

4.4 Leaf anatomy

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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 Despite the now outdated revision by Thoday (1924), boundaries of infrageneric taxa in *Passerina* remain a problem, mainly owing to the apparent lack of marked morphological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>	KwaZungu 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. arakensbergensis</i>	Endemic in Bergville District, KwaZulu-Natal	Zone between indigenous forest and alpine grassland, altitude ± 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. <i>nov.</i>	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. <i>nov.</i>	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 ± 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 Drapétees, 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.



Solereder (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>	<i>Thoday 212</i> *	WESTERN CAPE.—3320 (Montagu): Montagu Dist., near Concordia, (–CD).
<i>filiformis</i> subsp. <i>filiformis</i>	<i>Boucher 2833</i> *	WESTERN CAPE.—3118 (Van Rhynsdorp): Clanwilliam Dist., Diepkloof S of Verlorevlei, (–AD).
	<i>Bredenkamp 1039</i>	WESTERN CAPE.—3318 (Cape Town): Signal Hill, (–CD).
<i>filiformis</i> subsp. nov.	<i>Schlechter 5125</i> *	WESTERN CAPE.—3218 (Clanwilliam): Alexander's Hoek, (–BC).
	<i>Taylor 1542</i> *	WESTERN CAPE.—3218 (Clanwilliam): Malmesbury Div., Vredenburg, Steenberg's Cove, (–CC).
<i>glomerata</i> subsp. <i>glomerata</i>	<i>Bredenkamp 988</i> *	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Eikeboom, (–AC).
	<i>Bredenkamp 994</i>	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Kromrivier, (–AC).
	<i>Bredenkamp 1002</i>	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Algeria, (–AC).
	<i>Bredenkamp 984, 985</i>	WESTERN CAPE.—3219 (Wuppertal): Citrusdal, Piekenierskloof Pass, (–CD).
	<i>Bredenkamp 977</i>	WESTERN CAPE.—3219 (Wuppertal): Groenfontein, (–DC).
	<i>Bredenkamp 973</i>	WESTERN CAPE.—3319 (Worcester): Tulbagh, (–AC).
<i>glomerata</i> subsp. nov.	<i>Stokoe 8040</i> *	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains.
	<i>Esterhuysen 28587</i>	WESTERN CAPE.—3319 (Worcester): Hex River Mountains.
sp. nov. 1	<i>Goldblatt & Manning 8627</i>	WESTERN CAPE.—3220 (Sutherland): Roggeveld Escarpment, (–AB).
sp. nov. 3	<i>Stokoe 9302</i> *	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, Prince Albert area, (–AC).
	<i>Schlechter 5846</i> *	WESTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–CD).
	<i>Esterhuysen 10734</i> *	EASTERN CAPE.—3323 (Willowmore): Kouga Mountains, (–DA).
	<i>Esterhuysen 28006</i> *	EASTERN CAPE.—3324 (Steytlerville): Cockscomb, Uitenhage area, (–BD).
sp. nov. 4	<i>Killick 238</i>	KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (–CB).
	<i>Bredenkamp 1016*, 1017*</i>	KWAZULU-NATAL.—3030 (Port Shepstone): Oribi Gorge, (–CB).
	<i>Van Wyk & Bredenkamp 1, 1012*</i>	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (–AA).
	<i>Bredenkamp 1327</i>	KWAZULU-NATAL.—3130 (Port Edward): Mkambati Nature Reserve, (–AC).
	<i>Gillett 4537</i>	WESTERN CAPE.—3422 (Mossel Bay): en route to Knysna from George, (–BB).
	<i>Keet s.n.</i>	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 Soleeder (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 acroscopically, 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 Type B	Type C	Type D		arranged randomly Group A	arranged in rows Group B	Smooth	Papillate	Striate
<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
<i>P. comosa</i>		B2			X			X		
<i>P. paludosa</i> (Figure 3C)		B2								X
<i>P. galpinii</i> (Figure 2C)		B2, B3								X
<i>P. drakensbergensis</i>		B3						X		
<i>P. ericoides</i> (Figure 3D)		B3				X		X		
<i>P. sp. nov. 2</i>		B3						X		
<i>P. sp. nov. 3</i>		B3			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	
<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

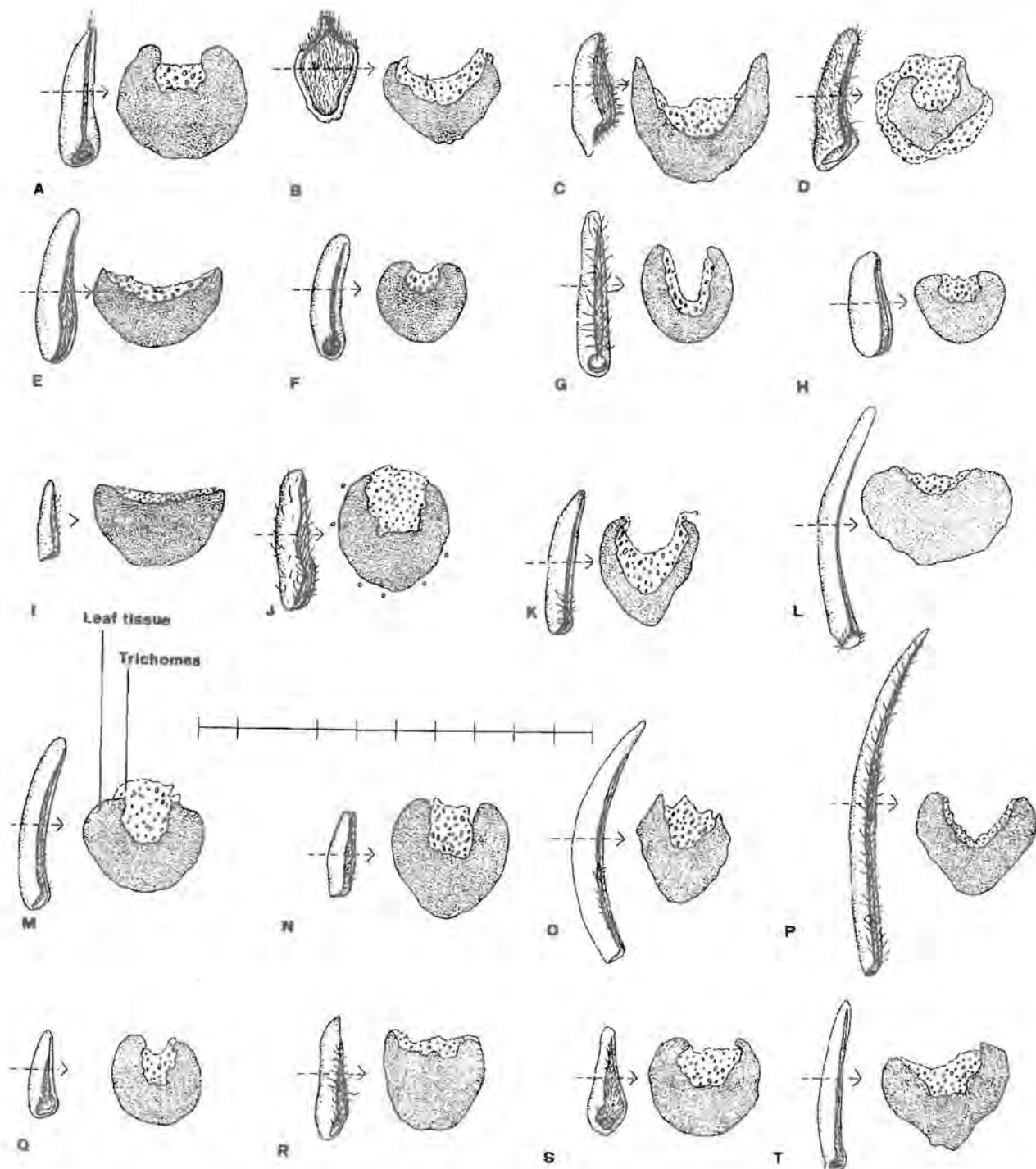


FIGURE 1.—Camera lucida drawings of leaves of *Passerina* species arranged according to leaf structural type (Table 3), correlating leaf shape to outline of leaves in *t/s*: A, *P. sp. nov. 1*, Bredenkamp 1044; B, *P. burchellii*, Bolus 684; C, *P. pendula*, Bredenkamp 908; D, *P. comosa*, Andreae 1288; 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. obrusifolia*, 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 *t/s* not to scale.

Tanniferous substances

Tanniferous 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.

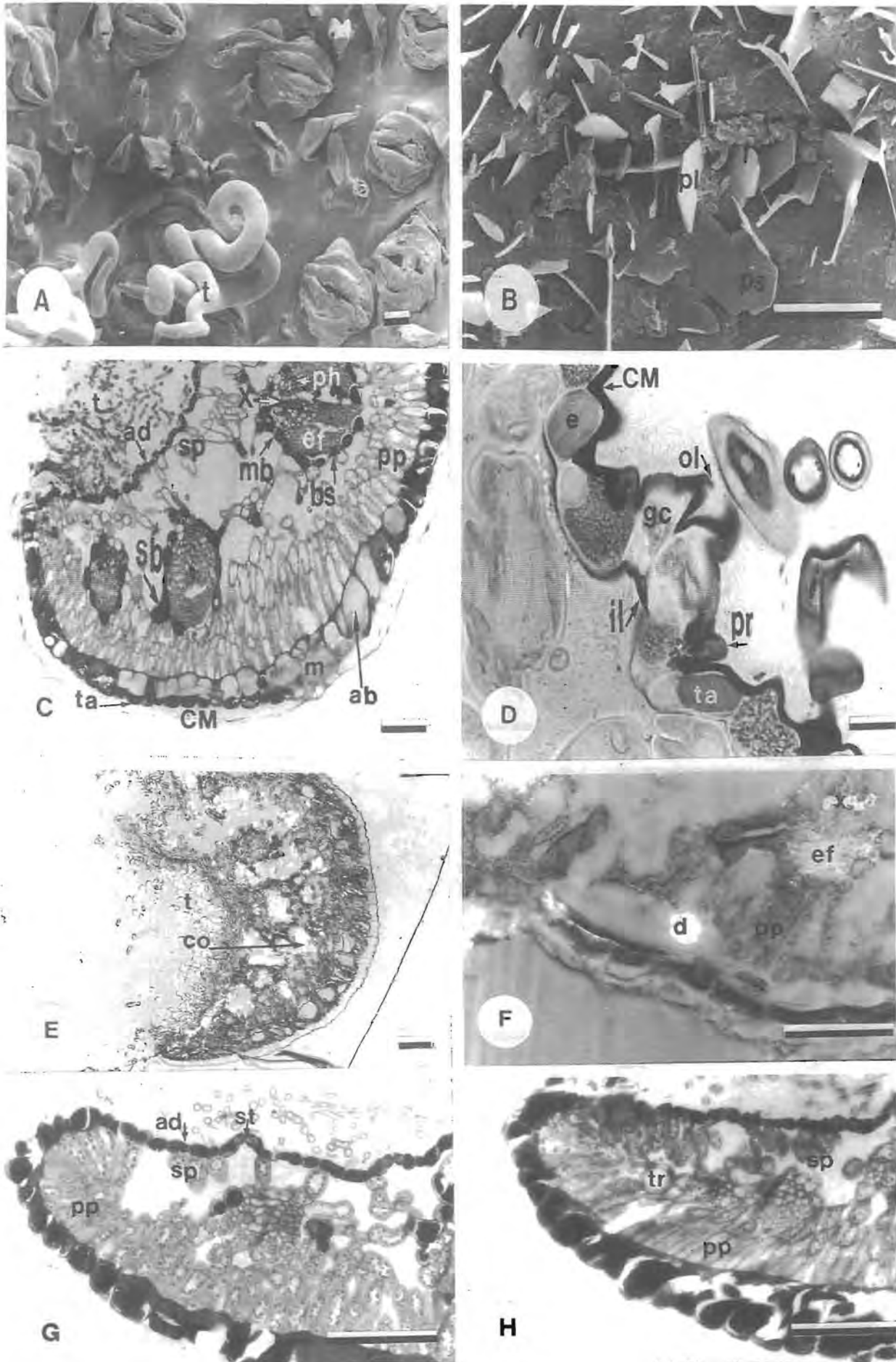


FIGURE 2.—A, B, SEM micrographs of trichomes and epicuticular waxes: A, *P. falcifolia*, Bredenkamp 915; B, *P. rigida*, Bredenkamp 1013. C–H, LM photographs of leaf: C, *P. galpinii*, Bredenkamp 946; D, *P. pendula*, Bredenkamp 909, stomatal apparatus in adaxial epidermis stained with Sudan Black B; 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 and tracheid 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, extraerythral sclerenchyma fibres; gc, guard cell; il, inner ledge; m, mucilage; mb, median vascular bundle; ol, outer ledge; ph, phloem; pl, plates; pp, palisade parenchyma; pr, peristomatal 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 μ m; C, E–H, 100 μ m.

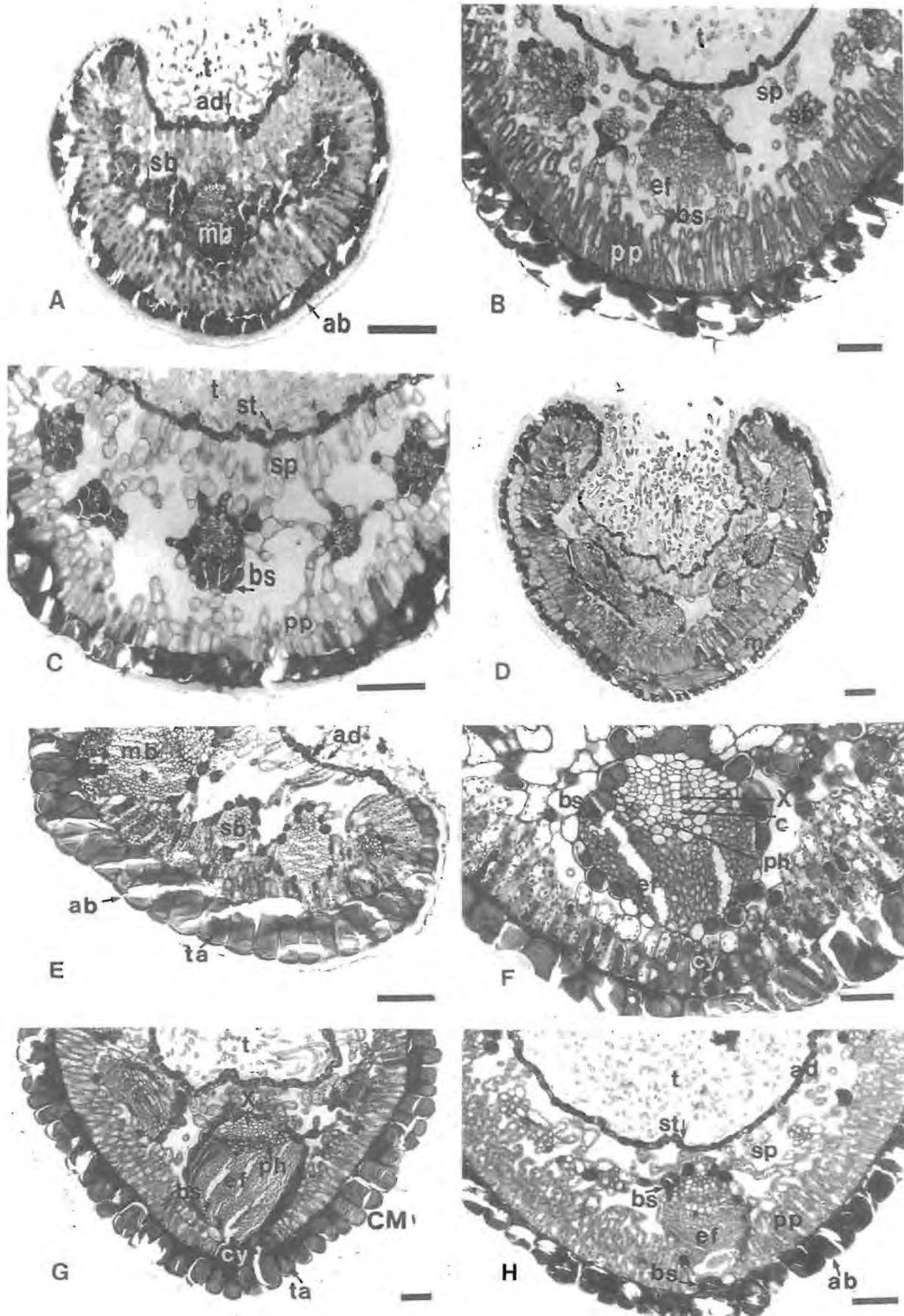


FIGURE 3.—LM photographs of leaf structural types A and B. Type A: A, *P. sp. nov.* 1, *Bredenkamp* 1044. Type B1: B, *P. pendula*, *Bredenkamp* 908. Type B2: C, *P. paludosa*, *Bredenkamp* 1035. Type B3: D, *P. ericoides*, *Bredenkamp* 962. Type B4: E, *P. filiformis* subsp. *filiformis*, *Bredenkamp* 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 μ m.

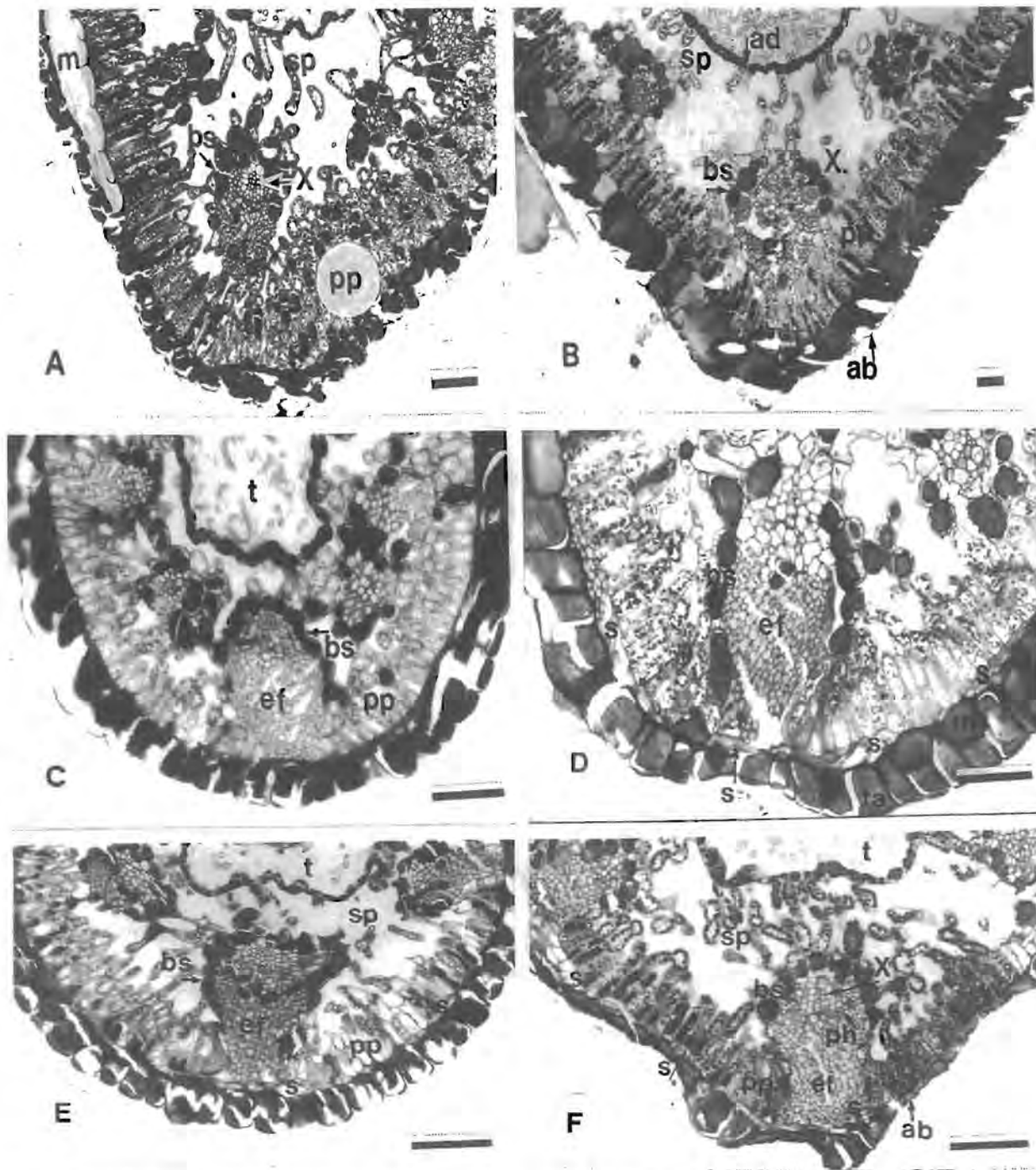


FIGURE 4.—LM photographs showing leaf structural types C and D. Type C: A, *P. falcifolia*, Bredenkamp 917; B, *P. sp. nov.* 4, Bredenkamp 1016. Type D1: C, *P. montana*, Bredenkamp 889. Type D2: D, *P. paleacea*, Bredenkamp 960; E, *P. rigida*, Bredenkamp 962; F, *P. vulgaris*, Bredenkamp 901. Abbreviations as for Figure 2. Scale bars: A–F, 100 μ 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) μ m. *Midrib* often raised below owing to supporting sclerenchyma fibres,

cymbiform leaf folding along reinforced midrib; thickness of main vein (260–)440(–560) μ 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 μ 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,



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; tanniniferous deposits ample. *Vascular tissue* collateral with adaxial xylem and abaxial phloem, surrounded by a layer of colourless parenchymatous cells, becoming tanniniferous or sclerenchymatous abaxially, separating vascular tissue from abaxial sclerenchyma fibres. *Xylem* arranged in a ± semilunar band or in ± 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, ± separated by irregular layer of parenchyma often containing tanniniferous 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, ± 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 \times anticlinal dimensions in *t/s* 30–65 \times (–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 tanniniferous, mucilagination minimal, periclinal \times anticlinal dimensions in *t/s* (20–)30–45(–50) \times (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 \times anticlinal diam. in *t/s* 30–65 \times 45–60 μm :
 13a Leaf outline in *t/s* canaliculate; secondary vascular bundles \pm 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 tanniniferous, periclinal \times anticlinal cell diam. in *t/s* (35–)40–45 \times 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 tanniniferous 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, \pm absent abaxially; cells rounded or longitudinally lobed, containing ample amounts of tanniniferous 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 tanniniferous 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, \pm 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 µm. 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			Abaxial fibrous sheath	Main vein Width μm	Main vascular bundle Shape	Bundle sheath enveloping main vascular bundle			Secondary vascular bundles No. (each side of main bundle)	Palisade parenchyma			Spongy parenchyma
	Structural type	Outline	Width μm				Completely	Adaxial cap	No. cells		Shape	No. layers	No. cells per $50 \mu\text{m}$	
<i>P. sp. nov. 1</i> (Figure 3A)	A	transversely elliptic	± 850		± 450	widely ovate	X		19–25	3 or 4		adaxial 3 abaxial 4		
<i>P. burchellii</i>	B1	narrowly transversely elliptic	± 1480		± 540	widely ovate	X		± 20	4	horseshoe	1 or 2	4	aerenchymatic
<i>P. pendula</i> (Figure 3B)	B1	canaliculate	780–860		± 340	widely ovate	X		17–19	4–9	horseshoe	1 or 2	4 or 5	aerenchymatic
<i>P. comosa</i>	B2	transversely elliptic	± 940		± 460	oblate	X		± 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		± 22	3	horseshoe	2 or 3	3	aerenchymatic
<i>P. sp. nov. 2</i>	B3	depressed obovate	± 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	± 820		± 400	widely ovate	X		± 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	± 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)	± 25 (B2, B3) or ± 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	X	400–570	obovate	X (B2, B3, B4)	X (D2)	± 23 (B2, B3, B4) or ± 17 (D2)	3 or 4	U	1–3	5	mesomorphic
<i>P. rigida</i> (Figures 3H, 4E)	B3, B6, D2	transversely elliptic	680–780	X	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	X	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 μm) 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 μm 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 μm 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 adaxial 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 tanniferous 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.

Tanniferous 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 (Brendenkamp & 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. falcifolia* 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 polyporate 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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4.5 Inflorescences and flowers

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Taxonomic significance of inflorescences, floral morphology and anatomy in *Passerina* (Thymelaeaceae)

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Keywords: anatomy, androecium, exotegmen, flower, gynoecium, morphology, *Passerina*, phylogeny, taxonomy, Thymelaeaceae, vasculature

ABSTRACT

Comparative studies were undertaken on the inflorescence, bracts and floral morphology of all taxa of the genus *Passerina* L. in southern Africa. Information is given in tabular form and a key based on bract morphology is presented. Floral morphology supported the status of the infrageneric taxa and also proved to be of taxonomic significance in the genus. Controversy surrounding the interpretation of a number of floral morphological structures in *Passerina* has been resolved. Morphological and anatomical evidence allowed a re-interpretation of the structure of the receptacle, hypanthium and sepals, ovary type and position, structure of the seed coat, ovule type and position, obturator, fruit and seed. On this basis an authentic generic description of the floral morphology was compiled. *Passerina* is distinguished by the following set of characters, a very short floral receptacle, tubular hypanthium, petaloid calyx, absence of petals and petaloid scales, diplostemonous dimorphic androecium, extrorse anthers, superior ovary, anatropous, ventrally epitropous ovule, an obturator of elongated cells, a 1-seeded berry or an achene and tegmic seed with nuclear endosperm becoming cellular throughout. On this basis the flower in *Passerina* is considered a phylogenetically advanced structure, supporting the view that the genus is advanced within the Thymelaeoideae. The proposed taxonomic relationship between Thymelaeaceae and Malvales is confirmed by floral morphological evidence.

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INTRODUCTION

The infrageneric taxonomy of *Passerina* L. is a problem, due to the apparent lack of marked morphological differences between species. The latest revision by Thoday (1924), is now mostly outdated.

Most species of *Passerina* are endemic to the Cape Floristic Region and adapted to a Mediterranean or semi-Mediterranean climate. The distribution of *P. sp. nov.* 4 and *P. montana* extends eastwards and northwards along the eastern mountains and Great Escarpment of southern Africa, predominantly summer rainfall areas. The species are apparently all wind-pollinated.

The controversy surrounding the interpretation of certain floral structures in the genus became obvious during the present study. Heinig (1951) did not include *Passerina* in her study of the floral morphology of the Thymelaeaceae. From the sexual system of Linnaeus (1781, 1784) to Domke (1934), floral morphology played an integral part in the intrafamilial classification of the Thymelaeaceae and in the circumscription of the family (Table 1). Between ± 1960 and 1996, vast leaps were taken in the classification of the flowering plants by making use of anatomical, floral, palynological, embryological and chemical evidence. During this period, disagreement on the circumscription of the Thymelaeaceae was common (Table 2). Since 1990, many higher-level phylogenetic relationships in angiosperms were based on evidence from *rbcL* and 18S nuclear ribosomal DNA sequence data. In many cases these studies confirmed previously proposed phylogenetic patterns and trends within the family, based on morphological evidence; in other cases, however, profound changes in the circumscription and relationships of the Thymelaeaceae were suggested (Table 3).

The present paper emanated from a monographic study of the genus currently in progress. Available evidence suggests the presence of at least four new species and four new subspecies, to be added to 16 previously recognized species, mostly endemic to southern Africa (Thoday 1924; Bond & Goldblatt 1984) (Table 4). Here we report on a comparative morphological study of the inflorescence, bract, flower, fruit and seed. Specific

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TABLE 1.—Classification of *Passerina* within the Thymelaeaceae according to different authors, based mainly on floral, fruit and seed morphology

Rank	Wikstrom 1818	Endlicher 1837, 1847	Meisner 1857	Bentham & Hooker 1880	Gilg 1891, 1894	Leandri 1930	Domke 1934
Undefined	Thymelaeorum						
Class		Thymelaeae					
Order		Daphnoideae	Thymelaeaceae	Thymelaeaceae			
Family					Thymelaeaceae	Thymelaeaceae	Thymelaeaceae
Subfamily					Thymelaeoideae		Thymelaeoideae
Tribe		Thymelinae	Gnidieae	Euthymelaeae	Daphneae	Thymelaeoideae	Gnidicae
Subtribe		Passerineae	Diplostemonae		Passeriniinae	Passeriniinae	Passeriniinae
Series				Series 1			
Division	Octandria						
Inflorescence, floral, fruit and seed morphology at genus level							
Inflorescence		flowers lateral					terminal spikes
Floral arrangement		perigynous	perigynous			perigynous	
Floral tube		perigone, infundibular, limb 4-fid	calyx tube hypocrateriform, persistent	perianth articulate above ovary	receptacle cylindrical, articulate in upper half	floral tube: fusion of 4 external whorls, articulate	calyx tube flask-shaped, articulate
Calyx	0		limb 4-partite				4-lobed
Corolla	infundibular, 4-fid, persistent	scales 0	petaloid scales 0	perianth scales 0	petaloid scales 0	petaloid scales 0	petals 0
Androecium (A)	A = 8	diplostemonous, A = 8, in incisions of perigone	A = 8, exserted, alternating with sepals	diplostemonous, exserted	diplostemonous, A = 8	diplostemonous, A = 8	diplostemonous, A = 8
Gynoecium (G)		unilocular, ovule pendulous		unilocular, ovule single			unilocular, ovule single
Fruit	nux	nux	nucula, pericarp crustaceous	indehiscent			berry or achene
Seed	1-seeded	1-seeded					black, crustaceous testa, micropylar beak-like

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TABLE 2.—Classification of *Passerina* within the Thymelaeaceae according to different authors, based on morphological, anatomical, palynological, embryological and chemical characters

Rank	Melchior 1964	Hutchinson 1973	Dahlgren 1975a, b	Dahlgren 1980, Dahlgren & Thorne 1984	Cronquist 1981, 1988	Thorne 1992a, b	Takhtajan 1997
Undefined Class	Thymelaeales				Magnoliopsida	Angiospermae (Magnoliopsida)	
Subclass					Rosidae	Dicotyledonae (Magnoliidae)	Dilleniidae
Superorder			Thymelaeanae	Malviflorae (= Dilleniiflorae)		Malvanae	Euphorbianae
Order		Thymelaeales	Thymelaeales	Thymelaeales	Myrtales	Euphorbiales	Thymelaeales
Family	Thymelaeaceae	Thymelaeaceae		Thymelaeaceae [excluded from Myrtales (1984)]	Thymelaeaceae	Thymelaeaceae	Thymelaeaceae
Subfamily	Thymelaeoideae					Thymelaeoideae	Thymelaeoideae
Tribe	Thymelaeae (= <i>Gnidieae</i>)						
Subtribe							
Series							
Division							
Relationships	Myrtales: perianth tube Malvales: pollen morphology	placed between Bixales and Proteaceae	placed between Dilleniaceae (including Malvales) and Myrtaceae	Myrtales: anatomical evidence. Euphorbiales—Malvales: chemical, embryological, palynological evidence	Myrtales: strongly perigynous, polypetalous to apetalous flowers. Other families: pseudomonomerous ovary, crotonoid pollen	Euphorbiaceae, Simmondsiaceae, Dichapetalaceae, Gonystylaceae	Gonystylaceae only other family in order

Floral, fruit and seed morphology described at different ranks

Character	Tribe	Family	Order	Family	Family	Family
Flower		hypogynous, bisexual, wind-pollinated	hypogynous, bisexual	perigynous, 4-merous		bisexual
Floral tube	perianth tube articulated	calyx tube	hypanthium	cylindrical, brightly coloured		calyx tube cylindrical
Calyx	4-lobed	perianth tubular, 4-lobed, imbricate		4-lobed, arising from upper rim of hypanthium		lobes imbricate
Corolla		petals or staminodes 0	petals or scale-like structures 0	petaloid scales considered as true petals (Dahlgren & Van Wyk 1988)		petaloid appendages 0
Androecium (A) Gynoecium (G)	pseudomonomerous	diplostemonous ovary superior	diplostemonous: unilocular, ovules pendulous, epitropous, bitegmic, crassinucellate; endosperm nuclear	diplostemonous pseudomonomerous; ovules pendulous	pseudomonomerous; ovules solitary	diplostemonous style sublateral; stigma papillose; carpels 2, monolocular; ovule solitary
Fruit		indehiscent	nut or drupe	indehiscent	indehiscent	indehiscent, nut-like, baccate, or drupaceous, enveloped by base of persistent calyx tube
Seed		solitary	endosperm scanty; embryo straight	endosperm scanty; embryo straight		caruncle-like or tail-like appendage, without aril; embryo straight; endosperm scanty



TABLE 3.—Classification of the Thymelaeaceae according to different authors, based on molecular data

Rank	Conti <i>et al.</i> 1996	APG 1998*	Alverson <i>et al.</i> 1998	Magallón <i>et al.</i> 1999
Undefined		Eudicots		Eudicot Clade
Supraordinal subgroup		Core Eudicots		Core Eudicots
Clade (Subclass)	Rosids	Rosids (subclass Rosidae)	Rosidae	Rosid Clade: Geraniaceae, Capparales, Sapindales, Malvales, Myrtales. Core Rosids
Subgroup	Expanded Malvales: Thymelaeaceae, Sarcocaulaceae, Malvales	Eurosids II	Expanded Malvales: Core Malvales, Thymelaealean Clade, Bixalean Clade, Dipterocarpean Clade	Expanded Malvales: Malvales, Thymelaeaceae, Sarcocaulaceae, Dipterocarpaceae, Bixaceae, Cistaceae, Sphaerocephalaceae, Neuradaceae, <i>Muntingia</i>
Order		Malvales		
Family	Thymelaeaceae (excluded from Myrtales)	Thymelaeaceae	Thymelaealean clade	Thymelaeaceae
Relationships	sister groups of Expanded Malvales: Myrtales, Sapindales, Expanded Capparales	sister group: Myrtales	sister groups of Expanded Malvales: Expanded Capparales, Sapindales, Myrtales	sister group of Malvales: Thymelaeaceae, Sarcocaulaceae, Dipterocarpaceae basal to Malvales

* Angiosperm Phylogeny Group.

results in leaf anatomy, indicating the arrangement of taxa in *Passerina* (Bredenkamp & Van Wyk 2001), are associated with floral morphological structures as well as fruit and seed types in the present study.

MATERIALS AND METHODS

As far as possible, material was collected from at least five different localities for every taxon. Live and preserved (dried and in liquid preservatives) material of all the species, subspecies and varieties in *Passerina* was studied (Table 4). Illustrations were made from herbarium material by means of a drawing tube. Measurements were taken by using a dissection microscope and a calibrated eyepiece.

Flowers were 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)]. Light microscopy (LM) was used to study the floral anatomy of *P. ericoides* (Bredenkamp 956, 962), which has fleshy fruit and *P. vulgaris* (Bredenkamp 944, 951) with dry fruit. As the flowers are quite small, whole flower buds, flowers directly after anthesis and young fruits enveloped in the floral tube were washed in water, dehydrated and embedded in glycol methacrylate (GMA) following the methods of Feder & O'Brien (1968). Embedded floral material was serially sectioned from the base of the receptacle to the anthers. 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).

Terminology

Terminology is used according to the following authorities: inflorescences (Weberling 1983, 1989; Weberling & Herkommer 1989); hypanthium (Bunniger 1972; Dahlgren 1975a, b, 1980; Dahlgren & Thorne 1984); stamen morphology (Heinig 1951; Fahn 1967; Noel 1983);

gynoecium (Heinig 1951; Davis 1966; Corner 1976); fruit (Spjut 1994).

Floral envelope

The authors regard the floral envelope ('outer floral whorl') as a hypanthium (fused calyx and androecium), differentiating into four petaloid sepals and a diplostemonous androecium, arising from the hypanthium rim at the separation of the sepals. For the description of colour, texture and measurement of total floral length, only the hypanthium and sepals are considered—the stamens are excluded.

Phylogeny

Speculations on phylogeny are based on prevailing family characters representing the ancestral state and derived characters, indicating a reduction in tissue 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

Inflorescences

Polytelic synflorescences present in all species; main florescences and co-florescences spicate (Figures 1A; 2A), often extended, forming multiflowered polytelic florescences in most species, sometimes strongly reduced (*P. burchellii*) (Table 5). *Proliferating spikes* with inflorescence apex growing out and returning to vegetative growth, common; main florescences and co-florescences subterminal. *Spikes* sometimes artificially resembling terminal subcapitulate inflorescences, but each characterized by two terminal leaves with axillary blind-ending rudimentary flowers, enveloping minute growing point (*P. montana*, *P. paleacea*, *P. glomerata*, *P. sp. nov.* 3); proliferating growth less common in subcapitulate inflorescences.



TABLE 4.—*Passerina* specimens examined and housed at PRE.

Species	Collector	Locality
<i>burchellii</i> Thoday	Bredenkamp 1545	WESTERN CAPE.—3319 (Worcester): Jonaskop, (–DC).
<i>comosa</i> C.H.Wright	<i>Bolus</i> 687*, <i>Stokoe</i> 2542	WESTERN CAPE.—3419 (Caledon): Baviaanskloof, Genadendal, (–BA).
	Thoday 212	WESTERN CAPE.—3320 (Montagu): Montagu District, near Concordia, (–CD).
<i>drakensbergensis</i> Hilliard & B.L.Burt	<i>Andrae</i> 1288*	WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (–AD).
	<i>MacDonald</i> 2125	
	<i>Edwards</i> 974	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
<i>ericoides</i> L.	Bredenkamp 1018, 1019, 1020, 1021*	KWAZULU-NATAL.—2829 (Harrismith): Ndedema Gorge, Cathedral Peak Forest Reserve, (–CD).
	Bredenkamp 956*	WESTERN CAPE.—3318 (Cape Town): Milnerton, (–CD).
<i>falcifolia</i> C.H.Wright	Bredenkamp 962*	WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD).
	Taylor 4042	WESTERN CAPE.—3419 (Caledon): Pearly Beach, (–CB).
	Bredenkamp 917*	WESTERN CAPE.—3323 (Willowmore): Gouna State Forest, (–CC).
<i>filiformis</i> L. subsp. <i>filiformis</i>	Bredenkamp 915	WESTERN CAPE.—3324 (Steytlerville): opposite Tsitsikama Lodge, (–CD).
	Tyson 1449	WESTERN CAPE.—3423 (Knysna): Knysna, (–AA).
<i>filiformis</i> L. subsp. nov.	Bredenkamp 1039*	WESTERN CAPE.—3118 (Van Rhynsdorp): Clanwilliam Dist., Diepkloof S of Verlorevlei, (–AD).
	Schlechter 5125*	WESTERN CAPE.—3318 (Cape Town): Signal Hill, (–CD).
<i>galpinii</i> C.H.Wright	Taylor 1542	WESTERN CAPE.—3218 (Clanwilliam): Alexander's Hoek, (–BC).
	Bredenkamp 946*	WESTERN CAPE.—3218 (Clanwilliam): Malmesbury Div., Vredenburg, Steenberg's Cave, (–CC).
<i>glomerata</i> Thunb. subsp. <i>glomerata</i>	Bredenkamp 932	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD).
	Bredenkamp 933	WESTERN CAPE.—3421 (Riversdale): Riethuiskraal, (–AD).
	Bredenkamp 923	WESTERN CAPE.—3421 (Riversdale): Still Bay, (–AD).
	Bredenkamp 988	WESTERN CAPE.—3422 (Mossel Bay): Mossel Bay, (–AA).
	Bredenkamp 994	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Eikeboom, (–AC).
<i>glomerata</i> Thunb. subsp. nov.	Bredenkamp 1002	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Kromrivier, (–AC).
	Bredenkamp 984, 985*	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Algeria, (–AC).
	Bredenkamp 977	WESTERN CAPE.—3219 (Wuppertal): Citrusdal, Piekensklou Pass, (–CD).
	Bredenkamp 973*	WESTERN CAPE.—3219 (Wuppertal): Groenfontein, (–DC).
<i>montana</i> Thoday	<i>Stokoe</i> 8040	WESTERN CAPE.—3319 (Worcester): Tulbagh, (–AC).
	<i>Esterhuysen</i> 28587*	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains.
<i>obtusifolia</i> Thoday	<i>Giess</i> 13136	WESTERN CAPE.—3319 (Worcester): Hex River Mountains.
	Bredenkamp 1024	NAMIBIA.—2217 (Windhoek): Auas Mountains, Molteblich, (–CA).
	Bredenkamp 1025	MPUMALANGA.—2430 (Pilgrim's Rest): World's View, (–DD).
	Bredenkamp 889, 890	MPUMALANGA.—2430 (Pilgrim's Rest): God's Window, (–DD).
<i>obtusifolia</i> Thoday	Bredenkamp 893*	FREE STATE.—2828 (Bethlehem): Golden Gate National Park, (–DA).
	Bredenkamp 971	FREE STATE.—2927 (Maseru): Ladybrand, (–AB).
	Bredenkamp 967	WESTERN CAPE.—3319 (Worcester): Karoo National Botanical Garden, (–CB).
<i>paleacea</i> Wikstr.	Bredenkamp 1033, 1034	WESTERN CAPE.—3319 (Worcester): Jonaskop, (–CD).
	Bredenkamp 929	WESTERN CAPE.—3321 (Laingsburg): Seweweekspoort, (–AD).
	Bredenkamp 919*	WESTERN CAPE.—3321 (Ladismith): Rooiberg, (–CB).
	Bredenkamp 960*	WESTERN CAPE.—3322 (Oudtshoorn): Perdepoort, (–CD).
	Bredenkamp 961	WESTERN CAPE.—3418 (Simonstown): Kommetjie, (–AB).
	Bredenkamp 952	WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD).
	Bredenkamp 950	WESTERN CAPE.—3418 (Simonstown): Harold Porter National Botanical Garden, (–BD).
<i>paludosa</i> Thoday	Bredenkamp 949	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD).
	Bredenkamp 940	WESTERN CAPE.—3420 (Bredasdorp): Waenhuiskrans, (–CA).
	Bredenkamp 1035	WESTERN CAPE.—3421 (Riversdale): Puntjie, (–AC).
	<i>Jangle</i> 156*	WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (–BA).
<i>pendula</i> Eckl. & Zeyh.	Thoday 100	WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (–BA).
	<i>Fourcade</i> 3043	WESTERN CAPE.—3418 (Simonstown): Riet Valley, Cape Flats, (–BA).
<i>rigida</i> Wikstr.	Bredenkamp 908, 909*	EASTERN CAPE.—3324 (Steytlerville): Zuur Anys, (–CB).
	Bredenkamp 1013*	EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB).
	Bredenkamp 899	KWAZULU-NATAL.—2832 (Mtubatuba): St Lucia Park, (–AD).
	Bredenkamp 898	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Mouth, (–AA).
	Bredenkamp 897	EASTERN CAPE.—3326 (Grahamstown): Kenton-on-Sea, (–DA).
<i>rubra</i> C.H.Wright	Bredenkamp 911	EASTERN CAPE.—3326 (Grahamstown): Port Alfred, (–DB).
	Bredenkamp 914*	EASTERN CAPE.—3327 (Peddie): Kleinmond West, (–CA).
	Bredenkamp 905	EASTERN CAPE.—3424 (Humansdorp): Jeffreys Bay, (–BB).
	Bredenkamp 900	EASTERN CAPE.—3424 (Humansdorp): en route to Kareedouw, (–CD).
<i>vulgaris</i> Thoday	Bredenkamp 926	EASTERN CAPE.—3325 (Port Elizabeth): Colchester, (–DB).
	Bredenkamp 907	EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD).
	Bredenkamp 901	WESTERN CAPE.—3321 (Ladismith): en route to Korenthe River Dam, (–CC).
	Bredenkamp 951*	EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB).
	Bredenkamp 944*	EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD).
sp. nov. 1	Bredenkamp 924	WESTERN CAPE.—3418 (Simonstown): Betty's Bay, Harold Porter NBG, (–BD).
	<i>Goldblatt & Manning</i> 8627	WESTERN CAPE.—3420 (Bredasdorp): Cape Infanta, (–BD).
	Bredenkamp 1044, 1046, 1047	WESTERN CAPE.—3422 (Mosselbaai): Kleinbrak, (–AA).
sp. nov. 2	<i>Oliver</i> 9281*	WESTERN CAPE.—3220 (Sutherland): Roggeveld Escarpment, (–AB).
	<i>Esterhuysen</i> 12189, 26859*	WESTERN CAPE.—3319 (Worcester): Waboomberg, Ceres, (–AD).
sp. nov. 3	<i>Stokoe</i> 9302	WESTERN CAPE.—3218 (Clanwilliam): Northern Cederberg Mountains, (–BB).
	<i>Schlechter</i> 5846	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, Prince Albert area, (–AC).
sp. nov. 4	<i>Esterhuysen</i> 10734*	WESTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–CD).
	<i>Esterhuysen</i> 28006*	EASTERN CAPE.—3323 (Willowmore): Kouga Mountains, (–DA).
	<i>Killick</i> 238	EASTERN CAPE.—3324 (Steytlerville): Cockscomb, Uitenhage area, (–BD).
	Bredenkamp 1016, 1017	KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (–CB).
	<i>Van Wyk & Bredenkamp</i> 1, 1012	KWAZULU-NATAL.—3030 (Port Shepstone): Oribi Gorge, (–CB).
	Bredenkamp 1327*	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (–AA).
	<i>Gillett</i> 4537	KWAZULU-NATAL.—3130 (Port Edward): Mkambati Nature Reserve, (–AC).
	<i>Keet</i> s.n.	WESTERN CAPE.—3422 (Mossel Bay): en route to Knysna from George, (–BB).
		WESTERN CAPE.—3423 (Knysna): Knysna, Redlands, (–AA).

* Illustrated specimens; *specimens used for light microscopy.

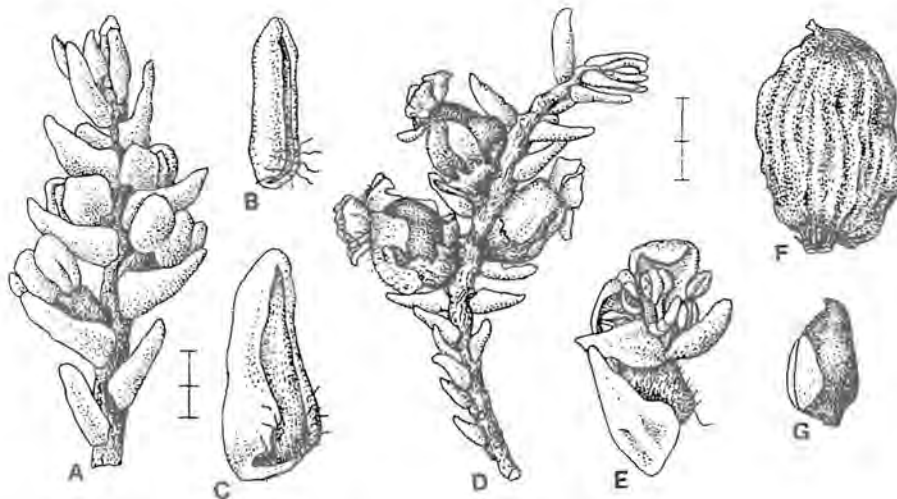


FIGURE 1.—*Passerina ericoides*. A–G, Bredenkamp 962. A, young inflorescence; B, leaf exposing adaxial surface; C, bract exposing adaxial surface; D, fruiting branchlet; E, flower enveloped by bract; F, fleshy one-seeded berry; G, seed with black tegmen and white fragment of endocarp. A, D, $\times 10$; B, C, E–G, $\times 20$. Scale bars: 10 mm.

Bracts

Arrangement subterminal in proliferating spikes, pseudoterminal in subcapitulate spikes; youngest bracts closest to growing point, enlarging along florescence axis; bracts enveloping flowers and fruits (Figures 1A, D, E; 2A, D), largest after anthesis of flowers, becoming more coriaceous and rounded at fruit set, gradually acquiring leaf shape at proximal end of florescence axis, decussate, sessile, imbricate, often conspicuously enlarged, resulting in longer spikes (*P. falcifolia*, *P. filiformis*, *P. sp. nov.* 4, *P. rubra*). *Lamina* inversely ericoid; adaxial surface (inside) concave, facing inflorescence axis, abaxial surface (outside) convex; cymbiform (boat-shaped) or helmet-shaped; in outline (plane shape), oblong, lanceolate, ovate and obovate to widely ovate and obovate, rhombic and narrowly obovate to obovate (Figures 3; 4; Table 5); bracts without leaf-like point, length $\times \frac{1}{2}$ width (2.5–)3.5–4.5(–5.5) \times (0.9–)1.0–1.5(–2.4)

mm; bracts with leaf-like point, length $\times \frac{1}{2}$ width (4.0–)5.1–6.3(–7.3) \times (1.4–)1.5–2.0(–2.6) mm; outside glabrous, seldom tomentose (*P. comosa*, *P. sp. nov.* 3), inside, base or midrib tomentose with glabrous wings or completely comose, tomentose, villous or setose; trichomes nonglandular, uniseriate, mostly strongly spiralled, white; coriaceous or chartaceous, rugose or smooth, \pm succulent or thin, outline of epidermal cells often macroscopically visible; often \pm 3–5-ribbed or reticulately veined on each side of main vein. *Wings* absent, or bordering lamina or distinct from lamina and conspicuously rounded or bullate; mostly glabrous, coriaceous, chartaceous or membranous, often straw-coloured and rosy-tinted. *Base* sessile or cuneate. *Midrib* strongly developed, forming spine of cymbiform bract, often keeled, extending to form a leaf-like point in many species. *Apex* obtuse, rounded or acute, mostly coriaceous. *Margins* often ciliate to setose (*P. burchellii*, *P. sp. nov.* 4, *P. pendula*).

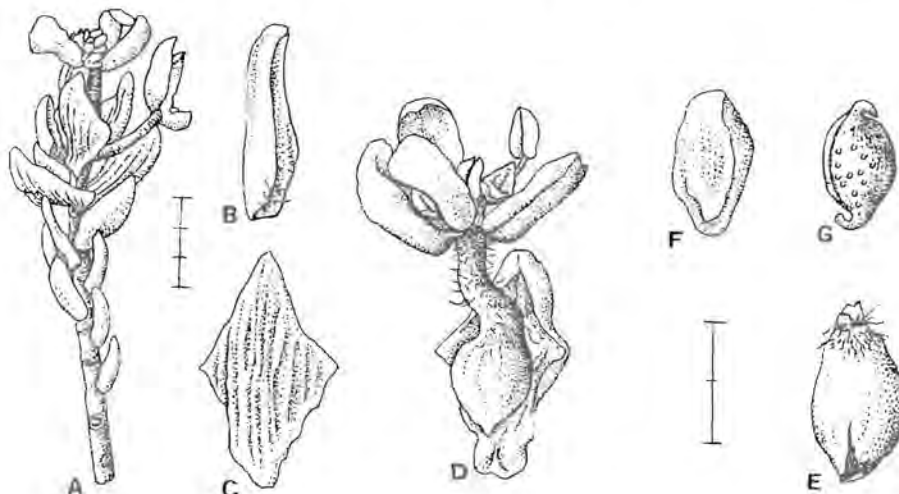


FIGURE 2.—*Passerina vulgaris*. Bredenkamp 944. A, inflorescence; B, leaf exposing adaxial surface; C, bract exposing abaxial surface; D, flower enveloped by bract; E, fruit enveloped by hypanthium, with fragmentation at neck base; F, achene; G, seed with black tegmen and white spots. A, $\times 10$; B–G, $\times 20$. Scale bars: 10 mm.

Key to taxa based on bract characters (Figures 3; 4; Table 5)

- 1a Bracts hairy outside *P. comosa* (Figure 3A), *P. sp. nov.* 3 (Figure 3B, C)
- 1b Bracts glabrous outside:
 - 2a Bracts shorter than 4.5 mm:
 - 3a Bracts rhombic in outline:
 - 4a Bracts dark green when fresh, dark brown in dried specimens, coriaceous; membranous wings absent *P. burchellii* (Figure 3D)
 - 4b Bracts blue-green (glaucous) in fresh and dried specimens, softly coriaceous; membranous wings present *P. pendula* (Figure 3E)



- 3b Bracts variously shaped, but not rhombic in outline:
- 5a Membranous wings present:
- 6a Wings present as membranous rims along lamina margins:
- 7a Lamina convex, ovate to obovate, thinly coriaceous, obscurely ribbed *P. montana* (Figure 3F)
- 7b Lamina helmet-shaped, widely obovate, thinly chartaceous, smooth *P. sp. nov. 2* (Figure 3G)
- 6b Wings variously shaped, but not as membranous rims along lamina margins:
- 8a Wings widely ovate, evenly concave, main vein forming small, obtuse apex *P. paleacea* (Figure 3H)
- 8b Wings oblate or obovate, often bullate:
- 9a Main vein extended into leaf-like point *P. galpinii* (Figure 3I)
- 9b Main vein shortly extended into subacute apex *P. sp. nov. 1* (Figure 3J)
- 5b Membranous wings absent:
- 10a Bracts oblong in outline, apex obtuse *P. ericoides* (Figure 3K)
- 10b Bracts widely ovate or obovate to widely obovate in outline, apex various:
- 11a Bracts widely ovate with distinct, short acute point, glaucous, coriaceous; lamina with 2 or 3 shallow folds *P. rigida* (Figure 3L)
- 11b Bracts obovate to widely obovate, point obtuse to acute, thickly coriaceous; lamina ribbed and reticulately veined *P. glomerata* subsp. *glomerata* (Figure 4A), *P. glomerata* subsp. nov. 1 (Figure 4B)
- 2b Bracts longer than 4.5 mm:
- 12a Bracts lanceolate and glaucous *P. drakensbergensis* (Figure 4C)
- 12b Bracts variously shaped and coloured, but not lanceolate and glaucous:
- 13a Main vein shortly extended into an acute apex; lamina rhombic to obtusulate, distinctly angled, 4- or 5-ribbed *P. vulgaris* (Figure 4L)
- 13b Main vein extending beyond lamina into a leaf-like point:
- 14a Leaf-like point obtuse at apex; lamina closely 2-ribbed at margins *P. obtusifolia* (Figure 4D)
- 14b Leaf-like point not obtuse; lamina extending into a membranous margin:
- 15a Adaxial (inner) surface of bracts basally to centrally setose or tomentose over entire length of midrib; wings glabrous:
- 16a Midrib and leaf-like point stout and strongly developed, apex acute *P. puludosa* (Figure 4E)
- 16b Midrib shortly extended or forming a straight or filiform, leaf-like point:
- 17a Midrib shortly extended, wings ovate-acuminate, gradually narrowing to a point *P. filiformis* subsp. nov. (Figure 4F)
- 17b Midrib extended, forming a straight or filiform, leaf-like point:
- 18a Midrib extended into a filiform, slightly falcate point; wings widely obovate, narrowing abruptly into a leaf-like point *P. filiformis* subsp. *filiformis* (Figure 4G)
- 18b Midrib extended into a straight point or slightly incurved point; wings ovate with margins hairy in upper half, or obtusulate, narrowing abruptly into a leaf-like point *P. sp. nov. 4* (Figure 4H, I)
- 15b Adaxial (inner) surface of bracts completely villous:
- 19a Midrib extended, leaf-like point falcate; wings \pm 4-ribbed *P. falcifolia* (Figure 4J)
- 19b Midrib shortly extended into a short point, apex acute; wings \pm 5-ribbed *P. rubra* (Figure 4K)

Generic description of floral morphology

Flowers actinomorphic, bisexual, hypogynous. *Floral envelope* membranous during pollination and yellowish in *P. rigida*, *P. paleacea*, *P. sp. nov. 1* and *P. sp. nov. 2*, slightly succulent and greenish in *P. ericoides*, mostly yellow-pink in all other species, dehydrated after shedding of pollen, becoming papyraceous or coriaceous, yellow-pink tones turning red, (4.0–)5.3–7.3(–8.4) mm long. *Pedicel* very short or absent. *Receptacle* very short. *Hypanthium* a membranous to coriaceous cylindrical tube; indumentum variable in density, trichomes nonglandular, uniseriate, often spiralled, whitish, density of indumentum at ovary ranging from glabrous to tomentose or strigose; neck (narrowed tube between apex of ovary and sepals) (0.3–)0.6–2.6(–3.0) mm long, density of indumentum ranging from glabrous to tomentose on outside, inside often hairy, abscission tissue not macroscopically discernible, articulation plane absent, after fruiting fragmentation of neck base caused by dehydration and torsification of tissue, shedding sepals and androecium (Figure 2D, E; Table 8) in most species. *Sepals* petaloid (Figures 1E; 2A, D); lobes 4, imbricate in bud (Figure 8C, D), flexed in flower, often setose with up to 5 long trichomes on outer surface and glabrous to tomentose on inner surface; outer lobes cymbiform or concave; inner lobes oblong, elliptic or obovate. *Corolla* absent. *Petaloid scales* absent. *Androecium* dimorphic diplostemonous, inserted at rim of hypanthium, filaments of antipetalous whorl (0.4–)0.7–1.2(–1.5) mm long, anti-

sepalous whorl (1.2–)1.4–2.2(–2.4) mm long; anthers (0.5–)0.7–0.9(–1.1) \times (0.2–)0.3–0.4(–0.7) mm, subbasifixed, 2-thecous and 4-locular (Figure 9A), extrorse. *Disc* absent. *Ovary* superior, (1.6–)2.0–2.5(–2.7) \times (0.5–)0.6–1.4(–1.7) mm, bicarpellate during embryonic stage (Bunniger 1972), pseudomonomerous (Heinig 1951) at maturity, placentation parietal, uniloculate, with 1 pendulous ovule laterally attached near top of ovary; style separating laterally from top of ovary, maintaining lateral position in hypanthium neck, reaching beyond hypanthium rim; stigma \pm globose, mop-like or penicillate (wind-pollination). *Fruit* enveloped by persistent, loosely arranged hypanthium fragmented at neck base or, in some species, fragmenting over widest circumference of fruit, shedding fragmented hypanthium, sepals and androecium (Figures 1D; 2E), in *P. ericoides* (Figure 1F) and *P. rigida* a fleshy 1-seeded berry, 5.3 \times 4.0 mm, in all other species (Figure 2F; Tables 6, 7) an achene, pericarp membranous and dry, 2.5 \times 1.2 mm. *Seed*: tegmen black and shiny, often with white spots, broadly fusiform with outgrowths at both micropylar and funicular ends (Figures 1G; 2G), 2.2(–2.9) \times 1.2(–1.6) mm.

Generic description of floral anatomy (as seen in transverse section)

Receptacle base: vascular tissue arranged in a central stele from which 8 traces are derived in a single whorl (Figure 5A). *Receptacle at apical position*: carpillary bundles arranged in continuous central cylinder; 8 vas-

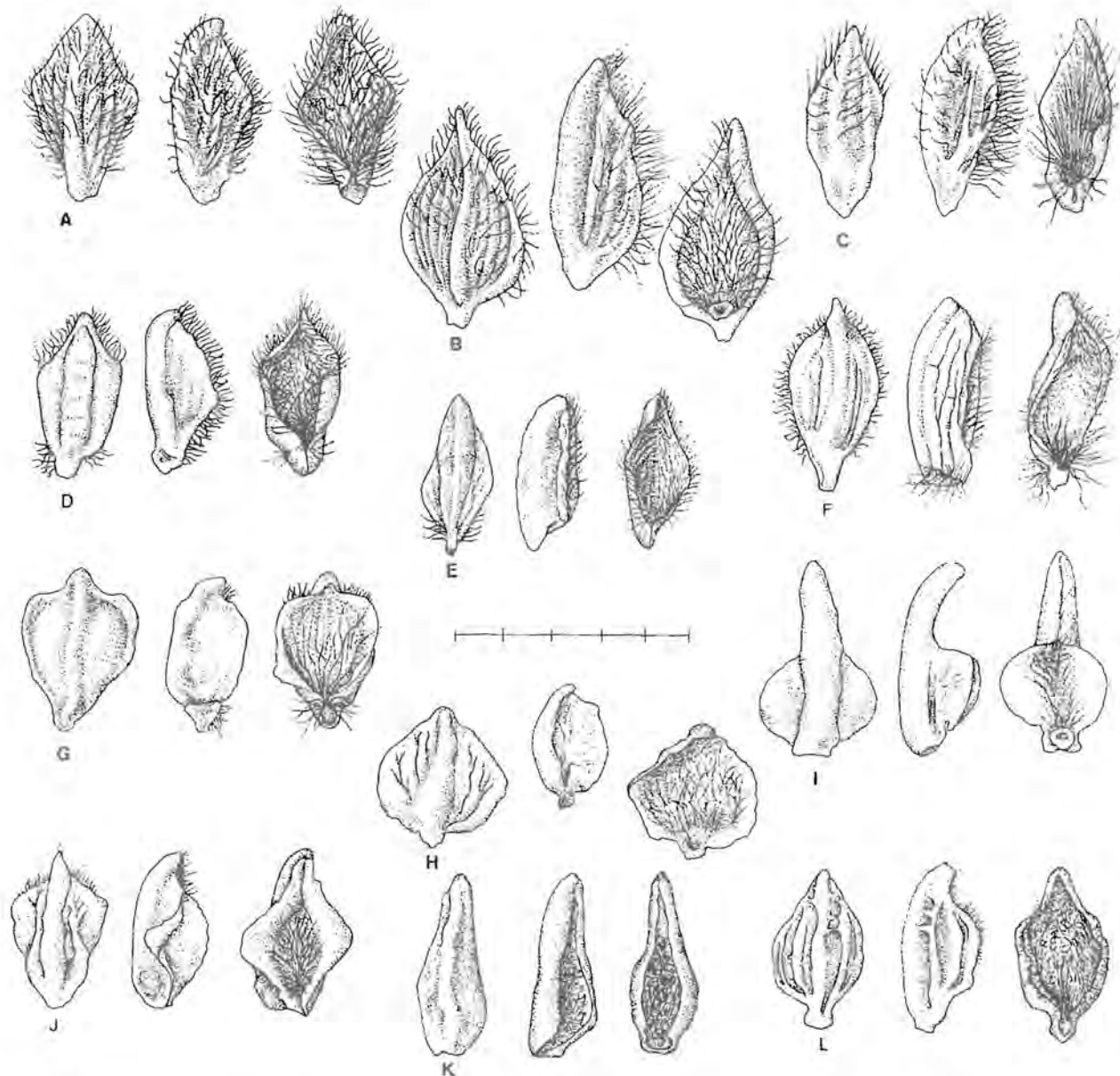


FIGURE 3.—Camera lucida drawings of abaxial, lateral and adaxial views of bracts of *Passerina* taxa, arranged according to sequence in key. A, *P. comosa*, Andreae 1288; B–C, *P. sp. nov. 3*, Esterhuysen 10734, 28006; D, *P. burchellii*, Bolus 687; E, *P. pendula*, Bredenkamp 908; F, *P. montana*, Bredenkamp 893; G, *P. sp. nov. 2*, Esterhuysen 26859; H, *P. paleacea*, Bredenkamp 960; I, *P. galpinii*, Bredenkamp 946; J, *P. sp. nov. 1*, Oliver 9281; K, *P. ericoides*, Bredenkamp 962; L, *P. rigida*, Bredenkamp 1013. A–L, $\times 20$, Scale bar: 5 mm.

cular bundles, fused sepal and stamen traces occupying peripheral position (Figure 5B); cells at periphery of cortex arranged in rows (abscission tissue), differentiation of inner epidermis of hypanthium and outer epidermis of ovary wall, separating hypanthium from ovary wall (Figure 5C, D). *Hypanthium* irregularly lobed or scalloped; outer and inner epidermis variously hairy; cuticle sometimes strongly developed; 8 vascular bundles stretching over entire length (Figure 5E, F). *Calyx* with 4 imbricate lobes developing at hypanthium rim, each containing 3 vascular bundles; epidermal and hypodermal layers containing large amounts of pigment; spongy parenchyma aerenchymatic (Figure 8C, D; Table 6). *Androecium*: each of the 4 fused commissural sepal and antipetalous stamen bundles (cs–pst) split into 2 sepal lateral bundles (sl) and 1 antipetalous stamen bundle (pst), resulting in the first whorl of 4 antipetalous stamens (situated slightly lower in the hypanthium) and

each sepal containing 3 vascular bundles (Figure 8A, B); each of the 4 fused sepal midrib and antisepalous stamen bundles (s–sst) split into a sepal midrib bundle (s) and an antisepalous stamen bundle (sst), forming the second whorl of 4 antisepalous stamens (Figure 8B, C); anthers extrorse, with wall of locule comprising epidermis and endothecium only, periclinal walls of epidermis thin and folded inwards, cell wall thickenings of endothecium \pm stellate, with rib-like extensions directed towards epidermis (Figure 9B), partitions between loculi withered and ruptured (Figure 9C), accompanied by final rupturing of outer walls of thecae (Figure 9D). *Ovary base*: wall independent of hypanthium or loosely adhering to hypanthium at distal side away from placenta (Figure 5E, F; Table 6); outer and inner epidermal walls strongly developed, containing ample amounts of tanniferous substances (Figure 5E) or less sturdy (Figure 5G); mesophyll of densely arranged parenchy-

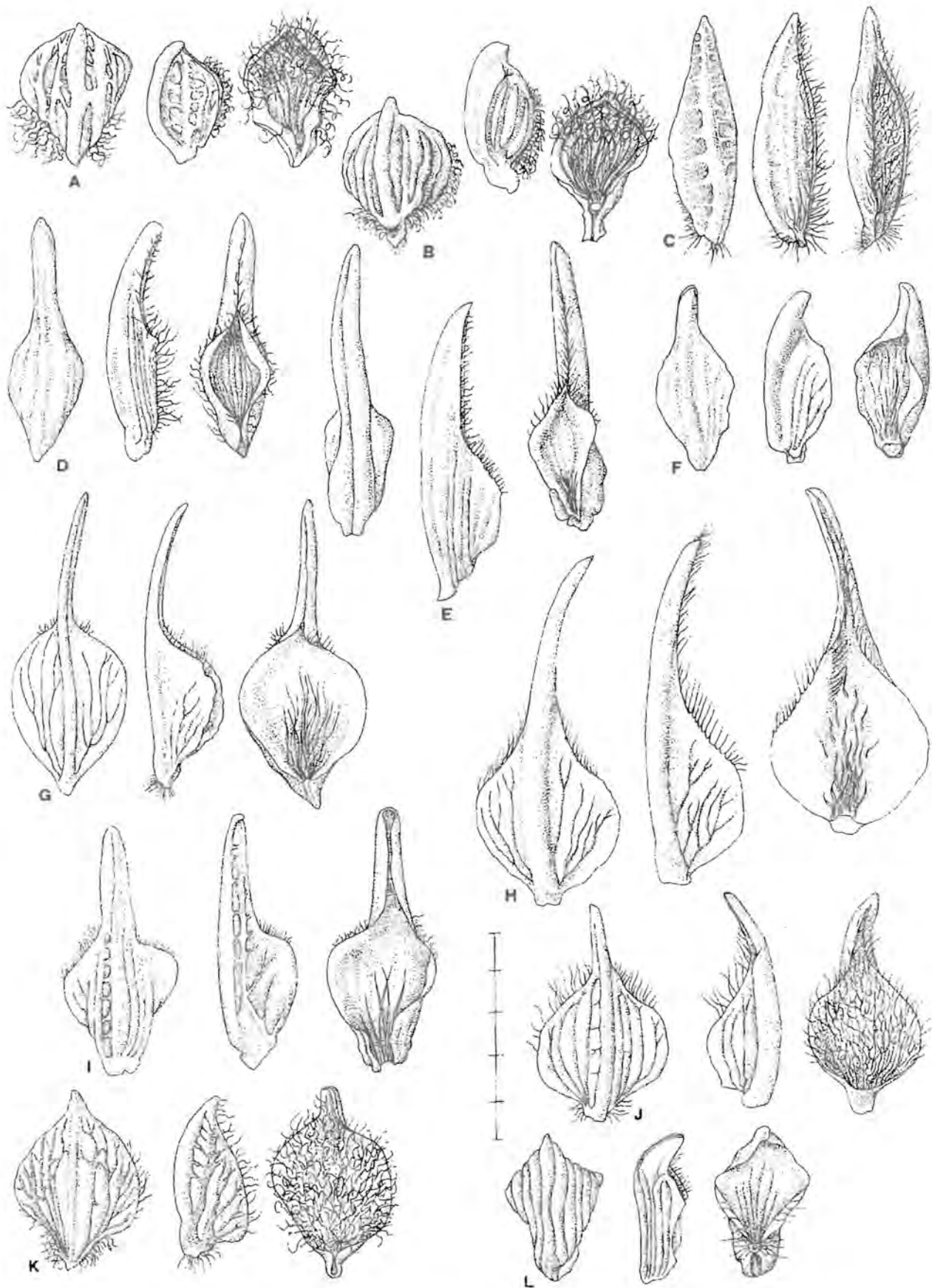


FIGURE 4.— Camera lucida drawings of abaxial, lateral and adaxial views of bracts of *Passerina* taxa, arranged according to sequence in key. A. *P. glomerata* subsp. *glomerata*, Bredenkamp 973; B. *P. glomerata* subsp. nov., Esterhuysen 28587; C. *P. drakensbergensis*, Bredenkamp 1012; D. *P. obtusifolia*, Bredenkamp 919; E. *P. paludosa*, Jangle 156; F. *P. filiformis* subsp. nov., Schlechter 5125; G. *P. filiformis* subsp. *filiformis*, Bredenkamp 1039; H. *P.* sp. nov. 4 from Knysna, Gillett 4537; I. *P.* sp. nov. 4, Bredenkamp 1327; J. *P. falcifolia*, Bredenkamp 917; K. *P. rubra*, Bredenkamp 914; L. *P. vulgaris*, Bredenkamp 944. A–L, $\times 20$. Scale bar: 5 mm.

TABLE 5.—Comparison of inflorescences and bracts in *Passerina*. Sequence of taxa according to key based on bract characters (see text)

Taxa	Polytelic inflorescence			Cymbiform bracts					
	Spikes subcapitulate	reduced	Multi-flowered main and co-florences	abaxial	Indumentum adaxial	Size length × ½ width (mm)	Plane shape	Lamina (per side of main vein)	Wings (per side of main vein)
<i>comosa</i>			X	tomentose	comose	(3.0–)5.5 × 1.5(–1.8)	widely ovate, apex acute	± 3-ribbed, coriaceous, rugose	margins submembranous
sp. nov. 3	X			tomentose	comose	(4.5–)4.9 × 1.5(–1.8)	widely ovate, apex acute	± 3-ribbed, coriaceous, rugose	margins submembranous
<i>burchellii pendula</i>		X	X		villous comose	(3.2–)3.5 × 1.5 (3.0–)4.2 × 1.0(–1.5)	rhombic, apex involute, acute rhombic, apex obtusely angled	coriaceous, smooth softly coriaceous, smooth	smooth margins membranous
<i>montana</i>	X				villous	(3.2–)4.0 × 0.9(–1.6)	ovate to obovate, apex subacute	thinly coriaceous, obscurely ribbed	margins membranous
<i>paleacea</i>	X				villous, wing borders glabrous	(2.5–)2.7 × 1.2(–1.9)	widely ovate, apex obtuse	chartaceous, smooth	membranous, obscurely veined
<i>galpinii</i>			X		midrib tomentose, wings glabrous	(3.6–)4.5 × 1.1(–2.2)	oblate, leaf-like point, apex subacute	chartaceous	membranous, broadly rounded, bullate
sp. nov. 1			X		midrib tomentose, wings glabrous	(3.2–)3.5 × 1.4(–1.9)	widely obovate, apex subacute	chartaceous	membranous, bullate
96 sp. nov. 2			X		setose	3.1 × 1.4	helmet-shaped, widely obovate, apex subacute	thinly chartaceous, smooth	smooth, membranous rims
<i>ericoides</i>			X		villous	3.6 × 1.5	leaf-like, oblong, obtuse	smooth, slightly succulent	absent
<i>rigida</i>			X		villous	(2.6–)3.4 × 1.4(–1.9)	widely ovate, distinct, short, acute point	coriaceous, 2 or 3 shallow folds	absent
<i>glomerata</i> subsp. <i>glomerata</i>	X				villous	4.0 × 1.4(–2.4)	obovate to widely obovate, point obtuse	thickly coriaceous, ribbed and reticulately veined	absent
<i>glomerata</i> subsp. nov.	X				villous	(2.5–)2.9 × 1.5	obovate to widely obovate, point obtuse to acute	thickly coriaceous, ribbed	absent
<i>drakensbergensis</i>			X		villous	5.5 × 1.5	lanceolate, apex obtuse to acute	coriaceous, obscurely ribbed and reticulately veined	absent
<i>obtusifolia</i>			X		setose	(4.0–)5.8 × 1.5(–1.7)	narrowly obtrullate, point leaf-like, apex obtuse	coriaceous, closely 2-ribbed at margins	absent
<i>paludosa</i>			X		basally setose, wings glabrous	(5.2–)7.0 × 1.8(–2.0)	narrowly obtrullate, point leaf-like, apex acute	coriaceous, ± 2-ribbed	membranous with obscure venation
<i>filiformis</i> subsp. nov.			X		centrally setose, wings glabrous	4.6 × 1.5	ovate acuminate, gradually narrowing to point	coriaceous	membranous with distinct venation
<i>filiformis</i> subsp. <i>filiformis</i>			X		basally to centrally setose, wings glabrous	7.3 × 2.0	widely obovate, narrowing abruptly into filiform point	chartaceous	membranous with distinct venation
sp. nov. 4			X		basally setose, wings glabrous	6.3 × 1.6	obtrullate, narrowing abruptly into straight, leaf-like point	coriaceous	chartaceous, ± 3-ribbed, obscurely veined
<i>falcifolia</i>			X		villous	(5.3–)5.8 × 1.7(–2.0)	widely ovate, narrowing into falcate point	coriaceous	coriaceous, ± 4-ribbed, reticulately veined
<i>rubra</i>			X		villous	(4.3–)5.1 × 1.8(–2.0)	widely ovate, with short, acute point	coriaceous	coriaceous, ± 5-ribbed, reticulately veined
<i>vulgaris</i>			X		shortly villous	(4.4–)5.1 × 1.4(–1.7)	rhombic to obtrullate, distinctly angled	coriaceous	coriaceous, distinctly 4- or 5-ribbed

X, character present.

TABLE 6.—Distinction between *P. ericoides* and *P. vulgaris* based on floral anatomy, seen in *Us* (Figures 5; 7; 10)

Floral part	<i>P. ericoides</i> (fruit fleshy)	<i>P. vulgaris</i> (fruit dry)
Hypanthium	Lobed. Outer and inner epidermis hairy (Figure 5E–G).	Scalloped. Outer epidermis hairy, inner epidermis glabrous (Figure 5F, H).
Ovary wall	Independent of hypanthium. Outer and inner epidermal wall strongly developed, containing tanniferous substances. Mesophyll of densely arranged parenchyma cells. Dorsal carpellary bundle strongly developed (Figure 5G). Commissural bundles densely arranged, often fused (Figure 5E, G).	Loosely adhering to hypanthium distally away from placenta (Figure 5F). Epidermal walls less sturdy with less tanniferous substances. Mesophyll aerenchymatic. Dorsal carpellary bundle rudimentary or absent (Figure 5F, H). Commissural bundles closely arranged, often separate (Figure 5F, H).
Style	Four-lobed. Vascular bundles 4, 1 per lobe (Figure 7C).	Elliptic. Vascular bundles inconspicuously arranged in a row along long axis of elliptic style (Figure 7D).
Fruit	Pericarp fleshy: exocarp tanniferous, mesocarp of a few layers of parenchyma, endocarp disintegrating with outer integument (Figure 10A, B).	Pericarp membranous: exocarp degenerated, mesocarp lacking, endocarp degenerated (Figure 10D).

ma cells (Figure 5E, G) or aerenchymatic (Figure 5F, H); vascular bundles arranged in a single ring-like whorl (Figure 5B), median and dorsal carpellary bundles separating from stele (Figure 5C, D), vascular bundles differentiating into dorsal carpellary bundle as well as median and commissural carpellary bundles (Figure 5E, G), or dorsal carpellary bundle absent or poorly defined (Figure 5F, H); funiculus ventral (Figures 5; 6); ovule bitegmic, outer integument (oi) consisting of outer epidermis (oeoi), mesophyll and inner epidermis (ieoi), inner integument consisting of palisade-like outer epidermis (oeii), mesophyll and tanniferous inner epidermis (ieii) (Figures 5G, H; 6A, B), crassinucellate; embryo sac with 1 cell of functional macropore (Figure 5G, H). *Ovary at median position*: ovule wall, integuments and nucellus remaining the same; embryo sac with 2 cells of functional macropore (Figure 6A, B). *Ovary at apical position*: placental vascular bundles and funiculus strongly developed; ovule anatropous, position ventrally epitropous; obturator of elongate cells extending from base of style to micropyle (Figures 6C, D; 7A, B); outer integument horseshoe-shaped, opening close to funiculus facing placenta (Figures 6C; 7A, B); micropyle formed by inner integument, initially facing upwards (Figures 6C, D; 7A), but close to base of style, incurved towards placenta (Figure 7B). *Style* four-lobed or elliptic, styler channel well developed (Figure 7C, D), lined by conducting tissue; vascular bundles 4, 1 per lobe (Figure 7C) or inconspicuously arranged in a row along the long axis of elliptic style (Figure 7D; Table 6). *Stigma* reaching beyond hypanthium rim, penicillate, ramified into numerous simple papillae, dispersed between filament bases (Figure 8A–C). *Seed* exotegmic, outer integument undergoing atrophy; outer epidermis of inner integument (oeii) lengthening and becoming palisade-like, mesophyll consisting of 2 or 3 layers of parenchyma, inner epidermis of inner integument (ieii) tanniferous (Figure 10A, B); tegmen black, lignified, still portraying palisade origin (Figure 10C, D); outer layer of nucellus ornate with cellulose thickenings, nucellus 3–5 cell layers thick; endosperm formation nuclear (Davis 1966), but later becoming cellular throughout (Figure 10D), absorbed by cotyledons containing no starch but copious amounts of oil.

Floral morphology at species level

Floral morphological characters and taxonomically important fruit characters are summarized in Table 7, and specialized hypanthium and sepal characters in Table 8. All these are associated with specific leaf anatomical characters (Bredenkamp & Van Wyk 2001).

DISCUSSION

Inflorescences

Weberling (1989) regards polytelic synflorescences as dominant within the Thymelaeaceae. He found monotelic synflorescences in the Gonystyloideae, a relatively primitive group, as well as certain genera of the Thymelaeoideae and Aquilarioideae. In the Gnidiaceae, it was found in *Lachnaea* L. (= *Cryptadenia* Meisn.) (Beyers & Van der Walt 1995; Beyers 1997), a genus endemic to the Cape Floristic Region (Beyers 1992). Weberling (1989) nevertheless concluded that it appears impossible to draw any taxonomic conclusions from the existence of monotelic synflorescences within these taxa. *Passerina* is characterized by polytelic synflorescences. Most species have multi-flowered main and co-florescences, and a reduction of florescences to single and subcapitulate spikes is clearly shown (Table 5).

Bracts

In their descriptions of the Thymelaeaceae, Domke (1934) reports the presence or absence of bracts and bracteoles, sometimes involucre, and Peterson (1978) mentions that deciduous or persistent bracts are often present. In *Passerina*, single flowers are always enveloped by persistent bracts. In the present study, this constant taxonomic character has been employed in a key for application in herbarium and field work (Figures 3, 4; Table 5).

Floral morphology and anatomy at generic level

Receptacle

Historically the interpretation of the receptacle in the Thymelaeaceae has been controversial. Tables 1 and 2

TABLE 7.—Floral morphological and fruit characters in *Passerina*, correlated with leaf anatomy

Taxon	*Leaf structural type	Fruit		Floral envelope (hypanthium and sepals)						Ovary	Filaments		Anthers	
		Fleshy	Dry	Colour at pollination			Texture			Total length in mm	Length × width in mm	Anti-petalous in mm	Anti-sepalous in mm	Length × width in mm
				green	yellow	yellow-pink	coriaceous	mem-branous	papy-raceous					
sp. nov. 1	A		X		X	X		X		5.3	1.7 × 0.5	0.4	1.2	0.5 × 0.3
<i>ericoides</i>	B3	X		X			X			5.0	2.1 × 1.7	0.5	1.3	0.9 × 0.7
<i>rigida</i>	B3, B6, D2	X			X			X		4.0	2.2 × 1.4	0.5	1.5	0.8 × 0.4
<i>paleacea</i>	B2, B3, B4, D2		X		X			X		4.2	2.4 × 1.4	0.7	1.4	0.6 × 0.5
sp. nov. 2	B3		X		X			X		4.6	1.8 × 0.5	0.4	1.2	0.7 × 0.3
<i>galpinii</i>	B2, B3		X			X			X	5.3	2.0 × 1.1	1.4	2.1	0.6 × 0.5
<i>glomerata</i> subsp. <i>glomerata</i>	B2, B3, B5		X			X			X	6.4	2.4 × 0.9	0.9	1.4	0.8 × 0.4
<i>glomerata</i> subsp. nov.	B6		X			X			X	4.9	2.5 × 0.9	1.2	1.4	0.9 × 0.4
<i>obtusifolia</i>	B2, B3, B4, B5		X			X			X	6.8	2.5 × 1.1	1.2	2.2	1.1 × 0.5
<i>burchellii</i>	B1		X			X			X	4.7	1.6 × 0.6	0.7	1.5	0.5 × 0.3
<i>pendula</i>	B2		X			X		X		6.5	2.0 × 0.7	1.5	2.0	0.8 × 0.4
<i>comosa</i>	B2, B3, D1		X			X			X	7.3	2.7 × 1.0	0.7	1.5	0.7 × 0.4
<i>paludosa</i>	B2		X			X			X	7.2	2.3 × 1.0	1.2	2.4	0.7 × 0.5
<i>montana</i>	B2, B3, D1		X			X			X	5.8	2.1 × 0.6	0.6	1.5	0.8 × 0.4
sp. nov. 3	B3		X			X			X	5.9	1.6 × 1.0	1.1	2.2	0.7 × 0.2
<i>drakensbergensis</i>	B3		X			X			X	5.9	2.4 × 0.9	1.2	2.0	0.9 × 0.3
<i>rubra</i>	B4		X			X			X	8.4	2.7 × 1.1	0.7	1.7	0.9 × 0.3
<i>filiformis</i> subsp. <i>filiformis</i>	B3, B4		X			X			X	6.0	2.3 × 0.5	1.1	2.2	0.8 × 0.3
<i>filiformis</i> subsp. nov.	B6		X			X			X	6.5	2.5 × 0.6	1.2	2.2	0.8 × 0.3
sp. nov. 4	C		X			X			X	6.6	2.2 × 0.7	0.8	1.7	0.8 × 0.3
<i>falcifolia</i>	C		X			X			X	8.4	2.5 × 0.7	1.4	2.1	1.0 × 0.4
<i>vulgaris</i>	D		X			X			X	6.2	2.1 × 1.1	0.7	1.4	0.9 × 0.4

* From Bredenkamp & Van Wyk (2001).
 X, character present.

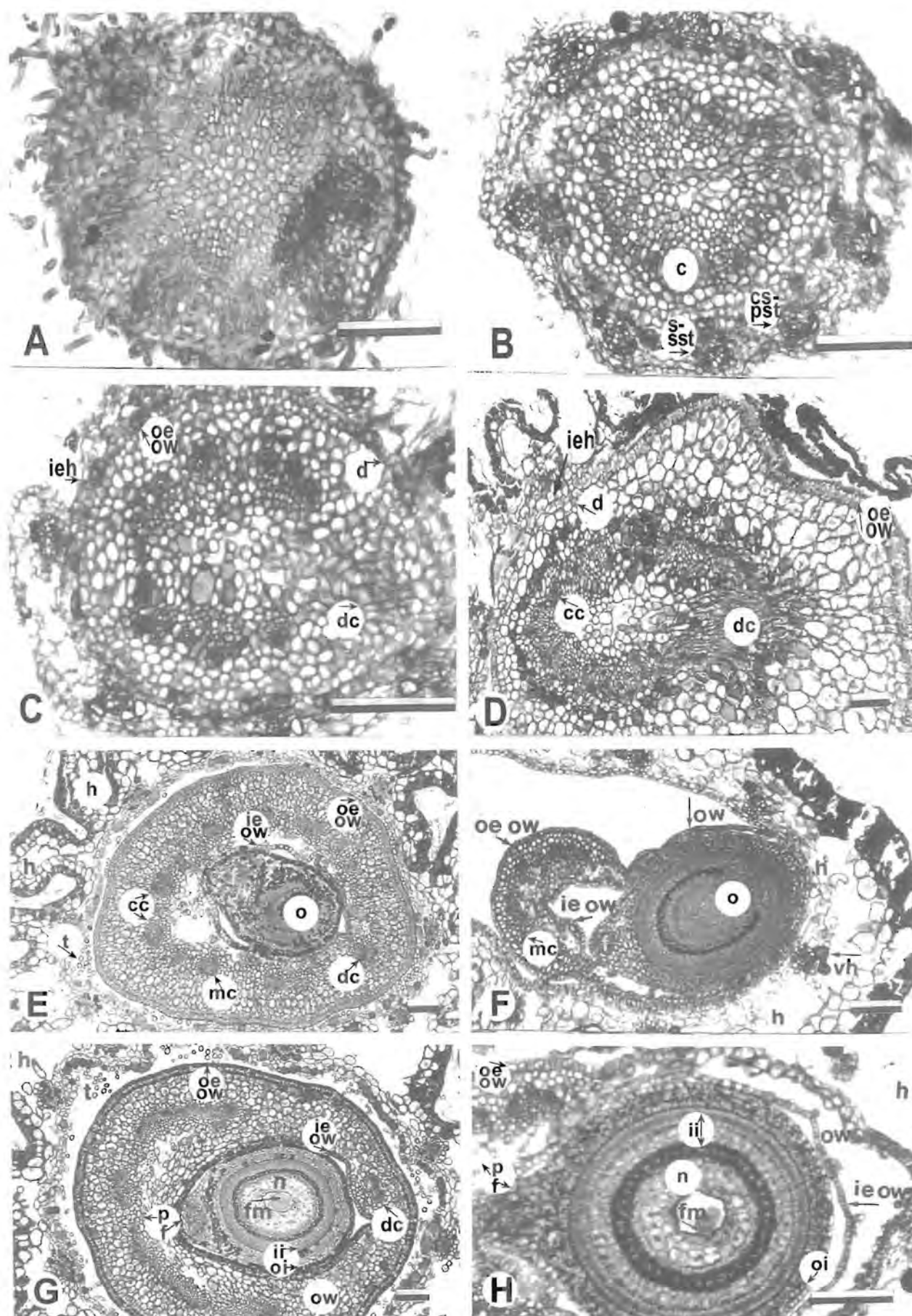


FIGURE 5.—LM photographs of *P. ericoides*, Bredenkamp 956, with fleshy fruit, and *P. vulgaris*, Bredenkamp 951, with dry fruit, showing structure of receptacle and base of ovary. A–D, *t/s* at different levels of receptacle. A–C, *P. vulgaris*: A, departure of eight traces from central stele; B, carpellary bundles arranged in ring, fused stamen and sepal traces in peripheral position; C, differentiation of cortex tissue into inner epidermis of hypanthium and outer epidermis of ovary wall, separation of dorsal carpellary bundle. D, comparison to similar stage in *P. ericoides*. E–H, *t/s* at base of ovary showing vasculature of ovary wall, funiculus and chalaza of pendulous ovule: E, *P. ericoides*, ovary wall independent of hypanthium, carpellary bundles in a single whorl; F, *P. vulgaris*, young bud, ovary wall loosely adhering to hypanthium distally; G, *P. ericoides*, one cell of functional macrospore; H, comparison to similar stage in *P. vulgaris*, reduction of dorsal carpellary bundle. c, carpellary bundle; cc, commisural carpellary bundles; cs-pst, fused commissural sepal and antipetalous stamen bundles; d, area of tissue differentiation; dc, dorsal carpellary bundle; h, hypanthium; ieh, inner epidermis of hypanthium; ieow, inner epidermis of ovary wall; ieow, inner integument; mc, median carpellary bundle; n, nucellus; o, ovule; oeow, outer epidermis of ovary wall; oi, outer integument; ow, ovary wall; p, placenta; s-sst, fused sepal midrib and antisepalous stamen bundle; t, trichome; vh, vascular bundle of hypanthium. Scale bars: A–H, 100 μ m.

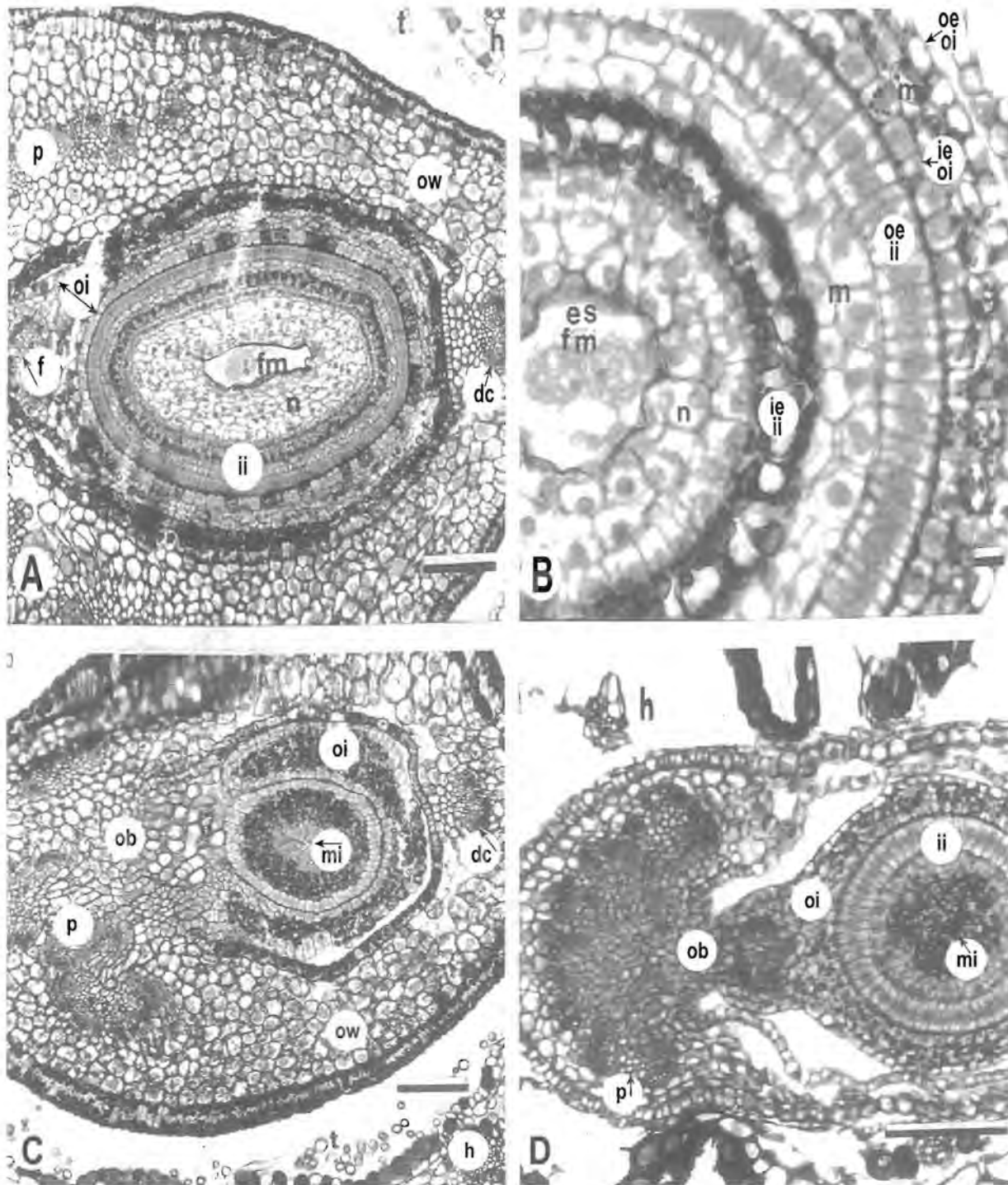


FIGURE 6.—LM photographs of *P. ericoides*, Bredenkamp 956, with fleshy fruit, and *P. vulgaris*, Bredenkamp 951, with dry fruit, showing structure of ovary and ovule. A, B, *ts* in median position of ovary: A, *P. ericoides*, embryo sac and two cells of functional macrospore; B, higher magnification of similar stage in *P. vulgaris*. C, D, *ts* at top of ovary: C, *P. ericoides*, placenta, obturator and micropyle originating from inner integument; D, comparison of similar stage in *P. vulgaris*. Abbreviations as in Figure 5. es, embryo sac; ieii, inner epidermis of inner integument; ieoi, inner epidermis of outer integument; m, mesophyll; mi, micropyle; ob, obturator; oeii, outer epidermis of inner integument; oeoi, outer epidermis of outer integument. Scale bars: B, 10 μ m; A, C, D, 100 μ m.

show that Meisner (1857) regards the floral envelope as perigynous and hypocateriform, implying a cup-shaped receptacle or hypanthium. Gilg (1891, 1894) describes the floral envelope as a cylindric receptacle which is articulate in the upper half, and Endlicher (1837, 1847), Leandri (1930) and Dahlgren & Thorne (1984) regard the floral arrangement as perigynous. The present study indicates that the receptacle (in *ts*) is very short (Figure 5A, B) and definitely not cup-shaped. This is evident from the arrangement of peripheral cortex cells in rows, followed by differentiation into the inner epidermis of the hypanthium and the outer epidermis of the ovary wall (Figure 5D), finally by the separation of the hypanthium (including the vascular bundles differentiated from the stele) from the ovary wall and the presence of trichomes in the space subsequently formed (Figure 5D–F).

Hypanthium and androecial position

Owing to reduction of the receptacle, the hypanthium in *Passerina* is here interpreted as being formed by the fused calyx and androecium only. The vascular tissue of the hypanthium constitutes the fused sepal and stamen traces (Heinig 1951), separating from the central stele in a single whorl and forming a peripheral ring of eight vascular bundles (Figure 5A, B), which persist throughout the length of the hypanthium. A similar pattern of fusion and distribution of vascular tissue has been reported by Heinig (1951) and for the genus *Lachnaea* (= *Cryptadenia*) by Beyers (1992) & Beyers & Van der Walt (1995). In *Passerina* the central stele differentiates into carpellary bundles after the separation of the fused sepal and stamen traces (Figure 5C–E). It can therefore be concluded that

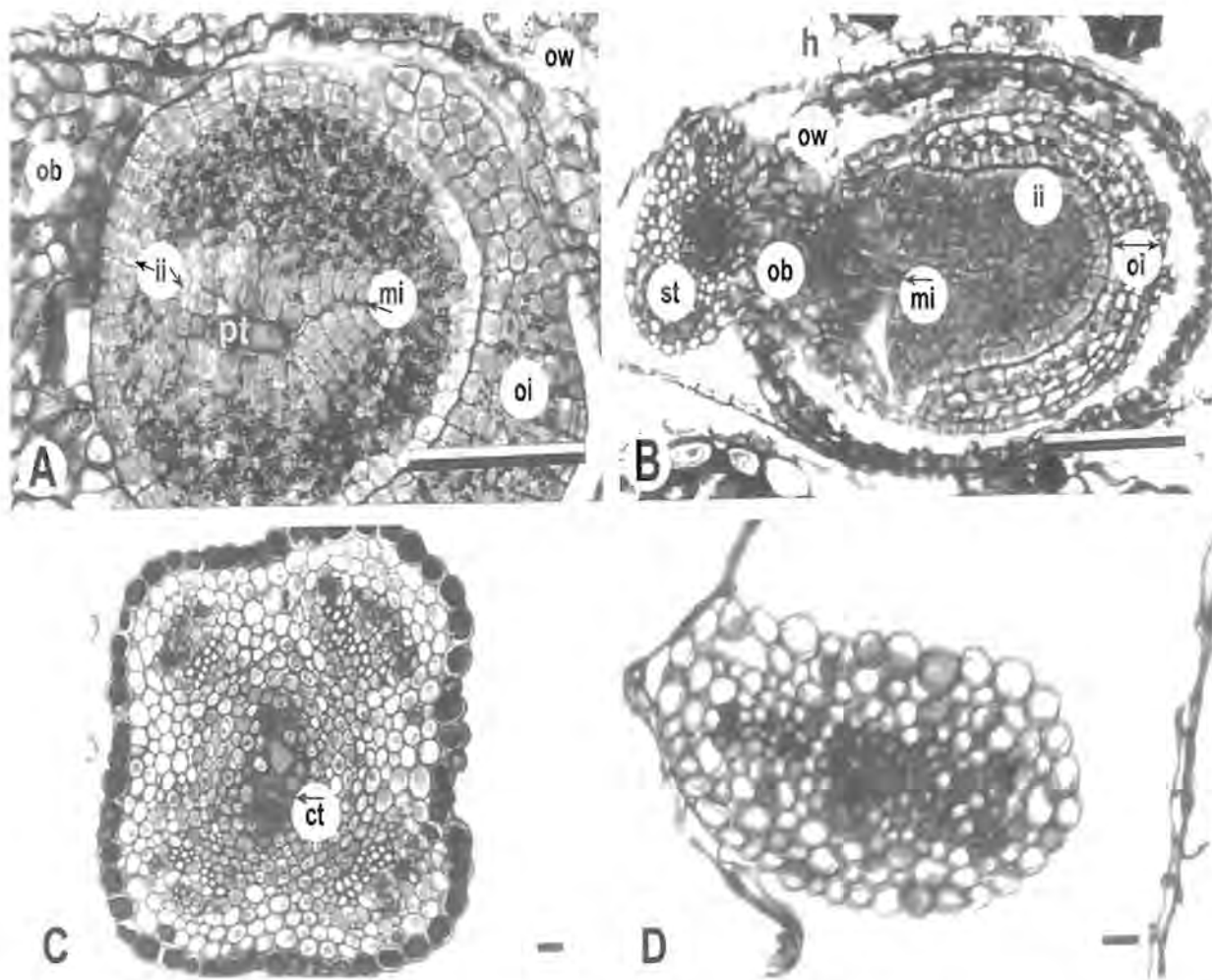


FIGURE 7.—LM photographs of *P. ericoides*, Bredenkamp 956, with fleshy fruit, and *P. vulgaris*, Bredenkamp 951, with dry fruit, showing structure of micropyle and style. A, *P. ericoides*, obturator, pollen tube penetrating micropyle, opening of outer integument towards micropyle. B, similar stage in *P. vulgaris*, style departing laterally. C, D, *t/s* of style. C, D, four-lobed style in *P. ericoides*. D, elliptic style in *P. vulgaris*. Abbreviations as in Figure 5. ct, conducting tissue; mi, micropyle; ob, obturator; pt, pollen tube; st, style. Scale bars: C, D, 10 μ m; A, B, 100 μ m.

the segments of the floral envelope and the androecium arise below the gynoecium, the floral arrangement being hypogynous and the ovary superior (Weberling 1989).

Identity of floral envelope

From Wikstrom (1818) to Takhtajan (1997) (Tables 1; 2) the floral envelope in Thymelaeaceae and, in many cases *Passerina*, was variously interpreted as an infundibular corolla, hypocateriform hypanthium, infundibular perigone, perianth, cylindric receptacle, floral tube formed by coalescence of four external whorls, perianth tube, or a hypanthium. Heinig (1951) supports the interpretation of Leandri (1930) and Domke (1934) of the floral tube as appendicular in origin, composed of the fused bases of the sepals and adherent stamen filaments, also pointing out that the sepal is with few exceptions a three-trace organ. Bunniger (1972) is of the opinion that the hypanthiums in families of the Myrtales and Thymelaeales have a similar origin. Our results show eight vascular bundles running along the length of the hypanthium and separating into sepal and stamen bundles, each sepal lobe eventually with three vascular bundles (Figure 8A, B). We regard the floral envelope as a hypanthium (fused calyx and androecium), differentiating into four petaloid sepals and a diplostemonous androecium, arising from the hypanthium rim at the separation of the sepals. A very short receptacle (Heinig 1951), which does not contribute to the hypanthium,

indicates a reduction in tissue and a possible advanced state. This is indeed the case in *Passerina*.

A study of petaloid scales in Thymelaeaceae has added further evidence to the interpretation of the floral envelope. These scales have been regarded by various authors as perigynous scales or glands, perigynous nectaries, petals or staminodes, petaloid scales and petaloid appendages (Tables 1; 2). Heinig (1951) is convinced that the morphology and vascularization of the petaloid scales resemble that of stipules, an opinion shared by Rao & Dahlgren (1969) on the floral anatomy and relationships of the Oliniaceae. In their floral description of *Olinia*, Dahlgren & Van Wyk (1988) consider the petaloid scales as true petals. Heinig (1951) concludes that the Thymelaeaceae is apetalous. In *Passerina* there are no petaloid scales or corolla (Tables 1; 2). Our results have shown the separation of antipetalous as well as antisepalous stamens, but petaloid scales or even vestiges of them were not observed. We therefore regard *Passerina* as truly apetalous. The complete reduction of the corolla or the absence of petaloid scales can be regarded as an advanced state in the Thymelaeaceae; it could also be interpreted as part of the anemophilous syndrome displayed by the genus. Based on both the pattern of the vascular tissue and the absence of petaloid scales, we consider the floral envelope in *Passerina* as a hypanthium consisting of the fused calyx and androecium, differentiating into four sepals and the diplostemonous stamens.

TABLE 8.—Specialized characters of the floral envelope in *Passerina*, correlated with leaf anatomy

Taxon	Leaf structural type	Fragmentation of hypanth. after fruiting		Hypanthium			Sepals							
		at neck base	at circumf. of ovary	neck length*	indumentum		indumentum				inner lobe: l × w*	outer & inner	shape of lobes	
					at ovary	at neck	outer lobe surface adaxial	surface abaxial	inner lobe surface adaxial	surface abaxial			outer	inner
<i>sp. nov. 1</i>	A	X		1.2	tomentose	tomentose	glabrous	apex setose	glabrous	glabrous	1.9 × 1.2		cymbiform	widely ovate
<i>ericoides</i>	B3		X	0.6	strigose	strigose	puberulent	glabrous	puberulent	glabrous	1.6 × 2.0	concave, widely ovate		
<i>rigida</i>	B3, B6, D2		X	0.8	glabrous	tomentose	midrib tomentose	glabrous	tomentose	glabrous	1.8 × 0.9		cymbiform	obovate
<i>puleacea</i>	B2, B3, B4, D2		X	0.3	glabrous	glabrous	glabrous	glabrous	glabrous	glabrous	1.8 × 1.5	concave, elliptic or subrotund		
<i>sp. nov. 2</i>	B3		X	0.7	tomentose	tomentose	apex tomentose	apex setose	glabrous	apex setose	1.8 × 1.0		concave, oblong	concave, obovate
<i>galpinii</i>	B2, B3		X	1.0	pubescent	pubescent	glabrous	glabrous	apex margin tomentose	glabrous	2.4 × 1.6		concave, elliptic	obovate
<i>glomerata</i> subsp. <i>glomerata</i>	B2, B3, B5		X	0.8	glabrous	tomentose	scantly pubescent	glabrous	scantly pubescent	glabrous	2.3 × 0.8		cymbiform	oblong-elliptic
<i>glomerata</i> subsp. nov.	B6		X	0.7	apex tomentose	tomentose	apex tomentose	glabrous	tomentose	glabrous	2.6 × 1.6		concave, ovate	widely obovate
<i>obtusifolia</i>	B2, B3, B4, B5		X	1.8	glabrous	tomentose	tomentose	glabrous	tomentose	glabrous	2.8 × 0.9		cymbiform	narrowly oblong
<i>burchellii</i>	B1	X		0.8	glabrous	tomentose	midrib setose	apex setose	tomentose	apex setose	2.3 × 0.6		cymbiform	obovate
<i>pendula</i>	B2	X		0.6	glabrous	tomentose	scantly tomentose	glabrous	scantly tomentose	glabrous	2.9 × 1.5		cymbiform	oblong
<i>comosa</i>	B2	X		0.9	glabrous	tomentose	glabrous	tomentose	glabrous	tomentose	2.8 × 1.0		cymbiform	elliptic
<i>paludosa</i>	B2	X		2.6	shortly tomentose	strigose	glabrous	apex setose	apex margin tomentose	apex setose	2.2 × 1.2		cymbiform	oblong
<i>montana</i>	B2, B3, D1		X	1.3	glabrous	tomentose	scantly tomentose	glabrous	tomentose	glabrous	2.1 × 1.0		cymbiform	obovate
<i>sp. nov. 3</i>	B3	X		1.4	glabrous	scantly tomentose	glabrous	apex setose	glabrous	apex tomentose	2.7 × 1.5		concave, ovate	obovate
<i>drakensbergensis</i>	B3	X		1.7	scantly tomentose	tomentose	glabrous	tomentose	tomentose	tomentose	2.4 × 0.8	concave, lanceolate		
<i>rubra</i>	B4	X		2.0	glabrous	pubescent	glabrous	glabrous	scantly tomentose	glabrous	2.9 × 1.7		cymbiform	obovate
<i>filiformis</i> subsp. <i>filiformis</i>	B3, B4	X		1.7	tomentose	tomentose	glabrous	apex setose	glabrous	apex setose	2.2 × 1.4		concave, obovate	obovate
<i>filiformis</i> subsp. nov.	B6	X		1.5	scantly tomentose	scantly tomentose	glabrous	apex setose	glabrous	apex setose	2.5 × 1.5	concave, obovate		
<i>sp. nov. 4</i>	C	X		2.3	upper half tomentose	tomentose	glabrous	apex setose	glabrous	apex setose	2.1 × 1.3		cymbiform	obovate
<i>falcifolia</i>	C	X		3.0	scantly tomentose	tomentose	scantly tomentose	glabrous	tomentose	glabrous	2.5 × 1.3		concave, obovate	obovate
<i>vulgaris</i>	D2	X		1.6	glabrous	scantly tomentose	scantly tomentose	glabrous	scantly tomentose	glabrous	2.5 × 1.3		cymbiform	obovate

X, character present; * average in mm.

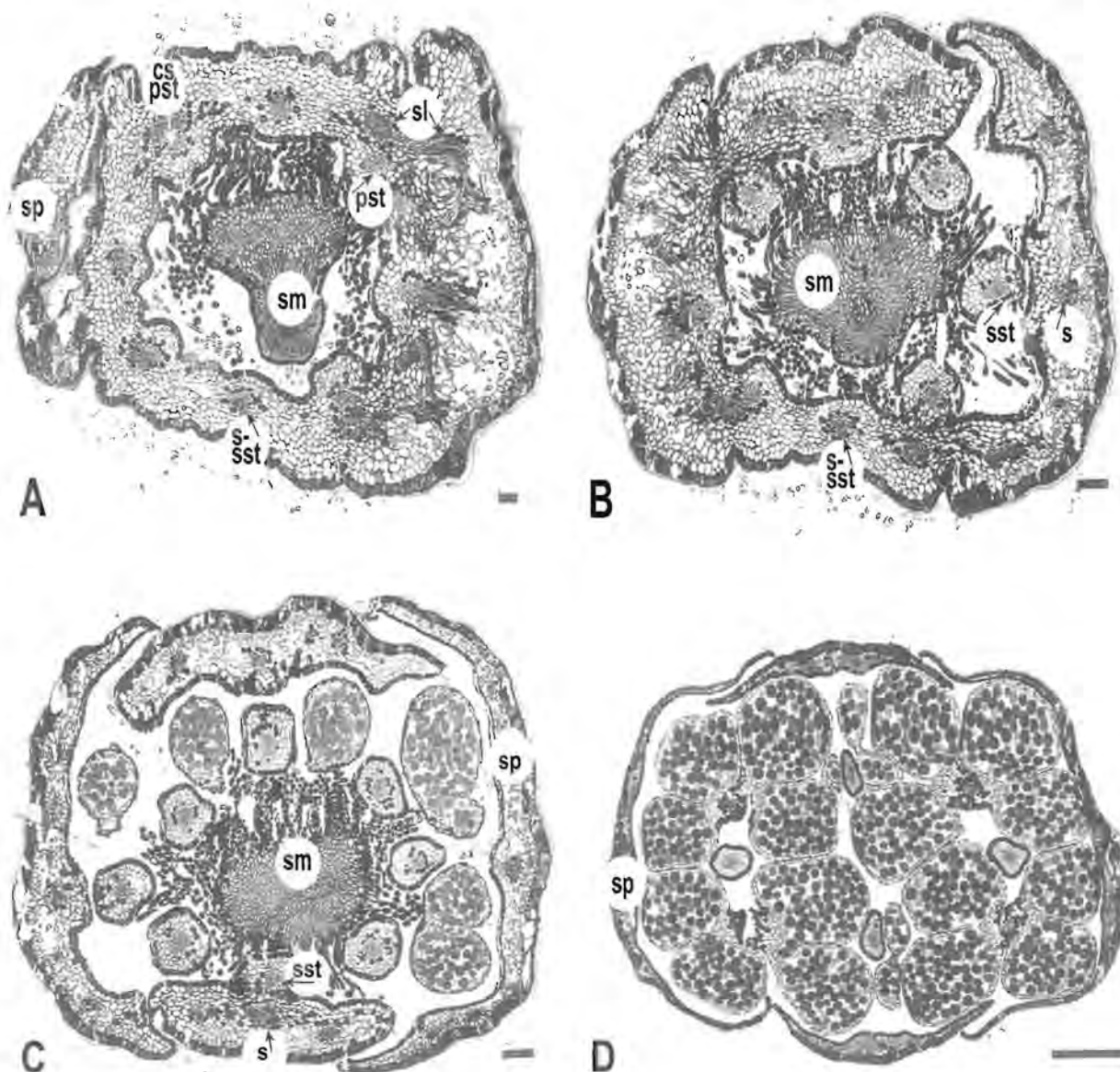


FIGURE 8.—LM photographs of *P. ericoides*, Bredenkamp 956, with fleshy fruit, and *P. vulgaris*, Bredenkamp 951, with dry fruit, showing structure of androecium. A–D, serial *U*s of sepals and two anther whorls. A–C, *P. ericoides*: A, each of fused commissural sepal and antipetalous stamen bundles splitting into two sepal laterals and one antipetalous stamen bundle; B, fused sepal midrib and antisepalous stamen bundle, splitting into sepal midrib and antisepalous stamen bundle; C, final stage in separation of antisepalous stamen bundles. D, *P. vulgaris*, *U*s through both anther whorls. Abbreviations as in Figure 5. pst, antipetalous stamen bundle; s, sepal midrib bundle; sl, sepal lateral bundle; sm, stigma; sp, sepal; sst, antisepalous stamen bundle. Scale bars: A–D, 100 μ m.

Fragmentation of hypanthium

The fruit in *Passerina* is enveloped by a persistent, loosely attached hypanthium. Bentham & Hooker (1880), Gilg (1891, 1894), Domke (1934) and Melchior (1964) mention that the hypanthium is articulated above the ovary. We found no definite articulation point in the hypanthium neck (narrowed part of hypanthium between apex of ovary and sepals) in *Passerina*, possibly because of the absence of receptacle tissue and the appendicular nature of the hypanthium. The base of the neck fragmented as a result of desiccation and torsification of cells (Figure 2E). In some species, fragmentation of the hypanthium takes place over the widest circumference of the fruit, shedding the fragmented distal part of the hypanthium, sepals and androecium (Figure 1D). A strong association was found between flowers with a short hypanthium neck and fragmentation of the hypanthium over the widest part of the fruit, and also between flowers with a long hypanthium neck and fragmentation at the base of the neck (Table 8).

A plane of circumscession, dividing the floral tube into a basal and upper portion, is clearly illustrated in *Gnidia* and *Struthiola* (Peterson 1978) and *Lachnaea* (Beyers

1992; Beyers & Van der Walt 1995). We hypothesize that the plane of circumscession possibly indicates a difference in tissue composition between the basal and upper portions of the hypanthium and that this articulation can be of morphological importance in the Thymelaeaceae. The basal portion of the floral tube below the plane of circumscession possibly indicates the inclusion of receptacle tissue in the hypanthium, whereas the upper portion consists of calyx and androecium tissue only (accepting the apetalous state). An alternative interpretation, offered by one of the referees of this paper, regards the vasculature as a prerequisite to decide whether one is dealing with a hypanthium (appendicular in origin) or a receptacle (axial in origin). The significance of an articulation indicating a distinction between parts of the hypanthium of different derivation, should be further investigated.

Androecium

In his description of Thymelaeaceae, Peterson (1978) describes the stamens as twice as many or as many as the sepals (rarely reduced to two or one), in one or two whorls, the outer whorl antisepalous. In the subfamily Aquilarioideae (Heinig 1951), stamens are of approximately

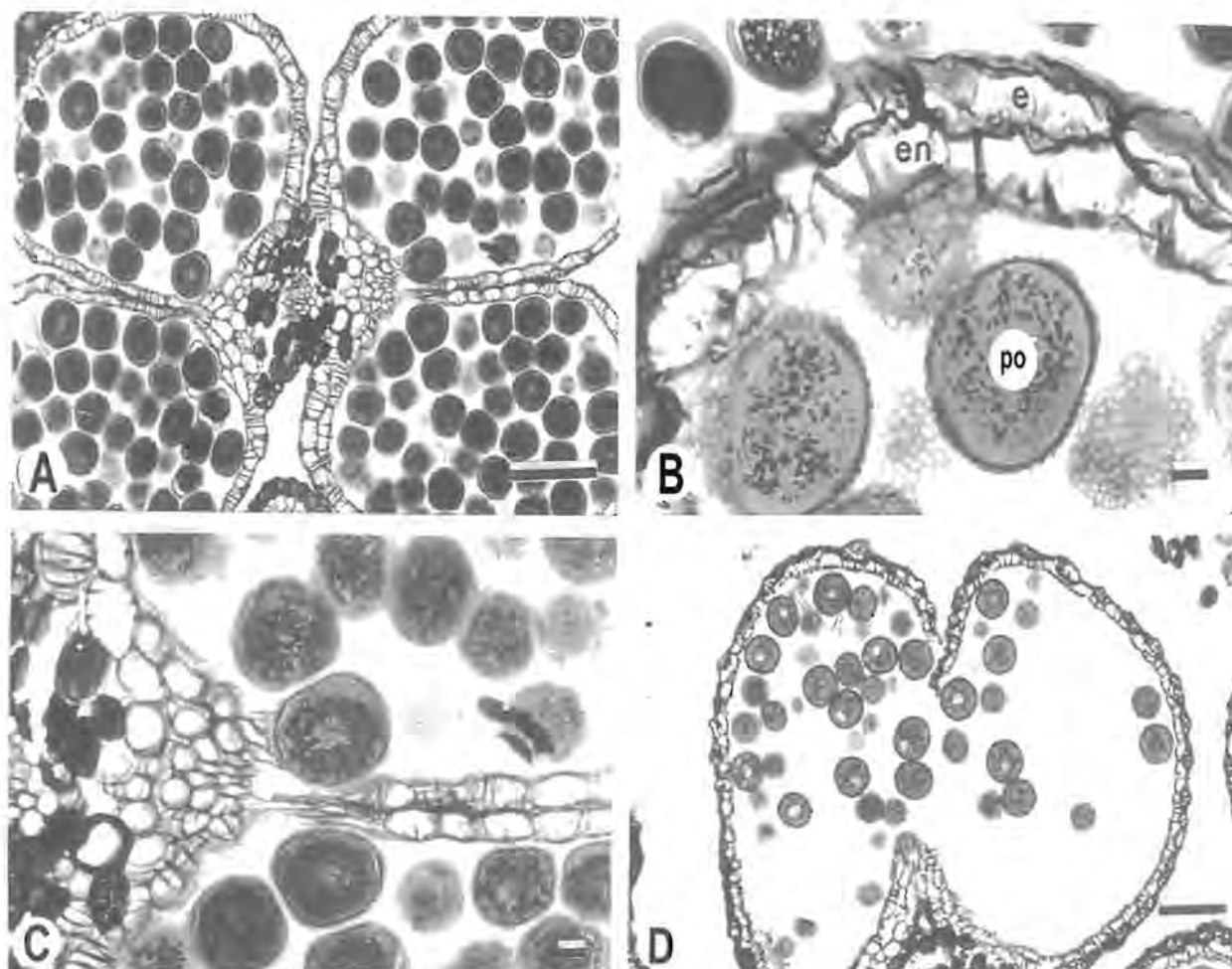


FIGURE 9.—LM photographs of *P. ericoides*, Bredenkamp 956 and *P. vulgaris*, Bredenkamp 951, showing structure of anther locules in *t/s*: A, *P. vulgaris*, 4-locular anther; B, *P. ericoides*, cell wall thickenings of endothecium rib-like; C, *P. vulgaris*, rupturing of partition between loculi; D, *P. ericoides*, rupturing of outer walls of thecae, extrorse. e, epidermis; en, endothecium; po, pollen. Scale bars: B, C, 10 μm; A, D, 100 μm.

equal length and the traces supplying them separate from the sepal traces, practically in a single whorl. The Thymelaeoideae is characterized by stamens arising as two distinct whorls at two distinct levels in the floral tube. The dimorphic diplostemonous nature of stamens in *Passerina* (Thymelaeoideae), in which the antipetalous stamens are shorter than the antisepalous ones, has been confirmed by our observations (Figure 8A–C). According to Heinig (1951) evolution within the androecium has been from polystemony to diplostemony to dimorphic diplostemony, indicating the advanced state of the androecium in *Passerina*. Peterson (1978) describes the anthers as usually introrse, rarely extrorse. Species of *Passerina* have large, exerted, extrorse anthers, clearly an adaptation to the anemophilous syndrome of the genus.

Separation of fused sepal and stamen traces

Heinig (1951) is of the opinion that a foreshortening of the floral axis has resulted in a fusion of the calyx and androecium and that progressive stages of adnation can be observed in the family. In all species the antipetalous stamen traces are fused to the commissural sepal traces and the antisepalous stamen traces to the sepal midrib traces at their point of origin from the stele. In the Aquilarioideae, in *Octolepis dinklagei*, they become separated in the receptacle or, in other cases, low down in the floral tube. Except for *Gnidia splendens* (= *Lasio-siphon splendens*), in which the separation of the antipetalous and antisepalous stamen traces takes place in the receptacle, Thymelaeoideae is characterized by

separation higher up in the floral tube, e.g. at the top of the ovary in *Dirca occidentalis* and below the origin of the sepals in *Gnidia subulata* (Heinig 1951). In *Passerina* the separation of the antipetalous stamen traces takes place at the origin of the sepals (Figure 8A, B) and separation of the antisepalous traces slightly higher up (Figure 8C), indicating what appears to be a phylogenetically advanced tendency.

Pollen

Pollen grains of most members of Thymelaeaceae are monads, spheroid and pantoporate, characterized by a typical croton pattern, comprising rings of more or less trihedral sexine units mounted on an underlying reticulum of circular muri (Bredenkamp & Van Wyk 1996). In *Passerina*, the basal reticulum, as in the typical croton pattern, is no longer discernible as it is replaced by a secondary reticulum derived from fused sexine. The supra-rectal subunits are fused completely to form a continuous reticulum which replaces the underlying reticulum. The reticulum in *Passerina* is therefore secondary in origin and considered phylogenetically advanced. This modification of the crotonoid pattern is probably also of functional significance as pollen in *Passerina* is adapted to anemophily.

Disc

In Aquilarioideae a hypogynous disc is generally absent, but is almost always present in Thymelaeoideae

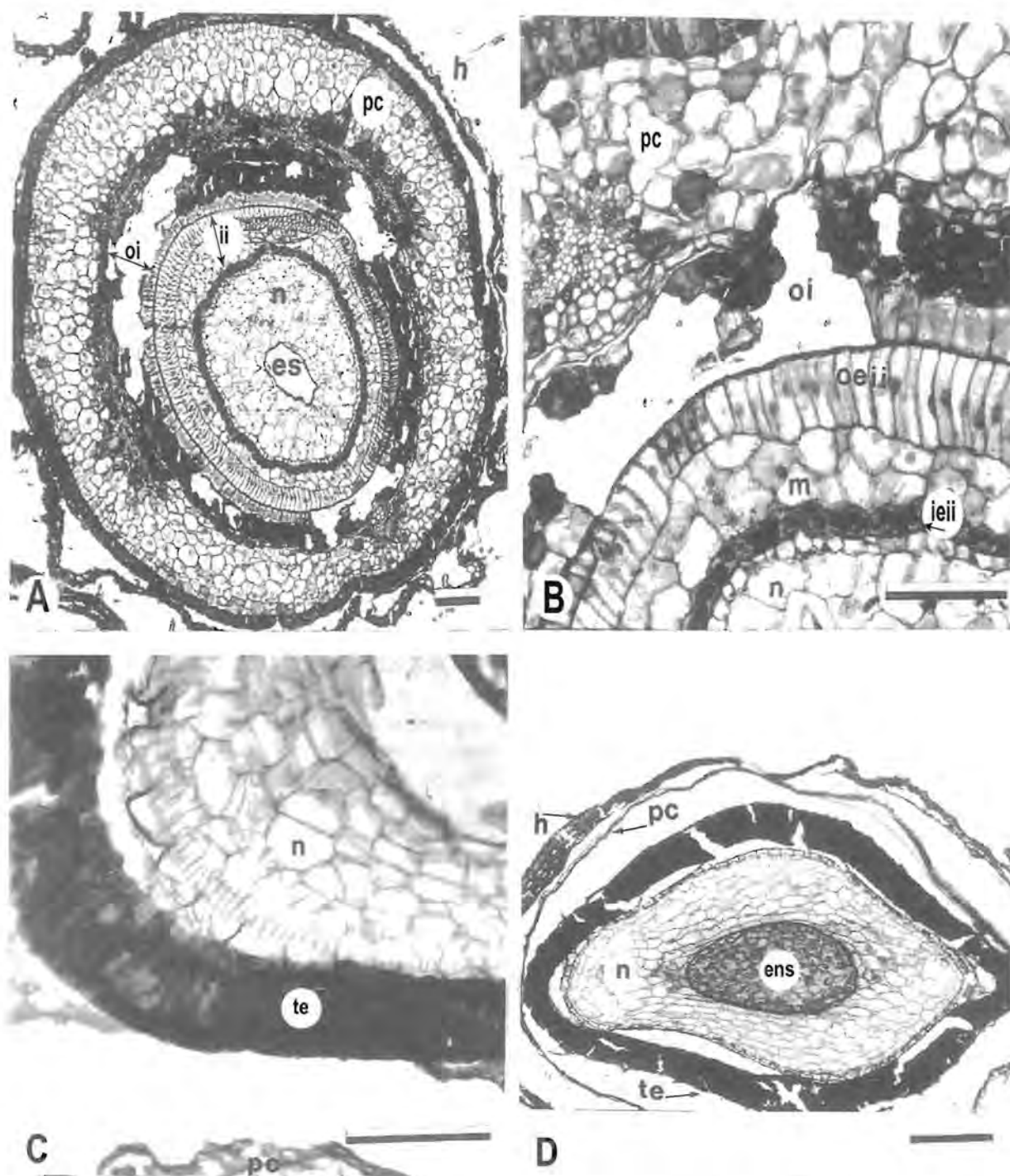


FIGURE 10.—LM photographs of *P. ericoides*, Bredenkamp 956, with fleshy fruit, and *P. vulgaris*, Bredenkamp 951, with dry fruit, showing structure of young fruit and developing seed in *t/s*. A, B, *P. ericoides*: A, pericarp fleshy, atrophy of outer integument; B, higher magnification, outer epidermis of inner integument palisade-like, mesophyll, inner epidermis of inner integument tanniferous. C, D, *P. vulgaris*: C, palisade-like exotegmen discernable in tegmen. D, tegmen black and lignified, crassinucellate, endosperm initially nuclear. Abbreviations as in Figure 5. ens, endosperm; es, embryo sac; ieii, inner epidermis of inner integument; m, mesophyll; oeii, outer epidermis of inner integument; pc, pericarp; te, tegmen. Scale bars: A–D, 100 μm.

(Heinig 1951; Peterson 1978). Possibly because of a reduction of tissue, no disc was observed in *Passerina*, a state confirmed by Bunniger (1972).

Ovary

The ovary in *Passerina* was described as unilocular up to the time of Domke (1934) (Table 1). The pseudomonomerous state is mentioned by Eckardt (1937), Melchior (1964), Dahlgren & Thorne (1984) and Cronquist (1988) (Table 2), while most authors agree that ovules are solitary and pendulous. According to Takhtajan (1997) the ovary in Thymelaeoideae consists of two carpels, it is monolocular and the ovule is solitary. Heinig (1951) is convinced that within the carpellary

whorl a reduction series may be observed, ranging from four- or more-carpellate members in the Aquilarioideae to the two-carpellate members of the Thymelaeoideae in which one carpel is markedly contracted, thus a pseudomonomerous ovary. According to Heinig (1951) the ovules have been reduced to one per locule in the entire family. In *Passerina*, at the base of the ovary, the dorsal and median carpellary bundles initially separate from the central stele (Figure 5C, D). After differentiation has taken place, the dorsal, median and commissural carpellary bundles (Figure 5E) can be distinguished. Because of a redistribution of carpellary bundles, the single dorsal carpellary bundle is arranged at the opposite side of the horseshoe-shaped median and commissural carpellary bundles (Figure 5G). In *Dirca palustris*,

Heinig (1951) has illustrated the authenticity of the pseudomonomerous ovary by the presence of two dorsal carpellary bundles, one in the fertile carpel and one in the second, reduced, sterile carpel positioned between two groups of commissural carpellary bundles. Bunniger (1972) showed the presence of two carpels in the flower primordia of *P. filiformis*. In the present study, which included the young bud stage of *P. vulgaris* (Figure 5F), no indication of a second carpel or a second dorsal carpellary bundle was found, possibly because of reduction and fusion processes, which had already taken place in the formation of the young ovary, consequently we consider the ovary of *Passerina* as pseudomonomerous.

Ovule type and position

Domke (1934) describes the ovule in Thymelaeaceae as pendulous, anatropous, with a ventral funiculus, exceptionally hemi-anatropous or orthotropous, indicating a phylogenetic tendency. Our study clearly indicates a pendulous, anatropous ovule in *Passerina* (Figure 6C, D). The funiculus is ventral and has been sectioned from the base of the ovule (Figures 5E–H; 6A) to the point of attachment with the placenta (Figure 6C, D). Close to the embryo sac the micropyle is a trilete opening formed by the inner integument (Figures 6C, D; 7A), facing upward. Towards the micropyle, the outer and inner integuments become horseshoe-shaped (in *ts*), resulting in the micropyle being directed towards the elongated obturator cells, located at the base of the style (Figure 7B). Based on these results, we agree with Dahlgren (1975b), who regards the ovule as pendulous and epitropous.

Obturator

Davis (1966) defines an obturator as any structure associated with directing the growing pollen tube towards the micropyle, but elongated cells extending from the base of the style to the micropyle are considered exclusive to the Thymelaeaceae. In *Passerina* such elongated obturator cells can be clearly seen at the level of the placenta, at the departure of the funiculus, touching on the inner integument (Figures 6C; 7A) and finally these cells extend from the base of the style entering the micropyle (Figure 7B).

Fruit

Most authors (Tables 1; 2) agree that the fruit in Thymelaeaceae is indehiscent. In *Passerina*, Wikström (1818), Meisner (1857) and Endlicher (1837, 1847) consider the fruit as a nut or a nutlet. Domke (1934) concludes that the fruit of *Dais*, *Gnidia*, *Lachnaea* (= *Cryptadenia*) and many taxa of *Passerina* can be defined as an achene, and that of *P. ericoides* as a berry. Dahlgren (1975b) considers the fruit of Thymelaeaceae as a nut or drupe, Peterson (1978) regards it as a berry, a nut, a drupe or a loculicidal capsule and Takhtajan (1997) describes them as nut-like, baccate or drupaceous. A relevant family character, that the outer integument of the ovule disintegrates and the inner integument becomes palisade-like and hardens to form a seed coat or tegmen (Figure 10A–D), is illustrated by the present study. Structurally the dry, membranous fruit in *Passerina* conforms to an achene (Spuyt 1994) and the reduction in pericarp tissue can probably be considered as

a specialized adaptation. A reduction in tissue from a drupe to a membranous 1-seeded berry or an achene can be illustrated in Thymelaeaceae and therefore the fruit in *Passerina* could be considered advanced within the family. We agree with Domke (1934) that *P. ericoides* (Figures 1F; 10A) and *P. rigida* are characterized by a fleshy 1-seeded berry, while all the other species have an achene (Figure 2F; Table 7). The achene remains enveloped in the remnants of the papyraceous hypanthium, nestled adaxially in the tomentum of the concave, persistent cymbiform bracts.

Seed

The existing confusion concerning the state of the tegmen in *Passerina* is a reflection of the total lack of information of this aspect in descriptions of the group by various authors (Tables 1; 2). Meisner (1857) describes a crustaceous pericarp and Domke (1934) a black, crustaceous testa. The ovule in *Passerina* is bitegmic (Figures 6; 7; 10). Corner (1976) refers to outer integument (oi) and inner integument (ii), the product of the outer integument becoming the testa and that of the inner integument, the tegmen. In *Passerina* the outer integument disintegrates, whereas the inner integument remains (Figure 10A), its outer epidermis becoming palisade-like (Figure 10A, B). Hence, the seeds of *Passerina* are exotegmic with a palisade, a state common to the family (Corner 1976). In *Passerina* the tegmen is black and lignified, and in *ts*, still portraying its origin from the palisade-like epidermis (Figure 10C, D).

Floral and fruit morphology at species level (Tables 7; 8)

In the present study, specific results in leaf anatomy indicating the arrangement of taxa in *Passerina* (Bredenkamp & Van Wyk 2001), are associated with floral morphological structures as well as fruit and seed types. In Table 7, leaf structural types A and especially B3 are associated with four species that have smaller, yellow, membranous flowers (up to 5.3 mm long). Leaf structural types B4, B5, B6, C and D are associated with most species having larger, yellow-pink, papyraceous flowers (up to 8.4 mm long). The same tendency in the length of the neck, and the size of the inner sepals is shown in Table 8.

Fruit

Fleshy fruit in *P. ericoides* (Figure 1D, F) and *P. rigida* is possibly correlated with the moist maritime climate of the coastal habitat of these species; it is possibly also an adaptation to bird dispersal. Both species occur in the Western Cape, and the range of *P. rigida* extends along the coast to St Lucia. *P. ericoides* has red berries and *P. rigida* has yellow berries. All other species are characterized by achenes and are adapted to drier habitats, from mountainous areas along the Great Escarpment to the arid Karoo. In *Passerina*, each achene is enveloped by papyraceous remnants of the fragmented hypanthium and enclosed within the tomentum of an enlarged bract (Figure 2D, E), which often takes on a rounded shape and turns yellow, red or brownish.

The fruits of *Passerina* clearly illustrate the phenomenon of transfer of function from protection to dispersal

(Stebbins 1974). In *P. ericoides* and *P. rigida*, with fleshy fruit, the pericarp has the double function of protecting the ovules during early stages of development and dispersal. The mature fruit enlarges beyond the bracts and is protected by the coriaceous pericarp, while the patent bract does not have a protective function (Figure 1D). The pericarp of the fruit is yellow or red when it is ready for dispersal, probably by birds or small mammals (Richards 1986), and the dispersal unit is the berry. In all other species which are characterized by achenes, the protection of the ovule is apparently transferred from the pericarp to the persistent bract. The bract enlarges around the achene, protecting it in the woolly tomentum of the concave adaxial surface (Figure 2D). The mature fruit is often still enveloped by the reddish, papyraceous remnants of the hypanthium. Both *P. montana* and *P. glomerata* are characterized by subcapitulate inflorescences, with proliferating growth more common in the latter species. In *P. glomerata* (growing in the arid Karoo) the accompanying bract turns yellow and becomes more patent when the fruit is mature; the achene is shed after abscission. The yellow colour is associated with senescence of the bracts and these structures are eventually shed, leaving conspicuous bract scars on the remaining, often terminal, woolly inflorescence axis. The unit of dispersal, in this case, is the achene, assisted by the patent senescing bract. The achene falls to the ground where it could either be dispersed by ants or small mammals or germinate under favourable conditions. In *P. montana* (growing along the Great Escarpment), the margin of the fruiting bract turns red and it becomes more patent, exposing the achene enveloped in the beak-like, reddish, papyraceous hypanthium, which fragments at the neck base. Perhaps birds, attracted by the red colour (Richards 1986), feed on the exposed achenes. Leafless, terminal, woolly branchlets, with terminal scars are a conspicuous feature of the plant after fruiting and it therefore also seems possible that the subterminal capitulum with several achenes is broken off as a unit. In this case the dispersal unit could be the achene or the achene accompanied by the bract or perhaps even the entire subcapitulum. There is a need for further observations on seed dispersal in the field to test some of these suggestions.

Filament length

For a comparison of filament length, it is easier to measure the antisepalous filaments as they are \pm twice the length of the antipetalous ones. Both *P. sp. nov. 1* and *P. sp. nov. 2* have short antisepalous filaments of \pm 1.2 mm, corresponding to their small flowers. *P. paludosa*, *P. filiformis* and *P. falcifolia* have exerted stamens because of their long (2.1–2.4 mm) filaments.

Anthers

Conspicuous differences in anther size have been noticed among the species; this has also been reported by Thoday (1924). In relation to flower size, most species have large exerted anthers between $0.7(-0.9) \times 0.3(-0.7)$ mm, possibly an anemophilous adaptation. *P. ericoides* has \pm elliptic anthers (Figure 1), whereas those of *P. drakensbergensis* are narrowly oblong, 0.9×0.3 mm. The largest anthers of 1.0×0.5 mm are found in *P. obtusifolia* and *P. falcifolia*.

Floral envelope

The hypanthium and sepals in *P. ericoides* are characterized by their coriaceous (almost fleshy) appearance and dull green to pinkish colour. The floral envelope in *P. rigida*, *P. paleacea*, *P. sp. nov. 1* and *P. sp. nov. 2* is pale yellowish and quite membranous. *P. pendula* is distinguished by a pinkish floral envelope, with a membranous texture. In all the other species the floral envelope is yellow-pink at anthesis, with a papyraceous texture. After pollination these flowers turn red and the hypanthium and sepals become thinly papyraceous and dry.

For practical purposes the total length of the floral envelope indicates flower size, and its taxonomic importance is clearly illustrated by the general increase in size from species 1–20 (Table 7). *P. rigida*, *P. paleacea* and *P. sp. nov. 2* are characterized by small flowers, the length of the floral envelope 4.0–4.6 mm. In most other species it ranges from 5.3–7.3 mm long. *P. rubra* and *P. falcifolia* are characterized by large flowers, the floral envelope being 8.4 mm long.

Specialized characters (Table 8)

a. Fragmentation of hypanthium after fruiting

During the fruiting phase, the persistent hypanthium fragments over the broadest part of the ovary, in eight of the 20 species. Except in *P. obtusifolia*, the hypanthium of all these species is characterized by a short neck of 0.3–1.0 mm. Anatomically their leaves also correlate with leaf structural type B (Bredenkamp & Van Wyk 2001). When fragmentation occurs at the neck base, the hypanthium usually has a long neck length of mostly 1.3–3.0 mm, and such species are associated with leaf structural types A, B, C and D.

b. Indumentum of hypanthium

In certain species of the genus *Lachnaea* (Beyers 1992; Beyers & Van der Walt 1995), different trichome types are found below and above the articulation plane in the hypanthium. This state could possibly also be present in other genera of the Thymelaeaceae. In *Passerina* the trichome type remains constant over the length of the hypanthium, possibly because there is no articulation plane in the hypanthium. As *Passerina* is distributed over a wide range of habitats, the density of the indumentum has been important in the distinction of certain species (Table 8). *P. ericoides* is distinguished by the strigose indumentum over the length of the hypanthium, whereas the indumentum of the neck is strigose in *P. paludosa*. A completely glabrous hypanthium is characteristic of *P. paleacea*. In 12 of the species, the hypanthium surrounding the ovary is glabrous, scantily tomentose or tomentose at the apex, with the neck scantily tomentose or tomentose. In *P. sp. nov. 1*, *P. sp. nov. 2* and *P. filiformis* subsp. *filiformis* the hypanthium is tomentose over its entire length. In *P. galpinii* the whole of the hypanthium is pubescent, whereas in *P. rubra* only the neck is pubescent and the rest of the hypanthium is glabrous.

A strong correlation was found between the indumentum of the lower hypanthium and of the bract. There is a



tendency for species characterized by a glabrous hypanthium base (Table 8) to have a protective bract with a very hairy adaxial surface (Table 5), whereas species with a hairy hypanthium base have a less hairy to almost glabrous adaxial bract surface. When the hypanthium neck is not covered by a bract, it tends to be hairy in varying degrees. Only *P. paleacea* has a completely glabrous hypanthium. In this species the entire hypanthium is completely covered by the hairy adaxial surface of the bract because of the very short hypanthium neck. This tendency shows that the function of protection of the ovule is partly transferred from the hypanthium to the hairy bract (Stebbins 1974).

c. Indumentum of sepals

Thoday (1924) uses the character 'outer sepals bearded behind the apex' in his key to distinguish between species. The abaxial surfaces of the outer and inner lobes of seven species are setose at the apex only and the adaxial surfaces range from glabrous to variously hairy (Table 8). In *P. comosa* abaxial surfaces of both outer and inner lobes are tomentose and adaxial surfaces are glabrous, *P. drakensbergensis* is similar except for the tomentose adaxial surface of the inner lobes. All sepals are completely glabrous in *P. paleacea*. The indumentum of the sepals varies infraspecifically and should, however, be used with discretion to distinguish between groups of species.

d. Size and shape of sepals

The size of the inner sepals is of taxonomic importance (Table 8). *P. sp. nov. 1*, *P. ericoides*, *P. rigida*, *P. paleacea* and *P. sp. nov. 2* are characterized by shorter and broader inner sepals, varying from widely ovate, obovate, widely obovate to subrotund. All other species have longer, narrower inner sepals, the shape varying, with one exception, from narrowly oblong, oblong, oblong-elliptic, elliptic, to obovate. *P. drakensbergensis* is distinguished by lanceolate sepals arranged in the shape of a cross.

Less important taxonomic characters

Ovary size (Table 7) has been considered less important, as it is difficult to measure all ovaries at the same developmental phase. In *Passerina* the size of the ovary increases markedly after anthesis and the enlarged ovary, enveloped by the persistent hypanthium, can already be observed in older flowers, rapidly followed by maturation of the fruit.

Taxonomic relationships

Up to 1930, priority was given to the definition of subordinal or subfamilial taxa in Thymelaeaceae, based mainly on floral morphology (Table 1). Applying both morphological and anatomical evidence, Domke (1934) proposed a satisfactory subfamilial classification system and envisages a phylogenetic relationship between the Thymelaeaceae, Malvaceae and Euphorbiaceae. Modern techniques have enabled taxonomists to find relationships between families and to arrange them into higher hierarchies, with ranks such as superorders or subclass-

es. Thus Dahlgren (1980) placed the Thymelaeaceae in the superorder Malviflorae (= Dilleniiflorae), Cronquist (1981, 1988) placed it in the subclass Rosidae, Thorne (1992a, 1992b) in the superorder Malvanae and Takhtajan (1997) in the subclass Dilleniidae (Table 2).

Heinig (1951) discussed the relationships of the Thymelaeaceae with the Myrtales, Saxifragaceae, Lythraceae, Gonystylaceae and Malvales on the basis of floral morphology and concluded that a polyphyletic origin of the Thymelaeaceae could be sought in both the Flacourtiaceae and Tiliaceae.

Cronquist (1968, 1981, 1988) considered the Thymelaeaceae as completely at home in the Myrtales (Rosidae) on account of the strongly perigynous polypetalous to apetalous flowers, internal phloem, vested pits and obturator. However, he admitted a possible relationship with other families, based on the pseudomonocarpous ovary and crotonoid pollen. Dahlgren (1975a, b) placed the superorder Thymelaeanae between the Dilleniaceae (Dilleniaceae, Cistaceae, Malvaceae, Urticales, Euphorbiales) and the Myrtales. Within the superorder Malviflorae, Dahlgren (1980) recognized a close affinity between the Malvales and Euphorbiales, and indicated a strong relationship with the Urticales and the Thymelaeales, but a phylogenetic affinity between the Malviflorae and Myrtiflorae was not supported. The inclusion of the Thymelaeaceae in the Myrtales was reviewed by Dahlgren & Thorne (1984). They argued that anatomically, most members of the family possess Myrtalean characters. On the other hand, embryological, chemical and palynological evidence strongly indicates an affinity with the Malviflorae. Thorne (1992a) accepted the superorder Malvanae, but included the Thymelaeaceae in the order Euphorbiales. Takhtajan (1969) considered the Thymelaeales to have a common origin with the Euphorbiales and Malvales, all arising from a Flacourtiaceae-type ancestor, and Takhtajan (1997) placed the Thymelaeales in the superorder Euphorbiana, with the Gonystylaceae as the only other family in the order.

Palynological evidence indicates that the very distinctive pollen in Thymelaeaceae is totally different from that of any Myrtales and similar to that of most Euphorbiaceae. Archangelsky (1971) concluded that both the Euphorbiales and the Thymelaeales belong to the subclass Dilleniidae and originated from ancestral lines of the Dilleniaceae \rightarrow Violales \rightarrow Malvales. In a paper on palynology of *Passerina*, Bredenkamp & Van Wyk (1996) supported Dahlgren (1980) in placing the Thymelaeales in the Malviflorae (= Dilleniiflorae).

In *Passerina*, the structure of the integuments surrounding the ovule provides taxonomically useful embryological evidence. We have shown the disintegration of the outer integument and the differentiation of the inner integument into a palisade-like outer epidermis, a mesophyll layer and an inner epidermis (Figure 10A, B). It is also clear that the mechanical part of the seed coat is derived from the palisade-like outer epidermis, hence it is an exotegmen (Figure 10C, D). Corner (1976) distinguished the Euphorbiales-Malvales-Thymelaeales-Tiliales (Malvlean complex) on the basis of the exo-



tegmic palisade. He dismissed the derivation of the Malvacean complex from the Dilleniales (endostele seeds) or Violales and looked towards the Myristicaceae (Magnoliales–Ranales) for the origin of the Malvacean seed.

Recent evidence from molecular phylogeny (Table 3) should be interpreted in context with the evidence from other botanical fields. The primary focus of The Angiosperm Phylogeny Group (APG 1998) is on orders, with a secondary focus on families of flowering plants. Above the ordinal level, ranks are defined as subgroups, clades or supraordinal subgroups. Magallón *et al.* (1999) attempted to compare these groups to the existing systems mentioned in the preceding paragraphs. Both APG (1998) and Magallón *et al.* (1999) recognized the Eudicots, a group characterized by tricolpate pollen, as well as the supraordinal group Core Eudicots, supported by pentamerous and isomerous flowers. Thymelaeaceae is designated to the Rosid clade by most authors. APG (1998) placed the Thymelaeaceae in the subgroup Eurosids II and order Malvales, whereas all the other authors placed it in the Expanded Malvales. The Malvacean relationship of the Thymelaeaceae seems to be strongly supported by molecular phylogeny, as well as floral morphology, anatomy, embryology and palynology.

The Euphorbiales–Malvales–Thymelaeales relationship indicated by embryology and palynology is, however, not supported by molecular data. APG (1998) placed the Euphorbiaceae in the order Malpighiales in the subgroup Eurosids I and Magallón *et al.* (1999) placed it in the Core Rosid Clade. Cronquist (1968, 1981, 1988) was convinced that if the Thymelaeaceae is not placed in the Myrtales, it would stand next to it. Conti *et al.* (1996), APG (1998), and Alverson *et al.* (1999) all regarded the Myrtales as a sister group of the Malvales or the Expanded Malvales to which the Thymelaeaceae is designated.

Speculations on phylogeny

Within Thymelaeaceae, both Domke (1934) and Heinig (1951) agreed that the subfamily Thymelaeoideae is phylogenetically more advanced than the Aquilarioideae. On the basis of the advanced pollen, Bredenkamp & Van Wyk (1996) raised the subtribe Passerininae to the tribe Passerineae, a decision supported by the present study. Although many of the following advanced character states are present in other genera of the Thymelaeoideae, these advanced character states are all found together in *Passerina*: receptacle reduced to a ± lenticular structure; departure of the fused sepal and stamen bundles before carpellary bundles; hypogynous floral arrangement; petal-like floral envelope comprising a hypanthium (fused calyx and androecium), differentiating into four sepals and a diplostemonous androecium; separation of stamen bundles high up in hypanthium, at formation of sepals; exserted, extrorse anthers; anemophilous habit; secondary reticulum of pollen; complete absence of petals or petaloid scales; asymmetric development of the style; superior, pseudomonomerous, unilocular ovary; asymmetric attachment of ovule at top of ovary; ventrally epitropous ovule; distinctive obturator; bitegmic ovule with exotegmic palisade; fruit a 1-seeded berry or an achene; seed with lignified, black exotegmen.

Considering all the characters mentioned, *Passerina* is considered highly advanced in relation to other genera in Thymelaeoideae.

Systematic value

Family level

The exotegmic palisade and the distinctive obturator are regarded as family characters. They form the basis of Corner's (1976) Euphorbiales–Malvales–Thymelaeales–Tiliales complex.

Subfamily level

The Thymelaeoideae is distinguished on the basis of the calyx tube (hypanthium in the present study), diplostemonous androecium and pseudomonomerous ovary (Domke 1934; Heinig 1951).

Tribal level

On the basis of the secondary reticulum, unique to the pollen of *Passerina*, Bredenkamp & Van Wyk (1996) raised the subtribe Passerininae to the tribe Passerineae.

Genus level

The present study indicates the exserted, extrorse anthers and the anemophilous habit as unique to *Passerina*.

Species level

Characters useful at species level are summarized in Tables 7 and 8.

CONCLUSIONS

The evidence on floral morphology not only confirmed the identity of 20 species and four subspecies, but also proved significant in the taxonomy of the genus. The status of the following taxa is confirmed by the present floral morphological study: *P. burchellii* Thoday, *P. comosa* C.H.Wright, *P. drakensbergensis* Hilliard & B.L.Burt, *P. ericoides* L., *P. falcifolia* C.H.Wright, *P. filiformis* L. subsp. *filiformis*, *P. filiformis* L. subsp. nov., *P. galpinii* C.H.Wright, *P. glomerata* Thunb. subsp. *glomerata*, *P. glomerata* Thunb. subsp. nov., *P. montana* Thoday, *P. obtusifolia* Thoday, *P. paleacea* Wikstr., *P. paludosa* Thoday, *P. pendula* Eckl. & Zeyh., *P. rigida* Wikstr., *P. rubra* C.H.Wright, *P. vulgaris*, *P. sp. nov. 1*, *P. sp. nov. 2*, *P. sp. nov. 3* and *P. sp. nov. 4*.

For almost three centuries evidence from floral morphology has been basic to plant taxonomy and applied at all hierarchical levels. Our research on the flowers in *Passerina* has produced new morphological and anatomical evidence, especially as Heinig's classical study of floral morphology in Thymelaeaceae (1951) did not include *Passerina*. The present study has succeeded in resolving the floral morphology in *Passerina*, as many mistakes have been perpetuated by previous authors. We conclude that the flower in *Passerina* is a phylogenetically advanced structure and consider the genus advanced



within the Thymelaeoideae. Possible taxonomic relationships of the Thymelaeaceae with the Malvales are strongly supported by the presentation of floral morphological, anatomical, embryological and palynological information to which this study has also contributed. Finally, all the above-mentioned evidence serves to form a firm taxonomic basis for future comparative studies, especially in the expanding molecular field.

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