

# Leaf anatomy of the genus *Passerina* (Thymelaeaceae): taxonomic and ecological significance

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**Keywords:** anatomy, epidermis, mesophyll, *Passerina*, sclerenchymatous sheath, southern Africa, Thymelaeaceae, vascular bundles

## ABSTRACT

A comparative anatomical study was made of the genus *Passerina* comprising 20 species and four subspecies, most of which are endemic to southern Africa. It showed that anatomical variation is useful in species recognition and classification. Anatomical characters typical of Thymelaeaceae and displayed in *Passerina* include isobilateral leaves, a papillate cuticular membrane, mucilaginous epidermal cell walls, a parenchymatous bundle sheath and extraxylary sclerenchyma fibres. Vascular bundles of the leaf lack intraxylary phloem. Characters common to *Passerina* are inverse-dorsiventral and epistomatic leaves, inverted palisade parenchyma and an abaxial hypodermal sclerenchymatous sheath. Orientation of the main vascular bundle in relation to the epidermis and mesophyll allows the recognition of four leaf structural types and ten states, according to which all species can be characterized and grouped. Functionally many anatomical features of the leaf in *Passerina* are interpreted as adaptations to the Mediterranean climate of the Cape Floristic Region, where most species occur.

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## INTRODUCTION

This paper emanates from a comparative leaf anatomical survey of the genus *Passerina* L., undertaken as part of a monographic study of the group. Work undertaken thus far has revealed at least four new species and four new subspecies, to be added to the 16 existing species, of which most species are endemic to southern Africa (Thoday 1924; Bond & Goldblatt 1984). Despite the now outdated revision by Thoday (1924), boundaries of infrageneric taxa in *Passerina* remain a problem, mainly owing to the apparent lack of marked morphological differences between the species. This paper explores the importance of leaf anatomy in *Passerina* as a source of potential taxonomic evidence.

Physiography and climate are important in the distribution of *Passerina* (Table 1). Most species of *Passerina* are endemic to the Cape Floristic Region. The climate of this region is mostly Mediterranean or semi-Mediterranean. Winter rainfall occurs in the west and along the south coast, complemented by some summer rain, which increases eastwards. The western Karoo and Namaqualand (Succulent Karoo Biome) are characterized by winter precipitation and summer drought. Only two species, *P. sp. nov. 4* and *P. montana* are distributed to the east and north along the eastern mountains and eastern escarpment of southern Africa, areas that receive predominantly summer rainfall.

Anatomical research in *Passerina* was initiated by Pick (1882a, b), who studied the effect of light on the orientation of assimilation tissue and discussed the inverse-dorsiventral leaf. Gilg (1891) published a taxonomic account on the Thymelaeaceae, indicating that the anatomical structure of stems was similar throughout the family and subsequently of no taxonomic value; he followed Endlicher (1847) in distinguishing the subtribe Passerininae on the basis of floral morphology. Van Tieghem (1893) described the anatomy of the root, stem and leaf for all the genera of the Thymelaeaceae known

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TABLE 1.—Distribution and habitat of *Passerina* species (order of taxa according to leaf structural type referred to throughout paper)

Leaf structural type	Taxon	Distribution	Habitat
A	<i>P. sp. nov. 1</i>	High altitudes, Ceres Karoo	Rocky areas, often covered by snow in winter
B1	<i>P. burchellii</i>	High mountains of Genadendal and Villiersdorp	South-facing rocky outcrops on mountain summits
B1	<i>P. pendula</i>	KwaZunga Catchment Basin and Zwartkops River area of Eastern Cape	On mountain slopes, zone between valley bushveld and fynbos, also on plains and roadsides
B2	<i>P. comosa</i>	Kamiesberg, Great Winterhoek and Klein Swartberg Ranges	Mountain slopes and summits
B2	<i>P. paludosa</i>	E of Muizenberg	Rare in salt marshes on lowland flats
B2, B3	<i>P. galpinii</i>	Agulhas Plain area	Calcrete, in stony areas, fields, disturbed areas and roadsides
B3	<i>P. drakensbergensis</i>	Endemic in Bergville District, KwaZulu-Natal	Zone between indigenous forest and alpine grassland, altitude $\pm$ 1 500–1 980 m. Also along streams and river banks
B3	<i>P. ericoides</i>	Beaches of Western Cape	In salt spray, on cliff faces overhanging sea, on primary dunes
B3	<i>P. sp. nov. 2</i>	Northern Cederberg Mountains	Between large rocks at mountain tops
B3	<i>P. sp. nov. 3</i>	Mountain tops of Uitenhage area and Swartberg Pass, Kouga Mountains and Montagu Pass	In rocky areas and rock crevices
B4	<i>P. rubra</i>	Port Elizabeth to Uitenhage with outliers in Swellendam and Bredasdorp Dist.	In rocky areas, on flatter areas, roadsides and disturbed areas
B3, B4	<i>P. filiformis</i> L. subsp. <i>filiformis</i>	Common in Cape Peninsula, distributed from Piquetberg across Hex River Mountains, to Attaquaskloof in Western Cape	In rocky areas mostly on south-facing mountain slopes
B6	<i>P. filiformis</i> L. subsp. nov.	From Malmesbury NE to Vredendal	Deep acid sands
B2, B3, B4, B5	<i>P. obtusifolia</i>	From Worcester in Western Cape to Alice in Eastern Cape. On some mountain ranges in and around Little Karoo	On lower mountain slopes in zone between Karoo vegetation and fynbos, otherwise large range of Karoo habitats, mostly dry rocky areas
B2, B3, B5	<i>P. glomerata</i> subsp. <i>glomerata</i>	Worcester to Tulbagh, in Clanwilliam area, extending to Witteberg S of Matjiesfontein	Large range of Karoo habitats, mostly dry rocky areas
B6	<i>P. glomerata</i> subsp. nov.	From Cederberg Mountains, along mountain summits to Cape Peninsula	Rocky crevices on mountain tops and slopes
C	<i>P. falcifolia</i>	Mountainous areas between George and Uitenhage	On rocky slopes, on mountain passes, roadsides and in flatter field areas
C	<i>P. sp. nov. 4</i>	From Mossel Bay and Oudtshoorn to Eastern Cape and along escarpment northwards to Zimbabwe, with outliers in Tanzania	In rocky places and rock sheets, also in valleys along streams
B3, B2, D1	<i>P. montana</i>	Eastern mountains and Great Escarpment of southern Africa to Zimbabwe and Malawi	In rocky places and rock sheets, also in valleys along streams, altitude $\pm$ 1 200 m
B2, B3, B4, D2	<i>P. paleacea</i>	Beaches and salt marshes of Western Cape	On primary and secondary dunes as well as rocky areas near sea shore
B3, B6, D2	<i>P. rigida</i>	Along coast from northern KwaZulu-Natal to Cape Peninsula	Pioneer and sand binder on primary dunes and rocky crevices, common along most of coast
D2	<i>P. vulgaris</i>	From Western Cape to East London in Eastern Cape	In rocky places on mountain slopes and valleys, pioneer in disturbed places, along roads, even on secondary dunes on coast

at the time and classified the family into three groups, namely Drapétées, Thyméléés and Aquilariées, with *Passerina* in the Thyméléés. In his key, the genera *Lachnaea* L., *Cryptadenia* Meisn., *Gnidia* L. and *Chymococca* Meisn. are grouped on the basis of gelatinized epidermal cells, whereas *Passerina* is distinguished by the absence of these cells. Subsequent work by Bredenkamp & Van Wyk (1999, 2000) has shown the presence of these cells in *Passerina*. Supprian (1894) studied the stem and leaf anatomy of the Thymelaeaceae, describing the epidermis ('Hautsystem'), the mechanical system ('Mechanisches system'), the assimilation system ('Assimilationsystem'), the vascular structure ('Leitungssystem'), the aeration system ('Durchlüftungssystem') and excretion management ('Excretbehälter') for all the

known genera. He classified the family into the subfamilies Aquilarioideae and Daphnoideae and placed *Passerina* into the latter, under the tribe Euthymeleae. Gilg (1894) studied the relationships in the Thymelaeaceae, using mainly floral anatomy, and classified the family into the subfamilies Aquilarioideae, Phalerioideae, Thymelaeoideae and Drapetoideae. *Passerina* is classified in the subfamily Thymelaeoideae, tribe Daphneae, subtribe Passerininae. In the same article, he gave a full account of the anatomical method applied by Van Tieghem (1893) and Supprian (1894), concluding that many of the characters used by them were not constant, that there would always be criticism against the anatomical method and that floral characters were more reliable in the delineation of the Thymelaeaceae.

Solereider (1899, 1908) summarized the anatomical work on the Thymelaeaceae up to the beginning of the twentieth century. The most prominent subsequent anatomical study in the Thymelaeaceae was done by Leandri (1930), who delimited the Thymelaeoideae on the basis of intraxylary phloem in the stem. He classified *Passerina* in the tribe Daphneae, and because of the absence of floral nectaries, into the subtribe 'Passeriniinae', thus combining anatomical and floral characters. Hereafter the most significant works on the Thymelaeaceae comprised the compilation of all the available knowledge. Domke (1934) proposed a widely adopted classification system for the family based on previous anatomical and floral morphological evidence, classifying *Passerina* under the subfamily Thymelaeoideae, tribe Gnidiaceae and subtribe Passeriniinae. Finally Metcalfe & Chalk (1950) and Metcalfe (1979, 1983) published accounts of the Thymelaeaceae in their standard works on the anatomy of the dicotyledons.

With the genera in Thymelaeaceae delineated on the basis of anatomy and floral morphology, the focus changed to generic revisions. Anatomical work on *Passerina* was done by Thoday (1921), who described the structure and behaviour of the ericoid leaves of *P. filiformis* L. and *P. cf. falcifolia* C.H. Wright under drought conditions and supplied some notes on their anatomy. Kugler (1928) described the inverse-dorsiventral leaves of *P. filiformis* (= *P. pectinata* Hort.). Recent comparative studies on Thymelaeaceae in southern Africa include those on leaf anatomy of the genera *Lachnaea* and *Cryptadenia* (Beyers 1992; Beyers & Van der Walt 1995) and on leaf and involucre bract morphology of systematic use in *Gnidia* (Beaumont *et al.* 1994). Previous studies of leaf anatomy identified mucilagination of the epidermal cells as being of possible taxonomic importance. Recently Bredenkamp & Van Wyk (1999) clarified the structure of these epidermal cells and the origin of the mucilage, indicating that this character is of taxonomic importance mainly at the family level. The present comparative anatomical study of the leaves in *Passerina* is the most comprehensive to date. Our primary objective has been to assess the infrageneric taxonomic significance of leaf anatomy in the genus.

The most outstanding anatomical feature of the Thymelaeaceae, namely the presence of sclerenchyma fibres, may well be an adaptation of members of the family to their environments. However, sclerenchyma fibres in the leaves of *Passerina* have never been studied at infrageneric level before, and this study meets that need. The presence of tough sclerenchyma fibres in the stems of *Passerina*, is well known among indigenous people, who use especially the bark for making ropes, straps and whips.

The wide distribution of *Passerina* in the Cape Floristic Region, the southern and eastern coastline of South Africa and along the eastern escarpment of southern Africa to Zimbabwe, and with outliers as far north as Tanzania, provides an opportunity to study the possible leaf anatomical adaptations of these plants to a wide range of habitats, experiencing both Mediterranean and summer rainfall conditions. For example, we suspect the decreasing rainfall from the eastern escarpment to the northwestern parts of the Northern Cape to be reflected

by adaptations in the leaf structure of the group. The present paper provides a description of anatomical characters in *Passerina* as well as an assessment of their taxonomic and ecological significance.

## MATERIAL AND METHODS

Leaves, both fresh and from herbarium material, of all infrageneric taxa in *Passerina* were studied. Additional *Passerina* specimens examined since Bredenkamp & Van Wyk (2000: 70) are listed in Table 2. Leaves from herbarium material were rehydrated in water for 5 minutes at boiling point. All leaf material was fixed and stored in a 0.1 M phosphate-buffered solution at pH 7.4, containing 2.5% formaldehyde, 0.1% glutaraldehyde and 0.5% caffeine [modified Karnovsky fixative; Karnovsky (1965)]. Whenever possible, material from at least five different localities was included.

### Light microscope (LM) studies

The light microscope was used for general leaf anatomy and epidermal studies. Unless otherwise stated, the tenth leaf from the growing point of a twig was used in all comparative studies. To prepare semi-thin transverse sections, a 1 mm wide segment of leaf material was cut from the centre of each leaf, thus including the main vein as well as both leaf margins. Samples were dehydrated, embedded in glycol methacrylate (GMA) and sectioned according to the methods of Feder & O'Brien (1968). Sections were stained in toluidine blue 'O', subjected to the periodic acid-Schiff's (PAS) reaction and mounted in Entellan (Art. 7961, E. Merck, Darmstadt).

The following three methods were followed in the study of the cuticles (Bredenkamp & Van Wyk 2000):

1. GMA sections of leaves in transverse section were stained with 1% Sudan Black B dissolved in 70% ethanol.
2. Macerated cuticular mounts were stained with a 1% aqueous safranin solution.
3. Epidermal mounts, obtained by removing small pieces of ad- and abaxial epidermis manually and by making paradermal hand sections, were stained with 1% safranin dissolved in 50% ethanol.

### Scanning electron microscope (SEM) studies

The scanning electron microscope was used to study the epidermal surface features (including epicuticular waxes) and to verify the structure of the cuticle (Bredenkamp & Van Wyk 2000).

### Transmission electron microscope (TEM) studies

The transmission electron microscope was used for the study of the structure of mucilaginous epidermal cell walls in *Passerina* (Bredenkamp & Van Wyk 1999).

### Measurements of leaf in transverse section (t/s)

Using LM, all measurements were done by using a calibrated eyepiece.

TABLE 2.—Additional *Passerina* specimens examined and taxonomical changes made since Bredenkamp & Van Wyk (2000: 70)

Species	Voucher specimen	Locality
<i>comosa</i>	Thoday 212*	WESTERN CAPE.—3320 (Montagu): Montagu Dist., near Concordia, (–CD).
<i>filiformis</i> subsp. <i>filiformis</i>	Boucher 2833*	WESTERN CAPE.—3118 (Van Rhynsdorp): Clanwilliam Dist., Diepkloof S of Verlorelei, (–AD).
	Bredenkamp 1039	WESTERN CAPE.—3318 (Cape Town): Signal Hill, (–CD).
<i>filiformis</i> subsp. nov.	Schlechter 5125*	WESTERN CAPE.—3218 (Clanwilliam): Alexander's Hoek, (–BC).
	Taylor 1542*	WESTERN CAPE.—3218 (Clanwilliam): Malmesbury Div., Vredenburg, Steenberg's Cove, (–CC).
<i>glomerata</i> subsp. <i>glomerata</i>	Bredenkamp 988*	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Eikeboom, (–AC).
	Bredenkamp 994	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Kromrivier, (–AC).
	Bredenkamp 1002	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Algeria, (–AC).
	Bredenkamp 984, 985	WESTERN CAPE.—3219 (Wuppertal): Citrusdal, Piekenierskloof Pass, (–CD).
	Bredenkamp 977	WESTERN CAPE.—3219 (Wuppertal): Groenfontein, (–DC).
	Bredenkamp 973	WESTERN CAPE.—3319 (Worcester): Tulbagh, (–AC).
<i>glomerata</i> subsp. nov.	Stokoe 8040*	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains.
	Esterhuysen 28587	WESTERN CAPE.—3319 (Worcester): Hex River Mountains.
sp. nov. 1	Goldblatt & Manning 8627	WESTERN CAPE.—3220 (Sutherland): Roggeveld Escarpment, (–AB).
sp. nov. 3	Stokoe 9302*	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, Prince Albert area, (–AC).
	Schlechter 5846*	WESTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–CD).
	Esterhuysen 10734*	EASTERN CAPE.—3323 (Willowmore): Kouga Mountains, (–DA).
	Esterhuysen 28006*	EASTERN CAPE.—3324 (Steytlerville): Cockscomb, Uitenhage area, (–BD).
sp. nov. 4	Killick 238	KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (–CB).
	Bredenkamp 1016*, 1017*	KWAZULU-NATAL.—3030 (Port Shepstone): Oribi Gorge, (–CB).
	Van Wyk & Bredenkamp 1, 1012*	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (–AA).
	Bredenkamp 1327	KWAZULU-NATAL.—3130 (Port Edward): Mkambati Nature Reserve, (–AC).
	Gillett 4537	WESTERN CAPE.—3422 (Mossel Bay): en route to Knysna from George, (–BB).
	Keet s.n.	WESTERN CAPE.—3423 (Knysna): Knysna, Redlands, (–AA).

\* Material used for the SEM study of the ad- and abaxial epidermis. All specimens are housed at PRE.

### Thickness of the main vascular bundle

The shortest distance between the outermost points of the ad- and abaxial epidermis through the main vascular bundle, was measured.

### Leaf width

Measurements from leaf margin to leaf margin would be unreliable considering the cymbiform shape of the leaf, the involute nature of the leaf margins, and the fact that leaf margins correspond to changes in turgor pressure. Leaf width was therefore measured as the shortest distance between the outer epidermal walls of the abaxial epidermis, parallel to the adaxial epidermis, but perpendicular to the axis of the main vascular bundle.

## Terminology

### Epidermal structure

Epidermal structure was described by Bredenkamp & Van Wyk (1999, 2000).

### Cuticle

Following Jeffree (1986), we distinguish the cuticle proper, the cuticular layer and the cell wall.

### Cuticular ornamentation (LM and SEM)

We follow Wilkinson (1979) in our choice of terminology.

### Epicuticular wax

The recognition of soft waxes is based on the criteria proposed by Amelunxen *et al.* (1967). Further interpretation of epicuticular waxes and crystals was done according to Wilkinson (1979) and Barthlott *et al.* (1998).

### Leaf anatomy

The definitions of dorsiventral and isobilateral leaves (Eseau 1965; Metcalfe 1979; Fahn 1982; Mauseth 1988) are accepted in the present study. However, we follow Kugler (1928) who coined the term 'inverse-dorsiventral' for leaves where the palisade parenchyma develops abaxially, because the abaxial epidermis is exposed to the environment. In addition to leaf symmetry, the works of the above-mentioned authors as well as those of Sole-reder (1908) and Metcalfe & Chalk (1950) have been used for the interpretation of leaf anatomy.

### Crystals

Crystals were interpreted according to Metcalfe (1983). Unstained GMA sections of leaves were used to

identify the presence and position of crystals by means of polarized light, after which they were tested for the presence of flavonoid glycosides, such as diosmin, according to the method of Jackson & Snowdon (1990). The identity of the crystals was finally confirmed using energy dispersive spectrometry (EDS).

### Phylogeny

Speculations on phylogeny are based on the prevailing family characters representing the ancestral state and derived characters at genus and species levels considered as possibly advanced. A cladistic analysis based on anatomical and morphological characters in *Passerina* is scheduled for the final stages of the study.

## RESULTS

### Macromorphology of leaf

*Leaf arrangement* decussate, sometimes imbricate, closely adpressed to stem or spreading at an angle of 5°–20°(–60°); spreading of leaves often prominent in juvenile plants. *Lamina* inversely ericoid; adaxial surface concave, villous, often forming a groove facing the stem; abaxial surface convex, orientated more or less acropically, thus exposing a large surface area to the environment; cuticle often amber-coloured (in herbarium material) and outline of epidermal cells often macroscopically visible. *Leaf shape* cymbiform, falcate or cigar-shaped; plane shape linear, oblong, lanceolate, or narrowly trul-

late. *Leaf base* sessile or cuneate. *Leaf apex* truncate and hump-backed, obtuse, rounded, acuminate or acute to almost spine-tipped. *Margins* sometimes ciliate. *Size* (1.5–) 2.5–4.0(–8) × (0.8–)1.2–2.0(–3.0) mm. Figure 1.

### Leaf anatomy

#### Trichomes

*Adaxial surface* of leaf villous, with uniseriate trichomes forming a felty layer over adaxial epidermis; trichomes bordering leaf margin often conspicuous. *Abaxial surface* of leaves mostly glabrous, young leaves tomentose to sparsely hairy in a few species (Table 3; Figure 2A).

#### Epidermis

*Lamina* epistomatic. *Adaxial epidermis* uniseriate, following concave leaf surface; stomata anomocytic; cuticular membrane 2–5 µm thick; epidermal cells irregularly shaped, outer periclinal wall convex in t/s, polygonal in surface view. *Abaxial epidermis* uniseriate, convex (following leaf surface curvature), glabrous or sparsely hairy; cuticular membrane well developed, (10–)20–30(–70) µm thick in t/s; epicuticular waxes coating entire surface, crystalloids, wax platelets and plates present or absent (Figure 2B–D). Anatomical structure and taxonomic value of abaxial epidermis are discussed by Bredenkamp & Van Wyk (2000), and correlated with leaf structural types in Table 3.

TABLE 3.—Correlation between leaf structural type and epidermal characters (Bredenkamp & Van Wyk 2000) in *Passerina*

Taxon	Leaves				Abaxial hair	Epidermal cells		Ornamentation of cuticular membrane		
	Isobilateral Type A	Inverse-dorsiventral				arranged randomly Group A	arranged in rows Group B	Smooth	Papillate	Striate
		Type B	Type C	Type D						
<i>P. sp. nov. 1</i> (Figure 3A)	A					X		X		
<i>P. burchellii</i>		B1				X		X		
<i>P. pendula</i> (Figure 3B)		B1					X			X
<i>P. comosa</i>		B2			X		X		X	
<i>P. paludosa</i> (Figure 3C)		B2					X			X
<i>P. galpinii</i> (Figure 2C)		B2, B3					X			X
<i>P. drakensbergensis</i>		B3					X		X	
<i>P. ericoides</i> (Figure 3D)		B3				X		X		
<i>P. sp. nov. 2</i>		B3					X		X	
<i>P. sp. nov. 3</i>		B3			X		X	X	X	
<i>P. rubra</i>		B4					X			X
<i>P. filiformis</i> subsp. <i>filiformis</i> (Figure 3E)		B3, B4					X			X
<i>P. filiformis</i> subsp. nov.		B4, B6					X			X
<i>P. obtusifolia</i> (Figure 3G)		B2, B3, B4, B5				X			X	
<i>P. glomerata</i> subsp. <i>glomerata</i> (Figure 3F)		B2, B3, B5				X		X		
<i>P. glomerata</i> subsp. nov.		B6				X			X	
<i>P. falcifolia</i> (Figure 4A)			C				X			X
<i>P. sp. nov. 4</i> (Figure 4B)			C				X			X
<i>P. montana</i> (Figure 4C)		B2, B3		D1			X	X	X	
<i>P. paleacea</i> (Figure 4D)		B2, B3, B4		D2			X			X
<i>P. rigida</i> (Figures 3H, 4E)		B3, B6		D2			X			X
<i>P. vulgaris</i> (Figure 4F)				D2			X			X

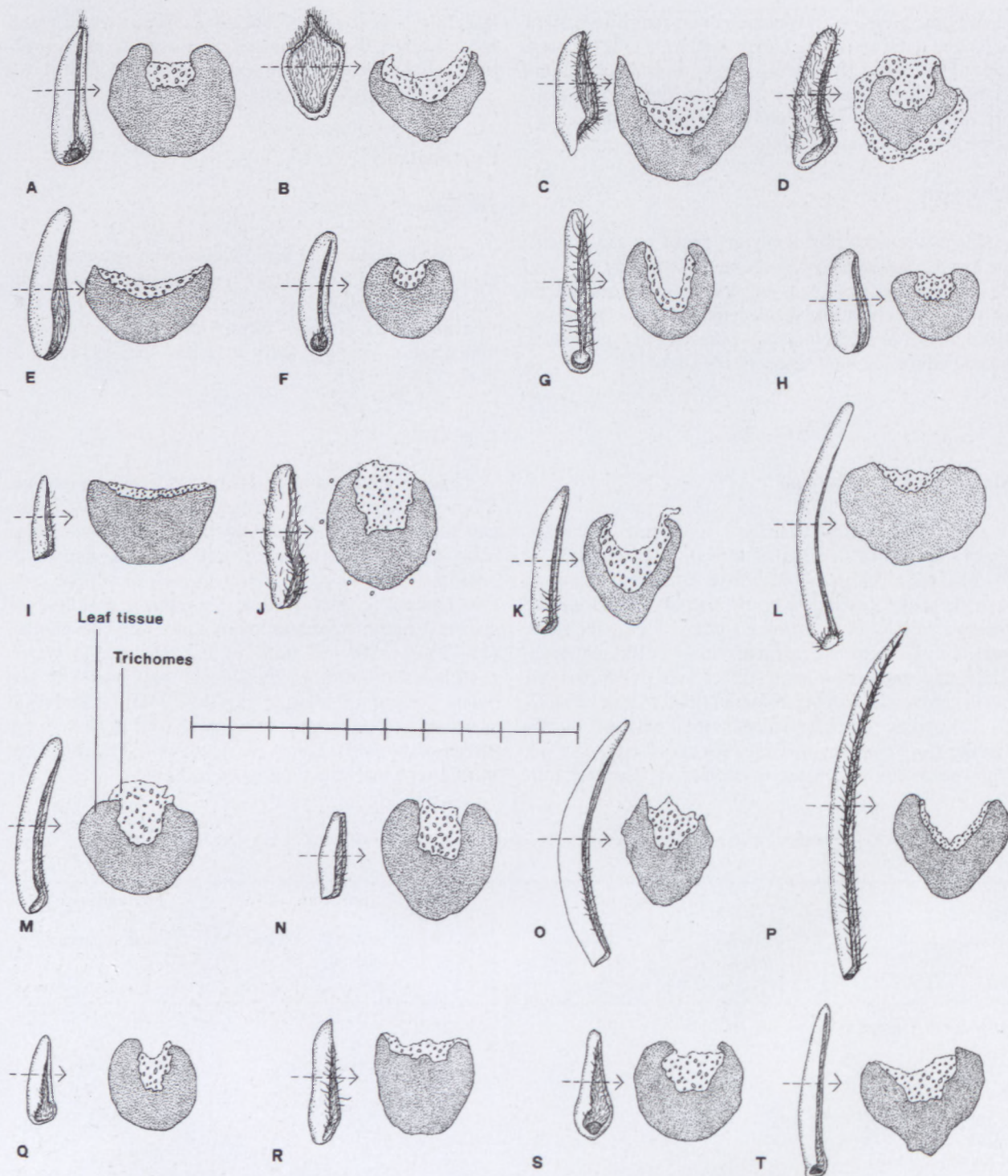


FIGURE 1.—Camera lucida drawings of leaves of *Passerina* species arranged according to leaf structural type (Table 3), correlating leaf shape to outline of leaves in *ts*: A, *P. sp. nov. 1*, Bredenkamp 1044; B, *P. burchellii*, Bolus 684; C, *P. pendula*, Bredenkamp 908; D, *P. comosa*, Andreae 1288; E, *P. paludosa*, Bredenkamp 1035; F, *P. galpinii*, Bredenkamp 946; G, *P. drakensbergensis*, Bredenkamp 1019; H, *P. ericoides*, Bredenkamp 962; I, *P. sp. nov. 2*, Esterhuysen 26859; J, *P. sp. nov. 3*, Esterhuysen 28006; K, *P. rubra*, Bredenkamp 914; L, *P. filiformis* subsp. *filiformis*, Bredenkamp 896; M, *P. obtusifolia*, Bredenkamp 919; N, *P. glomerata* subsp. *glomerata*, Bredenkamp 984; O, *P. falcifolia*, Bredenkamp 917; P, *P. sp. nov. 4*, Bredenkamp 1016; Q, *P. montana*, Bredenkamp 889; R, *P. paleacea*, Bredenkamp 960; S, *P. rigida*, Bredenkamp 911; T, *P. vulgaris*, Bredenkamp 901. Leaf size A–T  $\times 20$ . Scale bar: 10 mm; leaves in *ts* not to scale.

#### Tanniniferous substances

Tanniniferous substances (Figure 2C, D) present in ad- and abaxial epidermis, mesophyll, bundle sheaths, parenchyma abaxial of vascular tissue in vascular bundle, staining homogeneously or with vesicular appearance.

#### Crystals

Calcium oxalate crystals (Figure 2E, F) present in mesophyll, clustered crystals (druses) in parenchyma, fragmented calcium oxalate crystals, resembling crystal sand, present in intercellular spaces; flavonoid glycosides (diosmin) absent.

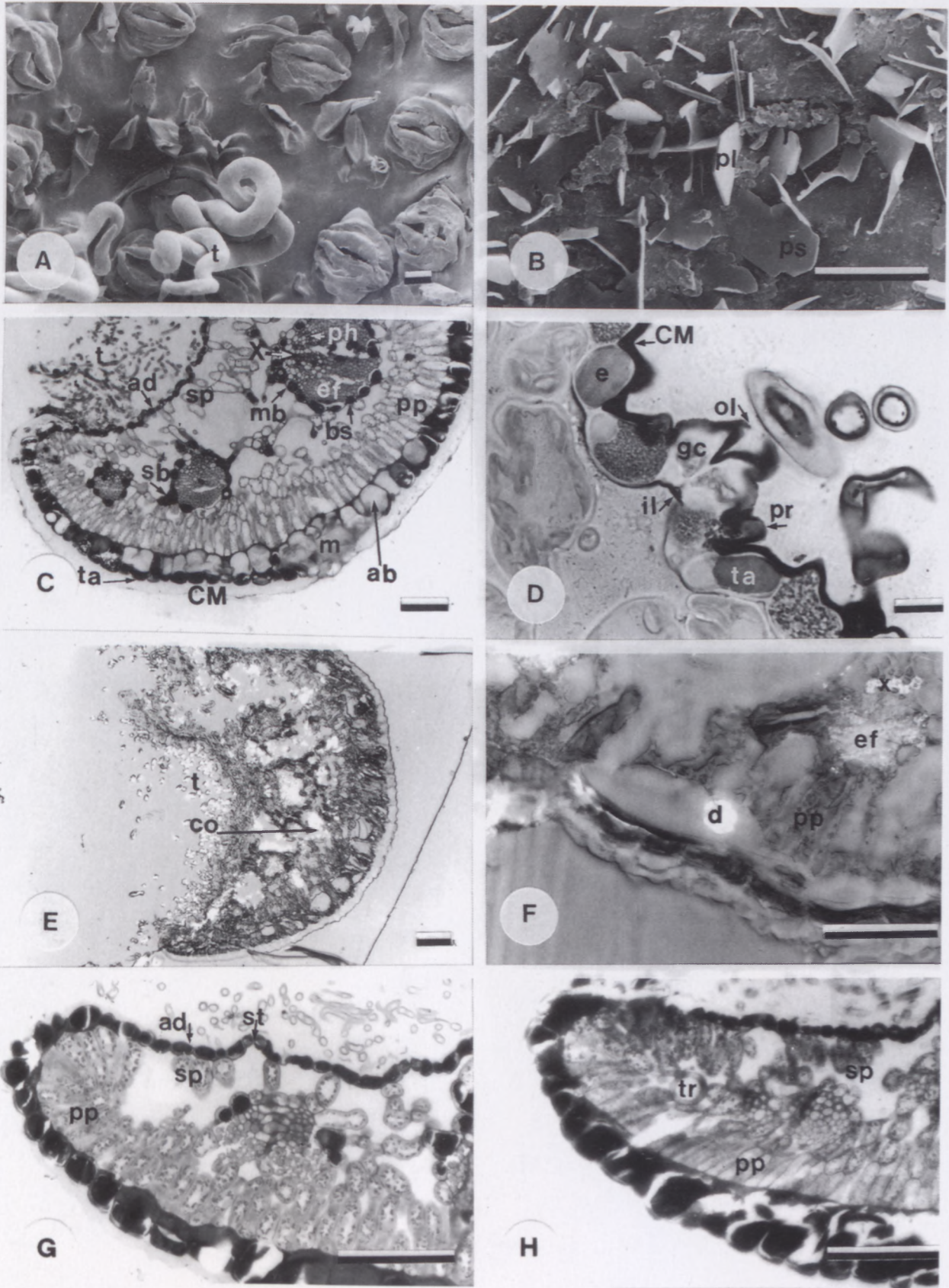


FIGURE 2.—A, B, SEM micrographs of trichomes and epicuticular waxes: A, *P. falcifolia*, Bredenkamp 915; B, *P. rigida*, Bredenkamp 1013. C–H, LM photographs of leaf: C, *P. galpinii*, Bredenkamp 946; D, *P. pendula*, Bredenkamp 909, stomatal apparatus in adaxial epidermis stained with Sudan Black B; E, *P. paleacea*, Pillans 3783, calcium oxalate crystals and druses in polarized light; F, *P. falcifolia*, Tyson 1449, cluster crystal from ruptured palisade parenchyma in polarized light; G, *P. drakensbergensis*, Bredenkamp 1019, mesophyll in leaf margin; H, *P. glomerata* subsp. *glomerata*, Bredenkamp 977, mesophyll and tracheid in leaf margin. ab, abaxial epidermis; ad, adaxial epidermis; bs, bundle sheath; c, cambial cells; CM, cuticular membrane; co, calcium oxalate crystals; cy, collenchyma; d, druse; e, epidermal cell; ef, extra-xylary vascular bundle; pr, peristomal rim; ps, platelets; s, sclerenchymatous hypodermal sheath; sb, secondary vascular bundle; sp, spongy parenchyma; st, stomata; t, trichome; ta, tanniferous compounds; tr, tracheid; X, xylem. Scale bars: A, B, D, 10  $\mu$ m; C, E–H, 100  $\mu$ m.

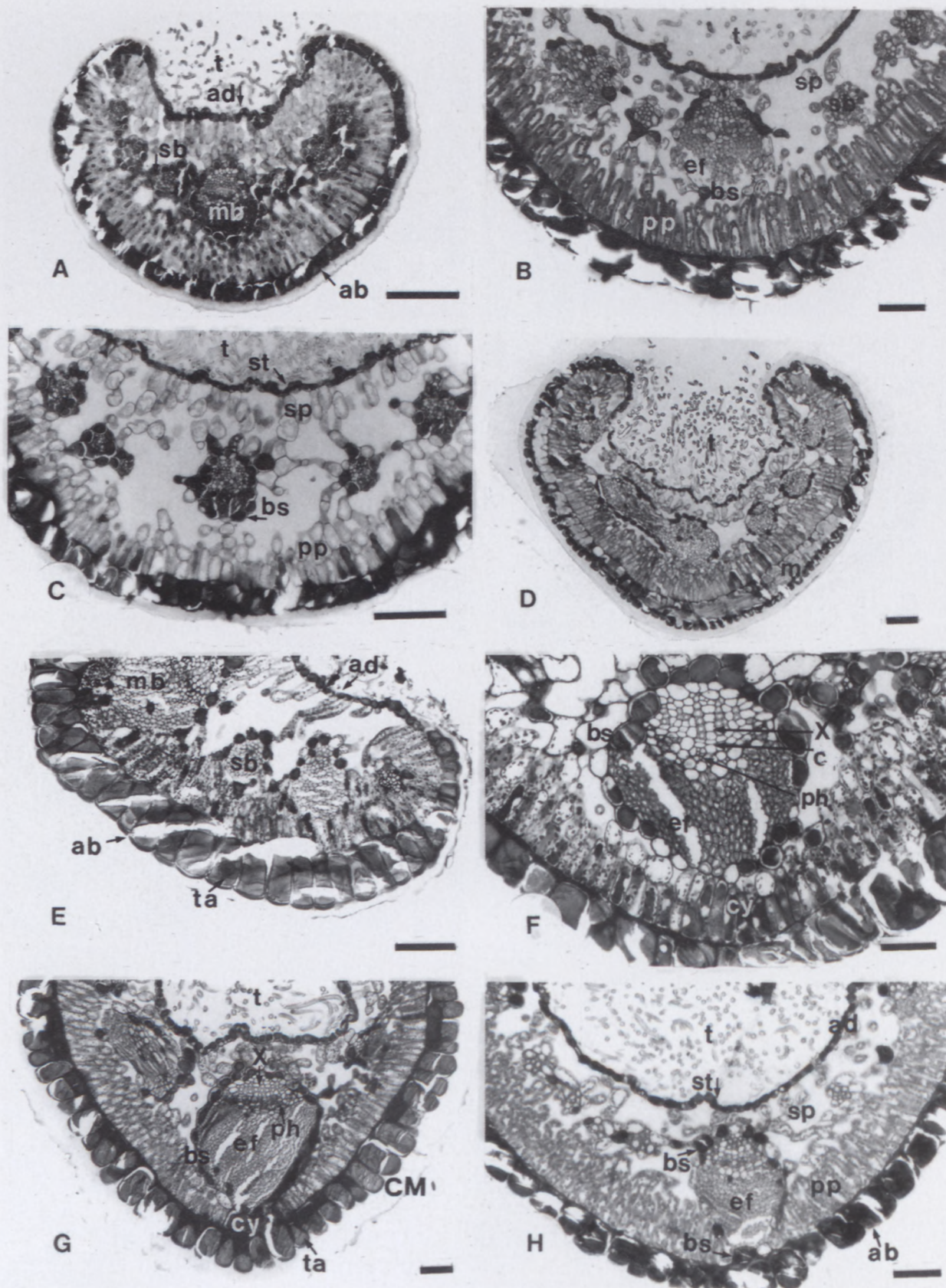


FIGURE 3.—LM photographs of leaf structural types A and B. Type A: A, *P. sp. nov. 1*, Bredenkamp 1044. Type B1: B, *P. pendula*, Bredenkamp 908. Type B2: C, *P. paludosa*, Bredenkamp 1035. Type B3: D, *P. ericoides*, Bredenkamp 962. Type B4: E, *P. filiformis* subsp. *filiformis*, Bredenkamp 1039. Type B5: F, *P. glomerata* subsp. *glomerata*, Bredenkamp 984, with secondary tissue in vascular bundle; G, *P. obtusifolia*, Bredenkamp 919. Type B6: H, *P. rigida*, Bredenkamp 1013. Abbreviations as for Figure 2. Scale bars: A–H, 100  $\mu$ m.



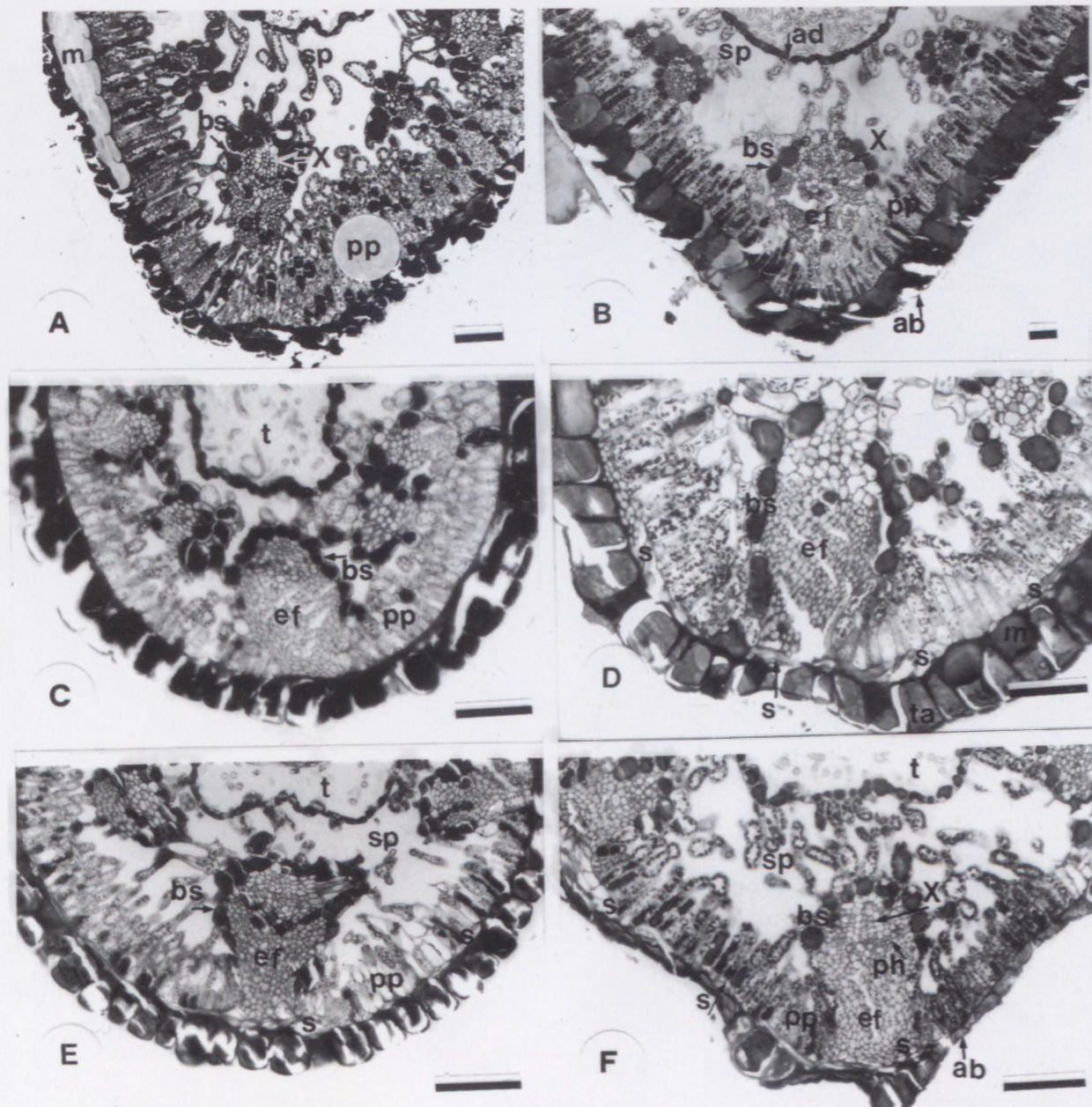


FIGURE 4.—LM photographs showing leaf structural types C and D. Type C: A, *P. falcifolia*, Bredenkamp 917; B, *P. sp. nov. 4*, Bredenkamp 1016. Type D1: C, *P. montana*, Bredenkamp 889. Type D2: D, *P. paleacea*, Bredenkamp 960; E, *P. rigida*, Bredenkamp 962; F, *P. vulgaris*, Bredenkamp 901. Abbreviations as for Figure 2. Scale bars: A–F, 100  $\mu\text{m}$ .

#### *Leaf structure, mesophyll, vascular and sclerenchyma tissue in t/s*

*Leaf* isobilateral or inverse-dorsiventral. *Outline* variable, narrowly transversely elliptic in flatter leaves, transversely elliptic (Figures 1F; 3A; 4C, E) or transversely oblong (Figure 1R) in cymbiform leaves, also canaliculate (Figures 1G; 3H) or carinate (Figures 1O–P; 4A, B, F); adaxial epidermis slightly concave in flatter leaves or leaf lamina and margins strongly upturned to involute forming a central groove or furrow. *Margins* filled with palisade parenchyma extending to adaxial epidermis, abruptly becoming irregular adaxially, conforming to shape and size of spongy parenchyma (Figure 2G); terminal vein endings often present, ultimately consisting of a single tracheid (Figure 2H). *Width* (570–)880(–1480)  $\mu\text{m}$ . *Midrib* often raised below owing to supporting sclerenchyma fibres,

cymbiform leaf folding along reinforced midrib; thickness of main vein (260–)440(–560)  $\mu\text{m}$ . *Mesophyll* palisade-like and homogeneous or inverted—spongy parenchyma situated adaxially and palisade parenchyma abaxially. *Palisade parenchyma* horseshoe-, U- or V-shaped, 1- or 2-layered, or 2- or 3-layered, (3)4 or 5(6) cells per 50  $\mu\text{m}$ ; cells narrowly elliptic to elliptic in isobilateral leaves or elongated in inverse-dorsiventral leaves, containing chloroplasts, tanniferous deposits and druse crystals. *Spongy parenchyma* in isobilateral leaves  $\pm$  uniform in shape, cells narrowly elliptic to elliptic, densely arranged with larger intercellular spaces in centre of leaf, aerenchymatic, meso- or xeromorphic in inverse-dorsiventral leaves, often resembling palisade parenchyma adaxial to veins, rounded, pentagonal or heptagonal with lobes connecting neighbouring cells; cells either loosely arranged with large intercellular spaces or densely arranged with small,

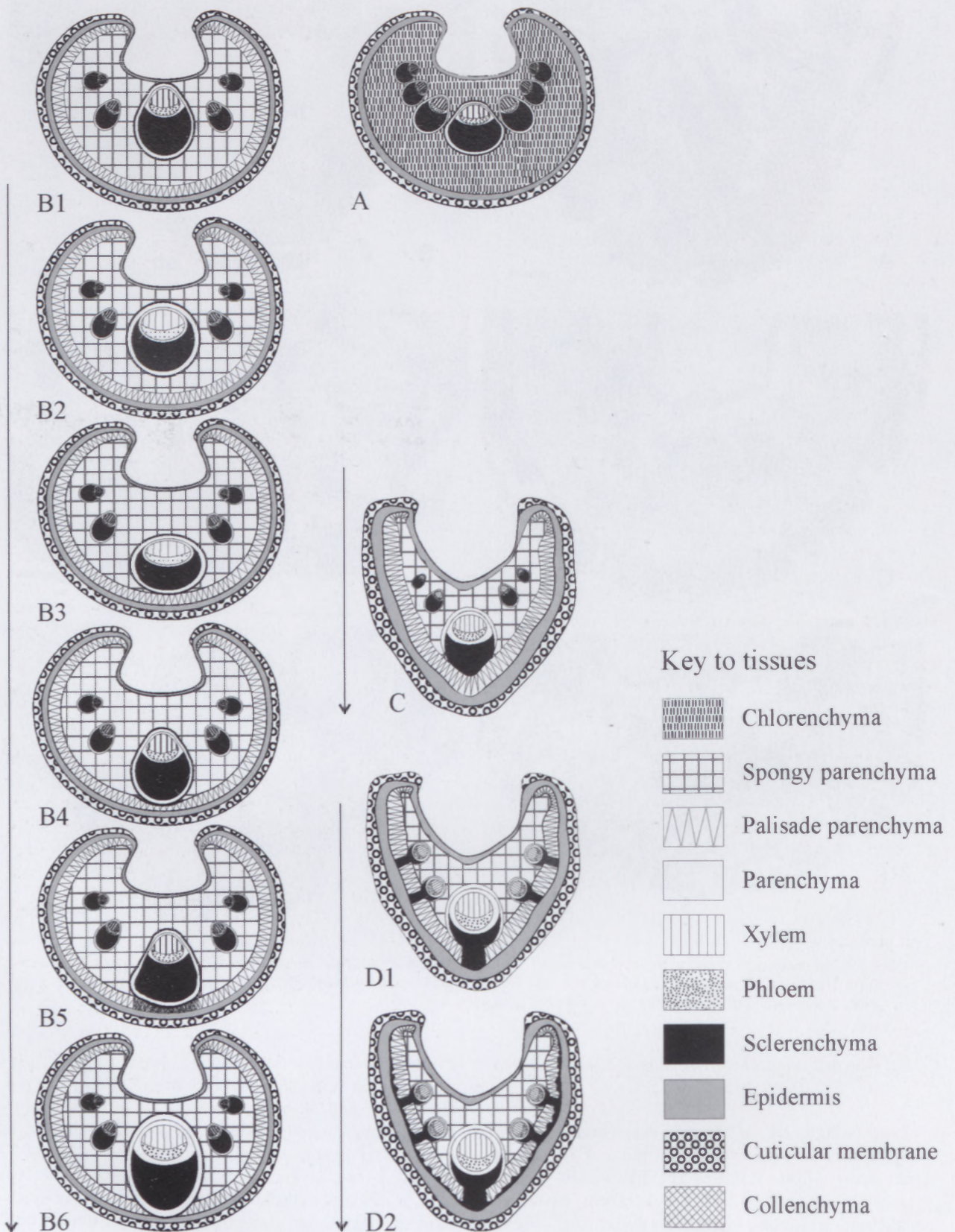


FIGURE 5.—Diagrammatic representation of leaf structural types A, B, C and D, also indicating increasing xeromorphic gradient within types B and D, as well as for type B to D.

centrally orientated intercellular spaces in xeromorphic leaves; elongated cells connecting bundles laterally, constituting a paraveinal mesophyll; chloroplasts and tanniferous deposits present; calcium oxalate crystals present in crystalliferous cells (presence in intercellular

spaces possibly due to processing) (Figure 2E, F). *Main vascular bundle* centrally arranged in isobilateral leaves (Figure 3A), variously orientated in relation to mesophyll of inverse-dorsiventral leaves (Figures 3–5). *Shape* ovate, widely ovate, very widely ovate, obovate or

obovate. *Bundle sheath* completely enveloping vascular bundle (Figure 3A–H) or present adaxially only (Figure 4A–F); number of cells (12–)14–28(–32), mostly one layer of parenchymatous cells or irregularly two-layered; cells larger than other tissues in vascular bundle, roundish or often longitudinally or transversely elongated; tanniferous deposits ample. *Vascular tissue* collateral with adaxial xylem and abaxial phloem, surrounded by a layer of colourless parenchymatous cells, becoming tanniferous or sclerenchymatous abaxially, separating vascular tissue from abaxial sclerenchyma fibres. *Xylem* arranged in a  $\pm$  semilunar band or in  $\pm$  7 radial tiers, alternating with xylem parenchyma (Figures 2C; 3F–G; 4A, F), often separated from phloem by thin-walled parenchyma cells. *Phloem* arranged in shallow band, sieve tubes and companion cells interspersed with phloem parenchyma. *Secondary growth* indicated by cambial cells and thin-walled derivatives arranged in rows between secondary xylem and secondary phloem; primary xylem situated in most adaxial position between large parenchymatous cells and primary phloem bordering on sclerenchyma fibres, conspicuous in *P. glomerata* subsp. *glomerata* (Figure 3F). *Extraxylary fibres* bordering phloem tissue abaxially,  $\pm$  separated by irregular layer of parenchyma often containing tanniferous substances and becoming sclerenchymatous (Figures 2C; 3F, H); enclosed in bundle sheath or extending beyond bundle sheath and palisade parenchyma up to abaxial epidermis. *Secondary vascular bundles* (5)6–13(–19) corresponding to main vascular bundles in orientation, shape, bundle sheath and arrangement of vascular tissue. *Sclerenchymatous hypodermal sheath* formed by sclerenchyma fibres extending paradermally, often up to leaf margins ('wandering' fibres *sensu* Thoday 1921), connecting with fibres from main and secondary vascular bundles in *P. paleacea*, *P. rigida*, and *P. vulgaris* (Figures 4D–F; 5); sclerenchyma fibres in mesophyll ('Spicularzellen' *sensu* Supprian 1894) absent.

## Leaf structural types

The isobilateral and inverse-dorsiventral states of the leaf dictate the orientation of the main vascular bundle. The main vascular bundle is central in isobilateral leaves (Figure 3A), and either close to the adaxial epidermis, situated centrally, or variously arranged in relation to the abaxial epidermis in inverse-dorsiven-

tral leaves (Figure 5). In this transformation series, four leaf structural types and ten states are identified (Tables 3; 4).

## Key to leaf structural types

- 1a Leaf isobilateral ..... type A (Figures 3A; 5A)
- 1b Leaf inverse-dorsiventral:
  - 2a Bundle sheath completely enveloping main vascular bundle, extraxylary sclerenchyma fibres enclosed in bundle sheath ..... type B (Figures 3B–H; 5B)
  - 2b Bundle sheath capping main vascular bundle adaxially,  $\pm$  absent abaxially, extraxylary sclerenchyma fibres not enclosed in bundle sheath:
    - 3a Main vascular bundle bordering on palisade parenchyma, extraxylary sclerenchyma fibres fitting into V-shaped palisade parenchyma ... type C (Figures 4A, B; 5C)
    - 3b Main vascular bundle extending beyond palisade parenchyma, extraxylary sclerenchyma fibres in contact with abaxial epidermis:
      - 4a Sclerenchymatous hypodermal sheath absent ..... type D1 (Figures 4C; 5D)
      - 4b Sclerenchymatous hypodermal sheath present ..... type D2 (Figures 4D–F; 5D)

## Leaf structural type A

*Leaf isobilateral. Main vascular bundle* central; bundle sheath completely enclosing vascular tissue. *Secondary vascular bundles* close to one another, with bundle sheaths adhering, forming a central plate of veins. *Sclerenchymatous hypodermal sheath* absent (Tables 3; 4; Figures 3A; 5A). Species represented: *P. sp. nov.* 1 (Figure 3A).

## Leaf structural type B

*Leaf inverse-dorsiventral. Palisade parenchyma* horseshoe-shaped. *Main vascular bundle* variously orientated in relation to mesophyll: adhering to adaxial epidermis (type B1), centrally arranged with strands of spongy parenchyma (type B2), touching palisade parenchyma abaxially (type B3), sunken into palisade parenchyma (type B4), extending beyond palisade parenchyma with collenchyma wedged between main vascular bundle and abaxial epidermis (type B5) or adhering to abaxial epidermis (type B6). *Shape* ovate, widely ovate, very widely ovate, oblate or obovate. *Bundle sheath* completely enveloping main and secondary vascular bundles. *Extraxylary sclerenchyma fibres* enclosed in bundle sheath. *Sclerenchymatous hypodermal sheath* absent (Tables 3; 4; Figures 3B–H; 5B).

## Key to subtypes of leaf type B and relevant taxa

- 1a Main vascular bundle close to or adhering to adaxial epidermis ..... type B1: *P. burchellii*, *P. pendula* (Figure 3B)
- 1b Main vascular bundle central or abaxial:
  - 2a Main vascular bundle central ... type B2:
    - 3a Mesophyll inverse-dorsiventral, spongy parenchyma more homogenous and palisade-like:
      - 4a Main vascular bundle surrounded by aerenchymatic spongy parenchyma, strands of spongy parenchyma connecting main vascular bundle to adaxial epidermis, palisade parenchyma and secondary vascular bundles ..... *P. paludosa* (Figure 3C)
      - 4b Main vascular bundle surrounded by mesomorphic spongy parenchyma, secondary vascular bundles closely arranged ..... *P. comosa*
    - 3b Mesophyll inverse-dorsiventral, palisade and spongy parenchyma clearly distinguished:
      - 5a Mesophyll xeromorphic ..... *P. obtusifolia*, *P. glomerata* subsp. *glomerata*
      - 5b Mesophyll aerenchymatic or mesomorphic:
        - 6a Outline of leaf in *t/s* transversely elliptic ..... *P. galpinii* (Figure 2C), *P. montana* (Figure 1Q)
        - 6b Outline of leaf in *t/s* transversely oblong ..... *P. paleacea* (Figure 1R)
  - 2b Main vascular bundle abaxially arranged or interfering with palisade parenchyma:

- 7a Main vascular bundle touching palisade parenchyma abaxially . . . type B3:
- 8a Abaxial epidermal cells large, strongly mucilaginous, periclinal × anticlinal dimensions in *t/s* 30–65 × (–35)55–60 (–70) μm:
- 9a Palisade parenchyma U-shaped . . . . . *P. paleacea*
- 9b Palisade parenchyma horseshoe-shaped . . . *P. galpinii*, *P. drakensbergensis*, *P. ericoides* (Figure 3D), *P. rigida*, *P. montana*
- 8b Abaxial epidermal cells exceptionally large, abundantly tanniferous, mucilagination minimal, periclinal × anticlinal dimensions in *t/s* (20–)30–45(–50) × (25–)30–75(–105) μm:
- 10a Outline of leaf in *t/s* transversely elliptic to cordiform . . . . .
- . . . *P. obtusifolia* (Figure 1M), *P. glomerata* subsp. *glomerata* (Figure 1N), *P. filiformis* subsp. *filiformis* (Figures 1L)
- 10b Outline of leaf in *t/s* not transversely elliptic, depressed obovate or canaliculate respectively . . . . .
- . . . . . *P. sp. nov.* 2 (Figure 1I), *P. sp. nov.* 3 (Figure 1J)
- 7b Main vascular bundle sunken into palisade parenchyma, causing specialization of, or extending beyond palisade parenchyma:
- 11a Palisade parenchyma indented because of sunken main vascular bundle . . . type B4:
- 12a Abaxial epidermal cells strongly mucilaginous, periclinal × anticlinal diam. in *t/s* 30–65 × 45–60 μm:
- 13a Leaf outline in *t/s* canaliculate; secondary vascular bundles ± 6 on each side of main bundle . . . *P. rubra* (Figure 1K)
- 13b Leaf outline in *t/s* transversely oblong, margins erect; secondary vascular bundles 3 or 4 on each side of main bundle . . . . . *P. paleacea* (Figure 1R)
- 12b Abaxial epidermal cells strongly tanniferous, periclinal × anticlinal cell diam. in *t/s* (35–)40–45 × 45–75 (–105) μm . . . . . *P. filiformis* subsp. *filiformis* (Figure 3E), *P. filiformis* subsp. *nov.*, *P. obtusifolia*
- 11b Palisade parenchyma abaxial of main vascular bundle specialized, or main vascular bundle extending beyond palisade parenchyma:
- 14a Main vascular bundle separated from abaxial epidermis by collenchyma containing ample amounts of tanniferous substances . . . . . type B5: *P. glomerata* subsp. *glomerata* (Figure 3F), *P. obtusifolia* (Figure 3G)
- 14b Main vascular bundle extending beyond palisade parenchyma, bordering on abaxial epidermis, abaxial cells of vascular bundle sheath often collenchymatous . . . type B6:
- 15a Main vascular bundle abaxially orientated, shape ovate to very widely ovate . . . . .
- . . . . . *P. filiformis* subsp. *nov.*, *P. glomerata* subsp. *nov.*
- 15b Main vascular bundle exceptionally large, situated close to adaxial epidermis, reaching and touching abaxial epidermis, shape elliptic . . . . . *P. rigida* (Figure 3H)

### Leaf structural type C

Leaf inverse-dorsiventral. Palisade parenchyma V-shaped. Main vascular bundle bordering on palisade parenchyma abaxially; shape obovate; bundle sheath 1 or 2 layers of parenchymatous cells capping main vascular bundle adaxially, ± absent abaxially; cells rounded or longitudinally lobed, containing ample amounts of tanniferous substances. Extraxylary sclerenchyma fibres not enclosed in bundle sheath, bordering on and fitting into the V-shaped palisade parenchyma. Sclerenchymatous hypodermal sheath absent (Figures 4A, B; 5C).

#### Key to species

- 1a Bundle sheath cells longitudinally lobed, radiating outwards adaxially, containing ample amounts of tanniferous substances . . . . . *P. falcifolia* (Figure 4A)
- 1b Bundle sheath cells rounded . . . . . *P. sp. nov.* 4 (Figure 4B)

### Leaf structural type D

Leaf inverse-dorsiventral. Palisade parenchyma horseshoe-, U- or V-shaped. Main vascular bundle extending beyond palisade parenchyma, ultimately in contact with abaxial epidermis. Shape obovate. Bundle sheath 1 or 2 layers of parenchymatous cells capping main vascular bundle adaxially, ± absent abaxially; cells rounded or lobed. Extraxylary sclerenchyma fibres extending beyond bundle sheath, running through palisade parenchyma up to abaxial epidermis; not enclosed in bundle sheath (ultimate stage in *P. montana*, type D1). Sclerenchymatous hypodermal sheath formed by hypodermal fibres extending paradermally in direction of leaf margins, often connecting with fibres from main and secondary vascular bundles. Present in all species of leaf

structural type D2, absent in *P. montana* (type D1) (Figures 4C–F; 5D).

#### Key to species

- 1a Sclerenchymatous hypodermal fibres absent . . . . .
- . . . . . type D1: *P. montana* (Figure 4C)
- 1b Sclerenchymatous hypodermal fibres present . . . type D2:
- 2a Outline of leaf in *t/s* transversely oblong; parts of lamina extending beyond adaxial epidermis narrow, containing terminal vascular tissue only; margins upturned; central furrow wide and shallow; palisade parenchyma U-shaped, density 5 cells per 50 μm . . . . .
- . . . . . *P. paleacea* (Figures 1R; 4D)
- 2b Outline of leaf in *t/s* transversely elliptic or carinate; parts of lamina extending beyond adaxial epidermis varying in width, each containing (2)3(–6) secondary vascular bundles; margins diverging outward or involute; central groove deep; palisade parenchyma horseshoe- or V-shaped, density (3)4(5) cells per 50 μm:
- 3a Outline of leaf in *t/s* transversely elliptic; margins involute; palisade parenchyma horseshoe-shaped . . . . .
- . . . . . *P. rigida* (Figure 4E), less often *P. vulgaris*
- 3b Outline of leaf in *t/s* carinate; margins diverging outward or involute; palisade parenchyma V-shaped . . . . .
- . . . . . 20. *P. vulgaris* (Figure 4F)

Intermediate states, with main vascular bundle orientated in more than one position in relation to the ad- and abaxial epidermis and mesophyll, were recorded in *P. glomerata* subsp. *glomerata*, *P. obtusifolia*, *P. montana*, *P. paleacea* and *P. rigida*. All states were accounted for in Tables 3 and 4, as well as in the construction of keys.

#### Comparative leaf anatomy at infrageneric level

In order to facilitate the interpretation of existing data for all infrageneric taxa, data are summarized in Tables 3 and 4.

## DISCUSSION AND ADDITIONAL OBSERVATIONS

**Leaf structure***Prevailing characters in Thymelaeaceae*

Leaf structure in Thymelaeaceae exhibits a transformation series from mainly dorsiventral, the prevailing state in the family, to isobilateral or centric in *Diarthron* Turcz., *Pimelea* Banks & Sol. and *Thymelaea* Juss. (Leandri 1930; Metcalfe & Chalk 1950), all these states being present in *Lachnaea* and *Cryptadenia* (Beyers 1992; Beyers & Van der Walt 1995) and the inverse-dorsiventral state prominent in *Passerina*. Thoday (1921) recorded the isobilateral state in juvenile leaves in selected species of *Passerina*, possibly reflecting its primitive status in the genus. Leaves of *P.* sp. nov. 1 (Figures 3A; 5A) are isobilateral, whereas the leaves of all the other species are inverse-dorsiventral, possibly representing the more advanced state (Figures 3B–H; 4A–F; 5B–D).

Most species of *Passerina* are adapted to the dry, warm summers and humid winters of the winter rainfall area of the Cape Floristic Region, others survive in the arid conditions of the Karoo, some grow in a range of habitats along the eastern escarpment and some are adapted to maritime conditions along the southern African coast (Table 1). What appears to be adaptations to these varying environments are reflected in the leaf structure of the various species. Weiglin & Winter (1991), studying the morphological-anatomical features of perennial halophytes, pointed out the importance of curvature of outer epidermal cell walls, epicuticular waxes, mesophyll orientation, enrolled leaves and fortification of tissue—characters present in most *Passerina* species. Other important leaf adaptations in *Passerina* are the decussate and appressed arrangement, the cymbiform shape and the inverted palisade parenchyma, developing on that side of the leaf which is exposed to the highest light intensity. Structural support is rendered by the presence of sclerenchyma in the main and secondary vascular bundles and in some Western Cape species these fibres proliferate beyond the vascular bundle sheath to join with hypodermal fibres, forming a sclerenchymatous hypodermal sheath. The importance of many of these characters is further discussed below.

**Epidermal tissue***Prevailing characters in Thymelaeaceae*

According to Metcalfe & Chalk (1950) the cuticular membrane (CM) of the leaf is usually smooth. Epidermal cells are arched outwards in *Linostoma* Wall. ex Endl. and papillose on the lower surface in species of *Daphne* L.

Speculations on functions and ecological aspects of the leaf epidermis in *Passerina* have been dealt with by Bredenkamp & Van Wyk (1999, 2000). Leaf arrangement in *Passerina* causes the abaxial epidermis to be largely exposed to the atmosphere, resulting in epider-

mal characters being more affected by environmental change. However, the arrangement of the epidermal cells and the ornamentation of the cuticular membrane (CM) correlate well with leaf structural type (Table 3). Species with epidermal cells arranged randomly and with smooth or papillate cuticular ornamentation, all have leaf structural type B. With the exception of *P. montana* (type D1) with epidermal cells arranged in rows and smooth or papillate cuticular ornamentation, structural types C and D correlate with epidermal cells arranged in rows with striate cuticular ornamentation. Finally, structural type D is also characterized by a well-developed sclerenchymatous hypodermal sheath (Table 4), possibly representing the more advanced state.

**Mesophyll***Prevailing characters in Thymelaeaceae*

Palisade cells are generally short. Mesophyll, including irregular sclerenchymatous fibres, is found in species of *Daphne* L., *Daphnopsis* C.Mart., *Enkleia* Griff., *Gyrinops* Gaertn., *Peddiea* Harv. and *Stephanodaphne* Baill. (Metcalfe & Chalk 1950).

In the isobilateral leaf of *P.* sp. nov. 1, mesophyll is palisade-like and homogeneous. All other species of *Passerina* display the possibly more advanced state in which the mesophyll is inverted, with elongated, abaxial palisade parenchyma and adaxial spongy parenchyma. The orientation of the mesophyll in relation to leaf shape, sclerenchyma and vascular tissue (Table 4), forms the basis of various leaf structural types distinguished in this study. The palisade parenchyma is horseshoe-shaped in all species with narrowly transversely elliptic, cordiform or canaliculate leaves in *t/s* and with leaf structural type B (Figure 3B–H). In *P. paleacea*, the leaf is transversely oblong in *t/s* and the palisade parenchyma is U-shaped (Figures 1R; 4D). Palisade parenchyma is V-shaped (Figure 4A, B, F) in species with structural types C and D, in which the leaves are typically carinate in *t/s*. In the most xeromorphic state, sclerenchyma extends through the V-shaped palisade parenchyma, joining other hypodermal fibres to form a sclerenchymatous hypodermal sheath (Figure 4F). Irregular sclerenchymatous fibres are absent in the mesophyll of leaves in *Passerina*.

The mesophyll of the leaf is seemingly adapted to survive arid conditions and high light intensity, thus becoming xeromorphic in most species. This is reflected by the palisade parenchyma which usually occurs in 1–3 layers, quite densely arranged with 3–6 cells per 50  $\mu\text{m}$ . Palisade cells contain large numbers of chloroplasts, ample amounts of tanniferous substances and crystals of calcium oxalate. In contrast, the spongy parenchyma is usually adaxially arranged and aerenchymatous in most species, corresponding to the epistomatic state of the leaves. With spongy parenchyma around the stomata, molecules of carbon dioxide would penetrate deep into the leaf and the large intercellular spaces of aerenchyma surrounding the vascular bundles would possibly have a moist atmosphere critical to physiological processes such as photosynthesis, respiration and transpiration.

TABLE 4.—Selected morphological and anatomical characters of all leaf structural types in *Passerina*

Taxon	Leaf		Axial fibrous sheath		Main vascular bundle		Bundle sheath enveloping main vascular bundle		Secondary vascular bundles No. (each side of main bundle)	Palisade parenchyma		Spongy parenchyma
	Structural type	Outline	Width $\mu\text{m}$	Width $\mu\text{m}$	Shape	Completely	Adaxial cap	No. cells		Shape	No. layers	
<i>P. sp. nov. 1</i> (Figure 3A)	A	transversely elliptic	$\pm 850$	$\pm 450$	widely ovate	X	19–25	3 or 4	adaxial 3 abaxial 4			
<i>P. burchellii</i>	B1	narrowly transversely elliptic	$\pm 1480$	$\pm 540$	widely ovate	X	$\pm 20$	4	horseshoe	1 or 2	4	aerenchymatic
<i>P. pendula</i> (Figure 3B)	B1	canaliculate	780–860	$\pm 340$	widely ovate	X	17–19	4–9	horseshoe	1 or 2	4 or 5	aerenchymatic
<i>P. comosa</i>	B2	transversely elliptic	$\pm 940$	$\pm 460$	oblate	X	$\pm 22$	3–5	horseshoe/V	3 or 4	4 or 5	mesomorphic
<i>P. paludosa</i> (Figure 3C)	B2	narrowly transversely elliptic	990–1140	410–460	ovate	X	19–20	3–5	horseshoe	1	3 or 4	aerenchymatic
<i>P. galpinii</i> (Figure 2C)	B2, B3	transversely elliptic	1000–1150	520–550	widely ovate	X	18–25	3	horseshoe	1 or 2	3 or 4	aerenchymatic
<i>P. drakensbergensis</i>	B3	canaliculate	720–830	370–400	widely ovate	X	17–19	3 or 4	horseshoe	1 or 2	3 or 4	aerenchymatic
<i>P. ericoides</i> (Figure 3D)	B3	transversely elliptic	910–1100	390–470	oblate	X	$\pm 22$	3	horseshoe	2 or 3	3	aerenchymatic
<i>P. sp. nov. 2</i>	B3	depressed obovate	$\pm 720$	300–360	widely ovate	X	23–28	2 or 3	horseshoe	1 or 2	4 or 5	mesomorphic
<i>P. sp. nov. 3</i>	B3	canaliculate	810–880	380–430	very widely ovate	X	18–27	3	horseshoe	1 or 2	4 or 5	aerenchymatic
<i>P. rubra</i>	B4	canaliculate	800–920	330–400	widely ovate	X	23–28	6	horseshoe	1 or 2	4 or 5	aerenchymatic
<i>P. filiformis</i> subsp. <i>filiformis</i> (Figure 3E)	B3, B4	cordiform	780–860	350–420	widely ovate	X	13–15	3 or 4	horseshoe	1 or 2	3–5	aerenchymatic
<i>P. filiformis</i> subsp. nov.	B4, B6	transversely elliptic	$\pm 820$	$\pm 400$	widely ovate	X	$\pm 27$	2 or 3	horseshoe	2	5	aerenchymatic
<i>P. obtusifolia</i> (Figure 3G)	B2, B3, B4, B5	transversely elliptic	730–1090	370–470	widely ovate	X	20–26	3 or 4	horseshoe	2	4 or 5	xeromorphic
<i>P. glomerata</i> subsp. <i>glomerata</i> (Figure 3F)	B2, B3, B5	transversely elliptic	570–980	290–500	very widely ovate	X	21–32	3 or 4	horseshoe	2 or 3	4 or 5	xeromorphic
<i>P. glomerata</i> subsp. nov.	B6	canaliculate	770–830	420–430	ovate	X	22–25	2–4	horseshoe	2	3 or 4	mesomorphic
<i>P. falcifolia</i> (Figure 4A)	C	carinate	900–960	520–550	obovate	X	12–14	3 or 4	V	1 or 2	3 or 4	aerenchymatic
<i>P. sp. nov. 4</i> (Figure 4B)	C	carinate	820–1280	400–700	obovate	X	$\pm 21$	3 or 4	V	2	3 or 4	aerenchymatic
<i>P. montana</i> (Figure 4C)	B2, B3, D1	transversely elliptic	560–710	260–360	obovate	X (B2, B3)	X (D1) $\pm 25$ (B2, B3) or $\pm 19$ (D1)	3 or 4	horseshoe	1 or 2	4–6	mesomorphic
<i>P. paleacea</i> (Figure 4D)	B2, B3, B4, D2	transversely oblong, margins erect	620–860	400–570	obovate	X (B2, B3, B4)	X (D2) $\pm 23$ (B2, B3, B4) or $\pm 17$ (D2)	3 or 4	U	1–3	5	mesomorphic
<i>P. rigida</i> (Figures 3H, 4E)	B3, B6, D2	transversely elliptic	680–780	270–390	obovate (large in B6)	X (B3, B6)	X (D2) 13–20 (B3, B6) or 18–22 (D2)	4–6	horseshoe	1–3	3–5	aerenchymatic
<i>P. vulgaris</i> (Figure 4F)	D2	carinate	660–870	330–500	obovate	X	14–23	3 or 4	horseshoe/V	1 or 2	4 or 5	aerenchymatic

X = present.

### Ecological significance

The xeromorphic character of the mesophyll can be expressed in terms of the number of cell layers and the density (reflected by the number of cells per 50  $\mu\text{m}$ ) of the palisade parenchyma as well as the appearance of the spongy parenchyma (Table 4). Possible adaptation to physiological drought is shown by the homogeneous and palisade-like mesophyll of *P. sp. nov. 1*, which grows on the high mountains of the Karoo, where it is often covered by snow in winter. Among the remainder of the species, the most xeromorphic state is found in *P. glomerata* subsp. *glomerata* (Figure 3F), *P. obtusifolia* (Figure 3G) and *P. comosa*, all growing in the NW parts of Western Cape; their leaves have (1)2 or 3 layers of cells in the palisade parenchyma, a density of 4 or 5 cells per 50  $\mu\text{m}$  and the spongy parenchyma is densely arranged. The mesophyll of *P. ericoides* (Figure 3D), *P. paleacea* (Figure 4D) and *P. rigida* (Figures 3H; 4E) can also be considered xeromorphic, possibly in response to the effect of salt spray, as these species grow on the sea shore. A xeromorphic mesophyll is also indicated for *P. montana* (Figure 4C), which occupies a wide range of habitats along the eastern escarpment. On the other hand, *P. paludosa* (Figure 3C), a rare species from marshy areas in the Cape Peninsula, has an inverse dorsiventral leaf with one layer of palisade parenchyma, a density of 3 or 4 cells per 50  $\mu\text{m}$  and a large aerenchymatic spongy parenchyma, corresponding to the general trend towards aerenchymatic tissue in marsh plants.

### Leaf structural types: orientation and structure of main vascular bundle in relation to epidermis and mesophyll

#### *Prevailing characters of vascular bundles in Thymelaeaceae*

In Thymelaeaceae, large portions of vascular bundles are often occupied by sclerenchyma and surrounded by a sheath of parenchymatous cells containing tannin (Van Tieghem 1893; Gilg 1894; Supprian 1894; Metcalfe & Chalk 1950). Both these characters are present in *Passerina*. Intraxylary phloem in the petiole and midrib was recorded by Leandri (1930) and cited by Domke (1934) for many genera, excluding *Passerina* (= *Chymococca*). The lack of intraxylary phloem in leaves of *Passerina* was confirmed by the present study (Tables 3; 4; Figure 5).

#### *Xeromorphic gradient*

The progressive change in orientation of the main vascular bundle in relation to the mesophyll shows a xeromorphic gradient (Figure 5). Leaf structural type A was defined on the basis of the isobilateral leaf, which is probably an ancestral state. The xeromorphic character of the leaf is strongly supported by the associated homogenous mesophyll and central vascular system. The leaves are inverse-dorsiventral in all other structural types. A xeromorphic gradient is clearly expressed in leaf structural type B. In types B1 and B2 the mesophyll is aerenchymatic and the main vascular bundle adaxially or centrally arranged. An increase in the density, the num-

ber of cells and layers and specialization of tissues takes place in types B3 and B4, with B5 and B6 representing the most xeromorphic forms. A similar increase in xeromorphism can be shown in structural types C and D1 and D2, with the abaxial arrangement of the main vascular bundle, the increase in sclerenchyma tissue and the ultimate formation of the sclerenchymatous hypodermal sheath, in type D2, as the most xeromorphic state.

### Ecological significance

Replacement of the main vascular bundle from the ad- to the abaxial position with the sequential increase in xeromorphism suggests an adaptive strategy (Figure 5). In type B the main vascular bundle is close to the adaxial epidermis and stomata, possibly enhancing transpiration. It is furthermore completely surrounded by aerenchyma. Vascular tissue in close contact with aerenchyma provides water, causing a moist atmosphere and a high water potential in the large intercellular spaces. Inorganic and organic substances are transported by the xylem and phloem for various physiological processes taking place in the mesophyll of the leaf. The more xeromorphic arrangement mechanically strengthens the leaf, allows enough moisture for photosynthesis and respiration, but possibly retards loss of water through transpiration. Increasing xeromorphism is illustrated by the vascular bundle becoming abaxially orientated and finally by sclerenchyma tissue of the vascular bundle abaxially projecting beyond the vascular bundle sheath and reaching up to the abaxial epidermis, leaving only the adaxial part of the vascular bundle in contact with aerenchyma. Vascular tissue, providing moisture for the critical physiological processes, is thus separated from aerenchyma by one or two layers of the parenchymatous bundle sheath cap. These adaptations, associated with geographical distribution (Table 1), can clearly be illustrated at species level and for all the leaf structural types.

Type A: the main and secondary vascular bundles are closely arranged with bundle sheaths adhering, forming a central plate of veins surrounded by two or three layers of palisade-like mesophyll, possibly acting as a protective sheath against the minimum temperatures, which are often below freezing point in the habitat of *P. sp. nov. 1* (Table 1; Figure 3A).

Type B1: *P. burchellii* and *P. pendula* (Figure 3B) are both mountainous species often surrounded by mist. The main vascular bundle is more or less against the adaxial epidermis close to the stomata and is completely surrounded by aerenchyma, possibly enhancing transpiration and aeration of the leaf.

Types B2, B3 and B4: these are the most common leaf types, found in  $\pm$  two-thirds of *Passerina* species (Table 4; Figure 3C–E). The possible adaptive significance of these structural types remains much the same as in B1, except that the leaf becomes sequentially more xeromorphic as the main vascular bundle borders on or sinks into the palisade parenchyma, possibly curtailing water loss.

Type B5: xeromorphism is enhanced in *P. glomerata* subsp. *glomerata* and *P. obtusifolia* (Figure 3F, G), both growing in the warm, arid Karoo. The main vascular

bundle is abaxially embedded in palisade parenchyma which differentiates into collenchyma and the spongy parenchyma surrounding the main vascular bundle which is more densely arranged with smaller intercellular spaces. This more xeromorphic arrangement mechanically strengthens the leaf, allows moisture for physiological processes but possibly retards loss of water.

Type B6: found in *P. glomerata* subsp. nov. occurring on mountain tops from the Cederberg to the Cape Peninsula and *P. filiformis* subsp. nov. which grows between Malmesbury and Vredendal. In this xeromorphic leaf the main vascular bundle is adaxially surrounded by spongy parenchyma, enhancing aeration, and is abaxially strengthened by palisade parenchyma and the vascular bundle sheath which differentiates into collenchyma. In *P. rigida* (Figure 3H), which grows in salt spray along the coast, the exceptionally large main vascular bundle is close to the adaxial epidermis and borders on the tanniniferous abaxial epidermis, with the possible adaptive advantage of strengthening the leaf and allowing transpiration and associated physiological processes at the same time.

Type C: found in *P. falcifolia* (Figure 4A) and *P. sp. nov. 4* (Figure 4B), growing in relatively moist environments (Table 1). The abaxial surface of the carinate leaf is in contact with the atmosphere, but the obovate main vascular bundle, situated abaxially, is well protected in the V-shaped palisade parenchyma. The adaxial parenchymatous bundle sheath cap and the vascular tissue are in close contact with the aerenchyma, providing moisture for the various physiological processes.

Type D1: in *P. montana* (Figure 4C) the extraxylary sclerenchyma fibres touch the abaxial epidermis, but hypodermal fibres are absent. This arrangement indicates a high degree of mechanical strengthening and xeromorphism, possible adaptations to the wide range of habitats along the eastern escarpment where these plants grow (Table 1).

Type D2: present in *P. paleacea* (Figure 4D), *P. rigida* (Figure 4E) and *P. vulgaris* (Figure 4F), all growing in Western Cape, the centre of diversity for *Passerina* and from where certain species extend west-, north- and eastwards. Orientation and structure of the main vascular bundle are the same as for type C, except that the sclerenchyma tissue of the vascular bundle projects beyond the vascular bundle sheath and reaches up to the abaxial epidermis forming a sclerenchymatous hypodermal sheath, thus strengthening the leaf and making it more xeromorphic. Vascular tissue remains in close contact with the aerenchyma, providing moisture for the various physiological processes.

## Sclerenchyma

### *Prevailing characters in Thymelaeaceae*

Van Tieghem (1893) described extraxylary fibres, specially mentioning those without lignification in *Daphne mezereum* L. and with lignification in *D. cneorum* L. Supprian (1894), mentioned the presence of fibres in the mesophyll of the leaves, which he called 'Spicularzellen' and regarded as a constant taxonomic character. In a subsequent paper, Gilg (1894), critically

discussed the anatomical method applied by the two previous workers, doubting the constant taxonomic value of 'Spicularzellen'. Thoday (1921) described a sclerenchymatous hypodermal sheath extending to the margins of the leaves in *P. filiformis* and *P. cf. falcifolia*, introducing the term 'wandering fibres'. Metcalfe & Chalk (1950) acknowledged the previous works, also mentioning the presence of bundles of sclerenchymatous elements supporting leaf margins in species of *Daphnopsis* C.Mart., *Dicranolepis* Planch. and *Passerina*.

During this study variation concerning leaf structural types was taken into consideration and amply documented. Considering the wide distribution of especially *P. montana* and *P. rigida*, variation in leaf structural type could be expected. In *P. montana* (Figure 4C), hypodermal fibres are absent although lignified fibres project beyond the vascular bundle sheath and reach the abaxial epidermis (type D1). Hypodermal sclerenchyma fibres have been recorded in *P. paleacea* and *P. rigida* with leaf structural types B2, B3 and B4 (Tables 3; 4), but without the development of a hypodermal sclerenchymatous sheath. The hypodermal sclerenchymatous sheath is usually associated with leaf structural type D2 as in the following description. The state in which the main vascular bundle is abaxially orientated, the sclerenchyma extending beyond the vascular bundle sheath, through the inverted palisade parenchyma, reaching the abaxial epidermis (type D) and connecting with the hypodermal sclerenchymatous fibres to form a hypodermal sclerenchymatous sheath, often reaching up to the leaf margins. Leaf structural type D2 is regarded by the present authors as the 'ultimate' adaptation, in *Passerina*, to the Mediterranean climate of the Cape Floristic Region. Figures 4D–F; 5.

## Less important taxonomic characters

### *Leaf width*

Considering the cymbiform, canaliculate or carinate shape of leaves as well as the movement of the lamina due to turgor pressure in the leaf, leaf width can at most be used to interpret leaf shape, but is not regarded as taxonomically significant.

### *Crystals*

Calcium oxalate crystals or lime crystals were considered as taxonomically valuable in the Thymelaeaceae and certain species of *Passerina* by Supprian (1894). Solereder (1908), Metcalfe & Chalk (1950) and Metcalfe (1983) report the presence of both druses and crystal sand in the Thymelaeaceae, but do not consider these crystals of much taxonomic value. In the present study, druses were recorded in the parenchyma cells of the mesophyll in all taxa of *Passerina*. Calcium oxalate crystals in the intercellular spaces are regarded as fragments of druses resulting from processing.

### *Tanniniferous substances*

The substances are abundantly present in the epidermis, mesophyll as well as vascular bundle sheath and parenchyma in all taxa of *Passerina*. No significant interspecific variation was recorded.



## Phylogenetic considerations

### *Leaf structural type correlated with epidermal structure*

A phylogenetic gradient for the leaf structural types cannot be shown, as various characters probably evolved separately. Thoday (1921) reported that juvenile leaves in *Passerina* were isobilateral in transverse section, indicating the possible ancestral state of leaf structural type A. The central arrangement of the vascular bundle in leaf structural type B is probably a primitive state, as rearrangement of the vascular bundle and consequent differentiation of tissues probably represent derived states. Species with epidermal cells arranged randomly and smooth or papillate cuticular ornamentation (Group A in Table 3) which correlate with leaf structural type B, probably represent a primitive state. The hypodermal sclerenchymatous sheath could have evolved as an adaptation to the Mediterranean climate of the Cape Floristic Region and is therefore considered to be a derived character. In conjunction with leaf structural type D, this state is possibly advanced. Epidermal cells arranged in rows with striate cuticular ornamentation (Group B) and associated with leaf structural type D possibly represent the most derived state.

### *Mesophyll*

Parenchyma cells are palisade-like and homogeneous in the isobilateral leaf. All other species possibly represent the derived state in which the mesophyll is inverted, with elongated, abaxial palisade parenchyma, horseshoe, U- or V-shaped and with adaxial spongy parenchyma.

### *Sclerenchyma*

Sclerenchyma (notably extraxylary fibres) in the leaves of *Passerina* could possibly be regarded as primitive as it is a prevailing state in the Thymelaeaceae. Within *Passerina* the hypodermal sclerenchymatous sheath in certain species could have evolved as an adaptation to the Mediterranean climate of the Cape Floristic Region and in conjunction with leaf structural type D, regarded as a possible advanced state.

## Taxonomic significance

The present study has clarified the taxonomic significance of various anatomical leaf characters at the following levels:

### *Family level*

Most family characters prevail in *Passerina* in their unmodified forms, e.g. the epidermis with a papillate cuticular membrane (CM) and mucilaginous epidermal cells, as well as the presence of extraxylary sclerenchyma in the vascular bundle. Other characters have been modified, for example the parenchymatous bundle sheath cap in leaf structural types C and D (Tables 3, 4) and the absence of intraxylary phloem in the leaves.

Irregular sclerenchymatous fibres present in the mesophyll of leaves in many species, have been modified into a sclerenchymatous hypodermal sheath in *Passerina*.

### *Genus level*

In most genera of Thymelaeaceae, leaves are isobilateral, dorsiventral or inverse-dorsiventral (Kugler 1928). *P. sp. nov. 1* (leaf structural type A) is characterized by isobilateral leaves. In all other species, the inversely ericoid leaves are arranged close to the stem, with the abaxial epidermis exposed to the environment. The palisade parenchyma develops abaxially, the mesophyll is inverted and the leaf is regarded as inverse-dorsiventral (Kugler 1928).

### *Species level*

Based on leaf epidermal characters, two groups (A and B) of species are recognized, in which many species could be classified to species level (Bredenkamp & Van Wyk 2000). The correlation of epidermal characters with the leaf structural types has confirmed the authenticity of both these character sets (Table 3). On the basis of anatomical evidence the delimitation of the various species and infraspecific taxa was confirmed (Tables 3, 4). *P. sp. nov. 1*, growing on high mountains in the Ceres Karoo, is characterized by isobilateral leaves and leaf structural type A. *P. glomerata* subsp. *glomerata* (types B2, B3, B5), common to a large range of Karoo habitats, could be distinguished from *P. glomerata* subsp. nov. (type B6), growing on mountain tops from the Cederberg range to the Cape Peninsula. *P. filiformis* L. was previously considered a taxon with a wide distribution from Western and Eastern Cape, along the eastern escarpment of southern Africa, possibly up to Tanzania. The present study and the morphological study indicate that plants growing in southern parts of Western Cape, Eastern Cape and the escarpment can clearly be distinguished from those of Western Cape. Consequently *P. filiformis* was split into *P. filiformis* subsp. *filiformis* (types B3 and B4), *P. filiformis* subsp. nov. (types B4, B6) and *P. sp. nov. 4* (type C). *P. filiformis* subsp. *filiformis* is common in the Cape Peninsula, and distributed from Piquetberg, across the Hex River Mountains, to Attaquaskloof in the southern parts of Western Cape. *P. filiformis* subsp. *glutinosa* occurs in the area between Malmesbury and Vredendal. *P. sp. nov. 4* has a wide distribution from Mossel Bay and Oudtshoorn to Eastern Cape and along the escarpment northwards to Zimbabwe, with outliers in Tanzania. Furthermore, the study of the leaf structural types revealed four leaf structural types and ten states, according to which all species can be characterized and grouped. Leaf type A occurs in *P. sp. nov. 1*; type B in *P. burchellii* Thoday, *P. pendula* Eckl. & Zeyh., *P. comosa* C.H.Wright, *P. paludosa* Thoday, *P. galpinii* C.H.Wright, *P. drakensbergensis* Hilliard & B.L.Burt, *P. ericoides* L., *P. sp. nov. 2*, *P. sp. nov. 3*, *P. rubra* C.H.Wright, *P. filiformis* L. subsp. *filiformis*, *P. filiformis* L. subsp. nov., *P. obtusifolia* Thoday, *P. glomerata* Thunb. subsp. *glomerata*, and *P. glomerata* Thunb. subsp. nov.; type C in *P. falctifolia* C.H.Wright, *P. sp. nov. 4*; type D in *P. montana* Thoday, *P. paleacea* Wikstr., *P. rigida* Wikstr. and *P. vulgaris* Thoday.

## CONCLUSIONS

Leaf anatomical evidence proved extremely useful in the classification of *Passerina*. Four leaf structural types and ten states are associated with specific habitats and geographical distribution, illustrating a xeromorphic gradient. On the basis of leaf structural types, four new species and four subspecies were identified. Certain phylogenetic tendencies were proposed and the systematic value of the various characters at family, genus and species levels were assessed, thus enabling the anatomical characterization of all infrageneric taxa in *Passerina*.

This study illustrates prevailing Thymelaeaceae characters as well as their modification and newly evolved tendencies in *Passerina*. Observations correlate with those obtained from other studies in the genus. Based on the secondary reticulum of the polyforate pollen grain of *Passerina*, the subtribe Passeriniinae Endl. was raised to the tribe Passerineae (Endl.) Bredenkamp & Van Wyk (1996). The unique leaf structural types and states identified by the present leaf anatomical study, provide more evidence in support of the tribe Passerineae.

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# A lexicon of plants traded in the Witwatersrand *umuthi* shops, South Africa

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**Keywords:** families, medicinal plants, plant parts, survey, trade, *umuthi*, vernacular names

## ABSTRACT

At least 511 medicinal plant species are traded commercially in 50 Witwatersrand *umuthi* shops. The plants are listed alphabetically by genus and common (vernacular) name. The orthographic vernacular names, as well as the orthographic variations in these names, are incorporated into the list. Annotations include the plant family, the number of *umuthi* shops stocking the species, the language of the common name, and the plant part traded. The plant family in the region which has the highest number of species and infraspecific taxa in trade is Liliaceae *sensu lato.*, followed in descending order by Fabaceae, Asteraceae, Euphorbiaceae and Amaryllidaceae. Approximately 88.6% of the vernacular names are in Zulu. The mean number of *umuthi* shops per species is 12.3, ranging from 1 to 41. Three hundred and fifty three species (69.2%) occur in the four northern provinces, and 23 species are listed as threatened on the Red Data List.

## INTRODUCTION

In 1994, a semiquantitative survey of 50 Witwatersrand *umuthi* shops was undertaken. Prior to the survey, no attempt had been made to describe the commercial market for medicinal plants and parts in the region. The dynamics of the medicinal plant trade in Witwatersrand *umuthi* shops have now been quantitatively described in terms of the species used, sources and suppliers of plants, the adequacy of the sample size, the diversity and equitability of species being traded and the probability of certain taxa being utilized based on their availability in the southern African flora and biomes (Williams *et al.* 2000). In addition, that paper lists the species most commonly available in at least two-thirds of the *umuthi* shops on the Witwatersrand. The purpose of this paper is to present a checklist of species in trade on the Witwatersrand. In addition, a list of all orthographic vernacular names and their variants referred to in this study is provided, with cross references to the appropriate botanical names. The list will be useful to researchers wanting to identify species in trade.

## METHODS

A stratified random sample of 50 *umuthi* shops was surveyed on the Witwatersrand in 1994. The research participants selected (including traditional healers who owned shops) were proportionately representative of the geographical distribution, ethnicity and gender of the herb traders on the Witwatersrand at the time of the survey (Williams *et al.* 1997). The vernacular names for the plants sold in each *umuthi* shop were recorded—either from a label on the shelf, or from the name cited by the research participant. The language of the plant names was also recorded to aid identification. It was not determined whether the plants sold were used as medicine or for charm purposes.

Forty-three references were used to identify most of the plants (Watt & Breyer-Brandwijk 1932, 1962; Gerstner 1938a, b, 1939a, b, c, 1941a, b; Miller 1941; Ferreira 1949; Watt 1956; Bryant 1966; Hanekom 1967; Stayt 1968; Jacot Guillarmod 1971; Immelman *et al.* 1973; Netshiungani & Van Wyk 1980; Liengme 1981; Netshiungani 1981; Von Breitenbach 1981a, b, 1984, 1986, 1989, 1991; Arnold & Gulumian 1984; Cunningham 1988; Scott-Shaw 1990; Hutchings 1992, 1996; Moll 1992; Veale *et al.* 1992; Pooley 1993; Loxton *et al.* 1994; Hahn 1994; Brandt *et al.* 1995; Estes 1995; Nichols 1995; Van Wyk *et al.* 1997; Kroon 1999). In addition, species were identified from descriptions of aerial plant parts given by the herb traders, or from specimens purchased at the market and identified at the C.E. Moss Herbarium (J), University of the Witwatersrand. An incomplete set of voucher specimens was purchased, and is presently being incorporated into the traditional medicine collection at the Adler Museum of the History of Medicine, University of the Witwatersrand.

Species identification from plant parts recorded in a trade survey is a problem, especially when tracing the plants through their vernacular names in the literature. Errors in identification are sometimes made by the recorders of this information, and there are likely to be citation errors of the vernacular names given by the traders. However, the scientific names allocated to these plants are, for the most part reliable, especially for the names recorded in the Zulu vernacular for which an extensive body of literature exists.

Following species identification, the data were entered into a relational database designed in the program DATAEASE by modifying the herbarium management system of the C.E. Moss Herbarium. This obviated entry of every scientific name encountered. The data capture format was designed specifically for the entry of the survey records, and the data were entered under some of the following fields for each species recorded in an *umuthi* shop, including: 1, genus and species number (Genspec No., following Arnold & De Wet 1993); 2, genus and species; 3, common names; 4, language of the

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common name, and 5, trader information and code. Herb traders were given codes denoting the region and order in which they were surveyed, for instance 'JB30' for 'Johannesburg Shop 30'. The number of records entered for the fifty herb traders totalled 6 285.

In the commercial medicinal plant market, the names cited for plants are generally not orthographically correct. Quite often in Zulu, for example, the prefix of the stem word is omitted or shortened. Therefore, to identify plants from Zulu names from some species lists requires searching for stem words that are orthographically or phonetically similar. In order to produce a 'user friendly' list, both the orthographic names and their variants were captured on this database. The correct, or orthographic, form of the vernacular names in this paper was checked by A. Ngwenya from the Natal Herbarium (NH) in Durban.

Following data capture, a complete checklist of all families, genera, species, plant parts, orthographic vernacular names and orthographic variants, was extracted from the database, as well as the number of citation records per species; authors of the botanical names are provided in this list (Appendix 1). Citation records were extracted according to the vernacular names, thus it was not possible to discriminate between the species. In Appendix 1, the number of shops cited is for the applicable vernacular name, not necessarily the precise species (e.g. seven species of *Helichrysum* called imphepho are cited as being recorded in 35 shops, as imphepho was recorded from 35 shops). The checklist was compared with the Red Data List (Hilton-Taylor 1996a, b, 1997) to compile a list of red data taxa traded medicinally on the Witwatersrand. The checklist was also compared with the flora found in the four northern provinces (Retief & Herman 1997) to examine the extent to which species may be harvested in areas other than KwaZulu-Natal, where most of the harvesting occurs (Williams *et al.* 2000).

#### RESULTS AND DISCUSSION

Five hundred and eleven species from 328 genera and 119 families were identified as being traded on the Witwatersrand (Appendix 1). The most commonly traded families in terms of the number of genera (in parenthe-

TABLE 1.—Broad floristic analysis of taxa traded on the Witwatersrand

Major families and groups	No. families	No. genera <sup>†</sup>	No. taxa*
Monocotyledonae	11	52	110
Iridaceae		6	8
Amaryllidaceae		6	15
Orchidaceae		7	10
Liliaceae <i>s.l.</i>		23	57
Dicotyledonae	97	263	384
Asclepiadaceae		7	11
Celastraceae		9	13
Rubiaceae		13	14
Euphorbiaceae		14	28
Asteraceae (Compositae)		20	34
Fabaceae (Leguminosae)		28	38
Angiospermae	108	315	494
Gymnospermae	5	6	6
Pteridophyta	6	7	10
Total	119	328	510

<sup>†</sup> only families with  $\geq 6$  genera are included in this listing.

\* including species, subspecies and varieties.

ses), are: Fabaceae (Leguminosae) (28), Liliaceae *sensu lato* (23), Asteraceae (Compositae) (20), Euphorbiaceae (14) and Rubiaceae (13) (Table 1). The largest families traded, in terms of the number of species and infraspecific taxa, are: Liliaceae *s.l.* (57), Fabaceae (Leguminosae) (38), Asteraceae (Compositae) (34), Euphorbiaceae (28) and Amaryllidaceae (15) (Table 1; Figure 1).

A mean of  $126 \pm 65.9$  (SD) species was recorded per *umuthi* shop, ranging from a minimum of 10 species to a maximum of 294 species in a shop (Williams *et al.* 2000). On average, a species was recorded in  $12.3 \pm 11.3$  shops. Seventy eight species were recorded in only one shop, and no species was recorded in more than 42 out of a maximum 50 *umuthi* shops (Williams *et al.* 2000). *Drimis* spp. had the highest recorded frequency of occurrence (82%), followed by *Eucomis autumnalis* and *Scilla natalensis* (78% each) (Williams *et al.* 2000). Thirty six species were found in more than 33 of the shops surveyed.

A comparison with the flora of the four northern provinces (Retief & Herman 1997) shows that 353 of the 510 species (69.2%) are found in the Northern Province, North-West, Gauteng and/or Mpumalanga. A mean of

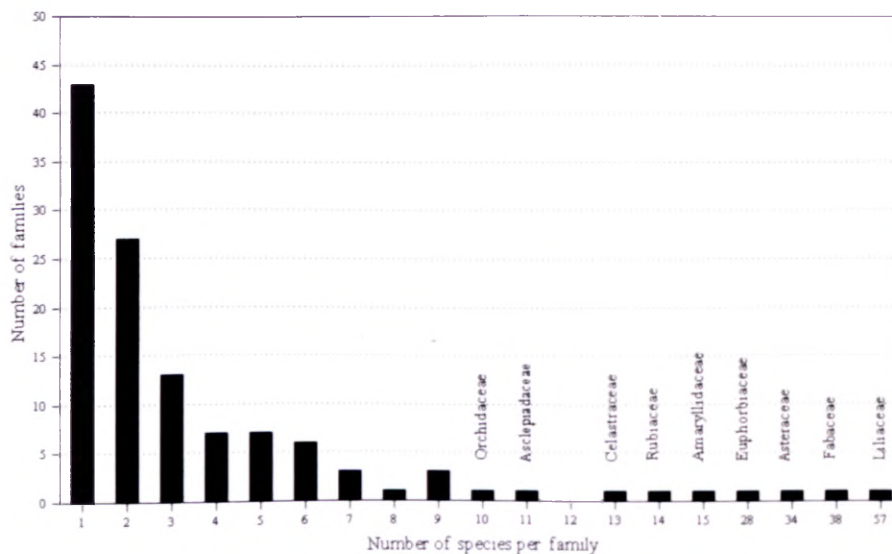


FIGURE 1.—The number of families with particular number of species traded on the Witwatersrand.

27.6% of the species are known to be harvested from this region, compared to 42.1% for KwaZulu-Natal (Williams *et al.* 2000). Therefore, the pressure on plant resources in KwaZulu-Natal could be relieved if commercial gatherers harvested plants in one of the four northern provinces. However, the predominance in utilization, demand and trade of and for Zulu medicinal plants in the region, and the familiarity (or lack thereof) of other ethnic groups with the Zulu plant pharmacopoeia are constraints to accessing and harvesting these resources from elsewhere.

Twenty one species (4.1%) from 17 genera and 16 families represent alien plant species. These species are naturalized in the regions harvested by commercial gatherers. In addition to the exotics harvested in southern Africa, there are at least five plants imported from India by Asian traders.

A total of 23 species (4.7%) traded on the Witwatersrand are threatened according to the Red Data List (Hilton-Taylor 1996a, b; 1997) (Table 2). A further 28 species are on the Red Data List, but are characterized as 'not threatened'. The global conservation status of *Siphonochilus aethiopicus* is listed in Table 2 as 'Not Threatened', even though subsequent corrections to the Red Data List (Hilton-Taylor 1997) have listed the species as extinct in the wild in KwaZulu-Natal. The plant is only obtainable from farmers in KwaZulu-Natal,

or collected in the veld in Mpumalanga and Swaziland. *Schlechterina mitostemmatoides* is also reported to be threatened (A. Hutchings pers. comm.).

The common names of medicinal plants in trade are predominantly in the Zulu vernacular. Eighty-nine percent of the plant names recorded were Zulu (Table 3) (Appendix 2). Despite the inclusion of Sotho, Venda, Shangaan and Swazi traditional healers (who were shop owners) in the survey, the proportion of plant names traded in these languages was low. This shows how traditional healers of other ethnic groups have adapted to the trade and become familiar with the names of plants in the language that dominates the trade, i.e. Zulu.

There is practical value in listing both the orthographic plant names and the orthographic variants in the plant checklist. Firstly, species identification is made easier, and secondly, the checklist provides a guide by suggesting the correct form of vernacular names to be used in the future. The justification for using capitals to separate the prefix from the stem of the noun, while not strictly correct in Zulu, is incorporated in the paper for the benefit of those using this list who are familiar with the structure of Zulu nouns. Most Zulu dictionaries enter nouns under the stem, but for readers not being able to identify the stem it is useful to capitalize it (A. Koopman pers. comm.). It is the authors' experience that this separation makes species identification from vernacular

TABLE 2.—Global conservation status of taxa traded on the Witwatersrand, according to the Red Data List for southern Africa (Hilton-Taylor 1996a, b; 1997)

IUCN Categories*			
Vulnerable (V)	Rare (R)	Insufficiently known (K)	Not threatened (nt)
<i>Encephalartos</i> sp.	<i>Alberta magna</i>	<i>Bowiea volubilis</i>	<i>Agathosma ovata</i>
<i>Gasteria croucheri</i>	<i>Aloe microcantha</i>	<i>Eucomis autumnalis</i>	<i>Ansellia africana</i>
<i>Haworthia limifolia</i>	<i>Bauhinia bowkeri</i>	<i>Scilla natalensis</i>	<i>Blighia unijugata</i>
<i>Warburgia salutaris</i>	<i>Begonia dregei</i>		<i>Boscia foetida</i>
	<i>Begonia homonyma</i>		<i>Bridelia cathartica</i>
	<i>Cassipourea flanaganii</i>		<i>Catha edulis</i>
	<i>Diaphanathe millarii</i>		<i>Celtis mildbraedii</i>
	<i>Euphorbia woodii</i>		<i>Clivia miniata</i>
	<i>Faurea macnaughtonii</i>		<i>Clivia nobilis</i>
	<i>Haworthia fasciata</i>		<i>Commiphora harveyi</i>
	<i>Pellaea rufa</i>		<i>Cyathea dregei</i>
	<i>Sandersonia aurantiaca</i>		<i>Dianthus mooiensis</i>
	<i>Stangeria eriopus</i>		<i>Elaeodendron croceum</i>
	<i>Strophanthus luteolus</i>		<i>Entada rheedii</i>
	<i>Vitellariopsis dispar</i>		<i>Euphorbia bupleurifolia</i>
			<i>Gardenia thunbergia</i>
			<i>Harpagophytum procumbens</i>
			<i>Mondia whitei</i>
			<i>Noltea africana</i>
			<i>Ocotea bullata</i>
			<i>Protea gagedi</i>
			<i>Schlechterina mitostemmatoides</i>
			<i>Siphonochilus aethiopicus</i> ‡
			<i>Stapelia gigantea</i>
			<i>Strychnos mitis</i>
			<i>Uvaria lucida</i>
			<i>Widdringtonia nodiflora</i>
			<i>Zantedeschia albomaculata</i>

\* The old IUCN categories (Davis *et al.* 1986) rather than the new categories (IUCN 1994) were used by Hilton-Taylor because many of the southern African data are still too sparse to apply the new criteria and categories (Hilton-Taylor 1996a).

‡ Hilton-Taylor (1996a) listed *Siphonochilus* as Endangered (E) in KwaZulu-Natal and the former Transvaal and Indeterminate (I) in Swaziland. The overall global conservation status of the species was listed as Not Threatened (nt). A subsequent correction to the conservation status of the species in KwaZulu-Natal listed *Siphonochilus* as Extinct (Ex) in the province (Hilton-Taylor 1997). However, no changes to the global conservation status of the taxon was recommended, hence the species is cited as Not Threatened in the above table.