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, vasculation

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.

CONTENTS

Introduction	213
Materials and methods	216
Terminology	216
Phylogeny	216
Results	216
Inflorescences	216
Bracts	218
Key to taxa based on bract characters	218
Generic description of floral morphology	219
Generic description of floral anatomy (as seen in	
transverse section)	219
Floral morphology at species level	223
Discussion	223
Inflorescence	223
Bracts	223
Floral morphology and anatomy at generic level.	223
Floral and fruit morphology at species level	232
Less important taxonomic characters	234
Taxonomic relationships	234
Speculations on phylogeny	235
Systematic value	235
Conclusions	235
Acknowledgements	236
References	236

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.

MS. received: 2000-08-22.

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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Undefined Thymela Class Order Family	m 1818	Endlicher 1837, 1847	Meisner 1857	Bentham & Hooker 1880	Gilg 1891, 1894	Leandri 1930	Domke 1934
Class Order Family	tearum						
Order Family		Thymelaeae					
Family		Daphnoideae	Thymelaeaceae	Thymelaeaceae			
					Thymelaeaceae	Thymelaeaceae	Thymelaeaceae
Subfamily					Thymelaeoideae		Thymelaeoideae
Tribe		Thymelinae	Gnidieae	Euthymelaeeae	Daphneae	Thymelaeoideae	Gnidieae
Subtribe		Passerineae	Diplostemoneae		Passerininae	Passeriniinae	Passerininae
Series				Series 1			
Division Octandri	ia						
		Inflor	escence, floral, fruit and s	eed morphology at genus le	vel		
Inflorescence		flowers lateral					tarminal enibae
Floral arrangement		perigynous	perigynous			Derigynous	envide minimo
Floral tube		perigone, infundibular, limb 4-fid	calyx tube hypocrateri- form, persistent	perianth articulate above ovary	receptacle cylindric, articulate in unner half	floral tube: fusion of 4	calyx tube flask-shaped,
Calyx 0			limb 4-partite		in adds in announ		4-lobed
Corolla infundib persisten	ular, 4-fid, t	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	nucula, pericarp crustaceous	indehiscent			berry or achene
Seed 1-seeded		I-seeded					black, crustaceous testa, micropyle beak-like

214

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	
Subclass					Rosidae	(Magnoliopsida) Dicotyledonae (Magnoliidae)	Dilleniidae
Superorder		Ē	Thymelacanae	Malviflorae(= Dilleniiflorae)		Malvanae	Euphorbianae
Order Family	Thymelaeaceae	I nymelaeales Thymelaeaceae	Inymelacates	Thymelacales Thymelacaceae [excluded	мупаles Thymelaeaceae	Eupnorblates Thymelaeaceae	Thymelaeaceae Thymelaeaceae
Subfamily Tribe Subtribe Series	Thymelaeoideae Thymelaeeae (= <i>Gnidieae</i>)					Thymelaeoideae	Thymelaeoideae
Relationships	Myrtales: perianth tube	placed between Bixales	placed between Dillenianae	Myrtales: anatomical evi-	Myrtales: strongly	Euphorbiaceae, Simmond- siaceae Dicharetalaceae	Gonystylaceae only other family in order
	Malvales: pollen morphology	ally Flocaccac	инслоинд мауагсэ) анд Мугталас	cence. ruppionace- Malvales: chemical, em- bryological, paiynological evidence	pergynow, purperation to apetalous flowers. Other families: pseudomonomerous ovary, crotomoid pollen	Gonystylaceae	
			Floral, fruit and seed morp	phology described at differen	it ranks		
Character	Tribe	Family	Order	Family	Family		Family
Flower		hypogynous, bisexual,	hypogynous, bisexual	perigynous, 4-merous			bisexual
Floral tube	perianth tube articulated	calyx tube	hypanthium	cylindrical, brightly			calyx tube cylindric
Calyx	4-lobed	perianth tubular, 4-lobed,		4-lobed, arising from upper			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)		diplostemonous	diplostemonous	diplostemonous	neardomonomerone.		diplostemonous etvle sublateral: stiema
uynoccium (U)	pseudomonomerous	ovary superior	unitocular, ovures pendutous, epitropous, bitegmic, crassinucellate; endosperm	pendulous	ovules solitary		papillose; carpels 2, mono- locular; ovule solitary
Fruit		indehiscent	nut or drupe	indehiscent	indehiscent		indehiscent, nut-like, baccate, or drupaccous, 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; endo- sperm scanty

215

Rank	Conti et al. 1996	APG 1998*	Alverson et al. 1998	Magallón et al. 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, Sarcolaenaceae, Malvales	Eurosids II	Expanded Malvales: Core Malvales, Thymelaealean Clade, Bixalean Clade, Dipterocarpalean Clade	Expanded Malvales: Malvales, Thymelaeaceae, Sarcolaenaceae, 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, Sarcolaenaceae, Dipterocarpaceae basal to Malvales

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

* 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.

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

Floral envelope

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 phosphatebuffered 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); 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 politelic 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.

Bothalia 31,2 (2001)

TABLE 7. Tussering specificity chaining and noused at the	TABLE 4.—Passerina	specimens	examined	and	housed	at	PRE
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Species	Collector	Locality
burchellii Thoday	Bredenkamp 1545	WESTERN CAPE.—3319 (Worcester): Jonaskop, (-DC).
	Bolus 687*. Stokoe 2542	WESTERN CAPE.—3419 (Caledon): Baviaanskloof, Genadendal, (-BA).
comosa C.H.Wright	Thoday 212 Andreae 1288*, MacDonald 2125	WESTERN CAPE.—3320 (Montagu): Montagu District, near Concordia, (-CD). WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (-AD).
drakensbergensis Hilliard	Edwards 974	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (-DB).
& B.L.Burtt	Bredenkamp 1018, 1019,	KWAZULU-NATAL.—2829 (Harrismith): Ndedema Gorge, Cathedral Peak Forest
arianidae I	1020, 1021* Prodomkum 056	Reserve, (-CD).
ericolaes L.	Bredenkamp 950• Bredenkamp 962•*	WESTERN CAPE.—3318 (Cape Town): Millietton, (–CD). WESTERN CAPE —3418 (Simonstown): Cape Maclear (–AD)
	Taylor 4042	WESTERN CAPE.—3419 (Caledon): Pearly Beach. (–CB).
falcifolia C.H.Wright	Bredenkamp 917*	WESTERN CAPE.—3323 (Willowmore): Gouna State Forest, (-CC).
	Bredenkamp 915	WESTERN CAPE.—3324 (Steytlerville): opposite Tsitsikama Lodge, (-CD).
filiformis L subsp filiformis	Tyson 1449 Roucher 2833	WESTERN CAPE — 31423 (Knysna): Knysna, (-AA). WESTERN CAPE — 3118 (Van Bhynsdorn): Clanwilliam Dist. Diankloof S of Varlore
Jugornus L. suosp. jugornus	Doucher 2000	vlei. (-AD).
	Bredenkamp 1039*	WESTERN CAPE.—3318 (Cape Town): Signal Hill, (-CD).
filiformis L. subsp. nov.	Schlechter 5125*	WESTERN CAPE.—3218 (Clanwilliam): Alexander's Hoek, (-BC).
	Taylor 1542	WESTERN CAPE.—3218 (Clanwilliam): Malmesbury Div., Vredenburg, Steenberg's
galpinii C.H.Wright	Bredenkamp 946*	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (-AD).
	Bredenkamp 932	WESTERN CAPE.—3421 (Riversdale): Riethuiskraal, (-AD).
	Bredenkamp 933	WESTERN CAPE.—3421 (Riversdale): Still Bay, (-AD).
elomerata Thunh subsn	Bredenkamp 925 Bredenkamp 988	WESTERN CAPE
glomerata	Bredenkamp 994	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Electroom, (-AC).
0	Bredenkamp 1002	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Algeria, (-AC).
	Bredenkamp 984, 985*	WESTERN CAPE.—3219 (Wuppertal): Citrusdal, Piekenierskloof Pass, (-CD).
	Bredenkamp 9// Bredenkamp 973*	WESTERN CAPE. — 3219 (Wuppertal): Groenfontein, (–DC). WESTERN CAPE = 3310 (Worrester): Tulbach (–AC)
elomerata Thunb. subsp. nov	Stokoe 8040	WESTERN CAPE — 3219 (Wundertal): Cederberg Mountains
8	Esterhuysen 28587*	WESTERN CAPE.—3319 (Worcester): Hex River Mountains.
montana Thoday	Giess 13136	NAMIBIA. —2217 (Windhoek): Auas Mountains, Molteblick, (-CA).
	Bredenkamp 1024	MPUMALANGA. —2430 (Pilgrim's Rest): World's View, (–DD).
	Bredenkamp 1025 Bredenkamp 889–890	FREE STATE —2828 (Bethlehem): Golden Gate National Park (-DA)
	Bredenkamp 893*	FREE STATE.—2927 (Maseru): Ladybrand, (–AB).
obtusifolia Thoday	Bredenkamp 971	WESTERN CAPE3319 (Worcester): Karoo National Botanical Garden, (-CB).
	Bredenkamp 967	WESTERN CAPE.—3319 (Worcester): Jonaskop, (–CD).
	Bredenkamp 1055, 1054 Bredenkamn 979	WESTERN CAPE
	Bredenkamp 919*	WESTERN CAPE.—3322 (Oudtshoorn): Perdepoort, (-CD).
paleacea Wikstr.	Bredenkamp 960*	WESTERN CAPE3418 (Simonstown): Kommetjie, (-AB).
	Bredenkamp 961	WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (-AD).
	Bredenkemp 952 Bredenkamp 950	WESTERN CAPE — 3418 (Simonstown): Harold Porter National Botanical Garden, (-BD). WESTERN CAPE — 3420 (Bredavdorn): De Hoon Natura Pacartia (-AD)
	Bredenkamp 949	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (-AD). WESTERN CAPE.—3420 (Bredasdorp): Waenhuiskrans, (-CA).
	Bredenkamp 940	WESTERN CAPE.—3421 (Riversdale): Puntjie, (-AC).
paludosa Thoday	Bredenkamp 1035	WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (-BA).
	Jangie 150* Thoday 100	WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (–BA).
pendula Eckl. & Zeyh.	Fourcade 3043	EASTERN CAPE.—324 (Stevilerville): Zuur Anys. (–CB)
	Bredenkamp 908, 909*	EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (-CB).
rigida Wikstr.	Ward 7211	KWAZULU-NATAL.—2832 (Mtubatuba): St Lucia Park, (-AD).
	Bredenkamp 1015" Bredenkamp 800	K WAZULU-NAIAL.—5130 (Port Edward): Umtamvuna River Mouth, (–AA).
	Bredenkamp 898	EASTERN CAPE.—3326 (Grahamstown): Port Alfred. (–DA).
	Bredenkamp 897	EASTERN CAPE 3327 (Peddie): Kleinmond West, (-CA).
rubra C H Wright	Bredenkamp 911 Bredenkamp 014*	EASTERN CAPE. 3424 (Humansdorp): Jeffreys Bay, (-BB).
mora C.H. wright	Bredenkamp 914" Bredenkamn 905	EASTERN CAPE.—3324 (Sicylierville): en route to Kareedouw, (-CD). EASTERN CAPE.—3325 (Port Elizabeth): Colchester (_DB)
	Bredenkamp 900	EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD).
vulgaris Thoday	Bredenkamp 926	WESTERN CAPE
	Bredenkamp 907	EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB).
	Bredenkamp 901 Bredenkamp 951•	EASTERN CAPE — 3320 (Granamstown): Granamstown, (-AD). WESTERN CAPE — 3418 (Simonstown): Betty's Bay Harold Porter NBG (BD)
	Bredenkamp 944•*	WESTERN CAPE.—3420 (Bredasdorp): Cape Infanta, (-BD).
	Bredenkamp 924	WESTERN CAPE.—3422 (Mosselbaai): Kleinbrak, (-AA).
sp. nov. 1	Goldblatt & Manning 8627	WESTERN CAPE.—3220 (Sutherland): Roggeveld Escarpment, (-AB).
	Бтеаепкатр 1044, 1040, 1047	wESTERN CAPE.—3319 (worcester): waboomberg, Ceres, (-AD).
	Oliver 9281*	
sp. nov. 2	Esterhuysen 12189, 26859*	WESTERN CAPE3218 (Clanwilliam): Northern Cederberg Mountains, (-BB).
sp. nov. 3	Stokoe 9302 Seblechter 5946	WESTERN CAPE
	Schlechler 3840 Esterhussen 10734*	WESTERN CAPE. — 5522 (Oudtshoorn): Montagu Pass, (-CD). EASTERN CAPE. — 3323 (Willowmore): Konne Montaging (DA)
	Esterhuysen 28006*	EASTERN CAPE.—3324 (Steytlerville): Cockscomb Hitenhage area (_RD)
sp. nov. 4	Killick 238	KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (-CB).
	Bredenkamp 1016, 1017	KWAZULU-NATAL3030 (Port Shepstone): Oribi Gorge, (-CB).
	van Wyk & Bredenkamp	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (-AA).
	Bredenkamp 1327*	KWAZULU-NATAL3130 (Port Edward): Mkambati Nature Reserve (-AC)
	Gillett 4537	WESTERN CAPE.—3422 (Mossel Bay): en route to Knysna from George, (-BB).
	Keet s.n.	WESTERN CAPE.—3423 (Knysna): Knysna, Redlands, (-AA).

* 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, × 10; B, C, E–G, × 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 (boatshaped) or helmet-shaped; in outline (plane shape), oblong, lanceolate, ovate and obovate to widely ovate and obovate, rhombic and narrowly obtrullate to obtrullate (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, ± 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 rosytinged. 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).



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

a Bracts hairy outside	P. comosa (Figure 3A), P. sp. nov. 3 (Figure 3B C)
b Bracts glabrous outside:	(1.610 0.0)
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, so	ftly 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 <i>P. paleacea</i> (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
5b Membranous wings absent:
10a Bracts oblong in outline, apex obtuse
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
11b Bracts obovate to widely obovate, point obtuse to acute, thickly coriaceous; lamina ribbed and reticu-
lately 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
12b Bracts variously shaped and coloured, but not lanceolate and glaucous:
13a Main yein shortly extended into an acute apex; lamina rhombic to obtrullate, distinctly angled, 4- or 5-
ribbed
13b Main vein extending beyond lamina into a leaf-like point:
14a Leaf-like point obtuse at apex: lamina closely 2-ribbed at margins
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; wines glabrous:
16a Midrib and leaf-like point stout and strongly developed, apex acute
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 oboyate 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 unper half, or obtrullate, narrowing abruntly into a leaf-like point \dots P sp. nov. 4 (Figure 4H, I)
15b Adaxial (inner) surface of bracts completely villous:
19a Midrib extended, leaf-like point falcate: wings + 4-ribbed P falcifolia (Figure 41)
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 cylindric 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, antisepalous 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 ± 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, 5.3×4.0 mm, in all other species (Figure 2F; Tables 6, 7) an achene, pericarp membranous and dry, 2.5×1.2 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*: carpellary 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, × 20. Scale bar: 5 mm.

cular bundles, fused sepal and stamen traces occupying peripheral position (Figure 5B); cells at perifery 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 commisural 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 ± 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 tanniniferous 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, × 20. Scale bar: 5 mm.

Taxa	Poly	telic infloresc	ence				Ymbiform bracts		
	Subcapitulate	reduced	Multi- flowered main and co- florescences	abaxial	lumentum adaxial	Size length $\times^{1/2}$ width (mm)	Plane shape	Lamina (per side of main vein)	Wings (per side of main vein)
comosa			×	tomentose	comose	$(3.0-)5.5 \times 1.5(-1.8)$	widely ovate, apex acute	± 3-ribbed,	margins submembranous
sp. nov. 3	x			tomentose	comose	$(4.5-)4.9 \times 1.5(-1.8)$	widely ovate, apex acute	coriaceous, rugose ± 3-ribbed, coriaceous, rugose	margins submembranous
burchellii pendula		×	x		villous comose	$(3.2-)3.5 \times 1.5$ $(3.0-)4.2 \times 1.0(-1.5)$	rhombic, apex involute, acute rhombic, apex obtusely	coriaceous, smooth softly coriaceous,	smooth margins membranous
montana	х				villous	$(3.2-)4.0 \times 0.9(-1.6)$	angled ovate to obovate, apex	smooth thinly coriaceous,	margins membranous
paleacea	x				villous, wing borders alabrous	$(2.5-)2.7 \times 1.2(-1.9)$	subacute widely ovate, apex obtuse	obscurely ribbed chartaceous, smooth	membranous, obscurely
galpinii			x		midrib tomentose,	$(3.6-)4.5 \times 1.1(-2.2)$	oblate, leaf-like point,	chartaceous	veined membranous, broadly
sp. nov. 1			х		wings glabrous midrib tomentose,	$(3.2-)3.5 \times 1.4(-1.9)$	apex subacute widely obovate, apex	chartaceous	rounded, bullate membranous, bullate
sp. nov. 2			Х		wings glabrous setose	3.1×1.4	subacute helmet-shaped, widely	thinly chartaceous,	smooth, membranous rims
ericoides			х		villous	3.6×1.5	obovate, apex subacute leaf-like, oblong, obtuse	smooth smooth, slightly	absent
rigida			х		villous	$(2.6-)3.4 \times 1.4(-1.9)$	widely ovate, distinct,	succulent coriaceous, 2 or	absent
glomerata subsp. glomerata	×				villous	$4.0 \times 1.4(-2.4)$	short, acute point obovate to widely obovate, point obtuse	3 shallow folds thickly coriaceous, ribbed and reticu-	absent
glomerata subsp. nov.	х				villous	$(2.5-)2.9 \times 1.5$	obovate to widely	lately viened thickly coriaceous,	absent
drakensbergensis			x		villous	5.5 × 1.5	obovate, point obtuse to acute lanceolate, apex obtuse to acute	ribbed coriaceous, obsurely ribbed and reticu-	absent
obtusifolia			х		setose	$(4.0-)5.8 \times 1.5(-1.7)$	narrowly obtrullate,	coriaceous, closely	absent
paludosa			х		basally setose,	$(5.2-)7.0 \times 1.8(-2.0)$	point lear-like, apex obtuse narrowly obtrullate,	2-ribbed at margins coriaceous, ± 2-ribbed	membranous with obscure
filiformis subsp. nov.			Х		wings glabrous centrally setose,	4.6×1.5	point leaf-like, apex acute ovate acuminate.	coriaceous	venation membranous with distinct
filiformis subsp. filiformis			x		wings glabrous basally to centrally	7.3×2.0	gradually narrowing to point widely obovate,	chartaceous	venation membranous with distinct
			,		setose, wings glabrous		narrowing abruptly into filiform point		venation
sp. nov. +			~		basally setose, wings glabrous	6.3×1.6	obtrullate, narrowing abruptly into straight, leaf-like point	coriaceous	chartaceous, \pm 3-ribbed, obscurely veined
falcifolia			x		villous	$(5.3-)5.8 \times 1.7(-2.0)$	widely ovate, narrowing	coriaceous	coriaceous, ± 4-ribbed,
rubra			Х		villous	$(4.3-)5.1 \times 1.8(-2.0)$	widely ovate, with	coriaceous	reticulately veined coriaceous, ± 5-ribbed,
vulgaris			Х		shortly villous	$(4.4-)5.1 \times 1.4(-1.7)$	short, acute point rhombic to obtrullate, distinctly analod	coriaceous	reticulately veined coriaceous, distinctly 4- or

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

222

X, character present.

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

Floral part	P. ericoides (fruit fleshy)	P. vulgaris (fruit dry)
Hypanthium	Lobed.	Scalloped.
	Outer and inner epidermis hairy (Figure 5E-G).	Outer epidermis hairy, inner epidermis glabrous (Figure 5F, H).
Ovary wall	Independent of hypanthium.	Loosely adhering to hypanthium distally away from placenta (Figure 5F).
	Outer and inner epidermal wall strongly developed, containing tanniniferous substances.	Epidermal walls less sturdy with less tanniniferous substances.
	Mesophyll of densely arranged parenchyma cells.	Mesophyll aerenchymatic.
	Dorsal carpellary bundle strongly developed (Figure 5G).	Dorsal carpellary bundle rudimentary or absent (Figure 5F, H).
	Commissural bundles densely arranged, often fused (Figure 5E, G)	Commissural bundles closely arranged, often separate (Figure 5F, H).
Style	Four-lobed.	Elliptic.
5	Vascular bundles 4, 1 per lobe (Figure 7C).	Vascular bundles inconspicuously arranged in a row along long axis of elliptic style (Figure 7D).
Fruit	Pericarp fleshy: exocarp tanniniferous, 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 tanniniferous inner epidermis (ieii) (Figures 5G, H; 6A, B), crassinucellate; embryo sac with 1 cell of functional macrospore (Figure 5G, H). Ovary at median position: ovule wall, integuments and nucellus remaining the same; embryo sac with 2 cells of functional macrospore (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, stylar 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) tanniniferous (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 Gnidieae, 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 multiflowered 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 involucral, 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

		Fru	uit			Floral envelop	e (hypanthium	and sepals)			Ovary	Filam	ents	Anthers
Taxon	*Leaf structural	Fleshy	Dry	Col	our at pollin	lation		Texture		Total	Length	Anti-	Anti-	I enoth
TOO TOO	type			green	yellow	yellow-pink	coriaceous	mem-	papy-	length	× width	petalous	sepalous	× width
								branous	raceous	in mm	in mm	in mm	in mm	in mm
sp. nov. 1	V		×		x	x		x		5.3	1.7×0.5	0.4	1.2	0.5×0.3
ericoides	B3	X		x			x			5.0	2.1×1.7	0.5	1.3	0.9×0.7
rigida	B3, B6, D2	×			×			×		4.0	2.2×1.4	0.5	15	0.8×0.4
paleacea	B2, B3, B4, D2		X		×			X		4,2	2.4×1.4	0.7	4	0.6×0.5
sp. nov. 2	B3		×		×			X		4.6	1.8×0.5	0.4	1.2	0.7 × 0.3
galpinii	B2, B3		x			×			x	5.3	2.0×1.1	1.4	2.1	0.6×0.5
glomerata subsp. glomerata	B2, B3, B5		×			×			x	6.4	2.4×0.9	0.9	1.4	0.8×0.4
glomerata subsp. nov.	B6		X			×			x	4.9	2.5×0.9	1.2	Р I	00200
obtusifolia	B2, B3, B4, B5		X			X			X	6.8	11×50		с с	11005
burchellii	B1		X			×			X	4.7	16×06	2.0	1 V 1	C.0 × 1.1
pendula	B2		X			×		X		6.5	2.0×0.7	51	00	FU~ 80
comosa	B2, B3, D1		X			x			X	7.3	27×10	2.0	2 I Z	10~00
paludosa	B2		×			X			X	7.2	2.3×1.0	1.2	P C	50×10
montana	B2, B3, D1		×			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
drakensbergensis	B3		×			x			X	5.9	2.4×0.9	1.2	2.0	04×03
ruhra	B4		×			X			X	8.4	2.7×1.1	0.7	17	0 9 × 0 3
filiformis subsp. filiformis	B3, B4		X			Х			X	6.0	2.3×0.5	II	66	0.8×03
filiformis subsp. nov.	B6		X			X			X	6.5	2.5×0.6	0		08403
sp. nov. 4	C		×			×			X	6.6	72×07	8.0	1 1	20200
falcifolia	С		X			×			X	8.4	25×07	1.4		C.0 < 0.0
vulgaris	D		×			X			×	6.2	2.1×1.1	0.7	1.1	0 0 × 0 4

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

224

* 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 vasculation 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; c, commissural carpellary bundles; cs-espt, fused commissural sepal and antipetalous stamen bundles; d, area of tissue differentiation; do, dorsal carpellary bundle; f, functulus; fm, functional macrospore; h, hypanthium; ie,h, inner epidermis of hypanthium; ieow, inner epidermis of ovary wall; ii, inner integument; mc, median carpellary bundle; n, nucellus; o, ovule; oeow, outer epidermis of ovary wall; oi, outer integument; wo, 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 µm.



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, Us 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, Us 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 µm; A, C, D, 100 µm.

show that Meisner (1857) regards the floral envelope as perigynous and hypocrateriform, 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 t/s) 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, 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 μm; A, B, 100 μm.

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, hypocrateriform 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.

Taxon	Leaf struc-	Fragme hypanth. a	ntation of fiter fruiting		Hypanthiu	Ξ				Sc	spals			
	tural type	at neck base	at circumf. of ovary	neck length*	indun at ovary	nentum at neck	outer lo adaxial	be surface abaxial	nentum inner lo adaxial	be surface	inner lobe $1 \times w^*$	outer & inner	shape of lobe outer	inner
sp. nov. 1 ericoides	A B3	×	×	1.2 0.6	tomentose strigose	tomentose strigose	glabrous puberulent	apex setose glabrous	glabrous puberulent	glabrous glabrous	$\begin{array}{c} 1.9 \times 1.2 \\ 1.6 \times 2.0 \end{array}$	concave, wide-	cymbiform	widely ovate
rigida	B3, B6, D2		x	0.8	glabrous	tomentose	midrib	glabrous	tomentose	glabrous	1.8×0.9	iy upovate	cymbiform	obovate
paleacea	B2, B3, B4, D2		×	0.3	glabrous	glabrous	glabrous	glabrous	glabrous	glabrous	1.8×1.5	concave, ellip- tic or subrotund		
sp. nov. 2	B3		×	0.7	tomentose	tomentose	apex tomen-	apex setose	glabrous	apex setose	1.8×1.0		concave,	concave, obo-
galpinii	B2, B3		×	1.0	pubescent	pubescent	glabrous	glabrous	apex margin	glabrous	2.4×1.6		concave, ellintio	obovate
glomerata subsp. glomerata	B2, B3, B5		×	0.8	glabrous	tomentose	scantily pubescent	glabrous	scantily	glabrous	2.3×0.8		cymbiform	oblong-elliptic
glomerata subsp. nov.	B6		X	0.7	apex tomen- tose	tomentose	apex tomen- tose	glabrous	tomentose	glabrous	2.6×1.6		concave, ovate	widely obovate
obtusifolia	B2, B3, B4, B5		×	1.8	glabrous	tomentose	tomentose	glabrous	tomentose	glabrous	2.8×0.9		cymbiform	narrowly oblong
burchellii pendula	B1 B2	××		0.8	glabrous glabrous	tomentose tomentose	midrib setose scantily	apex setose glabrous	tomentose scantily	apex setose glabrous	2.3×0.6 2.9×1.5		cymbiform cymbiform	obovate oblong
		;					tomentose		tomentose					
comosa paludosa	B2 B2	××		2.6	glabrous shortly tomentose	strigose	glabrous glabrous	apex setose	glabrous apex margin tomentose	apex setose	2.8×1.0 2.2×1.2		cymbiform cymbiform	elliptic oblong
montana	B2, B3, D1	×		1.3	glabrous	tomentose	scantily tomentose	glabrous	tomentose	glabrous	2.1×1.0		cymbiform	obovate
sp. nov. 3	B3	×		1.4	glabrous	scantily tomentose	glabrous	apex setose	glabrous	apex tomen- tose	2.7 × 1.5		concave, ovate	obovate
drakensbergensis	B3	× ;		1.7	scantily tornentose	tomentose	glabrous	tomentose	tomentose	tomentose	2.4×0.8	concave, lanceolate		
rubra	B4 D2 D4	×		2.0	glabrous	pubescent	glabrous	glabrous	scantily tomentose	glabrous	2.9×1.7		cymbiform	obovate
juljormis suosp. juljormis filiformis subsp. nov.	B6	<		1.5	scantily	scantily	glabrous	apex setose	glabrous	apex setose apex setose	2.5 × 1.5	concave,	concave, obovate	obovate
sp. nov. 4	C	×		2.3	tomentose upper half tomentose	tomentose	glabrous	apex setose	glabrous	apex setose	2.1×1.3	obovate	cymbiform	obovate
falcifolia	U	×		3.0	scantily tomentose	tomentose	scantily tomentose	glabrous	tomentose	glabrous	2.5×1.3		concave, obovate	obovate
vulgaris	D2	x		1.6	glabrous	scantily tomentose	scantily tomentose	glabrous	scantily tomentose	glabrous	2.5×1.3		cymbiform	obovate

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

228

X, character present; * average in mm.

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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 t/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, t/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 µm.

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 circumscission, 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 circumscission 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 circumscission 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 loculae 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, exserted, 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 commisural 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* (= *Lasiosiphon 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 supratectal 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 tanniniferous. 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 t/s), 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, Wikstrom (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 nutlike, 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 t/s, 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, membraneous 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

Bothalia 31,2 (2001)

(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 exserted 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 exserted anthers between $0.7(-0.9) \times 0.3(-0.7)$ mm, possibly an anemophilous adaptation. *P. ericoides* has ± 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 subclasses. 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, vestured pits and obturator. However, he admited a possible relationship with other families, based on the pseudomonomerous ovary and crotonoid pollen. Dahlgren (1975a, b) placed the superorder Thymelaeanae between the Dillenianae (Dilleniales, Cistales, Malvales, Urticales, Euphorbiales) and the Myrtanae. 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 Euphorbianae, 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 Dilleniales \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 disintigration of the outer integument and the differentiation of the inner integument into a palisade-like outer epidermis, a mesophyl 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 (Malvalean complex) on the basis of the exo-

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

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), diplostemous 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.Burtt, *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 hierachical 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

ACKNOWLEDGEMENTS

The authors wish to thank Dr E. Stevn for assistance with the LM, Ms G. Condy for the line drawings and Ms A. Romanowski for the developing and printing of the photographs.

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