longer than adult leaves (Fig. 4a, b). The shoot system lacks a differentiation into long- and short shoots (Fig. 4b), with alternate leaves (Fig. 4b, c). The internodes are short and densely covered with whitish trichomes (Fig. 4b, c). The leaf base is strongly adnate to the shoot axis so that the shoot cortex is mostly surrounded by leaf tissue. The lamina is spreading and may vary between juvenile and adult being reflexed at from 20° to 80° from the horizontal (Fig. 4b, c; illustrations in Leeson and Rozefelds 2003). The adaxial surface is light exposed and the abaxial one shaded (Fig. 4b, c). The lamina is ovate, 0.3–1.4 mm long and 0.3–1.0 mm wide. The leaves have a bifacial structure, with palisade parenchyma located towards the light exposed adaxial surface and spongy parenchyma towards the abaxial one (Fig. 4d). There are no sclerenchymatic tissue layers, except the xylem in the vascular bundle. The leaves are amphistomatic. Stomata are not encrypted, but placed between numerous small cylindric, multicellular trichomes (Fig. 4e) that do not cover the stomata (Fig. 4e). Stomata are slightly raised above the general level of the epidermis (Fig. 4g), are surrounded by a distinct cuticular rim (Fig. 4g, h) and are underlain by a large sub-stomatal cavity (greater than 30 µm). The epidermis is covered with a cuticle 3–4 µm thick (Fig. 4f, g). There are numerous collateral vascular bundles, with xylem located towards adaxial and phloem abaxial surfaces. Each bundle is surrounded by a distinct bundle sheath (Fig. 4i).

Ozothamnus scutellifolius

This is an erect plant with a shoot system that has no long-shoot/short-shoot differentiation (Fig. 5b). The primary axis of the seedling is densely pubescent and covered with whitish trichomes (Fig. 5a). The 2 cotyledons, the 2 primary leaves and the subsequent foliage have a comparatively broad lamina (Fig. 5a) but the size of subsequent leaves on juveniles becomes strongly reduced. The petiole is long, erect and closely appressed to the shoot axis. The margin of the lamina is markedly reflexed and strongly convex (Fig. 5d–f). The adaxial leaf surface is sparsely covered with short (< 50 µm), multicellular trichomes (Fig. 5g) while the abaxial surface is densely pubescent with cottony, whitish trichomes (Fig. 5a–d). Mature leaves are even more reduced in their overall size (Fig. 5d, e). The distal free part of the lamina is broadly ovate and 0.3–1.0 mm long and 0.3–0.8 mm wide. The adaxial surface is light-exposed while the abaxial one is shaded. The epidermis is covered with a cuticle (10–19 µm on the adaxial surface) that is at least twice as thick as the outer wall of the epidermal cells (Fig. 5j, k). Stomata are developed exclusively on the pubescent abaxial

surface and densely covered by the trichomes (Fig. 5h). They are not encrypted and are located more or less in the same plane as the epidermis (Fig. 5k) where each is surrounded by a distinct cuticular rim (Fig. 5k). The leaves have a bifacial structure with dense palisade parenchyma located towards the light exposed adaxial and spongy parenchyma with large intercellular spaces towards the shaded abaxial surface (Fig. 5k).

Phaenocoma prolifera

This plant is an erect densely branched shrub. The shoot system of adult shrubs is differentiated into long- and short-shoots (Fig. 6a, b). Long leader shoots produce alternate, closely arranged lateral short branches bearing very reduced, densely packed leaves (Fig. 6b, c). The main photosynthesis is carried out by the short shoot leaves. The leaves are alternate, ovate to triangular, about 0.3–0.6 mm broad, 0.6–1.0 mm long and slightly convex (Fig. 6e). They are erect and strongly appressed to the shoot axis so that the abaxial surface is light exposed and the adaxial shaded (Fig. 6d). The leaves are weakly imbricate and cover each other slightly (Fig. 6b, c). The young, still developing leaves are non-peltate (Fig. 6f) but develop a minor peltation in basal parts as they mature (Fig. 6e). Peltation is caused by pronounced expansion of the spongy mesophyll cells on the abaxial side of the vascular bundle distal to where the petiole attaches to the leaf lamina. The petiole is extremely short and located in the lower fourth on the adaxial surface (Fig. 6g). The light exposed abaxial surface is glabrous with no stomata. On very young leaves of adult plants platey material staining blue to violet is very thick (up to 57 µm) on the abaxial surface but becomes thinner (~ 33 µm) as the leaf expands (Fig. 6e, h). This is cuticular material as shown by the SEM image and the fact it can be removed by the solvent Trichloromethane (CHCl₃). The adaxial shaded surface is covered by dense unicellular hairs (Fig. 6d) and the cuticle is markedly thinner (1–2 µm) than the abaxial one. The cells of the abaxial epidermis are much more inflated than those of the adaxial shaded side (Fig. 6e, i) and stomata are developed exclusively on the adaxial surface. They are not encrypted and are more or less in the same plane as the epidermal cells (Fig. 6i, j, k). Each stoma is surrounded by a distinct raised cuticular rim (Fig. 6k). The inner sub-stomatal cavity is large (> 40 µm) and in contact with the larger intercellular spaces of the spongy parenchyma (Fig. 6h). The leaves are inverse-bifacial. A single layer of palisade parenchyma is located towards the abaxial side and spongy parenchyma towards the adaxial one. There is one main vascular bundle supplying the leaf and smaller, more peripheral ones (Fig. 6e, i). It has a collateral structure with xylem located towards adaxial and phloem towards abaxial and a distinct bundle sheath of parenchymatic cells (Fig. 6i). There is no

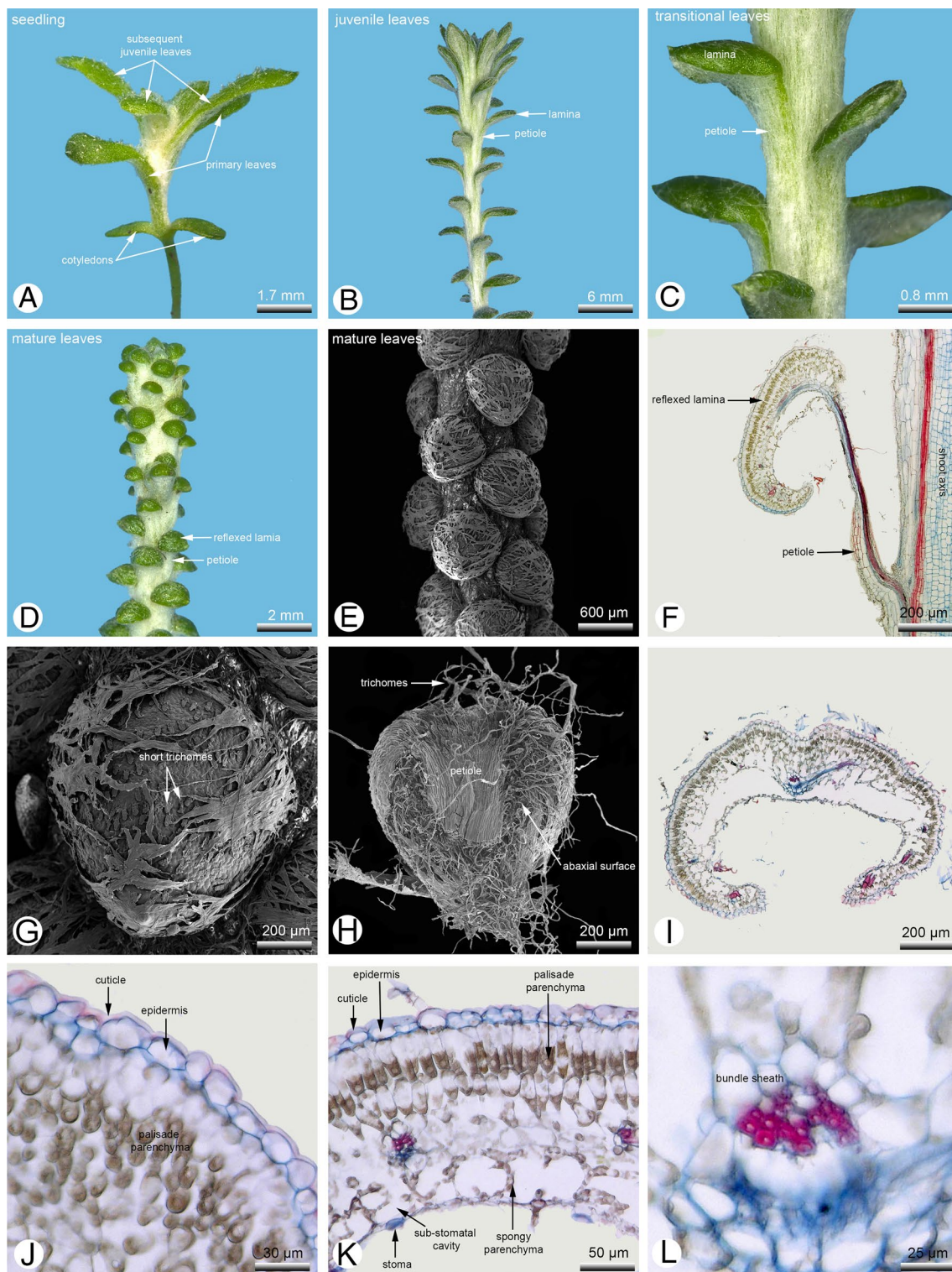


Fig. 5 *Ozothamnus scutellifolius*, **a** seedling; **b** juvenile shoot; **c** shoot of a juvenile showing transitional leaves leading towards the mature leaf type; **d–l** mature leaves; **d**, **e** foliate shoot; **d** shoot axis; **e** SEM-image; **f** longitudinal section of a leaf and shoot axis; **g** adaxial lamina surface; there are no stomata (SEM-image); **h** abaxial surface; **i**

bifacial leaf structure, (the adaxial epidermis that has separated from the mesophyll is a preparation artefact, microtome transverse section); **j** epidermis with a cuticle thicker than the outer epidermal cell wall; **k** stomata in the same plane as the epidermal cells; **l** collateral vascular bundle

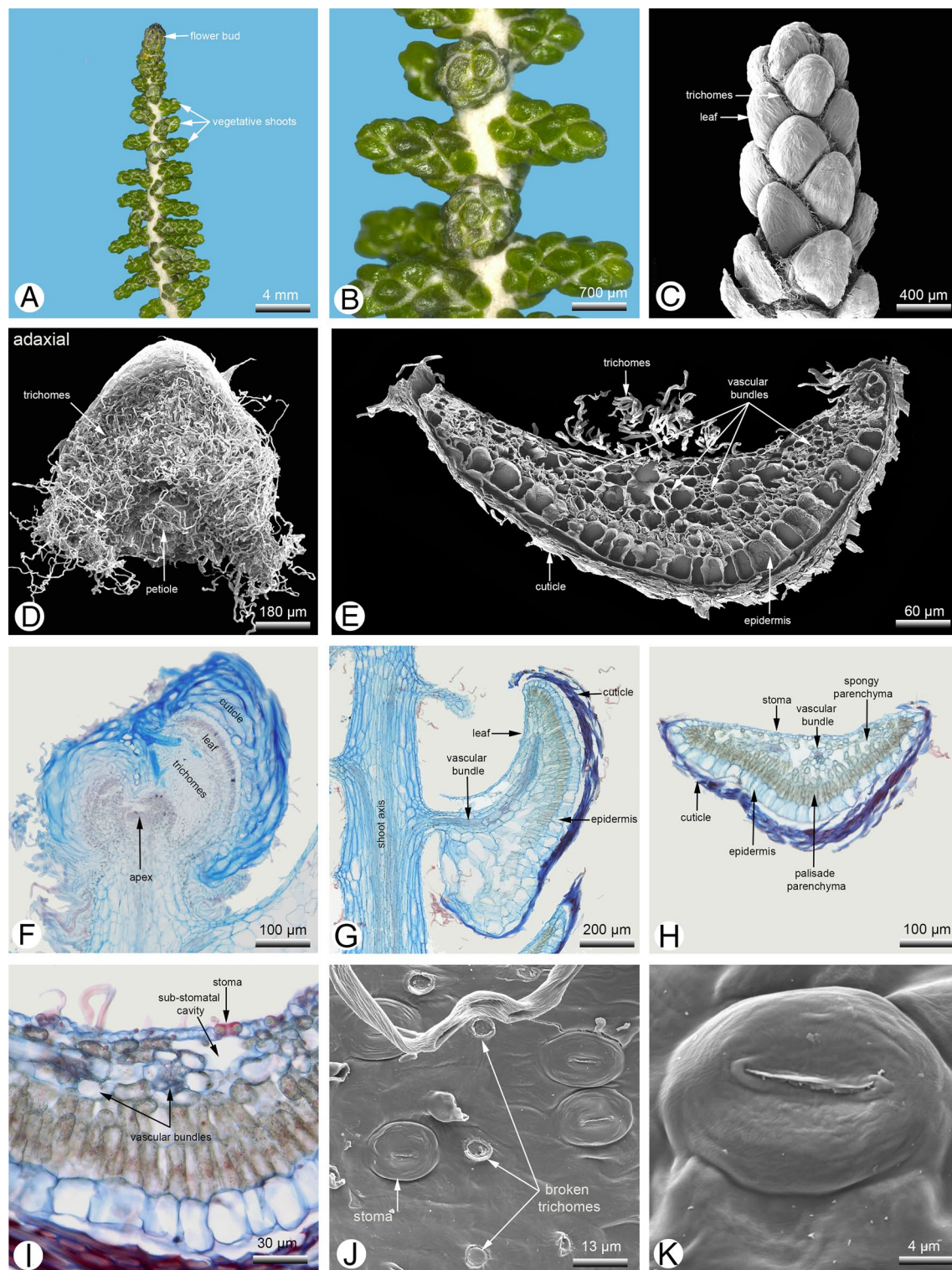


Fig. 6 *Phaenocoma prolifera*, **a** mature long shoot with short axillary branches; **b** detail of **a**; **c** shoot axis (SEM-image); **d** adaxial leaf surface (SEM-image); **e** cross section (SEM-image) of a mature leaf showing the large abaxial epidermal cells compared with the much smaller adaxial epidermal cells, the cuticle shows a platey structure and is separated from the abaxial epidermis (preparation artefact); **f** longitudinal section of the shoot apex; young leaves not peltate; **g** longitudinal section of a shoot axis and a peltate leaf; **h** cross sec-

tion of a mature leaf above the insertion of the petiole showing the inverse bifacial structure; the detachment of the cuticle from the epidermis is a preparation artefact; **i** vascular bundle; the detachment of the cuticle from the epidermis is a preparation artefact; **j** adaxial surface (for a clearer view most trichomes were removed); stomata not encrypted and located between the trichomes (SEM-image); **k** stoma surrounded by a distinct cuticular rim (SEM-image)

evidence of non-vascular additional sclerenchymatic fibers (Fig. 6i).

Melaleuca diosmifolia

Melaleuca diosmifolia is an upright shrub with almost virgate stems. The leaves have a distinct petiole approximately 1 mm long. Depending on the age of the shrub the petiole is either plagiotropic with young leaves spreading from the shoot axis, (Fig. 7a) or is markedly recurved leading to strongly reflexed mature leaves (Fig. 7b–d). Thus, adult leaves overlap each other, so that only about two-thirds of the lamina is directly light exposed. The leaves are alternate, narrow ovate to narrow elliptic, 6–8 mm long and 4–5 mm wide. The petiole is narrow and cylindrical and consists of small densely packed equidimensional cells, which are rich in phenolic substances, marked by the intensive red-violet staining (Fig. 7e, f). There is a sharp border between the tissues of the petiole and the lamina (Fig. 7e). Below the petiole insertion there is a strip of corky tissue (phellem) that extends to a lower node on the stem. A strip of heavily staining phelloderm cells attached to the shoot cortex passes abruptly to regular files of phellem cells that show sparse cell contents and are lignified towards the outside of the tissue (Fig. 7e, f). The lamina is flat and isobilateral with a palisade parenchyma on both sides of the leaf (Fig. 7g, h) but with more elongate cells on the adaxial side (Fig. 7h). The spongy parenchyma has only small intercellular spaces and is more extensive with slightly larger intercellular spaces on the abaxial side than the adaxial. The lower and upper epidermal cells are of similar size. Cuticle on the adaxial side is slightly thicker (3–4 µm) than on the abaxial surface (~ 1 µm, Fig. 7h). Numerous large oil glands are located in the mesophyll of the lamina and also in the petiole. In the collateral vascular bundles xylem is located towards adaxial and phloem towards abaxial with a considerable sclerenchyma developed below the phloem. The vascular bundle and phloem fibres are surrounded by a distinct bundle sheath consisting of large-sized (> 20 µm) parenchymatic cells (Fig. 7k). The leaves are amphistomatic with stomata developed on both sides (Fig. 7g). The stomata are not encrypted but are surrounded by a distinct raised cuticular rim (Fig. 7i, j) and have a relatively large sub-stomatal cavity (Fig. 7g, h).

Regelia inops

The 2 cotyledons, the 2 primary leaves and the subsequent juvenile leaves have a well-developed lamina approximately 10 mm long and 2 mm wide, spread widely from the shoot axis (Fig. 8a) and are non-peltate (Fig. 8a). The primary shoot axis of the seedlings is glabrous. The adult plant is erect with a shoot system differentiated into long- and short shoots. Long erect leader shoots produce branches

of smaller, densely spaced leaves from leaf axils at intervals along the stem. On juveniles, the leaves become more and more reduced, so that they are finally strongly reduced on adults (Fig. 8b). The leaves are ovate to lanceolate and on leaders they are twice the length of those on the lateral branches (5–7 mm vs. 2–3 mm). The mature leaves are opposite, erect and strongly appressed to the shoot axis so that the abaxial surface becomes light exposed and the adaxial one shaded (Fig. 8b). The leaves on the leaders are much more closely appressed to the stem than the shorter leaves that have an angle of about 25 degrees away from the stem. The leaves are imbricate and cover each other so that only about one half or one third of the lamina is light exposed (Fig. 8b). They are weakly peltate, with an extremely short petiole located in the lower fifth on the adaxial surface (Fig. 8d, f, g, h) so that the leaves are attached closely to the stem, which leads to the formation of a circular depression in the basal part of the leaf at its attachment (Fig. 8d, f, g, h). There is a very narrow extension at the leaf base that expands as the leaf ages to form the lower part of the peltate morphology. Both surfaces are glabrous with a cuticle from 3–7 µm on the adaxial surface (Fig. 8i, j, l) and sparse trichomes are only developed on the leaf margin (Fig. 8c, d, h). The leaves are inverse-bifacial with palisade parenchyma located towards the light exposed abaxial and distal adaxial side but with spongy parenchyma towards the shaded proximal part of the adaxial surface. Cells of the palisade parenchyma are rich in phenolic substances, marked by the intensive red staining. Large oil glands occur in the mesophyll (Fig. 8e, f). The leaves are amphistomatic with stomata on both surfaces, the abaxial ones having larger sub-stomatal cavity than the adaxial ones (Fig. 8e, j). Stomata are not encrypted and are more or less in the same plane as the epidermal layer (Fig. 8j, l). There is no pubescence, and each stoma is surrounded by a distinct cuticular rim (Fig. 8k). Cells of the abaxial light exposed epidermal layer are larger and have thicker walls than the adaxial ones (Fig. 8e). The vascular bundles have a collateral structure with xylem located towards ad- and phloem towards abaxial surfaces. There is a bundle sheath that is more distinct in LS than TS (Fig. 8e, l). Sclerenchyma with strongly thickened and lignified walls occurs below the phloem of each vascular bundle (Fig. 8e, l).

Discussion

Our study extends previous work examining the change in morphology and anatomy of selected species with very small adult leaves in their transition from juvenile to mature forms (Dörken and Parsons 2018; Dörken et al. 2019a, b). All the species for which we had juvenile and adult foliage are characterised by marked changes in leaf size, shape and orientation with plant age. In all of them

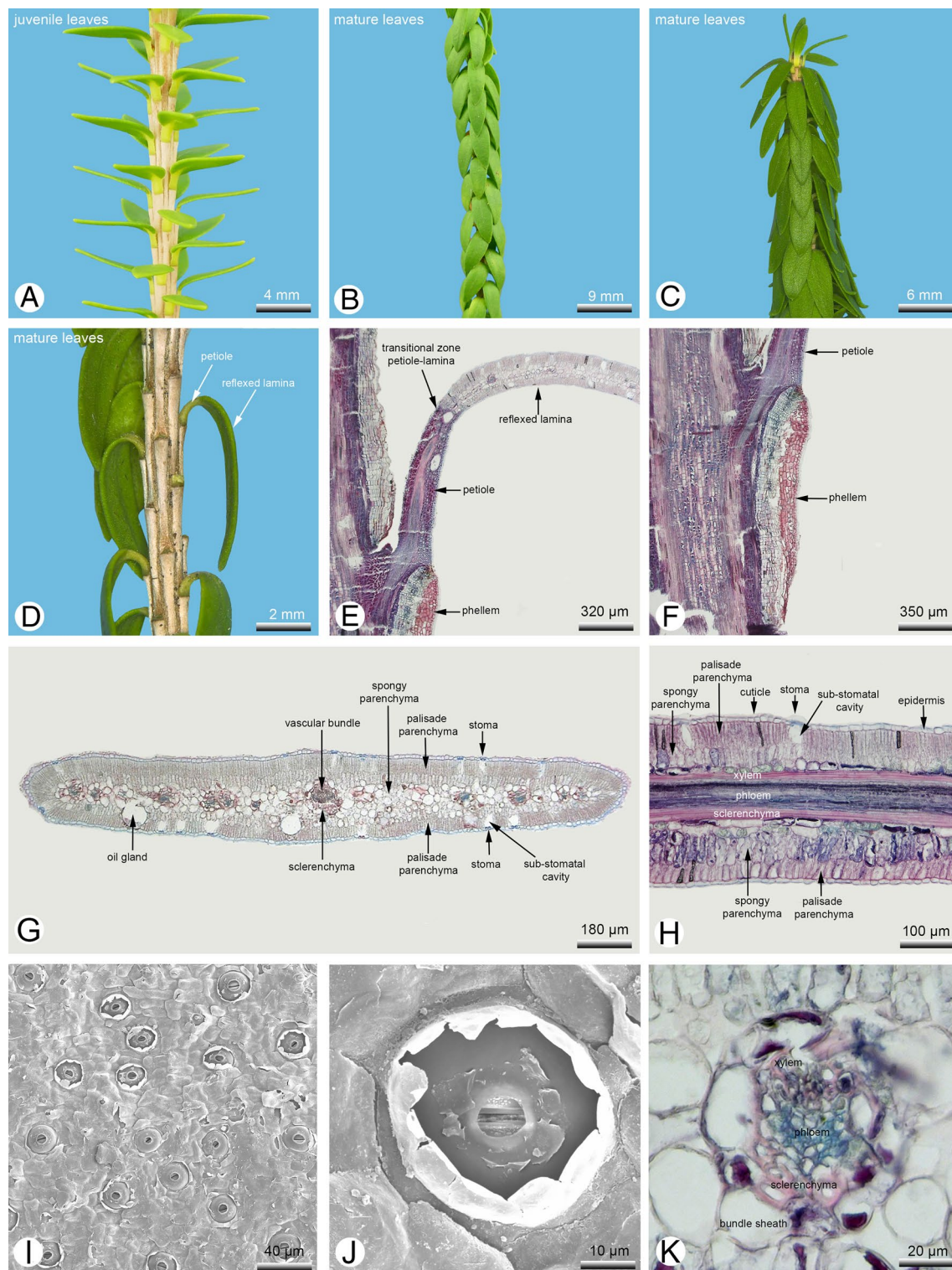


Fig. 7 *Melaleuca diosmifolia*, **a** juvenile leaves; **b–l** mature leaves; **b** mature shoot; **c** tip of a shoot; **d** reflexed leaf (some leaves removed for clarity); **e** longitudinal section of a shoot axis and a leaf; **f** longitudinal section of a leaf base; below all petioles there is a strip of corky tissue (phellem) that extends to a lower node on the stem; **g** cross sec-

tion of a leaf showing the isobilateral and amphistomatic structure; **h** longitudinal section of a leaf; **i** adaxial surface, stomata not encrypted (SEM-image); **j** stomata not encrypted but surrounded by a distinct cuticular rim (SEM-image); **k** vascular bundle with bundle sheath

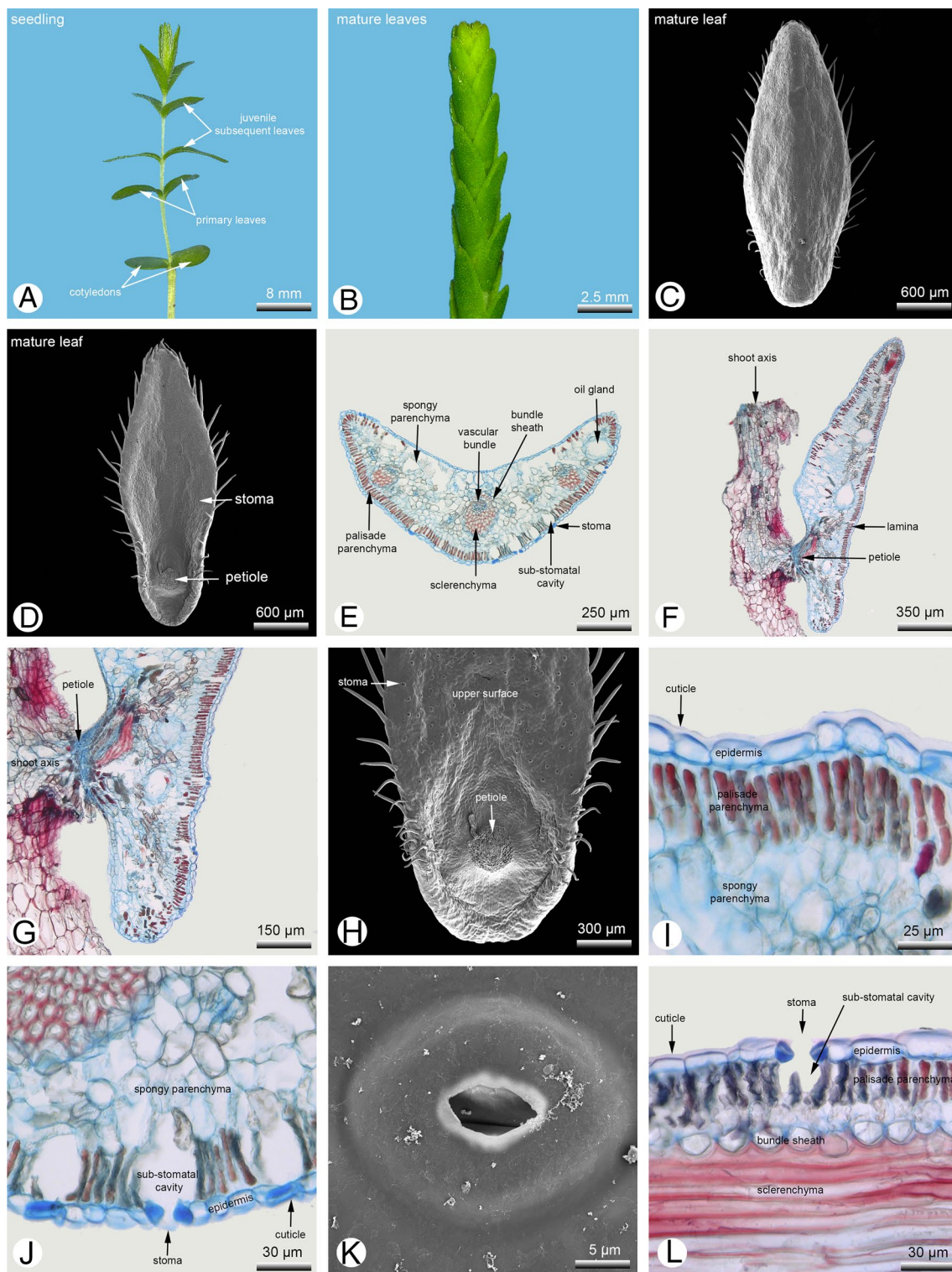


Fig. 8 *Regelia inops*, **a** seedling with the juvenile leaf types; **b** mature short shoot; **c–l** mature leaves; **c** abaxial view (SEM-image); **d** adaxial view (SEM-image); **e** inverse-bifacial leaf structure (microtome transverse section); **f–h** mature leaves are peltate; **f** longitudinal section of a shoot axis; **g** basal part of a leaf showing the peltation;

h basal part of the leaf showing the insertion of the petiole (SEM-image) **i** epidermis with a thick cuticle; **j** stomata not encrypted; **k** stoma surrounded by a distinct cuticular rim (SEM-image); **l** stomata in the same plane as the epidermal cells

leaves of seedlings have larger laminae and project from the stem at right angles which changes as new leaves are produced as the plant ages. This may be explained by the change in environmental pressures as a plant grows. It is common to observe that the leaves of juvenile plants seem to have a more mesomorphic structure than adult leaves and, while there has been little physiological work on this, in some studies it is shown that the leaves of juvenile plants are often larger and have lower water use efficiency than leaves on adult plants (Brodrribb and Hill 1993; Hansen and Steig 1993) and the xylem of seedling leaves is more susceptible to cavitation than cells in leaves on adults (Lucani et al. 2019). In a desert shrub (*Encelia farinosa* Torr. & A.Gray) survival of juvenile plants was lowest during years of severe drought. Size and higher intrinsic water use efficiency were positively related to seedling survival. However, seedlings with poorer water use efficiency that did survive showed an increase in their water use efficiency through time (Ehleringer and Driscoll 2022). Thus it is somewhat of a paradox that seedlings are often more mesomorphic than the adults they become. The usual explanation, particularly for species that regenerate after a disturbance such as fire, is that conditions post disturbance, which would include increased moisture, are more conducive to growth (Lamont and Enright 2000; Pausas and Lamont 2022) so seedlings are better able to survive. In xeric environments, in particular, as plants mature they need to increase water use efficiency which can be achieved in a number of ways such as leaf orientation, morphology and anatomy.

In the species we examined three groups can be recognised for leaves on adult plants (Table 4) as follows: (1) scale leaves erect, not peltate; (2) leaves erect with adaxial surface

strongly appressed to the shoot axis, and peltate (3) laminae spreading to reflexed to the shoot axis, not peltate.

The leaves of all the species except *R. inops* and *P. prolifera* are petiolate with orientation varying from erect through moderately spreading to reflexed. *Ozothamnus hookeri* is the only species we examined with erect nonpeltate leaves on adult plants (Group 1 leaves). In *R. inops* (Group 2 leaves) the leaves on seedlings are virtually sessile and this becomes more pronounced in the leaves on adults that move from spreading to erect. Due to the minute petiole the leaves appear nearly sessile and are closely appressed to the stem. The base of the leaf extends to form a peltate structure as found in at least 11 *Melaleuca* species (Bentham 1866; Carrick and Chorney 1979; Byrnes 1984) including *Melaleuca micromera* Schauer (Dörken and Parsons 2018) and also in the investigated *P. prolifera* that results in the leaves being erect and closely appressed to the stem. The peltation in these microphyllous species is very different from the typical peltate leaf morphology mostly found in species growing in subtropical or tropical zones where they occur in shady, humid to wet habitats (Wunnenberg et al. 2021). Such leaves are flat, large-sized, with a broad dorsiventral lamina on a more or less erect and long petiole and are at their most extreme in *Euryale* and *Victoria* (Nymphaeaceae) with leaves several metres across. In contrast the microphyllous leaves dealt with here are erect, often isobilateral and likely to be an adaptation to limiting heat gain in high light environments. With palisade mesophyll on both sides of the leaf, light of photosynthetic use can still be effectively captured as palisade tends to have a greater density of chloroplasts than spongy mesophyll cells (Esau 1965).

Microphyllous peltation is a characteristic of a group of species in *Melaleuca* recognised by Barlow (1986) but

Table 4 Adult leaf morphology, arrangement and disposition for the species studied

Group/species	Length (mm)	Shape	Arrangement	References
Group 1				
Leaves erect, nonpeltate				
<i>Ozothamnus hookeri</i>	1.0–1.5	Ovate	Alternate	Ohlsen et al. (2010)
Group 2				
Leaves erect, peltate				
<i>Phaenocoma prolifera</i>	0.6 – 1.0	Ovate	Alternate	Hind (1996)
<i>Regelia inops</i> , long shoot	5.0–7.0	Ovate	Decussate	Personal observation
<i>Regelia inops</i> , short shoot	2.0–3.0	Ovate	Decussate	Personal observation
Group 3				
Leaves reflexed				
<i>Olearia lepidophylla</i>	(0.3) 1 (-2)	Orbicular—broad ovate	Alternate	VicFlora (2023)
<i>Ozothamnus reflexifolius</i>	0.3–1.4	Obovate	Alternate	Leeson and Rozefelds (2003)
<i>Ozothamnus scutellifolius</i>	0.3–1.0	Globoid	Alternate	Curtis (1963)
<i>Melaleuca diosmifolia</i>	6.5 – 8.0	Narrowly ovate	Alternate	Brophy et al. (2013)

Table 5 Measurements of epidermal cell size, cuticle thickness and estimation of spongy mesophyll density from transverse leaf sections (values are listed as minimum and maximum)

Species	Cuticle thickness adaxial (µm)	Cuticle thickness abaxial (µm)	Epidermal cell size on light exposed surface (µm)	Epidermal cell size on shaded surface (µm)	Estimated spongy mesophyll cell density
<i>Olearia lepidophylla</i>	3.2–8.7	2.1–3.2	26.5–49.5	9.8–21.1	Low density
<i>Ozothamnus hookeri</i>	3.8–8.2	1.4–1.6	12.4–13.8	5.6–8.8	Dense
<i>Ozothamnus reflexifolius</i>	2.9–4.4	1.8–2.2	11.5–18.6	11.2–14.3	Low density
<i>Ozothamnus scutellifolius</i>	10.2–19.2	3.2–4.4	14.3–22.5	11.6–14.9	Low density
<i>Phaenocoma prolifera</i>	32.5–56.8	1.4–2.0	31.4–42.9	2.9–5.2	Low density
<i>Melaleuca diosmifolia</i>	6.4–12.6	3.8–6.4	15.6–17.1	12.3–15.8	Dense
<i>Regelia inops</i>	3.3–7.3	1.8–3.5	13.7–18.9	7.5–8.8	Low density

subsequent phylogenetic analysis of the Tribe Melaleuceae by Edwards et al. (2010) has placed the few species that were analysed from that group in clade C of the three groups recognised. In that analysis *Regelia inops* and *Petraeomyrtus punicea* (Byrnes) Craven (listed as *Melaleuca punicea* Byrnes in earlier treatments) that are both peltate-leaved species are included in Clade A and are sister taxa in that phylogeny. So peltate leaves seem to have arisen at least twice in the *Melaleuca* sensu lato clade. In these microphyllous species the method of forming the peltate leaf is different from that typically found where the extension of the leaf blade is due to a marginal meristem and a meristematic fusion/bridge for leaves that are usually in shaded locations. Orthodox peltation is advantageous for light interception in low light conditions (Givnish and Vermeij 1976) and most species are herbaceous and grow in mesic environments (e.g. *Tropaeolum*) or have annual photosynthetic tissues (e.g. *Drosera* spp.). This is not the case for *Regelia* or *P. prolifera* as they grow in open environments with seasonally dry soils. The peltate development with the attachment on the adaxial surface forces the leaf into an erect orientation. This is the reverse of *Olearia lepidophylla*, *Ozothamnus reflexifolius*, *Ozothamnus scutellifolius* and *Melaleuca diosmifolia* where the leaves are reflexed and close to the stem.

In a phylogenetic study of *Ozothamnus* and related genera in the Asteraceae, Schmidt-Lebuhn and Constable (2013) recognised eight leaf types including one where species often have reflexed leaves (Group 3 leaves in this study), namely leaf type four which is distinguished by reflexed leaves and some other characters. This type contains six species from Tasmania one of which also occurs on mainland Australia, clearly suggesting a close genetic relationship between them. Since 2013 a further two endemic Tasmanian *Ozothamnus* species with reflexed leaves have been described (de Salas and Schmidt-Lebuhn 2018) while *Ozothamnus lepidophyllus* Steetz with reflexed leaves is endemic to Western Australia (Florabase 2022, accessed November).

All the species we examined are low shrubs and all except *P. prolifera* have very upright growth form tending towards

being virgate so many of the shoots on the outside of the plant are vertically orientated. While morphologically dissimilar the result of reflexed and erect leaves on vertical stems is physiologically the same with the leaves forming a “column” of photosynthetic tissues that is orientated in such a way that light interception at midday would be lower than in the morning and evening and thus likely to lead to less heat load during the hottest part of the day (Falster and Westoby 2003). This would ameliorate heat-induced water loss. This agrees with a survey of leaf characteristics of species along a gradient of rainfall from 400–1500 mm/year in Western Australia that showed that species with leaf angles greater than 45° from the horizontal, that were amphistomatic and isobilateral were much more frequent at the lower end of the rainfall gradient and concomitantly where total daily photosynthetic active radiation was highest (Smith et al. 1998). This is consistent with the species in our study and as Onstein and Linder (2016) note this can be an advantage under water or nutrient stress.

The species we have studied here have more characteristics associated with xeromorphy than scleromorphy (Table 1). Thick cuticle is strongly associated with reducing water loss. In a study of cuticle mutants of *Nicotiana glauca* Graham it was found that although the alkanes in the cuticle of the leaves did not reduce transpiration in nonstressed conditions, under drought conditions they enabled the plant to seal the cuticle upon stomatal closure reducing leaf death and helping recovery (Negin et al. 2023). However there seems to be no direct relationship between cuticle thickness and xeric environments because for Asteraceae from the Patagonian desert the range in cuticle thickness was from 1 to 45 µm (data from Pyykkö 1966) and in a Mexican xeric environment much thinner values (0.19–1.15 µm, Rivera et al. 2017). In our species the range of cuticle thickness was from approximately 1–57 µm (median 3.8–8.2 µm adaxial surface, 1.8–2.2 abaxial surface) but only *Phaenocoma* had the very thick cuticle, which is up to 57 µm on very young leaves, but becomes thinner (~20 µm) as the leaf expands. It seems that the decrease in thickness is caused by the leaf

expansion. The cuticle consists of platelets that on immature leaves are loosely arranged. These can move to accommodate the leaf expansion but become poorly attached to the outer epidermal cell walls so can partially detach during the processing of the leaf for sectioning (Fig. 6e, h; Table 5).

Sclerenchyma that is more associated with scleromorphy is only found in *Melaleuca diosmifolia* and *R. inops*, and is there only associated with the vascular bundles, as found in the two *Melaleuca* species with very reduced leaves illustrated in a previous study (Dörken and Parsons 2018).

While all species studied here had very small leaves, three of the four Asteraceae species had slightly to strongly recurved margins, abundant trichomes (except *Ozothamnus reflexifolius*), particularly dense on the abaxial surface. Leaves were amphistomatous in all species except *Ol. lepidophylla* (which is hypostomatous) and stomata were not sunken in the epidermis but may have a cuticular rim formed by extension of the cuticle beyond the edge of the guard cells. Palisade parenchyma occurred on the light exposed side of the leaves independent of whether it is ad- or abaxial and all species have spongy parenchyma with approximately more than 20% of the leaf occupied by airspaces (except *Ozothamnus hookeri*). The isobilateral (=aequifacial leaves) leaves of *Melaleuca diosmifolia* were also amphistomatic and palisade parenchyma was located toward ad- and abaxial sides (Fig. 7g, h). At first glance, the isobilateral leaf structure of the strongly reflexed leaves of *Melaleuca diosmifolia* might appear as a contradiction, because an inverse-bifacial structure is much more to be expected. However, the structure of the mesophyll is strongly influenced by light exposure in the earliest developmental stages. Depending on their age, leaves of *Melaleuca diosmifolia* change their orientation. After emerging, young leaves spread upright from the shoot axis so that both leaf surfaces are similarly exposed to direct solar radiation before turning into a reflexed position (Fig. 7c). Thus, the isobilateral structure of the mature reflexed leaves results from a different leaf orientation and light exposure in early development. The morphological characteristics of most of the species such as the small leaves with recurved margins and abundant trichomes can be assigned to xeromorphic adaptations (Shields 1950; de Micco and Aronne 2012) but anatomically the leaves are not particularly xeromorphic or scleromorphic, in most cases lacking sclerenchyma, or dense parenchyma with small intercellular spaces (Table 1). A number of fynbos species examined by van der Merwe et al. (1994) had bundle sheath extensions that were considered to perhaps aid moisture distribution from the vascular bundle to the mesophyll as has also been claimed for sclereids in conifer leaves (Brodrick 2015). However, the species here, all with very small leaves, lack these structures and these are probably unnecessary as the leaves are so small that water moving from the vascular

system to the mesophyll has only a very short distance to travel.

All the species occur in relatively mesic environments, although usually with a summer water deficit. Only *Ol. lepidophylla* extends into an arid environment and paradoxically also occurs in the second highest rainfall of all the species. Plant–water relations of species are likely to be phylogenetically related and structural characteristics rather than physiological traits have a stronger phylogenetic signal (Avila-Lovera et al. 2023). Many of the characteristics of the leaves are likely to be associated with the ancestral characteristics of the family (e.g. Vivian and Cary 2012; Anderregg 2023). As noted above *R. inops* is related to certain *Melaleuca* species with similar to identical, morphology and anatomy. *Cassinia laevis* R.Br., *Metalasia* and *Brachyleana* species, all Asteraceae from shallow nutrient poor soils, have a very similar leaf anatomy and dense adaxial or abaxial indumentum (although broader leaves) to the asteraceous species here (van der Merwe et al. 1994; Burrows 2001). The consistency of characters in species in a particular clade (e.g. Anderregg et al. 2022) is particularly well illustrated in the Burrows study by the ericaceous species that all have similar leaf sclerenchyma patterns and stomata restricted to deep abaxial furrows on the leaf. However, as well as there being similarities in morphology and anatomy in particular clades there is also convergent evolution of morphological form in plants from similar environments (e.g. Felger and Henrickson 1997). This is shown in the Burrows (2001) study by two pea species (*Dillwynia* spp.) and the daisy *Metalasia densa* (Lam.) P.O.Karis (van der Merwe et al. 1994) that have the same inverse dorsiventral mesophyll as *R. inops*, although in very unrelated families.

Despite the generally “Köppen oceanic” climate in which all the species occur the summer rainfall is a very low proportion of the annual rainfall and points towards a summer water deficit for the species. The small leaf size and somewhat globose form, of the asteraceous species in particular, means that the ratio of surface area to volume is low and this would increase water use efficiency during drought conditions (de Micco and Aronne 2012). In addition the recurved leaf margins also increase the apparent volume of the leaf without increasing the surface area and revolute leaf margins in general are correlated with strongly seasonal environments (Wang et al. 2022). In an examination of LMA of Proteaceae species that are considered sclerophyllous, LMA was inversely related to rainfall and it was the leaf thickness that was specifically negatively correlated with rainfall and intrinsic water use efficiency (Lamont et al. 2002; 2015). In the species studied here the recurved leaf margins and dense abaxial trichomes of three of the species would simulate a thicker leaf than a planar lamina indicating better water relations during dry summer conditions.

Lamont et al. (2015) hypothesised that the increasing sclerophylly of *Hakea* species through the Tertiary in southern Australia was due to an increasingly arid climate over that time and the most sclerophyllous species in the world is a *Hakea* from south western Australia. The extensive range of *Ol. lepidophylla* into the arid zone may be the result of long distance dispersal as identified for the Asteraceae by Byrne and Murphy (2020) as well as the species being pre-adapted to low water availability due to its small leaves. Some cupressoid angiosperms ('whipcord plants') have similarly reduced leaves to the species studied here and occur in alpine areas of New Zealand, south eastern Australia and some in lowland areas, often on cliffs (Parsons 2010). While the environments in which they occur are not particularly arid most would still experience seasonally or edaphically dry conditions at some times of the year. Thus the tiny leaves are likely correlated with water deficit. This means that such plants can survive because competition from other species is reduced by the inhospitable growing conditions.

Under conditions of higher resource availability plants would be expected to develop the capacity for more extensive branching enabling greater leaf area in contrast to situations of less predictable resources where leaf production would be more restricted (Novoplansky 2009). Species with large leaves generally occur on nutrient rich soils and in mesic environments. However if these resources are absent species with small leaves can be competitive as vegetation will be relatively open, there will be high light availability, they require fewer nutrients and have better water use efficiency. An example is species in the Rhamnaceae described by Onstein and Linder (2016) that ancestrally had nonsclerophyllous leaves but evolved sclerophylly prior to the development of Mediterranean climates in the southern hemisphere. With the development of the winter rainfall regime in southern Australia and Africa, radiation occurred in the southern groups. With the intensification of summer drought and increasing nutrient impoverishment of soils, species with sclerophyllous characteristics radiated (Lamont et al. 2015; Onstein and Linder 2016)—in the Proteaceae leaves became thicker and with abundant sclerenchyma while in the Rhamnaceae most of the species have very small leaves with strongly recurved margins, similar to the species studied here and hence with conservative water relations.

There is a paradox between the fact that smaller leaves lose water more rapidly than larger leaves due to a smaller boundary layer, at least in forest trees (Wang et al. 2019), while in dry environments plants tend to have small leaves (Carlson et al. 2010; Wang et al. 2022) which would seem to be counterproductive for water economy. However, morphological and anatomical characteristics other than size will also affect both water relations and leaf heat load at different times of the year. Narrow leaves enable radiant heat loss during hot, dry conditions with less need for transpiration to

cool the leaf. In cooler conditions when water is abundant in Mediterranean climates small leaves allow high transpiration when evaporative demand is low and may increase nutrient uptake from nutrient poor soils when soils are moist in winter (Yates et al. 2010). This is an advantage in terms of water conservation in summer and nutrient uptake in winter. As species with small leaves occur in a diversity of habitats from nutrient poor soils with low water holding capacity, to cold alpine and acidic waterlogged environments, different leaf modification combinations may occur depending on the limiting conditions of where they grow. Boundary layer will be influenced by leaf tomentum, appression of the leaf to the stem, stomatal location and leaf margin morphology (such as recurved edges). Different combinations of these characteristics occur in small-leaved species and different combinations determine drought tolerance (Dias et al. 2020). Erect or reflexed leaves approximate a photosynthetic column that reduces exposure to mid day excess light and would limit heat load during the hottest parts of the day in summer (Falster and Westoby 2003). However in winter, low sun angle would provide slightly more leaf heating that would increase the gas phase conductance of water which is an important pathway for water in the leaf (Buckley 2015) and would facilitate the uptake of soil water in accordance with the suggestions of Yates et al. (2010).

Formation of a peltate leaf is unusual in species with small leaves and is only a minor modification to the extent of the lamina. However in the species we studied it served to orient the leaf parallel, and close to, the stem that would increase the boundary layer around the adaxial stomata. Similarly recurved leaf margins increase the boundary layer over stomata, aiding water conservation in dry, hot conditions (eg. Jordan et al. 2008) and leaf pubescence has been found to increase in response to drought (Sandquist and Ehleringer 2003) in some species from arid environments. There is a strong phylogenetic signal in leaf form indicating radiation of particular leaf morphologies has been important in responding to both water and nutrient limitation in temperate environments. However disparate groups have adopted similar solutions to particular environments indicating convergent evolution in response to specific selective forces.

Concluding discussion

In this paper dealing with microphyllous woody plants, we give the first detailed accounts of peltation and leaf reflexion. So far, these topics have been merely mentioned in passing in the taxonomic literature, in the case of peltation first by Bentham in 1866. Here, our novel findings show in exactly what ways microphyllous peltation differs from the normal type and we provide the first recognition that an

extreme form of leaf reflexion can become established in some lineages as a microphyllous leaf type.

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Data availability All data in this paper are presented in the tables and figures.

Declarations

Conflict of interest The authors declare no conflict of interest.

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